A Dynamical Systems Framework for Modelling Plant Community Organisation

By

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Abstract

This thesis reports the results of ecological modelling research based on the use of absolute fossil pollen data as a proxy for actual measurements of historic vegetation change. The theme of this project is community organisation while the topic of special interest is community behaviour.

The theory of community organisation includes some of the most fascinating and controversial problems in ecology. As defined in this thesis, community organisation is the study of the forces or mechanisms responsible for shaping the structure and behaviour of a community through time.

An unresolved and persistent problem in community ecology has been the question of whether or not natural communities are capable of equilibrium behaviour. During the 1970s, key theoretical developments led community ecologists to question this traditional assumption. Today, the non-equilibrium paradigm is considered to be a more likely model for community organisation.

The history of these major theoretical changes is reviewed in this thesis with the objective of deriving and testing hypotheses of plant community organisation. The hypothesis testing reported in this thesis is based on a new modelling paradigm. This framework required a flexibility that would permit its application to a wide range of ecological models and a sensitivity to the limitations of fossil pollen accumulation rate (PAR) data.

Field data has been obtained from two plant communities: a Mangrove community located on the coastal plains of the Fijian island of Totoya and a lowland mixed beech forest, located within the ring plain of one of New Zealand's active volcanoes (Mt. Ruapehu). This combination of study sites permits the research hypotheses that are advanced in this thesis to be tested in plant communities of varying environmental, temporal, spatial and structural characteristics.

The results of this research indicate that the plant communities studied exist in a low to intermediate density region, well below any theoretical region of density-dependency. The density vague behaviour of these communities appears to the result from stochastic domination. In conclusion, these results support the non-equilibrium model of community organisation. The implications of this research for palynologists involved in human impact studies and empirical modelling research are evaluated. Future objectives for theoretical modelling research in this area are suggested.

Preface

As an undergraduate student I had the pleasure of attending a course of lectures in biogeography given by Professor John Flenley (H.O.D., Geography, Massey University), my principal PhD supervisor. One of the requirements for the course was to write a three thousand word essay on the theory of ecological stability. Despite my best efforts, I found it very difficult to comes to terms with the notion of equilibrium and stability as applied to ecological systems. Being a curious person by nature, the subject of stable equilibria presented itself as an unfinished chapter in my undergraduate course of study.

As a possible PhD research direction, Professor Graeme Wake (H.O.D., Mathematics, Massey University) (my second PhD supervisor) had suggested the idea of using coupled systems of logistic equations to determine coefficients of interaction between competing populations in a plant community. Other palynologists had used the logistic equation with apparent success and this seemed like a natural extension of earlier work.

As I began modelling experiments, using Mangrove data from Fiji, I was puzzled by the fact that the behaviour of my first data set did not look anything like the behaviour of classical equilibrium models - coupled or uncoupled. Furthermore, I felt very uncomfortable with the idea of invoking natural process, sampling and measurement error in order to explain all the residual error in my data.

The first breakthrough to these problems came from some observations of the first Fijian data set. The behaviour of the two Mangrove species at this site looked almost oscillatory and appeared to be strongly correlated with abundances of microscopic charcoal fragments in the core sediments. It looked as if the charcoal was forcing the pollen signal. A simple way to test this hypotheses was to add a forcing function to the coupled logistic model, making the specific growth rate parameter dependent to both density feedback and environmental forcing. While this solution seemed like a good idea at the time, is yielded poor results, complicated by increased computational problems and processing time.

As an experiment, I decided to exchange the Malthusian growth term in the logistic equation for a constant growth term, also driven by the charcoal data. Having implemented this new model, I was amazed at the sudden change in the behaviour of the model during computer simulations. For the first time, I had a model that was producing behaviour close to that of my field data.

However, even this discovery was doomed to a disappointing end when I discovered that the optimisation software was providing parameters that produced an almost linear model - it ignored the charcoal data completely. Eventually, it dawned on me that the optimisation software may not be able to interpret cause - effect processes if a reaction time delay was involved and this now appears to be the case. Without realising what I was doing, I had produced a non-equilibrium model of community organisation.

Shortly after these discoveries, I found the 1987 review article of DeAngelis and Waterhouse in ecological monographs. To begin with, I was shocked to discover that theoretical ecology had taken such great strides over the last two and a half decades toward the non-equilibrium paradigm. As a palynologist, these were theoretical advances that I knew very little about. However, soon my initial concerns turned to delight as I realised that independent of any knowledge of current research developments in theoretical ecology - I had come to the very same conclusions.

Furthermore, I then realised that the theme of my project was no longer classical competition theory. More to the point, my research efforts had been directed at fundamental questions concerning the validity of the equilibrium paradigm as a model of community organisation. I had discovered an association between community behaviour and causal mechanisms that were distinctly non-equilibrium in nature. To this end, I believe that the following thesis represents a meaningful and exciting contribution to theoretical ecology and palynology.

The idea of non-equilibrium behaviour is not completely new to palynologists. However, strong linkages between ideas of this kind and theoretical ecology do not appear to have been made. This thesis represents an attempt to define a theoretical foundation that links the present research paradigm of theoretical ecology with the present empirical modelling paradigm of palynology. For this reason, the topic of community organisation is developed in detail in this thesis.

On a personal note, this thesis represents an accomplishment of a different kind. Firstly, I now have the satisfaction of understanding the meaning of stable equilibria. Secondly, it has been a privilege to work alongside Graeme Wake and a number of other mathematicians who have helped me to come to terms with the mathematical focus of this project.

Acknowledgments

I would like to express my sincere thanks to my two supervisors, Professor John Flenley and Professor Graeme Wake, for their untiring support throughout this project and for proof reading this manuscript. I wish to express my special thanks to Professor John Flenley for encouraging me to attempt a PhD, for introducing me to the field of theoretical ecology and for teaching me the importance of objectivity and innovation. I wish to express my special thanks to Professor Graeme Wake for imparting to me in two and a half years what no other teacher had successfully imparted to me during a lifetime of education - a love for mathematics. Also, I would like to express my gratitude to Charles Krebs for his textbook on ecology, now in its fourth edition. More than any other textbook, this fine publication has made ecology come alive for me. It has provided not only endless hours of enjoyable reading, but a primary source of references, historical information and inspiration for this thesis.

My thanks also to the staff of the Massey University Geography, Ecology and Mathematics Departments for their encouragement and assistance. Special thanks to Dr. Jill Rapson, Dr. Alistair Robertson, and Professor Brian Springett of the Ecology Department for encouragement, discussions and ideas. My thanks to Dr Robert McKibbin, Mr. Adrian Swift, Dr Robert McLachlan, Dr Kee Teo, Dr Bruce van-Brunt and Mr Richard Rayner of the Mathematics Department for their assistance with MatLab and computational aspects of the project. My special thanks to Dr. Robert McLachlan and Mr. Adrian Swift for their ideas and assistance with the scripting in MatLab.

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List of Mathematical Notation

Mathematical notation is listed in the order in which it appears in the text.

r (see addendum)[1]	is a parameter expressing the specific population growth rate (rate per year) for a continuous time system.
r (see addendum)[1]	is a parameter expressing the net reproductive rate of a population (number of female offspring produced per female per generation) in a discrete time system.
r_c (see addendum)[1]	is a parameter expressing a constant population growth rate (individuals per year) for a continuous time system.
r_c (see addendum)[1]	is a parameter expressing the constant reproductive rate of a population (individuals per generation) in a discrete time system.
N	is the state variable (population size).
t	is a discrete unit of time, scaled to make 1 the unit of a generation in a discrete time system.
$t \rightarrow t+1$	represents the step from generation t to that of generation $t+1$ (*i.e.* the step length of unity for a discrete time difference equation).
rN	the exponential growth term of Malthus (1798).
K	is a parameter expressing the upper asymptote or maximum value of N for a population in isolation.
N_{t+1}	the state variable N at the time interval $t+1$.
N_t	the state variable N at the time interval t.
$\overline{N}$	a parameter denoting an equilibrium solution.
$\overline{N}_n$	the subscript n denotes the number of feasible equilibrium states for $\overline{N}$.
N'_t	a small perturbation of the equilibrium state $\overline{N}$.
$N_{(0)}$	is a parameter expressing the initial population size of population N.
z	is a parameter expressing a deviation from equilibrium density.
N_{eq}	is a parameter expressing an equilibrium population size (where $R=1$).
R	is a parameter expressing the net reproductive rate.
B	the slope of the line B determines the rate at which the net reproductive rate R decreases with increasing density.
a	is a parameter expressing a known quantity obtained by computing the derivative of a linearised function f and evaluating it at $\overline{N}$.
β	is a coefficient expressing interspecific competition.

α	is a coefficient expressing interspecific competition.
N_1	the state variable of equation 1 (size of population 1).
N_2	the state variable of equation 2 (size of population 2).
N_t	the state variable of a discrete time equation at time t.
T	is a parameter expressing the development time of a resource.
c	is a parameter expressing the response of a population to environmental stress.
B	is a parameter denoting the maximum population size which an environment can support.
θ	is the parameter (theta) used to allow different forms of density-dependence to be described in the logistic and Lotka-Volterra competition equations.
$-PN_n$	is a term expressing the extent of density-dependent predation of the nth equation. Slobodkin (1964) added this term to the Lotka-Volterra competition equations.
w	is a parameter expressing the standard deviation of the resource utilisation function of May and MacArthur (1972).
d	is a parameter expressing a measure of spacing between species (May and MacArthur 1972).
k_i	is a parameter expressing the suitability of an environment for the ith species.
α_{ij}	is a coefficient which measures the degree of overlap in the resource utilisation functions of the ith and jth species.
k_i	is a parameter expressing a constant mean value of i.
$\gamma_i(t)$	is a term expressing Gaussian white noise with variance σ^2.
w	is a parameter expressing a reaction time delay
T_r	is a parameter expressing the characteristic return time of a population to equilibrium.
g	is a parameter expressing the reproductive time delay of a population.
τ_n	is a parameter expressing the density-dependence time delay of the nth species.
$d\pi(\lambda;t)$	is a term expressing a small increment of a Poisson process.
ε	is a parameter expressing the magnitude of a disturbance event.
P_E	is a parameter expressing the probability of extinction.
d	is a parameter expressing an instantaneous death rate.
b	is a parameter expressing an instantaneous birth rate.
$M_{(n,m)}$	are transition matrix elements, n(current), m(next).

d	is a parameter expressing the probability of death.
c	is a parameter expressing clutch size.
b	is a parameter expressing the probability of giving birth.
D	is a parameter expressing the diameter of a tree.
H	is a parameter expressing the height of a tree.
L_a	is a parameter expressing a leaf area index.
$D_{\max}$	is a parameter expressing maximum tree diameter.
$H_{\max}$	is a parameter expressing maximum tree height
$F(R)$	is a parameter expressing the probability of achieving radius R.
D	is a parameter expressing initial density.
y	is a parameter expressing the observation or field data.
Y	is a parameter expressing the fitted model.
e	is a parameter expressing the residual error.

Addendum$_1$

In order to avoid confusion, the reader should note that the meaning of the parameters r and r_c must be derived from the context in which a given equation is used. These two parameters differentiate between the specific growth / net reproductive rate terms (r) of classical equilibrium models (in Ecology) and the constant growth / constant reproductive rate terms (r_c) of the Constant Growth Trend models developed in this project. The same parameters have also been used in both continuous and discrete time (difference) equations. In continuous time equations these terms refer to a growth rate. In discrete time equations these terms refer to a reproductive rate.

List of Equations

Equations are listed in the order in which they appear in the text.

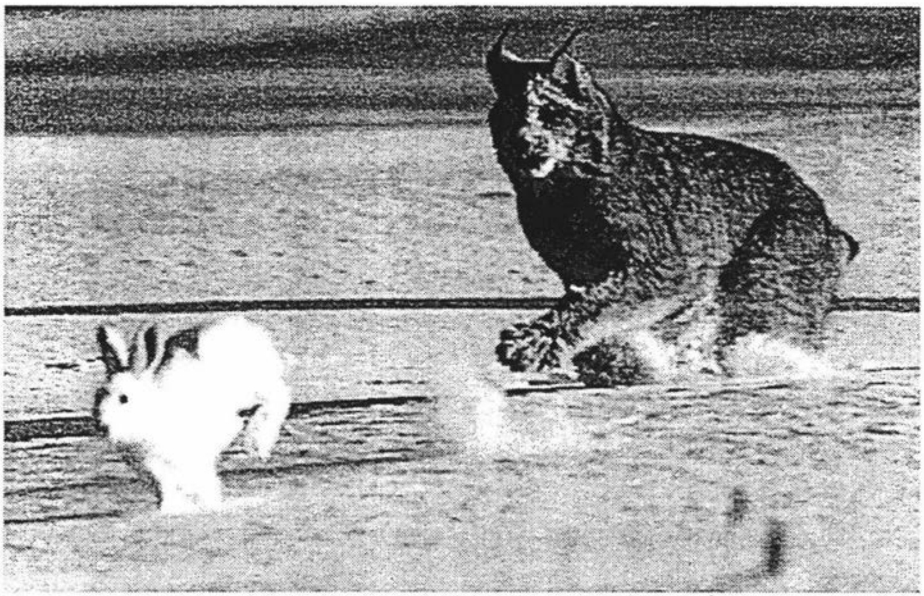
$\frac{dN}{dt} = rN$	The differential form of the exponential growth model.
$\frac{dN}{dt} = rN\left(\frac{K-N}{K}\right)$	The differential form of the logistic growth model.
$N_{t+1} = f(N_t)$	General form of a 1st order difference equation.
$N_{t+1} = N_t + rN_t(1-N_t)$	Discrete form of the logistic growth model re-scaled.
$N_{t+1} = N_t + rN_t\left(\frac{K-N_t}{K}\right)$	Discrete form of the logistic growth model.
$N_{t+1} = N_t + rN_t$	Difference equation form of the discrete exponential growth model.
$N_{t+1} = \left(1 - B_{Z(t)}\right)N_t$	Difference equation form of the discrete logistic growth model expressed as a deviation from equilibrium density.
$(3) \Leftrightarrow \left\| \frac{df}{dN}\right\|_{\overline{N}} \right\| \prec 1$	Local stability theorem (from Edelstein-Keshet 1987).
$\frac{dN_1}{dt} = r_1 N_1 \frac{(K_1 - N_1 - \alpha N_2)}{K_1}$ $\frac{dN_2}{dt} = r_2 N_2 \frac{(K_2 - N_2 - \beta N_1)}{K_2}$	Differential form of a two species system of coupled logistic equations.
$\frac{dN}{dt} = N\left(r - kN_{t-T}\right)$	Logistic growth equation with resource limitation time delay (Hutchinson 1948).
$\frac{dN(t)}{dt} = r(t)N(t)\left[1 - \frac{N(t)}{K(t)}\right]$	Non-autonomous logistic growth equation (Hallam and Clark 1981).

$\frac{dN(t)}{dt} = N(t)\left(r - \frac{c}{K}N(t)\right)$	Modified logistic sensitive of population responses to environmental stress (Hallam and Clark 1981).
$\frac{dN(t)}{dt} = N(t)\left[r(t) - c\frac{N(t)}{B(t)}\right]$	When this form of the logistic growth equation is non-autonomous, either a deteriorating growth rate or environment ensures extinction (Hallam and Clark 1981).
$\frac{dN_1}{dt} = rN_1\left(1 - \left({N_1}/{K_1}\right)^{\theta} - {\alpha N_2}/{K_1}\right)$ $\frac{dN_2}{dt} = rN_2\left(1 - \left({N_2}/{K_2}\right)^{\theta} - {\alpha N_1}/{K_2}\right)$	The theta logistic competition equations (Gilpin and Ayala 1973).
$\frac{dN_1}{dt} = rN_1\left(1 - \frac{N_1 + \alpha N_2}{K_1}\right) - PN_1$ $\frac{dN_2}{dt} = rN_2\left(1 - \frac{N_2 + \beta N_1}{K_2}\right) - PN_2$	Predator mediated competition equations (Slobodkin 1961).
$\frac{dN_i}{dt} = N_i\left[k_i - \sum_{j=1}^{n}\alpha_{ij}N_j\right]$	The logistic growth equation reformulated (May and MacArthur 1972) The coefficients α_{ij} measure the degree of overlap in the resource utilisation functions of the ith and jth species.
$k_i = k_i + \gamma_i(t)$	Environmental variability expressed by the addition of Gaussian white noise with variance σ^2 (May and MacArthur 1972).
$\frac{dN}{dt} = rN\left(\frac{K - N_{t-w}}{K}\right)$	The reaction time delay version of the classical logistic growth equation in differential form (Cunningham 1954).
$T_r = \frac{1}{r}$	Characteristic return time of a population to equilibrium following a disturbance (Maynard Smith 1968, May 1973).
$\frac{dN_1}{dt} = r_1N_1\left[\frac{(K_1 - N_1 - \alpha N_2)}{K_1}\right]_{(t-\tau_1)}$ $\frac{dN_2}{dt} = r_2N_2\left[\frac{(K_2 - N_2 - \alpha N_1)}{K_2}\right]_{(t-\tau_2)}$	Lotka-Volterra competition equations with density-dependent time delay for species one and two (Wangersky and Cunningham 1957).

$\frac{dN}{dt} = rN\left(1-\frac{N}{K}\right) - \varepsilon d\pi(\lambda;t)$	The logistic growth equation with environmental disturbance term defined by a Poisson process (Hansen and Tuckwell 1978).
$N_{(t+1)} = r\left(N_{(t)}\right)N_{(t)}$	Discrete time growth equation for which the growth rate (r) is totally governed by a stochastic environment rather than the current population size. At each time interval, (r) is chosen from a probability distribution (Lewontin and Cohen 1969).
$(P_E) = \left(\frac{d}{b}\right)^{N_0}$	Probability of population extinction (Pielou 1969).
$M_{(n,m)} = \sum_{i=0}^{n}\sum_{j=0}^{n} P_{cmij}\left(\frac{n}{i}\right)b^i(1-b)^{n-i}\left(\frac{n}{j}\right)d^{n-j}(1-d)^j$	Population growth based on demographic stochasticity (Gilpin 1992).
$\frac{d\left[D^2H\right]}{dt} = rL_a\left(1-\frac{DH}{D_{\max}H_{\max}}\right)$	Annual tree increment equation (Shugart 1984).
$F(R) = \frac{1}{1+2\pi R^2 D}$	Competition for space model (Slatkin and Anderson 1984).
$y = Y + e$	A classic equation used to express the relation between observations, the fitted model and residual error (Nelder 1972).
$\frac{1}{y^2}$	An error weighting term used to fit a model to data with large variance (Kuo and Fox 1992).
$\frac{dN}{dt} = r(1+mf(t))N\frac{(K-N)}{K}$	Classical logistic growth equation modified with forcing function which influences the Malthusian growth term.
$N_{t+1} = N_t + r(1+mf(t))N_t\left(\frac{K-N_t}{K}\right)$	Discrete logistic growth equation with forcing function.
$N_{t+1} = N_t + r_1 N_t\frac{(K_1 - N_t - \alpha M_t)}{K_1}$ $M_{t+1} = M_t + r_2 M_t\frac{(K_2 - M_t - \beta N_t)}{K_2}$	Difference equation form of the discrete couple logistic growth equation.

$N_{t+1} = N_t + r_1(1+m_1 f(t))N_t \frac{(K_1 - N_t - \alpha M_t)}{K_1}$ $M_{t+1} = M_t + r_2(1+m_2 f(t))M_t \frac{(K_2 - M_t - \beta N_t)}{K_2}$	The discrete coupled logistic equation with forcing function.
$\frac{dN_1}{dt} = r_1(1+m_1 f(t))N_1 \frac{(K_1 - N_1 - \alpha N_2)}{K_1}$ $\frac{dN_2}{dt} = r_2(1+m_2 f(t))N_2 \frac{(K_2 - N_2 - \beta N_1)}{K_2}$	The continuous coupled logistic equation with forcing function.
$\frac{dN}{dt} = r(1+mf(t))N$	The continuous exponential growth equation with forcing function.
$N_{t+1} = r(1+mf(t))N_t$	The discrete form of the exponential growth equation with forcing function.
$\frac{dN}{dt} = r_c + N$	The continuous time formulation of the exponential constant growth trend model.
$\frac{dN}{dt} = r_c + (mf(t))N$	The continuous time formulation of the exponential constant growth trend model with forcing function.
$N_{t+1} = r_c + (mf(t))N_t$	The discrete time formulation of the exponential constant growth trend model with forcing function.
$\frac{dN}{dt} = r_c + (mf(t) + sf(t))N$	The continuous time formulation of the exponential constant growth trend model with two forcing functions.
$\frac{dN}{dt} = r_c + (mf(t))N\left(\frac{K-N}{K}\right)$	The continuous time formulation of the logistic constant growth trend model with forcing function.
$N_{t+1} = N_t + r_c + (mf(t))N_t\left(\frac{K-N_t}{K}\right)$	The discrete time formulation of the logistic constant growth trend model with forcing function.
$\frac{dN_1}{dt} = r_c + (m_1 f(t))N_1\left(\frac{K_1 - N_1 - \alpha N_2}{K_1}\right)$ $\frac{dN_2}{dt} = s_c + (m_2 f(t))N_2\left(\frac{K_2 - N_2 - \beta N_1}{K_2}\right)$	The continuous time formulation of the coupled logistic constant growth trend model with forcing function.

Preview to Chapter one



(from Bright 1991)

Introducing the Study of Community Organisation

Predation is one of the three biotic mechanisms thought to be responsible for community organisation. In this picture, a Canadian Lynx chases a snowshoe hare through the snow. For at least two hundred years, Canadian Lynx populations have exhibited large scale oscillations as recorded by the numbers of fur returns of the famous Hudson Bay Company. For many ecologists, empirical evidence of this type provided convincing proof for the existence of stable equilibrium points in natural systems - a view that is now being seriously questioned. The following PhD thesis is dedicated to the study of this fascinating topic which forms the cornerstone of the much larger theme of community organisation.

Chapter one

Introducing the Study of Community Organisation

1.1 Objectives

The aim of this research project is to test hypotheses derived from community organisation theory. Absolute fossil pollen data from two different plant communities have been used to provide test data to permit the evaluation of community organisation theory in environments of differing spatial scale and resolution. Fossil pollen counts from two different study sites have been obtained with the aid of close resolution palynology. Modelling the fossil pollen field data required the development of a modelling framework based on dynamical systems theory.

The following chapter provides a more detailed description of these objectives and an introduction to the central topic of this research project - the study of community behaviour.

1.2 Introduction

The aims and modelling objectives of this research project are interdependent. The development of a modelling framework is driven by the need to test theory, while limitations of the same framework constrain to a degree the modelling process. A further objective involves the use of fine resolution palynology to provide proxy test data.

The palynology objectives should not be considered unimportant simply because they are not explicitly stated in the title to this thesis. Their absence indicates an analytical emphasis; an attempt to progress from the descriptive and narrative stages of palynology's past (Birks 1992).

The central theme of this research project is plant community organisation while the principal topic of interest is community behaviour as characterised by equilibrium and non-equilibrium theory. The testing of theory related to community organisation is one of current interest to many community ecologists. Until it is known which of the two contending equilibrium paradigms best imitates community behaviour, it will remain very difficult to prescribe management strategies for ecological reserves (Krebs 1985) or to formulate long term plans for sustainable resource management.

The methodology followed in this research project is common to most scientific research (Mentis 1988). An initial statement of working hypotheses was followed by experimental design, fieldwork in which samples were collected and lab-work in which the samples became data. Running concurrent with the data collection stage was the development of a modelling framework based on dynamical systems theory. This stage involved the scripting and debugging of software (Math Works Inc. 1991) in order to construct a mathematical framework (Robertson *el al.* 1991) that would solve and plot coupled systems of equations and estimate equation parameters based on non-linear optimisation procedures (Grace 1992). Finally, the software had to be validated, before the modelling work could begin.

The second and final stage of this project involved computer laboratory work in which the behaviour of various ecological models was tested against the behaviour of actual field data. Modifications were made to the models in order to test various hypotheses regarding the operation and behaviour of the systems under study.

In determining the layout of this thesis, the author considered it too restrictive an exercise to write from a formal scientific point of view (*i.e.* aims, method, results, discussion, conclusion *etc.*). To do so would be to place an unjustified emphasis on a sequence of research events at the cost of what this project is really all about - community organisation theory and its testing.

For this reason, a format more common to mathematics theses has been chosen with the justification that it provides a more natural grouping of the ideas being developed in a context of the natural stages of the project: to derive, to develop and to compare, *i.e.*

(a) to derive working hypotheses and models from existing theory

(b) to develop a mathematical framework for testing the models

(c) to compare field and model data.

1.2.1 Derive Working Hypotheses

Chapters one, two and three develop the theory of community organisation in three natural parts. Chapter one is primarily concerned with defining community organisation and introducing the topic of community behaviour by stressing its relationship to the activity of causal agents. Chapter one also sketches a descriptive theoretical outline of the equilibrium and non-equilibrium models of community behaviour. Chapters two and three develop in more detail the historical, ecological and mathematical significance of community behaviour with the objective of defining a set of testable research hypotheses.

1.2.2 Develop a Mathematical Framework

Chapter four takes up a discussion of ecological modelling and the current contribution being made in this field of research by palynologists. A further objective of this chapter is to define the modelling methodology used in this project. This will introduce subjects like the computational software and its validation along with the theory of parameter estimation as used in hypothetico-deductive scientific methodology.

1.2.3 Compare Actual and Model Data

Chapters five and six contain two case studies in which the field data is introduced, modelled and evaluated. Chapter seven contains a brief summary and statement of conclusions.

1.3 Community Organisation Introduced

Simply stated, community organisation is the study of the forces or mechanisms responsible for community structure and behaviour (fig 1.1). The problem with this definition is that it pre-supposes a knowledge of the word community - not yet defined. Attempts to develop a definition of community have a long history in ecology and involve an ongoing debate into some of the most controversial aspects of community organisation. For these two reasons, an acquaintance with the historical trends in the community definition debate is a pre-requisite to a working definition of community organisation.

1.3.1 A Working Definition of Ecological Community

A simple definition of an ecological community is: populations of living organisms in a prescribed area or habitat. Krebs (1985) suggests that there are three main ideas involved in all definitions of ecological community: species aggregation in a defined area, the idea of a fundamentalunit of community structure and the idea of homeostasis or self regulation (fig 1.2).

The second and third concepts of community listed above have been actively disputed. The extreme supporters of the third view consider that synergistic attributes belong to communities as a consequence of internal stability maintained by homeostatic control (Clements 1916, Tansley 1920, 1935, Braun-Blanquet 1932, Lovelock 1988).

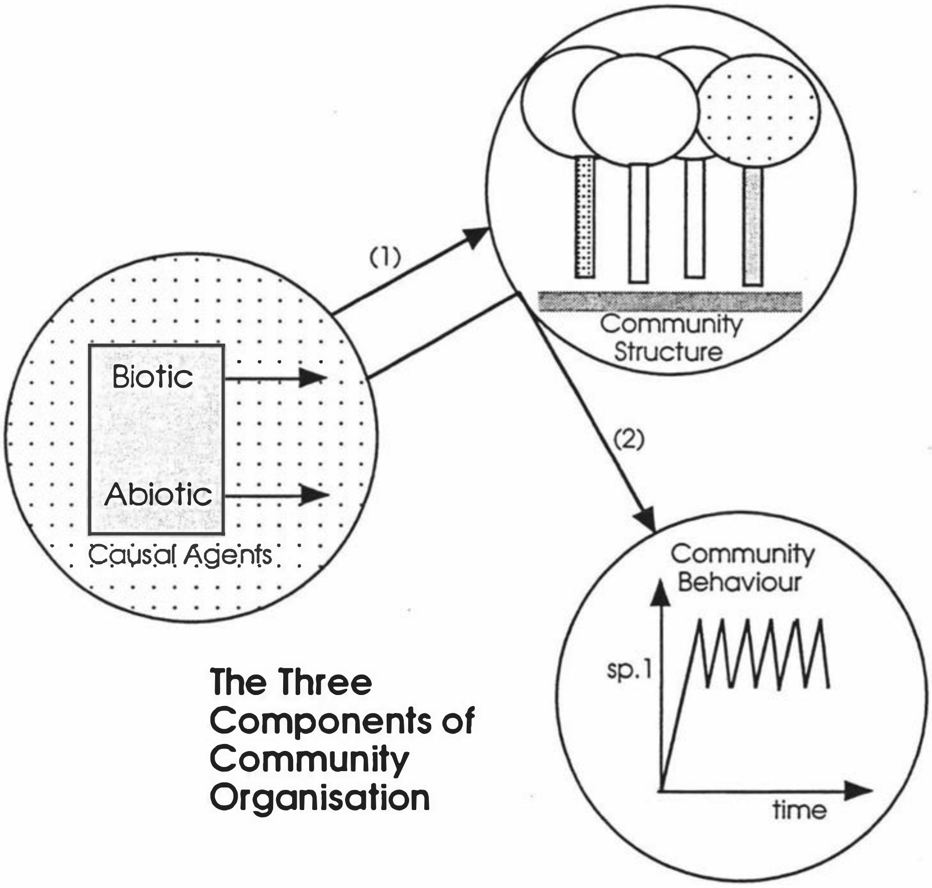


Fig 1.1 The three components of community organisation: causal agents, community structure and behaviour. Community organisation is the study of the forces or mechanisms responsible for community structure and behaviour. Causal agents may work directly upon the structure of a community (arrow 1) and in some cases are a part of the community structure itself (*e.g.* a predator or competing individuals). Causal agents work through the structure of a community in order to influence community behaviour (arrow 2).

The second concept of a fundamentalunit of community types or classes is a further major assumption of the Clements-Tansley-Braun-Blanquet holistic school - an idea that found wide endorsement in North America, Great Britain and Europe. Gleason (1926, 1939), an ardent critic of the super-organism paradigm, argued that communities were simply collections of populations with the same environmental requirements. This view became the central tenet of the individualistic school of community ecology.

The individualistic school argued that while communities could be recognised and classified, it was for the convenience of the human observer and *not a description of the fundamental structure of nature* (Krebs 1985). Furthermore, communities are not of fixed composition (Whittaker 1962, 1967), vegetation change through time is continuous (Raup 1964) and thought to occur as a result of essentially two factors: plant immigration and environmental fluctuation (Gleason 1926, 1939).

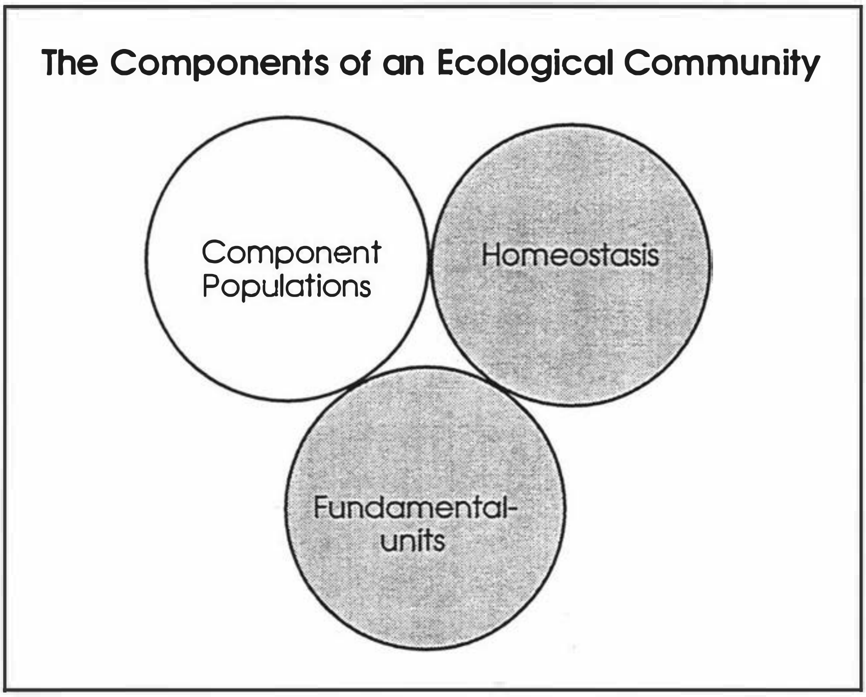


Fig 1.2 There are three main ideas involved in all definitions of ecological community: species aggregation in a defined area, the idea of a fundamentalunit of community structure and the idea of homeostasis or self regulation (Krebs 1985).

Simberloff (1980), argues that 1947 was a watershed year for the demise of the super-organism paradigm. Three respected plant ecologists (Egler, Cain and Mason) all published papers in Ecological Monographs forcefully attacking the Clementsian paradigm and citing Gleason's individualistic concept as the first articulation of their views.

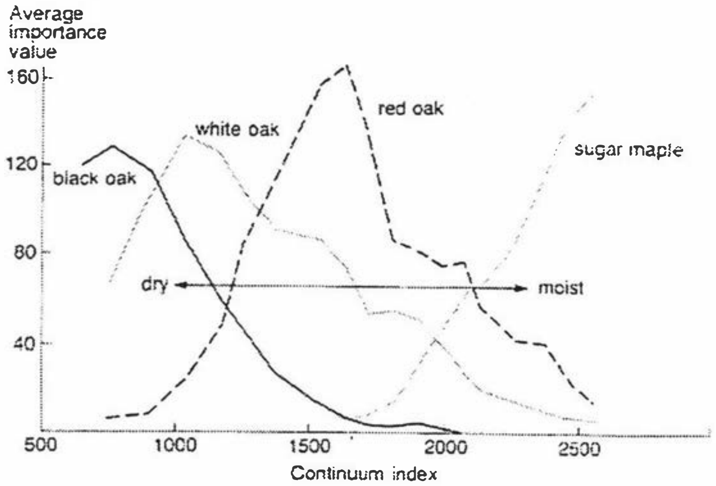


Fig 1.3 Curtis and McIntosh (1951)demonstrated that the so called climax vegetation of southern Wisconsin was actually a continuum of forest - the result of an environmental gradient. Soil moisture, exchangeable calcium, and pH increase to the right.

A few years later, two further groups of independent opposition followed with the vegetational continuum concept of Curtis and McIntosh (1951) (fig 1.3) and Whittaker's (1967) gradient analysis.

In reply, the holistic supporters claimed that the research evidence used to discredit the fundamentalunit hypothesis was invalidated on two counts. The stands studied by gradient analysis were disturbed and constituted non-equilibrium conditions. Therefore, the individualistic researchers had found by virtue of their methodology exactly what they were looking for (*ie.* non-equilibrium conditions) (Langford and Buell 1969, Daubenmire 1966).

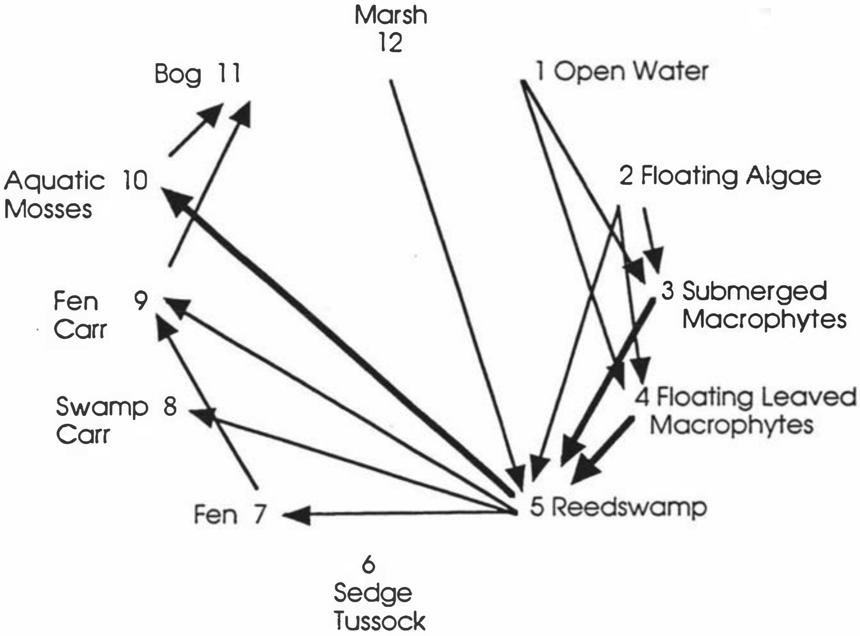


Fig 1.4 Hydroseral transitions in Britain as proposed by Walker (1970). Thick lines denote dominant courses. Evidence provided from the stratigraphy of lake basin sediments and the analysis of fossil pollen data (after Walker 1970).

The individualistic supporters objected that the subjective selection of homogeneous equilibrium stands should be made a criterion for determining fundamentalunits. Cottam and McIntosh (1966) argued that all species present must be used to look for the boundaries of *natural units* if the community concept is to be meaningful.

According to Clements, community change occurred by gradual process of succession from one state to another driven by autogenic mechanisms. In 1970, Walker brought an important temporal dimension into this essentially spatial controversy (fig 1.4) by demonstrating that historic hydroseral vegetation changes did not conform to the successional facilitation model postulated in the original Clementsian hypothesis. Actually, the term facilitation was coined by Connell and Slayter (1977) who presented further empirical evidence in favour of their own inhibition model.

The super-organism, Ecology's first paradigm (Simberloff 1980), in its original form is no longer considered useful in directing research along the lines suggested by Kuhn (1970). The present view of an ecological community lies closer to Gleason's individualistic view, than to Clements' super-organism interpretation. Species groups do not appear to be consistent from place to place. Communities are not discrete but grade continuously in space and time. Community classification is not considered to be a description of fundamental structure in nature (Krebs 1985).

Apparently, the super-organism has been revived. Simberloff (1980) contends that the *first ecological ideal, Clements' super-organism, is not dead but rather transmogrified into a belief that holistic study of ecosystems is the proper course for ecology* (Simberloff 1980). The ecosystem paradigm purports to have corrected the super-organism's shortcomings, primarily by noting that succession need not always lead to the same climax (Odum 1969).

Simberloff (1980) points out that one reason for the apparent paradigmatic status of the ecosystem concept is that it *lends itself to cybernetic interpretation via systems analysis, a vogue vocation in the United States about two decades ago.* Furthermore, *it provides support for the notion of self regulatory powers,* not to mention *the attraction of holism,* yet it has largely failed *to add substantially to our understanding of the workings of nature* while its most fundamental features are deterministic and synergistic as evidenced by its successional genesis and the claims of its strongest advocates (Odum 1969).

What is an ecological community? Populations of living organisms in a prescribed area or habitat. It is interesting to note that attempts to amend this simple structuralist definition of community call into question a fundamental inability to define properties of community function or organisation.

Gleason (1926, 1939) argued that communities were simply collections of populations with the same environmental requirements. This position suggests that communities may be organised by environmental controls which destine that community to track environmental fluctuations based on the genotypic constitution of component populations. If this position is correct, then communities may be characterised by unstable transient behaviour as the system moves from one state to another. This non-equilibrium view suggests that communities are open systems, characterised by collections of populations connected in time and space by dispersal mechanisms.

At the other end of the spectrum, Clements and Tansley argued for synergism - attributes that belong to communities as a consequence of internal stability maintained by homeostatic control. This position suggests that communities may be organised by internal community processes such as competition, predation and symbiosis. If this position is correct, then the study of communities is restricted to the behaviour of closed systems at or near an equilibrium point. Until recently, community ecologists have been divided over the question of whether communities should be considered equilibrium or non-equilibrium systems.

Community Property	**Gleason**	**Clements**
Community Structure	Individualistic	Fundamentalunit
Agents of community organisation	Abiotic Disturbance	Biotic disturbance and regulation
Community behaviour	Transient Non-equilibrium	Equilibrium centred
Stability	Unstable	Globally Stable
Type of System	Open (connected)	Closed

Table 1.1 A descriptive comparison of the two conflicting models of community organisation based upon various properties of natural communities.

In summary, this discussion on the nature of an ecological community has introduced some of the important concepts of community organisation in the historical context of ecologists' efforts to develop a working definition of an ecological community. A summary of these ideas is listed in Table 1.1.

It is now time to consider just how the four groups of biotic and abiotic mechanisms (competition, predation, symbiosis and abiotic disturbance) mentioned above may operate as agents of community organisation.

1.3.2 Community Organisation Defined & Illustrated

Community organisation has been defined as the study of forces or mechanisms responsible for community structure and behaviour. A more rigorous definition of community organisation awaits better understanding of which of the two equilibrium paradigms more accurately models community structure and behaviour. For this reason, at present, community ecology is composed of numerous strands of mechanistic, structural and behavioural theory that has yet to be completely unified. This thesis is not an attempt at unification. It is an attempt to probe more deeply into the nature of the mechanisms (causal agents) that regulate and force the component populations (structure) of natural communities. In this context, community behaviour may be defined as a time series record of changes in community structure (fig 1.5).

This objective will be accomplished by seeking to identify the association between the historic activity of causal agents and the behaviour of plant communities affected by them. The modelling work used in this project will focus upon the behaviour of plant communities. In order to interpret the behaviour of a community correctly, an acquaintance with the general theory of community organisation is essential.

For this reason, the theme of this project is undoubtedly community organisation, but the topic of special interest is community behaviour.

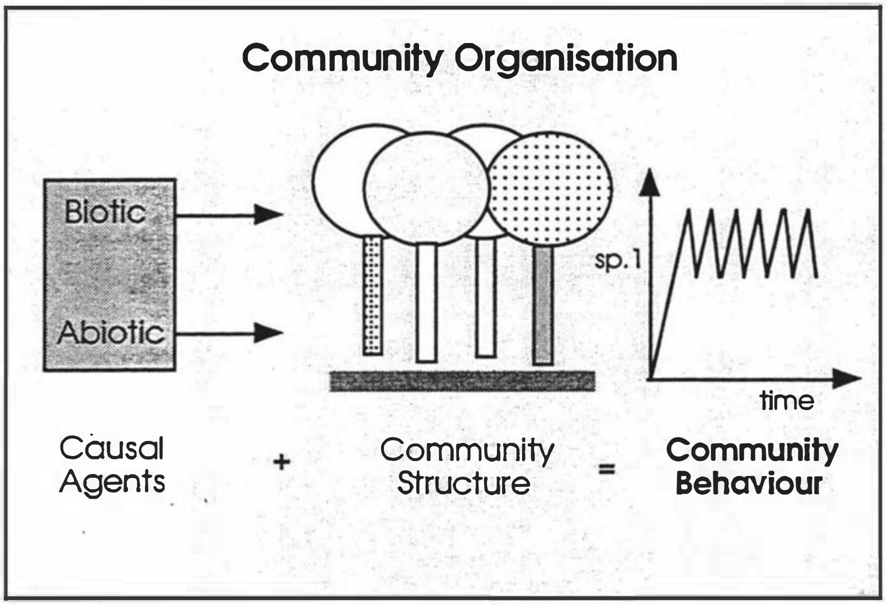


Fig 1.5 Community organisation is the study of the causal agents, forces, or mechanisms responsible for community structure and behaviour. Community ecologists are especially interested in understanding the complex interactive relationships between causal agents and community structure. The behaviour of an ecological community may be defined as a time series record of changes in community structure.

The remainder of this chapter provides a background discussion and review of important theoretical developments in community organisation. It is not possible in one chapter to review the entire field of community organisation theory, nor is it all relevant to this project. The present study will be limited to changes in population density caused by population natality (birth rate) and mortality (death rate). Immigration and emigration rates will be assumed to be at equilibrium. This assumption prevents the need to factor in complex spatial effects and temporal changes in community diversity.

Furthermore, the evaluation of population natality and mortality will be undertaken with respect to four possible forcing and regulating mechanisms (competition, predation, symbiosis and abiotic disturbance). Undoubtedly, processes which force and regulate the all important spatial and biodiversity attributes of communities must eventually be factored into the behavioural dynamics equation. Illustrations of this type of modelling research will be reviewed in chapter three.

Biotic causal agents are thought to be related to community behaviour through the effect of density-dependence. Classical equilibrium models of community behaviour have been developed on the assumption that food shortages caused by high population numbers will result in the regulation of these populations by internal biotic forces (competition, predation, symbiosis). Density-dependent *biotic* feedback mechanisms are believed to be the cause of equilibrium behaviour. The ecological and mathematical significance of this mechanism will be developed more fully in chapter two. As an introduction to Chapter Two, section 1.3.2.1 provides a background discussion which seeks to characterise the activity of biotic causal agents and to describe broadly the characteristics of equilibrium behaviour. A formal statement of the equilibrium paradigm is included in the summary to this section.

A range of modelling approaches has been explored in order to understand the relationship between abiotic disturbances and community behaviour. Abiotic disturbance is able to act on community structure independent of density. The concept of regulation is not at all useful in describing the behaviour of non-equilibrium systems which are forced from one state to another by abiotic disturbance events. Furthermore, the probabilistic nature of abiotic disturbance means that it is virtually impossible to predict future non-equilibrium behaviour. The ecological and mathematical significance of non-equilibrium systems will be developed more fully in chapter three. As an introduction to Chapter Three, section 1.3.2.2 provides a background discussion which seeks to characterise the activity of abiotic causal agents and to describe broadly the characteristics of non-equilibrium behaviour. A formal statement of the non-equilibrium paradigm is included in the summary to this section.

1.3.2.1 The Study of Biotic Causal Agents

There are at present three biotic causal agents thought to be responsible for community organisation - competition, predation and symbiosis. Biotic causal agents are traditionally associated with the self-regulatory, organisational strategies of the equilibrium paradigm. Under equilibrium conditions exogenous forcing by abiotic agents is considered to be damped-out by global stability; an attribute of self-regulation (Krebs 1985). Today, very few modern ecologists would support this notion. At present, there is a growing awareness of the importance of abiotic disturbance in community organisation. Furthermore, the interplay between biotic and abiotic mechanisms may account for a *major portion of the organisation and spatial patterning of natural communities* (Sousa 1984). This theme is more fully discussed in Chapter Three.

While it is possible to advance hypotheses about how biotic causal agents may work to organise community structure and behaviour, it has proved more difficult to test these theories. This has especially been the case for competition theory which has an extensive and controversial literature (Grinnell 1904, Kropotkin 1914, Lotka 1925, Volterra 1926, Gause 1932, 1934, 1935, Lack 1944, 1945, Crombie 1945, Park 1948, 1954, Hutchinson and Deevey 1949, Birch 1953, 1957, Ross 1957, Fryer 1959, Hardin 1960, Cole 1960, Miller 1967, Hutchinson 1958, 1959, 1961, de Wit 1961, DeBach and Sundby 1963, Slobodkin 1964, May 1974, Schoener 1974, Wiens 1977, Harper 1977, Mac Arthur 1958, 1968, 1972, Whittaker *et al.* 1973, Strong 1980, Simberloff and Boecklen 1981, Lewin 1983, Aarssen 1983, Abrams

1983, 1986, Ghilarov 1984, den Boer 1986, Grace and Tilman 1990, Rydin and Bengtesson 1990, Taper 1993, Hopf 1993)[1].

Connell (1980) and Connor and Simberloff (1979) are strongly critical of much of the published evidence presented in support of competition theory. According to Roughgarden (1983), these criticisms imply that *competition theory, including its extension to the co-evolution of competitors, is irrelevant to natural processes and is unworthy of testing regardless of whether the testing is feasible.* Furthermore, Roughgarden (1983) claims that the arguments of Connell (1980) and Connor and Simberloff (1979) are philosophically untenable and technically flawed; facts that amount to a general misrepresentation of the central objectives of community ecology. For the reply to Roughgarden (1983), see: Strong (1983), Connell (1983) and Simberloff (1983).

The role of competition in community organisation is thus difficult to summarise. Wiens (1977) contends that competition may be rare for some populations because of high environmental fluctuation. Such populations typically exist well below the carrying capacity of their environment where the negative effects of high density are not relevant. Occasionally, a time of food shortage may come in which competition does occur. If this occurs once every ten to fifteen years, competition may be hard to detect in short term studies.

At this point it is tempting to diverge into a more detailed discussion of the origins and development of the controversy that surrounds competition theory. Such a discourse is outside the focus of the present study for at least three reasons. Firstly, the literature on competition theory is so extensive that it deserves a thesis of its own. Secondly, the objective of this research has been to look for evidence of causal mechanisms *(plural)* by evaluating field data recording long term plant community behaviour. To accomplish this objective, the behavioural side of community organisation must be more fully developed.

Thirdly, Strong (1983) in his reply to Roughgarden (1983), argues for the importance of *alternative and complementary forces in communities, in contrast to a singular emphasis on competition.* The objective of the present study is to take a more holistic approach (McIntosh 1987) to community organisation. In order to give a fair and equal weighting to the *manifold mechanisms of ecological communities* (Strong 1983), the temptation to become involved in the semantic muddles and vague tautologies (Peters 1976) of competition theory must be resisted. For these reasons, the following discussion is representative and generalised.

---

[1] Key historic references on competition theory in ecology. These do not include numerous references to niche theory, reviews of which are given by Vandermeer (1972), Colwell and Fuentes (1975), Whittaker and Levin (1975) and Krebs (1985). For a review and discussion of competition theory consult MacArthur (1972), Connell (1983), Grace and Tilman (1990).

Most communities contain so many species it is literally impossible to study each species separately. One way of reducing the complexity of communities is to group species according to functional roles and feeding classes. Functional roles might include the activity of: herbivory, primary producers, and predator-prey relations. The transfer of energy from primary producers through herbivores to carnivores is referred to as a food chain. Elton (1927) was one of the first to apply this concept in ecology. Food chains rarely exist in isolation. Usually, they are interconnected to form a food web. In this way, any of the links of one food chain may, through the activity of decomposers, saprophytes, or parasites, interconnect with other food chains. Furthermore, most plants and herbivores have a number of different predators, a fact that again favours the food web approach. Feeding classes might include: the activity of mobile links, guilds, keystone and dominant species.

The following discussion draws on published work to illustrate ways in which competition, predation, and symbiosis may be studied in complex communities by research approaches focusing on: food webs, guilds, keystone species, Predator-prey relations, herbivory and dominant species. The purpose of this discussion is to characterise the complex workings of biotic mechanisms in community organisation.

1.3.2.1.1 ***Food webs***

Food web analysis is based on functional relationships and emphasises the connections between populations.

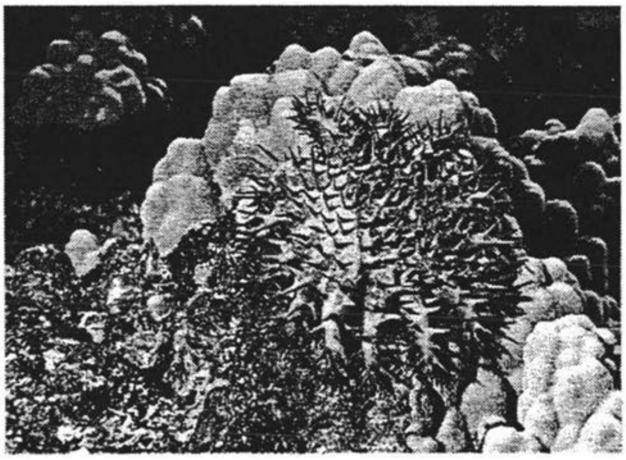


Fig 1.6 The Crown-of-Thorns Starfish is found in Indian and West Pacific oceans, from the east African coast to Hawaii. The size of the adult Starfish varies from 300 to 610 mm, while they are known to live for up to 8 years. Like *Heliaster* and *Pisaster*, the Crown-of-Thorns Starfish is a marine predator. Its strong digestive juices dissolve the soft-bodied polyps of coral. During the 1980s, populations of this starfish grew to enormous sizes and damaged extensive areas of coral reef in Western Samoa and Australia. Marine ecologists suspect that this sudden population explosion may have been related to the overfishing and poisoning of the Crown-of-Thorns natural predators (from Bright 1991).

Not all producers are consumed by all herbivores. Cohen (1989) suggests that food web analysis has greater power than ecosystem analysis to differentiate community structure because it includes species level information about the community. For example, Paine (1966) experimented with a food web containing four levels of marine carnivores found in a rocky intertidal coastal zone of the California coast. The starfish *Heliaster* was found to dominate as a top level carnivore until the size of two gastropods *(Hexaplex and Muricanthus)* in the level immediately below *Heliaster* reached a critical size. Having grown to this critical size range, both gastropods *(Hexaplex and Muricanthus)* also became top carnivores with *Heliaster*.

Other examples of the food web studies include: work on food relations among lemmings and their predators (Pitelka *et al.* 1955), the activity of herbivorous and detritus feeding fauna in a Georgia salt marsh (Teal 1962), the use of radioactive tracers to define food lines (Marples 1966), and a more detailed study of fauna and flora comprising a food web in an English Woodland by Elton (1966). Finally, food webs may be a useful concept for the theoretical analysis of community organisation as proposed by Cohen (1978) and Pimm (1982).

1.3.2.1.2 ***Guilds***

Guilds may be defined as groups of species that exploit a common resource base in a common fashion (Root 1967). Root (1967) suggested three advantages in the use of the word guild. Firstly, guilds focus attention on all sympatric competing species, regardless of their taxonomic relationship. Secondly, guilds eliminate the dual usage of the term niche as meaning both the functional role of a species and a description of the environmental factors that limit its existence. Thirdly, guilds are useful for comparative studies of communities.

Simberloff and Dayan (1991) suggest that the term guild holds a central place in ecology and point to a fourth goal in the study of guilds that has been recently articulated. Guilds may represent *basic building blocks* of communities (Hawkins and MacMahon 1989). The idea that species in a community fill fixed functional roles has a long history in ecology the discussion of which has usually centred upon niches which were *construed as individual species functional roles* (Simberloff and Dayan 1991). If guilds really are fundamental units; an emergent property (Salt 1979), then the elusive grail of community ecology might be found in the nature of guilds that form a community (Simberloff and Dayan 1991).

A group of species that exploit a common resource base will be subject to competition during times of food scarcity or high population density. Feinsinger (1976) studied nectar-eating birds of successional montane forests in Costa Rica illustrating the roles of guilds organised around competition for food. According to MacNally (1994), the guild structure of forest and woodland birds differs in a consistent manner from habitat to habitat. This may indicate that factors such as physiography, substrate and resource availability act as determinants of guild structure on a local basis.

Intra-guild predation (IGP) is a combination of species interactions based on competition, predation and parasitism. By definition, IGP is predation that must occur among guild members. Polis *et al.* (1989) define IGP as the *killing and eating of species that use similar, often limiting resources and are thus potential competitors.* In other words, IGP refers to potential competitors that eat each other.

The co-authors use the term *guild* more broadly than Root (1967) and suggest that a guild should include all taxa in a community that use and compete for similar resources regardless of the *tactics of resource acquisition* (Polis *et al.* 1989). In their review of the ubiquity and importance of IGP, the co-authors conclude that IGP significantly affects the distribution, abundance and evolution of many species. Furthermore, IGP appears to be important in promoting the *occurrence of alternative stable states in many circumstances* (Polis *et al.* 1989).

1.3.2.1.3 ***Keystone Species***

The keystone species concept was first introduced by Paine (1969). The presence of a keystone species and its role in organisation may be of critical importance to a community. Paine (1969) suggested that the activity of keystone species may determine community structure. Removal experiments are one of the easiest ways to test this hypothesis (Harper 1969). Paine (1974) applies this technique to the starfish *Pisaster ochraceous* in rocky intertidal communities of western North America.

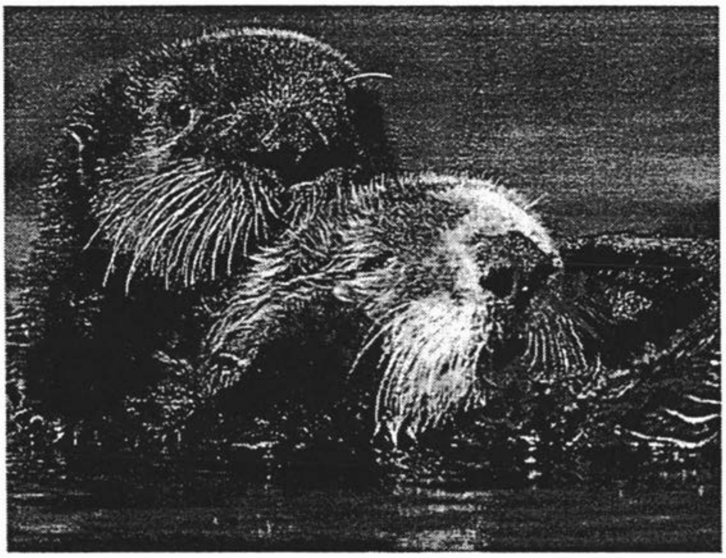


Fig 1.7 Sea Otters are usually found in North American and Russian/Pacific coastal Waters. These creatures measure up to 1.4 m in body length, weigh from 36 to 54 kg and are known to live for up to 20 years. Duggins (1980), suggests that Sea Otters may be a keystone species responsible for regulating sea urchins. (from Bright 1991)

The manual removal of *Pisaster* enabled the mussel *Mytilus californianus* to dominate the community to the exclusion of other invertebrates and algae needing attachment sites. There have been other keystone species research efforts.

Menge *et al.* (1994) have tried to reconstruct the earlier experiments of Paine (1969) and raise three important points regarding the keystone species concept. Firstly, the effect of *Pisaster* as a keystone predator is correlated spatially with wave disturbance (see Paine 1980, Robles 1987, Foster 1990, Robles and Rob 1993). Secondly, Menge *et al.* (1994) provide and draw on published evidence which suggests that this variation may be due to factors such as mussel recruitment, sand burial, algal turf, and the responses of whelks. Finally, the co-authors conclude that keystone predation is but one of several predation models.

Duggins (1980), shows how Sea Otters along the Pacific Coast of North America regulate sea urchins thereby preventing excessive disturbance by grazing sea urchins known to prevent the colonisation of algae and seaweed (fig 1.7). Mann and Breen (1972) suggest that the predatory influence of rock lobster may be critical in regulating population explosions of sea urchins *(Strongylocentrotus droebachiensis)* known to result in the elimination of the seaweeds *Laminaria* and *Alaria* .

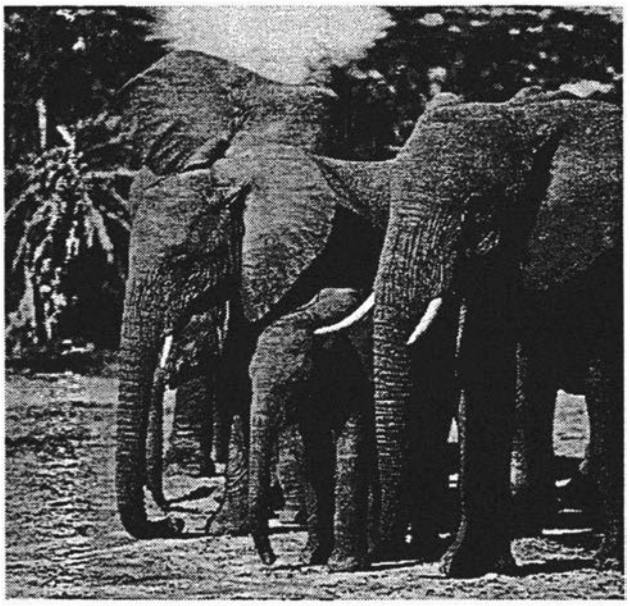


Fig 1.8 The African Elephant can be found living south of the Sahara and is now largely confined to national parks and reserves. During the rainy season when there is plenty of food, these elephants feed in open grassland. In the dry season, they move to wooded areas to find shelter and feed on trees. The African elephant can measure up to 3.4 m at shoulder height, weigh 4 to 6 tons and live between 55 and 60 years (from Bright 1991).

Laws (1970) considers the African Elephant (fig 1.8) to be a keystone species responsible for the destruction of woodland and its conversion to grasslands, much needed by grazing ungulates. Finally, the asynchronous fruiting phenology of *Ficus,* along with its large crop sizes and availability in lowland Malaysian forest when other fruits are scarce makes this genus an important keystone plant resource (Lambert and Marshall 1991).

1.3.2.1.4 Predator-Prey Relations

Three of the illustrations used above to support the idea of keystone species involve predator-prey interactions. The complex dynamics of predator-prey interactions were suggested independently by the work of Lotka (1925) and Volterra (1926). Based on equilibrium theory, the mathematical models of Lotka and Volterra demonstrated that it was possible for a predator and its prey to co-populate an area by being locked into periodic oscillatory behaviour of alternating prey and predator dominance.

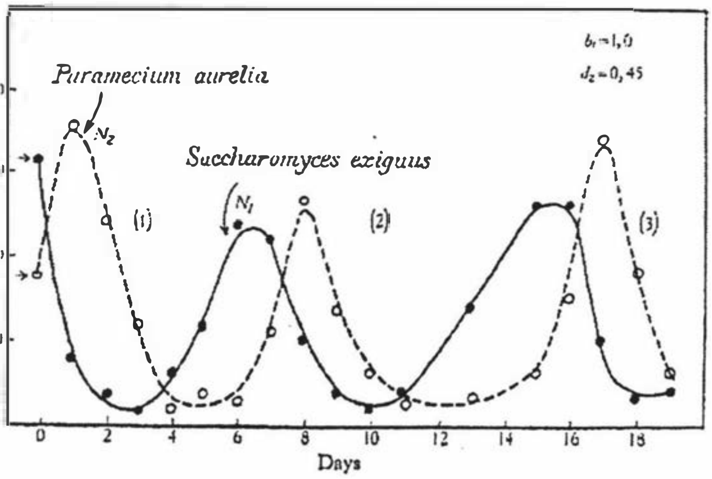


Fig 1.9 Portrayal of results from the 1935 publication of Gause who found conclusive evidence for periodic oscillations in the density of a predator *(Paramecium aurelia)* and prey *(Saccharomyces exiguus)*. These results appear to contradict his earlier findings (Gause 1934a) and may indicate that the predator-prey model is species specific.

For many years, the ultimate illustration of a natural system of oscillating predator and prey was considered to be recorded in the fur returns of the famous Hudson Bay Company (Elton and Nicholson 1942). These results appeared to give solid evidence to support the predictions of the Lotka-Volterra model. However, Gilpin (1973) points out that the data used to support this research was biased; the number of furs collected being a function of the effort of the trappers, the efforts of the trappers being a function of how much money each fur was worth at the time.

Gause (1934a) tried to replicate the periodic behaviour of the Lotka-Volterra model in test tube experiments using *Paramecium* and its predator *Didinium*. Gause found that he could imitate periodic behaviour by increasing the heterogeneity of the mixture by adding a prey refuge or by allowing for immigration. From these results, Gause concluded that by nature, predators will tend to annihilate their prey which explains why periodic oscillatory behaviour resulted from immigration.

Gause (1934a) had discovered that the model's periodic behaviour could not be replicated without some form of interference that enabled the prey to keep one step ahead of the predator. The following year Gause (1935) published further results using Paramecium along with two prey species: *Saccharomyces exiguous* and *Saccharomyces pombe* (fig 1.9). In these results Gause found conclusive evidence for periodic oscillations without interference mechanisms.

Huffaker (1958) and Huffaker *et al.* (1963), demonstrated similar results using interference mechanisms with systems of mites - one a predator and the other phytophagous on oranges (fig 1.10).

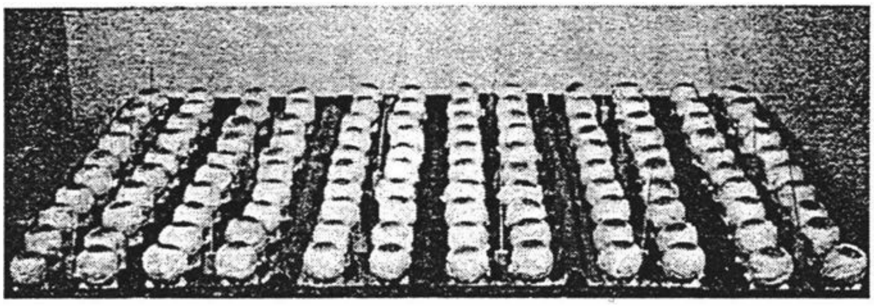


Fig 1.10 Part of the intricate network of impediments used by Huffaker (1958) to demonstrate that periodic predator-prey behaviour must be interference mediated. 120 oranges, each with 1/20 of the orange-area exposed, occupying positions in three wooden trays with partial barriers of vaseline and wooden posts.

Subsequent laboratory and glasshouse studies have shown that a number of phytophagous-predatory mite interactions tend to be unstable at small spatial scales. These populations are only able to persist through interactions among patches (Takafuji 1977, Fernando and Hassell 1980, Nachman 1981). Likewise, Walde (1994) studied predator-prey systems of mites at the scale of an orchard and concluded that the predator mite *(Typhlodromus pyri)* is able to drive the prey mite *(T. ulmi)* locally extinct in the absence of exogenous disturbance. In this system, long term persistence at the spatial scale of an orchard depends on recolonisation events within or between orchards.

Ende (1973), demonstrated apparent stable cycles in a homogeneous environment but on closer inspection discovered that the walls of the test tubes he was using were acting as a refuge for bacteria. In summary, laboratory experiments that replicate the famous periodic solution require some form of interference mediation while the results of Gause (1935) appear to indicate that the Lotka-Volterra model may be species specific.

MacArthur (1972) suggests that predation may regulate a community in one of two directions. Firstly, predators can increase the number of species living in an area by selectively eliminating the dominant species. By keeping species in lower tropic levels below their carrying capacity, competition is alleviated and new species can invade the system.

This is a restatement of the predation hypothesis of Paine (1969, 1971). Janzen (1970) suggested that the high species diversity of tropical trees is due to predation of seeds, lowering the probability of a seedling surviving near its parent. Smith *et al.* (1989) have evidence which suggests that preferential predation of various species of Mangrove seed pods is an important determinant of the diversity and spatial patterning of Mangrove forests. Secondly, while predation may limit the density of a given species, it can also disrupt the effects of competition.

The competition hypothesis suggests that high diversity communities arise in abiotic environments that are stable over long time periods. Stable environments allow most species to reach the carrying capacity which results in interspecific competition. Interspecific competition maintains niche diversification which in turn maintains high diversity (Dobzhansky 1950, Pianka 1974). The classical predation and competition hypotheses appear contradictory. Predation promotes high diversity by preventing competitive dominance and maintaining low density. In the competition hypothesis, high diversity results from density-dependent competition which maintains niche diversification.

The inter-relationships between the predation and competition hypotheses have been explored in work on intertidal invertebrate communities (Connell 1961, Menge 1976). Menge and Sutherland (1976) suggest that predation and competition are complementary in their effect, *the relative importance of each depending on the trophic level being considered and the overall trophic complexity in a community.* To test their hypotheses, the co-authors present empirical evidence derived from studies in the rocky intertidal communities of New England.

The co-authors conclude that the maintenance of high diversity by competition appears to be more important at higher trophic levels, while the maintenance of diversity by predation appears to be more important at lower trophic levels. Furthermore, predation is probably the dominant organising force in complex tropical communities which attain greater complexity as a consequence of stable environmental conditions. Trophic complexity implies an increase in predator abundance and activity following decreasing environmental instability. Fewer occurrences of competitive exclusion follow increased predator intensity. A failing of the competition hypothesis was the supposition that environmental stability promotes trophic complexity for primary producers, herbivores and *predators.*

Finally, the above implies that competition is probably the dominant organising force in trophically simple communities. Environmental disturbance prevents the establishment of top level predators common to trophically complex communities. In the absence of predator pressure, the densities of lower trophic levels approach the carrying capacity and interspecific competition results. A failing of the predation hypothesis was the supposition that animals are usually physiologically adapted to their environment. Therefore, the environmental instability that reduces trophic complexity does not reduce the density of prey species. A fuller treatment of competition theory is given in Mac Arthur (1972) and Slobodkin (1966).

A complicating factor in the study of natural systems of predator and prey is the fact that predation rates vary among habitats and seasons, creating spatial and temporal gradients in predation intensity (Bulter 1989). Brown trout alter their feeding patterns in winter in order to buffer a potential energy deficit caused by adverse environmental condition (Heggenes *et al.* 1993).

In summary, to the extent that predators cause mortality of larvae, juveniles and adults, predation is a process that contributes to the structuring and, in turn, the behaviour of natural communities (Hixon and Betts 1993).

1.3.2.1.5 ***Herbivory***

Herbivory is really a form of predation: herbivores are simply predators that prey on plants. What mechanism regulates predator populations? Like all populations it is possible that predators may be self regulated by intraspecific competition resulting from a large numbers of predators or a shortage of prey. Herbivore predators may be regulated by top level predators. A final possibility for the regulation of herbivore predators is the suggestion that *all that is green may not be edible* (Krebs 1985).

In a classic publication, Erlich and Raven (1964) proposed that plants and their predators may be locked into a co-evolutionary interaction. Plants, through mutation and recombination, produce chemical compounds (secondary plant substances) which are by-products of primary metabolic pathways. Some of these compounds serve to destroy or reduce the palatability of plants for herbivores.

On the other hand, herbivores can also evolve in response to physiological and structural obstacles. To overcome the ill-effects of plant defensive substances, herbivores have evolved detoxification mechanisms (Rhoads 1984). Therefore, the *diversity of plants not only may tend to augment the diversity of phytophagous animals (Hutchinson 1959), the converse may also be true* (Erlich and Raven 1964). In this respect, herbivory may organise plant communities by enhancing plant and herbivore diversity.

The idea that co-evolution is dependent on the co-occurrence of co-evolving species is a point that has been seriously challenged by Hairston *et al.* (1960) and Connell (1980). The basis of this question is found in the fact that herbivores usually consume only a small fraction of the net primary production - the world is green! according to Hairston *et al.* (1960). Cases of obvious depletion of green plants by herbivores or by meteorological catastrophe are exceptions. If this is the case then plants must be resource limited which in turn suggests that they are not regulated by herbivores. Because all populations must be regulated by something, Hairston *et al.* (1960) propose that herbivores must be regulated by predators.

If herbivores are not food limited, then they must seldom compete with each other (Rhoads 1984) and this suggests that because of abundant variety, herbivores rarely co-occur with plant species. The basis of this argument has long survived, despite bitter and sometimes scathing criticism (Murdoch 1966, Erlich and Birch 1967). Crawley (1983) suggests that there are two principal flaws in this argument. Firstly, the world is not always green and herbivore population regulation may well occur during these non green periods (e.g. winter, drought, fire, flooding). Secondly, all that is green is not food. Plant food quality varies in digestibility, nutrient status, toxins and repellents. These facts indicate that most green matter is inedible to most herbivores (Sinclair 1975).

Monarch and Queen butterflies (fig 1.11) are able to feed on Milkweed *(Asclepias curassavica)* which contains secondary plant substances called cardiac glycosides which are poisonous to mammals and birds. These butterflies are somehow able to neutralise cardiac glycosides and store these compounds in their bodies so that they become distasteful to insect-eating birds (Brower 1969).

Fig 1.11 Monarch butterflies migrate ca. 3200 km every year in order to reach their breeding grounds by spring. The eggs of the monarch butterfly are laid on the underside of milkweed leaves, the caterpillar's food plant. Both the caterpillar and butterfly are poisonous to predatory birds (from Bright 1991).

Feeney (1976), introduced the concept of *plant apparency*. Because late successional plants are more apparent to herbivores, Feeney reasoned that they must invest more energy in the production of secondary plant substances compared with early successional plants, which are less apparent. Herbivores have been used to test the palatability of early and late successional plants and the results of this research appear consistent with Feeney's hypothesis (Cates and Orians 1975, Edwards 1981).

Edwards and Wratten (1983, 1985) found evidence for wound-induced chemical changes in plant foliage which appear to render these species less palatable to predator activity. The speed and duration of chemical response was found to vary from plant to plant.

The co-evolution of plants and herbivores provides striking illustration of the existence of inter-dependency in community organisation. Inter-dependency suggests that these relations may involve elements of mutual benefit. Empirical support has come from a number of research quarters.

McNaughton (1976) noted that the grazing of Serengeti Migratory Wildebeest (fig 1.12) converted senescent grassland into a highly productive food source which supported herds of Thompson's Gazelle. In this case, the grassland, Wildebeest and Gazelle all receive mutual benefit.

Fig 1.12 Blue Wildebeest and Burchell's zebras grazing on the Serengeti Plains of East Africa. The Blue Wildebeest measures 1.2 - 1.5 m shoulder height and weighs ca. 160 - 260 kg. Their life expectancy is 16 - 20 years (from Krebs 1985).

Competition for food does not occur between the Blue Wildebeest and Thompson's Gazelle even though they graze the same area. Grazing facilitation occurs when the grazing of one herbivore species improves the food supply available to a second species. According to Sinclair (1975) competition for grass in the Serengeti may occur among grasshoppers and rodents.

Owen and Wiegert (1976) demonstrated that by hastening the recycling of nutrients, phytophagous insects and other herbivores may sometimes increase the fitness of plants. Owen (1980) suggests that the *mutually beneficial relationships between flowers and their pollinators and between fruits and the fruit-eaters can be extended to cover a much wider range of plant consumer interactions.* Owen cites several published sources in support of this claim. Many of the examples involve the return of nutrients to plant species via the activity of plant consumers.

Southwood (1985) suggest that *positive effects on the evolutionary fitness of a plant through interaction with animals arise most frequently from the latter's* *mobility.* There are numerous published examples. Firstly, the role of pollinator insects (Kwak *et al.* 1985), birds (Ford 1985), and butterflies (Gilbert 1980).

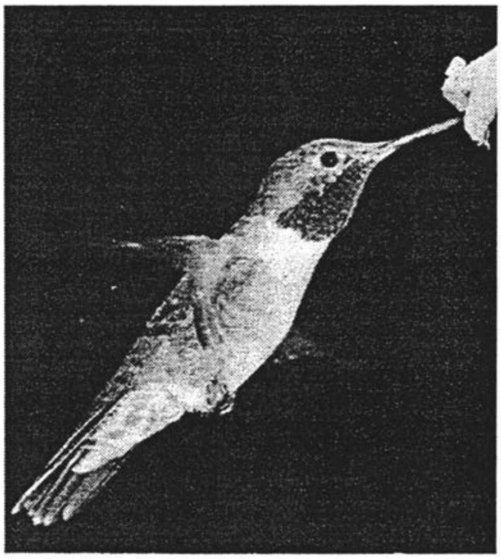


Fig 1.13 The Hummingbird is an active forager that loses heat energy rapidly. These birds survive on a diet of sugar solution combined with amino acids and other high-nutrition ingredients supplied in this photo by the trumpet creeper. The Hummingbird lifestyle can be used by plants to facilitate pollen dispersal (from Colinvaux 1993).

Secondly, the role of *mobile links* which connect rare and dispersed neotropical forest plants. These plants are obligate outcrossers (Bawa 1974) and rely on hummingbirds (fig 1.13) (Feinsinger 1976), bees (Delgado and Sousa-Sanchez 1977), hawk moths and bats (Heithaus *et al.* 1975) for pollination. Mobile links also constitute the major neotropical seed dispersers (McKey 1975).

Thirdly, on the other side of the relationship, Gilbert (1980) suggests that Keystone Mutualists (typically plants) are organisms which provide *critical support to large complexes of mobile links.* Howe (1977) suggests that the canopy tree *Casearia corymbosa* is a *pivotal species* because it supports several obligate frugivores which depend on it almost entirely during an annual food scarcity. Howe (1977) predicts that the loss of this tree would lead to the loss of several key mobile links.

Finally, ants defend many plants against herbivores (Bentley 1977). Leston (1978) introduced the concept of an *ant mosaic* which consists of an overlapping patchwork of dominant and subdominant ant communities. Research in the old world tropics and neo-tropics indicates that the *immunity of a plant to disease and defoliating animals is a function of its position in the ant mosaic* (Leston 1978).

1.3.2.1.6 ***Dominant Species***

The concept of functional dominance has a long history in ecology and is closely related to the concept of diversity (McNaughton 1968, Margurran 1988). Dominant species are recognised by their numerical abundance and may be quantified by measurement of density, biomass or productivity. Fager (1968), in his studies of invertebrate communities occupying rotting logs always found numerically dominant species even though the dominant species varied from log to log. This led Fager to propose that a principal determinant of dominant species may simply be who gets there first and monopolises the rotting log. The idea of competitive dominance is here brought to view.

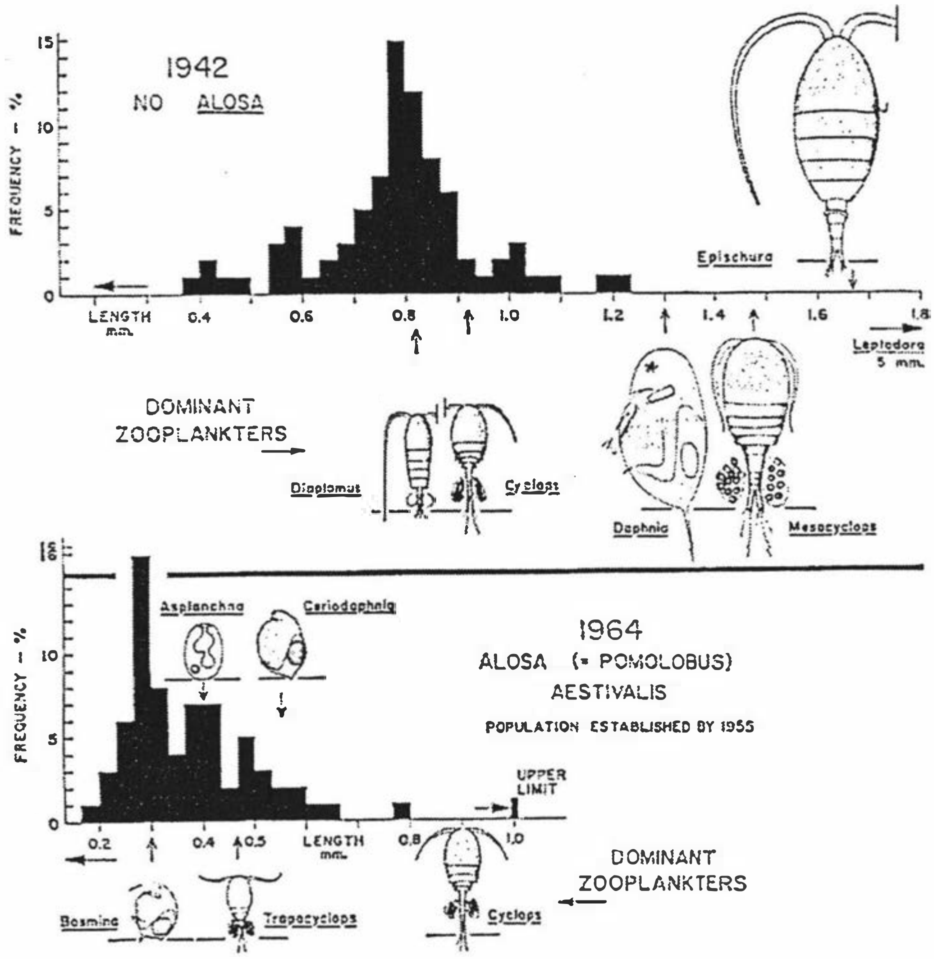


Fig 1.14 Size Dominance of crustacean zooplankton of Crystal Lake, Connecticut, before (1942) and after (1964)a population of Alewife (Alosa aestivalis) became well established (from Brooks and Dodson 1965).

Models of intraspecific competition that may facilitate species dominance by competitive exclusion have been advanced by Buss (1980). Co-existence, driven by competitive displacements internal to the community, may be a further outcome according to the competitive network theory of Buss and Jackson (1979). Price (1971) suggests that dominance may be accomplished by Fager's hypothesis of first arrival advantages that pre-empt competitive struggles and two further strategies accomplished by a species specialising on widely available specific resources or widely available general resources.

Freshwater plankton communities have been actively studied in order to understand a fascinating shift in size dominance of zooplantkon communities associated with the presence and absence of predatory fish (Brooks and Dodson

1965). Dominance in zooplankton herbivores (fig 1.14) may be determined by intraspecific competition when fish predators are absent and by predation when fish present. Recent studies have confirmed the role of predatory fish in structuring zooplankton communities (Zaret 1980).

1.3.2.1.7 Biotic Causal Agents - General Statements

Food webs highlight the complex nature of functional relationships in a community. These relationships are dynamic and may change in response to species size (Paine 1966), changes in niche preference, or competitive ability (MacNally 1994), the effect of IGP (Polis *et al.* 1989), the gain or loss of keystone species (Paine 1969, 1974), herbivory (Erlich and Raven 1964) and shifts in species dominance (Brooks and Dodson 1965).

The idea that species may fill fixed roles in a community has a long history in ecology. Functional roles have traditionally been envisaged as an extension of the niche concept (Simberloff and Dayan 1991), while more recent interest has focused on the notion that guilds may represent fundamental building blocks of communities.

The study of guilds has highlighted the importance of competition as an organising agent (Feinsinger 1976) as well as the influence of spatial heterogeneity on competitive interactions. Furthermore, Polis *et al.* (1989) clearly demonstrates that intra-guild relations, in general, are far more complex than as described by intraspecific competition theory - many potential competitors eat each other (IGP: Intra-guild predation). IGP appears to be an important mechanism responsible for promoting stable states in a some communities.

The activity of keystone species may be responsible for determining the fundamental structure of a community. The role of keystone species is varied and includes: the prevention of competitive dominance in lower trophic levels which would reduce community diversity (Paine 1974), the interference of competitive processes in lower trophic levels (Duggins 1980), keystone mutualistic relations between guild members (Laws 1970) providing key food resources for community members during times of annual food shortage (Howe 1977) and the activity of keystone mobile links which provide for the pollination (Heithaus *et al.* 1975) and seed dispersal (McKey 1975) of rare and spatially dispersed plants.

Lotka (1925) and Volterra (1926) independently introduced the theory of predator-prey interactions to ecology. Laboratory experiments appear to indicate that periodic oscillatory behaviour is interference mediated (Huffaker 1958, Ende 1973). More recent research suggests that predator-prey behaviour may be unstable at small spatial scales and that long term persistence requires inter-patch interactions (Takafuji 1977).

Many top level predators appear to be keystone species, a fact that highlights the role of top level predators in community organisation. Predation appears to be important for competition interference and preventing competitive dominance (MacArthur 1972). Menge and Sutherland (1976) suggest that the traditional competition and predation hypotheses are complementary, *the relative importance of each depending on the trophic level being considered and the overall trophic complexity in a community.*

The co-authors suggest that predation may organise trophically complex communities in which predator and prey densities are maintained by stable environmental conditions. Competition may be the dominant regulatory agent in trophically simple communities in which the densities of predator and prey are restricted by frequent abiotic disturbance. A further complicating factor in the study of predator-prey relations is that predation rates vary among habitats and seasons creating both spatial and temporal gradients in predation intensity (Butler 1989).

Herbivory is a special type of predation which introduces the notion of co-evolutionary interaction. While the concept of co-evolution seems intuitively appealing and empirically supported (Rhoads 1984), it has also been bitterly disputed (Crawley 1983). Contemporary herbivory has found empirical support from a number of quarters including: evidence for wound induced chemical defence in plants (Edwards and Wratten 1983) and chemical defence differentiation based on plant successional status (Feeney 1976). There is also evidence for mutualistic herbivory (McNaughton 1976) including: evidence for nutrient recycling (Owen and Wiegert 1976), mobile links (Bawa 1974), keystone mutualists (Howe 1977) and ant mosaics (Leston 1978).

Finally, the concept of functional dominance also has a long history in ecology (McNaughton 1968). Buss (1980) provides competition models which suggest that species dominance may not necessarily be detrimental to community diversity, even though this has been the traditional view of ecologists (Paine 1966, Connell 1978). Dominance appears to result from competitive superiority (Fager 1968) and resource specialisation (Price 1971). Dominance may not always be prevented or determined by the action of predators. Studies of dominance shifts in zooplankton herbivores suggest that dominance may be determined by intraspecific competition when fish predators are absent and by predation when fish are present (Brooks and Dodson 1965).

1.3.2.1.8 Conclusions

With respect to the present study, two important conclusions may be drawn from this review of key publications concerning biotic causal agents of community organisation. Firstly, this review demonstrates that the activity of biotic causal agents in determining community structure and behaviour is extremely complex. One pattern that emerges in evaluating the historical development of many of these theories is that they usually follow a reliably familiar path - from generality to complexity. This fact reflects both a gradual awakening by many ecologists to the complexity of natural systems on the one hand and perhaps the optimism of ecological modellers on the other.

Secondly, the complexity of interaction involved in community organisation raises serious questions about the utility of generalist equilibrium models. Such models usually have a strong reductionist flavour (Wiegert 1988, Hall 1988, Lomnicki 1988) and involve numerous assumptions. The Lotka (1925) and Volterra (1926) competition theory is a good example of a generalist model. This model was developed on the assumption that density-dependent competition is the sole arbiter of long term behavioural trends in multi-species systems (Nicholson 1933, Nicholson and Bailey 1935, Nicholson 1954a, 1954b, 1958). Gause (1932), Birch (1953) and Park (1948, 1954, 1964) all demonstrated the validity of the Lotka-Volterra competition theory and equations in controlled laboratory experiments. Unfortunately, research of this kind has accomplished little in bridging the gap between theory and the behaviour of natural communities (Cousens 1995).

In comment on the Volterra (1931) logistic theory of interspecific competition, MacArthur (1972) states that *it showed that simple equations might lead to co-existence or to one species replacing another, and it told us which to expect* and in this respect the Volterra theory *has been an unqualified success.* In comment on the limitations of the theory, MacArthur (1972) suggests that *it is probably never correct* and *very likely no population ever grows exactly according to Volterra's equations.* The basis of these comments may be derived from the fact that ecologists now recognise that most, if not all natural communities contain mechanistic and behavioural complexities which violate the numerous assumptions of the Lotka-Volterra competition model:

(i) It is unlikely that there is a direct inverse linear relationship between increasing density and growth rate decline in natural populations (Andrewartha and Birch 1954, Erlich and Birch 1967, Wiens 1984, Wangersky 1978, DeAngelis *et al.* 1985).

(ii) It is unlikely, that the outcomes of competitive interactions are completely insensitive to changes in the growth rates of component populations (Dorschner *et al.* 1987, Abdelkader 1980).

(iii) It is unlikely that the carrying capacity or equilibrium point of a system is invariant (Boyce and Daley 1980).

(iv) It is *very likely* that interacting systems of dimensionality greater then two species will be affected by instabilities caused by the driving mechanisms of a competitive system (Gilpin 1975).

(v) An extension of point four is the discovery that abiotic disturbances may work to moderate the adverse effects of biotic instabilities common to higher order systems (Hutchinson 1953, 1961, Connell 1978, Sousa 1980, Levin 1979, DeAngelis and Waterhouse 1987).

(vi) It is unlikely that competition is the sole arbiter or necessarily even the most important determinant of long term trends in community behaviour (May 1973, McNaughton 1976, Connor and Simberloff 1979, Nisbet and Gurney 1982, Connell 1980, Connell 1983, Simberloff 1983, Strong 1983).

(vii) It is unlikely that spatial effects are of little consequence. In this point is included the fact that immigrations and emigrations of component species may be critical in determining the long term stability of a system subject to biotic instabilities or frequent stochastic disturbance (Levins 1969, Cohen 1970, Levins and Culver 1971).

(viii) It is *very likely,* that equilibrium systems of the type described by the Lotka-Volterra competition equations are affected by abiotic disturbance (May and MacArthur 1972, Hansen and Tuckwell 1978, Birch 1953, Park 1948, 1954, 1964). Furthermore, it is even more likely that the interaction of biotic and abiotic disturbance is a major determinant of the rich dynamic behaviour evident in natural communities (Leslie and Gower 1960, Woodin and Yorke 1974, Sousa 1984a).

(ix) It is very unlikely that competition intensity is predictable and persistent. Competition may be an artefact of irregular periods of environmental fluctuation which cause sudden food shortages (Wiens 1977). Furthermore, environmental heterogeneity undoubtedly results in temporal and spatial gradients of competition intensity (Levin 1976, Horn and MacArthur 1972, Comins and Blatt 1974) .

(x) It is very unlikely that the effects of high density work instantaneously to slow population growth rates. Furthermore, it is very unlikely that reproductive success will ever be instantaneous (Wangersky and Cunningham 1956, Wangersky 1978, Krebs 1985, Holyoak 1994). Time lags are an important part of the biotic and abiotic processes of community organisation. The implication of this statement is that community behaviour must be interpreted in terms of the effect of current and historic causal agents.

(xi) It is very likely that predation plays an important role in regulating and interfering in competition common to lower tropic levels in complex communities characterised by stable environments (Menge and Sutherland 1976). Furthermore, it is evident that IGP is ubiquitous among guild members (Polis *et al.* 1989). Predation itself has a temporal and spatial dimension (Bulter 1989). Some plants respond almost instantly to herbivore browsing by producing defensive chemicals (Edwards and Wratten 1983, 1985).

(xi) It now appears very likely that the spatial scale at which a system is observed may be a primary determinant of equilibrium or non-equilibrium behaviour (DeAngelis and Waterhouse 1987).

As these theoretical developments indicate, community ecologists appear to have recognised the need for a modelling paradigm with a stronger holistic emphasis. To illustrate this point further, during the 1970s, the former omission of spatial extent in classical models was corrected by a large number of ecologists (e.g. Cohen 1970, Levins and Culver 1971, Horn and MacArthur 1972, Vandermeer 1973, Comins and Blatt 1974, Maynard-Smith 1974, Slatkin 1974, Levin 1974, 1976, Steele 1974, Levin and Paine 1974, 1975, Roff 1974a, b). DeAngelis *et al.* (1985) and DeAngelis and Waterhouse (1987) provide an excellent review of much of this current research - a development that has also been greatly influenced by the availability of personal computers.

The discovery of these mechanisms also suggests that the historic tendency of ecologists to look for unified general theories (Slobodkin 1961, Margalef 1963, Mentis 1988, Hall 1988) has tended to obscure the vision of some to the complex realities of natural systems. It also suggests that the failure of generalist models like the Lotka-Volterra competition equations to portray community behaviour comes as no surprise. DeAngelis and Waterhouse (1987) suggest that equilibrium conditions may be an emergent property of large spatial systems composed of numerous local patches connected in time and space by dispersal mechanisms.

Another factor that may have brought about a more holistic emphasis in models of community behaviour could be a general acceptance (on the part of ecologists) of the importance of abiotic disturbance as an agent of community organisation. This causal agent is evaluated in section 1.3.2.2.

1.3.2.1.9 The Equilibrium Paradigm

Having illustrated the operation of competition, predation and symbiosis as agents of community organisation, the self-regulatory aspects of the Clementsian equilibrium view of community organisation are more evident. The super-organism model of Clements (1916) and Tansley (1920) suggests that communities are closed, homogeneous patches of component populations, self-regulated, stable and equilibrium centred. Local populations are thought to be regulated and organised at the community level by competition, predation and symbiotic interactions. Exogenous disturbance is believed to be damped out by global stability. Species diversity is determined by niche diversification, while competitive superiority is the determinant of habitat allocation. This is a formal statement of the equilibrium model of community organisation - known as the equilibrium paradigm.

The question of whether populations are regulated by density-dependent or density-independent agents has caused much controversy in ecology and is more fully explored in the next section on the study of abiotic causal agents. The study of abiotic causal agents is considered as a precurser to a formal statement of the newer and less accepted, non-equilibrium paradigm of community organisation.

1.3.2.2 The Study of Abiotic Agents

In the equilibrium model of community organisation, structure and behaviour are determined by the operation of three biotic mechanisms -

competition, predation and symbiosis. Even though competition and predation have received most of the empirical and theoretical attention of ecologists, there is a growing realisation that abiotic disturbance may play as great a role in community organisation. In this final section on community organisation, the activity of abiotic disturbance is characterised, the limitations of formal descriptive approaches used to define abiotic disturbance are outlined and a brief historic review of the density-dependence controversy is presented. These three lines of evidence introduce a number of important concepts into the discussion of community organisation which will be summarised and drawn together in a formal descriptive statement of the non-equilibrium paradigm.

1.3.2.2.1 Defining Disturbance

Disturbance is a term that has been in use for many years in ecology and yet its meaning is not so clear as numerous attempts at definition illustrate (Pickett and White 1985, DeAngelis *et al.* 1985, Rykiel 1985, Sousa 1984a, Spurr and Barnes 1980, Odum *et al.* 1979, Bormann and Likens 1979, Grime 1979, Weaver and Clements 1938). Recent reviews of disturbance theory in ecology have been given by Sousa (1984a, Rykiel 1985 and Pickett *et al.* 1989).

Rykiel (1985) points out that a number of semantic and conceptual hurdles have complicated attempts to utilise and define disturbance. Firstly, in their English renderings, the words disturbance and perturbation are synonyms, further complicated by their close association with the word stress; thus indicating the inadequacy of conventional usage to convey ecological concepts. Secondly, the term disturbance is commonly used to describe both cause and response. For example, fire can be described as an agent of forest disturbance, while it can also be stated that a forest was disturbed (damaged, destroyed) by fire.

Further semantic problems occur whenever an effect becomes the cause of another effect as illustrated in attempts to define ecological systems in terms of circular causal systems (Patten *et al.* 1976). Terms used to define disturbance must distinguish between cause and effect as far as possible.

In using the term disturbance without a descriptive prefix, a further semantic problem is immediately obvious - both biotic and abiotic processes may act as agents of disturbance. Furthermore, there is a growing awareness among ecologists that the interplay between abiotic and biotic disturbance *seems to account for a major portion of the organisation and spatial patterning of natural communities* (Sousa 1984a).

The interplay between biotic and abiotic mechanisms will be discussed more fully in Chapter Three. Abiotic disturbance includes the activity of such agents as: fire, ice storms, floods, high winds, droughts, landslides, storm events, large waves, extremes of temperature and radiation (*e.g.* sunlight and ultra-violet). While abiotic forms of disturbance are generally external to the system under study, the previous statement is misleading if it suggests that it is a simple thing to differentiate between endogenous and exogenous forms of disturbance. This problem is evaluated in the following section.

1.3.2.2.2 Exogenous and Endogenous Disturbance

From a mathematical point of view, a disturbance may be defined as any exogenous action that moves the variables of a system away from their equilibrium values. This definition, while mathematically precise, has serious limitations when applied in an ecological context - the terms *exogenous and equilibrium are themselves poorly defined in real ecological systems* (DeAngelis *et al.* 1985). Firstly, to illustrate this point, DeAngelis *et al.* (1985) point out that a forest tree fall may be caused by an *exogenous* force like high winds. However, the aging or death that predisposes the same tree to blow down is an *endogenous* process. It is possible to argue that many disturbances are both endogenous and exogenous.

A second problem involves defining the equilibrium or non-equilibrium status of a forest in the first place. DeAngelis *et al.* (1985) and DeAngelis and Waterhouse (1987) argue that equilibrium conditions appear to be an emergent property of large spatial scales. If this is correct, then many forest systems may be classified as non-equilibrium at the patch level of scale and as equilibrium at the landscape level of scale. These problems highlight the fact that a correct interpretation of disturbance must be based on a clear definition of the terms equilibrium and non-equilibrium.

Ecological modellers have dealt with the question of temporal and spatial scale in differing ways. Caswell (1978) (Table 1.2) has attempted to classify ecological models on the basis of scale and distinguishes between open and closed, equilibrium and non-equilibrium systems. Caswell (1978) defines an open system as being one composed of many cells among which organisms can disperse.

closed non-equilibrium models	open non-equilibrium models
closed equilibrium models	open equilibrium models

Table 1.2 Types of population, community and ecosystem models based on their treatment of temporal and spatial scale (after Caswell 1978).

An open system, according to Caswell (1978), can exhibit long-time-scale behaviour that is quite different from the behaviour of a single patch. In this system of classification, temporal scale is implicit in the distinction between equilibrium and non-equilibrium models. A system that manifests stable equilibrium behaviour at one time scale, may also manifest non-equilibrium behaviour on shorter or longer time scales. DeAngelis *et al.* (1985) have used a slightly more complex version of Caswell's (1978) classification to classify models of disturbance (Table 1.3).

closed non-equilibrium	multicell non-equilibrium	open non-equilibrium
closed loose equilibrium	multicell loose equilibrium	open loose equilibrium
closed equilibrium	multicell equilibrium	open equilibrium

Table 1.3 The classification of disturbance in ecological systems based on Caswell's (1978) classification of the treatment of time and space in ecological models (from DeAngelis *et al.* 1985).

DeAngelis *et al.* (1985) define a *closed system* as an isolated patch, a *multicell system* as a collection of patches or cells connected by dispersal mechanisms and an *open system* as a system of cells of any size which is able to receive inputs of immigrants or propogules from an external environment.

In an *equilibrium system,* the system's variables tend to have preferred values that will be returned to after an imposed deviation from the preferred state. A *loose equilibrium system* has variables that tend to remain within fixed upper and lower bounds, but do not appear to have preferred values. An imposed deviation of the variables within these bounds is not mediated by density-dependent feedback mechanisms which act to return the system to a former preferred state. Strong (1984) referred to this type of system behaviour as *density-vagueness.*

In the third and final class of system behaviour, DeAngelis *et al.* (1985) differentiate between two types of non-equilibrium state. In a biotically disturbed *non-equilibrium system,* interaction among the variables will push one or more variables toward zero (type I). These disturbances result from endogenous biotic interactions (competition, predation, symbiosis). In a non-equilibrium system that is dominated by abiotic disturbance, random exogenous forces are acting to drive one or more system variables toward zero (type II).

There are a number of problems even with this classification. Firstly, some equilibrium systems are very sensitive to changes in values and will manifest (by definition) equilibrium behaviour in some regions of parameter space and non-equilibrium behaviour in other regions. This suggests that equilibrium and non-equilibrium systems should be defined according to regions of parameter space.

Secondly, the term non-equilibrium is often used merely to define a system driven to extinction by random exogenous abiotic disturbances such as: fire, storms, floods, droughts, volcanic activity *etc*, No attempt is made to differentiate between exogenous abiotic disturbance and endogenous biotic disturbance - both are forms of non-equilibrium behaviour. DeAngelis *et al.* (1985) suggest that in order to differentiate between endogenous biotic disturbance and random, exogenous, abiotic disturbance, the latter should be referred to as stochastic domination.

In summary, for an equilibrium system, a disturbance is a force which acts exogenously on the system to abruptly change the sizes of at least one of the system's variables. DeAngelis *et al.* (1985) suggest that the term abruptly distinguishes disturbance from stress which produces slow changes in variables.

Two types of non-equilibrium disturbance have been defined. For a biotically disturbed system, disturbances may be required to maintain species diversity. In this case, disturbances must be seen as a part of the whole system, or endogenous to it. For a stochastically dominated system, the disturbance events which drive certain species in the system to extinction are exogenous to the system.

1.3.2.2.3 ***Equilibria, Thresholds & Genotypic Changes***

Sousa (1984a) identifies three further problems in defining disturbance related to: assumed equilibrium conditions, defining a disturbance threshold and the effects of genotypic changes. To illustrate these deficiencies, Sousa (1984a) outlines the following definition of disturbance which he claims is accepted and used by many ecologists. Disturbance is defined as *uncommon, irregular events that cause abrupt structural changes in natural communities and move them away from static, near equilibrium conditions* (Sousa 1984a).

To begin with, this definition assumes prior equilibrium conditions. Sousa (1984a) argues that for many communities a stable equilibrium state may only exist as an average condition at large spatial scales, while even this has yet to be rigorously demonstrated. There is a significant body of published work which can be called upon to support Sousa's claim (Levin and Paine 1974, 1975, Connell and Slayter 1977, Caswell 1978, Crowley 1979, Hastings 1980, Paine and Levin 1981, Anderson *et al.* 1981, Shugart and West 1981, Sutherland 1981, Sale and Williams 1982, Flenley 1984, Slatkin and Anderson 1984, DeAngelis *et al.* 1985, DeAngelis and Waterhouse 1987).

Furthermore, Sousa (1984a) suggests that few populations or communities persist at or near an equilibrium state on small spatial scales. Once again, a significant body of published work can be called upon to support these claims (Jones 1945, Whittaker 1953, Raup 1957, Gilbert and Hughes 1968, 1971, Botkin et. al. 1972, Levin and Paine 1974, 1975, Maguire and Porter 1977, May and Anderson 1978, Pickett and Thompson 1978, Paine and Levin 1981, Connell and Sousa 1983, Menges and Loucks 1984, Slatkin and Anderson 1984, Forman 1981, Karlson and Jackson 1981, Godron and Forman 1983, Roughgarden *et al.* 1985, Murdoch *et al.* 1985). Also, a growing body of evidence appears to suggest that climatic shifts occur at time intervals shorter than those required by communities at even large spatial scales to reach competitive equilibrium (Amundson and Wright 1979, Botkin and Sobel 1975, Davis 1981, Green 1982, Walker and Chen 1987).

Secondly, changes caused by a disturbance agent may vary in intensity from negligible to extreme and a relevant question involves determining the point on this continuum that constitutes an initial disturbance threshold. In making this point, it is important to introduce the idea that not all disturbance is necessarily detrimental to a community. Sousa (1979) has demonstrated that algal colonies on three classes of intertidal marine boulders found on the California coast have levels of diversity directly related to the amount of disturbance a given size of boulder receives as it is rolled around by coastal wave action. The agent of disturbance in this example includes all the forces exerted on these boulders by wave action, which exerts a periodic form of disturbance. What is surprising is that while the largest boulder was moved the least (and therefore disturbed the least) it did not contain the highest levels of algal diversity.

Highest levels of algal diversity were found on the middle size class of boulder which suggests that intermediate levels of disturbance maintain highest levels of diversity. Sousa (1979) and Connell (1978) have suggested that intermediate levels of disturbance may promote high diversity by preventing competitive dominance.

loose- equilibrium type I	biotic disturbance
non-equilibrium type II	stochastic domination
non-equilibrium type III	biotic instability

Table 1.4 Three type of non-equilibrium behaviour. Type I, biotic disturbance is caused by the endogenous activity of biotic causal agents responsible for community organisation. Type II, stochastic domination results when a community is frequently driven near or to extinction by exogenous abiotic disturbance. Type III, biotic instabilities results from the over sensitivity of a system to parameter changes in certain regions of parameter space.

The intermediate disturbance hypothesis of Connell (1978) is thought to be an important mechanism for moderating the adverse affects of biotic instabilities in non-equilibrium communities (type III). Biotic instability is a third type of disturbance, characteristic of non-equilibrium communities. Biotic instabilities occur as a result of a system's extreme sensitivity to small changes in one or two parameters over certain regions of parameter space, (Table 1.4). Such instabilities have been identified in a number of classical ecological models (DeAngelis and Waterhouse 1987).

Furthermore, this illustration demonstrates that the determination of a detrimental threshold of disturbance for a given community is likely to be anything but intuitive. Karr and Freemark (1984) suggest that the *objective definition of a threshold at which a periodicity becomes a disturbance* is *difficult at best.*

A final problem identified by Sousa (1984a) is that species are able to adapt to a given disturbance agent. This implies that the environmental fluctuations that a species is able to respond to today, with effective homeostatic control, previously represented a hazard. An environmental fluctuation that once represented a hazard, does so no longer - so illustrating the dynamic relationship that exists between an organism and the environmental disturbances it encounters.

1.3.2.2.4 Scale, Resolution & State

A further problem encountered in definitions of disturbance is the level of ecological organisation and degree of resolution to which the definition is applied. A failure to take scale and resolution into account limits a definition of disturbance in its application. To illustrate this point, Bormann and Liken (1979) define disturbance as disruption of the pattern of the ecosystem, principally by external physical forces. In comment on this definition, Rykiel (1985) points out that firstly, pattern is not defined and secondly, the concept of disturbance is limited to *one organisational level and a low level of resolution.*

To illustrate this point, consider a single tree fall that produces a gap in the canopy for populations to invade and establish. A single tree fall is of tremendous relevance at the population and community levels of organisation where there is a high degree of resolution for such detail. At the ecosystem or landscape level of scale and resolution the event passes by almost unnoticed. Scale and resolution must be defined in describing the cause and effect of a disturbance, since the consequences and mechanisms of disturbance are different at each hierarchical level (Rykiel 1985).

Furthermore, Rykiel (1985) argues that the definition of disturbance must be made according to a specified reference state. Unless a reference state is specified, it is impossible to detect, let alone to measure a disturbance. The problem with this idea is how to define a benchmark state. Rykiel suggests two alternative methods and is realistic about their limitations. Firstly, the researcher could define a steady state expected to occur under optimal conditions. The problem with this approach is that a steady state itself may be an idealisation that only exists as an emergent property of large spatial scale (Sousa 1984a).

A second approach is simply to accept a pre-existing state, regardless of its dynamic status. The problem with this approach is that acceptance of a pre-existing state may fail to encompass all realistic possibilities of ecological behaviour inherent in the system (Rykiel 1985).

1.3.2.2.5 ***Guiding Principles***

In summary of this discussion on the difficulties of defining the word disturbance as used in ecology, it is evident that at present there exists no single working definition. Instead, there are guiding principles that a researcher should follow in defining disturbance in the context of a given research project. A summary of these is as follows;

1. Confusion with non-ecological usage of disturbance, perturbation and stress can be avoided by careful definition of a reference state.
2. Semantic problems can be avoided by distinguishing between cause and effect.
3. Spatial and temporal scales need to be defined.
4. An attempt needs to be made to identify and state operational thresholds for individual community members and boundaries that demarcate sudden changes in the system due to the action of a given agent or group of them.
5. Hierarchical scale and level of resolution need to be defined since the effect of a disturbance depends on *the organisational level used as a frame of reference, the scale at which the system is observed, and the ecological processes that can propagate the disturbance across levels at the specified scale* (Sousa 1984a).
6. Define the effect of the disturbed system. Descriptive terms are here implied and include quantification of: destruction, decomposition, interference, suppression (Rykiel 1985).
7. Define temporal scale with reference to the possible adaptive capabilities of the species involved.
8. The definition of equilibrium or non-equilibrium states awaits the outcome of future research in this area of community ecology. At present, DeAngelis *et al.* (1985), DeAngelis and Waterhouse (1987), distinguish between exogenous and endogenous disturbance in equilibrium behaviour and three types of non-equilibrium behaviour. A further class of behaviour could be to define to equilibrium behaviour over various ranges of parameter space.
9. Distinguish between the initial effects (are these deleterious or beneficial impacts?) to a reference state and the long term effects (are these deleterious or beneficial impacts?).

The guiding principles listed above should not be considered definitive. Further understanding of the need to define disturbance in areas not listed will doubtless come as the use of such strategies is applied to future research efforts. The above strategy is not only a useful system for classifying disturbance in an ecological context, but it serves to re-emphasise the far reaching influence and complex nature of disturbance as an agent of community organisation. Having dealt with the difficulties of defining disturbance, attention must now be turned to a further question that concerns the action of both biotic and abiotic mechanisms. Is the action of these mechanisms density-dependent or density-independent?

Again, ecologists have been largely divided over this question. The debate itself and the issues it raises draws some important concepts into the present discussion of abiotic disturbance and community organisation. For this reason, it is included in this section as a precursor to an evaluation of current research into abiotic disturbances that will illustrate to some degree the nature and working of these agents of community organisation.

1.3.2.2.6 The Density-Dependence Debate

The study of population regulation itself pre-dates Thomas Malthus (1798) but was at least formalised by him in his thesis on the consequences of long term unchecked human population growth. Charles Darwin (1859) drew on the work of Malthus by taking the problem of population regulation into account in his theory of evolution. Darwin (1859) suggested that competition for limited resources regulated population density and selected the fittest of each generation to survive and reproduce. Neither Malthus or Darwin really investigated the causes of population regulation. Controversies over the mechanisms of population regulation began in the 1930's with attempts better to understand the regulation of animal populations (Elton 1927).

Since the time of these pioneering research efforts at the turn of the century, the study of population regulation has come a long way. In describing the temporal behaviour of natural populations and communities, one of the striking features that has become evident is their temporal and spatial variability (Den Boer 1981, Titmus 1983). It is generally recognised that some of this variability may be the result of inappropriate sampling (Downing 1979, Titmus 1983), climate (Andrewartha and Birch 1954), resource abundance (Wiens 1976), disturbance (Denslow 1985), spatial heterogeneity (Horn and MacArthur 1972, Comins and Blatt 1974) and biotic instability (Gilpin 1975).

Some ecologists now view variation in data as a form of noise that obscures simpler phenomena. Examples of such noise might include: stochastic events that destabilise a community, or exogenous and endogenous disturbances that interrupt biological interactions (Chesson and Case 1986, DeAngelis and Waterhouse 1987 for reviews). Yet these current views of population regulation are in sharp contrast to those presented in earlier research which focused almost solely on the regulatory activity of density-dependent biotic causal agents.

During the 1950's ecology was almost split into two separate camps over a conflict that raged over questions of population regulation (Hassell 1986). The purpose of this survey will be to identify the two schools of opinion by reference to key publications. The present view of the density dependence question will then be advanced. A large share of the conflict involved in this historic debate has its origins in misunderstandings of a complex subject, studied by researchers from differing academic backgrounds. To avoid detailed discussion of semantic problems (and further confusion) the survey presented here is stated within the context of terms common to the discussion already developed in this thesis.

Early in this controversy, two dominant schools of thought emerged. The biotic school (supporters of homeostasis) naturally argued for competition, predation and symbiosis as mechanisms of population regulation. Not surprisingly, the biotic school also ardently supported the idea of 'density-dependence', a natural extension of equilibrium theory; probably aided (by the 1950s) by the conceptual equilibrium framework provided in the mathematical models of Lotka (1925) and Volterra (1926).

The abiotic school (supporters of Gleason's individualistic concept) also naturally argued for environmental agents (primarily weather) as mechanisms of population regulation. Furthermore, the abiotic supporters are usually associated with the term 'density-independence' related to the activity of disturbing forces independent of the effects of density.

Mechanisms of biotic regulation increase their effect as the density of the regulated population increases and approaches an equilibrium point. Abiotic factors tend to exert their effects regardless of the density of the regulated population. The distinction between density-dependence and independence may not be a realistic representation of nature. As Andrewartha and Birch (1954) have argued - weather can certainly be a density-dependent factor.

The terms *density-dependent* and *density-independent* were coined by Smith (1935) who was also a supporter of the idea that climate can act in a density-dependent manner. These ideas existed prior to this time, but different terms were used to describe them.

Howard and Fiske (1911) were first to advance the idea of *facultative* agents that acted more effectively as conditions increased that favoured the growth of a given species. They also coined the term *catastrophic agents* (such as climate) which they considered to act independently of species abundance. Nicholson (1933), in agreement with Howard and Fiske (1911), proposed two ideas that formalised a theoretical basis for most of the controversy that transpired in the density-dependence debate. Firstly, Nicholson subscribed to the biotic school by supporting the idea of a *balance of nature* - a conceptual pre-cursor to equilibrium theory. Secondly, he suggests that *the action of the controlling factor must be governed by the density of the population controlled* (Nicholson 1933).

By assuming equilibrium conditions, Nicholson was able to disregard all factors that did not conform to balance of nature theory. Not surprisingly, Nicholson reasoned that competition is the only factor that can regulate a population and supported these general views by publication of his work well into the 1950s (Nicholson and Bailey 1935, Nicholson 1954a, 1954b, 1958).

Stirrings among the abiotic supporters preceded the controversial publication of Nicholson in 1933. In 1928, Bodenheimer had suggested that only abiotic factors (climate) were important in the regulation of animal species. In 1931, Uvarov published a literature review on *Insects and Climate* supporting the idea of climate as an *ever-present factor in insect life.*

The Distribution and Abundance of Animals by Andrewartha and Birch (1954) appears to be the most important single publication representative of the abiotic school. In chapter 14 entitled *A General Theory of the Numbers of Animals in Natural Populations* the co-authors make several important contributions to the study of population regulation. Firstly, they reject the classification of agents as density- dependent and independent pointing to the fact that any agent can be density-dependent. Secondly, they reject the balance of nature approach judging Nicholson's ideas as wanting in empirical support. In their own strongly empirical approach they divide regulatory agents into weather, food, other organisms and a place to live.

While this list of agents carries the appearance of an apparently comprehensive compromise theory, in reality it is strongly biased toward weather as the only regulatory mechanism. Birch (1958) re-emphasised this position in a symposium presentation entitled *The Role of Weather in Determining the Distribution and Abundance of Animals,* the same idea is repeated in Ehrlich and Birch (1967). Latter, in a paper stressing the importance of genetic factors in determining population density, Birch appears to have revised his earlier position (Birch 1960).

There is a further class of theories on population regulation that may be termed compromise theories in that they attempt to find common ground between the two conflicting camps. Thompson (1929) argued for a mixture of biotic and abiotic regulation, further suggesting that the theoretical sum of these agents rendered the environment more or less optimal for a given species. Milne (1962) combined the best of Thompson, Nicholson, Andrewartha and Birch, adding that an ultimate factor of population regulation, intraspecific competition, was the only truly density-dependent factor.

Orians (1962) compares the book of Andrewartha and Birch (1954) supporting density-dependence, with Lack's (1954) book supporting the density-independent school and concludes that evolutionary pressures are a prerequisite for any generalist theory. Horn (1968), a former student of Orians, takes a novel approach at reconciling the two opposing camps by placing the two dominant density theories at opposite ends of a continuum. Horn attempted to show how density-dependent and density-independent agents could interact to regulate populations.

In a publication that must rank amongst one of the most thought provoking and profound thesis on ecological theory ever published, Hairston, Smith and Slobodkin (1960) raised support for the biotic school by proposing that decomposers, producers and predators, as whole trophic levels, are resource limited and therefore must be regulated by competition as proposed in the classical density-dependent theory. Murdoch (1966) claimed that the hypothesis of Hairston *et al.* had not been formulated in a way that enabled it to be tested by standard falsification. It wasn't necessarily wrong, but could not be tested because there existed no criteria for rejection of the hypothesis.

In summary, the two main theories in the population regulation debate have been defined and discussed in an historical context. A range of compromise theories has also been advanced that add very little in the way of developments that aid in discriminating between the question of density-dependent and density-independent regulation. Compromise theories for the most part are simply attempts to reconcile the two opposing views.

As suggested by Andrewartha and Birch (1954), any factor can act in a density-dependent manner and it seems that this point at least is now undisputed. To this end, the population regulation controversy appears to have ended with ecologists trying to focus their efforts on determining exactly which density-dependent factor regulates populations. A subtle undercurrent in this debate has been the suggestion made on both sides at times, that populations are either solely regulated by biotic agents (Nicholson 1933) or solely regulated by abiotic mechanisms (Birch 1958). A fundamental division on community level organisation is again illustrated.

Biotic mechanisms are no longer considered to be the sole regulatory forces of a community (Hassell 1986, DeAngelis and Waterhouse 1987). Hassell (1986), suggests that *there is wide spread agreement that dynamical patterns of persisting populations are the result of both density-dependent and density-independent processes.* This conclusion suggests that feedback processes acting in a density-dependent manner (via competition, herbivory, predation, parasitism, disease, or shifts in sex ration, fecundity, dispersal rate etc.) are necessary, at least for some of the time, in order to maintain the long term persistence of a population. If sufficiently severe, density-dependence can also be the cause of chaotic population fluctuations. However, it now appears equally likely that the chaotic behaviour of a natural system may result from the vagaries of an unpredictable environment affecting population birth and death rates (Hassell 1986).

The detection of density-dependence is clearly of major importance to population and community ecology. Evidence now suggests that for a given time series of population data there will be a mix of several of these different processes acting at different developmental stages. This in turn highlights the difficulties of disentangling the density-dependent signal from the accompanying noise. Noise may arise from either demographic or environmental stochasticity and result in either density-independent processes or reinforcement of the existing density-dependent processes (Hassell 1986).

From the historic equilibrium (density-dependent) view of population regulation, has emerged a more complex picture which stresses the activity of both biotic and abiotic, density-dependent and density-independent mechanisms of community organisation. In the preceding discussion it has been demonstrated that there are four principal forms of disturbance related to community organisation which operate in a complex array of density-dependent and independent processes. These form types of disturbance are summarised in Table 1.5.

Behavioural Status	**Causal Disturbance**	**Density**	**Regulatory Mechanism**	**Disturbance Activity**
equilibrium	abiotic	dependent or independent	exogenous	stochastic
loose equilibrium (type I)	biotic disturbance (competition, predation, symbiosis)	density vagueness (Strong 1984)	endogenous	weak feedback
non-equilibrium (type II)	abiotic (stochastic domination)	dependent or independent	exogenous	stochastic
non-equilibrium (type III)	biotic (instability)	dependent	endogenous	density-dependent negative feedback

Table 1.5 Classes of disturbance behaviour summarised. Classical equilibrium behaviour may be disturbed by abiotic forces which are quickly moderated by strong density-dependent feedback forces within the system. Three types of non-equilibrium behaviour are identified.

In Table 1.5, random, exogenous, abiotic disturbance may work to temporarily force an equilibrium system away from its equilibrium values. Classical equilibrium theory holds that populations fluctuate about an equilibrium in response to a tension between *environmental disturbances that push them away from the equilibrium and density-dependent forces that pull them back* (DeAngelis *et al.* 1985).

Endogenous biotic disturbance (non-equilibrium - type I) may work to destabilise an equilibrium system. Strong (1984) referred to this type of behaviour as density-vagueness, DeAngelis *et al.* (1985) have labelled this behavioural type a *loose equilibrium*. In such a system, an imposed deviation of the variables is not mediated by density-dependent feedback mechanisms which would normally act to return the system to a former preferred state.

Exogenous abiotic disturbance events (stochastic domination - type II) may dominate a community to the extent that some of the local populations are driven locally extinct. Finally, endogenous biotic instabilities (type III) may dominate a community to the extent that it remains in a transient non-equilibrium state. Independently, these forms of disturbance may be quite disruptive to the long persistence of a non-equilibrium community. Recently, ecologists have focused considerable attention on Type II and type III disturbances.

At intermediate levels, type II disturbances may enhance and maintain the diversity of a community by interrupting competitive differentiation or by preventing competitive dominance (Connell 1978). Furthermore, both types of disturbance may be strongly inter-related. Stochastic domination may work to moderate the adverse effects of biotic instabilities, while biotic instabilities may in turn moderate stochastic processes. A number of modelling approaches have been developed to explore these inter-relationships. These are more fully discussed in chapter three.

Having introduced and defined the present state of disturbance theory in ecology, it is now time to review representative publications documenting the activity of disturbance as an agent of community organisation.

1.3.2.2.7 Abiotic Disturbance Illustrated

Wind is an important agent of disturbance in both temperate and tropical latitudes. Wind causes gaps in the forest canopy by blowing down large branches or trees (Brokaw 1984, Bormann and Likens 1979, Hartshorn 1978, Runkle 1984, Whitmore 1974, 1975). The susceptibility of a given tree to wind throw is probably related to many factors including; age, structural decay or weakening by insect attack, disease, heavy epiphyte loading (Strong 1977), lightning strike, physiological stress resulting from things like drought or flooding, soil type, topography and aspect. Gap size is related to the size of the tree fall. Very large gaps may be a response to many trees collapsing in a given area. Small gaps may result from the gradual decay *in situ* of an aged tree. Jonsson and Esseen (1990) suggest that treefall disturbances are important for maintaining the persistence of colonists and high levels of bryophyte diversity in boreal forest ecosystems.

Ecologists now realise that the formation of gaps in a forest canopy plays an important role in community organisation (Denslow 1987). The first discussion of this idea is attributed to Watt (1925, 1947), who suggested that *following the death of a large tree and its fall, a canopy gap forms. The area below this gap becomes the site of increased regeneration and survival of trees. Trees grow, the forest builds, the canopy closes, and the gap disappears. Eventually, the now mature forest in the vicinity of the former gap suffers the mortality of a large tree and a new gap is formed and the cycle is repeated.*

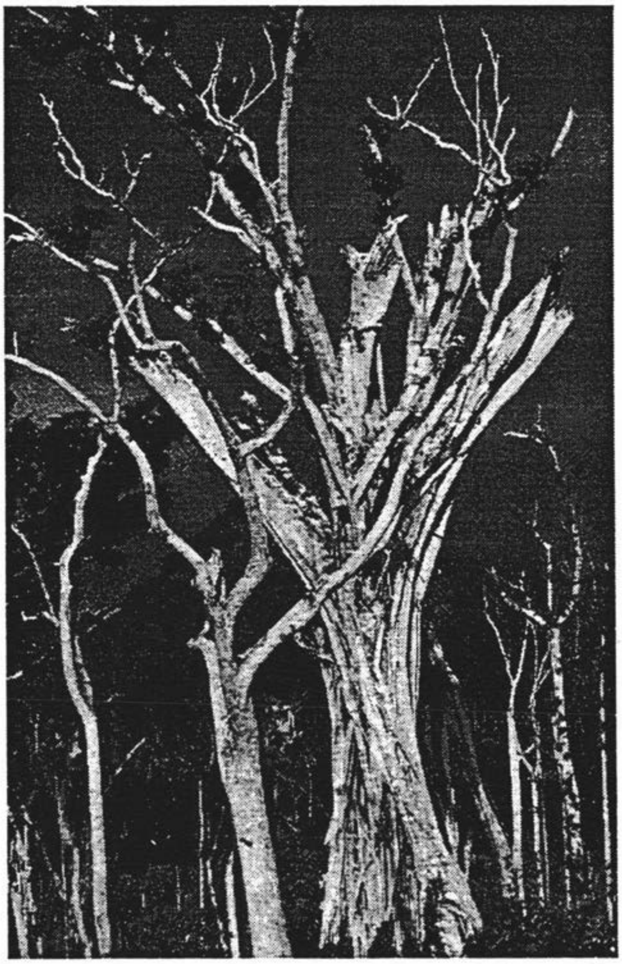


Fig 1.15 Forest reserve on the island of Savaii, Western Samoa. Large branches have been torn from these canopy trees during tropical cyclones that repeatedly lash the pacific islands (from Crawford 1993).

The theory of patch dynamics (Raup 1957, Whittaker and Levin 1977, Connell and Slayter 1977, Strong 1977, Pickett and White 1985, Denslow 1987) emphasises that important changes in forest community composition occur within patches caused by light gaps in the forest canopy resulting from tree or branch falls (Pickett and White 1985, Downes 1990). Patches of vegetation resulting from canopy gaps are now considered to be the fundamental building blocks of natural forests (fig 1.15).

Ecological modellers have recently given much attention to the gap level of organisation in their efforts to model and understand forest community behaviour (Levin and Paine 1974, 1975, Murdoch *et al.* 1985, Paine and Levin 1981, Botkin *et al.* 1972, Menges and Loucks 1984, Maguire and Porter 1977, Slatkin and Anderson 1984, Karlson and Jackson 1981, Roughgarden *et al.* 1985, May and Anderson 1978, Gilbert and Hughes 1968, 1971, Pickett and Thompson 1978, Forman 1981, Godron and Forman 1983).

Wind throw is a mechanism of forest gap formation that works at a variety of spatial scales, suggesting a range of possible patch sizes and dynamics. Individual trees or branches may come down (Bormann and Likens 1979, Brokaw 1984, Hartshorn 1978, Runkle 1984, Whitmore 1975, 1978). Epiphyte loading may be an important pre-conditioning for large branch falls, thought to be a likely cause of patch size and forest compositional heterogeneity in the tropics where epiphytes are most prevalent (Strong 1977).

Fig 1.16 The Aftermath of Mt. St. Helens volcanic eruption. An extensive area of plantation forestry was laid to the ground by the fierce blast of hot gases and ash that issued forth from Mt. St. Helens during its most recent eruption (from Colinvaux 1993).

Hurricanes are known to be responsible for the formation of larger disturbance patches (Brokaw 1984, Webb 1958, Whitmore 1974, 1978, Foster 1988, Sugden 1992, Boose *et al.* 1994).

Wind is but one of many abiotic agents that may be responsible for the formation of forest gaps. Abiotic agents that cause forest canopy gaps may include: heavy snowfall, landslides (Guariguata 1990), avalanches, flooding, volcanic activity (fig 1.16), frost damage (Duncan 1993), drought and fire. Fire is an important agent that may be controlled by a complex system of local factors including: weather conditions, landscape heterogeneity, chemical and structural composition of the fuel, the rate of fuel accumulation, fuel moisture content and seasonal availability (Sousa 1984a).

Fire ignition might be caused by lightning strike (Taylor 1973, Vogl 1974), spontaneous combustion (Viosca 1931), sparks from falling rocks (Henniker-Gotley 1936) and volcanic eruptions (Veblen and Ashton 1978). It is interesting to note that only ca. 0.03% of lightning discharges that strike vegetation result in forest fires (Taylor 1974). Sousa (1984a) suggests that the pre-condition of a forest determines, in an approximate sense, the likelihood, intensity and spatial extent of fire in a given area.

Aside from clearing small to large patches, less severe ground fires may work to thin a forest community by selectively destroying life forms or demographic classes such as seedlings, thereby delaying or preventing regeneration. In some instances, small scale disturbance may be vital for seedling establishment (Klinkhamer and De Jong 1988). A range of complex interactions are implied.

There has been some study into the disturbance of freshwater and marine environments by water motion. Aquatic organisms may be killed or displaced by sediments and particle matter carried and redeposited by water movement (Littler *et al.* 1983). Fluvial environments and communities are considered to be in a constant state of abiotic change - *you cannot step twice into the same river* (Krumholz and Neff 1970). The role of patch dynamics in the community organisation of lotic and lentic environments has been studied (Downes 1990, Frid and Townsend 1989). Generally, research into the role of disturbance in stream ecology is in its early stages, (Hemphill and Cooper 1983, Kimmerer and Allen 1982, McAuliffe 1983, 1984, Resh 1988).

Wave disturbance on temperate, rocky intertidal shores has been well studied, (Dayton 1971, Paine and Levin 1981, Sousa 1979, Sousa 1984b), as have the effects of wave action on tropical coral reefs (Connell 1978, Connell and Keough 1984, Dollar 1982, Pearson 1981). Wave action is highest during storm events and hence, the disturbance wave action causes, may be highly seasonal. Substrate plays an important part in determining the damaging action of waves, as does the physiological and morphological adaptations of the marine organisms effected.

Some sessile organisms may become more vulnerable to wave disturbance as their size and number increase. Dense, multi-layered beds of the mussel *Mytilus californianus* are more easily torn from substrate that supports small single layered beds under the same wave action (Harger and Landenberger 1971, Paine 1974, Paine and Levin 1981).

In the examples of abiotic disturbance given so far, the effects of extreme intensities on community organisation have been discussed. It is now time to consider more fully the action of intermediate levels of disturbance.

The intermediate disturbance hypothesis was proposed by Connell (1978) to explain high species diversity in tropical rain forests and coral reefs. Watt (1947) and Hutchinson (1953, 1961) had stated parts of the concept in various terms, but it was Connell's article that catalysed the current resurgence of interest in non-equilibrium mechanisms of community organisation. The model presumes a competitive hierarchy of species, with competitive outcomes being consistent and asymmetrical, *i.e.* one of a pair of competitors always winning over the other (Sousa 1984a).

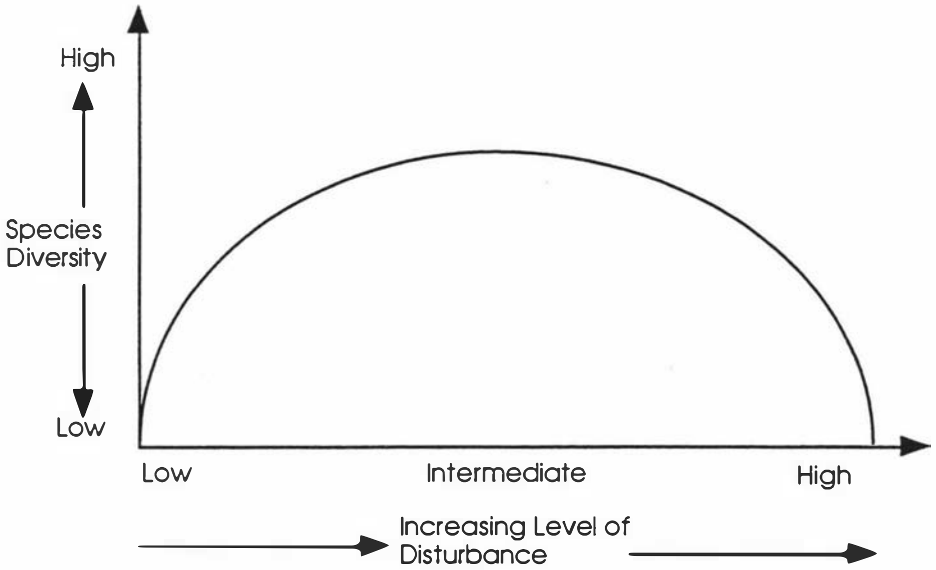


Fig 1.17 The intermediate disturbance hypothesis. Intermediate levels of disturbance maintain high levels of community diversity (after Connell 1978).

Intermediate disturbance allows species to colonise in a patch but prevents it from being dominated by one or a few species (fig 1.17). Such an assemblage is maintained in a non-equilibrium state. The local co-existence of species is ensured as long as the system remains open and between patch dispersal is allowed to occur (Connell 1978, 1979, Hemphill and Cooper 1983, Pickett 1980, Sousa 1979).

A further possible role for disturbance in community organisation has been proposed by Huston (1979) who suggested the idea of a *dynamic equilibrium* model. Huston regarded community organisation as a trade off between growth rates, rates of competitive exclusion and frequency of population reductions. If the return time of a disturbance is shorter than the time required for competitive exclusion, then species that are poorer competitors would persist in the system - increasing species diversity. If disturbance is too frequent or to severe, species diversity is reduced by the elimination of community members with long life cycles. Huston concluded that diversity is determined by the influence of the environment on the net outcome of species interactions.

The problem with Huston's hypothesis in its present form is that it cannot be tested because the theory of competitive exclusion cannot be tested. The theory of competitive exclusion can be traced back to Gause (1934) and before that to Grinnell (1917) the author of the concept. While initial research efforts focused on testing for competitive exclusion in laboratory and field experiments (Park 1948, Inger and Greenberg 1966, Istock 1966, Ayala 1971), it soon became evident that the competitive exclusion principle cannot be disproved. The theory proposes that no two similar species can occupy the same niche forever. The problem with this definition is that the theory itself recognises more than one species, so there must be differences between them (Den Boer 1986).

Initially, the intermediate disturbance hypothesis was considered to be the most likely mechanism for non-equilibrium community behaviour (Krebs 1985). Ecologists now recognise that the persistence of non-equilibrium communities may be traced to the operation of not one, but several moderating mechanisms (DeAngelis and Waterhouse 1987).

1.3.2.2.8 Abiotic Causal Agents - General Statements

A number of important conclusions may be drawn from the illustrations used to characterise the action of abiotic agents in community organisation. Firstly, the local variation, intensity, timing and spatial distribution of disturbing forces determines the nature of a disturbance regime for a given habitat. The regime of disturbance may represent a complex interplay between the properties of various organisms and characteristics of the abiotic forces involved. According to Bormann and Likens (1979, 1979a) it is probably not wise to attempt to distinguish between exogenous and endogenous disturbance.

DeAngelis *et al.* (1985) have devised a preliminary system of classification for differentiating between exogenous and endogenous disturbance based on the spatial and temporal properties of a population or community and its behavioural status. In this section, the classification of DeAngelis *et al.* (1985) has been related to population density and the characteristics of disturbing forces (Table 1.5). Four disturbance types have been identified, based on their relationship to: the equilibrium status of a system (equilibrium, loose equilibrium, non-equilibrium type II and type III), the type of causal agent (biotic or abiotic), the level of density dependency (density-dependent, density vague, density-independent), the nature of the organising mechanism (exogenous or endogenous) and its method of operation (stochastic, weak density feedback and density-dependent feedback).

Vulnerability to a given disturbing force may be determined by: factors that influence physical pre-condition, age, as well as species and assemblage differences. These differences are not static conditions and at the community level, vulnerability may change with succession (Sousa 1984a). The action of disturbing agents is diverse, both in space and time and appears to be an effectiv agent of community organisation primarily by promoting spatial heterogeneit through gap or patch formation. The theory of patch dynamics appears to b broadly applicable to both aquatic and terrestrial systems (Resh *et al.* 198 Alvarez-Buylla and Garcia-Barrios 1993).

Identifying thresholds that delimit non-lethal and lethal disturbanc regimes may be difficult, given that intermediate levels of disturbance appear t promote high levels of diversity. Compensatory mechanisms that moderat stochastic domination on the one hand and biotic instabilities on the other further complicate attempts to derive an operational definition of a disturbanc threshold.

The intermediate disturbance hypothesis of Connell (1978) provides likely, but not exclusive, mechanism for the non-equilibrium paradigm o community organisation. This point will be further developed in chapter thre in which the two main types of departure from a stable equilibrium state will b discussed. Ecologists have identified a number of mechanisms, like intermediat disturbance, which may work to moderate instabilities caused by the activity o biotic and abiotic agents of community organisation.

1.3.2.2.9 The Non-equilibrium Paradigm & Summary

The individualistic concept of Gleason (1926, 1939) suggests that communities are collections of populations with the same environmental requirements. If this is correct, then communities may be organised by environmental agents of disturbance which destine that community to track environmental fluctuations based on the changing genotypic make up of individuals and populations.

DeAngelis *et al.* (1985) refer to such a community as stochastically dominated (type II). More recently, it has become evident that many of the models designed to portray the behaviour of equilibrium systems, have parameters which are extremely sensitive in certain regions of parameter space. In these regions of parameter space, classical equilibrium models manifest biotic instabilities that constitute non-equilibrium behaviour (type II).

A final class of non-equilibrium behaviour has been identified by Strong (1984). Endogenous biotic disturbance (non-equilibrium - type I) may work to destabilise an equilibrium system. Strong (1984) referred to this type of behaviour as density-vagueness, DeAngelis *et al.* (1985) have labelled this behavioural type a *loose equilibrium.* In such a system, an imposed deviation of the variables is not mediated by density-dependent feedback mechanisms which would normally act to return the system to a former preferred state.

In general, non-equilibrium community behaviour is characterised by unstable, transient behaviour as the system moves from one state to another.

This non-equilibrium view suggests that communities are open systems, characterised by collections of patches connected in time and space by dispersal mechanisms. Immigration and dispersal mechanisms may compensate for local extinctions and in this way enable non-equilibrium communities to persist for long periods of time.

In the non-equilibrium view of community organisation, community composition is always changing and never in balance. There is no global-stability for communities in the real world - resilience or persistence is a far more relevant index of community behaviour. Stability is an equilibrium centred concept. Holling (1973) introduced the concept of resilience as an alternative way of looking at communities. Resilience is a boundary oriented view of communities that measures the ability of a system to persist in the presence of perturbations or disturbances.

It is likely that non-equilibrium systems are organised by a range of density-dependent, density-independent and density-vague processes that interact in a complex manner. Connell's intermediate disturbance hypothesis is now considered to be one of several mechanisms responsible for the non-equilibrium paradigm in ecology. Abiotic intermediate levels of disturbance may act to renew resources such as space at a rate sufficient to allow continued recruitment and persistence of species that would otherwise be driven locally extinct.

1.4 Community Organisation - Final Remarks

Discussion of community organisation so far has been undertaken on the basis of two simplifying assumptions - a distinction between biotic and abiotic mechanisms and a hierarchical focus which has been principally limited to the patch level of organisation. It has not always been easy to identify these assumptions in examples provided to illustrate the operation of biotic and abiotic mechanisms.

For example, what causes a forest canopy gap? - the excessive growth of epiphytes on a large branch (the biotic agent) or a strong gust of wind (the abiotic agent) that finally brings the branch in question down? Obviously, the growth of epiphytes pre-disposes a branch to brakeage, as may the action of borer or other biological forms of decay. The action of the wind is biologically mediated in this case and the interplay of biotic and abiotic processes is illustrated. It is very unlikely that abiotic mechanisms work independently of biotic agents. Sousa (1984a) suggests that *the interplay between disturbance and these biological processes seems to account for a major portion of the organisation and spatial patterning of natural communities.* This view represents an important turning point in the study of community organisation, a point that will be further discussed in chapter two.

A further limiting assumption used in this chapter has been the hierarchical level of organisation stressed - the patch. This level of organisation is not necessarily the level of greatest ecological significance or interest to community ecologists. Is it possible to average out the behaviour of within patch non-equilibrium conditions? Would this approach yield a picture of equilibrium conditions at a landscape level of organisation? There appears to be evidence both for (Bormann and Likens 1979, 1979a, Sprugel 1976, Zackrisson 1977, Sprugel and Bormann 1981, DeAngelis and Waterhouse 1987), and against (Romme 1982, Romme and Knight 1982) this idea. Romme (1982), has found evidence for cyclic rather than steady-state behaviour at a landscape level of organisation.

Shugart and West (1981) have conducted patch dynamics simulation studies using landscape scale, computer driven models. These studies suggest that large scale steady-state conditions are a function of total landscape area and the spatial extent of individual disturbance events.

If a large patch is affected by a disturbance event, a larger total landscape area is required to average out the effects of the disturbance. This suggests that for landscapes of relatively small total spatial area, that are affected by disturbances of large spatial extent, the likelihood of ever finding steady-state conditions is small.

Chapter one has introduced the study of community organisation within a simplifying and limiting context. Chapters two and three develop this theme by exploring more deeply the meaning of community behaviour. In chapter two the mathematical, ecological and historical significance of equilibrium theory is explored.

Chapter three explores the historical, ecological and mathematical significance of type II and type III non-equilibrium community behaviour as introduced in chapter one. The purpose of these two chapters will be to develop the theory of equilibrium and non-equilibrium community behaviour in an historical context that provides a review of key publications and theoretical developments.

A further objective of chapter three is to define and evaluate compensatory mechanisms (like intermediate disturbance) that may be responsible for moderating extremes of non-equilibrium behaviour. The concept of persistent non-equilibrium behaviour is introduced in chapter three as an alternative to the equilibrium centred concept of stability traditionally used to define long term stable community behaviour that is equilibrium centred.

1.5 Chapter Summary

The objective of chapter one has been to define community organisation within a context of the historic controversy in ecology over the two contending equilibrium paradigms. Within the central theme of community organisation the topic of special interest in this research project is community behaviour.

Community organisation has been defined as a study of the forces or mechanisms responsible for community structure and behaviour. In this definition, an ecological community is defined as populations of living organisms in a prescribed area or habitat. The individualistic (Gleason 1926, 1939) and super-organism (Clements 1916, Tansley 1920) concepts are traditional extensions of the community concept that represent two opposing schools of thought regarding community organisation.

The individualistic concept of Gleason (1926, 1939) suggests that communities are collections of populations with the same environmental requirements. If this is correct, then communities may be organised by environmental controls which destine that community to track environmental fluctuations based on the changing genotypic make up of individual populations. Such communities may be characterised by unstable transient behaviour as the system moves from one state to another. This non-equilibrium view suggests that communities are open systems, characterised by collections of patches connected in time and space by dispersal mechanisms.

In the non-equilibrium view of community organisation, community composition is always changing and never in balance. There is no global-stability for communities in the real world - resilience or persistence is a far more relevant index of community change. Defining disturbance with reference to non-equilibrium ecological systems has proven to be very difficult. The classification of DeAngelis *et al.* (1985) has been used to identify four classes of disturbance, three of which have relevance to non-equilibrium behaviour. The determination of disturbance thresholds creates further problems for empirical ecologists. This problem is illustrated by Connell's intermediate disturbance hypothesis, thought to be one of several possible compensatory mechanisms responsible for maintaining persistent non-equilibrium behaviour.

The super-organism concept of Clements (1916) and Tansley (1920) suggests that communities are closed, homogeneous patches of species, self-regulated, stable and equilibrium centred. Local populations are thought to be regulated and organised at the community level by competition, predation and symbiotic interactions. Exogenous disturbance is believed to be damped out by the activity of density-dependent feedback mechanisms. Species diversity is determined by niche diversification, while competitive superiority determines habitat allocation (Krebs 1985). This is a formal statement of the equilibrium model of community organisation - known as the equilibrium paradigm.

While the equilibrium paradigm has featured as a major theme in the development of theoretical ecology, there are very few modern community ecologists who would support this model. Most importantly, ecologists have come to realise that community organisation is extremely complex and involves significant contributions from both biotic and abiotic causal agents.

Historically, the role of abiotic disturbance in community organisation has been largely overlooked, with the exception of some temperate-forest ecologists. One important reason for this neglect is that abiotic disturbances rarely operate at time scales that render them suitable for observational based field research. A second reason for this oversight may be that abiotic disturbance and its implications challenge an all pervasive paradigm-stronghold in ecology, a model of community structure and behaviour that assumes constant environment - the equilibrium paradigm.

DeAngelis and Waterhouse (1987) suggested that the 1970s saw a key transition in ecological thinking as *ecologists gradually de-emphasised the role of classical mathematical models in ecology that assume the existence of equilibrium points.* Prior to the 1970s the equilibrium paradigm appears to have derived its all pervasive influence in ecology from the relative simplicity of its ecological constructs and mathematical relations - based on the concept of equilibrium as formalised in the mathematical models of Lotka (1925) and Volterra (1926). A number of lines of historic evidence may be drawn upon to illustrate this point.

Firstly, the controversy over the definition of an ecological community that divided ecology into the individualistic and super-organism schools at the turn of the century is essentially a dispute over the traditional *balance of nature* view of natural systems. In this historic context, the terms homeostasis and individualism are synonyms with equilibrium and non-equilibrium.

Secondly, the controversy between density-dependence and density-independence that split ecology into two camps during the 1950s, is a further demonstration of the dominance of the equilibrium paradigm as supported by Nicholson (1954b, 1958) and fellow supporters of the biotic school of population regulation.

Thirdly, the theory of island biogeography (MacArthur 1972, MacArthur and Wilson 1963, 1967, Williamson 1981, Wilson 1969) appears to have been a further attempt to forge ecological reality from the equilibrium-mould given to ecology in the models of Lotka (1925) and Volterra (1926). One of the principal assumptions of island equilibrium theory is that the environment remains quasi-constant, while the long term biological predictions of the model are equilibrium centred and empirically flawed according to Gilbert (1980).

At a time when ecologists are turning their experimental attention away from the equilibrium paradigm, opportunities now exist to test equilibrium and non-equilibrium theory with the aid of absolute fossil pollen data as a proxy indicator for historic vegetation change. A number of palynological modellers have already begun empirical modelling research in this area.

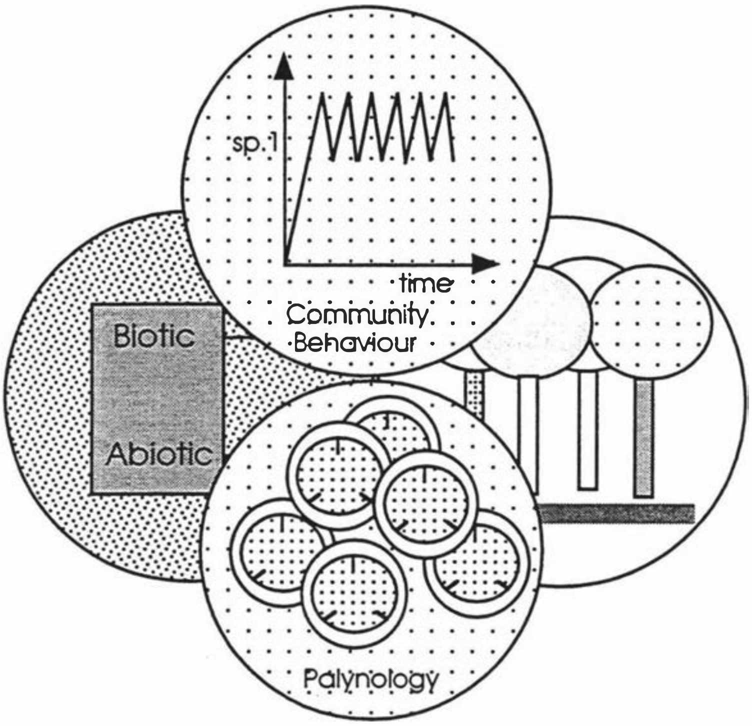
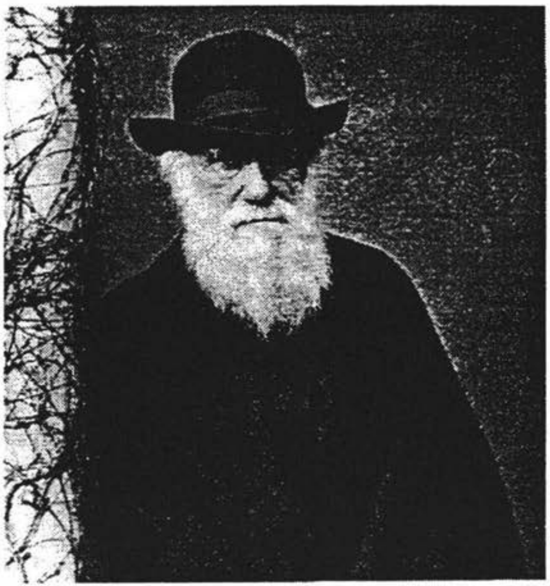


Fig 1.17 A wining combination - palynology and theoretical ecology. Future palynologists who come to terms with theoretical ecology will be able to make an exciting and meaningful contribution toward unravelling the complexities of community organisation.

It is the opinion of the present author that there is no limit to the exciting contributions that will be made by future palynologists who work in co-operation with theoretical ecologists to unravel the complexities of community organisation. The results documented in this thesis are undoubtedly, a small foretaste of better things to come.

Preview to Chapter two



(from Keeton and Gould 1986)

Community Behaviour Part One ~ the Equilibrium Paradigm

Darwin's *Origin of Species* (1859) must rank as one of the most controversial theories of natural history ever advanced. The theory of evolution accomplished much more than providing the world with an alternative explanation for the origin of species. Natural selection and the struggle for existence overturned a system of belief in the reality and power of a providential God. Prior to the *Origin of Species*, belief in creation and the balance of nature by a supreme God had been a pervasive premise in human reckoning dating from antiquity. Having overturned providential balance of nature, natural historians turned their attention toward the last bastion of providential design - the equilibrium paradigm.

Chapter two

Community Behaviour Part One ~ the Equilibrium Paradigm

2.1 Introduction

Chapter two provides an introduction to a more detailed study of community behaviour as contained in Chapters two and three. Community behaviour is one topic of the much larger theme of community organisation presented in Chapter one. In practice, it is virtually impossible to isolate the topic of community behaviour from the study of causal agents and community structure - all three topics are closely linked.

Community behaviour is an extensive field of study and for this reason the present discussion has been divided into two separate chapters. Chapter two will deal with the ecological, mathematical and historic significance of equilibrium theory. Chapter three covers three important topics which focus on the causes of departure from classical equilibrium behaviour defined and illustrated in Chapter two. Firstly, the two main causes of non-equilibrium behaviour will be identified. Secondly, mechanisms that work to restabilise and moderate departures from equilibrium behaviour will be explored. Finally, the question of spatial scale will be discussed with an aim to understanding whether non-equilibrium behaviour on a local scale has emergent equilibrium properties at the landscape level of organisation.

Chapters two and three have been modelled on a key publication reviewing the state of equilibrium theory in ecology co-authored by DeAngelis and Waterhouse (1987). This publication provides an excellent review of key publications covering major developments in the use of equilibrium and non-equilibrium theory in ecological modelling over the last two and a half decades. The co-authors have defined the historical development of equilibrium and non-equilibrium theory in the context of a super-model of community behaviour.

The term super-model is used in this context to imply the high level aggregation of individual theories into a single super-model that carries paradigm-like status. The co-authors themselves do not use the term super-model although their work effectively has this status. The publication of DeAngelis and Waterhouse (1987) represents what this author considers to be the clearest articulation of the state of community behavioural theory that has been published in the current ecological literature. A further quality of the super-model is its focus on modelling research which forms the methodological approach outlined in this thesis on the study of plant community behaviour, by modelling absolute fossil pollen data.

A further objective of Chapters two and three is to present current theory in a way that will permit a set of testable hypotheses to be derived. The nature of fossil pollen data precludes the testing of hypotheses related to every aspect of community organisation theory. This research project will focus on the activity of two causal agents (competition and disturbance) and the study of behavioural changes in plant communities organised by these two mechanisms. As outlined in Chapter one, disturbance may include a broad range of biotic and abiotic causal mechanisms and must be defined with reference to the behavioural status of the community being studied. Historic data for these types of causal mechanisms is usually very hard to find. Complementary lines of fossil evidence are used in this study to provide a proxy for actual measurements of historic disturbance events.

A disadvantage of the DeAngelis and Waterhouse (1987) review is that it assumes considerable prior theoretical knowledge. In this respect it has limited usefulness as a tool for portraying a conceptual understanding of equilibrium and non-equilibrium behaviour in an ecological context - an important objective of the present study.

For this reason, various mathematical approaches will be employed to define equilibrium behaviour and departure from it, in the next two chapters. There is a good reason for this approach. Mathematical models which portray community behaviour are attempts to capture the behaviour of natural systems in mathematical form. The ecological significance of this mathematical form must be clearly understood if correct interpretations are to be made of the similarities and differences between model and field data.

A further limitation of the DeAngelis and Waterhouse (1987) paper is its historic brevity. An historic perspective of equilibrium theory is important for two reasons. Firstly, current acceptance on the part of ecologists of a non-equilibrium model of community organisation represents a major paradigm shift (Judson 1994). Also, the acceptance of an alternative behavioural model of community organisation overturns the last stronghold of providential balance of nature theory that has dominated human perceptions of the natural world since antiquity. It is important to evaluate the history behind these changes in order to understand just why they have occurred.

Secondly, important theoretical contributions to present equilibrium theory in ecology begin with the empirical work of demographers during the seventeenth century. Many of the ideas introduced at this time are still of great interest to community ecologists. An appropriate way to bring these theories into the present discussion is to introduce them in their historic context.

A final objective of Chapters two and three is to review current literature in equilibrium theory. The efforts of ecological modellers have tremendously enriched community organisation theory with a variety of mathematical approaches. While reviewing this work, an effort will be made to stress the ecological significance of these models. This is important since much of the current modelling work is still of a theoretical nature derived from the insights of computer simulation studies. Chapter two begins in the following section with an introduction to the super-model of DeAngelis and Waterhouse (1987). The full significance of the super-model will become evident as the reader progresses through the next two chapters.

2.2 The Super-model Introduced

In Chapter one, the two equilibrium paradigms were presented as strictly alternative views. In Chapter two, this simplifying assumption is removed and the two paradigms are viewed as parts of a continuum of possible community behaviour, characterised by four model behavioural states: stably interactive, weakly interactive, unstably interactive and persistent. These four states are defined by DeAngelis and Waterhouse (1987):

(i) *Stably interactive* community behaviour results when populations hover around fixed equilibrium points. This is a re-statement of the traditional equilibrium paradigm.

(ii) *Weakly interactive* community behaviour is principally a departure from classical equilibrium theory into the realm of stochastic dominance - community organisation dominated by abiotic causal agents.

(iii) *Unstably interactive* community behaviour is principally a departure from classical equilibrium theory into the realm of biotic instability - limit cycles and chaotic behaviour.

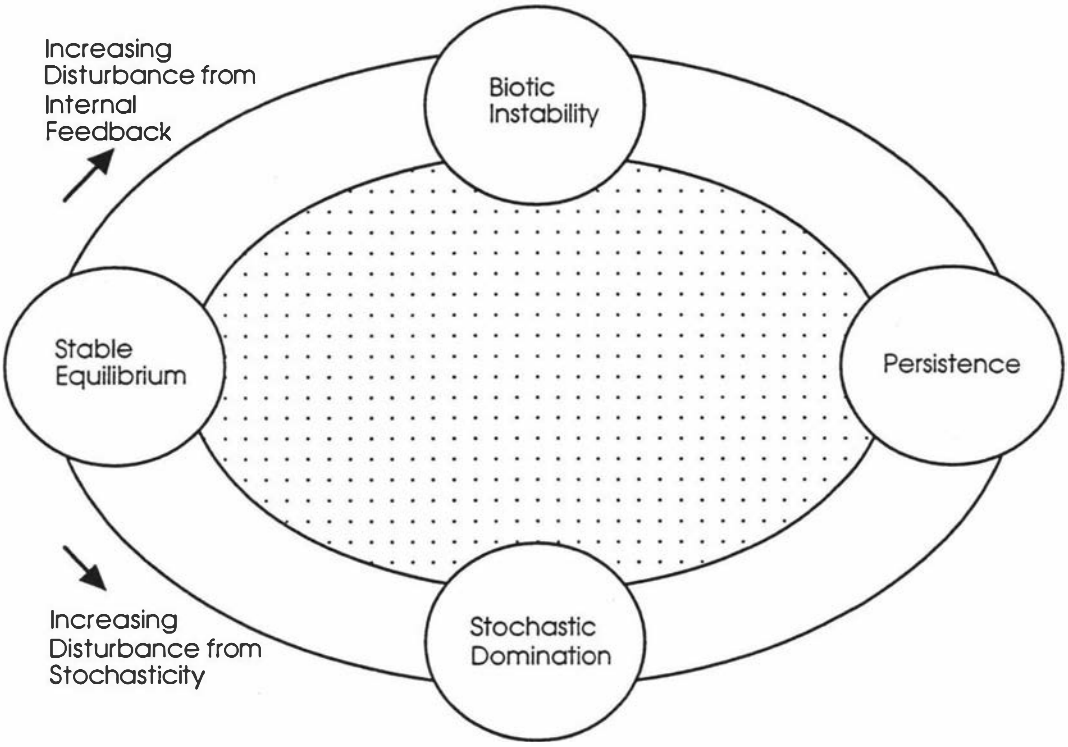


Fig 2.1 A super-model of community behaviour. Biotic instabilities and stochastic domination can both destabilise a community. The central hatched area symbolises a region of complex combinations of biotic and abiotic disturbance (after DeAngelis and Waterhouse 1987).

(iv) *Persistent* behaviour is a recent model of community behaviour which recognises that communities at a local patch level are inherently unstable and focuses upon mechanisms that promote long term persistence. This is a re-statement of the more recent non-equilibrium paradigm. Persistence is a non-equilibrium concept which refers to the tendency of populations to remain within acceptable limits of size despite disturbance (Holling 1973, Reddingius 1971, Innis 1974, Botkin and Sobel 1974, Chesson 1978, Harrison 1979, Gard and Hallam 1979).

DeAngelis and Waterhouse (1987), building on earlier work by Weins (1984a, 1984b), suggest that communities may exist along a continuous spectrum from which stably interactive (classical equilibrium) community behaviour grades away into unstably interactive (biotically unstable) behaviour in one direction and weakly interactive (stochastically dominated) behaviour in the other fig 2.1.

In figure 2.1, biotic instability and stochastic dominance are both unstable states. A persistent community is a non-equilibrium system that does not go to extinction despite the very high probability of this occurring. How are communities, characterised by mixtures of biotic instabilities and stochastic dominance, able to persist for long periods of time? This question is explored in

Chapter three by discussion of mechanisms that may moderate the damaging effects of these instabilities. The following chapter explores the rich mathematical, ecological and historic significance of stably interactive behaviour - the classical equilibrium paradigm.

2.3 The Historic Significance of Equilibrium Theory

The conceptual pre-cursor of modern equilibrium theory is believed to be the pervasive *balance of nature* and *divine providence* premises which date back to antiquity (DeAngelis and Waterhouse 1987, Ehrlich and Birch 1967). To early civilisations, the idea of a balance of nature implied that natural populations which remained constant for long periods of time were controlled or regulated. Drastic changes in the abundance of a population were considered to be the result of upsetting the balance of nature. In antiquity, a divine or supernatural agency was considered to be at work (*e.g.* the plagues that fell upon Egypt) (Ehrlich and Birch 1967).

The following review traces key developments in the balance of nature and divine providence concepts down through the centuries to ecology's current non-equilibrium focus. Important contributions made to equilibrium theory in the work of Malthus (1798), Verhulst (1838), Pearl and Reed (1920) and Darwin (1859) are outlined to introduce and identify key theoretical developments that paved the way for the beginning and end of ecology's first paradigm (Simberloff 1980).

Early conceptions of nature were strongly influenced by systems of belief in the controlling power of a supreme being, or God. Bible history records numerous references to early civilisations which offered animal and human sacrifices in order to appease the wrath of angry gods - believed to control the elements of nature (*e.g.* KJV. 1 Kings 18:23, Deuteronomy 18:10).

Perhaps most famous and well known of all providential events in antiquity are the plagues of frogs, lice, flies and apparently unnatural disasters that accompanied the efforts of the Hebrew prince Moses to free the children of Israel from Egyptian bondage (fig 2.2) (KJV. Exodus 7: 14-12). In a second example, according to Herodotus (485-425 B.C.), the Egyptians believed that the army of Sennacherib (an Assyrian King) was defeated at Pelusium in 701 B.C. because divine intervention caused plagues of mice to devour the quivers and bowstrings of his army (Egerton 1968a). Both the Egyptians and Babylonians recorded their fear of locust plagues in pictures, prayers and oral traditions (Egerton 1968a).

The Medo-Persian empire followed Egyptian and Babylonian ambition for world supremacy, a time in classical history of the presocratic philosophers who debated whether or not nature was in a state of flux. Presocratic philosophy marks an early turning point in the demise of the balance of nature premise. The

Grecian school of Socrates began to emphasise the concept of providential balance of nature in a new theoretical framework of natural regulation (Egerton 1968a).

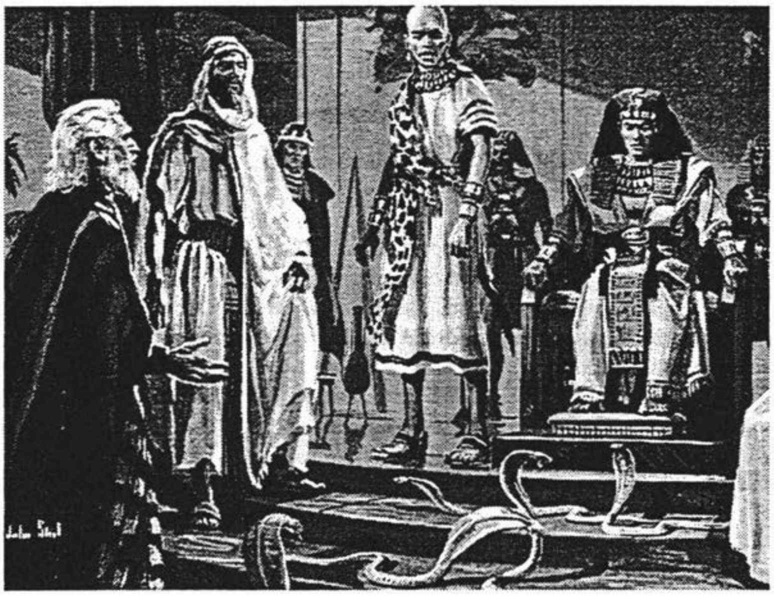


Fig 2.2 The Hebrew prince Moses and his brother Aaron stand before a bewildered Pharaoh who observes Moses serpent consume the serpents of his magicians Jannes and Jambres. Events, of a supernatural character, such as the plagues that fell upon the Egyptian nation, provided convincing evidence in favour of providential balance of nature. John Steel (Artist) has captured the reality of this belief in this portrayal (from White 1890).

The dominant theory of health in antiquity had been developed by Hippocratic physicians, who believed that bodily health was dependant upon a critical balance of body humors (Jones 1946). During the time of the Greek philosophers, a preoccupation with natural balance and its regulation is also evident. Greek science was built upon the assumption that nature was constant and harmonious (Kirk and Raven 1960).

The writings of Herodotus and Plato reveal a number of concepts related to the maintenance of natural balance by regulatory forces - a conceptual departure from the emphasis of providential intervention which had dominated human reckoning in antiquity. Ideas expressed by Herodotus and Plato include concepts of species stability, possible causes of population regulation and the notion of differential reproductive rates for predator and prey (Egerton 1968a).

Aristotle was familiar with the writings of both Herodotus and Plato but formulated his own ideas on the balance of nature suggesting that in each individual was an organising principle that guided its development. Aristotle's theory of teleology was later challenged by his successor Lyceum Theophrastus (372-287 B.C.) who seriously questioned Aristotle's deterministic assumptions. Cicero's *De natura Deorum* contains the first written synthesis of providential balance of nature in which concepts of differential reproduction, mutualism, ecological niche, and species survival were brought together as proofs that nature was designed to work harmoniously for the benefit of man (Egerton 1968a).

Fig 2.3 Thomas Robert Malthus (1766-1834), (from Keeton and Gould 1986).

The writings of Cicero (106-43 B.C.), were ahead of their time and represent an important landmark in the history of balance of nature theory. Little theoretical progress was made in the development of natural balance and harmony in nature until students of natural history and human ecology began to focus their ideas in a more analytical framework.

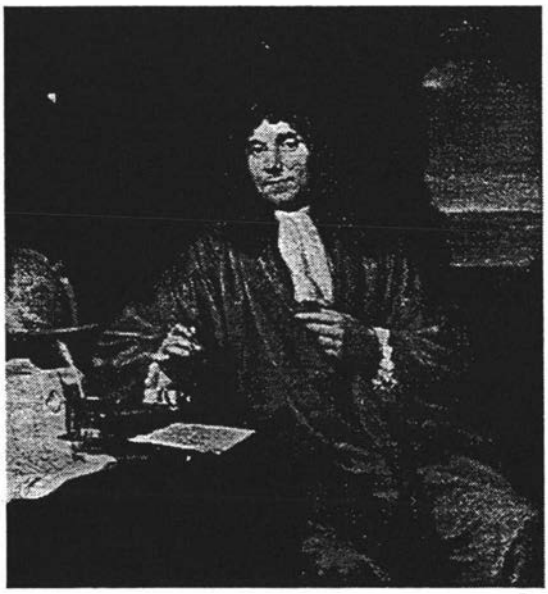


Fig 2.4 Antony van Leeuwenhoek (1632-1723) made one of the first attempts to calculate rates of increase for animal populations. Also responsible for the invention of the microscope and discovery of bacteria (from Keeton and Gould 1986).

Cole (1958) suggests that the father of demography was Graunt (1662) who described human populations in quantitative terms by estimating the rate of population growth for London. In 1687, Leeuwenhoek (fig 2.4) made one of the first attempts to calculate theoretical rates of increase for animal species (Egerton

1968b). Buffon (1756) in his *Natural History* touched on many aspects of population regulation. These early developments in descriptive and theoretical demography laid an important foundation for the controversial thesis of Malthus (fig 2.3) (1798).

Malthus suggested that geometric human reproductive rates (1) must eventually be limited by arithmetic rates of food production (Glass 1959, Himmelfarb 1960).

$$\frac{dN}{dt} = rN \tag{1}$$

where

r is a parameter expressing the specific population growth rate (rate per year) for a continuous time system,

N is the state variable (population size).

Interest in the mathematical aspects of demography increased after the time of Malthus. In 1835, Quetelet suggested that the potential ability of a population to grow exponentially was balanced by resistance to growth.

Fig 2.5 Pierre-Francois Verhulst (1804-1849). Responsible for the formulation of the Logistic equation as based upon ideas suggested by his teacher Quetelet (from Hutchinson 1978).

In (1838) his student Verhulst (fig 2.5) formulated an equation (2) that produced S-shaped population growth based on human population data. Verhulst called this model the logistic curve (Hutchinson 1978).

$$\frac{dN}{dt} = rN\left(\frac{K - N}{K}\right) \qquad (2)$$

where

rN the exponential growth term of Malthus (1798),

K is a parameter expressing the upper asymptote or maximum value of N for a population in isolation,

N is the state variable (population size).

The logistic equation utilised the geometric growth term of Malthus (rN) and provided for a feedback function of N reducing that rate. The same equation was later independently derived by Pearl and Reed (1920) as a description of the growth of the population of the United States. The same equation was later applied experimentally by Pearl (1927), (fig 2.6).

The idea, that the rate of growth of a population declined with time as the population, increased had gradually developed during the seventeenth and eighteenth centuries. During his lifetime, the Logistic equation of Verhulst excited practically no interest. The publications of Verhulst were later discovered by Pearl, in 1921, who gave them formal recognition (Hutchinson 1978).

Fig 2.6 Raymond Pearl (1879-1940). Pearl and Reed (1920) independently derived the Logistic equation and applied it to the United States population (from Kingsland 1985).

The logistic equation (2) is the first clear mathematical articulation of an understanding that limited environmental resources work through density-dependent mechanisms like competition to regulate population growth. The Logistic equation represents an important theoretical breakthrough. The concept of balance of nature unchanged since the time of Plato, was now formalised in a mathematical model that carried biological significance.

During the eighteenth and nineteenth centuries, two ideas that finally overturned the divine-providence concept in natural regulation gradually gained support. It became increasingly evident that many species had become extinct and that density-dependent competition was an important mechanism of population regulation. The consequences of these two ideas became clear with the work of Malthus (1798), Verhulst (1838) and Darwin (1859) (fig 2.7). Acts of providence were replaced by natural selection and the struggle for existence as stated in Darwin's theory of evolution (Stebbins 1982, Egerton 1968c).

Fig 2.7 Charles Darwin (1809-1882). Darwin's Origin of Species was instrumental in overturning the pervasive premise that acts of divine providence were responsible for maintaining the balance of nature (from Curtis 1983).

Darwin's (1859) *Origin of Species* did not overturn the concept of balance *in* nature. In his thesis, Darwin often makes reference to mechanisms of population regulation that appeared to maintain natural balance. For example, in comment on the *doctrine of Malthus,* Darwin states that a *struggle for existence inevitably follows from the high rate at which all organic beings tend to increase...* otherwise according to the *principle of geometric increase its numbers would become so inordinately great that no country could support the product* (Darwin 1859). Darwin's *Origin of Species* replaced acts of divine providence with the struggle for existence as a mechanism of population regulation.

Even though Darwin drew heavily upon the prevailing theory of his time, his conclusions concerning the Christian doctrines of creation and divine providence drew a storm of opposition from the church (Bratchell 1981, Huxley *et al.* 1958). Darwin's own recantation of creation is recorded in the introduction to his book - the Origin of Species. Darwin states, *I can entertain no doubt, after the most deliberate study and dispassionate judgement of which I am capable, that the view which most naturalists until recently entertained, and which I formerly entertained - namely, that each species has been independently created - is erroneous* (Darwin 1859).

Up until the time of Darwin, the focus of natural historians had been primarily upon population regulation. After Darwin's (1859) *Origin of Species* the time was right for a theory of community organisation based on the equilibrium concepts formalised in the mathematical model of Verhulst (1838) and Darwin's own theory of evolution.

The early 1800's saw the coming of age of natural history. Formal recognition of interrelations between community members began with the pioneering research of Forbes (1844) who described the distribution of marine organisms in British coastal waters, and recognised that species composition and abundance varied with habitat.

Similar ideas were expressed by Mobius (1877) who coined the term biocoenosis to describe a community as a collection of unified species. Forbes S. (1887), suggested that there was a steady balance of nature which maintained species within limits. In his classic paper *The Lake as a Microcosm,* Forbes (1887) described the aquatic species in a lake as an organic complex and stressed the notion of interdependence between species. Warming (1895, 1909), raised questions about the structure of plant communities and the associations of species within them. The concept of community succession was largely developed by Warming (1896) and Cowles (1899, 1901) who studied the stages of sand dune development at the southern end of Lake Michigan.

Classical succession theory was elaborated on in great detail by Clements (1916, 1936), who developed a complete theory of plant succession and community development called the monoclimax hypothesis. According to Clements, a biological community could be defined as a highly integrated super-organism capable of development by process of succession to a single end point in any given area. The climax community for a given region was determined by climate, which according to Clements, determined the state of equilibrium vegetation for an area. For this reason, Clements argued that the natural classification of communities must be based on the climatic climax or equilibrium hypothesis.

Simberloff (1980) refers to the Clementsian super-organism as ecology's first paradigm. The succession theory of Clements (1916, 1936) represents a major turning point in the history of equilibrium theory. To begin with, the super-organism paradigm was to result in a polarisation of ecologists into two opposing schools of thought as Gleason (1926, 1939) and fellow individualistic supporters argued against the fundament-unit and synergistic assumptions of the super-organism paradigm (ref. section 1.3.1/Chapter one).

Secondly, the historic balance of nature concept was now formalised in a theory bearing paradigmatic status at the community level of organisation. Thirdly, the super-organism met with strong opposition which appears to have catalysed support for a non-equilibrium alternative (ref. section 1.3.1/Chapter one).

Fourthly, the existence of an equilibrium state carries with it an assumption of density-dependent population regulation; a notion that was also to divide the ranks of ecology (ref. section 1.3.2.2.6 /Chapter one). Finally, the influence of an ecological paradigm presuming a stable community equilibrium state was to permeate ecological thought and attempts to model community organisation for decades to come (Lotka 1925, Volterra 1926, Odum 1969, Wynne-Edwards 1962, 1986, Margulis 1970, 1981, Lovelock 1979, Wilson and Sober 1989).

Are natural populations and communities regulated by mechanisms that promote equilibrium behaviour? Stable equilibria are a fundamental assumption of the super-organism paradigm that now appears to be unacceptable to a growing number of ecologists (Reddingius 1971, Caswell 1978, Murdoch 1979, Connell and Sousa 1983, Weins 1984a, DeAngelis and Waterhouse 1987). Dissatisfaction does not rest upon questions of system stability, but upon the fundamental validity of defining an equilibrium state at all - stable or unstable (DeAngelis and Waterhouse 1987).

In summary, early civilisations associated balance in natural systems with divine intervention. Greek philosophers and eighteenth century demographers advanced important descriptive, mathematical and theoretical constructs which were later formalised in the work of Malthus (1798), Verhulst (1838) and Darwin (1859). With the publication of Darwin's (1859) *Origin of Species* came the end of the general acceptance of divine providence as a mechanism of natural regulation.

The concept of stable community equilibria, as articulated in the climax succession theory of Clements, was a natural consequence of the work of early demographers, Darwin, Verhulst, Malthus, and the contributions of nineteenth century natural historians. Clementsian succession theory demarcates the beginning of the end for balance of nature (equilibrium theory) in ecology. The fundamentalunit, synergistic and density-dependent assumptions of the super-organism paradigm drew a storm of opposition, just as Darwin's theory of evolution had done almost a century before.

Succession theory turned the attention of ecologists toward the last stronghold of providential ecology. The historic concept of balance in nature is now being replaced with a view of community organisation based on unstable transient behaviour. For this reason, the development of Clementsian succession theory ranks with Darwin's theory of evolution as a major turning point in the history of equilibrium theory. Post-Clementsian history in ecology has seen the development and testing of numerous models based on equilibrium theory. A review of key publications covering this period is presented toward the end of this chapter following a discussion of the mathematical significance of equilibrium states in natural systems.

DeAngelis and Waterhouse (1987) suggest that the 1970s was an important transition period for ecologists during which time the role of equilibrium points in ecological models was gradually de-emphasised. The dawning of a non-equilibrium age had come in ecology. Ecologists began to give formal mathematical recognition to the fact that both *internal biotic feedback interactions and stochasticity were seen as prevalent and capable of disrupting ecological systems* (DeAngelis and Waterhouse 1987). The long term persistence of disturbed communities was then perceived to be a phenomenon that needed explanation. A search for mechanisms that would act to maintain the persistence of ecological communities was begun. Published evidence will be presented in Chapter three to cover this important period, during which the non-equilibrium paradigm has gained considerable attention and favour.

In Chapter three a review of published works on non-equilibrium theory in ecology, dating back over the last two and a half decades, provides a final line of evidence to support the arguments presented here concerning the demise of equilibrium theory. This review of published works provides conclusive evidence that the noonday of equilibrium theory in ecology has passed.

2.4 Stably Interactive Community Behaviour

According to the DeAngelis and Waterhouse (1987) super-model of community behavioural types, *stably interactive* behaviour defines populations that hover around fixed equilibrium points. This behavioural type is simply a redefinition of the classical equilibrium paradigm.

As used in this context, the term *stable* needs to be more carefully defined. Mathematicians refer to three types of system stability: neutral, local and global. The mathematical approach used in the following sections is limited to an evaluation of local stability. Global stability is evaluated over much longer time periods and requires more complicated mathematical techniques.

The concept of *interactive* community behaviour implies that a system is regulated by biotic causal agents. The mathematical and ecological significance of *stably interactive* community behaviour will be explored in the following sections.

Mathematical models are of tremendous benefit to theoretical ecologists, who wish to communicate the conceptually rich insights of their research into community behaviour. The following sections are based on a mathematical approach that begins with the simple case of single population behaviour and then works toward the more complex case of community behaviour. Many of the techniques introduced in this discussion will also be employed in the evaluation of field data later in this thesis. For this reason, the models, mathematical techniques and ecological concepts developed in the remainder of this chapter are of tremendous importance.

A number of topics are covered in the following sections. Firstly, the descriptive definition of an equilibrium state forms an introduction to a more detailed mathematical discussion. Secondly, aspects of the modelling and measurement of community behaviour are discussed. Thirdly, the ecological significance of equilibrium states in natural systems is explored in a section that addresses the question of why an equilibrium state exists. The answer to this question is found in the activity of density-dependent feedback mechanisms. This discussion will provide greater meaning to community behaviour that is biotically *interactive* (DeAngelis and Waterhouse 1987).

How stable will an equilibrium state be? The answer to this question provides a fourth line of discussion concerning mathematical techniques used in local stability analysis and the ecological significance of local stability, basins of attraction and strange attractors! Finally, discussion of these concepts provides an opportunity to introduce the concept of phase-space. Phase portraits, generated using a coupled system of logistic equations, will be used to illustrate a qualitative approach to the identification of stable equilibria. As an introduction to all these topics, the next section briefly considers the ecological and mathematical meaning of an equilibrium state in descriptive terms.

2.4.1 Equilibrium Defined

The concepts of homeostasis, equilibrium and steady-state all relate to the absence of change in a system (Edelsteïn-Keshet 1987). When reference is being made to the equilibrium state of an ecological community, what part of the community is it that does not change? The equilibrium state of a community usually refers to the changeless density of component populations. Although more specific, such a definition is conceptually lifeless and not at all helpful in providing insight into the real workings of population or community equilibrium behaviour. Homeostasis, equilibrium and steady-state all have tremendous ecological significance that is virtually impossible to comprehend with conventional descriptive English.

Mathematicians use the term steady-state to define a system in which there is a steady or changeless condition in the state of the system. The term equilibrium is synonymous with steady state, as used in this context. Mathematicians also refer to a periodic steady state and a dynamic equilibrium; terms which appear to contradict the fundamental notion of changeless behaviour.

These terms should be reserved for oscillatory behaviour, which maintains a long term changeless *trend*. The classical view of equilibrium in ecology accepts that species can deviate from changeless behaviour and manifest oscillations about an equilibrium point. However, the same view attaches fundamental significance to the existence of a steady state (DeAngelis and Waterhouse 1987). Therefore, the equilibrium paradigm in ecology by definition precludes the use of descriptive terms like periodic and dynamic. This fact is supported by the existence of equilibrium points in numerous models of ecological systems (Verhulst 1838, Lotka 1925, Volterra 1926, Pearl and Reed 1920, Nicholson 1933, Nicholson and Bailey 1935, Leslie 1948, Rosenweig and MacArthur 1963, Horn 1975a, 1975b).

In summary, the equilibrium state of an ecological community can be defined, in general descriptive terms, by the unchanging behaviour of its component populations. Two further questions can now be asked. How is an equilibrium state identified mathematically? and how stable will this state be? Before addressing these two questions it is important to make a brief mention of some aspects of the measurement and modelling of population behaviour.

2.4.2 The Measurement of Community Behaviour

The present research project focuses on behavioural aspects of community organisation. Population and community behaviour is usually studied with the aid of time series data. Time series data sets record changes in population and community structure. Populations are composed of individuals of the same species, and individuals per unit area is an accepted measurement of population density or concentration (Krebs 1985).

Traditionally, ecological modellers who have developed general population and community models have used population density as the state variable. There are limitations with this approach (McCauley and Murdoch 1987), including lack of realism and predictability. In response to these weaknesses, modellers have tended to add greater complexity, which has improved realism, but reduced generality (Judson 1994).

Furthermore, there have been recent murmurings among the ranks of ecological modellers concerning the perceived limitations of even complex models. This concern stems from the fact that more complex models ignore two fundamental aspects of biology. Firstly, that each individual is different as a result of genetics and environment or a combination of both. Secondly, interactions between individuals occur locally (Huston *et al.* 1988, DeAngelis and Gross 1992).

These concerns appear to have been important in stimulating the recent development of a new class of individual-based models. These models either track each individual in a population separately, or track groups of individuals separately, based on some common characteristic (Judson 1994). The present study is a further attempt to add complexity to classical ecological models which have used population density as the state variable. The more recent trend toward individual-based models will be discussed further in Chapter four.

Absolute population density may be determined by a count of total individuals per unit area (*e.g.* sheep per hectare). The idea of counting all the trees of each species in a forest is possible, but not so practical. In this case sampling methods based on quadrats or capture-recapture techniques (for animals) are used to give a sample from which the total population can be statistically estimated (Krebs 1985). Alternatives to estimates of population density are sampling methods that provide an index of population abundance. There are many examples of this type of methodology which include: trap returns, counts of faecal pellets, vocalisation frequency, pelt records, catch per fishing effort, percentage cover, feeding capacity *etc.* (Krebs 1985).

According to this system of classification, the absolute fossil pollen data used in this research project represents an *index* of population abundance. As the classical example of fur returns from the famous Hudson Bay Company illustrates, conclusions need to be drawn from this type of data with great caution. The reason for such caution stems from the fact that the exact nature and structure of error in index data is usually not known. For this reason, full statistical confidence cannot be specified, and therefore, heuristic evaluation of the data is by far more appropriate. In practical terms this will usually mean that assumptions need to be made concerning the quality of the data. This topic will be more fully discussed in Chapter four.

Once collected, the data is generally used for developing and evaluating the predictions of mathematical models. The logistic equation (2) of Verhulst (1838) and Pearl and Reed (1920), illustrates attempts to model the behaviour of individual populations based on an equilibrium state that results from intraspecific competition caused by increases in population density.

Ecological communities are composed of populations which may interact intraspecifically and interspecifically, if the predictions of the traditional equilibrium paradigm are correct. Models of equilibrium community behaviour must therefore express the outcomes of interspecific interactions which may result in co-existence, co-extinction, or the survival of some competing species and the local extinction of others.

The mathematical techniques used to evaluate models that describe equilibrium states in natural communities are more complex than those used to describe the behaviour of single populations. In principle, the same fundamental concepts are involved. For this reason, in the following discussion, the quantitative determination of stable equilibrium states for single species systems will be discussed first. This illustration uses the discrete logistic equation. This is a simple case, the principles of which are easily applied to the more complex case of interacting populations at the community level of organisation.

The Lotka-Volterra competition equations will then be used to illustrate qualitative techniques that may be used to evaluate the more complex case of community equilibria and stability. This will involve the use of coupled systems of ordinary differential equations.

2.4.3 Quantitative Technique

First order difference equations take the form (after Edelstein-Keshet 1987, Wake 1996 pers. comm.).

$$N_{t+1} = f(N_t). \qquad (3)$$

where

$f(\ )$	is a function describing the dependence of the next generation size on the current level of N_t,
N_{t+1}	is the state variable N at the time interval $t+1$,
N_t	is the state variable N at the time interval t,
t	is the unit of time, scaled to make 1 the unit of a generation,
$t \rightarrow t+1$	represents the step from generation t to that of generation $t+1$ (*i.e.* step length of unity).

In the context of difference equations, an equilibrium solution $\overline{N}$ is defined to be the value that satisfies the relation

$$N_{(t+1)} = N_{(t)} = \overline{N} \qquad (4)$$

so that no change occurs from generation t to generation $t+1$. From equation (3) it follows that $\overline{N}$ also satisfies the relation

$$\overline{N} = f(\overline{N}). \qquad (5)$$

where $\overline{N}$ is a value that the function *f* leaves unchanged and is frequently referred to as a fixed point, steady state, or equilibrium value (Edelstein-Keshet 1987, Wake 1966 pers. comm.).

There are two options available for determining the equilibrium state of a first order difference equation (3). It is often true that solving an equation such as

(5), for the fixed point of the function f, is simpler than finding a general solution to a full nonlinear difference equation (3) problem. This is a distinctly quantitative technique.

The solution of a full nonlinear difference equation problem can be plotted against time to provide a model of the qualitative behaviour of a system from which equilibrium states can be heuristically identified. This technique generally requires the use of computers and will be illustrated more fully in relation to the identification of community equilibria. The identification of equilibrium states for the single species logistic model will be used to illustrate the quantitative technique outlined above.

The difference equation form of the logistic model (6) can be written with scaling (after Edelstein-Keshet 1987),

$$N_{t+1} = rN_t(1 - N_t) \qquad (6)$$

where

N_{t+1}	is the state of the population N at the time interval $t+1$,
rN_t	is the exponential growth term of Malthus (1798),
$(1-N)$	is a feedback function of N that reduces r,
r	is a parameter expressing the net reproductive rate (the number of female offspring produced per female per generation) (from Krebs 1985).

The steady states are computed by setting

$$N_{t+1} = N_t \equiv \overline{N} \qquad (7)$$

so that

$$r\overline{N}^2 - \overline{N}(r-1) = 0 \qquad (8)$$

assuming that

$$N_{(0)} > 0$$

where

$N_{(0)}$ is the initial population size of N

The solutions to this equation indicate that there are two possible equilibrium states, one of which is trivial. Equation (8) is equal to 0 when

$$\overline{N_1} = 0$$

or when

$$\overline{N}_2 = 1 - \frac{1}{r}$$

where

$\overline{N}_n$ the subscript n denotes the number of feasible equilibrium states for $\overline{N}$

assuming that

$N_{(0)} > 0$

A trivial solution occurs when $\overline{N_1} = 0$, the population stays at 0 because of the absence of an initial condition. If it satisfied the conditions required to initiate population growth and r is sufficiently large enough, then the population will grow exponentially until it approaches the second non-trivial equilibrium state at $\overline{N}_2 = 1 - \frac{1}{r}$, ecologically known as the carrying capacity (after Edelstein-Keshet 1987, Wake 1996 pers. comm.).

2.4.4 Why Does an Equilibrium State Exist?

From an ecological point of view, the quantitative identification of an equilibrium state is not nearly as interesting as the question, why does it exist in the first place? In answer to this question, the existence of a population or community equilibrium state is a result of density-dependent population growth. The mechanism responsible for density-dependence in the logistic difference equation is a feedback function of N that reduces r (the net reproductive rate) as the population approaches the equilibrium point. Ecologically, this mechanism has tremendous significance which can best be illustrated by some simple mathematical relations. The scaled logistic equation,

$$N_{t+1} = rN_t(1 - N_t), \qquad (9)$$

is composed of two biotic mechanisms, the exponential growth term of Malthus (1798) and the density-dependent feedback mechanism embodied in the factor $(1 - N_t)$ of Verhulst (1838) on the right hand side of equation (9) (Wake 1996 pers. comm.). The combination of these two mechanisms resulted in a net reproductive rate that was regulated by population size. The dawn of natural history came with a growing realisation, during the eighteenth and nineteenth centuries, that populations do not grow with a constant multiplication rate as Malthus had proposed.

As a population increases exponentially, the effects of overcrowding led to intraspecific competition for limiting resources. In this explanation, the negative feedback mechanism (competition) is triggered and driven by increasing density. Verhulst (1838) assumed that there was an inverse linear relationship between density and population growth rate. The logistic difference equation can be re-expressed (10) as a deviation from the equilibrium density (z), in order to illustrate this concept (from Krebs 1985).

$$z = N - N_{eq} \tag{10}$$

where

z is a deviation from equilibrium density
N is the observed population size
N_{eq} is the equilibrium population size (where $r = 1$)
r is the net reproductive rate

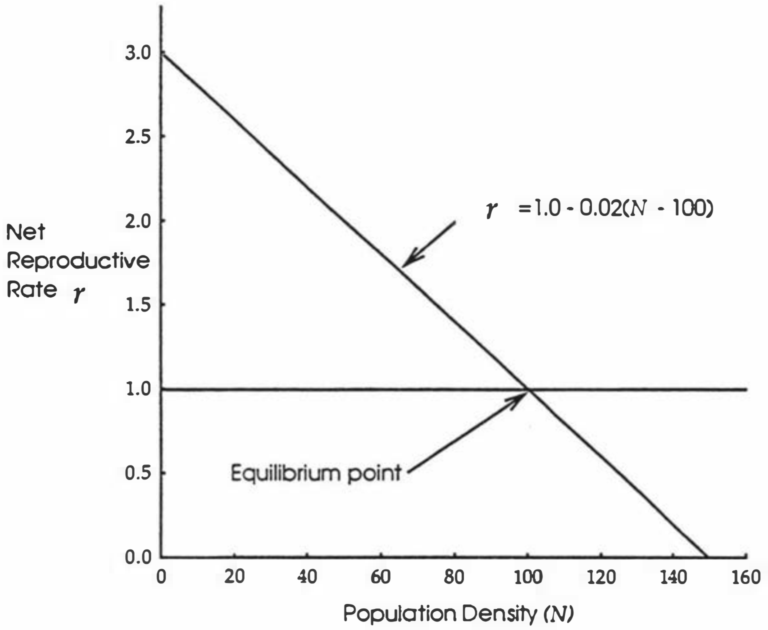


Fig 2.8 Net reproductive rate as a linear function of population density. The point indicated at a population density of 100 is equivalent to the carrying capacity k in the differential form of the logistic equation (2) illustrated in fig (2.9) (after Krebs 1985).

The equation of the straight line depicted in fig (2.8) is

$$r = 1.0 - B(N - N_{eq})$$

$$r = 1.0 - B_z \tag{11}$$

where

$(-)B$ is the slope of the line

The slope of the line $(-)B$ (fig 2.8) determines the rate at which the net reproductive rate r decreases with increasing density. A workable form of the logistic difference equation based upon deviations from equilibrium density can now be written (from Krebs 1985)

$$N_{t+1} = rN_t \tag{12}$$

in an expanded form

$$N_{t+1} = (1 - B_{Zt})N_t \tag{13}$$

To observe the qualitative behaviour of this model, equation (13) can be solved using a simple MatLab routine (Appendix I) based on an initial population size of $N_{(0)} = 10$, an equilibrium density of 100 and a slope of 0.013 (fig 2.8) (Krebs 1985).

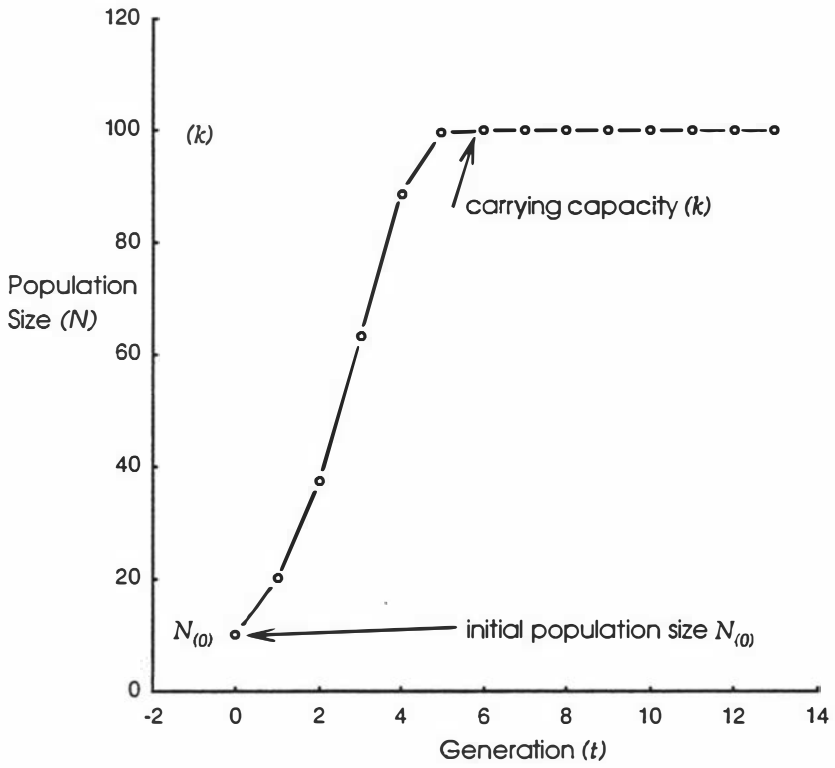


Fig 2.9 The logistic curve. In this illustration, population growth is based on discrete generations and a multiplication rate as an inverse linear function of population density. Initial population size is 10 and equilibrium density is 100.

In the traditional equilibrium model of community organisation, the existence of an equilibrium state for a single population was believed to be a direct result of a density-dependent feedback mechanism. In the logistic model there is an inverse linear relationship between the reproductive rate r and the population density N (fig 2.8). This feedback function reduces the net reproductive rate as the population approaches the equilibrium density which is 100 in this example.

The reason for this mathematical exercise is that it illustrates, as nothing else can, the activity of the biotic causal agent thought to be primarily responsible for regulating individual population growth. Remove the density-dependent feedback mechanism from the logistic model and the result is unhindered exponential growth. Having established the existence and primary cause of an equilibrium state, the question of its stability can now be considered.

2.4.5 How Stable is an Equilibrium State?

The concept of stability must be introduced to distinguish between three types of equilibrium solution, often defined with reference to illustrations like figure 2.10.

An equilibrium state is termed stable if neighbouring states are attracted to it, as in the case of ball C, and unstable if the converse is true, as in the case of ball

B. Ball B is precariously balanced on the top of a hill and can be defined as an equilibrium state. Once ball B is disturbed it will not return to this former state and is therefore an unstable equilibrium state. Ball A is neutrally stable and if disturbed it will have no tendency to either return to A or move away from it. Finally, ball D is clearly a non-equilibrium state, since the ball and system represented by it are in a state of change.

A limitation with this type of illustration is that it gives a misleading concept of the behaviour of ecological systems as represented by a ball of somewhat deterministic trajectory.

DeAngelis and Waterhouse (1987) argue that a more accurate representation would be a pollen grain migrating through a column of still water, but subject to stochastic fluctuations in pressure from water molecules. The importance of random buffeting would depend on the size and density of the grain, relative to the water it displaces. In this scenario, ball D might sink slowly and erratically towards ball A, redefining position A as a stable equilibrium point in a noisy system. In this case, stochasticity actually extends the range of initial conditions for which position A is stable.

Another possible scenario is that grain D simply drifts randomly in water with no predictable tendency toward position A. In this case, the existence of an equilibrium point could not be inferred from the movement of grain D, which is now stochastically dominated.

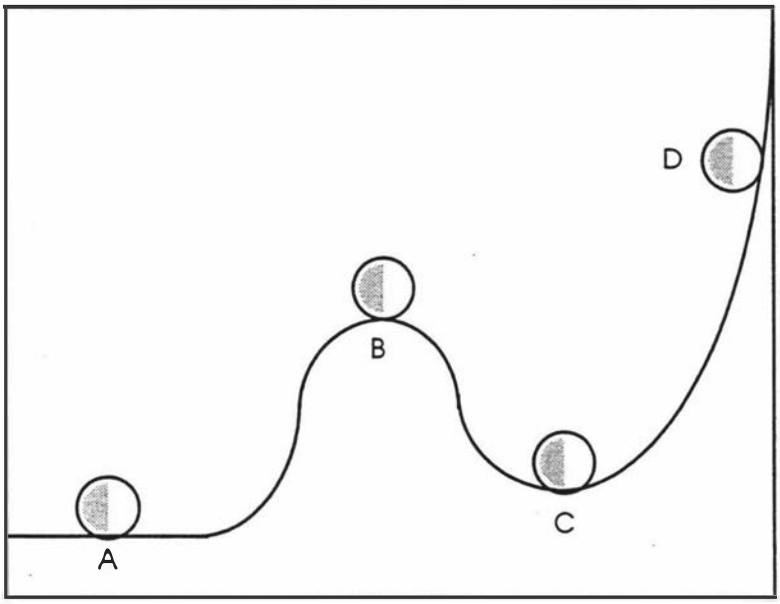


Fig 2.10 Types of equilibrium points: balls B and C are at rest and represent steady state situations. Ball C is locally stable, while ball B is unstable. Ball D is not in a steady state, since its position and velocity are continually changing. Ball A is neutrally stable (after DeAngelis and Waterhouse 1987).

Stochastic domination is a form of non-equilibrium behaviour which may be maintained by properties of the environment and the influence of spatial scale. If the spatial scale (or pollen grain) is large enough, there is a greater likelihood of it staying within the proximity of a fixed point. This suggests that equilibrium may be a useful concept when applied to some spatial scales, but not when applied to others (Connell 1978, Harris 1980, DeAngelis and Waterhouse 1987, Wiens 1989, Allen and Hoekstra 1990).

Having determined the existence of an equilibrium state (section 2.4.3), it is a simple mathematical procedure to test for local stability. This would be equivalent to giving ball C a small push and waiting to see if it returns to position C. Firstly, it is assumed that $N_{(t)}$ is a point very close to the equilibrium state $\overline{N}$, while $N'_{(t)}$ is a small perturbation of this same state. This relation can be stated

$$N_{(t)} = \overline{N} + N'_{(t)}. \tag{14}$$

This type of problem may be solved using partial derivatives or linearization. Linearization is ideally limited to local stability analysis where small squared perturbation terms can be ignored. These terms cannot be so easily ignored if a larger perturbation is applied when testing for global stability. Linearization is generally combined with the use of partial derivatives as outlined by Edelstein-Keshet (1988). In this case, from equations (5) and (14) it follows that the perturbation $N'_{(t)}$ satisfies

$$N'_{(t+1)} = N_{(t+1)} - \overline{N} = f\left(N_{(t)}\right) - \overline{N} = f\left(\overline{N} + N'_{(t)}\right) - \overline{N} \tag{15}$$

The value of the function f evaluated at $\left(\overline{N} + N'_{(t)}\right)$ is generally unknown, however it can be approximated by exploiting the fact that $N'_{(t)}$ is a very small quantity. The function f can be rewritten using a Taylor expansion series:

$$f\left(\overline{N} + N'_{(t)}\right) = f\left(\overline{N}\right) + \left(\frac{df}{dx}\Big|_{\overline{N}}\right)N'_{(t)} + \underbrace{0\left(N'^{2}_{(t)}\right)}_{small-term} \tag{16}$$

Close to the equilibrium state the small squared term can be ignored and some further terms cancelled, based on equation (5).

$$\overline{N} = f\left(\overline{N}\right) \tag{5}$$

$$N'_{(t+1)} \cong f\left(\overline{N}\right) - \overline{N} + \left(\frac{df}{dx}\Big|_{\overline{N}}\right)N'_{(t)} \tag{17}$$

Equation (17) is an approximation of the function f with cancelled terms removed. This approximation can be written as

$$N'_{(t+1)} = aN'_{(t)} \tag{18}$$

where

$$a = \left(\frac{df}{dx}\Big|_{\overline{N}}\right) \tag{19}$$

The constant (a) is a known quantity, obtained by computing the derivative of f and evaluating it at $\overline{N}$. $\overline{N}$ is an equilibrium state of equation (3) if the derivative of f evaluated at $\overline{N}$ is less than one

$$N_{t+1} = f(N_t). \qquad (3)$$

where equation (3) is the general form of a first order difference equation (Edelstein-Keshet 1987). This can be summarised as follows (after Edelstein-Keshet 1987) where the absolute value of a<1.

Condition for Stability

$$\overline{N} \text{ is a stable steady state of (3)} \Leftrightarrow \left|\frac{df}{dN}\Big|_{\overline{N}}\right| < 1 \qquad (20)$$

To illustrate the use of this technique the logistic difference equation will be tested for stability. The discrete logistic equation (6) highlights some interesting effects of the density-dependent feedback term caused by exceeding critical values of the net reproductive rate r (after Edelstein-Keshet 1987). The scaled difference equation form of the logistic model is described in equation (6).

$$N_{t+1} = rN_t(1 - N_t) \qquad (6)$$

$$r\overline{N}^2 - \overline{N}(r-1) = 0 \qquad (8)$$

The solutions to this equation (8) indicate that there are two possible equilibrium states, one of which is trivial. Equation (8) is equal to 0 when

$$\overline{N_1} = 0$$

or when

$$\overline{N}2 = 1 - \frac{1}{r}$$

where

$\overline{N}_n$ the subscript n denotes the number of feasible equilibrium states for $\overline{N}$ assuming that

$N_{(0)} \succ 0$

According to equation (20), a perturbation about $\overline{N}_2$ will satisfy

$$N'_{t+1} = aN'_t$$

where

$$a = \left(\frac{df}{dx}\Big|_{\overline{N}2}\right) = r(1-2N)\Big|_{\overline{N}2} = (2-r) \qquad (21)$$

According to the linear stability theorem of equation (20), N_2 will be stable whenever $|a| < 1$. Furthermore, the stability of this equilibrium state requires that the parameter r must satisfy the condition that $1<r<3$. This means that the stability of the non-trivial equilibrium state is conditional on the parameter r. When r exceeds the critical values of 1 or 3, the equilibrium state is not stable and in this context r is referred to as a *bifurcation value.* Equation (6) provides striking illustration of the influence of bifurcation values, defined as thresholds beyond which there are sudden abrupt changes in the qualitative behaviour of the equation or of the system that it models (after Edelstein-Keshet 1987).

The logistic difference equation (6) is sometimes known as the discrete logistic equation and first came to public attention in a classic paper by May (1976). May demonstrated the capacity of simple difference equations to manifest complex behaviour. The qualitative behaviour and ecological significance of this model will be considered further in a section of Chapter three entitled *unstably interactive population* behaviour.

As a final consideration to the present topic of stably interactive community behaviour, the principles of identifying equilibrium states and determining local stability will now be applied to a multi-species system. This line of discussion will focus on qualitative techniques for identifying stable equilibrium states. Illustrations will be drawn from a two species system of coupled differential equations developed independently by Lotka (1925) and Volterra (1926).

2.4.6 Qualitative Technique

The purpose of this section is to identify and explore the behaviour of equilibrium states at the community level of organisation. Discussion so far has been limited to individual populations; the following section focuses on evaluating the behaviour of a two species system in order to illustrate equilibrium behaviour in a more complex multi-species community.

If the predictions of the equilibrium paradigm are correct, then it is not possible to model populations in a multi-species community using the logistic equation. To do so is to assume that no interspecific interactions exist. For this reason, before attempting to model a plant population, it would be very desirable to know if the population being studied is conforming to behaviour that is at, or near an equilibrium point. Qualitative techniques can be used to determine if field data from multi-species systems confirms to equilibrium behaviour.

Having evaluated the qualitative behaviour of field data, the same techniques can be used to identify the behavioural characteristics of a given mathematical model. By following this procedure, it is possible to determine if a proposed model is capable of manifesting the type of behaviour found in the natural system.

Analysis of this kind must form the first step in modelling work, if time is not to be wasted trying to determine the parameters of an equilibrium equation that is being used to model non-equilibrium behaviour. The following discussion is limited to the qualitative evaluation of a two species model. The same techniques can, and will, be used later in this thesis to evaluate field data.

2.4.6.1 *Qualitative Technique Defined*

In order to model ecological communities of interacting species, a coupled system of logistic equations may be used. The coupling in these equations provides a mechanism that describes interspecific competition. Gause (1934) in his now classic book, referred to these equation couplings as coefficients of the *struggle for existence.* A group of species modelled by these equations are regulated by density-dependent interspecific and intraspecific competition. As mentioned, the interspecific mechanism is missing in the classical logistic equation (2), a fact that limits its use to the study of isolated single populations.

Interspecific and intraspecific competition may involve relationships that depend on variables like density in ways that are far more complicated than simple proportionality. Lotka (1925), recognised that these equations represented a rather idealised case which would probably find poor agreement with reality. Further to this, Lotka suggested that *there is room here for further analysis along more realistic lines....* and that *it must be admitted that this may lead to considerable mathematical difficulties.* Models of such complicated behaviour usually contain nonlinearities that are difficult at best and often, impossible to solve explicitly in closed analytic form.

Qualitative solutions, and especially phase-plane methods have been developed by mathematicians to deal with these problems (Edelstein-Keshet 1987, Odell 1980). Most of these methods are beyond the scope of the present study which will be confined to the use of portrayal and phase-plane techniques.

The objective of most qualitative approaches is to circumvent the need for an explicit solution to complex systems of equations. Instead, a range of techniques are used to determine *qualitative or behavioural* features of the equations. In this context, the term qualitative has two meanings. Firstly, to determine the critical limits of an equation without an explicit solution; secondly, to use these limits with some intuition, to *describe the behaviour of solutions and thus understand the phenomena captured in a model in a pictorial form* (Edelstein-Keshet 1988).

The following section focuses on the second of these two techniques. Computer simulations will be used to generate data that would normally be provided by qualitative techniques that circumvent the need for explicit solutions to these equations. This procedure has the advantage of harnessing the speed and power of modern computers to handle the difficulties of computational work.

2.4.6.2 Understanding Community Behaviour

The differential form of the logistic equation (2) can be written for two species, N_1 and N_2, including, in each equation, a contribution from the influence of the second species.

$$\frac{dN_1}{dt} = r_1 N_1 \frac{(K_1 - N_1 - \alpha N_2)}{K_1}$$

(22a, b)

$$\frac{dN_2}{dt} = r_2 N_2 \frac{(K_2 - N_2 - \beta N_1)}{K_2}$$

The coupling terms, αN_2 and βN_1, of equations 22a and b respectively epresent coefficients of interaction. Setting $\alpha = 0$ and $\beta = 0$ results in uncoupled logistic growth for each of the two populations. This form of equation coupling requires an assumption that under all conditions of density there is a constant conversion factor between the competitors (Krebs 1985).

What will be the outcome of competition between these two equations? As in the case of the single species logistic equation (2), an equilibrium state for these equations can be identified quantitatively by solving a system of simultaneous equations at equilibrium.

$$\frac{dN_1}{dt} = 0 = \frac{dN_2}{dt} \qquad (23)$$

Four solutions exist to these coupled equations depending on the values of α and β relative to the ratios of K_1 and K_2 (Harper 197, May 1981, Silvertown 1987, Renshaw 1991). The four solutions listed below are independent of the values r_1 and r_2.

(i) If $\alpha > \frac{K_1}{K_2}$ and $\beta > \frac{K_2}{K_1}$ then only one of the two species will persist and the outcome of this interaction will be determined by the initial conditions or starting proportions of each species.

(ii) If $\alpha > \frac{K_1}{K_2}$ and $\beta < \frac{K_2}{K_1}$ then species 1 will go to extinction.

(iii) If $\alpha < \frac{K_1}{K_2}$ and $\beta > \frac{K_2}{K_1}$ then species 2 will go to extinction.

(iv) If $\alpha < \frac{K_1}{K_2}$ and $\beta < \frac{K_2}{K_1}$ then both species will co-exist at an equilibrium state.

In the case of the single species logistic equation, only one non-trivial equilibrium state existed. In the case of the two species coupled logistic equation (22 a, b), there are three possible equilibrium states (ii), (iii), and (iv) in which the outcome of the interaction involves either the co-existence of both species or the extinction of one or the other. Case (i) is an equilibrium state in which the competitive outcome is determined by the initial size advantage of each population. Of the four solutions (i - iv) listed above, only (ii-iv) are stable, according to the definition of stability outlined in section 2.4.5, which states that an equilibrium state is termed stable if neighbouring states are attracted to it.

These outcomes can be portrayed pictorially by solving equation (22 a, b) for various values of α and β determined by the four potential equilibrium solutions (case (i) - (iv)) above. In order to provide comparative portrayals of this system of coupled equations all parameters, constants and initial values will be standardised in the following way (Table 2.1, 2.2, 2.3).

parameter	*value*
r_1	65
r_2	50
K_1	1000
K_2	1200

Table 2.1 Equation parameters used in simulations 1-4.

$N_{(0)}$	*species 1*	*species 2*
simulation 1	100	250
simulation 2	150	150
simulation 3	700	900
simulation 4	750	750

Table 2.2 Initial conditions used in simulations 1-4.

	α	β
case (i)	0.9	1.3
case (ii)	0.9	1.1
case (iii)	0.7	1.3
case (iv)	0.7	1.1

Table 2.3 Competition coefficients used in simulations 1-4. α and β are determined according to cases (i) - (iv).

The equation parameters in Table 2.1 will remain constant in all four simulations. Each case listed in Table 2.3 contains parameters which have been calculated according to the four possible equilibrium states, identified for equation (22 a, b) (cases (i) - (iv)). The parameters of each case in Table 2.3 will be simulated under four different initial conditions, as listed in Table 2.2.

Data for each of the case studies listed above will be generated by solving equation (22 a, b) using a MatLab differential equation solver (Appendix II). To begin with, the solutions derived from these computer simulations can be portrayed by plotting the state variables N_1 and N_2 against the independent variable (time). To illustrate this procedure, plots of this kind will be used to portray the outcomes of case (i). This case predicts that an unstable equilibrium state exists for these equations in which only one species will survive long term, as determined by the initial conditions or population sizes. The competition coefficients of case (i) are listed in Table 2.3 and the equation parameters in Table 2.1. Fig 2.11 portrays the outcomes of the four different initial conditions listed in Table 2.2. Annotation indicates species 1 and 2.

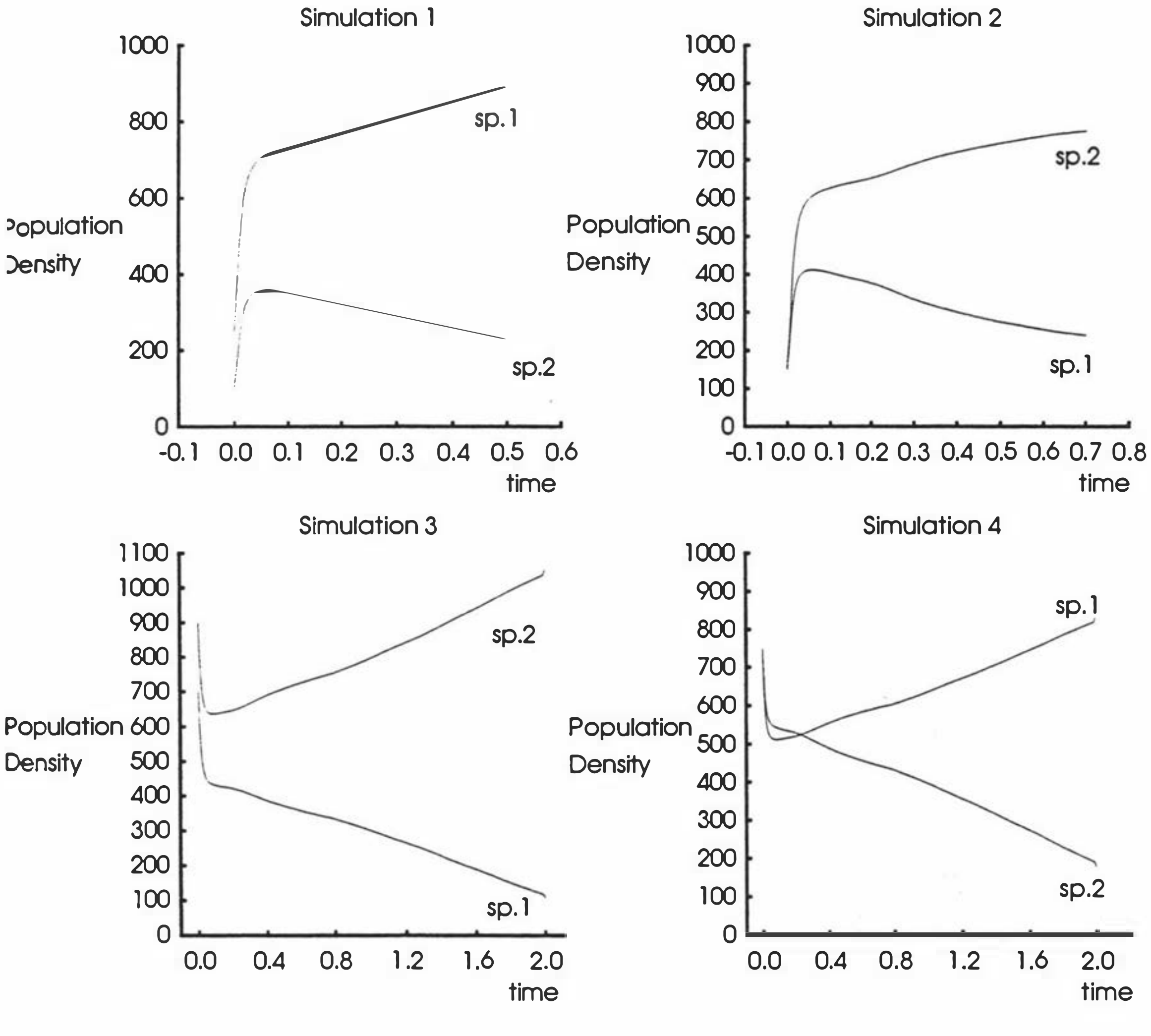


Fig 2.11 Portrayal of a coupled system of logistic equations based on competition coefficients in case (i), and initial conditions in table 2. Only one species survives the competitive interaction and the survivor is determined by initial population size.

Plots such as those illustrated in fig 2.11 are commonly used to portray single species behaviour. From these plots the behaviour of the case (i) competition coefficients can be more easily visualised. It is now clear that differing initial conditions are the determinants of who wins and who loses in this system of equations. Only the species with highest initial population advantage is able to survive the competitive encounter and reach an equilibrium state. This type of community equilibrium state is unstable since it results from the extinction of one species. Ecologically, this suggests that in the simplest of natural systems, the history of that system may have a critical effect on its future. This implies that the present structure and behaviour of some communities may be nothing more than an accident of history.

There is a more powerful way of portraying the information contained in these four plots. The axes of a phase portrait are the magnitudes of the two state variables or population densities for N_1 and N_2. Phase space is synonymous with vector space. For each time *t*, a point is plotted, the co-ordinates of which are the densities of the two interacting species. Connecting the points in temporal sequence results in an orbit or trajectory. If this procedure is repeated for a number of initial conditions (or population densities), a picture called a phase portrait is obtained (Schaffer 1984). In fig 2.12 is plotted the data from the four simulations of fig 2.11. In explanation of this portrait, phase space consists of four primary regions. At the population densities of:

(0, 0)	both species have become extinct,
(1000, 1000)	both species coexist,
(0, 1000)	species one is extinct and species two survives,
(1000, 0)	species two is extinct and species one survives.

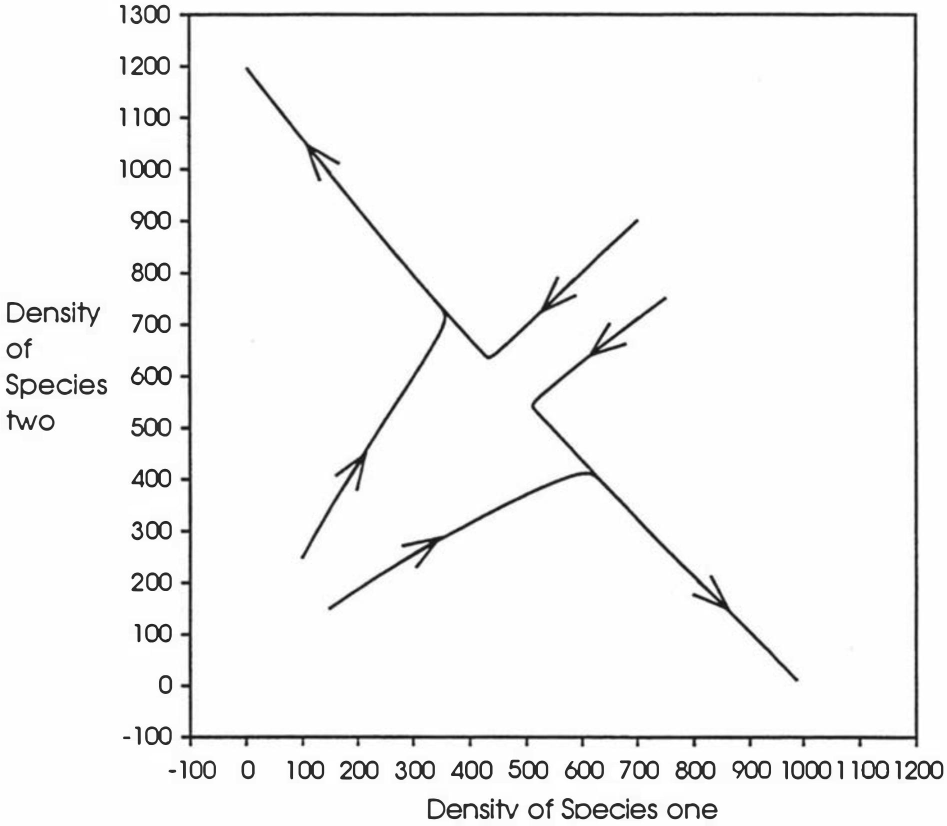


Fig 2.12 A phase portrait (saddle point) of species one interacting with species two based on the competition coefficients of case (i) and all four sets of initial conditions in Table 2.2. The arrows indicate the direction of time.

In this phase portrait, the four sets of initial conditions are identical tc those used in fig 2.11. The symmetry of this unstable equilibrium state can now be seen. Initial conditions that provide species one with a superior population size compared with that of species two, always result in the extinction of species two. The reverse is true for initial population densities that favour species two. A much richer concept of community equilibrium behaviour can now be visualised with the aid of phase space.

The fixed point values (1000, 0) and (0, 1200) in this phase portrait are referred to as attractors. An attractor is equivalent to the basin in which ball C is resting in fig 2.10. By definition, an attractor is an object in phase space which attracts initial conditions from the region around it called a basin of attraction (Schaffer 1984, Farmer *et al.* 1983). The location and behaviour of attractors and their basins of attraction are an artefact of parameter space; a multi-dimensional response surface defined by equation parameters.

The concept of an ecological niche of multi-dimensional space, defined by axes of resource tolerance and preference, equates to the concept of parameter space, as used in the context of attractors in the above illustration. Equation parameters are effectively resource axes on a very low scale of resolution. For example, the co-efficients of competition (α and β) may be viewed as high level functions which define a range of individual adaptive strategies which collectively determine the competitive ability of a species for a given habitat.

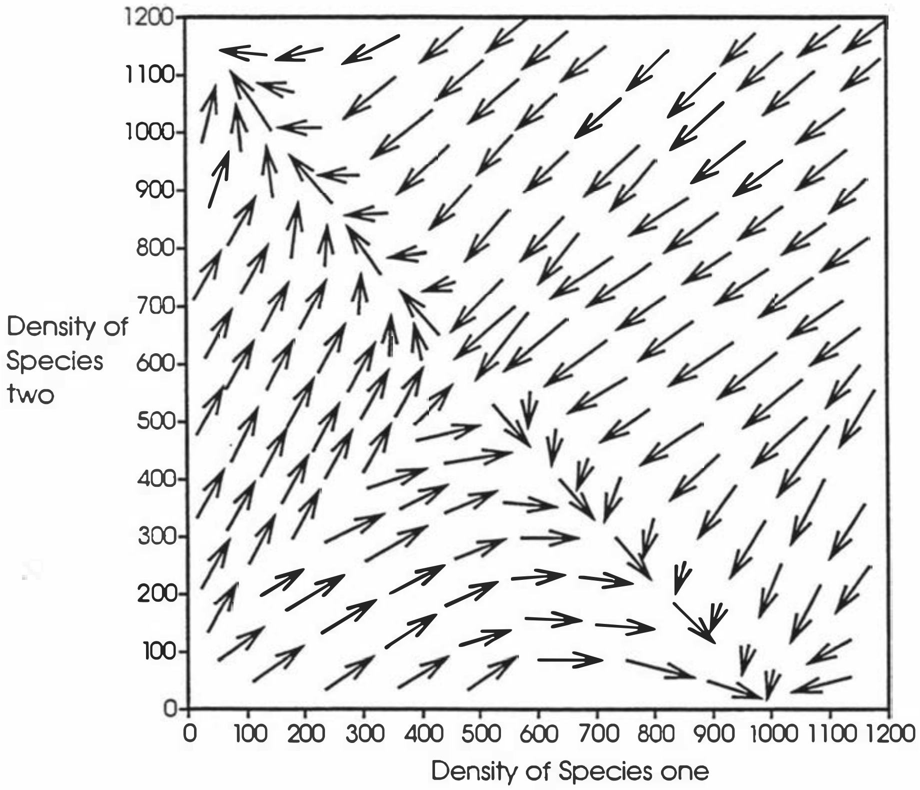
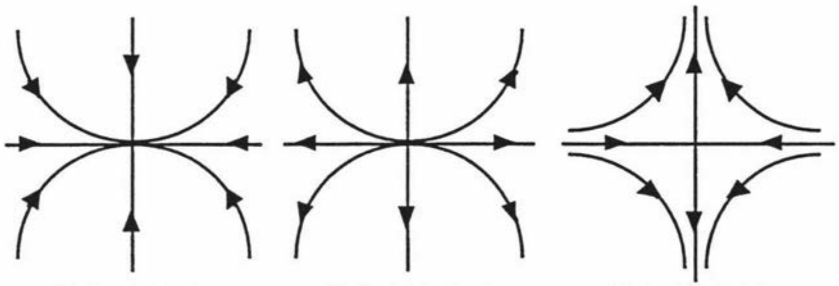
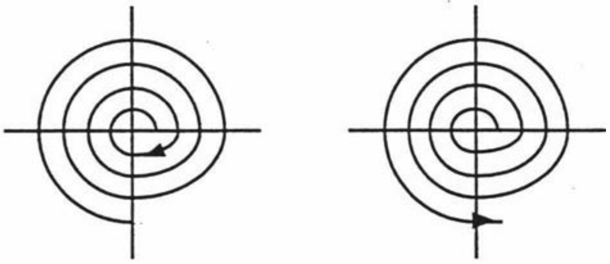


Fig 2.13 A vector field which illustrates more effectively the nature of an attractive basin. In this system of two interacting species, two parallel basins of attraction exist.

A trajectory that starts inside a basin of attraction will remain in it forever and be drawn towards an equilibrium state defined by the parameters in the system of equations - an ecological black hole. In interactive systems such as that represented in fig 2.12 based on case (i), there are two basins of attraction side by side and the region between these two attractors represents an area of initial uncertainty. It is possible to portray the nature of an attractive basin more effectively by constructing a vector field (fig 2.13), inferred from the trajectories of the initial conditions, portrayed in fig 2.12. This type of unstable system equilibrium is referred to as a saddle point. The vector field identifies the location of the saddle point at ca. (500, 500). Initial conditions are attracted to a saddle point only to be pushed away again (fig 2.13).



(1) Stable Node (2) Unstable Node (3) Saddle Point



(4) Stable Spiral (5) Unstable Spiral

Fig 2.14 In phase space, an equilibrium point (0, 0) can be characterised by one of the five feasible parameter planes illustrated above (after Edelstein-Keshet 1987, Wake 1996 pers. comm.).

Three characteristic types of attractor have been identified, point attractors, periodic attractors and strange attractors (Ruelle and Takens 1971, Ruelle 1980). Point and periodic attractors have more clearly defined basins, as in the case of the saddle point already illustrated. Strange attractors generate highly irregular or chaotic motion and have been identified in three dimensional phase space (Schaffer 1984).

Five different types of point attractor can be identified: saddle points, stable nodes, unstable nodes along with stable and unstable spirals (fig 2.14). The ecological significance of point attractors is especially relevant to succession theory. Field data from an ecological community that could be characterised by a stable node would provide convincing evidence of the existence of a climax community. The unstable node and saddle point of fig 2.14 reflect biotic instabilities and illustrate the working of competitive exclusion.

The coupled logistic equation (22 a, b) is also capable of manifesting stable equilibrium behaviour as indicated by the solution in case (iv). The representation of a stable node in fig 2.14 suggests that case (iv) should be a large attractive basin with a valley bottom or fixed point. Initial conditions started anywhere inside this basin are attracted toward the fixed point. The coefficients of case (iv) were simulated for the four sets of initial conditions and plotted (fig 2.15).

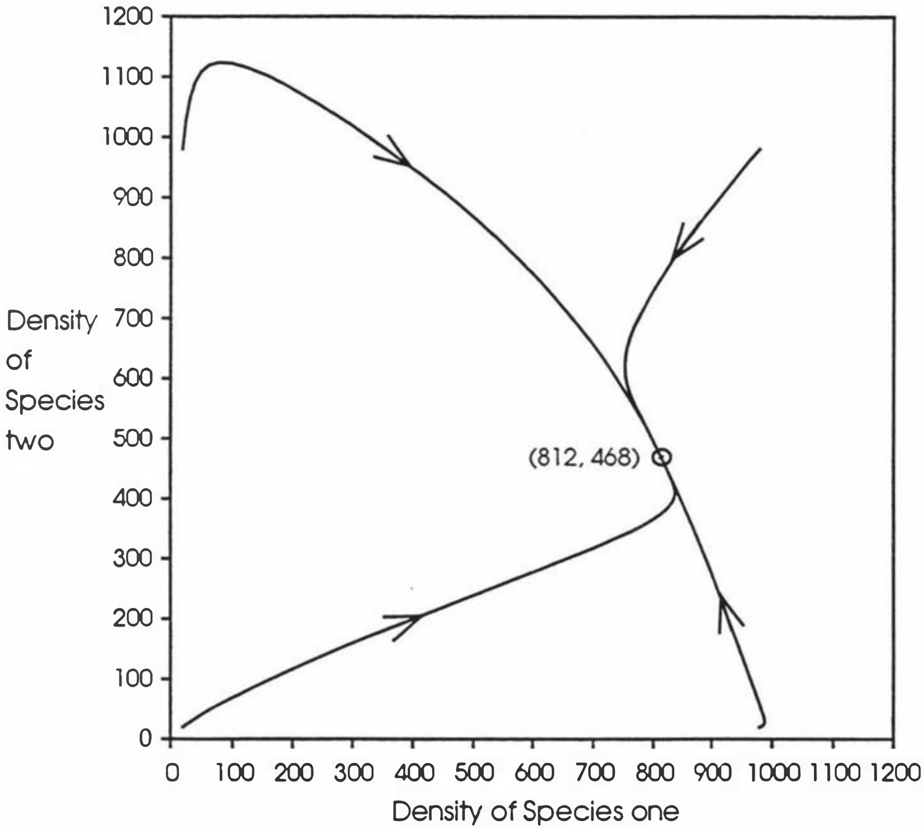


Fig 2.15 A stable node based on the competition coefficients of case (iv). An initial condition started anywhere inside this attractive basin will be drawn toward the fixed point at (812, 468).

A further unstable equilibrium state of the coupled logistic equation (22 a, b) is that of the local extinction of one species independent of initial conditions. Unlike case (i), the outcome of cases (ii) and (iii) are independent of initial conditions. This fact is illustrated using the four initial conditions of Table 2.2 with the competition coefficients of case (ii).

The prediction of case (ii) is that species 1 will be eliminated and species two will find an equilibrium point. The outcome is plotted as a phase portrait in fig 2.16.

The mathematical language of equilibrium theory is conceptually very rich. This section has attempted to draw upon mathematical metaphors in order to build a conceptual picture that gives meaning to the well rehearsed descriptive definitions of equilibrium and stability theory. A summary of these ideas is presented in the next section.

2.4.6.3 Summary

This section has defined and explored the conceptually rich theory of stably interactive community behaviour, a term used by DeAngelis and Waterhouse (1987) to define one of four possible community behavioural states. Classical theory suggests that an interactive community manifests behaviour that is driven by biotic causal agents. An equilibrium state exists as a direct result of density-dependent interactive processes which shut down the growth rate of a community as it reaches its theoretical equilibrium point or carrying capacity.

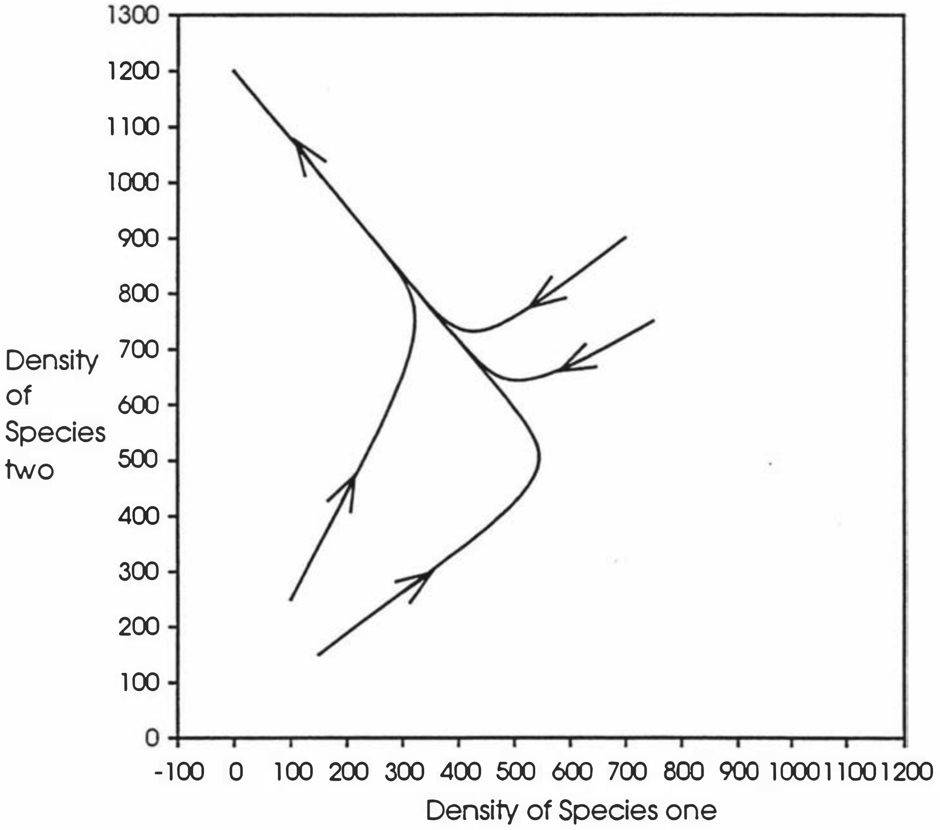


Fig 2.16 Case (ii) represents a further stable node according to fig 2.14.

An equilibrium state has been defined with reference to both population and community dynamics. The identification of an equilibrium state has been illustrated with both quantitative and qualitative mathematical techniques. Analysis of the qualitative behaviour of a multiple species system provides a useful means of identifying stable and unstable equilibria which can be characterised by three types of attractor in phase space: stable node, unstable node and saddle point.

For a single population or a multi-species community, an equilibrium state can be defined by the unchanging behaviour of component populations. Quantitative determination of the stability of an equilibrium state is undertaken by assuming that $N_{(t)}$ is a point very close to the equilibrium state $\overline{N}$, while $N'_{(t)}$ is a small perturbation of this same state(14).

$$N_t = \overline{N} + N'_t \qquad (14)$$

This type of problem may be solved using partial derivatives or linearization. The concept of a stable equilibrium state at the community level of organisation is conceptually quite difficult to grasp. A simple two species system of equations has been used to illustrate these concepts. The qualitative behaviour of a community is powerfully portrayed with the aid of phase portraits.

In phase space, a point attractor is an object which attracts initial conditions to itself from a surrounding region called a basin of attraction. Depending on its level of species diversity, a community may have several possible equilibrium states, but not all of these will be stable.

Three types of point attractor have been identified of which only one is globally stable. Classical equilibrium theory in ecology suggests that stable nodes and saddle points are characterisations of the early stages of community succession during which time niche specialisation and competitive exclusion operate to organise a structure that will eventually support a climax community. In this context, a stable node represents the condition of a climax community.

The discussion undertaken in the preceding sections has been largely theoretical. The next section provides a review of key publications, recording research efforts aimed at testing the predictions of the equilibrium paradigm. This review has a strong historic perspective and will cover the development of research efforts in equilibrium theory from the time of ecology's first equilibrium paradigm (the super-organism) until the 1970s. An appropriate label for this period in the history of ecology is *the Logistic era* (after Pearl 1927). The logistic era is a time in the history of ecology in which ecologists have sort to bridge the gap between the predictions of equilibrium theory and the reality of nature. Chapter three takes up the history of ecology during the 1970s until the present day and reviews state of the art developments in non-equilibrium theory.

2.5 The logistic era - the Study of Theory and Reality

As stated earlier in this chapter, Clementsian succession theory demarcates the beginning of the end for balance of nature (equilibrium theory) in ecology. The fundamental unit, synergistic and density-dependent assumptions of the super-organism paradigm drew a storm of controversy and opposition, just as Darwin's theory of evolution had done almost a century before (Clements 1928). In this context, succession theory turned the attention of ecologists toward the last stronghold of providential ecology - the concept of balance or equilibrium *in* nature. In Darwin's theory of evolution, the struggle for existence had replaced acts of divine providence as the mechanism of population regulation. During this century, research efforts aimed at bridging the gap between equilibrium theory and reality have largely failed to provide conclusive evidence for the existence of stable equilibria in natural systems. The following section reviews and discusses key aspects of this research which has largely contributed to the final demise of the equilibrium paradigm.

2.5.1 *Introduction*

At the turn of the century, the focus of much mathematical population theory was the logistic equation (2) of Verhulst (1838), later independently derived by Pearl and Reed (1920). From the logistic equation, Lotka (1932) and Volterra (1931) independently developed competition equations (22 a, b). These two sets of equations formed the basis of important theoretical developments in ecology during much of the remainder of this century (Murray 1979). The following discussion is restricted to these two models for a number of reasons.

Firstly, the power of a mathematical model lies in its predictive capability and in the robustness of its assumptions. Both the predictions and assumptions of these two models have been subjected to extensive testing. Secondly, the process of extensive testing has acquainted ecologists with the limitations of these two models as prescribed in their original formulations. Thirdly, because the limitations of these models are well understood, they provide an important test of the core equilibrium theory from which they were derived. In fig 2.17, the historic formulation, testing, re-assessment and current rejection of the logistic and Lotka-Volterra model formulations is portrayed.

The logistic and Lotka-Volterra equations were formulated on the assumption that natural populations were regulated by density-dependent mechanisms that maintained stable equilibrium conditions. In fig 2.17, the assumption of equilibrium behaviour is represented as a core paradigm from which the models and their most obvious assumptions were derived.

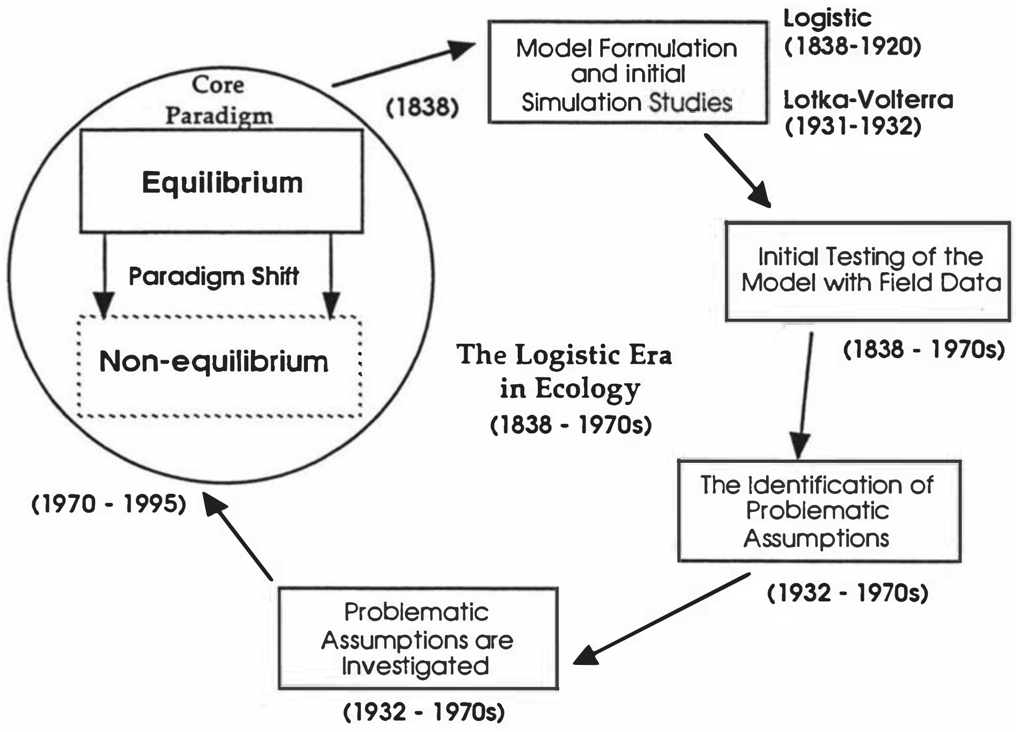


Fig 2.17 The logistic era in ecology has involved the formulation, rigorous testing and development of equilibrium theory as described in the logistic and Lotka-Volterra competition models. Approximate dates are given for the various stages identified.

The initial formulation of the equations as given by Verhulst (1838), Pearl and Reed (1920), Lotka (1931) and Volterra (1932) was used to fit the predictive behaviour of the models to field data. Key research work from this period will be cited in the following review. These research efforts led ecologists to realise that the predictive power of these models was faulted on the grounds of invalid assumptions. Research efforts were then initiated to explore more fully the nature of problematic assumptions. One way of improving invalid assumptions is to add greater complexity to the original formulation of a model and in the case of the logistic and Lotka-Volterra equations, this has been an active area of research. This period of revision and further research was conducted within a context of other major theoretical developments in ecology.

It is now generally accepted that most of the assumptions of the logistic and Lotka-Volterra models are violated in natural systems most of the time. During this long process of testing, ecologists have become better acquainted with the limitations of these models and the theory from which they were derived. Ecology is now undergoing a major shift away from the traditional core equilibrium paradigm toward a non-equilibrium alternative (DeAngelis *et al.* 1985, DeAngelis and Waterhouse 1987).

Modelling is a burgeoning field in ecology and alternative equilibrium models exist. However, it is the opinion of this author that none of these models is as far advanced in the process of testing outlined in fig 2.17 as is the logistic and Lotka-Volterra competition models. Many of the alternative models are still at the formulation / simulation study / field data testing stage. There are many examples of such models in the literature. Some examples include: a coupled system of two predators and one prey (McGhee and Armstrong 1977), single species growth models (Hubbell 1973, Khanin and Dorfman 1973, Streifer and Istock 1973, Varley *et al.* 1973, Coulman et. al. 1971, Timin and Collier 1971, Trubatch and Franco 1974), two species competition models (Kolmogorov 1936, Herbert *et al.* 1956, Gomatam 1974a, b, Stewart and Levin 1973), a two species host parasite model (Nicholson and Bailey 1935), competition models with nonlinear growth rates (Armstrong and McGhee 1976a, b, Koch 1974, Smith *et al.* 1975), discrete competition models (Hassell and Comins 1976, Haussmann 1971).

In these alternative equilibrium models, favourable correspondence between model behaviour and field data are important, but incomplete if the assumptions of the models remain untested (Facelli and Pickett 1990).

An illustration of an alternative modelling formulation and framework based on equilibrium theory is the Markov succession model introduced to ecology by Horn (1975, 1975a). From the time of Clements, various models had been developed to study ecological succession, but none of them provided much in the way of predictive power. Markovian succession models were favourably greeted as an answer to these limitations.

The theory behind the application of Markovian chains to succession was developed by Horn (1975, 1975a), Usher (1979) and van Hulst (1979, 1979a). The method had earlier been applied by Anderson (1966), Usher (1966), Bosch (1971) and Botkin *et al.* (1972).

Briefly, a Markov model consists of a state vector and a transition matrix containing the probabilities of different transitions in the system. The product of the vector times the matrix produces a new vector representing the state of the system at a future time interval. In its simplest form, the model has been widely applied (Enright and Ogden 1979, Culver 1981, Hobbs 1983, Ogden 1983, Lippe *et al.* 1985, Lough *et al.* 1987, Isagi and Nakagoshi 1990, Alvarez-Buylla 1994).

Markov succession models have been formulated on a number of major assumptions including: a homogeneous seed source, that the system converges on a stationary composition (May 1976), that the transition probabilities do not change, that successional deletion of species involves uniform probability, that the stationary distribution is a geometric series, that the dynamics of the system depend on its present state and are independent of past states, that interactions are instantaneous and therefore the history of a system is unimportant in determining its future. Most importantly, the model assumes long term equilibrium behaviour.

Facelli and Pickett (1990) suggest that while Markovian succession models were greeted as *the ultimate tool for the analysis, description and prediction of succession,* they have produced only *meagre results.* The co-authors point out that in fitting model behaviour to data, mimicry *is not good evidence of the Markovian nature of succession,* since the model's *assumptions remained largely untested.*

May (1976) has also reviewed the Markov succession modelling approach and concludes that the *only sweeping generalisation that can be made about succession is that it shows a bewildering variety of patterns.* Succession may *be rapidly convergent on a stationary vegetational composition... be slow and apparently dependent on accidents of history... lead to alternative stationary states... change in response to more or less random changes in the physical environment... change cyclically by responding to and perhaps reinforcing an environmental cycle.* The utility of Markovian succession rests largely upon the validity of the first of the successional pathways identified by May (1976) - the assumption that vegetation converges on a stationary composition.

The logistic equation has been traditionally accepted as a general mathematical description of population growth despite repeated criticism (Gray 1929, Hogben 1931, Kavanagh and Richards 1934, Feller 1940, Andrewartha and Birch 1954, Smith 1952, 1954, Pielou 1969, 1977). General descriptions of the logistic equation are common to most ecology text books (Maynard Smith 1974, May 1974, 1976, Pielou 1977, Hutchinson 1978, Murray 1979, Hutchinson 1978, Freedman 1980, Slobodkin 1980, Emlen 1984, Hendrick 1984, Krebs 1985, Ginzburg and Golenberg 1985, Ehrlich and Roughgarden 1987, Ricklefs 1990, Renshaw 1991, Colinvaux 1993).

The Lotka-Volterra competition equations (22 a, b) also have a well rehearsed history in ecology (Maynard Smith 1974, Pielou 1977, Murray 1979, Hutchinson 1978, Freedman 1980, Slobodkin 1980, Emlen 1984, Hendrick 1984, Krebs 1985, Ginzburg and Golenberg 1985, Ricklefs 1990, Renshaw 1991, Colinvaux 1993) and suffer from all of the limitations of the underlying logistic. They also assume instantaneous competition and have competition coefficients (α and β) that are invariant with respect to N_1 and N_2 (Pielou 1977, Emlen 1984, Krebs 1985).

In the following review, discussion of the Lotka-Volterra competition model will be restricted to competition theory. A burgeoning literature also exists for positive density-dependence (mutualistic) theory, derived from, tested and applied using the Lotka-Volterra competition model formulation (May 1976, Freedman 1980, Dean 1983, Wolin and Lawlor 1984, Adicott and Freedman 1984, Boucher 1985).

A number of case studies and theoretical developments are reviewed in the following section in order to evaluate more fully these models which have provided a primary source of empirical testing and theoretical development of equilibrium theory in ecology up until the 1970s.

2.5.2 *Empirical Testing - The Logistic Model*

Carlson (1913) ran laboratory experiments (fig 2.18) in which he grew cultures of yeast and noted the tendency of these populations toward an equilibrium. Carlson's work was later used by Pearl (1927) who calculated logistic curves for the data.

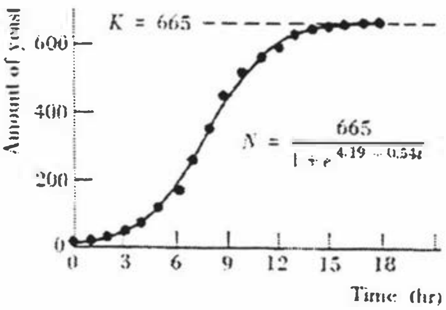


Fig 2.18 The yeast data of Carlson (1913) fitted to the logistic equation by Pearl (1927), (from Krebs 1985).

In 1927, Pearl fitted a logistic curve to data recording the growth of *Drosophila melanogaster* laboratory populations (fig 2.19) which he maintained in bottles with yeast as a food source (see also Lotka 1925). Pearl also worked to fit the logistic to national populations including those of Sweden, France, North America and the world population.

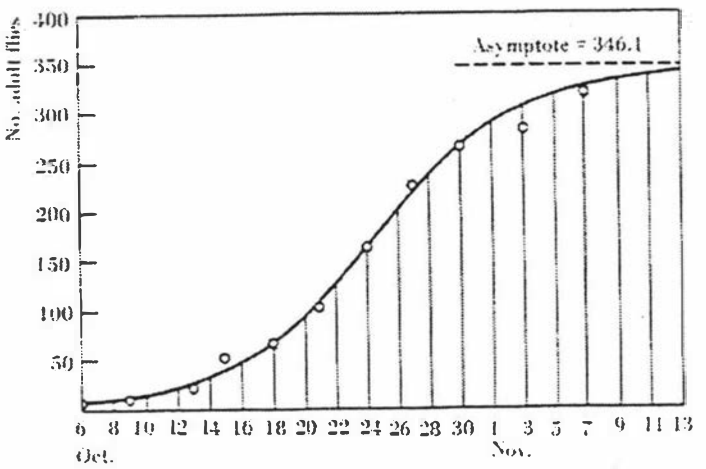


Fig 2.19 The growth of an experimental population of fruit fly *Drosophila*. The data points have been fitted to the logistic curve by Pearl (1927), (from Krebs 1985).

Pearl hailed his results as the ushering in of the *Logistic era.* (see fig 2.19). He suggested that the logistic curve was a universal law of population growth. Sang (1950) criticised the application of the logistic to *Drosophila* and identified complexities that Pearl had overlooked. Firstly, the food source Pearl had used for *Drosophila* was itself a growing population and therefore not a constant food supply. Secondly, Pearl had counted only the adults of *Drosophila* which has several stages to its life cycle in which both adults and larvae consume food.

By contrast to yeast, flour is a dead food medium more suitable for use as a constant food source. Beetles that live in flour, *(Tribolium)* and wheat *(Calandra)* have been used by ecologists for experimental population studies (Chapman 1928, Park 1948, 1954, 1962, Birch 1953). Like *Drosophila,* beetles tend to have quite complex life cycles, although in this case both the adults and larvae eat much the same food.

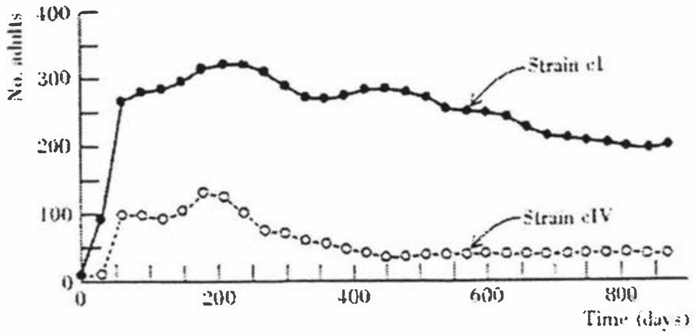


Fig 2.20 Population growth of the flour beetle Tribolium castaneum over an extended time period of 800 days. Both strains show a tendency away from stable equilibrium conditions (Park *et al.* 1964) (from Krebs 1985).

Thomas Park (1964), reared populations of *Tribolium* for several years and found that the long term behaviour of the *Tribolium* population tended away from an upper asymptote (fig 2.20). The density of the population did not stabilise after the initial sigmoid increase. Instead, the population showed a long term decline. In work on *Calandra oryx,* Birch (1953) found similar results in which the initial sigmoid rise was followed by large fluctuations.It is now thought that these fluctuations in population numbers, brought about under constant environmental conditions, may be the result of social behaviour. Krebs suggested that there has been no case demonstrated of an organism with a complex life history settling to a steady-state at the upper asymptote of the logistic curve (Krebs 1985).

In support of Krebs' (1985) claims concerning complex life history and variation of populations around an equilibrium point, Davidson (1938, 1938b) provides evidence from Tasmanian and South Australian sheep populations.

The data recorded by Davidson (1938), (fig 2.21) for south Australian sheep populations shows fair correspondence with the logistic curve. Davidson explains the variance about the upper asymptote in terms of the dependence of the carrying capacity on the power of pasture to recover from overgrazing. In the arid climate of South Australia, pasture recovery is dependent on annual rainfall and the prevalence of wet and dry spells.

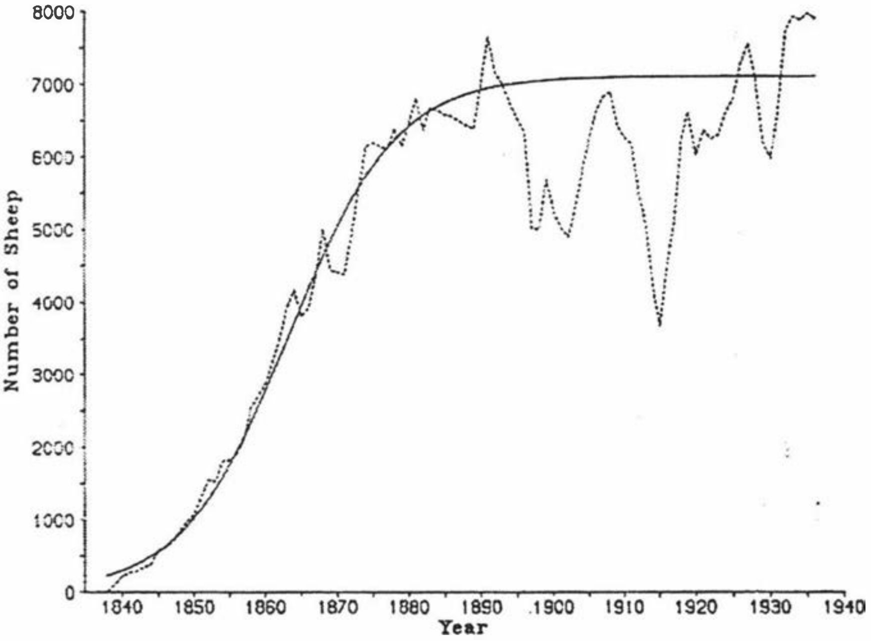


Fig 2.21 Growth of South Australian Sheep Population (broken line) and fitted logistic curve (solid line), (Davidson 1938), (from Renshaw 1991).

Bacterial population growth has also been studied under laboratory conditions. Jordon and Jacobs (1947) grew *Escherichia coli* in a constant environment with continuously renewed food supply. They counted both viable bacteria and total cells (fig 2.22). At 35°C, the growth of the bacteria was logistic, but at 25°C, the bacteria grew rapidly in a non-logistic manner. These results demonstrate that behavioural responses can be mediated by environmental variables like temperature.

A limitation of experiments with laboratory based populations is that a full range of environmental variables and stochasticity are missing. One of these missing variables may be responsible for mediating deviant behaviour caused by temperature change. This concept of compensatory behaviour is explored more fully in Chapter three.

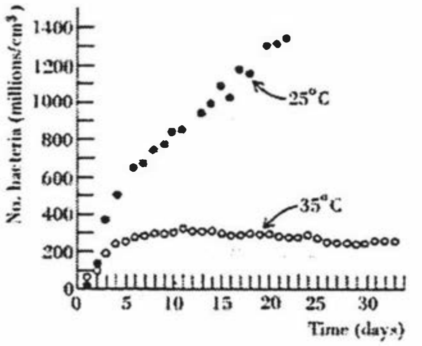


Fig 2.22 Jordon and Jacobs (1947) grew laboratory populations of *Escherichia coli* under constant environmental conditions. Variation in temperature resulted in non - logistic growth behaviour (from Krebs 1985).

The first ecologist to consider the importance of time delays for the dynamics of ecosystems was Hutchinson (1948) who built a resource limitation time delay into the logistic equation (23)

$$\frac{dN}{dt} = N(r - KN_{t-T}) \qquad (23)$$

where

N_t the state of the system N at time t.

T the development time of a resource.

The reasoning behind this delay function came from the idea that as the density of a species increases, the resources available to it decrease in classical density-dependent fashion. However, in a real ecosystem resources are self-renewing, therefore the level of resource availability at a given time t will depend on the density of the regulated species at time T in the past. In this context, T is the development time of the resource species. The classical logistic equation assumed instantaneous resource availability. According to Hutchinson's revised equation (23), if T is large compared to $1/r$, divergent oscillations result. This is in sharp contrast with the behaviour of the logistic equation. When $(T) = 0$ a stable non-oscillatory equilibrium results.

The resource-availability-time-delay model of Hutchinson (1948) was tested by Nicholson (1954). In an intricate laboratory experiment Nicholson (1954) showed that populations of the blowfly *Lucilia cuprina*, supplied with food at a constant rate, oscillated with large amplitude and regular period. This result ran contrary to the predictions of the logistic model which assumes instantaneous resource availability and predicts stable equilibria. Nicholson applied the experiment in two ways.

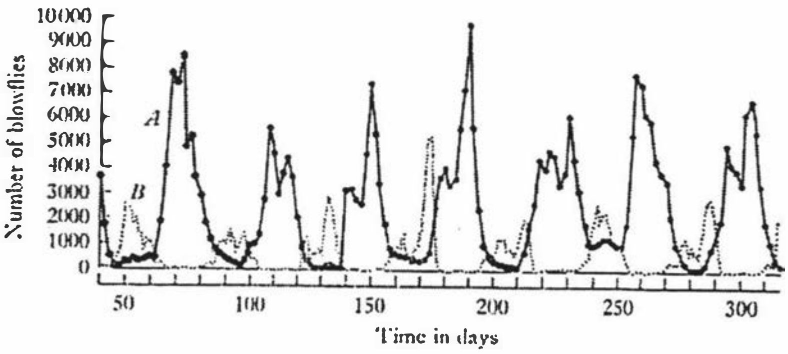


Fig 2.23 Number of blowfly (line A) *Lucilia* in an experiment devised by Nicholson (1954, 1958), (from Maynard Smith 1974).

Firstly, adult and larval *Lucilia* were kept in a cage in which unlimited food was supplied to the larvae and constant, but limited food was supplied to adults. The result was oscillations of large amplitude and regular period (fig 2.23). Maynard-Smith (1974) suggested that two mechanisms may be responsible for regulating this system. Firstly, as the population of blowflies increases in number, more food is required to maintain the population and as a result of this feedback mechanism, the rate of egg laying declines.

Secondly, there must be a time delay in the development of larvae before they become egg laying adults.

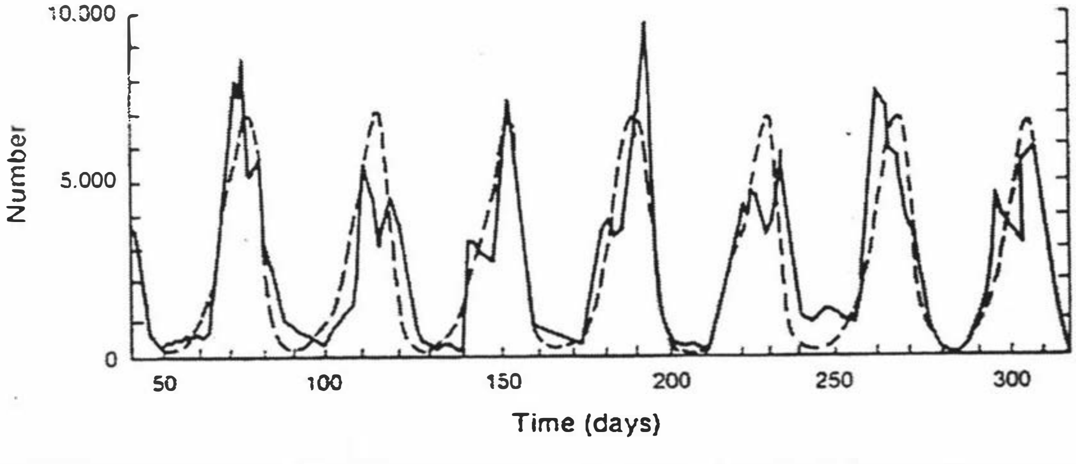


Fig 2.24 Experimental data from Nicholson (1954, 1958, 1958a), (solid line). Broken line represents the behaviour of the logistic model with a nine day development time lag (May 1975), (from Hendrick 1984).

Nicholson also observed sustained oscillations when unlimited food was supplied to adults and limited amounts to larvae. In this case, the existence of oscillations suggests that as the number of eggs laid on a limited food resource increases, the numbers of adults produced should decline. Nicholson found this to be the case and suggested that when many eggs are laid food is wasted by being eaten by larvae who die before pupation. The greater the number of eggs laid, the greater the waste and the result is a decline in adult numbers (Maynard-Smith 1974).

Nicholson (1954, 1958), distinguishes between two types of competition for limited resources. The case of *Lucilia* illustrates scramble-competition in which the efficiency of food utilisation for a limited resource declined as population numbers increased. Scramble-competition appears to result in oscillatory behaviour. In contest-competition, the distribution of adequate food resources is limited to a class of individuals - the strongest. logistic growth is the result of contest competition.

May (1975), revisited the work of Nicholson (1954, 1958) and attempted to modify the logistic equation so as to capture the behaviour of Nicholson's blowflies (fig 2.24). May found that a time lag of nine days adequately explained this pattern of population change - the time required for the larva to mature to the adult stage (a developmental time delay).

The growth of intertidal barnacle populations that are limited for space appear to grow in a manner that is consistent with the predictions of the logistic model. Connell (1961a) suggested that, for a barnacle population, the limit to population size is space on a rock. Once all of the available space is taken, further increases in density cannot occur (fig 2.25). This type of growth behaviour was demonstrated by Connell (1961a) using two newly exposed rocks. Both the carrying capacity and pattern of density increase are similar for the two rocks.

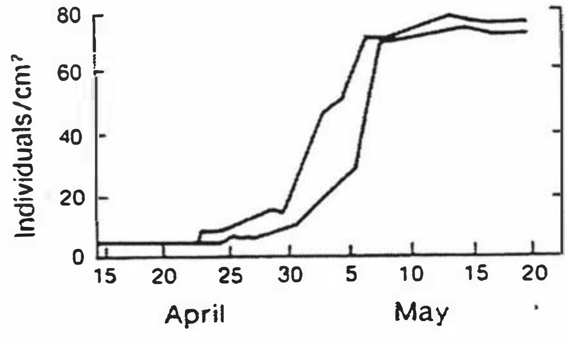


Fig 2.25 The growth of a two barnacle populations on two exposed rocks (Connell 1961a). Both populations demonstrate similar response to the effects of increasing density (from Hendrick 1984).

While the behaviour of Connell's barnacle populations appears to conform to the predictions of the logistic model, the results are really site specific. Firstly, Connell just happened to choose a species which apparently has little ability to change its environment in the way that plant communities and terrestrial animal populations can. In this case the carrying capacity is invariant.

Secondly, barnacle populations are exposed to two forms of disturbance. Firstly, it is well known that barnacles are a food resource for other marine predators. Secondly, excessive low tide exposure or high tide storm damage may slowly or drastically reduce population numbers. These facts suggest that the long term behaviour of these populations is very unlikely to be equilibrium centred. For these reasons, Connell's results are probably an artefact of life history characteristics, temporal and spatial resolution.

Two further predictions of the logistic model are: the existence of an inverse linear relationship between decreasing growth rate and increasing density and a negative growth rate inversely related to density if a population overshoots its carrying capacity. MacArthur (1960) published experimental results from a study of oven birds, *Seiurus aurocapillus,* which appears to support these predictions (fig 2.26).

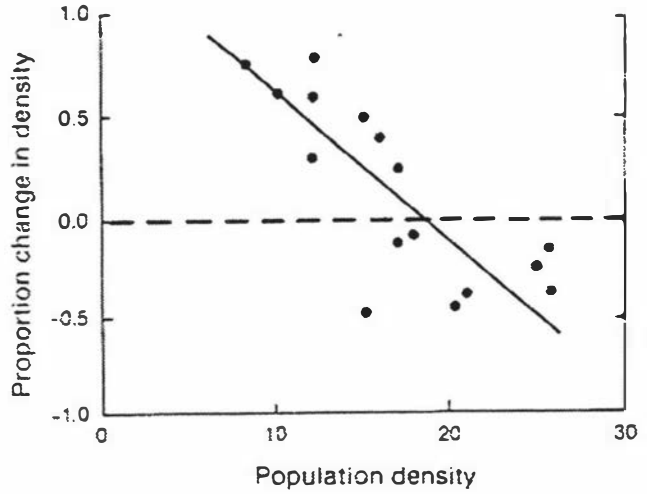


Fig 2.26 Empirical evidence to support the existence of an inverse linear relationship between reproductive change and increasing population density (MacArthur 1960), (from Henrick 1984).

While the density of the ovenbird population was between 15 and 20, the population size increased and decreased part of the time. This suggested to MacArthur that the carrying capacity of the population was between 15 and 20 birds.

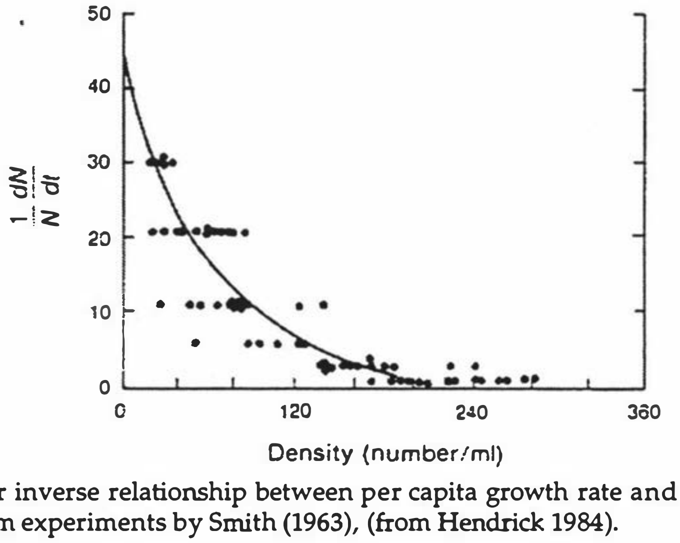


Fig 2.27 A nonlinear inverse relationship between per capita growth rate and population density. Population data from experiments by Smith (1963), (from Hendrick 1984).

Respectfully, it needs to be said that MacArthur's choice of model for this data and fitting techniques *leave much to be desired.* If a nonlinear model was chosen, the same data could be used as evidence to support the idea of an inverse nonlinear relationship. The equilibrium point identified in this illustration is certainly not invariant.

In contrast to MacArthur's (1960) results, Smith (1963) experimented with *Daphnia* and provided empirical evidence (fig 2.27) which suggested that an inverse linear relationship between per capita growth rate and density did not exist in this case. Smith (1963) demonstrated, that the relationship may be concave, with the per capita growth rate lower at intermediate densities than a linear relationship would predict.

Ziswiler (1967), presented evidence based on historic census records which demonstrates just how vulnerable natural populations can be to disturbance.

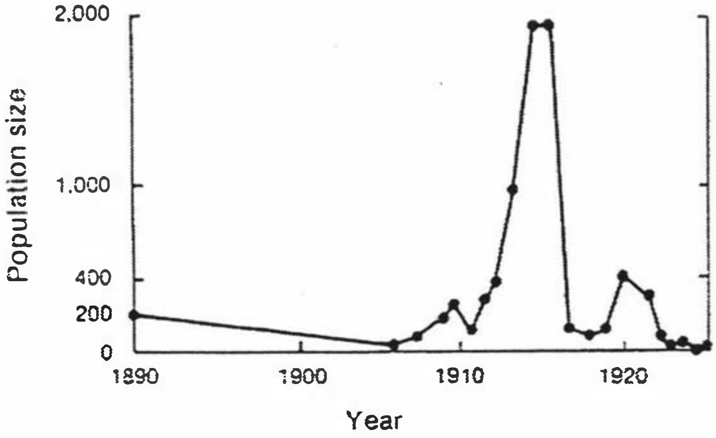


Fig 2.28 Numbers of North American heath hen just prior to their extinction in 1932 (Ziswiler 1967), (from Hendrick 1984).

As a result of former habitat destruction and recreational hunting, the North American heath hen fell to a dangerously low population size of 100 at the turn of the century. An intensive breeding program was started and the population rebounded in classical logistic fashion reaching an equilibrium point about 1914. A few years later, the population suddenly crashed after a fire destroyed much of its natural habitat. The heath hen finally became extinct in 1932 (fig 2.28). The exact cause of the population crash is not clear. These birds were known to form large mating aggregations and it may be that it was the disruption of this social behaviour that prevented the population from maintaining itself (Krebs 1985).

In xeric *Picea* and *Abies* forest of the central Rockies, Aplet *et al.* (1988) suggest that neither the equilibrium or non-equilibrium model alone has proved adequate to explain existing forest community structure. The authors point out that some forest stands investigated are undergoing postfire development and indicate the existence of non-equilibrium processes. However, a mature stand of Spruce in late development is also cited as evidence of the existence of equilibrium processes.

There have been a number of attempts made in past and recent times to improve the form of the logistic equation in order to deal with some of its more obvious deficiencies. Richards (1959), Pearl (1940) and Jolicoeur and Pontier (1989), have all proposed four parameter versions of the logistic, the last of which is capable of describing population growth and decline.

The logistic equation has sometimes been used to model situations with changing levels of environmental support and changes in the intrinsic growth rate (24). This is simply accomplished by allowing the parameters r and K to vary with time in the case of the logistic (Boyce and Daley 1980) and Lotka-Volterra competition equations (Abdelkader 1980).

$$\frac{dN(t)}{dt} = r(t)N(t)\left[1 - \frac{N(t)}{K(t)}\right]. \tag{24}$$

Ecologically, variation in r and K is indicative of environmental instability. Hallam and Clark (1981) identify an untenable contradiction apparent in this non-autonomous version of the logistic equation (24). The behaviour of the model is such, that a population with a small intrinsic growth rate parameter is barely able to persist under favourable conditions, while it is able to do *well or better in an intolerable environment.* The co-authors claim that these deficiencies result from the domination of the intrinsic growth rate in the equation and advance the following equation (25) in an effort to overcome these deficiencies

$$\frac{dN(t)}{dt} = N(t)\left(r - \frac{c}{K}N(t)\right). \tag{25}$$

The intrinsic growth rate r, is expressed in the units (time) $^{-1}$ as is the positive parameter c. The parameter c is a measure *of the population response to environmental stress as represented by the ratio N/K* (Hallam and Clark 1981). In the classical logistic equation, the parameter K can be interpreted as either a population carrying capacity or a steady state - definitions which need not be equivalent. To overcome this problem, the co-authors reformulate equation (25) as

$$\frac{dN(t)}{dt} = N(t)\left[r(t) - c\frac{N(t)}{B(t)}\right], \tag{26}$$

where B denotes *the maximum population which the environment can support* (Hallam and Clark 1981). When r and B are constants, equation (26) has a stable equilibrium at $N = rB/c$. In the case that equation (26) is non-autonomous, either a deteriorating growth rate or environment ensures extinction (Hallam and Clark 1981).

More general discussion concerning the ecological significance (Murray and Garding 1984), necessity (Lotka 1925, Volterra 1931, Volterra and D'Ancona 1935, Kostitzin 1939, Spiegelman 1946) and interpretation (Caughley 1966, Caughley and Birch 1971, Ayal and Safriel 1979) of the parameters of the continuous and discrete (Birch 1948) versions of the logistic equation have been undertaken.

Underlying all of the historic debate concerning the adequacy (or inadequacy) of the logistic equation is a more pointed question concerning the adequacy (or inadequacy) of any first-order equation as a model of population dynamics (Turchin 1993). One-dimensional models such as the logistic cannot exhibit limit cycles or chaos. Turchin (1993) points out that equations of at least two dimensions are required for cycles and three for chaos. For this reason, attempts to quantify the frequency of complex dynamics in natural populations with one-dimensional models biases the results in favour of stability (Turchin 1993). Furthermore, Turchin (1993) points out that the *paper that is most often cited as evidence for the rarity of complex dynamics in nature* ... (Hassell *et al.* 1976) ... *used a one dimensional approach.*

Witteman *et al.* (1990) provide evidence which appears to support Turchin's (1993) concerns regarding the utility of the single dimension model used by Hassell *et al.* (1976). The authors used auto-correlation analysis and lag-plot reconstruction techniques on 71 long term population studies and demonstrate that complex dynamics are far more prevalent in natural population behaviour than is suggested by the earlier publication of Hassell *et al.* (1976).

2.5.3 *Empirical Testing - The Lotka-Volterra Equation*

Lotka (1932) and Volterra (1931), used the logistic equation as the basis of their competition equations. Important theoretical developments and applications of these equations are reviewed by Wangersky (1978).

For some time after the initial formulation of the Lotka-Volterra competition models, it was assumed that the outcomes of these interacting equations was independent of changes in the specific growth rate parameters of the two equations. Dorschner *et al.* (1987) present the results of computer simulation studies along with analytical arguments to show that *this earlier interpretation of the effect of r on the outcome of competition in the indeterminate case is in error.*

The authors demonstrate that when biotic potentials are similar, it is possible to reverse the competitive outcome of an initial set of densities based on competition coefficients and equilibrium values as per the Lotka-Volterra indeterminate case (Dorschner *et al.* 1987).

The theta (θ) form of the logistic equation was developed by Gilpin and Ayala (1973) to allow for different forms of density-dependence to be described. If theta is small, per capita birth or death rates decrease rapidly with increasing population size, even at small population densities. If theta is large, the probabilities of birth and death do not change much until the prey population reaches its carrying capacity. The competition form of the theta logistic model (27 a, b) appears to give a better fit to experimental data with *Drosophila pseudoobscura* and *D. serrata* (Ayala 1969). With the exception of the theta term, the parameters and coefficients of this equation are identical to those specified in equation (22 a, b).

$$\frac{dN_1}{dt} = rN_1\left(1-\left(N_1/K_1\right)^{\theta} - \alpha N_2/K_1\right)$$

$$\frac{dN_2}{dt} = rN_2\left(1-\left(N_2/K_2\right)^{\theta} - \alpha N_1/K_2\right) \qquad (27a, b)$$

Initially, Ayala (1969) interpreted his results as disproof of the principle of competitive exclusion. Gilpin and Justice (1972), pointed out that Ayala's results with *Drosophila pseudoobscura* and *D. serrata* could more usefully be thought of as illustrating the inadequacy of the logistic competition equation formulation (22 a, b) to analyse all cases of competition.

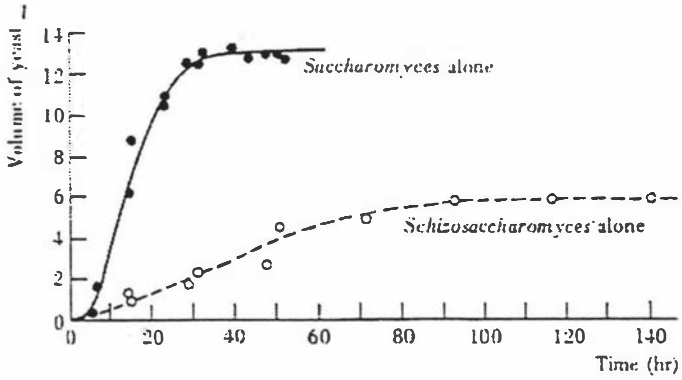


Fig 2.29 The two experimental yeast populations of Gause (1932) fitted to the logistic model (from Krebs 1985).

Istock (1977) studied the behaviour of two species of waterboatmen *(Corixidae)* and fitted seasonal data to the Lotka-Volterra model. Both species were found to co-dominate in their pond environment and were present at all times. One species *(Hesperocorixa lobata)* was found to be numerically dominant in the spring and early summer while the other species *Sigara macropala)* dominated in the latter half of the summer. Istock concludes that *S. macropala* is able to inhibit the development of *H. lobata,* but the interaction is not necessarily reciprocal. The behaviour of these two populations appears to be equilibrium centred and yet quite dynamic on an annual basis.

Much of the early research and theoretical developments that have come from the Lotka-Volterra equations can be traced back to the research efforts of the Russian microbiologist named Gause. Gause (1932) studied the mechanisms of competition between two species of yeast *Saccharomyces cervisiae* and *Schizosaccharomyces kephir*. To begin with, Gause (1932) grew the two yeast species separately and found that he could obtain a good fit between their growth data and the logistic model (fig 2.29).

Before the research efforts of Gause in 1932, Richards (1928), had discovered that the action of alcohol produced by the breakdown of sugar for energy under anaerobic conditions would slow down the rate of growth of yeast populations. Richards discovery suggested that yeast were principally limited by ethyl alcohol accumulation and this association could be illustrated by plotting alcohol concentration alongside population growth (fig 2.30).

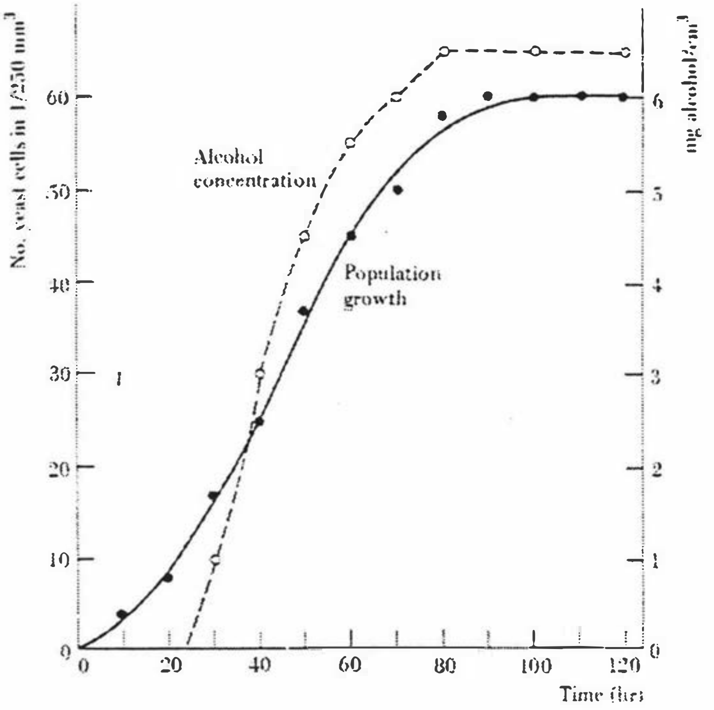


Fig 2.30 Experimental data for the growth of yeast fitted to the logistic model (solid line). Accumulation of ethyl alcohol (Richards 1928), (from Krebs 1985).

In a nice example of lateral thinking, Gause (1932) reasoned that if alcohol accumulation was indeed a critical limiting factor then it should be possible to determine the coefficients of competition in the Lotka-Volterra equations by measuring the alcohol production rates of the two yeasts. To test this hypothesis, Gause grew the two yeast species in a single culture, fitted the data to the Lotka-Volterra model and compared the competition coefficients with those determined by direct measurements of alcohol production rates. While the two sets of coefficients were not identical, they were very close. Gause attributed differences to the presence of other waste matter.

Birch (1953) experimented with interacting populations of grain beetles *Calandra oryzae* and *Rhizopertha dominica.* Birch found that the outcome of interaction between the two beetles in a mixed culture was dependent on temperature. At 29°C, *Calandra* would usually eliminate *Rhizopertha*, while at 32°C, *Rhizopertha* would eliminate *Calandra*. Once again, it is interesting to note that in the experimental results of Birch plotted in figure 2.31, the species which wins out in the competitive encounter does not reach a stable equilibrium point as predicted by the Lotka-Volterra model.

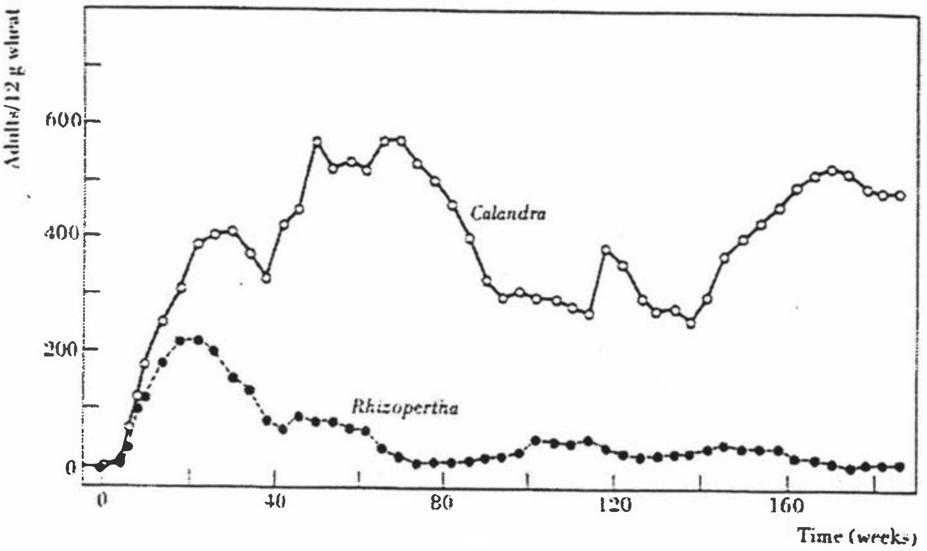


Fig 2.31 A plot showing the outcome of a competitive interaction between the two species of grain beetle grown in a mixed culture by Birch (1953). In this example from the work of Birch, both species of grain beetle are raised in wheat at 14% moisture content and 29.1°C constant temperature (from Krebs 1985).

Park (1948) explored interspecific competition by experimenting with mixed cultures of two flour beetles *Tribolium confusum* and *Tribolium castaneum*. Park experimented with a range of environmental variables including: space, initial densities, food quantities, climate, genetic variability and the addition of sporozoan parasites. Park found that space did not greatly affect the outcome of competition between these two species.

Park (1948), also noted that it was not possible to predict outcomes with any certainty. The results appeared to be more probabilistic in nature. This was especially the case at intermediate climates when sometimes *T. confusum* would win and sometimes *T. castaneum* would win. Furthermore, Park found that different genetic strains of *Tribolium* differed greatly in their competitive ability.

The work of Park was instrumental in demonstrating that the outcome of competition is not always invariant and may depend on abiotic factors like weather and internal biotic factors like genetic composition. In the examples of interacting populations considered so far, the outcome of the interaction has also meant the loss of one species.

Crombie (1945) raised two species of grain beetle in wheat and found that they could coexist indefinitely. The mechanism of coexistence appeared to be difference in food preference. The larvae of *Rhizopertha* live and feed on the inside of the wheat grain while the larvae of *Oryzaephilus* live and feed on the outside of the wheat grain. Crombie reasoned that these differences were enough to allow coexistence of the two species.

Both the logistic and Lotka-Volterra equations assume that competition occurs independent of other forms of community interaction such as predation or symbiosis. This assumption will almost never be upheld in multi-species communities. Slobodkin (1961), was one of the first people to investigate the possible implications of predation for competing species. To accomplish this, Slobodkin added complexity to the basic Lotka-Volterra competition equation by adding a density-dependent predation term (28 a, b) to each equation $-PN_{(n)}$.

$$\frac{dN_1}{dt} = rN_1\left(1 - \frac{N_1 + \alpha N_2}{K_1}\right) - PN_1$$

(28a, b)

$$\frac{dN_2}{dt} = rN_2\left(1 - \frac{N_2 + \beta N_1}{K_2}\right) - PN_2$$

Slobodkin (1964) applied the insights gained in this theoretical study to an experimental situation with two species of hydra and discovered some fascinating results. To begin with, *Chlorohydra viridissima* (green hydra) was found to win in competition with *Hydra littoralis* (brown hydra) in the absence of any forms of predation and the presence of heavy light. Slobodkin then ran these same experiments, first in darkness and then under intense predation.

The predation took the form of Slobodkin removing fixed amounts of total hydra population at fixed intervals. As the extent of predation rose from 0% to 25% to 50% per day, the green hydra required longer and longer time intervals to exclude its competitor. At 90% predation per day, the two hydra coexisted. Slobodkin had discovered that in the case of hydra, coexistence could be predator mediated - behaviour that was not a part of the original Lotka-Volterra competition formulation. These results strongly suggest that in at least some cases, coexistence will be predator mediated.

In another example of lateral thinking and careful observation, Gause (1935) discovered that he could get two species of *Paramecium* to coexist in a test tube containing a yeast suspension. *P. aurelia* would feed on the yeast suspended in the upper layers of the test tube while *P. bursaria* would feed on the lower layers. The results of these last three case studies all point to a phenomena that the Lotka-Volterra equations did not predict. The idea was articulated by Gause (1934) and later became known as Gause's hypothesis.

As a result of competition, two similar species scarcely ever occupy similar niches, but displace each other in such a manner that each takes possession of certain particular kinds of food and modes of life in which it has an advantage over its competitor.

Hardin (1960) stated the principle quite succinctly; *complete competitors cannot coexist.* The idea became known as the competitive exclusion principle and was destined to become yet another field of controversial inquiry in ecology. There is not space nor justification for reviewing the full history of this debate. However, some key aspects of this controversy do have an important bearing on the present theme. Briefly, the study of Gause's hypothesis makes it even more difficult to treat the mechanism of interspecific competition in the Lotka-Volterra equations with any real certainty.

2.5.4 Empirical Testing - Competitive Exclusion

From the beginning, the competitive exclusion principle seemed shrouded in controversy. Hutchinson and Deevey (1949), claimed that it was the *most important development in theoretical ecology* and *one of the chief foundations of modern ecology.* Cole (1960), virtually ignored the idea and referred to it as a *trite maxim.* The cause of the difficulty could be traced back to two primary areas.

Firstly, competitive exclusion assumed the existence of a niche for each species that defined the role of a species in a community, according to Elton (1927) and subdivisions of the species habitat, according to Grinnell (1917). These early ideas were incorporated into Hutchinson's (1958) redefinition of a fundamental niche, as conceptualised by an array of multi-dimensional resources axes for each species. Practical difficulties with defining a niche stem from the problem of determining an infinite number of resource dimensions for a given species. Furthermore, many biotic dimensions are not amenable to linear measurement. Finally, the definition of a niche is a snap shot in time which ignores the fact that competition is a dynamic process. MacArthur (1968), suggested that a way of getting around these difficulties was to restrict the discussion of differences between species to one or two primary resource axes.

Armed with a rather pragmatic definition of ecological niche, ecologists then set themselves to address the question of whether two species in the same community could coexist. According to Hardin's (1960) definition, *complete competitors cannot coexist.* It soon became evident that a second major difficulty faced the competitive exclusion hypothesis. Plant ecologists pointed out that in a field of plants it was possible to find examples of many species living together in the same general habitat. Two main theoretical positions have been advanced and tested by ecologists in attempts to resolve this apparent contradiction (Krebs 1985).

Firstly, it is possible that competition is rare in nature, that species do not compete for limited resources and therefore are not excluded from potential niches by competitive interactions. A second view, holds that competition is common enough to be a guiding force in the evolution and development of species. In a third pseudo-view of the competitive exclusion principle, Hutchinson (1961) invoked non-equilibrium conditions as a possible explanation for the paradox of phytoplankton. The first and third of these two views does not provide much in the way of hope for the idea of Lotka-Volterra competition.

It has proven to be very difficult to test the first of these three hypotheses. Krebs (1985) suggests, that the best examples of competitive exclusion in nature come from introduction experiments used in attempts to control agricultural pests. Krebs (1985) cites the introduction of three parasitic wasps into California and points to the fact that each time a new wasp species was introduced, it displaced the one introduced before it. The problem is, these exclusions occurred during times of super-abundance of food and without any harm being done to two other parasites that attack the same food source. In other words, the mechanism of exclusion is obviously not density-dependent, not Lotka-Volterra, and not at all obvious (DeBach and Sunby 1963).

May and MacArthur (1972) made an attempt toward determining the extent of difference required to ensure coexistence in a varying environment. The co-authors assumed that a series of species compete for a resource which varies along a single dimension. This approach can be illustrated by assuming that each species has an individual resource utilisation function (fig 2.32). By further assuming that the shapes of the resource utilisation functions are the same for all species, then *the degree of competition can be measured by w/d, where w is the standard deviation of the resource utilisation function and d the spacing between species* (Maynard Smith 1974).

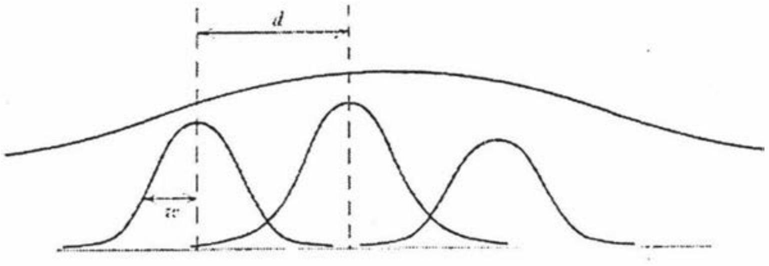


Fig 2.32 May and MacArthur's resource utilisation curves. The upper curve represents total resource availability. The lower curves represent resource utilisation functions for different species. The model assumes that species compete for a resource that varies along a single dimension (May and MacArthur 1972), (from Maynard Smith 1974).

In a system of equations of n species, which have densities $N_1 \ldots, N_i \ldots, N_n$, the equations (22 a, b) may be rewritten in abbreviated form

$$\frac{dN_i}{dt} = N_i\left[k_i - \sum_{j=1}^{n} \alpha_{ij} N_j\right]. \qquad (29)$$

The constant k_i represents the suitability of the environment for the ith species. The coefficients α_{ij} measure the degree of overlap in the resource utilisation functions of the ith and jth species. May and MacArthur (1972) discovered that when the k's and α's were treated as constants, as in the case of a uniform environment, it was found that component species could be packed indefinitely close and stable equilibrium still existed. The co-authors then tried introducing environmental variability into the models by putting

$$k_i = k_i + \gamma_i(t) \qquad (30)$$

where

k_i is a constant mean value

$\gamma_i(t)$ is Gaussian white noise with variance σ^2

This form of the model assumes a one dimensional resource utilisation and that any resource item taken by one species is not available for another species. The co-authors discovered that community stability is now dependent on a threshold value of d/w related to the noise level σ^2. Stability was also influenced by the diversity of the community. The importance of this model is that it has provided a theoretical basis upon which to begin a more detailed evaluation of community diversity. It also demonstrates, yet again, the limitations of the Lotka-Volterra formulation. The assumption of a stable environment is unlikely to be upheld for most natural communities.

In an attempt to approach the competitive exclusion principle from a different direction, MacArthur (1972) reasoned that if complete competitors cannot coexist, *how different do two species have to be in order to coexist in the same habitat?* This line of questioning led MacArthur to the idea of a identifying a resource utilisation threshold. A limiting similarity was defined by MacArthur, as the differences that species evolve to minimise the impact of competition and thus to permit coexistence. However, there appears to be no ecological constant that describes limiting similarity for all situations (Abrams 1975). Pianka (1976) and May (1976) provide well referenced discussions on the topics of niche theory, limiting similarity and resource utilisation theory.

There is a danger in amassing evidence and claiming that this proves that niches in natural communities are organised in ways consistent with Lotka-Volterra competition theory. The point is, at present it is not known how niches could be organised in communities that have no competitive pressures (Krebs 1985). A more recent trend in the study of limiting similarity has been the use of null models (Strong 1980) which advance the following type of question: how much overlap in niches would be expected if no competition occurred in nature? Even the use of null models has been met with controversy (Strong 1980, Quinn and Dunham 1983, Lomnicki 1988, Wiegert 1988, Mentis 1988) although, Krebs (1985) suggests that the root of this unrest is the *role of interspecific competition in natural communities.*

2.5.5 **Summary**

The empirical work reviewed in this section records attempts to test the predictions of the logistic and Lotka-Volterra competition equations in some way. It is now evident, that none of these laboratory based experimental results can be used to provide unquestionable empirical support for the existence of stable equilibrium behaviour. To evaluate these results better, each publication has been summarised and placed in one of five categories listed below:

(1) equilibrium centred single population behaviour
(2) unstable equilibrium single population behaviour
(3) non-equilibrium single population behaviour
(4) evidence of Lotka-Volterra competition
(5) evidence against Lotka-Volterra competition

These five categories sort the publications into single (1-3), versus multi species (4-5) experiments. Attempts to test the predictions of the logistic equation have yielded three types of results, providing empirical support for equilibria, unstable equilibria or non-equilibrium population behaviour. Category one is called equilibrium centred, because the data presented is unsuitable to assess long term stability. Finally, attempts to test the predictions of the Lotka-Volterra equations have yielded empirical evidence either for or against the theory of Lotka-Volterra competition.

This evaluation cannot be based upon numerical support for the discovery of a certain type of result, because the author has purposefully biased the results by trying to gather across the field representative publications. However, the results do provide an important empirical perspective which gauges the level of uncertainty involved in these models under a fundamental assumption of the existence of stable equilibrium behaviour.

The five categories and summaries of each relevant research publication reviewed in this section are listed below.

(1) Empirical Evidence of Equilibrium Behaviour in Single Populations

Pearl (1927) fitted national population data to the logistic model.

Carlson (1913) and Pearl (1927) undertook laboratory experiments on yeast populations and fit the data to the logistic model.

Gause (1932) fitted the logistic curve to yeast data.

(2) Empirical Evidence of Unstable equilibrium Behaviour for Single Populations

Park *et al.* (1964) undertook laboratory experiments with *Tribolium* and fitted data to the logistic model. Population declined after initial sigmoid rise.

Davidson (1938) used data recording the growth of Australian sheep populations. Population fluctuated after initial sigmoid rise.

Connell (1961) provided experimental data from coastal barnacle populations which appeared to support the predictions of the logistic model. Connell's results are probably an artefact of temporal and spatial resolution.

Birch (1953) undertook laboratory experiments with *Tribolium* and fitted the data to the logistic model. Population fluctuated after initial sigmoid rise. This form of unstable population behaviour may be due to complex social interactions.

(3) *Empirical Evidence of Non - equilibrium Behaviour for Single Populations*

Pearl (1927) fitted experimental data from *Drosophila* to the logistic curve. Sang (1950) refuted the validity of these results.

Jordon and Jacobs (1947) undertook laboratory experiments with populations of *Escherichia coli*. logistic behaviour is found to be temperature dependent.

Nicholson (1954) undertook laboratory experiments with populations of blowfly *(Lucilia)*. Constant food source produced periodic oscillatory behaviour.

May (1975) supported the experimental results of Nicholson by modelling Nicholson's blowfly data with the logistic equation based on a nine day time delay.

MacArthur (1972) attempted to use data from populations of ovenbird to support the existence of an inverse linear relationship between density and growth rate. Howeyer, MacArthur's fitting technique is questionable.

Smith (1963) advanced statistically sound empirical evidence in support of a nonlinear inverse relation between density and growth rate.

Ziswiler (1967) presented data on the logistic rise and unexplainable crash of a now extinct population of North American heath hen.

Aplet *et al.* (1988) found evidence for both equilibrium and non-equilibrium behaviour in a single community of xeric *Picea* and *Abies* forest of the central Rockies.

Hallam and Clark (1981) identified inconsistencies in the behaviour of the non-autonomous logistic equation and advanced a four parameter logistic which eliminated these problems.

Turchin (1993) suggested that any first-order equation will not be able to capture the dynamics of cycles and chaos in natural populations and communities.

Whitteman *et al.* (1990) advanced empirical evidence which supported the claims of Turchin (1993).

Hassell *et al.* (1976) the paper most often cited as evidence for the rarity of complex dynamics in nature, has its claims based on the behaviour of a one dimensional model.

(4) *Empirical Evidence Supporting Community Behaviour as Predicted by the Lotka-Volterra Competition Equations.*

Istock (1977) undertook experimental studies with interacting water boatmen and discovered evidence which supported the predictions of the Lotka-Volterra formulation in most cases. Competition intensity is not constant.

Gause (1932) determined coefficients of interaction for two species of yeast based on fitted population data and ethyl-alcohol production.

Crombie (1945) demonstrated coexistence of two species of grain beetle which have differing food preferences during adult and larval developmental stages.

(5) *Empirical Evidence Not Supporting Community Behaviour as Predicted by the Lotka-Volterra Competition Equations.*

Dorschner *et al.* (1987) advance simulation studies and analytical evidence to highlight a predictive error in the indeterminate case of the Lotka-Volterra equations. The authors show that indeterminate outcomes may be sensitive to certain ranges of values for the intrinsic growth rate parameter (r).

Ayala (1969) discovered that different forms of density-dependence are required in order to improve the fit of interacting species of *Drosophila.* The theta logistic competition equation was developed by Gilpin and Ayala (1973).

Gilpin and Justice (1972) pointed out that Ayala's results with *Drosophila* are suggestive of inadequacies with the Lotka-Volterra formulation.

Birch (1953) discovered that the outcome of interactions between grain beetles was dependent on environmental temperature - a factor not included in the Lotka-Volterra formulation.

Park (1948) noted that the outcome of interaction between interacting species of *Tribolium* was probabilistic and this was especially the case at intermediate climatic conditions.

Slobodkin (1964) demonstrated that the coexistence of two species of hydra was mediated by predation.

Gause (1935) demonstrated coexistence of two species of *Paramecium* in a yeast suspension contained in a single test tube. Sang (1950) points out that yeast is not a constant food supply - an assumption of the logistic equation.

2.5.6 *Conclusions*

Most of the models used in theoretical ecology involve numerous assumptions and approximations. The present review and summary indicates that in the case of the logistic and Lotka-Volterra competition equations, empirical evidence indicates that many of these models have assumptions and linear approximations which are violated to varying degrees.

While the present results do not support unbiased numerical conclusions, the present author has not been able to find published evidence supporting the existence of a locally or globally stable single population equilibrium, as predicted by the logistic model. This fact appears to be consistent with Connell and Sousa (1983) who question whether any ecological community yet studied has conclusively been shown to be stable. Silvertown (1987) claims there is evidence that meets the rigour of Connell and Sousa's (1983) stability criteria and he questions whether stability is as rare as the co-authors claim.

Three examples of apparent equilibrium behaviour are cited in category (1), (Pearl 1927, Carlson 1913, Gause 1932). The brevity of the data sets prevents conclusions being drawn concerning the long term stability of this equilibrium. Aplet *et al.* (1988), also report evidence of equilibrium behaviour, but their results are observationally based and involve no behavioural modelling work.

The four publications placed in category (2), provide evidence for long term equilibrium behaviour in which instabilities are evident (Park *et al.* 1964, Davidson 1938, Connell 1961, Birch 1953). The likelihood of long term instabilities in the data of Connell (1961), is inferred from the highly disturbed nature of the intertidal marine environment.

In category (3), four publications (Jordon and Jacobs 1947, Nicholson 1954, May 1975, Ziswiler 1967), present data and modelling evidence for the existence of distinctly non-equilibrium behaviour. Pearl (1927), also belongs in this category by virtue of Sang's (1950) refutation of his research method. It seems quite likely that Pearl's results would have been quite different had he systematised his counting procedure and used a truly constant food source. These conclusions are strongly supported by the results of Nicholson (1954). Again, Aplet *et al.* (1988) have observational evidence for non-equilibrium behaviour.

MacArthur (1972) and Smith (1963), present evidence concerning the adequacy or inadequacy (depending on how MacArthur's results are viewed), of the assumption of inverse linear density-dependency. Ayala (1969) and Gilpin and Ayala (1973), Gilpin and Justice (1972), advance various lines of evidence which suggest that inverse linear density-dependence is inadequate for the Lotka-Volterra competition model, in some cases.

A final four publications are cited in category (3), (Hallam and Clark 1981, Turchin 1993, Witteman *et al.* 1990, and Hassell *et al.* 1976), which present evidence concerning inadequacies in the non-autonomous logistic and predictive capability of first-order equations. The use of first-order models is clearly of heuristic value as is evidenced by the wealth of empirical research and theoretical developments that have come from the logistic and Lotka-Volterra models.

Most of the published examples of single population behaviour reviewed in this section have turned up unexpected behaviour. These anomalies are suggestive of fundamental inadequacies in the assumptions and linear approximations of the logistic model. Evidence appears to exist for the presence of equilibrium points in the behaviour of some laboratory and natural populations. In most cases, intraspecific competition is assumed to be the mechanism responsible for this behaviour. Furthermore, it may be very difficult to test for the existence of intraspecific competition (Wiens 1977, Roughgarden 1983). Evidence in favour of local or global stability is clearly wanting.

As mentioned earlier, the Lotka-Volterra competition equations suffer from all of the inadequacies of the underlying logistic. These equations also have greater degrees of freedom and are capable of manifesting dynamics which are in advance of those predicted by the logistic. In category (4), Istock (1977), Gause (1932) and Crombie (1945), all present empirical evidence supporting the predictions of the Lotka-Volterra competition model.

However, in category (5), Birch (1953), Park (1948), Slobodkin (1964) and Gause (1935), present evidence which essentially contradicts the predictions of the Lotka-Volterra competition model. Birch (1953), demonstrates that competitive interactions can be temperature mediated. Park (1948), demonstrates that interactive outcomes can be probabilistic. Slobodkin (1964), demonstrates that coexistence can be predator mediated. Gause's results must be questioned on the basis of Sang (1950).

Also in category (5), Dorschner *et al.* (1987), Ayala (1969), Gilpin and Ayala (1973), Gilpin and Justice (1972), identify further inadequacies related to nonlinear density-dependency and the outcome of interaction being dependent on certain values of the intrinsic growth rate in the indeterminate case. To provide a more effective overview of these results each major assumption of these two models and its empirical invalidation is listed in Table 2.4.

As was demonstrated in Chapter one, there is a number of other lines of research evidence which can be drawn upon to support the information in Table 2.4. However, the present discussion has been limited to the logistic and Lotka-Volterra competition equations which provide sufficient evidence concerning the inadequacy of many of the assumptions and approximations of these models.

Some of the assumptions listed above are generalised for the sake of space and could be expanded upon. For example, spatial independency implies that: crowding affects all individuals equally, individuals are homogeneously distributed and equilibrium conditions are independent of observational scale.

Assumption or Approximation	Assumption or approximation Violated ?	Published Authority
inverse linear density - dependency	nonlinearities	Smith 1963, Ayala 1969, Gilpin and Ayala 1973, Gilpin and Justice 1972
growth rate dependency	nonlinearities	Dorschner *et al.* 1987, Hallam and Clark 1981
environmental independency (*i.e.* globally stable)	disturbance drives instabilities	Davidson 1938, Jordon and Jacobs 1947, Ziswiler 1967, Birch 1953, Park 1948, Slobodkin 1964, May and MacArthur 1972
invariant equilibria	nonlinearities	Boyce and Daley 1980, Hutchinson 1958, Nicholson 1954, May 1975
dimensional stability	unstable above one dimension	Turchin 1993 Witteman *et al.* 1990
dynamics captured using first-order equations	instabilities are likely for multi species systems	Turchin 1993 Witteman *et al.* 1990
regulated by density feedback, (*i.e.* competition) social behaviour is not a determining factor in community behaviour	disturbance moderated and driven, (biotic disturbance includes social behaviour	Davidson 1938, Jordon and Jacobs 1947, Ziswiler 1967, Birch 1953, Park 1948, Slobodkin 1964, May and MacArthur 1972
migration, emigration and spatial independency	spatially dependent	Hallam and Clark 1981, Ziswiler 1967, Gause 1935
deterministic	probabilistic shochasticity	Park 1948, Aplet *et al.* 1988, Turchin 1993, Davidson 1938
competition intensity is invariant	equilibria and intrinsic growth rate are not invariant	Boyce and Daley 1980, Hutchinson 1958, Nicholson 1954, May 1975 Dorschner *et al.* 1987, Hallam and Clark 1981
historical independency	time lags	Hutchinson 1948
independent of genetic variation	interactive outcomes dependent of genetic variation	Park (1948)

Table 2.4 Summary table of the results of experimental testing of hypotheses (model constructs) derived from the equilibrium paradigm.

Inverse linear density-dependency implies that the growth rate is density-dependent even at the lowest densities. It may be more reasonable to suppose that there is a threshold density below which individuals do not interfere with each other (Pielou 1977).

An invariant growth rate assumes that there is a stable age distribution and that females in a sexually reproducing population always find mates, even when the density is low (Pielou 1977). The assumption of a stable age distribution rests upon Lotka (1922), who concluded that a population growing geometrically develops a stable age distribution.

There is also a number of assumptions regarding the instantaneous nature of regeneration, resource supply and the outcome of competitive interactions. Both regeneration and resource supply (reaction) time lags have been adapted for the logistic equation (Hutchinson 1948, Wangersky and Cunningham 1956, Wangersky 1978).

Finally, the Lotka-Volterra competition model assumes that the competition coefficients (α and β) are invariant with respect to N_1 and N_2. It is unlikely this assumption is upheld in every case as is demonstrated by Istock (1977).

The competitive exclusion principle has been a major theoretical development of the Lotka-Volterra competition equations which has proven very difficult to substantiate. Furthermore, Krebs (1985) cites examples of exclusions which have occurred in the existence of a super-abundant food supply. May and MacArthur (1972) discovered that closely packed species coexisted in a stable environment. The same result could not be produced when threshold levels of environmental instability were introduced. MacArthur's (1972) idea of limiting similarity and Strong's null models have also largely failed to find conclusive evidence of interspecific competitive exclusion.

As noted earlier, Wiens (1977) contends that competition may be rare for some populations because of high environmental variability. Such populations exist well below any carrying capacity and are only affected by competition during times of infrequent food shortage. In essence, the same hypothesis was invoked by Hutchinson (1958) to account for the paradox of plankton. Both explanations are distinctly non-equilibrium in nature. At present, this appears to be the most plausible explanation, a position that has been argued by Strong (1984, 1986).

With reference to the present discussion, competitive exclusion provides further uncertainty concerning the validity of Lotka-Volterra interspecific competition. If the non-equilibrium hypotheses of Hutchinson (1958) and Wiens (1977) are correct, then the intraspecific competition mechanism of the logistic equation is also invalidated in its initial form. While the details of the competition controversy will continue to be debated, it now seems quite clear, that initial assumptions concerning the existence and intensity of competition are probably invalid in the case of some, if not most, natural populations. Furthermore, it now seems likely that competition intensity is closely related to the degree of environmental stochasticity present in a given habitat (Wiens 1977).

These conclusions acknowledge the apparent existence of equilibria in some cases. Exceptions to what appears to be a non-equilibrium rule may be explained by the following:

(i) It is assumed that intraspecific competition is the biotic mechanism primarily responsible for the form of the logistic curve. The existence of intraspecific competition needs to be clearly demonstrated. Presumably, biotic or abiotic disturbance is also capable of driving short term logistic growth.

(ii) Apparent equilibrium behaviour must be demonstrated across a range of different scales. In the absence of testing of this nature, it can always be claimed that apparent equilibrium behaviour is simply an artefact of temporal and spatial scale.

(iii) Apparent equilibrium behaviour can be driven by non-equilibrium processes. It now seems evident that biotic and abiotic disturbance plays a major role in community organisation and represents what this author considers to be the greatest failing of the logistic and Lotka-Volterra competition equations.

Points (i) - (iii) above are supported by Facelli and Pickett (1990) who contend that good correspondence between a model and field data constitutes a poor test of a model, if its assumptions remain untested. Perhaps some of the great achievements of the logistic and Lotka-Volterra equations, are the discoveries that have resulted from attempts to test the assumptions of these models.

Having identified invalid assumptions, the difficulty then remains of trying to identify just which combination of neglected complications is causing the problem. Pielou (1977) maintains that the skill of a good modeller lies in being able to distinguish experimentally between important and unimportant causal variables. In a word of caution, Pielou suggests that good correspondence between predicted and observed events *cannot be taken to imply that the model's simplifying assumptions are reasonable in the sense that neglected complications are indeed negligible in their effects* (Pielou 1977).

The conclusion of the logistic Era in ecology appears to have been characterised by a realisation that many previously neglected complications, such as nonlinear density-dependency, growth rate dependency, environmental independency, invariant equilibria, dimensional stability, the adequacy of first-order models, spatial independency, determinism, invariant competition intensity and historical independency, *apparently matter a lot.*

One possible answer to these deficiencies is to add greater complexity to the existing formulations of the logistic and Lotka-Volterra competition models. There are a number of difficulties in this approach. One problem, is in determining which simplifying assumptions are *too simple*. Pielou (1977) points out that obviously *no model can allow for all conceivable complications; if it did, it would (by definition) cease to be a model*. Furthermore, attempts to improve the realism of a model accomplish little, if they remove one objectionable assumption, only to replace it with a much *larger number of other assumptions; and any assumption in this context is merely a guess, perhaps a wild one* (Pielou 1977).

In adding greater complexity to a model, the degree and nature of a violated assumption needs to be considered. Some simplifying assumptions demarcate paradigm boundaries. If this is the case, then the addition of greater complexity to an existing model amounts to a paradigm shift. Some of the assumptions and approximations of the logistic and Lotka-Volterra models demarcate the equilibrium / non-equilibrium boundary in ecology. To replace these assumptions with greater complexity is effectively to construct a non-equilibrium model.

To illustrate this point, the equilibrium paradigm portrays stable equilibrium conditions[1] as a tension maintained between biotic density feedback mechanisms and exogenous disturbance. In other words, the equilibrium paradigm accepts the existence of exogenous disturbance, but not as a regulatory or driving mechanism (Clements 1928).

If the addition of exogenous disturbance is required in the logistic or Lotka-Volterra competition equations in order to predict the behaviour of a natural population or community, the product of this combination is essentially a non-equilibrium model. The only exception to this condition would be if the level of the disturbance is low enough, to enable the density-feedback mechanism to dominate as the sole regulatory force.

Non-equilibrium behaviour is primarily driven by abiotic and biotic forms for disturbance. For this reason, the illustration used above generalises a range of non-equilibrium scenarios.

DeAngelis *et al.* (1985), DeAngelis and Waterhouse (1987) argue that during the 1970s theoretical ecology took a major paradigm shift. The logistic era has come to an end. The present non-equilibrium trend in ecological modelling appears to indicate that theoretical ecologists (in general) see little point in using greater complexity to improve equilibrium models. DeAngelis and Waterhouse (1987) claim that dissatisfaction with the equilibrium paradigm *does not hinge on the mere question of system stability, but on whether it is valid to define the existence of an equilibrium state at all, stable or unstable.*

Where does this leave the logistic and Lotka-Volterra competition models? In an increasingly pluralistic discipline such as ecology this question is very hard to answer and time will doubtless be the final test of any attempted explanations. Clearly, with all of the research evidence presented in the previous two chapters it is very difficult to justify the use of these models in their initial formulations.

Very few of the many laboratory populations that have been modelled on the logistic or Lotka-Volterra competition equations manifest predicted behaviour. If it is not possible to generate stable equilibrium behaviour under the controlled conditions of a laboratory, then it must be at least one hundred times less likely that this behaviour will ever be found in natural populations and communities, affected by abiotic disturbance.

Not all natural populations and communities have been tested by the logistic and Lotka-Volterra models. The controversy over density-dependent competition is yet to be resolved. Hypotheses based on alternative mechanisms and applied to differing temporal and spatial scales have yet to be adequately tested. One reason for this has been the expense and difficulties of obtaining long term data (Pielou 1974). As these difficulties are overcome, the logistic and Lotka-Volterra competition equations will doubtless be used again and again. However, the primary justification for the application of these models must be different and should not express the unchallenged assumption that equilibrium behaviour is the basis of community organisation.

In the light of historic research evidence, theoretical developments and current trends in ecological modelling, future research should seek to test the behaviour of these equations across temporal, spatial, mechanistic and paradigm boundaries.

Finally, the logistic and Lotka-Volterra competition equations provide an important benchmark for characterising equilibrium behaviour and exploring deviations from it. They have provided a wealth of scientific discovery and will doubtless continue to do so as they are used as instructive tools with due regard given to their mechanistic and behavioural limitations.

Palynologists have access to a wealth of long term data from plant communities that has traditionally been used for descriptive and narrative purposes. Recently, a number of palynologists have begun to use their absolute pollen data for ecological modelling research. Some of this research has involved the use of the logistic and Lotka-Volterra competition equations. This work will be evaluated more fully in Chapter four.

2.6 Working Hypotheses - the Equilibrium Paradigm

The purpose of this chapter has been to provide a detailed evaluation of the present status of equilibrium theory in ecology. Much of this review has focused upon the mathematical, behavioural, ecological and experimental performance of the logistic and Lotka-Volterra equations. Both of these models, have been extensively tested and found to be supported by unsound simplifying assumptions. Where does this leave the equilibrium paradigm?

Once again, this is a very difficult question to answer and one of the primary reasons for this is the increasing influence of pluralism (McIntosh 1987) in ecology - the existence and acceptance of alternative theoretical positions. Most scientists would agree that pluralism is to be encouraged in any academic or scientific discipline. However in ecology, pluralism appears to result from the absence of a single body of core theory that may be recognised as a central, unifying, theoretical standard and guiding paradigm. In this case, pluralism is not so helpful.

Amid such a pluralistic atmosphere it is important to be objective, thorough and systematic in evaluating theory, while theoretical positions need to be cautiously stated. Furthermore, in a field as vast as ecology, any stated position can only reflect the educated opinion and limited knowledge of the author from whom it comes. The opinion of the present author, reflects the weight of theoretical, historic and empirical evidence presented in the first three chapters of this thesis. That opinion is that it appears that the unified sentiments expressed by Reddingius (1971), Caswell (1978), Murdoch (1979), Connell and Sousa (1983) and Wiens (1984) questioning the validity of defining the existence of an equilibrium state in natural systems - stable or unstable, is probably quite correct.

(i) Biotic mechanisms undoubtedly play a part, some of the time, in the regulation of populations and communities.

(ii) It is now patently clear however, that abiotic disturbance and biotic instabilities play a much greater role than has been historically recognised by early ecologists and natural historians.

(iii) As Sousa (1984a) has suggested, the interplay between biotic and abiotic causal agents may account for *a major portion of the organisation and spatial patterning of natural communities.*

(iv) Community organisation is vast, diverse, complex and involves intricate mechanisms. It may be quite unrealistic to expect that the behaviour of such complex systems will ever be captured with mathematical models of the dimensions, determinism and mechanistic simplicity of the logistic and Lotka-Volterra competition models.

The present study provides a number of opportunities to test the strength of these predictions by means of hypothetico-deductive research methodology (Mentis 1988). The basis of this methodology is developed more fully in Chapter four. Briefly, experimentally testing the strength of a hypothesis derived from base theory is a problem of deduction that involves two different methodological problems. Firstly, validation (Loehle 1983) involves the use of *a priori* refutation criteria for evaluating the predictive power of a working hypothesis (or model formulation). This is usually accomplished with various curve fitting techniques.

Secondly, validation alone is not sufficient to test the explanatory power of a working hypothesis, this can only be accomplished by strong inference (Platt 1964) which involves the use of competing hypothesis. Alternative theories might be genuine attempts at explanation or one might be a null hypothesis (Strong 1980). Competitive models are rejected on the grounds of *inferior explanatory power, conflict with background theory and lack of internal consistency and parsimony* (Mentis 1988).

Evaluation of the predictions of the equilibrium paradigm in this chapter leads to the following hypotheses.

1. communities are closed systems,
2. present behaviour is influenced by past events (time lags),
3. patches are of homogenous composition,
4. landscapes are composed of fundamental units,
5. biotic feedback is strong and frequent,
6. alternative stabilising mechanisms are not required in the presence of strong biotic coupling,
7. community behaviour is non-transient and stable,
8. community behaviour is not driven by abiotic disturbance,
9. community behaviour is deterministic,
10. community behaviour is not subject to biotic instabilities,
11. mechanisms responsible for population behaviour are complex and involve nonlinearities,
12. because of global stability, community behaviour exists in the high density region,
13. biotic feedback is adequately described by a linear relationship,
14. a stable equilibrium is the result of strong negative feedback,
15. predation is not an major determinant of long term population and community behaviour,
16. competition is the major determinant of community behaviour
17. social behaviour is not an important determinant of long term population and community behaviour.

In order for the predictive and explanatory power of these hypotheses to be tested, they must be given a mathematical form - in accordance with hypothetico-deductive methodology. While there are many equilibrium model formulations to choose from, the logistic and coupled logistic are central to the present line of discussion and will be used for this reason. These two models capture much of the reality of the equilibrium paradigm as described in the seventeen hypotheses listed above.

In some respects these seventeen hypotheses are generalised and do not represent every possibility. Not every stated hypothesis can be tested within the limitations of the present study. Despite this fact, it is important to keep the landscape view of a theoretical position in mind if sound conclusions are to be drawn from individual parts of a larger body of theory. The alternative non-equilibrium hypotheses and chosen model formulation will stated at the completion of Chapter three. The properties and form of the equilibrium and non-equilibrium model constructs to be tested in this research will be outlined toward the end of Chapter four.

In summary, these hypotheses have both predictive and explanatory qualities which must be tested using two distinctly different experimental approaches. The predictive capability of the models will be tested by heuristic evaluation (the refutation criteria) of the behavioural performance of the model constructs compared with field data derived from absolute fossil pollen data. The explanatory power of the models will be tested by evaluation of predictive capability, explanatory superiority, harmony with background theory, internal consistency and parsimony. This twofold approach forms the basis of the modelling framework[1] adopted in this project, outlined more fully in Chapter four.

2.7 Chapter Summary

Chapter two has covered three topics of the much larger theme of equilibrium behaviour, set forth in Chapters two and three. Community behaviour has traditionally focused on two contending models and is but one topic, of the much larger theme of community organisation as presented in Chapter one. In summary, the purpose of this chapter has been to explore the historical, ecological and mathematical significance of equilibrium theory. Furthermore, this discussion has centred upon the super-model of DeAngelis and Waterhouse (1987) which was introduced earlier in the chapter.

This super-model is an attempt to provide a portrayal of the current state of community behavioural theory in ecology. The model defines the existence of a classical equilibrium state, as a benchmark from which two forms of deviant (non-equilibrium) behaviour have been identified (biotic instability and stochastic domination). The long term persistence of these two non-equilibrium states, suggests that these systems have complex compensatory mechanisms which moderate the adverse affects of biotic instabilities and stochastic domination.

The conceptual precursor to the equilibrium paradigm in ecology is believed to be the balance of nature and divine providence premises which have dominated human views of nature since antiquity. The first major theoretical challenge to the divine providence premise came with Darwin's *Origin of Species* (1859). Darwin's theory of evolution did not overturn the concept of balance *in* nature; it provided an alternative explanation for what had historically been viewed as the supernatural or providential regulation of nature.

In his monoclimax theory of succession, Clements (1916) drew heavily upon the prevailing theory of his time, as Darwin had done almost a century before. Not surprisingly, the succession theory developed by Clements recognised the existence of a stable equilibrium community, of fundamental unit composition, with emergent (organism like) properties and self regulated by homeostatic biotic mechanisms (Clements 1928).

The historic balance *in* nature theory lived on in Clements' super-organism, claimed by Simberloff (1980), to be ecology's first paradigm. Just as Darwin's theory of evolution had done almost a century before, Clements' theory of succession met with a storm of opposition. This opposition has effectively catalysed key theoretical controversies and developments; instrumental in the demise of balance of nature (equilibrium) theory in ecology.

The influence of an ecological paradigm presuming a stable equilibrium state permeated ecology and led to a host of other theoretical developments based on the assumption of equilibrium behaviour. In this chapter, the empirical testing of two distinctly equilibrium centred ecological models is presented to demonstrate, how the claims of the equilibrium paradigm have been invalidated. The logistic and Lotka-Volterra models, are based on density-dependent feedback and interspecific biotic mechanisms. The models are distinctly equilibrium centred and have been extensively tested with laboratory and to a lesser degree, field data.

The evaluation of published research reveals that many of the assumptions of these two models are empirically flawed. In researching these historical records it has not been possible to find a single example of laboratory or field data that supports the fundamental predictions of the logistic model - long term stable equilibrium behaviour.

The sentiments of Reddingius (1971), Caswell (1978), Murdoch (1979), Connell and Sousa (1983) and Wiens (1984), appear to be symptomatic of feelings shared by a growing number of ecologists (ref. DeAngelis and Waterhouse 1987). These ecologists have abandoned the classical equilibrium paradigm to explore the behaviour of what appears to be a more promising field of theoretical labour - the non-equilibrium paradigm.

The last bastion of providential ecology has finally fallen.

A final objective of this chapter has been to explore the mathematical significance of equilibrium theory. The difficulties of defining stable equilibrium behaviour, using conventional descriptive terms common to mathematics and ecology has been discussed. Mathematics is, by far, a more powerful, conceptually rich and explicit language, that provides many wonderful insights into the possible workings of community organisation and behaviour.

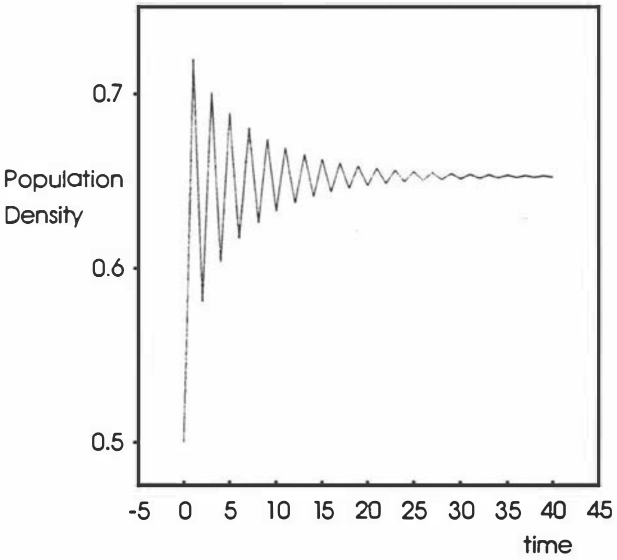
During this discussion, quantitative mathematical techniques have been used with a single population model, to illustrate just how an equilibrium point is mathematically defined for an ecological system. In relating the existence of an equilibrium point to ecological theory, the question of why an equilibrium point exists has been explored. To answer this question, the logistic equation has been rewritten in terms of deviations from equilibrium density. This analysis clearly identifies the existence and nature of the density-dependent feedback mechanism responsible for equilibrium behaviour in these models.

The local stability of an equilibrium state (for a single population), has been evaluated quantitatively using partial derivatives and linear approximation techniques. These techniques have been illustrated using the discrete logistic equation. The behaviour of this simple difference equation was highlighted by Robert May (1976) and will be more fully considered in Chapter three.

The mathematical treatment of community equilibria is both conceptually and mathematically more difficult to accomplish using quantitative techniques. This is especially the case in models involving nonlinearities. Mathematicians have developed a number of qualitative approaches, which can be combined with the speed and power of modern computers, to provide an intuitive and conceptually powerful methodology to characterise and portray community equilibria and stability.

The qualitative and quantitative techniques presented in this chapter will be used later in this thesis to model and evaluate the behaviour of field data based on the hypotheses advanced in Chapters two and three.

The main conclusions of this chapter are drawn from historical, theoretical and experimental evidence. This evidence provides explanation for the major theoretical shift that has occurred in ecology during the 1970s, away from the traditional equilibrium paradigm to a newer non-equilibrium alternative. The hypotheses advanced in this chapter are statements of the equilibrium paradigm, the predictions and explanatory power of which will be tested according to hypothetico-deductive methodology.



Community Behaviour Part Two ~ the Non - equilibrium Paradigm

The fascinating behaviour of the discrete logistic equation first came to public attention in a classic publication by May (1976). The stability of one of the steady states of this equation is conditional on the growth rate parameter (r). Critical changes in the value of (r) over certain regions of parameter space demarcate thresholds of abrupt changes in the qualitative behaviour of the equation, or the system that it models.

The behaviour of this simple difference equation drew the attention of ecologists to two important insights. Firstly, the simplest of ecological systems appear to be capable of manifesting a diverse spectrum of dynamic behaviour. More importantly, the nature of this behaviour is distinctly non-equilibrium and driven by instabilities in the biotic mechanisms of the system.

Chapter three

Community Behaviour Part Two ~ the Non-equilibrium Paradigm

3.1 Introduction

Chapter three is the final chapter in this thesis on the theory of community organisation. The purpose of this chapter is to explore the historical, ecological and mathematical significance of the non-equilibrium model. These objectives will be achieved by focusing on three main topics. Firstly, in Chapter two, the two principal causes of non-equilibrium behaviour identified by DeAngelis and Waterhouse (1987) were introduced. In this chapter, these two types of behaviour will be more fully evaluated. Secondly, mechanisms that work to restabilise and moderate departures from equilibrium behaviour will be explored. Finally, the question of spatial scale will be discussed with an aim to understanding whether non-equilibrium behaviour at a local scale has emergent equilibrium properties at the landscape level of organisation.

3.2 History

In Chapter two, historic and empirical evidence was evaluated in order to identify weaknesses in the experimental results and assumptions of two of ecology's most tested equilibrium models. Evaluation of this research has raised serious questions regarding the adequacy of first-order deterministic equilibrium models to explain the complex dynamics of natural communities (Pollard 1981, Turchin 1993). The post 1970s trend in non-equilibrium modelling in ecology was partly an extension of insights gained during the decades in which ecologists developed and tested equilibrium models. More importantly, the early 1970s was a time of watershed publications which advanced two important theoretical positions that catalysed the non-equilibrium era in ecology.

Ecologists gradually realised that density-dependent feedback may not be adequate to damp out every form of abiotic or biotic disturbance. Furthermore, the traditional concept of density-feedback may be quite inadequate to explain more complex forms of regulation in real populations and communities. With these realisations, ecologists began to look for other compensatory mechanisms that would act to restabilise a disturbed equilibrium state. It was generally assumed by most ecologists that, if equilibrium models could be made more complex (diverse) by including a larger number of species, the systems behaviour would be stable. The stability/diversity controversy has a long history in ecology (MacArthur 1955, Preston 1969, Lewontin 1969, Orians 1975, Margalef 1975, Whittaker 1975, May 1973, 1975, 1979, McNaughton 1977, King and Pimm 1983, Pimm 1984).

May (1972) demonstrated that in randomly assembled linear ecosystem models, this long held assumption was quite misleading. For a randomly assembled model of a multi-species community in which the population of each species would by itself be stable, ... *too rich a web connectance, ... or too large an average interaction strength, ... leads to instability ... the larger the number of species, the more pronounced the effect* (May 1972). Zaret (1982), provided empirical support for May's diversity/instability hypothesis.

The publication of May in 1972 drew criticism from Roberts (1974), who claimed that May's ecosystem model was invalidated because of unfeasible negative equilibrium values for some populations. Despite this refutation, the implications of May's discovery could not be ignored. May's results made *theoretical ecologists acutely aware that there are real difficulties with the idea of the ecosystem as a balance of interacting species* (DeAngelis and Waterhouse 1987).

In a second watershed publication, May (1974) drew the attention of ecologists to another sobering fact. Because the simplest of nonlinear equations were capable of giving rise to chaotic and therefore intrinsically unpredictable behaviour, the hope *of deriving simple, general laws for systems in which non linearity is the norm must be illusory* (Judson 1994).

May's (1974) observations of chaotic behaviour in the discrete logistic equation suggested to theoretical ecologists that simple principles in ecology will be the exception, accidents of history are important, apparently random fluctuations in natural communities may be due to deterministic chaos and that chaotic systems are inherently unpredictable (Judson 1994, Berryman and Millstein 1989, DeAngelis and Waterhouse 1987).

These two publications of May are important landmarks in the shift of theoretical ecology from an equilibrium to a non-equilibrium model of community organisation. The 1972 publication of May provided a decisive theoretical answer to the long standing assumption that increased species diversity would stabilise community functional properties and, by virtue of this, their behaviour (McNaughton 1977). Zaret (1982) supported these conclusions with empirical evidence.

The equilibrium paradigm had largely rested upon the axiom that equilibrium conditions involved a balance of interacting species. If the very functional property of a community that was supposed to regulate population behaviour (at equilibrium), instead gave rise to internal instabilities, ecologists saw little hope for the concept of balance in nature.

Furthermore, in the equilibrium paradigm, biotic interactions were thought to be responsible for damping out the adverse affects of environmental stochasticity. If this regulatory mechanism was itself subject to instability, a community would be vulnerable to stochastic domination in the absence of other more effective compensatory mechanisms.

Finally, the 1974 publication of May further confirmed the existence of biotic instability in even the simplest nonlinear difference equations. If natural communities are subject to internal biotic instabilities that give rise to chaotic behaviour, then again, the functional simplicity of the equilibrium paradigm is flawed. Simple principles will be the exception, accidents of history will be important, apparently random fluctuations in natural communities may be due to deterministic chaos which is inherently unpredictable.

The theoretical positions advanced by May (1972, 1974) are suggestive of two principal forms of non-equilibrium behaviour. In the super-model of DeAngelis and Waterhouse (1987) the co-authors suggest that unstably interactive communities are dominated by internal biotic instabilities. Equilibrium points may exist for such systems, but these points are not stable. Species extinctions may result, or *violent limit cycle oscillations drive the system away from the equilibrium between populations.* The co-authors also refer to this type of community behaviour as *biotic feedback instability.* The interactive forces between component populations are too strong for the system to survive in a stable condition.

Chaotic behaviour of this kind requires positive feedback loops and/or unstable (over compensatory) negative feedback loops. Since negative feedback reactions (like density-dependence) always induce asymptotic stability, over-compensation can only occur if time lags are present in the negative feedback loops (Berryman and Millstein 1989).

In weakly interactive communities, *stochastic fluctuations are likely to nock populations away from average values.* In communities dominated by tochastic fluctuations, the disturbing forces are *as strong as or stronger than any omeostatic biotic forces between the populations acting to restore them* DeAngelis and Waterhouse 1987). The co-authors also refer to this situation *as eing stochastically dominated.*

In fig 2.8 (Chapter two), the two non-equilibrium community types nentioned above are shown as points on a continuous spectrum - departures rom classical equilibrium behaviour. The co-authors suggest that the spectrum hould be *bent around representing the fact that both stochastic dominance and iotic feedback instability are associated with reduction in the stability of the ystem. Systems that contain aspects of both stochastic effects and biotic interaction can be placed in the semi-enclosed hatched area.*

In the next two sections, the ecological and mathematical significance of the two non-equilibrium community types defined above will be explored. This discussion will draw upon published research in order to illustrate the types of approaches ecological modellers have used in exploring the mechanisms, assumptions and behaviour of non-equilibrium models.

3.3 Unstably Interactive Community Behaviour

DeAngelis and Waterhouse (1987) suggest that when the *earliest kinetic equations representing population interactions, the Lotka-Volterra equations, were developed in the 1920s, it was quickly recognised that such systems easily give rise to instabilities when certain biotic feedbacks are increased sufficiently.* As pointed out by the co-authors, competitive exclusion is itself a form of biotic instability in the system. After decades of observation and experimentation it is now clear that natural populations manifest a fascinating range of dynamic behaviours. Some populations have been observed to fluctuate apparently randomly over small or large amplitudes while others appear to cycle in a regular manner. Lawton (1987), suggests that there are two *ways of reproducing this range of behaviour in mathematical models.*

The first option is to vary the model by incorporating structural components like host refuges and increased species diversity. Changes in structural complexity have been observed to alter the dynamics of populations and this is currently an active field of research. For example, the adverse affects of non-equilibrium behaviour may be moderated by structural elements in a community. This hypothesis is explored more fully later in this chapter.

In a second option, model behaviour may be changed by holding structure constant and varying parameter values. One of the simplest ways of demonstrating this phenomenon is provided by the time-lagged logistic equation which describes the growth of a single species population. While the structure of this model remains constant, a diverse spectrum of behaviour can be generated by varying the time-lag parameter (Wangersky and Cunningham 1956, Cunningham 1954, Cook 1965).

In its unmodified form, the logistic equation assumes an instantaneous reaction time between changes in density and changes in the growth rate. Wangersky (1987) referred to this assumption as a logical absurdity. Cunningham (1954), found that a reaction time delay destabilises the behaviour of this equation. The delay is incorporated into the density-dependent feedback term $(K-N)/K$ in the following way

$$\frac{dN}{dt} = rN\left(\frac{K-N_{t-w}}{K}\right), \qquad (31)$$

where

w is the reaction time delay

t is time

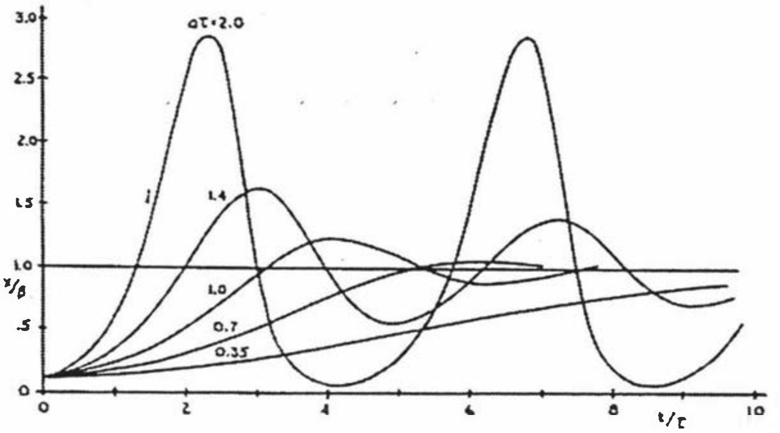


Fig 3.1 The behaviour of the logistic Model with increasing time delays. Cunningham (1954) found that, in general, longer time delays produce greater numerical instability (from Cunningham 1954).

Cunningham (1954), discovered that the behaviour of the well known logistic equation with reaction time delay manifested cyclic behaviour with the amplitude of each wave determined by the size of the time delay (fig 3.1). The model was capable of manifesting a stable population when

$\left(0 < rT < e^{-1}\right)$, or damped oscillations when

$\left(e^{-1} < rT < \pi/2\right)$, or stable limit cycles when

$\left(rT > \pi/2\right)$.

Lawton (1987) suggests that *even the most sceptical field naturalist would probably concede that structural changes to species interactions are likely to alter population behaviour. But what evidence is there that simply altering parameter values under structurally constant conditions changes the behaviour of field populations?*

In a classic series of experiments, Pratt (1943) noticed that *Daphnia,* grown at a critical temperature of 18^{o}C, manifested behaviour closely resembling the predictions of the logistic curve (fig 3.2a).

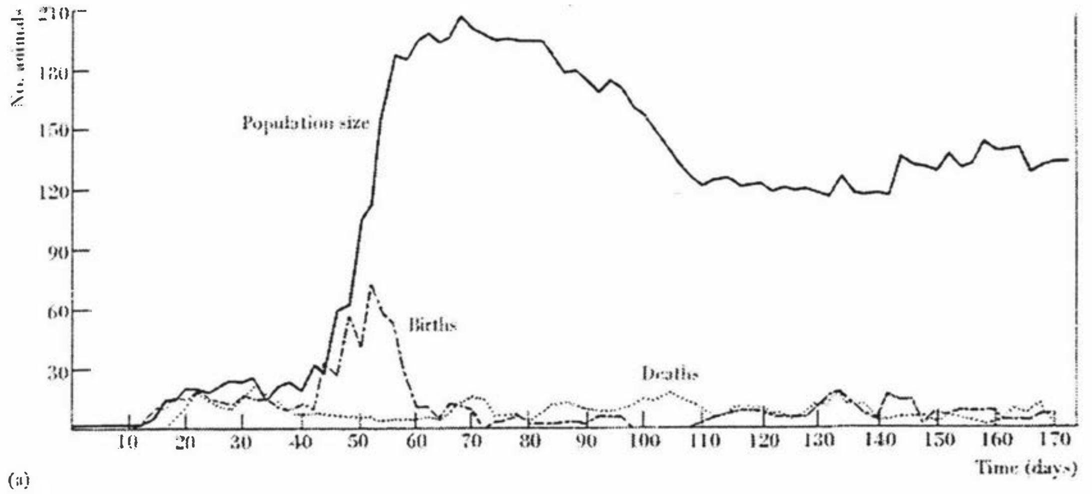


Fig 3.2a Pratt's population data for the water flea *Daphnia magna* raised in 50 cc of pond water at 18^{o}C.

However, *Daphnia* grown at 25^{o}C showed unpredictable oscillations in number (fig 3.2b).

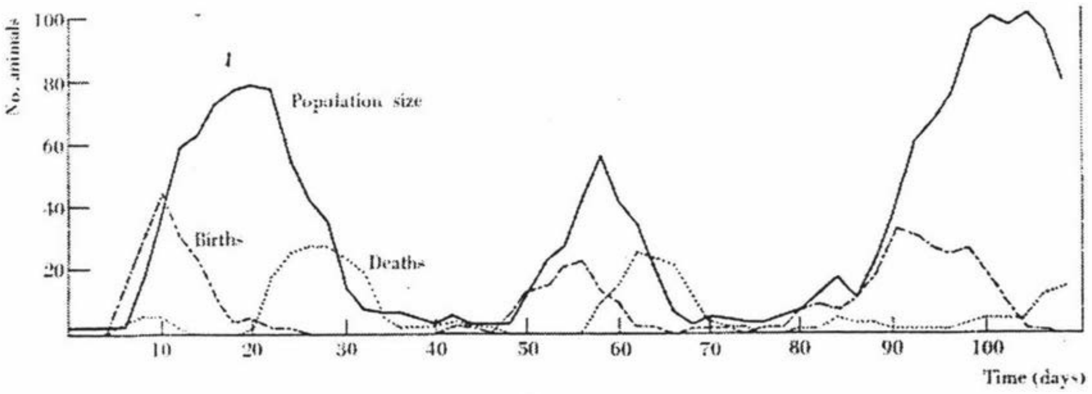


Fig 3.2b Pratt's population data for the water flea *Daphnia magna* raised in 50 cc of pond water at 25^{o}C.

Pratt (1943) concluded that *Daphnia* grown at 25^{o}C oscillated because there was a delay in the depressing effect of population density on birth and death rates which caused this *Daphnia* population to overshoot its equilibrium point and then to crash towards extinction.

The mechanisms responsible for this oscillatory behaviour in *Daphnia* are now well understood (Goulden and Horning 1980). *Daphnia* store energy during times of superabundant food supply in the form of oil droplets or triacylglycerols. They then utilise these food reserves once food supply has collapsed. Because of this mechanism *Daphnia* are not instantaneously affected by low food supply and, therefore, carry on reproducing when food supply is limited. This in turn causes them to overshoot their carrying capacity, resulting in population collapse when their food reserves run out. The importance of this fascinating behaviour is that these oscillations are an intrinsic part of the biological system and not caused by exogenous forcing of the population.

The food reserve mechanism of *Daphnia* is a positive feedback that temporarily overrides the negative density-dependent feedback mechanism which is an intrinsic part of the logistic model. However, eventually this positive feedback mechanism fails and engages an undamped negative feedback (total food depletion) which causes the population to collapse. The introduction of time delays causes the stable trajectory of the logistic model toward its upper asymptote to be replaced by oscillatory behaviour that may be stable or converge toward, an equilibrium.

Murdoch and McCauley (1987) suggest that simple algal-herbivore interactions made up of *Daphnia* and their prey phytoplankton provide ideal subjects for studying chaotic behaviour. In their experiments with this simple food web, the co-authors have identified three classes of behaviour of *Daphnia* - algal populations under structurally identical conditions.

In the first class, stable *Daphnia* and algal populations were observed in six examples. The dynamics of class two were stable limit cycles in which *Daphnia* lagged behind the algae, as predicted in classical predator-prey dynamics. A total of 15 populations cycled in this manner. Finally, the co-authors found four examples of stable algae, but cyclic *Daphnia*.

Murdoch and McCauley (1987) suggest that the mechanism responsible for cyclic behaviour, at least in laboratory populations of *Daphnia*, is what they have termed *dominance and release.* Cyclic behaviour appears to be caused by the effects of *Daphnia* on their own vital rates, via delayed intraspecific competition for food as predicted by the logistic equation with reaction time delay.

Lawton (1987) applied the logistic equation (31) to the *Daphnia*-algae data of Murdoch and McCauley and determined growth rate values of ca. 0.2, very close to the published results of the co-authors which ranged from 0.09-0.33. Lawton concludes that *Daphnia and their algal food supply provide the most unequivocal support available for a central assumption of mathematical population biology, namely that changing parameter values, but not the structure of an interaction, is sufficient markedly to alter patterns of population behaviour*.

May *et al.* (1974), evaluated stability criteria in relation to time delays for a range of continuous and discrete single species equations. The reason for their inquiry was prompted by May (1972) - that increased complexity tends to produce instability. This hypothesis suggests that the stability of most ecosystems is the result of special strategies which have evolved to meet necessary stability criteria. The authors discovered that a relationship appears to exist between the characteristic return time of a population T_r, and time delay. This relationship determines whether a population approaches an equilibrium monotonically or overshoots and oscillates.

The concept of a return time in the logistic model is discussed by Maynard Smith (1968) and May (1973) and simply defines the time taken for a population to return to equilibrium following a disturbance. In this case, larger values of r lead to a more rapid return to equilibrium.

$$T_r = \frac{1}{r} \tag{32}$$

where

T_r is the characteristic return time

r is population growth rate

In their analysis of both discrete and continuous single species models, the authors conclude that a general requirement for stability is that the characteristic return time T_r be larger than both reaction and regeneration time delays.

Regeneration time delays are a further amendment of the logistic equation which assumed that reproductive capacity was instantaneous, allowing no time for possible time delays caused by gestation or its equivalent (Krebs 1985, Renshaw 1991). A reproductive time delay may be important in slowing the rate of growth of a species during the early phases of population growth and can be incorporated into the logistic equation as follows:

$$\frac{dN}{dt} = rN_{t-g}\left(\frac{K - N_{t-w}}{K}\right) \tag{33}$$

where

w is the reaction time delay

g is the reproductive time delay

t is time

Nisbet and Gurney (1982) found that in some situations the birth rate may depend not just on one particular time t, but on a weighted average of times. Obviously, the field of all possible time delays is vast and those mentioned in this section are intended only to illustrate the concept and its application. Furthermore, the present line of discussion involves considerable abstraction, as is illustrated by a few carefully chosen publications.

In the organisation of natural communities, time delays undoubtedly operate in a far more complex context. Empirically, the detection of time lags appears to be closely associated with temporal and spatial scale (Holyoak 1994). Renshaw (1991), has explored the behaviour of time delayed systems influenced by the operation of stochastic processes. Cushing (1977a, 1977b) provides a more detailed mathematical study of the effect of time delays on the nature of oscillations of species density in single and multi-species systems.

In a novel application of time delay theory, May (1973), evaluates the effects of time delays in population models with two and three trophic levels and illustrates how intricately time delays may be associated with the organisation of communities. May applied a known stabilising resource limitation effect to a herbivore population with an additional time delay. The behaviour of the herbivore population was simulated with and without the activity of predators. May discovered that of the two simulations, only the vegetation-herbivore-carnivore community was stable. May (1973a) concludes that *herbivore population numbers may often be set neither by predators alone nor by vegetation alone, but by an explicit interplay between both effects.*

Biotic instabilities are not only generated by time delays. In single species, discrete-time-difference equations, instabilities appear to be related to the sensitivity of certain parameters to the smallest of changes in value. Berryman and Millstein (1989) suggest that following May's (1974) observation of chaotic behaviour in the discrete logistic equation (fig 6.2), *the idea has arisen that apparently random fluctuations in natural ecosystems may in fact be due to deterministic chaos.* Chaos theory has introduced some important concepts into ecology which can be simply illustrated by brief discussion of the behaviour of the discrete logistic equation (6).

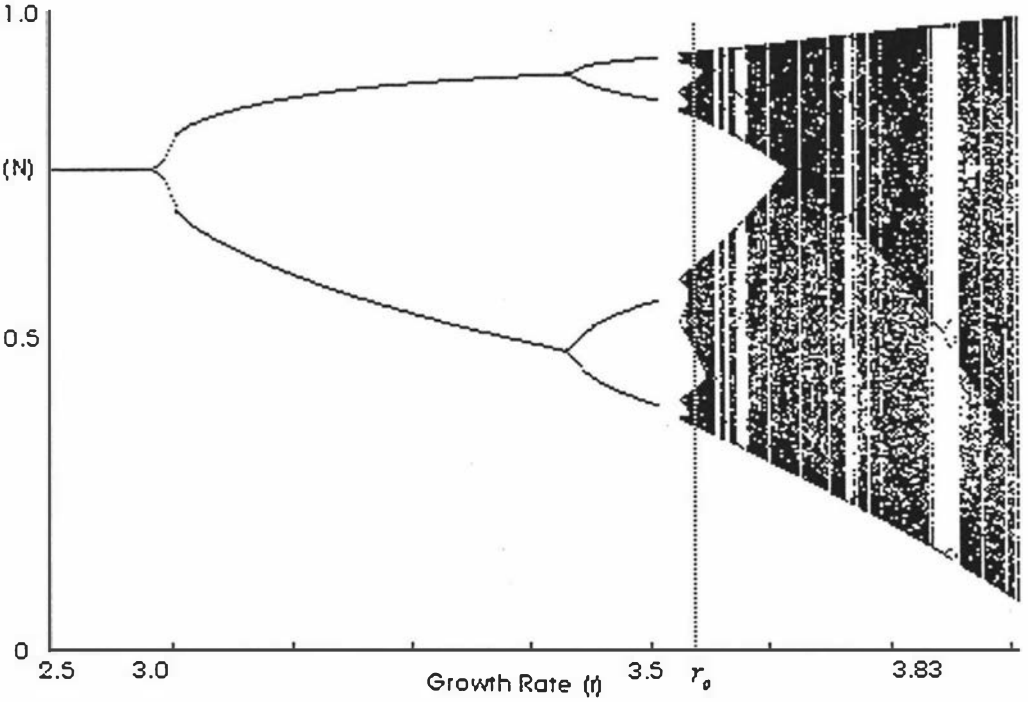


Fig 3.3 A hierarchy of stable fixed points (N) of periods 1, 2, 3, 4, 8, ..., 2^n (corresponding to stable limit cycles of periods 2^n), which are produced by the discrete logistic equation (6) for increasing values of r. Each pair of points arrises by bifurcation as a previous fixed point becomes unstable. This sequence of stable cycles of period 2^n is bounded by the parameter value r_c; beyond which lies the chaotic region (after fig 2.1, May 1981).

The form of the discrete logistic (scaled) is expressed in equation 6,

$$N_{t+1} = rN_t(1 - N_t). \qquad (6)$$

The stability of the non-trivial equilibrium state is conditional on the parameter r and must satisfy the condition that $1 < r < 3$. When r is outside the critical range of $1 < r < 3$, the equilibrium state is not stable and in this context r is referred to as a bifurcation value. The bifurcation map of fig 3.3 portrays the behaviour of the discrete logistic equation as it exceeds successive bifurcation thresholds - behaviour that is sometimes referred to as a cascade. On the bifurcation map portrayed in fig 3.3, N becomes unstable as the parameter r reaches the first instability threshold (3.0), at which point N bifurcates to produce two new and locally stable fixed point cycles of period two. The population will oscillate stably in a 2 point limit cycle.

However, with increasing values of r, these two points in turn become unstable and bifurcate to give four, locally stable, fixed points of period four. In this same way there arises by *successive bifurcations, an infinite hierarchy of stable limit cycles of period* 2^n *- a cascade of period doubling* (May 1981). This sequence of stable limit cycles eventually converges on a limiting parameter r_c beyond which the system is no longer stable and may be termed chaotic. For any parameter value in this domain there is an infinite number of different periodic orbits (May 1981, Li and Yorke 1975, May and Oster 1976).

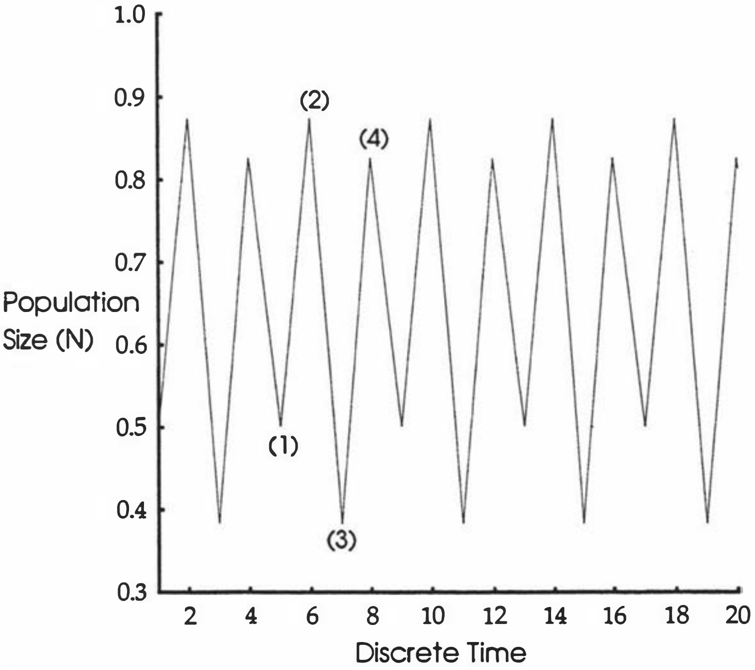


Fig 3.4 Illustrating the dynamical behaviour of a population N_t as described by the discrete logistic equation (6) for a parameter value (r) of 3.5. The nature of a stable 4 point limit cycle is indicated by annotation of the 4 stable fixed points (1) - (4).

The concept of a stable limit cycle simply implies that the oscillatory behaviour of the system is limited to a stable equilibrium point of period 2^n.

This can be illustrated by solving the discrete logistic equation (6) for a parameter value r of 3.5 which yields a stable limit cycle of period 4 (fig 3.4). The four equilibrium states of this four point limit cycle are indicated by the annotation (1) - (4). The concepts of stable limit cycles and chaotic behaviour may also be related to the theory of attractors in phase space.

For a simple discrete or continuous time model, the attractor can be a single point (an equilibrium), two points (two point cycle), up to a finite number of points (a more complex cycle) (May 1977). Empirical support of the existence of attractors has been demonstrated for *Tribolium* (Desharnais and Liu 1987). Chaotic attractors of deterministic systems are usually strange attractors. Empirical support for the existence of a strange attractor has been demonstrated by Schaffer (1984). The attractor in phase space is chaotic only if at least one of the Lyapunov exponents is positive. Furthermore, in *a continuous time differential equation system there must be at least one negative Lyapunov exponent for the attractor to attract* (Hastings *et al.* 1993).

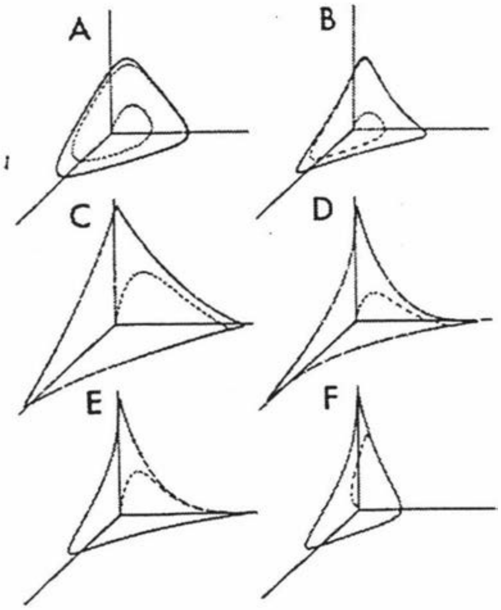


Fig 3.5 Three dimensional interference limit cycles generated by the solution of a 3 dimensional system of Lotka-Volterra equations (from fig 2, Gilpin 1975).

Cyclic and chaotic behaviour has been demonstrated for a range of classical models. Gilpin (1975) demonstrates that competition systems of three or more species based on the Lotka-Volterra competition equations are capable of having limit cycles as an attractor manifold (fig 3.5). Gilpin (1979) further demonstrates that chaotic behaviour can occur for systems of Lotka-Volterra equations over certain regions of parameter space.

May (1972) reviews a wide class of models which have been proposed in the ecological literature for predator-prey systems. May demonstrates that all such models *possess either a stable equilibrium point or a stable limit cycle.*

Wangersky and Cunningham (1957) have demonstrated that it is possible to determine the outcome of a competitive struggle by varying the reaction time delays in coupled systems of logistic equations:

$$\frac{dN_1}{dt} = r_1 N_1 \left[\frac{(K_1 - N_1 - \alpha N_2)}{K_1} \right]_{(t-\tau_1)}$$

and $$\frac{dN_2}{dt} = r_2 N_2 \left[\frac{(K_2 - N_2 - \alpha N_1)}{K_2} \right]_{(t-\tau_2)} \qquad (34)$$

where

τ_1 is the density-dependence time delay for species 1
τ_2 is the density-dependence time delay for species 2

Hassell and Comins (1976) have applied time delays to coupled systems of discrete logistic equations making time delays of a fixed length an implicit part of the system. They found oscillatory solutions resembling some of Wangersky and Cunningham's (1957) results (fig 3.6). Time delays result in greater system instability in single and coupled systems of equations.

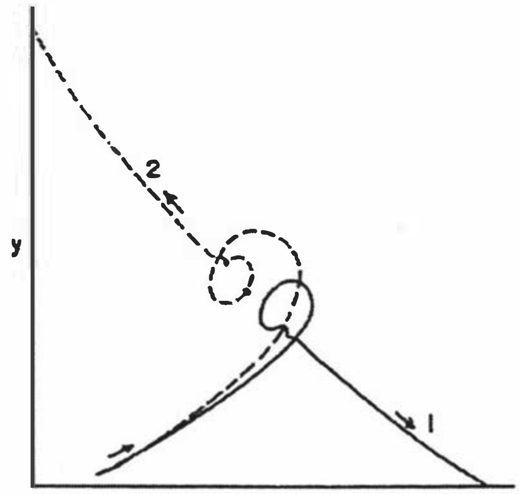


Fig 3.6 Illustration of competition between two species (x, y), with the outcome determined by the size of time delays (dashed and solid line) (from Wangersky 1978).

Apart from its intrinsic mathematical interest, the discrete logistic equation used above to illustrate cyclic and chaotic behaviour raises some interesting ecological issues.

Firstly, the dynamic behaviour of this system mimics that of a random process and yet the model itself is deterministic. This suggests that chaotic population fluctuations need not be due to random environmental fluctuations or sampling errors. The nature of this equation suggests that chaotic behaviour may reflect the workings of a deterministic and strongly density-dependent population model (Berryman and Millstein 1989).

Secondly, Judson (1994) claims that the lessons of chaos suggest simple principles in ecology will be the exception, accidents of history are important and *because predictions are impossible, the only way to find out more about what is going on in some dynamic systems is to simulate them exactly.* Judson (1994) argues that individual based simulations may be the only way to find *the texture of a system.* In recent times, individual based modelling in ecology has found strong support (DeAngelis and Gross 1990).

Thirdly, a characteristic of chaotic systems is their extreme sensitivity to the slightest changes in initial conditions. Judson (1994) suggests that this fact implies the importance of historic events in determining the future behaviour of a dynamical system. Godfray and Grenfell (1993) in their review of chaos theory in ecology suggest that chaos should not be viewed purely as a property of deterministic systems. Rather, chaos is a result of extreme sensitivity that can arise through *the interaction of the deterministic and stochastic components of a system.*

Fourthly, Hess *et al.* (1993) sound a word of caution concerning the properties of discrete and continuous time as handled by a digital computer. The authors point out that simple maps are not derived from continuous physical systems described by differential equations *but are constructed ab initio as discrete, finite difference equations.* This fact implies that their dynamics involve a chaotic richness quite different from that found in real continuous systems.

Fifthly, chaotic behaviour is closely associated with density-dependence, since it requires the operation of either positive feedback loops or delayed, unstable (over compensatory) negative feedback loops. For these reasons, chaotic behaviour may usefully be thought of as a deviation from stable equilibrium conditions. Furthermore, human impact on the environment is quite capable of forcing positive feedback loops and imposing over compensatory negative feedback on natural systems. Berryman and Millstein (1989) argue that these facts suggest that the lessons of chaos are important for ecologists, not because ecological systems are normally chaotic, but because they can be made chaotic by human actions.

Hastings *et al.* (1993) review the history of chaos theory in ecology from the time of May's early work on discrete time models in population ecology (May 1974, 1976, May and Oster 1976). The work of May was followed by Hassell *et al.* (1976) who tested the hypothesis of chaos in natural insect populations *by fitting a first-order discrete time equation to census data.*

Turchin (1993) suggests that it is not surprising that Hassell *et al.* (1976) failed to find conclusive evidence for chaotic behaviour in their insect data. The authors had used a first-order equation which is incapable of capturing the dynamics of cycles and chaos in natural populations and communities.

Whitteman *et al.* (1990) provide evidence which supports the existence of omplex dynamics in natural population behaviour. These authors abandoned he use of first-order equations in favour of auto-correlation analysis and lag-lot reconstruction techniques.

Unfortunately, the publication of Hassell *et al.* (1976) was not without its nfluence and suggested to many ecologists that chaos was unimportant in atural populations. However, the theme of chaos in ecology appears to have een rekindled by Schaffer (1984) and Schaffer and Kot (1985, 1986).

Unstably interactive models by themselves are an incomplete picture of real ommunities because they ignore environmental and demographic stochasticity. Stochastic domination is the theme of the next section.

3.4 Weakly Interactive Community Behaviour

The name which DeAngelis and Waterhouse (1987) have given to a community type dominated by stochastic processes is weakly interactive which is suggestive of inferior homeostatic control. In these communities, strong stochastic fluctuations cause component populations to deviate from trajectories that would otherwise be dominated by stably interactive behaviour.

Population growth may be regarded as a stochastic process for at least two reasons. Firstly, even in a constant environment, population size may vary in response to chance events in reproductive success and ecologists refer to this process as *demographic stochasticity* (May 1973). Secondly, parameters traditionally viewed as constants in classical deterministic models, r, K, α, β, *may be defined as variables that take different values through time based on some probability distribution* (Roughgarden 1975). Fluctuations in parameter values of this kind are used to represent environmental stochasticity (May 1973).

3.4.1 To What Degree is Stochasticity Still Deterministic ?

Most of the models that have been discussed in preceding sections of this chapter have been deterministic. A deterministic model predicts *a single outcome from a given set of circumstances* or initial conditions while a *stochastic model predicts a set of possible outcomes weighted by their likelihood's or probabilities* (Taylor and Karlin 1994). In ecology, stochastic models vary in the degree to which they have abandoned deterministic elements. The question may now be asked, to what extent does the behaviour of a stochastically dominated population or community still reflect the operation of deterministic processes?

Deterministic models have a long history in ecology, intricately bound with the assumptions of equilibrium theories of community organisation. Classical competition theory (Hutchinson 1959) is of particular interest to the present discussion. Classical competition models have traditionally been used to suggest that natural communities have a highly predictable structure, an argument that was dependent on at least five major assumptions and on some empirical data.

Firstly, it was assumed that life history characteristics could be summarised in a single parameter - the per capita growth rate. Secondly, it was assumed that deterministic equations could be used to model population growth in which environmental fluctuations were ignored. Thirdly, as a community grows, its structure was assumed to approach a stable age distribution. Fourthly, it was assumed that competition was the only important biological interaction (Hutchinson 1959, Grant 1986). Finally, is was assumed that coexistence required a stable equilibrium point.

The second, third, fourth and fifth of these assumptions are of special interest to the present discussion. The degree to which these assumptions are relaxed determines the extent to which the modified model retains predictive capability.

Community predictability is also closely associated with stability, a property shared by all forms of classical equilibrium theory (competition, predator-prey) to varying degrees. Competitive systems were traditionally considered to have global stability. A globally stable system would show little tendency to lose species, the community being able to recover from events that drive species to low densities. Communities would be assembled by immigration and because the system approaches equilibrium, historical changes in abundance could be considered unimportant in determining a future state.

Some ecologists have argued that these properties of global stability may also be shared by models of non-equilibrium theories (Chesson and Case 1986). For example, a system that demonstrates non-equilibrium behaviour at a local scale, may have emergent equilibrium properties at a higher, landscape level of scale. This hypothesis is currently an area of active research and will be discussed more fully later in this chapter.

In summary, the predictability of a community as proposed in classical stable equilibrium theory rests primarily upon the following seven assumptions:

(1) community regulation by competition,
(2) community structure approaches a stable age distribution,
(3) environmental fluctuations can be ignored,
(4) coexistence requires stable equilibria,
(5) a community has a stable species composition,
(6) communities recover from perturbations,
(7) historical events are not important for stable equilibria.

In the previous section, an important point was made concerning May's (1974) observation of chaotic behaviour in the discrete logistic equation. Following May's observation, ecologists were led to realise that apparently random fluctuations in natural populations and communities may in fact be due to deterministic chaos. This same observation may now be made concerning stochastic domination. Research efforts appear to indicate that elements of determinism or predictability are present in stochastic systems.

This proposition can be illustrated by reviewing published research in this area. Most of this work has ignored intrinsic stochasticity. Randomness is introduced by replacing one of the model's parameters by stochastic processes. The dynamics of the resulting model are then compared with those of its deterministic parent in an attempt to identify behavioural differences and properties of stability in the stochastic counterpart (Turelli 1978).

3.4.2 Environmental Stochastic Domination - Empirical Research

The addition of environmental stochasticity does not necessarily imply the existence of unpredictable, non-equilibrium behaviour. With strong internal biotic forces, the extent to which a community is affected by environmental stochasticity is dependent on factors like the frequency, magnitude and spatial extent of disturbance events. This assumes, of course, that competition is a valid regulatory process.

Armstrong and McGhee (1980) demonstrate that population limit cycles can actually facilitate coexistence for many species on a limiting resource - a conclusion that invalidates one of the key predictions of classical theory. Classical competition theory requires that at least *n* limiting resources are required for the coexistence of *n* species (Chesson and Case 1986).

In order to explain the paradox of plankton, Hutchinson (1961) turned this axiom around and reasoned that the existence of more species of plankton than limiting resources must imply that the hypothesis of an equilibrium is wrong. Hutchinson went on, to suggest that intermediate disturbance may work to moderate potential instabilities caused by strong competitive forces in the plankton community, that would normally result in competitive exclusion.

The results of Armstrong and McGhee (1980), appear to complement the conclusions of Hutchinson (1961). In the model of Armstrong and McGhee, the environment does not vary, fluctuations in population density and resource levels result from biotic instability (limit cycles) in the model's equilibrium point (Emlen 1984).

May and MacArthur (1972), introduced white noise into competition communities modelled by a variant of the deterministic logistic equation (29). The co-authors discovered that when the equation's parameters were held constant, as in the case of a uniform environment, stable equilibrium was the result. The co-authors then introduced environmental variability into the model in the form of Gaussian white noise and discovered that community stability was now dependent on a threshold level of white noise.

Turelli (1978), pointed out that May's proposed scenario of competing deterministic and stochastic forces was quite sound. However, some of the assumptions implicit in May's use of white noise could only be upheld in very specific circumstances.

Another approach to modelling environmental fluctuations was used by Hanson and Tuckwell (1978) who assumed that the logistic model described an equilibrium state that was disturbed and continually reduced, by discrete disturbance occurring at return intervals, defined by Poisson processes.

$$\frac{dN}{dt} = rN\left(1-\frac{N}{K}\right) - \varepsilon d\pi(\lambda;t) \qquad (35)$$

where

$d\pi(\lambda;t)$ is a small increment of a Poisson process

ε is the magnitude of the disturbance

$N_{(0)}$ is the initial population size

Models like (35) exhibit thresholds in the size of the disturbance (noise) (ε) beyond which the stability of the equilibrium changes (see Wake and Watt 1996 in press). From the stochastic formulation of the logistic, Hanson and Tuckwell (1978) calculated expected time to extinction as functions of r/λ and $N_{(0)}/\varepsilon$. The general conclusion of Hanson and Tuckwell was that expected extinction time increases dramatically as the carrying capacity increases. Although the model was capable of extinctions, these were found to require extremely long time intervals when the carrying capacity was large and λ was of intermediate value.

A third type of modelling approach used to explore environmental variability has been applied to the logistic (Boyce and Daley 1980) and discrete logistic (Lewontin and Cohen 1969). The basic idea is illustrated by the use of a discrete time growth equation,

$$N_{t+1} = r(N_t)N_t, \qquad (36)$$

in which the growth rate (r) is totally governed by a stochastic environment rather than the current population size. At each time interval the growth rate (r) is chosen independent of N_t from a probability distribution (Lewontin and Cohen 1969). These studies show that even when a population initially grows toward infinity, extinction is the inevitable long term outcome.

In summary, each of the four models reviewed in this section relax classical equilibrium assumptions to varying degrees. All four models maintain competition, stable age distributions, and equilibria as a driving deterministic force. The results appear to indicate that coexistence and stability are feasible for a community dominated by environmental stochasticity. However, this feasibility is very dependent on the extent of environmental opportunity (carrying capacity), individual life history, community structure as well as the nature and severity of the disturbing force.

3.4.3 *Demographic Stochasticity - Empirical Research*

The modelling of stochastic birth and death processes has a long history in ecology (Feller 1939, Kendall 1949, Skellum 1955, Bartlett 1957, 1960, Bartlett *et al.* 1960, MacArthur and Wilson 1976, Cohen 1979, Mode and Pickens 1986, Yoldzis 1989, Gilpin 1992). Various studies have attempted to extend the concept of demographic stochasticity to the dynamics of interacting species (Chiang 1954, Bartlett 1957, Leslie and Gower 1958, 1960, Tsokos and Hinckley 1973).

A birth and death model is stochastically dominated when both the birth and mortality rates are density-independent and therefore not characterised by equilibrium states (Yoldzis 1989). Stable equilibrium states are possible (Karlin and McGregor 1958) when species immigration counters the negative influence of local extinctions on population growth. A population dominated by probabilistic birth and death processes will either grow without bound, fall away to extinction or wander along in a random manner for a long period of time (Rodriguez 1989). The nature of a random walk depends on the initial population size and relative magnitudes of the birth and death rate parameters (Pielou 1969).

There have been two main conceptual approaches to the analysis of demographic stochasticity. A recursive model based on very small time steps was developed by MacArthur and Wilson (1967). The model population could be expected to change in size only by a single birth or death at a given interval. The co-authors showed that the average time to extinction varied inversely with population size and the ratio of population growth rate to birth rate (r/λ). However, their approach was not without its limitations. Firstly, small increments are an approximation of real temporal patterns of birth and death. Secondly, the approach only estimates the mean time to extinction, the model was not capable of predicting a probability distribution of future population sizes.

A variant of the MacArthur and Wilson approach, is given by Pielou (1969). This model is simple in its form and worthy of brief discussion since it illustrates a number of fundamental properties of stochastic demographic processes. The probability of extinction for a population based on stochastic birth and death processes for an initial condition $N_{(0)}$ is given by the following equation,

$$(P_E) = \left(\frac{d}{b}\right)^{N(0)} \qquad (37)$$

where

P_E is the probability of extinction
d is the instantaneous death rate
b is the instantaneous birth rate
$N_{(0)}$ is the initial condition or population size.

Pielou (1969) suggests two scenarios in explanation of this relationship. Firstly, assuming that the birth rate is greater than the death rate, a population should grow exponentially. The chance of extinction is obviously greatest during the first few time intervals. This first scenario can be illustrated (after Krebs 1985) using equation (37) to describe two cases in which d and b alternatively are numerically greater in two different chance events:

(i) birth rate is numerically greater (P_E is very low),

$$(P_E) = \left(\frac{0.25}{0.75}\right)^5 = 0.0041 \tag{37a}$$

(ii) death rate in numerically greater (P_E is much higher),

$$(P_E) = \left(\frac{0.45}{0.55}\right)^5 = 0.367. \tag{37b}$$

This relation suggests that the larger the initial population size and the greater the difference between birth and death rates, the more chance the population has of staying in existence. Secondly, it is possible that birth and death rates may be equal or stationary in which case:

(iii) stationary birth and death rates

$$(P_{(E)}) = \left(\frac{d}{b}\right)^{N_{(0)}} = (1.0)^{N_{(0)}} = 1.0. \tag{37c}$$

The probability of extinction (1.0), is relatively high for any stationary population that is subject to stochastic fluctuations in birth and death rates. This simple exercise effectively illustrates why populations driven by demographic stochasticity are capable of manifesting distinctly non-equilibrium behaviour (Krebs 1985).

A more recent approach to demographic stochasticity has been demonstrated by Gilpin (1992), who uses a Markovian transformation matrix to predict future population sizes on an annual basis. The elements of this matrix are,

$$M_{(n,m)} = \sum_{i=0}^{n}\sum_{j=0}^{n} P_{cmij}\binom{n}{i} b^i (1-b)^{n-i} \binom{n}{j} d^{n-j} (1-d)^j \tag{38}$$

where

$M_{(n,m)}$ are transition matrix elements, n(current), m(next)

d is the probability of death

c is clutch size

b is the probability of giving birth

and assuming that,

$p = 0$ if $(m = ic + j)$ or $(m = n \leq ic + j)$ is false,
$p = 1$ if $(m = ic + j)$ or $(m = n \leq ic + j)$ is true.

For a population with one living individual there are four possible transitions to states of $o, 1, c,$ and $c+1$ individuals, with probabilities of $d(1-b)$, $(1-b)(1-d)$, bd, and $b(1-d)$ respectively. The value of p is conditional because some of the transition elements are adjusted to prevent population sizes above K (the carrying capacity).

The value of Gilpin's approach lies in its ability to give the distribution of population states with time, so that it is easy to predict the extinction probabilities of populations with different initial conditions, carrying capacities, growth rates and clutch sizes. Gilpin (1992) uses this approach to compare several populations with differing clutch sizes for which birth and death rates are adjusted to hold the discrete growth rate and net reproductive rate constant. Gilpin (1992) discovered that increased variance in the annual growth rate of an individual gives populations with larger clutch sizes a much higher probability of extinction (Alstad 1994).

Mode and Pickens (1986) investigated an important assumption of models which describe demographic stochasticity for large populations. The co-authors discovered that for large populations with homogeneity in laws of reproduction and survivorship among members of the population, *the impact of demographic stochasticity on this uncertainty could be low*. However, for large populations in which the laws of reproduction and survivorship are heterogeneous among members of the population, *then demographic stochasticity could be a significant factor in measuring the uncertainty of a population projection.*

In summary, the types of models reviewed in this section have substituted the assumption of a stable age distribution for demographic stochasticity of varying degrees. The performance of single-species models has been tested under conditions of environmental constancy. Population growth under such conditions is dominated largely by random processes and the influence of initial conditions. The larger the initial population size and the greater the difference between birth and death rates, the more chance the population has of staying in existence. Variance in individual growth rates appears to result in a higher likelihood of extinction. A stationary population in a fluctuating environment has a greater probability of extinction.

Finally, the probability of fluctuations in large populations composed of individuals with heterogeneous laws of reproduction and survivorship appear to be greater. In a system of Lotka-Volterra competition equations, Leslie and Gower (1958) found that only the indeterminate case appears to be greatly influenced by demographic stochasticity.

The above results appear to indicate that population extinction increases as a consequence of demographic stochasticity under conditions of environmental constancy for single populations. In the case of competing species, coexistence is still feasible, while the indeterminate case is now subject to a stranger probabilistic outcome as suggested by the experiments of Park (1954) with *Tribolium.*

For the single populations mentioned in this section, local extinctions are not replenished by species immigration - a mechanism which may enable natural populations to persist long term. Classical competition theory assumed that immigration and emigration rates were stationary and therefore not factored into equilibrium models.

3.4.4 Demographic and Environmental Stochasticity

A third approach to the study of stochasticity is to allow fluctuation in demographic or environmental variables so that populations are density-independent most of the time. In this case the classical assumption of competitive constancy is relaxed. Density vagueness of this kind implies inherent stochasticity - *dispersion, inconsistency, weakness, and indistinctness in the key demographic functions* (Strong 1986a). The classical assumption of environmental constancy is also relaxed. Density vague population ecology has been elaborated on in great detail by Strong (1984, 1986).

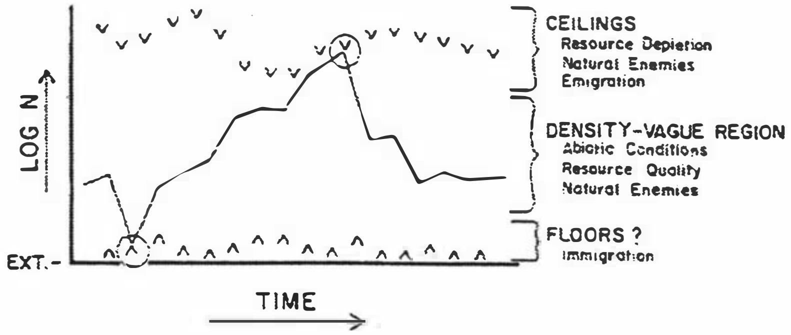


Fig 3.7 Density vagueness according to Strong (1986). Strong's liberal population regulation is vaguely related to intermediate densities, between ceilings and floors. Most change in this population is unrelated to density (from Chesson and Case 1986).

Strong's main argument reflects the inadequacies of the historic dichotomy between density-dependent and density-independent theory which he claims is inadequate to describe *the rich character of density relationships in nature* (Strong 1986a).

Strong's concept of liberal population regulation involves three primary regions of differing demographic conditions and density-dependence. Mechanisms termed floors are designed to prevent local extinctions, while ceilings involve a further range of mechanisms that regulate tendencies toward over-compensation. Population behaviour operates like a random walk at ntermediate densities, but differs from the classical idea of a truly random walk which was unlimited and assumed eventual species extinction.

The behaviour of communities organised by intermittent density-dependence and interspecific competition have been explored by Koch (1974), Huston (1979) and Chesson (1982). As expected, in all three cases, environmental stochasticity reduces the densities of several competing species to weak competition levels where population growth is temporally insensitive to density. In all cases, coexistence was promoted as a result of demographic and environmental uncertainty (Chesson and Case 1986).

3.4.5 Unconstrained Stochastic Domination

A fourth option is to allow environmental fluctuations in which the variance is not constrained about a single mean value. Davis (1986) argues that directional changes of climate can have a profound effect on the structure of biological communities. Ability to track and respond to annual and long term climatic shifts is species specific, which according to Davis (1986) implies that communities do not respond as units. These variations in *rates of change among component species cause faunal and floral disequilibrium and change the patterns of species abundances resulting from competition and predation.* Davis suggests that community behaviour will be difficult to interpret unless climatic variations in both space and time are taken into account.

A number of attempts have been made to study the tracking behaviour of different species explicitly with simple models (Hubbell 1973, Roughgarden 1975, Boyce and Daley 1980, Nisbet and Gurney 1982). In summary, Davis (1986) suggests that short lived organisms may well fit this picture since their population dynamics are fast, relative to the rate of change of the mean environment. However, long lived species such as forest trees, respond to changes in the mean environment with considerable time lag (see West *et al.* 1980, Shugart and Noble 1981, Fulton 1991). This may explain why some present-day forests appear to be genetically maladapted to current conditions. Davis points out that for such communities, an appeal to tracking theory cannot salvage traditional stable equilibrium community theories.

3.4.6 The Hubbell and Foster Model

Hubbell and Foster (1986) have proposed an explanation of apparently random fluctuations in populations that does not involve demographic or environmental stochasticity. The co-authors suggest that many tropical tree species are essentially identical in terms of their responses to environmental fluctuations and resource requirements. Assuming this to be true, then the only differences between these species amount to reproductive incompatibilities. Therefore, the difference in density of two interacting tree species is just as likely to increase as to decrease, independent of environmental conditions or the population densities of other species.

In the Hubbell and Foster model, there is complete competitive equality in the community. Elimination only occurs as a result of random drift in numbers. For these sorts of communities, chance and history may be the major factors shaping community structure (Chesson and Case 1986).

3.4.7 Summary

In summary, the main purpose of this section has been to evaluate the topic of stochastic domination for populations and communities organised according to the predictions of classical competition theory. Research work in this area indicates that for populations and communities modelled on the basis of classical equilibrium models with varying degrees of demographic and environmental stochasticity, elements of determinism are still evident in these systems.

This section provides an interesting contrast to the conclusions drawn from the research work reviewed in Chapter two. Also, these research efforts illustrate how equilibrium models and theory might usefully be employed to study natural systems. A general trend in this research indicates that deterministic behaviour is feasible, but clearly dependent on the formulation of a given model and the intensity of the disturbing force. These models are an attempt to address some of the limitations of untenable assumptions now evident in classical equilibrium models.

The evidence presented in this section, also demonstrates that there is a much higher probability of local extinction for populations dominated by stochastic processes - especially long term. Furthermore, in some model formulations, the behaviour of the system is characteristically unpredictable. DeAngelis and Waterhouse (1987) suggest that *for small spatially localised populations, isolated from new immigration and subject to stochastic fluctuations, extinction is inevitable.*

What enables a community to persist in an ecosystem over long periods of time when it is dominated by strong stochastic forces (because of weak interactive coupling) or subject to biotic feedback instabilities? At present, there are two possible answers to this question.

Firstly, the classical hypothesis of stable equilibria has led researchers to look for mechanisms which will damp out biotic instabilities and stochastic dominance, in order to return a disturbed equilibrium system to its former state. Scientists working in this field have attempted to incorporate stabilising mechanisms into classical equilibrium models. One problem with this approach is that stability is an equilibrium-centred concept. If transient behaviour is the norm for natural communities, then stability as a concept may be quite misleading.

A more recent view proposes that communities are always in a state of change and therefore the non-equilibrium paradigm is a more relevant behavioural model. Community behaviour of this kind may be a response to biotic feedback instabilities on the one hand or stochastic domination on the other, or a complex mixture of both.

The assumption that transient behaviour is the norm for natural populations and communities emphasises the need to search for mechanisms that will buffer and damp out extreme disturbances, so that communities may persist long term. Persistence is not an equilibrium centred concept. By contrast, it acknowledges the fact that change is an intrinsic part of community behaviour, caused by biotic and environmental instabilities. Persistence, refers to the ability of a population to remain within survival size limits, despite the existence of disturbance. (Reddingius 1971, Holling 1973, Innis 1974, Botkin and Sobel 1974, Chesson 1978, Harrison 1979, Gard and Hallam 1979).

DeAngelis and Waterhouse (1987) suggest that of these two responses to the question of long term community persistence, the non-equilibrium option has *opened up richer areas for investigation than the first.* A variety of non-equilibrium modelling approaches has been explored with an aim to identify mechanisms that may ensure the long term persistence of communities. To conclude this chapter, a review of these approaches will be given. The purpose of this discussion is to identify theoretical approaches to increasing the persistence of transient, non-equilibrium systems. This section is entitled the study of persistent community behaviour.

3.5 Persistent Community Behaviour

The super-model of DeAngelis and Waterhouse (1987) (fig 3.8), was first introduced in Chapter two (fig 2.1) in order to define the two principal behavioural departures from classical equilibrium conditions. Collectively, these three behavioural types have been more fully defined and discussed in Chapters two and three. It is now evident that both biotic instabilities and stochastic domination result in a much higher probability of extinction for local populations, at the patch level of ecological integration. Unless these small, local population units have strong connectivity with other units in the landscape, extinction is inevitable.

Having established the fact that non-equilibrium systems are inherently unstable and prone to local extinction, what mechanisms enable these populations to persist long term? During the early 1970s, ecologists began to devote a great deal of research effort toward this question. The five main hypotheses which have emerged from this research, are illustrated on the super-model (fig 3.8) by small numbered circles located near arrows as depicted below.

③ → pathway 3 (39)

The direction of these arrows in the super-model indicates the direction in which the given behavioural type will tend, as a result of the influence of a given stabilising mechanism. The five main stabilising hypotheses are indicated by the objects of (39), in fig 3.8. The combination of numbered circle and arrow represents a pathway as described by one of the five stabilising hypotheses. These five hypotheses can be further subdivided into two classes (equilibrium and non-equilibrium).

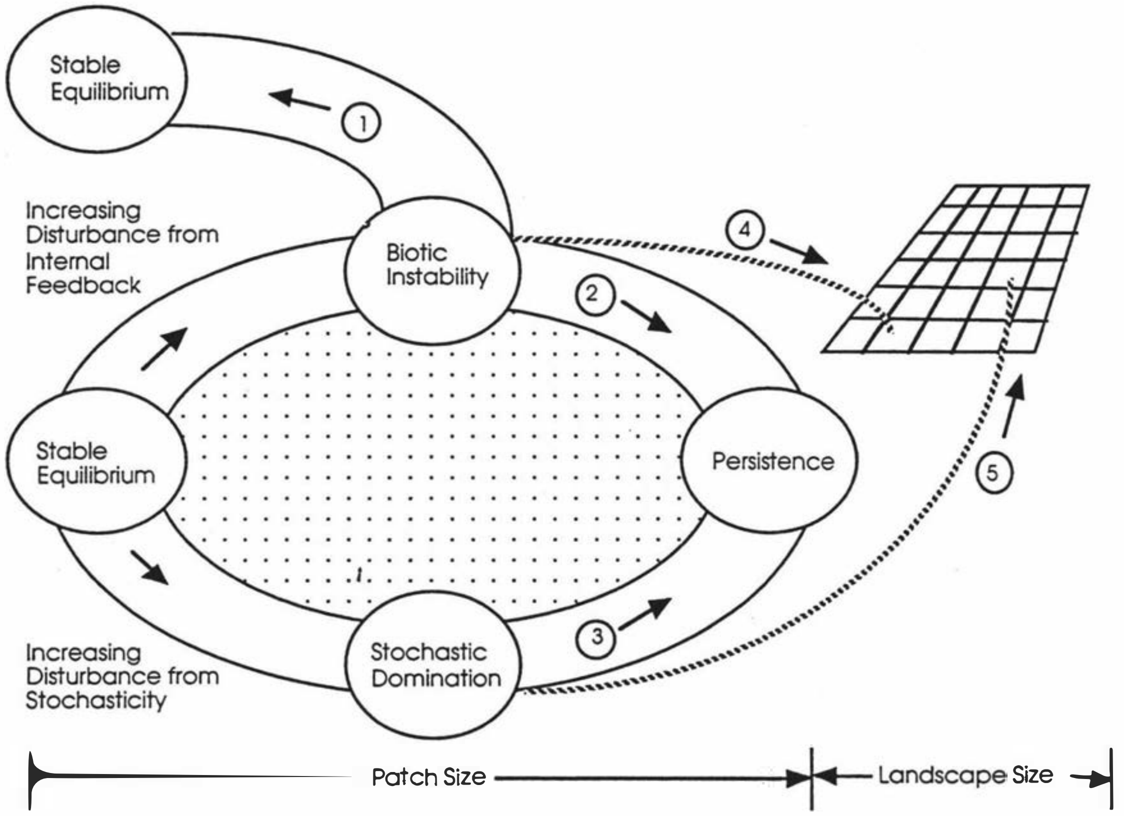


Fig 3.8 The Super-model of DeAngelis and Waterhouse (1987). The small circles with numbers and arrows indicate the five general types of hypotheses made by ecologists to explain why ecological systems persist or are stable despite the prevalence of biotic instabilities and stochastic domination (from DeAngelis and Waterhouse 1987).

Pathway one is the only equilibrium pathway and represents an attempt on the part of some ecologists, *to incorporate stabilising mechanisms into basic classical models that could preserve the stability of equilibrium states* (DeAngelis and Waterhouse 1987). Pathways two to five, are the non-equilibrium pathways and represent an attempt to abandon the idea of stable equilibria *as a fundamental property at the local scale and examine mechanisms ensuring long term persistence of communities* (DeAngelis and Waterhouse 1987). These five mechanisms are discussed more fully in the following five sections.

The following discussion considers the matter of community persistence (hypotheses two to five) on distinctly ecological time scales. Ecological time is by no means the only, nor necessarily the most relevant time scale at which to investigate ecological success. Wilson (1987) (fig 3.9) has suggested that *length of* *life through geological time ... may be ... the ultimate criterion of ecological success for a species or its descendants.*

Fig 3.9 E. O. Wilson. *Length of life through geological time* ... may be ... *the ultimate criterion of ecological success for a species or its descendants.* (from Wilson 1987, The Tansley Lecture to the British Ecological Society).

3.5.1 Pathway One - Restabilising a Disturbed Equilibrium State

As mentioned above, pathway one (fig 3.10) is an attempt to incorporate stabilising mechanisms into classical equilibrium models. DeAngelis and Waterhouse (1987), have identified five different research approaches to this problem.

3.5.1.1 Stabilising Functional Relationships

Firstly, the *recognition that simple predator-prey systems can exhibit instabilities* (*e.g.*, Gause 1934, Rosenweig and MacArthur 1963, May 1972) led ecologists to a search for functional relationships that would restabilise these systems.

Classical experiments and models of predator-prey interaction always assumed or experimentally forced predators to look for their prey in a spatially homogeneous environment. Huffaker (1958), demonstrated the crucial role of environmental heterogeneity in stabilising predator-prey systems. As a result of this discovery, further population models incorporating spatial heterogeneity have been formulated (Hassell and May 1973, 1974, Murdoch and Oaten 1975, Hassell 1980). Kaiser (1983), took the work of Huffaker (1958) a step further by demonstrating the role of size and *small-scale spatial heterogeneity* in stabilising predator-prey systems.

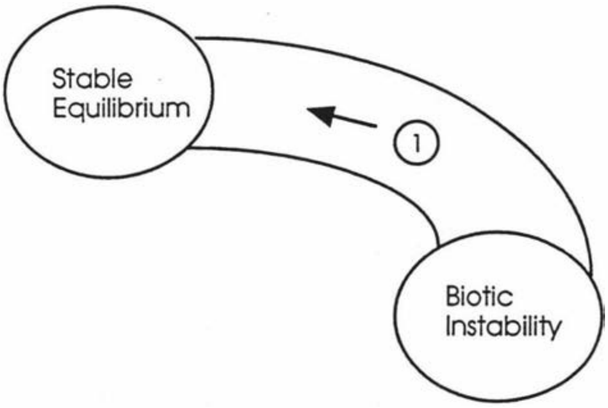


Fig 3.10 The Super-model of DeAngelis and Waterhouse redrawn to illustrate the location and nature of pathway one. In this pathway, various mechanisms work to restabilise a disturbed equilibrium system (redrawn from DeAngelis and Waterhouse 1987).

May (1975) and others have suggested that the stability of a community of competitors can be markedly affected by the addition of a higher trophic level. MacArthur (1972), further suggested that the activity of a predator that persistently switches its attention to the most abundant prey species at any time, might be capable of decreasing the limits of niche overlap consistent with stable equilibrium theory. Roughgarden and Feldman (1975) demonstrated that switching behaviour in predators can maintain a system of prey even where complete niche overlap occurs. Their model is a variant of the competition model of MacArthur and Levins (1967) and the classical predator-prey model of Lotka (1925) and Volterra (1926).

Building on the work of MacArthur (1972), May and MacArthur (1972) and May (1975), Comins and Hassell (1976) constructed an *n* dimensional prey system in the hope of finding a polyphagous predator, capable of increasing the stability domains of its prey (the competitors). The co-authors found that predator switching could produce stability, even when the prey species overlapped completely, or competition coefficients were greater than one. The co-authors conclude that in either case, predator switching allows predators *to coexist successfully with their prey over a wider range of conditions.* These results find general agreement with other research by Caswell (1978), Crowley (1979), Stenseth (1980), Tilman (1980, 1982) and Hassell and May (1973).

The response of a predator to changes in prey density is at the heart of the predator-prey-stability theory. A number of authors have explored this theme by connecting it with optimal foraging theory which suggests how predators will respond to changes in prey density (Schoener 1971, Krebs 1978, Abrams 1982, Sih 1984). The optimal foraging hypothesis, is based on an assumption that an optimal strategy exists, that will maximise the net rate of energy intake for a given species.

There have been a number of variations on the theme of predator switching. Kretzschmar *et al.* (1993), advanced the idea of direct and indirect interaction stabilisation. Murdoch (1969), showed that predator switching was associated with the strength of predator preferences and the opportunity to become trained to an abundant prey.

The dynamic nature of functional relationships is well illustrated by Estes (1990) and Dublin *et al.* (1990) who muster evidence for multiple population equilibria and seek to identify possible mechanisms for these feasible states.

3.5.1.2 Complexity, Connectivity and Stability

Gardener and Ashby (1970) and May (1972a, 1973), showed that as randomly connected systems become larger, they tended to be less stable near an equilibrium point - small deviations from equilibrium will tend to grow with time. For decades, the notion that increased complexity would stabilise ecosystem functional properties (see McNaughton 1977) had an intuitive and somehow irresistible appeal. It is therefore not surprising that the discovery of May (1972a, 1973), evoked a response of cautious re-evaluation on the part of many ecologists. Armstrong (1982), suggested that *MacArthur's* ... (1955) ... *argument, being so intuitively plausible, must be valid in some important sense.*

Austin and Cook (1974), assembled a model of a complex ecosystem and discovered unusual stability features. In conclusion, the co-authors suggest that with increased complexity, there is an increase in stable points due to compensating adjustments with increasing food web complexity. However, *stability declines, in the sense that the equilibrium points become less aggregated in the vector field* (Austin and Cook 1974).

DeAngelis (1975), demonstrated that a bias towards low assimilation efficiencies, strong self regulation in higher trophic levels, or increased donor dependence would serve to increase the probability of stability with increasing connectance.

Nunney (1980), used classical linearised ecosystem models to determine whether the explicit inclusion of specific nonlinear biological processes (*i.e.* greater realism), would improve ecosystem stability with increasing connectance. Nunney showed that the functional nature of a predator-prey relationship largely determined system stability with increasing ecosystem complexity. However, in a coarse grained (heterogeneous) environment (see Levins 1968), the central role of functional response disappeared.

Armstrong (1982), employed a two predator, two prey model for which the connectivity was continuously variable and found that the relationship between stability and connectivity was not a unitary problem. Some aspects of community stability reacted differently to the same change in connectivity. Armstrong (1982) concludes that MacArthur's (1955) conjecture that community stability was related to *patterns of interaction of the species forming a community* ... is correct, but ...*also shown to be a problem more complicated than MacArthur and others have supposed* .

3.5.1.3 Stabilising Operational Constraints

Taking a different approach to the stability/complexity hypothesis, Roberts and Tregonning (1980) do not assume classical equilibrium conditions. The traditional approach has been to assume equilibria and then to examine how the system reacts to departures from these conditions. The co-authors are critical of this *stability focus* and argue that one should first look *for factors which determine whether an equilibrium will be attained at all* ... noting that *the existence of an attainable equilibrium effectively guarantees stability anyway.*

The argument here raised is that for ecological systems to be mathematically feasible (*i.e.* all equilibrium states have positive values), certain properties of a system (constraints on structure and parameter values) must exist and be satisfied (Roberts and Tregonning 1980). The existence and operation of these constraints may also favour system stability. There appears to be some evidence to support this hypothesis.

Roberts and Tregonning (1980) present modelling evidence which identifies overlapping, nested, viable sub-systems, for which the co-authors claim there is *defence in depth.* Lawlor (1978) argues that real ecosystems have structural patterns which contribute to their stability (or lack of it). Gilpin (1975) evaluates the behaviour of a simple competitive system that appears unstable and random.

By modelling the system with a three dimensional system of Lotka-Volterra competition equations, Gilpin found that the system was capable of manifesting neutral or undamped oscillations. Two driving mechanisms appear to be involved. Neutral or undamped oscillations resulted from non-transitive (a competitive network) interference, while true limit cycles resulted from any mechanism that prevented local extinctions.

3.5.1.4 Stabilising Competitive Systems

May (1973) questioned the hypothesis of MacArthur (1955) (that web structure and community stability are related) by calling attention to four primary web features: species diversity, the nature of the interconnections, the number of connections per species and the intensity of interactions between web members. This focus has stimulated a search for stabilising mechanisms among researchers in a number of areas (see Pimm 1979).

The investigation of competitive communities stabilised by predation has a long history in ecology (Gause 1934, Lack 1949, Slobodkin 1961, 1964, Paine 1966, 1980, 1983, fig 3.11, Wilks 1994). A central idea in this research has been the hypothesis that local species diversity is related to the number *of predators in the system and their efficiency in preventing single species from monopolising some important, limiting requisite* ... like space.

Smith (1973), has suggested that trophic pathways might contribute little to ecosystem stability; the real answer may lie in the spatial patterning of the environment. Duggins (1983), demonstrated that some predators can stabilise a community, not only by reducing prey numbers, but by simply moving their prey around in space.

Fig 3.11 R. T. Paine *Local species diversity is directly related to the efficiency with which predators prevent the monopolisation of the major environmental requisites by one species* (Paine 1966) (from Paine 1984).

Different competitive strategies may also contribute to ecosystem stability by reducing the likelihood of competitive exclusion. Research on limit cycles in model communities (Gilpin 1975) and on competitive strategies in coral reef communities (Buss and Jackson 1975), has suggested that some systems may be characterised by competitive networks (Buss and Jackson 1979, Karlson and Jackson 1981), rather than the earlier idea of competitive hierarchies (Paine 1966, Dayton 1971, Connell 1975, Jackson and Buss 1975). The stabilising properties of competitive networks has been demonstrated in cryptic coral fish communities (Buss and Jackson 1979, Jackson 1979) and subtidal rocky substrata in New England (Osman 1977).

A hierarchy (*i.e.* a transitive pattern) occurs when all species of a higher rank out-compete all species of a lower rank, as illustrated for barnacle and mussel assemblages on temperate rocky intertidal shores (Paine 1974). Networks (*i.e.* non-transitive patterns), result when at least one species of lower rank out-competes one or more species of higher rank. The complexity of a network is enhanced with an increasing number of such reversals (*i.e.* feedback loops) (Buss and Jackson 1979, Karlson and Jackson 1981).

An underlying interest in much of the research into the operation, nature and stabilising properties of competitive interactions in ecosystems, has been to explain species diversity patterns. Vance (1985) points out that much of this research (*reviewed by* Armstrong and McGhee 1980), which focused on the question of coexistence, lacks explicit description of *how consumers use resources and how they interact with each other in seeking these resources.*

Petersen (1975) and Vance (1985), demonstrate theoretically that coexistence can depend upon species interference as well as resource exploitation properties.

Gillett (1962), Janzen (1970) and Connell (1971), concerned with explaining the high diversity of tropical rain forests, independently hypothesised that *natural enemies act to increase spacing within these tree populations through disproportionately high attack on progeny near adults* (Clark and Clark 1984). Ultimately, patterns of seedling recruitment, as influenced by seed dispersal, affect adult distributions (Janzen 1970, Connell 1971, Hubbell 1979, 1980). This bias in favour of species rarity has been supported by a review of twenty four woody plants (Clark and Clark 1984), and fieldwork investigating the relation between seedling survival and dispersal distance, light gaps and pathogens (Augspurger 1984). The persistence and stability of seed dispersed, forest species in island comunities has also been studied (Cohen 1970, Levins and Culver 1971, Slatkin 1974, DeAngelis *et al.* 1979).

3.5.1.5 Stabilising Predator-Prey Systems

Early experimental work on predator-prey systems (Gause 1934, 1936) had led to the conclusion among many ecologists that the predator-prey relationship is inherently self-annihilative. The long term persistence of such a system was thought to be dependent upon either immigration or the introduction of prey refuges restrictive to predators. Huffaker (1958), demonstrated that a predator-prey cycle could be extended to three successive oscillations by the introduction of spatial domain into laboratory experiments.

Park (1948) varied the spatial volume of competing species of *Tribolium* and was forced, by weight of evidence, to conclude that space was not important in determining the outcome of interactions. Park (1962) found similar results when attempting to manipulate the climatic conditions of *Tribolium* laboratory populations. Katz (1985) concluded that the predatory influence of the marine snail *Urosalpinx cinerea* effectively destabilised the prey population dynamics of the barnacle *Balanus balanoides*.

The research efforts which have characterised pathway one have focused upon identifying mechanisms that would restabilise disturbed equilibrium behaviour. The illustrations cited in this section cover a variety of mechanisms including: functional relationships, operational constraints, the influence of transitive and non-transitive pathways, climate and space. Much of this research involves modifications to classical equilibrium models, a fact which further serves to illustrate the inadequacies of these models and their simplifying assumptions.

As DeAngelis and Waterhouse (1987) have noted, the search for stabilising mechanisms has sometimes yielded negative results (Park 1948, 1962, Katz 1985). For this reason, *it seems unwise to .. base any theory of ecological communities solely on the notion of inherent stabilising mechanisms.* The discussion of pathway two (fig 3.12) evaluates the role of disturbance as a stabilising mechanism in biotically unstable systems.

3.5.2 *Pathway Two - Biotic Instability / Stochastic Stabilisation*

The commonplace observation of a single limiting resource supporting multiple species (coexistence), suggests that there exist in nature many groups of apparently competing species (Vance 1984). Early attempts to disprove the theory of competitive exclusion repeatedly resulted in the conclusion that such coexistence was just not possible (Volterra 1928, Lotka 1932, Rescigno and Richardson 1965, Levin 1970). Hutchinson (1953, 1959, 1961), turned the theory of competitive exclusion around and reasoned that the existence of multi-species systems supported by the same basic resources, must be suggestive of non-equilibrium conditions.

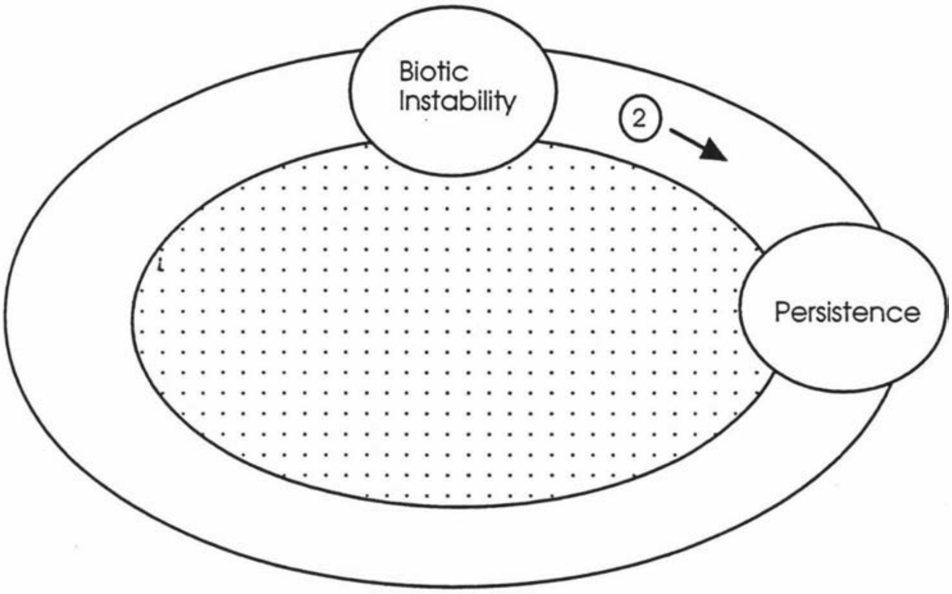


Fig 3.12 The Super-model of DeAngelis and Waterhouse redrawn to illustrate the location and nature of pathway two. In this pathway, disturbance acts as a stabilising mechanism in biotically unstable systems (redrawn from DeAngelis and Waterhouse 1987).

Hutchinson's (1961) idea that disturbance must interrupt the process of competition (fig 3.12) had earlier been suggested by Alex Watt (1947), who had studied pattern and process in terrestrial plant communities. Beginning with the work of Richerson *et al.* (1970), the notion of environmental disturbance as a stabilising factor in feedback-dominated systems received considerable attention. For some time, the intermediate disturbance hypothesis was considered to be the most likely mechanism for the non-equilibrium paradigm (Krebs 1985). The idea of disturbance moderated coexistence has found theoretical and empirical support in many branches of ecology.

Richerson *et al.* (1970), suggested that the coexistence of a high diversity phytoplankton community resulted from the slow mixing of lake waters, compared with the reproductive rate of the phytoplankton. This form of disturbance permitted phytoplankton communities to develop in distinct patches or temporary niches in space (Petersen 1975).

The explanations of Hutchinson (1961) and Richerson *et al.* (1970), are distinctly non-equilibrium compared with that of Petersen (1975), who advanced a mechanism which he claimed was capable of maintaining stable equilibria. In the Petersen model, an assemblage of coexisting phytoplankton may be limited by several nutrients, each species principally limited by the availability of a different nutrient.

Vance (1984) also argues for stable equilibria, claiming that traditional models *lack an explicit description of how consumers use resources and how they interact with each other in seeking these resources*. Vance overcomes these failings by describing competition mechanistically in terms of mathematical functions that depend on the morphological, physiological and behavioural properties of the organisms involved.

Apart from the occasional dissenter, evidence for the disequilibrium interpretation of Hutchinson (1961) appears to be growing. Loucks (1970) and Wright (1974) have suggested that the long term diversity and dynamics of forest communities are maintained by periodic *perturbations* (Loucks 1970). Similar conclusions are drawn by Kneidel (1984) who experimentally perturbed communities of carrion-breeding *Diptera*.

Grossman *et al.* (1982), evaluated data collected for over 12 years on stream fish assemblages and concluded that the *assemblage is ... regulated by stochastic factors*. Again, similar conclusions are advanced by den Boer (1968), who suggested that variation within natural populations, as well as in their environments, may result in a *spreading of the risk* of extinction resulting from environmental perturbations.

Connell (1978) and Sousa (1980), tested the intermediate hypothesis of Connell (1978) on tropical forests, coral reefs (Connell 1978) and intertidal algal communities (Sousa 1980). These authors not only found strong evidence of environmental disturbance as a stabilising mechanism, they were able to relate disturbance intensity to competition theory, confirming ideas that had earlier been expressed by Wiens (1977) and indirectly by other authors. Huston (1979) (fig 3.13) has attempted to reconcile non-equilibrium and competition theory in his dynamic equilibrium hypothesis.

As theoretical extensions of the fieldwork mentioned above, three different types of disturbance model have been advanced: (a) disturbances that affect population numbers directly, (b) disturbances that affect the resources that populations feed on and (c) endogenously generated disturbances caused by fluctuations in consumers and resources (DeAngelis and Waterhouse 1987).

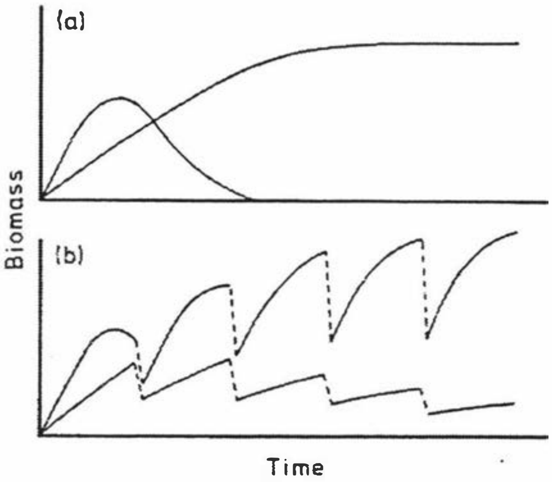


Fig 3.13 The effect of non-equilibrium conditions on the outcome of competition. (a) Simulation in which competitive equilibrium is attained by the K species. (b) Simulation in which competitive equilibrium is prevented by periodic disturbance. In this second case, the K species became extinct (from Huston 1979).

3.5.2.1 Disturbance that affects population numbers directly

In a model based on competition for space among marine bivalves, tube-building polychaetes and small crustaceans, Woodin and Yorke (1974) and Woodin (1981), discovered that long term persistence of these species was only possible with fluctuating rates of resource recruitment. Chesson and Warner (1981), building on the earlier work of Sale (1977, 1978), model the coexistence of coral reef fishes using a non-equilibrium model. The co-authors show that the probability of both species persisting is high, provided (environmental) variability (reflected) in birth rates is also sufficiently high. Leslie and Gower (1958, 1960), facilitated coexistence in an unstable predator-prey model by increasing the rate of mortality (a form of indirect environmental disturbance).

The intermediate disturbance hypothesis has been applied in differing natural systems and model forms. The modelling results of Huston (1979) (*i.e.* intermediate disturbance maintains high species diversity) have been confirmed in numerous cases: for filter feeding stream insects (Hemphill and Cooper 1983), for herbivorous *Diptera* and intertidal algae (Robles 1982), for a benthic stream community (McAuliffe 1984), for old field plant communities (Armesto and Pickett 1985) and for a tropical dry forest tree diversity (Hubbell 1979).

3.5.2.2 Disturbances that affect population resources

Levins (1979), programmed nonlinearities into the resources (R) of two competing species (N_1,N_2). In the absence of disturbance, N_2 would be competitively excluded. However, high values of (R) favoured the persistence of N_2. Kemp and Mitch (1979), apply the model of Levins (1979), to examine the hypothesis that physical turbulence in an aquatic system can modify interactive pressures between plankton populations and *allow coexistence of species competing for the same resource.*

DeAngelis and Waterhouse (1987) point out that an important distinction made in Levins application of the model is that the fluctuations in R provide two effective resources. The first resource is an averaged R^*, that is available to both species, the second is a high concentration of R, more readily available to species N_2. The interesting discovery presented in this work is that this form of resource partitioning results from temporal variation.

The effects of resource partitioning have some empirical support. Using Shannon's Diversity formula, Tramer (1969), shows that in breeding bird populations, diversity patterns are strongly correlated with *variation in the species richness (SR) component, the relative abundance (RA) component being relatively stable.* Tramer (1969), suggests that regulation of diversity by either the SR or RA component may represent alternative strategies suited to predictable / non-rigorous and unpredictable, rigorous environments, respectively.

Rotenberry (1978) and Nudds (1983), present results consistent with the hypothesis that in a stochastic environment, spatial heterogeneity or habitat patchiness (resource variability) may be more important than resource limitation and competition in determining bird community structure.

3.5.2.3 Endogenously generated fluctuations

Expanding on the work of Levin (1970), Kaplan (1970) and Koch (1974), Armstrong and McGhee (1976b) demonstrate that the resource partitioning manifested in the model of Levins (1979) and Kemp and Mitch (1979), can also be accomplished when the fluctuations are limit cycles. Powell and Richersen (1985) have provided empirical support for the Armstrong and McGhee (1976b) model with data from lake phytoplankton.

In summary of pathway two, it has become increasing evident that stochastic processes (often of intermediate intensity) play an important and varied role in moderating the adverse affects of biotic instability. In the next section, the activity of biotic restabilising mechanisms is evaluated, as a means of moderating the adverse affects of stochastically dominated populations and communities.

3.5.3 Pathway Three - Stochastic Domination / Biotic Compensation

As was illustrated earlier in this chapter, populations dominated by demographic and environmental stochasticity have a much greater probability of extinction. Two classes of possible biotic mechanisms (fig 3.14) have been identified - floors and ceilings.

3.5.3.1 Low Density Survival - Stable Floors

To explain the long term persistence of stochastically dominated populations, Errington (1946, 1947) has suggested that these populations may have compensatory mechanisms which ensure a higher probability of survival, when the populations reach low numbers - the idea of a stable floor (Strong 1984, 1986). There appears to be some empirical evidence to support this hypothesis.

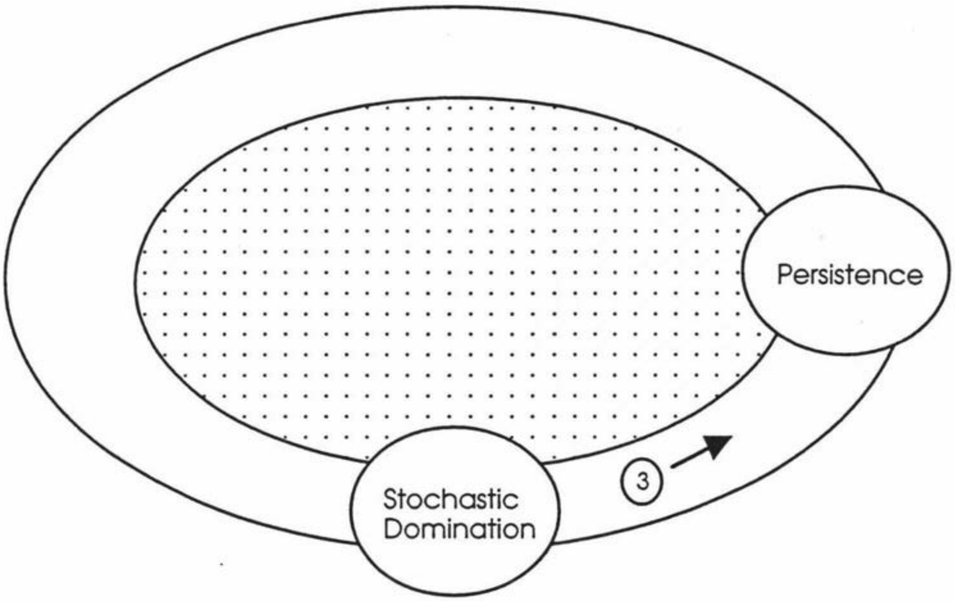


Fig 3.14 The Super-model of DeAngelis and Waterhouse redrawn to illustrate the location and nature of pathway three. In this pathway, biotic restabilising mechanisms act to moderate the adverse affects of stochastic domination (redrawn from DeAngelis and Waterhouse 1987).

Connell *et al.* (1984), found that seed recruitment for rare tropical forest trees, relative to more common species, was greater than would be predicted by simple linear proportionality. It appears that when a species is rare, the adverse affects of intraspecific competition may be reduced.

3.5.3.2 Low Density Elasticity - Stable Floors

In a more theoretical approach, Connell and Sousa (1983) suggest that ecological stability is composed of two important concepts - resistance and adjustment. An adjustment occurs when a given species is perturbed and returns to the same equilibrium point or limit cycle. Adjustment includes the idea of the amplitude of a disturbance and the elasticity (speed of return) of a response.

Errington (1939, 1940), studied the effects of drought and disease on North American Muskrat populations. The (speed of) recovery of the Muskrat population following local extinction was characterised by immigration and rapid reproductive return to former cyclic behaviour.

Lodge and Kelly (1985) studied the response of four snail species to one summer overkill event (the dramatic decline of a microphyte habitat under anoxic conditions caused by warm summer temperatures) in a shallow temperate pool. Following this sudden population crash, the co-authors observed that in the following year, the snail populations *showed relatively explosive and variable reproduction .. there were at least two generations with incomplete replacement*. Furthermore, the July cohort *had a high growth rate and itself reproduced in September-October* of the same year.

3.5.3.3 *Density Vague Regulation - Floors and Ceilings*

The concepts of floors and ceilings as mechanisms which ensure local species persistence has been elaborated on by Strong (1984, 1986) who referred to such behaviour as density vague regulation. A density vague population may wander a range of intermediate densities in response to environmental stochasticity. The danger of over compensation is prevented by ceilings of intraspecific competition (Milne 1962) and resource limitation (Pollard 1981), predation and emigration.

Floors may help to lessen the probability of population extinction at low density by mechanisms like those suggested above by Connell (1984) and Errington (1964, 1947). As illustrated in the example of Errington's (1939, 1940) muskrat studies, local immigration may provide the most effective floor. Another class of potential floors has been identified by Davis (1986). Process time lags may provide an important low density recovery mechanism for forest plant communities.

3.5.4 *Pathway Five - Stochastically Dominated Cells in a Landscape*

An attempt has been made to illustrate the significance of pathway five, in fig 3.15, by dividing the illustration into two distinct levels of ecological integration - the patch and the landscape.

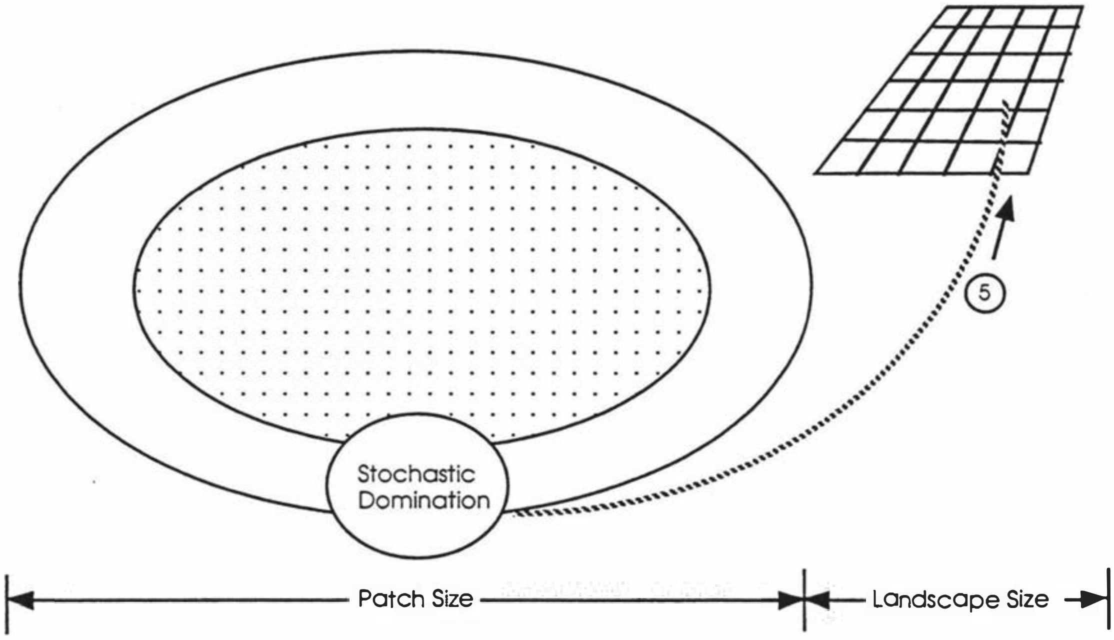


Fig 3.15 The Super-model of DeAngelis and Waterhouse redrawn to illustrate the location and nature of pathway five. In this pathway, an attempt has been made to add spatial extent to models of stochastic domination in order to enhance persistence (redrawn from DeAngelis and Waterhouse 1987).

The landscape level of integration is illustrated on the right hand side of the diagram, by a large landscape unit composed of many local cells (square units in this case). Pathway five connects the community type characterised by stochastic domination with the landscape level of scale.

Some ecologists have explored the hypothesis that stochastic domination may be stabilised by the addition of spatial extent (den Boer 1968, Reddingius and den Boer 1970 and Roff 1974a, b). The class of models used by these authors is based on the concept of a spatial *spreading of risk* (den Boer 1968).

3.5.4.1 Spreading of Risk Models

Most models of population dynamics assume that species resources are homogenous in space (*e.g.* Lotka 1925, Leslie 1945, Wiegert 1974, Bebbington *et al.* 1975, Anderson 1979, Hansen and Tuckwell 1981). In most cases, the reason for this assumption is that it simplifies mathematical analysis. It is now generally accepted that this assumption will be violated in most real populations - where resource distribution is usually patchy (Emmel 1976, Cowie and Krebs 1979, McNamara 1982). An illustration of resource patchiness occurs when areas of useable resource are separated by non-useable habitat. Observations of this kind led den Boer (1968) to propose the spreading of risk model.

There are two important ideas behind this class of model. Firstly, den Boer proposes that temporal variation and intensity has a spatial component. Natural populations reduce the danger of extinction by *spreading the risk* of local extinction from one to a number of places in a heterogeneous environment. Secondly, if a major perturbation event arises and local extinctions result, then locally extinct sub-populations can be restored by immigration from unaffected patches.

den Boer (1981) used the model described above to explain the regional coexistence of naturally occurring carabid beetles. den Boer (1981), concludes that *populations that are composed of large numbers of highly interconnected interaction groups (sub-populations) may show an impressive survival time, if the risk of extinction is sufficiently spread over a great part of these sub-populations.*

3.5.4.2 Dispersal Models

Vance (1984) evaluates a collection of dispersal models in order to examine the effect of dispersal on system stability. Vance (1984) concludes that dispersal mechanisms can exert either a stabilising or destabilising influence on the population growth process. In the models Vance evaluates, dispersal was found to increase stability in most cases, while those with opposite effect generally involved assumptions *unlikely* to be widely applicable in nature.

Dispersal between the cells of a landscape may provide a steady immigration which serves as a low density floor (Strong 1984, 1986). Connor *et al.* (1983), suggest that *the distribution and abundance of leafminers on oak should not be viewed as the turnover of reproductive populations on individual trees, but rather as the immigration and failed colonisation of species* *whose movements encompass several trees.* However, dispersal is not as simple a process as it might intuitively seem.

Gurney and Nisbet (1978) conclude that locally unstable populations in a patchy environment (containing N sites) can persist by balancing extinction and recolonisation. However, the long term persistence of such a population is feasible, *only if the average proportion of occupied patches is greater than a limiting value of order of magnitude* $3N^{-(1/2)}$.

Crowley (1977, 1981), shows that increasing the number of cells in a system can enhance stability, but only if the fluctuations in individual cells are asynchronous. Crowley (1977) suggests that his results imply that truly *natural ecosystems can be preserved only at scales large enough to provide stability and to quiet disruptive environmental noise.*

Fig 3.16 W. W. Murdoch. *Regulation arises as a result of potentially stabilising density dependent processes, even when brought about by non-equilibrium mechanisms* (from Murdoch 1994, MacArthur Award Recipient).

3.5.4.3 ***Biological Control Theory***

Finally, Murdoch *et al.* (1985), have evaluated this stochastic view of the landscape for biological control theory which they claim has traditionally focused on the notion of a stable pest equilibrium. Reviewing nine published cases of apparently stable pest equilibria, the authors demonstrate that *only one of nine real examples of successful control is convincingly a stable interaction.* In support of their non-equilibrium theory, the authors identify two possible strategies by which a natural enemy may control a pest in a non-equilibrium state.

Spreading of risk and dispersal theory is an attempt to add spatial extent to stochastic models in order to compensate for the higher probability of extinction associated with these systems. While the exact details of these stabilisation's are quite complex in some cases, it is evident that the addition of spatial extent generally increases system persistence.

The idea of adding spatial extent has also been applied to what DeAngelis and Waterhouse (1987) have called biotically unstable cells. The three different approaches to the problem are briefly discussed in the next section.

3.5.5 *Pathway Four - Biotically Unstable Cells in a Landscape*

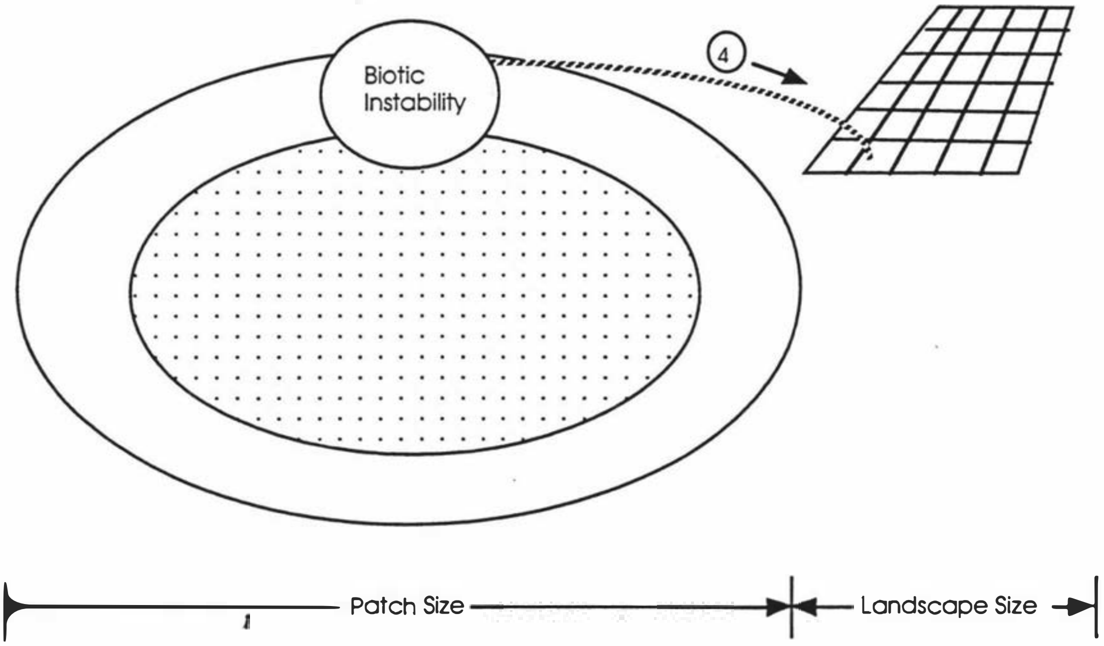


Fig 3.17 The Super-model of DeAngelis and Waterhouse redrawn to illustrate the location and nature of pathway four. In this pathway, an attempt has been made to increase persistence by adding spatial extent to biotically unstable populations (redrawn from DeAngelis and Waterhouse 1987).

The basic idea behind the class of models identified by pathway four (fig 3.17), is similar in spirit to the mechanism of extinction and recolonisation applied to the spreading of risk models. Populations in individual landscape cells are transient, but extinctions and recolonisations balance out over large landscapes composed of many cells. Most classical models of population dynamics (*e.g.* see reviews by: Royama 1971, Wiegert 1975, Van Dye and Abramsky 1975) assumed closed populations and thus no dispersal could take place. The models reviewed in the following section are exceptions to this traditional approach and can be categorised into three broad classes: deterministic dispersal and spatial extent (a), stochastic dispersal and spatial extent (b) and models which include both spatial extent and landscape heterogeneity (c).

3.5.5.1 *Models of Deterministic Dispersal with Spatial Extent*

The approach taken in these models is very similar in its mathematical form and was initially applied by Levins (1969), Cohen (1970) and later by Vandermeer (1973) and Slatkin (1974), for the simple case of two species and habitats of only one type. In these models, the state variables are not defined in terms of species densities, but the *numbers of habitats in a region which are colonised by each species* (Slatkin 1974). The variables $P_0, P_1, P_2,$and P_3, represent the fractions of the available habitat which are occupied by neither of the species (species 1 alone, species 2 alone or both species together). The rate of extinction, for each species individually or interactively, is defined as a probability per unit time. The rate of colonisation (Y) of an empty habitat by species 1, (Y_1), is proportional to the total fraction of habitats occupied by species 1 ($Y_1 = P_1 + P_3$).

The general results of this first model indicate that one species could still exclude another species from a geographic region, but not in a deterministic sense. Thus, the *equilibrium level of each species is determined by the parameters of the system and not by the initial conditions* (Cohen 1970). Furthermore, the models also demonstrate that predator-mediated prey coexistence is possible.

Levins and Culver (1971) produced a variant of the original model of Cohen (1970), however it led to the untenable result that a rare species was able to exclude another species from a region. Horn and MacArthur (1974), improved and extended the model of Levins and Culver (1971), to describe competition between two species over a mosaic of patches of two habitat types (1 and 2) for the respective fractions q_1 and q_2, of available patches actually occupied by species two.

The Horn and MacArthur (1974) model ignores direct reference to individual colonies or the number of habitable patches. The co-authors consider that these variables exert their influence through the various colonisation and extinction parameters. The main result of Horn and MacArthur's model is the definition of a criterion for species two to be able to invade a patchwork in which species one is already present, in equilibrial occupancy fractions $\hat{p}_1$ and $\hat{p}_2$.

Levins (1969), evaluated the consequences of environmental heterogeneity for biological control. Levins' (1969) model assumed that the local time scale was much faster than the regional one and that movement by individuals was possible between any two patches in the region. Hanski (1983) points out that these two assumptions are frequently incompatible and corrects these shortcomings in his own model. Hanski discovered that two like species may or may not coexist regionally, depending on the difference between the time scales and on the intensity of competition. In general, large differences in time scale tended to favour coexistence.

All of the above models were based on the assumption that the extinction rate is modified by the presence of other species (competitors) and migration rates from one habitat to another. Hastings (1978) adapted these earlier models to the case of two competing prey and one predator in an environment consisting of many discrete identical patches. One of the important predictions of Hasting's model was that intermediate levels of predation gave the greatest chance of prey coexistence.

All of the above models are based on assumptions of spatial homogeneity, unstable equilibria for individual patch cells and that the fractions of cells occupied by species over a large region have an equilibrium. In summary, it is assumed that spatial extent provides room for many species to coexist, although elimination can occur if *two or more species are confined to a single cell* (DeAngelis and Waterhouse 1987).

Armstrong (1976) constructed a variant of Levins and Culvers' (1971) model which assumed a heterogeneous environment The model was based on experimental work with two species of fungi and an unidentified species of *Penicillium*, grown in agar-filled petri dishes. Armstrong (1976), found that coexistence could be attained for the two species of fungi in a patchy environment *where local populations on occasion become extinct, with Penicillium playing the role of a fugitive species.* Fugitive species depend for their existence on an adequate supply of colonisable habitat, free of a previous occupant. The invasion of a fugitive species is accomplished by reproduction and dispersal that is competitively superior to that of the locally extinct species.

Fig 3.18 S. A. Levin. *Systems generally show characteristic variability on a range of spatial, temporal and organisational scales* (from Levin 1992, MacArthur Award Recipient).

Waser and Case (1981) have applied a modified version the fugitive species model to the coexistence of omnivorous forest primates in the Kibale forest, western Uganda. The model again illustrates that in complex communities, species abilities as fugitives can greatly affect their relative abundances. The assumptions of the Waser and Case (1981) model mean that it is not possible to determine if fugitive abilities alter the likelihood of coexistence.

Levin (1974), Yodzis (1977) and Allen (1983) have all investigated the hypothesis that spatial extent provides opportunities for the strategies of fugitive-type species. This work has been based on systems of reaction diffusion equations, advanced by Levin (1974) (fig 3.18) who uses population size variables for each spatial cell instead of the conventions described above which are variants of an earlier model of Levins (1969) and Cohen (1970).

Allen (1983) evaluates the behaviour of a Lotka-Volterra reaction-diffusion equation, in a heterogeneous environment. Allen (1983) shows that diffusion can alter the extinction or persistence of the Lotka-Volterra system. Random diffusion was shown to drive a competitive or predator-prey system to extinction, whereas a mutualistic system was shown to persist. Yodzis (1977) uses reaction-diffusion equations in a patchy environment to evaluate the likelihood of limit cycles in competing guilds. Yodzis (1977) shows that the likelihood of a limit cycle is high for increasingly complex (species rich) systems.

3.5.5.2 Models of Stochastic Dispersal with Spatial Extent

The deterministic class of models discussed in the previous section assume that the *possibility of stable equilibrium on the regional scale exists* DeAngelis and Waterhouse (1987). The next natural extension of these models was to stochastically determine migration transfers by Monte Carlo random number generation. In these models the possibility of stable equilibria over large spatial domains is not so obvious. For this reason, these models focus on the idea of persistence at larger spatial scales.

Hilborn (1975), explored the relationship between dispersal properties of predator and prey in a spatially complex environment by simulating the experimental system of Huffaker (1958). Hilborn concludes that for *spatially complex predator-prey interactions, a prime determinant of the system behaviour is the dispersal process.* Furthermore, Hilborn points out that traditionally most work on predation has concentrated on interaction within a given location and totally ignores the dispersal process.

Hilborn (1975) also found that an increase in the total number of system cells would increase the persistence of a system independent of the dispersal process. These results were later confirmed by Caswell (1978), who also notes that an increase in system cell number, reduced demographic stochasticity.

Hogeweg and Hesper (1981) introduced a new modelling framework called MICMAC which enabled them to model interaction within (internal cell dynamics) and between patches (migration dynamics). The within cell dynamics were governed by unstable deterministic equations - simulating a transient cell. Between cell migration, was driven by food shortages and density-dependency, rather than by random processes. The co-authors demonstrated that for their model formulation, episodic between cell migration gave rise to regional stability.

Using locally unstable Lotka-Volterra predator-prey systems, Zeigler (1977) also showed that regional persistence of locally unstable cells was impossible, when a discrete population exchange (migration) mechanism *is replaced by one of the continuous linear diffusion type.*

Similar results were found by Myers (1976) who used a more specific model to study the distribution and dispersal of insects among exhaustible food resources (food plants or cells). Myers (1976) found that those factors which tended to lead to resource exploitation *(high fecundity, low batch size and density-dependent dispersal),* all tended to reduce the persistence of the plant-consumer system. However, those factors which led to the maintenance of resource refuges *(episodic migration, large batch size and clumped egg batch distribution)* all tended to increase the persistence of the plant-consumer system.

These results in general find consensus among a range of modelling applications and predator-prey systems: a parasite-host system and a disease-host system (Hassell 1980), predator-mediated, non-equilibrium coexistence of tree-hole mosquitoes (Bradshaw and Holzapfel 1983), the effect of abiotic disturbance on a tropical butterfly population (Blau 1980) and a model simulation of two competitors based on resources division and aggregation of competitors (Atkinson and Sharrocks 1981).

The general conclusion of the models discussed in this section is that the exact nature of spatial dispersal can have an important effect upon the persistence of unstably interacting species. Once again, the details of individual models vary, but generally speaking, stochastic dispersal and spatial extent appears to stabilise biotically unstable systems. The next natural extension of these models is to add spatial heterogeneity to spatial extent. This class of model behaviour is investigated in the next section.

3.5.5.3 Models of Spatial Extent and Landscape Heterogeneity

There is an enormous amount of literature on the subject of modelling population and community dynamics in heterogenous environments. Detailed reviews of earlier research are given by Weins (1976), Giesel (1976) and Levin (1976). Two models are cited below as being indicative of the types of modelling work that has been undertaken in this area of modelling and field research.

As noted earlier, Horn and MacArthur (1974), improved and extended the model of Levins and Culver (1971), to describe competition between two species over a mosaic of patches of two habitat types (1 and 2) for the respective fractions q_1 and q_2 of available patches actually occupied by species two.

The Horn and MacArthur (1974) model ignores direct reference to individual colonies or the number of habitable patches. The co-authors consider that these variables exert their influence through the various colonisation and extinction parameters. The main result of Horn and MacArthur's model is the definition of the criterion for species two to be able to invade a patchwork in which species one is already present in equilibrial occupancy fractions $\hat{p}_1$ and $\hat{p}_2$.

Depending on the migration and extinction rates, stable coexistence was possible even between closely related species. The model of Horn and MacArthur (1974) is more fully evaluated by Levin (1974).

Comins and Blatt (1974), studied the effects of spatial heterogeneity on models of predator-prey systems. Their model environment was graded from favourable to unfavourable, which introduced the possibility of the prey taking refuge in a place less favourable to the predator. The co-authors modelled the response of the prey to this one-dimensional, heterogenous environment, by using an advection-diffusion equation which biased the movement of the prey toward a fertile area. The interaction of the prey and predators is described using Lotka-Volterra equation terms.

The co-authors test several model applications and show that the stability of the system is enhanced by introducing environmental heterogeneity, *and that this feature is not highly dependent on the details of the model chosen.* Secondly, the co-authors point out that it was not necessary to have inaccessible regions or discontinuity's in the environment in order to observe refuge behaviour. This effect was produced by a simple one dimensional gradient. Finally, the stabilising effect of heterogeneity was apparently not produced by simple diffusion or predator-prey behaviour. Comins and Blatt (1974) speculated that this effect might be due to the averaging out of slightly out-of-phase population cycles.

Models that include spatial heterogeneity have been applied across a vast field of empirical work which now appears to indicate that species coexistence is better explained by spatial and temporal heterogeneity, than by the behaviour of classical equilibrium theory as based on resource partitioning (DeAngelis and Waterhouse 1987).

3.5.6 Summary

Section five on persistent community behaviour has explored a diverse range of modelling applications and results which focus on two areas of community behaviour. Firstly, these publications record the efforts of some theoretical and field ecologists to identify and incorporate stabilising mechanisms into classical equilibrium models. Secondly, a larger portion of this research represents an attempt on the part of theoretical and field ecologists to moderate the adverse affects of biotic instabilities and stochastic domination in ecological communities.

3.5.6.1 Can a Disturbed Equilibrium State be Restabilised?

This review covers five main classes of mechanisms which have been explored and applied to classical equilibrium models in attempts to stabilise disturbed equilibrium behaviour. These mechanisms include: functional relationships, increased web complexity, operational constraints, variations to competitive and predator-prey systems. There are a number of observations and conclusions which may be drawn from this review.

Firstly, the stabilising mechanisms which have been built into these models are extensions of classical equilibrium models. This fact represents a further line of evidence concerning the inadequacies of the simplifying assumptions evident in classical equilibrium models. Secondly, this research provides an illustration of the ways in which classical equilibrium models can be modified and applied, in order to test hypotheses concerning the adequacy of classical assumptions and the nature and behaviour of the equilibrium systems they model. There is still much research that can and will be undertaken in this area.

Thirdly, it is difficult to draw firm conclusions concerning the nature of these results. In some cases, it is evident that the application of the five mechanisms listed above does lead to increased system stability. However, there certainly are exceptions to these trends (Park 1948, 1962, Gardener and Ashby 1970, May 1972a, 1973, Austin and Cook 1974, Gilpin 1975, Nunny 1980, Roberts and Tregonning 1980, Katz 1985, Vance 1985).

It must be admitted that an equally impressive list of publications could be mustered to support those mechanisms which clearly do restabilise a disturbed equilibrium state. Furthermore, the exceptions listed above are not all clear cut. Many of these papers record results which are subject to operational thresholds and working assumptions. In other cases the system is found to be more complex than initially suspected.

In conclusion, these results do suggest that the assumptions of classical models are inadequate. The inclusion of greater mechanistic complexity appears to stabilise these systems in some instances, although this is usually subject to further assumptions and in many cases operational thresholds and increased ecological complexity. If stable equilibria exist for natural populations and communities, it seems likely that such a state will be transient and buried beneath a complex framework of mechanistic nonlinearities and organisational complexity.

For these reasons, this type of research evidence cannot be used to support the equilibrium paradigm of community organisation. It is not surprising that the remaining four non-equilibrium pathways reviewed in this section have *seemingly opened up richer areas of investigation than the first* (DeAngelis and Waterhouse 1987).

3.5.6.2 *Can a Non-equilibrium State Persist?*

The four non-equilibrium pathways may be divided into two categories based on differing technical and theoretical approaches. The objective has been to stabilise non-equilibrium behaviour. The two classes of mechanism investigated are: (i) spatial extent and inter-cell dispersal and (ii) stochasticity and biotic feedback. Many of the comments already made concerning attempts to stabilise classical equilibrium models can also be made for the results of the four non-equilibrium pathways.

Firstly, the results are not clear cut. While there is generally a strong trend in favour of restabilisation, many of these results have uncovered greater mechanistic complexity and are subject to operational thresholds and working assumptions (Tramer 1969, Levins 1969, Cohen 1970, Horn and MacArthur 1974, Petersen 1975, Crowley 1977, 1981, Myers 1976, Zeigler 1977, Hastings 1978, Gurney and Nisbet 1978, Huston 1979, Chesson and Warner 1981, Hogeweg and Hesper 1981, Allen 1983, Vance 1984, Murdoch *et al.* 1985, Davis 1986).

However, in the case of non-equilibrium models, the discovery of loose assumptions, increased organisational and mechanistic complexity, is very much in keeping with the spirit and nature of these incredibly complex, dynamic and probabilistic systems. However, a very real limitation of these models is that many, if not most, of those cited here do not prove causality, they assume it. Rigorous empirical studies are now needed in order to apply and test these models and their mechanism on field data.

The 1970s saw the beginning of a significant shift in the way ecologists viewed ecological populations and communities. The last three and a half decades of research in this area confirms the inadequacy of classical equilibrium theory and represents the beginning of a distinctly new era in theoretical ecology and ecological modelling. DeAngelis and Waterhouse (1987) suggest that this new approach may *eventually introduce new rigour into the classical approach.* Furthermore, this new approach may also form the basis for determining *the temporal and spatial scales on which the equilibrium models are valid approximations of the dynamics* of natural populations and communities.

There remains one final question to investigate in this chapter. The present study has been largely limited to the patch or cell level of scale. The addition of spatial extent and dispersal mechanisms, was undertaken in order to determine the feasibility of *long term persistence* for non-equilibrium communities.

A further hypothesis suggests that it is unreasonable to look for equilibrium behaviour at the cell or patch level of integration, since these small scale systems are always in a state of change (Connell 1979). At a larger landscape level of organisation, emigrations and immigrations may balance out in such a way that these large scale systems manifest emergent equilibrium behaviour. The identification and definition of community behaviour must be undertaken with reference to observational scale (Levin 1992).

3.6 The Problem of Observational Scale

In section five of this chapter, the main objective has been to review models which attempt to demonstrate the feasibility of persistence for the haviour of transient populations, viewed at the cell or patch level of tegration. The success of modelling work of this type may suggest that non-uilibrium behaviour is the norm, for natural populations and communities of e real world. One problem with this view is that non-equilibrium behaviour ay also be an artefact of small spatial scales. In the following discussion, this ypothesis is referred to as *the problem of observational scale.*

The problem of observational scale has often been evident between cologists who have studied the same systems at differing temporal and spatial cales. (Anderson *et al.* 1981, Sutherland 1981, Sale and Williams 1982, Sousa 984a, Wiens 1984, 1989, Chesson and Case 1986, DeAngelis and Waterhouse 987, Sale 1988, Levin 1992). It is now evident, that a perception of *equilibrium* or *on-equilibrium* behaviour is dependent on the scale of observation (Wiens 989).

Not surprisingly, the topic of scale in ecology has received much attention n recent times (Levandowsky and White 1977, Allen and Starr 1982, Kaiser 1983, Flenley 1984, O'Neill *et al.* 1984, Davis 1986, Allen *et al.* 1987, Wiegert 1988, Wiens 1989, Allen and Hoekstra 1990, Holyoak 1994, Costanza and Maxwell 1994).

Levin (1992) has suggested that the question of just how the scale of observation influences the description of pattern is of central importance to ecological theory. Levin points out that each individual species experiences the environment on a unique range of scales (see Allen and Hoekstra 1990) and thus responds to variability on an individual basis. Therefore, no description of the variability and predictability of the environment will make sense, without *reference to the particular range of scales that are relevant to the organisms or processes being examined.*

Levin (1992) sets forth a number of guidelines, relating the need for clarification of the observational scale problem to just how this might be accomplished. Earlier on, Wiens (1989) had suggested that *current theory provides little guidance as to what we might expect.* Historically and more recently, the problem of observational scale has been tackled in three main ways.

Firstly, classical equilibrium models simply assumed that scale wasn't important. Secondly, a more recent trend involves the study of transient patches, based on an assumption of non-equilibrium conditions. These models also assume that the dynamics of a forest gap are representative of a larger non-equilibrium landscape system. Forest gap models, formulated on the individual-based-modelling paradigm, have produced some very impressive results in efforts to match field data with a predictive model.

Finally, another recent modelling trend involves actual attempts to test for stable equilibria in landscape systems composed of transient patches. These three main approaches are briefly discussed and illustrated in the following section.

3.6.1 Classical Equilibrium Models

Firstly, classical equilibrium models in ecology simply assumed that scale was not important (Hallam and Clark 1981, Ziswiler 1967, Gause 1935), and treated communities as closed, integrated, deterministic, homogeneous units (Clements 1916, 1928, 1936, Royama 1971, Wiegert 1975, Van Dye and Abramsky 1975). These models are simplifications of real systems and have provided a starting place to begin analysis. However, each of these assumptions must be relaxed if ecologists are to understand the factors governing the diversity and dynamics of real ecosystems (Levin 1992).

3.6.2 Modelling the Transient Patch

A second approach has emerged in more recent times which involves attempts to model transient patches by relaxing classical assumptions of equilibrium behaviour - an approach that reflects the individualist school of succession theory (Gleason 1926, 1939). There are two main subclasses of transient patch models: variants of traditional models and non-traditional individual-based-models.

3.6.2.1 The Transient Patch - Variants of Traditional Models

This first class of transient patch models are an extension of the traditional modelling paradigm in ecology. These models were usually deterministic and used some index (density, diversity or spatial component) as the state variable. Non-equilibrium, stochastic and spatial dimensions could be added to these models with increased mechanistic (and computational) complexity (eg. Gilbert and Hughes 1968, 1971, Levin and Paine 1974, 1975, May and Andersen 1978, Paine and Levin 1981, Roughgarden *et al.* 1985, Murdoch *et al.* 1985,).

These aggregated models, in general, have demonstrated greater realism than their simpler counterparts. However, a frequent criticism of this first class of models is that the addition of mechanistic complexity occurs at the cost of generality. The quest for generality in ecology began at least as early as the mid 1950s (reviewed by Macintosh 1985) and has been marked by vigorous debate (Ruse 1973, Mayr 1988).

Huston *et al.* (1988) argue that even these more complex variants of traditional ecological models ignore two fundamental aspects of biology: *that all individuals are different, whether by genetics or environment or both and that interactions between individuals takes place locally* (Judson 1994). These criticisms have stimulated the development of a new class of individual-based-models (IBMs).

3.6.2.2 Transient Patch - Individual-Based-Models (IBM)

This second class of individual-based-models has also arisen as a result of other perceived shortcomings in traditional ecological models. May's (1974) observation of complex dynamics and chaotic behaviour in simple nonlinear equations was suggestive of previously unforseen (or assumed) limitations in ecology's traditional modelling paradigm. Judson (1994) suggests that the lessons of chaos are *that simple principles will be the exception, incidents of history are important and that, because predictions are impossible, the only way to find out what is going on in some dynamic system is to simulate them exactly.* Hence the rise of individual-based-models (IBM) (DeAngelis and Gross 1992, Judson 1994).

The application and use of IBMs in ecology is increasing (Gilbert and Hughes 1968, 1971, Botkin *et al.* 1972a, b, Ek and Monserud 1974, Maguire and Porter 1977, Shugart and West 1977, May and Anderson 1978, Pickett and Thompson 1978, Karlson and Jackson 1981, Menges and Loucks 1984, Slatkin and Anderson 1984, Roughgarden *et al.* 1985) even though there are serious questions concerning their utility.

Huston *et al.* (1988) have suggested that individual based models will unify ecological theory. Other ecologists have questioned whether IBMs are sufficiently general to be useful (Murdoch *et al.* 1992, Lomnicki 1992). Metz and de Roos (1992) question whether the results of IBMs are anything more than an artefact of their construction. One class of individual based model is of particular relevance to the present thesis and will be briefly discussed in order to illustrate the application of IBMs to the problem of observational scale.

3.6.2.3 The Application of IBMs

The model JABOWA (Botkin 1972a, b), was first developed as a collaborative research effort between scientists of the Individual Based Modelling T. J. Watson Research Centre and ecologists from Yale university, who were involved in the Hubbard Brook Ecosystem study. Even though JABOWA was not used extensively in the Hubbard Brook study, its basic concepts (and much of its FORTRAN code) were used to proliferate a host of closely related forest succession and gap models (Shugart 1984, 1990).

JABOWA was first applied by Botkin (1972a, b) to simulate forest succession in Northern Hardwood forests. Since this pioneering study, the IBM concept has been applied by a growing group of researchers, interested in a range of causal mechanisms thought to be responsible for the dynamics of forest patches or gaps. The fundamental modelling unit in these models is the forest gap, hence the name of *forest gap, forest stand* or *forest succession model*. .

Gap models operate on the assumption that gaps in a forest canopy, formed by the death and fall of a canopy tree, become the localised sites of regeneration and growth. Jones (1945), Watt (1947), Bray (1956) and Curtis (1959) all considered that mature forest ecosystems could be considered as the relatively consistent average of regeneration in forest gaps (see Waring and Schlesinger 1985). The dynamic changes that occur in a forest ecosystem across a landscape, are represented in gap models as an aggregate response of homogeneous mosaic patches - a standard mathematical simplification. Shugart (1984) points out that a more complex alternative would be to represent the time and space dynamics of a forest ecosystem by partial differential equations.

Following the fall of a canopy tree, local regeneration occurs as a result of root sprouting and the introduction of local and external seed sources. The model's gap is small enough that the growth of each tree can be modelled. Annual tree increment (diameter in Botkin's 1972a, b, initial application) is expressed as a function of weather, competition and other factors as determined by a standardised equation (40),

$$\frac{d\left[D^2H\right]}{dt} = rL_a\left(1 - \frac{DH}{D_{\max}H_{\max}}\right). \qquad (40)$$

where

D is the tree's diameter
H is the tree's height
L_a is a leaf area index
r is another parameter affecting the growth rate
$D_{\max}$ maximum tree diameter
$H_{\max}$ maximum tree height

The growth equation (40) is based on the assumption that tree volume is a function of a tree's diameter D squared, times the tree's height H and that tree growth is based on an annual volume increment. The alternative parameters r, $D_{\max}$ and $H_{\max}$ can be related through empirical data to a range of environmental conditions such as relevant site factors, competition, climate, atmospheric conditions and soil type etc. Stochastic mortality for gap trees is determined annually according to a preset growth threshold value. Variation in the spatial scale of a model gap was investigated by Shugart and West (1979) who concluded that an optimal model gap size was between 0.04-0.08 ha. for a forest in which gap phase replacement is an established phenomena.

As mentioned earlier, the single most important operational assumption of gap models is that the local dynamics of a transient patch are representative of landscape dynamics. This assumption is defended by Shugart (1984). In terms of performance, gap models certainly appear to be capable of behaviour which shows impressive correlation with field data in some cases. Solomon (1980, 1981), used the FORET model to predict the long term behaviour of the forest vegetation surrounding Anderson Pond in White Country, Tennessee. The predictions of the FORET model were then placed alongside a percentage pollen diagram produced from a core sample taken from the lake sediments of Anderson pond (Delcourt 1979).

The temporal pattern of arboreal vegetation for the past 16,000 years (fig 3.19), (as recorded by fossil pollen data) was found to be in good agreement with the behaviour predicted by the FORET model (fig 3.20). The main driving mechanism of the model was climate variations, considered by Delcourt (1979) to be appropriate for eastern Tennessee for the past 16,000 years. As a test of goodness of fit, Solomon *et al.* (1980) calculated correlation coefficients for each 500 year segment of data. The correlation coefficient was significant in all twenty two cases analysed, while the r^2 values averaged ca. 0.5 (an r value of ca. 0.70) across the entire simulation. Such correlation is very impressive for data as variable as pollen data.

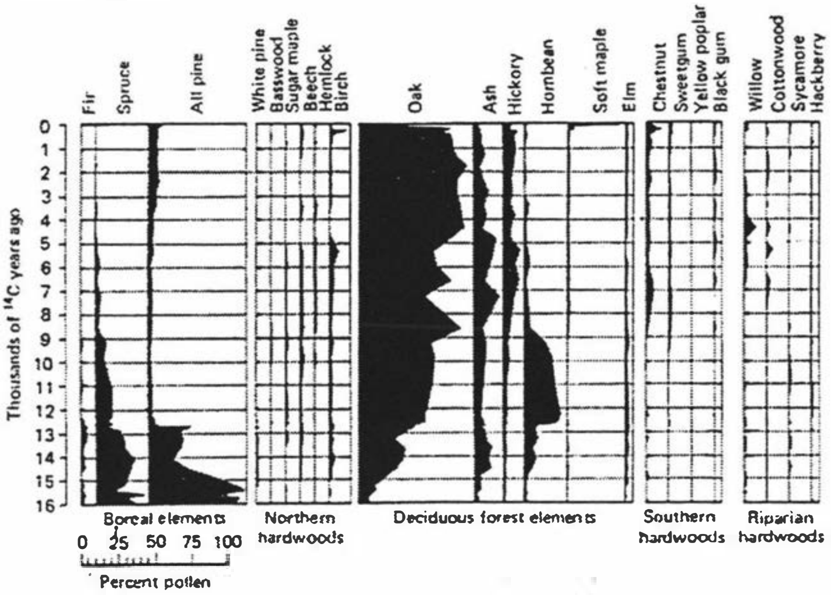


Fig 3.19 Arboreal pollen diagram from Anderson Pond, White County, Tennessee, for the past 16,000 ^{14}C years (from West *et al.* 1981).

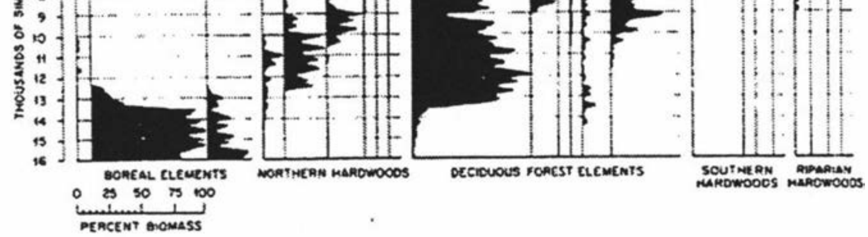


Fig 3.20 Simulated forest composition for the last 16,000 years (from West *et al.* 1981).

Shugart (1984) suggests that *extended tests on the ability of a model to predict forest composition can be a reasonably reliable way of gaining confidence in the model's reliability.* Climatic data and plant species immigration data, were both inferred from the fossil pollen data. The fossil pollen data was not corrected with r values (representation values, see Davis 1963) before the calculation of pollen percentages (ref. Davis 1963, Webb *et al.* 1978).

The versatility of gap models like FORET and JABOWA is also to be admired. Variants of the initial model formulation (Botkin *et al.* 1972a, b) have been applied to test the following: the response of a forest to chronic air pollution (West *et al.* 1980), forest response to timber harvest (Shugart *et al.* 1980), forest response to differing management techniques (Shugart and West 1981), the response of high altitude *Eucalyptus* forest to fire disturbance (Shugart and Noble 1981), delayed immigration due to climate change (Solomon *et al.* 1981), the impact of chestnut blight in an Appalachian deciduous forest (Shugart and West 1977), the response of forest to increased greenhouse gas concentrations (Emanuel 1977), the potential consequences of global climate change (Shugart 1990, Shugart *et al.* 1992, Smith *et al.* 1992), forest response to the effects of site conditions and disturbance (Fulton 1991), the impact of herbivory on forest growth (Dyer and Shugart 1992), and the model's performance against remotely sensed data (Weishampel *et al.* 1992).

The above list is by no means exhaustive, but serves to illustrate the incredible versatility of this modelling paradigm. In many of these cases, long term fossil pollen data was not available, in which case the model's behaviour has been verified using standard space-for-time substitution techniques. A range of applications with fossil pollen data and model limitations are cited by Solomon and Webb (1985).

DeAngelis and Waterhouse (1987) suggest that the possibilities for direct verification in the field and detailed modelling of local dynamics have a great appeal to many empirically minded ecologists. Furthermore, some theoretical ecologists regard the transient dynamics of patches as an essential consideration in the design and management of nature reserves, where extinction is a dominant population process (Pickett and Thompson 1978). Models of transient patch dynamics can also be extended to larger spatial scales to enable the evaluation of equilibrium behaviour at the landscape level of integration.

3.6.3 Landscape Dynamics

The study of landscape dynamics has been undertaken in order to test for the existence of stable equilibrium conditions at larger scales of observation. At the landscape level of scale, dispersal processes may work to balance out variations in species abundance, caused at the patch level of scale by local extinction. DeAngelis and Waterhouse (1987), point out that even regional equilibria may be thought of as transitory in nature. Over suitably long time periods, climatic shifts and regional stochasticity (Shugart 1984) and biotic instabilities may result in species extinction at a regional scale (Shugart and West 1981).

The models used to study landscape dynamics are variants of classical equilibrium models, adjusted for mechanistic and spatial complexity. Even though the mathematical detail is different, these models all show that equilibrium behaviour *is obtainable asymptotically by scaling up the spatial dimension* (DeAngelis and Waterhouse 1987).

Crowley (1979) constructed a spatially distributed analytical predator-prey model based on an earlier resource limiting, deterministic version of a simulation model by Caswell (1978). Caswell (1978), had earlier shown that the predator population worked to extend the persistence of the model system for which Caswell could find no equilibrium state. Crowley (1979), found that *conceptually shrinking* the system from an infinite number of cells to a finite number, introduced demographic stochasticity. This form of internal instability increased the probability of extinction of one or more species within a given time interval.

Crowley (1979) then increased the number of system cells toward infinity and identified a large region of parameter space where the system manifested stable equilibria.

Levin and Paine (1974) and Paine and Levin (1981) are critical of research efforts which ignore interregional interactions and concentrate on the equilibrium properties of closed systems. To overcome this spatial weakness, the co-authors view their study communities (intertidal mussel populations) as a regional system of component islands or patches. The overall system patterning of these communities is shown to be a balance *reached between extinctions and immigration and recolonisation abilities of the various* (component) *species* (Levin and Paine 1974, see also Levin 1969, 1970a). The co-authors use a system of input-output, partial differential equations, which recognise the stochastic nature of the local patch environment and allow for comparisons of areas with differing levels of disturbance.

Slatkin and Anderson (1984), have developed a modelling approach similar to that of Maguire and Porter (1977) who defined area (in their model) as a set of discrete square cells. The objective of Slatkin and Anderson's (1984) study was to analyse competition for space in coral growth. The co-author's model (41) is deterministic and almost parameter free, with the except of D, the initial density.

$$F(R)=\frac{1}{1+2\pi R^2 D}, \tag{41}$$

where

$F(R)$ is the probability of achieving radius R

D is the initial density.

Each individual is assumed to occupy a certain area and grows into a circle of increasing radius (R) according to a specified growth law, $R(t)$, which gives the radius measured in arbitrary units of time t after its birth. The co-authors assume that coral growth is continuous in space until it touches another individual, at which instant one or the other dies and immediately disappears.

The probability $F(R)$, that an individual survives to size radius (R) is given by equation 41. Slatkin and Anderson found that the model produced an *equilibrium distribution* of coral sizes.

3.6.4 Summary

Research approaches to the problem of observational scale can be categorised into three classes. Firstly, classical equilibrium theory ignored the problem of observational scale. A second, and more recent trend has been to relax classical assumptions of equilibrium behaviour and to model the patch level of scale as a sub-landscape unit with transient dynamics. Individual-based-modelling, (IBM) is a new modelling paradigm which has been developed, at least in part, to overcome perceived shortcomings in the use of classical models to study patch dynamics.

An important application of IBMs was introduced to ecology by Botkin *et al.* (1972a, b). Forest gap models such as JABOWA and FORET have made an impressive and important contribution to the study of non-equilibrium patch dynamics. The power of these models lies both in their application to a diverse range of causal mechanisms and in the quality of their predictions. Once again, it is the purpose of such models to identify association between possible causal mechanisms and patch behaviour. To prove causality is a different and more complex problem which will probably remain the domain of future empirical studies.

A third approach to the problem of observational scale has been the application of modified classical models to study the dynamics of landscape / regional / large spatial systems. Levin (1969, 1970a) referred to modelling of populations in large spatial systems as a study of metapopulation dynamics. A metapopulation (according to Levin 1969, 1970a), consists of a balance between colonisations and extinctions in large spatial systems (see Hastings and Harrison 1994). The notion of a metapopulation has been applied to the study of both *persistent* and *emergent equilibrium* behaviour in systems which include spatial.

For example, the present section has been concerned with equilibrium behaviour as an emergent property of large spatial scales. This form of equilibrium is an asymptotic limit of increasing size and not an intrinsic property of the system. In this sense, it is very different from the classical notion of stable equilibria which was an intrinsic property of the ecological model being used.

However, Levin's (1969, 1970a) definition of a metapopulation model is more broad and includes the modelling of individual cells with transient dynamics as components of a larger system in which *persistence* can be calculated. Although these two approaches are similar in spirit, they are designed to test distinctly different hypotheses.

In conclusion, the behaviour of model systems with spatial extent has been evaluated in this chapter in terms of both persistence and stable equilibria. These two views of community behaviour are closely related, in that they both have fundamental units based on non-equilibrium behaviour. Both model systems are connected by dispersal mechanisms and yet both systems can be defined in terms of characteristically different behaviour at large spatial scales.

The above conclusion suggests that it will probably be difficult to define a set of rules which will be appropriate to the behaviour of every metapopulation. For this reason, future development and application of metapopulation modelling may help to identify the limits of scale for which non-equilibrium and emergent equilibrium behaviour are appropriate definitions of systems with large spatial extent. As Levin (1992) has suggested, no description of the variability and predictability of the environment will make sense without *reference to the particular range of scales that are relevant to the organisms or processes being examined.* Consequently, the topic of ecological scale is likely to feature as a high priority in studies of community behaviour in the future.

3.7 Working Hypotheses

An objective of chapters two and three has been to define a set of working hypotheses based on current developments in theoretical ecology. The hypothetico-deductive scheme of hypothesis testing involves a number of important conceptual problems related to ecological modelling work (Mentis 1988). These issues will be considered more fully in chapter four which outlines the methodological approach used in this research project. The remainder of this section will be concerned with defining a set of non-equilibrium hypotheses derived from the review and evaluation of published work set forth in the present chapter.

3.7.1 The Equilibrium Hypotheses of Chapter Two

An objective of chapter two was to evaluate the historic, mathematical and ecological significance of equilibrium theory in ecology. Insights from this discussion led to the formulation of a series of equilibrium hypotheses. In order to test the explanatory power of these hypotheses a set of competing or alternative hypotheses is required (Platt 1964). Alternative theories might be genuine attempts at explanation or one might be a null hypothesis.

According to Strong (1980), a null hypothesis expresses the possibility that nothing has happened, *that a process has not occurred, or that change has not been produced by the cause of interest.* In this context, the use of null hypotheses are particularly helpful to test for the existence of alternative models of organisation and operation. Strong (1980) is critical of the paucity of null hypothesis testing in ecological research and cites numerous examples of theoretical controversies which might have been avoided.

Another approach to the statement of an alternative hypothesis is simply to define an alternative theory (or explanation) from which competing hypotheses and model constructs can be defined. This approach is not always possible because it is generally not known exactly what conditions might exist in the absence of assumed behaviour. In the case of community organisation, the non-equilibrium paradigm does provide an alternative explanation to classical equilibrium theory.

3.7.2 *Hypotheses Derived from the Non-equilibrium Paradigm*

Chapter three has reviewed the development of research into the non-equilibrium model of community organisation, a trend which began in ecology during the early 1970s. This body of theory and research will now be used to define alternative non-equilibrium hypotheses.

As was stated earlier, the limitations of fossil pollen data precludes the testing of every hypothesis derived from the non-equilibrium paradigm. While this is true, it is important to test and develop theory in relation to a base theory so that it is possible to assess the extent to which a new model formulation fits into the background predictions and explanations of existing theory. To keep things as orderly and simple as possible, the seventeen equilibrium hypothesis of chapter two are restated below as prediction of non-equilibrium community organisation and behaviour. Below each of these seventeen hypotheses are insights and refinements (in italics) gained from the present study of the non-equilibrium paradigm.

The reason for this approach is to commensurate equilibrium and non-equilibrium hypotheses into a common system of predictions and explanations. This will make the evaluation of the explanatory and predictive power of these hypotheses a much easier task.

1. Communities are open systems:
   - *immigration and migration assist in counteracting the negative affects of biotic instabilities and demographic stochasticity,*
   - *for small, spatially localised populations, isolated from new immigration and subject to stochastic fluctuations, extinction is inevitable.*
2. Present behaviour is influenced by past events (*i.e.* time lags):
   - *chaotic behaviour (overcompensation) requires the operation of time delays in negative feedback loops,*
   - *time lags will tend to destabilise a small scale spatial system,*
   - *reaction time lags exist for ecological systems,*
   - *reproductive time lags exist for ecological systems,*
   - *stability is feasible when the characteristic return time (T_r) is greater than both the reaction and regeneration time delays,*

- *reaction time lags can determine the outcome of a competitive interaction,*
- *historic events shape contemporary behaviour by the activity of time delay processes,*
- *long lived species such as trees respond to environmental fluctuations with considerable lag time.*

3. Patches are of heterogenous composition:
- *spatial heterogeneity stabilises predator-prey systems,*
- *spatial heterogeneity has a stabilising effect on systems of large spatial scale, subject to the nature of diffusion processes and variation in migration and extinction rates.*

4. Landscapes are composed of component patches:
- *increased complexity, web connectance, and interaction strength tends to destabilise community behaviour,*
- *both stochasticity and strong biotic feedback reduce the persistence of local landscape cells.*

4a. Adding spatial extent to stochastically dominated cells in a landscape:
- *local cells are unstable and spatially heterogeneous,*
- *species resources are heterogeneously distributed in space,*
- *populations reduce the danger of extinction by spreading the risk of local extinction,*
- *dispersal mechanisms facilitate community persistence,*
- *spatial extent is a stabilising mechanism only if fluctuations in individuals cells are asynchronous.*

4b. Adding spatial extent to biotically unstable cells in a landscape:
- *local cells are unstable and spatially heterogeneous,*
- *predator-prey and competition systems are stabilised with the addition of spatial extent,*
- *in heterogeneous cells, the activity of fugitive species may stabilise interacting populations,*
- *random diffusion will tend to destabilise a competitive, or predator-prey system,*
- *the behaviour of spatially complex predator-prey systems is determined by the nature of dispersal processes,*
- *spatial extent can increase persistence independent of dispersal mechanisms,*
- *episodic cell migration enhances regional persistence,*
- *high fecundity, low batch size and density-dependent dispersal decreases regional persistence.*

5. Biotic feedback is weak and infrequent:
- *competition as a regulatory process seldom operates,*

- *competition as a regulatory process only operates at levels sufficient to f facilitate natural selection,*
- *competition never operates,*
- *it is the activity of stochastic disturbing forces that causes localised extinctions and not competitive interactions,*
- *competitive exclusions seldom, if ever occur.*

6. Alternative stabilising mechanisms exist in the presence of weak biotic coupling and stochasticity.

6a. Increased persistence for biotically unstable local cells by stochastic stabilisation:

- *disturbance moderates coexistence in competition and predator-prey systems,*
- *intermediate disturbance maintains high diversity,*
- *periodic or cyclic disturbance facilitates resource partitioning which in t turn can promote coexistence on a single limiting resource.*

6b. Increased persistence for stochastically unstable communities by biotic compensation:

- *low density survival by compensatory floors (e.g. immigration),*
- *low density elasticity (e.g. rapid recovery),*
- *low density process time lags,*
- *high density ceilings (e.g. resource depletion, predation and natural enemies, emigration).*

7. Community behaviour is transient and unstable:
    - *persistence is a more appropriate concept for non-equilibrium systems.*

8. Community behaviour is driven by abiotic disturbance:

- *in the absence of stabilising mechanisms, a population affected by stochasticity will tend toward extinction long term,*
- *stochastic fluctuations knock populations away from average values,*
- *stochastic forces are stronger than homeostatic forces,*
- *severe disturbance can drastically alter the structure and behaviour of a community.*
- *community persistence is dependent on thresholds of disturbance,*
- *climate changes cause floral and faunal disequilibria,*
- *short lived species track environmental fluctuations,*

9. Community behaviour is probabilistic/random:

- *stochastically dominated systems contain deterministic elements,*
- *deterministic predictability in stochastically dominated systems is dependent on factors like the frequency, magnitude and spatial extent of a disturbance event,*
- *chaotic and stochastic behaviour is unpredictable,*

- *deterministic chaos may result from strong biotic feedback,*
- *deterministic chaos implies the existence of multiple unstable fixed points,*
- *chaotic behaviour reflects the operation of positive feedback loops and or unstable (over compensatory) negative feedback loops (ref. hypothesis 2 above regarding time delays in negative feedback loops),*
- *human impact is capable of forcing positive feedback,*
- *chaotic systems will be sensitive to small changes in initial conditions,*
- *birth and mortality rates are density-independent,*
- *a stationary population in a fluctuating environment has a greater chance of extinction,*
- *single to multiple point attractors exist for simple discrete or continuous time systems.*

10. Community behaviour is subject to biotic instabilities:
    - *changes in parameter values made while holding community structure relatively constant are sufficient to markedly alter patterns of population behaviour,*
    - *biotic instabilities result from over compensatory growth rates, positive feedbacks, undamped negative feedbacks that drive a system away from stable between species equilibria,*
    - *one or more equilibrium points exist for such systems but these are not stable,*
    - *species extinctions resulting from biotic instabilities or violent limit cycle oscillations drive the system away from the equilibrium between populations,*
    - *internal forces are too strong for the system to survive stably.*
11. Mechanisms responsible for population behaviour are complex and involve nonlinearities.
    - *the relationship between increasing density and population growth rates involves nonlinearities,*
    - *population age distributions are affected by stochasticity,*
    - *population birth and death processes are affected by stochasticity,*
    - *species composition is not stable,*
    - *the increased size of a carrying capacity will tend to increase the persistence of a population,*
    - *nonlinear diffusion processes enhance regional persistence.*
12. Community behaviour exists well below any theoretical carrying capacity:
    - *population behaviour is characteristically density-vague,*
    - *density-vague mechanisms exist (e.g. ceilings and floors),*
    - *coexistence can be promoted by density-vague regulation,*

- *density-vague regulation involves continuous variation in intra and interspecific competition.*

13. Density-dependence involves nonlinearities:
    - *density-dependent mechanisms operate infrequently.*
14. Equilibrium conditions may be an emergent property of large spatial scales:
    - *equilibrium behaviour that is an emergent property of large spatial scales represents an asymptotic limit of increasing size and not an intrinsic property of the system.*
15. Predation is an important determinant of long term population and community behaviour:
    - *herbivore regulation may be facilitated by an interplay between predator and vegetation abundances.*
16. Competition is one of the least important factors determining the spatial and temporal behaviour of natural populations and communities. At present there are three possible hypotheses:
    - *(a) competition never exists in natural systems.*
    - *(b) competition is weak and infrequent, but strong enough to drive evolution.*
    - *(c) density-vague behaviour is a more appropriate model of community organisation.*
17. Social behaviour is an important determinant of long term population and community behaviour.

In order for these hypotheses to be tested they need to be given a mathematical formulation. The constant growth trend model (CGTM) has been developed in this project in order to test the predictions and explanatory power of the non-equilibrium paradigm. Just like the classical logistic and coupled logistic equations, the CGTM has a discrete and continuous time model formulation. It also has a quasi-equilibrium formulation which can be used to test the density vague theory of community organisation. The mathematical properties, classification and characteristics of the equilibrium and non-equilibrium model formulations used in this project are outlined in chapter four.

3.7.3 Other Relevant Factors

The sixteen equilibrium hypotheses of chapter two have been restated with the addition of insights from current empirical and theoretical work on non-equilibrium systems. These hypotheses represent a distinctly non-equilibrium view of community organisation. As mentioned earlier, not all of these hypotheses can be tested with fossil pollen data.

Chapter four covers three important topics all related to the testing of the above hypotheses and begins with a discussion of the theory of ecological modelling in relation to hypothesis testing. This discussion is followed by a review and evaluation of the modelling research of palynologists. The objective of this review is to identify and evaluate the types of approaches palynologists have used in the study of plant population and community behaviour. Having accomplished this, it will be a simple matter to identify just how the modelling framework developed and used in this project differs from the contributions of other palynological modellers

In summary, a detailed set of alternative hypotheses have been derived from historic and current developments in community organisation theory. Not all of these hypotheses are relevant to the limitations of the data and observations used in this project. These issues are discussed more fully in the next chapter.

3.8 Chapter Summary

Chapter three has focused upon four main objectives. Firstly, to evaluate the two principal causes of departure from classical equilibrium behaviour. Secondly, to explore a range of possible stabilising mechanisms responsible for the long term persistence of local and regional communities. Thirdly, to review and evaluate recent research efforts aimed at addressing the problem of observational scale. Finally, the seventeen equilibrium hypotheses defined in chapter two have been used as a basis for developing a more detailed set of non-equilibrium hypotheses based on current research developments in non-equilibrium theory.

The ushering in of a non-equilibrium era in ecology appears to have been catalysed by two key theoretical developments. Firstly, the long controversy in ecology over the notion that increased complexity (biodiversity) would stabilise community functional properties has finally been resolved. The understanding, that too *rich a web connectance, ... or too large an average interaction strength, ... leads to instability (May 1972)*, has made theoretical ecologists acutely aware of the difficulties *with the idea of the ecosystem as a balance of interacting species* (DeAngelis and Waterhouse 1987).

Secondly, May's (1974) observations of chaotic behaviour in the simplest nonlinear equation suggested to theoretical ecologists, that there was little hope of deriving simple general laws for systems in which nonlinearity was the norm.

During the early 1970's, ecologists made a major theoretical shift from an equilibrium to a non-equilibrium centred view of community organisation. This shift expressed not only the theoretical contributions of Robert May, but a growing awareness of the inadequacies of classical equilibrium theory and models, on the part of many ecologists.

It is difficult to give an exact demarcation point for the rise of non-equilibrium theory in ecology. However, several lines of new research inquiry can be identified. These lines of research evidence identify departures from classical equilibrium systems and the ways in which these departures might be stabilised in order to account for long term community persistence. Two principal community types have been identified as departures from classical equilibrium behaviour.

In a community dominated by stochastic events, sudden and often extensive changes to community structure can drive component populations to localised extinction in the absence of restabilising mechanisms. Current research evidence suggests that these communities can be stabilised by a variety of compensatory mechanisms, termed *floors* and *ceilings* by Strong (1982) who argues for density vague behaviour.

In a community type dominated by strong positive feedback, undamped negative feedback, or high over compensatory growth rates, strong biotic forces (violent limit cycles) or local extinctions drive these systems away from equilibrium values. Current research evidence suggests that these populations may be stabilised by interruptive disturbance events that place a check on destructive biotic forces.

In this chapter, an important distinction has been made between two different effects which result from the addition of spatial extent to non-equilibrium systems. In many cases, it now seems evident that the addition of spatial extent, resource and habitat heterogeneity and dispersal mechanisms, (in general) appears to increase the long term *persistence* of communities dominated by stochasticity and biotic instabilities. Community persistence is a non-equilibrium concept which is not dependent on the existence of equilibria. A second approach to spatial extent involves the problem of observational scale.

The problem of observational scale has surfaced in ecology as the result of a growing awareness of the fact that community behaviour may be scale dependent. Recent research evidence suggests that for some communities, equilibrium behaviour may be an emergent property of large spatial systems connected by dispersal mechanisms. Equilibrium behaviour of this kind is not the result of internal biotic control (an intrinsic property of the system), but an asymptotic limit of increasing spatial size.

The quest for mechanisms that will stabilise non-equilibrium behaviour has also branched into attempts to identify mechanisms that will restabilise disturbed equilibrium systems. This line of research has involved the addition of mechanistic complexity to classical equilibrium models. While this approach has provided some important insights into the operation of theoretical equilibrium systems, it has been criticised for its loss of generality, its insensitivity to individuals and localised interactions. The identification of these short comings has added support for the rise of individual-based-models of community organisation in ecology.

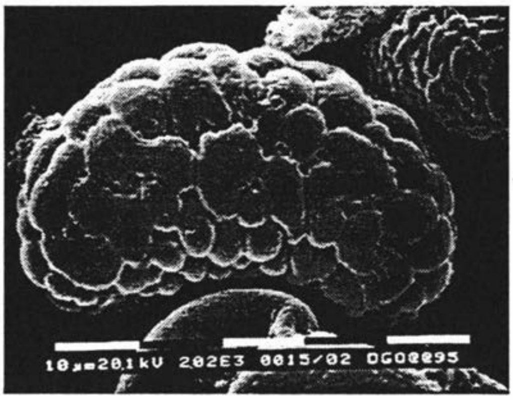
The application of individual-based-models to the modelling of forest stand or gap dynamics has resulted in a very adaptable and powerful modelling framework. IBM's have now been applied (with considerable success) to the study of a variety of causal mechanisms related to community organisation.

In conclusion, the evidence presented in chapters two and three of this thesis strongly indicates that non-equilibrium theory is a far more appropriate model of community organisation. There appear to be exceptions to this rule and in a subject as broad and complex as ecology, exceptions should come as no surprise. It is very likely that future research into the problem of observation scale will help to resolve these apparent contradictions.

The present thesis provides further insights into the workings of non-equilibrium communities with the aid of fossil pollen data, used in connection with a new constant growth trend model (CGTM). The CGTM is sensitive to the limitations of fossil pollen data and provides tremendous scope for exploring the mechanistic complexities of non-equilibrium systems of differing spatial and temporal dimensions.

Chapter four introduces this new model and describes its general properties, behaviour and assumptions in relation to the recent modelling work of palynologists.

Preview to Chapter four



Ecological Modelling & the Contribution of Palynologists

Palynologists have access to historic data recording the behaviour of plant populations and communities over geological and ecological time scales. Percentage fossil pollen data has traditionally been used by palynologists to describe and narrate the nature of long term vegetation changes. More recently, the main limitation of percentage fossil pollen data has been largely overcome with the development of absolute technique. Some palynologists have now begun to use their absolute fossil pollen data to model the behaviour of single and multi-species plant communities. Chapter four reviews the contribution of palynologists to ecological modelling and outlines a new model and dynamical systems modelling framework that has been developed with the intention of using fossil pollen data to model plant community organisation.

Chapter four

Ecological Modelling & the Contribution of Palynologists

4.1 Introduction

There are three objectives to be accomplished in chapter four. Firstly, the chapter begins with a discussion of a four part system of classification for ecological models. This highly integrative approach to classification provides a useful overview of the scope of modelling in ecology and provides a comprehensive basis for characterising the recent contributions of palynologists to ecological modelling research. Tremendous opportunities exist for palaeoecological studies to make important contributions toward unravelling the complexities of community organisation. This fact will be highlighted by a brief discussion of the emergence of palaeoecology and its contribution to the generation of long-term data.

Secondly, chapter four provides a detailed description of the dynamical systems modelling framework developed and used in this research project. Section two will include an introduction to the computer hardware, MatLab scripting language and modelling procedures used in this research project. The concepts and theory of nonlinear optimisation will also be introduced, along with a discussion of the nature and structure of error in fossil pollen data.

The ability to identify the nature and structure of error in time series data largely determines the utility of the data for modelling work.

The ability to identify the nature and structure of error in time series data largely determines the utility of the data for modelling work. Considerable effort has been made on the part of palynologists to quantify and understand the nature of sampling, laboratory and counting errors in fossil pollen technique. Considerable effort has also been made to understand the nature of errors introduced into fossil pollen data as a result of atmospheric pollen deposition and those geological processes that disorder the stratigraphic sequences from which sample cores are taken.

There is, unfortunately, very little that can be done to control the nature and structure of errors introduced via the natural processes of pollen deposition and sedimentation. For this reason, evaluation of the modelling work undertaken in this thesis will be heuristic rather than statistical. Justification for this approach will be briefly discussed along with the application of this heuristic refutation criterion to validating the predictive capability of model formulations.

In summary, the second objective of chapter four is to define the modelling framework and criteria used for the acceptance or rejection of alternative working hypotheses (Loehle 1983, Mentis 1988).

The third and final objective of chapter four is to introduce the main equilibrium and non-equilibrium model constructs to be tested in this project. The mathematical properties and characteristics of the logistic and coupled logistic models have already been well discussed in previous chapters. By contrast, the constant growth trend model is more fully discussed so that its origin, assumptions, behaviour and adaptation to modelling non-equilibrium systems is well understood. The discussion of these model formulations (or hypotheses) at the end of chapter four provides an introduction to their testing in the two case study chapters.

4.2 Ecological Modelling

The following section provides an introduction to the terminology, philosophy, methodology, classification and theory of mathematical modelling in ecology. This introduction also provides a conceptual and theoretical basis for the modelling work undertaken in this thesis as well as providing a basis for characterising and evaluating the recent contributions of palynologists to ecological modelling research.

4.2.1 Ecological Modelling Defined

The following discussion is limited to an evaluation of mathematical models in ecology (hereafter referred to as ecological modelling). A detailed classification of ecological models is given later in this chapter.

According to Kreb (1966), a model is a simplified system that represents some of the essential features of reality. Furthermore, a model provides explanations of experimental observations and insights which are in turn a starting point for fuller exploration of reality. In principle, ecological modelling and hypothesis building are the same since each *attempts to derive from nature some significant aspect of it* (Patil and Hazra 1983). Fortunately for ecology, the basic philosophical issues underlying model development and application find continuity throughout all the natural sciences (Skellam 1972).

Lomnicki (1988) suggests that while a model is generally considered to be the formal statement of a hypothesis, the relationship between a model and a hypothesis are generally not well understood. A scientific explanation of a phenomenon requires formulating a hypothesis which *implicates the given phenomenon and other related ones and at the same time is consistent with the remaining body of current theory* (Lomnicki 1988). Very often, mathematical models are the best or the only possible way of presenting a hypothesis and discovering its implications. Hypothesis testing is now accepted as an important part of the work of an ecological modeller in both theoretical and empirical research (Sugden 1987).

Rutter (1972) suggests that the aims of an ecologist, like all scientists, are to observe and describe natural phenomena, to systematise observations, to explain observations as well as to predict and extrapolate from observations what is likely to occur in uninvestigated situations provided by nature or experiment. The work of explanation, prediction and extrapolation all involve modelling of one form or another.

Furthermore, the study of complex natural systems requires the use of models in order to *capture the essence of observed patterns and processes without becoming enmeshed in details* (May and Oster 1976). A model that contains all of the complex features of a natural system would by definition cease to be a model (Pielou 1969). It is important that a model contains the *characteristic* features of a system which are essential in the context of a given research question or problem to be solved.

Jorgensen (1986) suggests that ecological models have traditionally been applied in the description of complex systems and the definition of system properties in order to highlight gaps and weaknesses in knowledge and to test scientific hypotheses. The last of these applications is of special interest to the present study. Because models can be used to simulate the reactions of natural systems, their behaviour can be compared with data obtained from fieldwork sampling and observations. Validation of this kind is an important but not exclusive part of hypothesis testing. This topic will be developed more fully in the next section.

Lomnicki (1988) proposes that two important lessons have come from the early history of ecology. Firstly, it is not possible to investigate ecological systems without models or analogies derived from other more familiar systems. Most ecologists of the first half of this century did not apply mathematical modelling but were preoccupied with less precise model analogies like the Clementsian super-organism. The second lesson is that the ecological modelling which in the first half of this century was practised by a few ecological theorists, has proved to be the most enduring and promising ecological methodology. While ecology's first paradigm (the super-organism) is now of only historic importance, the predator-prey and competition models of Lotka and Volterra still *form a fundamental part of ecology* (Lomnicki 1988).

In ecology, mathematical modelling has developed over the last three decades as a result of three main factors: the development of computing technology, more readily accessible high level programming languages along with data storage and access techniques (Jeffers 1972). The development of modelling in ecology has also been attended by some important and controversial theoretical and philosophical debates concerning the place of modelling in ecology. The key elements of these ongoing discussions are developed over the next two sections which cover the nature, application and classification of models in ecology.

4.2.2 Five Elements of Ecological Models

There are five fundamental elements of all ecological models: forcing functions, state variables, parameters and coefficients, constants and calibration procedure.

Forcing functions or external variables are functions or variables of an external nature that influence the state of a model system. State variables describe the state of a system. The correct structure of a model is usually dependent upon the right choice of state variables although in most cases this choice is obvious. The relationships between forcing functions and state variables are usually defined by mathematical equations. Because the same types of biological, chemical and physical processes can be found in many ecosystems the same equations can be used in different model applications. At present, it is not possible to have one equation which represents a given process in all ecological contexts. Many processes in ecological systems have several mathematical representations which are equally valid. This may be because the process is too complex to be understood in sufficient detail at present or because circumstances allow the use of simplifications.

The mathematical representation of natural processes contains coefficients or parameters. Parameters are constants which can be related to a scientific (mechanistic) definition in causal (analytical or theoretical) models (*e.g.* the specific growth rate of a population). Most parameter values are only ever known within certain limits. Jorgensen (1979) provides a comprehensive list of ecological parameters although only a few of these are known with any certainty. In most cases it is necessary to calibrate parameter values against actual field data.

Calibration is an attempt to find the best accordance between computed and observed state variables by fine tuning the parameters of a given equation. Calibration can be accomplished by iterative trial and error or by the use of more formal optimisation procedures (usually available in software form). In models aimed at simulating the dynamics of ecological processes, the calibration procedure plays an important part in determining the quality of the final model. Firstly, as indicated above, most parameter values are only ever known within certain limits.

Secondly, most ecological models do not distinguish between different species, but usually consider them as one state variable. Because the species composition of some communities varies through time (often annually) an exact average parameter value often cannot be found.

Thirdly, the influence of processes not included in the model can, to a certain extent, be considered by the calibration process when the results of a model are compared with field data. This may explain why model parameters can take on different values for the same model when applied to different ecosystems. In other words, the calibration can take site differences and processes of minor importance into account. It is important to avoid or reduce the use of calibration for this reason. To a certain extent the limitations of calibration can be overcome by the use of realistic parameters determined where possible from empirical studies. Sensitivity analysis can also be used to determine the influence of changes in parameters or forcing functions on the most crucial state variables.

Finally, some models will also contain universal constants such as the gas constant etc. Constants of this type do not require calibration (Jorgensen 1986).

In summary, ecological models can be defined in relation to five fundamental elements. Calibration procedure (optimisation) has been used quite extensively in this project and will be discussed more fully in the methodology section of this chapter.

4.2.3 The Classification and Application of Ecological Models

The following section will demonstrate the tremendous variety of ecological model types and the scope of their application. Models can be classified in many different ways. The semantic difficulties of trying to decide on a classificatory scheme for models has been thoroughly explored by Skellam (1972). The present discussion outlines four highly integrative systems of classification developed by four different authors concerned with different aspects of ecological modelling research. Model classification can be based on structural differences (Robertson *et al.* 1991) or provide insight into the strengths and weaknesses of various modelling approaches. Some systems of classification are more successful than others, while all those presented here introduce perspectives that are unique and relevant to the present discussion.

The model classification discussed in this section will be used to characterise and evaluate the modelling work of palynologists and the constant growth trend model developed in this research project. To prevent needless repetition, each system of classification has been illustrated so that the relationships between subclasses are presented in diagrammatic form. Only the subclasses of each scheme which are directly relevant to the present discussion will be defined. Furthermore, each subclass will be defined only once, after which the re-use of the same term should be taken by the reader to indicate that the previous definition is relevant. The definitions themselves have been closely paraphrased from original source text as indicated by references.

4.2.3.1 Classification Based on Intended Application

Robertson *et al.* (1991) distinguish between three fundamental models in ecology: statistical or descriptive models, analytical or theoretical models and simulation models (fig 4.1). The basis of this system of classification is the intended end use of the model and the mathematical paradigm from which it was derived.

Statistical models are mainly used to summarise or express large amounts of data in a condensed mathematical form that emphasises inherent regularities. The choice of a given statistical model has little or no theoretical justification and the model's parameter values usually have no ecological meaning. In its purest form, the statistical or descriptive model (Wangersky 1978) has terms which equate to fitting constants for which no mechanistic or physical quantities are implied. There is no unique descriptive model for a given system; it is usually possible to construct any number of equally valid descriptive models for the same collection of data. Statistical models are also referred to as empirical models by (Wiegert 1975).

Theoretical / analytical models are usually developed from simple theoretical considerations with little or no empirical evidence. These models are used to explore abstract ecological concepts. The models are frequently handled analytically. Mathematical tractability is generally regarded as of greater importance than ecological sense. Theoretical models usually require highly simplistic ecological assumptions which can render their conclusions of doubtful value.

Wangersky (1988) argues that most biological models are neither purely statistical (descriptive) or purely analytical (theoretical). More specifically, they are attempts to construct analytical models with descriptive terms inserted to make the model fit the available data. The problem with these composite models is that the terms which are really fitting constants assume names with mechanistic status.

Numerical simulation models involve the iterative solution of a mathematically-specified model. These models specify the changes that take place over a single time step. The model is solved by repeatedly computing the changes in the system thus updating the state of the system. Numerical simulation models may be formulated in terms of one of the main modelling paradigms.

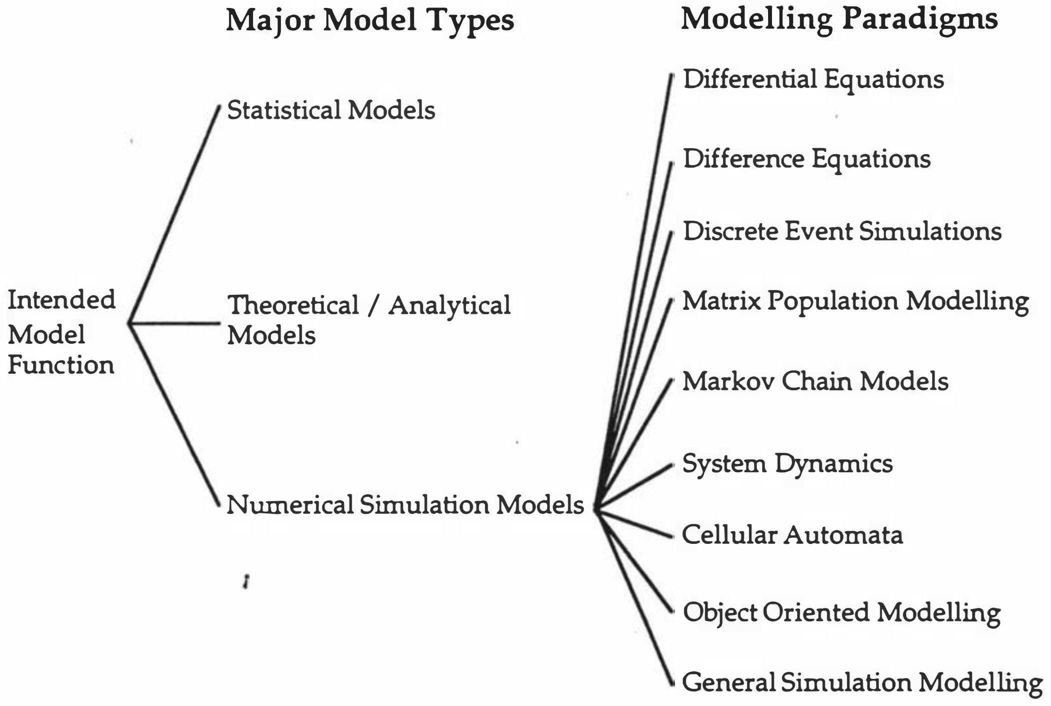


Fig 4.1 The classification of ecological models based on intended application and choice of modelling paradigm (after Robertson *et al.* 1991).

A modelling paradigm may be defined as the particular mathematical framework in which the system to be modelled is expressed. Robertson *et al.* (1991) suggest that the advantage of using a particular modelling paradigm is that it facilitates model construction by *channelling thought into the particular modelling structures recognised by the paradigm; computational tools are available for handling the constructed model; and communication between modellers is made easier by common understanding of the meaning of the modelling constructs allowable within the paradigm.* The major disadvantage of using a particular modelling framework (with numerical simulation or analytical models) is that ecological reality is frequently sacrificed.

Differential equations are used to model systems in which change is considered to be continuous and all rates of change are instantaneous functions of the current state of the system. Usually, the problem can be modelled as a system of ordinary linear or nonlinear differential equations (ODEs) although some ecologists have also used partial differential equations (PDEs) for investigating systems with spatial dimensions.

Difference equations are used for modelling systems in which discrete change in the system occurs over unit intervals of time. There are two main justifications for the use of difference equations. Firstly, many ecological processes occur more or less discretely (*e.g.* the life cycle of many species occurs over a very short period of time). Secondly, even though a process like plant growth may be continuous, it is often only possible to collect data on a discrete basis. Based on either of these justifications it is reasonable to model a system using corresponding discrete time units.

A modelling paradigm not mentioned in this classification or any of the others yet to be evaluated has been adapted to the present research project. A **dynamical system** is one whose state changes with time (t) as described by a set of first-order differential equations (Coddington 1961) in either discrete or continuous time (Arrowsmith and Place 1990). The traditional way to analyse such a system is by studying its trajectories in phase space. Geometrically, a dynamical system describes the motion of the points in phase space along the solution curves defined by a given system of differential equations (Perko 1991). Concepts like stability play a major role in dynamical systems theory (Rosen 1970, Silvert 1983). Comprehensive treatments of dynamical systems theory are given by Verhulst 1990, Medved (1992), Katok and Hasselblatt (1995).

The main advantage of the Robertson *et al.* (1991) scheme of classification is that it distinguishes between models on the basis of their intended application and the modelling framework in which they were formulated. It would be a misconception to assume from the simplicity of this three way end-use classification that the selection of a correct model for a particular ecological problem is an easy thing (Jorgensen 1979). This is not the case and the scope of ecological modelling outlined in the next three systems of classification will make this point very clear.

The concept of a modelling paradigm is also very useful. Different mathematical frameworks could be used as a basis for comparing the strengths and weaknesses of different modelling approaches, although this idea is not developed by the authors.

In fig 4.1 general simulation models have been illustrated as a subgroup of the main modelling paradigms. In reality, they represent a class of specific models which cannot easily be placed into one of three classes of ecological model types mentioned. There are a number of other more serious limitations to this scheme of classification.

Firstly, it provides no subdivision of the three main classes of model type (or end use) into the hundreds of analytical and simulation models that exist in population and community ecology alone. Furthermore, few of the modelling paradigms common to analytical and simulation models are used in statistical modelling and no mention is even made of regression models or time series analysis.

Secondly, the authors attempt to distinguish between three main types of ecological model on the basis of the method of determining a solution. For example, analytical models depend on mathematical manipulations alone to explore the relationships between variables (*i.e.*. they seek a closed-form solution to the state of the system at some equilibrium). Simulation models depend on numerical substitution (according to model defined rules) to find the expected outcome of a given mathematical formulation. The formal method of solution is really only one of several mathematical characteristics that can be used to classify models.

Finally, the authors make no attempt to classify models on the basis of the way in which models are amenable to validation. Caswell (1976) argues that the whole concept of the validation of ecological models is almost universally misconstrued by ecologists. The basic distinction which is not often made is between theoretical models (theories) and predictive models (calculation tools).

It should be pointed out that these three main weaknesses in the classification scheme of Robertson *et al.* (1991) may largely be considered as matters of abstraction. On the other hand, systems of classification which focus upon the three deficiencies of the Robertson *et al.* (1991) scheme provide valuable insights into those factors which distinguish different ecological models, their application, mathematical properties and relation to hypothetico-deductive methodology.

4.2.3.2 Classification Based on Validation Procedure

The following discussion evaluates a classification of ecological models based upon alternative methods of model validation. Loehle (1983) argues that the validation of ecological models is not based on a standard procedure. This criticism will be more fully evaluated.

4.2.3.2.1 Hypothesis Testing Introduced

In the positivist scientific methodology, theories are used as conceptual aids to understanding (Harper 1980) and the validity of a theory depends on how well it is supported by field data (verification) or on how well it stands up to attempts to find contradictory evidence (falsification). To validate means to devise and apply tests which prove that something is true, a test that is generally considered to include both verification and falsification procedures (ref. Jones 1983).

Harvey (1972) maintains that the need to determine the validity of a theory by verification and falsification is the biggest problem in scientific theory. Most scientific theorists insist that at least some of the statements contained in a theoretical proposition must be closely attached to real world observations. This requirement is usually met by hypothesis testing. If repeated testing shows that a given hypothesis is always true (or related to aberrant phenomena when not true) then the theory from which the hypothesis is derived is spoken of as being a true theory. There are many theories in the natural sciences which are regarded as true in this sense (Harvey 1972).

However, there is no general agreement as to what is meant by a true theory (Harvey 1972). According to Mankin (1975) it is just not sufficient to say that a model (or hypothesis) is invalid just because its behaviour is not perfect. Such a statement blurs the distinction between theories and calculation tools (predictive models). O'Neill (1975) also argues against the notion that almost any theory is as good as another since no model is true or false, just more or less useful.

As indicated by Mankin (1975) this problem is complicated by the use of theories of differing structure and intended application. For example, it is difficult to test the predictions of probabilistic theories against reality without collecting considerable information to determine just what the probabilities are. Having accomplished this, it is understood that the predictions of a probabilistic theory will reflect the operation of probabilistic and not deterministic processes.

As a second example, normative theories involve a large degree of abstraction (operational assumptions). Operational assumptions are usually close approximations of reality (*e.g.* linearity in the place of nonlinearity) or are known to be completely unrealistic but required for the sake of simplification. It is not correct to dismiss a normative theory as untrue because it does not accurately represent something that exists, or represents as true things that do not exist (Harvey 1972).

In summary, to validate means to devise and apply tests which prove that something is true. Loehle (1983) argues that different classes of model require different types of validation procedure, but theory can only ever be tested. A fundamental distinction is often not made between theoretical models (theories) and predictive models (calculation tools). These distinctions are discussed in the following sections.

4.2.3.2.2 Hypothetico-deductive Validation

A good theoretical model should do more than just predict; it should also offer explanation. The structure of a good theoretical model should be interpretable in terms of the real world. A multiple regression model has predictive power, but is a poor example of a theoretical model because the regression coefficients have *no biological meaning*. The validation of a theory involves the formulation of a hypothesis (or model) and its testing by strong inference (Platt 1964). Hypothesis testing is primarily a problem of deduction - the collection and analysis of data to evaluate the truth of an *a priori* hypothesis (Mentis 1988).

When testing hypotheses, none can ever be proved correct, although some might be found to fail or to conflict *with observation, experience and other* *theories* (Mentis 1988). For this reason, science should use strong inference (Platt 1964). It should try to falsify rather than verify hypotheses (Cousens 1985).

The process of strong inference (Platt 1964) recognises the iterative nature of hypothesis (or model) testing. Stage one involves the devising of alternative hypotheses. Stage two involves the devising of an experiment, the outcome of which will exclude at least one of the alternative hypotheses. In stage three, the experiment is undertaken, in stage four it is evaluated and the results interpreted, new hypotheses formed and the whole process repeated using a new data set. This process never ends because our theories never capture reality perfectly. Correct explanations cannot be proven deductively except by eliminating all possible alternative hypotheses. However, incorrect explanations may be disproved by contradictory experiments or observations (Popper 1959, 1972, 1983).

In ecology, strong inference has been integrated into the ecological modelling process (Caswell 1976). The three main steps involved in mathematical modelling are: formulation, solution or simulation and interpretation (Goodall 1972, Wake 1992). Model formulation is sometimes referred to as model specification and is described in some detail by Nelder (1972). Once there is confidence that a model has been correctly formulated and *validated* by simulation, it is possible to use the model to test theory. Collectively the model construction and hypothesis testing process would involve: model formulation, solution or simulation and strong inference which includes interpretation.

A number of critiques of the usefulness of a strong inference model of scientific method now exist. The limitations of purely deductive logic and the doctrine of disproof of specific hypotheses as a prerequisite to scientific progress have been debated at length by Lakatos (1968, 1970, 1974) and others. Feyerabend (1975) disputes the possibility of objective criteria for scientific truth in many kinds of investigation. Campbell (1979) questions the desirability of complete objectivity on the part of individual scientists. Furthermore, it is also evident that the history of scientific advances in ecology often corresponds poorly to the process envisaged in the hypothetico-deductive model of Kuhn (1970). Despite these questions and limitations, many ecologists appear to accept strong inference as the proper model for ecological investigation (Quinn and Dunham 1983).

In summary, when using strong inference, if it is discovered that a theoretical model fits the data 99% of the time, but fails to predict the data 1% of the time, it would be necessary to improve the model. However, this type of behaviour from a model would be quite acceptable, if it was a calculation tool - a purely predictive model (Loehle 1983).

4.2.3.2.3 ***Hypothetico-Inductive Validation***

By contrast, predictive models (calculation tools) are evaluated for their usefulness in predicting aspects of the real world, or on how well they meet design specifications - a multiple regression model is a good example.

Platt (1964) characterised explicit formal hypothesis testing in science as *strong inference* and argued that it is a hallmark of virtually all scientific progress. However, Mentis (1988) argues that the hypothetico-deductive scheme alone is not always sufficient for this task. There is more than one way in which knowledge can be, and is, developed. Even if the hypothetico-deductive approach is preferred, the *state of current knowledge might be insufficient for postulating non-trivial hypotheses* (Mentis 1988).

For example, to say that variable X and Y are correlated without quantification of the nature and strength of the relation is to state a *trivial hypothesis* (Mentis 1988).The validation of a trivial hypothesis is a problem of induction which *attempts to develop knowledge, generate hypotheses or derive general statements from specific data* (Mentis 1988). Correlation, regression, ordination, classification, biplots, correspondence analysis and the like, are statistical-ampliative techniques used by ecologists to generate *a posteriori* hypotheses. Popper (1965) has shown that there is no valid inductive technique for proving the truth of any theory.

The collection of data and use of ampliative techniques to partition data sets into pattern and noise leaves the degree to which the constructed model is a descriptor of the particular data set uncertain and the extent to which it has predictive value. The stating of an *a posteriori* hypothesis after the collection of data, risks accepting spurious hypotheses or rejecting null hypotheses *more frequently than the significance levels would lead one to expect* (Mentis 1988).

However, predictive quality can be evaluated: (1) internally (by removing a random fraction of the data and repeating an analysis to see how stable it is); (2) externally (by the addition of data and repeating of an analysis to see how a former pattern alters); and (3) by repeating the analysis on a fresh and independently collected data set (Mentis 1988). Extensive corroborative testing of predictions increases the degree of confidence in a model but can never be used as an absolute proof (Mentis 1988).

In summary, Loehle (1983) states that confusion has arisen in the ecological literature as a result of a failure to distinguish between theoretical and predictive models. Caswell (1976) shows that goodness of fit to ecological data is usually taken as the main criterion for model evaluation. However, goodness of fit is necessary, but not sufficient, as a criterion for the evaluation of a theoretical model. A predictive model can be accepted as sufficiently accurate, but it is only possible to *fail to reject a theory* (Loehle 1983).

4.2.3.2.4 The Validation of Logical Models

Logical models are a third class of model identified by Loehle (1983). Certain types of simulation models embody logical structures or operators which perform tasks precisely. This distinguishes them from any type of theory or calculation tool which is used to approximate reality. Processes which can be represented with logical models are fundamentally different from most biological systems. In summary, Loehle (1983) distinguishes between three fundamental classes of simulation models: logical, theoretical and predictive (fig 4.2).

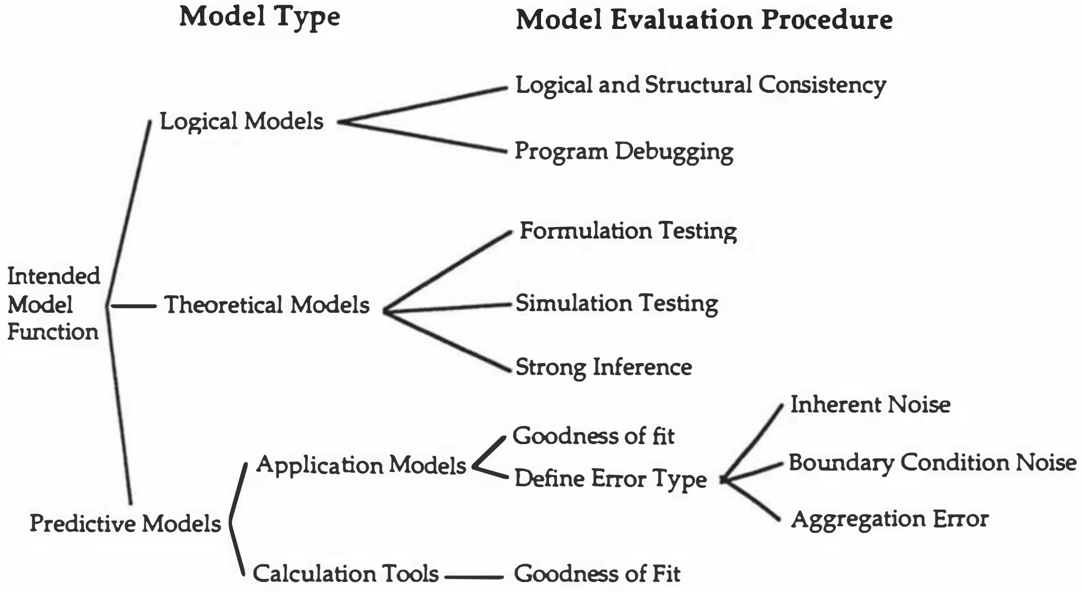


Fig 4.2 The classification of models based on evaluation procedure. Logical models are evaluated by logic and programming techniques common to computer science. Theoretical models are evaluated by the process of strong inference (Platt 1964). There are two classes of predictive models for which goodness of fit is an accepted test. However, application models also require evaluation of three types of internal error (after Loehle 1983).

Logical models (fig 4.2) are evaluated purely on a logical and structural basis which may include standard program debugging techniques common to computer science. The most important distinction between this class of model and the other two is that experimental design is not required as a part of the validation process. Models of ecological systems need a very different approach for their evaluation.

Theoretical models (fig 4.2) require three stages of validation: formulation testing, simulation testing and strong inference. *Formulation* testing validates the translation of a theory into mathematical model form. Obviously, conclusions about a theory cannot be drawn from the results of an incorrectly formulated model. *Simulation* validation involves testing for computer coding errors and the failure of mathematical or numerical techniques to calculate answers correctly.

The process of validation alone is not relevant for models which are theories. It is possible to validate a predictive model, a computer simulation or a model formulation. However, it is not possible to validate a theory. It is necessary to test a theory by strong inference.

Predictive models (fig 4.2) can be divided into two subclasses: application models and calculation tools. Application models are based on well established laws and theories *in which laws are applied to solve a particular problem* (Loehle 1983). The usefulness of such a model depends on the extent to which known laws have been correctly applied. The only things subject to change in an application model are the boundary conditions. This process involves the exclusion of minor factors and inclusion of other exogenous factors as driving variables. This process introduces boundary condition noise.

The system of an application model must also be simplified using aggregation and representation. This usually involves the aggregation of some system element to represent a single state variable. Inherent system noise can be eliminated to varying degrees. However, success in this area requires a knowledge of the nature and structure of measurement and inherent process errors.

A calculation tool is a method for obtaining an answer that may not be based on exact laws (*e.g.* a regression equation). Calculation tools can have predictive power even though it is biologically meaningless. Most parts of a calculation model are subject to adjustment while all sources of error are usually lumped into one error term in the model (42) (Nelder 1972).

$$y = Y + e \tag{42}$$

where

y	is the observation or data
Y	is the fitted model
e	is the residual error

A normal rule concerning equation 42 is that the model is not adequate if pattern is still discernible in the residuals. The converse may not be true since any residual pattern is relative to present knowledge and a new idea may turn up a variable highly correlated with residuals (Nelder 1972). It is possible to change the structure, the form of the equations and the parameters if it helps to reduce the error.

4.2.3.2.5 Refutation and Conceptual Problems

The present study is primarily interested in the formulation, simulation, testing and interpretation of theoretical models. The models advanced in this project have been formulated from existing ecological theories and, therefore, constitute test hypotheses. According to the hypothetico-deductive Popperian scheme (Popper 1959) there are three main types of hypothesis testing which can be considered as suitable grounds for refutation (Popper 1965). There are also certain conceptual problems associated with these tests. These problems derive both from the feasibility of formulating testable hypotheses and more deeply, from questions regarding the fundamental validity of the hypothetico-deductive approach.

Quinn and Dunham (1983) suggest that theories of causality in ecology rarely lend themselves to analysis by the formal method of hypothesis testing (strong inference). The co-authors point out that falsification by observation or experiment occurs only to the extent that a hypothesised cause can be shown not to operate at all. Therefore, if many causes contribute to an observed phenomenon, then none can be eliminated by a properly designed experiment.

The incompatibility of strong inference with ecological systems stems from the fact that no single cause can be shown to account for all of the observed variation in patterns of community behaviour. Most ecological studies seek to assign relative importance to all known causes. Attempting to force the study of highly overlapping mechanisms of ecological change into a rigid hypothetico-deductive mould has the potential to detract from understanding for at least three reasons (Quinn and Dunham 1983).

Firstly, the co-authors point out that in the hypothetico-deductive approach possible contributing causes are not hypotheses because in patterns with multiple causes *it is not possible in principle to perform critical tests to distinguish between the truth of processes occurring simultaneously.*

Secondly, the only way to treat possible contributing causes as distinguishable hypotheses is to use univariate tests. However, the behaviour of a multivariate process *may not be safely inferred from any combination of univariate tests if there are strong interactions among contributing causes* (Quinn and Dunham 1983).

Finally, in the hypothetico-deductive scheme, knowledge is only increased when a formal hypothesis or a null hypothesis (proposing the nonexistence of a cause) has been rejected. The problem is that reliable null hypotheses are often impossible to construct because it is generally not known what patterns would exist in the absence of any given biological process. Therefore, Quinn and Dunham (1983) claim that a null hypothesis has *no value in formal deductive logic* ... and that in practice, null hypotheses represent reference points *for measurement (an inductive procedure) rather than constructs of deductive logic.*

In summary, there are very few ecological systems (including those of the present study) which could be traced back to a single primary causal mechanism; it is very difficult to formulate null hypotheses; univariate tests cannot be used to discriminate between interactive multivariate systems. The hypothetico-deductive scheme and its application has its supporters (Strong 1980) but is not without its critics (Lakatos 1970, 1974, Feyerbend 1975, Campbell 1979, Murray 1986, Quenette 1993) or its problems (Quinn and Dunham 1983). Furthermore, there appears to be open acceptance among ecologists of the fact that ecology as a science has not always progressed as science is supposed to with a dialogue between theory and experiment (Sugden 1987).

In the light of these problems, the hope of a general predictive theory seems to fade (Slobodkin 1961, Orians 1962, Margalef 1963, Ruse 1973, Macintosh 1985, Huston *et al.* 1988, Mayr 1988). Despite these limitations and apparent problems, strong inference is generally accepted as the most suitable model for the investigation of complex ecological phenomena (Quinn and Dunham 1983).

Some further operational problems are associated with the refutation of various types of hypotheses. These problems are briefly described with the three main types of refutation criteria below.

The first refutation type concerns hypotheses or models used explicitly for prediction. The grounds for refutation in this case are whether the prediction meets some predefined accuracy. If the model fails such a test, then it requires improvement or replacement. A major conceptual problem in this type of test is in defining the level of accuracy and how to remedy it in the case of failure (Mentis 1988).

The second refutation type involves an assessment of the explanatory power of a model. The worth of any single explanatory hypothesis in isolation is difficult to evaluate and for this reason competitive theories are needed. Alternative theories might be genuine attempts at explanation or one might be a null hypothesis. Competitive models are rejected on the grounds of *inferior explanatory power, conflict with background theory and lack of internal consistency and parsimony* (Mentis 1988).

There are a number of conceptual problems associated with this second type of refutation procedure; the generation of viable competing theories, the relative weighting of various criteria for refutation and the determination of exactly what constitutes a satisfactory explanation (Mentis 1988).

A third type of refutation test concerns the use of a classical statistical null hypothesis H_0. A null hypothesis is framed in a way which states that there is no difference between the subjects of comparison. A significant result leads to H_0 being overthrown and a difference being assumed. Sampling design is one of the most important operational requirements for the use of statistical tests (Mentis 1988).

A common problem to all three types of refutation criterion is the existence of underlying value judgements. What ever hypothesis is at stake, rejection ultimately rests on an individual decision regarding *the nature and scale of the difference considered important, the accuracy of prediction desired or the level of explanation felt satisfactory ... considered, desired and felt have strong subjective bases* (Mentis 1988).

For this reason it is important that the criteria for difference, accuracy and explanation be specified before the fieldwork is conducted so that *it is possible to* *say a priori under what conditions the hypotheses will fail. A posteriori postulation and testing of hypotheses is inductive and conflicts with the essence of the hypothetico-deductive scheme* (Mentis 1988).

The present study is primarily concerned with the predictive and explanatory power of specific hypotheses derived from the two contending paradigms of community organisation. As suggested above, the use of refutation criteria involves certain problems which will be discussed more fully later in this chapter.

4.2.3.2.6 ***Summary***

Loehle (1988) has attempted to classify ecological models on the basis of model evaluation techniques. Three fundamental classes are evident in this scheme which relates these main model types to distinctly different systems of validation.

While the classification of Robertson *et al.* (1991) distinguishes between ecological models on the basis of end use, it provides no basis for comparing model type by the recognised hypothetico-deductive and inductive evaluation procedures advanced in this section. The next section adds an important dimension to the classification of theoretical (process) models by sub-classifying them according to their mathematical characteristics and traits.

4.2.3.3 ***Classification Based on Mathematical Characteristics***

The classification scheme proposed by Hurd and Kaneene (1993) was developed to aid in classifying epidemiologic models. However the scheme is sufficiently generalised to be directly applicable to ecological modelling. The classification is based on six mathematical characteristics: causal perspective, effect of chance, application perspective, mathematical treatment of time, computational treatment of individuals and method for determining solutions (fig 4.3). Causal perspective reflects the nature of the original hypotheses stated by an investigator.

Associative models in this context are the equivalent of predictive models in the previous classification of Loehle (1983). Predictive or associative models are inductive by nature and infer causality without a knowledge of the pathways or processes leading to the observed phenomena.

Process models are the equivalent of theoretical models according to the previous classification of Loehle (1983). Process models begin by defining hypothesised pathways and structural processes which may be responsible for the behaviour of the system under consideration.

The importance of the Hurd and Kaneene (1993), system of classification (fig 4.3) is in its development of the mathematical characteristics of the theoretical models discussed in the previous classification of Loehle (1983). Most of these terms are relevant to the present study and are described below.

A theoretical model deals with chance by being either stochastic or deterministic. However, as was demonstrated in chapter three, some stochastic model formulations have retained deterministic elements.

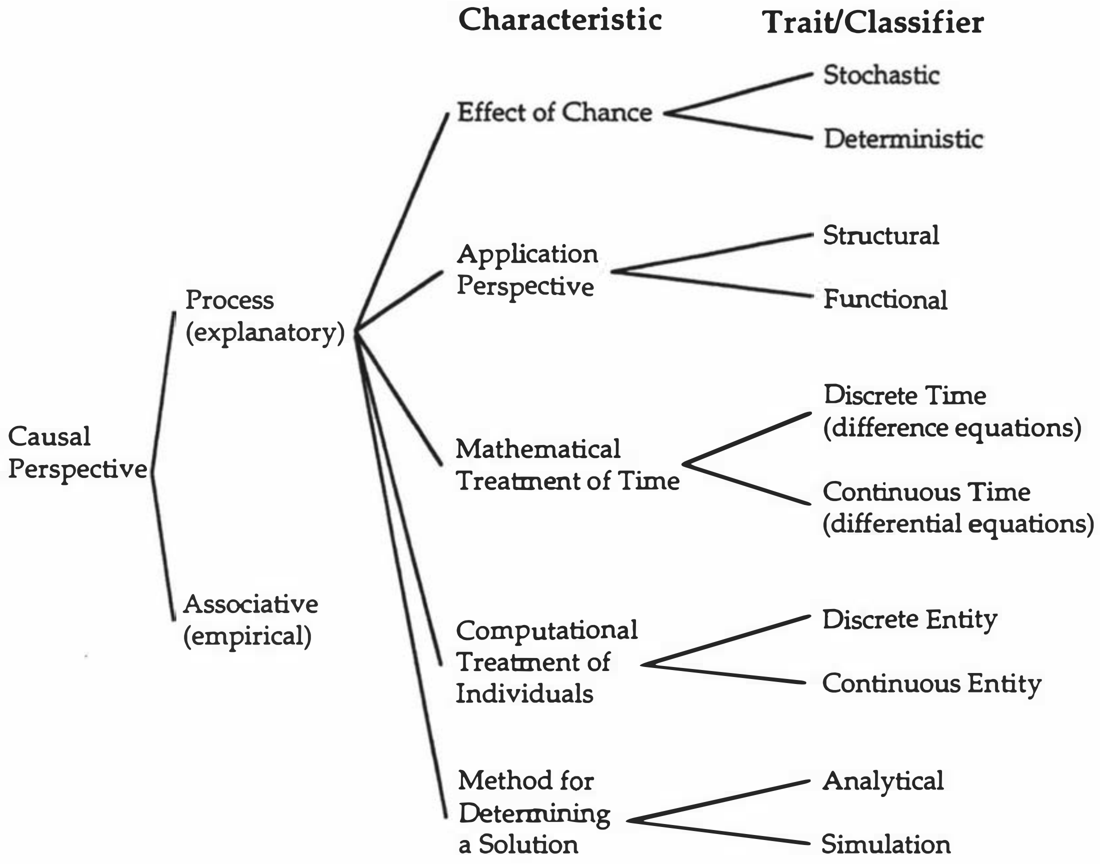


Fig 4.3 Method of classification for process (theoretical) epidemiologic models (from Hurd and Kaneene 1993).

Stochastic models include elements of random variation and chance and have the advantage of reflecting aspects of chance and uncertainty in a model's behaviour. The model's predictions are usually expressed with confidence intervals and expected values instead of the point estimates common to deterministic models.

A deterministic model will give the same result every time it is simulated. This property means that it is possible to determine consistently the state of the model for any given set of initial conditions and parameter values. Deterministic models are ideal for determining the sensitivity and thresholds of a system that result from changes in parameters values.

A theoretical model is usually the mathematical formulation of a hypothesis derived from a base theory. The nature of the hypothesis is reflected in the models' application perspective.

Structural models attempt to portray the underlying behavioural mechanism for the purpose of making *a priori* predictions or of exploring the implications of model's assumptions.

Functional models involve the use of *a posteriori* hypotheses which are derived with the aid of an established inductive (usually statistical) modelling process. Functional models are usually constructed using retrospective data and their primary use is to generate predictive models which can be used to quantitate observed phenomena.

A theoretical model formulation will deal with time in one of two ways:

Discrete time models divide time into units of equal duration and employ the algebra of finite-difference equations.

Continuous-time models treat time as a continuous variable and use differential equations to express instantaneous rates of change.

A theoretical model formulation treats individuals in two different ways:

Discrete-entity models are the equivalent of the individual-based models (IBMs) introduced toward the end of chapter three. These models track one individual at a time through the simulation process. The state variable of a given individual is modified by the operation of natural process mechanisms inherent in the individual's equation or as part of a pathway of process subequations which are often stochastic in nature.

Continuous-entity models treat the number of individuals in any state as a real number. Such models can be computed in either discrete or continuous time. These models usually assume homogeneously mixing populations, an assumption which can be a limitation where interactions are known to be on an individual basis. The advantage of continuous-entity models is that the size of the population being simulated will not affect the speed of the computer. The distinction of a continuous-entity blurs when a differential-equation model is simulated on a digital computer that divides time is into very small units for numerical integration.

In terms of how a model arrives at its solutions, it is possible to classify a model as either analytical or simulation.

Analytical models depend on mathematical methods alone to explore the relationships between variables. More specifically, these models seek a closed-form solution to the state of the system at some equilibrium. The advantage of these models is that they can be evaluated rigorously and stability criteria can be determined. Disadvantages include the fact that they are largely the domain of mathematicians and assume away reality in order to produce a more tractable model.

Simulation models depend on numerical substitution according to model defined rules in order to find the expected outcome of the mathematical formulation. Three general types (genera) of simulation model can be identified (fig 4.4). The individual simulation models listed in fig 4.4 have specific relevance to epidemiology, although many of these modelling paradigms are also in use in ecological modelling.

Mass action models treat spatial processes in terms of random and homogeneous mixing. These models can be deterministic or stochastic, discrete-time or continuous-time, but they are always continuous entity.

Chain-binomial models were developed in order to overcome limiting assumptions in mass action models. These models are fully stochastic, discrete time and continuous-entity. Markov models or chains are sometimes used for simulations and are mathematically equivalent to chain-binomial models with a finite state and discrete-time parameter.

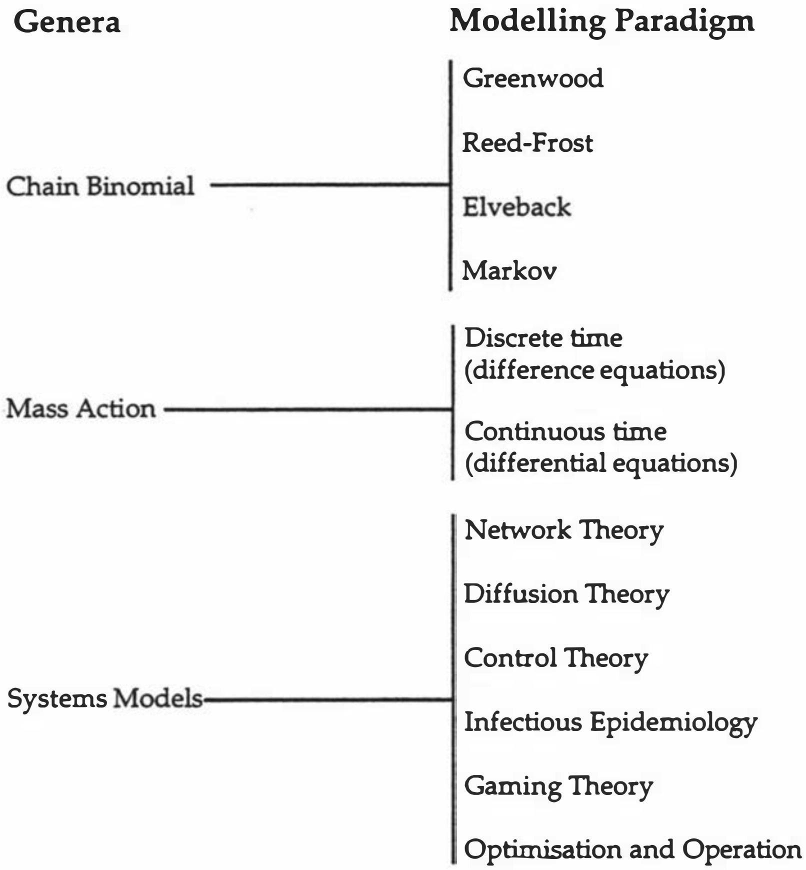


Fig 4.4 The genera of process simulation models (from Hurd and Kaneene 1993).

Systems models are not derived from a particular mathematical school of thought (Drummond 1976, Wright 1976). These models use whatever mathematical or simulation techniques are necessary to model a particular system of interest and consequently, are holistic by nature. Hurd and Kaneene (1993) suggest that systems models offer the greatest potential for future use as they are not limited by the assumptions of other modelling paradigms (Patil *et al.* 1983).

In summary, an advantage of the classification of Hurd and Kaneene (1993) is its ability to distinguish between a wide variety of theoretical models in existence by selecting combinations of various mathematical characteristics and traits. However, one distinct disadvantage of all the systems of classification presented so far has been a general failure to relate models to ecological theory. The super-model of DeAngelis and Waterhouse (1987) is unique in this sense. A brief evaluation and diagrammatic schema of the super-model is presented in the next section.

4.2.3.4 *Classification Based on Ecological Theory*

DeAngelis and Waterhouse (1987) do not define their super-model as a system of classification although it effectively is.

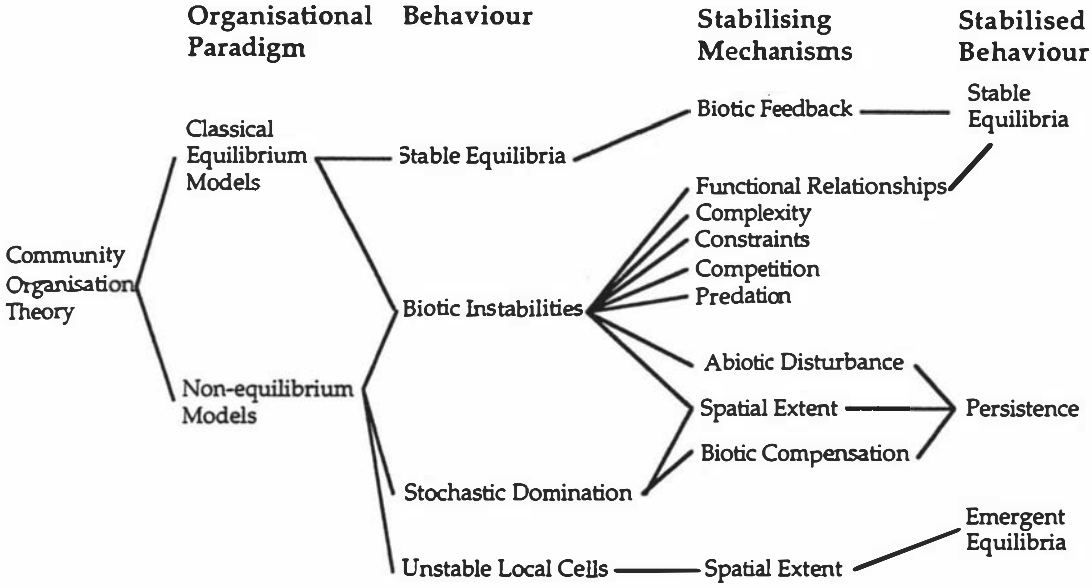


Fig 4.5 Classification of ecological models based on the alternative theories of community organisation. The classification scheme portrayed above represents the behaviour of equilibrium and non-equilibrium models with and without the addition of stabilising mechanisms. The nature of the stabilising mechanism is representative of the type of mechanistic complexity added to the parent model (after DeAngelis and Waterhouse 1987).

Because the super-model has already been extensively discussed in chapters one to three of this thesis, the terms and classes portrayed in fig 4.5 will be familiar to the reader.

The main benefit of this classification scheme is that it highlights the relationships between the theory of community organisation and the models that have been used to explore this theory base. The first class of behaviour (next to organisational paradigm in fig 4.5) reflects the outworking of the driving mechanisms inherent in the models of equilibrium and non-equilibrium systems. There are three classes of non-equilibrium behaviour, one of which (biotic instability) is also related to both equilibrium and non-equilibrium models.

The classic work of Robert May during the early 1970s led to the realisation that certain classes of equilibrium model were capable of manifesting inherent instabilities over certain regions of parameter space. A range of model mechanisms (functional relationships, complexity, constraints, competition, predation) were then investigated in order to attempt to discover how these systems might be restabilised.

Non-equilibrium models can be characterised by two fundamental classes of behaviour (biotic instability and stochastic domination). A third class of non-equilibrium behaviour (unstable cells) is representative of general non-equilibrium conditions at the local patch scale and may be produced by complex interactions of biotic instability and stochastic domination (density vague regulation).

A range of mechanisms (biotic compensation, abiotic disturbance and spatial extent) have been used in an attempt to stabilise non-equilibrium behaviour. These three main classes of stabilising mechanism were achieved by adding increased mechanistic complexity in earlier non-equilibrium models. The nature of the restabilising mechanism is also suggestive of the type of model complexity involved. For example, spatial extent requires the use of a systems modelling paradigm which is able to track the behaviour of individual model subunits and facilitate between cell (or subunit) dispersal based on stochastic or deterministic processes etc. The addition of spatial extent to unstable local cells is associated with a more recent behavioural discovery - emergent equilibrium behaviour.

Ecological models can also be classified on the basis of stabilised behaviour for which there are three subclasses in the DeAngelis and Waterhouse scheme: classical equilibria, persistence and emergent equilibria.

4.2.3.5 Summary and Conclusions

Of the four classification schemes presented in this chapter, the scheme of DeAngelis and Waterhouse (1987) requires that the user has a considerable background knowledge of ecological modelling and the structure and properties of various models. Despite this limitation, the scheme of DeAngelis and Waterhouse (1987) is perhaps the most valuable of all four schemes because it relates model type back to the fundamental organising paradigms in community ecology.

It is more difficult to rank the other three schemes of classification in order of importance because they are each unique in the contribution they make toward classifying ecological models. Combined, these four schemes of classification provide a highly integrative and comprehensive means of characterising the mathematical properties, the modelling paradigm, the research philosophy, the methodology and the theory base in community ecology where many of these models have been applied.

These elements of the four classification schemes reviewed in the preceding sections of this chapter will be used to classify the modelling research of palynologists, the constant growth trend model and modelling framework outlined later in this chapter. Most importantly, this highly integrative system of classification provides an excellent overview of the nature, variety and tremendous scope of mathematical modelling in ecology. In the next section, the contribution of palynologists to ecological modelling will be evaluated.

4.2.4 From Palaeo-ecology to Community Organisation

The purpose of this section is to provide a brief review and evaluation of the modelling research of palynologists. The integrative system of classification developed in the previous sections will be used as a basis for evaluation and classification of fossil pollen models. As an introduction to this discussion, a brief review will be made of developments in the recent scientific literature which have predicted and more recently evaluated the application of palaeoecological studies to theoretical ecology. As an introduction, the following section broadly defines palaeontology, palaeo-ecology, palaeolimnology and palynology.

4.2.4.1 Palaeontology

The present project is primarily concerned with the use of fossil pollen data as a proxy for actual measurements of long-term plant population behaviour. However, the main title to this section (from palaeo-ecology to community organisation) correctly indicates that the recent theoretical awakening among palynologists has also been experienced by palaeoecologists (Foster 1990, Gould 1981). In some areas of research palynologists use various lines of palaeoecological data as supporting evidence for their historic vegetation studies. This fact tends to blur the borders of demarcation between the two disciplines.

Kay (1947) defines palaeontology as *a means by which rocks are better classified in time and in environment of origin.* Gould (1981) suggests that traditional palaeontology *was the handmaiden of stratigraphic geology.* Although usually thought of as a descriptive science, palaeontology has recently allied itself with evolutionary biology and has experienced *all the challenge and excitement of its most rapidly developing sub discipline - theoretical ecology* (Gould 1981).

Traditionally, palaeontology was eminently a geological discipline although it did not ignore biology nor deny the importance of ecology. As a creation of the petroleum industry, palaeoecology became the fad subject of the 1940s and 1950s although it bears little relationship to anything an ecologist would recognise (Gould 1981).

The transformation of palaeoecology (former palaeontology) occurred during the early 1960s (West 1964) and 1970s - a change which appears to have come as a direct impact of theoretical population ecology. Palaeoecologists began to turn their research techniques toward the study of some of ecology's most theoretical and controversial questions such as community diversity (Deevey 1969, Stehli *et al.* 1969, Bretsky and Lorenz 1970, Valentine 1970, 1973), genetic variability (Schopf and Gooch 1972, Valentine and Ayala 1974), community succession (Walker 1970, Walker and Alberstadt 1975), competition theory (Stanley 1973), island equilibrium theory (Schopf 1974) and functional morphology (Deevey 1965).

Palaeo-ecology literally means the *ecology of the past* (Colinvaux 1993). Based upon the principles of uniformity and superposition (Roberts 1989) palaeoecologists study past fossil assemblages *to reconstruct the histories of populations or communities in order to test contemporary hypotheses* (Colinvaux 1993). Quaternary biogeographers also focus on contemporary ecological hypothesis testing as one of three strong traditions (Stott 1984) while palaeontologists traditionally used fossil evidence as a *time stratigraphic indicator* (Colinvaux 1993).

Palaeolimnology has emerged as a branch of contemporary limnology and focuses on the *interpretation of sedimentary sequences and on the diagenetic processes that can alter that record* (Wetzel 1983). Wetzel (1983) an eminent and well respected limnologist defines palaeolimnology from a methodological viewpoint as lake sediment dating, organic and stratigraphic sediment analysis along with lacustrine palynology and the study of macrofossil remains. Colinvaux (1993), an equally respected ecologist and palynologist defines palaeolimnology, lacustrine and terrestrial palynology as separate techniques of palaeoecology. Walker (1990) resolves this apparent contradiction by pointing out that *Quaternary palynology in America emerged, rather unexpectedly but with dramatic effect, from palaeo-limnology.*

Undoubtedly there is much technique shared by both palynologists and palaeolimnologists and it could be argued that time is the only difference between them. The time factor provides opportunity for lake ontogeny which differentiates lake ecosystems (and palaeolimnologists) from terrestrial mires and the palynologists who study them. Furthermore, palynologists are primarily concerned with the use of fossil pollen data to reconstruct terrestrial vegetation change. Palaeolimnologists are primarily concerned with the use of fossil evidence to study lake ecosystem productivity (Wetzel 1983).

Finally, an important assumption of palynological palaeoecology is that absolute fossil pollen values may be used as a suitable proxy measure of plant population density at any given site. This assumption involves more than just the suitability of fossil pollen data as a constant representative index of the living plant assemblage that existed in the surrounding area from which a core sample was taken. It must also be assumed that the living pollen assemblage deposited by natural processes at a core site location is consistently derived from the local vegetation source area.

The random deposition of extra-local pollen to the fossil assemblage results in a fossil pollen signal that does not accurately portray the long-term behaviour of the plant populations being studied. Palynologists have for many years investigated contemporary pollen deposition processes with the hope of discovering ways of minimising the influence of extra-local pollen contamination. The nature of this problem is now well understood (Tauber 1965, 1966, Oldfield 1970, Flenley 1973, Andersen 1973, Bonney and Allen 1984, Prentice 1985, 1988, Jacobson and Bradshaw 1980, Green and Dolman 1988, Traverse 1988, Di-giovanni *et al.* 1989, Sugita 1993, Davis 1994). The careful choice of research core site (Jacobson and Bradshaw 1980, Prentice 1985, 1988, Walker 1990, Sugita 1993) will to a large degree minimise this problem. However, even these methodological principles and procedures rely on the principle of uniformity - the assumption that present conditions have prevailed in the past.

The influence of extra-local pollen and the representative quality of fossil pollen as a proxy index for historic plant population density are generally considered to be the two most important and critical assumptions of palynological palaeoecology.

In summary, palaeontology is a distinct discipline of geology (Gould 1981) and has traditionally been concerned with the use of fossil evidence as *time stratigraphic indicator* (Colinvaux 1993). Palaeo-ecology emerged during the 1940s and 1950s as a product of the petroleum industry and was transformed with the advent of theoretical population ecology during the 1960/70s. Palaeolimnology and palynology may both be viewed as sub-branches of Quaternary palaeoecology, although Walker (1990) correctly points out that palynology has emerged from palaeolimnology.

By strict definition, the present research project draws on various lines of palaeoecological evidence (terrestrial forest and intertidal mangrove fossil pollen data as well as data derived from charcoal fragments and volcanic tephra). In the modelling of the two plant communities studied in this project, charcoal fragment and volcanic tephra data will be used as forcing functions responsible for driving the non-equilibrium behaviour of these systems. For this reason it is correct to refer to these two lines of evidence as palaeoecological and fossil pollen data.

The testing of hypotheses (models) according to the hypothetico-deductive technique requires the acquisition of suitable long-term data. Without doubt, one of the hindrances of formal ecological studies has been the difficulties and expense of obtaining long-term data of high statistical quality. Palaeo-ecology is increasingly viewed as a potential answer to the need for a temporal perspective (long-term data) in ecological studies. The next section briefly discusses the need for long-term data as an introduction to the rise of palaeoecology as a distinct academic discipline.

4.2.4.2 The Need for Long-term Data

In recent times the field of theoretical ecology has become known for its multitudinous simulation studies and paucity of model validation, with data generated from conventional long-term experiments or observational studies. The value of long-term studies (Taylor 1987) is reflected in the fact that the most *and Godwin but perhaps insufficiently developed, or inappropriately advertis since their days.*

To accomplish this objective, palynologists will probably need either work corroboratively with theoretical and empirical ecologists or to acquai themselves with state of the art developments in theoretical ecology.

The present thesis is an attempt to close the gap between theoretical ecolo and palynology as suggested by Davis (1994). Based on further research of t kind, palynology will hopefully find its *most expanding and exciting future what it is primarily and directly about, namely the numbers and locations plants* (Walker 1990).

In keeping with the objectives of the present thesis it is not the intention the present author to review the already well documented (*e.g.* Prentice 1 Schoonmaker and Foster 1991, Walker 1982, MacDonald and Edwards 19 contributions made by palynologists to their *existing modelling rese paradigm.* Such an approach will accomplish little more than restating what already been adequately said.

Instead, the approach taken by this author in reviewing the contribution palynologists will be to evaluate and characterise this work in terms of modelling paradigms of theoretical ecologists. The purpose of this evaluati to provide a distinctly new classification which identifies areas in which fu contributions to this field of research might be made. Finally, this evalu will assist in classifying the contribution of the present thesis in relatic existing studies in palynology.

4.2.4.5 The Contributions of Palynologists - an Eval

The procedure taken in this evaluation involves two parts. Firstly contributions of palynologists will be diagrammatically represented in ter each of the four classification schemes discussed earlier in this chapter. Secc these illustrations will be used as a basis for discussion and evaluation. Th system of model classification is based on the *intended application* mod paradigm of Robertson *et al.* (1991).

4.2.4.5.1 Classification Based on Intended Applicat

The three main classes of model application in the Robertson *et al.* scheme are statistical, theoretical and simulation (fig 4.6). The models u Palynologists have been related to these three general areas of applicatior model type listed under Modelling Paradigms represents a particular mo framework in use by one of the three main modelling schools in palynolo

Statistical Modelling is subdivided into two subclasses. The first s includes a range of inductive statistical modelling techniques like fact cluster analysis that have recently been used to generate environ hypotheses using fossil pollen data (see Moseholm *et al.* 1987, D'antc Schabitz 1990, Andersen 1991, Birks 1985, Birks and Gordon 1985). This response of taxa to historic environmental changes that are within the range of projected global changes.

Furthermore, Foster *et al.* (1990) present considerable research evidence to demonstrate that a fundamentally important lesson from palaeoecological studies has been a better understanding of the nature of communities and the non-equilibrium conditions (Davis 1994) that have shaped their destiny. Specifically, palaeoecological studies have provided information on the individualistic nature of species behaviour (Davis 1981), community structure (Clark 1990, Grimm 1983), the impact of past climate change (Schoonmaker and Foster 1991), the study of plant invasions (MacDonald 1993), community succession (Walker 1970), evolution theory (Schoonmaker and Foster 1991), community organisation (Delcourt and Delcourt 1987), refugia (Walker and Chen 1987, Colinvaux 1987), non-equilibrium behaviour (Wasson and Clark 1985) stability (Watts 1973, Foster *et al.* 1990) and change (Delcourt and Delcourt 1987).

Davis (1994) points out that while only twenty years ago there may have been resistance among ecologists to the idea that climate change is significant on ecological time scales, *ecologists of the 1990s not only accept the idea but embrace the challenge of predicting its effect on species interactions.* Much of the research quoted above is only representative of a much larger body of palaeoecological studies the most significant contribution of which has come from palynology.

4.2.4.4 The Contributions of Palynologists - Introduction

One of the first palynologists to recognise the potential of fossil pollen data derived by absolute technique for studies in population ecology was Watts (1973). An interesting feature of the application of the methodologies first articulated by Watts (1973) has been the development inside palynology of a distinct research paradigm. While this paradigm undoubtedly has its roots in ecology, it has developed largely independent of theoretical ecology and this is especially true of developments in this field over the last three decades.

This fact is a credit to the palynologists who have developed a research framework of their own based on the peculiar strengths and limitations of fossil pollen data. Furthermore, the development of this unique paradigm has been productive of insights that have already radically changed the theoretical perspective of plant ecologists in general (Davis 1981, 1986, 1994). The *possibilities are endless* (Flenley 1990). However, it is the belief of the present author that the full potential of the application of palaeoecology and more specifically palynology to the study of ecological theory exists in addressing questions at the very forefront of current theoretical ecology. As Walker (1990) has suggested, palynologists should begin to *build back toward main stream ecology and plant geography, picking up the threads first spun by Iversen, Firbas*

Treatment of Time: An interesting trend in this sub class is a noticeable absence of model formulations based on difference equations or discrete time. The exponential, logistic and coupled logistic can all be reformulated as difference equations. Justification for the use of difference equations may include the evidence of life history based on regular or annual processes or discrete sampling.

Computational Treatment of Individuals: The development and application of individual based model formulations (discrete entity) is so new (Judson 1994, DeAngelis and Gross 1992) that it comes as no surprise that this modelling paradigm has not been used by palynologists more extensively. The North American modelling research (Solomon *et al.* 1980, West *et al.* 1981 Green *et al.* 1983, Davis and Botkin 1985, Solomon and Webb 1985) based on th JABOWA and FORET forest stand models shows tremendous promise.

The constant growth trend model, forest stand model formulations and empirical modelling research of palynologists (Walker and Chen 1987, Chen 1988, Magri 1989, Tsukada 1980, 1981, 1982, 1982a, 1982b, 1983, Tsukada and Sugita 1982, Bennett 1983, 1986, 1988, Delcourt and Delcourt 1987) has all involved the use of mathematical models for which individuals are treated as continuous entities.

Method of Solution: Hurd and Kaneene (1993) define the term analytical in this context as a closed form solution to the state of a system at some equilibrium. Therefore, a prerequisite to an analytical solution is the use of an equilibrium model (*e.g.* Walker and Chen 1987, Chen 1988, Magri 1989, Tsukada 1980, 1981, 1982, 1982a, 1982b, 1983, Tsukada and Sugita 1982, Bennett 1983, 1986, 1988, Delcourt and Delcourt 1987).

The four types of simulation model listed in fig 4.8 (constant growth trend, forest stand, exponential and advection/diffusion) may be further sub classified as systems (constant growth trend, forest stand, exponential) and mass action (advection /diffusion) models according to the genera of process simulation models in fig 4.4.

In summary, the classification scheme of Hurd and Kaneene (1993) identifies an important trend in the research of palynologists involving theoretical model constructs. Primarily, palynologists have chosen to apply continuous entity, deterministic models to generate *a posteriori* hypotheses (a functional application perspective) and to test *a priori* hypotheses (in an applied or empirical domain) in continuous time equilibrium systems which require analytical solutions.

This approach highlights a strong equilibrium focus. The behaviour of stochastic systems (DeAngelis and Waterhouse 1987) or systems driven by deterministic chaos (Judson 1994), (based on simple difference equations) remain largely unexplored. The use of a structural application perspective is strictly speaking the domain of a theoretical modelling methodology. Initial research efforts involving the use of individual-based models (discrete entity) has produced very promising results (Solomon *et al.* 1980, West *et al.* 1981, Green *et al.* 1983, Davis and Botkin 1985, Solomon and Webb 1985).

Systems models are the favoured choice of model solutions based on simulation procedure with the exception of advection/diffusion models (Dexter *et al.* 1987) which are mass action models by definition. Chain binomial, mass action and systems modelling paradigms (see fig 4.4) in general have apparently been little used by palynologists.

The constant growth trend model advanced in the present project has both stochastic and deterministic elements It is used as an *a priori* hypothesis and can be formulated in either continuous or discrete time.

4.2.4.5.4 Classification Based on Ecological Theory

The classification of ecological models by DeAngelis and Waterhouse (1987) is based on two alternative models of community organisation which have been contributed to by theoretical modelling and a variety of empirical and simulation studies. Because of the difficulties of obtaining suitable long-term data for use in testing the mechanistic and predictive qualities of these new model formulations many of the new model-hypotheses advanced by theoretical ecologists remain in the simulation testing stage. Future fossil pollen researchers will undoubtedly make an important contribution in this area. The use of a theoretical modelling methodology is the necessary qualification for designation in this scheme of classification.

The validity of the present authors evaluation of the contributions of palynologists to this modelling paradigm rests on the acknowledged weakness of attempting to distinguish between empirical and theoretical palynological modelling studies. Assuming that this distinction is correct, then the modelling research of palynologists could be considered as a general class of insights and contributions to ecological theory derived from empirical studies.

Once again, time series analysis modelling is a little more difficult to classify under this scheme. The time series analysis of Green (1981, 1982, 1983, 1983a, 1986), Green and Dolman (1988), Green *et al.* (1988a) has focused upon identifying correlation between the absolute fossil pollen signal and other palaeoecological data (charcoal fragments) assumed to be an abiotic disturbance.

While this work is distinctly non-equilibrium in nature and therefore fits into the DeAngelis and Waterhouse (1987) scheme of classification, it involves the generation of *a posteriori* hypotheses which do not appear to be tested using hypothetico-deductive methodology.

The constant growth trend model, forest stand models and advection/diffusion models have also been used to test hypotheses related to the non-equilibrium paradigm of community organisation. The constant growth trend model and forest stand models have been used to evaluate the influence of abiotic disturbance as forces driving non-equilibrium systems. The advection/diffusion models have been used to model spatial effects based on an assumption of Malthusian growth as the mathematical form *that best represents the diffusion-like and source/sink mechanisms* (Dexter *et al.* 1987).

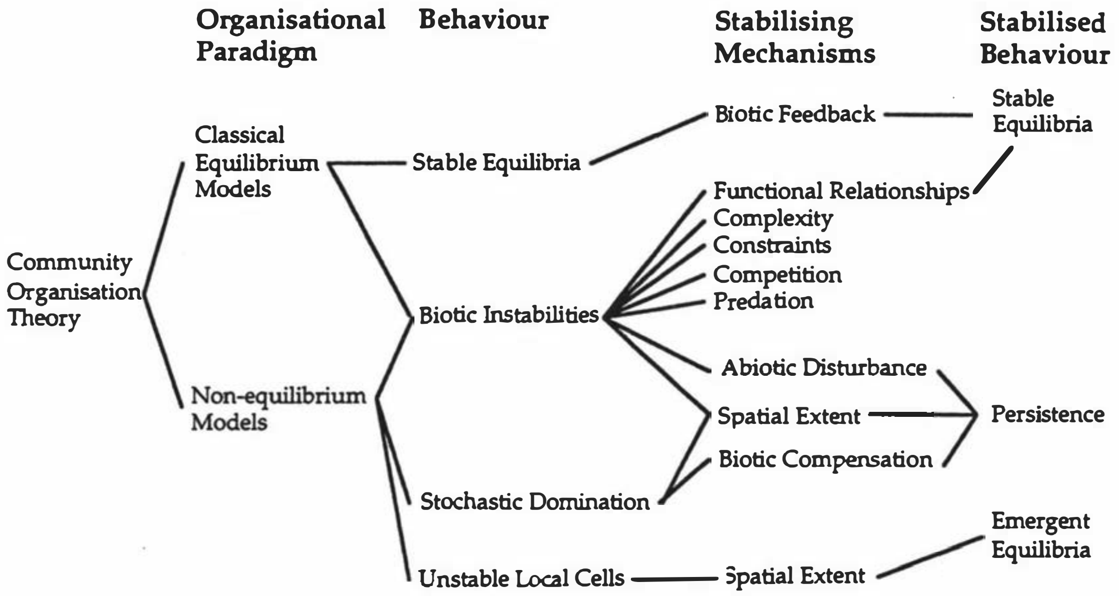


Fig 4.9 Classification of models used by palynologists based on ecological theory (after DeAngelis and Waterhouse 1987).

4.2.4.6 The Contributions of Palynologists - Summary

The present line of discussion has traced the emergence of palynology from palaeontology and stressed the tremendous opportunities that exist for using the palaeorecord (long-term data) to study community organisation. In many areas of palaeoecology and palynology important contributions have been and are being made to community ecology by way of traditional descriptive, narrative and analytical scientific methodology.

The importance of scientific methodology has been stressed in the context of a distinction between empirical and theoretical modelling. It is proposed that the modelling research of palynologists up until the present time has been primarily empirical. The distinguishing characteristic of theoretical modelling research is the use of an alternative hypothesis in order to evaluate the explanatory power of a given model formulation.

The present author acknowledges the possible limitations of attempting to classify palynological modelling research as reported in scientific publications in which it is not accepted convention to explicitly state the authors methodological philosophy. Despite this weakness, the present author believes that the issues are clear enough to venture upon a tentative classification as set forth above.

It has been acknowledged that insights from the empirical modelling research of palynologists have already made a significant contribution to theoretical ecology. These insights have especially been important in drawing the attention of contemporary community ecologists to the non-equilibrium nature of vegetation communities. In the above evaluation the present author has attempted to identify areas in which palynological modelling research might be directed in the future.

Firstly, at a time when palaeoecologists in general are seeking to close the gap between historical and mainstream ecology, it seems timely to consider the important distinctions between an empirical and theoretical modelling methodology. Secondly, it is evident from the above evaluation that there exists an enormous theory base in contemporary theoretical ecology which might be used by palynological modellers as a road map for future research questions and hypotheses. The possibilities are endless (Flenley 1990).

Thirdly, there appears to be an exciting range of model constructs and general modelling paradigms used by theoretical ecologists that might successfully be exploited by palynologists in their modelling research.

Finally, this evaluation has helped to identify in just which areas the present thesis attempts to make a contribution to palynological modelling research. Firstly, every effort has been made to bring this research project into line with recent developments in theoretical ecology. Secondly, the modelling framework used in this study is an adaptation of parts of various modelling paradigms designed to meet the peculiar needs of absolute fossil pollen data. Finally, the research methodology used in this project is hypothetico-deductive and involves the collection and analysis of data to evaluate the truth of an *a priori* hypothesis (Mentis 1988) by testing the predictive and explanatory power of model constructs.

In the remainder of this chapter there are two final objectives to be accomplished. Firstly, to outline the dynamical systems framework used in this project and secondly, to introduce the model formulations to be tested.

4.3 A Dynamical Systems Modelling Framework

The objective of the following section is to introduce the modelling framework used in this project and to define the criteria used for the acceptance or rejection of working hypotheses. In this context, the term modelling framework is synonymous with modelling paradigm (Robertson *et al.* 1991). The modelling framework developed in this project is an integration of parts from at least four modelling paradigms. Dynamical systems is undoubtedly the most dominant of the four. However, because modelling paradigms in general share so much in common, it is difficult to define exact boundaries.

4.3.1 Introduction

For the sake of definition the modelling paradigm used in this project (fig 4.10) consists of four components: the *hypothetico-deductive* research methodology, a collection of *model constructs* and *procedures* borrowed from various modelling paradigms and *evaluation* procedures based in dynamical systems methodology.

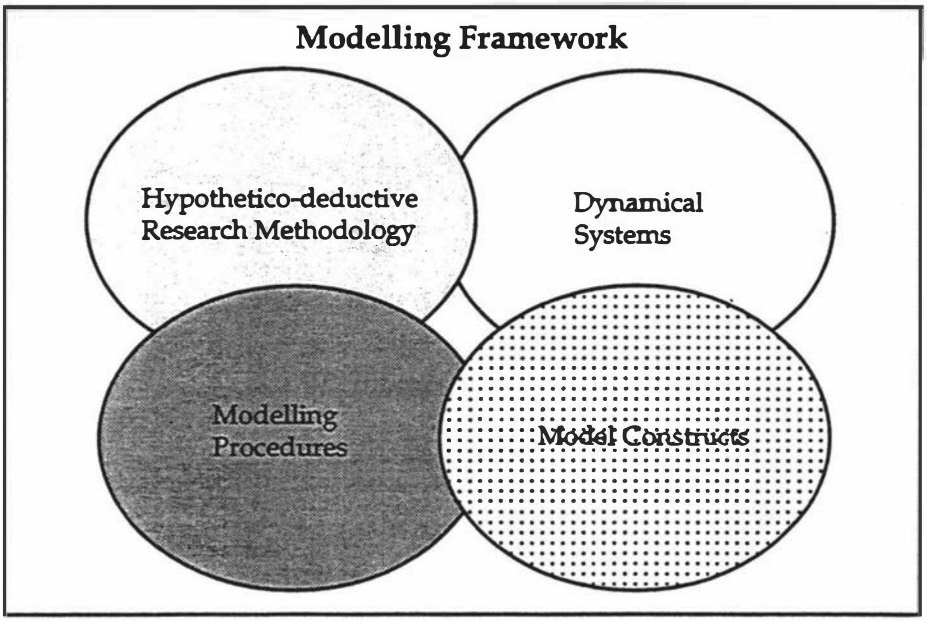


Fig 4.10 The four main components of the dynamical systems modelling framework developed in this project.

Most of these topics have already been defined in previous sections of this chapter and for this reason the emphasis of the following section will be to identify the way they have been applied to the present project.

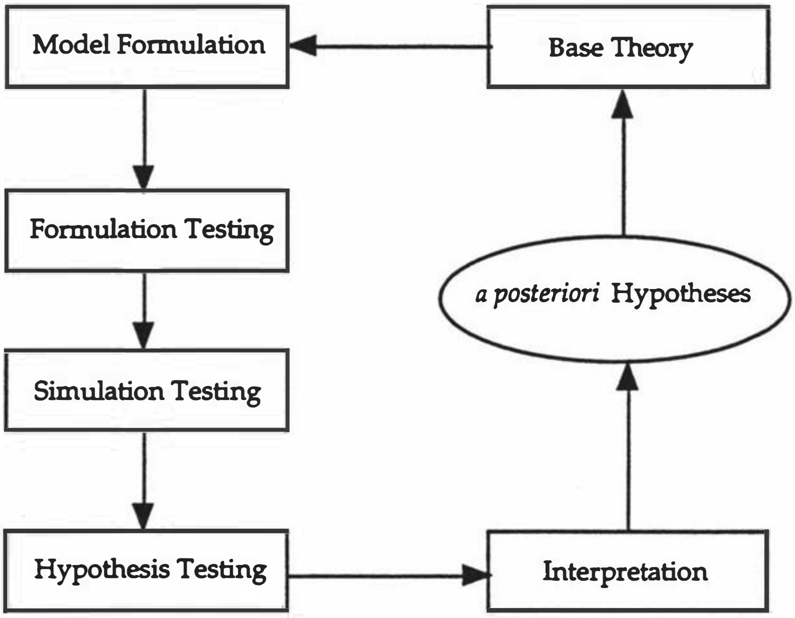


Fig 4.11 The four main stages of the modelling process used in this project. Model formulation and formulation testing represent one stage. Simulation testing, hypothesis testing and interpretation are the final three stages. The interpretation stage involves evaluating experimental results in the light of the original base theory or paradigm. This stage often involves the integration of *a posteriori* hypotheses into new model formulations for future testing. The original model formulation is an *a priori* hypothesis.

The following discussion covers these four topics in an integrative fashion. Firstly, the computer hardware and software will be introduced. This will provide an opportunity to evaluate MatLab's scripting language. Secondly, the modelling process (Wake 1992, Platt 1964, Loehle 1983, Mentis 1988) will be discussed. This involves a systematic description and evaluation of the four stages of modelling procedure (fig 4.11) used in this project: model formulation and testing, model simulation testing, hypothesis testing by calibration procedures and results interpretation.

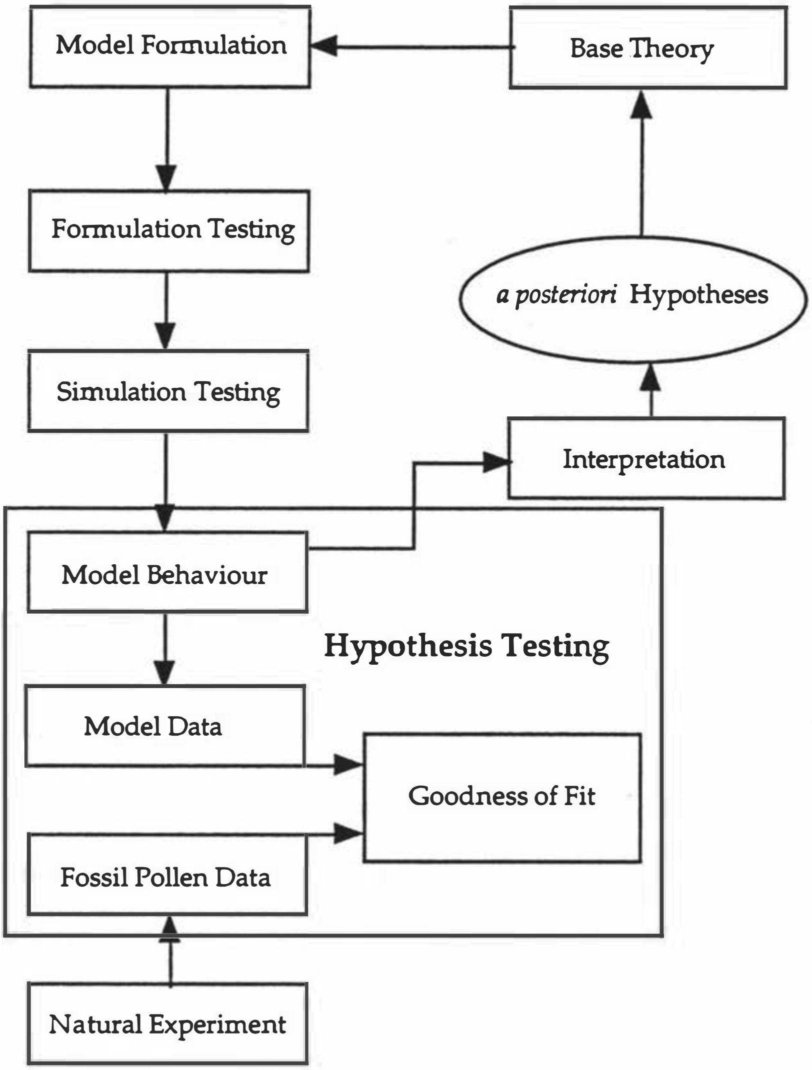


Fig 4.12 The modelling process of fig 4.11 modified to illustrate the two components of experimental design in hypothesis testing.

Finally, once the main operational procedures have been outlined, the model constructs used in this project will be introduced. These models reflect a variety of modelling paradigms and theoretical propositions. These models will be tested for predictive and explanatory capability in accordance with hypothetico-deductive methodology. Testing the predictive power of a model requires an experiment designed to compare the performance of a model against field data (fig 4.11).

As used in the context of this study, experimental design (or hypothesis testing) has two important components. Natural experiments (Diamond 1986) involve all the historic forces that influence the deposition and preservation of pollen. Through sampling and preparation techniques the fossil pollen record is converted into field data (fig 4.11). Palynologists have no input into natural *experimental design* unlike empirical ecologists involved in the design of laboratory and field experiments. By choosing a given core site location, palynologists determine which natural experiment they are to study and ultimately the quality of the experimental record, but they have no control over the initial experiment at the time it occurs.

Experimental design also involves the testing of field data against the predictions of a theoretical model. In the present study this will be referred to as *experimental design for hypothesis testing*. Optimisation procedures are used to fine tune the parameters of a model so that its behaviour as near as possible imitates that of the field data. Goodness of fit is commonly used to evaluate how well a model's behaviour imitates field data behaviour. In this project, the use of long sequences of fossil pollen data involves problems of experimental design that are not usually common to laboratory and field experiments. These points are discussed below as a general introduction to the modelling framework presented in this section.

4.3.1.1 Natural Experimental Design

Natural experimental design is somewhat of a problem for palaeoecologists who are unable to establish an experiment and replicate it as ecologists are able to do in other areas of neoecological research (Hurlbert 1984, Walker 1990, Delcourt and Delcourt 1991).

The essence of experimentation is control and replication (Walker 1990). It may be argued, that no experiment can be totally controlled and as Walker (1990) has pointed out *it is idle to think that every hole in the ground is the site of a natural experiment which palynology can interpret.* Not even laboratory experiments and field studies are totally free from these limitations (Diamond 1986).

No experimental procedure is perfect and palaeoecological studies have much to offer by complementing the weaknesses of laboratory and field experiments. Furthermore, while *experimental control and replication* is not available to the palaeoecologist, local and regional site replication most certainly is. Site replication tests the hypothesis of consistent results while controlled replication tests the hypothesis of predicted between-site differences. Walker (1990) has suggested that the *strongest methodology of Quaternary palynology is replication. It is important that its use be maximised and to do so it must be applied in a manner appropriate to the problem to be settled.*

The Fijian island of Totoya provides ideal conditions for regional site replication. Two of the six sites cored on this island have been used for testing the hypothesis of regional consistency while a third site which differed slightly in local physiographic conditions has been used as a control replicate. The opportunity for local and regional site replication was also available at the New Zealand core site but was not utilised because the size of this PhD project was considerable by this stage. These sites will make an ideal future companion study to test the results outlined in this thesis.

4.3.1.2 Experimental Design for Hypothesis Testing

Once the data from a natural experiment has been collected it can be compared with the predictions of a theoretical model (see fig 4.12). This component of experimental design is accomplished using some form of calibration procedure. Jorgensen (1979) uses calibration to define what most ecological modellers and mathematicians refer to as parameter estimation (O'Neill *et al.* 1980, Benson 1979, Richter and Sondgerath 1990). Parameter estimation is accomplished using an optimisation methodology (like least squares) that involves criteria for determining goodness of fit (Halfon 1980, Costanza 1989, Richter and Sondgerath 1990) between model and field data.

The design element of hypothesis or model testing involves an *a priori* decision concerning exactly what level of accuracy is required for the acceptance or rejection of a hypothesis. There are problems with this procedure when using long sequences of fossil pollen data. Firstly, the behaviour of a deterministic model is very precise and fitting such a model requires an adequate knowledge of the nature and structure of error in field data for goodness of fit to be evaluated.

Secondly, parameter estimation in linear data and short sequences of nonlinear data (*e.g.* a logistic rise) is a relatively simple procedure. However, this situation changes when attempting to estimate model parameters for long sequences of nonlinear data such as those used in this project. There are various error weighting (Grace 1992, Kuo and Fox 1992) and data smoothing techniques (Kuo and Fox 1992, Schaefer and Farber 1992, Minitab 1995a, b) that can be used to improve goodness of fit. However, these techniques also require an understanding of the nature and structure of error - a problem with fossil pollen data.

When the nature and structure of error is not known in data it is difficult to determine whether variance is the result of natural processes (Cousens 1995) or sampling and natural process errors (Chesson 1986). As a result of this problem it is difficult to determine why a model fails to fit field data. If the model has the wrong mechanisms it will poorly predict the behaviour of field data. If the model formulation is mechanistically correct and still fails to fit field data the tendency is to assume that the model is wrong. This may not be the case if variance in the field data is caused by unknown error.

For data derived from laboratory and field experiments this is less of a problem because the experimenter either has control or is able to assess experimental error by conventional forms of measurement. When the nature and timing of exogenous disturbance is known and accurately measured, it is possible to make allowance for these errors in evaluation of the data. Unfortunately, palaeoecologists have no control over the process errors of natural experiments. Therefore, they are not able to assess these errors by measurement or eliminate them during the experiment so as to simplify the system being studied.

Error can be introduced into fossil pollen data via two known natural processes and four sampling/laboratory procedures: pollen dispersal and deposition (Tauber 1965, 1966, Flenley 1973, Andersen 1973, Bonney and Allen 1984, Prentice 1985, 1988, Jacobson and Bradshaw 1980, Green and Dolman 1988, Traverse 1988, Di-giovanni *et al.* 1989, Sugita 1993, Davis 1994), disturbance during geological preservation (Davis *et al.* 1971, Davis 1973, Green 1983, Green and Dolman 1988, Green *et al.*. 1988a, Delcourt and Delcourt 1991, MacDonald and Edwards 1991), core sample removal and subsampling (Green and Dolman 1988, Larsen and MacDonald 1993), laboratory processing (Stockmarr 1971, Maher 1977, 1981, Regal and Cushing 1979, Clark 1984, Walker *et al.* 1994), dating of the core stratigraphy (Scott *et al.* 1984, Green and Dolman 1988, Jemmett and Owen 1990, Buck *et al.* 1994) and fossil pollen counting (Brookes and Thomas 1967, Faegri and Iversen 1975, Rull 1987).

Of these two classes of error, palynologist's have no control over the natural process errors of pollen dispersal and preservation. Considerable effort has been expended to understand the operation of these natural processes in contemporary vegetation. While important discoveries have been made in this area, especially regarding pollen source area (Oldfield 1970, Prentice 1985, 1988, Jacobson and Bradshaw 1980, Sugita 1993), it is still not possible to specify the nature and structure of errors introduced from the operation of these natural processes with any degree of certainty.

Palynologists do have greater control over errors introduced as a result of core removal, subsampling, the dating of core sample stratigraphy, laboratory preparation techniques and microscope counting. For example, Walker *et al.* (1994) have carefully calculated the statistical uncertainty involved in the several stages of pollen extraction from a lake mud to counted absolute data. The authors report 95% confidence intervals of about ± 17% and ± 9% of the mean total fossil pollen concentration estimates attained by the volumetric (Davis 1965) and exotic marker (Benninghoff 1962) methods respectively (ref. also to Maher 1972).

Green (1981, 1982, 1983, 1988) addressed the problem of interpreting fine resolution (closely sampled) absolute fossil pollen data by treating the data as a statistical time series. The time series techniques used by Green (reviewed in 1988) include filtering, sequence-splitting, correlogram, spectral analysis and process modelling. However, these techniques cannot improve the quality of poor data. They constitute inductive tools used to manipulate and interpret data.

For example, data filtering and weighted running averages are common time series procedures used for cleaning up *noisy data.* However, these techniques assume a knowledge of the nature and structure of error without which is not possible to know for certain if an averaging routine is removing noise or actual data.

In summary, parameter estimation requires goodness of fit criteria which, in turn, requires a knowledge of the nature and structure of error in field data. Palynologists are not able to obtain adequate knowledge of the errors introduced into fossil pollen data as a result of the natural processes of pollen deposition and preservation. For this reason, it is more appropriate to evaluate fossil pollen data heuristically.

Therefore, the refutation criteria used in hypothesis testing in this project will be to assess model behaviour by evaluating the morphological features of the model and field data. This is not a statistically sound basis for hypothesis refutation or acceptance and ultimately involves the danger of rejecting or accepting the wrong hypothesis (Mentis 1988). However, the alternative is to use statistical techniques as a criterion for refutation and to draw conclusions which may be equally as unsound.

The result of a heuristic evaluation will be a grading of goodness of fit based on subjective criteria. It is however the opinion of the present author that such an approach will be adequate to distinguish between extremes of performance (*e.g.* acceptable or poor) in model formulations and to identify weaknesses in predictive capability.

Ecology is still in the early days of understanding the causes of long-term vegetation behaviour. It is doubtful that fossil pollen data will ever be used to provide conclusive evidence. It should much rather be viewed as a complementary line of evidence to other empirical and theoretical research, an opportunity to test hypotheses within a temporal framework while recognising the possible limitations of the data. As Walker (1990) has suggested the *strongest methodology of Quaternary palynology is replication.* Consistent results based on within and between site replication will add greater confidence to palynological modelling research although the use of replication itself will often involve a trade off against increased core sample resolution.

Having defined the refutation criteria used in this project the modelling process, hardware, software and model constructs can now be described.

4.3.2 Computer Hardware and Software

Modelling nonlinear systems requires both computer power and software flexibility. The matching of computer software and hardware is an important consideration. There are three general classes of software available to ecological modellers, each of which requires differing amounts of computer processor speed.

4.3.2.1 Three Software Options

Modellers who are suitably proficient in mathematics and programming are able to script software from programming languages like FORTRAN, C, object oriented C and Turbo Pascal. These applications have small script overheads and consequently run very fast. They also provide unlimited flexibility at the cost of development time and programming expertise.

A second option is the use of high level languages like MatLab and Maple. Programming languages of this kind usually have facility for modular subroutines written in C. In a high level language, development time is greatly reduced and flexibility retained at a cost of high script overheads and poor performance unless supported by a very fast and efficient computer processor.

A final option is to use production or shelf software like STELLA™ (Costanza 1987) and Sigmaplot (Kuo and Fox 1992). STELLA™ is an object oriented modelling program for the Macintosh that allows a user to design and run a fairly elaborate model in a fraction of the development time required for high level and standard programming languages. Sigmaplot is a scientific plotting program for Macintosh or Windows which comes complete with transform language, optimisation software and differential equation solvers (version 5.0). These programs are a good compromise. For loss of flexibility, the user gains easily developed software that runs quite efficiently on slower computers.

This brief review demonstrates that operational speed is very much a result of the choice of software and to a lesser degree the capability and efficiency of the computer processor.

4.3.2.2 Computer Hardware

The modelling work undertaken in this project was developed and run on SUN workstations using the Unix operating system. It is difficult to compare Unix with the Macintosh and MS-DOS (or Windows). The central processor on a SUN workstation is very fast, however Unix is designed to support a multi-user environment which can hardly be compared with a stand alone machine. As a rough estimate, when MatLab is run remotely on a SUN workstation it probably runs a little slower than a 486/PC with maths co-processor.

The Sun workstation proved to be quite adequate for the development (or scripting) of routines and running simulations on single or low dimensional differential equations. However, the use of forcing functions, higher order dynamical systems and nonlinear optimisation virtually brought the SUN workstation to a standstill! A single optimisation run using classical equilibrium models with forcing functions was found to take anything from twelve to over twenty four hours. Due to the arrival of new hardware, the final results for this thesis were re-run on a Digital Alpha with a 200 MHz processor. Routines which had formerly taken twenty four hours could now be completed in thirty minutes to an hour.

One advantage of Unix is the ability to run background processes. A further advantage is the ability to log onto a workstation remotely and thereby monitor, start, stop or debug problems in long operations. By using a modem linked to a macintosh computer with Apple Remote Access (ARA) software it was also possible to perform these tasks from home.

In retrospect, the SUN workstation was probably not the ideal platform for this type of modelling work. The MatLab scripting language is also partly to blame - poor performance is the cost of a flexible high level language. MatLab would probably have run faster on a stand alone 486/PC with a maths-coprocessor. The latest Pentium range of personal computers, native and clone Power Macintosh computers operate at processor speeds ranging from 66 MHz to over 100 MHz. These systems offer tremendous computing power and would be ideal for this type of modelling work.

Constanza and Maxwell (1991) have developed an algorithm and software for using parallel processors to handle complex spatial systems based on GIS and dynamical systems models (STELLA™). Their spatial modelling workstation using eight transputers on a Macintosh IIci ran spatial ecosystem models in about the same time as a CRAY X/MP.

4.3.2.3 Matlab and the Optimisation Toolbox

The following discussion introduces the MatLab scripting language and illustrates its properties by an evaluation of the nonlinear optimisation program (Appendix 3) developed for this project. This program was based on MatLab's optimisation toolbox (Grace 1992). All of the script files used in this project for model simulation and optimisation will be located in the appendices at the rear of this thesis. Each script file is referenced to the place where it is mentioned in the text for the convenience of the reader.

The name MatLab stands for *matrix laboratory* - a software package suitable for scientific and engineering numeric computation. The strength of MatLab is its ability to integrate numerical analysis, matrix computation, signal processing and graphics in an easy-to-use environment where problems and solutions are expressed just as they are written mathematically. The basic data element of MatLab is a matrix that does not require dimensioning. This allows the user to solve numerical problems in a fraction of the time required to write a program in a language like FORTRAN, Basic or C (The Maths Works Inc. 1991).

The MatLab environment consists of a command window which is used to load data, define variables, print results and call MatLab subroutines stored as mfiles (MatLab files) - designated by the suffix *.m*. For example, ode45.m stands for differential equation solver 45. To call ode45.m the user simply types the filename of the mfile in the command window without the .m suffix.

```
>>ODE45     % the >> symbol stands for the MatLab command
            % window prompt.
```

The percentage sign (%) is used in the command window and mfiles to comment-out notes and unnecessary script.

Subroutines can be nested within new mfiles so that a quite complicated program can be constructed. This feature of the MatLab environment has been used in this project to construct a nonlinear optimisation program for parameter estimation. The elements of this program are illustrated in fig 4.13. The overall program is composed of three mfiles named zdu.m, lsfun.m and ode.m.

Zdu.m is the command file which contains the statements that would normally be entered into the command window (fig 4.13). The file lsfun.m stands for least-squares function (fig 4.13). This file contains a subroutine which calls the differential equation solver (ode45.m) on the model equations stored in the mfile named ode.m (ordinary differential equation mfile). The basic operation of the program is as follows.

The m-filename *zdu* is typed into the command window and this calls the mfile zdu.m. Firstly, all of the global parameters and variables are read into the MatLab workspace and held there for future reference. MatLab then loads all of the appropriate fossil pollen data files into its workspace. Data files are stored in an acsii format identified by the *filename* suffix (.dat). At this stage, the fossil pollen data has the dimensions of *total pollen grains per* cm^2 of sample sediment.

The sample depths and carbon 14 dates which have been used to determine the rate of sedimentation in the core are then loaded into MatLab's work space. A subroutine (interp1.m) is then used to interpolate a new data set from a three way table which contains the carbon 14 dates, sample depths and pollen data. Interpolation determines each new datum point based on the carbon 14 age of the stratigraphic depth from which the sample was taken. These data have the dimensions *total pollen grains per* cm^2 *of sample sediment per Calibrated year* (grains cm^{-2} CAL. yr^{-1}) (see fig 4.13). Interpolation has the effect of standardising all of the sample time intervals for the optimisation routine which requires data of equal time steps in order to compare field and model data behaviour using least squares. The interpolated absolute fossil pollen data is kept in the MatLab workspace for use by the least-squares function mfile (lsfun.m).

In the next step, initial equation parameters (PAR) are loaded into the MatLab workspace. Finally, the command mfile (zdu.m) calls the optimisation subroutine located in the mfile named lsfun.m.

When lsfun.m is called, it loads global variables, passes all relevant arguments (including PAR) and then calls the differential equation solver ode45.m to solve the differential equations located in the mfile ode.m. All of the model formulations used are stored in the ode.m mfile (equation statements not needed for a given optimisation run are commented out). In fig 4.13, the coupled logistic equation is being called and will be solved based on the initial equation parameters which the user has supplied to start the program.

Next the model data is picked up from the MatLab workspace by the lsfun.m mfile. The term *tem* is the difference between the field and model data. If this difference satisfies convergence criteria then the optimisation routine will converge and send the results (final parameters and model data) to the command window.

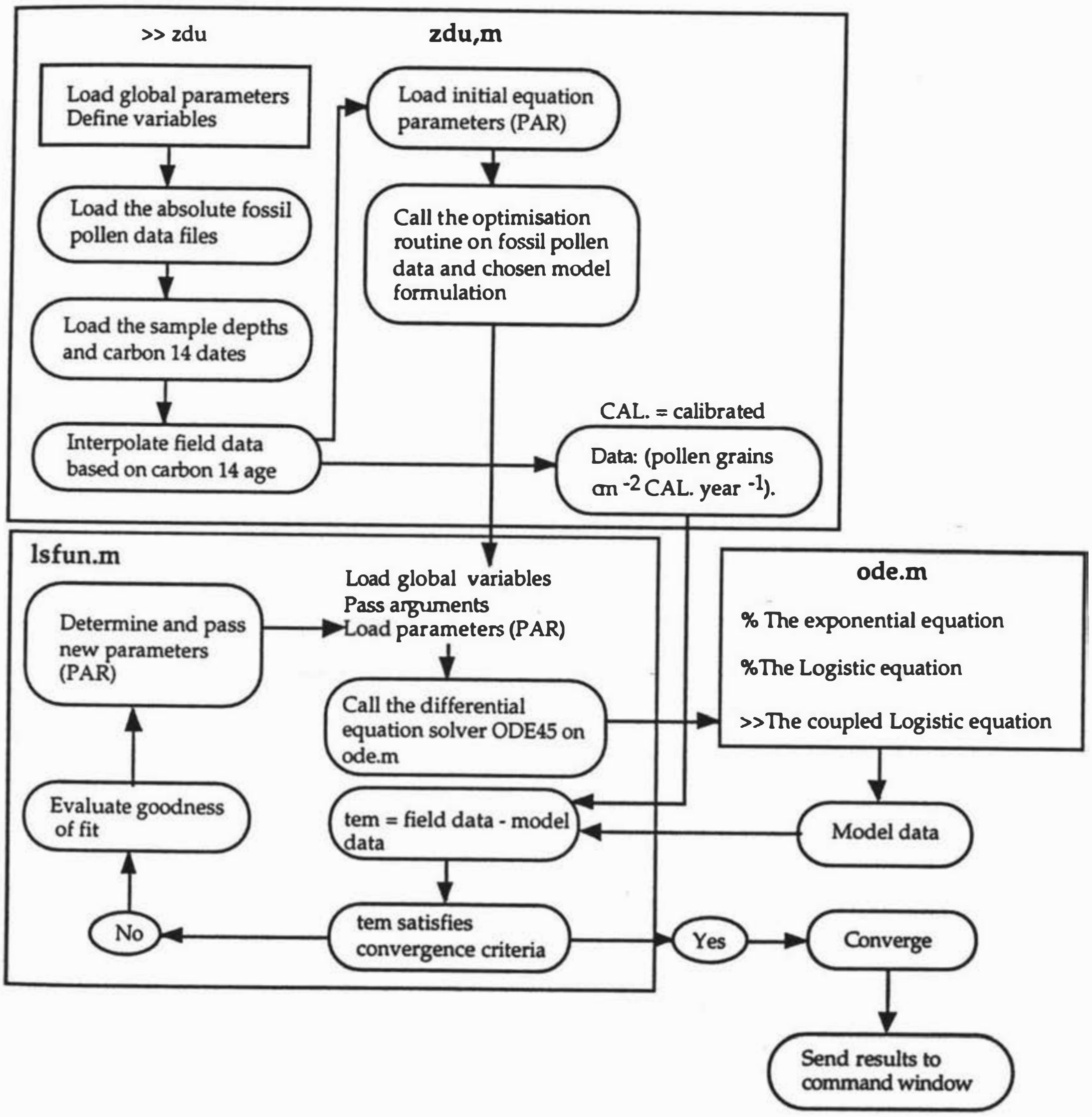


Fig 4.13 A flow diagram showing the interrelationships of the elements of the nonlinear optimisation program scripted in MatLab.

If *tem* does not satisfy the convergence criteria the search path function evaluates the present and past values of *tem* to determine if the range of parameters being used is improving or worsening the goodness of fit. Based on this evaluation, the optimisation software chooses a new set of parameters and repeats the model simulation process over again until the system converges.

In summary, the MatLab language was found to be quite adequate for these modelling needs of this project. MatLab offers flexibility, requires a relatively short development time and initial learning curve. The main limitation of the software was its poor operational speed - contributed to by the use of a Unix workstation. There were some problems with the use of the nonlinear optimisation program with fossil pollen data. These points are briefly outlined in the next section.

4.3.2.4 Optimisation Toolbox - Application Problems

At present, an ecological model with the predictive capability necessary to explain all of the variance in long sequences of fossil pollen data just does not exist. This fact casts some question over the use of nonlinear optimisation software with such data. The nonlinear optimisation program is designed to fine tune model parameters to provide an optimal fit between model and field data. This is accomplished with good quality data and a model formulation with high predictive capability. In certain branches of engineering, chemistry, physics and a few areas of biology this is a realistic expectation: for example, the growth of laboratory populations of *Drosophila* by Pearl (1927) (fig 2.19).

The nonlinear optimisation software was initially used in this project to test the hypothesis that interactive equilibrium models would explain the variance evident in absolute fossil pollen data. However, this hypothesis was shown to be quite incorrect. This failure also reflects the inadequacy of equilibrium model formulations and the fact that the optimisation software was not able to deal with the variance in fossil pollen data in a rational manner.

With experience it was discovered that running model simulations based on various regions of parameter space was an equally effective means of evaluating the qualitative behaviour and properties of model and field data without the use of nonlinear optimisation software (Appendix 4). In some cases it proved very difficult to locate feasible regions of parameter space in order to conduct simulation experiments and the optimisation program was quite useful in dealing with this computational problem.

Model simulations based on programming *for loops* (Appendix 4) were used in the place of nonlinear optimisation software. A simulation *for loop* enables the behaviour of a model to be evaluated over large ranges of parameters in a single simulation. These simulations can also be used to provide model parameters which, as approximations based on the limitations of the data and models being used are probably as accurate as the results of the optimisation software.

MatLab's optimisation subroutine (known as a toolbox) has various default parameter settings which can be adjusted to accommodate variance in field data. However, these are no substitute for good field data and reliable model formulations. To illustrate this point, the properties of some parameter settings are briefly discussed below.

The level of precision required for termination criteria can be adjusted to halt the search path in an optimal region of parameter space. However, this requires a tight fit between field and model data.

It is also possible to place constraints on the optimisation search path to prevent it from entering certain regions of parameter space. Most of the parameters of the models used in this project allow considerable freedom in this area, even as far as negative values were concerned. Good parameter results mostly depend on the conditioning of the initial model parameter matrix. Nonlinear systems seem to be attracted to solutions in select regions of parameter space, and outside these regions the behaviour of the model is simply not feasible.

The objective of optimisation is to find an optimum, a region in parameter space that gives the very best possible correspondence between model and field data. The existence of multiple optima usually indicates the use of a poor model formulation (*i.e.* there is no optimal solution). The testing of a model formulation over large regions of parameter space is also used to test for the possibility of multiple optima. This problem only ever occurred once or twice with equilibrium model formulations using forcing functions. As a safety measure, all model formulations were tested in this manner. The problem appears to have been isolated to this early class of models.

It is possible to control the step size of the optimisation routine as it searches parameter space for a local optimum. It is generally agreed that a relatively large initial step size is advisable until the search path finds an optimal basin (*i.e.* there is little change in the parameters). At this point it is advisable to use a small step size so that the true basin of an optimum can be located. In some systems a false convergence can result from too large a step size (Kuo and Fox 1992).

Least squares curve fitting operates on the assumption that the errors at all data points are equal. However, this assumption is flawed when there is large variance in the data - smaller y values have smaller errors. The optimisation program fits model behaviour to the field data by minimising the sum of the squares of the residuals. Because the squares of the residuals extend over an even larger range than the data, small residual squared numbers are essentially ignored.

The answer to this non-uniform error problem is to use weighting, so that all residual squared terms are approximately the same size. In this situation it is common practice to fit the model to the field data with a weighting variable - the inverse of the y variable squared (43)

$$\frac{1}{y^2} \tag{43}$$

which is proportional to the inverse of the variance of the y data. This improves goodness of fit for data with low values of y (Kuo and Fox 1992).

Experience indicated that the improvements in goodness of fit with nonlinear data are so small that it is only worth applying weighting techniques when the behaviour of a model is already very close to field data. In other words, weighting is not intended to improve the poor performance of a poor data or model formulation.

Scaling of the data is another important consideration when using the optimisation routine, especially if forcing functions are being used. Scaling does not influence the quality of the result, however it can drastically improve the speed of the equation solver used and thus improve overall efficiency. Unscaled forcing functions can result in problems with computational singularity.

Finally, the MatLab optimisation software offers a choice of two different search algorithms. The default setting is the Levenberg-Marquardt and the alternative is the Gauss-Newton which is generally faster when the residuals are small (Levenberg 1944, Marquardt 1963, More 1977, Dennis 1977).

In summary, the objective of this section was to introduce and illustrate the use of MatLab's scripting language by evaluating the nonlinear optimisation program developed for this project. The program was initially used on equilibrium model formulations. However, more extensive use of the software was abandoned as the limitations of this procedure became evident. Nonlinear optimisation software is designed for use with good data and model formulations of high predictive capability. Excessive variance in field data causes search path problems which cannot be corrected with standard error weighting or data smoothing techniques when fossil pollen data is being used.

Adjustments can be made to the default settings of the optimisation software but these are no substitute for model and data quality. Use of nonlinear optimisation in this project was mainly restricted to initial tests of the equilibrium model formulations, for evaluating the behaviour of models in various regions of parameter space where it was difficult to locate feasible initial parameters (a calculation tool) and for use with difference equations.

Model formulations based on difference equations in some cases provided striking correlation between model and field data. The optimisation program was more appropriate in this context. These results are described and evaluated in the two case study chapters.

4.3.3 The Modelling Process.

The modelling process used in this project is composed of two parts, model formulation and testing (Wake 1992) and hypothesis testing and evaluation

(Platt 1964, Loehle 1983). These two parts may be viewed as a circular process (fig 4.11, 4.12).

4.3.3.1 Introduction

Model formulation involves the transcription of a model from base theory (Loehle 1983). A model formulation is effectively an ecological hypothesis in mathematical form. The purpose of ecological modelling is to use experiments in order to discover if a given model hypothesis is an approximation to the truth (Harvey 1972). Consequently, ecological modelling is a circular process of model formulation, designing experiments for hypothesis testing, the interpretation of experimental results and integration of results and *a posteriori* observations into new hypotheses (fig 4.11, 4.12). New hypotheses must be tested with new field data.

This cyclic process is used for testing both the predictive and explanatory power of a model. When testing the predictive power of an ecological model the grounds for refutation are *whether the prediction meets some predefined accuracy* (Mentis 1988). The level of accuracy used to define goodness of fit in this project involves a heuristic grading of goodness of fit based on the qualitative properties of the model and field data.

As was earlier suggested, the predictive qualities of a model are only one part of the criteria needed to test the explanatory power of a model. The worth of any explanatory hypothesis in isolation is difficult to evaluate - competitive theories are needed (Caswell 1979). Competitive theories may include genuine attempts at explanation or one might be a null model (Mentis 1988).

Competitive models are rejected on the grounds of inferior explanatory power (predictive capability), *conflict with background theory and lack of internal consistency and parsimony* (Mentis 1988). The generating of viable competitive models and determination of weighting for the various criteria of refutation along with the definition of exactly what constitutes a satisfactory explanation are all conceptual problems with this approach (Mentis 1988).

The model formulation / hypothesis testing / interpretation process (fig 4.11, 4.12) requires access to numerous data sets in order that new model formulations may be tested. In this respect, the Fijian island of Totoya provided an ideal location from which a total of six cores were collected and three analysed for modelling research purposes. A fourth data set was added with the New Zealand Lake Rotokura core site.

For the sake of explaining just how the explanatory and predictive power of the model formulations used in this project were tested, the following sections provide a brief step by step account of the modelling experiments undertaken in this project.

4.3.3.2 Keteira Core Site - Experiment 1

To begin with, the predictive and explanatory power of the classical logistic and coupled logistic models was tested against the behaviour of absolute fossil pollen data from the Keteira core site (Fiji). The alternative hypothesis was the possibility of discrete time population growth as formulated in the discrete logistic and coupled logistic equations (fig 4.14).

The discrete logistic formulation is capable of three general classes of behaviour, logistic growth to a single equilibrium point, multiple point limit cycles and deterministic chaos. Upon testing these models against the field data it was found that the unstable behaviour of the discrete logistic provided the best fit with field data. This result ran contrary to classical equilibrium theory and the expectations of the author.

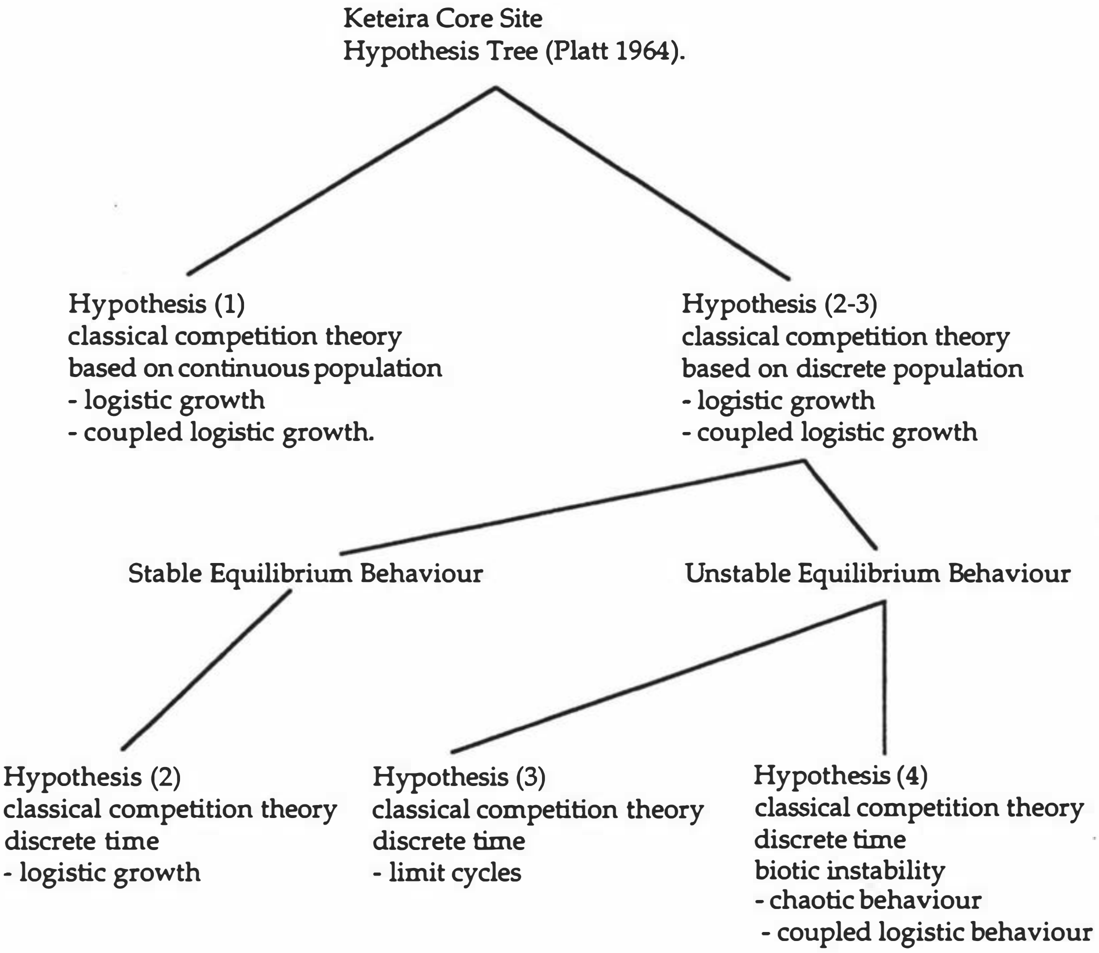


Fig 4.14 Hypothesis tree for the Keteira core site, Fiji. This tree shows the alternative hypotheses tested in experiment number one. The discrete form of the logistic equation is capable of both equilibrium and non-equilibrium behaviour based on critical values of the growth rate parameter r. This provides a total of four initial hypotheses.

4.3.3.3 Keteira Core Site - Experiment 1 (Interpretation Stage)

Added to this discovery was the observation of a very close correlation between the behaviour of the fossil pollen and charcoal fragment data. It appeared that the charcoal was forcing the fossil pollen signal. From these results it seemed apparent that the nature of the behaviour of this simple mangrove community was non-equilibrium and stochastically dominated. In order to test this hypothesis, forcing functions were added to the classical logistic model formulation with the intention of testing to see if the charcoal data could explain the variance in the data within the confines of an equilibrium model formulation.

Simulation and optimisation testing of this new model formulation showed that it was not capable of replicating the dynamic behaviour of the two mangrove species at the Keteira core site. This appeared to be a fault of the model formulation. In an attempt to correct this fault the Malthusian growth term in the logistic model was exchanged for a constant growth function. Initial simulation studies at the Keteira core site when used in conjunction with time delays indicated that this model formulation had many predictive and explanatory qualities. This constant growth trend model formulation was now ready for testing at the Udu core site (Fiji).

4.3.3.4 Udu Core Site - (Experiment 2)

The continuous exponential, logistic and coupled logistic, constant growth trend model formulations (hypothesis 5, fig 4.15) were tested on the Udu core site data against the initial equilibrium hypothesis (1) and the discrete exponential CGTM (hypothesis 6).

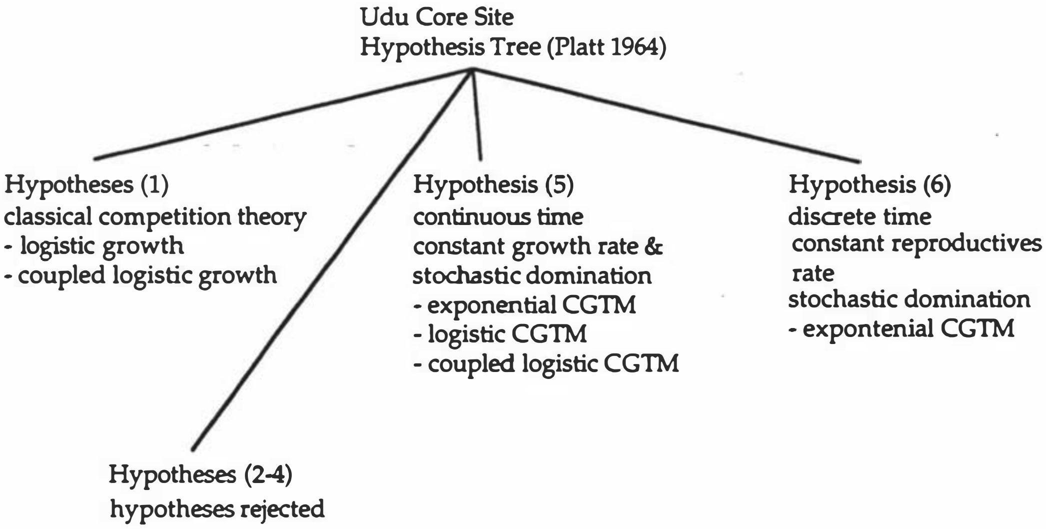


Fig 4.15 Hypothesis tree for the Udu core site, Fiji. The constant growth trend model formulations for continuous (hypothesis 5) and discrete (hypothesis 6) time are the new hypotheses to be tested.

Hypotheses (2-4) were eliminated during evaluation of the first experimental results when it was discovered that the *domain of application* of these models was limited to systems operating in the high to over-compensation density region. It will be demonstrated that the plant communities being tested in this study operate in the low to intermediate density region.

In the CGTM formulations, charcoal data was used as a forcing function with time delays determined using optimisation procedures. At this point the utility of the optimisation software came to an end and was replaced with for-loop simulation analysis which was quicker and provided adequate results. The results of this test indicated that the stochastic exponential constant growth trend model formulation provided superior predictive and explanatory capability - with one exception.

These results indicated that it was possible to obtain good fit between model and field data over the first half of the data set based on certain model parameters. Changes to the model parameters provided good model and field data fit over other sections of the data set. This *a posteriori* observation indicated that there had been a change in the nature of the disturbing forces driving this non-equilibrium system.

4.3.3.5 *Udu Core Site - Experiment 2 (Interpretation Stage)*

It seemed that a simple way to test for the existence of a change in the nature of the disturbing forces driving this system was to add a further forcing function which would have an increasing effect on the influence of the charcoal function with increasing time. This model formulation was simulation tested using Udu core site data and then experimentally tested using field data from the Lawakilevu core site, Fiji.

4.3.3.6 *Lawakilevu Core Site - Experiment 3*

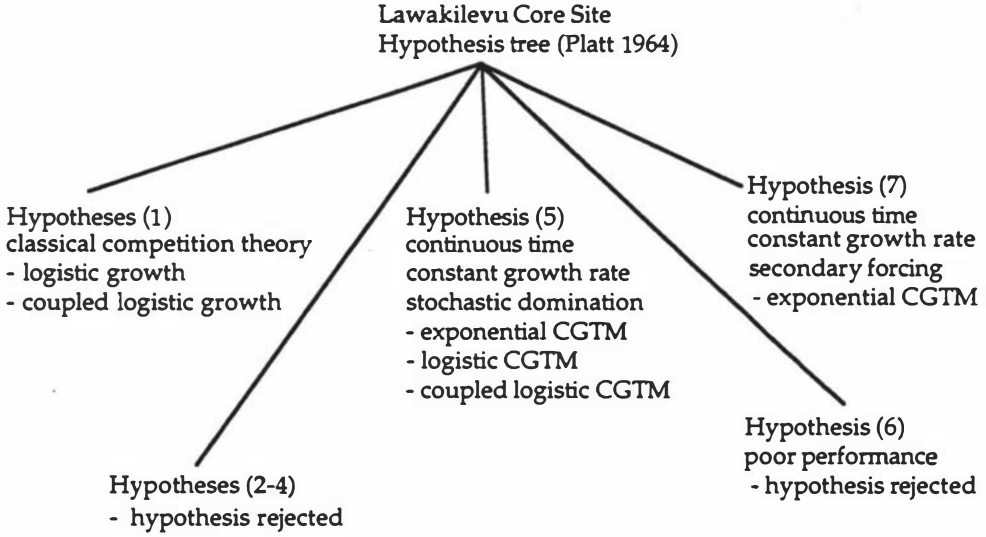


Fig 4.16 Hypothesis tree for the Lawakilevu core site, Fiji. Hypotheses (2-4) and (6) have now been eliminated. Hypothesis (7) is really the continuous exponential CGTM formulation of hypothesis (5) with an added function influencing the effect of the charcoal data with time.

The continuous exponential CGTM with charcoal forcing, charcoal forcing time delay and additional forcing function expressing an increasing effect of the charcoal function over the time period of the data set was tested on the Lawakilevu core site data.

This new model formulation was tested against the performance of the three continuous CGTM formulations of hypothesis (5) and the classical competition theory model formulations of hypothesis (1). Hypotheses (2-4) and (6) have now been eliminated. The results of experimental testing at this site co-favour hypotheses (5) and (7) for different reasons.

4.3.3.7 ***Lake Rotokura Core Site - Experiment 4***

While the effect of charcoal drives or inhibits the growth of mangrove through the action of physiological processes which appear to take time. It is unlikely that this is the case with the disturbing influence of volcanic tephra which probably acts almost instantaneously in its damaging affect upon vegetation. This hypothesis was tested on the New Zealand Lake Rotokura data set by replacing the charcoal forcing data in the continuous exponential CGTM with tephra data derived from measurements of tephra deposits in the Lake core sample. This model formulation was tested against the performance of the classical competition model formulations.

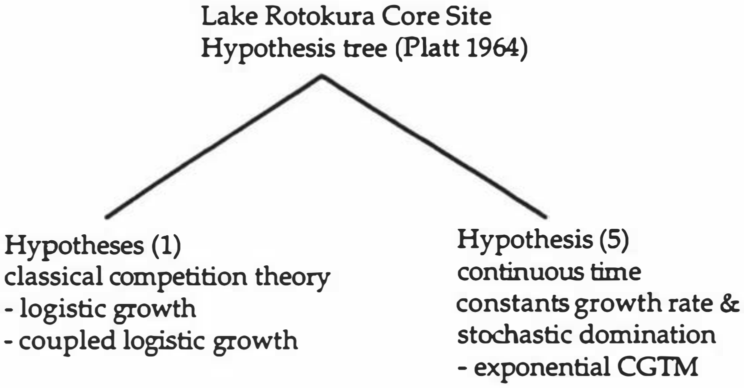


Fig 4.17 Hypothesis tree for the Lake Rotokura core site, New Zealand.

For the sake of keeping the above hypothesis tree illustrations concise, only very brief descriptions of the hypotheses to be tested have been made. It should also be noted that some of the main hypotheses (numbers 1 - 7) have more than one model construct (or hypothesis). These models have been grouped in this way because of their similarities and in order to keep things as simple as possible. These illustrations are given on a site by site basis. A summary hypothesis tree of all four core sites and experiments is given in fig 4.18.

Each of the circles in fig 4.18 represents one of the seven main hypotheses tested in this project. Each grouping of circles indicates a group of hypotheses which suggests that communities are primarily organised by different classes of causal mechanisms. The three main classes of causal mechanisms tested for (as suggested by DeAngelis and Waterhouse 1987) are represented by the three vertical columns in fig 4.18. These three classes include stable equilibria, stochastic domination and biotic instability.

In order to provide an explicit statement of hypotheses one to seven, these are listed below for the convenience of the reader. These statements integrate, where relevant, the equilibrium and non-equilibrium hypotheses of chapters two and three respectively. Each model construct to be tested has been described in terms of its driving and regulatory mechanisms, community structure and feasible behaviour.

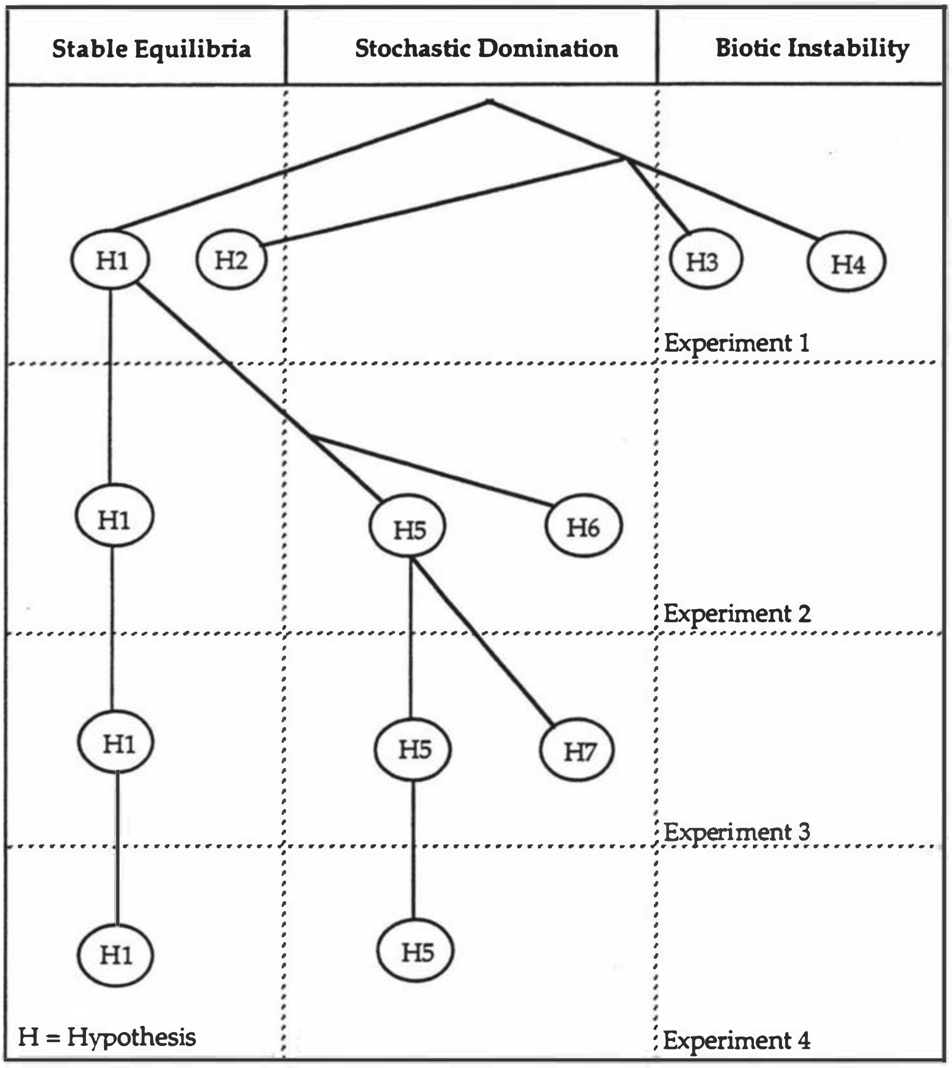


Fig 4.18 A summary diagram of the seven hypotheses tested in this project over four modelling experiments (after Platt 1964).

Stable Equilibria (column 1)

Hypothesis 1

(a) logistic equation	
driving mechanism	- continuous exponential growth
regulatory mechanism	- density dependent negative feedback - intraspecific competition - instantaneous negative feedback
population structure	- continuous entity - stable age distribution - stable birth and death processes - homogeneous mixing

	- homogeneous resource distribution
	- biotically stable
	- closed system
	- no spatial effects
behaviour	- globally stable equilibrium
	- non-transient
	- deterministic

(b) coupled logistic equations (two species)

driving mechanism	- continuous exponential growth
regulatory mechanism	- density dependent negative feedback
	- instantaneous negative feedback
	- intraspecific competition
	- interspecific competition
community structure	- continuous entity
	- stable age distribution
	- stable birth and death processes
	- stable species composition
	- homogeneous mixing
	- homogeneous resource distribution
	- interactive
	- biotically stable
	- closed system
	- no spatial effects
behaviour (phase space)	- saddle point
	- stable node
	- non-transient
	- deterministic

Hypothesis 2

(a) logistic equation

driving mechanism	- discrete exponential growth
regulatory mechanism	- density dependent negative feedback
	- instantaneous negative feedback
	- intraspecific competition
population structure	- continuous entity
	- stable age distribution
	- stable birth and death processes
	- homogeneous mixing
	- homogeneous resource distribution
	- biotically stable
	- closed system

	- no spatial effects
behaviour	- globally stable equilibrium - non-transient - deterministic

Biotic Instability (column 3)

Hypothesis 3

logistic equation

driving mechanism	- discrete exponential growth
regulatory mechanism	- density dependent negative feedback - instantaneous negative feedback - intraspecific competition
population structure	- continuous entity - stable age distribution - stable birth and death processes - homogeneous mixing - homogeneous resource distribution - biotically unstable - closed system - no spatial effects
behaviour	- unstable equilibria - multiple point limit cycles - transient - deterministic

Hypothesis 4

logistic equation

driving mechanism	- discrete exponential growth
regulatory mechanism	- unstable over-compensatory negative feedback with time delay - instantaneous negative feedback - intraspecific competition
population structure	- continuous entity - stable age distribution - stable birth and death processes - homogeneous mixing - homogeneous resource distribution - biotically unstable - closed system - no spatial effects
behaviour	- highly unstable equilibria

	- transient
	- deterministic chaos

Stochastic Domination (column 2)

Hypothesis 5

(a) exponential CGTM

driving mechanism	- continuous constant growth
	- constantly scaled exogenous forcing
	- time delayed exogenous forcing
regulatory mechanism	- no high density ceiling
	- low density floor
	- (stochastic boundedness)

Chesson (1978) defines stochastic boundedness as favourable environments that are common enough that sparse populations will tend to increase rather than wander to extinction.

population structure	- continuous entity
	- stable age distribution
	- stable birth and death processes
	- homogeneous mixing
	- homogeneous resource distribution
	- weak biotic coupling
	- closed system
	- no spatial effects
behaviour	- non-equilibrium (density-vague)
	- persistent
	- transient
	- slight density-vague (S.D.V.)

Strong (1986) defines S.D.V. as mixed deterministic and stochastic influence at intermediate density.

(b) logistic CGTM

driving mechanism	- continuous constant growth
	- constantly scaled exogenous forcing
	- time delayed exogenous forcing
regulatory mechanism	- high density ceiling (competition)
	- low density floor
	- (stochastic boundedness)
population structure	- continuous entity
	- stable age distribution
	- stable birth and death processes
	- homogeneous mixing

	- homogeneous resource distribution
	- unstable biotic coupling
	- closed system
	- no spatial effects
behaviour	- equilibrium (stability conditional on the exact magnitude of the stochastic forcing)
	- non-equilibrium (density vague)
	- persistent
	- transient
	- slight density-vague (S.D.V.)

(c) coupled logistic CGTM

driving mechanism	- continuous constant growth
	- constantly scaled exogenous forcing
	- time delayed exogenous forcing
regulatory mechanism	- high density ceiling (competition)
	- interspecific competition
	- low density floor
	- (stochastic boundedness)
community structure	- continuous entity
	- stable age distribution
	- stable birth and death processes
	- stable species composition
	- homogeneous mixing
	- homogeneous resource distribution
	- unstable biotic coupling
	- closed system
	- no spatial effects
behaviour (phase space)	- saddle point
	- stable node
	- stability of the equilibria is again conditional on the exact magnitude of the stochastic forcing.
	- non-equilibrium (density vague)
	- persistent
	- transient
	- slight density-vague (S.D.V.)

Hypothesis 6

(a) exponential CGTM

driving mechanism	- discrete constant growth
	- constantly scaled exogenous forcing

	- time delayed exogenous forcing
regulatory mechanism	- no high density ceiling
	- low density floor
	- (stochastic boundedness)
population structure	- continuous entity
	- stable age distribution
	- stable birth and death processes
	- homogeneous mixing
	- homogeneous resource distribution
	- weak biotic coupling
	- closed system
	- no spatial effects
behaviour	- non-equilibrium (density-vague)
	- persistent
	- transient
	- slight density-vague (S.D.V.)

Hypothesis 7

*(a) exponential CGTM*__________________________________

driving mechanism	- continuous constant growth
	- constantly scaled exogenous forcing
	- a second exogenous forcing function which influences the long-term behaviour of the first.
	- time delayed exogenous forcing
regulatory mechanism	- no high density ceiling
	- low density floor
	- (stochastic boundedness)
population structure	- continuous entity
	- stable age distribution
	- stable birth and death processes
	- homogeneous mixing
	- homogeneous resource distribution
	- weak biotic coupling
	- closed system
	- no spatial effects
behaviour	- non-equilibrium (density-vague)
	- persistent
	- transient
	- slight density-vague (S.D.V.)

4.3.3.8 Summary

The purpose of the above narrative is to illustrate the way in which the theoretical modelling process has been applied in the present study, to provide an introduction to the two case study chapters and to give an explicit statement of the competing hypotheses to be tested in this project. Although some mechanistic issues are mentioned, the above discussion focuses on the testing of these hypotheses based on validation procedure. Testing the explanatory power of the models involves evaluation of theoretical issues which must be reserved for the two case study chapters. Chapters one to three provide a very important theoretical foundation for the explanatory testing component of this research.

The testing of competing hypotheses has an experimental testing stage which is designed to test the predictive and explanatory power of a model formulation on a given set of field data. From the results of this test, the superior performance of one hypothesis is evident. During the interpretation and reformulation stage *a posteriori* observations are integrated into a new hypothesis or model formulation which must be tested for translation and computational accuracy before they too can be tested on new core site data - so the process continues. The details and discussion of these results are recorded in the two case study chapters.

4.3.3.8.1 Testing for Translation Accuracy

In this project, new model formulations were tested for correctness of mathematical formulation and theoretical translation from ecological base theory.

The first of these tests was accomplished by ensuring that any new mathematical formulation was checked by two independent parties (qualified mathematical modellers) who had suitable mathematical competence to identify any mistakes. The second test is by far more difficult to perform since it requires a thorough knowledge of both the mathematical formulation and the ecological theory from which the equation is translated.

For this reason, model formulation mistakes can be very difficult to identify. All of the model formulations used in this project have been subjected to the scrutiny of suitably qualified ecologists and mathematicians. Simulation testing was also used in order to ensure that the qualitative behaviour of the models matched that which was expected by the new hypothesis being advanced.

The main translation problem came with an attempt to add a forcing function to the classical exponential, logistic and coupled logistic equations. While this mathematical formulation appeared to be quite sound the behavioural performance of the model was poor. The details of this problem are further discussed in the first case study chapter.

4.3.3.8.2 *Simulation Testing*

This type of testing refers to the computational procedures used to solve model formulations. There are several types of computational procedures which require testing in this modelling process, the optimisation software, equation solvers, forcing functions and time delays.

Firstly, the optimisation program was tested by using a sine function in MatLab to generate a logistic rise. The optimisation program was then used to fit a model to this data. The process was then repeated using a sine function with the addition of random error. A model was also fitted to this data.

The optimisation program is structured in such that the very first data points are *passed* by the program as initial parameters so that the search routine has perfect freedom to locate the fitted curve. The scripting in the optimisation program was debugged until perfect goodness of fit was experienced with the sine test. When used with the addition of random error, the curve fitter was required to locate a logistic rise directly between the variance caused by the random numbers. Repeated testing proved the reliability of software.

Before the optimisation routine could be tested, the differential and difference equation solvers used in this program also had to be independently tested for behavioural accuracy. The use of MatLab subroutines for solving differential and difference equations made this testing stage relatively easy. The output from the equation solvers could be directly plotted against known model standards.

The addition of forcing functions simply involved the changing of model formulations and the loading of appropriate data files. An assumption of the MatLab equation solvers is that all data points represent equal units of time. This meant that all data had to be interpolated against a sample depth / carbon 14 age standard for use by the equation solvers.

With this type of time step structure, time delays could be easily scripted into the optimisation program or simulation routines by passing the argument $(t - par(n))$ where t is the argument for time and $(par(n))$ is a time delay parameter to be optimised. While this approach worked perfectly, it excessively slowed the computer and was abandoned for this reason. As an alternative to the optimisation of a time delay parameter, the delay parameter was determined by direct simulation trails.

In this case a time delay was accomplished by shifting the values of the forcing data one data point at a time and by truncating the field data in order to maintain the same length between field and forcing data. This approach was unsophisticated, but saved time and produced acceptable results. There is no way in MatLab of interpolating between sample time points while using Runge-Kutta differential equation solvers (ode 23 and 45).

The last elements of the modelling paradigm introduced in this section of chapter four are the equilibrium model constructs (hypotheses 1-4).

4.3.4 *Hypotheses (1 - 4) Classical Competition Models*

This first group of model constructs can be divided into differential (continuous time) and difference equation (discrete time) formulations. In the following discussion, each model will be written in its mathematical form with its behavioural characteristics and assumptions briefly described. The following discussion forms an introduction to the two case study chapters.

4.3.4.1 *The logistic Model*

The intuitive notion that an upper limit to population growth exists has been formalised in the logistic equation (46). The model consists of a Malthusian growth term and density-dependent feedback term that lowers the growth rate as the population size approaches an equilibrium point. The differential form of the equation is

$$\frac{dN}{dt} = rN\frac{(K-N)}{K} \qquad (46)$$

where

r	is a parameter expressing the specific population growth rate for a continuous time system,
N	is the state variable (population size),
K	is a parameter expressing the upper asymptote or maximum value of N for a population in isolation,
t	is time.

The model simply predicts a logistic rise to a stable equilibrium point and cannot satisfactorily be used to predict any other kind of long-term population behaviour. The model has many assumptions including an instantaneous feedback response to density, a specific growth rate, an invariant equilibrium point, a negative linear relation between increasing density and decreasing growth rate.

Ecologically, the model assumes that a population can be modelled as a continuous entity and that the specific growth rate adequately reflects stable demographic processes. Furthermore, the model is a closed, deterministic system that ignores spatial effects and stochasticity. Reproductive and population homogeneity are assumed, along with biotic stability and the fact that intraspecific competition is the prime determinant of population behaviour.

In order to give greater predictive capability, the classical logistic model was reformulated (47) to include a forcing function provided by a fossil charcoal fragment data set.

$$\frac{dN}{dt} = r(1+mf(t))N\frac{(K-N)}{K} \qquad (47)$$

where

$mf(t)$ is a term expressing a scaled forcing function for which m is a constant scaling coefficient.

The behaviour of this model formulation is critically evaluated in the first case study chapter. For the meantime it is worth noting that the model retains all the assumptions of its logistic parent with the exception of the fact that the specific growth rate parameter r is now dependent on both density-dependent feedback and the forcing effect of the charcoal function (a data set in this case). The sign of the specific growth rate r and scaling coefficient m determine the behaviour of the model.

When r and m are both positive, the population is only capable of increase. When r and m are both negative there is population increase for large values of m and population decrease for small values of m. The other indeterminate case occurs when r is positive and m is negative. In this case there is population increase for small values of m and population decline for large values of m. Finally, when r is negative and m is positive the population is only capable of population decline. The two indeterminate cases can be illustrated as follows.

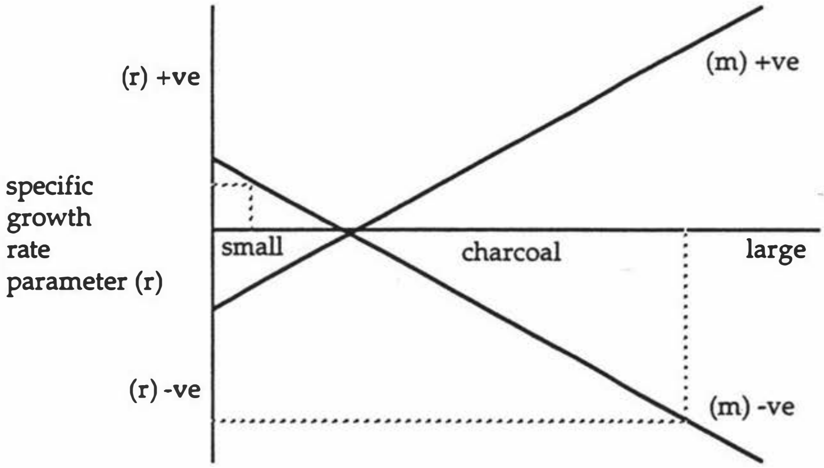


Fig 4.19 Illustrating the two indeterminate behavioural scenarios of equation (47). The slope of the line that intersects the horizontal charcoal axis is determined by the value and sign of the scaling coefficient m. When r is positive and m negative, small amounts of charcoal cause positive growth and large amounts of charcoal cause negative growth. These two cases are indeterminate in the sense that the value of the charcoal ultimately determines the direction of growth, but independent of the negative feedback mechanism.

Equation 47 also assumes a constant scaling coefficient m and a linear relationship between a change in the abundance of the charcoal data and that of the specific growth rate parameter r. An instantaneous reaction between changes in charcoal concentration and changes in the growth rate parameter r is also assumed. This assumption proved to be quite unrealistic for the Fijian data sets and was easily changed by the introduction of a reaction time delay in the forcing function term of equation 47,

$mf(t-T)$ is a term expressing a scaled forcing function for which m is a constant scaling coefficient and

T	is a reaction time delay in the influence of charcoal data upon the specific growth rate parameter r.

The logistic equation (46) can also be formulated as a population growth process in discrete time (48) by using simple difference equations.

$$N_{t+1} = N_t + rN_t\left(\frac{K-N_t}{K}\right) \tag{48}$$

where

r	is a parameter expressing the net reproductive rate of a population (number of female off spring produced per female per generation) in a discrete time system,
N_t	is the state variable (population size),
K	is a parameter expressing a logistic effect where
$K\left(1-\frac{1}{r}\right)$	is a carrying capacity,
t	is a discrete unit of time, scaled to make 1 the unit of a generation in a discrete time system.
$t \rightarrow t+1$	represents the step from generation t to that of generation $t+1$ (*i.e.* the step length of unity for a discrete time difference equation).

The continuous logistic equation with forcing function (47) can also be formulated as a population growth process in discrete time (49).

$$N_{t+1} = N_t + r(1+mf(t))N_t\left(\frac{K-N_t}{K}\right) \tag{49}$$

The parameters of equation (49) are identical to equation 48 with the exception that

$mf(t)$	is a term expressing a scaled forcing function for which $m$is a constant scaling coefficient and
$mf(t-T)$	is a term expressing a scaled forcing function for which m is a constant scaling coefficient and
T	is a reaction time delay in the influence of charcoal data upon the net reproductive rate parameter r.

4.3.4.2 The Coupled logistic Model

The coupled logistic equation includes the terms of the logistic equation and an equation coupling which is intended to describe instantaneous interspecific competition between interacting populations. This model formulation is a true dynamical system, the dimensionality of which can be adjusted to the number of species in the system being studied. In practice, this is not a good idea. Each extra dimension adds many more parameters (or degrees of freedom) for which an increasingly larger field data set is required to evaluate realistically the predictive capability of the model system.

The present study is limited to the evaluation of two interacting populations. The evaluation of a three dimensional system is feasible, but much more complicated (involving the possibility of deterministic chaos - see Gilpin 1975a) and therefore outside the scope of the present project.

The two dimensional differential form of this model is written as follows (48a, b).

$$\frac{dN_1}{dt} = r_1 N_1 \frac{(K_1 - N_1 - \alpha N_2)}{K_1}$$

(50a, b)

$$\frac{dN_2}{dt} = r_2 N_2 \frac{(K_2 - N_2 - \beta N_1)}{K_2}$$

where

N_1	is the state variable for population one,
N_2	is the state variable for population two,
r_1	is a parameter expressing the specific growth rate for population one,
r_2	is a parameter expressing the specific growth rate for population two,
α	is an interspecific competition coefficient,
β	is a interspecific competition coefficient,
K_1	asymptotic density for species 1 in isolation,
K_2	asymptotic density for species 2 in isolation.

This equation involves all of the assumptions of the logistic model and includes the fact that the interspecific interaction term is invariant, while response to interaction is instantaneous.

The continuous formulation of the coupled logistic equation can also be written to include the influence of a forcing function on the specific growth rate parameters r_1 and r_2.

$$\frac{dN_1}{dt} = r_1(1 + m_1 f(t))N_1 \frac{(K_1 - N_1 - \alpha N_2)}{K_1}$$

(51a, b)

$$\frac{dN_2}{dt} = r_2(1 + m_2 f(t))N_2 \frac{(K_2 - N_2 - \beta N_1)}{K_2}$$

The parameters and terms of this formulation are identical to equation (50a, b) with the exception that m_1 and m_2 are now the scaling coefficients for populations 1 and 2. The addition of forcing functions to this formulation of the coupled logistic involves all of the assumptions of equation (47) while a time delay is implemented in exactly the same manner.

The coupled logistic equation also has a discrete form which is illustrated below in the case of the two dimensional system (52a, b).

$$
\begin{aligned}
N_{t+1} &= N_t + r_1 N_t \frac{(K_1 - N_t - \alpha M_t)}{K_1} \\
M_{t+1} &= M_t + r_2 M_t \frac{(K_2 - M_t - \beta N_t)}{K_2}
\end{aligned}
\qquad (52a, b)
$$

The parameters and terms of these equations will already be familiar to the reader based on equation 48 a, b. The only difference is that the state variables (M) and (N) for each population are denoted by letters and not subscripts. This difference equation form of the coupled logistic equation can also be written to include a forcing function,

$$
\begin{aligned}
N_{t+1} &= N_t + r_1(1 + m_1 f(t)) N_t \frac{(K_1 - N_t - \alpha M_t)}{K_1} \\
M_{t+1} &= M_t + r_2(1 + m_2 f(t)) M_t \frac{(K_2 - M_t - \beta N_t)}{K_2}
\end{aligned}
\qquad (53a, b)
$$

The only change in equation 53 a, b is the addition of two independent and constant scaling coefficients m_1 and m_2 for the forcing functions of populations 1 and 2. The assumptions of the model, the forcing function and implementation of a reaction time delay are as per the general discrete logistic equation (49) and the discrete coupled logistic parent (52).

In practice, not all of the eight equations described in this section were used for experimental testing. Despite this fact their inclusion at this point is required for the sake of completeness since the qualitative behaviour of these equations was carefully evaluated. It was found that the addition of a forcing function to the logistic, discrete logistic, coupled logistic and discrete coupled logistic did not greatly improve their predictive capability. The reason for this failure appears to exist primarily in the Malthusian growth term used in these equations. The addition of a time delay makes little difference when the model's behaviour is poor in the first place.

4.3.5 Summary

In summary, this section on the modelling process used in this project has addressed many of the peculiar problems involved in using the hypothetico-deductive technique to test model formulations against fossil pollen data. The main points are as follows.

Firstly, it is not possible to determine the nature and structure of errors introduced into fossil pollen data as a result of pollen dispersal, deposition and geological preservation. Therefore, a heuristic approach will be used to evaluate the predictive power of model formulations against field data.

Secondly, the modelling process used in this project has been identified and consists of two main elements, model formulation and hypothesis testing. The nature of this developmental process of hypothesis testing has been evaluated in the light of the hypothetico-deductive scientific method.

In this scheme, the predictive power of model formulations is tested according to a predefined accuracy. The explanatory power of a hypothesis (or model formulation) is tested on the basis of predictive capability (partly), conflict with background theory, lack of internal consistency and parsimony.

Before the modelling process can begin, model formulations must be tested for mathematical correctness and theoretical translation accuracy. The computational techniques used for parameter estimation and curve fitting, model simulation, forcing and time delay effects also need to be tested for computation accuracy.

Finally, the modelling process of this project involved the testing of alternative equilibrium and non-equilibrium hypotheses as illustrated in the hypothesis trees drawn for each of the four modelling experiments undertaken.

The modelling framework of this project consists of four main components (hypothetico-deductive methodology, modelling procedures, a dynamical systems modelling paradigm and a collection of model constructs. The model constructs introduced in this section have been derived from classical competition theory. These model formulations are all capable of equilibrium behaviour while the discrete logistic and coupled logistic are also capable of unstable multiple point equilibria and deterministic chaos.

The constant growth trend model formulation was developed in response to the poor performance of these classical models when used in conjunction with a forcing function. This distinctly non-equilibrium model construct is introduced and evaluated in the final section of this chapter.

4.4 The Constant Growth Trend Model

The constant growth trend model was formulated in order to address theoretical and behavioural weaknesses in the classical logistic and coupled logistic equations. These two equilibrium models were developed on the assumption of a specific growth rate. The following discussion demonstrates that there is some theoretical evidence for justifying the use of a constant growth rate in place of the traditional Malthusian growth parameter. This new model formulation has greatly improved predictive capability based on the use of known stochasticity and thus provides a basis for evaluating the non-equilibrium theory of community organisation.

The following discussion begins with an evaluation of the exponential equation and its general properties as an introduction to the constant growth trend model.

4.4.1 Malthusian Growth

The most simple of all non-equilibrium model formulations is the exponential growth term of Malthus (1798). The Malthusian growth term describes population increase based on a constant specific growth rate term (growth rate per year). The model predicts uninterrupted population growth which in the real world would inevitably be followed by a population collapse - the consequence of exceeding a finite environmental resource base. The characteristics of this type of behaviour would differ from one population to another. The continuous exponential model has the following form

$$\frac{dN}{dt} = rN \qquad (54)$$

where

r is a parameter expressing the specific population growth rate (rate per year) for a continuous time system,

N is the state variable, (population size).

The exponential model is based on an assumption of non-equilibrium conditions and the existence of a specific (multiplicative) growth rate. Growth is feasible as long as r is positive in value (50). This model system is closed, spatial effects are not accounted for, exogenous forcing is ignored, population and reproductive homogeneity is assumed, biotic feedback does not exist, behaviour is deterministic and density-independent.

The qualitative behaviour of the model is very limited. It predicts unending geometric population expansion - a theoretical impossibility for any population. Furthermore, the model provides no prediction of the nature of a possible population collapse or the means of recovery.

Equation 54 can also be reformulated to include a forcing function, clearly this term is the basis of the logistic equation when used with forcing function described in the previous section.

$$\frac{dN}{dt} = r(1 + mf(t))N \qquad (55)$$

where

$mf(t)$ is a term expressing a scaled forcing function for which m is a constant scaling coefficient,

$mf(t-T)$ is a term expressing a scaled forcing function for which m is a constant scaling coefficient and

T is a reaction time delay in the influence of charcoal data upon the specific growth rate parameter (r).

The behaviour of this model is also determined by the combined influence of the sign of the specific growth rate parameter (r) and the scaling coefficient as in fig 4.19. Furthermore, the scaling coefficient is assumed to be constant and without a reaction time delay an instantaneous influence of the charcoal on the specific growth rate parameters is assumed.

The exponential equation can also be expressed as a discrete population growth model

$$N_{t+1} = N_t + rN_t \qquad (56)$$

where

r	is a parameter expressing the net reproductive rate of a population (number of female offspring produced per female per generation) in a discrete time system.
N_t	is the state variable (population size),
t	is a discrete unit of time, scaled to make 1 the unit of a generation in a discrete time system.
$t \rightarrow t+1$	represents the step from generation t to that of generation $t+1$ (*i.e.* the step length of unity for a discrete time difference equation).

In this formulation, the population increases geometrically without limit when (r) > 1 and decreases to extinction when (r) < 1 (Krebs 1985). In addition to the continuous model, this formulation also assumes a constant reproductive rate and the existence of discrete generations. The discrete form of this equation (56) with forcing function is likewise,

$$N_{t+1} = r(1 + mf(t))N_t \qquad (57)$$

where

$mf(t)$	is a term expressing a scaled forcing function for which m is a constant scaling coefficient,
$mf(t-T)$	is a term expressing a scaled forcing function for which m is a constant scaling coefficient and
T	is a reaction time delay in the influence of charcoal data upon the specific growth rate parameter (r).

The assumptions of this formulation are as per equation (55) with the exception that time is now measured in a discrete unit. As in equation (47), the behaviour of the model is determined by the combined influence of the sign of the forcing function scaling coefficient m and specific growth rate parameter r (see fig 4.19).

As introduced here, the exponential growth equation provides an important connecting link between the behaviour of the classical competition models used in this project and the constant growth trend model formulations.

The most successful CGTM was the non-equilibrium, continuous time, exponential growth formulation. In the case study chapters it will be come evident that the logistic and coupled logistic CGTM formulations do not add increased predictive capability to the much simpler exponential CGTM formulation.

4.4.2 The Constant Growth Trend Model - an Introduction

One of the limitations of equilibrium models is an inability to describe the long-term behaviour of a natural system that operates below the feasible region of density-dependency. High population density is at least theoretically required for an equilibrium point. Systems that operate below the region of strong density-dependence appear to wander through the intermediate density region in response to the influence of demographic and environmental stochasticity. Strong (1984, 1986, 1986a) refers to these systems as density vague. The theory of liberal (density vague) population regulation has been used as a basis for the development of the constant growth trend model.

4.4.2.1 Density Vague Regulation

Strong (1986) suggests that the most important accomplishment of the old debates over population dynamics is the understanding that while much population change is affected by density, virtually no natural population changes solely as a function of density alone (Solomon 1957, Klomp 1962, Bakker 1964). This fact and the existence of residual stochasticity mean that *a simple dichotomy between density-dependent and density-independent is inadequate to describe the rich character of density relationships in nature* (Strong 1986).

In Strong's (1984, 1986, 1986a) conception of liberal population regulation (fig 4.20) there exists a density vague region. The control, regulation and negative feedback mechanisms that return a population to intermediate densities *occur outside of fairly widely separated upper and lower bounds to population change. These bounds are likely to be soft and to increase their effect gradually, to cause gentle return toward intermediate densities* (Strong 1986). Furthermore, neither biotically nor abiotically created density bounds are likely to be static in position or in quantity.

In liberal population regulation, floors and ceilings are the lower and upper bounds to population transit. These two density regions have different mechanisms of density change and different demographic conditions from the central density region. Ceilings may be caused by density-dependent agents like resource depletion, predation, competition and emigration.

Floors are regions of density-independence. These regions are not as well understood as ceilings due to the fact that scarce populations are more difficult to find and study (Strong 1986). Floors may include immigration processes, higher survival probabilities or the existence of an environmental, exogenously imposed floor of *stochastic boundedness* (Chesson 1978). In this last case, favourable environments are common enough that sparse populations will tend to increase rather than wander to extinction.

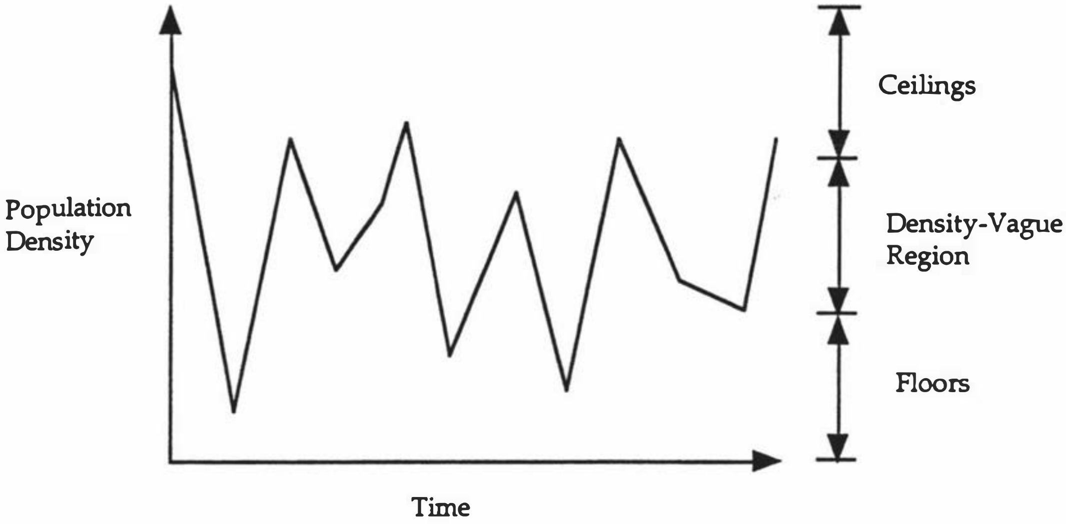


Fig 4.20 Liberal population regulation (after Strong 1986).

Density vagueness and its manifestation in liberal regulation predisposes a population neither to extinction nor to increase to enormous density. Having characterised density vague behaviour it is interesting to ponder exactly what causal mechanisms may be involved. Strong (1986) suggests that density vague behaviour may be driven by a grading of mechanisms from veiled to slight to dominant density vagueness.

In a *veiled density-vague* system, liberal regulation my be due to tight density relationships which can be explained by classical deterministic systems with the additional variable or two. This may include complicated versions of logistic type mechanisms - a variant equilibrium, nonlinear density relationships, time lags in density dependence or demographic stochasticity.

The slight density vague system is a grey area of mixed deterministic and stochastic influences at intermediate densities.

This grey area grades away into dominant density vagueness at intermediate densities which may be characterised by large numbers of *hard* and *soft* causal mechanisms (Strong 1986).

While the mechanisms of liberal population regulation will continue to be investigated, the characterising of density vague behaviour is very relevant to the present project. The type of density vague behaviour illustrated in fig 4.20 demands an explanation that cannot be adequately provided with conventional equilibrium models. As Strong (1986) has argued, *the literature is full of examples of density-vagueness and liberal regulation.* Causal agent will differ from site to site. The constant growth trend model has been formulated with an intention to test for the operation and influence of environmental stochasticity as a mechanism of liberal regulation.

4.4.2.2 The Constant Growth Trend Model - Behaviour

The constant growth trend model derives its name from its characteristic behaviour - a constant growth trend. The idea for this came from the observation that the Fijian and New Zealand data sets used in this project demonstrated a long-term constant growth trend (or density vague) behaviour. Just as Strong (1986) had suggested, this density vague trend showed no disposition to increase or to fall away to extinction.

For data that maintains a long-term trend in the intermediate density region it seemed reasonable to expect that this behaviour would best be modelled by a function that approximated a linear trend. As a first approximation to this, the specific growth rate of the exponential equation was exchanged for a constant growth rate with a very low parameter value that approximated a linear trend when plotted through the field data. The differential form of this exponential CGTM, (58), is as follows.

$$\frac{dN}{dt} = r_c + N \qquad (58)$$

where

r_c is a parameter expressing a constant growth rate,

N is the state variable.

The subscript c in the constant growth rate parameter is used to differentiate between this parameter and the specific growth rate parameter r of the Malthusian exponential equation (54). Equation (58) can be rewritten with a forcing function (59),

$$\frac{dN}{dt} = r_c + (mf(t))N \qquad (59)$$

where

$mf(t)$ is a term expressing a scaled forcing function for which m is a constant scaling coefficient,

$mf(t-T)$ is a term expressing a scaled forcing function for which m is a constant scaling coefficient and

T is a reaction time delay in the influence of charcoal data upon the specific growth rate parameter (r).

The behaviour of the exponential CGTM is very close to that of the Malthusian exponential model when identical parameter values are used. The difference can be seen in a simulation of model (58) and the exponential model (54). In this simulation, both models have the same growth rate value and the same initial condition. Based on fig 4.21 it can be seen that the initial behaviour of populations with the two growth rates is almost identical. However, in the long-term the population driven by a specific growth rate increases in number more quickly.

When used with a forcing function, this model formulation gives optimal results with a value of r that approximates zero (a horizontal line). When r has an actual value of zero, the predictive performance of the model is poor. This appears to indicate that the growth function is necessary but only at critically low values.

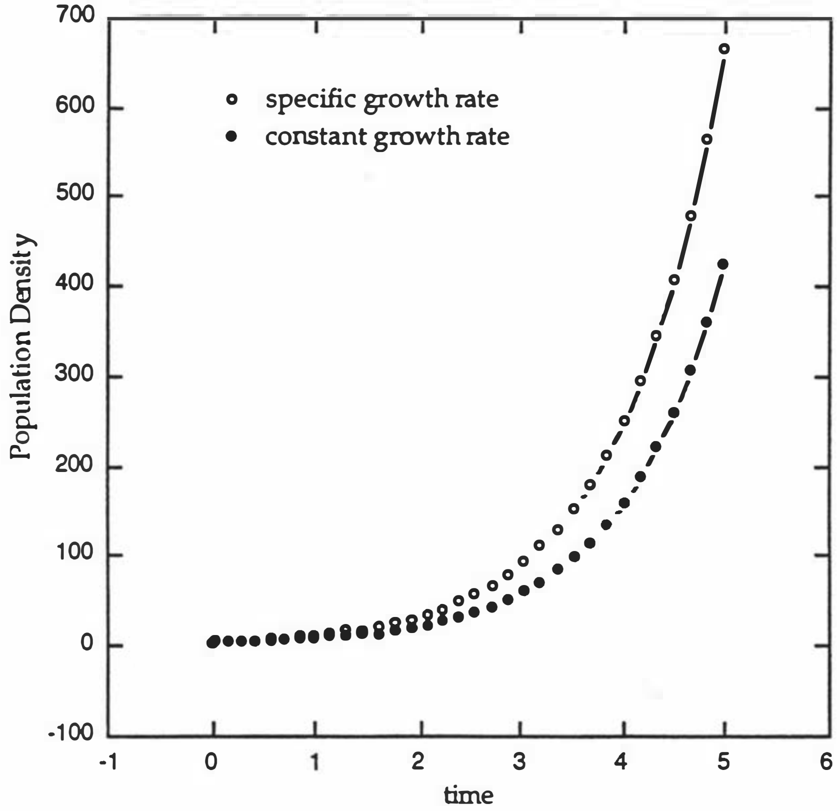


Fig 4.21 The behaviour of the constant and specific growth rate compared.

The position of this growth trend on the y axis is determined by the value of the initial population size. One theoretical problem with the CGTM formulation is that the population will grow from an initial population size of zero or indeed a negative number - behaviour that is an artefact of the constant growth rate. While this does not make ecological sense it should be recognised that the CGTM is probably an approximation of a function not yet discovered. It is very desirable now to implement further research that will identify the underlying ecological mechanisms.

The exponential CGTM also has a discrete form written below with forcing function.

$$N_{t+1} = r_c + (mf(t))N_t \qquad (61)$$

where

r_c is a parameter expressing the constant reproductive rate of a population (individuals per generation) in a discrete time system,

N_t is the state variable,

t is a discrete unit of time scaled to make 1 the unit of a generation,

$mf(t)$ is a term expressing a scaled forcing function for which m is a constant scaling coefficient,

$mf(t-T)$ is a term expressing a scaled forcing function for which m is a constant scaling coefficient and

T is a reaction time delay in the influence of charcoal data upon the specific growth rate parameter (r).

4.4.2.3 The Exponential CGTM - Properties

Even though the exact mechanism responsible for the behavioural performance of this model when used with forcing function remains unclear, its general properties are more evident. The exponential CGT model is clearly a closed, non-equilibrium, continuous entity system that assumes spatial effects are not important. The model also assumes demographic stability and population homogeneity. Stochasticity is assumed to be the dominant process driving this system which retains a deterministic element (the constant growth rate) but is free of any bias caused by density-dependent feedback.

Computationally, the model assumes that the constant growth rate is a near approximation to what is likely to be a more complicated growth function. Time delays are assumed to be adequately represented by the size of the time step between individual field and forcing data points. A linear relationship is assumed to exist between the forcing data and the constant growth rate. The behaviour of the model is once again determined by the sign and size of constant growth rate parameter r_c and scaling coefficient m. When m and r_c are either both negative or both positive, the population decreases or increases respectively. A combination of negative and positive terms results in two indeterminate cases where population increase or decrease is determined by critical values of charcoal data (fig 4.19).

4.4.2.4 The Constant Growth Trend Model - Disturbance Regions

When used with a forcing function the behaviour of the exponential CGTM appears to be composed of two components, an underlying constant growth trend and the variance caused in this growth trend by exogenous stochasticity. Furthermore, it is evident that the underlying growth trend is necessary for the performance of the system. Two relevant questions are what factors regulate the constant growth rate and the scaling coefficient.

The constant growth rate must be partly influenced by the inherent nature of demographic processes which in turn may be regulated by key environmental variables like climate, rainfall, drought etc. If this is the case, then it is to be expected that the constant growth rate will be maintained under a given set of environmental or demographic conditions - periods which may be referred to as a *disturbance region* in the behaviour of the system.

Changes to the constant growth parameter or scaling coefficient may be responsible for sudden changes in the qualitative behaviour of a population or community. A growth rate disturbance region may change at a variety of time scales ranging from variance caused by major climate shifts to annual and seasonal variations. Interpreting these changes will be difficult and requires the identification of those time points at which there are sudden changes in the qualitative behaviour of these systems (disturbance boundaries). Strong (1986) referred to this problem as changes in the density vague boundaries of the system - *neither biotically or abiotically created density bounds are likely to be static in position or in quantity.*

The existence of disturbance regions suggests that the behaviour of the exponential CGTM based on a given set of parameters will be inadequate to explain data sets which cover a single disturbance region. If a disturbance boundary exists somewhere in this disturbance region, the predictive power of the exponential CGTM will be limited by its invariant parameter values. There are at least five ways of tackling this problem.

Firstly, equation 59 could be reformulated with the addition of a second forcing function used to influence the effect of the first forcing function based on charcoal data,

$$\frac{dN}{dt} = r_c + (mf(t) + sf(t))N \qquad (62)$$

where (m) and (s) are simply the scaling coefficients of the two forcing functions. In practice, it was found that the use of identical time delays for the two forcing functions was quite adequate. Along with all of the afore mentioned assumptions of the forcing function, this formulation also assumes that the combined influence of these two functions is additive.

A second approach to dealing with the problem of an invariant constant growth rate is to reformulate the exponential CGTM as a logistic and coupled logistic model formulation. In this case the negative density-dependent feedback mechanism of these models (intraspecific competition) will shut down the constant growth rate whenever the population approaches a high density ceiling. The continuous logistic CGTM with forcing function may be written as follows,

$$\frac{dN}{dt} = r_c + (mf(t))N\left(\frac{K-N}{K}\right) \qquad (63)$$

The terms of this equation will be familiar to the reader by now. The discrete logistic CGTM is likewise,

$$N_{t+1} = N_t + r_c + (mf(t))N_t\left(\frac{K - N_t}{K}\right) \tag{64}$$

It is interesting to note that the discrete logistic CGTM is capable of the full dynamic range of behaviour shown in the true discrete logistic equation. This point is briefly developed in the case study chapters. A coupled logistic CGTM may also be written in continuous form,

$$\begin{aligned} \frac{dN_1}{dt} &= r_c + (m_1 f(t))N_1\left(\frac{K_1 - N_1 - \alpha N_2}{K_1}\right) \\ \frac{dN_2}{dt} &= s_c + (m_2 f(t))N_2\left(\frac{K_2 - N_2 - \beta N_1}{K_2}\right) \end{aligned} \tag{65a, b}$$

where r_c and s_c are the constant growth rate parameters for populations 1 and 2. The remainder of the parameters and terms used are identical to those of equation 51 (a, b).

A third and more difficult option is to accept the existence of a more complex function responsible for regulating the long-term value of the constant growth rate. There is no evidence in the present study which can be drawn upon to establish such a function.

A final, less sophisticated approach, is to approximate the behaviour of different disturbance regions by modelling each region separately, and accepting the fact that this is the nearest approximation to the problem presently available. The behaviour of a different disturbance regions may be combined into a composite plot for further qualitative evaluation.

4.4.2.5 Summary

In summary, the exponential constant growth trend model has its origin in the poor performance of classical equilibrium models to explain the dynamics of density vague population behaviour. The CGTM is a formulation of what Strong (1986) referred to as a mixture of *deterministic and stochastic influences at intermediate densities.*

4.5 Chapter Summary

Chapter four is written with the purpose of focusing on three closely related objectives. Firstly, to develop a working definition of ecological modelling and to use this as a basis for evaluating the contributions of palynologists to empirical and theoretical modelling research. Secondly, to outline the modelling paradigm developed and used in this project for modelling absolute fossil pollen data. Finally, to define and evaluate the constant growth trend model developed in this project for modelling density vague population behaviour in non-equilibrium systems.

Ecological modelling may also be referred to as hypothesis testing and this process requires the use of hypothetico-deductive scientific methodology.

The four systems of model classification presented in this chapter indicate something of the tremendous variety of ecological model types and the scope of their application. These four classification schemes provide an opportunity to evaluate ecological models on the basis of their intended application, validation procedure, mathematical characteristics and relationship to base theory in population and community ecology.

Palaeoecologists have begun to make important contributions to ecological theory, especially concerning the nature of communities and the non-equilibrium processes that have shaped their destiny. Palynologists have also become more actively involved in using model constructs in what appears to be a primarily empirical domain of application.

The modelling paradigm used in the present project draws on at least four well established existing modelling paradigms in order to develop a research methodology sensitive to the limitations and strengths of absolute fossil pollen data. The main features of this paradigm include the use of the hypothetico-deductive scientific methodology, evaluation procedures derived from dynamical systems, general modelling procedures and a range of model constructs.

These elements have been applied to develop a modelling process which is common to other modelling paradigms but designed to deal with the limitations of absolute fossil pollen data. The two main components of this modelling process are model formulation from base theory and the experimental design required to test the predictive and explanatory power of these model constructs.

The 1st experiment of this research project focused on testing the performance of classical continuous and discrete time competition models. From the results of this first experiment the exponential CGTM formulation was developed and tested at three further core sites. The performance of this new model was continually tested against the performance of classical continuous time competition models. This series of experiments is illustrated as a hypothesis tree in fig 4.18. The details if the experimental procedure, results and discussion are outlined in the next two case study chapters.

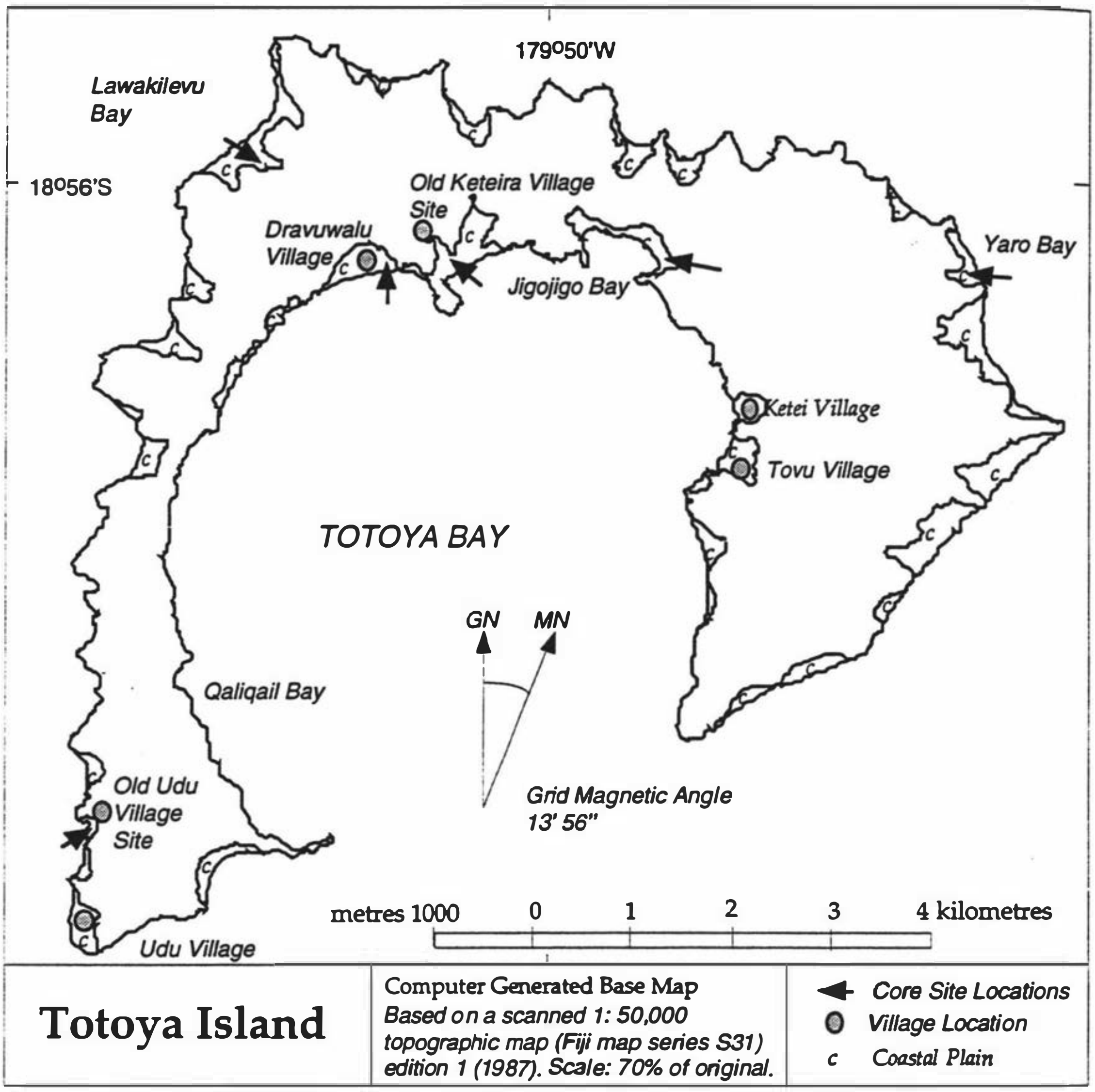


Fig 5.0 Base map of Totoya Island. Fringing and barrier reefs are not indicated. Approximate locations of the six Totoya core sites are indicated by small arrows (from Fiji Map Series 1987).

Modelling Plant Community Organisation ~ Mangrove Forest, Totoya, Lau Islands, Fiji

Two species of mangrove (*Bruguiera gymnorhiza* and *Excoecaria agallocha*) grow in sheltered parts of the coastal plain of Totoya island in a simple community structure. The results of the following case study indicate that modification of the island's inland forest is largely responsible for the non-equilibrium behaviour of this subtropical plant community.

Chapter five

Modelling Plant Community Organisation ~ Mangrove Forest Totoya, Lau Islands Fiji

5.1 Objectives

Chapters five and six provide two case studies of palynological modelling research designed to test the predictive and explanatory power of hypotheses derived from the equilibrium and non-equilibrium models of community organisation.

Chapter five records the results of three modelling experiments on fossil pollen data from mangrove forests on the Fijian Island of Totoya. The fourth and final experiment undertaken in this project is recorded in Chapter six.

The present chapter is divided into four sections. The introduction provides a brief description of the Island of Totoya, its physiography, climate, soils, vegetation and settlement history. Section two provides a detailed account of the methodology used in the collection of cores and their laboratory treatment. There are two methodologies used in this project.

Firstly, the collection of cores, laboratory processing and compilation of data (see section two of this chapter) involves techniques which are common to all palynological modelling studies (ref. Green 1981, 1982, 1983, 1983a, 1986, Green and Dolman 1988, Green *et al.* 1988a, Walker and Chen 1987, Chen 1988, Magri 1989, Tsukada 1980, 1981, 1982, 1982a, 1982b, 1983, Tsukada and Sugita 1982, Bennett 1983, 1986, 1988).

The modelling framework developed in this project is the second methodology which has already been fully presented in Chapter four and is not repeated in the present chapter. In Chapter four, the model constructs tested in this project were introduced and briefly evaluated in terms of their predictive capability, explanatory power and assumptions. In Chapters five and six the emphasis will shift from the predictions, explanations and assumptions of these models to their domain of application - the ecological setting in which they are applied and tested in this project.

The initial domain of application for the classical continuous and discrete competition models tested in experiment 1 resulted from questions related to the spatial structure of mangrove communities (mangal) on Totoya island. Hypotheses derived from classical mangrove succession theory are introduced in the first section of this chapter during discussion of the ecology of mangrove vegetation on Totoya. These hypotheses form a theoretical basis for testing in experiment one, from which new hypotheses and model constructs are derived to be tested in experiment two and then again in experiment three.

Theoretical modelling is an iterative process of theorising, testing and interpretation. In order to capture the line of thought followed in the model formulation and testing stages of this project, the modelling results (section three) are narrated in the order in which the modelling work was undertaken.

The third section of this chapter records the results of modelling experiments one to three which includes the initial testing of all seven hypotheses outlined in Chapter four. Hypotheses one and five are also tested on the New Zealand Lake Rotokura data set (experiment four recorded in Chapter six).

Section three is primarily illustrative, an approach which is in keeping with the heuristic method of evaluating model behaviour against field data chosen for this project. This approach will de-emphasise *the importance of model parameters* (in contrast with earlier palynological modelling studies) and concentrate on the qualitative behaviour of chosen model constructs over various ranges of parameter space. The justification for this approach lies in the level of statistical uncertainty inherent in all fossil pollen data. This problem was mentioned in chapter four and will be more fully discussed as an introduction to the discussion section of this chapter.

The results section of this chapter concentrates on portraying the predictive qualities of the various models being tested. These results are integrated into a discussion of both the predictive and explanatory power of the model constructs being tested in section four.

Finally, the two case study chapters are written with other important objectives in mind. The main theme of this thesis is community organisation while the topic of special interest is community behaviour. The experiments outlined in the next two chapters provide insights into community organisation in two ways. Firstly, theoretical modelling provides an opportunity to test natural systems for the operation of different classes of causal mechanisms. Secondly, known causal mechanisms are an important basis for understanding the behavioural (equilibrium or non-equilibrium) status of a community.

5.1.1 The Use of Equilibrium Model Constructs in Palynology

The first three chapters of this thesis were devoted to a detailed evaluation of the historic (equilibrium) and more recent (non-equilibrium) models of community organisation. The four experiments undertaken in this research project provided an opportunity to test the predictive and explanatory power of these two organisational models. There is a potential criticism of this approach which should briefly be discussed.

Palynological modellers have been severely criticised for their use of equilibrium models (Clark 1988). This fact comes as no surprise in the light of developments in theoretical ecology over the last two and a half decades. Although this criticism was levelled at the research of Delcourt and Delcourt (1987) who had used the coupled logistic equation (50a, b), the wider application of Clark's critique of *Lotka-Volterra models* to the other main equilibrium model used by palynologists (the logistic) can not be missed.

However, with the exception of the research by Delcourt and Delcourt (1987), other palynological modellers who have used the logistic equation have done so, not to test the explanatory power of the model but to use it as a calculation tool for determining population doubling times. A good review of this approach is given by Prentice (1988). As was pointed out in chapter four, this is an empirical modelling approach for which the use of the logistic model is quite acceptable.

The present study uses the logistic and coupled logistic (equilibrium) models in order to test their predictive and explanatory power against that of alternative non-equilibrium hypotheses. Based on the critique of Clark (1988) there needs to be justification for using such models and indeed there is.

Firstly, the initial use of these models in this project was made with the intention of using them as a first approximation of equilibrium behaviour that could be improved by adding greater model complexity. Other modelling research of this kind has been very successful and includes some of the most important discoveries identifying the limitations of the equilibrium model of community organisation (Hutchinson 1948, Cunningham 1954, Wangersky and Cunningham 1957, Slobodkin 1961, May and MacArthur 1972, Gilpin and Ayala 1973, Hansen and Tuckwell 1978, Hallam and Clark 1981).

Secondly, the present project is not only concerned with predicting community behaviour, but with explaining the causes of it. In order to test the explanatory power of a non-equilibrium model of community organisation, a competing equilibrium model is required (Mentis 1988, Platt 1964). Interpretation of the results of such tests must evaluate the performance of a model construct in terms of how well the mechanisms, assumptions and domain of application of the model agree with reality. The base theory from which the logistic and coupled logistic models were formulated can be tested to the extent that these models embody the causal mechanisms and predictions of this paradigm.

The logistic and coupled logistic equations are not the only equilibrium model formulations that could be used as alternative hypotheses. However, as mentioned earlier, of all the models that could be chosen from, these two model formulations have been the most thoroughly tested and are therefore the most well understood - for all their *plainly embarrassing* limitations (Clark 1988). Future palynological modelling studies will doubtless make refinements to and extend the application of the present study.

5.2 Introduction - the Island of Totoya

The following section gives a brief introduction to the physiography, climate, soils, vegetation and settlement history of Totoya Island. Descriptive information of this type provides an important background to the present study. The ecology of the two mangrove species that grow on Totoya is discussed in more detail in order to define a domain of application for the models tested in experiments one to three.

The palynological modelling of the mangrove forests on Totoya is only one part of a much larger interdisciplinary project which included contributions from ethnographers, archaeologists, geomorphology and palynology. The main palynological objective of project Totoya involved an attempt to reconstruct the island's late Holocene vegetation history. The archaeologists involved in project Totoya were hopeful that the fossil pollen record would cover the pre and post human settlement period so that evaluation of human impact on the island's vegetation could be made.

As it turned out, Totoya lacked inland core sites and for this reason cores were taken from coastal mangrove swamps. It will be shown in the present study that the time period covered by these cores postdates human settlement of the island as defined by archaeological evidence.

There are very few published sources of information which can be used to provide an authoritative basis for describing the contemporary vegetation of Totoya. Those that do exist are either very brief or in some cases inaccurate. For these reasons, the modern vegetation survey work undertaken by the present author during his stay on Totoya represents the most up to date information on the island's vegetation available. Even these results should be considered as only a pilot study, needed to provide a modern vegetation analogue for interpreting the island's fossil pollen record. A much larger and more detailed investigation of the island's vegetation is still needed, a priority there simply wasn't time to address during this first exploration.

For the convenience of the reader it should be noted that Fijian orthography instead of the Phonetic system has been used in the text, maps and figures of this chapter (Parham 1972). The use of common Fijian plant names is according to Wright (1919). The conventions of the Fijian system are as follows :

B	*is pronounced MB as in number,*
C	*is pronounced TH as in that,*
D	*is pronounced ND as in end,*
G	*is pronounced NG as in sing,*
Q	*is pronounced NG as in finger.*

Furthermore, *each syllable of a Fijian word ends in a vowel, where two vowels occur together each is given its normal sound and value, accent or stress is normally placed on the last syllable but one, consonants have approximately the same sounds as in English* .(Parham 1972 and Smith 1981). In this chapter, plant nomenclature follows Parham (1972) and Smith (1981, 1981a).

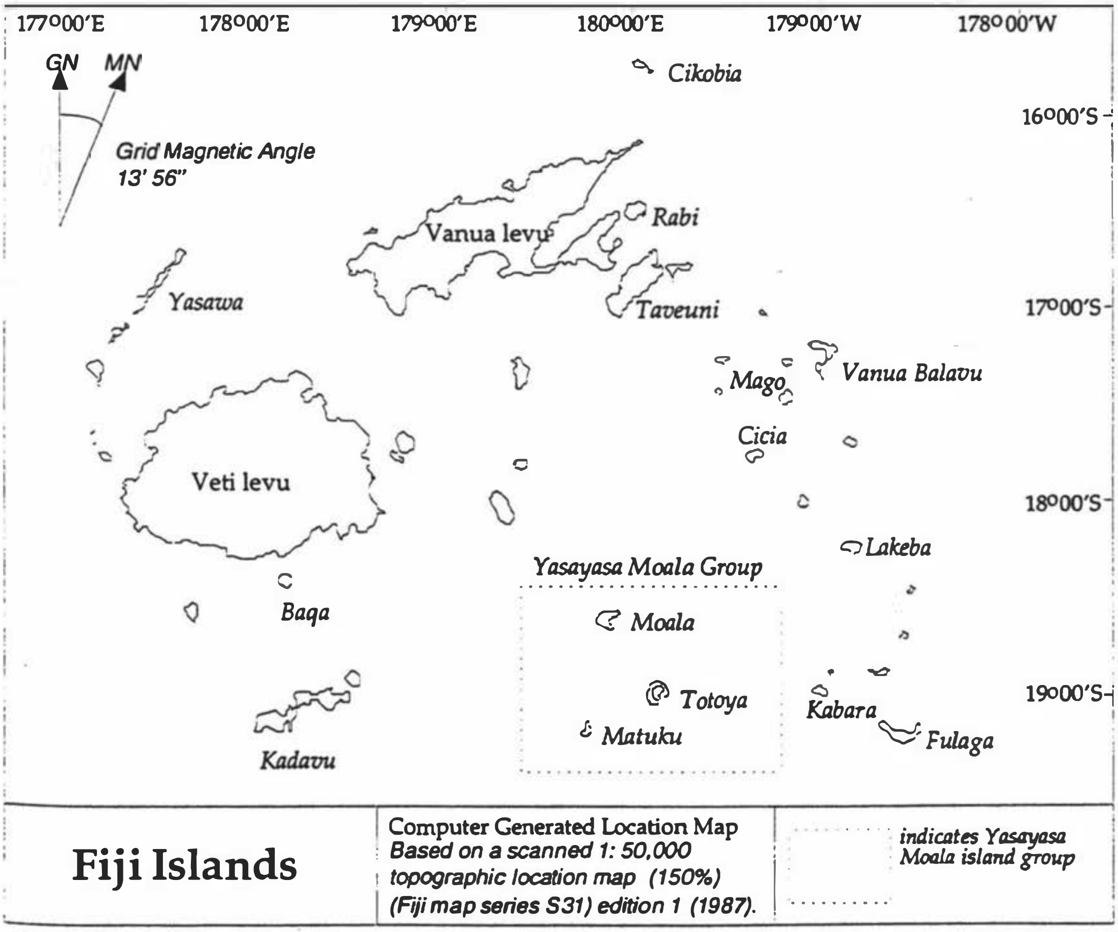


Fig 5.1 A map showing the location of the Yasayasa Moala islands within the Fijian island group. The island of Totoya is located between the neighbouring volcanic islands of Moala and Matuku. An outline map of Totoya island (fig 5.0) is located on the preview page to the present chapter (after Fiji Map Series S31/32 1986).

5.2.1 Totoya - Landscape Development

The beautiful island of Totoya is of volcanic origin and one of a three island group known to the Fijian people as the Yasayasa Moala (fig 5.1). Totoya provides one of the finest examples of an island caldera. The caldera probably formed from an explosion towards the end of the volcano's active life, a point in time which marks the beginning for landscape evolution (Nunn 1994a).

Nunn (1994a) identifies three stages in the post-eruptive landscape development of the island. Firstly, an asymmetrical caldera formed as *the results of explosion and subsidence of the centre of the old volcano.* Episodic subsidence would have formed terraces along the inner slopes of the island which were probably initially steeper that the outer slopes. Stage two of Totoya's landscape evolution involved *denudation of the valley sides, alluviation in valley bottoms and lateral erosion of the coastline - processes which altered in importance as the Pleistocene sea-level oscillated* (Nunn 1994a).

The third stage of landscape development identified by Nunn (1994a) was intimately associated with late Holocene sea-level rise and fall. Drowning of the *Totoya coast was followed by lateral shoreline erosion and reef establishment about 5000 years ago* (Nunn 1994a).

5.2.2 Late Holocene Sea-level Adjustment

In many parts of the Pacific Basin, sea-level is believed to have attained a late Holocene maximum about 3-4000 years ago (Clark and Lingle 1979). Nunn (1991) estimates that on average, sea-level was about 1.5 m above its present mean level having reached this maximum as a result of increase over the last 11,000 - 13,000 years. The effect of sea-level rise and fall would have differed from island to island and may have been a factor that gave impetus for *people to set out on the great colonising voyages of the late Holocene in the Pacific* (Nunn 1987, 1991, 1994a).

In figs 5.2a, b is illustrated the effect of sea-level rise on oceanic island coastline and reef development during the middle to late Holocene. This generalised scheme provided by Nunn (1994a) may be used to gain some idea of the mid to late Holocene coastline development of Totoya which has both fringing and barrier reefs.

In scenario (a) of fig 5.2 is illustrated the conditions likely to have existed at the time of the Holocene sea-level maximum ca 5000 years ago (Nunn 1990b). Because of a long term steady rise in sea-level there had been relatively little lateral erosion of the coastline which may have submerged in the case of some oceanic islands. Protection from offshore reefs *on many coasts may have been absent as reefs struggled to match the pace of sea-level rise* (Nunn 1994a).

The loss of reef protection may have subjected many coastlines to the influence of high energy wave activity. The existence of a high energy window combined with the stabilisation of sea-level about 3-4000 years ago would have resulted in *aggressive lateral erosion of island coastlines manifested along many by the creation of shore platforms* (Nunn 1994a).

Once sea-level began to fall (ca 3000 years ago), the coastal platforms cut at higher sea-level would have emerged and become the *foci for the accumulation of alluvium, colluvium and marine deposits including dune sands* (Nunn 1994a).

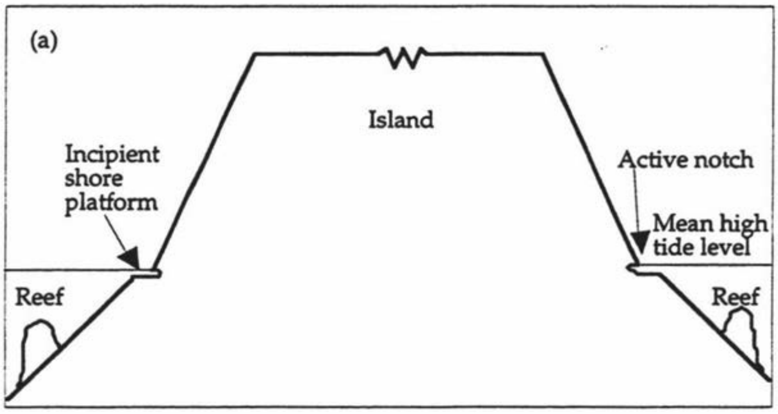


Fig 5.2a Geomorphological conditions likely to have existed on Totoya and other oceanic islands at the time of the Holocene sea-level maximum ca 5000 years B.P. (after Nunn 1994a).

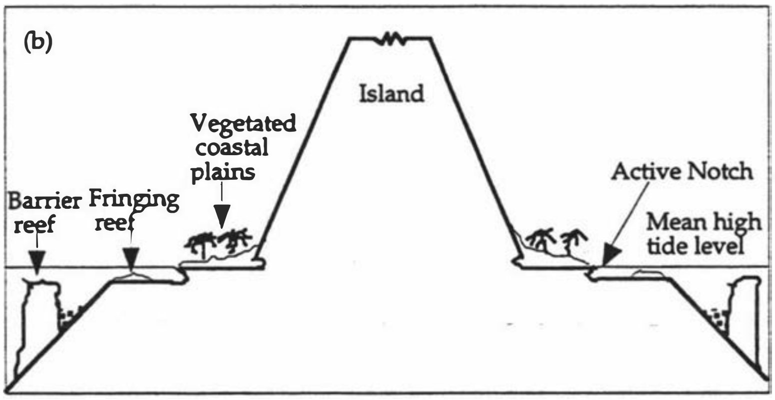


Fig 5.2b Geomorphological conditions likely to have existed on Totoya and other oceanic islands as a result of the late Holocene sea-level regression which is estimated to have begun ca 3000 years B.P. (after Nunn 1994a).

This model of late Holocene coastal platform construction fits the case of Totoya very closely. Firstly, Totoya has a very distinctive fringing and barrier reef system identical to that illustrated in fig 5.2b. Behind the current active notch cut by the present mean high tide level is a coastal plain. The coastal plain of Totoya is now well vegetated and dissected in places by ephemeral stream channels which meander their way across the plain out to sea. During the dry months of the year these stream channels are plugged at their seaward limit by a sand barrier. This results in the ponding of brackish waters in the stream channel just behind the sand barrier. The growth of mangrove on the coastal plains of Totoya is always associated with these stream channels and their muddy floodplains.

Although the exact form of these swamps varies from site to site, the Totoya mangrove swamps fits closely the *wave dominated barrier lagoon* environmental setting described by Thom (1979) (fig 5.3).

The exact timing of late Holocene sea-level regression on Totoya and the coastal progradation which followed it does not appear to closely match the model suggested by Nunn (1994a) by an order of 1000 years. The tentative date of 2000 - 3000 years B.P. quoted in Nunn (1994a) is based on a clustering of radiocarbon dates from earliest coastal sediments on 12 Southwest Pacific islands, five of which are located in the Fijian archipelago (Nunn 1990).

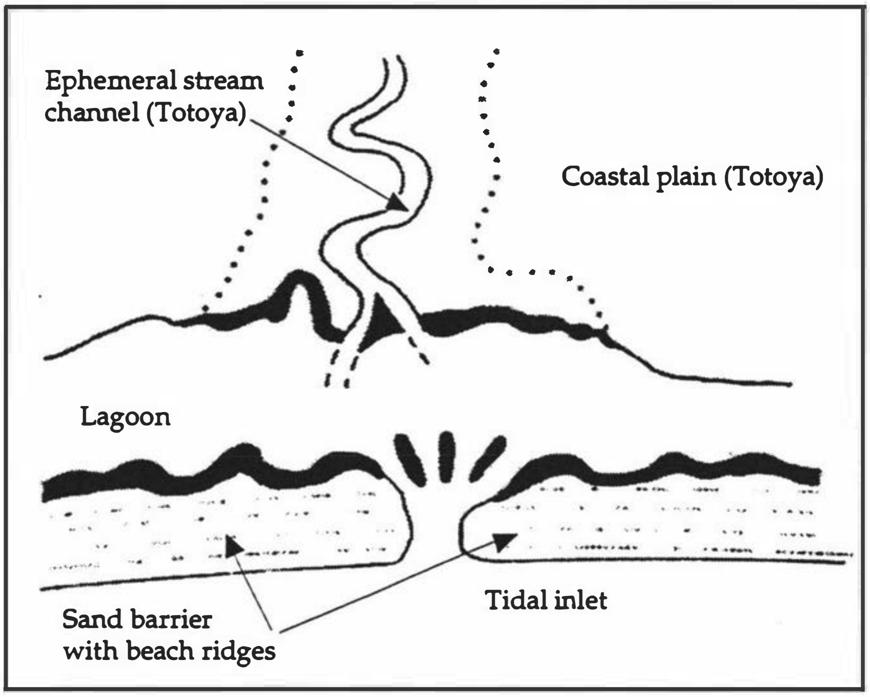


Fig 5.3 A generalised environmental setting for the mangrove swamps of Totoya (after Thom 1979).

Calibrated (CAL.) radiocarbon dates from Totoya based on basal sediments from the Keteira core site (inner lagoon) and Yaro Bay core site (outer island) are 1860 CAL. years B.P. ±239 (95% confidence / organic mud / ref. NZA 4603) and 1473 CAL. years B.P. ±162 (95% confidence / shell fragment / ref. NZA 4744) respectively. For the Keteira core site this places the beginning of sea-level regression and coastal progradation within a time frame of 2100 CAL B.P. to 1621 CAL. B.P. which is at least 1000 radiocarbon years outside the dates quoted by Nunn (1994a).

Radiocarbon dates on shell fragments found at the base of a cultural deposit on Totoya indicate an earliest possible human settlement date of ca 2500 CAL. years B. P. (Archaeologist Dr. Jeff Clark, North Dakota State University, USA. pers. comm.). It is interesting to note that the initiation of coastal progradation on Totoya based on the two basal core sediment samples falls well inside the time of human settlement of the island.

While it is undeniable that falling sea-level drove the process of coastal progradation on Totoya and other oceanic islands (Nunn 1990), the late initiation of coastal plain construction on Totoya suggests that other factors were involved. The coastal plains surrounding these core sites have been constructed at an average rate of 2.0 mm (Yaro) and 1.3 mm (Keteira) per year based on the averaged calibrated radiocarbon dates quoted above and total core lengths of 2950 mm and 2400 mm for Yaro and Keteira respectively.

A final line of evidence which gives possible insight to the mechanisms behind coastal plain construction is the existence of charcoal fragments in all six cores taken from the island. It will be demonstrated that peaks of charcoal are not correlated with sudden decline in mangrove fossil pollen, which suggests that it was not the mangrove forest that was being burnt. Combined with the very high rates of sedimentation (especially clay) mentioned above and occurring during a time of human settlement, these lines of evidence point to surface soil erosion caused by the burning of the island's inland forest.

The island's inland forest is today restricted to a number of small forest remnants, many of which are located along wet valley bottoms, flanks and upper margins of ridgelines - areas unsuitable for agricultural practices. Another group of remnant forests grows on top of rock pavements and outcrops common to many of the island's slopes. These forests probably escaped burning because of a general lack of forest understorey.

In summary, from the present line of discussion it is evident that sea-level change has played an important part in the landscape evolution of oceanic islands. On Totoya, the progradation of the present coastal plain was undoubtedly driven by falling late Holocene sea-level as Nunn (1994a) has suggested. However, basal radiocarbon dates from the two longest cores taken from mangrove swamps on Totoya indicate that the construction of coastal plains on Totoya is a more recent phenomenon, falling within a radiocarbon time frame of 1311 to 2100 CAL. years B.P. (based on the possible limits of the 95% confidence intervals for the Yaro and Keteira core sites).

This time period falls well within the period of earliest known human settlement of the island (ca 2500 CAL. years B.P.) and based on this and other lines of evidence, burning of the island's inland forest has been suggested as an important factor in the late Holocene construction of Totoya's coastal plains. While charcoal is clearly present in the cores taken from Totoya, it is only possible to speculate as to its origin and the author acknowledges this fact. The caution urged by Nunn (1992, 1994) in assigning environmental change to human causes (*e.g.* Ellison 1994) is also acknowledged. Further independent evidence is clearly needed.

By contrast, it is more evident from the fossil pollen record that these environmental changes have had a profound influence on the behaviour of the two mangrove species that grow in these swamps. This proposition will be further explored later in this chapter.

5.2.3 Physiography, Climate and Soils

The slopes of Totoya's volcanic cone are draped in a discontinuous soil mantle of shallow nigrescent steepland soils and humic latosols. Totoya is described as a class II climate, *having a moderate dry season* with soil water deficits resulting from exposure to the prevailing south easterly trade winds (Twyford and Wright 1965). Despite annual water deficits, the island's basaltic bedrock has weathered to form a deep red coloured clay rich humic latosol which is deep and free draining in most low lying areas. A more general description of climate for the South Pacific Islands is given by Streten and Zillman (1984).

The island's landscape can be divided into three main classes: moderate to very steep (ca. 74%), undulating (ca. 12%) and flat (ca. 14%), (Twyford and Wright, 1965). Hillside slope angle varies from less than 5 to ca. 43 degrees in some steepland areas.

Totoya is also divisible into broad ecological zones based on inner lagoon and outer island, windward and leeward locations regions. A 3.75 km breach in the southern wall of the remnant volcanic cone provides an important control on the inner island lagoon environment through the influence of prevailing south easterly trade winds which usually blow the strongest during the second half of the year. The hurricane season is usually between the months of December and April (Mead 1928). Nunn (1992) notes the existence of an environmental gradient on the island evident in the concentration of dry grassland vegetation at the leeward end of the island when compared with the dominance of forest in the wetter (windward) end of the island.

Written records of vegetation on the island are few. In 1845 Charles Wilkes (documenting early exploration of the Fiji islands) describes Totoya as covered with *luxuriant foliage* and having *many fertile valleys* (Wilkes 1970). The terms *luxuriant* and *fertile* are probably synonymous and intended to convey the idea of rapid growth, stately size, and plant health. Unfortunately, Wilkes' description provides no indication as to the type of vegetation then present or its extent.

In recent times a more generalised description of the island's vegetation has appeared in The Soil Resources of the Fijian Islands Vol 1, by Twyford and Wright (1965), as well as the latest 1: 50,000 topographical map series (ref. Fiji Map Series 31 S32), with vegetation zones inferred from aerial photos. The following description of the island's vegetation is based on the author's observations and quadrat sampling.

5.2.4 Vegetation Survey Methodology

Because of constraints on time, a restricted random sampling technique was used for the survey of core site, inland forest and coastal zone vegetation classes.

Two sets of voucher specimens (Macmillan 1968) were collected. One set was lodged with the herbarium at the University of the South Pacific in Suva where preliminary plant identification was conducted. A second set was returned to Massey University and a third set kept in a small spiral bound book, used in the field to facilitate consistent identification of samples during fieldwork.

The total number of survey quadrats used in this study was influenced by available sampling time and the modelling objectives of this project which focused on the mangrove swamp vegetation. For these reasons, although the survey involved the collection of data from 35 quadrats, only five of these are from an inland forest location (the Cibicibi forest at Qaliqali Bay see fig 5.0).

A total of five quadrats were used at each swamp site from which a core was taken. Of this five, one quadrat was randomly located within the *Inocarpus fagiferus* forest. Three quadrats were randomly located within the mangrove forest. A final quadrat was randomly located within the coastal zone vegetation. Coconut plantation covers much of the coastal plain except for small pockets of mangrove forest located near stream channels and the coastal zone vegetation. The coconut plantation association is not of direct interest to this study and was not surveyed for this reason. Many more sample quadrats could have been used, however the author considered the above approach to be adequate given the objectives of the project and available time.

Within each restricted sample area (*i.e. Inocarpus* forest, mangrove forest and coastal zone vegetation), a 20 m x 20 m quadrat was randomly laid by reading out random numbers from a set of statistical tables and pacing out the random numbers in steps. Direction was given by a compass bearing also determined by random number selection. Two direction changes and distances were paced out. On arrival at the random location, the first 20 m side of the sample quadrat was determined from a randomly chosen compass bearing with the next side at right angles to this based on whether the next number in the random number table was odd (right hand side) or even (left hand side).

Identification was made of every plant in the sample quadrat with generic names given to unknown plant species. A small cardboard tag (10X15 mm) with a synthetic fibre string was tied to every specimen and its herbarium number written in pencil on the tag. A master list was kept with tag numbers, generic and or common names. With the aid of the village people, initial identification of most of the samples could be made based on common Fijian names. DBH measurements were recorded for each tree species, abundance cover estimated as a percentage for non-tree species, site parameters listed (slope, aspect, map reference, site map) and observations of interest noted.

The only change to this sampling procedure was made when surveying a large track of inland forest at Qaliqali bay (fig 5.0). This area was surveyed using an altitudinal transect varying from 180° to 250° with five sample quadrats laid at successive altitudes (80m, 120m, 160m, 200m, 220m) . The direction of this forest transect (180° to 250°) was largely determined by the nature of the forest floor and its slope which varied from 30 - 42 degrees in some places. In most places it was impossible to make a direct ascent of this slope for sampling purposes. The first quadrat was located at ca. 80m in order to avoid compositional variation resulting from the inland forest merging with coastal zone forest near the waters edge. After this, a quadrat was located at successive 40m intervals in altitude (located with the aid of a handheld altimeter).

The survey of the Cibicibi forest at Qaliqali Bay involved one days work and represents the only opportunity the author had to sample inland forest vegetation. Further research is needed to determine the extent to which the Qaliqali Bay Cibicibi forest is representative of remaining forest cover in other parts of the island.

Only the more descriptive elements of this data are described below with the intention of providing an overview of the island's contemporary vegetation.

5.2.5 Totoya Island - Contemporary Vegetation

Within the contemporary vegetation of Totoya eight main plant associations were identified. Inland swamps and the wetland vegetation that is associated with them in other parts of Fiji (Ash and Ash 1984) appear to be missing on Totoya. Ash and Ash (1984) suggest that wetlands formed in other parts of Fiji as a result of forest clearance in areas of impeded drainage. The eight plant associations are:

1. Mangrove Forest
2. Coastal Zone Vegetation
3. Cibicibi Forest
4. Cau Forest
5. Talasiga (Fijian grassland association)
6. Coconut Plantation
7. Pine Plantation
8. Village Gardens

5.2.5.1 Mangrove Forest

Woodroffe (1987) lists seven species of mangrove in Fiji of which only two are found on Totoya, *Excoecaria agallocha* and *Bruguiera gymnorhiza.*

5.2.5.1.1 Bruguiera gymnorhiza

Bruguiera gymnorhiza is of the family Rhizophoraceae which includes many of the more common mangrove species found in the Fiji group of islands (*R. stylosa, R. mucronata, R. samoensis and R. selala)* (Parham 1972, Smith 1981). The genus *Bruguiera* differs from *Rhizophora* by the general absence of stilt roots *and the presence of knee pneumatophores which project in abundance above the surface of the mud* (Watson 1928).

According to Ding Hou (1960), a total of six species of the genus *Bruguiera* have been identified, all found in the East Africa, Indo Pacific region (Tomlinson 1986). Chapman (1976) suggests that birds as well as wind may assist in the pollination of *Bruguiera* (Tomlinson *et al.* 1979), while the anthers of *Bruguiera gymnorhiza* are held under tension which can be released by *touch or shock and the pollen is then scattered.* Tomlinson (1986) refers to the pollen release mechanism of *Bruguiera* as explosive, the anthers being released by a *visiting pollinator.* While flowers and fruits occur throughout the year, the principal flowering season is between November to February. The fruiting of *Bruguiera gymnorhiza* occurs profusely after March (Smith 1981).

Bruguiera gymnorhiza is probably the largest *and longest lived of the mangrove community* (Ding Hou 1958) It is known to grow 4 - 15 m in height (up to 36 m in Malesia) (Smith 1981). The stem of the mature adult is normally buttressed (Watson 1928, Lovelock 1993). Watson (1928) characterises *Bruguiera gymnorhiza* as a successional species that marks a final transition between mangrove forest proper and the establishment of inland forest species. *Bruguiera gymnorhiza* may grow on exposed shores or as a seaward to intermediate, inland component of riverine environments (Tomlinson 1986, Lovelock 1993).

5.2.5.1.2 ***Excoecaria agallocha***

Excoecaria is a genus of 35 to 40 species occurring *in tropical Africa and Asia to the Western Pacific* (Tomlinson 1986). Smith (1981) gives a more detailed distribution of *Hainan, India and Ceylon through Malesia and Micronesia into the Pacific as far as Tonga and Niue; perhaps also tropical Africa* (Smith 1981). Three members of the genus *Excoecaria (E. agallocha, E. acuminata, E. confertiflora)* occur in Fiji, the latter two of which are both endemic to Fiji (Smith 1981).

Excoecaria agallocha is a member of the Euphorbiaceae family and is the type of the genus *Excoecaria* (Tomlinson 1986). It is peculiar in being *almost or quite leafless during the flowering season when, owing largely to its catkin-like male flowers, it resembles a poplar or willow* (Watson 1928).

Smith (1981) classes *Excoecaria agallocha* as a tree which usually grows 4 - 15 m high although is occasionally found as a shrub (2 m high). Its preferred habitat is found at or *near sea level in mangrove swamps and beach thickets or along lower river courses, rarely occurring on bare basalt hillsides inland to an elevation of 415 m* (Smith 1981). Tomlinson (1986) notes that it is a characteristic associate of the mangrove community but prefers an open site toward the rear of the mangal. It occurs more commonly on exposed beaches and in sandy estuaries. Both Smith (1981) and Tomlinson (1986) note that its has been found in disturbed or open sites well above coastal plains but not exceeding 400m. For this reason, *Excoecaria agallocha* cannot be regarded as an exclusively mangrove component. Tomlinson (1986) notes that *the plant shows no obvious morphological adaptation to mangal; the root system is obviously not specialised.*

Like *Bruguiera gymnorhiza, Excoecaria agallocha* flowers all year round but is *most often found flowering between October and February, fruiting between January and July* (Smith 1981).

*5.2.5.2 **Fossil Pollen Identification***

Based on visible diagnostic characteristics of the fossil pollen the present author is doubtful as to whether it is possible to identify *Excoecaria agallocha* and *Bruguiera gymnorhiza* to species level. At a genus level the pollen of both species is quite distinctive.

Visual identification of the two mangrove species of Totoya was first made by Mr Saula Vodonaivalu (herbarium technician), based on leaf and flower specimens submitted to the South Pacific Herbarium, Suva, Fiji.

For *Bruguiera gymnorhiza,* pollen identification to genus level was accomplished by reference to two sources. Firstly, photo reprints of *Bruguiera parviflora* (ref. 250B and 254B) and *B. sexangula* (ref. 254B) were supplied from the pollen reference collection of the Geography Department, University of Hull, UK. Secondly, photos of *B. gymnorhiza* and morphological description is available in Tseng-Chieng (1972).

In fig 5.4 a, b, is portrayed equatorial (a) and polar (b) orientations of *Bruguiera gymnorhiza* from photographs of microscope slides prepared for the Keteira core site (for sample preparation please refer to the laboratory methodology section of this chapter).

Bruguiera gymnorhiza is a suboblate to oblate-spheroidal pollen grain (16-19µ by 19-21µ), tricolporate with no distinguishable surface patterning (psilate). The pore annulus is large and distinctive (see fig 5.4 a). Pollen morphology is based on Iversen and Troels-smith (1981) and Tseng-Chieng (1972).

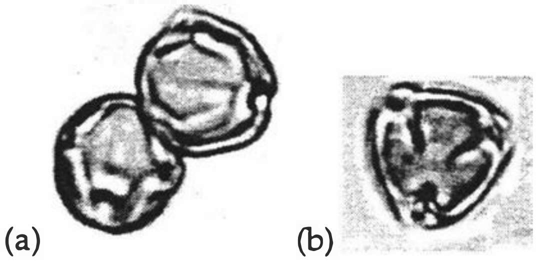


Fig 5.4 *Bruguiera gymnorhiza* pollen photographed and reproduced as scanned images (scale 150% original) - (a) equatorial and (b) polar orientation. Microscope magnification 1000x. Silicone oil slide mount. Film 28 section c and d frames 17 and 18 (Massey University Geography Department 1996).

Compare fig 5.4 a, b with fig 5.5 a, b. Fig 5.5 a, b are scanned images reproduced from microscope photographs of *Bruguiera pariflora,* equatorial (a) and polar (b) orientation (University of Hull reference collection).

For *Excoecaria agallocha*, pollen identification to genus level was accomplished by a photo reprint (245B) supplied from the pollen reference collection of the Geography Department, University of Hull, UK. Photos of *Excoecaria kawakamii* and morphological description of the same is given by Tseng-Chieng (1972).

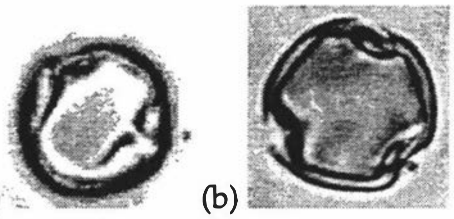


Fig 5.5 *Bruguiera parviflora* pollen photographed and reproduced as scanned images (scale 100% original) - (a) equatorial and (b) polar orientation. Microscope magnification 1000x oil immersion. Photo reference 250B/slide ref. 221-3-1H University of Hull, UK.

In fig 5.6 is portrayed equatorial views of *Excoecaria agallocha* from photographs of microscope slides prepared for the Keteira core site (for sample preparation please refer to the laboratory methodology section of this chapter).

Excoecaria agallocha is a spheroidal to subprolate (rarely oblate-spheroidal, (18-29μ by 21-28μ), tricolporate pollen grain with distinctive echinate surface patterning (fig 5.6 c). Distinctive surface echinate patterning visible at 1000x magnification with an intermediate focal plain (fig 5.6 b). The pores of *Excoecaria agallocha* have a distinctive "H" appearance when viewed with equatorial orientation and a surface focal plain (fig 5.6 c). Pollen morphology is based on Iversen and Troels-smith (1981) and Tseng-Chieng (1972).

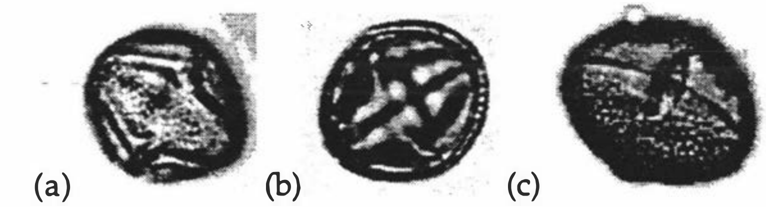


Fig 5.6 *Excoecaria agallocha* pollen photographed and reproduced as scanned images (scale 100% original) - (a-c) equatorial orientation. Microscope magnification 1000x and silicon oil slide mount. Film 28 section E frames 25, 27 and 28 (Massey University Geography Department 1996).

Compare fig 5.6 with fig 5.7 based on scanned photographic images of *Excoecaria agallocha* from the University of Hull pollen reference collection.

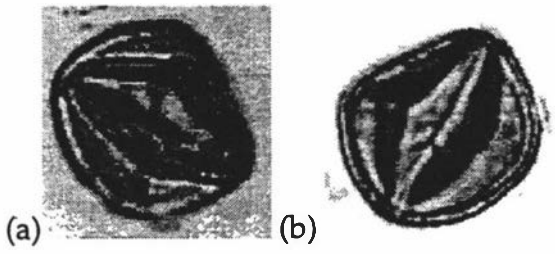


Fig 5.7 *Excoecaria agallocha* pollen photographed and reproduced as scanned images (scale 100% original) - (a-b) equatorial orientation. Microscope magnification 1000x and silicon oil slide mount. Photo ref. 245B University of Hull, UK.

5.2.5.3 *The Colonisation of Mangrove Species*

It seems quite likely that *Bruguiera gymnorhiza* and *Excoecaria agalloch* have been recent additions to the plant diversity of Totoya. To begin with, Totoya is located close to the southern and eastern limits of mangrove distribution (Saenger and Moverly 1985, Woodroffe 1987, Woodroffe and Grindrod 1991, Latham 1979).

Secondly, the process of colonisation itself is dependent on the availability of a suitable habitat. For mangrove species, available substrate, sediment supply and shelter from high energy waves are important factors (Woodroffe 1987). It is likely that an environment of this type was not available on Totoya until after the late Holocene sea-level maximum when the island's barrier reef re-emerged and offered protection from the high energy window of the sea-level maximum (Nunn 1994a). At present, Totoya's mangrove communities are located within sheltered embayments near or alongside ephemeral stream channels on the coastal plains.

Thirdly, how were the seed of these species dispersed? During a visit to the neighbouring islands of Matuku and Moala, large numbers of the mature seed pods of *Bruguiera sp.* were seen to be afloat in the water, adjacent to much more extensive communities of mangrove than those found on Totoya. These nearby islands may have acted as sources of seed propagation in more recent times. *Bruguiera sp.* is noted by Thaman and Ba (1979) as being a species valued in Fiji as a firewood and it seems possible that timbers and seed stock, a traditional food source (Parham 1943), were moved by the early Polynesian explorers. *Bruguiera sp.* is also mentioned as a drift disseminule by Smith (1990).

Chapman (1970) makes two interesting comments on the topic of dispersal. Firstly, he suggests that *Rhizophora mangle were carried to Fiji* by early explorers and proposes that the high tannin content of *Rhizophora* seeds would have rendered them ideal for *tanning ropes, nets and sails*. Secondly, he argues that while ocean currents may be invoked as a dispersal mechanism for *Rhizophora mangle* in the Fiji group, it would be expected that *Avicennia germinans with its viviparous seedlings* would have travelled as well. This is not the case. The topic of dispersal in the Pacific Basin is more fully covered in Chapman (1976).

5.2.5.4 *Disturbance of Mangrove Forests*

Chapman (1976) has observed that of the two mangrove species found on Totoya, *Bruguiera gymnorhiza* tends to be more tolerant of saline to brackish water conditions while *Excoecaria agallocha* tends to favour brackish to fresh water conditions. This physiological tolerance may partly explain the spatial distribution of the two species at four of the Totoya core sites (Yaro Bay, Keteira, Dravuwalu and Jigojigo Bay). At the other two core sites (Udu and Lawakilevu) both species grow intermixed at the front of the swamp, an association that grades away to *Excoecaria agallocha* at the rear of the swamp at both sites.

Chapman (1976) further notes that *Bruguiera gymnorhiza* may be characterised as forming a pioneer community that favours site conditions with frequent flooding (seaward of the swamp). By contrast, *Excoecaria agallocha* may be characterised as growing in more of an established forest community and will tolerate only sporadic flooding. These characteristics of the Totoya mangrove are generally well recognised by the main authorities on Fijian mangrove vegetation (Mead 1928, Parham 1972, Wattling 1978, Smith 1981).

The expansion and contraction of mangrove in the fossil pollen data indicates that past mangrove communities were more extensive than the present. Harvesting of mangrove for firewood, an established practice in other parts of Fiji (Wattling 1978) and Asia (Watson 1928), is at least one possible explanation for this behaviour. Parham (1972) further notes that the aerial roots of *Bruguiera gymnorhiza* were used by the Fijian people for making bows while smoke from the burning timbers of *Excoecaria agallocha* was reputed to have been a cure for leprosy. Bark from both species was considered to have medicinal uses (Smith 1981). In times of food shortage, Smith (1981) maintains that the seeds of *Bruguiera gymnorhiza* were used to make *mandrai* (bread).

However, the author noted during his stay on the island that mangrove forest is not harvested for fire wood or seed by the village people at the present time, if it ever was in the past. At Yaro Bay there had been evidence of mangrove trees being cut back, although the reasons for this are unclear. This site is one to two hours walk by foot from the nearest village.

It may be that this area was cleared to permit access to mud crabs or other food sources (Milward 1976) like fish in the large pond which the trees partly covered. However, it is clear that human harvesting (at times) cannot be wholly discounted as a possible mechanism of population behaviour.

Throughout the Totoya mangrove forests seed production is abundant, although it is questionable as to just how effective these seed stocks are in promoting regeneration due to predation by crabs. These crabs appear to be a well known seed predator in mangrove swamps (Watson 1928, Chapman 1976).Tomlinson (1986) claims that they prevent regeneration. In Fiji, the mangrove mud crabs are considered as a food delicacy and on Totoya were harvested almost daily by the local village people from various parts of the island.

The influence of crabs on regeneration is impossible to assess without further research into the question. Watson (1928) claims that in Malaysian mangrove forests, crabs are probably the worst enemy of mangrove. Damage includes predation on seedstock, ring barking young seedlings and in some cases even parent plants. There appears to be no obvious pattern to these attacks although Watson (1928) observed that its intensity appeared to increase after clear felling of forest when replanting was underway. Crab predation was less in dark understorey conditions.

The present author did observe that it was a very rare thing to find the seedlings of either *Bruguiera gymnorhiza* or *Excoecaria agallocha* regenerating anywhere near their own parents. While vivipary is common among mangrove species (Frodin *et al.* 1974, Cowan 1976), the present author has not been able to find a single published observation of this behaviour in either *Bruguiera gymnorhiza* or *Excoecaria agallocha.* This may indicate effective predation by crabs and if this is the case then these mangrove communities may have a form of predator mediated discrete population growth. The problem is, if seed predation by crabs is so effective at preventing regeneration as is claimed in the literature on Mangrove vegetation, how do these communities become established in the first place? Further research into this question is clearly needed.

A rather curious feature of the ecology of *Bruguiera gymnorhiza* was observed by Watson (1928) who notes that clear felled areas of *Bruguiera gymnorhiza* forest *often remain unregenerated in spite of frequent tidal inundation.* Watson suggests that *Bruguiera gymnorhiza* may have allelopathic tendencies which prevents regeneration anywhere near the parent plant. This does not appear to be a problem to inland plant species that may follow it where physical conditions allow. Furthermore, at two sites on Totoya (Udu and Lawakilevu), *Bruguiera gymnorhiza* and *Excoecaria agallocha* grow intermixed in a single forest stand.

Stoddart (1980) suggests that tropical cyclones may be an important disturbing agent in mangrove forests, recovery from which he estimated to exceed 25 years. Fiji has a annual tropical cyclone season (Mead 1928, Cooper 1966, d'Aubert 1994) and this is likely to be an important factor influencing the spatial extent of mangrove forests.

The forms of disturbance mentioned in the above section are of particular relevance to the mangal of Totoya. The whole question of mangrove zonation has been extensively debated in the literature with apparently little success in terms of elucidating precise causal mechanisms. Rodriguez (1987) recently suggests that the diversity of spatial organisation found in mangrove community structure, *on a global scale, appears as a chaotic mess of special cases without a unifying criterion which will allow the inference of general properties of the system.*

In evaluating fossil pollen from mangrove communities, spatial processes of mangrove expansion and contraction are recorded as a time series of rises and falls in fossil pollen concentration. In order to interpret these spatial processes as temporal behaviour it is necessary to review briefly the main theories that have been advanced to explain these processes.

5.2.5.5 The Zonation of Mangrove Forests

Reviews of literature on mangrove forest zonation are given in Tomlinson (1986), Chapman (1976), Clough (1979) and Rodriguez (1987).

In view of the meandering nature of the streams and channels that cut across mangrove forest zonations it is not surprising that these communities seem more readily interpretable as a mosaic (Thom 1979). Where mangrove communities grow along the sides of rivers or on steep or physically delimited shore fronts, there may be *insufficient space for zonation to develop* (Tomlinson 1986). In general, the species diversity and patterning of mangal appears to increase over a northerly latitudinal gradient (Bridgewater 1985).

The most common species of mangrove can be found in exclusive stands in at least some places, although genera like *Rhizophora* that grow together show pronounced zonation that is easily disrupted for a number of possible reasons. The substrate of most coastal swamps varies from coarse coral to sand to silt to clay to mangrove peat (in some places). On high energy coastlines or in estuaries subject to irregular freshwater discharge, sediment redistribution is highly variable. Differences in the supply and composition of mangrove sediments is another cause of instability in the spatial patterning of mangrove communities.

According to the space for time substitution theory of plant ecology (Pickett 1987), a zonation of species in space represents their succession in time. The notion that mangrove zonations represent a successional stage in the development of inland forest vegetation has featured as a dominant theme in the ecological literature that has been especially championed by Chapman (1976). This theory has strong links with the Clementsian school of plant ecology, denies the likelihood of a steady-state (mangal) interpretation and insists that there must be a climax vegetation (Johnstone 1983).

In sharp contrast to the climax interpretation of Johnstone (1983) is a steady-state interpretation of mangrove forest structure given by Woodroffe (1983). The community studied by Woodroffe persisted for at least 2000 years by building up deposits of peat exceeding 4m in places and this in spite of a local sea-level rise of ca 2m.

A long period of exponential growth expansion (ca 90 years) has been documented by Burns and Ogden (1985) for *Avicennia marina* forest in New Zealand. Also, Tomlinson (1986) notes the existence of mangrove peat beyond the seaward limit of existing *Rhizophora* forest in Biscayne Bay, Florida. In this case it appears that the existing mangrove zone has either shrunk or migrated landward. Other examples of long-term mangal persistence are documented by Chappell and Grindrod 1985, Clark and Guppy 1988, Kendrick and Morse 1990, Crowley *et al.* 1990.

In a classic publication on mangrove community structure, Davis (1940) suggested that the shoreline extends seaward as a result of the land building role of mangroves *in a continuous process of accretion and succession. This process is interrupted only when hurricanes, storm flushings or other natural destructive forces reverse it* (Rodriguez 1987). However, on stable coastlines, mangrove forests are now known to persist for long periods of time, behaviour that appears to result from the existence of some environmental factor independent of soil accretion (Lugo 1980).

Recently, the view of mangrove community structure as a spatial expression of successional processes and the land building role of mangroves has been seriously questioned. Tomlinson (1986) suggests that the *chief deficiency seems to be a lack of a direct demonstration of real successional processes in time (rather than imaginary ones in space).* Furthermore, one reason for this problem is that mangrove trees are not datable by tree ring analysis (Gill 1971). For this reason, the static analysis of spatial zonation cannot be converted to a dynamic one by comparing the relative ages of trees in the community (Tomlinson 1986).

A more recent trend in research in this area has seen a recognition of the multivariate nature of this problem. For example, Lugo (1980) identified 35 possible causal factors of mangrove zonation! In the history of mangrove research some of these factors have clearly received more attention than others and these main research themes (Bird and Barson 1979) are briefly as follows.

5.2.5.5.1 Abiotic Factors Influencing Zonation

The notion that *zonation is a spatial expression of plant succession and that mangrove vegetation is not a climax forest, but rather a number of seral communities arranged in fairly definite zones, were formally expressed for the first time by Davis for the Florida mangroves* (Rodriguez 1987). According to the scheme of Davis (1940), succession proceeds as a direct result of the land building role of mangroves (Bird 1972). This process is only interrupted when environmental disturbances (Oliver 1976) upset the construction process of seaward accretion. This traditional mangrove succession paradigm (Chapman 1970, 1976, Walsh 1974) was challenged by Thom (1979).

Research by Thom (1967) and co-workers in Mexico and Australia suggests that mangrove distributions follow but do not over-ride abiotic land building processes. Thom (1979) suggests that mangrove are opportunistic species which colonise available substrate (see also Stoddart 1980). Mangrove zonation is considered an ecological response to *external conditions of sedimentation, microtopography, estuarine hydrology and geochemistry* (Thom 1979).

A weakness in this explanation is its failure to account for differential biological adaptation to *contrasted physiographic factors* (Tomlinson 1986). In Thom's explanation, a steady-state may prevail and involve cyclic short-term instability or long-term self maintenance of a community facilitated by environmental factors independent of soil accretion. In this respect the explanation of Thom provides a sharp contrast to the successional theory of Davis (1940). Perhaps the classical pattern of succession (Davis 1940, Chapman 1970, 1976, Walsh 1974) represents only one of several possible patterns of spatial organisation (Rodriguez 1987). What are the factors that may be responsible for this variation and is there a unifying criterion?

It is also possible to ascribe species zonation to a narrow range of tidal inundation classes and this implies that a species may be restricted to a given class. This restriction could be modified by other factors like substrate type and these ideas, in essence, form the basis of Watson's (1928) inundation class theory of mangrove zonation.

Recent research into the factors responsible for spatial patterning in mangrove communities has involved the analysis of gradients caused by tidal factors, particularly salinity (Passioura *et al.* 1992). Is it possible that mangrove could respond physiologically to these gradients so that each mangrove species has an optimal growth region within the shore area? Research into the regeneration of *Rhizophora* suggest that for this genus, salinity tolerance may be related to interspecific competition (Rodriguez 1987). Similar conclusions were drawn from research on other mangrove species by Clarke and Hannon (1970). *Rhizophora* has been observed to do well in fresh water environments in the absence of competitors (Soto and Jimenez 1982, Jimenez 1985a,b).

The hypothesis of sediment salinity and mangrove zonation has been experimentally tested by Carter *et al.* (1973). In Florida mangroves these researchers demonstrated that mangrove respiration was positively correlated with soil salinity. However, as might be expected this is not the end of the story. Rabinowitz (1978a) experimented with garden plots of the four genera of mangrove found in Panama. She observed that some mangrove seedlings showed better survival in other mangroves' habitats than in their own, results that strongly indicate that mangrove pattern is not controlled by species preference.

Tomlinson (1986) suggests that a possible answer to this contradiction may be that for many ecologically constraining factors it is extreme conditions that are limiting and not the average. Salinity may determine zonation at the margin of a salt flat while the range of *salinities within the extended seaward zones subjected to frequent inundation ... may be so small as to be physiologically insignificant*. If this is indeed the case, then it seems likely that other limiting factors may also be involved. In the following section hypotheses explaining the influence of biotic factors on mangrove distribution are considered.

5.2.5.5.2 Biotic Factors Influencing Zonation

Following her reciprocal transplant experiments, Rabinowitz (1978a, b) formalised the idea that mangroves are interchangeable between zones into one of the simplest hypotheses attempting to explain the causes of mangrove zonation - the different tidal sorting of propagules. The positive correlation between an increasing size of mangrove propagules and the position of the species between the land and the sea may be explained by the fact that large propagules do not invade shallow water where their movements are restricted.

Likewise, smaller propagules can only establish if free from tidal disturbance. Contradictory evidence for the propagule sorting hypothesis is found in the presence of mangrove species with small propagules occupying the seaward margin of the mangrove swamp (Chai 1982). The hypothesis of Rabinowitz (1978b) assumes a biological explanation in the absence of a known physiological adaptation and that seedling establishment is representative of persistence to maturity. (Rabinowitz 1978b, Rodriguez 1987, Tomlinson 1986).

The question of whether mangal structure is the result of successional processes or a steady-state remains unanswered (Lugo 1980). Based on the discovery of Woodroffe (1983) and others it is evident that some communities of mangrove persist in one location for considerable periods of time. Clearly, different mangrove populations may co-exist in the same swamp, but the causal factors responsible for the organisation of these communities remains unclear.

The most likely biotic causal mechanisms proposed in the literature so far appear to be the propagule sorting hypothesis of Rabinowitz (1978b) and the salinity tolerance hypothesis applied to *Rhizophora* seedlings in the research of Soto and Jimenez (1982) and Jimenez (1985a,b).

The question is, to what extent are these or any other biotic mechanisms capable of causing competitive exclusion on the time scales for which mangrove communities are at present known to persist (*e.g.* Woodroffe 1983). If biotic mechanisms operate, then it may be more appropriate to evaluate mangrove communities in terms of the *gap phase dynamics* and *succession* theory familiar to community ecology.

In conclusion, the present status of mangrove zonation theory provides an opportunity to test the equilibrium and non-equilibrium status of mangrove communities by modelling their long term behaviour. This approach is very different from traditional ecological approaches to the study of mangrove zonation which have focused on geomorphological, spatial, physiological and biotic causal mechanisms and ecosystem (Golley *et al.* 1962, Lugo and Snedaker 1974) analysis.

Static research of this kind undoubtedly has a place; however, it is now equally evident that a new approach to the problem of mangrove zonation is badly needed. What is needed is an opportunity to study the dynamic (temporal) perspective so as to test the traditional static background theory. Recent studies reviewed by Grindrod (1988) suggest that palynology may be highly effective for the study of mangrove zonation and geomorphological process interactions

(Grindrod 1985). A deficiency in behavioural research of this kind is, according to Tomlinson (1986), *stultifying to the whole of tropical ecology*. The present research project provides an opportunity to address this deficiency by testing for the operation and influence of various biotic and abiotic causal mechanisms on mangrove community behaviour.

5.2.5.6 Mangrove Forest Structure - Totoya

An interesting characteristic of the mangrove forests of Totoya is their community structure which strongly resembles a spatial successional sequence. When viewed as an inland to seaward successional zonation, *Inocarpus fagiferus* forest is always found at the rear of Totoya mangrove swamps. *Bruguiera gymnorhiza* (a known pioneer mangrove species) always dominates at the seaward end of the swamp with *Excoecaria agallocha* dominating the intermediate zone. These three species are present at each of the six core sites on Totoya, although the exact spatial arrangement of the forest zones varies from site to site.

These observations are consistent with literature on mangrove forests in other parts of the Pacific basin (Parham 1965, Wattling 1978, Woodroffe 1987, Ellison 1986). *Bruguiera gymnorhiza* is always associated with a habitat at the seaward margin of mangrove swamps. *Excoecaria agallocha* is usually located in drier areas where evidence for occasional tidal inundation is present (ref. Mead 1928).

Finally, the Totoya mangrove forests are usually flanked by either physical barriers like a ridge line or vegetation communities like coconut plantation. The Ivi *(Inocarpus fagiferus)* forest at the rear of the swamp may be backed by coconut plantation or inland forest depending on its proximity from the rear of the coastal plain.

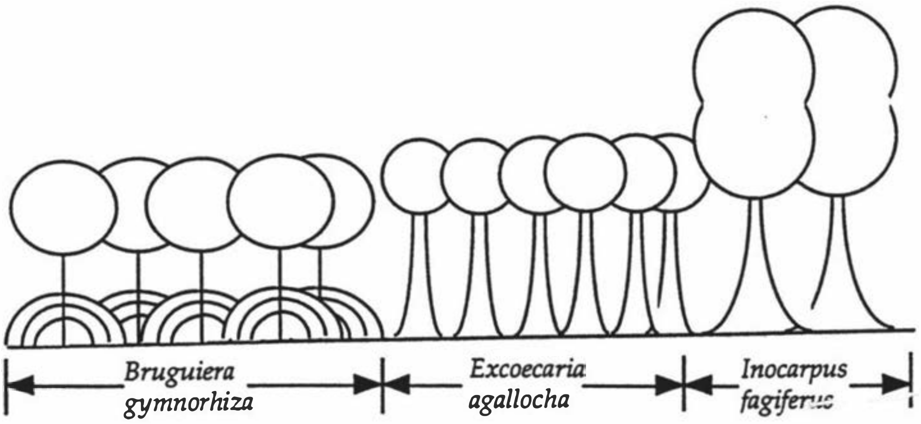


Fig 5.8 The peculiar spatial zonation of the two mangrove species and *Inocarpus fagiferus* forest at the Keteira, Dravuwalu, Jigojigo Bay and Yaro Bay core sites. *Bruguiera gymnorhiza* dominates the seaward zone, *Inocarpus fagiferus* forest dominates the rear of the swamp with *Excoecaria agallocha* dominating the intermediate zone.

Lianes are generally scarce in mangal (Chapman 1976) and this is evident on Totoya. Occasionally the Duva *(Derris trifoliata)* is found on mangrove foliage near swamp margins. The odd individual of Vesiwai *(Pongamia pinnata)* and Mulomulo *(Thespesia populnea)* can also be found near the swamp margins. Both species are found more commonly in coastal zone vegetation.

With the exception of two core sites (Udu and Lawakilevu) where the seaward mangrove forest is a mixture of both *Bruguiera gymnorhiza* and *Excoecaria agallocha,* all of the other four core sites (Dravuwalu, Keteira, Jigojigo Bay and Yaro Bay) show a distinctive sea to land zonation of *Bruguiera - Excoecaria - Inocarpus* (fig 5.8).

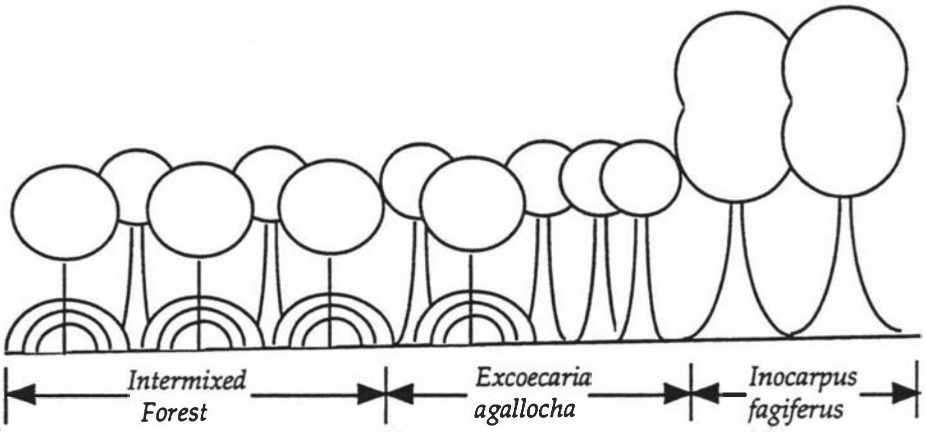


Fig 5.9 The peculiar spatial zonation of the two mangrove species and *Inocarpus fagiferus* forest at the Udu and Lawakilevu core sites. An intermixed forest of *Bruguiera gymnorhiza* and *Excoecaria agallocha* dominates the seaward zone, *Inocarpus fagiferus* forest dominates the rear of the swamp with *Excoecaria agallocha* dominating the intermediate zone.

At the Udu and Lawakilevu core sites, the seaward zone of mixed *Bruguiera gymnorhiza* and *Excoecaria agallocha* forest grades away inland to an exclusive stand of *Excoecaria agallocha* forest, with *Inocarpus fagiferus* forest at the rear of the swamp (fig 5.9).

Based on these static observations a tentative interpretation might suggest that the four core sites (Dravuwalu, Keteira, Jigojigo Bay and Yaro Bay) provide possible evidence of non-interactive successional processes which are driven by possible abiotic causal mechansims like coastal plain construction and physiological tolerance.

At the other two core sites, the longer term persistence of the two intermixed mangrove species is suggested in smaller swamp basins that probably don't provide space for the zonations found at the other four sites. Furthermore, at these two core sites the likelihood of a steady-state community is implied. The sedimentary history of these two sites falls within a time frame similar to that reported by Woodroffe (1983) on a Grand Cayman island.

The study of mangrove community structure involves a spatial dimension that is outside the modelling objectives of the present project. However, community structure also has a strong temporal dimension which can be used in this project to test hypotheses of community organisation. Changes in the spatial dimensions (number of individuals of a population present in a given zone of mangrove forest) should be recorded as temporal changes in the concentration of the fossil pollen of that same population over time.

Based on the two tentative observational hypotheses mentioned above, a domain of application has now been defined for testing hypotheses 1 - 4 outlined in Chapter four.

5.2.5.7 Domain of Application: Hypotheses 2 - 4

If the spatial behaviour of these populations conforms to a series of non-interactive seral population zones migrating across the coastal plain as an opportunistic response to coastal plain construction processes, then the temporal behaviour of these populations should be represented by a long term steady state - assuming that the populations are undisturbed and that regeneration is a continuous process.

Because of what is known of the ecology of these two mangrove species it is far more probable that regeneration (mediated by seed predators - crabs) will be a stochastic process. In a review of herbivory research on mangal, Robertson (1991) suggests that in research trials, crabs were responsible for consuming more than 70% of the seeds of five mangrove species and 30 - 80% of the annual leaf litter fall. If these results are indicative of the general trophic energy transfers in mangal then the temporal behaviour of these populations probably approximates a series of long term population rises and falls similar to the repeated behaviour of an annual reproductive process. To model community organisation of this kind in experiment one, the discrete logistic equation (48) is used.

This model simulates a discrete reproductive process and can be used to test for three different classes of behaviour (logistic growth, limit cycles and chaotic behaviour) based on critical values of the net reproductive parameter (r). Individual equations can also be coupled (52a, b) to test for the existence of discrete time interactive processes.

One immediately obvious problem is that the hypothesis proposed above assumes stochastic demographic processes while the discrete logistic has a stable net reproductive parameter. Furthermore, the behavioural instability of this model results from over-compensation caused by excessively high net reproductive rates - not demographic stochasticity.

These points are both quite valid. The problem is, at present there is no obvious way of determining the timing or quantifying the influence of the stochastic processes likely to be driving the regeneration of these populations. In this context, the explanatory power of the discrete logistic is likely to be poor. However, the test is useful for gaining some first hand indication of the behavioural nature of these populations that cannot be assessed as effectively using a continuous time logistic formulation (46).

This model formulation could be used to test for seral zonation behaviour at the four core sites on Totoya (Dravuwalu, Keteira, Jigojigo Bay, Yaro Bay) where spatial evidence of non-interactive behaviour is currently observed.

Because the initial focus of this project was on modelling plant community behaviour resulting from competitive causal mechanisms only one of these four core sites (Keteira) was chosen for use as a modelling data set. It was the intention of the author to use the Keteira core site as a control site, to test for the existence of between site behavioural consistency. The hypothesis being tested is that the behaviour of the two mangrove species at the Keteira core site is different from the behaviour of the two mangrove species at the Udu and Lawakilevu core site, if successional and steady-state processes are the main organisation differences between the two sites.

5.2.5.8 Domain of Application: Hypothesis 1

If the spatial behaviour of these populations does not conform to a series of non-interactive seral zones migrating across the coastal plain then what should be expected as an alternative behavioural type? The answer to this question is a steady-state community and there appears to be some justification for such a hypothesis.

Firstly, the physical intermixing of both species of mangrove is an important prerequisite for the operation of density-dependent processes like interspecific competition driven by competition for limited resources like light and space (Clarke and Myerscough 1993). Intermixing of mangrove has been investigated by Clarke and Hannon (1971) who attribute this behaviour to a number of causes including salinity, seed dispersal, competition for light and competition based on differential growth rates.

Core Site Location	Breadth (m)	Length (m)
Yaro Bay	500	825
Keteira	350	500
Dravuwalu	600	500
Jigojigo Bay	550	250
Udu	150	100
Lawakilevu	150	100

Table 5.1 A comparison of core sites on Totoya Island based on measurements of the coastal plain from a 1:50,000 topographic map (Fiji map series S 31/32). Breadth provides a measurement of the coastal plain from the front to the rear of the plain through the core site area. The length measurement provides an indication of the distance along the front of the coastal plain between physical boundaries.

Secondly, the swamp area at both sites is small and located in a natural basin with distinct physical boundaries. Such a site, while unsuitable for distinct seral zones, may be more suited to internal filling that results in a community being established long term on the basis of gap phase replacement dynamics as suggested by Tomlinson (1986) and more recently by Clarke and Myerscough (1993).

When the coastal plains of all six core sites are compared, Udu and Lawakilevu have the smallest total available area. Some indication of available area can be gained by measurements made from a 1:50,000 topographic map (Table 5.1).

The measurements of Table 5.1 are only intended for comparative purposes and should not be considered as an attempt to estimate available swamp area for a number of reasons. Firstly, the distance across the coastal plain (breadth) varies greatly and is determined by the presence of ridges and valleys at the rear of the plain as well as the curvature of the beachline. Secondly, while a coastal plain positioned between two ridge lines may be quite long (*e.g.* 825m for Yaro Bay), not all of the area indicated in this measurement would be suitable for mangrove swamp at the present time. Despite these limitations it can be seen that the measurements of the Udu and Lawakilevu core sites are very small compared with the measurements taken from the coastal plains of the other four core sites on the island.

Based on the small amount of total available area at these two core sites it seems very possible that a large intermixed mangrove community has persisted in the past based on gap phase dynamics. If this is the case, then this community may approach a continuously regenerating population because of the physical confinement of the site. Instead of a migration of discrete seral zones across the coastal plain, these sites are more likely to have experienced invasion and infilling of the swamp basin in which they are located. Intermixing was probably a gradual process as sediment supply changed the physiographic nature of the basin and altered local physiological gradients.

Inundation and physiological tolerance constitute a third possible mechanism. The spatial expression of the two mangrove species at these swamps gives the appearance of an interactive process resulting from the landward invasion into preferred habitat of *Bruguiera gymnorhiza* and the seaward advance of *Excoecaria agallocha*.

Fourthly, the seed sizes of *Excoecaria agallocha* and *Bruguiera gymnorhiza* are positively correlated to the location of these species in the swamp area - according to the propagule sorting hypothesis of Rabinowitz (1978a,b). The fruit of *Excoecaria agallocha* is three lobed and about 7mm in diameter while individual seeds measure approximately 3mm in diameter. The water born dispersal capabilities of these seeds could be superior to that of *Bruguiera gymnorhiza* which has a 25 cm hypocotyl, *cigar shaped, blunt apically and slightly angular* (Tomlinson 1986).

Is it possible that *Excoecaria agallocha* is able to out-compete *Bruguiera gymnorhiza* on the basis of superior water born seed dispersal capability? Clarke and Myerscough (1993) found that in communities of New Zealand *Avicennia*, distribution was not limited by seed dispersal capability. Instead, they found that propagule establishment was limited by physicochemical conditions, interspecific competition for light and seedling predation! Tamai and Iampa (1988) discovered that light conditions affected the growth of young trees (>1 year old) more than the establishment of new seedlings.

At core sites where there is a larger swamp area and tidal range, dispersal advantages would clearly give *Excoecaria agallocha* superior access to the rear of the swamp where *Bruguiera gymnorhiza* is presently excluded. In parts of the swamp where the two species intermix, competition for light and seedling predation by crabs may be important determinants of seedling survival according to the recent results of Clarke and Myerscough (1993). The results of Clarke and Myerscough (1993) find good agreement with earlier work by Burns and Ogden (1985) who found that *survivorship of the young tree class is the main determinant of the population growth rate; annual seed production is relatively unimportant*.

As a fifth consideration, *Bruguiera gymnorhiza* is known to have possible allelopathic tendencies toward nursing its own seedlings and those of other mangrove species (Watson 1928).

Finally, there is the indiscriminate predatory activity of crabs to factor into the above evaluation. According to the literature on mangal, the activity of these predators may be responsible for hindering or stopping regeneration. The exact impact of these predators may be extremely difficult to assess.

Firstly, their abundance will vary from site to site and with time, especially since they are harvested as a food source by the local village people. Secondly, it is possible that seeds are dispersed by tidal currents from one site on the island were there are few crabs at a given time and colonise successfully at other sites. The presence of the sand barrier at the front of these swamps would limit this colonisation process to times of flooding caused by heavy rainfall. Thirdly, neighbouring islands doubtless acted as centres for seed dispersal. Complicated dispersal mechanisms of this kind basically require equally complicated operational assumptions.

Based on the experimental approach used in this project it is not possible to prove the existence of a given causal mechanisms. Those mentioned above are intended only to demonstrate (at least initially) that the conditions present at the Lawakilevu and Udu core sites where the two species of mangrove grow intermixed may (theoretically) favour the establishment of a steady-state community. This, in turn, justifies the use of a continuous competition model in order to test for the existence of stable equilibrium conditions.

It is difficult to assess the extent to which the physical confinement of these two populations in a natural basin-like area will affect regeneration processes.

Clearly, such a community could never maintain a steady-state if continuous regeneration processes were not in operation and there is not some upper limit to population expansion - suggested to be exponential in nature according to Burns and Ogden (1985). It seems that the only way to test this hypothesis is to compare the behaviour of the two mangrove species at these sites with the behaviour of an interactive continuous model like the coupled logistic (50a, b).

5.2.5.9 Summary of A Priori Predictions

In an experiment designed to test the two hypotheses described above for the Keteira, Udu and Lawakilevu core sites, the following results are predicted - *a priori*.

Firstly, the Keteira core site will show evidence of behaviour approximating discrete demographic processes. This prediction corresponds to a succession of seral population zones advancing seaward over the coastal plain with time as the process of coastal plain construction advances. The limitations of the application of the discrete logistic model (48) have been outlined.

Secondly, the Udu and Lawakilevu core sites will show behavioural evidence of a long-term continuous, interactive growth process. This process should result in a trend toward a dominant species as the two species compete for suitable habitat under changing physiological and physiographic site conditions caused by sedimentation and seaward coastal plain construction.

This behavioural prediction is based on the assumption of population infilling of the swamp area. Because these swamps are blocked at the seaward margin by a sand barrier, seed dispersal for most of the year will be inhibited and concentrated within the swamp basin. Because this community does not have the same migrational behaviour of distinct forest zones as the other four sites on Totoya, internal replacement, increased density and forms of interspecific competition may be the only viable long-term organisational strategies.

The two hypotheses advanced in this section to explain the behaviour of these mangrove communities contain all of the assumptions involved in using discrete and continuous models (see Chapter four). Most importantly, these hypotheses assume that environmental conditions remain stable and have no serious impact on these individual and interactive populations.

5.2.6 Coastal Zone Vegetation

Coastal zone vegetation on Totoya varies with coastline morphology - an important controlling factor. This community has some affinity with the coastal zone associations described by Parham (1965, 1972), Kirkpatrick and Hassell (1981) and Morton and Ray (1980) for other parts of Fiji.

In places where valley sides and ridge tops at the coastal margin are still covered by inland Cibicibi forest, this association usually remains intact right down to the water's edge. In exposed locations this vegetation has an edge affect - likely to be disturbance related. Mangrove is always associated with the ephemeral stream channels which drain watersheds behind the coastal plain and are thus controlled largely by seasonal rains.

Coastal zone vegetation usually consists of a tree association often located at the seaward margin of the coastal plain in front of coconut and mangrove forests. In undisturbed places the vegetation merges back inland toward the forest behind it, but is often intersected by a pathway, regularly cleared to enable foot traffic about the island.

Tree specimens collected include: the Visivisiwai *(Pongamia pinnata)*, Dilo *(Calophyllum inophyllum)*, Drala *(Erythrina variegata)*, Niu *(Cocos nucifera)*, Makota *(Dysoxylum richii)*, Vaivai *(Leucaena leucocephala)*, Yagoyagona *(Macropiper sp.)*, Ivi *(Inocarpus fagiferus)*, Molokaka *(Vitex trifolia var bicolor)*, Dabi *(Xylocarpus moluccensis)*, Mulomulo *(Thespesia populnea)*, Vutu *(Barringtonia asiatica)*, and the Tavola *(Terminalia catappa)*.

Samples of the herb Tamole *(Hyptis pectinata)* and the grass Gasau *(Miscanthus floridulus)* were also collected, although these two species are by no means exclusive. In general, herbs and grasses were few. By contrast, the presence of lianes was more striking as ground cover in some places and canopy in others. The Duva, *(Derris trifoliata)* was most common, while the Wavoti *(Ipomoea Sp.)*, Wabosucu *(Mikania micrantha)*, Wavuli *(Ipomoea congesta)* and Matiavi *(Wilkstroema foetida)* were present in lesser amounts.

Plantations are a common feature of the vegetation located upon the coastal plain. Here the Voivoi *(Pandanus caricosus)* is cultivated and harvested for use in mat making. A second species of pandanus is found on Totoya.

5.2.7 Cibicibi Forest

The Cibicibi forest appears to be a forest association that is unique to the island of Totoya when compared with the rest of the Fiji group as described by Parham (1965, 1972). At present, it is appears to be the most prevalent forest association on Totoya from which other forest associations are but variants, differing in one or two species of tree and abundant in a more diverse ground layer of ferns and grass where gentle slope, light and stable substrate allow their presence.

Disturbance is a major factor controlling compositional variation within the Cibicibi forest. On some hillsides, long tongues of different vegetation can be seen intermixed within the Cibicibi forest association - compositional variation that is probably related to fire disturbance. In steepland areas slope instability may be a further means of vegetation disturbance. In other locations, human clearance of the forest has occurred in small areas for cultivation and here, the invasive nature of the reed grass Gasau *(Miscanthus floridulus)* and lianes are evident.

Finally, the grazing of livestock in some parts of the island was carried out in the past. Today, goats are usually penned and hence their browsing controlled.

However, it was commonly known among the people of Tovu village that cattle had been allowed to graze the moderate hillslopes on the outer side of the island near Yaro bay in recent times. Browsing animals may still disturb areas of Cibicibi forest as faecal pellets were found at survey sites at Qaliqali Bay. A detailed review of literature and assessment of the impact of introduced and native terrestrial vertebrates of Fiji is given by Pernetta and Wattling (1978).

Survey of the Cibicibi forest was conducted on the western side of the lagoon at Qaliqali Bay. Here, the composition of the Cibicibi forest is almost exclusively trees, lianes, a tree fern and a couples of grasses. An accessible transect line of 180 - 255 degrees was followed up a very unstable steepland face littered with large boulders. The first 20 m x 20 m quadrat was laid at an altitude of 80 m to avoid disturbed vegetation in the coastal zone, with successive quadrats at 120m, 160m, and 220m.

Cibicibi *(Maniltoa brevipes)* is the most common tree in this association followed by Bolavatu *(Homalium pallidum)*, Qalaka *(Planchonella grayana)* and the otherwise coastal zone tree Boiboida*(Barringtonia asiatica)*. Other trees in order of greatest abundance include, Sasagilu *(Dysoxylum sp.)*, Rewa *(Cerbera manghas)*, Sevua *(Vavala amicorum)*, Baka *(Ficus Sp.)*, Sekeci *(Aleurites molluccana)*, Qai *(Cordyline terminalis)*, Ramasa *(Alectryon samaensis)*, Siti *(Grewia crenata)* and Soni *(Caesalpinia sp.)*.

Abundance of the two grass species collected *(Digitaria sp. and Seleria lithosperma)* varied considerably and appeared to be related to disturbance providing openings in the forest canopy for light. The lianes also varied in abundance. The Wavoti *(Ipomoea sp.)* was the most prevalent: its hanging vines made passage through the forest difficult. Vono*(Alyxia sp.)* was found only in one quadrat at 120 m. Lastly the tree fern *Lygodium sp.* was present in very few places and usually attached to the lower trunks of trees.

At higher altitude, the forest loses its distinct canopy, trees become tufted by the outgrowth of long basal branches, tree density declines and grass cover increases as suggest for other high altitude forests of the Fiji group by Parham (1972).

5.2.8 **Cau Forest**

A second forest association on Totoya, very different in structure from the Cibicibi forest, is the Cau *(Casuarina nodiflora)* forest. This assemblage (located in few places) is usually situated on low altitude valley sides, ridge tops or near ridge lines. Parham (1972) describes the tree as *30 to 40 feet high with drooping branches and needle like branchlets*, a species *very common in the dry zones especially where the soil is poor*. On Totoya, Cau trees grow in association with the reed grass Gasau*(Miscanthus floridulus)*.

5.2.9 *Grassland Vegetation*

The Fiji grassland (Talasiga) association was described by Parham (1965, 1972). This class of vegetation on Totoya was not formally surveyed, although some aspects of their composition and distribution are worthy of mention.

Talasiga comprises a range of communities with an herbaceous stratum dominated by forbs (non-gramineous herbaceous species). Brackens are a principal component (Latham 1979). The Totoya Talasiga is easily divisible into 3 or 4 height classes related to a variety of factors including slope, aspect, surface morphology, soil quality and depth. It is floristically diverse, and shows marked variation when its compositional mosaic is observed on valley sides in the leeward (dry) end of the island. Totoya's grassland association is primarily composed of Gasau *(Miscanthus floridulus)* and bracken fern *(Pteridium esculentum)*. The *vadra (Pandanus odoratissimus)* can be seen growing as individual trees amidst some areas of the island's grassland vegetation.

Most grassland savannas of the everwet tropics have long been regarded as the result of anthropogenic disturbance (Parham 1955, 1972, Twyford and Wright 1965, Cochrane 1969, Flenley 1979, Barrau 1980, Kirch 1984). This view was questioned by Bartlett (1956) and later by Spriggs (1981) who proposed that a period of aridity may have seen rainforest replaced by savannas in some areas (see Nunn 1990a). Latham (1983) proposed that the grassland association may have developed during a period of pre-settlement aridity, evidence for which was found by Southern (1986) on Taveuni Island.

Nunn (1990a, 1992, 1994a) presents a very thought provoking and balanced evaluation of the questions which surrounding the origins of tropical grassland vegetation pointing out that much of the evidence used to support this theory is *inferred* from historical evidence *a posteriori* (Nunn 1994a). While acknowledging that *pre-settlement forests were severely decimated on most pacific islands within 1000 years of initial settlement* (Nunn 1990a), Nunn (1992) argues that sea-level changes, climatic changes, tectonic changes and catastrophic events are all factors equally capable of inducing the types of environmental changes traditionally interpreted as anthropogenic.

In other words, the explanation is not as simple as has traditionally been believed and while it is desirable *to limit human impacts, it is equally important to recognise the nature and potential contributions of non-human agencies to environmental change* (Nunn 1990a).

5.2.10 *Summary and Discussion*

The contemporary vegetation of Totoya can be divided into eight main classes, two of which (Coastal zone and Cibicibi forest) appear to be restricted to Totoya when compared with the generalised system of classification outlined for the Fiji group of islands by Parham (1965, 1972) (see Table 5.2).

Common Name	*Botanical Name*	*Coastal Zone*	*Pollen Data*	*Fiji Group*	*Cibicibi Forest*
Dilo	*Calophyllum inophyllum*	S	G		
	Diospyros samoensis	S	G		
Voivoi	*Pandanus caricosus*	S	G		
Vadra	*Pandanus odoratissimus*		G		
	Eugenia sp.		G	G	
Visivisiwai	*Pongamia pinnata*	S			
Drala	*Erythrina variegata*	S			
Niu	*Cocos nucifera*	S	F		
Makota	*Dysoxylum richii*	S	G		
Vaivai	*Leucaena leucocephala*	S		G	
Yagoyagona	*Macropiper sp.*	S			
Ivi	*Inocarpus fagiferus*	S			
Molokaka	*Vitex trifolia var bicolor*	S		G	
Dabi	*Xylocarpus moluccensis*	S			
Mulomulo	*Thespesia populnea*	S			
Vutu	*Barringtonia asiatica*	S	G	S	S
Tavola	*Terminalia catappa*	S		G	
Tamole	*Hyptis pectinata*	S			
Gasau	*Miscanthus floridulus*	S			
Duva	*Derris trifoliata*	S			
Wavoti	*Ipomoea sp.*	S			S
Wabosucu	*Mikania micrantha*	S			
Wavuli	*Ipomoea congesta*	S			
Matiavi	*Wilkstroemia foetida*	S			
Cibicibi	*Maniltoa brevipes*			G	S
Bolavatu	*Homalium pallidum*				S
Qalaka	*Planchonella grayana*		G		S
Sasagilu	*Dysoxylum sp.*		G		S
Rewa	*Cerbera manghas*	S	G		S
Sevua	*Vavala amicorum*				S
Baka	*Ficus Sp.*		G		S
Sekeci	*Aleurites molluccana*		G		S
Qai	*Cordyline terminalis*				S
Ramasa	*Alectryon sp*	G			S
Siti	*Grewia crenata*		G		S
Soni	*Caesalpinia sp.*				S
	Digitaria sp.				S
	Seleria lithosperma				S
Vono	*Alyxia sp.*		G		S
	Lygodium sp.		G		S

Table 5.2 Comparing Totoya's vegetation with that of the Fiji group of islands (Parham 1972). Coastal zone and Cibicibi forest associations are compared with the fossil pollen assemblage (over all six core sites) and other Fiji islands. The level of plant and pollen identification is indicated by G for Genus, S for Species, F for Family.

The post human settlement landscape of Totoya is dominated by a grassland association. The distribution of the Totoya grassland vegetation appears to be strongly correlated to moisture availability as noted by Nunn (1992). Scattered and mostly disturbed remnants of inland Cibicibi forest vegetation appear to remain along with smaller pockets of Cau *(Casuarina nodiflora)* forest. More detailed research is needed to determine the extent of compositional variation in the Cibicibi forest association.

Table 5.2 shows that the Coastal zone and Cibicibi forest associations on Totoya are quite distinctive and spatially separate. With the exception of *Alectryon sp.* all of the identifications of plant species in these two classes were able to be made to species level. A list of herbarium samples from Totoya is recorded in Appendix 5.

As mentioned earlier, pollen identifications were made on a variety of sources of reference material. Most identifications could only be safely made to genus level with the exception of *Cocos nucifera.* Based on these identifications it is possible to see both the coastal zone and Cibicibi forest associations present on Totoya are reasonably well represented in the fossil pollen record even though the core samples were not from inland swamp sites.

The coastal zone vegetation of Totoya has very little affinity with the other islands of the Fiji group. It seems unlikely that the Coastal zone and Cibicibi forest associations of Totoya are based on restricted endemic species since at a genus level, at least, many of these tree species are common in other parts of the Pacific (see Hargreaves 1970). Furthermore, Totoya is only one of a three island cluster including nearby Moala and Matuku. Before coming to any firm conclusions concerning the endemic nature of these forest associations it would at least be necessary to survey the vegetation on these neighbouring islands.

It is also evident that the vegetation of the Fiji group of islands does not appear to have been surveyed in a systematic manner. A detailed chronology and description of past research work (up until 1981) is given by Smith (1981), much of which is more detailed than earlier accounts given by Parham (1953, 1964, 1972). Further systematic and detailed survey work is clearly needed. Despite these words of caution, the forest associations of Totoya do appear to be quite distinctive when compared with the other islands of the Fiji group, as described by Parham (1972).

5.3 Methodology

The following section provides a detailed discussion of the methodology used in the selection of core sites, removal of cores, laboratory preparation, counting, dating and compiling of fossil pollen data sets for the experiments outlined in this chapter.

5.3.1 Selecting the Site of a Natural Experiment

As outlined in Chapter four, natural experimental design involves all of the historic forces that influence the deposition and preservation of pollen.

While palynologists have no input into natural experimental design, the careful choice of core site can have a significant influence on the quality of the data used in a project.

The use of mangrove swamp sediments for fine resolution sampling (Green and Dolman 1988) and modelling research may see a rather odd choice when lake sites (especially with varved sediments) (*e.g.* O'Sullivan 1983) and peat deposits (*e.g.* Green *et al.* 1988) potentially provide a more satisfactory temporal record.

The choice of core sites in Fiji was guided by the need to find a fossil pollen record from a low diversity plant community of two or three species. The tropics may seem like the last place on earth to go looking for such a community! Unlikely as it may seem, the mangrove forests of Totoya are only a two species community.

In this initial selection process a high priority was placed on the need for a low diversity plant community. This priority reflects the strong equilibrium focus that the author brought to this project. By contrast, the results of this research provide a strong non-equilibrium focus for future palynological modelling studies of this kind. In the selection of core sites, future studies need not be restricted by community diversity to the same degree that this one was.

5.3.1.1 **Taphonomy**

Pollen dispersal and geological sedimentation processes (diagenesis and weathering) largely determine the quality of the fossil pollen signal at a given core site (West 1972). The following factors are likely to have influenced pollen dispersal and geological preservation at the Keteira, Lawakilevu and Udu core sites on Totoya.

5.3.1.1.1 **Pollen Dispersal**

Of the two mangrove species found on Totoya only *Excoecaria agallocha* is anemophilous. Grindrod (1985) discusses the pollen dispersal of anemophilous *Rhizophora* and notes that the pollen of this genus is found in abundance both near the parent plant and ca. 2 km upwind from parent sources. *Excoecaria agallocha* forms a closed canopy just like *Rhizophora* and this suggests that its pollen is also dispersed locally, up and downwind for some distance.

The Lawakilevu core site is within reasonably close down wind proximity to the Dravuwalu and Keteira mangrove swamps. *Excoecaria agallocha* is the most dominant species (ca. 85%) at the Dravuwalu swamp and Keteira swamp (ca. 70%). Because of this, there is a strong likelihood of wind dispersed regional pollen contamination of this species at the Lawakilevu core site. One mitigating factor is the inland ridgeline between the two sets of swamps which rises to ca. 220 m. This would act as a physical barrier to wind dispersed pollen.

The Keteira core site is also located within a 2 km upwind radius from the Dravuwalu swamp site. A physical barrier (100 m ridgeline) also separates these two sites. Finally, by comparison to the Lawakilevu and Keteira core sites, the Udu core site is completely isolated from nearby swamps which could act as sources of extra-local or regional pollen contamination.

In contrast with the anemophily of *Excoecaria agallocha, Bruguiera gymnorhiza* is well known (Tomlinson 1986) for its zoogamous pollination, inefficient wind dispersal and abundant pollen deposition, localised near the parent plant (Grindrod 1985).

The present distribution of mangal on Totoya and fossil pollen records from these sites indicates that *Bruguiera gymnorhiza* and *Excoecaria agallocha* are the only two mangrove species. Both species have quite distinctive pollen morphology. Furthermore, Grindrod (1985) has observed that *pollen grains of the mangrove taxa maintain limited distributions once deposited in sediments, indicating a low degree of redistribution by either tidal or seasonal flooding.*

The above factors indicate that the two mangrove species should be well represented by pollen dispersal processes localised within each mangrove swamp. Regional and extra-local pollen sources should be minimal (Jacobson and Bradshaw 1980). Identification of the two mangrove taxa is simplified by an absence of other mangrove species with similar pollen morphology.

5.3.1.1.2 Geological Processes

The mangal of Totoya always grows in close proximity to a small ephemeral stream channel with distinctive floodplains. The exact location of these stream channels appears to be structurally controlled and for this reason, it seems unlikely that they have shifted course in the past. A 5 metre steel peat probe was used to locate the deepest possible basin for core removal.

An important control on sediment depth was proximity to the seaward end of the swamp, the location of the deepest part of the swamp basin. At the Lawakilevu and Udu swamps this effectively placed the location of core removal in a central area of the intermixed *(Bruguiera gymnorhiza* and *Excoecaria agallocha)* forest (fig 5.9). Thankfully, it was not a rainy time of the year so the removal of cores was a relatively easy process.

A factor which may not be so favourable to reliable pollen preservation is the activity of the mud crabs which inhabit the mangrove swamps of Totoya. Evidence of bioturbation (Jacobson and Bradshaw 1980) was evident in the swamp sediments of Totoya. The mud crabs leave raised mounds above the place where they are burrowing. While it is not possible to say with any certainty that the core samples taken have not been affected by bioturbation, every effort was made to avoid this problem.

Firstly, each core was removed from a part of the swamp where surface evidence of bioturbation was minimal. Secondly, of all the cores removed from the swamp, only one half metre section showed evidence of bioturbation and this core section (and site) was rejected.

5.3.2 *Core Removal*

Ideally, the removal of a core that is intended to be used for fine resolution pollen analysis should be accomplished using a coring device like a Mackereth lake corer (Mackereth 1958, Smith 1959) or a Sonic Drill (Duval 1981). These devices are capable of removing an entire (6m) core (for subsampling) in one complete section (Green and Dolman 1988). A Mackereth corer is clearly not suitable for a barrier lagoon swamp like those found on Totoya. It is also questionable whether or not it would be possible to winch a sonic drill casing back out of the muddy sediments of a mangrove swamp.

On Totoya, the removal of core samples was accomplished with the aid of a hand operated D section and Hiller corers (Moore *et al.* 1969). Half metre core sections were removed from alternate bore holes located ca. a half metre apart. The lower metre to half metre (differing from site to site) of the core sample consisted of a transition from a clay rich firm sediment to a sloppy matrix of coarse coral, sand and clay. This lower section of the core was successfully retrieved using the Hiller corer. Apart from this, the D section produced very good core sections.

Each half metre core section was removed from the coring device and placed directly into a 40 x 40 mm square PVC core casing box (Marley Electrical Mini Trunking). Each end of the core box was carefully labelled with permanent marker pen to indicate the sample depth. The site name and core section number was also written on each box. The end of the core boxes were sealed with numerous layers of masking tape. Finally, each group of core boxes from a given site were strapped together with masking tape in order to prevent the core sections from being disturbed while in transit.

The core boxes had to be transported by outboard powered boat, ferry, truck and aircraft before being landed safely in New Zealand. Where possible, the author insisted on carrying the core boxes himself, in order to prevent the cores being disturbed. The core boxes were package in a wooden crate for shipment by aircraft from Fiji to New Zealand. In retrospect, although it probably would have required more time, it would have been safer to subsample the cores in the field.

Because it was necessary to travel to each core site by boat there was not time (in one working day) to describe the properties of the core stratigraphy in the field. This was done when the cores were unpacked at the laboratory in New Zealand. The cores are at present stored at ca. 5^{o}C in the Palynology Lab of the Massey University Geography Department, New Zealand.

5.3.3 *Subsampling of the Cores*

Unlike time series analysis (Green 1981) which requires sampling intervals of equal time duration, the only requirement of the models used in the present project was that the sampling distance was the same. Despite this fact, the *pollen counts for pairs of samples extracted from the ends of adjacent core sections ...*

were inspected (see results section) to ensure that ... *adjacent core sections differed no more than would be expected from replication of a single sample* (Green 1981).

It would be very desirable to sample continuously a core so that a continuous time data set was produced. The benefits of this type of sampling approach are graphically illustrated by Green (1981). While very desirable, this type of approach is simply not realistic (at present) because of the large amounts of time required to prepare and individually count pollen samples. Recent progress made in automating pollen counting may soon change this situation (Prof. J Flenley pers. comm.).

For the present project, a sampling strategy was used that involved repeated subsampling of each core at progressively closer sample intervals of 500 mm, 100 mm, 50 mm and finally 25 mm centres. The data set resulting from each new sampling interval was observed in order to assess the degree to which the resultant data set showed evidence of behavioural trends (Green and Dolman 1988).

The underlying assumption in this strategy is that evidence of sample trends indicates an adequate sampling interval. If the core was sampled beyond this level, it is assumed that the trend which was already evident would remain. In practice this would probably not be the case, but the differences should be small. Although this approach involves assumptions, it helps to minimise the total amount of sampling required in order to gain an indication of the long-term behaviour of the fossil pollen signal.

The Lawakilevu and Udu cores were completely subsampled with the exception of the very lowest portions of these cores composed increasingly of a sand, coral and shell matrix. A total of 51 samples was taken from the Lawakilevu core and 73 samples from the Udu core. The control site core (Keteira) was subsampled to a lesser degree (33 samples). Because the control site was only required as a between site test of behaviour, only a short section of this core was analysed (0.0 - 800 mm depth).

The subsampling procedure involved the removal of 1cm^3 units of core sediment at a final (centred) sample interval of 25 mm. This sampling procedure was accomplished with the aid of a stainless steel spatula which was used to remove the outer surface of the core sediment in order to avoid contamination. The subsample was then carefully removed from the internal section of the core.

These portions of sediment were then compressed into a 1cm^3, polypropylene centrifuge tube section which had been cut in order to measure out 1cm^3 units of sediment. In order to ensure consistent filling of the 1cm^3 tube sections, the section was placed on a new plastic petri dish so that the sediment forced in from the top of the vessel did not fall out the bottom. The top of the vessel was finally levelled off using the spatula.

These 1cm^3 units of sediment were then placed directly into a 15 ml polypropylene centrifuge tube of the same diameter as the 1cm^3 sampling vessel. The transfer process simply involved using the stainless steel spatula to press the soft sediments out of the 1cm^3 sampling vessel into each tube. The centrifuge tube was then given a screw top lid and labelled with permanent marker pen.

Sections 5.3.4 and 5.3.5 (Appendix 7) cover all of the necessary procedures involved in the laboratory preparation and counting of the core samples, the compiling of the count data and radiocarbon dating of the cores.

5.4 Results

The results section of this chapter covers five main topics in the following order: description of the core stratigraphy, dating of the core stratigraphy, description of the fossil pollen data sets, correlation of stratigraphy with fossil pollen data and finally the presentation of experimental modelling results.

The three modelling experiments conducted in this chapter are each presented as a brief introductory model formulation (the hypotheses to be tested), a statement of results (portrayal of model and field data), an interpretation of the results and finally a simulation study which introduces the model constructs tested in the next experiment.

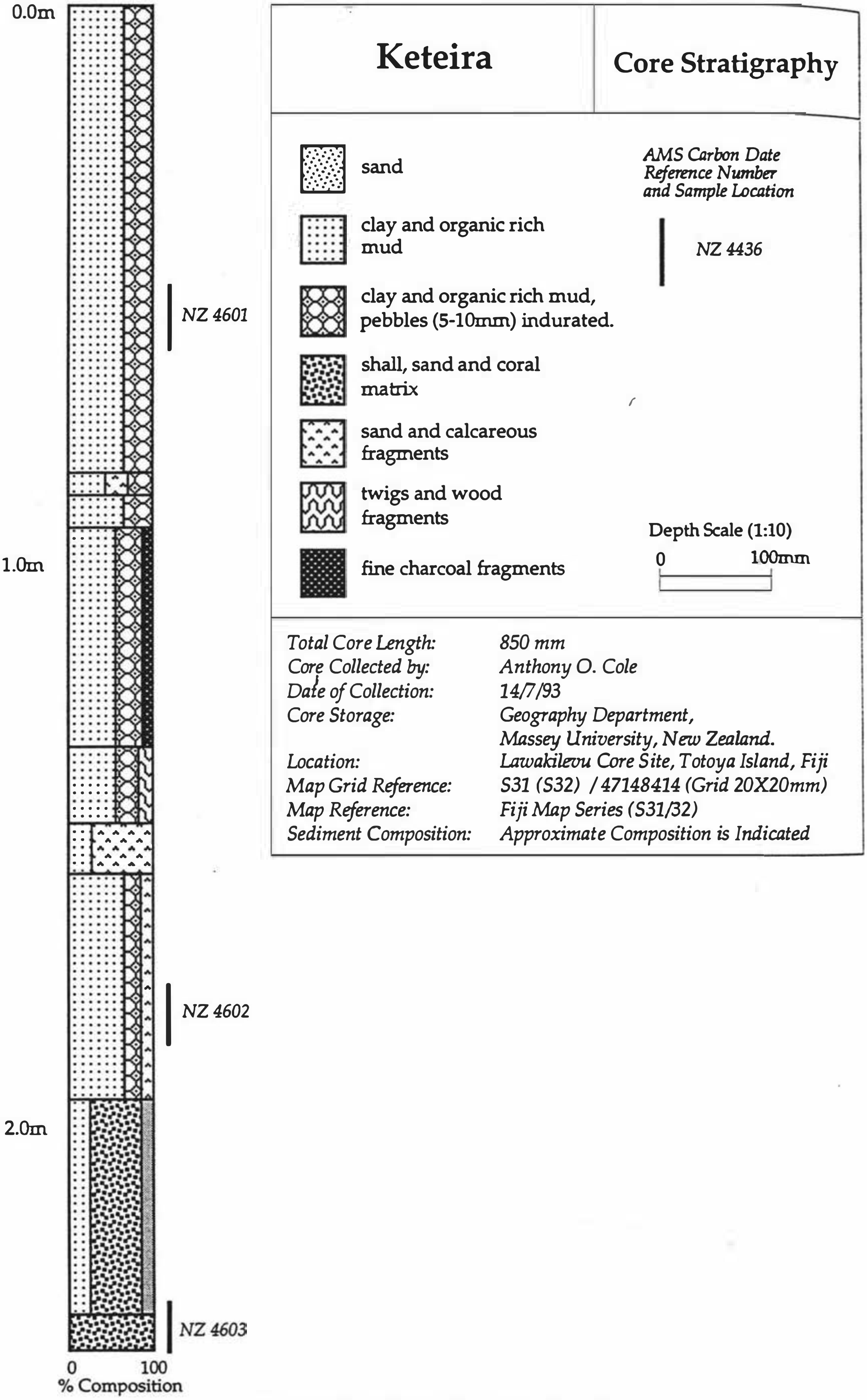
Most of the illustrations used in this section are so large (a standard A4 page) that it is not possible to insert them between individual paragraphs of text as has been done up until now in this thesis. Where possible, illustrations have been inserted between paragraphs or the pages of text that describe these figures. For the convenience of the reader, each illustration page has been labelled with a figure number as used in the earlier sections of this thesis.

5.4.1 Core Stratigraphy

Illustrations of the core stratigraphy for the three core sites (Keteira, Lawakilevu and Udu) are recorded in figures 5.10 (Keteira), 5.11 (Lawakilevu), and 5.12 (Udu). The stratigraphic column portrayed in these illustrations has two components. On the left of each column, a vertical scale (in metres) indicates the depth of the core sediments. Within the stratigraphic column, each stratigraphic unit of sediment is divided into proportions which represent approximate percentages of component parts. A depth scale, details of collection, storage and symbol key are also included with each figure.

5.4.1.1 Keteira: Core Stratigraphy

The stratigraphy of the Keteira core shows a number of interesting features which are good indicators of the history and environmental conditions of this site. Firstly, while the basal sediments of this core have a clay component they are primarily of marine origin. These sediments are located on top of an impervious pavement and doubtless represent conditions at the initiation of late Holocene sea-level regression.



Total Core Length:	*850 mm*
Core Collected by:	*Anthony O. Cole*
Date of Collection:	*14/7/93*
Core Storage:	*Geography Department,* *Massey University, New Zealand.*
Location:	*Lawakilevu Core Site, Totoya Island, Fiji*
Map Grid Reference:	*S31 (S32) / 47148414 (Grid 20X20mm)*
Map Reference:	*Fiji Map Series (S31/32)*
Sediment Composition:	*Approximate Composition is Indicated*

Fig 5.10 The Keteira Core Stratigraphy

Secondly, the dominant component of the remainder of the core is clay and organic rich mud. At present, it is only possible to speculate as to the causes of this sediment input. Because it is carried to the site of deposition by hydrological processes the sediment is doubtless derived from the watershed behind the swamp and may indicate steady background erosional processes, slope instability triggered by storm events or surface erosion caused by deforestation (burning) of the inland forest.

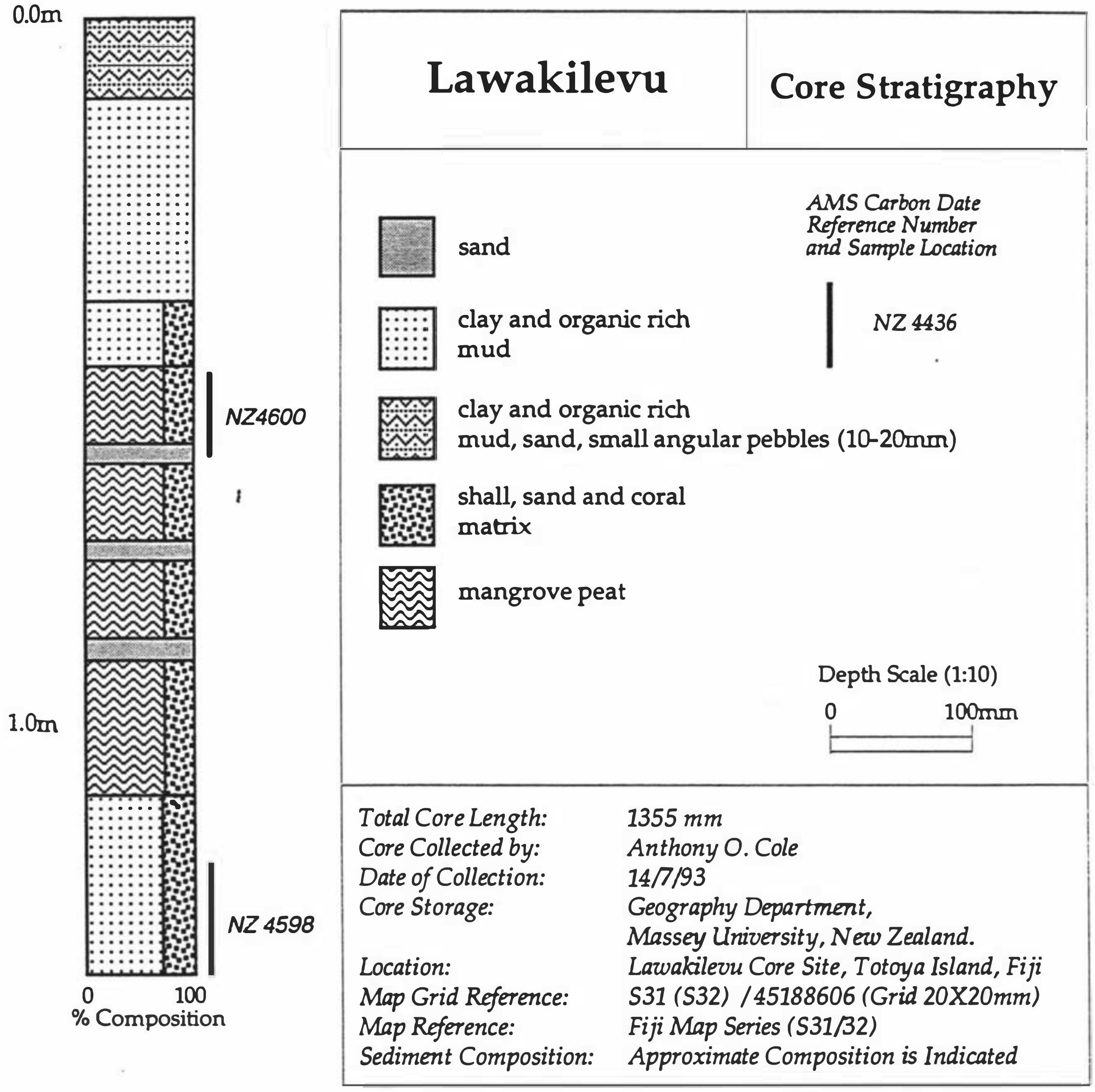


Fig 5.11 The Lawakilevu Core Stratigraphy

Thirdly, the fluvial nature of this environment is indicated by the presence of small pebbles (5-10 mm). Fourthly, the concentration of charcoal fragments in the unit at ca. 1.0 m are indicative of the charcoal fragments that are present in varying concentrations throughout the samples taken from this core. The watershed behind this swamp is today covered in Talasiga (grassland vegetation).

Finally, disturbance events are indicated by the non-uniformity of small units at ca. 1.5m and just above 1 m. Also, this is one of the longest cores (with the exception of Yaro Bay) recovered from the island.

5.4.1.2 Lawakilevu: Core Stratigraphy

The Lawakilevu core is one of the shortest cores recovered from the island and like the Keteira core shows a number of interesting features.

Firstly, the basal sediments are of a very similar composition to those found at the Keteira core site and doubtless indicate the beginning of sea-level regression and coastal progradation for this core site. Secondly, above the basal sediments is a large unit of mangrove peat intermixed with ca. 20% fine grain sand, shell and coral material. This unit indicates the existence of an established mangrove forest which experienced occasional sea-water intrusion. The peat unit has three distinctive non-conformities (composed of sand) which are probably related to storm events.

Thirdly, the stratigraphic unit above the peat grades into a solid unit of clay and organic rich mud. The surface unit is composed of the same organic clay rich sediment with the addition of sand and small angular pebbles (10-20 mm). The watershed behind this swamp is composed of a clay rich surface soil on top of an aggregate base. Apart from an area just behind the swamp that is now used for gardening by some of the people of near by Dravuwalu village, the area is totally covered in Talasiga.

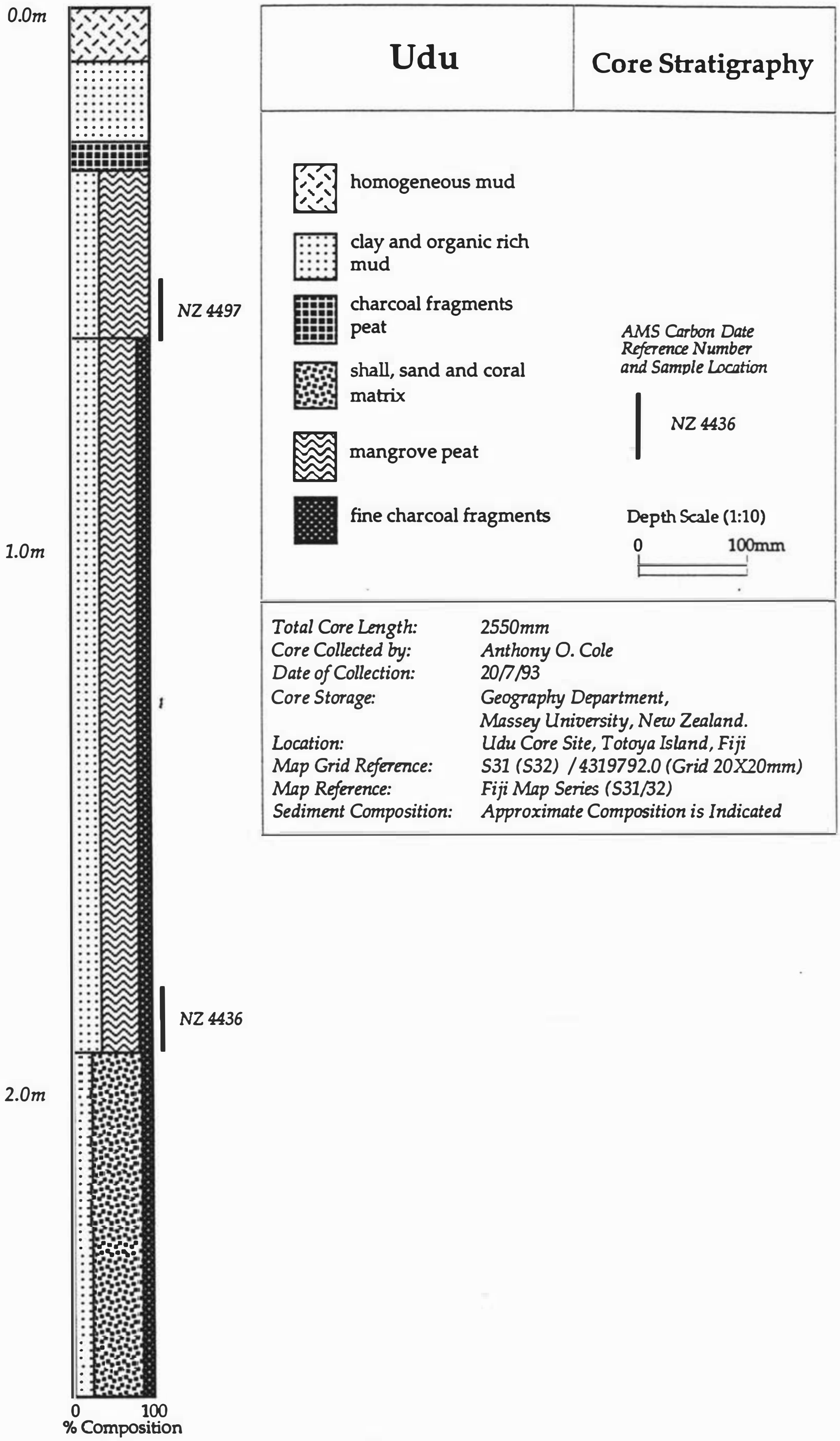
5.4.1.3 Udu: Core Stratigraphy

The Udu core stratigraphy has similar features to the Lawakilevu core: basal sediments dominated by marine deposits, an intermediate unit of clay rich peat with charcoal fragments grading away to surface units of clay and organic mud to homogeneous mud (fig 5.12). Finally, the watershed directly behind this swamp is still covered in inland forest which shows signs of disturbance (deforested areas, compositional variation and the presence of coconut trees) but despite this, is still largely intact.

5.4.1.4 Summary and Discussion

The three core sites discussed above may be divided into two distinct groups based on clear stratigraphic differences. Keteira is the only member of the first group. At this site, there is an absence of mangrove peat formation and the presence of small pebbles throughout the length of the core above the 2 m depth mark. The presence of organic mud and clay rich sediments indicates that this site has a history of pronounced fluvial activity and flood disturbance.

The site is located toward a central coastal area of the island's inner lagoon. It could be that the swamps in this vicinity are a geomorphological response to the annual heavy rainfalls that the prevailing Southeasterly weather patterns bring to this part of the island. By contrast, both the Lawakilevu and Udu core sites are located on the outside of the island.



Total Core Length:	*2550mm*
Core Collected by:	*Anthony O. Cole*
Date of Collection:	*20/7/93*
Core Storage:	*Geography Department,* *Massey University, New Zealand.*
Location:	*Udu Core Site, Totoya Island, Fiji*
Map Grid Reference:	*S31 (S32) / 4319792.0 (Grid 20X20mm)*
Map Reference:	*Fiji Map Series (S31/32)*
Sediment Composition:	*Approximate Composition is Indicated*

Fig 5.12 The Udu Core Stratigraphy

Both of these locations would have been sheltered from the full impact of Southeasterly storm fronts. Furthermore, these sites are located in the intermediate (Udu) to dry (Lawakilevu) rainfall regions of the island.

Shelter from prevailing storm fronts may be a factor which distinguishes the second group of core sites (Lawakilevu and Udu). By contrast to Keteira, both of these sites have an intermediate stratigraphic unit of peat with lower clay composition than the Keteira core site. The top units of these two sites are more clay rich indicating changed environmental and geomorphological conditions in more recent times. The dating of these core sites based on AMS dates is considered in the next section.

5.4.2 *The AMS Dating of Core Sediments*

Dating of the core sediments forms an important part of fossil pollen accumulation rate (PAR) calculations. Once again, it would be very desirable to have many radiocarbon dates to support a stratigraphic chronology. However, the present expense of AMS dates in New Zealand ($912.50 NZ per sample) prohibits such freedom. When selecting the samples for radiocarbon dating from the Udu, Keteira and Lawakilevu cores, generous portions of sample were submitted in the hope that they might contain enough carbon to make them suitable for gas counter dating method ($450 NZ per sample). Unfortunately, none of the samples submitted were suitable for gas counter dating and all had to be dated using the AMS (Accelerated Mass Spectrometry) method.

In the following section, plots of stratigraphic depth verses radiocarbon age are used to provide some indication of possible changes in sedimentation rates for the three Totoya cores (Udu, Lawakilevu, Keteira). These data form the basis of PAR calculations in the modelling work.

Site Reference	Depth (mm)	Conventional C 14 age (years B. P.)	Calibrated age (years B.P.)	95 % Confidence Calibrated (CAL. yrs B. P.)	Laboratory Reference NZA
Udu 001	500-610	165 ± 67	139	279 - (-4)	4497
Udu 002	1800-1920	792 ± 67	670	786 - 554	4436
Lawak 006	500-620	154 ± 70	139	279 - (-4)	4600
Lawak 007	1230-1355	421 ± 79	411	535 - 288	4598
Ketei 008	500-610	588 ± 77	562	663 - 461	4601
Ketei 009	1750-1850	1010 ± 80	1045	1054 - 1036	4602
Ketei 010	2350-2460	1967 ± 89	1860	2100 - 1621	4603

Table 5.4 A summary table of AMS CAL. age determinations for samples from the Keteira, Lawakilevu and Udu core sites.

It is convention to plot stratigraphic depth on the x axis and radiocarbon age on the y axis (since age is the dependent variable). Error bars are used to indicate both the total depth over which the date applies and 95% confidence intervals for the average, calibrated AMS dates which have been used. It is also assumed that the surface samples from these sites represent the date of core collection. A summary of the AMS dating results has been listed in Table 5.4.

The site reference number (Table 5.4) refers to the sample reference given by the author upon submission to the New Zealand Rafter Laboratory. The conventional and average calibrated (95% confidence) CAL. ages are given in years B. P. Finally the Rafter Laboratory reference number is quoted in the final column. These reference numbers are also quoted on various illustrations given in this chapter.

5.4.2.1 Keteira: AMS Dates

The three AMS dates for the Keteira core were all based on organic mud samples. As can be seen from fig 5.13 there is reasonable temporal agreement between the three dates. In interpreting these plots, it is good to remember that a positive linear relationship between stratigraphic depth and calibrated (CAL.) age determinations would indicate a constant rate of sedimentation in the core over the geomorphological history of the swamp.

By contrast, fig 5.13 shows three periods of different sedimentation rates based on averaged and calibrated AMS determinations. Rates of change can be calculated from this data by calculating an estimate of the total sedimentation for a period (i.e. between NZA 4601 - NZA 4602) and dividing this by an estimate of the total calibrated time required to accomplish this interval of sedimentation. The determination of these rates of change is very useful for between-core-site comparisons. These calculations are given for the Keteira core in Table 5.5.

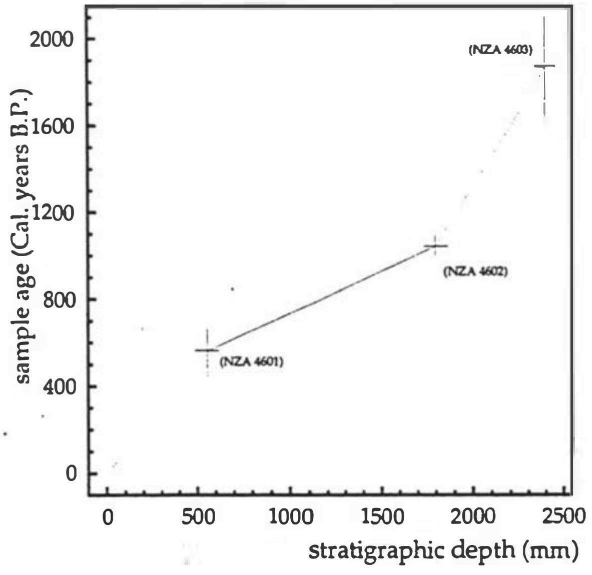


Fig 5.13 The results of AMS dating of mangrove mud samples taken from the Keteira core.

The Keteira core was subsampled from 0.0 mm - 800 mm, a time period which just catches the tail end of the faster sedimentation rate of 2.5 mm CAL. year $^{-1}$ (see Table 5.5).

Rafter lab. Reference NZA	Depth Interval (mm)	Total Depth (mm)	Time Period CAL. yrs. B.P.	Total Time CAL. yrs	Sedimentation Rate (mm/CAL. yr)
NZA 4601	0 - 555	555	0 - 562	562	0.98 mm/ yr
NZA 4601-4602	555 -1800	1245	562 - 1045	483	2.5 mm/ yr
NZA 4602-4603	1800 - 2405	605	1045 - 1860	815	0.74 mm/ yr

Table 5.5 Calculation of estimated sedimentation rates for the three different depth intervals represented by AMS dates based on mud samples from the Keteira core.

5.4.2.2 Lawakilevu: AMS Dates

One of the AMS dates for the Lawakilevu core was based on organic mud (NZA 4600) while the other date was based on shell fragments from the basal sediments of the core (NZA 4598). Once again, it is evident that there is very reasonable temporal agreement between the two dates (see fig 5.14).

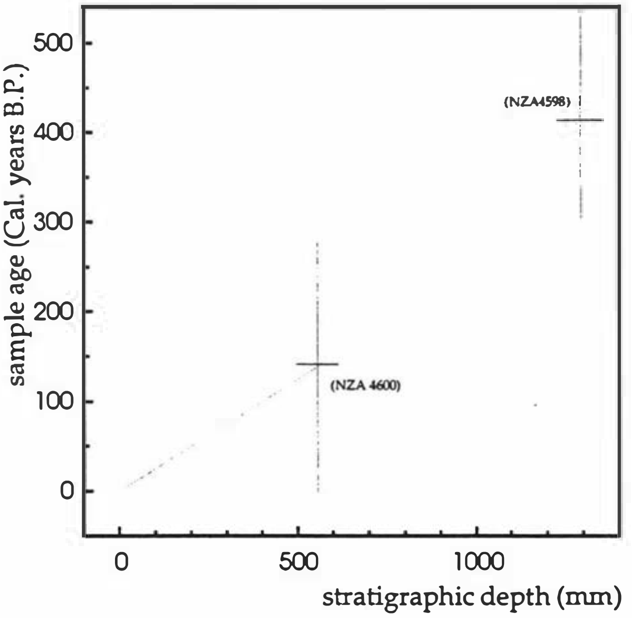


Fig 5.14 The results of AMS/CAL. dating of mangrove mud and shell samples taken from the Lawakilevu core.

From fig 5.14 it is evident that the 95% confidence intervals of these calibrated AMS dates are much wider than for the previous site. Once again, an average, calibrated date has been used (fig 5.14). The rates of sedimentation for the two depth intervals covered by these AMS dates are listed in Table 5.6. The Lawakilevu core was subsampled at 25 mm centred intervals from 0.0 mm to

1250 mm, a depth interval which is influenced by the two different rates of sedimentation.

Rafter lab. Reference NZA	Depth Interval (mm)	Total Depth (mm)	Time Period CAL. yrs. B.P.	Total Time CAL. yrs	Sedimentation Rate (mm/CAL. yr)
NZA 4600	0 - 560	560	0 - 139	139	4.0 mm/ yr
NZA 4600-4598	560 - 1292	732	139 - 411	272	2.7 mm/ yr

Table 5.6 Calculation of sedimentation rates for the two different depth intervals represented by AMS dates and based on mud and shell samples from the Lawakilevu core.

It is interesting to note from Table 5.6 that the estimated sedimentation rate for the depth interval of 560 mm - 1292 mm (ca. 139 - 411 CAL. years B.P.) is similar to that estimated for the depth interval of 555 mm - 1800 mm (ca. 562 - 1045 CAL. years B.P.) on the Keteira core. If the time periods covered by these depths had also matched, this might have suggested the existence of regional processes driving sedimentation. However, based on the dates quoted above, the processes driving sedimentation at these two sites are clearly out of time phase (even considering the 95% confidence intervals at the Lawakilevu site.

5.4.2.3 *Udu: AMS Dates*

Both of the AMS dates for the Udu core are based on organic mud samples. Once again, it is evident that there is very reasonable temporal agreement between the two dates (fig 15.5). The sedimentation rates for the depth intervals covered by these AMS dates are given in Table 5.7.

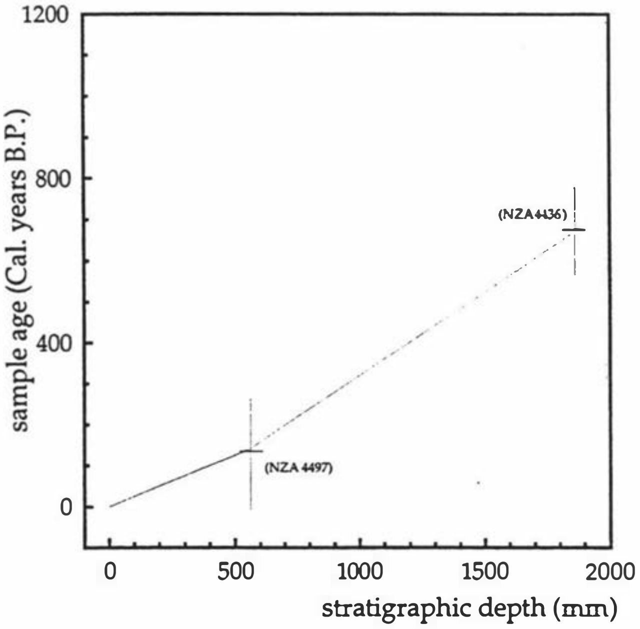


Fig 5.15 The results of AMS dating of mangrove mud samples taken m the Udu core.

The Udu core was subsampled from 0.0 mm to 1800 mm. This is the longest data set from Totoya that has been used for modelling. Furthermore, this data set covers the sedimentary depth and time period covered by the two AMS dates of fig 15.5.

Rafter lab. Reference NZA	Depth Interval (mm)	Total Depth (mm)	Time Period CAL. yrs. B.P.	Total Time CAL. yrs	Sedimentation Rate (mm/CAL. yr)
NZA 4497	0 - 555	555	0 - 139	139	3.97 mm/ yr
NZA 4497-4436	555 - 1860	1305	139 - 670	530	2.45 mm/ yr

Table 5.7 Calculation of sedimentation rates for the two depth intervals represented by AMS dates based on mud samples from the Udu core.

5.4.2.4 Summary and Discussion

The purpose of this section has been to present the results of the AMS dates that have been used to construct a time frame for the sedimentation of the three cores used in this modelling research. Based on the visual plots presented in this section it is evident that there is very reasonable temporal agreement between the depth samples dated by AMS and the radiocarbon ages they represent (see Table 5.7).

It is also interesting to compare the estimated sedimentation rates for the sedimentary depth intervals demarcated by the various AMS dates. A summary is presented in Table 5.8.

Site Name	Depth Interval (mm)	Total Depth (mm)	Time Period CAL. yrs. B.P.	Total Time CAL. yrs	Sedimentation Rate (mm/CAL. yr)
Udu	0 - 555	555	0 - 139	139	3.97
Udu	555 - 1860	1305	139 - 670	530	2.45
Lawakilevu	0 - 560	560	0 - 139	139	4.0
Lawakilevu	560 - 1292	732	139 - 411	272	2.7
Keteira	0 - 555	555	0 - 562	562	0.98
Keteira	555 -1800	1245	562 - 1045	483	2.5
Keteira	1800 - 2405	605	1045 - 1860	815	0.74

Table 5.8 A summary of estimated sedimentation rates for the Keteira, Lawakilevu and Udu core sites. Notice the similarity in AMS sample depth, CAL. age determinations and consequent estimated sedimentation rates for the Udu and Lawakilevu cores.

There are a couple of interesting trends in Table 5.7. Firstly, the estimated sedimentation rates for the three core sites are remarkably similar. This is especially the case between the Lawakilevu and Udu core sites. At these sites there is also very good correspondence between AMS samples and the CAL. ages they represent. For example, the Udu AMS sample of 555 mm has an age of 139 CAL. years while this depth interval (0 - 555 mm) has an estimated sedimentation rate of 3.97 mm CAL. year $^{-1}$. These figures are very close to the Lawakilevu AMS sample of 610 mm which also has an age of 139 CAL. years while this depth interval (0 - 610 mm) has an estimated sedimentation rate of 4.0 mm CAL. year $^{-1}$.

A second interesting trend is the contrast between the Lawakilevu and Udu core sites which are quite similar and the Keteira core site which is distinctly different. For example, the first AMS sample at Keteira of 555 mm has an age of 562 CAL. years B.P. while at the Udu site it represents an age of 139 CAL. years B.P. Furthermore, the sedimentation rates between the two sites are either different or the similarity applies to a different time period.

In summary, the dating results presented above appear to be internally consistent. Many more radiocarbon dates would be needed in order to permit a more detailed evaluation of between site sedimentation rates. Where there are differences, such as between the Keteira and Lawakilevu/Udu core sites, these are probably explainable by spatial, physiographic and environmental factors like inner and outer island locations, windward (wetter) and leeward (drier) environments and the influence of prevailing Northeasterly weather *etc*. This line of discussion raises an interesting question. Are the stratigraphic, sedimentary and temporal similarities between the Udu and Lawakilevu core sites environmentally controlled? More on this question later.

5.4.3 The Data Sets

The plots used to portray the fossil pollen and model data presented in this chapter have been systematised for the convenience of the reader. Firstly, each figure consists of three plots which are identifiable by the bracketed letters (a), (b), and (c) in the lower left hand corner of each plot. Secondly, the x axis (time measured in CAL. years B.P.) has been arranged so that the reader may interpret the behaviour of the data by reading from left to right (as in reading a book). The behaviour of the data (or system) begins at the oldest (negative) carbon age on the x axis and progresses toward time zero which is assumed to be the date of core collection.

Thirdly, the scale of the data which is being portrayed is indicated at the lower left hand corner of each plot. Fourthly, the dimensions of the data being portrayed are indicated by the labels given to the x and y axes. Finally, small black (filled) and white (unfilled) circles have been used in order to distinguish between fossil pollen and model data, or between different species of fossil pollen data. A circle legend is provided on the top axis of every plot and is used to define exactly what each circle represents.

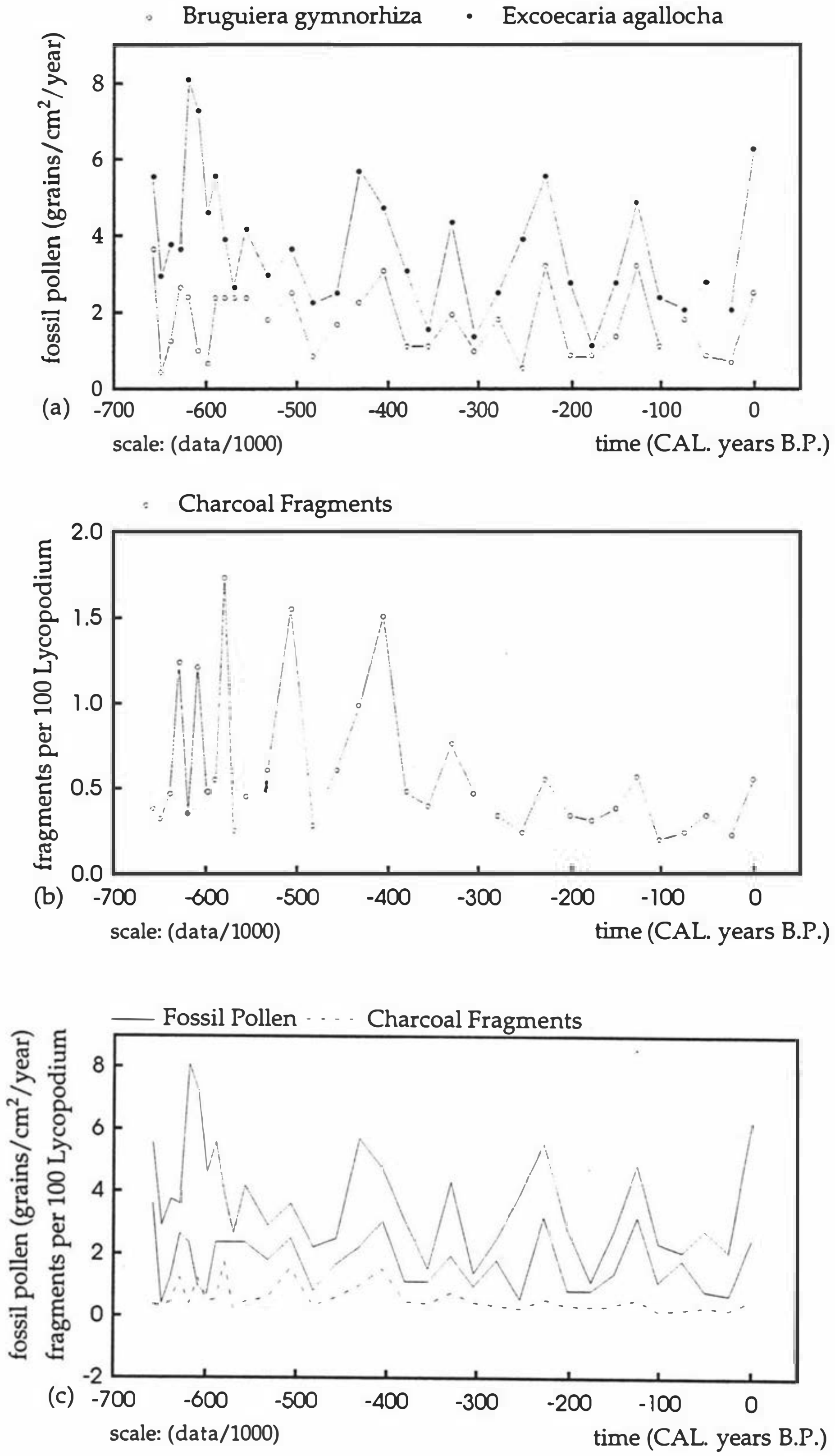


Fig 5.16 The Keteira core site - mangrove and charcoal fragment data.

The third plot (c) of some figures is commonly used to portray the residual ror about a central zero axis. Different types of line have been used to fferentiate between different species in these plots (circles tended to clutter the ɔt). A line legend is also provided on the top axis of these plots.

5.4.3.1 The Keteira Data Set

The Keteira data set covers a CAL. time period of ca 650 years B.P. During this time the behaviour of the two mangrove species (fig 5.16) is best described as variable and density vague. Although individual rises and falls in the data are often defined by 2 to 4 data points in a short trend, the long-term behaviour of the two species appears to follow no obvious trend. It is also interesting to note that the two mangrove species appear to be in phase in what might best be described as an irregular cycle.

The charcoal data (fig 5.16 b) has been portrayed as a continuous signal. In reality this is not the case. This approach is used to emphasize the similarity between the behaviour of the pollen signal and the rises and falls in charcoal fragment concentration. Furthermore, many of the peaks in charcoal concentration are correlated with peaks in the mangrove signal. Charcoal and mangrove data sets are portrayed together in fig 5.16 c where the peak to peak correlation between the three sites is still evident, but less distinct due to differences in scale between the two data sets.

5.4.3.2 The Lawakilevu Data Set

The Lawakilevu data set covers a CAL. time period of ca 400 years B.P. The mangrove data (fig 5.17 a) at this site shows distinct differences between the two species, unlike the Keteira data. Firstly, *Bruguiera gymnorhiza* remains at values close to zero for much of the history of this site. It also shows evidence of a strong behavioural response in more recent times (the last 75 -100 CAL. years B.P.). Secondly, *Excoecaria agallocha* is by comparison much more abundant and shows behavioural evidence of three distinct rises and two falls in concentration.

It is interesting to note that both major expansions of *Excoecaria agallocha* have lasted for ca. 100 CAL. years. Expansions of both mangrove species at the Keteira core site have also lasted for about the same time period (100 CAL. year cycles). Returning to Lawakilevu (fig 5.17 b), the charcoal data shows less obvious behavioural correlation with the mangrove data. In fig 5.17 c the mangrove and charcoal data sets are portrayed together and a distinct correlation between the first main rise in charcoal concentration and the fossil pollen of *Excoecaria agallocha* can now be seen (400 - 300 CAL. years B.P.). Correlation between charcoal and mangrove data over the rest of the data set appears to be poor.

5.4.3.3 The Udu Data Set

The Udu data set covers a CAL. time period of ca 400 years B.P (fig 5.18). As at the Lawakilevu core site, two important trends are obvious. Firstly, *Bruguiera gymnorhiza* hovers around zero for much of the time period covered by the core (fig 5.18 a). Secondly, *Excoecaria agallocha* shows evidence of a number of population expansions and contractions over ca. 100 CAL. year intervals.

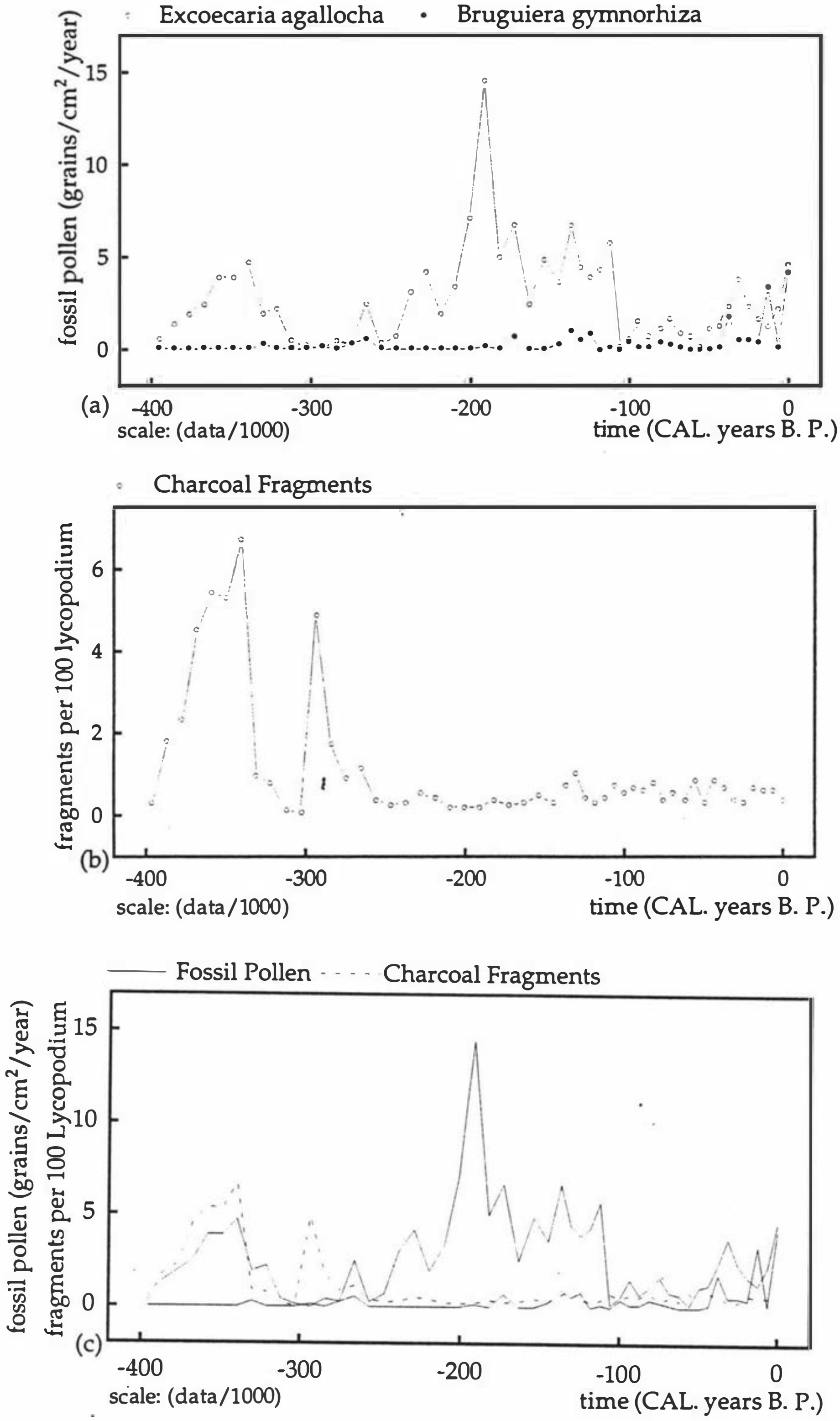


Fig 5.17 The Lawakilevu core site - mangrove and charcoal fragment data.

Both species show evidence of a strong population expansion in recent times (75 - 100 years B.P.). Thirdly, the overall behaviour of the two mangrove species is once again, density vague. The system shows no long-term tendency toward a favoured equilibrium value of any kind. It definitely rises to high densities, but does so only to fall away once again. Furthermore, at low density, both populations appear to be capable of avoiding localised extinction. These are the characteristics of a density vague population.

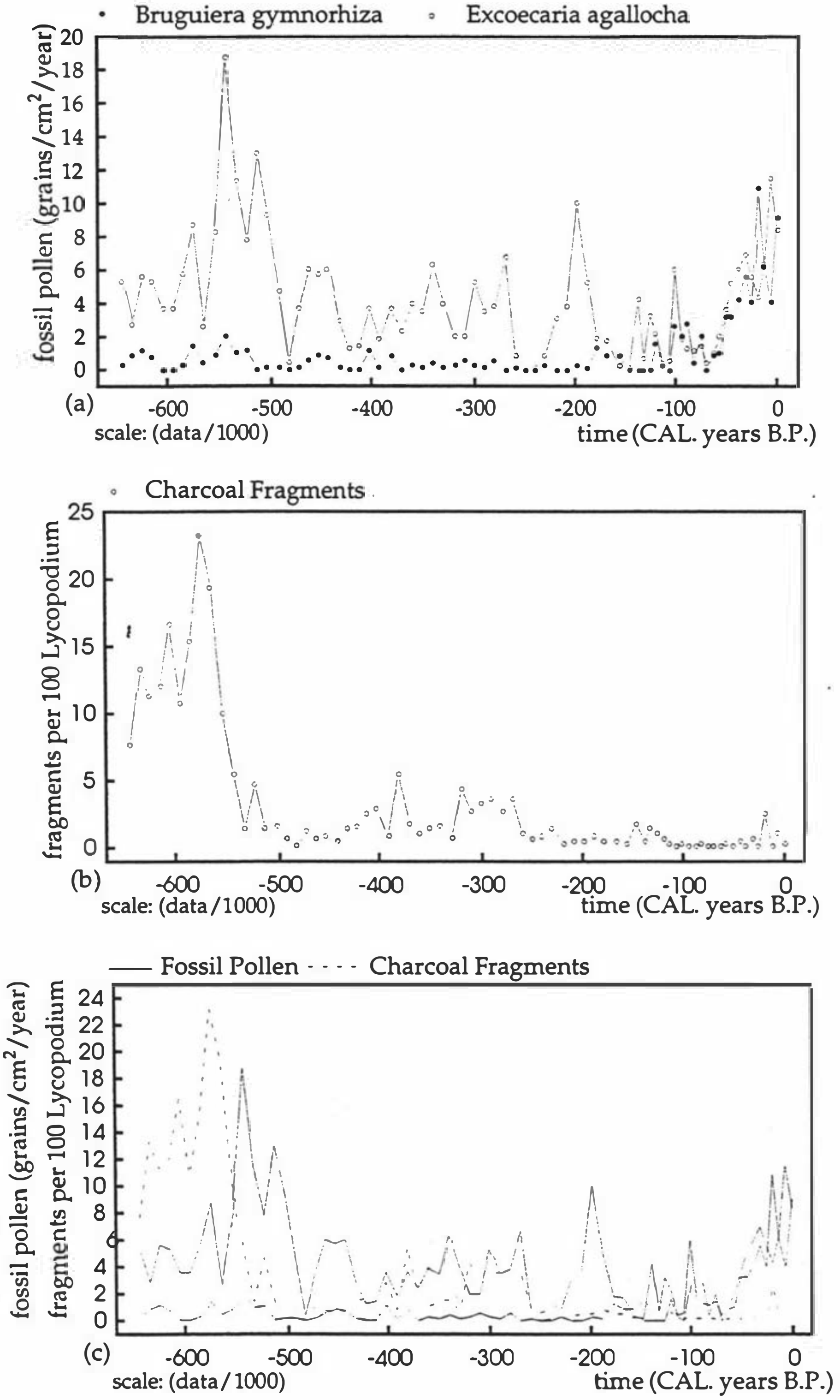


Fig 5.18 The Udu core site - mangrove and charcoal fragment data.

In fig 5.18 b the charcoal signal shows slightly stronger variance than at the previous Lawakilevu core site. In the composite plot of fig 5.18 c, some correlation can be observed between the behaviour of the charcoal signal and that of the mangrove fossil pollen data.

5.4.4 Stratigraphy and Fossil Pollen Data Correlated

In subsampling mangrove swamp deposits the palynologist is ever aware of the fact that non-uniformity in the sediments of a given core may be correlated with sudden changes in the fossil pollen signal. If this is the case, it may suggest that the behaviour of the system at this point was being influenced by geological processes. A further problem arises as a result of core collection using a short half metre collection device such as a standard D section or Hiller corer. If the ends of the half metre sections are not truly representative of the fossil pollen signal at that depth, then large variance between the samples at the ends of core may be experienced.

A simple way to test for these two problems is to plot the fossil pollen data against a graphic representation of the core stratigraphy for each site. In these illustrations, dotted lines have been used to indicate the location of half metre core boundaries.

5.4.4.1 Lawakilevu: Core Stratigraphy and Pollen Data

The Lawakilevu core has been subsampled over its entire length (fig 5.19). The stratigraphy of this core includes a number of non-uniform sedimentary units. From this portrayal it is evident that none of the major changes in pollen concentration is related to these non-uniform stratigraphic units. If a relationship did exist, then it would be expected that the pollen signal would change suddenly at the boundary of such a change. While there is variance in the data, it does not appear to be related to the core stratigraphy.

Two 500 mm core boundaries are indicated and the changes in fossil pollen data at these points are as would be expected.

5.4.4.2 Keteira: Core Stratigraphy and Pollen Data

In fig 5.20 it can be seen that the Keteira core has been subsampled over the entire length of a very uniform sedimentary unit near the top of the core (800 mm - 0.0 mm). There is only one 500 mm core boundary and the fossil pollen samples at this boundary are values that would normally be expected (*i.e.* there is not sudden change in value).

5.4.4.3 Udu: Core Stratigraphy and Pollen Data

The Udu core has also been subsampled over all of its length (fig 5.21). In this case, there does appear to be a correlation between the stratigraphic unit of ca. 280 mm - 600 mm and the fossil pollen data. The fossil pollen signal is at a very low value at the beginning of this unit and appears to return to a very low value at the end of it. It seems very likely that this correlation is coincidental. Firstly, the fossil pollen signal for this core is a consistent series of rises and falls lasting ca. 100 CAL. years based on fig 5.18 a. With this one exception, all of the other rises and falls are clearly independent of the stratigraphy. Secondly, the change in stratigraphy of the unit at 600 mm - 280 mm, compared to the unit which precedes it (1900 mm - 600 mm), only involves the loss of visible particles of charcoal fragments (clay and peat components remain). Three 500 mm core boundaries are indicated, the pollen values of which appear as would normally be expected.

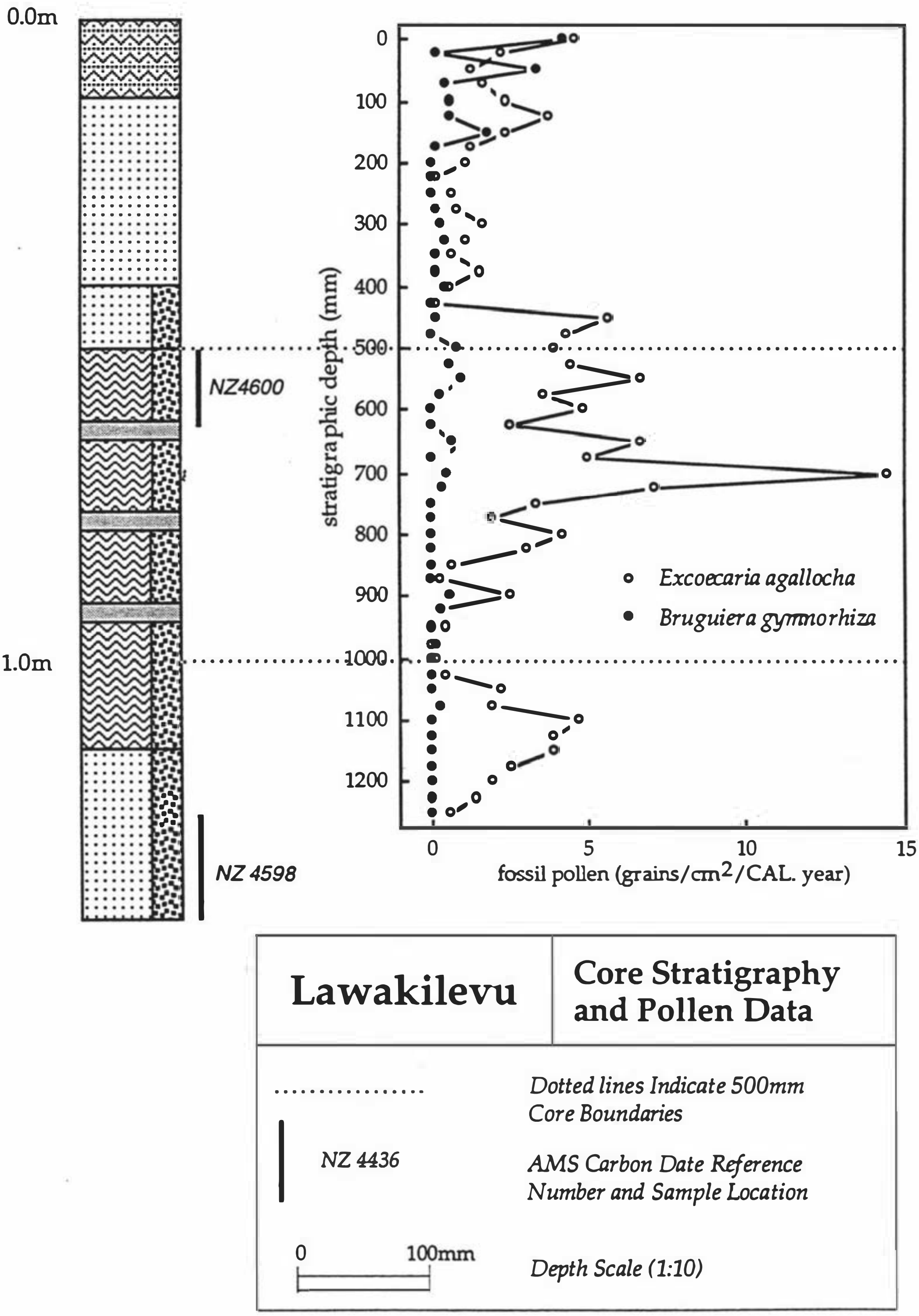


Fig 5.19 The Lawakilevu core stratigraphy and mangrove data.

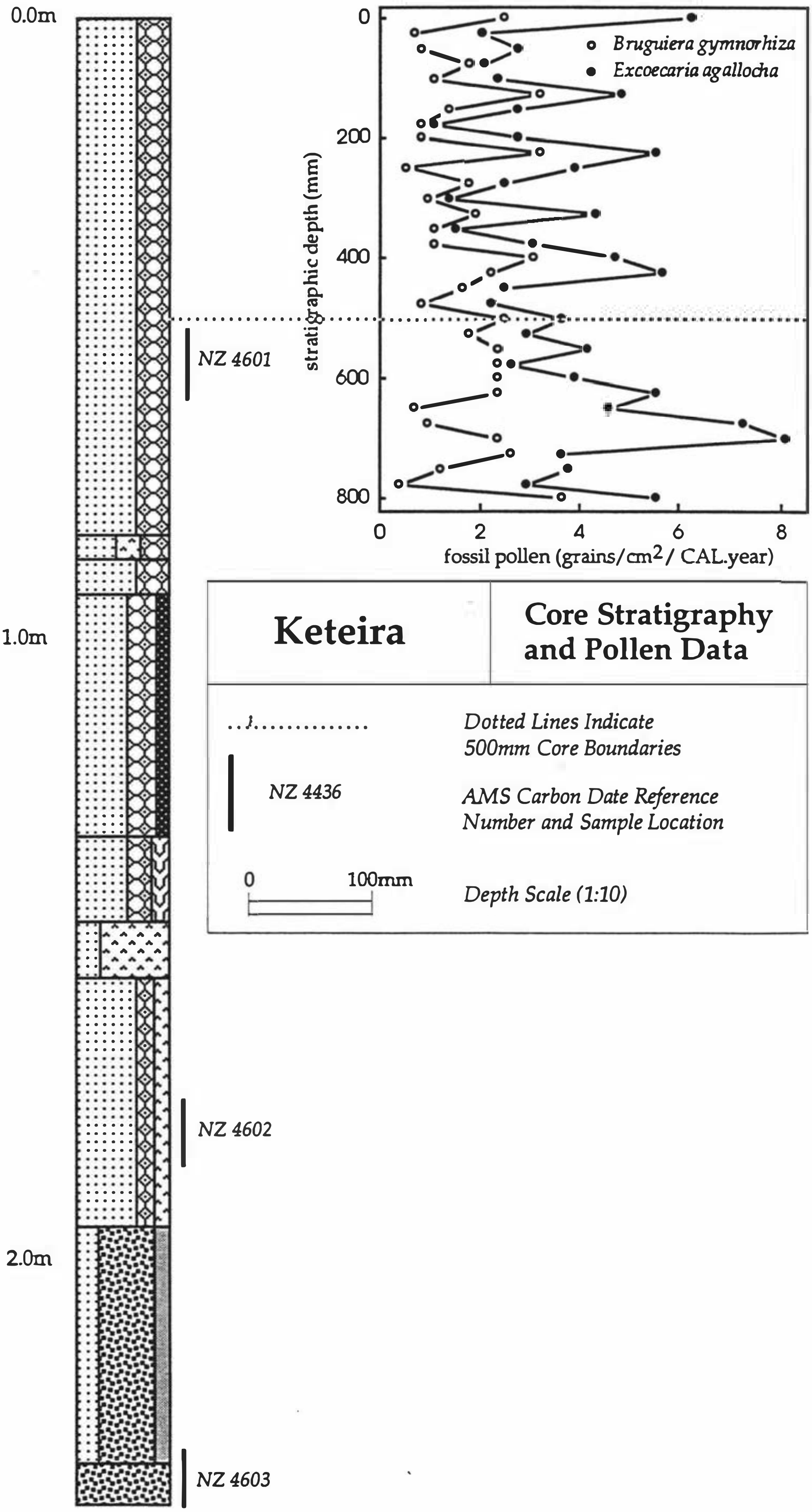


Fig 5.20 The Keteira core stratigraphy and mangrove data.

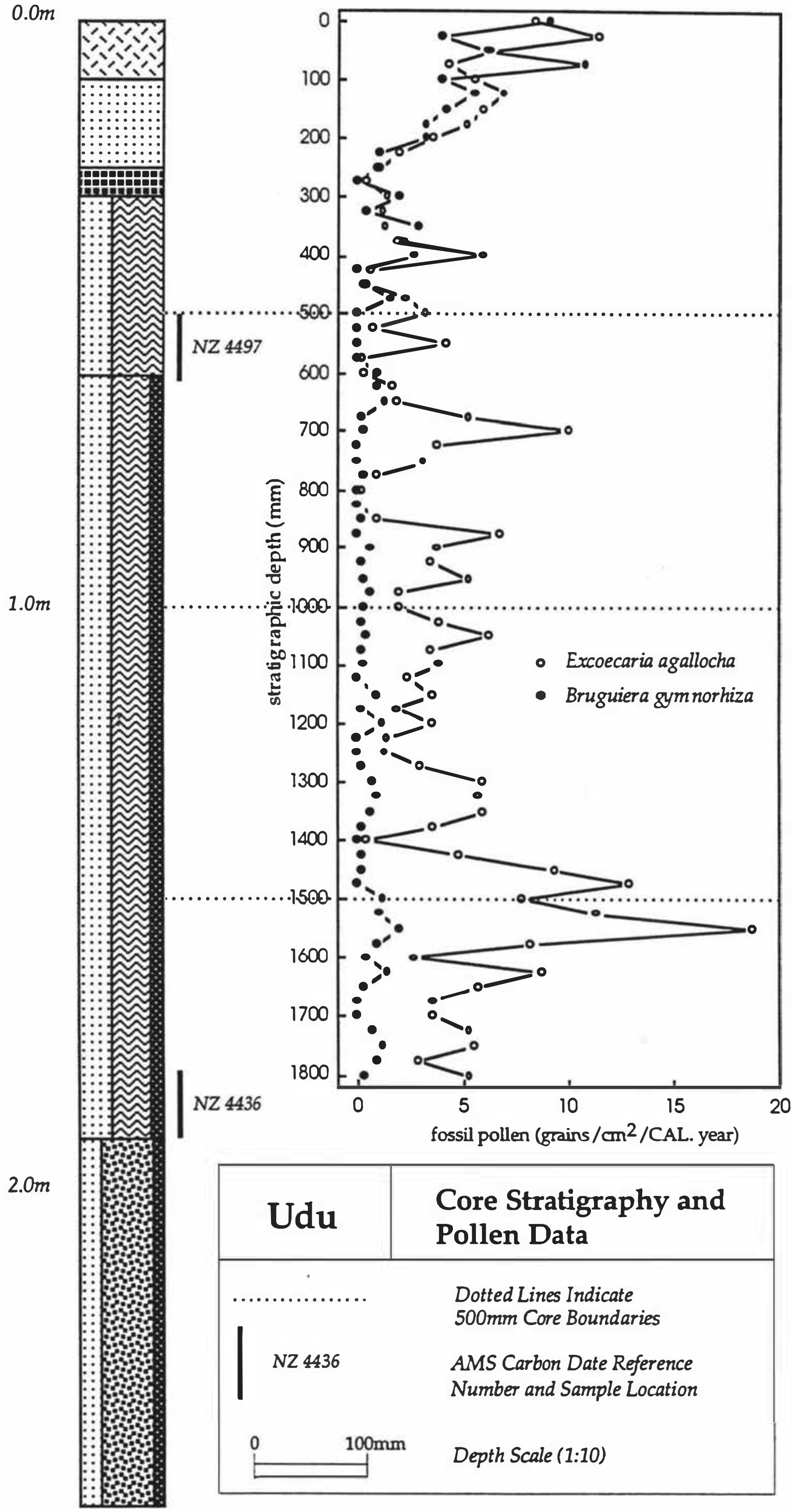


Fig 5.20a The Udu core stratigraphy and mangrove data.

5.4.5 Summary

In this section, the core stratigraphy, its radiocarbon dating, the fossil pollen and charcoal fragment data sets, correlation test of the same and fossil pollen data have all been presented. The quality and internal consistency of the fossil pollen data may be partly evaluated, based on these various lines of evidence.

Firstly, the core stratigraphy provides evidence of a transition from marine to terrestrial dominated sediments, indicative of late Holocene sea-level change. Secondly, the AMS dates from these sediments fall within a sea-level regression time frame, as would be expected. Thirdly, the AMS dates from these cores are internally consistent between the three sites. The main difference in AMS sample depth and CAL. age is between the Keteira and Udu/Lawakilevu core sites. This difference is probably explained by spatial, physiographic and differing environmental conditions between the two sets of sites.

Fourthly, estimated sedimentation rates have been calculated. These rates reflect the limitations of averaged, calibrated AMS dates. Despite this fact, the sedimentation rates are high, but reasonable and internally consistent between the three sites. An interesting question from this line of inquiry regards the causes of strong similarity in sedimentation rates between the Udu and Lawakilevu core sites. The most simple (parsimonious) explanation for this similarity is that environmental processes are the causal mechanism.

This explanation is not unreasonable, but does not account for existence of definite peaks and background variance in the charcoal fragment concentrations found in these cores. Inland forest burning has often been invoked to account for increased erosion rates accompanied with stratigraphic evidence of charcoal fragment concentrations. In this context, the Lawakilevu and Udu core sites may simply have been occupied and/or disturbed by Polynesian settlers during similar time periods.

Fifthly, the behaviour of the mangrove fossil pollen data at these sites appears to be independent of subsampling procedure. Also, the behaviour of the two mangrove species is poorly correlated with the core stratigraphy as would be hoped.

Finally, the general properties of the fossil pollen data sets have been briefly discussed. It should now be evident that these systems are density-vague and this raises many questions concerning the causes of the trends and variance that is evident in this data.

5.4.5 *Experiment One - Keteira Data*

The presentation of results in the following section includes: a statement of the hypotheses and models being tested, the experimental results, an interpretation of the results and reformulation of working hypotheses. The MatLab script files used in simulation and optimisation trials of the equations tested in experiments one to three are recorded in Appendix 10 and 11.

5.4.5.1 Hypotheses

Two alternative hypotheses have been proposed in order to explain the zonation and intermixed structure of mangal at the Keteira, Lawakilevu and Udu core sites on Totoya.

In experiment one, it is predicted that the Keteira core site will show behavioural evidence of non-interactive population rises and falls. In this model of community organisation the two mangrove species are considered as opportunistic strategists which take spatial advantage of the process of coastal plain construction on Totoya, resulting from late Holocene sea-level regression and inland forest clearance (*i.e.* mangrove succession theory).

In experiments two and three it is predicted that the Udu and Lawakilevu core sites will show behavioural evidence of long-term, continuous, interactive population growth processes. In this second model of community organisation, the two mangrove species are considered as competitors in a physically limited and changing environment (mangrove equilibrium theory).

The above predictions will be tested using a continuous interactive model of community organisation (the logistic (46) and coupled logistic (50 a, b) equations) and a discrete model of community organisation (the discrete logistic (48) and discrete coupled logistic (52 a, b)).

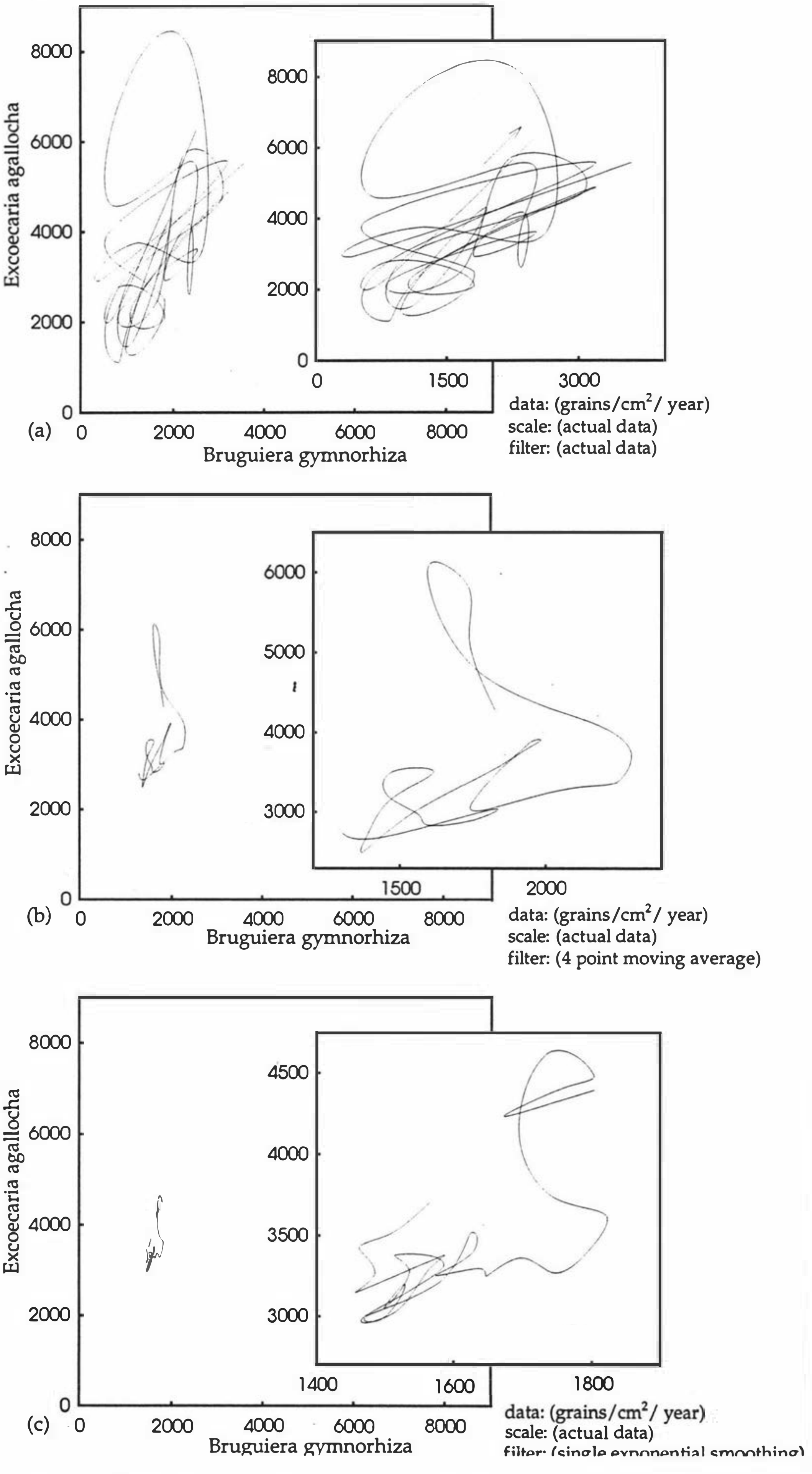
While the above results are predicted *a priori* for experiments one to three, it is important to attempt to find contradictory evidence and not to assume that a test need only be applied to the site where certain results are *expected to be found*. Therefore, the four model constructs chosen for this test should be applied to each core site data set with necessary changes made to model constructs (hypotheses) in order to improve their behavioural performance.

In experiment one, the Keteira core site data is modelled. This first experiment is testing for the possible existence of two different causal mechanisms of community organisation - competition and biotic instability.

5.4.5.2 Phase Portraits

One of the simplest ways to test for the operation of competitive causal mechanisms in a two species community is to evaluate the system in phase space. If the system is truly competitive, it should tend long-term to one of the four possible solutions predicted by the coupled logistic equations solved at equilibrium (section 2.4.6.2, Chapter 2).

The logistic and coupled logistic models predict behaviour that is based on steady trends which have long-term outcomes. In such a system, internal biotic forces must be greater than exogenous disturbing forces in order for the system to be locally or globally stable. If this is the correct interpretation of the Keteira data, then it must be accepted that there is a large component of noise in the fossil pollen signal for this site.



data: (grains/cm²/ year)
scale: (actual data)
filter: (actual data)

data: (grains/cm²/ year)
scale: (actual data)
filter: (4 point moving average)

data: (grains/cm²/ year)
scale: (actual data)
filter: (single exponential smoothing)

Fig 5.21 The Keteira core site - phase portraits based on actual and filtered data.

Figure 5.21 illustrates this situation by presenting the actual Keteira data set as a phase portrait and two further portraits based on a 4 point running average (fig 5.21 b) and single exponential smoothing filter (fig 5.21 c).

In figure 5.21 the direction of time is indicated by a small arrow (see fig 5.21 a). In the lower right hand corner of each plot the dimensions of the data, scale and type of noise filter used are indicated. For comparative purposes, the x and y axes of each three plots must be drawn to the same scale. This tends to obscure the behaviour of the filtered data. For this reason a second window provides an enlargement of each portrait.

In comment on these results, the behaviour of the actual Keteira data set (fig 5.21a) is incredibly complex and cannot be interpreted as an interactive system near equilibrium. Assuming that the variance in the data is noise, the 4 point running average (fig 5.21 b) and single exponential smoothing filter (fig 5.21 c) should clean up the data and make any interactive trend more evident.

In conclusion, none of the three phase portraits shown in fig 5.21 shows any indication of the four behavioural types predicted by the coupled logistic model. Based on this evaluation it is evident that the long-term behaviour of this system does not tend toward equilibrium behaviour as predicted by the coupled logistic equations. In the next section, the results of model fitting to fossil pollen data are evaluated.

5.4.5.4 The Logistic and Coupled Logistic Models.

The optimisation software was used in this part of experiment one in order to attempt to find optimal parameters for the logistic and coupled logistic models fitted to the Keteira mangrove data. An evolutionary approach was taken in fitting these models to the mangrove data. Initial parameters for the exponential model were determined by simulation. The optimal parameters from the exponential model were used as initial parameters for the logistic equation. Finally, optimal parameters were from the logistic were then used as initial parameters for the coupled logistic.

In this optimisation procedure, no attempt was made to examine the mangrove data for the existence of a logistic rise. It was assumed that the optimisation software would find such behaviour by least squares. Parameter estimation results are listed in Table 5.9.

Model	N_e	N_b	r_e	r_b	K_e	K_b	α	β
exponential	1.9720	4.5882	-0.0005	-0.0008				
logistic	1.9711	4.5806	-0.0005	-0.0008	40	40		
coupled logistic	1.3	2.8	0.00006	0.0065	40	40	-120	14

Table 5.9 Parameters for the logistic and coupled logistic equations tested on the Keteira data set. The subscript letters (e and b) for the various model parameters indicate which of the two mangrove species that parameter belongs to (e = *Excoecaria agallocha,* b = *Bruguiera gymnorhiza*). Scale: data/1000.

A problem with applying the logistic and coupled logistic models to fossil pollen data is in determining initial estimates for model parameters, especially K_e and K_b. In the absence of empirical data, the author either allowed the optimisation software to find a local solution or attempted to find possible parameter basins by trial and error using *for loop* simulation studies (Appendix 4). This involved running simulations of the coupled logistic equation over a range of possible values for K_e and K_b. This was done in order to see what effect changes to this parameter would have on the behaviour of the system.

Values tested ranged from 10 to 200 in incremental amounts of 10 and from 1 to 30 in increments of 1. The results highlighted two facts. Firstly, the equations cannot be solved if K is too small. Secondly, variation in this parameter made very little difference to the behaviour of the model.

As a result of this simulation experiment the author decided on a more ecological approach to the problem of determining K_e and K_b. This approach may be explained as follows.

Firstly, the fossil pollen concentration of *Excoecaria agallocha* in the surface sample (indicating time of core collection) is ca. 6000 grains cm^{-2} $year^{-1}$ and that of *Bruguiera gymnorhiza* is ca. 2500 grains cm^{-2} $year^{-1}$. Therefore, the fossil pollen concentration of total mangrove forest trees at this site at the present time is ca. 8500 grains cm^{-2} $year^{-1}$. Secondly, based on visual assessment of the swamp, the author estimated that the present mangrove forest density could be increased four or five times in theoretical terms. This estimation takes into account the present density of mangrove forest trees and total swamp area.

This assumption suggests that the behaviour of the two mangrove species recorded in the fossil pollen data from this site have existed in the lower feasible density region for the 700 CAL. years covered by this data set. In other words, these populations have not been able to reach their theoretical asymptotic density limit over this time period - assuming that the present environmental conditions and swamp area have been constant, which is not an unreasonable assumption.

The logistic (fig 5.22) and coupled logistic (fig 5.23) model fits to mangrove data indicate that the optimisation routine has interpreted the Keteira data sets as a long-term constant growth trend (ca. 700 CAL. years of the very initial stages of logistic growth!).

5.4.5.3.1 **Continuous Logistic Growth**

Fig 5.22 portrays the logistic model fitted to the Keteira mangrove data. The optimisation routine has interpreted the two mangrove species as having long-term negative growth rates.

5.4.5.3.2 **Continuous Coupled Logistic Growth**

Fig 5.23 portrays the coupled logistic model fitted to the Keteira mangrove data.

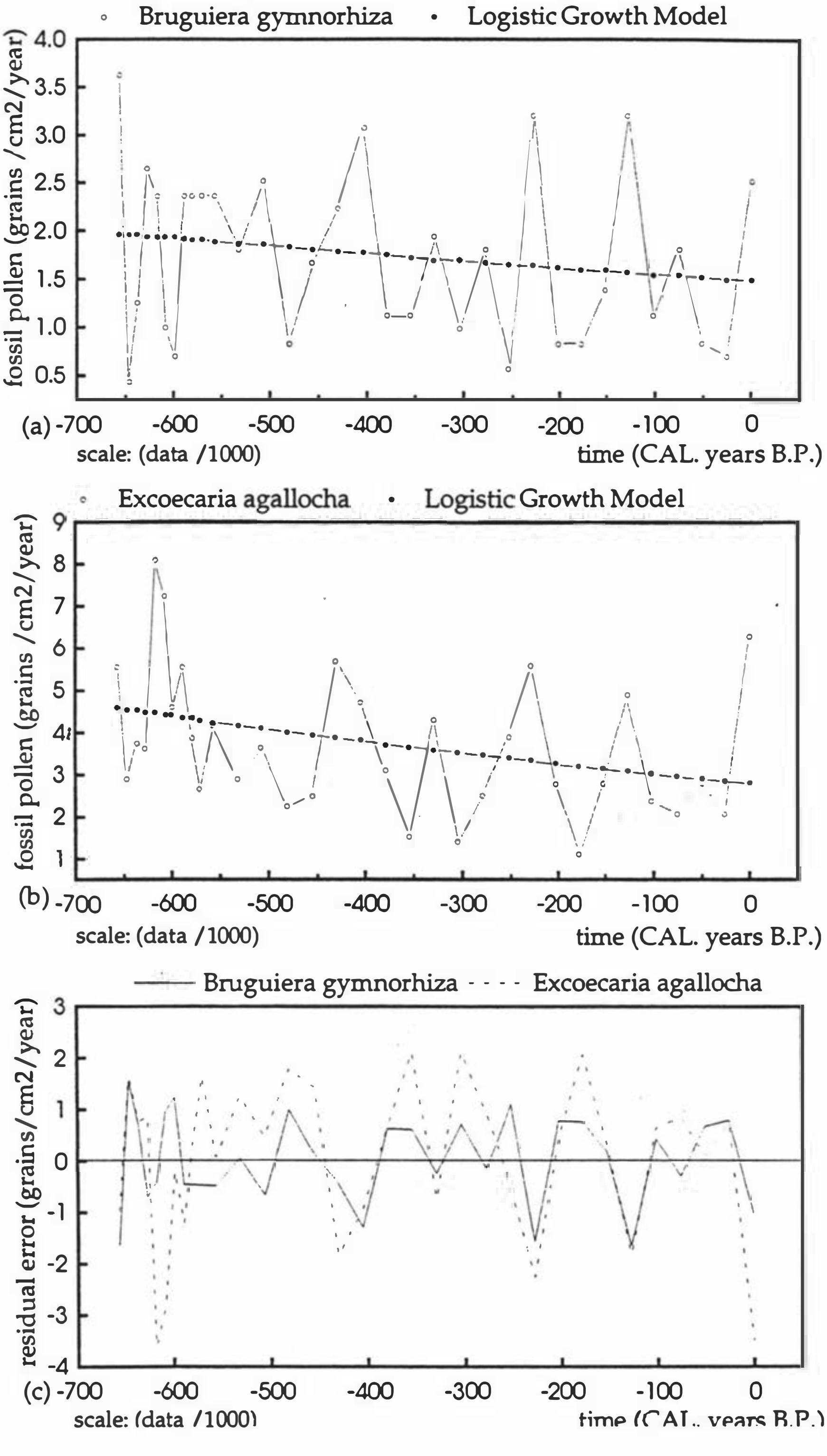


Fig 5.22 The Keteira core site - continuous logistic growth model fitted to (a) *Bruguiera gymnorhiza* and(b) *Excoecaria agallocha* with (c) residual error.

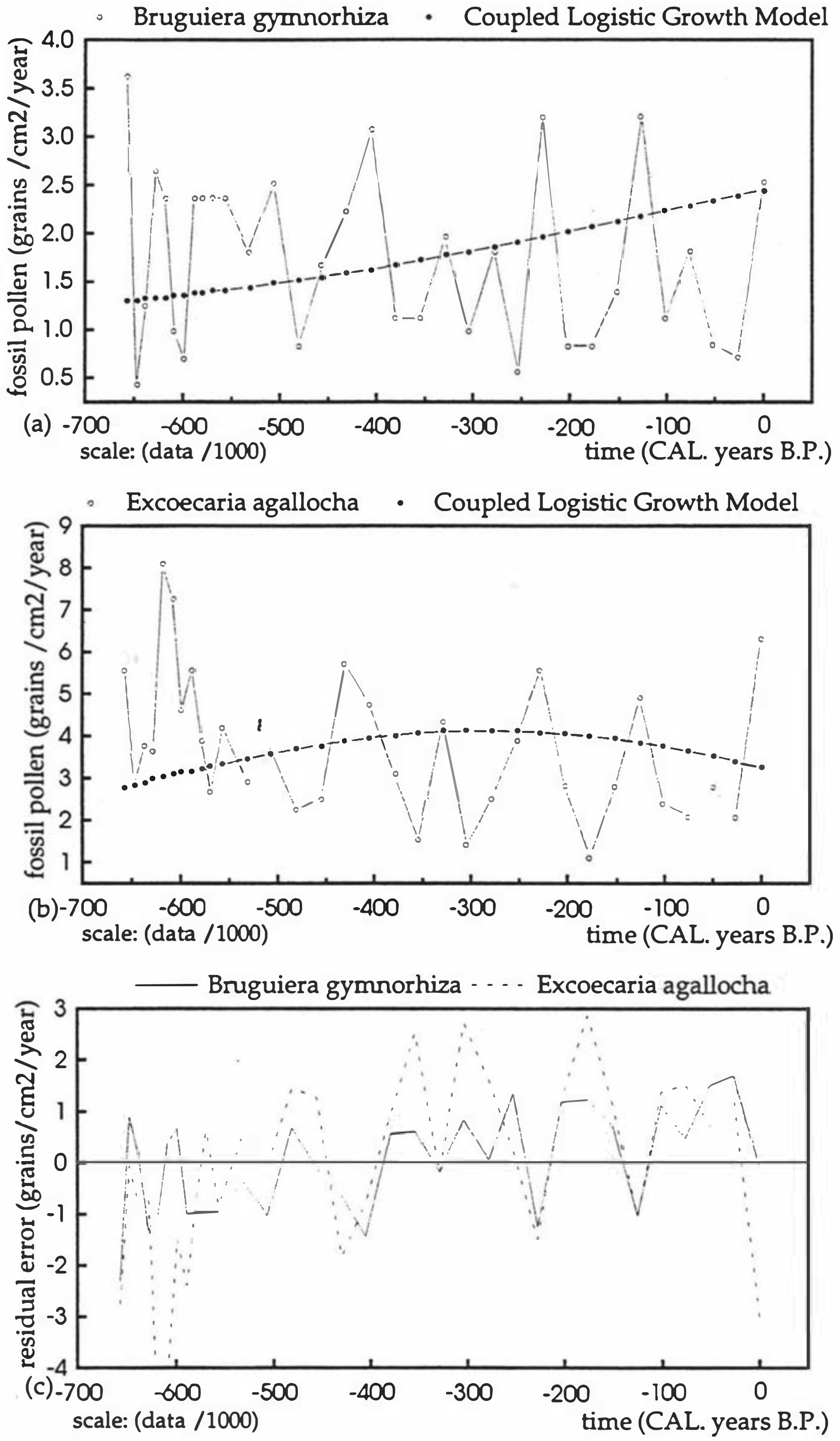


Fig 5.23 The Keteira core site - continuous coupled logistic growth model fitted to (a) *Bruguiera gymnorhiza* and(b) *Excoecaria agallocha* with (c) residual error.

The behaviour of the two mangrove species has been interpreted as an interactive struggle from which *Bruguiera gymnorhiza* is, at present, emerging as the dominant species.

Interpreting these results as logistic or coupled logistic growth is all very well, but overlooks one important point - these models obviously do not explain the variance in the data. This point is clearly illustrated by plots of the residual error (fig 5.22 c, 5.23 c) for these two models.

In summary, there are three key results from this section. Firstly, evidence of competitive interaction cannot be found in phase space for actual or filtered data. Secondly, approximation of upper asymptotic density limits suggests that these two mangrove species exist in the intermediate to lower density region. Finally, the logistic and coupled logistic models do not explain the variance in this mangrove data. Based on the qualitative evidence provided by phase portrait analysis of actual and filtered data, it seems unlikely that the variance in this data is entirely error that is obscuring competitive processes.

5.4.5.4 Discrete Time Models

A total of six optimisation runs were needed in order to fully evaluate the discrete logistic and coupled logistic equations.

Discrete Models	N_e	N_b	r_e	r_b	K_e	K_b	α	β
exponential	0.02021	0.0490	-0.0095	-0.0178				
logistic case I	0.0355	0.0459	1	1	0.2	0.0355		
logistic case II	0.007	0.0470	0.016	0.026	0.015	0.025		
logistic case III	0.0349	0.0460	2.7482	2.7518	0.0259	0.03947		
coupled logistic	0.0349	0.0460	2.7482	2.7518	0.0259	0.0394	0.01	0.1
coupled logistic	0.0349	0.0460	2.7482	2.7518	0.0259	0.0394	-0.01	-0.4

Table 5.10 Parameters for the logistic and coupled logistic equations tested on the Keteira data set. The subscript letters (e and b) for the various model parameters indicate which of the two mangrove species that parameter belongs to (e = *Excoecaria agallocha*, b = *Bruguiera gymnorhiza*). Scale: data/100,000.

The parameters determined from these runs are recorded in Table 5.10. As in the case of the continuous models of the previous section, the discrete exponential model is used only to provide initial parameter estimates for the discrete logistic and discrete coupled logistic model formulations.

5.4.5.4.1 The Discrete Logistic

In the present experiment, the discrete logistic equation has been fitted to the Keteira mangrove data by trying initial parameter estimates in different regions of parameter space. For the parameter values listed in Table 5.9, the discrete logistic manifests logistic growth in case I, limit cycles in case II and chaotic behaviour in case III. These three different behavioural types can be used to test for the existence of a stable equilibrium point (case I), multiple unstable equilibrium points (case II) and non-equilibrium deterministic chaos in case III.

Simulations of the parameters listed in Table 5.10 are plotted in figures 5.24, 5.25 and 5.26.

Fig 5.24 portrays the behaviour of the discrete logistic for the parameter values recorded in case I of Table 5.10. The result is rapid logistic growth to an upper density asymptote. The residual error (fig 5.24 c) once again demonstrates the poor performance of this model in explaining the variance of the Keteira mangrove data.

Fig 5.25 portrays the behaviour of the discrete logistic for the parameter values recorded in case II of Table 5.10. Of all the models tested so far, the discrete logistic model in this region of parameter space realistically begins to approximate the behaviour of the Keteira mangrove data. In fig 5.25 (a), there is a peak to peak correspondence between the model and the mangrove data in many places. Furthermore, some of the limit cycles are in reasonable phase with the mangrove data.

Fig 5.26 portrays the behaviour of the discrete logistic for the parameter values recorded in case III of Table 5.10. In this region of parameter space there is an even greater correspondence between the model and Keteira mangrove data. Does this suggest that this behaviour indicates deterministic chaos? This is probably not the correct interpretation for a number of reasons.

Firstly, the discrete logistic equation in this region of parameter space produces chaotic behaviour as a result of over-compensation caused by the extremely rapid reproductive processes of the system. This fact does not fit the ecology of these two mangrove species which are known to have very poor seedling survival, due to predation on seeds by crabs. This fact led to the hypotheses of stochastic demographic processes which may find a temporal expression in short-lived population behaviour.

Secondly, limit cycles such as those portrayed in fig 5.25 and over-compensatory are behaviour are both limited in their amplitude. Over-compensation is caused by rapid population growth which exceeds environmental limits and results in population crashes. If this behaviour is the result of over-compensation, then it suggests that the upper density asymptote is around 0.025 to 0.0394 (grains cm^{-2} CAL. years $^{-1}$) for the two Keteira mangrove species as indicated in Table 5.10.

However, at the other two core sites (Udu and Lawakilevu), *Excoecaria agallocha* reaches population densities (grains cm^{-2} CAL. years $^{-1}$) of 0.18 and 0.15 (values rescaled to data/100,000) - how is this explained if this behaviour is over-compensation? These densities are way above the upper asymptotic densit suggested by the discrete logistic model in case III.

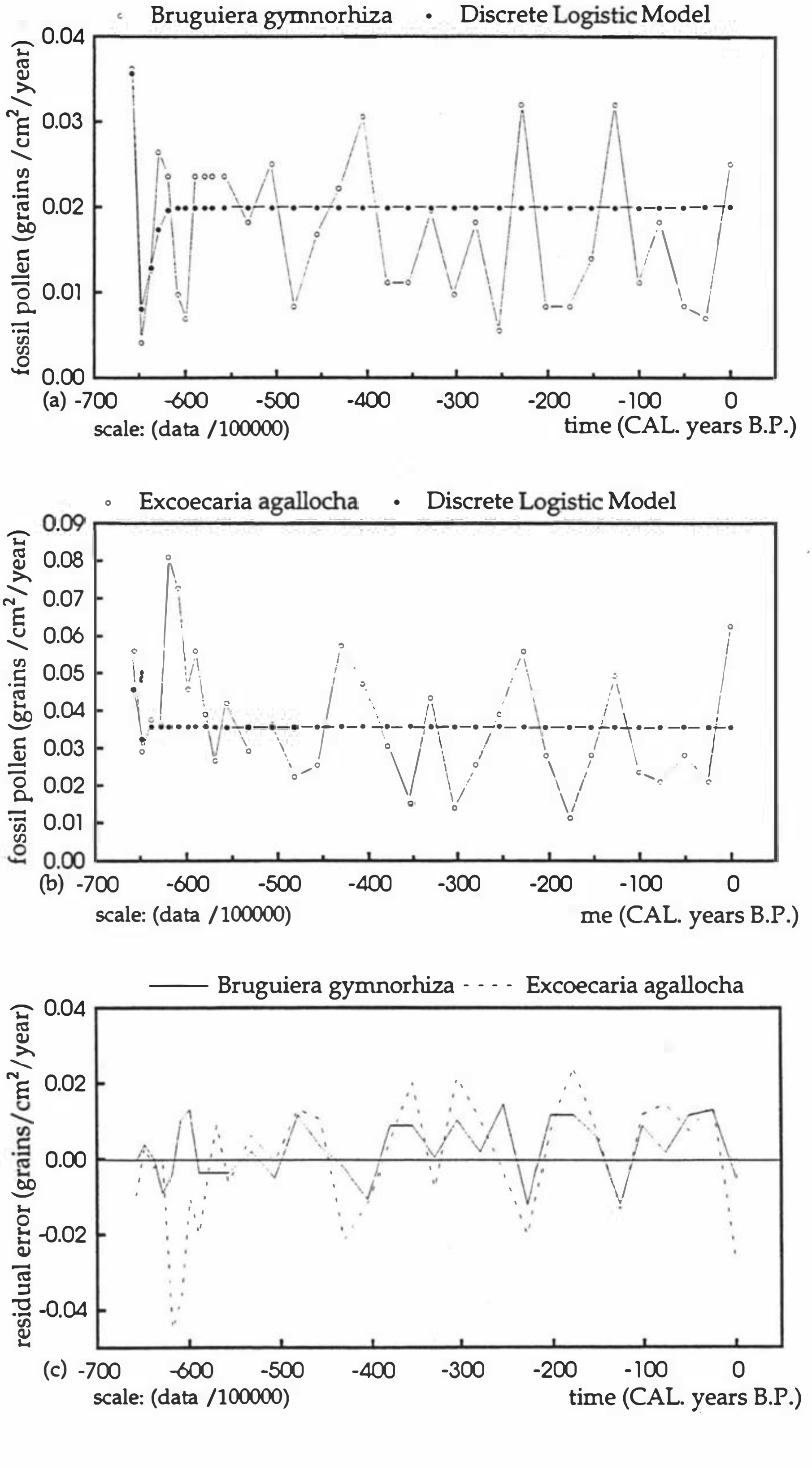


Fig 5.24 The Keteira core site - discrete logistic growth model (case I) fitted to (a) *Bruguiera gymnorhiza* and (b) *Excoecaria agallocha* with (c) residual error.

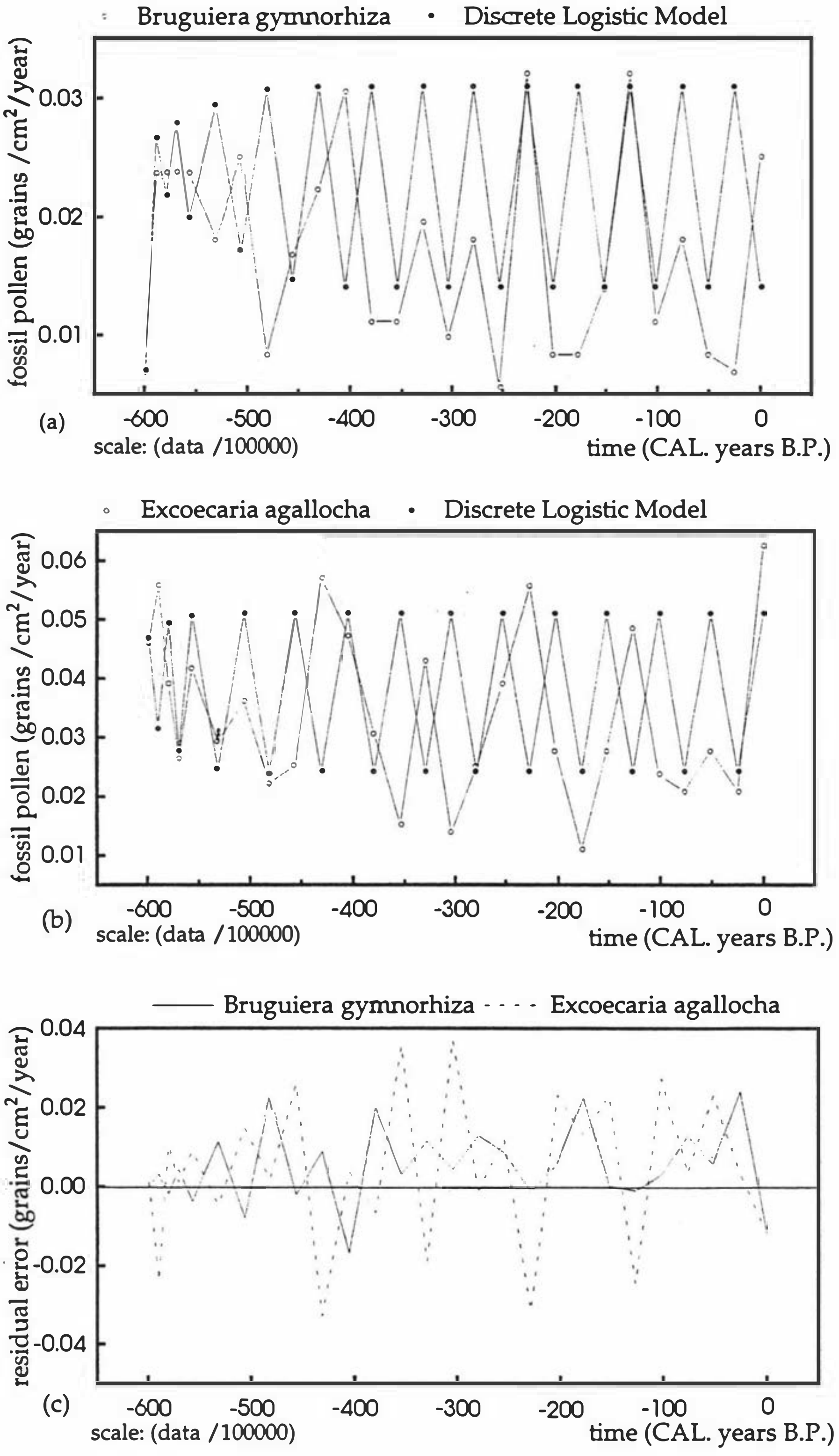


Fig 5.25 The Keteira core site - discrete logistic growth model (case II) fitted to (a) *Bruguiera gymnorhiza* and (b) *Excoecaria agallocha* with (c) residual error.

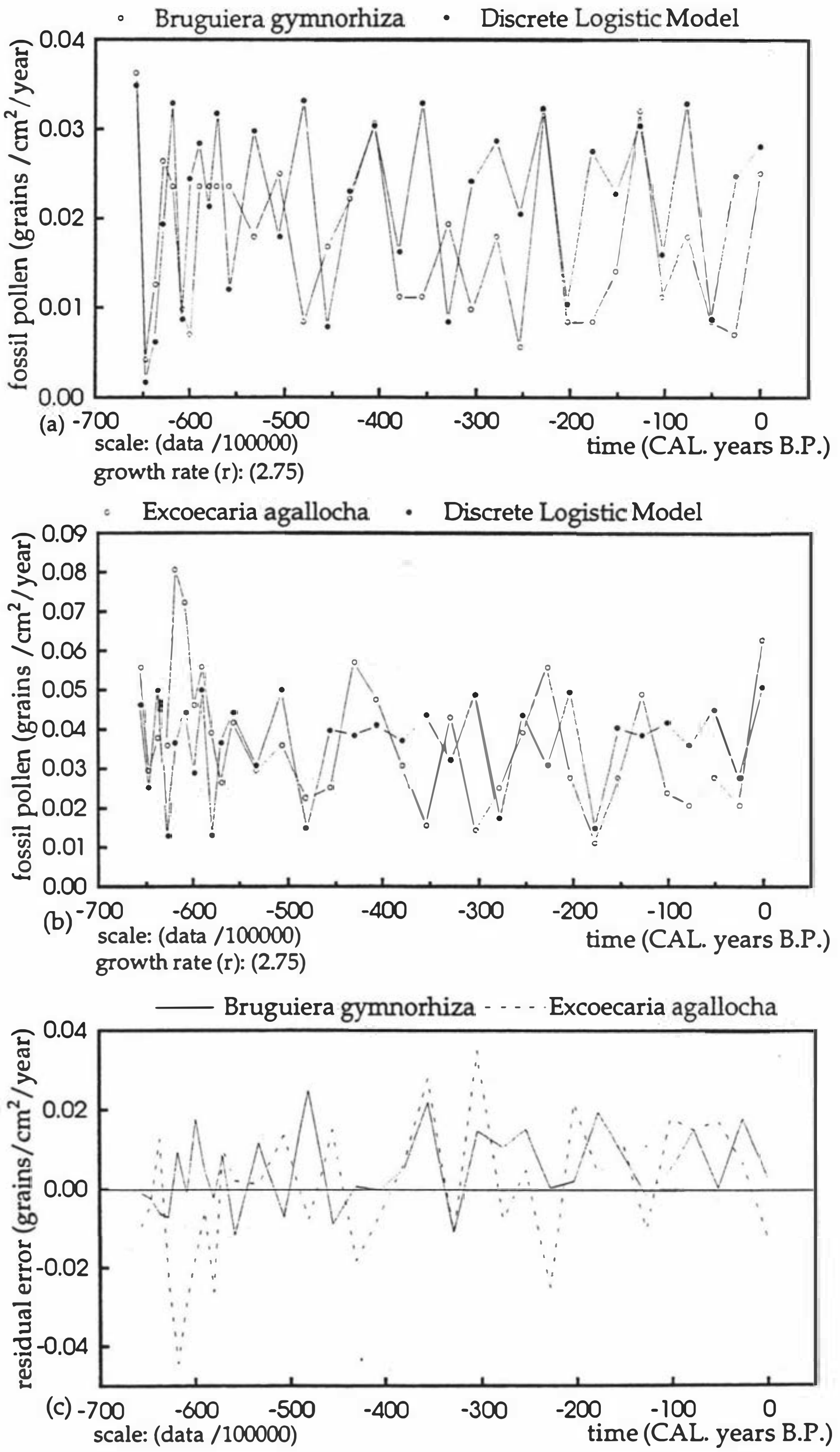


Fig 5.26 The Keteira core site - discrete logistic growth model (case III) fitted to (a) *Bruguiera gymnorhiza* and (b) *Excoecaria agallocha* with (c) residual error.

Thirdly, the Keteira core site has considerable area available for further expansion of mangrove forest (*i.e.* increased density). While mangrove succession theory suggests that mangrove zones expand in response to sediment trapping - not high growth rates.

The application of the discrete logistic to the present study of mangal is clearly limited in its explanatory power. However, of all the models tested so far, its non-equilibrium chaotic behaviour most closely resembles the behaviour of the Keteira mangal. This strongly suggests that some stochastic mechanism is involved. The question is, to what extent does this behaviour reflect the operation of internal (biotic) and external (abiotic) stochastic mechanisms? This question is considered later on.

The coupled discrete logistic has been used to test for the existence of competitive processes in discrete time. The results of this experiment are recorded in the next section.

5.4.5.4.2 *The Discrete Coupled Logistic*

The reader will notice that in Table 5.10 the coupled logistic equation has been listed twice. The reason for this is to illustrate a problem which has become evident in using this model formulation. The parameter values for the competitive couplings in these equation (α and β) should be negative if the system is driven by competition. The problem is, it is usually possible to find an equally feasible solution for the mangrove data using positive parameters for (α and β). Positive parameters indicate mutualism and not competition.

There are a number of examples of this problem given in this chapter, the first is recorded in Table 5.10 and portrayed in figures 5.27 and 5.28. These results were gained using a combination of optimisation and simulation techniques.

In fig 5.27, the competition coefficients are positive. With the negative term in the coupled logistic equation, a positive parameter will result in a negative competitive effect. The correlation between the model and the mangrove data is striking in some places, out of phase in other places and completely wrong in other places.

Now compare the results of fig 5.27 with those of fig 5.28 which were obtained for almost the same value (but negative) competition coefficients. These negative terms have a positive (mutualistic) effect in the coupled logistic equations. These results suggest that in some regions of parameter space the coupled logistic equation cannot be used to discriminate between competitive and mutualistic causal mechanisms.

5.4.5.5 *Interpretation*

The objective of the following section is to interpret the results of experiment one in order to determine if changes can be made to these initial model formulations in order to improve their predictive and explanatory capability. The results of experiment one have provided the following insights.

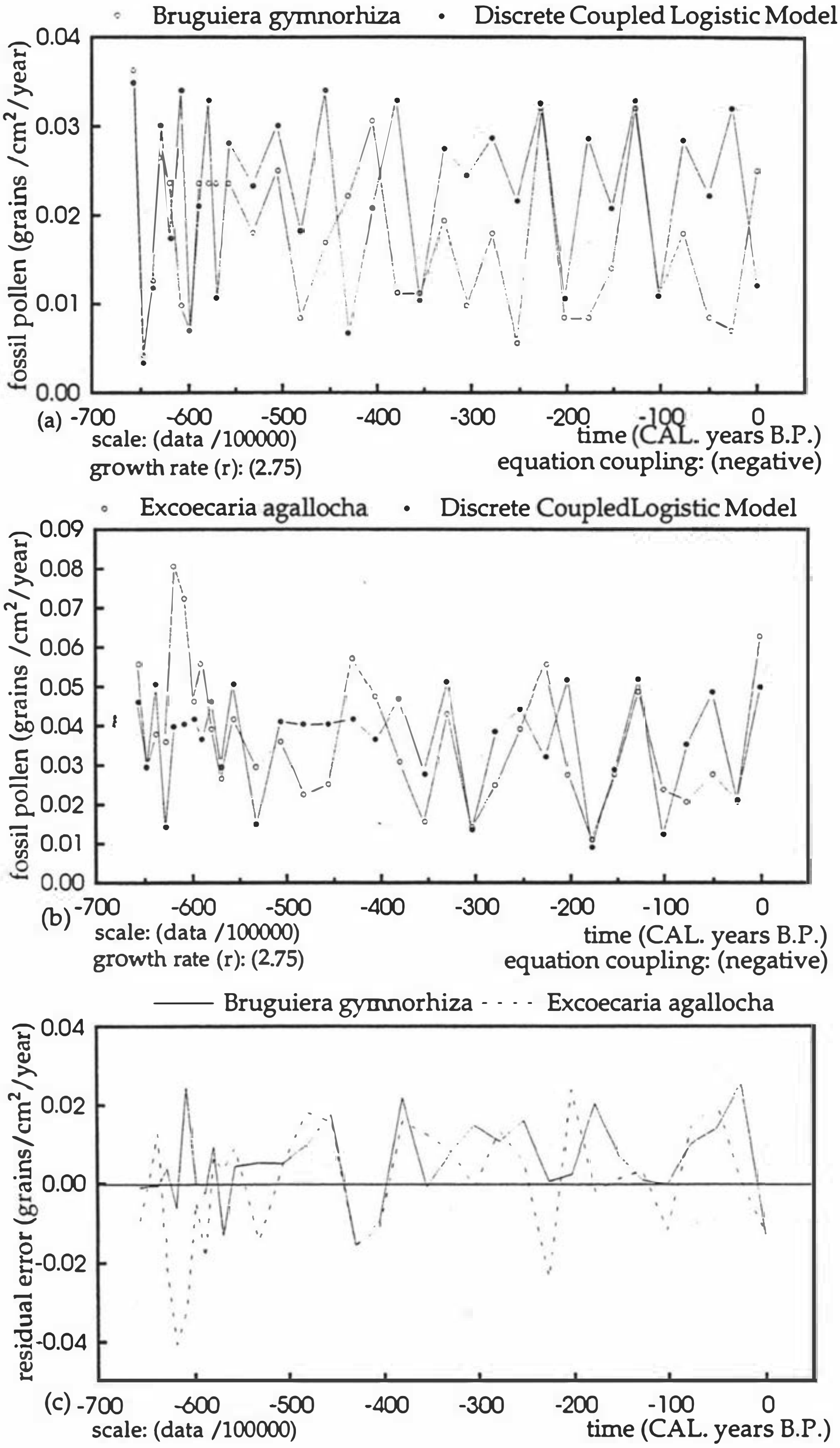


Fig 5.27 The Keteira core site - discrete coupled logistic growth model with negative equation couplings fitted to (a) *Bruguiera gymnorhiza* and (b) *Excoecaria agallocha* with (c) residual error.

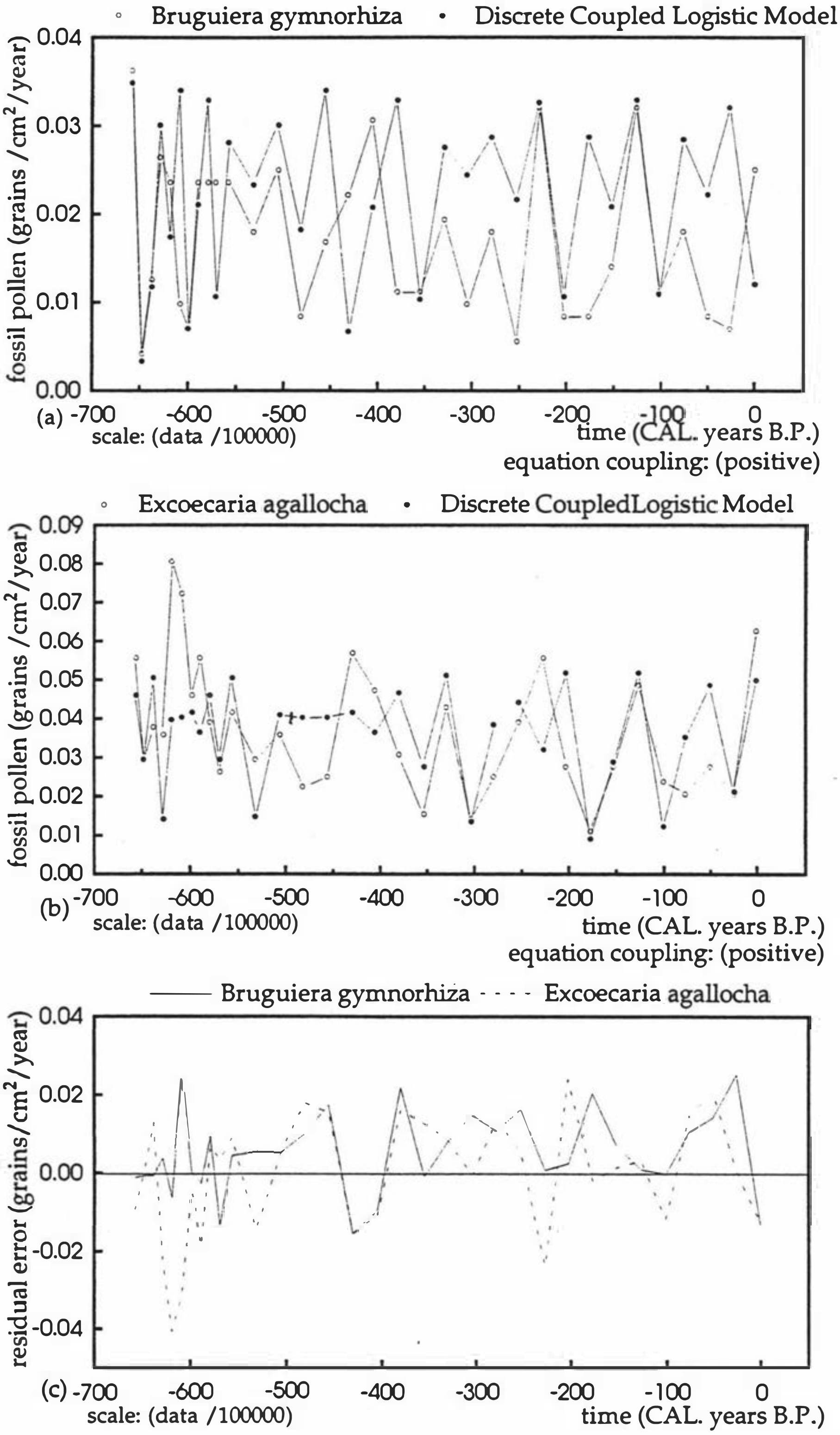


Fig 5.28 The Keteira core site - discrete coupled logistic growth model with positive equation couplings fitted to (a) *Bruguiera gymnorhiza* and (b) *Excoecaria agallocha* with (c) residual error.

Firstly, phase portraits of mangrove data derived from actual and filtered fossil pollen data show no evidence of the qualitative behaviour that would be expected of two interacting populations.

Secondly, the continuous logistic and coupled logistic models can be fitted to the Keteira mangrove data based on least squares non-linear optimisation, but variance in the data is not explained. Furthermore, 700 CAL. years is a long time for the initial stages of a logistic rise.

Thirdly, the Keteira mangrove data shows evidence of a repeated 100 CAL. year expansion and contraction. This behaviour is also evident in the other two data sets to varying degrees. The regularity of this behaviour suggests that some underlying process is involved and that these rises and falls should not be completely attributed to error.

Fourthly, the nature of the behaviour of the Keteira mangrove appears to be density vague for a number of reasons. Firstly, the present density of the mangrove forest and total area of available swamp suggest that a much larger community could be supported. Secondly, at the other two sites, *Excoecaria agallocha* reaches very high fossil pollen concentration. Therefore, it appears that the Keteira mangrove have been existing in an intermediate to low density region.

Fifthly, the very good predictive performance of the discrete logistic equation in a region of parameter space resulting in chaotic behaviour strongly suggests that the behaviour of these two mangrove species is influenced by stochastic processes.

Finally, the behaviour of the mangrove data at the Keteira core site shows a very close correlation with the behaviour of charcoal fragment concentration data. It appears that the charcoal data is in phase with the fossil pollen signal in places and may therefore be forcing it.

Of all the observations and insights gained from experiment one, the last one is probably the most important. Charcoal from the burning of inland forest is usually always associated with increased erosion of forest soils. Sedimentation is a process that appears to effect mangal by changing the physiological and geomorphological dynamics of a swamp.

A simple way of testing this new hypothesis is to use the charcoal data as a forcing function in the classical continuous logistic and coupled logistic equations. Such a formulation combines density-dependent processes with elements of stochastic environmental forcing. This combination may potentially explain the long-term density vague behaviour of the Keteira mangrove. Furthermore, it may help to explain the poor performance of the logistic and coupled logistic equations as recorded and illustrated in this first section.

The results and insights summarised above are *a posteriori* observations and should not be used to reformulate a model that is tested on the same data from which the observations came. For this reason, the new model formulation will only be simulation tested using the Keteira mangrove data and then tested in experiment two using the Udu mangrove data.

Further use of the discrete logistic model will not be made because of its poor explanatory power in the present domain of application. The mechanism of this model is biotic instability caused by extreme sensitivity to the rapid reproductive processes of the system. Based on the reasons given in the previous section, it is very unlikely that this is the mechanism responsible for the non-equilibrium behaviour of the Keteira mangal.

5.4.5.6 Model Reformulation

Based on the results of experiment one, it is now clear that the continuous logistic and coupled logistic equations are not capable of predicting the behaviour of the Keteira mangal. Poor predictive performance in a model suggests that there is either unknown error in the field data or incorrect mechanisms in the model formulation. As mentioned earlier, there is not much that can be done to evaluate the extent and nature of dispersal and geological process errors in fossil pollen data. However, it is possible to reformulate the logistic and coupled logistic equations so that they include the influence of environmental forcing based on the charcoal data.

5.4.5.6.1 The Logistic Equation with Charcoal Forcing

Charcoal forcing may be responsible for influencing the fundamental demographic (birth and death) processes of these populations by improving or worsening environmental conditions, thus causing one of the mangrove populations to expand or contract in response. The reformulation of the logistic (47) and coupled logistic (51a, b) equations to accomodate charcoal forcing was discussed in Chapter four. These two model constructs are rewritten below for the convenience of the reader.

$$\frac{dN}{dt} = r(1 + mf(t))N\frac{(K - N)}{K} \qquad (47)$$

where

$mf(t)$ is a term expressing a scaled forcing function for which m is a constant scaling coefficient.

and

$$\frac{dN_1}{dt} = r_1(1 + m_1 f(t))N_1\frac{(K_1 - N_1 - \alpha N_2)}{K_1}$$

$$\frac{dN_2}{dt} = r_2(1 + m_2 f(t))N_2\frac{(K_2 - N_2 - \beta N_1)}{K_2} \qquad (51a, b)$$

As was indicated in the description of these model formulations given in Chapter four (section 4.3.4.1), the behaviour of the system is now dependent on the value and sign of the specific growth rate parameter (r) and the charcoal scaling coefficient (m). The behaviour of this new model formulation can only be fully evaluated by simulation study of the four possible parameter scenarios for r and m outlined in Chapter four.

This was accomplished by using the *for loop* simulation routine (Appendix 4) to simulate the logistic model (47) for various values of the parameter m, based on four possible sign combinations for r and m. The logistic model (47) is the basis of the coupled logistic formulation (51a, b). Both model constructs were thoroughly tested, however, for the sake of simplification only the results of simulation trials using the logistic (47) model are presented here. These may be considered indicative of the general behaviour of both models.

The results of this study indicated that these new model formulations very poorly predicted the behaviour of the Keteira mangal. To demonstrate this fact, the four simulation trials are illustrated below (fig 5.29, 5.30, 5.31, 5.32) with tables listing the range and sign of the parameters tested.

In case I, r and m are both negative in sign so that the resultant population growth (fig 5.29) is positive for large values of m. The parameters tested in this simulation are listed in Table 5.11. In each case study, $K = 15$. The mangrove and charcoal data have been scaled by 1000.

In case II, r and m are both positive in sign so that the resultant population growth (fig 5.30) is positive for all values of m. The parameters tested in this simulation are listed in Table 5.12.

In case III, r is negative and m is positive in sign so that the resultant population growth (fig 5.31) is negative for all values of m. The parameters tested in this simulation are listed in Table 5.13.

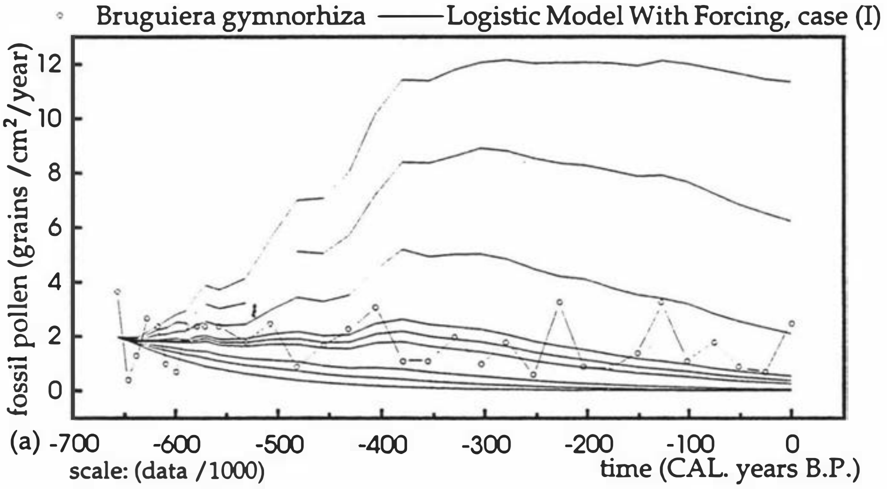
In case IV, r is positive and m is negative in sign so that the resultant population growth (fig 5.32) is negative for large values of m. The parameters tested in this simulation are listed in Table 5.14.

As can be seen from figures 5.29 - 5.32, model (47) does a poor job of replicating the variance in the Keteira mangrove data. Furthermore, this predictive weakness is obviously not the result of a reaction time delay of the population in responding to the charcoal forcing. The fundamental problem is an inability to replicate the degree of variance in the fossil pollen data.

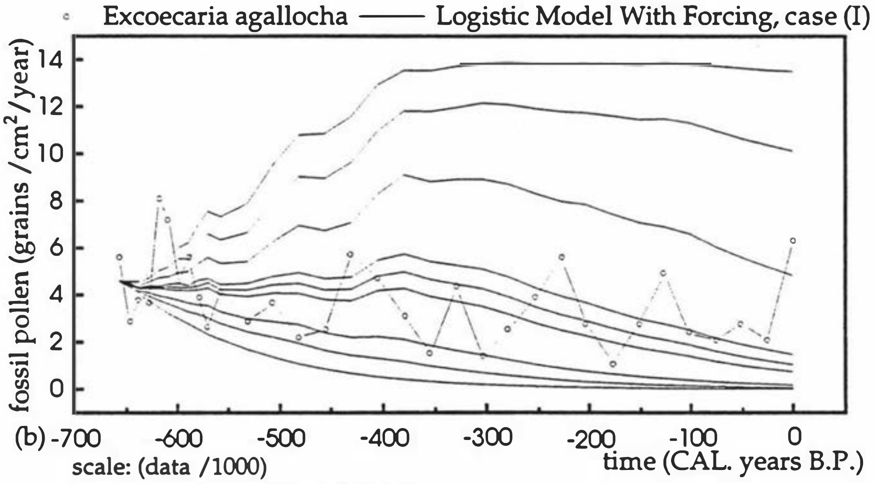
From a mathematical point of view, this weakness appears to result from the influence of the value and sign of the two parameters r and m. In case I, when the value of m reaches a critical level, it ceases producing variance and instead drives the system toward K, the upper asymptotic population density in model (47). In case II, growth is always positive and all values of m drive the system toward K. In case III, growth is always negative and drives the system toward a trivial equilibrium value at $N = 0$(where N is the state variable of equation 47). Case IV is probably the most successful of all four trials. The behaviour of the system is determined by the value of m which is negative.

Model Formulation	r	m
continuous logistic (47)	-0.01	0
"	"	-0.05
"	"	-0.08
"	"	-0.12
"	"	-0.13
"	"	-0.14
"	"	-0.18
"	"	-0.22
"	"	-0.26
"	"	-0.30

Table 5.11 Case I, a simulation study of the continuous logistic equation (47) for various values of the parameter m.



scale: (data /1000)
forcing function: (charcoal data)
scaling coefficient (-m): (negative)
specific growth rate (-r): (negative)



scale: (data /1000)
forcing function: (charcoal data)
specific growth rate (-r): (negative)
scaling coefficient (-m): (negative)

Fig 5.29 The Keteira core site - continuous logistic with forcing function. Simulation for various values of (r) and (m), (case I) plotted against (a) *Bruguiera gymnorhiza* and (b) *Excoecaria agallocha*.

Model Formulation	*r*	*m*
continuous logistic (47)	0	0
"	0.0001	0.0
"	"	0.5
"	"	1.5
"	"	2.5
"	"	4.5
"	"	8.5
"	"	12.5
"	"	18.5

Table 5.12 Case II, a simulation study of the continuous logistic equation (47) for various values of the parameter *m*.

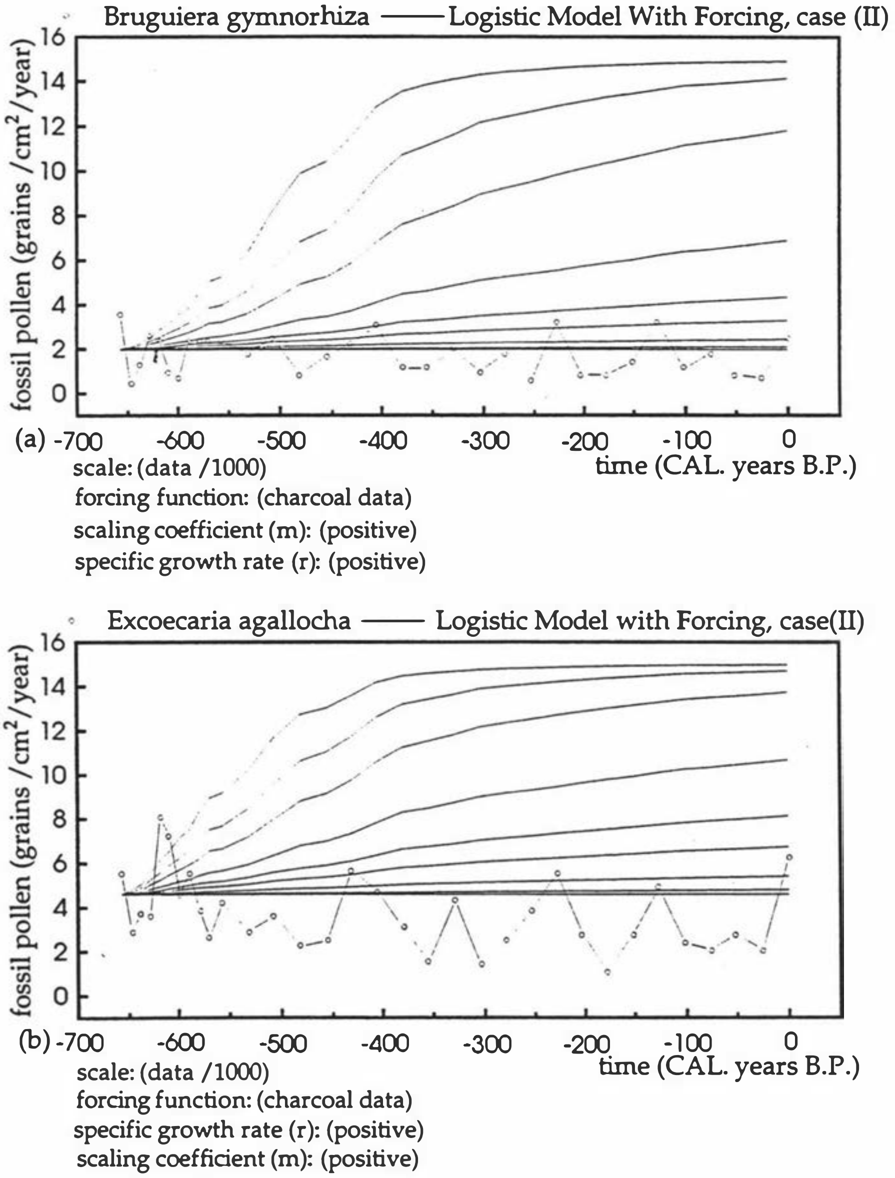
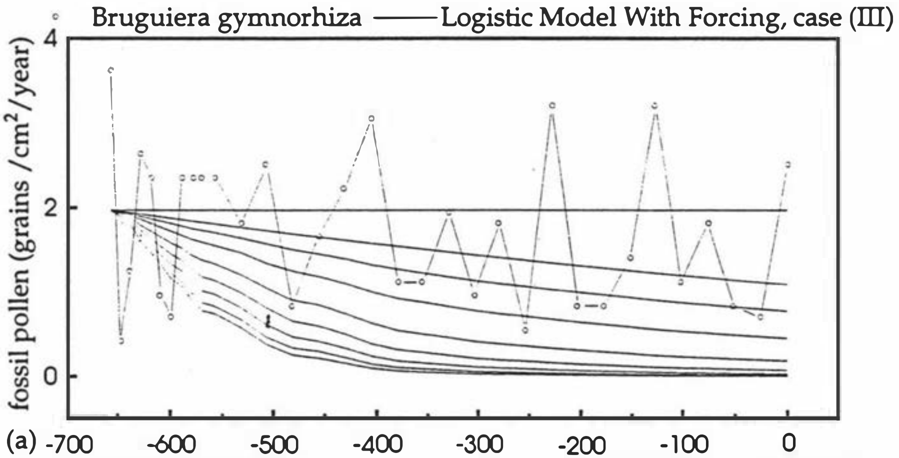


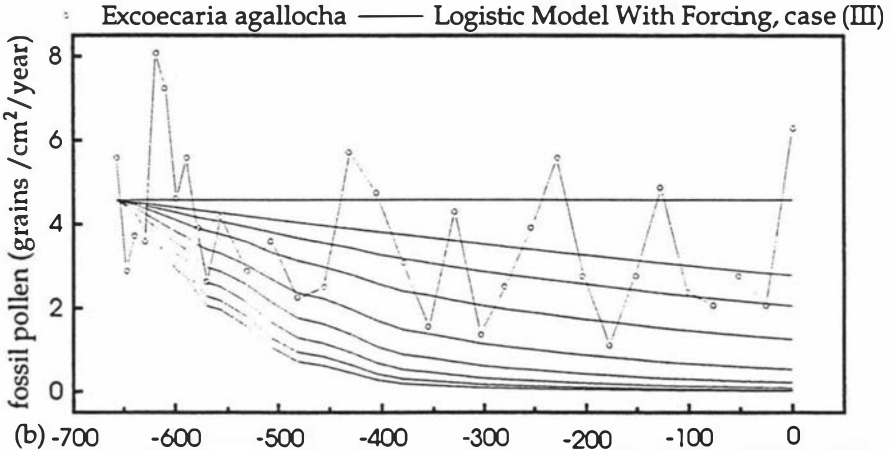
Fig 5.30 The Keteira core site - continuous logistic model with forcing function. Simulation for various values of (r) and (m), (case II) plotted against (a) *Bruguiera gymnorhiza* and (b) *Excoecaria agallocha*.

Model Formulation	*r*	*m*
continuous logistic (47)	0	0
"	-0.0001	0.001
"	"	0.1
"	"	0.25
"	"	0.5
"	"	0.75
"	"	1.0
"	"	1.25
"	"	1.5
"	"	2.0

Table 5.13 Case III, a simulation study of the continuous logistic equation (47) for various values of the parameter *m*.



scale: (data /1000)
forcing function: (charcoal data)
scaling coefficient (m): (positive)
specific growth rate (-r): (negative)

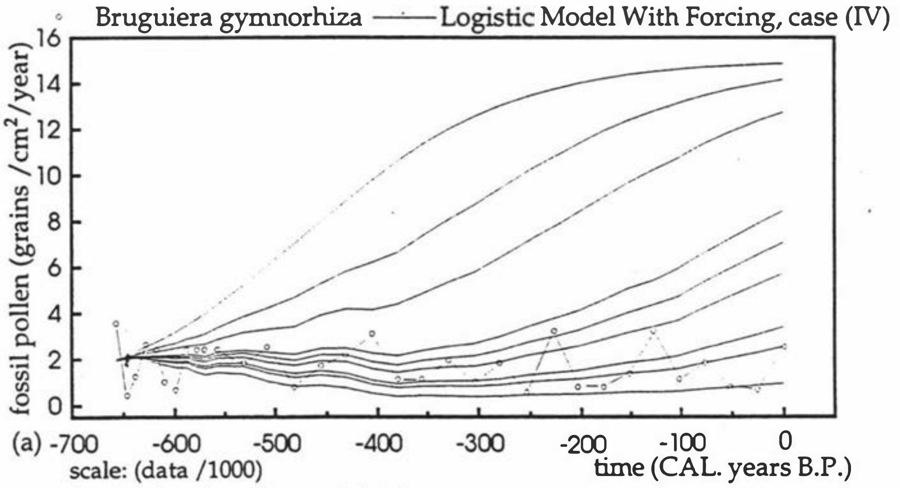


scale: (data /1000)
forcing function: (charcoal data)
specific growth rate (-r): (negative)
scaling coefficient (m): (positive)

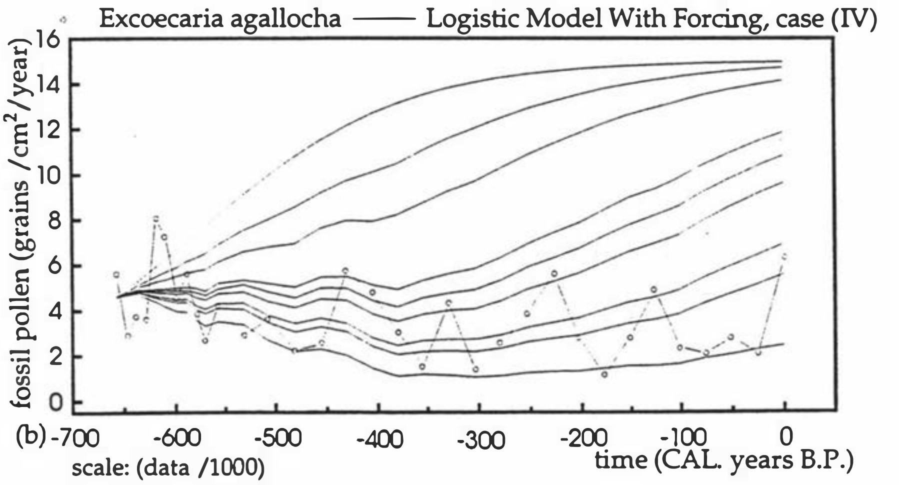
Fig 5.31 The Keteira core site - continuous logistic with forcing function. Simulation for various values of (r) and (m), (case III) plotted against (a) *Bruguiera gymnorhiza* and (b) *Excoecaria agallocha*.

Model Formulation	*r*	*m*
continuous logistic (47)	0.01	0
"	"	-0.05
"	"	-0.08
"	"	-0.12
"	"	-0.13
"	"	-0.14
"	"	-0.16
"	"	-0.17
"	"	-0.2
"	"	-0.24

Table 5.14 Case IV, a simulation study of the continuous logistic equation (47) for various values of the parameter *m*.



scale: (data /1000)
forcing function: (charcoal data)
scaling coefficient (-m): (negative)
specific growth rate (r): (positive)



scale: (data /1000)
forcing function: (charcoal data)
specific growth rate (r): (positive)
scaling coefficient (-m): (negative)

Fig 5.32 The Keteira core site - continuous logistic with forcing function. Simulation for various values of (r) and (m), (case IV) plotted against (a) *Bruguiera gymnorhiza* and (b) *Excoecaria agallocha*.

Intermediate values of $-m$ approximate the behaviour of the mangrove data, however the level of variance produced by the charcoal is clearly inadequate.The problem with equation (47) outlined above appears to result from the nature of the model formulation. To illustrate this point it is necessary to expand equation (47) so that,

$$\frac{dN}{dt} = rN + r(mf(t))N\left(\frac{K-N}{K}\right). \qquad (47a)$$

The terms of equation 47a will be familiar to the reader based on Chapter four (section 4.3.4.1). The behaviour of this model results from the two exponential growth terms rN and $r(mf(t))N$. The second of these growth terms is influenced by the charcoal forcing function. This is simply the charcoal fragment concentration data set (fragments per 100 *Lycopodium* scaled by 1000). The problem is, when the second growth term $r(mf(t))N$ reaches critical values it swamps the first exponential growth term and drives the system to equilibrium.

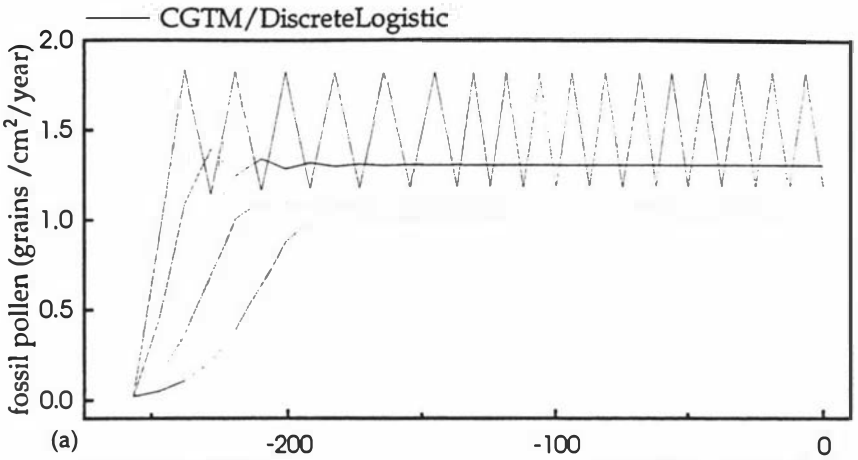
5.4.5.6.2 The Constant Growth Trend Model Formulation

Equation 47a can be reformulated in a way that overcomes the above problem. A simple, first approximation was to exchange the double exponential growth term for a constant growth term (r_c) and a second growth term $mf(t)N$, the basis of which is the forcing function.

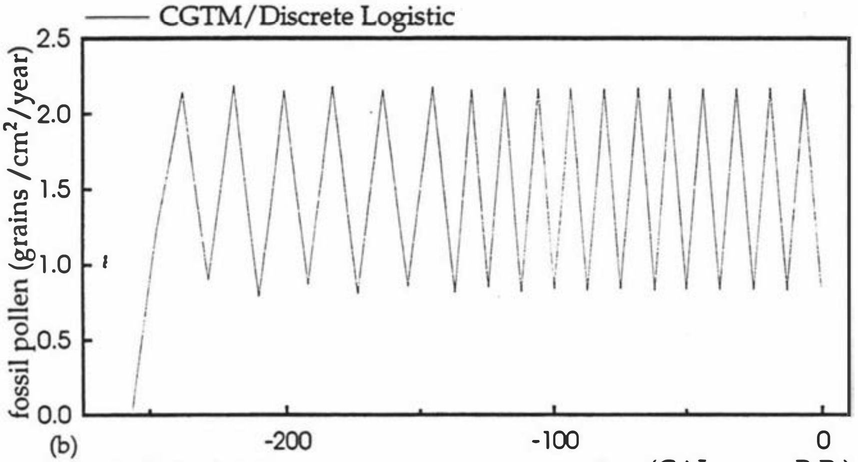
$$\frac{dN}{dt} = r_c + (mf(t))N \qquad (59)$$

In this formulation (the exponential CGTM), the exponential growth term (rN) of equation 47a has been replaced by a growth constant (r_c). The second, (forced) exponential growth term of equation 47a, has also been replaced. In the new growth term, the Malthusian (54) specific growth rate parameter (r), is replaced by a forcing function - a non-constant growth rate. The growth term of equation (59) was called the exponential constant growth trend model (CGTM). The name exponential identifies the parent model from which it is derived. The name, Constant Growth Trend Model (CGTM), comes from the behaviour of the model when the forcing function scaling parameter (m) is zero and the model produces a constant growth trend based on the value and sign of r_c.

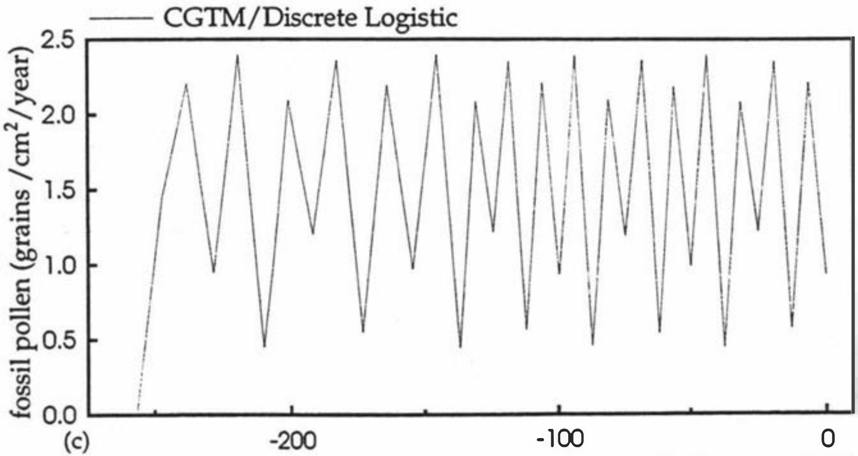
The exponential CGTM forms the basis of a range of model constructs which have been introduced in section 4.4.2 of Chapter 4. Of these model constructs, the author was interested to discover that the discrete logistic CGTM has all the behavioural characteristics of the parent discrete logistic equation (48) which, as shown earlier, is capable of three classes of behaviour - logistic growth, limit cycles and deterministic chaos. This fact is illustrated in figures 5.33 and 5.34 which show the results of simulation experiments using the discrete logistic CGTM based on critical values of the constant reproductive rate parameter (r_c).



scale: (data /1000)
constant reproductive rate (r_c): (0.01, 0.1, 0.4, 0.85)
equilibrium point (k): (1.0)



scale: (data /1000)
constant reproductive rate (r_c): (1.2)
equilibrium point (k): (1.0)



scale: (data /1000)
constant reproductive rate (r_c): (1.4)
equilibrium point (k): (1.0)

Fig 5.33 Simulations of the logistic CGTM in discrete me to illustrate the behaviour of this model based on changes in the constant reproductive rate parameter (r_C).

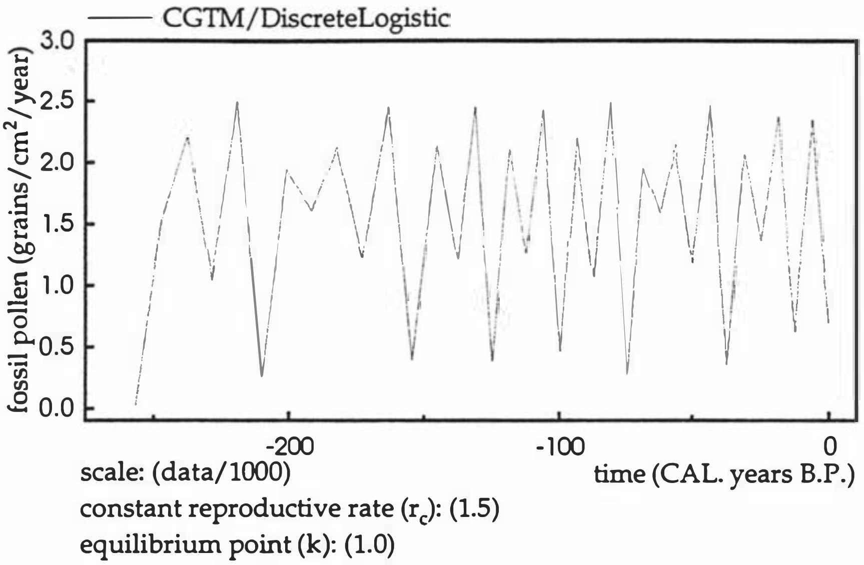


Fig 5.34 Simulations of the logistic CGTM in discrete time, to illustrate the period doubling behaviour of this model based on changes in the constant reproductive rate parameter (r_c).

Initial optimisation experiments with the exponential CGTM also yielded very poor results until it was realised that the optimisation software was not able to interpret the presence of a reaction time delay in the effect of the charcoal forcing on population growth. This problem was easily overcome by the use of a reaction time delay where:

$mf(t-T)$	is a term expressing a scaled forcing function for which m is a constant scaling coefficient and
T	is a reaction time delay in the influence of the charcoal data upon the specific growth rate parameter r (in a continuous time model).

CGT Model Formulations	N_e	N_b	$r_c(exc.)$	$r_c(brug.)$	m_e	m_b	K_e	K_b	α	β
exponential	1.25	7.154	0.16129	0.18971	-170	-111				
logistic	0.9738	7.2337	0.25	0.17	-320	-150	20	20		
coupled logistic case I	0.9738	7.2337	0.016	0.17	-260	-150	20	20	1	1
coupled logistic case II	0.9738	7.2337	0.016	0.17	-260	-150	20	20	-0.0001	-0.0001
discrete expon.	0.007	0.0470	0.014	0.02	-0.9	-0.9				

Table 5.15 Parameters for the logistic and coupled logistic equations tested on the Keteira data set. The subscript letters (e and b) for the various model parameters indicate which of the two mangrove species that parameter belongs to (e = *Excoecaria agallocha*, b = *Bruguiera gymnorhiza*). The constant growth/reproductive rate parameter (r_c) also has a subscript to indicate which mangrove species the parameter belongs to. Scale: data/1000 for continuous models and data/100,000 for discrete time models. In every model the scale of the charcoal data is charcoal/1000.

When used in conjunction with a reaction time delay the exponential CGTM gave very good model fits to the Keteira mangrove data. The parameters used to gain these results and the CGT model formulations tested are recorded in Table 5.15.

The parameters of Table 5.15 have been used to simulate the behaviour of these model constructs (fig 5.35, 5.36, 5.37, 5.38, 5.39) in order that their behaviour may be compared with that of the Keteira fossil pollen data. These illustrations are located on the next five pages.

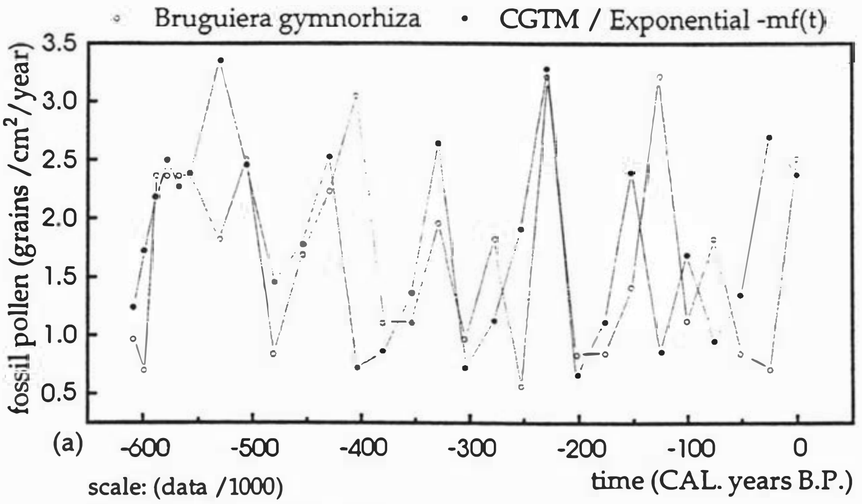
In fig 5.35, the behaviour of the exponential CGTM is plotted against the Keteira mangrove data. This model fit is based on a five sample point time delay which represents ca. 85 CAL. years B.P. Apart from the fact that parts of the model/fossil pollen data fit are slightly out of phase, the overall correspondence between the two data sets is clearly the best of all models tried so far.

In fig 5.36, the predictive performance of the logistic CGTM has been plotted against the Keteira fossil pollen data. When *m* is zero and *r* is positive, this model produces classical logistic growth to a single equilibrium point. In this context the logictic CGTM is a mixture of equilibrium and non-equilibrium (stochastic) forces. Once again, a reaction time delay of ca. 85 years (5 sample points) is required.

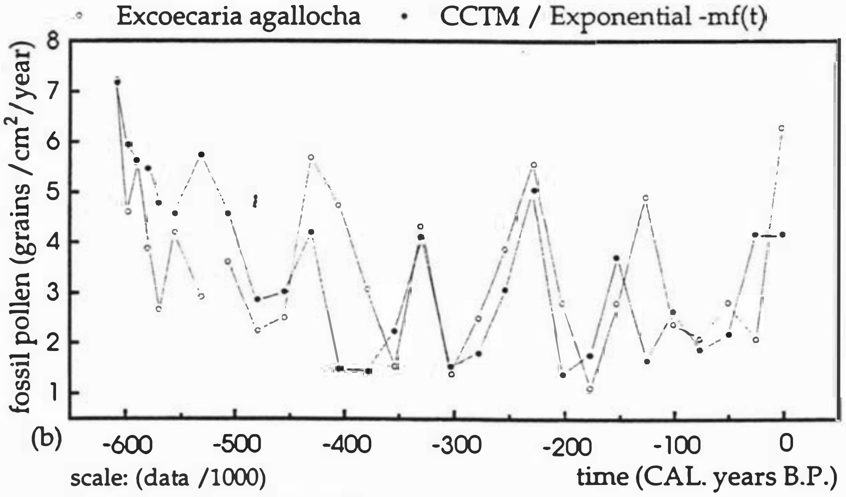
While the model fit is reasonably good, it is still evident that the model and mangrove data never leave a theoretical low density region - the initial stages of logistic growth. It could not be said that the density-dependent negative feedback mechanism of this model had significantly improved its behaviour.

In Table 5.15, the reader will notice that two sets of parameter values are recorded for the coupled logistic CGTM formulation. Once again, it is possible to replicate the results of this model using both positive (fig 5.37) and negative (fig 5.38) competition coefficients. This model is also a mixture of equilibrium and stochastic forces. As in the case of the logistic CGTM model, it cannot be said that the increased complexity of this model formulation has improved its behaviour in relation to the Keteira mangrove data. Based on the principle of parsimony, the exponential CGTM appears to have superior predictive capability.

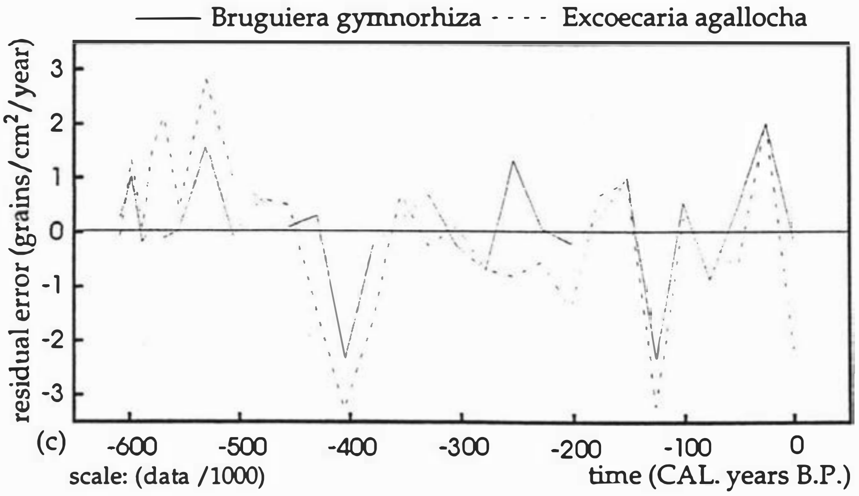
In fig 5.39, the discrete exponential CGTM has been plotted against the Keteira mangrove data based on the parameter values of Table 5.15. This model formulation clearly has inferior predictive capability when compared with the continuous exponential CGTM formulation. This discrete model seems to be less sensitive to lower values of charcoal between 200 - 0.0 CAL. years B.P. This test appears to indicate that the underlying demographic process may indeed be continuous.



scale: (data /1000)
time delay: (5 sample points)
forcing function: (charcoal data)

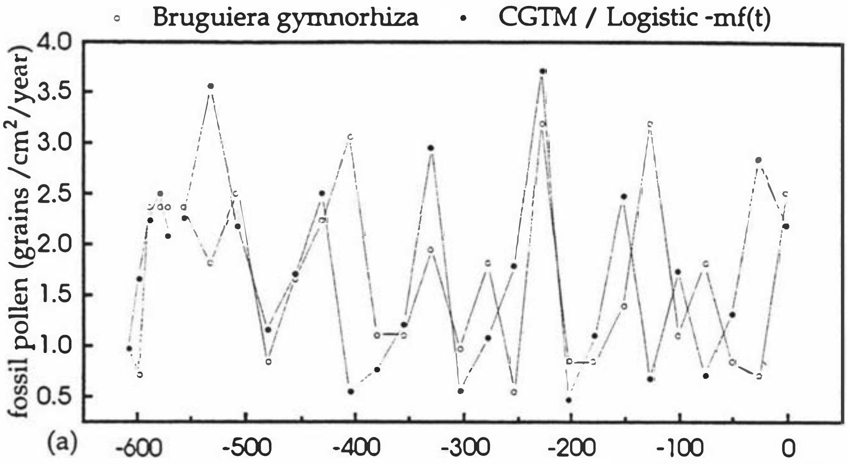


scale: (data /1000)
time delay: (5 sample points)
forcing function: (charcoal data)

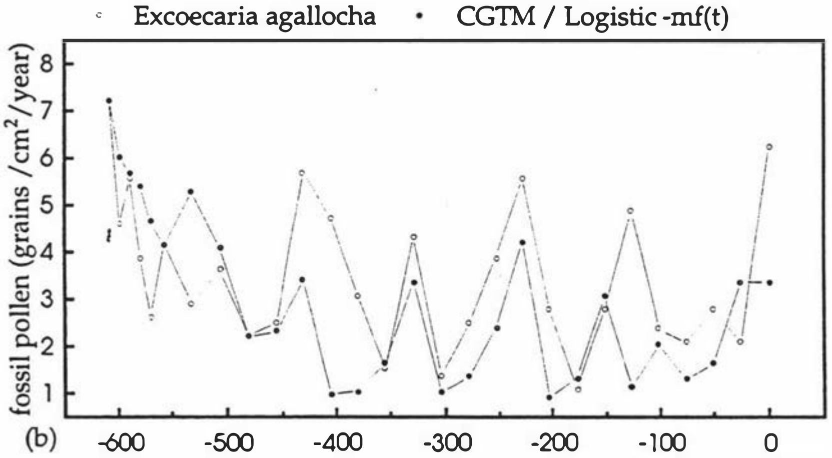


scale: (data /1000)

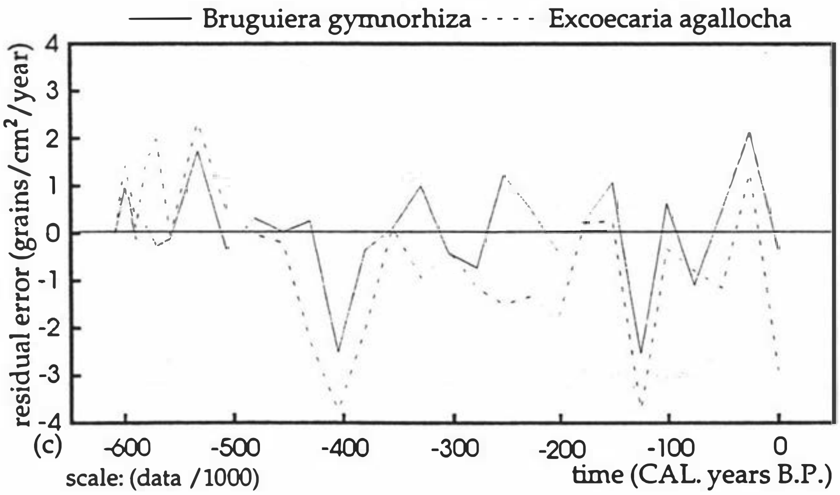
Fig 5.35 The Keteira core site - a simulation study of the exponential CGTM with 5 sample point time delay and negative scaling coefficient.



scale: (data /1000)
time delay: (5 sample points)
forcing function: (charcoal data)



scale: (data /1000)
time delay: (5 sample points)
forcing function: (charcoal data)



scale: (data /1000)

Fig 5.36 The Keteira core site - a simulation study of the logistic CGTM with 5 sample point time delay and negative scaling coefficient.

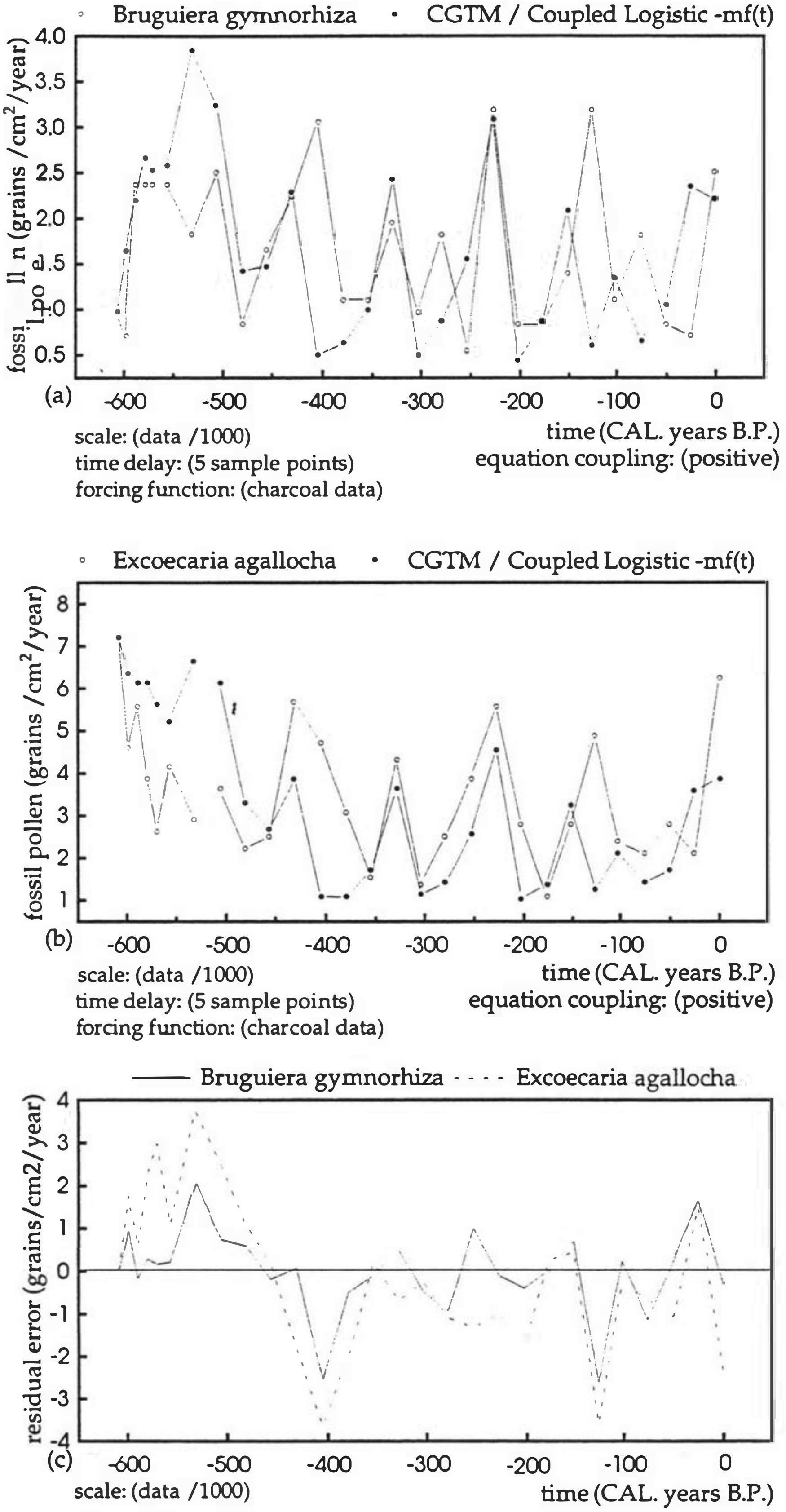


Fig 5.37 The Keteira core site - a simulation study of the coupled logistic CGTM with 5 sample point time delay and positive scaling coefficient.

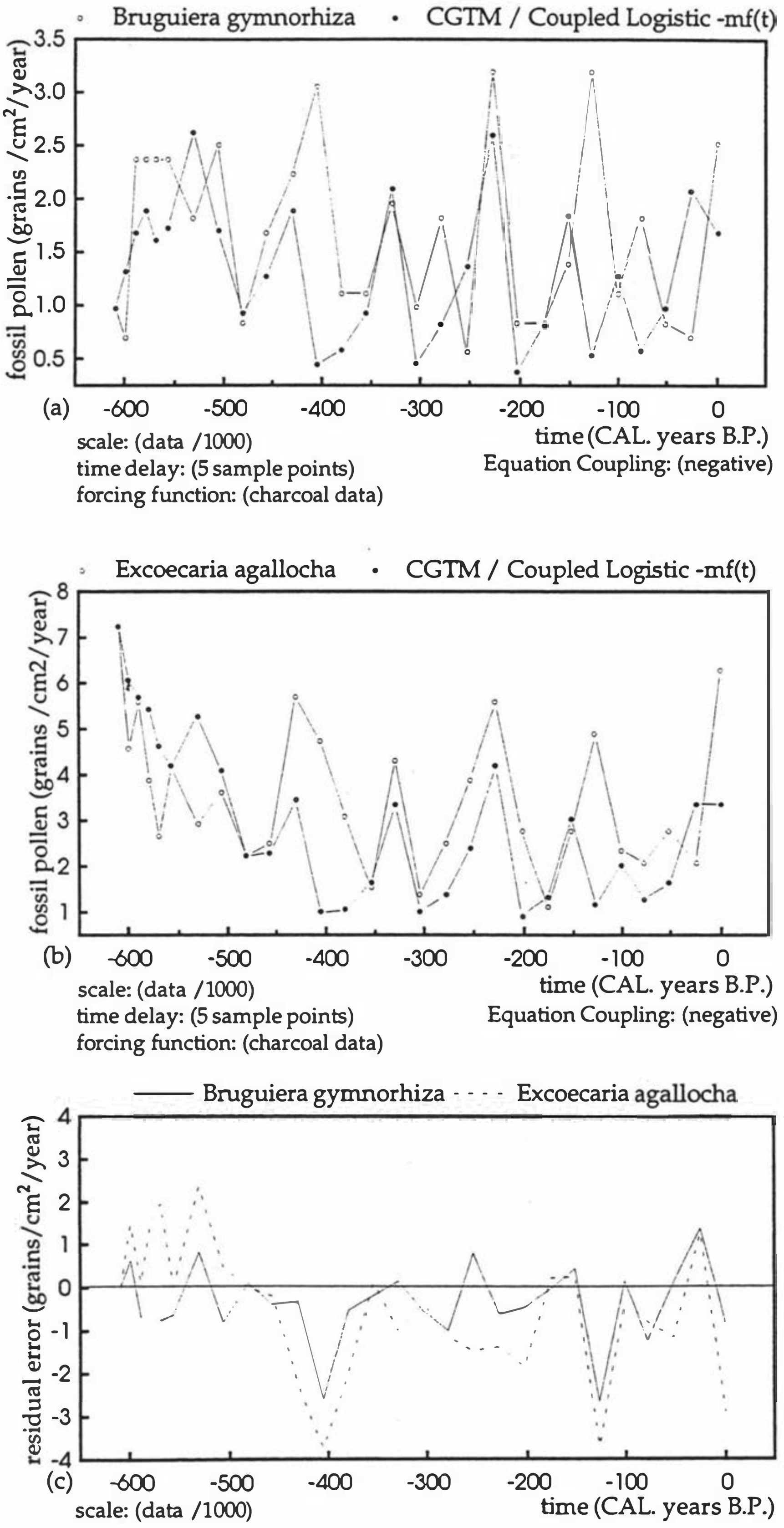


Fig 5.38 The Keteira core site - a simulation study of the coupled logistic CGTM with 5 sample point time delay and negative scaling coefficient.

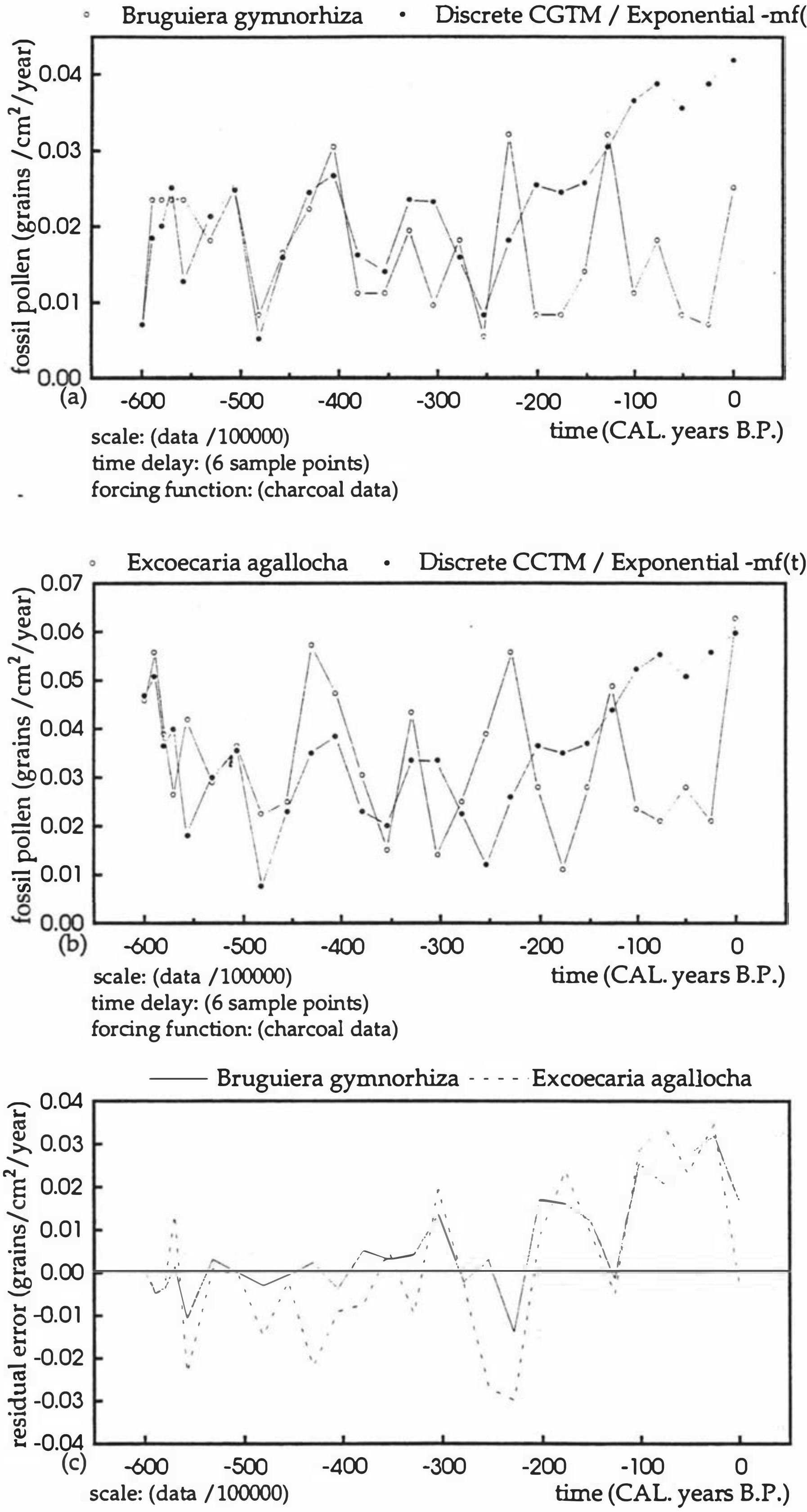


Fig 5.39 The Keteira core site, a simulation of the discrete exponential CGTM with 6 sample point time delay and negative scaling coefficient.

5.4.6 Experiment Two - Udu Data

Interpretation of the results of experiment one and reformulation of the initial model constructs presents a new hypothesis to be tested in experiment two. In experiment two, the following alternative hypotheses are tested against the Udu Mangrove data.

5.4.6.1 Mangrove Equilibrium Theory

The initial equilibrium hypotheses being tested in experiment one suggested that the spatial behaviour of mangal at the Lawakilevu and Udu core sites resulted from long-term, continuous, interactive growth processes, as described by classical competition models (the logistic and coupled logistic). This hypothesis was tested at the Keteira core site in an attempt to find contradictory evidence for the hypothesis of *demographic stochasticity* proposed for this site and based on classical mangrove succession theory.

It is now evident that the behaviour of the Keteira mangal cannot be explained by classical competition theory. Furthermore, attempts to reformulate these classical equilibrium model constructs using a forcing function have failed. Therefore, the initial equilibrium hypothesis remains and must now be tested at the Lawakilevu and Udu core sites.

5.4.6.2 Mangrove Succession Theory

The initial non-equilibrium hypothesis for experiment one suggested that the two mangrove species are opportunistic strategists which have taken spatial advantage of the geomorphological process of coastal plain construction on Totoya. It was also suggested that the demographic processes driving these populations were stochastic - based on seedling survival and predation.

The model used to test these hypotheses demonstrated that the behaviour of the Keteira mangrove approximates a non-equilibrium system driven by stochasticity. So far it has not been possible to determine if the stochasticity affecting this system is demographic or environmental. Finally, the domain of application for the discrete logistic model does not match the ecology of the Totoya mangal.

Based on the above conclusions, this is as far as it is possible to test this initial hypothesis. A new competing hypothesis must now be advanced for experiment two.

5.4.6.3 Density Vague - Stochastic Domination

Based on the simulation results of the exponential CGTM, it is now possible to advance a new hypothesis to explain mangrove community organisation at the Keteira core site. This hypothesis is based on *a posteriori* observations and cannot be tested against the original Keteira data set. Instead, it forms an alternative hypothesis to the mangrove equilibrium theory stated above. It is now predicted *a priori*, that contradictory evidence will be found at the Lawakilevu and Udu core sites to reject a density vague hypothesis.

It now seems evident that the Keteira mangal have been driven by a stochastic environmental forcing agent which is represented in the cores from this site by a fossil proxy - charcoal fragments. It seems likely that this charcoal has come from the burning of the island's inland forest. This in turn probably resulted in increased erosion of forest surface soils which were hydrologically deposited at the Keteira core site along with charcoal fragments.

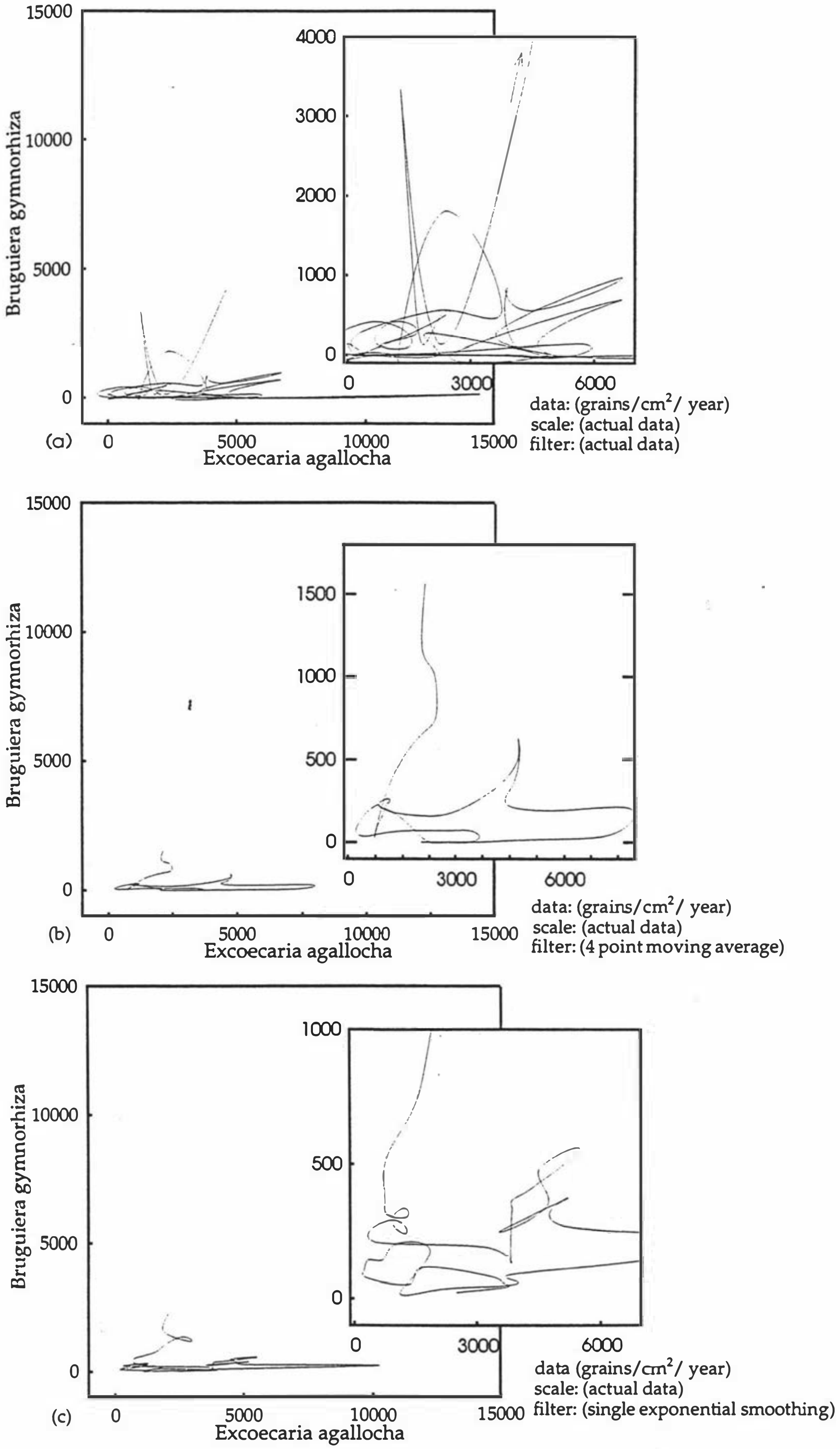
Increased rates of sedimentation have acted to change the geomorphological and physiological conditions of the mangrove swamp. As a direct result of these changes, the existing mangrove forest was forced to migrate seaward in order to maintain optimal physiological and geomorphological conditions. The time delay of approximately 85 CAL. years represents the time taken for the decline of an existing forest and establishment and expansion of a new one, seaward of the old site.

In this hypothesis, the causal mechanism of community behaviour is the changing sedimentation rate driven by inland forest burning and clearance. The population growth rate is constant, with an underlying stochastic mechanism. This growth process drives the mangrove forest structure at Keteira, resulting in non-equilibrium behaviour. This non-equilibrium behaviour is a temporal record of a spatial process - the seaward migration of mangrove forest across the coastal plain.

This hypothesis has been formulated into the exponential CGTM, logistic CGTM, coupled logistic CGTM and discrete exponential CGTM. The exponential CGTM contains a fully non-equilibrium causal mechanism whereas the logistic CGTM and coupled logistic CGTM formulations contain both equilibrium and stochastic forces. The long-term behaviour of these last two model constructs suggests a struggle between two main opposing forces (logistic growth and stochastic domination). Finally, the discrete exponential model tests for the existence of discrete demographic growth processes. In experiment two these model constructs are tested against the Udu mangal where equilibrium behaviour has been predicted and the rejection of this CGTM hypothesis is expected.

5.4.6.4 Phase Portraits

Fig 5.40 contains three phase portraits based on the state variables the two mangrove species at the Udu core site. Individual plot axes have been standardised for comparative purposes. In order to portray any underlying competitive behaviour more clearly, the actual mangrove data (fig 5.40a) has been transformed using a 4 point moving average (5.40b) and a single exponential smoothing filter (5.40c). None of the results portrayed in fig 5.40 give any indication of qualitative behaviour predicted by the coupled logistic equation (50a, b) (section 2.4.6.2, Chapter 2).



data: (grains/cm^2/ year)
scale: (actual data)
filter: (actual data)

data: (grains/cm^2/ year)
scale: (actual data)
filter: (4 point moving average)

data (grains/cm^2/ year)
scale: (actual data)
filter: (single exponential smoothing)

Fig 5.40 The Udu core site - phase portraits based on actual and filtered data.

These results suggest that the behaviour of the two mangrove species at this core site is not driven by density-dependent interspecific competition.

5.4.6.5 The Logistic and Coupled Logistic Models

Once again, the optimisation software was used in this part of experiment two in an attempt to obtain a model to mangrove data fit. An evolutionary approach to parameter estimation was also used and involved the exponential and logistic models in order to estimate feasible parameters for optimisation of the coupled logistic model against the Udu mangrove data. Parameter estimation results are listed in Table 5.16. The upper asymptotic population density (K) was estimated for this site using the same procedure outlined in experiment one for the Keteira core site. Based on this approach, the value of K is estimated as 30 grains cm^2 CAL. year $^{-1}$.

Model	N_e	N_b	r_e	r_b	K_e	K_b	α	β
exponential	0.5	4.3	0.003	0.0006				
logistic	0.5	4.3	0.003	0.0006	30	30		
coupled logistic	4.4577	1.6655	-0.0005	-0.0005	30	30	-36.28	-12.12

Table 5.16 Parameters for the logistic and coupled logistic equations tested on the Udu data set. The subscript letters (e and b) for the various model parameters indicate which of the two mangrove species that parameter belongs to (e = *Excoecaria agallocha,* b = *Bruguiera gymnorhiza*). Scale: data/1000.

5.4.6.5.1 Continuous Logistic Growth

Fig 5.41 portrays the logistic model fitted to the Udu mangrove data. The optimisation routine has interpreted these two species as having a long-term positive growth rate of very small value (see Table 5.16). A long-term, interactive steady-state was predicted for this small swamp basin.

It seems unlikely that either the model or data of fig 5.41 could reasonably be interpreted as stable logistic growth. Firstly, the expansion and contraction of *Excoecaria agallocha* approximates a 100 CAL. year cycle, as is evident in the data sets of the other two core sites (ref. section 5.4.3.2 Chapter 5). It seems unlikely that a trend which is consistent over three spatially separate core sites is the result of measurement, depositional or geological error.

Secondly, the concentration of *Bruguiera gymnorhiza* approximates zero for much of the history of the site. *Bruguiera gymnorhiza* is known to deposit pollen very close to the parent plant and these results could suggest that the *Bruguiera gymnorhiza* forest stand was some distance from the present day seaward end of the swamp from which this core was taken. However, the geomorphological setting of this small swamp basin suggests that this explanation is unlikely. It seems more likely that *Bruguiera gymnorhiza* has only been introduced in the late stages of the infilling of this swamp basin with mangrove forest.

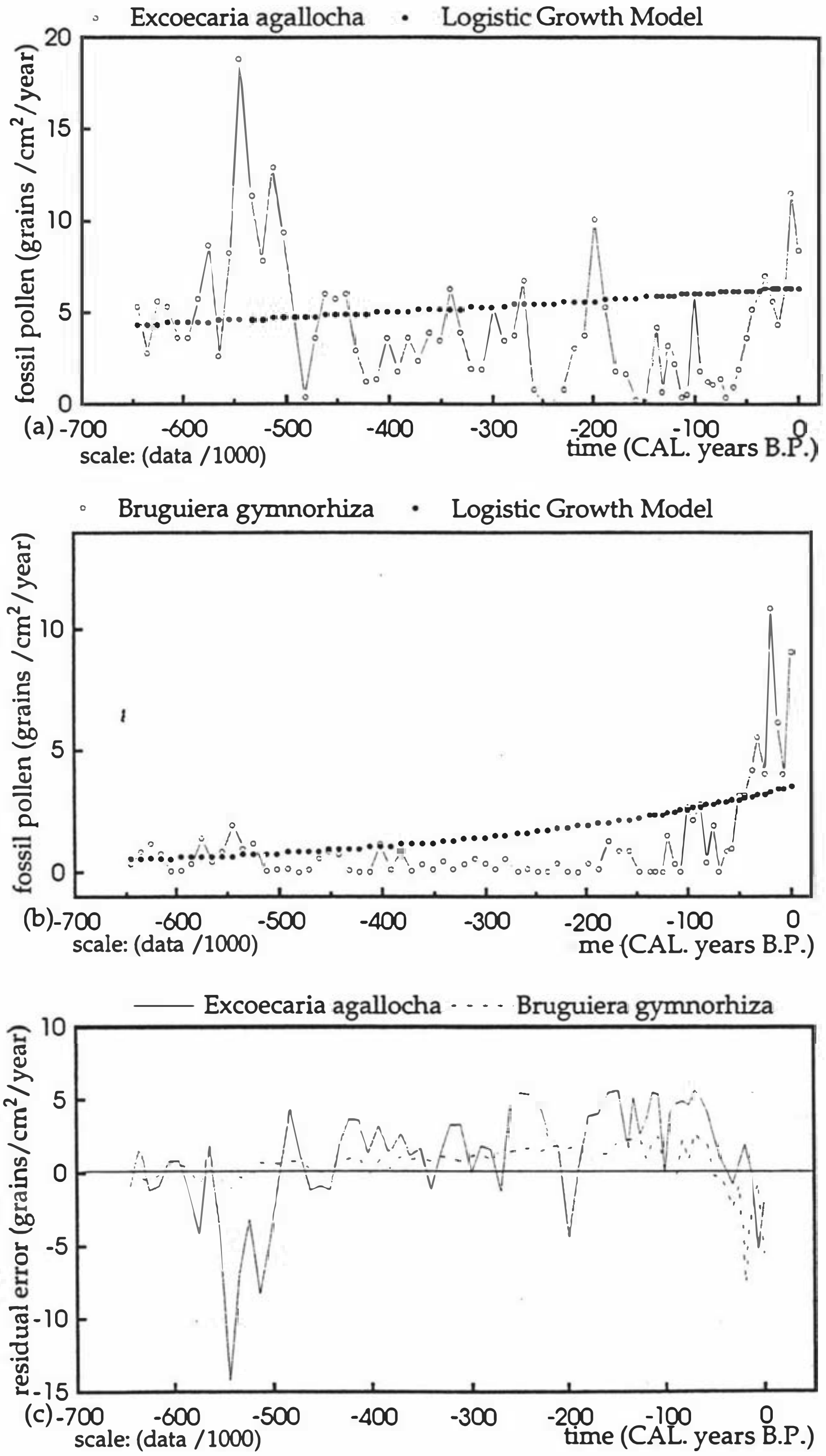


Fig 5.41 The Udu core site - logistic growth model fitted to (a) *Excoecaria agallocha* and (b) *Bruguiera gymnorhiza* with (c) residual error.

Thirdly, a logistic interpretation requires acceptance of the fact that *Excoecaria agallocha* has spent the last 650 CAL. years in the initial stages of logistic growth and it seems rather odd that during all this time it has never attained a steady-state. *Excoecaria agallocha* has expanded to very high concentrations of fossil pollen (population density) in the past, only to return to low values again.

5.4.6.6.2 Coupled Logistic Growth

Fig 5.42 portrays the coupled logistic model fitted to the Udu mangrove data. The fossil pollen data shows that this community has only existed in an intermixed state in very recent times (ca. 100 CAL. Years). Furthermore, the recent data of the two mangrove species actually shows evidence of mutualistic, not competitive behaviour. This behavioural observation appears to be reflected in the competition coefficients returned by the optimisation routine (see Table 5.16).

Negative competition co-efficients become positive when used in the coupled logistic equation which already has negative signs for these coefficients. The resultant positive coefficients are indicative of mutualistic behaviour. This in turn, implies that the density region up to approximately 10,000 grains cm^{-2} CAL. year^{-1} is a low density region.

It is interesting to speculate as to whether this mutualistic behaviour will eventually be curbed by density-dependent competition, or whether the mutual rise that can be seen at present will soon be followed by a fall, as has consistently been evidenced by the mangal of the Keteira core site.

Quite apart from those issues already mentioned, the coupled logistic model does a very poor job of explaining the variance in this data. This fact, coupled with current mutualistic behaviour, an absence of competitive effect in phase space, the recent introduction of *Bruguiera gymnorhiza* and the long term density vague behaviour of *Excoecaria agallocha* all indicate that this behaviour was not driven by competitive causal mechanisms.

5.4.6.6 The Constant Growth Trend Model Formulations

A total of five interactive optimisation and simulation trials were needed in order to fully evaluate the CGTM formulations tested in this experiment. The results of these trials are recorded in Table 5.17.

5.4.6.6.1 The Exponential CGTM

At the Keteira core site, the exponential CGTM gave the very best results of the all the CGTM formulations tested. Fig 5.43 records the results of modelling the Udu mangrove data with the exponential CGTM. This model fit involves an eight sample point time delay which equates to a time delay of ca. 71 CAL. years. A number of observations may be made from these results.

Firstly, the parameters listed in Table 5.17 for the exponential CGTM have produced a good fit to the mangrove data in more recent times, but not during the early history of the swamp, at which time *Excoecaria agallocha* was the dominant of the two species.

Secondly, the behaviour of the model does a slightly better job of predicting the variance in *Bruguiera gymnorhiza* than it does that of *Excoecaria agallocha*.

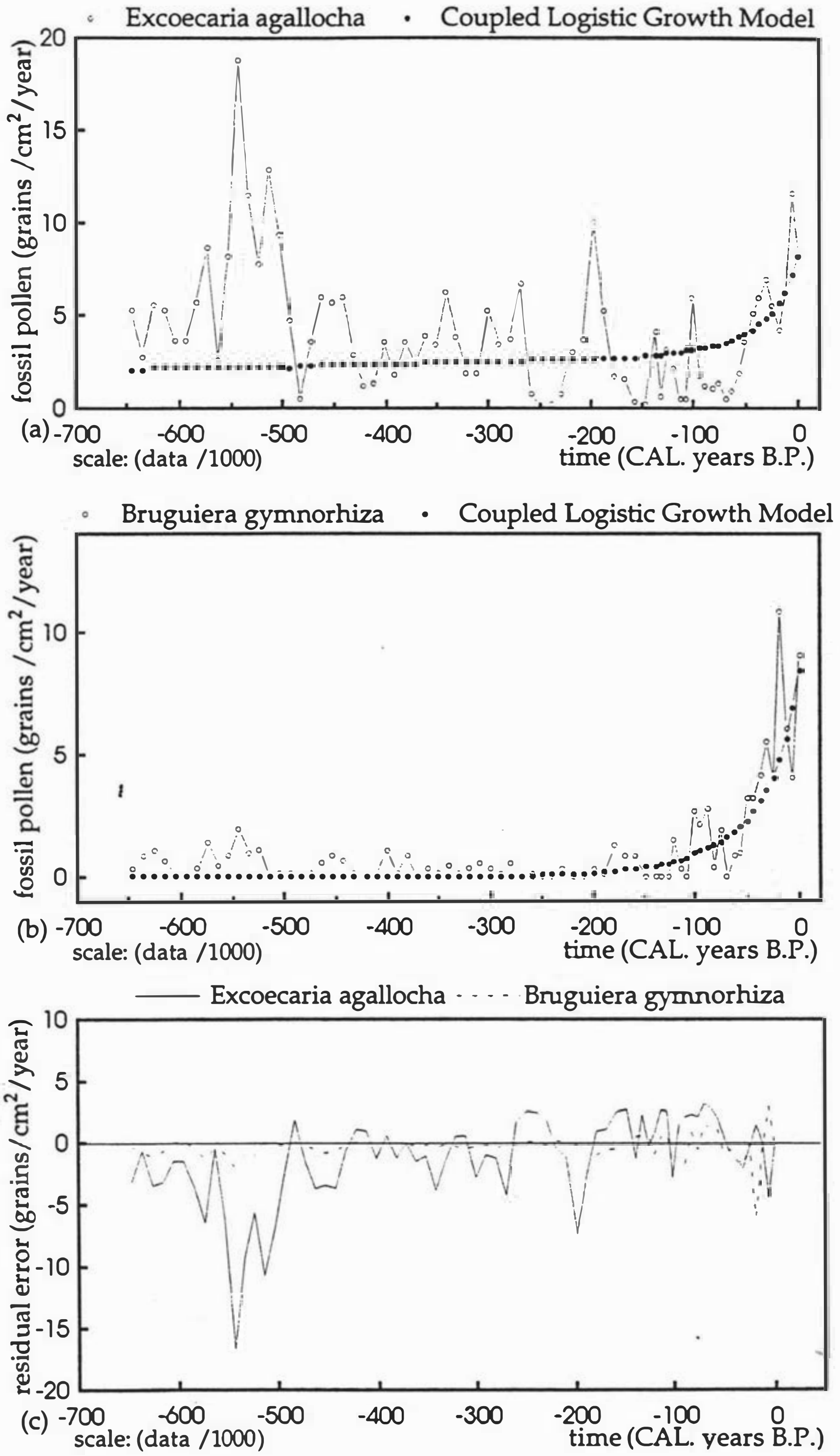


Fig 5.42 The Udu core site - coupled logistic growth model fitted to (a) *Excoecaria agallocha* and (b) *Bruguiera gymnorhiza* with (c) residual error.

Finally, much of the early history of *Excoecaria agallocha* is unexplained by the model. In this model formulation, the behaviour of the model is a response to the existence of variance in the charcoal fragment concentration. Therefore, poor model variance is a direct result of poor variance in the charcoal record for that time period. This explanation raises a question concerning the present site. Why is the final rise (100 - 0.0 CAL. years) of these two mangrove data sets modelled reasonably well when the greatest charcoal peaks occur in the earliest history of the core site (ca. 645 - 500 CAL. years B.P.)? (see fig 5.18). The above observation suggested to the author that two different levels of disturbance intensity may be represented at this site for which a constant charcoal scaling parameter is inadequate.

CGT Model Formulations	N_e	N_b	$r_c(exc.)$	$r_c(brug.)$	m_e	m_b	K_e	K_b	α	β
exponential	5.0484	7.7712	0.8	0.6524	-8.6	-7.1				
logistic	19.0484	2	0.1	0.1	-0.3	-0.8	30	30		
coupled logistic case I	19.041	2.008	0.0499	-0.870	-0.2	-0.8	30	30	-30	-3
coupled logistic case II	19.041	2.008	0.0499	-0.870	-0.2	-0.8	30	30	0.1	0.08
discrete exponential	0.1294	0.0001	0.007	0.004	-0.1	-0.1				

Table 5.17 Parameters for the logistic and coupled logistic equations tested on the Udu data set. The subscript letters (e and b) for the various model parameters indicate which of the two mangrove species that parameter belongs to (e = *Excoecaria agallocha,* b = *Bruguiera gymnorhiza*). The constant growth/reproductive rate parameter (r_c) also has a subscript to indicate to which mangrove species the parameter belongs. Scale: data/1000 for continuous models and data/100,000 for discrete time models. In every model the scale of the charcoal data is charcoal/1000.

This observation was tested in the interpretation stage of this experiment by trying to use a secondary forcing function (increasing sediment depth) to emphasise the effect of the charcoal in the early history of the site. The results of this experiment were very good and suggested that the charcoal scaling coefficient is not a constant and may change in response to non-linear processes like sedimentation rate.

5.4.6.6.2 The Logistic CGTM

Fig 5.44 portrays the behaviour of the logistic CGTM for parameter values recorded in Table 5.17. This model also has an eight sample point time delay which equates to a time delay of ca. 71 CAL. years. These results again show that the model is insensitive to the small changes in charcoal fragment concentration. While the model captures more of the long-term trend in the data, it largely fails to explain the variance. Furthermore, the model now appears to be out of phase with the Mangrove data in some areas. In other words, the variance that does exist in the model does not predict the exact timing of variance in the mangrove data.

5.4.6.6.3 The Coupled Logistic CGTM

Figures 5.45 and 5.46 portray the behaviour of the coupled logistic CGTM for the two sets of parameter values recorded Table 5.17.

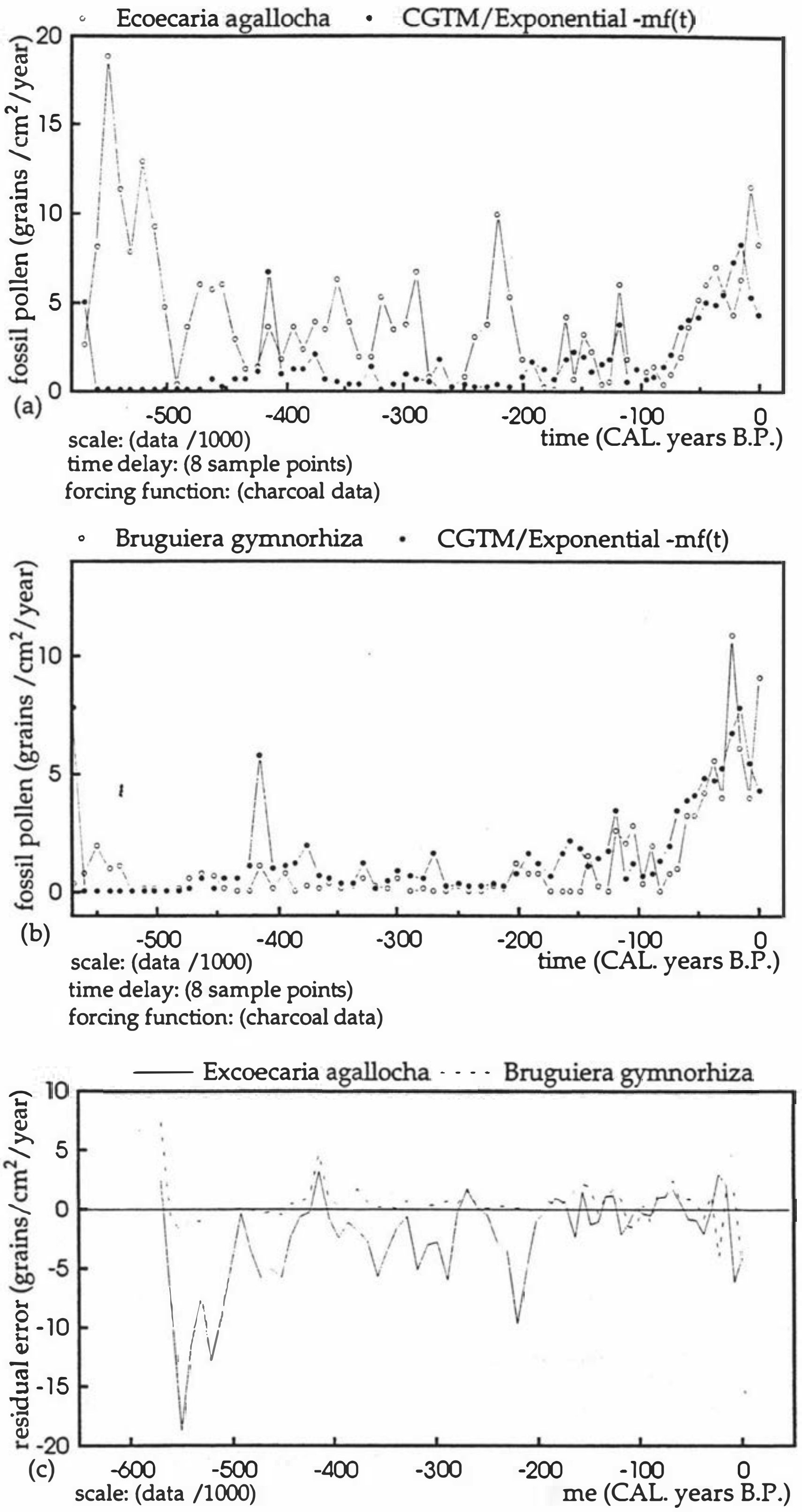


Fig 5.43 The Udu core site - exponential CGTM with 8 point time delay for (a) *Excoecaria agallocha* and (b) *Bruguiera gymnorhiza* with (c) residual error.

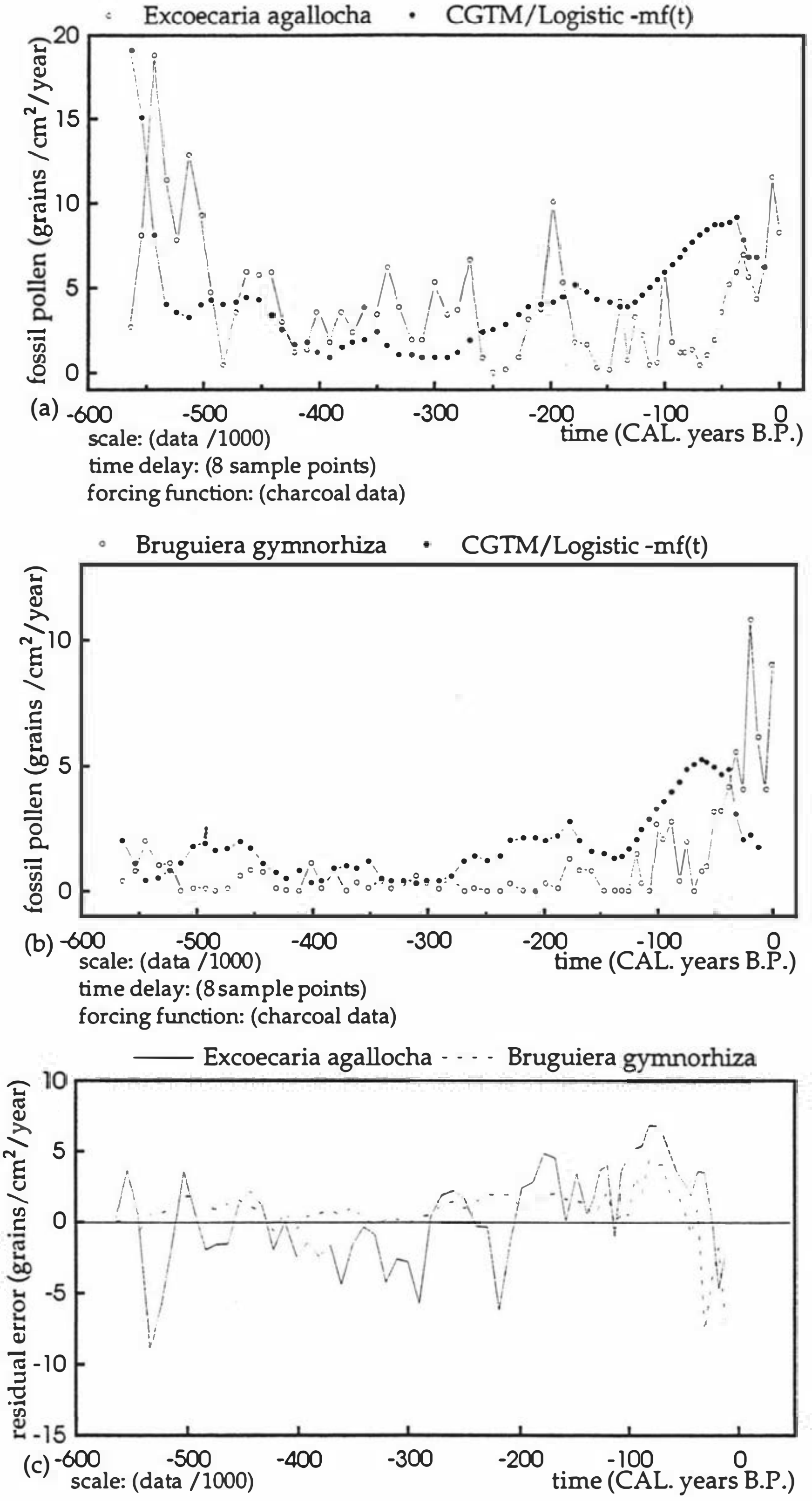


Fig 5.44 The Udu core site - logistic CGTM with 8 point time delay for (a) *Excoecaria agallocha* and (b) *Bruguiera gymnorhiza* with (c) residual error.

An eight sample point time delay is also involved in this data set. These results demonstrate once again, that it is possible to interpret this mangrove data as being competitive or mutualistic. This formulation of the Coupled Logistic

CGTM is not capable of discriminating between these two behavioural types in this region of parameter space. Secondly, the general comments made above, concerning the logistic CGTM, also apply to the results of the behaviour of this model.

5.4.6.6.4 The Discrete Exponential CGTM

Fig 5.47 portrays the behaviour of the discrete exponential CGTM based on the parameter values recorded in Table 5.17. A thirteen sample point time delay is now required and represents a time delay of ca, 113 CAL. years. These results once again indicate a long-term steady trend with rises and falls. However, the variance in the model now has little correspondence to the mangrove data. This model has similar behaviour performance to the logistic and coupled logistic CGTM, neither of which have done a particularly good job of predicting the mangrove data.

5.4.6.7 Interpretation

It requires careful evaluation of a model construct in order to determine just which causal mechanism is responsible for the failure of a model to predict field data behaviour. In this context, there are two distinct problems with the CGTM formulations tested above.

Firstly, poor predictive performance appears to be the result of insensitivity to extremes of charcoal fragment concentration.

It appears that a constant charcoal scaling parameter is just not adequate over very large and very small charcoal concentrations such as those found at the Udu and Lawakilevu core sites. Could this imply that the charcoal (as a proxy) has no effect on these populations? This seems unlikely in light of the results of experiment one. At this site, the charcoal signal is relatively even and therefore suits a constant scaling parameter. This explanation of parameter insensitivity can be easily tested and will be, later in this section.

Secondly, the poor predictive performance of the continuous logistic CGTM and coupled logistic CGTM appears to result from a range of problems that are compounded by insensitivity to the charcoal signal. For example, the optimisation results from the coupled logistic suggest that the behaviour of these two mangrove species is mutualistic and not competitive. Also, there is no evidence in phase space of interspecific competitive processes. Furthermore, persistence in a low density region will not only disfavour interspecific competition, it disfavours intraspecific competition and probably explains a lack of *logistic growth behaviour.*

The final CGTM formulation tested was the discrete exponential CGTM. This model construct is non-equilibrium and therefore not complicated by the equilibrium problems mentioned above. This model will be influenced to a degree by the charcoal parameter insensitivity problem mentioned above.

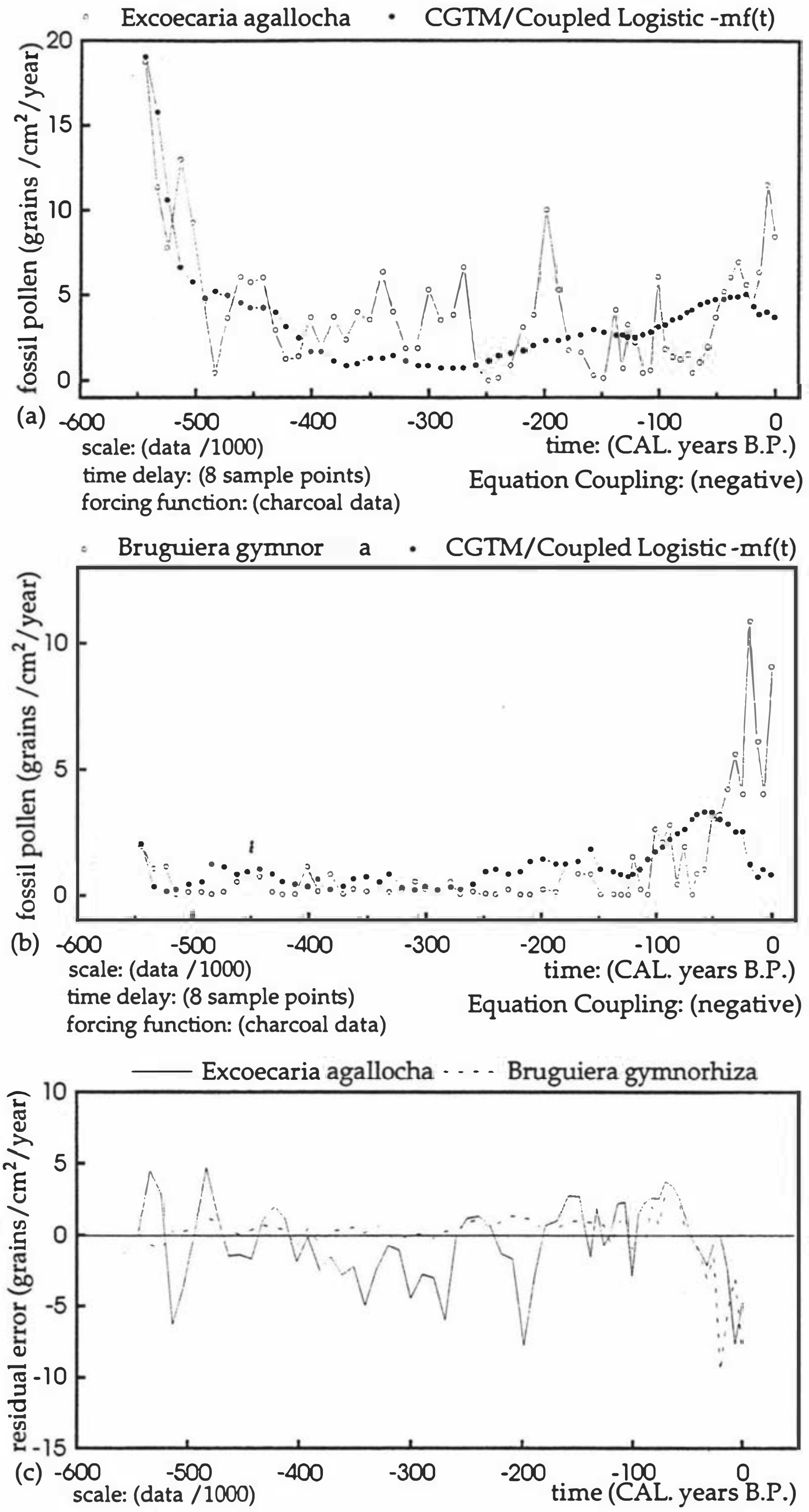


Fig 5.45 The Udu core site - coupled logistic CGTM (negative coefficient) with 8 point time delay for (a) *Excoecaria agallocha* and (b) *Bruguiera gymnorhiza* with (c) residual error.

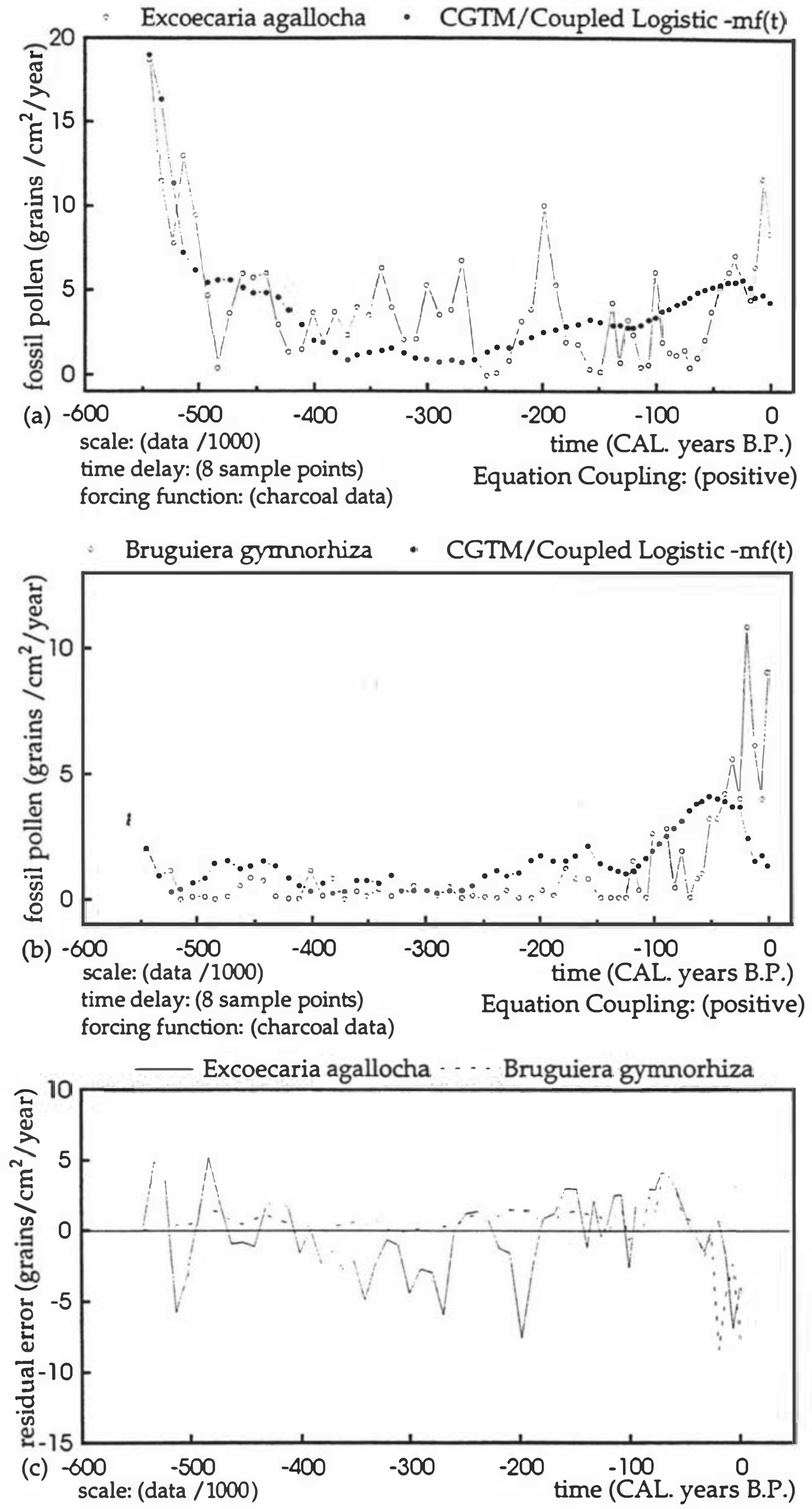


Fig 5.46 The Udu core site - coupled logistic CGTM (positive coefficient) with 8 point time delay for (a) *Excoecaria agallocha* and (b) *Bruguiera gymnorhiza* with (c) residual error.

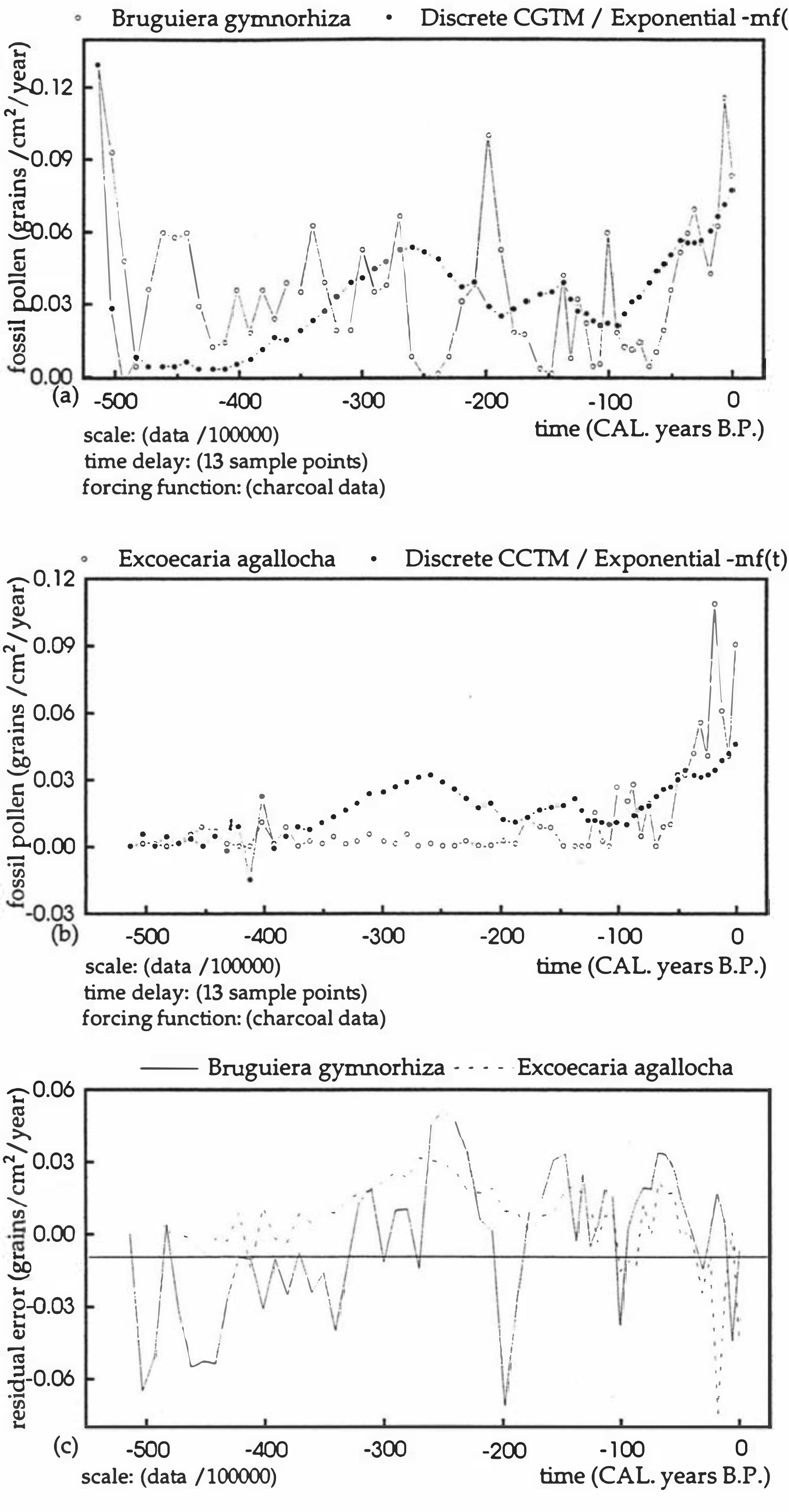


Fig 5.47 The Udu core site - discrete exponential CGTM with 8 point time delay for (a) *Excoecaria agallocha* and (b) *Bruguiera gymnorhiza* with (c) residual error.

However, taking these factors into consideration, the performance of this model is not nearly as good as that of the exponential CGTM (fig 5.43). It seems that the main failure of the continuous exponential CGTM is in its inability to respond to large variance in charcoal fragment concentrations. This *a posteriori* hypothesis is tested in the next section.

5.4.6.8 Model Reformulation

Based on the results of experiment two, it is now clear that the logistic, coupled logistic, logistic CGTM and coupled logistic CGTM are not capable of predicting the behaviour of the Udu Mangal. The causal mechanisms at fault appear to be both parameter insensitivity to charcoal forcing and low density community structure, which is unsuitable for competitive processes.

5.4.6.8.1 Parameter Insensitivity

The parameter insensitivity problem can be tested by the use of a secondary forcing function (62) (sediment depth data).

$$\frac{dN}{dt} = r_c + (mf(t) + sf(t))N \tag{62}$$

In equation 62, m and s are scaling constants for the two forcing functions. The reason for combining the effect of the two forcing functions is so that the charcoal forcing function is weighted by the influence of the sediment depth function. A plot of sediment depth against time for this site (fig 5.48) shows this relationship. Equation 62 was simulated using the parameter values recorded in Table 5.18.

The reason for choosing sediment depth as a secondary forcing function reflects an attempt at an approximation only. If the Udu mangrove forest responds to changes in sedimentation rate, then this is likely to be a quite complex nonlinear function, which would require lots of AMS dating in order to reconstruct. By contrast the present function is rather simplified but should be adequate to identify the existence of any relationship.

CGT Model	N_e	N_b	r_c *Exco.*	r_c *Brug.*	m_e	m_b	s_e	s_b
exponential	2.25	0.15	1.18	0.17	-0.03	-0.12	-.0006	-.0001

Table 5.18 Parameters used in simulating the exponential CGTM with secondary forcing function.

Fig 5.49 portrays the behaviour of the exponential CGTM with secondary forcing function based on the parameter values recorded in Table 5.18. These results are in sharp contrast with those presented earlier (fig 5.43) which shows the exponential CGTM without the addition of a secondary forcing function. The insensitivity of the exponential CGTM to large changes in charcoal concentration is evident from these two sets of results. In order to predict the Udu mangrove data adequately, two model constructs are required.

A composite plot illustrating the predictive power of both model constructs combined is given in fig 5.50. In this illustration, the limitations of the secondary forcing function can be seen.

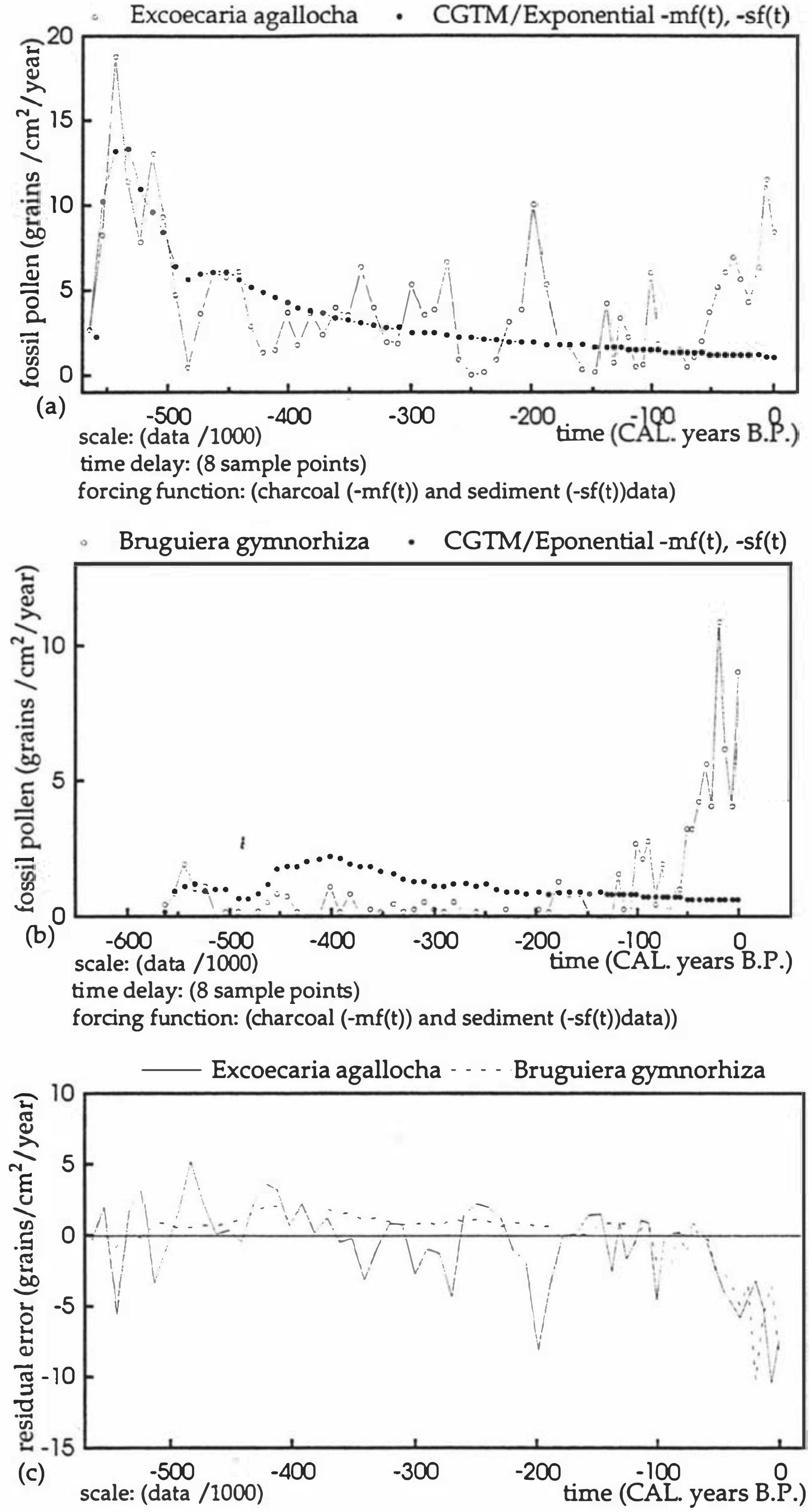
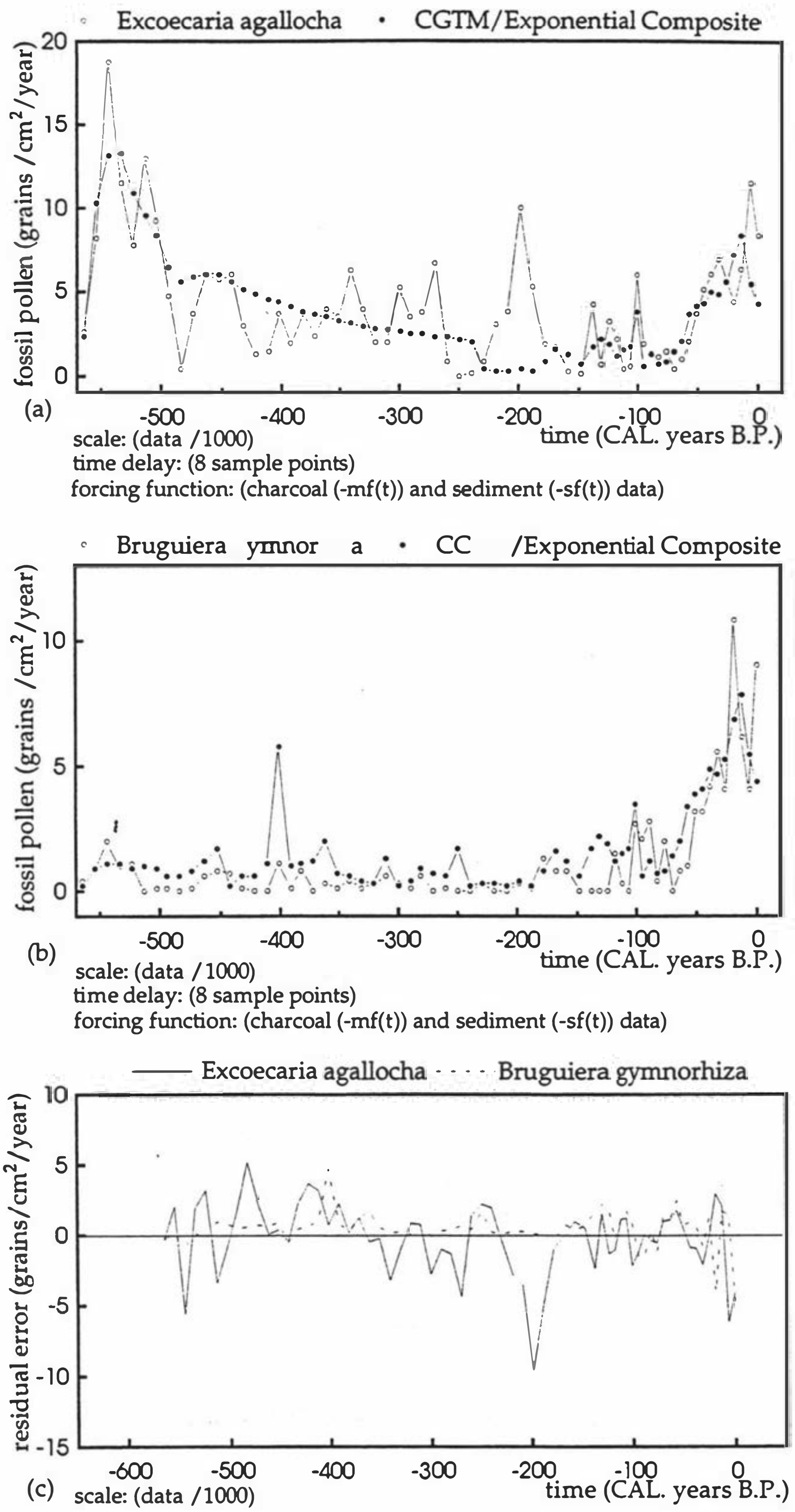


Fig 5.49 The Udu core site - exponential CGTM with 8 point time delay for (a) *Excoecaria agallocha* and (b) *Bruguiera gymnorhiza* with (c) residual error.



(a) scale: (data / 1000)
time delay: (8 sample points)
forcing function: (charcoal (-mf(t)) and sediment (-sf(t)) data)

(b) scale: (data / 1000)
time delay: (8 sample points)
forcing function: (charcoal (-mf(t)) and sediment (-sf(t)) data)

(c) scale: (data / 1000)

Fig 5.50 The Udu core site - exponential CGTM (composite plot) with 8 point time delay for (a) *Excoecaria agallocha* and (b) *Bruguiera gymnorhiza* with (c) residual error.

Fig 5.50 demonstrates that it is possible to predict the long term behaviour of the Udu mangal by using a complex non-linear forcing function to drive the behaviour of these populations. These models reflect behavioural limitations which may be improved by the use of a more complex secondary forcing functions.

Rather than finding contradictory evidence with which to reject the hypothesis of *stochastic domination* for this core site, these results support many of its predictions. Rather than finding supportive evidence with which to confirm the *mangrove equilibrium hypothesis,* these results allow the rejection of this hypothesis.

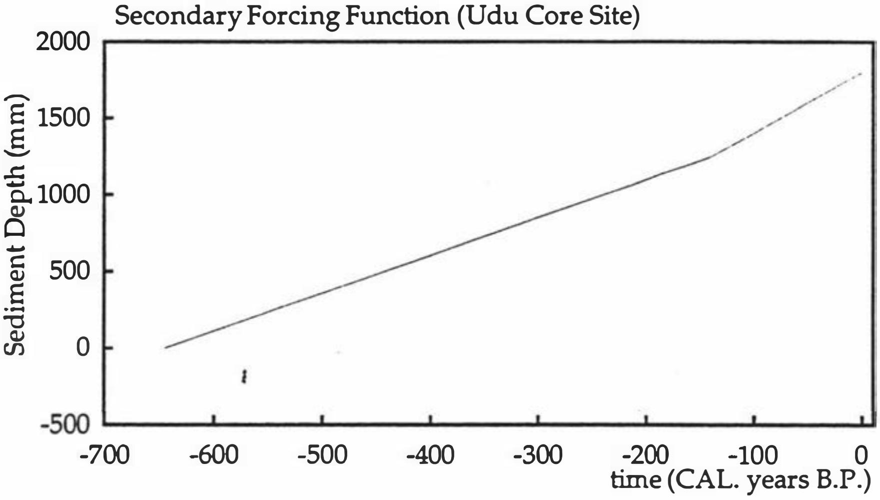


Fig 5.48 A secondary forcing function for the exponential CGTM.

5.4.7 Experiment Three - Lawakilevu Data

Interpretation of the results of experiment two and reformulation of the initial *stochastic domination* model construct presents a new hypothesis to be tested in experiment two. In experiment two, the following alternative hypotheses are tested against the Udu Mangrove data.

5.4.7.1 Mangrove Equilibrium Theory

The initial equilibrium hypothesis remains and must now be tested at the Lawakilevu core site.

5.4.7.2 Mangrove Succession Theory

The initial mangrove succession theory hypothesis was rejected, based on the results of experiment one. This hypothesis was replaced with a new hypothesis based on stochastic domination as a primary causal mechanism.

5.4.7.3 Stochastic Domination - New Hypothesis

It is now predicted *a priori,* that contradictory evidence will be found at the Lawakilevu core site to reject this hypothesis. Based on the reformulation results of experiment two, a new prediction can now be added to this hypothesis. It is now evident that over very long time periods the stochastic forces disturbing a community change in intensity. Each time period of characteristic disturbance results in population behaviour which may be defined by that *disturbance region* in the history of the site.

The existence of differing disturbance regions implies that it will not always be possible to model the behaviour of such a system using a constant forcing function scaling parameter. This procedure did work at the Keteira core site only because the time period covered by this site appears to have had a very constant level of disturbance which is reflected in the behaviour of the mangrove data. This hypothesis can be tested at the Lawakilevu core site by comparing the performance of the exponential CGTM with and without secondary forcing function (based on sedimentation rates as per fig 5.48). Lawakilevu sample depth and CAL. sample age data will be used to construct a secondary forcing function to test the strength of this prediction.

5.4.7.4 ***Phase Portraits***

Fig 5.51 portrays three phase portraits based on the state variables of the two mangrove species at the Lawakilevu core site. Individual plot axes have been standardised for comparative purposes. Once again, the data has been transformed using a four point moving average (fig 5.51b) and a single exponential smoothing filter (fig 5.51c).

None of the results portrayed in fig 5.51 give any indication of the qualitative behaviour predicted by the coupled logistic equation (50a, b) (section 2.4.6.2, Chapter 2). As was found at the other two core sites, these results suggest that the behaviour of the Lawakilevu mangal is not being driven by density-dependent interspecific competition.

5.4.7.5 ***The Logistic and Coupled Logistic Models***

Once again, the optimisation software and an evolutionary approach to parameter estimation were used in the following trials. Parameter estimation results are recorded in Table 5.19. The upper asymptotic population density (K) for this site has been estimated at 30 grains cm^2 CAL. years^{-1} B.P. using the same procedure outlined for the Keteira core site.

Model	N_e	N_b	r_e	r_b	K_e	K_b	α	β
exponential	0.5	0.2	0.0032	0.0037				
logistic	0.5	0.2	0.0032	0.0037	30	30		
coupled logistic	0.5564	0.0042	0.0103	0.0147	30	30	220	-0.1

Table 5.19 Parameters for the logistic and coupled logistic equations tested on the Lawakilevu data set. The subscript letters (e and b) for the various model parameters indicate which of the two mangrove species that parameter belongs to (e = *Excoecaria agallocha*, b = *Bruguiera gymnorhiza*). Scale: data/1000.

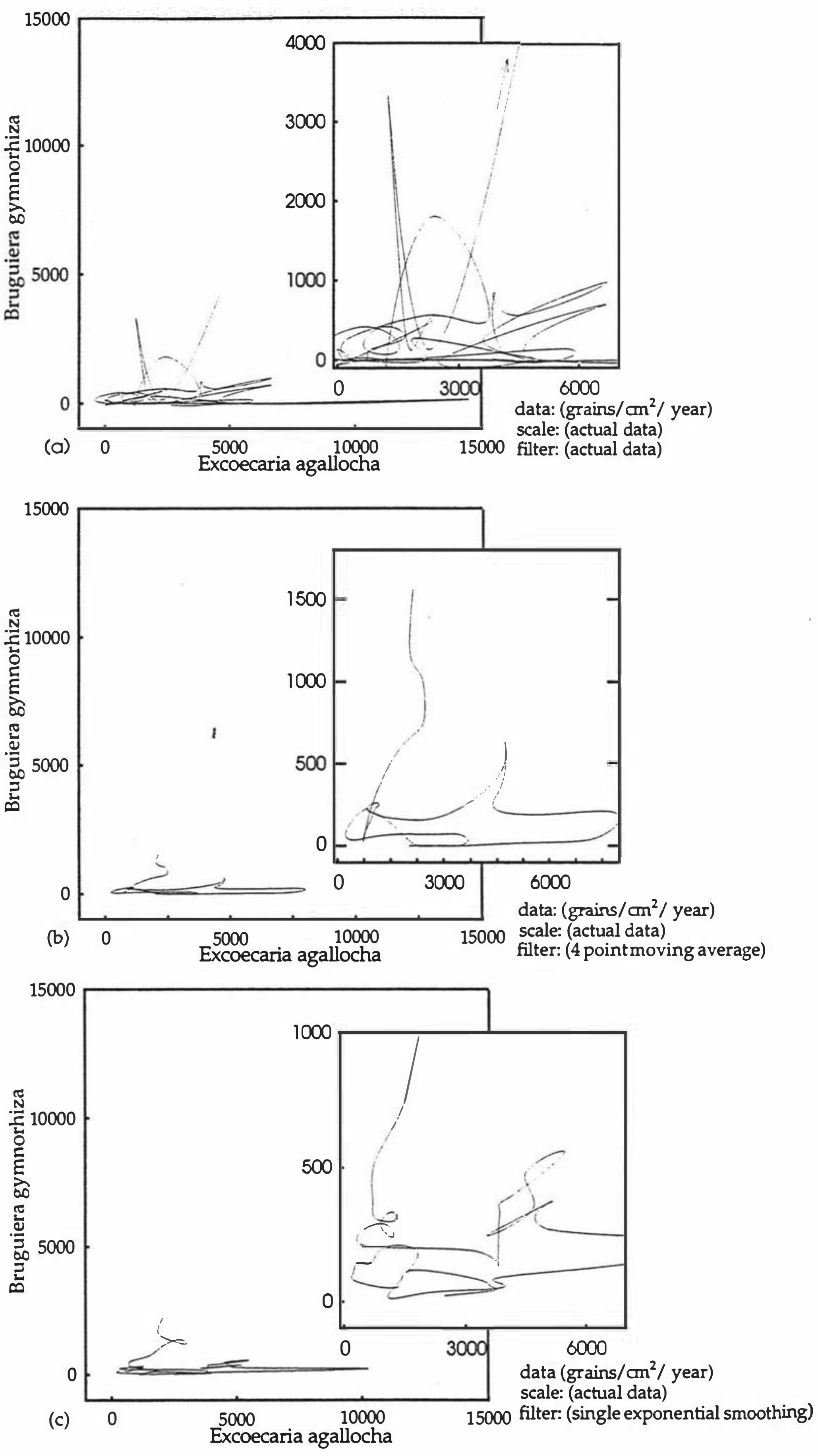


Fig 5.51 Phase Portrait for the Lawakilevu Core Site.

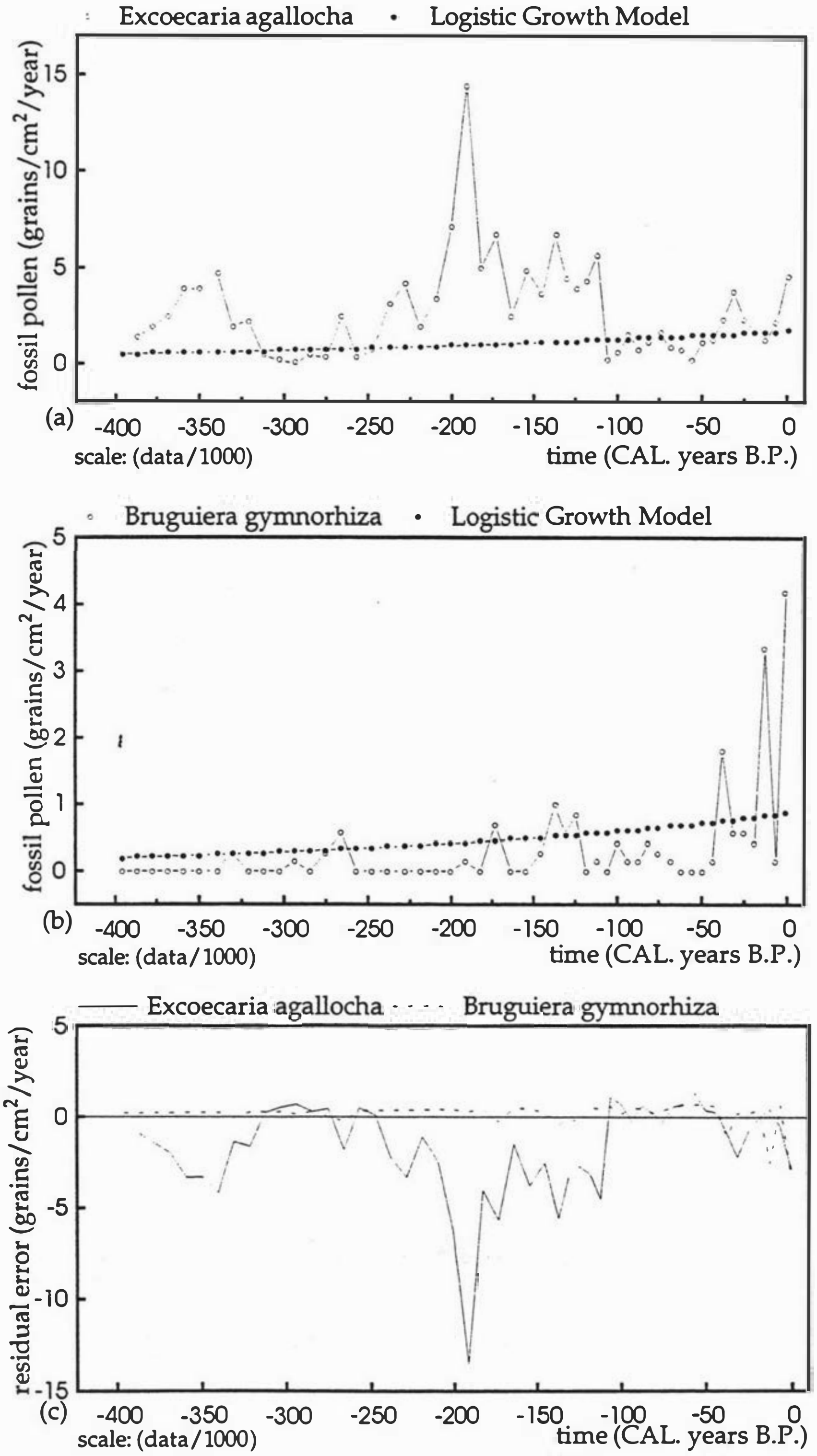


Fig 5.52 The Lawakilevu core site - logistic model fitted to (a) *Excoecaria agallocha*, (b) *Bruguiera gymnorhiza* and (c) residual error.

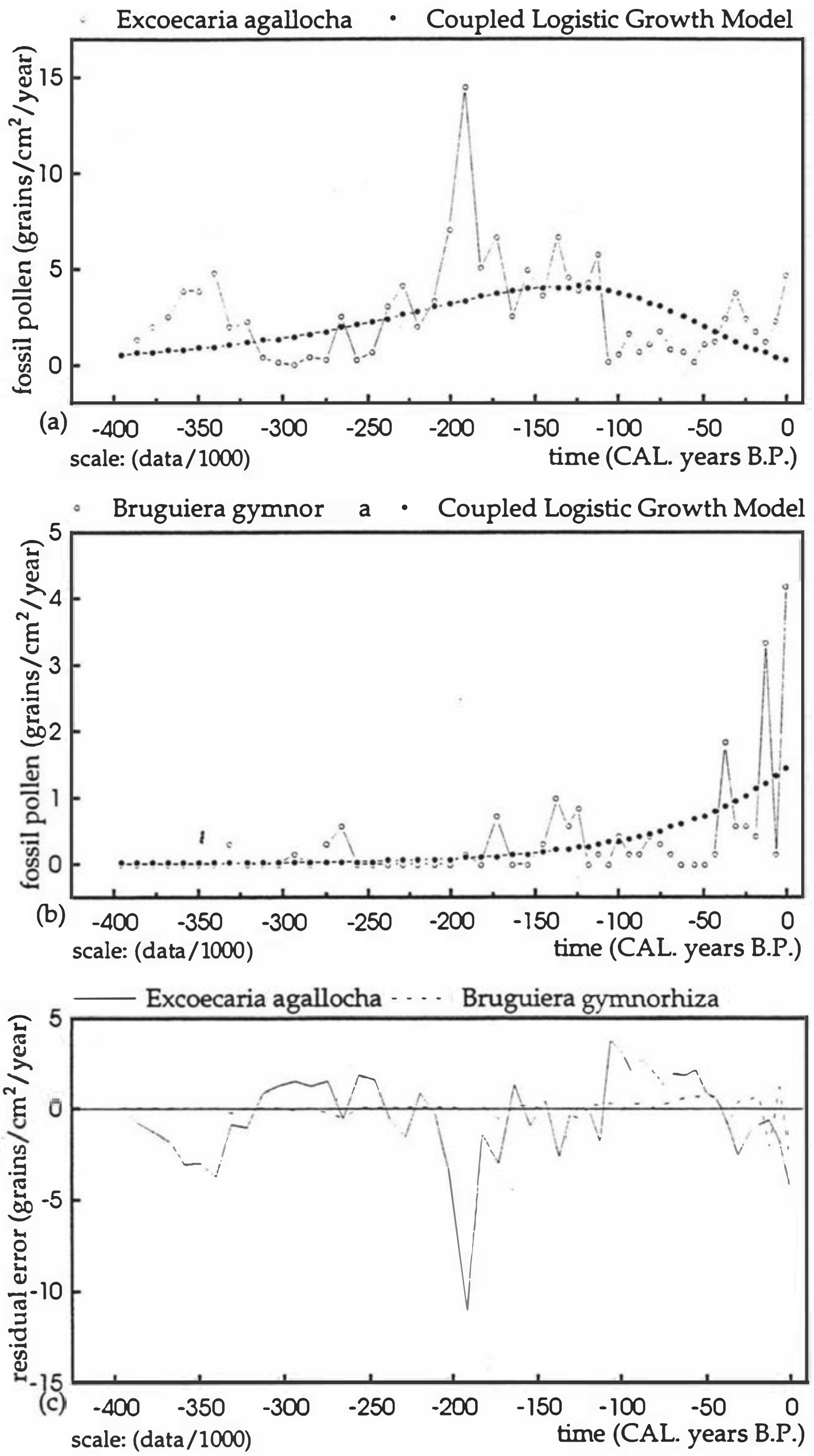


Fig 5.53 The Lawakilevu core site - continuous coupled logistic model fitted to (a) *Excoecaria agallocha,* (b) *Bruguiera gymnorhiza* and (c) residual error.

5.4.7.5.1 Continuous Logistic Growth

Fig 5.52 portrays the logistic model fitted to the Lawakilevu mangrove data for the parameter values listed in Table 5.19. There are some similarities between the mangrove data of this site and that of the Udu core site.

Firstly, the two main rises and falls of *Excoecaria agallocha* occur within time intervals that approximate 100 CAL. years (400 - 300, 250 - 100). This cyclical behaviour is suggestive of some common process between the three sites.

Secondly, both species remain within an intermediate to low density region, assuming that the upper asymptotic population density is ca. 40 (grains cm^{-2} year $^{-1}$). An intermediate to low density region may be insufficient to drive intraspecific competition and this probably explains the general absence of *logistic growth.*

Finally, the logistic model fails to explain the variance in the long-term behaviour of this system, none of which could easily be characterised as a logistic rise to a stable equilibrium.

5.4.7.5.2 The Coupled Logistic

Fig 5.53 portrays the coupled logistic model fitted to the Lawakilevu mangrove data, based on the parameter values outlined in Table 5.19. The optimisation software has interpreted the Lawakilevu mangrove data as a competitive struggle between the two mangrove species, although according to the parameters of Table 5.19, *Bruguiera gymnorhiza* has a mutualistic and not competitive relationship toward *Excoecaria agallocha.*

The same problems already mentioned for the other two core sites apply when interpreting the behaviour of the two mangrove species at Lawakilevu as interspecific competition. This fact highlights the importance of using the optimisation software carefully as a tool to interpret data.

Based on a purely visual evaluation of the data, it appears that the two mangrove species at this core site have only recently (ca. 100 CAL. years) become an intermixed community. Prior to this time, the concentration of *Bruguiera gymnorhiza* has remained at critically low levels which may be typical of an invasion sequence for this species.

The equilibrium hypothesis for this site proposed that the community might attain a long-term steady-state as a result of swamp basin infilling. However, it is now clear that if this process has occurred, it has not involved an intermixed community of both species. *Excoecaria agallocha* has been the dominant species at both the Lawakilevu and Udu core sites for most of the history of the site.

Finally, it is difficult to say whether the present expansion of both species at these two core sites will be followed by a future competitive struggle or the return of both species to the low density region, as is evident in the 100 CAL. year mangal cycle at Keteira. The system must remain undisturbed if it is to reach the upper intermediate, to high density region, where competitive forces will attract it to an equilibrium. At the Udu, Lawakilevu and Keteira core sites on Totoya, environmental stochasticity appears to have been historically responsible for preventing stable equilibrium behaviour.

CGT Model Formulations	N_e	N_b	$r_c(exc.)$	$r_c(brug.)$	m_e	m_b	Ke	Kb	α	β
exponential case I	3.895	0.001	0.3	0.05	-0.2	-0.2				
exponential case II	3.895	0.001	0.7	0.008	-0.3	-0.9				
exponential case III	3.895	0.001	0.7	0.008	-0.3	-0.9	-	-	s_e 0.008	s_b 0.0005
logistic	0.2	0.001	0.7	0.07	-0.5	-.07	30	30		
coupled logistic case I	0.199	0.0009	0.57	0.042	-0.7	-0.3	30	30	-0.008	-0.02
coupled logistic case II	0.199	0.0009	0.57	0.042	-0.7	-0.3	30	30	0.0001	0.0001

Table 5.20 Parameters for the CGTM formulations tested on the Lawakilevu data set. The subscript letters (e and b) for the various model parameters indicate which of the two mangrove species that parameter belongs to (e = *Excoecaria agallocha,* b = *Bruguiera gymnorhiza*). The constant growth/reproductive rate parameter (r_c) also has a subscript to indicate which mangrove species the parameter belongs to. Scale: data/1000 for continuous models and data/100,000 for discrete time models, charcoal/1000. Secondary forcing parameters are indicated by s_e and s_b.

5.4.7.6 The CGTM Formulations

A total of six interactive optimisation and simulation trials were needed in order to evaluate fully the CGTM formulations tested in this experiment with the Lawakilevu core site data. The results of these trials are recorded in Table 5.20.

5.4.7.6.1 The Exponential CGTM

Fig 5.54 portrays the behaviour of the exponential CGTM based on the parameter values recorded in Table 5.20. In case I of Table 5.20, the exponential CGTM has a delay of 4 sample points which equates to a time delay of ca. 28 CAL. years.

The above results may be contrasted with fig 5.55, which is based on the parameter values of the exponential CGTM in case II of Table 5.20. This model has a delay of 12 sample points which equates to a time delay of ca. 111 CAL. years. Comparing these two sets of plots involves an evaluation of good and bad points on both sides. The cause of these differences once again appears to result from an insensitivity of the model to very small values of charcoal concentration for most of the history of the community, compared with the very large values early in the history of the system (see fig 5.17).

In case I (fig 5.54), a 28 CAL. year time delay provides greater freedom for the model to explain the very low values of *Bruguiera gymnorhiza.* Also, the model does a reasonably good job of explaining the sudden decline in *Excoecaria agallocha* at ca. 120 - 100 CAL. years B.P. Furthermore, the sudden rise of *Excoecaria agallocha* at ca. 220 - 180 CAL. years B.P. is not included in the behaviour of this model with a 28 CAL. year time delay.

In case II (fig 5.55), an 111 CAL. year time delay makes it almost impossible for the model to predict the behaviour of *Bruguiera gymnorhiza* at its very low values. However, the model does predict the large expansion of *Excoecaria agallocha* at ca. 220 - 180 CAL. years B.P. very well, but fails to predict the sudden decline of *Excoecaria agallocha* at ca. 120 - 100 CAL. years B.P.

In case III (fig 5.56), an attempt has been made to improve the charcoal data insensitivity problem by adding a secondary forcing function to the exponential CGTM and using a 12 sample point delay. This change has slightly improved the predictive capability of the model for both species. Some of the variance in *Bruguiera gymnorhiza* is now predicted. Furthermore, the secondary function better approximates the behaviour of *Excoecaria agallocha* from ca. 100 - 0.0 CAL. years B.P. However, the sudden decline of this species at 120 CAL. years B.P. is still poorly modelled.

A difference between the case III model for this site and the exponential CGTM with secondary forcing function used for the Udu site lies in the total number of explanatory equations required. The Udu site required two equations (1 exponential CGTM + 1 exponential CGTM with secondary forcing function) in order to near predict the mangrove data. The behaviour of these two equations was presented in a composite plot (fig 5.50). The Lawakilevu data has been predicted in fig 5.56 with only one exponential CGT equation employing a secondary forcing function. Further equations could be used to improve this behaviour.

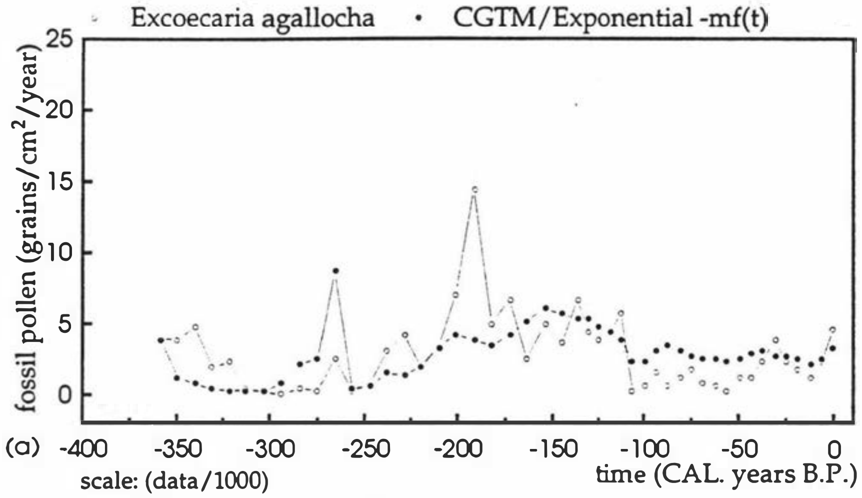
5.4.7.6.2 *The Logistic CGTM*

Fig 5.57 portrays the behaviour of the logistic CGTM based on parameter values recorded in Table 5.20.The behaviour of this model is also based on a 12 sample point delay and is very comparable to that of the exponential CGTM with 12 sample point delay (fig 5.55). By contrast, the logistic CGTM formulation does have greater freedom to explain the behaviour of *Bruguiera gymnorhiza* .

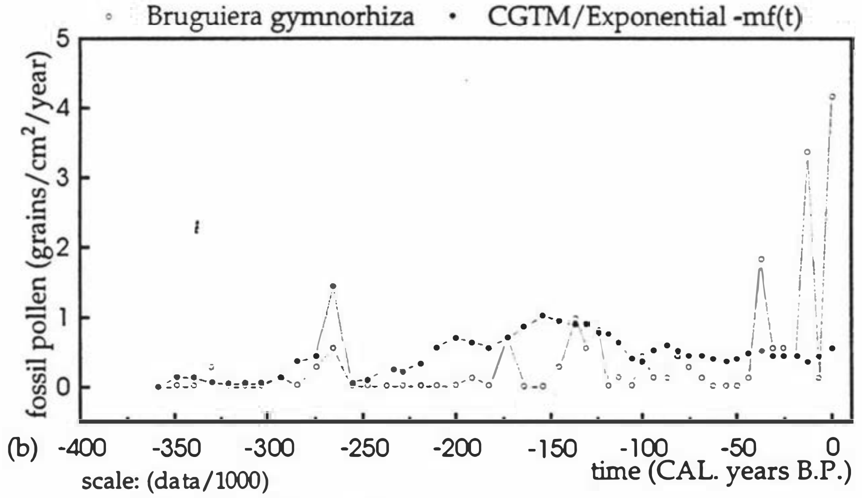
These differences in behaviour are very small, as are the differences in parameter values between the two models (see Table 5.20) - a fact that probably explains this behavioural similarity. In this context, the addition of an upper asymptotic density parameter makes very little behavioural improvement to the exponential CGTM. This is to be expected since the behaviour of the system is confined to an intermediate to low density region.

5.4.7.6.3 *The Coupled Logistic CGTM*

Fig 5.58 and fig 5.59 both portray the behaviour of the coupled logistic CGTM formulation based on parameter values for case I and case II in Table 5.20.



scale: (data/1000)
time delay: (4 sample points)
forcing function: (charcoal data)



scale: (data/1000)
time delay: (4 sample points)
forcing function: (charcoal data)

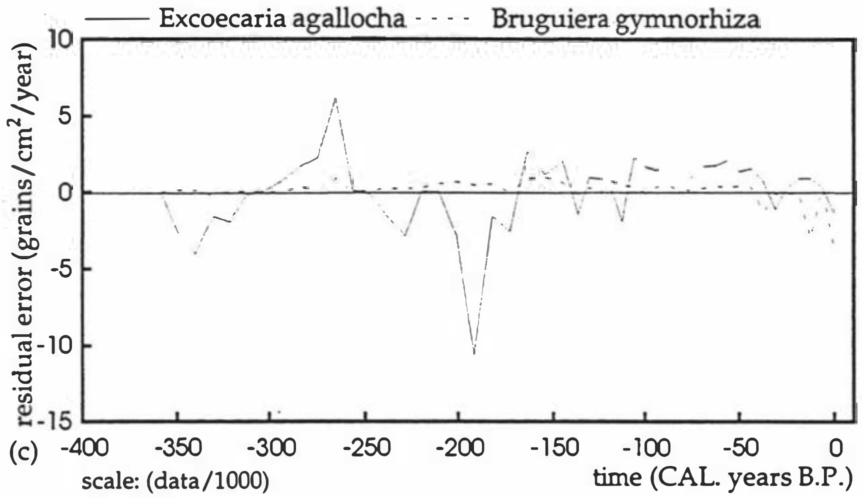


Fig 5.54 The Lawakilevu core site - exponential CGTM with 4 point time delay for (a) *Excoecaria agallocha* and (b) *Bruguiera gymnorhiza* with (c) residual error.

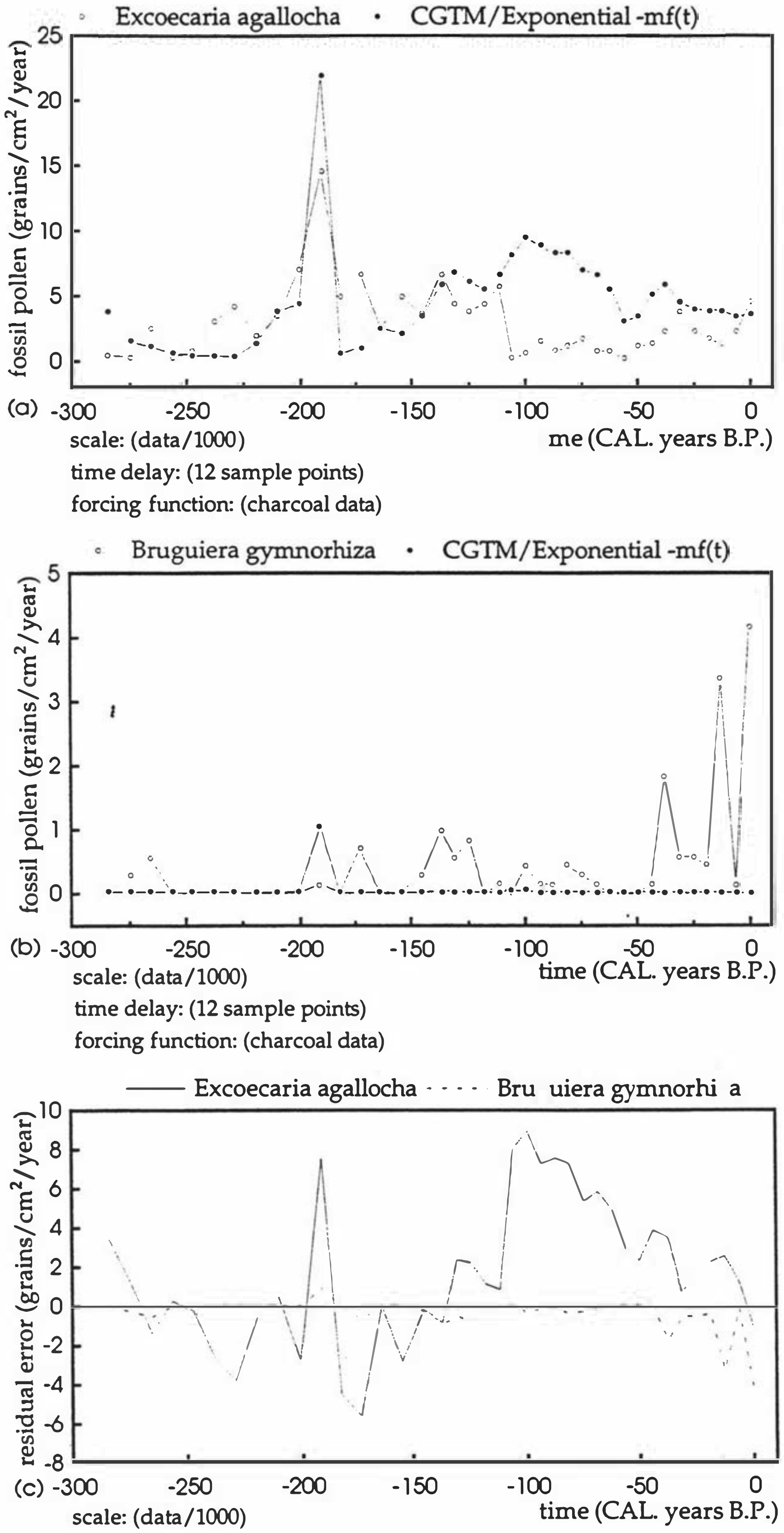
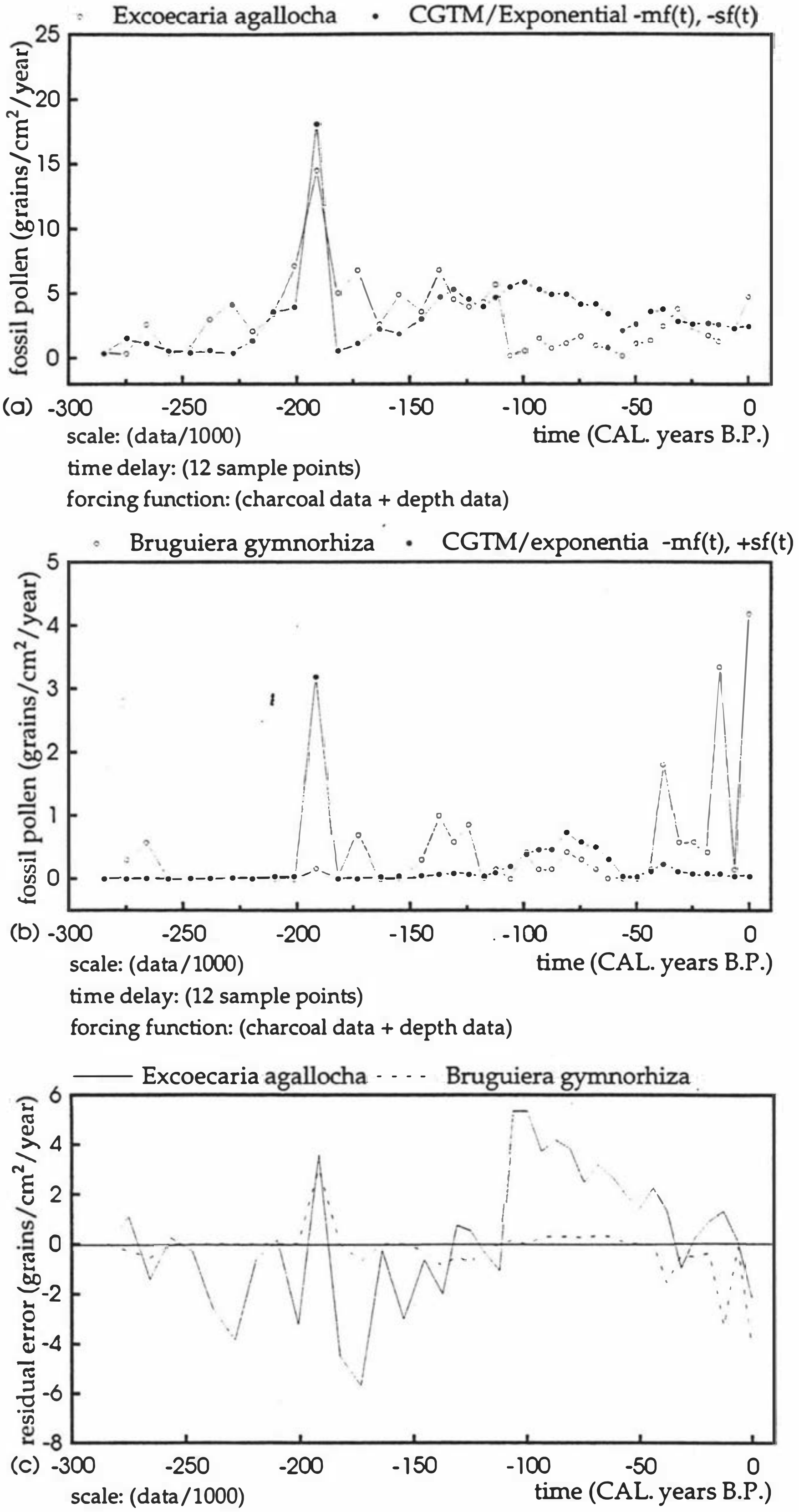


Fig 5.55 The Lawakilevu core site - exponential CGTM with 12 point time delay for (a) *Excoecaria agallocha* and (b) *Bruguiera gymnorhiza* with (c) residual error.



scale: (data/1000)
time delay: (12 sample points)
forcing function: (charcoal data + depth data)

scale: (data/1000)
time delay: (12 sample points)
forcing function: (charcoal data + depth data)

scale: (data/1000)

Fig 5.56 The Lawakilevu core site - exponential CGTM with 12 sample point time delay based on charcoal fragment and sediment data for (a) *Excoecaria agallocha* and (b) *Bruguiera gymnorhiza* with (c) residual error.

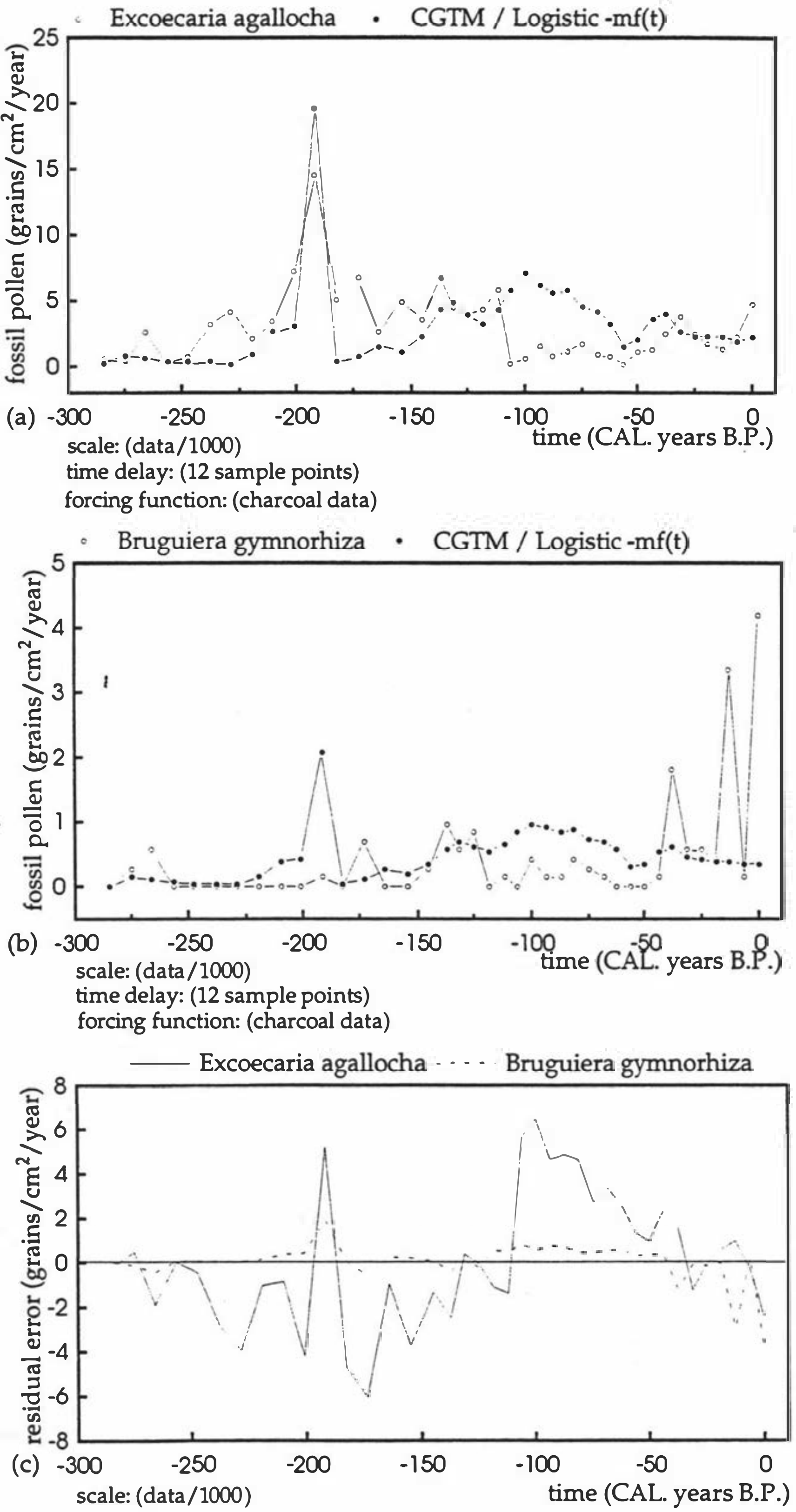


Fig 5.57 The Lawakilevu core site - logistic CGTM with 12 point time delay for (a) *Excoecaria agallocha* and (b) *Bruguiera gymnorhiza* with (c) residual error.

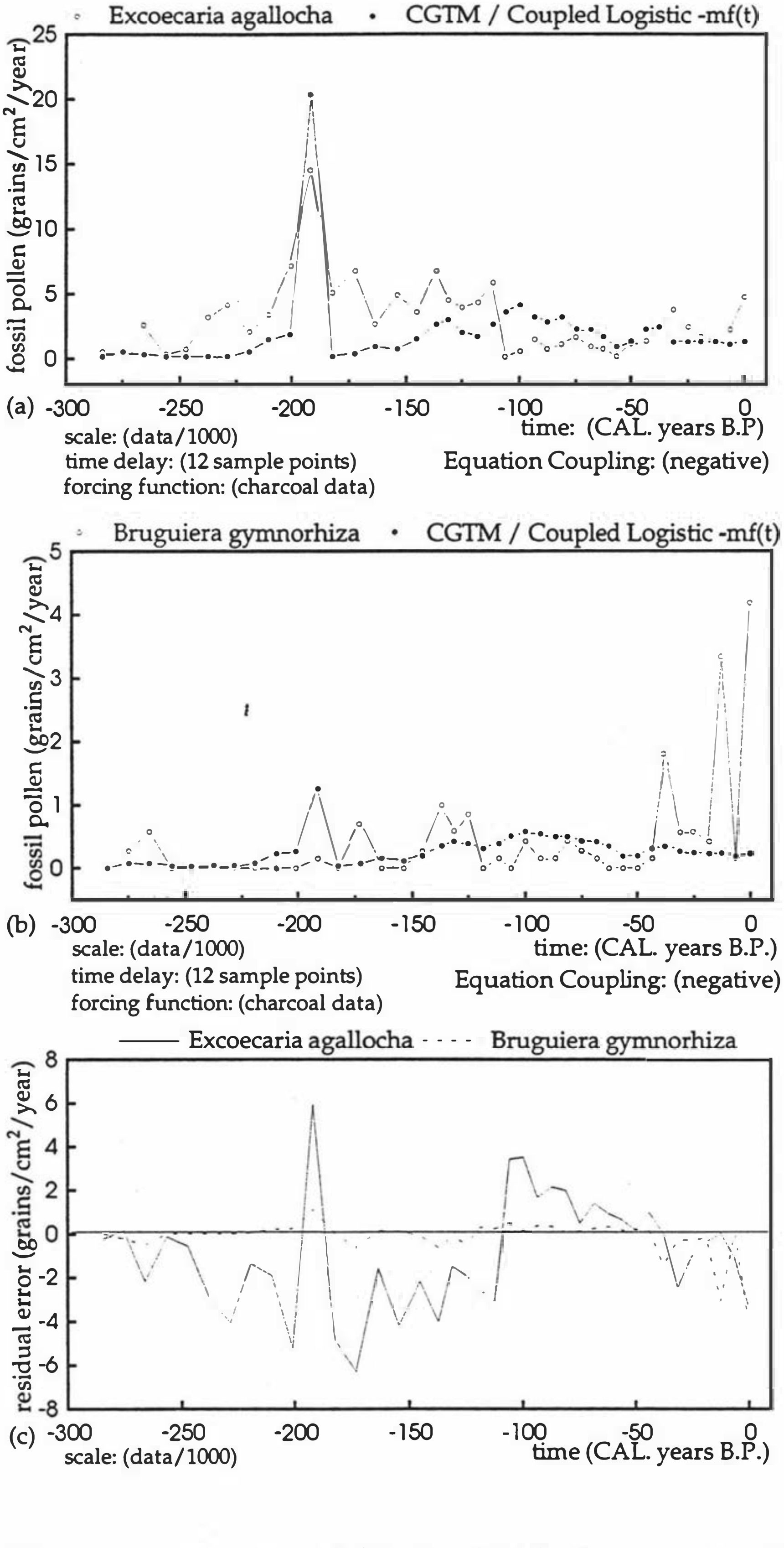


Fig 5.58 The Lawakilevu core site - coupled logistic CGTM with nega ive coupling and 12 poin time delay for (a) *Excoecaria agallocha* and (b) *Bruguiera gymnorhiza* with (c) residual error.

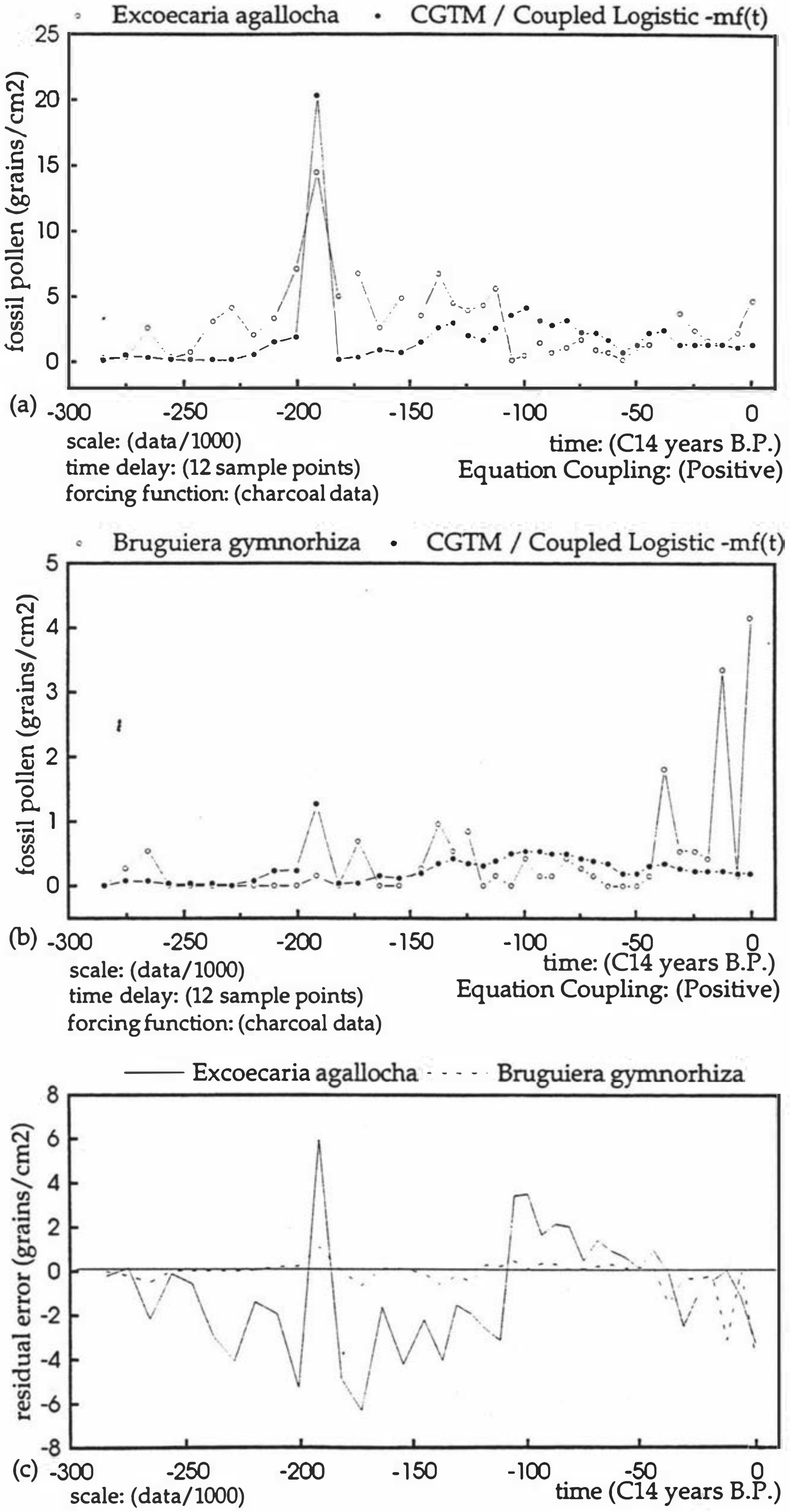


Fig 5.59 The Lawakilevu core site - coupled logistic CGTM with positive coupling and 12 point time delay) for (a) *Excoecaria agallocha* and (b) *Bruguiera gymnorhiza* with (c) residual error.

Using this model formulation, it is possible to replicate the same behaviour using positive and negative competition coefficients. This phenomenon suggests that in this region of parameter space, the coupled logistic CGTM is unable to discriminate between competitive and mutualistic behaviour.

Even with the additional complexity of this model it does a poor job of predicting the behaviour of the Lawakilevu mangal. The main reason for this failure is probably the low density conditions of this community.

5.4.7.7 Interpretation

The results of experiment three confirm those of earlier experiments. Firstly, it is not possible to interpret the behaviour of the Lawakilevu mangal in terms of classical competition theory. As might be expected, these models make a very poor job of predicting the variance in the mangrove data at all three core sites.

Secondly, the Lawakilevu mangal spends most of its time in a low density region. Expansion to a region of higher density is only ever short term and followed by a return to low density. This behaviour approximates a cyclic pattern, similar to that found at the Udu and Keteira core sites.

Thirdly, the Lawakilevu mangal has only become an intermixed community structure in very recent times. For most of the history of the site, *Excoecaria agallocha* has been the dominant species.

Fourthly, the behaviour of the Lawakilevu mangal is density vague. The CGTM formulations tested at this site represent a range of density vague mechanisms. Based on simplicity and predictive capability, the exponential CGTM is clearly the superior model at this site.

Finally, the performance of the exponential CGTM is hindered at the Udu and Lawakilevu core sites by insensitivity to large variance in the charcoal fragment data. An attempt has been made to overcome this problem by introducing a secondary forcing function. This solution has proved to be a mixture of success and failure in terms of model performance. These results suggest that the answer to parameter insensitivity is not a simple one and that nonlinearities are probably involved.

5.5 Discussion of Results

The following section is written as a critical evaluation of the three sets of experimental results recorded in this chapter. The main objective of this evaluation is to arrive at a model of community organisation for the Totoya mangal. As an introduction to the following evaluation, a set of interpretation principles is outlined. These principles provide an answer to the problems involved in interpreting modelling results based on fossil pollen accumulation rate (PAR) data that were mentioned in Chapter four. These principles also provide a basis for interpretation of the results of the next case study in Chapter six.

5.5.1 Interpreting Fossil Pollen Data

There are two different problems involved in interpreting theoretical modelling results based on absolute fossil pollen data. The first is the error that is likely to have been caused by pollen dispersal and geological preservation processes. Then there is the error which is involved in dating the sediments from which the fossil pollen is derived.

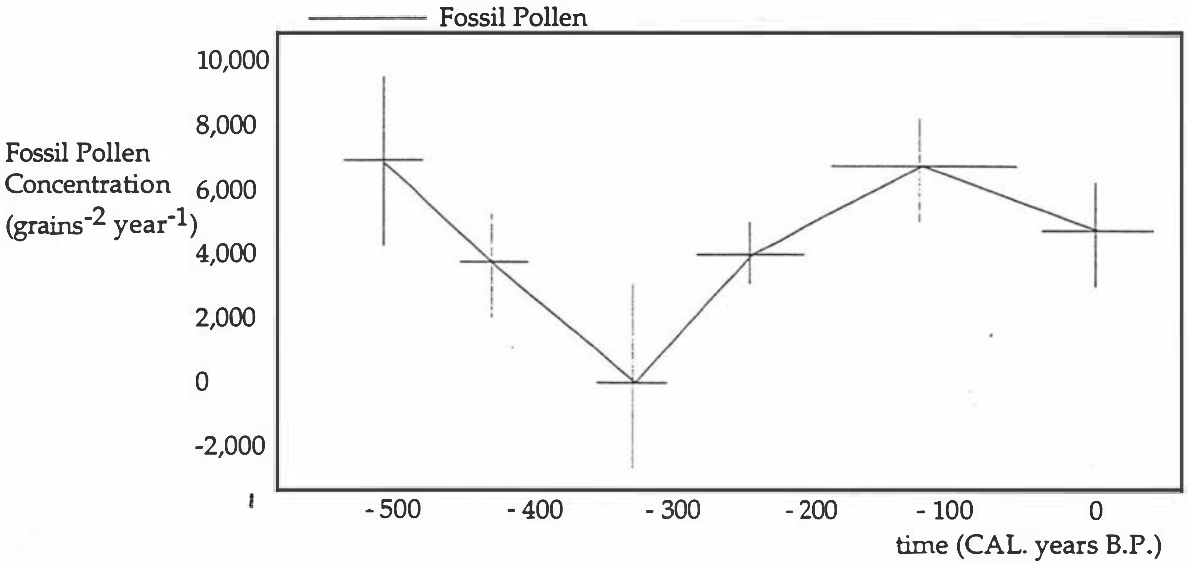


Fig 5.60 PAR data drawn with error bands based on 95% confidence intervals. The fossil pollen signal path has been drawn through average values of the two error bars.

In the plots of the results section of this chapter, absolute fossil pollen data has been expressed as a pollen accumulation rate (PAR). On an individual plot, the calibrated age scale (interpolated from sample depth and calibrated age data) is plotted on the x axis with fossil pollen concentrations (grains cm^{-2} $year^{-1}$) plotted on the y axis.

In evaluating PAR data there are two main sources of error to be dealt with. Firstly, there is the error involved in radiocarbon dating of the core sediments. Secondly, there are the many potential sources of error involved in the dispersal, preservation, collection of cores, concentration and counting of fossil pollen grains (as mentioned in Chapter four).

These two sources of error can be illustrated by plotting PAR sample points with two sets of error bars. The horizontal error bar indicates a 95% confidence interval for radiocarbon age, while the vertical error bar indicates a 95% confidence interval for fossil pollen concentration (fig 5.60). The important point to be drawn from this illustration (fig 5.60) is that each fossil pollen sample point could theoretically exist at a location anywhere within the area demarcated by the two 95% error bars. Likewise, the behaviour of a model which is fitted to this fossil pollen signal is quite acceptable, as long as its behaviour is located somewhere within the area demarcated by the two 95% error bars for each sample point (fig 5.61).

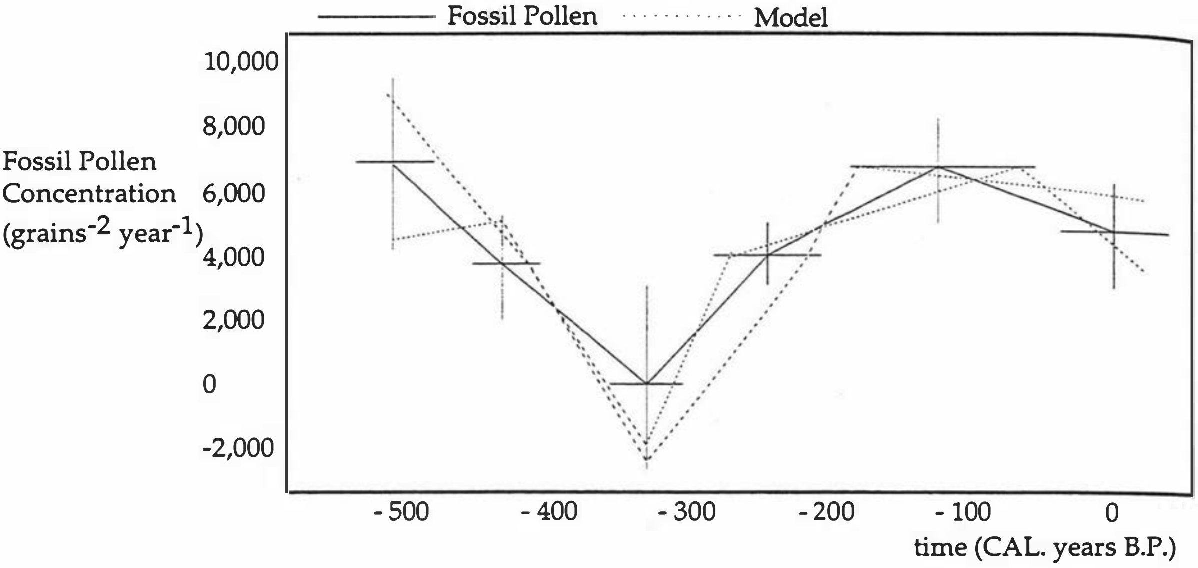


Fig 5.61 PAR data drawn with error bands based on 95% confidence intervals. The behaviour of fossil pollen and model data is indicated.

In fig 5.61, two different models have been plotted with the original fossil pollen signal. These two models are very different in spirit from the original fossil pollen signal and yet, they are still acceptable predictions of the behaviour of this system. The contrast between model and fossil pollen data can be seen more clearly in fig 5.62. The casual observer may be tempted to think that the behaviour of the two models pictured in fig 5.62 are a poor prediction of the field data (solid black line). If the 95% error bars were redrawn on this plot it would be more easy to see that the behaviour of these two models is actually quite an acceptable prediction of the behaviour of the field data.

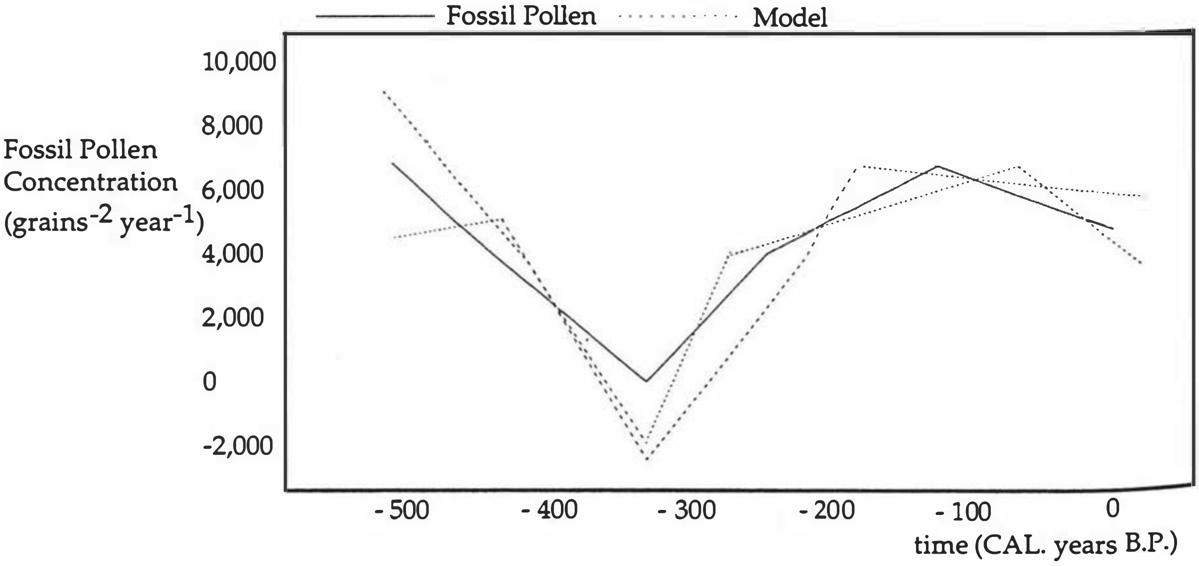


Fig 5.62 A comparative plot of the behaviour of fossil pollen and model data based on fig 5.61.

A problem with PAR determinations not mentioned above, is that at present it is not possible to determine with any certainty the vertical 95% error bar. This is because errors resulting from dispersal and geological processes cannot be measured in an absolute sense. It is possible to gain some indication as to the likely level of these two sources of error using site replication, pollen rain and dispersal studies.

Modern pollen rain studies can be used to estimate the percentage of a fossil pollen assemblage that is likely to have resulted from local, extra-local or regional pollen contamination. A limiting factor in such studies is that modern vegetational patterns may not accurately represent the past.

Secondly, pollen dispersal studies can be used to determine the levels of pollen deposited from various parts of a nearby plant community. The results of such a study may indicate if the understorey plants of a forest are well represented in relation to pollen from the forest canopy. Such a study might also indicate where the highest concentration of pollen is deposited, in relation to its source area. Studies of this kind have been undertaken on modern vegetation (see Chapter four) and now provide an important theoretical basis for understanding pollen dispersal and depositional processes.

Thirdly, replication is an important tool for determining the influence of geological processes or bioturbation on a fossil pollen assemblage.

In summary, the practical difficulties of estimating the 95% vertical error bar for absolute fossil pollen data have been discussed. Pollen rain studies, pollen dispersal studies and replication can all be used to assess the level of confidence in the vertical error bar. Future research could evaluate ways that palynologists might express the degree of vertical confidence that they have in their data, based on non-statistical methods of evaluation.

5.5.2 Interpretation of the Totoya Fossil Pollen

Because the mangrove swamps of Totoya are so spatially isolated and surrounded by coastal zone and inland forest vegetation, there is a very high likelihood that the fossil pollen assemblage from these swamp sediments represents only local pollen. It is more difficult to be as certain about the level of geological disturbance or bioturbation that may have affected these cores. However, a correlation check of stratigraphy and fossil pollen data for the three core sites has failed to find evidence of major changes in fossil pollen concentration that are correlated with stratigraphic changes (figs. 5.19, 5.20, 5.20a).

Finally, there are clear similarities and explainable differences in the fossil pollen data, stratigraphy and radiocarbon dating for the three Totoya core sites used in this study. These lines of evidence provide an indication of the general reliability of the fossil pollen data from Totoya. Despite this fact, great care must still be taken in interpreting this data.

5.5.2.1 *Principles of Model Interpretation*

The problems outlined in the previous section illustrate the difficulties involved in attempting to interpret PAR data. The present author has taken a heuristic approach to interpretation based on the following principles:

1. Goodness of fit is not a useful criterion for evaluating the degree of correspondence between the behaviour of model and PAR data. The idea of goodness of fit traditionally implies a point to point matching between field and model data. As illustrated in the previous section, this concept is not at all helpful. Each PAR sample point may potentially have quite large horizontal and vertical error bars associated with it.

2. Reference to the *behaviour of a system* is a more useful concept when interpreting PAR data.

3. When comparing the behaviour of model and PAR data, morphological form may be a more helpful concept than point by point correspondence.

4. Morphological form may be visually evaluated by remembering that each fossil pollen data point may be represented by horizontal and vertical error bars. These error bars demarcate a feasible confidence area or region within which the morphological form of a model may exist.

5. In some cases it will be possible to test the predictive power of a mechanistic model by comparing model parameter values with data generated by empirical studies. However, empirical studies of this kind are few. Therefore, it seems appropriate to de-emphasise the importance of parameter values when modelling PAR data.

6. A further problem, caused by the existence of an error region around each fossil pollen data point, is that the totally feasible behaviour possible for the living system represented by this data cannot be modelled by using finite parameter values. A range of parameter values is clearly more appropriate, along with the range of possible model behaviours generated by them.

Principle number six was applied in the modelling work of this project by simulation testing of each model construct over a range of parameter values. The parameter values reported in the results section of this chapter should not be considered as attempts to state *optimal values.* These parameters may be considered as *averaged values* of a possible range that reflects the feasible behaviour for these systems.

In summary, the behaviour of a system, its morphological form and the range of parameter values used to generate this behaviour are all concepts which seem more appropriate to modelling PAR data. This does not suggest that a single set of parameter values has no place in evaluating this type of research. Averaged values can be used, as long as it is remembered, that the total feasible range of behaviour possible exists within a range of parameter values either side of those stated. Further research into how to report and portray this type of information is clearly needed.

Because palynological modelling research does not meet the same statistical standards as research that is carried out in a laboratory, it should not be considered inferior. Palynologists are able to have confidence in their data, through replication experiments, pollen rain and dispersal studies. What is needed is some tangible way of communicating this level of confidence. The behaviour of a system, its morphological form and the concept of averaged parameter values, form the basis of the heuristic evaluation used to interpret model and PAR data in this project.

5.5.2.2 Evaluating the Modelling Results

The reason for developing a modelling paradigm in this project was to systematise a procedure that could be used with PAR data to model community organisation. Having done this, the objective of the discussion section of this chapter is to evaluate the results and arrive at a model of community organisation for the Totoya mangal. To accomplish this objective, refutation criteria must be used in order to determine which model constructs (tested in experiments 1-3) provide the best prediction and explanation of the competing hypotheses of community organisation being tested.

5.5.2.3 Refutation Criteria

The predictive power of a model can only be tested on the basis of an *a priori* refutation criterion. The refutation criterion chosen for this project involves the principles of model interpretation outlined in the previous section. The explanatory power of a model can only be tested with the aid of a competitive theory. Competitive models are rejected on the grounds of *inferior explanatory power, conflict with background theory and lack of internal consistency and parsimony* (Mentis 1988).

5.5.2.4 Summary of hypotheses

In the following evaluation, it is important to distinguish between the different hypotheses being tested in this project and the way in which they were derived.

The equilibrium and non-equilibrium models of community organisation provide general hypotheses which are difficult to test because they are too complex.

Because the two competing models of community organisation are too general to test by themselves, theoretical ecologists have formulated mathematical model constructs with much higher levels of abstraction from reality. Abstraction is accomplished by the use of working assumptions and approximations (usually in mathematical form).

The logistic and coupled logistic equations are both examples of specific model constructs which have been formulated from the equilibrium model of community organisation. These models incorporate high levels of abstraction (*e.g.* no community is driven solely by competition).

Models derived from the base theory of community organisation require domain of application in order that they may be tested. The domain c application for a model provides data from the real world against which th performance of a model construct may be tested.

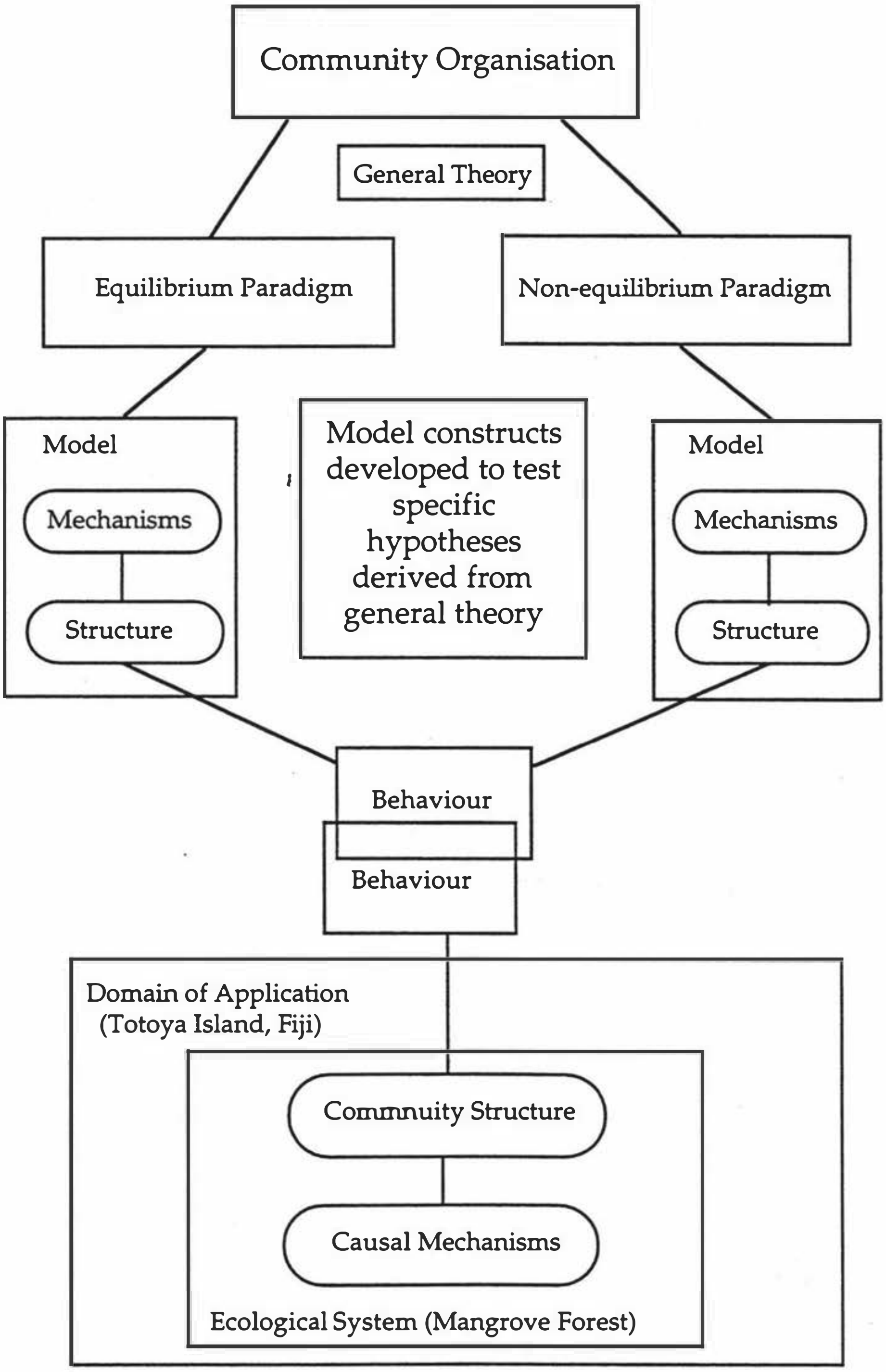


Fig 5.63 A summary diagram showing the relationship between the different classes of hypotheses tested in this case study chapter.

Field data records the behaviour of the ecological system which is the object of study in a given domain of application (fig 5.63). The Domain of application may be quite a broad area (*e.g.* Totoya Island) while the exact object of study may be a single ecological system (*e.g.* mangrove forest).

The domain of application effectively gives the theoretical model construct an ecological context in which it can be tested. The domain of application involves consideration of what is known of the ecology of the system being studied and provides important insights into the causal mechanisms and structure of this system.

Information of this type usually forms the basis of hypotheses which attempt to explain and predict the working of a given ecological system. Mathematical model constructs can be used to test the strength of these hypotheses. The testing process usually involves a dialogue between what is known of the ecology of a system on the one hand and how this relates to the predictions and explanatory power of the model on the other hand. Such a dialogue forms the basis of the evaluation of experiments one to three in the following section.

5.5.3 ***Keteira - Experiment One***

At the Keteira core site, two hypotheses were tested by using classical competition models and the discrete logistic equation. In terms of predictive capability, the discrete logistic (case III) (fig 5.26) clearly has superiority.

For the competition models, phase portraits give no indication of competitive behaviour. Both the logistic (fig 5.22) and coupled logistic (fig 5.23) models poorly predicted the long-term trends and variance of the mangrove data from this site.

The explanatory power of the logistic and coupled logistic equations involves a number of assumptions which are not upheld at this site. Firstly, competition is driven by high density, while the Keteira mangrove wanders the low to intermediate density region. Secondly, the Keteira data appears to be exogenously forced, while these two model constructs assume environmental constancy. Thirdly, these models assume a closed system, while immigration and emigration of seedstock between sites on the island cannot be discounted. Fourthly, the model assumes deterministic processes, while the exogenous forces acting at this site appear to be stochastic.

The explanatory power of the discrete logistic equation is poor compared with its predictive capability. Overcompensation requires extremely rapid reproductive processes which do not fit with the known seed predation problem of these two mangrove species. Secondly, the very high population peaks of the two mangrove species at Udu and Lawakilevu are hard to explain if this behaviour is driven by overcompensation. Thirdly, it is high density and intense intraspecific competition which causes the sudden crash in a population which has overcompensated. The estimated upper asymptotic density for this site (40 for data/1000 and 0.4 for data/100,000) suggests that this system is presently in a low density region.

Finally, the fact that this system appears to return continuously to low density values approximating zero, suggests that it is exogenously forced. The strong likelihood of exogenous forcing and seed dispersal are also violations of the assumptions of the discrete logistic model.

In conclusion, the logistic and coupled logistic models are rejected on the grounds of poor predictive capability. The explanatory power of these models is faulted on the grounds of conflict with background theory (violated assumptions). The use of these two models represented an attempt to find contradictory evidence (a steady-state) at a site where non-equilibrium behaviour was expected. Based on these results, contradictory evidence cannot be found.

The discrete logistic model (case III, fig 5.26) provides very good prediction of the mangrove forest behaviour at this site. However, the explanatory power of this model is faulted on the grounds of conflict with background theory (violated assumptions).

5.5.4 Keteira - Reformulation

Reformulation of the logistic and coupled logistic models (with forcing function) improved the predictive power of these two models in the low density region. However, this improvement was not enough to predict the variance in the data at this site. Furthermore, at critical parameter values, the forcing function would drive the system to equilibrium, instead of improving the variance in the model (figs 5.29 - 5.32).

The exponential CGTM formulation (fig 5.35) was developed in response to the poor predictive power and inferior explanatory capability of the logistic and coupled logistic models with forcing function.

Of all the models tested on the Keteira data, the exponential CGTM demonstrates the very best predictive capability. The explanatory power of this model involves a stochastic mechanism and therefore it is not disfavoured by low density conditions. Secondly, the model combines environmental stochasticity with a reaction time delay to predict almost perfectly the behaviour of the Keteira mangal. Finally, the model incorporates a constant growth rate in contrast to the exponential growth rate of the logistic formulation. The constant growth mechanism is likely to be an approximation to a more complex demographic process. At present, there appears to be no obvious ecological reason why this growth mechanism should be so successful. The mathematical weakness of the logistic equation with forcing function has been discussed in the results section.

The logistic CGTM (fig 5.36) and coupled logistic CGTM formulations (figs 5.37, 5.38) were also tested on the Keteira data. These model formulations have increased mechanistic complexity (intraspecific and interspecific competition) and should therefore make a better job of predicting the Keteira mangrove data. However, this is clearly not the case. At best, their predictive capability matches that of the exponential CGTM.

Reformulation tests, while instructive, cannot be used to prove the truth of any theory. Reformulation of the above models is based on *a posteriori* observations. These models must now be tested on new data.

5.5.5 Udu - Experiment Two

In contrast to the Keteira core site, at the Udu core site, conditions approximating a long-term steady state were predicted as a result of swamp basin infilling. This hypothesis must be rejected in favour of the density vague hypothesis, which was tested for with the CGTM formulations.

The predictive power of the logistic (fig 5.41) and coupled logistic (fig 5.42) equations at this site was, once again, very poor. Morphologically, these models fail to even approximate any long-term trend or variance in the data. Furthermore, the phase portraits for this site give no indication of interactive behaviour. The logistic and coupled logistic model assumptions violated at the Keteira core site are also violated at this site.

A further violation is the introduction of *Bruguiera gymnorhiza* during the last two hundred CAL. years and possible localised extinction of this species on occasions during the earlier history of the site. Neither of these model constructs has any ability to deal with spatial effects of this kind. Finally, contrary to the hypothesis predicted for this site, the optimisation software actually suggests that these two mangrove species are presently engaged in a mutualistic relationship (see Table 5.16).

The predictive power of four different CGTM formulations was tested at the Udu core site. Once again, it can be stated without any fear of contradiction that the morphological form of the exponential CGTM (5.43) is superior to that of any of the other CGTM formulations (*i.e.* the logistic CGTM fig 5.44, the coupled logistic CGTM figures 5.45, 5.46 and the discrete logistic CGTM fig 5.47).

Despite the above assertion, it is also evident that even the exponential CGTM is limited in its predictive power on this data. This fault was traced back to an insensitivity in the model to large variance in charcoal fragment concentrations. The problem was partly solved by the use of an additional model with a secondary forcing function based on sedimentation rate (fig 5.48). A composite plot (fig 5.50) shows the predictive power of the two models. It seems likely that the secondary forcing function chosen for this reformulation experiment, is only an approximation of a much more complex nonlinear function.

In terms of its explanatory power, the exponential CGTM may still be considered superior when compared with the continuous models and other

CGTM formulations tested. The justification for this conclusion lies in the simplicity of this model construct. The addition of interspecific and intraspecific competitive mechanisms involves greater model complexity that should result in a noticeable improvement in predictive power. This is clearly not the case. Based on the principle of parsimony, the exponential CGTM is a superior model.

The explanatory power of the logistic and coupled logistic CGTM formulations is faulted once again on the basis of violated assumptions as for the continuous models tested at this site. Furthermore, the model seems unable to discriminate between competitive and mutualistic interaction, as illustrated by almost identical behaviour, based on completely different signs, for the competition coefficients (see Table 5.17).

The explanatory power of the discrete exponential CGTM (fig 5.47) must also be faulted, although the grounds for this rejection are a little more difficult to see. Firstly, the model retains the mechanistic simplicity of the continuous exponential CGTM and should therefore equal its predictive capability - this is clearly not the case. Secondly, to obtain reasonable behaviour with this model, the use of a much longer time delay was needed (113 CAL. years).

For some reason, its predictive capability is out of phase with the time delay of the other CGTM formulations (71 CAL. years). Thirdly, the explanatory power of the model is based on a constant, discrete reproductive process. All that can be said is that the predictive failure of the model suggests that this is not the correct reproductive mechanism for the Udu mangal. This model formulation is also rejected on the grounds of poor predictive performance. There is not enough ecological information available to reject the model on the basis of inferior explanatory power. Further research into this matter is clearly needed and especially the influence of crab seed predation, which has featured as a topical issue in mangrove publications.

In summary, the exponential CGTM is, once again, the superior model construct for the Udu core site. Based on the morphological form of its behaviour, the model is unrivalled in its predictive power. The continuous logistic and coupled logistic, logistic CGTM and coupled logistic CGTM can all be faulted on grounds of conflict with background theory (violated assumptions). Furthermore the coupled logistic CGTM appears to be internally inconsistent, in that it is not able to discriminate between competitive and mutualistic behaviour. In some cases there has been enough ecological information available to fault these models on the grounds of inferior explanatory power. This is not the case with the discrete exponential CGTM.

The charcoal parameter insensitivity problem, identified at this site, has been partly remedied by the use of a secondary forcing function. These behavioural results appear to indicate that this problem involves a more complex function than that used in the secondary forcing function. Where the variance in the charcoal signal is relatively even, there are very good results (*e.g.* Keteira). Where this variance is not even, there are poor results. Therefore, the problem appears to lie in the use of a constant charcoal scaling parameter.

5.5.6 Lawakilevu - Experiment Three.

At the Lawakilevu core site it is more difficult to distinguish between the results of the various models tested on the basis of predictive power. Firstly, as has consistently been the pattern at the other two core sites, the logistic and coupled logistic models are incapable of predicting the main trend and variance in this data. Furthermore, phase portraits give no indication of the existence of competitive behaviour in this system.

By contrast, it is more difficult to discriminate between the predictive power of the various CGTM formulations at this site. This problem, once again, appears to be a direct result of insensitivity of the model to large variance in the charcoal fragment concentrations at this site (fig 5.17).

The predictive power of the exponential CGTM was contrasted on the basis of 4 (fig 5.54) and 12 (fig 5.55) sample point time delays. The 12 sample point time delay version of these two simulations provides the best overall prediction of the behaviour of *Excoecaria agallocha* and the worst prediction of the behaviour *Bruguiera gymnorhiza*. Increasing the scaling parameter (m) for *Bruguiera gymnorhiza* (fig 5.55 b) with 12 sample point time delay caused a large rise in the model behaviour at ca. -200 CAL. years B.P. This rise corresponds to the large expansion of *Excoecaria agallocha* at the same time (ca. -200 CAL. years B.P) in plot (a) of fig 5.55. This is clearly a charcoal parameter sensitivity problem once again.

The predictive power of the exponential CGTM, with the addition of a secondary forcing function, makes a noticeable improvement to the above problem (see fig 5.56).

The predictive power of the logistic CGTM (fig 5.57) is, in many respects, equal to that of the exponential CGTM with secondary forcing function. This similarity appears to be the result of the same parameter values shared between the two equations (especially for *Excoecaria agallocha* see Table 5.20). The slightly different parameter values for *Bruguiera gymnorhiza* could be swapped between the two equations. These facts suggest that the addition of an upper asymptotic density limit (K) makes virtually no predictive improvement to the logistic CGTM formulation.

In contrast with the above, the coupled logistic CGTM has quite poor predictive capability (figures 5.58 and 5.59), compounded, by an inability to discriminate between competitive and mutualistic behaviour.

There is no need to discuss the explanatory power of the model constructs tested at this site. With the exception of the exponential CGTM, these model constructs may be rejected on exactly the same grounds as those for the Udu core site. In summary, the main faults include: conflict with background theory (violated assumptions), lack of internal consistency in the coupled logistic CGTM, generally inferior explanatory power and parsimony.

In summary, the exponential CGTM emerges from this evaluation with superior predictive and explanatory power. This result is internally consistent over the three Totoya core sites that have now been tested.

5.5.7 Mangal Community Organisation - Totoya

Based on the interpretation of the modelling results of experiments 1 to 3, it is now possible to construct a tentative model of community organisation for the mangrove forests of Totoya. This model is based on the assumptions, approximations and mechanistic limitations of the exponential CGTM.

5.5.7.1 Sea-level Regression - an Environmental Setting

The environmental setting of the mangrove forests of Totoya involves the construction of coastal plains as a result sea-level regression following the late Holocene sea-level maximum ca. 3 - 4000 years ago (Clark and Lingle 1979, Nunn 1991). It is now evident that the process of coastal progradation on Totoya occurred ca. 1000 CAL. years later than the figures quoted by (Nunn 1994a). Since the initiation of coastal progradation on Totoya, thousands of tonnes of terrestrial clay rich sediments have been deposited onto the coastal plains of this island.

The core samples taken from the Totoya mangrove swamps show a large variance in charcoal fragment concentration. It has been demonstrated that the timing of the fires which caused these charcoal concentrations does not coincide with a noticeable destruction of mangrove forest - nor is there any reason to expect that this might be so. This evidence appears to point to the burning of the island's inland forests. The resulting loss of forest cover was probably responsible for surface soil erosion and the very high levels of sediment that have been deposited on the coastal plains and mangrove swamps of Totoya over the last fifteen hundred CAL. years.

The present author has no evidence by which to say with absolute certainty that the burning of the island's inland forest was caused by human deforestation practices. Because forest clearance occurred during a time of known human settlement, this explanation is quite possible, at least in part. As suggested by Nunn (1992, 1994), there is need for further research into the whole matter of human induced environmental change. Furthermore, this issue is not of critical importance to the results presented above.

5.5.7.2 Causal Mechanisms of Community Organisation

The model of community organisation advanced in this thesis, is based on three components: causal mechanisms, community structure and community behaviour. Based on the modelling results of this case study, it is now evident that the deposition of terrestrial sediments into the mangrove swamps of Totoya is a critically important mechanism, responsible for driving the temporal and spatial dynamics of these communities.

These modelling results provide supporting evidence for the recent geomorphological model of mangrove forest organisation that has been advanced by Thom (1967, 1979). Thom (1967) suggested that mangrove distributions follow, but do not override abiotic land building processes. Evidence to support this hypothesis may be found in three observations from the coastal plains and swamps of Totoya.

Firstly, as suggested by Thom (1967), mangrove distribution follows, but does not override abiotic land building processes. Evidence for this behavioural response to land building processes may be found in the time delayed response of Totoya mangal to sediment loading of the swamps. Sediment loading appears to precede any behavioural response on the part of the mangrove forest by a period of time ranging from 71 - 111 years (see Table 5.21).

Site	Model Name	CAL. time delay
Keteira	exponential CGTM	ca. 85
Udu	exponential CGTM	ca. 71
Lawakilevu	exponential CGTM	ca. 111

Table 5.21 Behavioural time delays for the three core sites on Totoya.

Because there is not a direct linear relationship between sediment depth and CAL. age, the estimates of time delay listed in Table 3.9 should only be considered as approximations. The exact time is not so important as the fact that a time delay actually exists. It requires ca. 70 to 110 CAL. years for the mangrove forest to respond to sediment loading of the swamp caused by inland forest clearance. This pattern appears to be very consistent, so that even relatively small rises in charcoal have a short-term effect on mangrove forest behaviour.

Secondly, the influx of terrestrial sediments into the coastal plains of Totoya appears to be a direct result of inland forest clearance, which occurred independent of the existence of mangrove. Terrestrial sediments were hydrologically flushed out into the shallow waters of the coastal platform where they decelerated and settled. This process is still in operation today. During his stay of Totoya, the author noted, with great interest, the enormous distance between low and high tide marks at Jigojigo bay.

Jigojigo bay, is a large, crescent shaped embayment, located on the eastern shores of the island's inner lagoon (see Totoya map on chapter preview page). At low tide, it is not the beautiful fringing reef that emerges, it is clay rich mud, mixed with marine sediments. It seems very likely, that within a few years the floor of this embayment will begin to emerge above the present tidal range and ultimately become covered in coastal vegetation. Two stream channels empty out into this embayment and these are likely to be the location of future mangrove forests.

Secondly, the mangrove swamps comprise only a small area of the total coastal plain at a given location. This implies that these large coastal plain deposits were laid without the aid of mangrove forests. Mangrove forests on Totoya only grow where small, ephemeral stream channels meander their way across the coastal plain. The location of these stream channels is controlled by inland geomorphology (valley bottoms - the focal points of inland drainage basins). This suggests that any historic expansions of mangrove forest would have been limited to the swampy areas around these streams.

Thirdly, a further point of interest is that all of the charcoal scaling constants from the three core sites are negative (Table 5.22). This fact implies that sediment loading (indicated by charcoal fragments) causes forest decline. In other words, the long-term behavioural response of the mangrove forest to sediment loading of the swamp is population decline - not population increase. It is only possible to speculate as to the exact mechanism causing this behaviour. It could be a response, on the part of the mangrove, to either changed tidal range or physiological conditions. Thom (1979), has argued that mangrove are simply opportunistic species which colonise available substrate.

Site	Model Name	$m_{Exec.}$	$m_{Brug.}$
Keteira	exponential CGTM	-170	-111
Udu	exponential CGTM	-8.6	-7.1
Lawakilevu	exponential CGTM	-0.2	-0.2

Table 5.22 Forcing function scaling coefficients.

The important point to be noted from Table 5.22 is that in every case, sediment loading of the mangrove swamp results in population decline. This fact makes it difficult to support the mangrove succession theory of Davis (1940), who proposed that succession proceeds as a direct result of the land building role of mangrove. These results suggests that both *Excoecaria agallocha* and *Bruguiera gymnorhiza* are poorly adapted to the role of sediment trapping.

The size of the inland forest disturbance and resultant sediment loading of the coastal plain and mangrove swamps appears to be reflected in the behaviour of the mangrove forests. At Keteira, a relatively even level of variance in charcoal concentration results in a relatively even level of variance in the mangrove forest. It now seems quite likely that these regular behavioural cycles, approximating 100 CAL. years, are related to inland forest disturbance or associated processes.

Without further research, it is only possible to speculate as to the spatial behaviour represented in these rises and falls in mangrove fossil pollen. It now seems evident that the Udu and Lawakilevu core sites have been largely dominated by *Excoecaria agallocha,* while there is also evidence of a recent invasion of *Bruguiera gymnorhiza* at both sites.

At the Keteira core site, there are six expansions and contractions of both mangrove species (fig 5.16a), while the present one is the seventh. This behaviour has occurred over a time period of ca. 700 CAL. years (*i.e.* one major disturbance every 100 CAL. years on average). The behaviour of the mangrove correlates well with noticeable peaks in charcoal concentration (fig 5.16b).

At the Lawakilevu core site, there are only two main expansions and contractions in *Excoecaria agallocha* (Fig 5.17a), along with two main peaks of charcoal fragment concentration (fig 5.17b, c). There is the beginning of a recent expansion at the site which involves both species. These three behavioural responses have occurred over a ca. 400 CAL. years (*i.e.* one major disturbance every 133 CAL. years on average).

At the Udu core site, there is only one main expansion and contraction of the mangrove data (fig 5.18a) and only one main peak in the charcoal data (fig 5.18b). There are ca. six smaller expansions in the mangrove data and it is more difficult to correlate these with charcoal peaks. However, the time period covered by this behaviour is still ca. 700 CAL. years (*i.e.* one major disturbance every 100 CAL. years on average).

The period of the expansion and contraction of the mangrove forest appears to cover approximately 100 CAL. years, although this varies from site to site and from one rise in mangrove fossil pollen to another. To add confidence to this behaviour, many of these rises are described by groupings and clear sub trends in the fossil pollen data. It is unlikely that this time period reflects the operation of a background regional process since the rise and falls in mangrove are not in phase between sites. The irregularity of the time period at individual sites strongly suggests that this long-term behaviour simply reflects a stochastic process. The timing of inland forest clearance appears to be the cause.

The very large time delays involved in the behavioural response of the mangrove forest to sediment loading provides a fascinating insight into the behaviour of stochastically dominated plant communities. From these results it is evident that disturbance events which occurred 70 - 110 CAL. years ago, are responsible for determining the temporal and spatial behaviour of these mangrove forests at the present time! This fact suggests, that in some plant communities, memory effects of this kind will mean that it is simply not possible to correlate present vegetational distribution patterns with environmental variables using static, short term research projects.

In summary, the exponential CGTM has limitations, but still appears to provide the most consistent explanation and prediction of the behaviour of the Udu, Lawakilevu and Keteira mangrove forests. To complete this discussion of results, it is important to consider the exponential CGTM and the organisation of the Totoya mangal, in relation to the DeAngelis and Waterhouse (1987) super-model. This will help to identify just where the results of this case study fit into the present non-equilibrium paradigm of community ecology.

5.5.7.3 *Classifying the Exponential CGTM*

The exponential CGTM is a classical case of stochastic domination, according to the DeAngelis and Waterhouse (1987) super-model of community organisation. The sediment loading of the mangrove swamps of Totoya is a stochastic event, which operates through a time delay, to knock these two mangrove species away from a trajectory which tends toward a high density region.

In a system dominated by stochastic environmental fluctuations, there is a higher probability of eventual local extinction, unless compensatory mechanisms operate at critically low densities. Compensation may counteract stochastic forces by ensuring that populations have an increased probability of survival. A number of possibilities exist for the Totoya mangal.

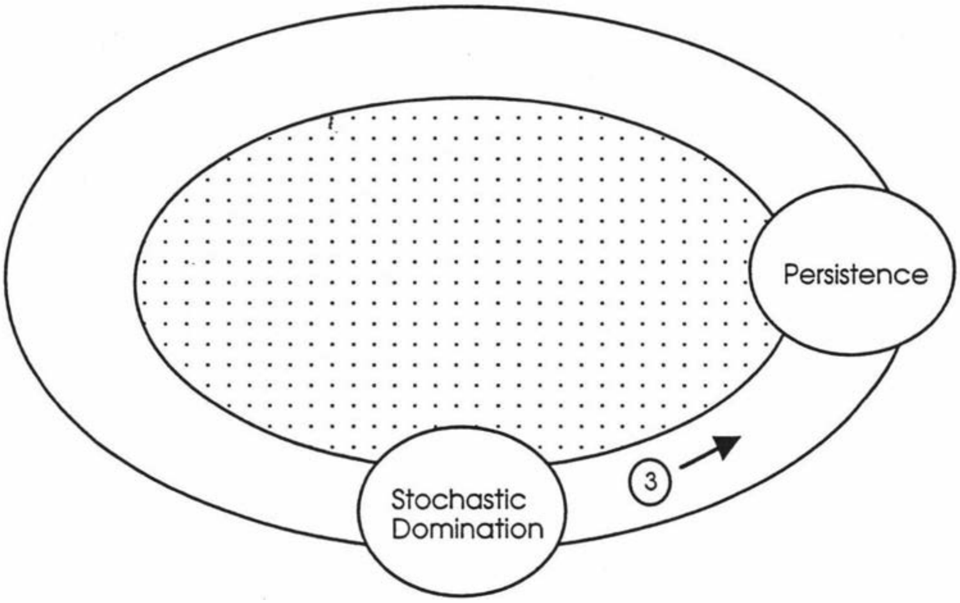


Fig 5.64 The Super-model of DeAngelis and Waterhouse, redrawn to illustrate the location and nature of pathway three. In this pathway, biotic restabilising mechanisms act to moderate the adverse affects of stochastic domination (redrawn from DeAngelis and Waterhouse 1987).

Firstly, a stable floor may be present in the existence of both local and regional seed dispersal processes. A stochastic event like sediment loading or a hurricane may result in the localised extinction of one or both species of mangrove in a single patch or island cell. However, the persistence of other cells on a local (within island) or regional (inter island) basis may ensure a continued supply of seed stock for recolonisation.

Secondly, while it is true that the Totoya mangal shows evidence of successive population reductions, it is equally true, that these communities manifest an amazing capacity to recover after these events. Assuming that Thom

(1969, 1979) is correct about mangrove being opportunistic species, then it seems likely that they are well adapted to recolonisation strategies. The Totoya mangal appears to respond to sediment loading by seaward migration across the coastal plain.

Density vague ceilings, like resource limitation and intraspecific competition do not appear to exist on Totoya. The mangrove populations of Totoya spend most of their time in a low density region, where intraspecific competition and resource limitation do not operate. Wandering the density low region appears to be a direct result of the frequency of local disturbance events.

Pathway three of fig 5.64 is located between the community type characterised by stochastic domination and the community type characterised by persistence. The compensatory mechanisms of pathway three are portrayed as promoting long-term persistence (ability to withstand disturbance), rather than being a pathway to equilibrium conditions.

The interpretation given to the Totoya mangal in this discussion is clearly non-equilibrium. It is now interesting to consider if this interpretation is an artefact of spatial scale. The problem of observational scale was briefly discussed in Chapter three and involves the idea that interpretation of equilibrium or non-equilibrium conditions may be scale dependent. Classical equilibrium models dealt with the problem of observational scale by simply assuming that it was not important. Communities were thereby treated as closed, deterministic, homogeneous units.

The exponential CGTM is a variant of the classical equilibrium models referred to above that relaxes the assumptions of classical equilibrium behaviour - an approach that reflects the individualistic school of succession theory (Gleason 1926, 1939). The observational level of scale of the exponential CGTM is the patch. A major problem with this level of scale is that seed immigration on an island like Totoya may be a critical factor, ensuring the long-term persistence of localised populations.

The interpretation of non-equilibrium behaviour, given in this case study to the Mangrove forests of Totoya, appears to be perfectly correct for the patch level of observational scale. A future palynological modelling study of Totoya and the neighbouring Yasayasa Moala islands, could be directed toward testing for the existence of emergent equilibrium conditions at the island and inter island levels of observational scale. Interconnected systems of patch models, like the exponential CGTM, could be used as a basis for this approach. Empirical studies could be used to estimate contemporary seed dispersal probabilities as a basis for interpreting the fossil pollen record.

5.6 Chapter Summary

The objective of this research project was to develop a dynamical systems methodology for modelling absolute fossil pollen data, in order to test hypotheses derived from community organisation theory. This first case study provides an illustration of the application of the dynamical systems methodology developed in this project. It also demonstrates something of the potential for future palynological modelling research of this kind.

The mangrove forests of Totoya provide an unlikely, but suitable site for palynological modelling research. The author's greatest concern in collecting cores from these sites was the strong possibility of sediment resorting and bioturbation. However, a carefully conducted pilot study, the correlating of the core stratigraphy with mangrove fossil pollen data, the between site consistency of radiocarbon results and the consistency of the data, all testify to the suitability of these cores for modelling research. Despite the above, dispersal and geological problems can never be fully dismissed as potential causes of error in fossil pollen data.

As a further aid to reducing possible error in the fossil pollen data, a pilot study was used in order to gain experience in the laboratory preparation of samples. The technique developed in this pilot study was consistently applied to all samples. Furthermore, the pilot study samples were not used for modelling research.

In this case study, the interpretation of PAR data in relation to the behaviour of model data has been described as a problem involving vertical and horizontal errors. Of the two, it is not possible to quantify vertical error caused by pollen dispersal and geological resorting in an absolute sense. By comparison, it is more easy to quantify errors involved in radiocarbon dating. A final problem involves portraying the level of non-conventional confidence that palynologists have in PAR data. Further research is clearly needed in this area.

The problem of interpreting vertical and horizontal error in fossil pollen data was addressed in this project by developing a set of heuristic interpretation principles. In discussion of these principles, it was pointed out that the traditional modelling concepts of goodness-of-fit and optimal parameter values are just not appropriate for use with PAR data. In place of these two rejection criteria, behavioural morphology and parameter range were used. In this case study, averaged parameter values are reported. However, it needs to be remembered that the behaviour of a model is related to PAR data by a range of behavioural types, produced by a range of parameter values.

The results of this case study suggest that it is not possible to support a steady-state or successional explanation for the mangrove forests of Totoya. Firstly, coastal progradation on Totoya has occurred, independent of the existence of mangrove forests. Secondly, these results show that sediment loading of the mangrove swamps causes population decline. This suggests that these two species are poorly adapted to sediment trapping.

The exponential CGTM has been used to identify an underlying abiotic causal mechanism which appears to have a profound influence on the structure and behaviour of this community. There are a number of important insights which have come from the present study.

Firstly, this model demonstrates that the traditional Malthusian exponential growth parameter may not be the correct, or most appropriate, or closest approximation, of a function that describes a population growth mechanism limited by birth and death processes. Further research is clearly needed in this area.

Secondly, the exponential CGTM formulation not only provides prediction, but explanation of causal mechanisms determining the behaviour of these systems. The model suggests that these ecological systems are dominated by strong stochastic forces which regulate population growth and effectively prevent transit to a high density region where competitive forces would regulate the community near equilibrium.

Thirdly, at the Udu and Lawakilevu core sites, both species are presently growing in an intermixed forest. The recent introduction and rise of *Bruguiera gymnorhiza* over the last 120 - 100 CAL. years may be interpreted as a mutualistic form of interaction with *Excoecaria agallocha* (both species are in phase, in a low density region).

Fourthly, it is now evident that sediment loading of these swamps causes mangrove forest decline and that the stochastic forces driving these populations has a memory effect of ca. 70 - 110 years. The behaviour of the present forests is being shaped by historic environmental changes. In the equilibrium model of community organisation, historic events were not considered to play an important part in influencing population dynamics.

These results may be scale dependent and the only way to answer this question is by further palynological modelling research at a local (island) and regional (inter island) scale. Seed dispersal may be a necessary compensatory mechanism, responsible for preventing local patch extinctions.

Chapter five has illustrated something of the tremendous potential that exists for palynological modelling research along the lines presented in this thesis. In the next chapter, this same technique is used to study the community organisation of a lowland New Zealand beech forest, at the landscape level of organisational scale.

Preview to Chapter six

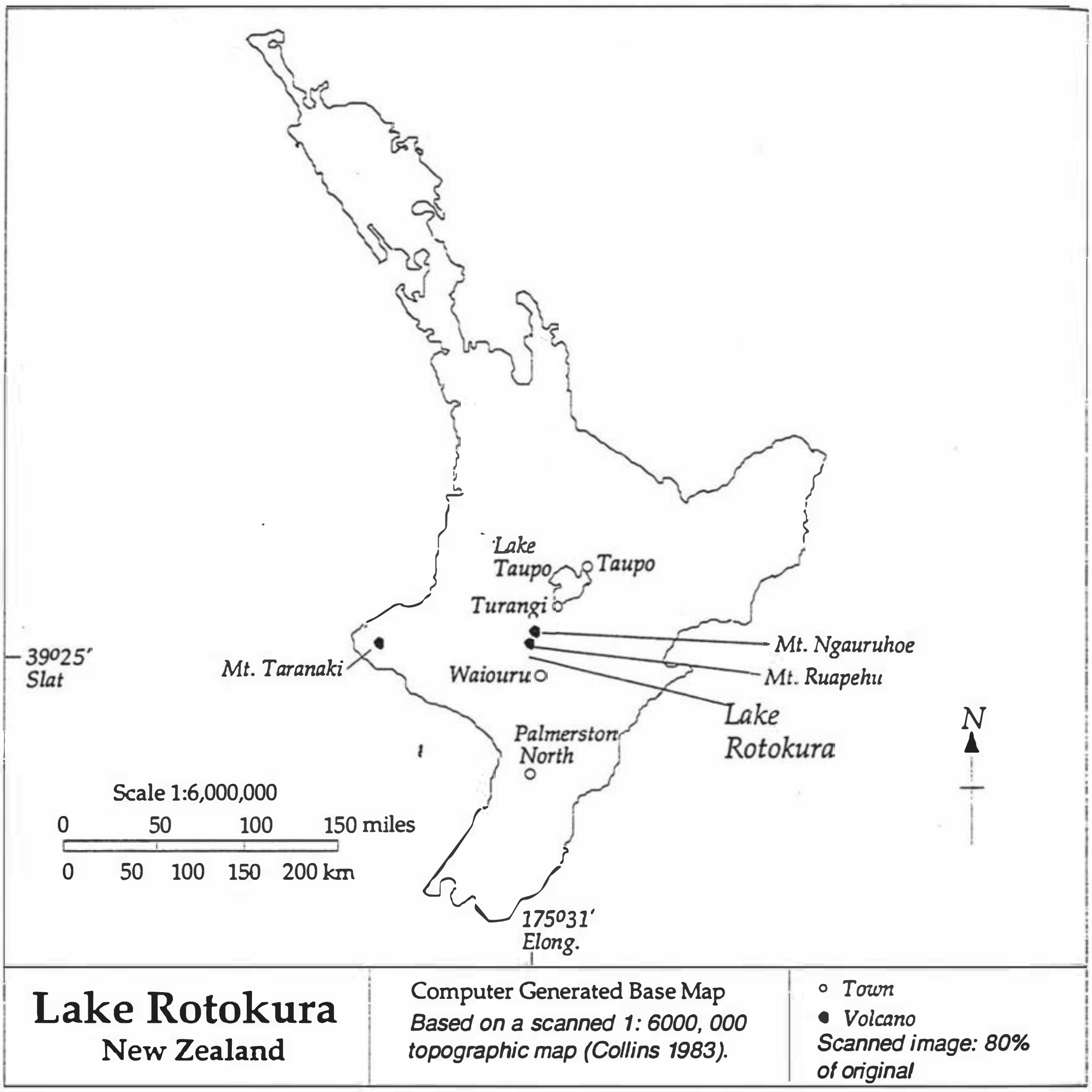


Fig 6.0 Base map showing the location of Lake Rotokura (after Collins 1983).

Modelling Plant Community Organisation ~ Podocarp-Hardwood-Beech Forest, North Island, New Zealand.

In the following case study, the palynological modelling methodology developed in this thesis is applied to a domain of very different complexity and spatial scale from the mangrove forests of Totoya. The modelling results presented in this chapter provide additional evidence to verify the predictive and explanatory power of the exponential CGTM and non-equilibrium paradigm.

Chaptersix

Modelling Plant Community Organisation ~ Podocarp-hardwood-Beech Forest, North Island, New Zealand.

6.1 Objectives

The case study outlined in the following chapter provides another opportunity to test the predictive and explanatory power of the exponential CGTM against the performance of a classical equilibrium model (the logistic). In contrast with the mangrove forests of Totoya, the New Zealand podocarp - hardwood - beech forest modelled in this case study provides an opportunity to test the exponential CGTM at the landscape level of ecological scale. In the previous case study, the level of ecological resolution involved a simple two species community. By contrast, the Lake Rotokura forest is a far more complex community and for this reason, the theoretical modelling of this system involves a high degree of abstraction. Once again, the objective of this study is to construct a model of community organisation.

The format of the following chapter is identical to that of Chapter five. Section two provides an introduction to the physiography, climate and vegetation of the podocarp-hardwood-beech forest that surrounds the Lake Rotokura basin from which the cores for this case study were taken. Section three records the methodology used in the collection of cores, laboratory processing and compiling of results. Because a detailed account of laboratory methodology was given in Chapter five, the methodology section of this chapter simply only notes differences in the technique and treatments used for the Lake Rotokura core samples. The results of experiment four are recorded in section four, with a discussion of these results recorded in section five.

In contrast with the previous case study, the Lake Rotokura research project was more problematic and, for this reason, the reliability of the fossil pollen data more uncertain.

Firstly, the landscape level of scale provides an important and interesting ecological context in which to test for the existence of equilibrium behaviour. However, a regional pollen signal may be influenced by compositional irregularities in the forest vegetation and long distance dispersal (see Myers 1973, Moar and Myers 1978, McGlone 1982). New Zealand *Nothofagus* pollen has been recorded in pollen rain up to 60 km from the source forest (Myers 1973). It is more difficult to identify such problems without a large scale survey of the vegetation which would involve a PhD sized project all of its own.

Secondly, none of the three AMS radiocarbon dates used to date the Lake Rotokura core is reliable. Instead, the core has had to be dated on tephra deposits, which have very large confidence intervals. Because of constraints on time and funding, it was not possible to collect and process replicate core samples to use for cross correlation checking of the regional pollen signal and stratigraphic position of the tephra deposits.

Thirdly, the possibility of overturning of lake sediments cannot be completely discounted. The likelihood of this is strengthened by the poor results of AMS radiocarbon dating.

Fourthly, it was not possible to identify all of the New Zealand beech pollen to species level. To solve this problem, the beech species were grouped together into two different genera. This solution made fossil pollen identification very easy, but resulted in a loss of resolution in a forest dominated by beech trees.

Despite the above problems, the results of the present study appear to be internally consistent with the predictions of the exponential CGTM. For this reason, they are worth reporting and provide an important basis for identifying weaknesses in the modelling methodology and its use in this particular domain of application. Future research will doubtless address and correct many of these problems.

6.2 Introduction - the Rotokura Ecological Reserve

The Rotokura ecological reserve is located at the Southern limit of the ring plain of New Zealand's Mount Ruapehu (fig 5.0). The Rotokura ecological reserve (fig 5.1) forms one small part of the Rangataua state indigenous forest, listed under the Wellington Conservancy (NZ Forest Service 1966).

At its Northern and Western boundaries, the Rangataua state forest borders onto the Southern end of the much larger Tongariro National park region. This park encloses the Mount Ruapehu and Mount Ngauruhoe ring plains and much of the desert region to the west of the main state highway connecting Waiouru to the South and Turangi to the North. At its northern and western boundaries, the Rangataua state forest borders onto the Karioi exotic forest.

The Rangataua forest is composed mainly of *virgin or lightly logged forest, of mixed podocarp-hardwood and beech below an altitudinal limit of Rimu (Dacrydium cupressinum)* (NZ Forest Service 1974). At its northern boundary, the composition of the Rangataua forest gives way to a stand of *virgin and lightly logged or secondary growth* beech forest (NZ Forest Service 1974).

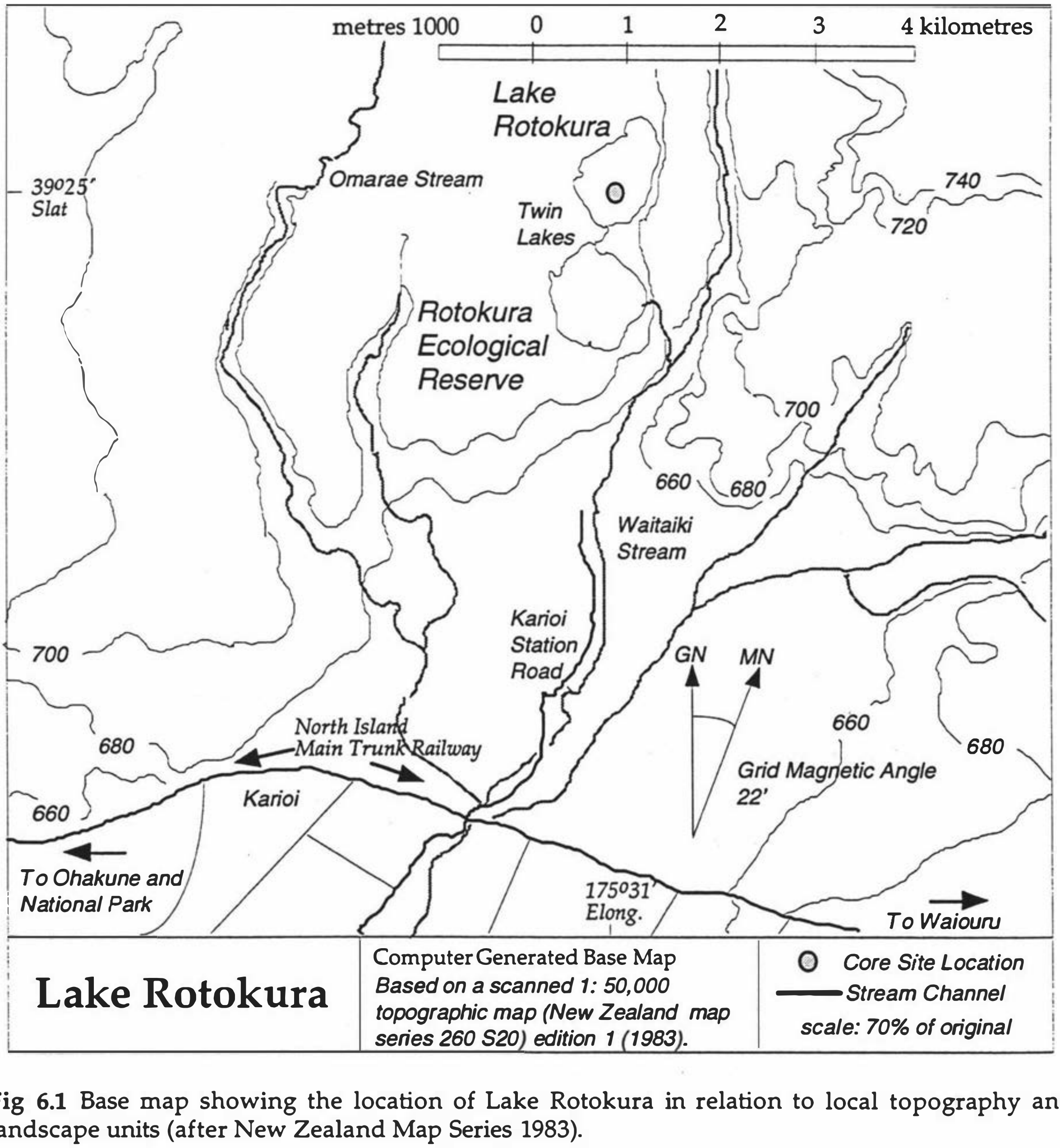


Fig 6.1 Base map showing the location of Lake Rotokura in relation to local topography and landscape units (after New Zealand Map Series 1983).

Lake Rotokura is one of two lake basins known by the local name of *the Twin Lakes.* The Lakes are located within the Rotokura ecological reserve, an ecological subunit of the Rangataua Forest. Lake Rotokura is the northern basin of the Twin lakes and is located at ca. 175°31' east longitude and 39°25' south latitude, with a grid reference of 268493 (New Zealand Map Series 1983).

6.2.1 *Geology*

A detailed account of New Zealand's geology may be found in Suggate (1982). The geomorphology of the central volcanic region is described in Healy (1982). Located just within the southernmost reaches of the Mount Ruapehu ring plain, the Twin Lakes are situated at an altitude of ca. 700 m on lahar deposits known as the Hawera series (Waimean, Otiran). The lake basins are believed to be constructed of andesitic volcanic and assorted intrusive bedrock material (New Zealand Geological Survey 1973).

6.2.2 *Soils*

The forest soil group of the Rotokura ecological reserve, is classified as a Taupo/Tokoroa yellow brown pumice soil. The Twin lakes are located just to the north of the Ohakune and Pokaka yellow/brown loam soil group boundary (New Zealand Map Series 1973).

6.2.3 *Climate*

The Rangataua forest is classified as a high rainfall region, for which local conditions vary greatly with altitude and exposure (New Zealand Map Series 1983). Mean annual rainfall, is between the 1200 and 1400 mm isobars (New Zealand Map series 1979). General descriptions of New Zealand's regional and local climates are given in Tomlinson (1976), Salinger (1988), Maunder (1971) and McKenzie (1967). A detailed treatment of contemporary climate for the central North Island region is given by Garnier (1958).

Long-term climate trends for the Tongariro region have been inferred primarily from palynological studies (McGlone and Topping 1973, 1977, 1983). McGlone and Topping (1977) suggest that the glaciers of the last glacial maximum began to retreat well before 14,000 years B.P. by which time podocarp - hardwood forest had begun to replace the grassland and scrub vegetation of this colder period. The co-authors identify three post-glacial pollen zones. From 14, 000 to 10, 000 years B.P., the Tongariro forests were dominated by *Prumnopitys spicatus*, in a dry climate with annual temperatures only 2 - 3° C lower than the present time.

From 10,000 to 5,000 years B. P., the Tongariro forests were dominated by *Dacrydium cupressinum*, in a climate that was wetter and milder than the present day. During the last 5,000 years there has been a return of *Podocarpus spicatus* forest and an increase in *Nothofagus* forest, during a drier and more frost prone climate (McGlone and Topping 1977).

6.2.4 *Physiography*

The Twin Lake basins have been formed by a mixture of both geomorphological and human causes. The northern most basin (Lake Rotokura) has formed on the surface of a lahar flow (a lahar lake). The southern most lake basin was dammed sometime during the early 1970s (of human origin). Lake Rotokura has no inflow channel, but now empties into the southern Twin Lake basin which was originally a natural landscape depression, covered in swamp vegetation and trees. From this lower basin, an outflow stream has been cut to allow the lake to empty into the Waitaiki Stream, situated in a valley bottom, ca. 40m below the level of this lake (fig 6.1).

The physical landscape around the two lakes is varied. The main landform unit, a lahar, provides gentle sloping terrain from the Northeast to the Southwest. The forest composition of the Rotokura ecological reserve has been classified as podocarp-hardwood-beech (NZ Forest Service 1974). While these three components are undoubtedly present in the forest, the overall composition is varied and reflects a patch-like pattern rather than homogeneous mosaic.

6.2.5 Vegetation Survey Methodology - Lake Rotokura

In the following text, the taxonomy of the New Zealand Podocarpaceae and Fagaceae is according to Connor (1985). General taxonomic nomenclature is according to Allan (1961), Moore and Edgar (1970), Edgar (1971), Edgar and Connor (1978, 1983) and Brownsey *at al.* (1985).

The forest vegetation around Lake Rotokura up to ca. 100 metres from the water's edge was surveyed with the aid of a twenty by twenty metre sample quadrat. The main objective of this survey was to determine the composition of the forest (especially the main canopy trees) in the local forest surrounding the lake. This was simply accomplished by a systematic sampling strategy based on an access track which goes right around the lake. The vegetation survey was conducted by pacing out ca. 80 m intervals along this track and then randomly positioning a twenty by twenty metre sample quadrat (marked out using a 100 m plastic tape).

The positioning of the quadrat involved choosing four 3 digit random numbers from a set of standard statistical tables. The first number provided an initial compass bearing (between 0 - 360 degrees). The second number provided a distance (in paces) from the access track. At this point the first axis of the quadrat was positioned by a compass bearing determined once again by random number selection. A final random number was used to locate the second axis of the quadrat (to the right hand side of the first axis if an odd number was selected and to the left hand side of the first axis if an even number was chosen).

Once the quadrat had been laid out, an effort was made to identify all of the plant species in the quadrat. A field notebook was kept with leaf samples of every new species found and herbarium specimens (Appendix 8) were also collected (MacMillan 1968). General site parameters (aspect, slope, site profile, substrate, disturbance type and intensity) were recorded along with breast height girth measurements (cm) for trees and abundance cover for small trees, shrubs and ground cover species. Using this procedure, samples were collected from a total of fourteen quadrats. By the end of fourteen quadrats, the number of new species found in each quadrat was restricted to the occasional discovery of a fern or shrub species.

The Rotokura lake basin measures ca. 600 by 800 m at its widest points. This suggests that the fossil pollen assemblage in the sediments of this lake will be composed of pollen from a local, extra local and regional source area, as suggested by Jacobson and Bradshaw (1980). More recent research on pollen source area for lake basins (Prentice 1985, Sugita 1993) has confirmed the general principles outlined by Jacobson and Bradshaw (1980).

6.2.6 ***Lake Rotokura Forest Vegetation***

A general vegetation survey of the Tongariro National Park Region has recently been undertaken in order to compile a 1:50,000 vegetation map (Atkinson 1985). In contrast, the objectives of the present vegetation survey are only designed to provide a species list and a basis for description of the forest vegetation as tools for interpreting the fossil pollen record. Using this approach, it is assumed that the composition of the local vegetation is indicative of the regional forest. Much more detailed research would be required to gain more accurate information on the composition of the regional and local forest.

Initial observation of 'the local forest appeared to indicate that its composition was reasonably homogeneous, however the vegetation survey indicates that this is not the case. The forest composition around Lake Rotokura is very patchy, a condition that probably reflects a high degree of disturbance (large openings in the forest canopy, fallen trees and large branches, a patchy understorey composition and patches with a high density of small DBH poles (regeneration pole forest).

The results of the vegetation survey are illustrated in fig 6.2. This drawing shows the approximate location of boundaries separating the main vegetation associations around the lake perimeter in relation to the fourteen survey quadrats. The exact positioning of the quadrats and vegetation boundaries are not drawn to any scale.

The vegetation survey results presented in the following discussion are intended for descriptive purposes only. A much larger scale vegetation survey would be needed to quantitatively define the vegetation association boundaries in this forest. This approach is outside the objectives of the present project.

Finally, in fig 6.2, *Nothofagus ? truncata* has been labelled with a question mark to indicate that the identification of this species is yet to be confirmed. Preliminary identification of all forest species was made by Dr. Alistair Robertson (Plant Ecologist, Massey University). Dr Robertson suggested that the specimens which he had identified as *Nothofagus truncata* could be a hybrid of *Nothofagus fusca.* If this specimen is positively identified as *Nothofagus truncata* then it will represent the discovery of a new area for this species (see fig 6.5).

6.2.6.1 Forest Quadrat One

In forest quadrat one, the forest canopy is dominated by *Nothofagus solandri var. cliffortioides* with the odd tree of *Podocarpus totara* and *Nothofagus menziesii.* The understorey is composed primarily of *Cyathodes fasciulata* growing in association with a variety of shrubs *(Coprosma rotundifolia, Pittosporum divaricatum, Coprosma robusta, Melicope simplex* and *Pseudopanax simplex)* and ferns *(Pteridium esculentum, Blechnum colensoi, Blechnum chambersii* and *Grammitis billardierei).*

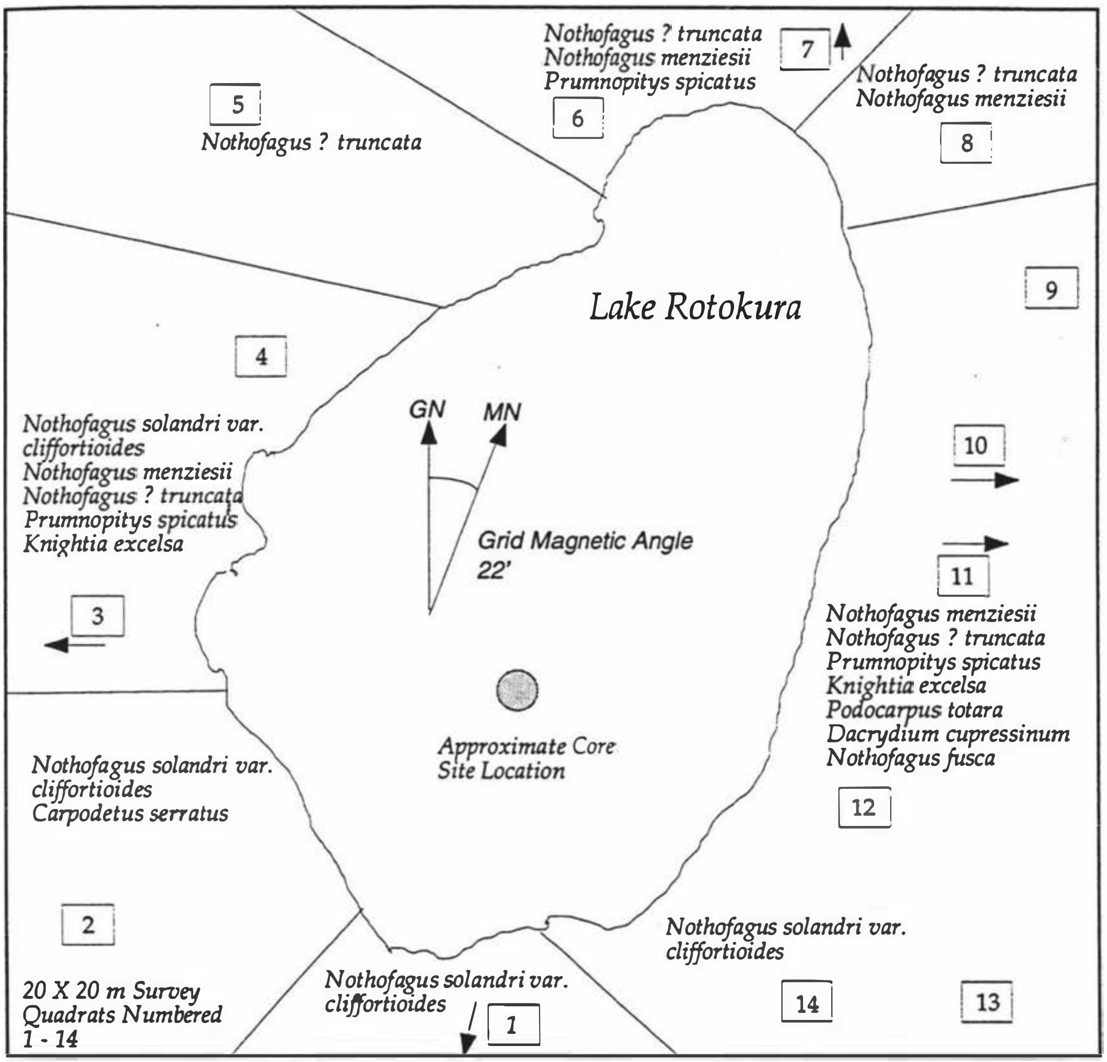


Fig 6.2 A sketch map showing the zonation of the major vegetation associations around Lake Rotokura, Twin Lakes, Rotokura Ecological Reserve. Approximate locations of the fourteen vegetation survey quadrats are indicated. Some of the quadrats are located quite a distance from the lake edge. Small arrows have been used to show the direction in which these quadrats should be located.

6.2.6.2 Forest Quadrat Two

In forest quadrat two, the forest canopy is still dominated by *Nothofagus solandri var. cliffortioides* mixed with *Carpodetus serratus* and the odd tree of *Nothofagus menziesii, Prumnopitys spicatus* and *Pseudopanax colensoi.* The understorey is virtually missing in this zone and is replaced by a ground layer of *Coprosmas, (Coprosma* sp. (hybrid of australis) and *Coprosma rotundifolia).*

Ferns are a dominant component of the ground layer and include *Cyathea dealbata, Blechnum chambersii,* and *Grammitis species.*

6.2.6.3 Forest Quadrats Three and Four

In forest quadrats three and four, the forest canopy is composed of four dominant species *(Nothofagus solandri var. cliffortioides, Nothofagus menziesii, Nothofagus ? truncata* (hybrid of fusca?) and *Prumnopitys spicatus).* There are also minor components of *Pseudopanax crassifolius, Dacrydium cupressinum, Nothofagus fusca* and *Knightia excelsa.* The understorey is composed primarily of *Cyathodes fasciulata,* with *Pseudopanax colensoi, Pittosporum divaricatum, Melicope simplex, Pennantia corymbosa, Coprosma australis* and *Pseudopanax crassifolius.* A more diverse ground layer of ferns is present in this zone *(Grammitis* spp., *Asplenium flaccidum, Polystichum richardii, Blechnum kiokio, Blechnum banksii, Grammitis billardierei* and *Blechnum chambersii).*

6.2.6.4 Forest Quadrat Five

In forest quadrat five, there is a sudden shift in forest canopy tree dominance. The canopy is dominated almost exclusively by *Nothofagus ? truncata* (hybrid of fusca?) with the odd tree of *Prumnopitys spicatus* and *Nothofagus menziesii.* The forest understorey is sparse and dominated by *Cyathodes juniperata and Cyathodes fasciulata.* The ground layer consists of a patchy and often dense layer of small shrubs *(Pittosporum divaricatum, Coprosma australis, Pseudopanax simplex, Coprosma* sp. (hybrid of australis), *Coprosma rotundifolia)* and ferns *(Pteris cretica, Grammitis billardierei and Blechnum kiokio).*

6.2.6.5 Forest Quadrats Six and Seven

In forest quadrats six and seven, forest canopy dominance is shared by *Nothofagus ? truncata, Nothofagus menziesii* and *Prumnopitys spicatus.* This area of the forest has an understorey of only a few shrubs *(Pittosporum divaricatum, Griselinia lucida, Coprosma* sp. (hybrid of australis) *and Melicope simplex),* in association with the small trees *(Aristolia fruticosa, Cyathodes fasciulata, Pseudopanax colensoi, Carpodetus serratus).* As in other parts of the forest, the ground layer is dominated by ferns *(Pteris cretica, Blechnum kiokio, Blechnum chambersii, Grammitis billardierei, Histiopteris incisa, Microsorium diversifolium, Asplenium flaccidum, Cyathea dealbata, Hymenophyllum multifidum, Grammitis* sp.*).*

6.2.6.6 Forest Quadrat Eight

In forest quadrat eight, dominance of the forest canopy has returned once again to *Nothofagus ? truncata* (hybrid of fusca?) with *Nothofagus menziesii* as a minor component. The understorey is now dominated by small shrubs *(Coprosma tenuifolia, Coprosma* sp. (hybrid of australis) and *Melicope simplex).* The ground layer is again dominated by ferns *(Asplenium flaccidum,* *Hymenophyllum multifidum, Blechnum chambersii, Grammitis billardierei, Blechnum colensoi and Histiopteris incisa).*

6.2.6.7 ***Forest Quadrats Nine to Fourteen***

In the remaining forest quadrats (9 - 14), the composition of the forest changes very little. The forest canopy is dominated by *Podocarpus totara, Dacrydium cupressinum, Nothofagus menziesii, Knightia excelsa, Nothofagus fusca, Prumnopitys spicatus* and *Nothofagus ? truncata*. The understorey of the forest is much more closed than the western side of the lake and dominated in places by *Cyathodes fasciulata*. The remainder of the understorey is composed of small shrubs and dominated by *Coprosmas (Coprosma* sp. (hybrid of australis), *Melicope simplex, Coprosma rotundifolia, Coprosma robusta, Coprosma tenuifolia, Coprosma rigida, Pittosporum divaricatum* and *Olearia* sp.*)*.

The ground layer is composed of a variety of ferns *(Grammitis billardierei, Histiopteris incisa, Blechnum colensoi, Blechnum chambersii, Polystichum richardii, Asplenium flaccidum, Grammitis* sp., *Cyathea dealbata, Lastreopsis glabella, Blechnum colensoi, Pellaea rotundifolia* and *Hymenophyllum multifidum)*.

6.2.6.8 ***Discussion and Summary***

The vegetation survey shows that there are clear patterns in the distribution of the forest canopy species around the lake. *Nothofagus solandri var. cliffortioides* is found in the Southern end and Western side of the lake (quadrats 1-4), while *Nothofagus ? truncata (hybrid of fusca?)* is found in the Northern and Eastern sides of the lake (quadrats 5-14). The podocarp-hardwood-beech assemblage for which the Rangataua state reserve is so well known, is at present, most dominant on the Eastern side of Lake Rotokura. A full species list is given in Appendix 8 along with presence, absence and abundance data for tree main tree species.

Compositional variation around the lake is likely to be strongly influenced by disturbance events acting through a complex mixture of local site conditions. Evidence of disturbance is easier to identify. For example, quadrat 5 is located in the middle of a patch of large DBH trees which have fallen in a Southeasterly direction, a fact that suggests a past windthrow event.

Quadrats 6 and 7 are dominated by small DBH *Nothofagus ? truncata* (even age) poles, a regeneration process that indicates a past disturbance event (Wardle 1984). Throughout the forest, canopy gaps exist as a result of the collapse of older trees and large branches.

In summary, these evidences demonstrate that at a landscape level of scale, the spatial composition of the forest located directly around Lake Rotokura is representative of the podocarp - hardwood - beech assemblage for which the Rangataua forest is so well known (New Zealand Forest Service 1966, 1974).

However, this larger landscape unit is clearly composed of many small, disturbance related subunits.

6.2.7 The New Zealand Beech Forest Associations

There is now an extensive literature on New Zealand beech forest, much of which is reviewed in Wardle (1984), Poole (1988) and Wardle (1991). The purpose of the following discussion is to review key aspects of the beech literature in order to arrive at a theoretical model of community organisation for the Lake Rotokura beech forest. From this model, testable hypotheses will be derived.

Within the context of the present study, the focus of this review must be limited to the mixed beech forest association. In this discussion, the term hardwood is used to define all *dicotyledonous trees except the beeches* (Wardle 1984). The term podocarp is used to define *all indigenous Coniferales other than Agathis australis (i.e. Phyllocladus, Podocarpus, Dacrydium and Libocedrus)* (Wardle 1984).

6.2.7.1 Characteristics of the Genus

The genus *Nothofagus* belongs to the Fagaceae, *a family of woody shrubs and trees with alternate (rarely whorled), spatulate leaves; small unisexual flowers; and a fruit which is a nut enclosed in an often hardened cupule* (Wardle 1984). Fagus (the Northern beech genus) is the closest relative of *Nothofagus* (the Southern beech genus). Together, these two genera form the sub-family Fagoideae. The two genera differ in a number of ways including arrangement of the male flowers, style length, pollen grain morphology, wood anatomy, chemical composition of the cambial sap, chromosome numbers and extent of deciduousness.

There are thirty four species of *Nothofagus* that are currently recognised and these share many ecological characteristics. Hybrid Southern beeches have been described by Poole (1950) and provenance variation by Wilcox and Lengard (1983). Most species occur as elements of rain forest vegetation, favour harsh sites, increase along environmental gradients which *lead away from the moist, mild, fertile optimum for growth* and are relatively poor competitors at the seedling stage of development (Wardle 1984).

Nothofagus is known to form *extensive, relatively uniform* (Wardle 1984) montane forests which become intermixed with hardwood and podocarp components of the New Zealand forest flora at lower altitudes. The podocarps and hardwoods are generally considered to be better competitors in these mixed associations. In these low altitude forests *Nothofagus* becomes limited to *low fertility and poorly drained soils, dry sites such as ridge crests and areas of recent forest disturbance* and tends to favour *discrete pure stands* rather than intermixing with other forest species (Wardle 1984). van Steenis (1971) has suggested that this discrete spatial behaviour may be related to mycorrhizal symbionts. Wardle (1984) suggests that another reason may be related to *reproductive behaviour and conditions required for seedling establishment.*

Both *Fagus* and *Nothofagus* species are wind pollinated, while seed production, in at least some species, is irregular (Burrows and Allen 1991). *Nothofagus* are also known for generally poor seed dispersal which is accomplished by gravity and wind. Rudimentary wings aid wind dispersal in some species. The nuts of *Nothofagus* are also known to float in streams and rivers, but not in salt water. Long distance dispersal by birds is not common, the nuts are poorly adapted to withstand fire and only remain viable for only one season after being released from the parent plant. Seed *is seldom carried more than a few hundred metres from the parent tree* (Wardle 1984, Allen 1987a).

6.2.7.2 Nothofagus Taxa in New Zealand

The red beech *(Nothofagus fusca),* the hard beech *(Nothofagus ? truncata),* the silver beech *(Nothofagus menziesii),* the black beech *(Nothofagus solandri var. solandri)* and the mountain beech *(Nothofagus solandri var. cliffortioides)* comprise the five main taxa of *Nothofagus* currently recognised in the New Zealand flora. Leaf shape *is the major diagnostic characteristic used in taxonomic separation of the species* (Wardle 1984). All five New Zealand species may be found growing in the forest communities surrounding Lake Rotokura. Their main ecological characteristics and distributions (see also Poole 1960) are described below.

6.2.7.2.1 Nothofagus menziesii (Silver beech)

The Silver beech averages 20 - 25 m in height and is an evergreen which is known for its enormous spreading branches. In a forest, the trunk is usually devoid of branches for more than half the height of the tree while the base of the trunk may be buttressed on *larger trees growing on poorly drained sites at low altitude* (Wardle 1984). This species is also known to become dwarfed at high altitudes, on poor soils and exposed sites (Wardle 1984). For a detailed life history see Manson (1974).

The distribution of Silver beech is illustrated in fig 6.3. In the north of New Zealand, it is restricted to montane and subalpine forests, while in the South, its range almost reaches sea-level in some places. Wardle (1984) notes that it is usually a *component of the wetter beech forests near and to the West of the main axial mountain ranges and in these areas it is often the main tree species forming the timberline.* It is known to co-dominate with Red beech *(Nothofagus fusca)* at lower altitudes, but often forms a pure forest with only a few other species at higher altitudes in wetter mountain regions (Wardle 1984). For a more detailed discussion of *N. menziesii* refer to Wardle (1967).

Fig 6.3 The distribution of *Nothofagus menziesii* (Silver beech) in New Zealand (from Wardle 1984).

6.2.7.2.2 Nothofagus fusca (Red beech)

The Red beech normally reaches a height of 24 - 30 m, is evergreen and well known for its enormous spreading crown in those trees that emerge above the main forest canopy. Large root buttresses are also known to develop on this species in deep soils of lower slopes, terraces and poorly drained sites (Wardle 1984).

The distribution of Red beech is illustrated in fig 6.4. This species is usually found in lowland or montane forests, although it is also known to form a subalpine timberline in some places. It favours deep fertile soils of the lower valley slopes and terraces and rarely ascends above 1000 m. The Red beech forms either exclusive stands or will associate with other tree species like Mountain beech (in drier conditions) and Podocarps (especially *Dacrydium cupressinum*) at lower altitudes (Wardle 1984).

6.2.7.2.3 Nothofagus ? truncata (Hard beech)

The Hard beech averages 24 - 30 m in height, is evergreen and also develops large root buttresses on gentle slopes and on poorly drained soils. The trees of this species are known to reduce their trunk diameter and height on spurs, ridges and headlands.

The distribution of Hard beech is illustrated in fig 6.5. In contrast with the other New Zealand beeches, Hard beech favours lower altitudes and is more restricted to Northern districts. It is usually found in lowland and montane forests up to about 600 m, growing in association with *Dacrydium cupressinum* and the *broad-leaved hardwoods, Weinmannia racemosa* and in the North Island, *Beilschmiedia tawa* (Wardle 1984).

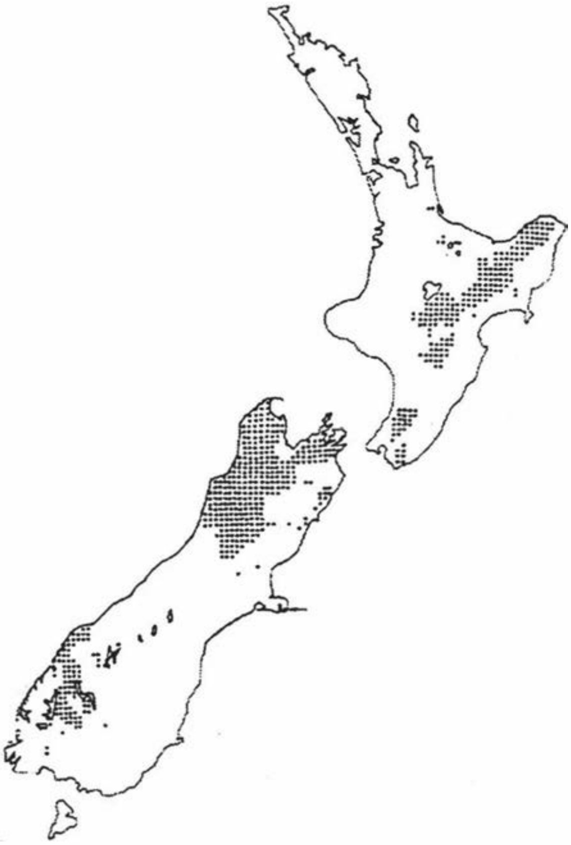


Fig 6.4 The distribution of *Nothofagus fusca* (Red beech) in New Zealand (from Wardle 1984).

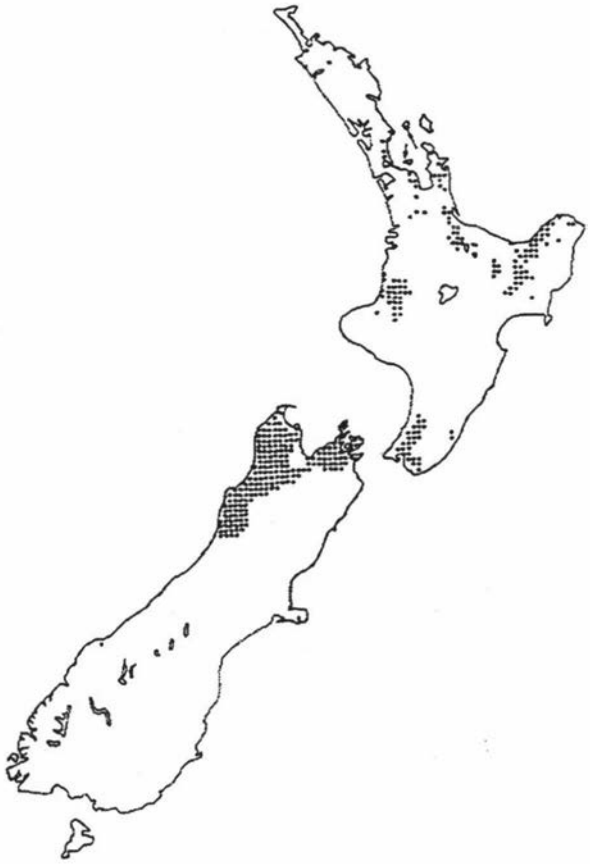


Fig 6.5 The distribution of *Nothofagus ? truncata* (Hard beech) in New Zealand (from Wardle 1984).

This species also favours its own company and is known to form exclusive stands on ridges, drier spurs and on poor soils, while intermixing with other species on slopes and in gullies (Wardle 1984).

6.2.7.2.4 ***Nothofagus solandri var. solandri (Black Beech)***

The Black beech averages 20 - 25 m in height (occasionally 30 m) and is also an evergreen. Neither Black nor Mountain beech usually forms a buttress. The overall growth form of these trees is reduced on poorly drained, low fertility soils, spurs and exposed ridges (Wardle 1984).

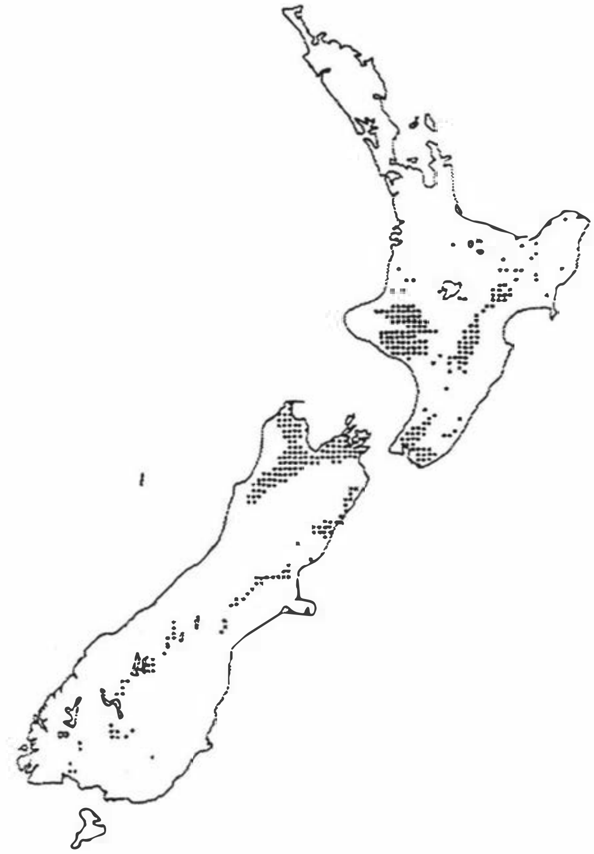


Fig 6.6 The distribution of *Nothofagus solandri var. solandri* (Black beech) in New Zealand (from Wardle 1984).

The distribution of Black beech is illustrated in fig 6.6. Black beech tends to favour the same sites as Hard beech and has also been known to occupy river terraces in the montane and lowland forests. Once again, this species favours exclusive stands (especially in drier Eastern locations) but will intermix with podocarps in deep soil that is fertile and free draining (Wardle 1984). For a detailed description of the distribution and life history of Nothofagus *solandri* see Wardle (1970, a, b, c).

6.2.7.2.5 ***Nothofagus solandri var. cliffortioides (Mountain beech)***

Unlike the other New Zealand beech species, Mountain beech usually only grows to average heights of 12 - 15 m and has been estimated to reach a maximum age of 350 - 400 years (Jowett *et al.* 1987). The form of these trees is usually devoid of lower branches in forest locations while open sites encourage large spreading crown formation.

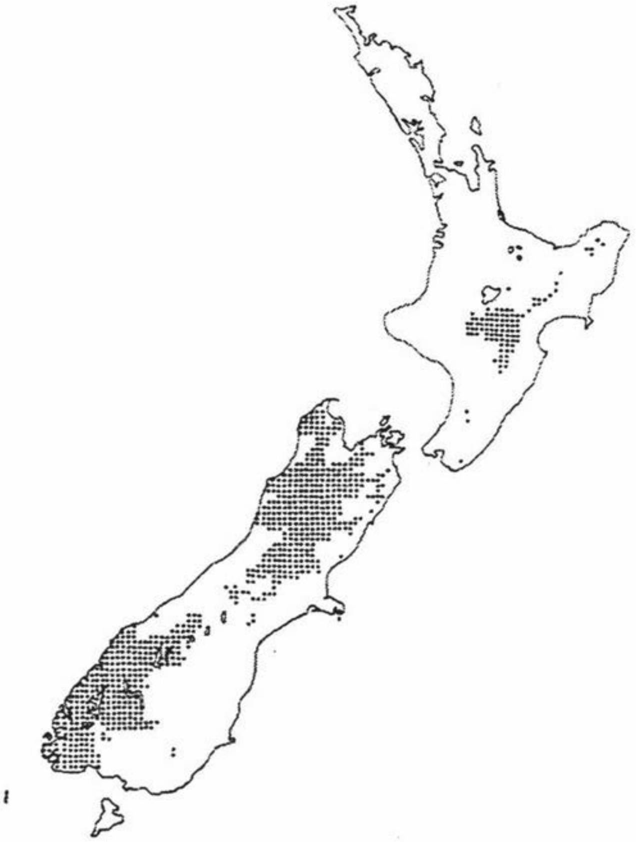


Fig 6.7 The distribution of *Nothofagus solandri var. cliffortioides* (Mountain beech) in New Zealand (from Wardle 1984).

Poorly drained soils, ridges and spurs are all sites that engender stunting in Mountain beech. In high altitude exposed sites of poor soil, this species is known to be reduced in size to a small shrub (ca. 45 cm high). Mountain beech is also known to develop highly specialised growth forms in drifting and avalanching snow, found usually in high altitude locations (Wardle 1984). For a more detailed life history see Wardle (1974).

The distribution of Mountain beech is illustrated in fig 6.7. This species is again restricted to montane and subalpine zones and well drained infertile soils of lowland regions. It is known to ascend above 1200 to 1300 m, but rarely exceeds 1500 m. Mountain beech forms exclusive stands in *drier subalpine eastern regions* but will also intermix with the taller podocarps and hardwoods on shallow and poorly drained subalpine soils (Wardle 1984).

6.2.7.3 ***Pollen Identification***

Identification of the fossil pollen from the Lake Rotokura core presents a number of problems. Firstly, there appears to be adequate evidence to correlate the flowering success of the Southern beeches with *average temperature - and possibly rainfall - of the preceding season* (Poole 1948, 1955). If this is the case, then variation in weather patterns from year to year may influence pollen productivity.

Secondly, the *Nothofagus* genus cannot be identified to species level. The five known species of New Zealand *Nothofagus* can be classified into two separate groups (Fusca type and Menziesii type) beyond which further identification is not possible at the present time (Cranwell 1941a, b, Harris 1956).

The Fusca type pollen group includes *N. solandri var. cliffortioides, N. fusca, N. solandri var. solandri and N. ? truncata,* while the Menziesii pollen type includes only *N. menziesii.* This grouping of the New Zealand *Nothofagus* pollen into two separate groups causes a problem for the modelling experiments.

In order to evaluate interspecific competition using the coupled logistic equation, it is desirable to be able to identify fossil pollen to species level. Because there is no way around this problem, the present study has used the identification of *Nothofagus* to a type level only.

There are definite limitations to this approach. The main limitation is that the ecology of individual species is different. By grouping species, individual ecological characteristics are being *averaged* together. While this is true, the most important aspect of the ecology of the New Zealand genus of *Nothofagus* is shared by all species. The New Zealand *Nothofagus* are thought to be poor competitors in podocarp - hardwood forests.

While grouping the *Nothofagus* pollen into types, it should still be possible to identify the existence of competitive behaviour between this genus and the dominant podocarp components, *Dacrydium cupressinum* (Wardle 1963, Franklin 1968) and *Podocarpus totara* of the Lake Rotokura forest. This approach simply involves a different level of resolution than would normally be used in a palynological study of this kind.

By grouping the *Nothofagus* pollen into two types it is also possible to reduce the total number of possible competitive interactions and thereby the complexity of the model being used. Another difficult decision needed to be made in selecting the most important podocarp - hardwood species to use in the modelling experiments.

The inclusion of every tree species found in the forest would result in a model of unmanageable size and computational complexity. Furthermore, the greater the number of parameters a model has, the greater the degree of freedom and therefore, the easier it becomes to fit any type of behaviour. In the light of these limitations, it seemed appropriate to limit the choice of podocarp - hardwood species to the two most dominant canopy species which, as it happens, both belong to the family Podocarpaceae. These two species are *Dacrydium cupressinum* and *Podocarpus totara.*

As it turned out, the pollen of the other forest canopy trees and understorey species was very poorly represented in the fossil assemblage from the Lake Rotokura core. This is a common problem with a *Nothofagus fusca* type pollen assemblage. The *Nothofagus fusca* pollen type tends to have a masking affect on other taxa (Bussell 1988 and McGlone 1988). These other taxa *show correspondingly reduced percentages and thus become under-represented with respect to their abundance in some vegetation* (Bussell 1988).

The identification of the Fusca type and Menziesii type pollen groups is so simple that it could not easily be mistaken. Detailed, illustrated accounts of the morphology of these pollen types may be found in Cranwell (1941a, b) and Harris (1956). The identification of the two podocarp species (*Dacrydium cupressinum* and *Podocarpus totara*) is also a very simple procedure and is outlined in detail in Pocknall (1981). Because the identification of these pollen types is so straightforward and so well documented in published sources, the present author has not included a detailed description of pollen identification in this text. Such an approach was more appropriate for the Totoya mangal, the identification of which is not as well described in published sources as the above New Zealand types.

6.2.7.4 Beech Forest in New Zealand

Wardle (1984) suggests that the New Zealand forest has the characteristics of *evergreen rain forest in which four major physiognomic elements can be recognised.* These elements are the softwoods (all softwood, indigenous *Coniferales* including *Agathis australis*), the broad - leaved - hardwoods (all dicotyledonous, hardwood trees except beeches), and the beeches. The softwoods can be further subdivided into their own class (the podocarps) which excludes *Agathis australis* but includes all of the indigenous *Coniferales* (*Phyllocladus, Podocarpus, Dacrydium and Libocedrus*). For a detailed classification of the North Island forests, see McKelvey and Nicholls (1957) and Nicholls (1976).

The beeches may be considered as the single major element in New Zealand forest vegetation. They either occur as pure beech forest (ca. 46% of New Zealand's 6.247 million ha of indigenous forest) or as mixed beech forest (ca. 22% or 1.38 million ha as mixtures of beech with softwoods and broad-leaved hardwoods) with various amounts of the other three main elements. The remaining 32% of New Zealand's indigenous forest has *little or no beech* (Wardle 1984). In the South Island, 84% of the total indigenous forest is beech or mixed beech. In the North Island only 40% of the total indigenous forest is beech or mixed beech(Wardle 1984).

6.2.7.4.1 The Mount Ruapehu Beech Forest

A detailed description of New Zealand beech forest composition and distribution is given in Wardle (1984). The Mount Ruapehu forests are of special interest to the present study. These forests are mostly beech softwood (podocarp) and often give way to pure beech forest at higher altitudes. The timberline around Mount Ruapehu is irregular (ca. 1510 m), formed by mountain beech and considered to be the highest timberline in the North Island (Wardle 1984).

Between 1400 m and 1510 m, mountain beech has an understorey of *Coprosma pseudocuneata, Gaultheria depressa, Phyllocladus alpinus and Podocarpus nivalis.* Between 1400 m and 1200 m *Libocedrus bidwillii* and *Dacrydium biforme* usually appear and begin to co-dominate with Mountain beech at ca. 1250 m. At 1220 m, Silver beech appears and co-dominates with red beech below 1065 m. At this lower altitude, mountain beech begins to become restricted while the understorey of this red - silver beech community usually includes *Griselinia littoralis, Pseudopanax crassifolius, Pseudopanax simplex, Carpodetus serratus, Podocarpus hallii, Myrsine divaricata and Coprosma foetidissima, with Blechnum discolor dominating the ground vegetation* (Wardle 1984).

In these lowland forests, the podocarps (*Dacrydium cupressinum, Podocarpus ferruginous and P. spicatus)* co-dominate with red and silver beech and are generally considered to be superior competitors. Below 975 m, the hardwoods *(Elaeocarpus dentatus, Elaeocarpus hookerianus* and *Weinmannia racemosa,* begin to dominate the forest and on *well drained sites completely exclude the beeches* (Wardle 1984). This red and silver beech forest fades out on the Western side of Mount Ruapehu and completely disappears on the Northern side of the mountain (Wardle 1984).

6.2.7.5 Mechanisms of Beech Forest Disturbance

Wardle (1984) suggests that beech forest disturbance types can be divided into two categories. Firstly, climate change, vulcanism and fire act to change the composition, internal structure and stability of beech forests. Factors of this kind are able to act at both local and regional scales and in this way, may act through time to cause changes in the composition of these forests.

A second class of disturbance seldom results in extensive compositional changes and may be more slow in their action. In this class, mass movement is triggered by tectonic activity, rainfall and *weather related factors such as wind, snow and flood* (Wardle 1984). This type of disturbance does not result in the loss of seed stock *so that the overall physiognomy of the forest does not alter significantly* (Wardle 1984). The following discussion of causal mechanisms responsible for beech community organisation concentrates on vulcanism, since this is the mechanism being investigated in the present study.

There has also been considerable debate in the literature as to whether long-term climate changes are more important in determining distributional patterns of beech forest in some parts of New Zealand. This question is also briefly considered.

6.2.7.5.1 Climate Change

There has been much debate in New Zealand as to the possible effects of long-term climate change on the persistence and distribution of beech forests. The details of this debate are recorded in a wide range of published sources, a good review of which is given in Wardle (1984). Climate change is a slow acting causal mechanism of community organisation. The influence of climate change on forest vegetation is likely to be complicated by response time delays resulting in faunal and floral disequilibria (Davis 1986).

Very early on in the climate change debate in New Zealand, Cockayne (1919, 1928) argued that any long-term climate change resulting in an increase of temperature would competitively disadvantage the beech forest elements in favour of the tropical elements of the New Zealand flora. As a result of climate warming of this kind, the tropical elements in the New Zealand flora would respond by advancing southward while the subantarctic element of the New Zealand flora would retreat to higher altitudes in colder, lowland regions (see Wardle and Coleman 1992). A long-term change to a colder, drier climate would, on the other hand, favour the beeches (Wardle 1984).

The present consensus of opinion appears to be that present distributional patterns of beech forest in the New Zealand flora are a result of incomplete readjustment since the last major retreat of the Pleistocene ice about 14,000 years ago (Suggate 1965). It is possible that in the initial stages of readjustment, the podocarps and broad-leaved hardwoods had a competitive advantage over the beeches as a result of *more effective mechanisms for long distance seed dispersal, such as dissemination by fruit eating birds* (Wardle 1984).

6.2.7.5.2 Vulcanism

Vulcanism is an important causal agent of forest community organisation in the North Island of New Zealand. McCraw (1973) suggests that the greater part of the North island has been covered in tephra at some time in the past while at least 20% of the modern landscape is covered in a more or less continuous tephra deposit (Poole 1953). Of all past volcanic events affecting the North Island of New Zealand, those which were centred around the Taupo area (1800 years B.P.) have left the *greatest imprint on the present forest and its distribution in the central North Island* (Wardle 1984).

The full extent of the Taupo eruption is difficult to assess. McKelvey (1963) suggests that hundreds of thousands of hectares of forest were destroyed, while an equal amount of forest was probably severely damaged. Elder (1963) estimated that forest destruction occurred within a 50 km radius of the eruption centre, while Grange (1931), Rice (1964) and Cunningham (1964) have identified charcoal from the Taupo eruption ca. 65 - 80 km from the eruption centre. Despite the severity and extent of the Taupo eruption, there appears to be evidence to suggest that post eruption forest recolonisation occurred very rapidly (McKelvey 1953).

The impact of vulcanism on forest communities would vary according to their distance from the eruption centre, differences in local site conditions, the prevalence of fire, the ability of a species to tolerate ash deposits and to regenerate after the event (Clarkson 1990). It seems likely that tree species adapted to long distance dispersal would have had an advantage in the recolonisation process. In some places, ash deposits may have worked to improve soil drainage, structure and fertility. This in turn, would have favoured the *competitive, fertility demanding, broad-leaved hardwood species over the beeches* (Wardle 1984). In summary, vulcanism is a causal mechanism of community organisation which has far reaching consequences for the spatial and temporal behaviour of forest communities.

Both Nicholls (1963) and McKelvey (1963) argue that beech forest was once more extensive in the regions surrounding the Taupo volcanic centre. Their present scattered distribution may have resulted from post-eruption conditions that favoured podocarps and broad-leaved hardwood species over the beeches.

McGlone and Topping (1977) consider that Nicholls (1963) and McKelvey (1963) have largely ignored the influence of climate as a causal mechanism of central North Island beech distributions. McGlone and Topping (1977) suggest that beech forest was almost eliminated after the last glacial maximum. The retreat of the glaciers in this area was driven by a climate change that favoured the podocarps and broad-leaved hardwood species which were also able to disperse more rapidly than the beeches. The slow dispersal of the beeches may explain their absence from high altitude forests, where they meet competitive resistance from the more quickly established upland podocarp/hardwood associations. This hypothesis proposes that volcanic eruptions in the central North Island have served to retard the expansion of beech that has occurred more successfully in other parts of the North Island.

Taupo was not the only volcanic centre likely to have influenced the forests and vegetation of the central North Island region where Lake Rotokura is situated. Neall (1995) has evidence of *18 sandy ash deposits from Ruapehu in the last 1800 years, one every 100 years* on average. The most recent of these eruptive events occurred in September 1995 and is believed to be the first *eruption of Ruapehu of this magnitude recorded since the European settlement of New Zealand* (Neall 1995).

This latest eruption covered thousands of hectares of forest, desert and farmland vegetation with a dark grey cover of ash. The direction of the prevailing westerly weather at the time of the eruption carried almost all of the ash fallout to the East and Northeast of the mountain. This fact implies that not all of the mountain's eruptive events will be recorded in the sediments of Lake Rotokura which lies to the South of the mountain.

6.2.7.5.3 ***Fire***

Prior to the human settlement of New Zealand, forest fires caused by either volcanic activity or lightning strike may have been responsible for forest destruction (Cameron 1961, New Zealand Forest Service 1964, Molloy 1969, 1977).

Wardle (1984) argues that fire resulting from natural causes is unlikely to have been a long-term control of forest vegetation, since *the interval between successive burns in any one area would have permitted succession back to forest.*

The human settlement of New Zealand greatly changed this situation. Cameron (1961) (see also Newsome 1991) estimates that ca. half of the original primeval forest of New Zealand (11.5 million hectares) was destroyed by the original Polynesians. Those areas burnt by the Polynesians were prevented from reverting back to *forest by the later land clearing activities of the European Pastoralists* (see Dick 1955). In other areas of *merchantable forest, logging and burning was deliberate policy* (Wardle 1984).

It seems unlikely that forest fires caused by natural agents like lightning would be an inadequate long-term control of forest vegetation. It may certainly be responsible for composition variation and undoubtedly involve a complex interaction of environmental conditions. A number of examples may be used to illustrate this point; local regeneration may fail if seedlings are scorched and ultimately die (McQueen 1951), a crown fire may be sufficient to cause the fall of a dead standing tree, strong winds may carry embers and cause many small localised fires, or a localised fire may smoulder underground until drought conditions cause it to flare up into a more damaging conflagration (Wardle 1984).

6.2.7.5.4 Other Factors

Climate change, vulcanism and fire are the main causal agents of interest to this present study. Other forms of beech forest disturbance may include local or regional damage from windthrow (Jane 1986), physical damage from heavy snow, insect damage (Milligan 1974, Hosking and Kershaw 1985, Hosking and Hutcheson 1986), earthquakes (Rawlings 1964), winter desiccation of small stems in exposed locations (Sakai and Wardle 1978, Greer and Wardle 1989), drought (Jane and Green 1983, Grant 1984, Hosking and Hutcheson 1988), a shift in the local watertable, flood damage, mass movement (Wardle 1984), and the influence of introduced animals in more recent times (Conway 1949, Grant 1955, Widdowson 1959, Silvestor 1964, James and Wallis 1969, Barton 1972, James 1974, Cunningham 1979).

6.2.7.6 Forest Recovery

Beeches are generally poor competitors in podocarp - hardwood forests and tend not to become established where a fern or herbaceous ground cover already exists. Baylis (1980) has suggested that *the beeches may not be able to obtain suitable ectomycorrhizal symbionts in softwood soils, and therefore cannot become established, because they are not able to take up sufficient phosphorus for growth.* However, more recent research appears to indicate that this problem is unlikely to be universal (Allen 1987).

Beech seedlings are more commonly found on new sites - especially in mixed forests. In these locations, phosphorus levels from newly weathering rock are *sufficiently high to support non-mycorrhizal seedlings. These seedlings should be able to grow on such sites, at least in the absence of competition, until they can encounter suitable fungi* (Baylis 1980).

In pure and mixed beech forest, regeneration after a disturbance event that leaves a light gap in the canopy will be slow, unless *advance growth seedlings are already present in the forest floor* (Wardle 1984). In this situation, the establishment of new beech seedlings will be limited to elevated sites (Allen 1987) like tree stumps and *fallen logs which provide a seed bed above the level of the dense understorey* (Wardle 1984).

6.2.8 Domain of Application: Hypotheses 1 and 5

The Lake Rotokura beech forest provides a completely new domain of application for testing the predictive and explanatory power of the coupled logistic and exponential CGTM formulations. Furthermore, what is known of the ecology of this type of forest ecosystem provides two alternative hypotheses which may explain the nature and operation of the causal mechanisms and long-term behaviour of this community.

6.2.8.1 An Equilibrium Hypothesis

In this hypothesis, the present distribution of beech forest in the central North island region is considered to be a response to long-term climate amelioration following 'the last glacial maximum (Wardle 1963). In this model, the podocarp - hardwood elements of these forests gained an initial competitive advantage over the beech, as a result of superior seed dispersal mechanisms. As a result of this advantage, these elements of the central North island forests were able to establish more quickly in a post glacial climate that favoured these species. A review of hypotheses developed to explain the long-term successional progress of these forests is given by Chapman (1958).

As a result of the above competitive struggle, the beech element of these forests was initially slow to recover and was later resisted from invading (Wardle 1964, 1980, Rogers 1989, Haase 1989, 1989a) higher altitude sites by the existence of already well established podocarp - hardwood forests.

Both Cockayne (1928) and Holloway (1954) proposed that in mixed beech forest there was a long-term trend toward the replacement of podocarps (Cameron 1960, Burke 1973) by beeches (see Baylis and Mark 1963).

Today, the existence of beech elements in the Lake Rotokura forest may suggest that an invasion on the part of beech has taken place (see Wardle 1985 regarding South island beech forest recovery) and resulted in a displacement of former podocarp - hardwood elements. This hypothesis reflects the deterministic Clementsian model of community structure which implied that *a change in one species, especially a physiognomic dominant, would have profound effects on the remainder of the community* (Wilson and Allen 1990). In contrast with this model, the individualistic model of Gleason suggests there would be little effect (see the non-equilibrium hypothesis below).

This interactive process probably occurred on a local patch by patch basis and it therefore needs to be assumed that the overall displacement should be evident at the landscape level of scale used in this project. This is not an unreasonable assumption, especially in light of the fact that the beech forest trees have been aggregated into two groups (pollen types) and may now be considered as a landscape, rather than forest elements.

Vulcanism is accommodated into this equilibrium hypothesis by recognising that an eruptive event may either push the forest system away from equilibrium and therefore delay an eventual competitive outcome, or reset initial conditions. If initial conditions are reset, then a competitive interaction may be observed from its initial state. Both Cockayne (1928) and Holloway (1954) suggest that beech will slowly displace the podocarp-hardwood element under the current climate conditions.

This equilibrium hypothesis will be tested by using a coupled system of logistic equations of two dimensions (as used in Chapter five). In order to simplify the modelling of this complex community, the total number of interacting elements in the forest will be reduced to two, the podocarps (*Dacrydium cupressinum and Podocarpus totara)* and the beeches (Fusca type and Menziesii type).

Competitive behaviour can also be tested for by plotting the state variables of interacting forest elements in phase space. For example, *Dacrydium cupressinum* could interact in the landscape with *Podocarpus totara*, or either of the beeches (Fusca type and Menziesii type). In the same manner, *Podocarpus totara* could interact with either of the beeches (Fusca type and Menziesii type). A total of six interactions is possible. The behaviour of these interactions should approximate the equilibrium solutions of the coupled logistic model (see section 2.4.6.2, Chapter 2).

6.2.8.2 A Non-equilibrium Hypothesis

The idea of evaluating New Zealand forest dynamics in terms of a non-equilibrium model of community organisation has been proposed by Ogden (1985). In the non-equilibrium hypothesis, the invasion of beech into a new high altitude forest zone is also a possibility, however this process is opportunistic and not competitive.

In this hypothesis, volcanic disturbance is considered to be disruptive (McGlone *et al.* 1988, Leathwick and Mitchell 1992) and intermediate to high in intensity and frequency. This level of disturbance maintains the forest in a low density region where intra and interspecific competition does not occur (Haase 1991). Gap phase dynamics (Stewart *et al.* 1991, Ogden *et al.* 1991) and resource heterogeneity provide an opportunistic environment for an invading species like beech to become established in response to local patch disturbances.

The long-term behaviour of such a system will be density vague. At the landscape level of scale, localised extinctions in a landscape subunit may be restored by seed dispersal processes. This spatial effect cannot be tested for with the non-spatial models used in this project. Non-equilibrium community organisation will be tested for by using the exponential CGTM. The forcing function for this model will be supplied by measurements of the size of tephra deposits in the core sample - a proxy for actual data of past volcanic events.

The use of such a forcing function does have some limitations. It must be assumed that the depth of the tephra layer in the core represents the nature and extent of a given volcanic event. It is unlikely that this will always be true. For example, a drought may dry out the forest and predispose it to a high level of fire risk. If a volcanic event coincides with a drought of this kind, fire may do considerable damage. If the same volcanic event occurred in the middle of winter, during a time of heavy rain, the level of damage caused by fire would be minimal.

Another assumption required for the forcing function is that the tephra was deposited in a single event of short time duration. It is very difficult to factor this time effect into the equation solvers used for this model which operate, on an almost linear relationship between sample depth and CAL. radiocarbon time.

A further problem is that the differential equation solvers require a forcing function with sample intervals coinciding with the same sample intervals used by the fossil pollen data. These two intervals do not always coincide. This problem was solved by fitting a spline curve to the tephra data which comprises a total of 73 data points at depth intervals not corresponding to the fossil pollen samples. A MatLab interpolation routine was then used to interpolate out a new data set of 60 data points (0 - 59) at 100 mm sample intervals (the exact sample interval of the fossil pollen data). The main problem with this approach was that the spline fit tends to exaggerate the tephra signal and for this reason must be considered as an approximation to a more complex function. Further research is needed in this area. The interpolated tephra data is recorded within Appendix 9.

6.2.8.3 Summary of A Priori Predictions

In an experiment designed to test the two hypotheses described above for the Lake Rotokura beech forest, the following results are predicted *a priori.*

The equilibrium hypothesis predicts that if the frequency and level of volcanic disturbance is low enough, opportunity will be provided for this forest to reach a high density region. This will result in competitive behaviour between the established podocarp elements of the forest and the invading beech elements under the present climate conditions.

This equilibrium interpretation recognises the existence of local disturbing events, but predicts that these will not be as strong as internal biotic causal mechanisms (intra and interspecific competition) which maintain this system at or near equilibrium.

In the non-equilibrium hypothesis, the frequency and intensity of volcanic disturbance is intermediate to high. Exogenous disturbance of this kind will effectively maintain this system in a low density region where competition does not exist. The resultant behaviour will be density vague.

In both of the above hypotheses it is assumed that the expansion of *Nothofagus* is possible as a result of generally drier and more frost prone climatic conditions over the last 5,000 years (McGlone and Topping 1977, McGlone and Moar 1977). The essential difference between the two hypotheses is that in the equilibrium model, strong internal biotic forces drive the community while in the non-equilibrium model the forest community is stochastically dominated.

The two hypotheses advanced in this section to explain the community organisation of this beech forest contain all of the assumptions involved in using the continuous coupled logistic and exponential CGTM formulations. The use of continuous time models is undertaken in the absence of any ecological information regarding the existence of discrete reproductive processes in these systems. Finally, the refutation criteria stated in Chapter five also applies in testing the above hypotheses. Due allowance must be made for the limitations of the tephra forcing function as discussed above.

6.3 Methodology

The following section provides a detailed discussion of the methodology used in the selection of the New Zealand core site, removal of cores, laboratory preparation, counting, dating and compiling of fossil pollen data sets for experiment four outlined in this chapter. To save repetition, references are provided in some places to the methodology section of Chapter five, where common procedures, treatments and discussion of important issues has already been given.

6.3.1 Site Selection

The selection of the Lake Rotokura core site occurred in the very early stages of this project, when the objectives of the modelling experimentation were still focused on classical equilibrium theory and the use of coupled logistic equations. At this time, the Lake Rotokura site seemed attractive for a number of reasons. Firstly, the forest vegetation around the lake appeared to be of homogeneous composition and low diversity. Secondly, the lake basin was small and lacked any inflow stream channel.

A vegetation survey of the forest vegetation around the lake was not completed until after the core from this lake had been removed. In retrospect, the site might have been abandoned, had the results of the vegetation survey been completed before the removal of the core. The vegetation survey showed that the forest vegetation was not homogeneous and what appeared to be a low diversity community revealed the existence of four New Zealand beech species. A positive identification of *Nothofagus truncata* would mean that all five New Zealand beech species are present in this forest. Needless to say, with limited time and funding in a PhD project, the temptation to abandon a site must be carefully considered.

By the time the data from the Lake Rotokura site had been prepared, the Totoya experiments were nearing completion and the project had developed a very strong, alternative, non-equilibrium hypothesis. The Lake Rotokura site was now viewed in a different light. The known volcanic history of this site provided an ideal opportunity to test for the existence of possible non-equilibrium community organisation. The possibility of non-equilibrium causal mechanisms and behaviour had been completely overlooked in the initial equilibrium focus of the project.

Perhaps the lesson to be learned from this experience, is that in the choosing of a site for palynological modelling research, the formulation of the hypotheses to be tested is equally as important as consideration of the local site conditions.

6.3.1.1 ***Taphonomy***

The following factors are likely to have influenced pollen dispersal and the preservation of fossil pollen in the organic mud sediments of Lake Rotokura.

6.3.1.1.1 ***Pollen Dispersal***

Amongst the New Zealand trees and shrubs, anemophily is very uncommon. Only the conifers *(i.e. Podocarpus etc.)* and two other genera *(Nothofagus and Laurelia)* have this type of reproductive strategy (McGlone 1988). It is therefore, not surprising, that both *Podocarpus* and *Nothofagus* tend to be over represented in fossil pollen assemblages (Bussell 1988). *Nothofagus fusca* is evidently the worst (McGlone 1988).

A further complication with *Nothofagus* is the fact that its pollen is known to travel such a long way by wind from a local source area (see Myers 1973, Moar and Myers 1978, McGlone 1982). The extent to which these two problems (over representation and long distance dispersal) have adversely influenced the fossil pollen assemblage of the Lake Rotokura site is very difficult to assess.

Over representation is probably less of a problem, especially because *Nothofagus and Podocarp elements (i.e. Podocarpus totara and Dacrydium cupressinum)* are all anemophilous.

Long distance dispersal may be more of a problem. One mitigating factor may be that the prevailing airstream over this central New Zealand region is Westerly, a source area from which *Nothofagus* forest is almost completely absent (a beech gap) (see figs. 15.8 - 16.2). Assuming that these conditions have persisted, then the fossil pollen of *Nothofagus* in the Lake Rotokura sediments is probably a regional signal. It is more difficult to be as certain about the podocarps.

Another factor which is not so favourable, is that the timberline on Mount Ruapehu (at ca. 1510 m) is composed almost exclusively of mountain beech *(Nothofagus solandri var. cliffortioides).* Katabatic winds may be responsible for the dispersal of mountain beech pollen down onto Lake Rotokura at ca. 700 m. Katabatic winds usually blow at night when the prevailing Westerly wind would have died down. The westerly wind would be a compensating factor, at least some of the time.

The dense structure of the New Zealand podocarp - hardwood - beech forests tends to block the passage of understorey pollen and thereby exacerbates the under representation problem (McGlone 1988). The modelling objectives of the present project are restricted to the beech and podocarp components of the forest (canopy trees). Therefore the general absence of understorey pollen does not cause a problem.

In summary, the source area for the fossil pollen used in this study *(N. fusca type, N. menziesii type, P. totara and D. cupressinum)* will include local, extra local and regional components - a landscape level of ecological scale. The possibility of long distance dispersal cannot be completely discounted for any of the forest elements used in this study.

6.3.1.1.2 ***Geological Processes***

There are two possible problems connected with the preservation of pollen in the sediments of Lake Rotokura. Firstly, while conducting fieldwork at the site, the author was told by some of the local people that the lake becomes cloudy or mixed at certain times during the year. It is very difficult to ascertain the reliability of this observation - the same people also told the author that the Lake Rotokura basin was bottomless and somehow connected to volcanic vents on nearby Mount Ruapehu. The story about the lake being bottomless is clearly not correct. For this reason, the author wonders if the notion of the lake overturning is not somehow connected, in the minds of the observers, with the idea of volcanic gases ascending from the bottom of the lake! The possibility of overturning cannot be completely discounted.

Measurements of the depth of the lake indicate that its floor descends quite rapidly to a central focal depth of ca. 8 m. The author assumes that the structure of the lake floor is quite stable, since a gradient is clearly present and is presumably in a form of constructional equilibrium. However, Mount Ruapehu has an eruption frequency of ca. 100 years and earthquake events have doubtless been a part of these episodes. Furthermore, New Zealand is frequently affected by earthquakes of various intensities. Therefore, the possibility of land sliding or slumping of lake sediments cannot be completely discounted.

A fact which makes the likelihood of slumping or land sliding much greater, is that none of the three AMS radiocarbon dates from this site are internally consistent with dated tephra deposits. This problem is discussed in detail later. One compensating factor, is that all of the tephra deposits in the central region of the core appear to be where they should be - based on visual identification (Prof V. Neall pers. comm.) and one tephra probe. For this reason, the core has been dated on the basis of this tephra chronology and not the anomalous AMS radiocarbon dates.

In summary, overturning and sediment slumping are potential problems which cannot be completely discounted when interpreting this core. The effect of overturning at worst may be to average out the pollen signal over various parts of the core. The effect of slumping presents a more serious problem. However, the internal consistency of the tephra deposits in the core give greater confidence.

6.3.2 Core Removal

The Lake Rotokura core was removed by using a modified Livingstone Piston Corer (Walker 1964) from a raft, secured to trees at the side of the lake by ropes. The deepest part of the lake was located by traversing up and down the lake in an inflatable dingy, measuring the depth of the water with a 20 m plastic tape tied to a heavy weight.

The removal of the core was a simple procedure. The very firm, organic rich, lake mud sediments of Lake Rotokura, were retained in the barrel of the piston corer perfectly. No section or part of the core was distorted or lost as a result of sloppy sediments.

Once each 1 m unit of core was removed from the casing pipe, it was taken to shore in an inflatable dingy before being extruded out into a core box (40 X 40 mm square PVC core casing box). The cores were sealed with many layers of masking tape to prevent possible leakage and the core boxes labelled. The core sections were transported back to Massey University, where they are now stored at ca. 5^{o}C in the Palynology lab of the Geography Department.

6.3.3 X-ray Analysis

Before subsampling, the entire core sections were x-rayed in order to locate possible tephra deposits. The X-ray procedure was carried out by the Radiology staff in Veterinary Clinical Sciences at Massey University. Optimal radiation intensities for the cores were found by trial and error. This approach is necessary, since the composition of core sediments changes from site to site and in some cases with the depth of a core.

6.3.4 Subsampling of the Core

The subsampling strategy developed for the Totoya cores was also used on the Lake Rotokura core. A sample volume of 1 cm^3 was removed and each subsample was spiked with 2 Lycopodium tablets (batch 710961) (Stockmarr 1971).

The Lake Rotokura core was subsampled at 500 mm and then 100 mm centred intervals with a final total of 59 samples (5900 mm). For the details of the subsampling procedure used, please refer to section 5.3.3 of Chapter five.

6.3.5 Laboratory Procedure

Overall, the Lake Rotokura samples were very easy to prepare and yielded very rich and clean residues. In contrast to the Totoya samples, these preparations were almost free of charcoal fragments and had only very small traces of clay and silica (diatoms). The treatments used are outlined in sections 5.3.4.1 - 5.3.4.10 of Chapter five. The only exceptions to this schedule of treatments and procedures are as follows. Firstly, only one treatment of hot sodium pyrophosphate (followed by sieving) was required to remove the clay content of these samples. Secondly, a thorough sieving and distilled water wash was required before alcohol dehydration, in order to clean up the samples, by removing fine grained organics. Finally, a series of volcanic glass slide mounts were also made in order to aid in the identification of the core's tephra deposits.

6.3.6 Counting Procedure

The counting procedure outlined in section 5.3.5 of Chapter five was not used in counting the samples from this core. Instead, a total pollen count of at least 200 pollen grains was used as a basis for gaining a suitable count size of the four fossil pollen elements in the Lake Rotokura forest vegetation used in this study. The data from the cores were converted to absolute fossil pollen counts by performing the necessary calculations on Tilia (ref. section 5.3.5.4 Chapter five for details) (ref. Appendix 9 for count data).

6.3.7 Dating of the Core Stratigraphy

Three lake mud samples were removed from the Lake Rotokura core and submitted to the Rafter radiocarbon laboratory (the Institute of Geological and Nuclear Sciences, Lower Hutt, NZ). These samples were dated using AMS radiocarbon techniques. Details of the core sections submitted for radiocarbon dating are listed below.

Site Name	*Sample*	*Depth (mm)*
Rotokura	Rot 012	5920-5970 mm
Rotokura	Rot 013	5600-5650 mm
Rotokura	Rot 014	2600 - 2650 mm

Table 6.1 Lake Rotokura core samples submitted for radiocarbon dating.

6.4 Results

The results section of this chapter covers five main topics in the following order: description of the core stratigraphy, dating of the core stratigraphy, description of the fossil pollen data set, correlation of the core stratigraphy with fossil pollen data and presentation of the experimental modelling results. The results presented in this case study differ from the Totoya study in two ways. Firstly, because only one core has been recovered from the Lake Rotokura site, it is not possible to cross correlate the cores for stratigraphic and forest community behaviour. Secondly, the lake Rotokura modelling experiment is the last of the four experiments conducted in this project. Therefore, while it is possible to speculate about how the results might be improved by further model reformulation, it is not possible to test such formulations without obtaining further data. All of the MatLab script files used in experiment four (for optimisation and simulation trials) are recorded in Appendix 10 and 11.

6.4.1 Core Stratigraphy

The Lake Rotokura core stratigraphy is illustrated in fig 16.3. A total of 5900 mm of core sediment was retrieved from Lake Rotokura. As with the Totoya core stratigraphy, illustrated in the previous chapter, the stratigraphic columns portrayed in these illustrations have two components. On the left of each column, a vertical scale (in metres) indicates the depth of the core sediments. Within the stratigraphic column, each stratigraphic unit of sediment is divided into proportions which represent approximate percentages of the component parts. A depth scale, details of collection and symbol key are located as a separate table on the top of the page following fig 16.8.

The stratigraphy of the Lake Rotokura core is primarily composed of a homogeneous lake mud (gyttja), which is present throughout most of the length of the core. This lake mud has a low clay fraction and high organic content. The next noticeable feature of the core is the presence of tephra and diatom deposits. With the exception of the Taupo and Waimihia tephra deposits, most of these units were identified only as a result of X-ray analysis. Using the X-ray photo plates as a guide, samples were taken from each deposit and visually checked under a low power microscope in order to verify that the deposits were in fact tephra. As is indicated by fig 16.8, many of these deposits turned out to be diatoms - a field for future research.

The Waimihia tephra was identified by Mr Shane Cronin, of the Massey University Soil Science Department, who conducted a tephra probe on the WDS electron microprobe at Victoria University in Wellington. The results of the probe show that a Taupo volcanic source is indicated by the glass chemistry (Orthopyroxene 73%, Magnetite 17% and Clinopyroxene 10%) which correlates most closely (3.225) with the Waimihia tephra (3.972).

The Taupo tephra was visually identified by Prof. Vince Neall of the Massey University Soil Science Department. The characteristics used to identify this tephra include its rhyolitic composition, gritty structure and the presence of elongate vesicles of a vesiculate nature. The Whakaipo and Marpara tephra deposits were also visually identified by Prof. Vince Neall, although it is more difficult to be as certain about these identifications without further tephra probes.

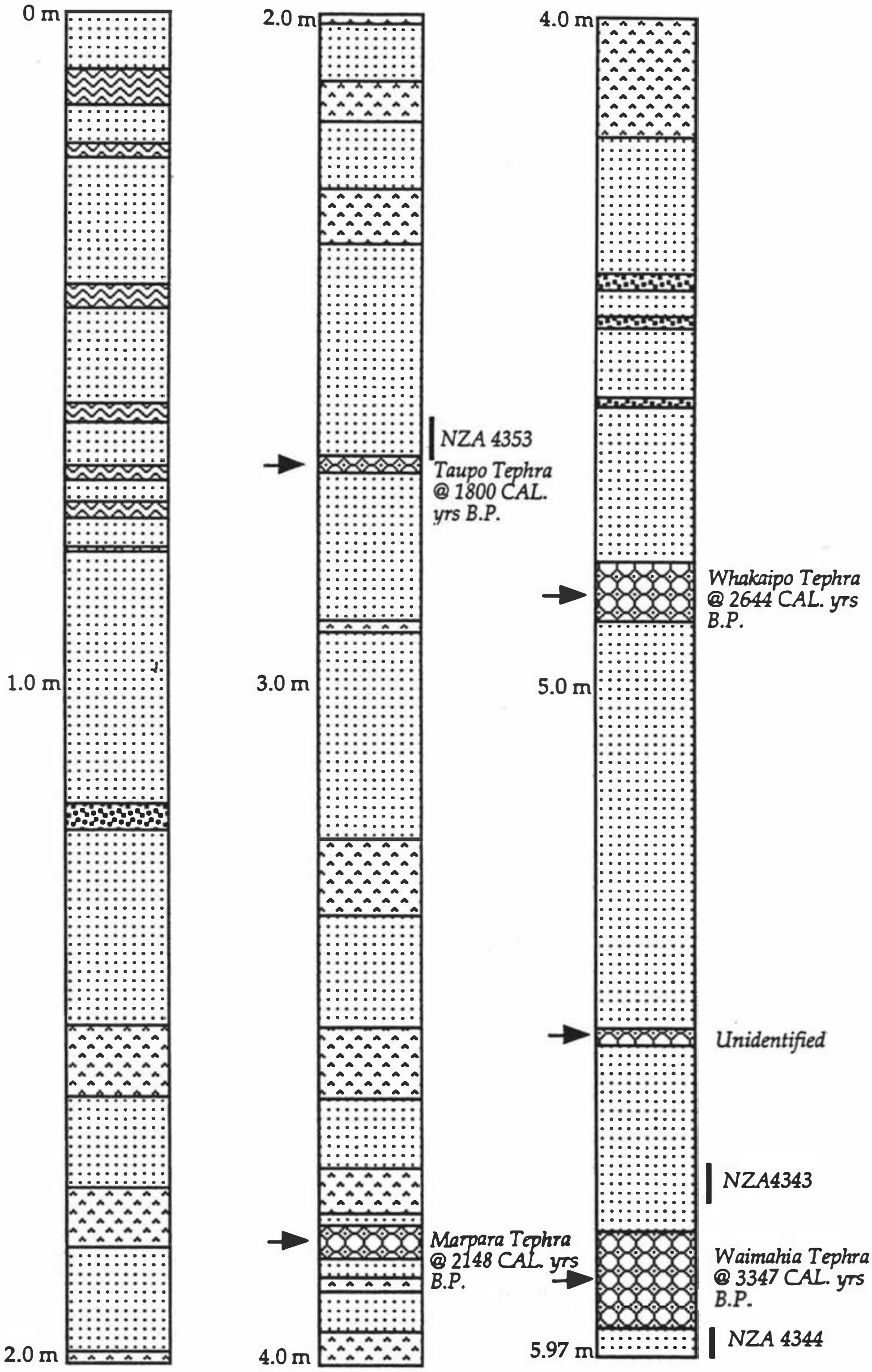


Fig 6.8 The Lake Rotokura core stratigraphy. The symbol key for 6.8 is located at the top of the following page (Table 6.2).

Lake Rotokura		Core Stratigraphy
⁙ homogeneous mud (gyttja)	▓ andesitic tephra	≋ andesitic tephra / diatoms
^ diatoms/gyttja	⊠ rhyolytic tephra	
Total Core Length:	*5970 mm*	Depth Scale (1:10)
Core Collected:	*Anthony O. Cole*	0 100mm
Date Collected:	*21/12/93*	

Table 6.2 Key for the interpretation of the Lake Rotokura core stratigraphy (for fig 6.8).

The size of these deposits, their composition (rhyolitic) and their location between the Waimihia and Taupo tephra deposits are the main diagnostic characteristics. A review of late Quaternary silicic and other tephra formations from New Zealand, along with their stratigraphy, nomenclature, distribution, volume and age is given by Froggatt and Lowe (1990).

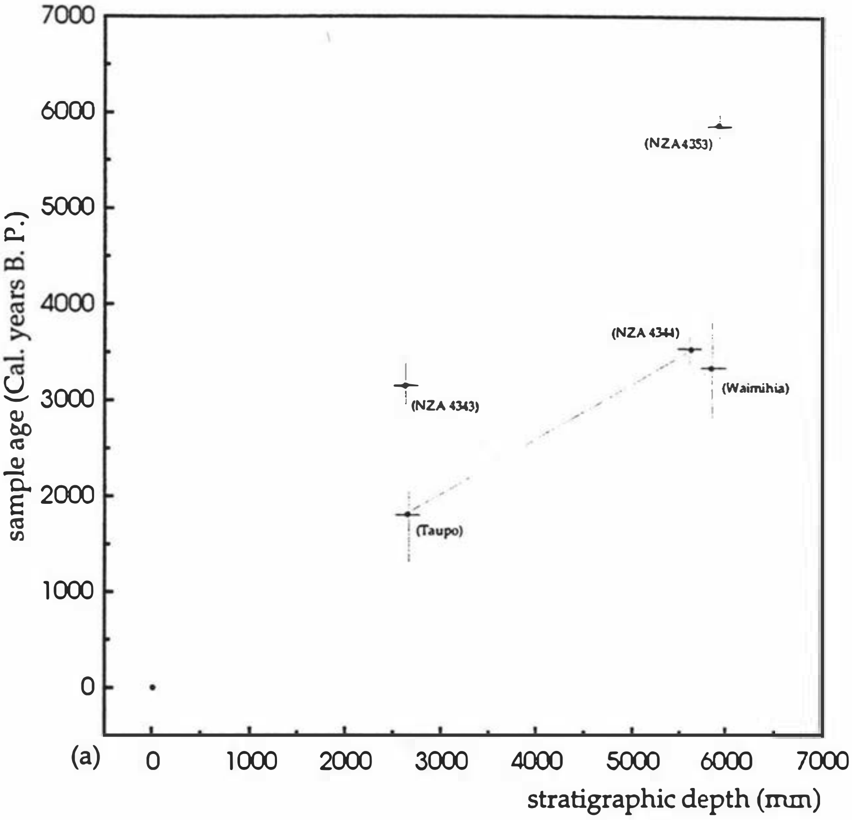
6.4.2 The AMS Dating of the Core Sediments

The results of AMS dating of the Lake Rotokura core do not correlate well with the stratigraphic position and known ages of the tephra deposits. This evaluation accommodates the fact that the tephra deposits tend to have very large confidence intervals, based on numerous published dates (ref. Froggatt and Lowe 1990). The results of the AMS radiocarbon dating of the Lake Rotokura core are listed in Table 6.3.

Site Reference	Depth (mm)	Conventional C 14 age (years B. P.)	Calibrated CAL. age (years B.P.)	95 % Confidence Calibrated (CAL yrs B. P.)	Laboratory Reference NZA
Rot 012	5920-5970	4918 ±83	5851.5	5879-5824	4344
Rot 013	5600-5650	3347 ±66	3533.5	3685-3382	4343
Rot 014	2600-2650	3019 ±67	3146.5	3338-3019	4353

Table 6.3 A summary table of AMS CAL. age determinations for samples from the Lake Rotokura core. These three samples were AMS dated as sediment units (lake mud).

The results listed in Table 6.3 can be more effectively displayed by plotting the average calibrated radiocarbon ages against stratigraphic depth. In order to illustrate just how poorly these dates correlate with tephra deposits in the core, average CAL. radiocarbon tephra ages have been included in this plot. Error bars around the tephra deposit ages indicate the total range of available published dates for that deposit (ref. Froggatt and Lowe 1990). Error bars on the three AMS radiocarbon ages represent a 95% confidence interval for the average calibrated age and the amount of sample submitted from the core on the depth axis (fig 6.9).



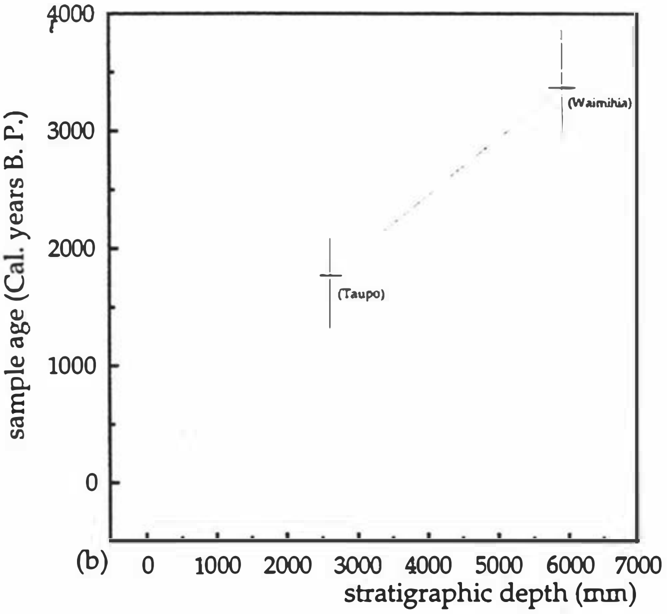


Fig 6.9 The results of AMS/CAL. dating of lake mud samples taken from the Lake Rotokura core.

Fig 6.9 (a) is a plot which includes both AMS radiocarbon ages for given sample depths, along with the average CAL. age of the Waimihia and Taupo tephra deposits. In this plot, each age sample point is identified by either an AMS reference number, or name, in the case of the two tephra deposits. These plots effectively portray the discrepancy between the AMS dates and average CAL. tephra ages. Furthermore, this discrepancy is so large that it is not possible to draw a line of best fit by using the error bars around the AMS dates and tephra ages. Of the three Lake Rotokura AMS dates, the one which raises the most concern is located below the Waimihia tephra (NZA 4353) and has an average calibrated age of 5851.5 CAL. years B.P (fig 6.9 a).

This age implies that there has been virtually no sediment deposition into the lake basin between this time and Waimihia eruption at 3347 CAL. years B.P. (a period of 2504.5 CAL. years). This discrepancy is almost certain to be the result of a geological problem with the core stratigraphy. There appears to be a large sediment unit missing from this part of the core.

The remaining two AMS radiocarbon dates (NZA 4343 and 4344) are both much older than known ages for the Taupo and Waimihia tephra deposits in the core. There is at present, no obvious explanation as to why this should be the case. For this reason it seems safer to trust the known ages af the Taupo and Waimihia tephra deposits as a basis for dating the core sediments (see fig 6.9 b).

6.4.3 The Lake Rotokura Data Set

The total period of time covered by this fossil pollen record is ca. 3300 CAL. years. The four Lake Rotokura fossil pollen data sets are plotted in fig 6.10 and 6.11 along with the volcanic tephra data. The format of these plots is similar to those of Chapter five (section 5.4.3), with a couple of differences. Firstly, the Totoya charcoal fragment data has been replaced by tephra data. Secondly, there is much more variance in the Lake Rotokura data. In order to make the behaviour of the data easy to see in these plots, the y axis (fossil pollen in grains cm^{-2} CAL. year^{-1}) has been adjusted to 500 in fig 6.10 a and 150 in fig 6.11 a. This makes the plots easier to interpret, but has cropped the very first part of the PAR signal at time interval -2500 CAL. Years B.P. in both plots. To compensate for this problem, a preview window has been located in the top right hand corner of these plots, which shows the over all behaviour of the data, including the very first rise (but at a loss of detail).

The data from Lake Rotokura is a striking contrast to what would be expected for a forest community of this kind, operating in a high density region, near equilibrium. The behaviour of these four forest tree types, should be viewed in relation to the two largest volcanic events which have affected this forest community. Firstly, the Waimihia eruption occurred at approximately 3347 CAL. years B.P. which coincides with the very first major fall in fossil pollen concentration.

Secondly, the Taupo eruption occurred at approximately 1800 CAL. years B.P. which also coincides with another decline in fossil pollen concentration.

These observations indicate that there is a strong correlation between the long-term behaviour of this forest system and the occurrence of volcanic events. The tephra data plotted in these portraits (see plot b/figs 6.10 and 6.11) has been generated by interpolation of spline fitted actual tephra data.

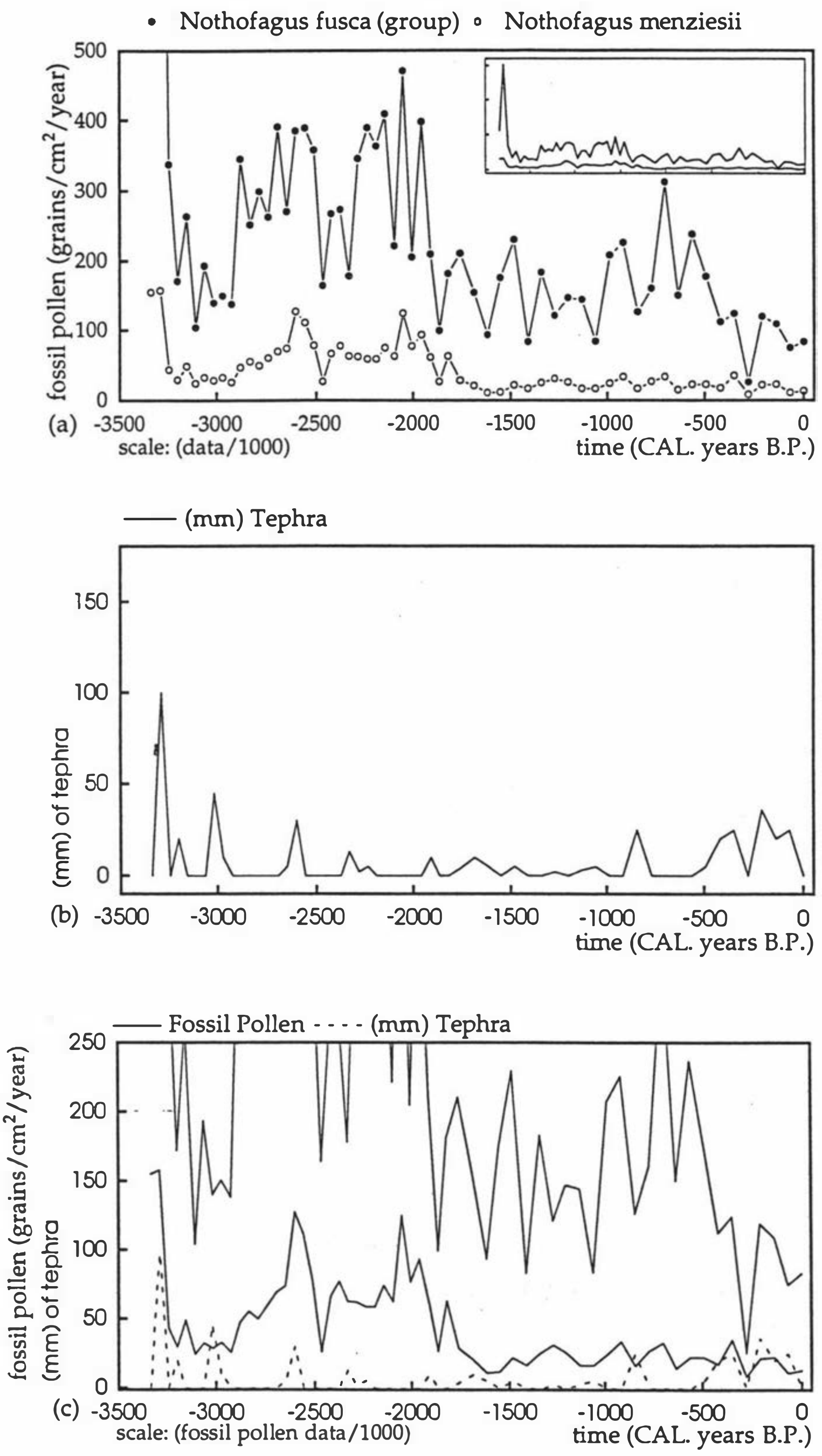


Fig 6.10 Lake Rotokura core site showing *Nothofagus menziesii type and Nothofagus fusca type* fossil pollen and interpolated volcanic tephra data.

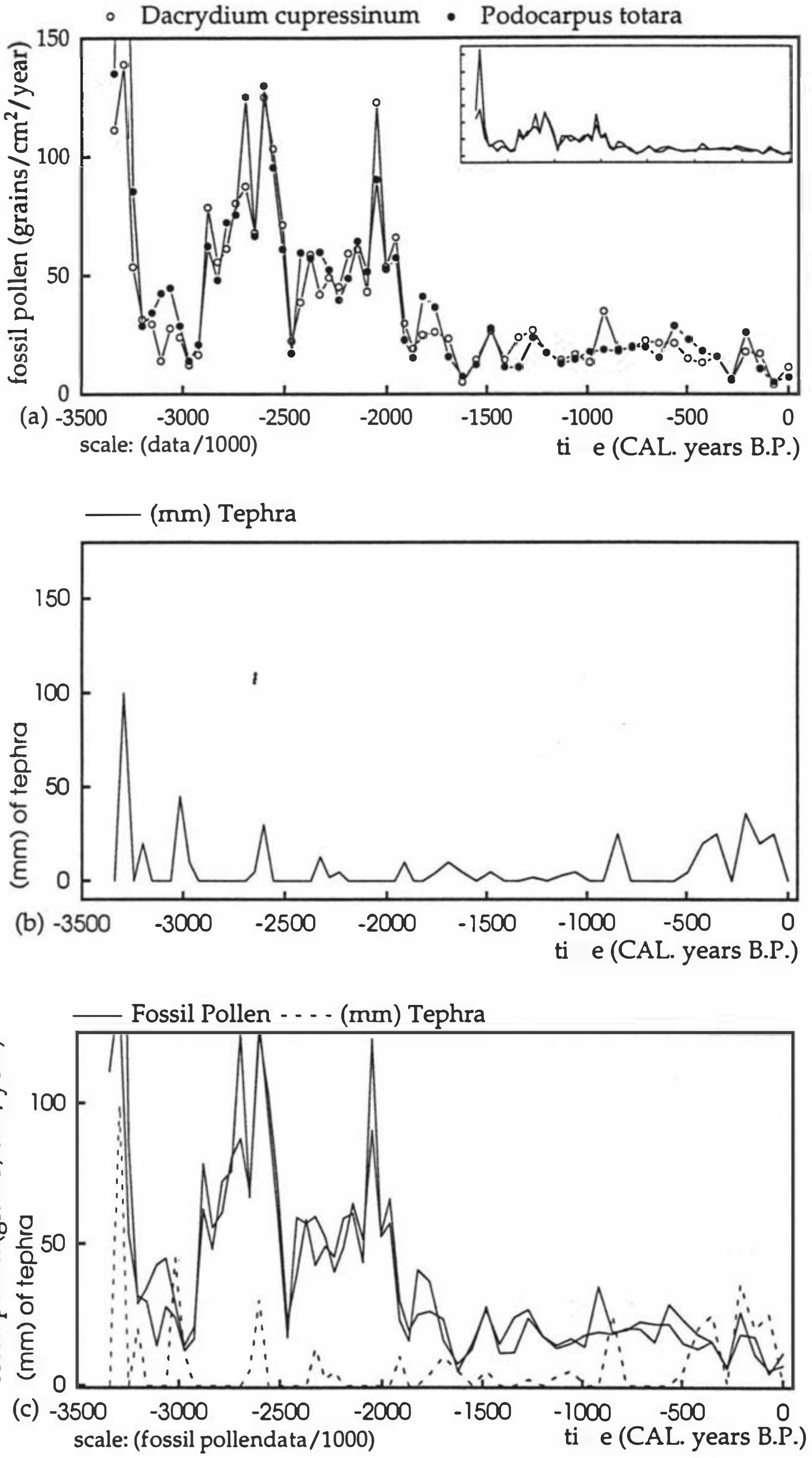


Fig 6.11 Lake Rotokura core site showing *Podocarpus totara and Dacrydium cupressinum* fossil pollen data along with interpolated volcanic tephra data.

When this interpolated data is plotted against the fossil pollen data (plot c/figs 6.10 6.11), the peak to peak correlation between the tephra data and the fossil pollen data is more evident - but not perfect.

The next important characteristic of these data is that all four species appear to respond to the influence of the tephra data (volcanic events) in unity. While there is not a perfect peak to peak rise and fall in all four forest tree types, the overall trend is remarkably similar.

Determining an upper asymptotic population density for this system involves all of the theoretical problems discussed in the previous case study. If it is assumed that the highest point that the fossil pollen signal rises to is an approximation of the upper asymptotic population density, then all four forest tree types are operating in the intermediate to low density region.

Overall, the behaviour of the forest tree species in this system may be described as density vague. The recovery of the forest following the Waimihia and Taupo eruptions, does not involve a return to a steady state, as would be predicted by classical equilibrium theory. A continual series of volcanic events appears to maintain the forest in a low density region, where competition does not appear to occur.

Another noticeable characteristic of these data, is that the forest does not appear to have recovered to the same high density after the Taupo eruption (@ 1800 CAL. years B.P.). This trend is evident in all four forest tree types. Long-term, it looks as if the density of the forest is slowly declining. Once again, this behaviour is evident in all four forest tree types. On a regional scale, this behaviour could have resulted from the large scale destruction of a formerly more extensive podocarp - hardwood - beech forest around this Southern end of Mount Ruapehu. If this is the case, what is portrayed in this data is a fall in regional pollen and not a decline in local pollen.

However, it seems unlikely that this interpretation is correct in light of the very strong recovery of all four forest tree types following the Waimihia eruption at ca. 3300 CAL. years B.P. (see figs 6.10a, 6.11b). These evidences suggest that the podocarp - hardwood - beech forest in this region is declining and not increasing in dominance as McGlone and Topping (1977) had earlier suggested. Could this behaviour be a result of recent climate change toward warmer and more moist conditions? This is possible, but unlikely, in view of the fact that both the podocarp and beech elements of the forest are responding in the same manner - warmer conditions should favour the podocarp - hardwood elements of the forest.

A more likely explanation is that these forests are maintained in a low density region by repeated volcanic disturbance of intermediate to high frequency and intensity. This level of disturbance prevents competitive exclusion.

6.4.4 Phase portraits

It is possible to test for the existence of competition by replotting this data in phase space. If this forest system exists in a high density region, then there should be evidence of a long-term trend toward an equilibrium value for pairs of interacting forest elements. In order to help identify such a trend, the fossil pollen data has been transformed using a four point moving average. Based on four forest tree types *(N. fusca type, N. menziesii type, P. totara and D. cupressinum)* a total of six paired interactions are possible; these are recorded figs 6.12, 6.13, 6.14.

A number of trends may be identified in the behaviour of these six phase portraits, for which the direction of time is indicated by a small arrow in each plot. Firstly, none of the six phase portraits provide any indication of the classical equilibrium behaviour predicted by the coupled logistic equations for a two dimensional system.

Secondly, all of the six phase portraits show a steady, long-term trend toward the zero / zero (low density) region. The present state of the system is a long way from its initial high density conditions. Thirdly, in the process of reaching the low density region, all of the six interactions show evidence of a type of intermediate density orbit. The morphology of this orbit is masked by noise, but evident in each case. Orbits of this kind are usually associated with predator prey systems. The exact reason for this behaviour in the present system is unclear.

In summary, a number of lines of evidence have now been presented which all indicate that this forest system has operated a long way from equilibrium over the past three thousand years. As was mentioned in Chapter five, it is possible that the long-term behaviour of a forest based on fossil pollen evidence may be partly influenced by sampling procedure (including core removal) and major disturbance events recorded in the core stratigraphy. It is reasonably easy to test for these problems by plotting the fossil pollen data along side of an illustration of the core stratigraphy and using this as a basis for cross correlation checking.

6.4.5 Correlation of Core Stratigraphy and Pollen Data.

In fig 6.15, the first two metres (0.0 - 2.0 m) of the Lake Rotokura core stratigraphy have been illustrated along side the fossil pollen data of all four forest tree types for this section of the core. The Nothofagus *fusca* type data set has been scaled by ten in order to group all four pollen signals in the same area of the plot.

The piston corer, used in collecting the Lake Rotokura core, has a barrel which measures exactly one metre in length. Not all of the sediment units collected were exactly one metre long, however the subsampling of the core at 100 mm intervals coincides with these one metre boundaries.

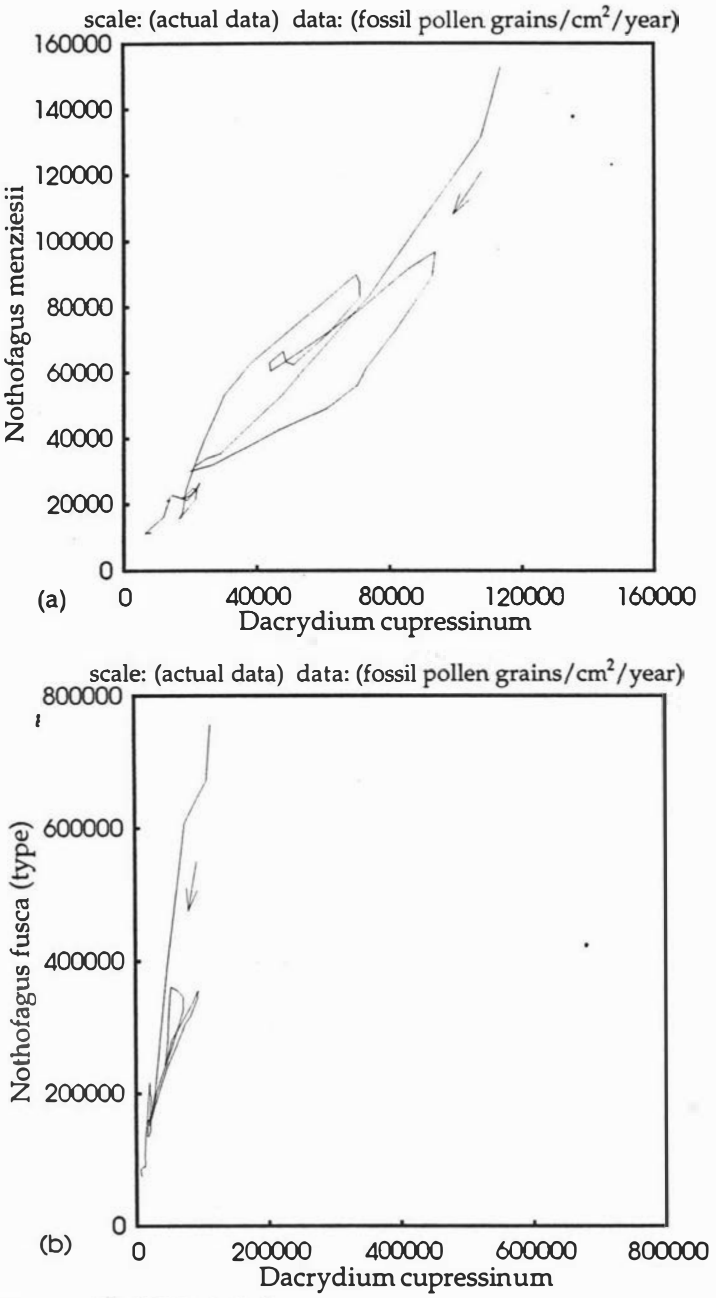
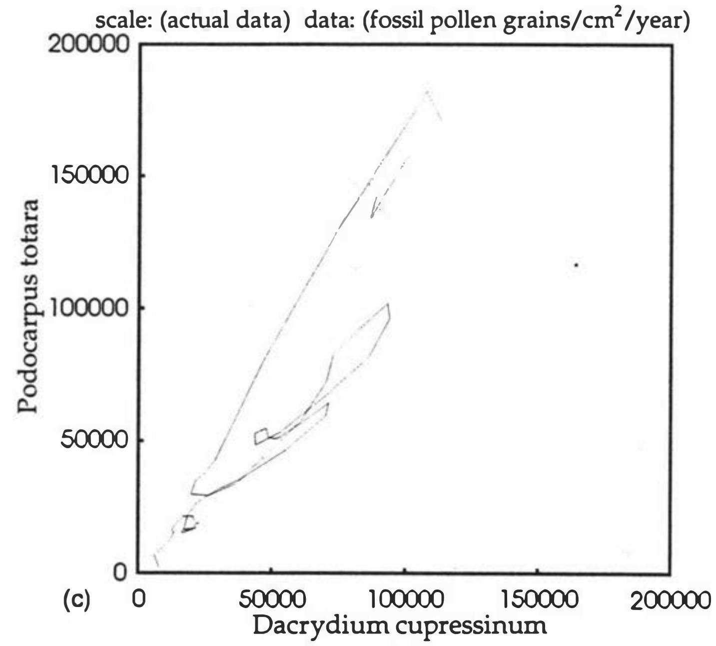


Fig 6.12 Lake Rotokura core site, phase portraits of Dacrydium cupressinum interacting with (a) *Nothofagus menziesii*, (b) *Nothofagus fusca (type)*. Data prepared using a four point moving average.



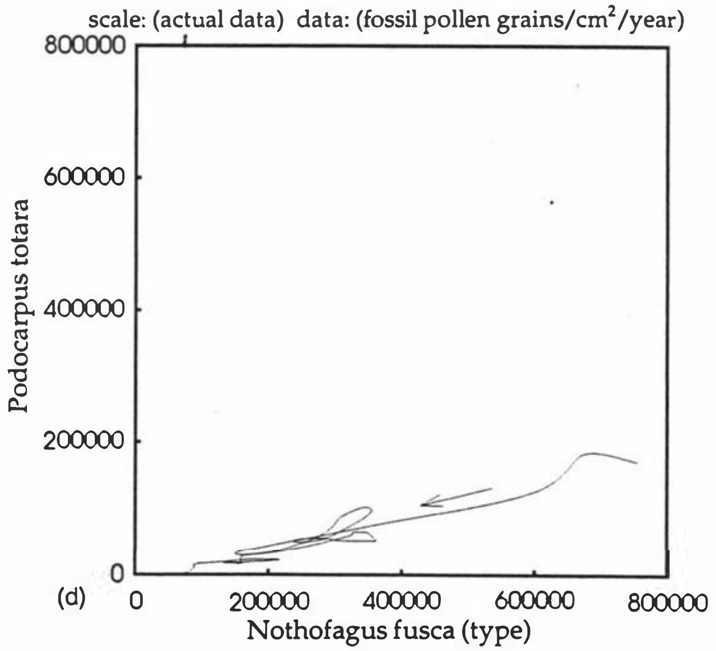


Fig 6.13 Lake Rotokura core site, phase portraits of Dacrydium cupressinum interacting with (c) *Podocarpus totara*, and *Nothofagus fusca (type)* interacting with (d) *Podocarpus totara*. Data prepared using a four point moving average.

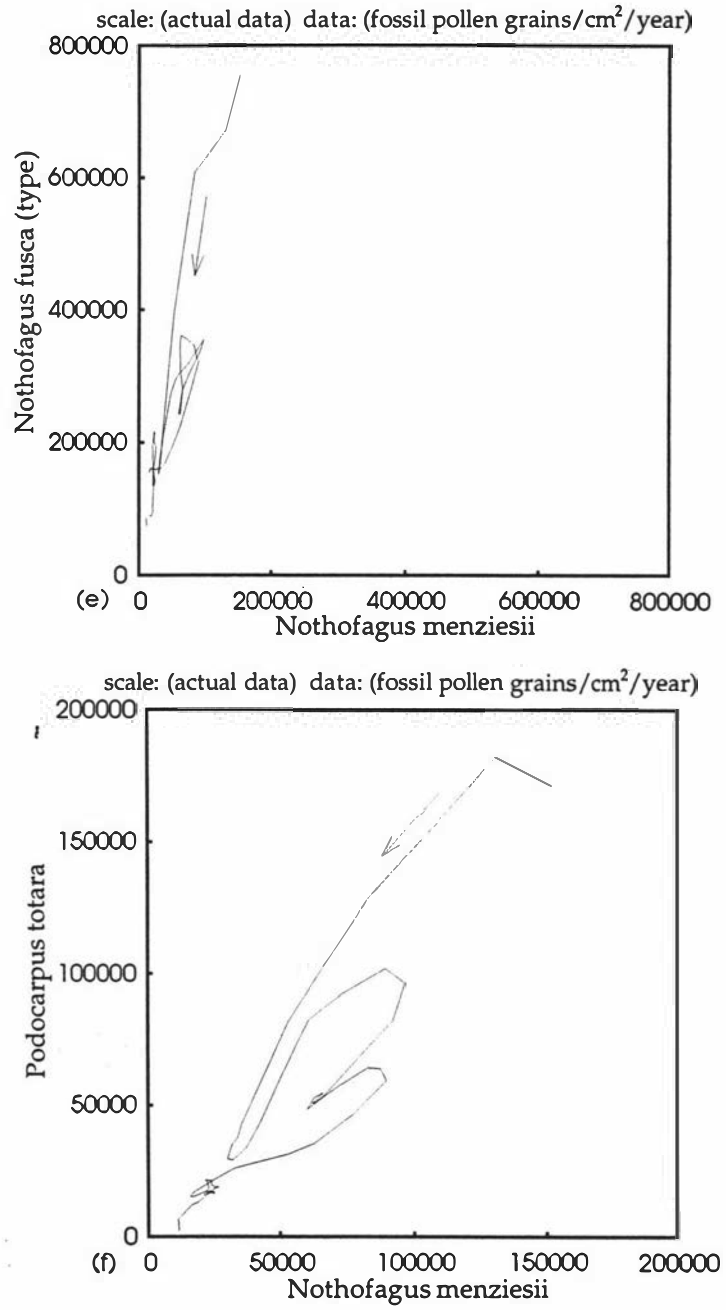


Fig 6.14 Lake Rotokura core site, phase portraits of *Nothofagus menziesii* interacting with (e) *Nothofagus fusca (group) and* (f) *Podocarpus totara*. Data prepared using a four point moving average.

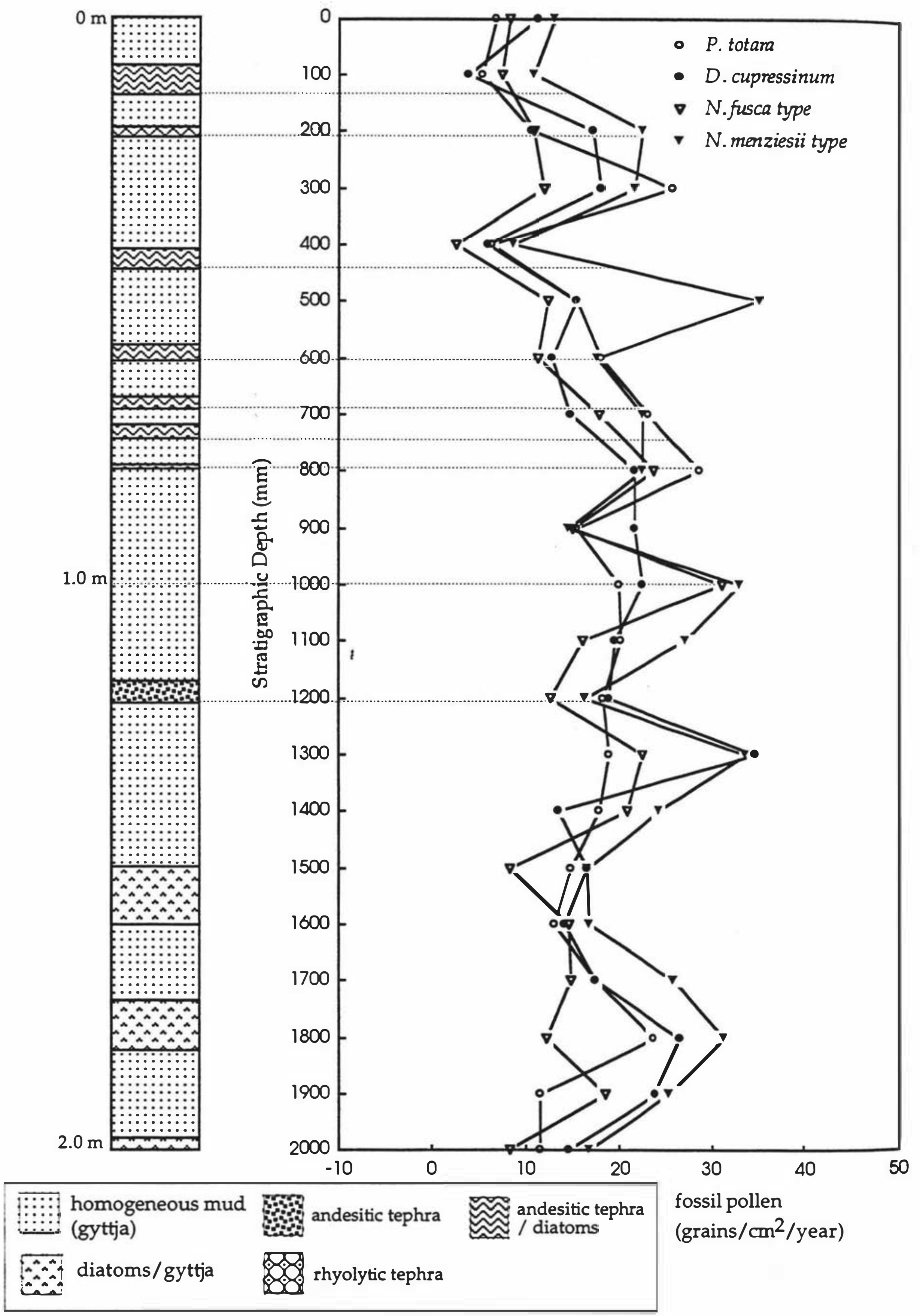


Fig 6.15 A correlation test of the Lake Rotokura core stratigraphy and fossil pollen data. This first illustration portrays the 0.0 mm to 2000 mm section of the core. The *Nothofagus fusca* data set has been scaled by 10. Correlation points are indicated by dotted lines.

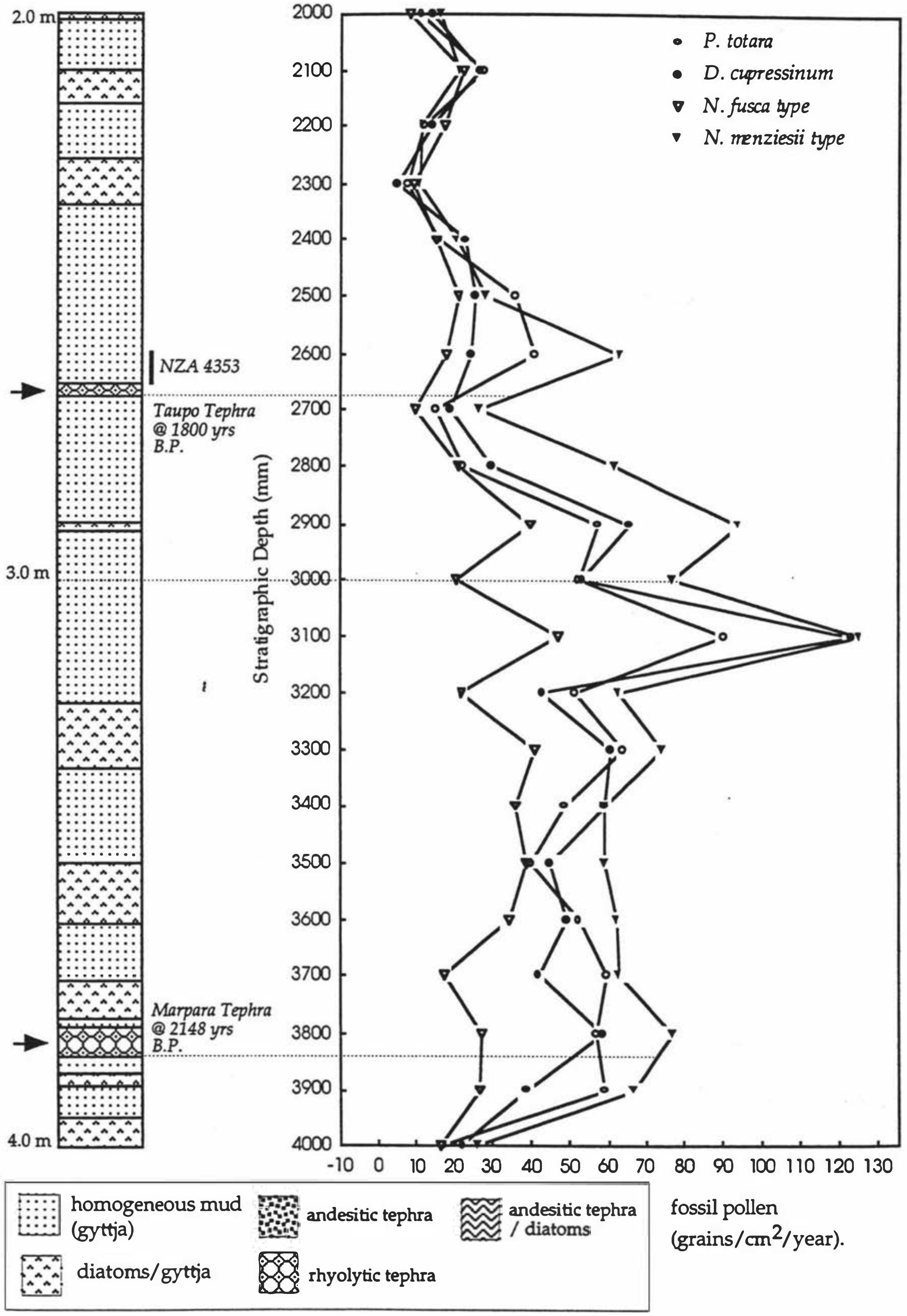


Fig 6.16 A correlation test of the Lake Rotokura core stratigraphy and fossil pollen data. This first illustration portrays the 2000 mm to 4000 mm section of the core. The *Nothofagus fusca* data set has been scaled by 10. Correlation points are indicated by dotted lines. The fossil pollen concentration scale in this illustration has been adjusted to provide better visual presentation of the data.

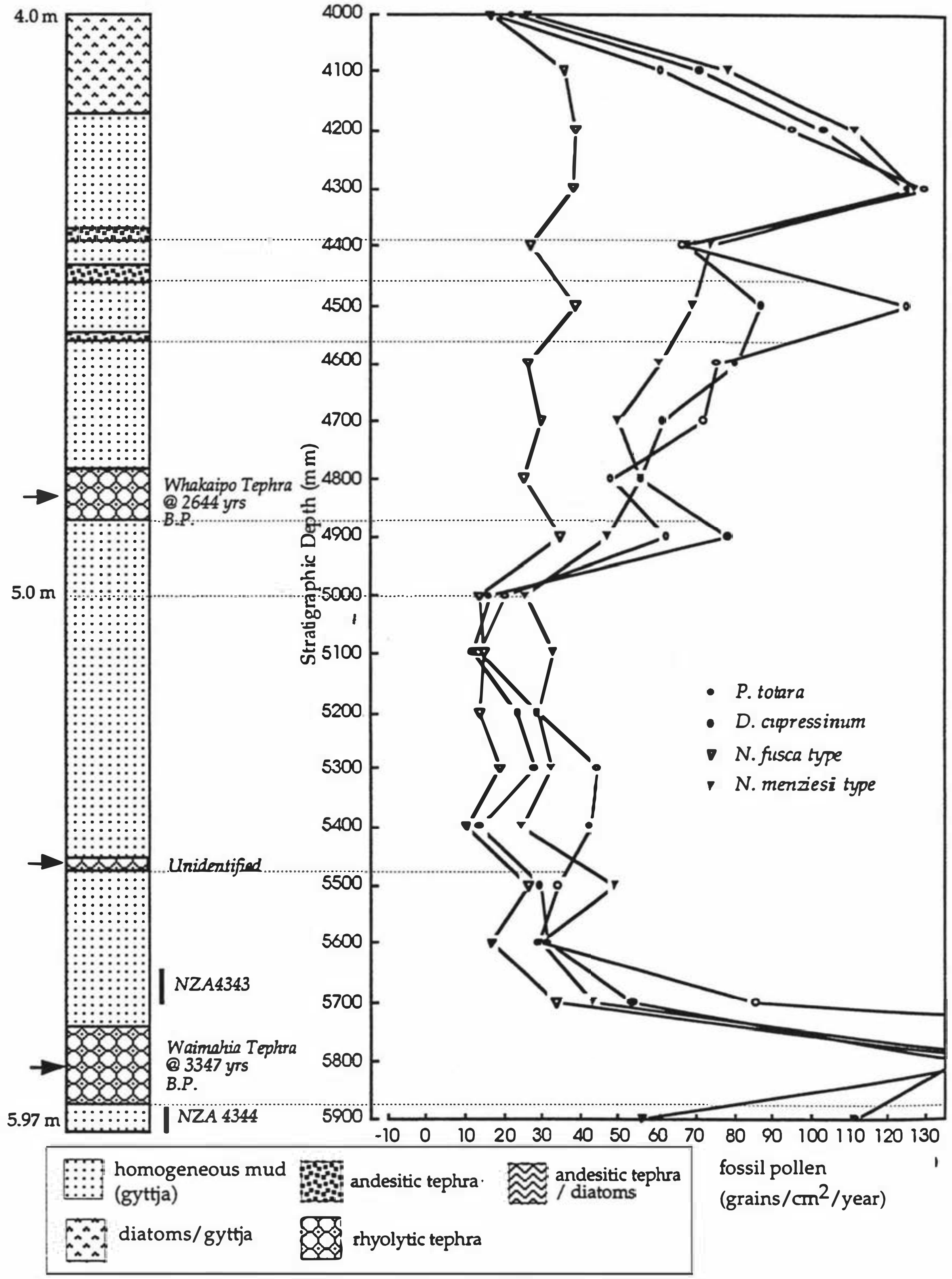


Fig 6.17 A correlation test of the Lake Rotokura core stratigraphy and fossil pollen data. This first illustration portrays the 4000 mm to 5970 mm section of the core. The *Nothofagus fusca* data set has been scaled by 10. Correlation points are indicated by dotted lines.

In fig 6.15, the pollen values at the 1000 mm and 2000 mm boundaries are as would be normally expected.

In many places the correlation between the position of tephra in the core and corresponding declining trends in fossil pollen is quite strong. The tephra deposits in this section of the core appear to be andesitic (dark coloured angular glass) and possibly originated from nearby Mount Ruapehu. As noted earlier, Mount Ruapehu has erupted once every one hundred years since the last major Taupo eruption (Neall 1995).

Not all of the post Taupo (Ruapehu) tephra deposits are recorded in this core. There are a total of eight in this two metre section of the core.

In fig 6.16, the second two metres (2.0 - 4.0 m) of the Lake Rotokura core stratigraphy has been illustrated along with the fossil pollen data of all four forest tree types for this section of the core. This section of the core includes the Taupo tephra at ca. 2650 mm. It is interesting to note that the Taupo eruption event (tephra) coincides with a steady decline in fossil pollen, however it is clearly not the initial cause of this behaviour. Locating the beginning of this downward trend is quite difficult. It is possible that it could have begun at ca. 3100 mm, or at 3800 mm, just after the (unconfirmed) Marpara tephra at ca. 3850 mm.

In fig 6.17, the final 1.97 metres (4.0 - 5.97 m) of the Lake Rotokura core stratigraphy have been illustrated along side the fossil pollen data of all four forest tree types for this section of the core. This section of the core includes the Waimihia tephra which clearly precedes a major fall in the concentration of all four forest tree types. This tephra is the largest of all those found in the core and its correlation with this major behavioural change suggests that it had a very damaging affect on the forests of this region. It also appears that the Lake Rotokura forest has never fully recovered to the pre - Waimihia level of density.

The forest recovery phase following the Waimihia eruption includes a number of smaller andesitic tephra deposits and the (unconfirmed) Whakaipo tephra. These tephra deposits are also correlated with forest tree decline, although the nature of this relationship is not as clear as in other parts of the core. Finally, the 5000 mm core boundary in this section of the core has pollen values as would normally be expected.

6.4.6 Experiment Four

The experimental modelling results presented in this section follow the format used in Chapter five. A brief statement of the hypotheses and models being tested is followed by the modelling results and their interpretation.

6.4.6.1 Hypotheses

Two hypotheses have been proposed in order to explain the long-term community organisation of the Lake Rotokura podocarp - hardwood - beech forest. The equilibrium hypothesis predicts that the frequency and intensity of volcanic disturbance will be low enough to allow competitive exclusion in this forest. Invasion of the Lake Rotokura forest region by beech is predicted by McGlone and Topping as a result of a mid Holocene climate change toward drier and more frost prone conditions.

In the non-equilibrium hypothesis, the frequency and intensity of volcanic disturbance is intermediate to high and therefore sufficient to maintain the Lake Rotokura forest in a low density region where competition cannot occur. The resultant behaviour will be density vague.

The results already presented in this chapter provide several lines of evidence which strongly suggest that the Lake Rotokura forest is stochastically dominated by volcanic disturbance events. For example, the composition of the contemporary forest is patchy, the Lake Rotokura core has numerous tephra deposits, many of which are correlated to declines in fossil pollen concentration. Furthermore, the long-term behaviour of the four forest tree populations does not appear to exist near equilibrium. Instead, the behaviour is more density vague and suggestive of a high degree of disturbance. Finally, there does not appear to be any evidence of competitive behaviour in phase space.

6.4.6.2 The Coupled Logistic Model

As a final attempt to identify classical equilibrium behaviour, the author tried to model this system using coupled logistic equations over a range of dimensions (2, 3 and 4 interacting equations) and regions of parameter space. None of these model formulations was capable of replicating the behavioural characteristics of these forest tree populations.

Overall, the model behaviour was capable of reproducing long-term trends in the data, but this involved a number of problems. Firstly, how should the upper asymptotic density for each interacting population be determined? Secondly, should the upper asymptotic density be the same for all populations? Thirdly, when the optimisation routine did work (a rarity with these larger systems), it consistently chose negative growth rate parameters, interpreting the long-term behaviour of the system as population decline. This is an interpretational problem based on the limitations of least squares.

Fourthly, simulation trials also proved to be unsuccessful, largely because of the difficulties of finding suitable initial parameters. The author used an evolutionary approach to parameter estimation, as outlined in the previous chapter, however even this proved unsuccessful when the more complex equations were being solved.

For the above reasons, the simulation results of the coupled logistic model are not reported here in any formal sense. In summary, the simulations from this site are not quite as good as the Totoya results. It is not possible to interpret the long-term behaviour of these forest trees as near equilibrium - at least as far as the macro-modelling approach, used in this project, is concerned. With a much finer resolution sampling interval, it would be possible to fit models like the logistic or coupled logistic to much shorter sequences of data.

For example, in fig 6.16, there appears to be a logistic type recovery which begins at 4000 mm and levels off to an apparent steady state at ca. 3800 mm. One problem is that this apparent steady state is nowhere near the upper asymptotic density region that this forest system is clearly capable of reaching. Does this suggest that a short term steady state is feasible in an intermediate density region?

One of the main limitations of the coupled logistic model formulation, as used in this context, is that it is not able to predict population decline and recovery. Its deterministic mechanisms simply predict a competitive interaction and long-term, unchanging outcome. This type of model clearly lacks the level of complexity necessary to predict and explain long-term forest community organisation of this kind.

6.4.6.3 The Continuous Exponential CGTM

A series of simulations were used to test the behaviour of the exponential CGTM over a wide region of parameter space. The approach taken involved varying one parameter at a time over large regions of parameter space. The tephra data was used without a reaction time delay (it seems fair to assume that the impact of a volcanic disturbance would be immediate). Averaged parameter values for the exponential CGTM are recorded in Table 6.4.

The logistic CGTM was also tested in this experiment, however as was consistently found in the Totoya experiments, the addition of an upper asymptotic density to this model made virtually no difference to the performance of the model. Therefore, based on the principle of parsimony, the exponential CGTM is clearly the superior model, since it combines simplicity along with explanatory and predictive power.

CGT Model Form	N fusca	N menz.	N Dac.	N Podo.	r_c fusca	r_c menz.	r_c Dac.	r_c Podo.	m fusca.	m menz.	m Dac.	m Podo.
expon	5.6	1.6	1.15	1.6	0.009	0.002	0.002	0.002	-0.01	-0.01	-0.01	-0.01

Table 6.4 Parameters for the exponential CGTM formulation. The subscript letters for the various model parameters indicate which of the four forest populations (or types) that parameter belongs to. Scale: data/100,000 and tephra/10,000.

Fig 6.18 portrays the results of the exponential CGTM plotted along with the Lake Rotokura fossil pollen data for *Nothofagus menziesii* and *Nothofagus fusca* type pollen (according to the parameters listed in Table 6.4). Fig 6.19 portrays the results of the exponential CGTM plotted along with the Lake Rotokura fossil pollen data for *Dacrydium cupressinum* and *Podocarpus totara* type pollen (according to the parameters listed in Table 6.4).

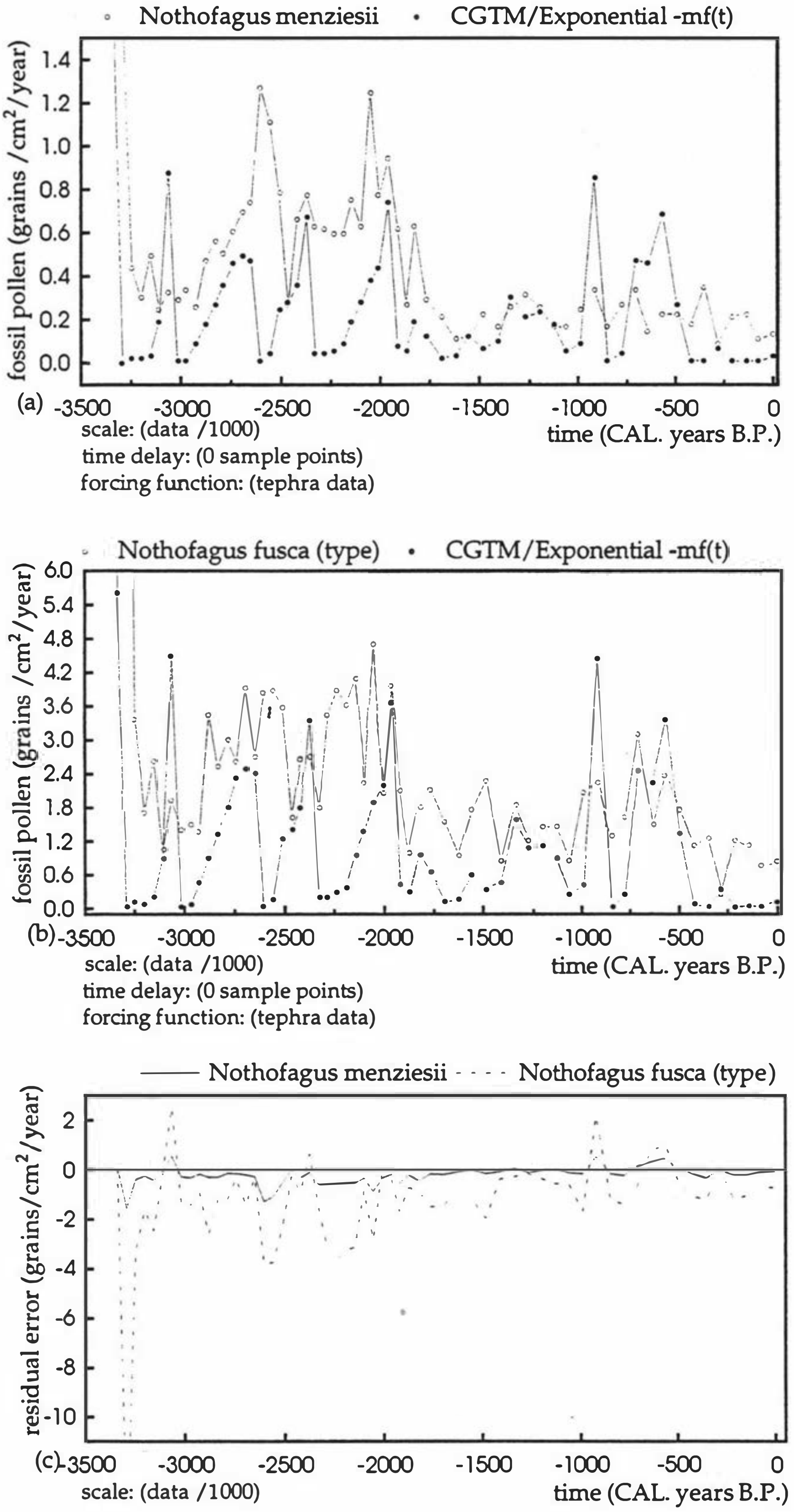


Fig 6.18 Lake Rotokura core site, exponential CGTM with forcing function based on interpolated volcanic tephra data for (a) *Nothofagus menziesii* and (b) *Nothofagus fusca* (group) with (c) residual error.

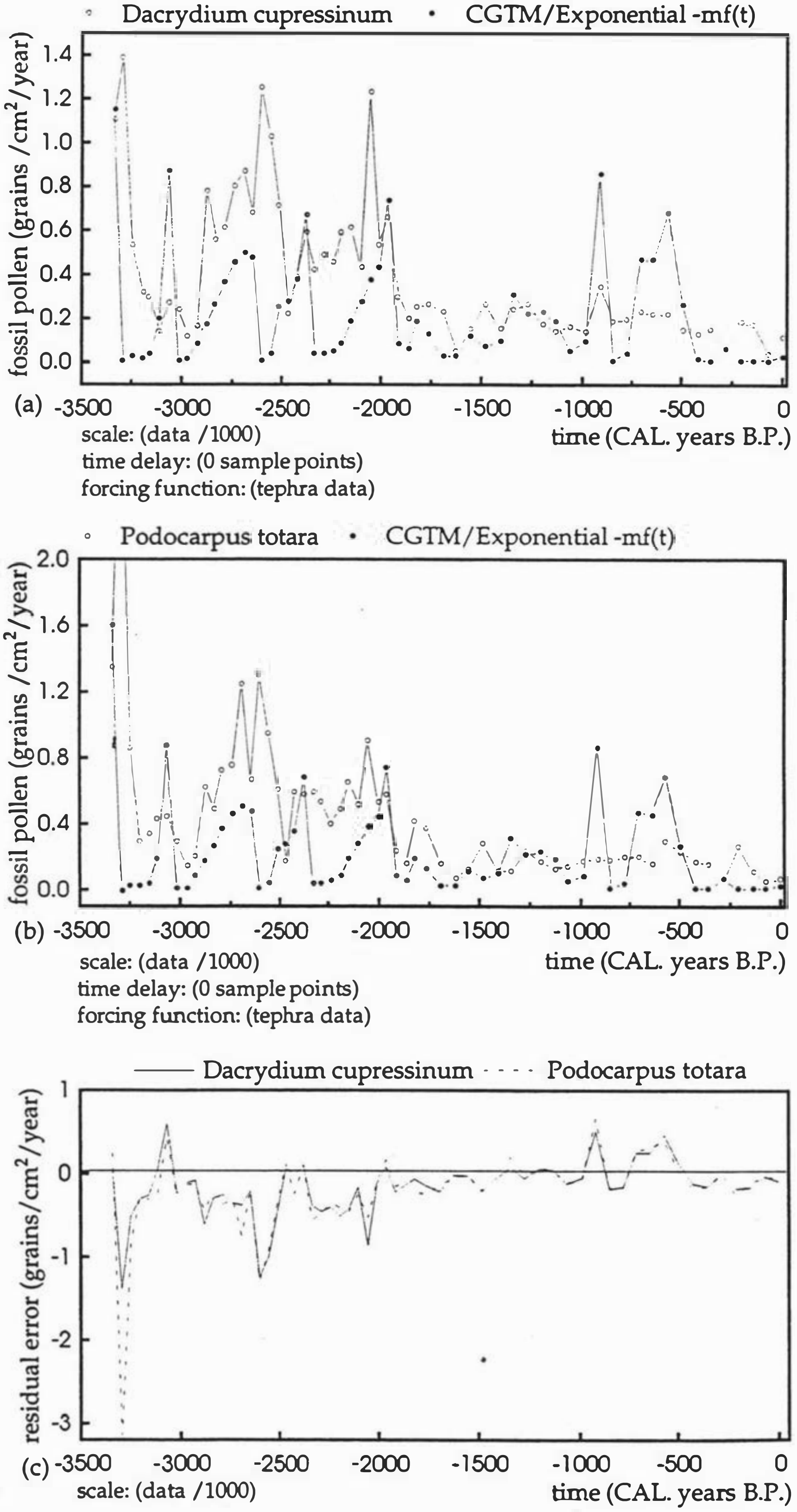


Fig 6.19 Lake Rotokura core site, exponential CGTM with forcing function based on volcanic tephra data for (a) *Dacrydium cupressinum* and (b) *Podocarpus totara* with (c) residual error.

As would be expected, the tephra scaling parameter (m) for all four models is negative. This indicates that larger values of tephra cause forest decline, as would be expected. There are a number of important features in these plots.

Firstly, the model behaviour portrayed in these plots may be varied across a range of parameter space, based on those averaged parameter values reported in Table 6.4. This region of parameter space both improves and worsens the behaviour of the model in different ways.

Secondly, earlier in this chapter it was pointed out that the tephra data used in this model formulation were very much an approximation to a more complex function. Despite this fact, there is an impressive correspondence between the model and fossil pollen data in many places. Overall, the general morphology of the model and fossil pollen data is very similar (although not on a peak to peak basis).

Thirdly, the parameter insensitivity problem which was discovered in the behaviour of the exponential CGT models used on the Totoya data, also seems to be a problem for the Lake Rotokura models. The tephra scaling parameter (m) is too severe for the behaviour of the model in some places, and apparently insensitive in other places. This problem once again arises as a result of the large variance in the Lake Rotokura data. The problem suggests that there may be a secondary process involved in this system, that is modifying the effect of the tephra.

6.4.6.3.1 Disturbance Regions

On visual evaluation of the data, there do appear to be different disturbance regions where a given level of disturbance may operate for a short period of time. In all four forest tree population plots, the region from 3300 CAL. years B.P. to ca. 3000 CAL. years B.P. may be considered as a post Waimihia eruption disturbance region.

From 3000 CAL. years B.P. to ca. 1500 CAL. years B.P. may be defined as a second disturbance region, where the forest system has repeatedly recovered to and fallen from, a high density region.

From 1500 CAL. years B.P. to the present time, there is a third distinctive disturbance region in the forest, where its behaviour has remained in a low density region.

The last disturbance region shows behaviour that appears to result from two main causal mechanisms. Firstly, the major impact of the Taupo eruption event followed by a period of short term recovery. Secondly, there is a very good correlation in this part of the core between andesitic tephra and decline in the forest tree pollen (see fig 6.15). The problem with this explanation is that it is very unlikely that these are the only causal mechanisms. The recovery phase following the Waimihia eruption event also shows evidence of andesitic eruption events in the core stratigraphy (fig 6.17) (although not as many as the post Taupo eruption period) and yet this forest recovered to a very high density region. What is the difference between these two disturbance regions?

6.4.6.3.2 Climate Change

It does not seem likely that climate change was responsible for these changes since this causal mechanism should have preferentially favoured one of the forest elements (either the podocarp-hardwood or beech) but not both. In contrast to a predicted climate change explanation, the four forest tree types at this site all respond in concert to the causal mechanisms of the third disturbance region.

6.4.6.3.3 Fire

Another (very controversial) explanation, is that the third disturbance region may coincide with the Polynesian burning of the forests of this inland central New Zealand region. This would place the arrival of Polynesians in this region of New Zealand at a very early time ca. 1250 - 1000 CAL. years B.P. Further research would be needed to clarify these issues. Polynesian burning of inland forest is usually associated with compositional changes in vegetation that are more clearly recorded in the local pollen record. The Lake Rotokura site records a regional picture in which forest canopy tree types dominate and smaller compositional changes are therefore under represented.

6.4.6.3.4 'Hydrology

A final (and less controversial) explanation is that there has been a general fall in the water table around Lake Rotokura coinciding with the timing of the Taupo eruption event. Evidence for this proposition comes from a general increase in Cyperaceae fossil pollen types in this part of the core (fig 6.20). The Cyperaceae fossil pollen increases during the post Taupo eruption period. This increase could be associated with a fall in the water level of Lake Rotokura, providing more substrate for the Cyperaceae to colonise. A fall in the water level of the lake may also be associated with a fall in the water table of the surrounding forest, which could generate physiological stress and the preferential death of the weaker canopy trees.

The problem with this explanation, is that it only accounts for a decline in local forest tree density, while the Lake Rotokura fossil pollen signal is more likely to be of a regional source area. Finally, testing of this hypothesis was undertaken by introducing the Cyperaceae fossil pollen data as a secondary forcing function into the exponential CGTM (with tephra data). The results indicate that the Cyperaceae made very little difference to the performance of the existing exponential CGTM without secondary forcing function.

6.4.6.3.5 Other Causal Mechanisms

A final characteristic of the behaviour of the exponential CGTM formulation, used in modelling the behaviour of the Lake Rotokura forest, is that the model fails to predict much of the smaller variance in the forest tree data. Apart from the scaling parameter insensitivity problem, it is very likely that the regional forest has been influenced by other forms of disturbance.

As mentioned earlier, the beech / mixed beech forest in New Zealand is susceptible to a variety of environmental forces including: windthrow (for which there is evidence at the Lake Rotokura site), damage from heavy snow, insect damage, earthquakes, drought, changes in the water table, flood damage (in lowland regions only) and the ravages of introduced animals.

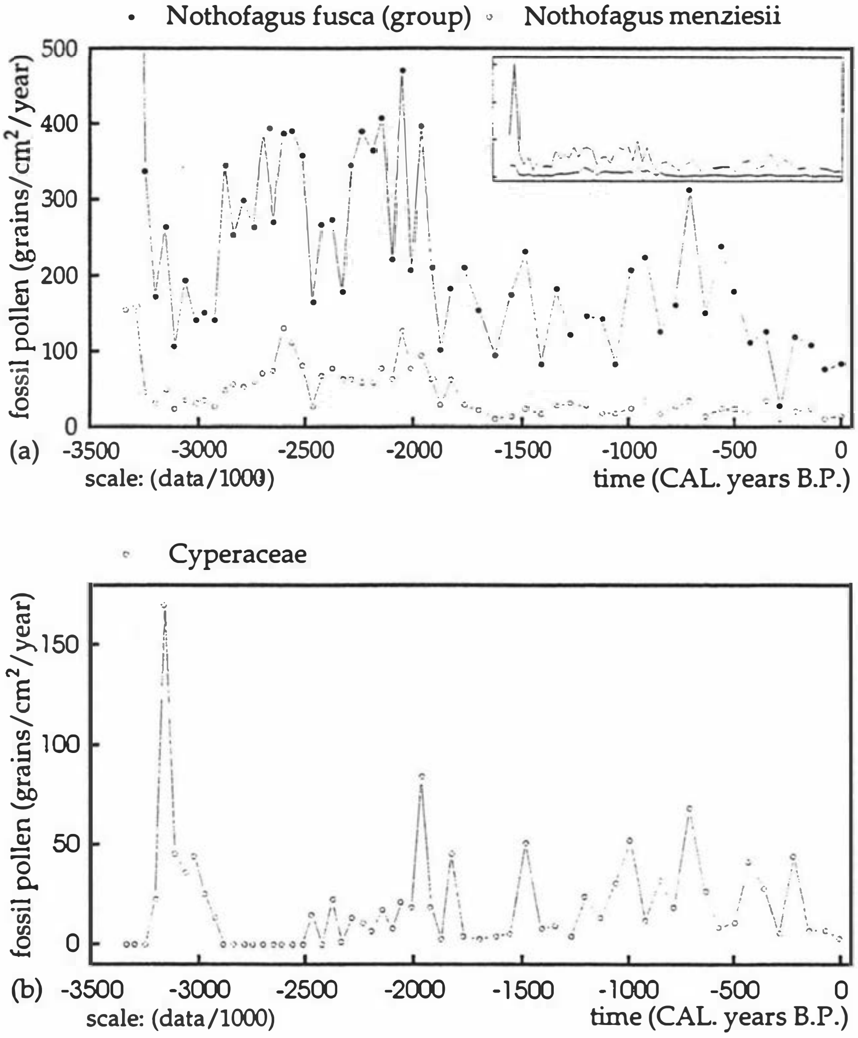


Fig 6.20 The long-term behaviour of Lake Rotokura Cyperaceae fossil pollen as an indicator of changes in Lake water level and possibly, the local forest water table.

In summary, the results of the exponential CGTM experiment indicate that this model is capable of explaining some, but not all of the variance in the behaviour of Lake Rotokura forest tree types used in this study. Insensitivity on the part of the tephra scaling parameter is partly the cause of the poor performance of this model. The main cause, lies in the fact that this forest system is likely to be driven by any number of the potential abiotic and biotic causal mechanisms mentioned in this chapter. From this point of view, it seems evident that the tephra forcing function does explain a high degree of the behaviour of this forest system. It may therefore, be classed as a primary causal agent of community organisation in this forest system.

6.4.7 Interpretation of Results.

The discussion of the results of experiment four has so far focused on the causal mechanisms operating in the Lake Rotokura forest and just how well these explain the behaviour of this system. It is now time to evaluate the explanatory and predictive power of the mathematical models, in terms of their operational assumptions and domain of application

6.4.7.1 The Coupled Logistic

The poor performance of the coupled logistic model formulations used in this experiment may be traced back to the violation of many, if not most, of the model's assumptions in this domain of application.

Firstly, the main regulatory mechanism of this model is instantaneous, density-dependent, negative feedback on population growth. In contrast to these mechanisms, the Lake Rotokura forest appears to exist in a low density region where competitive exclusion (competition) is prevented.

Secondly, the model assumes stable demographic processes, an assumption that is very unlikely to be met in this forest, as a result of the local disturbance regime. This is more likely to be a problem on a patch level of scale. At a regional level, it is more likely that gains and losses in individual local patches level out. However, even regional demographic stochasticity cannot be completely discounted as a causal agent of community organisation. This could happen if a disturbing force continually affects demographic processes at a regional level of scale.

Thirdly, the model assumes homogeneous population mixing and resource distribution, while the local Lake Rotokura forest is clearly heterogeneous in population distribution and available resources.

Fourthly, the coupled logistic model assumes a closed system with no spatial effects. For a regional pollen signal, this assumption could never be upheld. Seed dispersal is known to be the primary mechanism of forest migration and recolonisation.

Fifthly, the coupled logistic is a deterministic model while the causal mechanisms driving the Lake Rotokura forest are clearly stochastic.

Finally, there are computational problems involved in the use of this model with systems of higher dimensions. These appear to be caused by sensitivity of the model to initial starting parameters. Further research is needed in this area.

The explanatory and predictive power of the coupled logistic model tested at this site must be rejected for all of the above reasons. These include: inferior predictive and explanatory power, conflict with background theory (assumptions violated) and inappropriate domain of application.

6.4.7.2 The Exponential CGTM

The exponential CGTM blends together a variety of causal mechanisms which clearly have superior predictive capability, when compared with the well known performance of the coupled logistic model.

Firstly, the main driving mechanism of the model is a constant growth rate of value approximating zero (see Table 6.4). Despite the fact that this growth mechanism is so small, it is still needed. If the constant growth rate parameter is set to zero, the model loses its predictive capability.

Secondly, the model assumes a constant forcing function scaling parameter and this is clearly inadequate. The ecological implications of a variant scaling parameter are quite fascinating. This suggests that many disturbance processes are mediated by other environmental variables. Modelling such complex organisation will be very difficult.

Thirdly, the model proposes that volcanic stochasticity acts to limit transit of this forest system to high density regions. In other words, stochastic vulcanism is a high density ceiling. This explanation is in perfect harmony with what is known of the ecology of the New Zealand mixed beech forests. The low density floor of this system may be accounted for by the seed dispersal capabilities of the podocarp - hardwood elements of the forest and the seed masting, for which the beech species are so well known (Wardle 1984). Furthermore, the frequency and intensity of volcanic stochasticity appears to be low enough to ensure long term persistence of this forest community. Chesson (1978) refers to this as stochastic boundedness.

The exponential CGTM also assumes stable demographic processes, homogeneous population mixing and resource distribution, a closed system and no spatial effects. All of these assumptions are violated as per the coupled logistic model mentioned above. This fact indicates that the major weakness in the coupled logistic model is not so much these assumptions, but a failure to account for abiotic (and possibly biotic) forms of disturbance.

Based on the above evaluation, the exponential CGTM clearly has limitations, but must be accepted as the superior explanation and prediction of the community organisation of the Lake Rotokura forest.

6.4.8 Community Organisation

As was indicated at the beginning of this chapter, the Lake Rotokura case study involves a very high level of abstraction and in many respects, may be considered as pioneering research in this area. The exponential CGTM with tephra forcing function does not provide a complete picture of the organisation of this forest community. However, the present study has demonstrated something of the extent to which this forest community is affected by stochastic volcanic events. Their frequency and intensity shapes the long-term behaviour of this system to a very high degree. The failure of the exponential CGTM to explain all of the variance in the data suggests that other causal mechanisms are involved

6.4.8.1 Climate Change

McGlone and Topping (1977) have suggested that the last 5000 years of the late Holocene have been marked by a drier and more frost prone climate that has favoured the expansion of the beech, although this expansion has been retarded by volcanic disturbance. The present study does not provide evidence to support this hypothesis. Firstly, the long-term behaviour of the Lake Rotokura forest is a decline to the low density region - not a long-term increase. Secondly, there is no evidence for the preferential increase or decline of either the podocarp or beech elements of the forest. Finally, the influence of volcanism appears to have been under-estimated in their hypothesis and emerges from this study as the primary determinant of long-term forest change, independent of possible climatic effects.

6.4.8.2 Stochastic Vulcanism

To suggest that stochastic volcanic events are the primary determinant of long-term forest behaviour requires that the influence of climate must be shown not to operate. This appears to be the case. A drier, more frost prone climate should preferentially favour the beeches, but in this forest, all of the forest canopy dominants are declining together. Furthermore, they all respond in concert to volcanic events.

In could be argued, that the failure of the Lake Rotokura forest to recover to former levels of density after the Taupo eruption, has been caused by mechanisms other than climate. In this case a climate driven expansion of beech would have occurred, had it not been for these other forms of disturbance. Such alternative mechanisms might include: Polynesian burning of the forest, hydrological changes, increased volcanic activity and other more general causes. However, only increased volcanic activity seems adequate to explain such behaviour.

Firstly, hydrological changes will be very difficult to prove on a regional basis. Secondly, the timing of Polynesian forest fires appears to be too early for this part of the island. Thirdly, the other causes mentioned do not operate at a frequency and intensity that would be likely to cause a regional forest decline. Finally, this leaves vulcanism as the most parsimonious explanation.

In summary, for the climate change hypothesis to be accepted, this site should show evidence of a long-term increase in the beech element of the forest and by contrast, a decline in the podocarp element. This evidence is not present in the Lake Rotokura fossil pollen data. The overall decline in the forest elements of this forest over the last 1800 CAL. years B.P. cannot easily be explained by causal mechanisms other than volcanic activity. Further research is clearly needed in this area, especially in the light of a recent palaeontological research discovery which places the earliest arrival of Polynesians in New Zealand at ca. 2000 years B.P. (The Dominion 1996).

6.4.8.3 Stochastic Domination

In terms of the DeAngelis and Waterhouse (1987) super-model, the Lake Rotokura regional forest may be defined as an ecological system that is stochastically dominated. Stochastic volcanic activity prevents the transit of this community to a higher density region. Its intensity and frequency appears to be intermediate to high, which is just enough to prevent competitive exclusion.

Compensatory seed dispersal processes and stochastic boundedness prevent these populations from wandering to extinction and ultimately, may be responsible for the long-term persistence of this forest community.

In experimenting with a regional fossil pollen signal, the present author was very interested to see if the localised effects of all combined disturbance events would be balanced out at the landscape level of scale. This does not appear to be the case. In other words, the behaviour of this system does not provide evidence of emergent equilibrium conditions as a result of this higher level of scale.

Once again, the interpretation given to this case study is distinctly non-equilibrium in nature and reflects the individualistic school of succession theory. Furthermore, these results do not appear to be an artefact of observational scale.

6.5 Chapter Summary

The Lake Rotokura core site provides an opportunity to evaluate the modelling methodology developed in this thesis in a domain of application very different from that of Totoya Island in Fiji. The Lake Rotokura site is an inland forest of much greater species diversity and structural complexity than the mangrove forests of Totoya. The Totoya mangrove forests provided an opportunity to model a plant community based on the strong certainty of a local pollen signal. At Lake Rotokura, the basin size and pollen dispersal characteristics of the four forest tree types used in this study are suggestive of a regional pollen source area.

The dating of the core stratigraphy of the Totoya mangal was accomplished with AMS radiocarbon dates, which were internally consistent over the entire island and within individual cores. By contrast, the Lake Rotokura core was far more problematic. None of the AMS radiocarbon ages from this core match with the position and age of well known tephra deposits. Based on these anomalous AMS dates there appears to be evidence for the loss of at least one sedimentary unit from the base of the Lake Rotokura core.

Despite the above problems, the internal consistency of the Lake Rotokura core is evident in a number of lines of evidence. Firstly, the fossil pollen signal appears to respond to the effect of known volcanic events at the appropriate time and in an appropriate way, in almost every case. There are exceptions to this observation. The performance of the exponential CGTM is probably a reasonable guide to the strength of this relationship.

Secondly, cross correlation checking shows that the procedures used to collect and subsample the core have not influenced the behaviour of the fossil pollen signal otherwise than would be expected.

The modelling of the Lake Rotokura mixed beech forest has been based on the behaviour of four main forest tree types: *Nothofagus fusca* type, *Nothofagus menziesii* type, *Dacrydium cupressinum and Podocarpus totara.* The fossil pollen assemblage was reduced to these four tree types for a number of reasons. Firstly, the pollen of the five New Zealand beech species present in the Lake Rotokura forest can only be identified into two groups (*Nothofagus fusca* type and *Nothofagus menziesii* type). Secondly, the use of the coupled logistic equation required that the model system be kept to a low number of dimensions.

The initial focus of this study was strongly centred on equilibrium theory and this is another reason why the number of species used in this study was kept to a minimum. The results of this study indicate that the behaviour of this forest community remains in a low density region. This suggests that this forest community is not driven by competition as a causal mechanism and furthermore, that the system operates a long way from equilibrium. This being the case, a future study of this kind need not be limited to a few species.

One of the most important discoveries of this study has been a clarification of the extent to which this New Zealand mixed beech forest is dominated by stochastic volcanic events. Further studies of this kind are very much needed and should ultimately build a much clearer picture of late Holocene plant community organisation in New Zealand and other parts of the world.

In conclusion, this case study must lead to a rejection of a classical equilibrium interpretation of the community organisation of the Lake Rotokura mixed beech forest, in favour of a non-equilibrium hypothesis. A number of problems have been identified and associated with interpreting the fossil pollen data from this site. Despite these problems, the stratigraphy of the core and behaviour of the fossil pollen data appear to be internally consistent. As such, this case study demonstrates the tremendous potential of palynological modelling research. Furthermore, it has identified a number of areas where this modelling methodology may be refined and applied in future studies.

Thesis
Summary and Conclusions

7.1 Objectives

The objective of the following section is to provide a brief summary of the main points, contributions and discoveries that have been outlined in the six chapters of this thesis. Firstly, the introduction begins with a brief summary of Chapters one to six. Secondly, the contributions and discoveries made in this research project are outlined. Finally, future research directions and conclusions are outlined.

7.2 Chapter Summary

The central aim of this research project has been to test hypotheses derived from community organisation theory. In order to achieve this aim, three subobjectives needed to be accomplished. Firstly, a detailed base theory had to be constructed from recent and historic developments in theoretical ecology. This base theory is developed in the first three chapters of this thesis and uses the DeAngelis and Waterhouse (1987) super-model as a foundation.

Secondly, in Chapter four, a new mathematical modelling framework has been developed for modelling research based on absolute fossil pollen data. Finally, the strengths and limitations of this new modelling approach have been demonstrated by two case studies, recorded in chapters five and six.

7.2.1 Chapter One

The definition of an ecological community has been a matter of great controversy in the history of ecology. While most ecologists would agree with the idea of a community as a collection of populations in a defined area, there has been much debate about the possible synergistic attributes of a community and its fundamentalunit structure.

The fundamentalunit, individualistic debate may be translated into questions concerning the causal mechanisms, structure and long-term behaviour of communities. These questions were explored in Chapter one by evaluating the two classes of causal mechanisms thought to be responsible for all community behaviour - abiotic and biotic causal agents.

From the study of biotic and abiotic causal mechanisms has emerged two distinctly different models of community organisation. The equilibrium paradigm is the classical model which proposes that communities are primarily organised by biotic causal agents (competition, predation and symbiosis). This view of ecological communities suggested that they were essentially closed, fundamental units, constructed through process of time by niche differentiation and the process of competitive exclusion. The climax community was a product of these strong, internal, biotic organising processes which resulted in a globally stable equilibrium state.

In contrast, the non-equilibrium paradigm is the more recent and less accepted model of community organisation. This model suggests that while equilibrium behaviour may be the ideal, in reality it is never realised because of fundamental instabilities in the biotic processes of communities and the influence of stochastic domination (abiotic disturbance). Stochastic domination is thought to maintain communities in intermediate to low density regions where competitive exclusions cannot occur. Compensatory mechanisms are believed to operate and enable local populations to persist long-term.

In summary, Chapter one introduces the topic of community organisation and briefly defines the equilibrium and non-equilibrium paradigms. These two paradigms are explored in more detail in Chapters two (the equilibrium paradigm) and three (the non-equilibrium paradigm).

7.2.2 Chapter Two

Chapters two and three explore and develop the super-model of community organisation discussed by DeAngelis and Waterhouse (1987). Chapter two covers the historical, mathematical and ecological significance of the equilibrium paradigm.

The historical significance of the equilibrium paradigm has its roots in the all pervasive notion of a balance of nature maintained by a divine or supernatural power. Chapter two traces out the key historical developments that have led to ecology's modern equilibrium paradigm. Important preliminary reasons for the abandonment of equilibrium theory by theoretical ecologists in the 1970s, may be found in Charles Darwin's book, The Origin of Species and Fredrick Clements' succession theory. The former overturned a historic system of belief in a Creator God as the cause of balance in nature, while the latter became a seeding ground for intense debate that questioned the fundamentalunit and synergistic assumptions of succession theory (*i.e.* the assumption that a balance of nature actually existed in natural systems).

The mathematical significance of equilibrium theory is explored in Chapter two by the use of quantitative and qualitative mathematical techniques. The concepts of equilibria and stability are defined with mathematical models, used to illustrate just how these concepts may be applied to the study of populations and communities.

The ecological significance of equilibrium theory is explored by a review of modelling research based on the classical logistic and coupled logistic equations. These equations have provided powerful tools to ecologists who have used them to explore the assumptions of equilibrium theory. This body of research provides one illustration after another of the limitations of these classical model constructs and the base theory from which they were derived.

Chapter two concludes with a list of the types of hypotheses that have been derived from the equilibrium paradigm. Many of these hypotheses have been tested in the present project by the use of classical competition models (the logistic and coupled logistic).

7.2.3 Chapter Three

Chapter three reviews the implications of a number of key theoretical developments of the late 1960s and early 1970s which led theoretical ecologists finally to abandon the equilibrium paradigm as a model of community organisation. This introduction develops into a theoretical discussion of the two primary departures from stable equilibria recognised in the non-equilibrium paradigm (*i.e.* biotic instability and stochastic domination).

In section three there is a discussion of the concept of community persistence and the compensatory mechanisms that ecologists have explored in their efforts to understand the survival strategies of populations and communities which exist a long way from equilibrium. Finally, Chapter three also explores the problem of observational scale and reviews some of the recent research that has been directed toward testing this hypothesis.

While Chapters one and two provide a very necessary theoretical background, the literature reviewed in the above sections of Chapter three forms the fundamental basis of the hypotheses tested in the case study Chapters of this thesis. A detailed list of non-equilibrium hypotheses is provided at the end of Chapter three. Many of these are tested in the four modelling experiments of this project.

7.2.4 Chapter Four

While descriptive theory has a place in ecology, the development and application of mathematical models has formed the basis of many of the major theoretical developments in this field of research. Chapter four takes up a new line of inquiry and investigates the development and testing of mathematical models. A detailed and integrative system of classification has been developed and used in the classification of ecological models and the more recent contributions of palynologists to this field of research.

In the above evaluation of the modelling research of ecologists and palynologists, the importance of the hypothetico-deductive research methodology has been stressed. This approach to model formulation, testing, interpretation and reformulation, forms the operational basis of the modelling framework developed in this thesis. This new modelling framework is defined in detail in Chapter four and consists primarily of a collection of model constructs, various modelling procedures, dynamical systems techniques and the hypothetico-deductive methodology.

To conclude Chapter four, the model constructs and hypotheses to be tested in the two case study projects are discussed and listed in detail. These models are used to accomplish two objectives. Firstly, to test for the existence of equilibrium or non-equilibrium conditions. Secondly, to be reformulated as part of the modelling processes, so as to develop a mathematical model of community organisation for the four plant communities studied in this project. A total of four experiments is used to test these model formulations.

A mathematical model, as used in ecology, is derived from base theory. To test the predictive and explanatory power of such a model, a domain of application is required. Theoretical modelling is a process of comparing the mathematical model construct, derived from base theory, against a model of reality, derived from observations and research into real ecological systems.

7.4.5 The Case Study Chapters

The two case study chapters are designed to accomplish a number of objectives, the main one of which is to illustrate the strengths and weaknesses of the modelling framework developed in this project. More specifically, the two case study chapters record the results of experiments designed to test the equilibrium and non-equilibrium model constructs used in this project.

Both chapters begin with a review of published research into the two ecological communities being investigated. From this review, two alternative hypotheses are derived, based on what is known of the possible equilibrium and non-equilibrium organisation of these plant communities. These hypotheses are then tested by using the equilibrium and non-equilibrium model constructs outlined in Chapter four.

A methodology section in both case study chapters provides a detailed account of the choice of core site, removal of cores, dating and subsampling of the cores, laboratory treatment of the core samples along with the procedure used for counting the fossil pollen and compiling the data.

The results sections of the two case study chapters has been written in a manner that outlines the modelling results within the formulation, testing, interpretation and reformulation structure of the modelling framework developed in this project.

Finally, each case study chapter concludes with an attempt to construct a model of community organisation for the plant communities studied in each set of experiments, based on the outcome of the modelling results. This discussion also relates the findings of the modelling experiments back to the DeAngelis and Waterhouse (1987) super-model. In this way, the contributions and discoveries made in the present research are related back to current developments in theoretical ecology. The major contributions and discoveries of this research project are summarised in the following section.

7.3 Contributions and Discoveries

The main contributions and discoveries made in the present project are outlined in the following section, according to the various fields of research covered in this study.

7.3.1 Palynological Modelling

The present project provides three main contributions to palynological modelling. Firstly, the present thesis outlines a theoretical foundation which provides a strong connecting link between palynology and theoretical ecology. Secondly, the present project has been used to develop an alternative modelling framework for palynological modelling research.

Combined, these two contributions provide a basis upon which to design, mathematically implement and interpret future palynological modelling research of this kind in terms of current developments in theoretical ecology.

Thirdly, the results of the case studies outlined in this thesis demonstrated to the author the tremendous potential of a modelling approach designed to test hypotheses. Traditional palynology has focused on attempting to derive hypotheses *a posteriori* from palynological data. This approach has especially been used in archaeological studies - a hallmark of palynological studies of which Nunn (1992) (and others) is very critical.

The dangers of generating hypotheses *a posteriori* were powerfully illustrated to the present author on two occasions in this project. Firstly, the author brought to this project a very strong equilibrium focus which has now been rejected. Secondly, initial observations of the Totoya mangrove data led the author to conclude that the large falls in mangrove fossil pollen must have resulted from human harvesting and destruction of these plant communities. At the completion of this study, the author now realises that it is possible to explain this behaviour by ecological mechanisms, without invoking the human impact paradigm.

These lessons impressed the author with the need for a stronger ecological theory base in palynology and a methodological approach to fossil pollen interpretation based on the testing of *a priori* hypotheses according to *a priori* refutation criteria. It is the author's hope that the methodological and theoretical approach outlined in this thesis will successfully be applied to future palynological studies.

7.3.2 Theoretical Ecology

The present project makes a number of important contributions and discoveries to the theory base of theoretical ecology.

7.3.2.1 Community Organisation Defined

Firstly, the present project has been built upon the conceptual and theoretical model of community organisation described in the first chapter of this thesis. While is it very simple, the author believes that this model is an important clarification and crystallisation of various ideas of community organisation that have been presented in various places in the ecological literature. This model provides an important connecting link between community ecology, palynology and ecological modelling.

7.3.2.2 The Exponential CGTM

The exponential CGTM represents an interesting discovery, the full implications of which will need to be carefully evaluated in future modelling and empirical research. The basis of this model is a constant growth term, based on the constant growth rate parameter (r_c), which provides an alternative to the classical Malthusian exponential growth term. This new constant growth term, is doubtless an approximation of a more complicated growth function. Future research is needed in this area.

The logistic and coupled logistic CGTM formulations are variants of the exponential CGTM which provide a mathematical basis for testing some of the predictions of Strong's non-equilibrium theory of liberal regulation (the basis of density vague behaviour) (Strong 1984, 1986).

7.3.2.3 Stochastic Domination

The modelling research conducted in this project provides further evidence for the existence of natural communities dominated by stochasticity. Possible compensatory mechanisms have also been outlined. Finally, the existence of non-equilibrium behaviour in the mixed beech forest of New Zealand's Lake Rotokura does not appear to be an artefact of a low level of observation scale.

7.3.2.4 Mangrove Ecology - Fiji

One of the most fascinating discoveries which has come from the modelling of the Totoya mangal is the realisation that these ecological communities have a form of disturbance memory. Present community organisation is being shaped by disturbance events that occurred ca. 70 - 100 CAL. years B.P.

In this modelling research the classical mangrove succession paradigm of Davis (1940) was rejected in favour of the opportunistic, non-equilibrium paradigm of Thom (1967, 1979). Finally, this project has demonstrated something of the tremendous potential that exists for future palynological modelling research in mangrove communities.

7.3.2.5 Mixed Beech Forest Ecology - New Zealand

An interesting discovery that has come from the modelling of the Lake Rotokura mixed beech forest is a realisation of the extent to which this forest system is stochastically dominated by volcanic disturbance.

In this modelling research, a classical equilibrium interpretation of the community organisation of this forest community was rejected in favour of a non-equilibrium model. Finally, the modelling and fossil pollen evidence present in this study, clearly shows that the beech element of this mixed forest is not responding to drier and more frost prone climates as McGlone and Topping (1977) had suggested. Instead, both the podocarp and beech elements of the forest appear to respond in concert to stochastic volcanic events.

7.4 Future Research

Throughout this thesis, many comments have been made regarding the need for future research. Many of the problems identified by these comments are related to methodological issues for which research is needed to streamline and refine this new modelling approach. While these research priorities are all important and valid, the present author believes that the most important challenge for palynological modellers lies in the area of building back toward mainstream theoretical ecology.

This objective can only be accomplished by future research priorities that cross the interdisciplinary boundaries between palynology, mathematical modelling, environmental science and theoretical ecology.

In order to accomplish this objective, it would be very good to see the establishment of an international palynological modelling research group, with a charter to systematically work at testing and developing theory in community and population ecology. Such a group could be a focal point for international - interdisciplinary projects, publishing and education.

Concerning education, there is an urgent need to focus tertiary education toward the training of future palynologists with much broader educational backgrounds in: ecology, mathematics, modelling, computer programming, statistics and the environmental sciences. There is also a need for research, to plan educational programs of this kind.

Concerning the present project, there are a number of important research questions that need to be addressed. Undoubtedly, the most important of these is the problem of dealing with vertical and horizontal error in palynological modelling research (see section 5.5.1, Chapter five).

There is also the need to streamline and refine the computational aspects of the modelling work and to investigate ways in which PAR fossil pollen data may be portrayed with modelling results of the kind presented in this thesis. The use of simulation studies over various ranges of parameter space, the use of ranges of parameter values and model behaviour are all unconventional approaches to portrayal which need refining.

There is also a need for further application of the modelling framework outlined in this project. While further modelling research could easily be planned for the Twin Lake Basins at the Rotokura Ecological Reserve, there are many other sites around the Tongariro National park region which could be used to build a clearer picture of late Holocene forest behaviour in this region of New Zealand.

In Fiji, there are numerous research opportunities involving a group of islands that have had only three large scale palynological studies, undertaken by Southern (1986), Latham (1979) and the present author. Nunn (1992) raises important questions regarding the use of palynological data as an indicator of vegetation and environmental change, resulting from human causes. Palynological modelling may provide an important dimension to this problem.

Finally, the full implications of the constant growth rate term in the exponential CGTM need to be further investigated. Also, in the theoretical ecology and mathematical modelling literature there are many model formulations which have been halted at the simulation study stage for the want of suitable data to test these model constructs and the hypotheses they represent. Palynological modellers have an important contribution to make in this area.

7.5 Conclusions

As outlined above, the present project makes a number of important contributions toward palynological modelling research, theoretical ecology and the understanding of how Fijian mangal and New Zealand mixed beech forest communities are organised.

This thesis outlines a new direction for palynological modelling research based on a strong theoretical and methodological basis, as well as a new mathematical modelling framework. The strengths and weaknesses of this approach have been identified.

The case studies reported in this thesis serve to illustrate both the strengths and weaknesses of this new modelling framework, along with the tremendous potential that exists for future palynological modelling research of this kind.

Appendix 1

Text Reference

Chapter two, *Equation, 13, the discrete logistic, section 2.4.4,*

Description

The following Matlab script file is designed to solve the difference equation (13) listed below, based on an initial population size of $N_{(0)} = 10$, an equilibrium density of $N_{(eq)} = 100$, and slope of 0.013. The equation is solved by calling a Matlab *for loop* subroutine over the time period t = 1:12, for equation (13). The *for loop* is scripted in an mfile named 4loop.m and called from the Matlab command window.

Command Window

```
>>                                  % (>>) command window prompt
>> 4loop                            % calls the mfile 4loop.m
```

Function mfile (4loop.m)

```
clg;                                % clear previous graph settings
clear all;                          % clear workspace
B = 0.013;                          % slope of density feedback
N(1) = 10;                          % initial population size
NE = 100;                           % equilibrium density
for t = 1:12, N(t+1) = (1 - B*(N(t) - NE))*N(t);
end;                                % Matlab's for loop called
plot (x);                           % plot command
axis([0, 12, 0, 120]);              % scale plot axis
```

References

For further information concerning the use of Matlab's for loop subroutine refer to the Matlab Users Guide for Sun Workstations, subsection 3.81 (Matlab 1991).

Appendix 2

Text Reference
Chapter two, *Equations (22 a, b), the coupled Logistic, section 2.4.6.2.*

Description

The following Matlab Scripts are designed to solve a couped system of differential equations over the time period t_0 to t_f, based on the initial conditions $N_{(0)}$. Equation parameters are defined by the global variable "par" and stated in numerical order according to their position in the equations xdot(1) and xdot(2). The differential equation solver ode45 is called to solve the equations xdot(1) and xdot(2) contained in the matlab file (mfile) "DEquat.m". Explanatory text is commented out using a percentage symbol (%).

Command Window

```
>>                                      % (>>) command window prompt
>>com                                   % calls the mfile com.m
```

Command mfile (com.m)

```
clg;
global par;
par=[65 1000 0.4 50 1200 0.9]';         % par=[r, k, α, r, k, β ]
t0=0; tf=2;                             % time
x0=[980  980]';                         % initial conditions
[t,x] = ode45('DEquat', t0, tf, x0);    % call ode45
axis([0, 0.5, 0, 1200]);
subplot(221), plot(t, x(:,1));          % subplot commands
axis([0, 0.5, 0, 1200]);
subplot(222), plot(t, x(:,2));
axis([0, 1200, 0, 1200]);
subplot(223), plot(x(:,1),x(:,2));
%plot(x(:,1),x(:,2));                   % plot phase portrait
%data=[x(:,1) x(:,2)]                   % data defined
%save data.dat data -ascii              % data saved to the file data.dat
```

Function mfile (DEquat.m)

```
function xdot = DEquat(t,x);            %pass arguments (t, x)

% coupled logistic equation
xdot(1) = par(1)*x(1)*(par(2)-x(1)-par(3)*x(2)/par(2));
xdot(2) = par(4)*x(2)*(par(5)-x(2)-par(6)*x(1)/par(5));
```

References

For further information, on the use of differential equation solvers ode23 and ode45, refer to the Matlab Users Guide for Sun Workstations, reference section 3-137 (Matlab 1991).

Appendix 3

Text Reference
Chapter Four, *Matlab and the Optimisation Toolbox, section 4.3.2.3*

Description

The following three mfiles have been developed as parts of the nonlinear optimisation program used for curve fitting and parameter estimation. Various changes have been made to these scripts in order to accommodate forcing functions and time delays (Appendix 10 and 11).

Command Window

```
>>                                    % (>>) command window prompt
>>zdu                                 % calls the mfile zdu.m
```

Command mfile (zdu.m)

```
clear all;                            % clear current workspace
global par                            % define global variables
global pc

%-----------------------------Load Data ------------------------------
load lawak.dat;                                  % load lawakilevu data
      data = [lawak(:,3), lawak(:,4)]
       depth = lawak(:,1);                       % load depth data
            t = [0;  560; 1292.5 ];              % average sample depth for C14
                                                 % ... core samples.
             p = [0;  139.5; 411.5 ];            % calibrated C14 ages
              pc =interp1(t, p, depth);          % interpolation subroutine
               pc = -pc                          % invert the time vector
             pc = pc(length(pc):-1:1)
            time = pc;
        data = data(length(data):-1:1,:)/1000    % invert and scale the data

%------------------------Parameters for 2-D Model -------------------------
PAR= [0.2   0.2   0.3  -0.2  0.05  -0.2 ]              %1st Estimate

%-----------------------Changes to Default Settings -----------------------
options(14) = 200           % specify number of iterations
option(18) = 0.001          % specify search path step size

%--------------------Call Least Squares Optimisation-----------------------
optimum = leastsq('lsfun', PAR, options, [ ], time, data)

% optimum are the model parameters used at convergence. Optimum calls %
% the least squares subroutine on the mfile lsfun.m using the parameters
% specified by PAR on the x and y data defined as time and data.
```

Function mfile (lsfun.m)

```
function tem=lsfun(PAR, t, dat);      % pass arguments
global par                            % par is a global variable
```

```
    par = PAR ;                          % define par
          ns = size(dat); n=ns(2);       % determine data length
           nstep=length(t);              % specify data timesteps
              u = zeros(nstep,n);        % u is a zeros matrix
         u(1,:) = par(1:n);              % the first row of u contains
                                         % .. row one of par
    [tm,uo] = ode45('odefn',t(1),t(nstep),u(1,:)',1e-4);

% [tm, uo] is an output matrix for the results of the differential equation
% solver ode45 which solves the equations of odefn.m based on initial
% and final time steps, initial conditions of u and a desired solution
% accuracy of 1e-4

    tem = [interp1(tm,uo(:,1),t) interp1(tm,uo(:,2),t) ] - dat ;

% tem is the difference between the model and field data.
```

Function mfile (odefn.m)

```
function udash=odefn(t, u, par)          % pass arguments
global sc;                               % define global variables
global par;

%---------------------------------------Model Formulations-----------------------------
% exponential equation
%udash(1)=par(3)*u(1);
%udash(2)=par(4)*u(2);

% logistic equation
%udash(1)=par(3)*u(1)*(par(4)-u(1)/par(4));
%udash(2)=par(5)*u(2)*(par(6)-u(2)/par(6));

% coupled logistic equation
udash(1)=par(3)*u(1)*(par(5)-u(1)-par(4)*u(2)/par(5));
udash(2)=par(6)*u(2)*(par(8)-u(2)-par(7)*u(1)/par(8));
```

References

For further information on the use of differential equation solvers ode23 and ode45 and general subroutines used in this program refer to the Matlab Users Guide for Sun Workstations, reference section 3-137 (Matlab 1991). For further information on the use of the least squares optimisation routine refer to Grace (1992).

Appendix 4

Text Reference

Chapter Four, *Optimisation Toolbox - Application Problems, section 4.3.2.4.*

Description

The mfile named sim.m has been developed for simulation studies using the Matlab *for-loop* subroutine. This small program operates by calling the differential equation solver nested in the lsfun.m mfile (see Appendix 3). The differential equation solver calls the equations recorded in the function mfile named odefn.m. The *for-loop* function enables the user to solve an equation over a range of specified parameters values. It is also possible to simulate a range of two or more parameters at any one time by nesting sub-for-loops within the first for-loop statement.

Command Window

```
>>                                  % (>>) command window prompt
>>sim                               % calls the mfile sim.m
```

Command mfile (sim.m)

```
clear all;                          % clear current workspace
global par                          % define global variables
global pc

%-----------------------------Load Data ------------------------------------
load lawak.dat;                               % load lawakilevu data
      data = [lawak(:,3), lawak(:,4)]
       depth = lawak(:,1);                    % load depth data
            t = [0;  560; 1292.5 ];           % average sample depth for C14
                                              % ... core samples.
             p = [0;  139.5; 411.5 ];         % calibrated C14 ages
              pc =interp1(t, p, depth);       % interpolation subroutine
               pc = -pc                       % invert the time vector
             pc = pc(length(pc):-1:1)
            time = pc;
        data = data(length(data):-1:1,:)/1000  % invert and scale the data

for i = 0.00001:0.00001:0.0001,          % i is the range of parameter values
                                         % ... to be simulated.
w= [data(1,:) i  -0.30  -0.0001 0.008  -0.96  0.00050]

% the eight parameters of the coupled logistic equation based on two
% dimensions. The specific growth rate (r) of equation one (parameter 3)
% has been replace by the variable i (a range of parameter values 0.00001:
% 0.00001: 0.0001).

lsfun(w, time, data)                     % calls the lsfun function mfile
                                         % on the parameters w and the
                                         % arguments time and data.
```

```
error = ans;                            % define error as simulation output
plot(time, data(:,2), time, data(:,2)+error(:,2)) % plot command
hold on
end;

% the plot command used above produces a composite plot of all of the
% simulation results for which the parameter variable i has been specified.
```

Function mfile (lsfun.m)

```
function tem=lsfun(PAR, t, dat);              % pass arguments
global par                                    % par is a global variable
          par = PAR ;                         % define par
           ns = size(dat); n=ns(2);           % determine data length
            nstep=length(t);                  % specify data timesteps
                u = zeros(nstep,n);           % u is a zeros matrix
          u(1,:) = par(1:n);                  % the first row of u contains
                                              % .. row one of par
     [tm,uo] = ode45('odefn',t(1),t(nstep),u(1,:)',1e-4);

% [tm, uo] is an output matrix for the results of the differential equation
% solver ode45 which solves the equations of odefn.m based on initial
% and final time steps, initial conditions of u and a desired solution
% accuracy of 1e-4

     tem = [interp1(tm,uo(:,1),t) interp1(tm,uo(:,2),t) ] - dat ;

% tem is the difference between the model and field data.
```

Function mfile (odefn.m)

```
function udash=odefn(t, u, par)         % pass arguments
global sc;                              % define global variables
global par;
%-----------------------------------------Model Formulations--------------------------------
% exponential equation
%udash(1)=par(3)*u(1);
%udash(2)=par(4)*u(2);

% logistic equation
%udash(1)=par(3)*u(1)*(1-u(1)/par(4));
%udash(2)=par(5)*u(2)*(1-u(2)/par(6));

% coupled logistic equation
udash(1)=par(3)*u(1)*(1-u(1)/par(5))-(par(4)*u(2)/par(5));
udash(2)=par(6)*u(2)*(1-u(2)/par(8))-(par(7)*u(1)/par(8));
```

References

For further information on the use of the for-loop sub routine and general subroutines used in this program refer to the Matlab Users Guide for Sun Workstations, reference section 3-137 (Matlab 1991).

Appendix 5

Totoya Island Plant Species List
With Vegetation Survey Identification Numbers
Collector: Anthony O. Cole

Item	Botanical Name	Life Form	Survey ID
1	*Bruguiera gymnorhiza*	Tree	FJT 01
2	*Excoecaria agallocha*	Tree	FJT 02
3	*Pongamia pinnata*	Tree	FJT 03
4	*Macropiper timothianum*	Tree	FJT 04
5	*Ficus vitiensis*	Tree	FJT 05
6	*Erythrina variegata*	Tree	FJT 06
7	*Cocos nucifera*	Tree	FJT 07
8	*Dysoxylum richii*	Tree	FJT 08
9	*Inocarpus fagiferus*	Tree	FJT 09
10	*Vitex trifolium*	Tree	FJT 10
11	*Diospyrus samonensis*	Tree	FJT 11
12	*Calophyllum inophyllum*	Tree	FJT 12
13	*Thespesia populnea*	Tree	FJT 13
14	*Xylocarpus granatum*	Tree	FJT 14
15	*Cordyline terminalis*	Tree	FJT 15
16	*Tree 1*	Tree	FJT 16
17	*Tree 2*	Tree	FJT 17
18	*Maniltoa brevipes*	Tree	FJT 18
19	*Vavala amicorum*	Tree	FJT 19
20	*Planchonella grayana*	Tree	FJT 20
21	*Hibiscus tiliaceus*	Tree	FJT 21
22	*Aleurites moluccana*	Tree	FJT 22
23	*Micromelum minutum*	Tree	FJT 23
24	*Terminalia catappa*	Tree	FJT 24
25	*Dillenia biflora*	Tree	FJT 25
26	*Geniostoma uninervium*	Tree	FJT 26
27	*Homalium pallidum*	Tree	FJT 27
28	*Tree 3*	Tree	FJT 28
29	*Alectryon samaensis*	Tree	FJT 29
30	*Gyrocarpus americanus*	Tree	FJT 30
31	*Grewia crenata*	Tree	FJT 31
32	*Cerbera manghas*	Tree	FJT 32
33	*Ficus sp.*	Tree	FJT 33
34	*Caesalpinia sp.*	Tree	FJT 34
35	*Euodia hortensis var. swampifolia*	Tree	FJT 35
36	*Barringtonia asiatica*	Tree	FJT 36
37	*Pandanus sp.*	Tree	FJT 37
38	*Dendrocnide harveyi*	Tree	FJT 38
39	*Diosyros sp.*	Shrub	FJS 01

40	*Mariscus javanicus*	Aquatic	FJA 01
41	*Scleria lithosperma*	Aquatic	FJA 02
42	*Eulophia macgregori*	Orchid	FJO 01
43	*Miscanthus floridulus*	Grass	FJG 01
44	*Digitaria sp.*	Grass	FJG 02
45	*Phymatosorus nigrescans*	Fern	FJF 01
46	*Nephrolepis sp.*	Fern	FJF 02
47	*Nephrolepis sp.*	Fern	FJF 03
48	*Asplenium australasicum*	Fern	FJF 04
49	*Pyrrosia adnascens*	Fern	FJF 05
50	*Hyptis pectinata*	Herb	FJH 01
51	*Derris trifoliata*	Liane	FJL 01
52	*Ipomoea sp.*	Liane	FJL 02
53	*Mikania micrantha*	Liane	FJL 03
54	*Ipomoea sp.*	Liane	FJL 04
55	*Clerodendrum inerme*	Liane	FJL 05
56	*Liane 1*	Liane	FJL 06
57	*Alyxia sp.*	Liane	FJL 07
58	*Jasminum simplicifolium*	Liane	FJL 08

Taxonomic nomenclature in the above table is according to Parham (1972) and Smith (1981). Herbarium specimens are to be located in the Massey University Herbarium. Only the authors herbarium reference numbers are listed in the above table.

Appendix 6

Fossil Pollen Count Data

Number of Lycopodium per Tablet:	13911 ± 308
Lycopodium Batch Number:	710961
Number of Lycopodium Counted for Charcoal Counts:	100

The Keteira Count Data (Control Site)

Depth (mm)	Charcoal Frag.	*Exco. pollen*	*Brug. pollen*	*Lycop. /pollen*	Sample Volume	Tablets Added
0.0	550	45	18	200	1 cm^3	2
25	222	15	5	200	1 cm^3	2
50	339	20	6	200	1 cm^3	2
75	238	15	13	200	1 cm^3	2
100	192	17	8	200	1 cm^3	2
125	562	35	23	200	1 cm^3	2
150	376	20	10	200	1 cm^3	2
175	306	8	6	200	1 cm^3	2
200	339	20	6	200	1 cm^3	2
225	551	40	23	200	1 cm^3	2
250	244	28	4	200	1 cm^3	2
275	337	18	13	200	1 cm^3	2
300	468	10	7	200	1 cm^3	2
325	755	31	14	200	1 cm^3	2
350	395	11	8	200	1 cm^3	2
375	471	22	8	200	1 cm^3	2
400	1513	34	22	200	1 cm^3	2
425	979	41	16	200	1 cm^3	2
450	609	18	12	200	1 cm^3	2
475	286	16	6	200	1 cm^3	2
500	1548	26	18	200	1 cm^3	2
525	601	21	13	200	1 cm^3	2
550	456	30	17	200	1 cm^3	2
575	250	19	17	200	1 cm^3	2
600	1736	28	17	200	1 cm^3	2
625	546	40	17	200	1 cm^3	2
650	478	33	5	200	1 cm^3	2
675	1215	52	7	200	1 cm^3	2
700	357	58	17	200	1 cm^3	2
725	1233	26	19	200	1 cm^3	2
750	467	27	9	200	1 cm^3	2

775	318	21	3	200	1 cm^3	2
800	3600	40	26	200	1 cm^3	2

The Lawakilevu Count Data

Depth (mm)	Charcoal Frag.	*Exco.*	*Brug.*	*Lycop .*	Sample Volume	Tablets Added
0.0	365	33	30	200	1 cm^3	2
25	349	16	1	200	1 cm^3	2
50	578	9	24	200	1 cm^3	2
75	529	12	3	200	1 cm^3	2
100	608	17	4	200	1 cm^3	2
125	789	27	4	200	1 cm^3	2
150	674	17	13	200	1 cm^3	2
175	857	9	1	200	1 cm^3	2
200	330	8	0	200	1 cm^3	2
225	842	1	0	200	1 cm^3	2
250	374	5	0	200	1 cm^3	2
275	550	6	1	200	1 cm^3	2
300	365	12	2	200	1 cm^3	2
325	803	8	3	200	1 cm^3	2
350	585	5	1	200	1 cm^3	2
375	674	11	1	200	1 cm^3	2
400	525	4	3	200	1 cm^3	2
425	746	1	0	200	1 cm^3	2
450	401	41	1	200	1 cm^3	2
475	308	31	0	200	1 cm^3	2
500	430	28	6	200	1 cm^3	2
525	1007	32	4	200	1 cm^3	2
550	694	48	7	200	1 cm^3	2
575	303	26	2	200	1 cm^3	2
600	466	35	0	200	1 cm^3	2
625	299	18	0	200	1 cm^3	2
650	246	48	5	200	1 cm^3	2
675	371	36	0	200	1 cm^3	2
700	200	104	1	200	1 cm^3	2
725	191	51	0	200	1 cm^3	2
750	214	24	0	200	1 cm^3	2
775	408	14	0	200	1 cm^3	2
800	529	30	0	200	1 cm^3	2
825	300	22	0	200	1 cm^3	2
850	263	5	0	200	1 cm^3	2

875	394	2	0	200	1 cm^3	2
900	1550	18	4	200	1 cm^3	2
925	910	2	2	200	1 cm^3	2
950	1740	3	0	200	1 cm^3	2
975	4900	0	1	200	1 cm^3	2
1000	96	1	0	200	1 cm^3	2
1025	110	3	0	200	1 cm^3	2
1050	790	16	0	200	1 cm^3	2
1075	930	14	2	200	1 cm^3	2
1100	6700	34	0	200	1 cm^3	2
1125	5300	28	0	200	1 cm^3	2
1150	5400	28	0	200	1 cm^3	2
1175	4500	18	0	200	1 cm^3	2
1200	2300	14	0	200	1 cm^3	2
1225	1800	10	0	200	1 cm^3	2
1250	300	4	0	200	1 cm^3	2

The Udu Count Data

Depth (mm)	Charcoal Frag.	*Exco.*	*Brug.*	*Lycop .*	Sample Volume	Tablets Added
0.0	362	60	65	200	1 cm^3	2
25	961	83	29	200	1 cm^3	2
50	165	45	44	200	1 cm^3	2
75	2574	31	78	200	1 cm^3	2
100	125	40	29	200	1 cm^3	2
125	612	50	40	200	1 cm^3	2
150	180	43	30	200	1 cm^3	2
175	537	37	23	200	1 cm^3	2
200	111	26	23	200	1 cm^3	2
225	295	14	7	200	1 cm^3	2
250	127	7	6	200	1 cm^3	2
275	71	3	0	200	1 cm^3	2
300	126	10	14	200	1 cm^3	2
325	200	8	3	200	1 cm^3	2
350	181	9	20	200	1 cm^3	2
375	165	13	15	200	1 cm^3	2
400	272	43	19	200	1 cm^3	2
425	149	4	0	200	1 cm^3	2
450	361	3	2	200	1 cm^3	2
475	597	16	11	200	1 cm^3	2

500	975	23	0	200	1 cm^3	2
525	1477	5	0	200	1 cm^3	2
550	503	30	0	200	1 cm^3	2
575	1707	1	0	200	1 cm^3	2
600	209	2	6	200	1 cm^3	2
625	499	12	6	200	1 cm^3	2
650	513	13	9	200	1 cm^3	2
675	861	38	1	200	1 cm^3	2
700	526	72	2	200	1 cm^3	2
725	472	27	0	200	1 cm^3	2
750	362	22	0	200	1 cm^3	2
775	1405	6	2	200	1 cm^3	2
800	814	1	0	200	1 cm^3	2
825	618	0	0	200	1 cm^3	2
850	940	6	1	200	1 cm^3	2
875	3605	48	0	200	1 cm^3	2
900	2590	27	4	200	1 cm^3	2
925	3598	25	1	200	1 cm^3	2
950	3314	38	2	200	1 cm^3	2
975	2605	14	4	200	1 cm^3	2
1000	4367	14	2	200	1 cm^3	2
1025	638	28	1	200	1 cm^3	2
1050	1548	45	3	200	1 cm^3	2
1075	1379	25	1	200	1 cm^3	2
1100	1016	28	2	200	1 cm^3	2
1125	1836	17	0	200	1 cm^3	2
1150	5462	26	6	200	1 cm^3	2
1175	772	13	1	200	1 cm^3	2
1200	2779	26	8	200	1 cm^3	2
1225	2418	10	0	200	1 cm^3	2
1250	1654	9	0	200	1 cm^3	2
1275	1397	21	1	200	1 cm^3	2
1300	426	43	5	200	1 cm^3	2
1325	760	41	6	200	1 cm^3	2
1350	719	43	4	200	1 cm^3	2
1375	1145	26	1	200	1 cm^3	2
1400	39	3	0	200	1 cm^3	2
1425	653	34	1	200	1 cm^3	2
1450	1607	67	1	200	1 cm^3	2
1475	1319	93	0	200	1 cm^3	2
1500	4646	56	8	200	1 cm^3	2
1525	1390	82	7	200	1 cm^3	2
1550	5370	135	14	200	1 cm^3	2

1575	10082	59	6	200	1 cm^3	2
1600	19360	19	3	200	1 cm^3	2
1625	23200	62	10	200	1 cm^3	2
1650	15350	41	2	200	1 cm^3	2
1675	10800	20	0	200	1 cm^3	2
1700	16500	26	0	200	1 cm^3	2
1725	12000	38	5	200	1 cm^3	2
1750	11300	40	8	200	1 cm^3	2
1775	13300	20	6	200	1 cm^3	2
1800	7600	38	2	200	1 cm^3	2

Appendix 7

5.3.4 Laboratory Procedure

The subsamples from Totoya mangrove cores were very rich in terrestrial clay sediments and fine grained charcoal fragments. For this reason the sample preparation procedure had to be slightly adapted to deal with processing this type of material. In the following discussion, a step by step description of both the chemical treatments used and laboratory procedures followed is given.

The need for uniform sample preparation has been stressed by Green and Dolman (1988). Uniformity ensures that errors introduced *by laboratory processing will be systematic, rather than random and will therefore not affect the interpretation of the resulting sediment record.* Uniform procedure has been applied to all of the Totoya samples. This was aided by a series of pilot samples, which were used to evaluated the suitability of these cores for further research. Insights gained from the laboratory treatment of this first batch were consistently applied to the 157 samples processed for modelling data sets.

The following procedure has been adapted from Faegri and Iversen (1989), Moore *et al.* (1991), Walker *et al.* (1994) and Jemmett (1995). Refinements are based on the author's experience and suggestions given by Mrs Leighanne Signal (Laboratory Supervisor, Geography Department, Massey University).

5.3.4.1 10% HCl Treatment

The 1cm3 samples located in 15 ml polypropylene centrifuge tubes were initially treated in a 10% solution of HCl in order to dissolve carbonates. Some of the samples had large amounts of carbonates and therefore the HCl had to be added very carefully so as not to induce a violent reaction resulting in sample loss. This mixture was then centrifuged at 3500 rpm for 5 minutes and decanted.

5.3.4.2 Addition of Lycopodium Tablets

Two *Lycopodium* tablets (batch 710961) (Stockmarr 1971) were added to each sample preparation (Green 1983). First, the two tablets were dissolved in a 50 ml conical flash by adding ca. 10 ml of 10% HCl. When the tablets were completely dissolved and had finished reacting, the HCl/*Lycopodium* mixture was added to the next sample tube with gentle stirring of the mixture. This preparation was then centrifuged at 3500 rpm for 5 minutes and decanted. The sample was then washed with distilled water and a couple of drops of dilute sodium lauryl sulphate to help prevent flocculation. This preparation was then centrifuged at 3500 rpm for 5 minutes and decanted.

5.3.4.3 10% KOH Treatment

Next, 10% KOH solution (Moore *et al.* 1991, Faegri and Iversen 1989) was added to each sample tube (to remove humic acids) with the tubes being heated on a hotblock to a steady temperature of 95^{o}C and held at this temperature for ca. five minutes. During this time the contents of each tube were periodically stirred and continuously watched to avoid boiling over and sample loss. The contents of each sample tube were then emptied, through a multilayered 180 micron terylene sieve element, held in a glass funnel in the mouth of a 50 ml conical flask.

The tube and terylene sieve were then washed clean with distilled water. The terylene sieve element was placed in a labelled petri dish to be kept for analysis of macro-remains (inorganic and large organic particles). The contents of the conical flask was poured back into the centrifuge tube and the flask washed clean with distilled water.

This preparation was then centrifuged at 3500 rpm for 5 minutes and decanted. The sample was then washed with distilled water and a couple of drops of sodium lauryl sulphate to help prevent flocculation. The sample tube was then centrifuged at 3500 rpm for 5 minutes and decanted. The distilled water wash procedure was repeated until the supernatant was clear. For the Totoya samples it was not necessary to repeat the KOH treatment.

5.3.4.4 ***Hot $Na_4P_2O_7$ Treatment***

The samples were next treated with 10% hot sodium pyrophosphate ($Na_4P_2O_7$) in order to deflocculate clays (Bates *et al.* 1978). This procedure was successful in removing a very large percentage of the clay sediments in these samples. The procedure involves filling sample tubes with $Na_4P_2O_7$ and then heating them on a hot block to 105°C for ca. 10 - 20 minutes.

The sample tubes were then centrifuged for 5 minutes at 3500 rpm and then decanted. This treatment was repeated (two or three times) until the clay content had been reduced to ca. one third of the original total.

Finally, the samples were given a water wash and passed through a reverse flow suction sieve apparatus containing a 5 micron nylon sieve element. The remaining clay in the sample was washed through the sieve using large amounts of distilled water dispensed from a high pressure squirt bottle.

The sample remaining on the sieve element was then washed free into a 500ml beaker and then poured and washed back into the original centrifuge tube for centrifuging down and decanting. Step 5.3.4.4, including both the hot $Na_4P_2O_7$ treatment and sieving was found to be required in order for the next step (HF treatment) to work effectively at removing large silicates and the remaining fine grained clays.

5.3.4.5 ***40% HF Treatment***

Treatment with 40% Hydrofluoric acid is normally a slow gentle reaction, however this was not the case with most of the Totoya samples which proved to be extremely reactive and had to be treated with great caution for this reason (Jemmett 1995). The procedure used involved measuring out ca. 7ml of cold HF into each sample tube and stirring the sample into the HF with a polypropylene stirring rod. The preparation was stable and unreactive at this stage.

Next, the tubes were heated on a hot block to a steady temperature of 95°C. At this point the samples had to be watched for evidence of reactivity (like boiling water). Reactive tubes needed to be removed from the hot block immediately if HF spills were to be avoided. Sample tubes which did over react were abandoned and repeated from the subsampling stage.

A period of 5 minutes at 95°C was found to be adequate for cleaning up fine grained clays and removing silicates. After this time period, the sample tubes were removed from the hot block and had ca. 5 ml of hot 10% HCl added. Hot HCl (10%) is used to keep the dissolved silicates in solution until the decanting process. The mixture of hot 40% HF and 10% HCl was then stirred, the polypropylene stir rods removed and screw top lids placed on each sample tube to contain flumes and avoid HF spills. The sample tubes were then centrifuged at 3500 rpm for 5 minutes and decanted. This was followed by a wash with distilled water and a couple of drops of sodium lauryl sulphate. The samples tubes were then centrifuged at 3500 rpm for 5 minutes and decanted (Moore *et al.* 1991, Faegri and Iversen 1989).

5.3.4.6 Acetolysis Treatment

A standard acetolysis pre-treatment and treatment (Moore *et al.* 1991, Faegri and Iversen 1989) was next applied to the samples in order to remove organic material and prepare them for oxidation which more successfully destroyed lignins (step 5.3.4.7).

The pre-treatment involved washing each sample in dilute acetic acid and then glacial acetic acid in order to dehydrate the sample (acetolysis mix is extremely reactive with water). The sample tubes are then centrifuged at 3500 rpm for 5 minutes and decanted after the glacial acetic acid wash.

Next, a mixture of 9 ml of acetic anhydride and 2 ml of concentrated sulphuric acid is made up. The conc. H_2SO_4 was added to the acetic anhydride solution (in a 500 ml beaker) and the mixture allowed to react until it settles down. In the next step, ca. 3 ml of acetolysis mixture was poured into each sample tube and brought up to a temperature of 90°C for 5 minutes on a hotblock. After heating, the samples were removed from the hot block and the reaction stopped by adding 5 ml of cold glacial acetic acid. The sample tubes were then centrifuged at 3500 rpm for 5 minutes and decanted. The wash, centrifuge and decant procedure was repeated using glacial acetic acid, dilute acetic acid and finally water with a coupled of drops of sodium lauryl sulphate to help prevent flocculation.

5.3.4.7 Oxidation Treatment

Oxidation (Faegri and Iversen 1989) mixture is best applied to each sample tube separately since the reaction runs very fast and must be neutralised quickly if sample loss is to be avoided. To begin this process, each sample is suspended in glacial acetic acid and then 1 ml of concentrated HCl is added to the sample tube.

The sample and acid were mixed together well to ensure an even reaction. In the next step, five or six drops of saturated $NaClO_3$ solution is added to the acid and sample mixture. A violent reaction follows and the sample is bleached (solution turns yellow) after only a couple of seconds.

During the reaction, the contents of the sample tube are mixed using a glass pipette and then the contents of the sample tube emptied into a 50 ml beaker containing ca. 10 ml of distilled water. This mixture is then poured back into the original centrifuge tube, aided by a wash with distilled water. The tube was then centrifuged at 3500 rpm for 5 minutes and decanted.

5.3.4.8 Acetolysis and Sieving

In step number 5.3.4.8, the acetolysis procedure outlined in step number 3.4.6 was repeated. Step number 5.3.4.8 was not required to remove further organic particles, but to add colour back to the pollen grains that had been bleached out during the oxidation procedure. This made the fossil pollen grains easier to identify under a light microscope. After this step, a final sieve (using the reverse suction sieve apparatus - step 5.3.4.4) with distilled water was found to be ideal for removing fine grained organics from the sample.

5.3.4.9 Alcohol Dehydration

After step 5.3.4.8, samples were ready for dehydration with alcohol before mixing in silicone oil prior to mounting on microscope slides (Moore and Webb 1978). The dehydration procedure involved washing each sample with absolute ethanol, followed by a 50/50 mixture of absolute ethanol and Tertiary Butyl Alcohol (TBA) and then finally, a wash in 100% TBA. After each wash the sample tube was centrifuged at 3500 rpm for 5 minutes and decanted.

Finally, a little fresh TBA was added to each sample tube, mixed thoroughly with the sample and then the total contents of the tube transferred to a 5 ml storage vial which had been appropriately labelled. Silicone oil (Andersen 1960) (ca. 0.5 ml) was then added to the storage vial and mixed into the TBA. The lids were left off the storage vials over night so that the TBA could evaporate leaving a mixture of fossil pollen and silicone oil. This mixture was checked the following morning. Each sample was stirred again and further silicone oil added if necessary.

5.3.4.10 Slide Mounts in Silicone Oil

The silicone oil/fossil pollen mixture was next mounted onto standard glass microscope slides. The slides were first cleaned and then heated on a slide warmer. A large drop of silicone oil/fossil pollen mixture was placed in the centre of the slide and mixed around using a small glass rod. A cover slip was then placed onto the drop of silicone oil/fossil pollen mix. As this mixture spread out under the weight of the cover slip, a ring of hot paraffin wax was run around the outside of the cover slip.

The slide was then removed from the slide warmer and the hot paraffin wax allowed to cool and set hard. Excess wax was removed from around the cover slip using a wooden toothpick. Finally the slide was polished with a tissue and labelled ready for use.

The procedure described above was applied consistently to all of the subsamples taken from the three core sites (Keteira, Udu and Lawakilevu) used in this modelling project. Most of the sample preparations produced using this procedure were very clean and the fossil pollen easy to count with two exceptions. Firstly, in some of the early preparations it proved to be very difficult to completely remove all of the fine grain organic particles. This problem was largely overcome by thorough distilled water washing (step 5.3.4.8) when using the reverse suction sieve apparatus.

Secondly, some of the early preparations clumped together and this also made counting more difficult. This problem was also largely overcome with the consistent use of sodium lauryl sulphate in the distilled wash water and the thorough washing of the samples with distilled water during sieving (step 5.3.4.8).

Finally, some of the preparations were very rich in fine charcoal particles which the author noted were present (at times) in decanted wash water. This appears to be a problem related to water tension. The use of sodium lauryl sulphate once again appeared to correct this problem, although further research on this point is clearly needed. A standardised treatment procedure is important so that losses of charcoal fragments as a result of decanting and sample treatments are consistent across all samples in accordance with Clark (1984).

Sample preparations which were very rich in charcoal fragments were also difficult to count and the author experienced this problem in some cases. The addition of larger amounts of silicone oil when mounting these charcoal rich samples helped to thin the sample down and thereby made counting easier.

5.3.5 Counting Procedure

There are three important factors that needed to be considered in the counting procedure: pollen distribution on microscope slides, determination of count size and the procedure used to count charcoal fragments.

5.3.5.1 Pollen Distribution on Microscope Slides

The first problem concerns the statistical distribution of pollen grains on a sample slide as considered by Brookes and Thomas (1967). Although the richness of fossil pollen in a preparation tends to vary from sample to sample, the Totoya samples were intermediate to poor in pollen richness. For this reason, it was necessary to count a number of slides in order to gain fossil pollen counts based on a minimum number of 200 marker pollen grains *(Lycopodium).*

For most sites an average of two slides was counted, however it was not uncommon to count three to five slides for some samples. Because of this problem, all of the fossil pollen located in the silicone oil region of each slide was completely counted. The only exception to this was the last slide which was counted until the complete number of *Lycopodium* marker grains had been achieved.

5.3.5.2 ***Determination of Count Size***

The counting strategy used involves a compromise between counting effort and the level of reliability required from pollen counts (Rull 1987). Obviously, large counts give very reliable estimates (the width of the 95% confidence interval decreases with increasing count size) but requires an equally large investment of time to accomplish. Maher (1972) has shown that based on a multinomial distribution, percentages stabilise as the pollen sum increases. Rull (1987) has attempted to locate a critical point *from which no significant shifting of these confidence intervals occurs* despite the general opinion which appears to be that the objectives of a given project should determine the count size and therefore no standard sample size will ever be fixed (Faegri and Iversen 1964, Moore and Webb 1978, Birks and Birks 1980, Maher 1981). The present project involves two further complicating factors.

Firstly, research into optimal counts sizes has focused on the total pollen assemblage. At the three core sites on Totoya, the two species of mangrove are the only objects of interest to this project. Inland forest pollen was also represented in the mangrove fossil pollen assemblage, but there seemed little justification for counting all of this as well.

Secondly, assuming a total assemblage (inland forest and mangrove fossil pollen) count size of at least 200 pollen grains, the mangrove fossil pollen in this total count would probably only represent a small percentage of the total pollen sum. Therefore, it seems equally extreme to solve the first problem above by counting a total of two hundred mangrove fossil pollen!

A simple and obvious solution to the above problems has been devised for the present study. This approach involves assumptions which there is not the time to evaluate in the present thesis. The full answer to these problems will doubtless require future research. To determine a count size for the present project the following procedure was used. The objective of this strategy was to develop a procedure for which reliable estimates could be gained by counting only the two mangrove species.

Firstly, the cores were subsampled at 500 mm intervals (a pilot study), and samples prepared for counting. These samples were counted using a standard technique involving counts of all fossil pollen present on the microscope slide to a total pollen sum of 200 grains. *Lycopodium* marker spores were also counted so that it could be determined that 100 to 150 *Lycopodium* marker spores was necessary to produce a count size of ca. 200 grains.

Therefore, the total number of mangrove fossil pollen encountered in the process of counting 200 *Lycopodium* marker spores was used as a count strategy for all of the Totoya samples used in this project. As suggested above, the statistical implications of this approach need to be investigated. The main assumption is that a total of 200 *Lycopodium* is an adequate number for all of the core samples. This assumption rests on observed numbers of 100 - 150 *Lycopodium* for initial 500 mm samples at the six core sites on the island.

Finally, the procedure assumes that the mangrove counts gained using this approach, are those that would have been gained, had a total pollen sum been counted. The main advantage of this approach was that it saved considerable time over the total 157 samples counted for the three modelling data sets.

5.3.5.3 Counting Charcoal Fragments

There is now a growing body of literature (Clark 1984, Winkler 1985, Clark 1982, 1988a, b,) on the subject of charcoal analysis for palaeoecological and palaeoenvironmental interpretation. Recent research by Swain (1973), who compared preserved charcoal particle concentrations with fire scar records, has showed that preserved charcoal particles in high concentration provide an almost perfect indicator of local fire occurrence. An excellent summary of the issues surrounding the dispersal, treatment, counting and interpretation of charcoal fragments as an indicator of fire is given in Patterson *et al.* (1987). Two of the issues (dispersal and counting) mentioned by these authors have an important bearing on the present project.

Firstly, the core sites on Totoya are suitably distanced apart and the island's total land mass small enough that the presence of charcoal fragments in a core sediment may be taken as an indication of localised fire. The main mechanism of charcoal fragment transport to the core site is likely to have been hydrological. This in turn suggests that the charcoal fragments in the core samples were derived from the watershed behind the core sites (Patterson *et al.* 1987).

Secondly, having established the fact that charcoal fragments in these cores is an indicator of local fire histories, a method of quantifying the charcoal fragments was needed. A variety of approaches has been used by various authors including: counts of charcoal particles or measurements of area by point counts (Clark 1982), classification according to size (Waddington 1969). Number and area may be expressed as a percentage of the pollen sum (Maguire 1983), as a total content per unit of sediment (Innis 1981) or as influx per unit area per year (Green 1981). Once again, the method of counting derives from the objectives of individual projects.

In the present project, the charcoal fragment data was used as a forcing function in differential and difference equation model formulations. In an application of this kind what is ideally wanted is a temporal record of the changing concentrations of charcoal in core sediments, independent of sedimentation rate.

A simple way of accomplishing this was to take counts of charcoal fragments over all size ranges for a standard number of *Lycopodium* marker spores (100 in this case). This approach is similar in principle to that outlined above for the counting of mangrove pollen. In retrospect, this approach was very time consuming because most of the samples had very high levels of charcoal. A smaller number of *Lycopodium* would have been more appropriate.

5.3.5.4 Compiling the Data

The compiling of absolute fossil pollen data usually involves calculations which convert the actual fossil pollen counts into a value which expresses the total number of fossil pollen grains per unit of sample sediment (absolute pollen frequency). This is illustrated in the following calculations based on

10,319 ± 100	total *Lycopodium* marker spores added to sample
50	total pollen grains counted
25	*Lycopodium* marker spores counted
APF (total)	is the total pollen grains per unit of sediment, and of the 50 pollen grains counted

$$APF\ (total) = 10{,}319 \times \frac{50}{25}$$

where

20 grains were *Bruguiera gymnorhiza*
30 grains were *Excoecaria agallocha.*

Therefore;

$$\text{APF of } Bruguiera\ gymnorhiza = APF(total) \times \frac{20}{50}$$

and

$$\text{APF of } Excoecaria\ agallocha = APF(total) \times \frac{30}{50}.$$

There are software packages available for transforming fossil pollen count data to pollen concentration (grains cm $^{-3}$) as illustrated above. The package used in the present project was Tilia which is available from Dr Eric Grimm, Associate Curator of Botany, Illinois State Museum.

Pollen accumulation rates (PAR) (used in the modelling experiments and results portrayal) were obtained from the following formula (Birks and Birks 1980)

$$\text{PAR (grains cm}^{-2}\text{ yr}^{-1}) = \text{pollen concentration (grains cm}^{-3}) \times \text{sediment accumulation rate (cm yr}^{-1}).$$

The actual count fossil pollen data sets are recorded in Appendix 6. Each *Lycopodium* tablet of batch 710961 used in the preparation of these samples contains 13,911 ± 308 *Lycopodium* marker spores.

Although the charcoal data were counted at the same time as the mangrove pollen counts, they were not utilised in the modelling experiments until quite late in this project. As a result of this fact, the data were never transformed using the above APF calculations. This occurred initially because it did not seem appropriate to include charcoal fragment counts into calculations involving fossil pollen data. Later, when the data was used, the need to transform it was completely overlooked by the author.

As it turns out, this does not cause a problem because the total number of *Lycopodium* marker spores counted was standardised for all sample counts (100). Therefore, transforming the charcoal data makes no difference to the behaviour of the data in time and therefore does not affect the modelling results. In retrospect, the charcoal data should have been transformed and expressed as charcoal fragments per sample unit (as per Green 1981). In recognition of this problem, the plots of the charcoal data in the results section of this chapter has been labelled (charcoal fragments per 100 *Lycopodium*) instead of charcoal fragments per cm^{-2} of sediment.

5.3.5.5 Dating of the Core Stratigraphy

Dating of the Fijian cores used in this project was accomplished with the aid of AMS (Accelerated Mass Spectrometry) dates processed by the Rafter radiocarbon laboratory, the Institute of Geological and Nuclear Science, Lower Hutt, New Zealand. Details of the core sections submitted for radiocarbon dating are recorded below in Table 5.3.

Site Name	*Sample*	*Depth (mm)*
Udu	Udu 001	500 - 610 mm
Udu	Udu 002	1800 - 1920 mm
Lawakilevu	Lawak 006	500 - 620 mm
Lawakilevu	Lawak 007	1230 - 1355 mm
Keteira	Ketei 008	500 - 610 mm
Keteira	Ketei 009	1750 - 1850 mm
Keteira	Ketei 010	2350 - 2460 mm

Table 5.3 Core samples submitted for AMS radiocarbon dating.

Appendix 8

Lake Rotokura Plant Species List
Collector: Anthony O. Cole

In the following tables, the taxonomy of the New Zealand Podocarpaceae and Fagaceae is according to Connor (1985). General taxonomic nomenclature is according to Allan (1961), Moore and Edgar (1970), Edgar (1971), Edgar and Connor (1978, 1983) and Brownsey at al. (1985).

Item	Botanical Name	Life Form	Survey ID
1	*Cyathodes fasciulata*	Tree	NZT 01
2	*Pseudopanax colensoi*	Tree	NZT 02
3	*Nothofagus ? truncata*	Tree	NZT 03
4	*Prumnopitys spicatus*	Tree	NZT 04
5	*Nothofagus Solandri var. solandri*	Tree	NZT 05
6	*Aristolia fruticosa*	Tree	NZT 06
7	*Carpodetus serratus*	Tree	NZT 07
8	*Dacrydium cupressium*	Tree	NZT 08
9	*Podocarpus totara*	Tree	NZT 09
10	*Cyathodes juniperdta*	Tree	NZT 10
11	*Nothofagus fusca*	Tree	NZT 11
12	*Galtheria antipoda*	Tree	NZT 12
13	*Nothofagus menziesii*	Tree	NZT 13
14	*Nothofagus solandri var. cliffortioides*	Tree	NZT 14
15	*Brachyglottis repanda*	Tree	NZT 15
16	*Knightia excelsa*	Tree	NZT 16
17	*Pseudopanax crassifolius*	Tree	NZT 17
18	*Hebe stricta*	Shrub	NZS 01
19	*Griselinia lucida*	Shrub	NZS 02
20	*Coprosma tenuifolia*	Shrub	NZS 03
21	*Coprosma sp. (hybrid of australis)*	Shrub	NZS 04
22	*Coriaria arborea*	Shrub	NZS 05
23	*Coprosma australis*	Shrub	NZS 06
24	*Coprosma robusta*	Shrub	NZS 07
25	*Melicope simplex*	Shrub	NZS 08
26	*Coprosma rotundifolia*	Shrub	NZS 09
27	*Pittosporum divaricatum*	Shrub	NZS 10
28	*Pseudopanax simplex*	Shrub	NZS 11
29	*Pennantia corymbosa*	Shrub	NZS 12
30	*Olearia sp.*	Shrub	NZS 13
31	*Coprosma rigida*	Shrub	NZS 14
32	*Olearia cheesemanii*	Shrub	NZS 15
33	*Coprosma cheesemanii*	Shrub	NZS 16
34	*Grammitis billardierei*	Fern	NZF 01
35	*Histiopteris incisa*	Fern	NZF 02

36	*Microsorium diversifolium*	Fern	NZF 03
37	*Blechnum chambersii*	Fern	NZF 04
38	*Blechnum colensoi*	Fern	NZF 05
39	*Pellaea falcata*	Fern	NZF 06
40	*Polystichum richardii*	Fern	NZF 07
41	*Blechnum kiokio*	Fern	NZF 08
42	*Blechnum green bay kiokio*	Fern	NZF 09
43	*Pteridium esculentum*	Fern	NZF 10
44	*Asplenium flaccidum*	Fern	NZF 11
45	*Grammitis sp.*	Fern	NZF 12
46	*Cyathea dealbata*	Fern	NZF 13
47	*Blechnum banksii*	Fern	NZF 14
48	*Pteris cretica*	Fern	NZF 15
49	*Hymenophyllum multifidum*	Fern	NZF 16
50	*Pallaea rotundifolia*	Fern	NZF 17
51	*Lastreopsis glabella*	Fern	NZF 18
52	*Hyptis pectinata*	Herb	NZH 01
53	*Ranunculus sp.*	Herb	NZH 02
54	*Phormium tenax*	Herb	NZH 03
55	*Herb 1*	Herb	NZH 04
56	*Herb 2*	Herb	NZH 05
57	*Herb 3*	Herb	NZH 06
58	*Rubus parvis*	Lianne	NZL 01
59	*Clematis sp.*	Lianne	NZL 02
60	*Parsonia capularis*	Lianne	NZL 03
61	*Clematis paniculata*	Lianne	NZL 04
62	*Lianne 1*	Lianne	NZL 05
63	*Mulinbeckia australis*	Lianne	NZL 06
64	*Poa trivialis*	Grass	NZG 01
65	*Stipa variabilis*	Grass	NZG 02
66	*Triticale spp. (hybrid)*	Grass	NZG 03
67	*Dactylis glomerata*	Grass	NZC 04
68	*Earina mucronata*	Orchid	NZO 01
69	*Orchid 1*	Orchid	NZO 02
70	*Pterostylis sp.*	Orchid	NZO 03
71	*Orchid 2*	Orchid	NZO 04

Herbarium specimens from the Lake Rotokura vegetation survey are to be stored at the Massey University Herbarium. Listed above are the authors New Zealand survey reference numbers.

Appendix 8
Lake Rotokura Beech Forest
Tree Species Abundance by Vegetation Survey Quadrat

Item	Botanical Name	Total DBH (cm)													
	Survey Quadrat Number	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1	*Cyathodes fasciulata*	24	1	1	1	1	1		1	88	1	1	1	1	1
2	*Pseudopanax colensoi*	1	1	33.5	1		1	1						1	1
3	*Nothofagus ? truncata*			1579	1344	2812	1680	3911	8903	2730	2044	1032	145	204	1
4	*Prumnopitys spicatus*	1	64	547	166	9	382	1	380	1	707	125	172	62	505
5	*Nothofagus Solandri var. solandri*	1									1				
6	*Aristolia fruticosa*		1	18.5	1	1	1	1		1			1		
7	*Carpodetus serratus*		594			1	32	34	34		1		17	17	1
8	*Dacrydium cupressium*	1	516	349	1					515	324	310	266		470
9	*Podocarpus totara*	47								23	92	19	249	348	274
10	*Cyathodes juniperata*	1									1	1	1	1	
11	*Nothofagus fusca*			1						1		30	388		300
12	*Galtheria antipoda*			1						1					
13	*Nothofagus menziesii*	110	74	412	124	1	581	227	910	741	858	319	70	244	258
14	*Nothofagus solandri var. cliffortioides*	2514	1141	1442	1238						397	10636	1880	3149	2163
15	*Brachyglottis repanda*												1		
16	*Knightia excelsa*			1	16			25	25	24	78				
17	*Pseudopanax crassifolius*	1	38.5	9.5		1	1			1	1	1	1	1	

The above table lists (by quadrat) the presence and relative abundance of the main forest tree species that were identified during the Lake Rotokura vegetation survey. A blank cell in the above table indicates the absence of a given species from the quadrat indicated by that column of the table. The value one represents presence only. All values greater than one are the sum total breast height measurements (cm) of the girth of a given species of tree in that survey quadrat.

Appendix 9

Fossil Pollen Count Data

Number of Lycopodium per Tablet: 13911 ± 308

Lycopodium Batch Number: 710961

Tephra data is interpolated (see section 6.2.8.2, Chapter 6).

The Lake Rotokura Count Data

Depth (mm)	*N. Fusca*	*N. Menzi.*	*Dac. cup.*	*Podo. totara.*	*Lycop. counts.*	Tephra (mm) interp.	Sample Volume	Tabs. Added
0.0	244	38	33	16	81	2.4	1 cm^3	2
100	213	31	11	11	79	6.6	1 cm^3	2
200	204	42	32	18	52	6.4	1 cm^3	2
300	193	35	29	31	45	4.3	1 cm^3	2
400	177	37	25	18	119	4.4	1 cm^3	2
500	201	57	25	17	45	2.7	1 cm^3	2
600	218	34	25	27	54	4.0	1 cm^3	2
700	229	29	19	19	36	1.0	1 cm^3	2
800	264	25	24	22	31	7.1	1 cm^3	2
900	216	21	31	12	40	2.6	1 cm^3	2
1000	235	25	17	8	21	6.7	1 cm^3	2
1100	231	39	28	16	40	1.8	1 cm^3	2
1200	209	27	31	24	46	3.1	1 cm^3	2
1300	227	34	35	10	28	1.1	1 cm^3	2
1400	246	29	16	14	33	5.1	1 cm^3	2
1500	199	39	39	25	66	3.0	1 cm^3	2
1600	244	28	24	18	47	1.2	1 cm^3	2
1700	238	42	28	19	45	2.3	1 cm^3	2
1800	205	53	45	29	47	3.5	1 cm^3	2
1900	237	33	31	11	30	9.2	1 cm^3	2
2000	235	47	41	26	78	7.4	1 cm^3	2
2100	231	22	27	22	28	5.0	1 cm^3	2
2200	265	18	22	15	42	5.2	1 cm^3	2
2300	250	29	13	17	74	3.7	1 cm^3	2
2400	244	33	37	17	44	2.5	1 cm^3	2
2500	242	33	30	35	32	3.4	1 cm^3	2
2600	196	68	27	40	30	4.5	1 cm^3	2
2700	197	53	38	27	55	2.5	1 cm^3	2
2800	211	62	30	19	28	1.8	1 cm^3	2
2900	299	54	38	27	16	8.3	1 cm^3	2
3000	199	75	52	42	27	1.8	1 cm^3	2
3100	203	54	53	33	12	2.0	1 cm^3	2

3200	215	61	42	38	27	7.2	1 cm^3	2
3300	235	43	35	32	16	1.7	1 cm^3	2
3400	209	34	34	24	16	6.9	1 cm^3	2
3500	224	34	26	22	16	1.0	1 cm^3	2
3600	211	38	30	30	17	1.3	1 cm^3	2
3700	173	61	41	51	27	1.0	1 cm^3	2
3800	186	53	40	36	19	2.1	1 cm^3	2
3900	144	36	21	30	15	0.0	1 cm^3	2
4000	242	39	33	19	41	1.4	1 cm^3	2
4100	206	45	41	31	16	0.0	1 cm^3	2
4200	196	56	52	37	14	0.0	1 cm^3	2
4300	166	155	1	49	12	0.0	1 cm^3	2
4400	175	48	44	37	18	0.0	1 cm^3	2
4500	197	35	44	58	14	0.0	1 cm^3	2
4600	170	39	52	45	18	0.0	1 cm^3	2
4700	215	36	44	43	20	0.0	1 cm^3	2
4800	199	44	44	37	22	0.0	1 cm^3	2
4900	211	29	48	35	17	0.0	1 cm^3	2
5000	159	30	19	24	32	1.3	1 cm^3	2
5100	173	38	14	38	32	2.5	1 cm^3	2
5200	141	29	24	29	28	4.3	1 cm^3	2
5300	160	27	23	37	23	3.6	1 cm^3	2
5400	135	18	18	55	36	4.5	1 cm^3	2
5500	161	30	18	21	17	1.7	1 cm^3	2
5600	179	31	33	30	29	2.3	1 cm^3	2
5700	170	22	27	43	14	0.0	1 cm^3	2
5800	163	17	15	34	3	0.0	1 cm^3	2
5900	140	39	28	34	7	0.0	1 cm^3	2

Appendix 10

Text Reference

Chapters five and six.

Description

The following Matlab script files are designed to solve the three classes of continuous time model formulations used in this project (tested in Chapters five and six of this thesis). The command file (zdu.m) calls the MatLab optimisation subroutine *leastsq.* The mfile named lsfun.m calls the differential equation solver named ode45 on the equations being optimised (contained in the mfile named odefn.m).

The mfile named sim.m calls a *for loop* routine for running simulations of a model formulation (contained in the mfile named ode45.m). The *for loop* routine permits a model formulation to be tested over a range of parameter values at any one time.

The following mfiles also contain the scripting that is necessary for using the CGTM formulations with a time delay and secondary forcing function. Unnecessary script is commented out using a % sign.

Command Window

```
>>                                      % (>>) command window prompt
>> zdu                                  % calls the mfile zdu.m
>> sim                                  % calls the mfile sim.m
```

Command File (zdu.m)

```
clear all;
global par
global count;
global pc
global sc
%global cc              %to enable succession data

%——————————————————Load Data ——————————————————————————————
load udu.dat;
load charc.dat
count =0;
%data, charc and depth are all contained in the ascii data file udu.dat
        data = [udu(:,3), udu(:,4)]
                %charc = udu(:,2);
                        depth = udu(:,1);
                                t = [0; 555; 1860 ];          %depth
                                        p = [0; 165; 670 ];   %CAL. age (years B.P.)
                                pc =interp1(t, p, depth);
                        pc = -pc
                pc = pc(length(pc):-1:1)                      %invert time vector
        time = pc;
data = data(length(data):-1:1,:)/1000
```

```
charc = charc(length(charc):-1:1,:)/10000
sc = spline(time, charc);
%--------------------------Secondary Forcing Function--------------------------------
load soil.dat                                          % load soil data
succession = soil/1000;
cc = spline(time, succession);                         %spline

%--------------------------------------------Initial Parameters--------------------------------
 PAR=[ 5.3008  8.1598  0.8400 0  -0.00105  0.6850  0  -0.0000105 ];

%--------------------------------Settings for the Optimisation Routine----------------
options(2) = 1e-10
options(14) = 200
option(18) = 0.001
%call the optimisation routine
optimum = leastsq('lsfun', PAR, options, [ ], time, data)
optimum1 = leastsq('lsfun', optimum, options, [ ], time, data)
```

Function mfile (lsfun.m)

```
function tem=lsfun(PAR, t, dat);
        global count;
        global par
                par = PAR ;
count;
        ns = size(dat); n=ns(2);
                nstep=length(t);
                        u = zeros(nstep,n);
                u(1,:) = par(1:n);
        tic
[tm,uo] = ode45('odefn',t(1),t(nstep),u(1,:)',1e-4);
tem = [interp1(tm,uo(:,1),t) interp1(tm,uo(:,2),t) ] - dat ;

%------------------------------------------ Output Data --------------------------------
        count = count+1;
        toc;
        best_abs = max(abs(tem));
        best_so_far = sum(abs(tem));

%------------------------------------------- Output Files ----------------------------
fid = fopen('Uduout', 'a');
        fprintf(fid, 'iteration_timelapse = %10.12f \n', toc);
                fprintf(fid, 'par = %10.12f \n', par);
                        fprintf(fid, 'Abs_Max_error = %10.12f \n', best_so_far);
                fprintf(fid, 'Sum_of_error = %10.12f \n', best_abs);
        fprintf(fid, 'Iteration_Number = %d \n', count);
fprintf(fid, '\n' );
fclose(fid);
```

Function mfile (odefn.m)

```
function udash=odefn(t, u, par)
global sc;
global par;
```

```
%global cc;                             %to enable succession data
%charci = ppval(sc, t - par(7));        %implements time delay
charci = ppval(sc, t);
%successiondat = ppval(cc, t);          %interpolate successiondat
%-------------------------Classical Model Formulations--------------------------------------
%exponential growth model
%udash(1)=par(3)*u(1);
%udash(2)=par(4)*u(2);

%logistic model
%udash(1)=par(3)*u(1)*(par(4)-u(1)/par(4));
%udash(2)=par(5)*u(2)*(par(6)-u(2)/par(6));

%coupled logistic model
%udash(1)=par(3)*u(1)*((par(5)-u(1)-par(4)*u(2))/par(5));
%udash(2)=par(6)*u(2)*((par(8)-u(2)-par(7)*u(1))/par(8));

%-----------------------------------Classical Growth Models + mf(t)---------------------
%exponential +mf(t)
%udash(1)= par(3)*(1 + par(4)*charci)*u(1);
%udash(2)= par(5)*(1 + par(6)*charci)*u(2);

%logistic +mf(t)
%udash(1)= par(3)*(1 + par(4)*charci)*u(1)*(1 - u(1)/par(5));
%udash(2)= par(6)*(1 + par(7)*charci)*u(2)*(1 - u(2)/par(8));

%coupled logistic + mf(t)
%udash(1)= par(3)*(1 + par(4)*charci)*u(1)*(1-u(1)/par(6))-(par(5)*u(2)/par(6));
%udash(2)= par(7)*(1 + par(8)*charci)*u(2)*(1-u(2)/par(10))-(par(9)*u(1)/par(10));

 %---------------------------------CGTM formulations------------------------------------
%exponential CGTM
udash(1)= par(3)+(par(4)*charci)*u(1);
udash(2)= par(5)+(par(6)*charci)*u(2);

%exponential CGTM with secondary forcing function
%udash(1)= par(3)+(par(4)*charci + par(5)*successiondat)*u(1);
%udash(2)= par(6)+(par(7)*charci + par(8)*successiondat)*u(2);

%logistic CGTM
%udash(1)= par(3)+(par(4)*charci)*u(1)*((par(5)-u(1))/par(5));
%udash(2)= par(6)+(par(7)*charci)*u(2)*((par(8)-u(2))/par(8));

%coupled logistic CGTM
%udash(1)= par(3)+(par(4)*charci)*u(1)*(1-(u(1)/par(5)) - (par(6)*u(2)/par(5)));
%udash(2)= par(7)+(par(8)*charci)*u(2)*(1-(u(2)/par(9)) - (par(10)*u(1)/par(9)));
```

Function mfile (sim.m)

```
% for loop simulation routine
clear all;
global par
global count;
```

```
global pc
global sc
%global cc   %to implement the secondary forcing function

%------------------------------------------ Load Data ----------------------------------------
load ket.dat;
load charc.dat
count =0;
        data = [ket(:,3), ket(:,4)]
                %charc = ket(:,2);
                        depth = ket(:,1);
                                t = [0;  555; 1800 ];                    % depth
                                p = [0;  562; 1045 ];                    %CAL. age
                        pc =interp1(t, p, depth);                        %Time  Interpolation
                pc = -pc
        pc = pc(length(pc):-1:1)
time = pc;
data = data(length(data):-1:1,:)/1000
charc = charc(length(charc):-1:1,:)/1000
sc = spline(time, charc);
plot(time, data)

%--------------------------------Secondary Forcing Function--------------------------------
load soil.dat                                   % load soil data
succession = soil/1000;
cc = spline(time, succession);                  %spline

%-------------------------------------------for loop command--------------------------------
for w = 0.1:0.1:0.9,
par= [ 1.25  7.154  w  -170.768  0.18711  -111.92];
lsfun(par, time, data);
error = ans;
%plot(time, data, time, data+error);    %plot  command
%axis([-600, 0, 0, 10]);
end;
```

References

For further information concerning the use of Matlab's for loop subroutine and differential equation solvers refer to the Matlab Users Guide for Sun Workstations (Matlab 1991). For further information on the use of the least squares optimisation routine refer to Grace (1992).

Appendix 11

Text Reference

Chapters five and six.

Description

The following Matlab script files are designed to solve the two classes of discrete time model formulations tested in Chapters five and six of this thesis. The command file (zdu.m) calls the MatLab optimisation subroutine *leastsq*. The mfile named lsfun.m calls a *for loop* equation solver on the equations being optimised and contained in the same mfile. The mfile named sim.m calls a *for loop* routine for running simulations of a model formulation that is contained in the mfile named lsfun.m. In the following files, unnecessary script is commented out.

Command Window

```
>>                              % (>>) command window prompt
>> zdu                          % calls the mfile zdu.m
>> sim                          % calls the mfile sim.m
```

Command File (zdu.m)

```
clear all;
global par;
global charci;
global count;

%----------------------------------------Load files----------------------------------------
load ket.dat;
depth = ket(:,1);
count =0;
        t = [0; 555; 1800 ];                              %stratigraphic depth
                p = [0; 562; 1045 ];                      %CAL. age
                        pc =interp1(t, p, depth);         %Time Interpolation
                                pc = -pc;
                        pc = pc(length(pc):-1:1);
                time = pc;
        data = [ket(:,3) ket(:,4)]/100000;
data = data(length(data):-1:1,:);
load charci.dat;
charci = charci(length(charci):-1:1,:)/1000;
ntimes = length(time);
discretetimes = time(1) : (time(ntimes)-time(1))/(ntimes-1) : time(ntimes);
charci = interp1( time, charci, discretetimes ) ;

%----------------------------------------Initial Parameters----------------------------------------
par = [0.019905612359, 0.038963172352, -0.011927214112, -0.010585291951];

%----------------------------------------Optimisation Options----------------------------------------
options(2) = 1e-8
options(14) = 300
```

```
option(18) = 0.0001

%---------------------------Call the Optimisation Routine--------------------------------
optimum = leastsq('lsfun', par, options, [], time, data)
optimum1 = leastsq('lsfun', optimum, options, [], time, data)
optimum2 = leastsq('lsfun', optimum1, options, [], time, data)
optimum3 = leastsq('lsfun', optimum2, options, [], time, data)
optimum4 = leastsq('lsfun', optimum3, options, [], time, data)

%-------------------------Plot Final Results--------------------------------------
lsfun(optimum4, time, data);
error=ans;
plot(time, data, time, data+error)
```

Function mfile (lsfun.m)

```
function tem=lsfun(par, t, dat);
        global count
        global charci;
count;
        ns = size(dat);
                n=ns(2);
                        nstep=length(t);
                                u = zeros(nstep,n);
                        %u(1,:) = par(1:n);
                %charcdelay = charci - par(7);                    %time delay
        %ones(nstep,1);
tic
u(1,1) = par(1);
u(1,2) = par(2);
for i = 1:nstep-1

%----------------------------------Discrete CGTM Formulations------------------------
%discrete exponential CGTM
%u(i+1,1) = par(3) + (par(4)*charci(i))*u(i,1);
%u(i+1,2) = par(5) + (par(6)*charci(i))*u(i,2);

%discrete logistic CGTM
%u(i+1,1) = u(i,1) + par(3) + u(i,1)*(par(4)-(u(i,1)/par(4)));
%u(i+1,2) = u(i,2) + par(5) + u(i,2)*(par(6)-(u(i,2)/par(6)));

%------------------------------Discrete Classical Growth Models--------------------
%discrete exponential
u(i+1,1) = u(i,1) + par(3)* u(i,1);
u(i+1,2) = u(i,2) + par(4)* u(i,2);

%discrete logistic
%u(i+1,1) = u(i,1) + par(3)* u(i,1)*(par(4) - u(i,1)/par(4));
%u(i+1,2) = u(i,2) + par(5)* u(i,2)*(par(6) - u(i,2)/par(6));

%discrete coupled logistic
u(i+1,1) = u(i,1) + par(3)*u(i,1)*((par(5)-u(i,1)-par(4)*u(i,2))/par(5));
u(i+1,2) = u(i,2) + par(6)*u(i,2)*((par(8)-u(i,2)-par(7)*u(i,1))/par(8));
```

```
end
tem=u-dat;
count =count + 1;
toc;
        best_abs = max(abs(tem));
        best_so_far = sum(abs(tem));

%-----------------------------------------Output File--------------------------------------------
fid = fopen('Uduout', 'a');
        fprintf(fid, 'iteration_timelapse = %10.12f \n', toc);
                fprintf(fid, 'par = %10.12f \n', par);
                        fprintf(fid, 'Abs_Max_error = %10.12f \n', best_so_far);
                                fprintf(fid, 'Sum_of_error = %10.12f \n', best_abs);
                        fprintf(fid, 'Iteration_Number = %d \n', count);
                fprintf(fid, '\n' );
        fclose(fid);
```

Function mfile (sim.m)

```
%clear all;
global par;
global charci;
global count;
load ket.dat;
depth = ket(:,1);
count =0;
        t = [0;  555; 1800 ];                           %stratigraphic depth
                p = [0; 562; 1045 ];                    %CAL. age
                        pc =interp1(t, p, depth);       %Time  Interpolation
                                pc = -pc;
                        pc = pc(length(pc):-1:1);
                time = pc;
        data = [ket(:,3) ket(:,4)]/100000;
data = data(length(data):-1:1,:);
load charci.dat;
charci = charci(length(charci):-1:1,:)/1000;
ntimes = length(time);
discretetimes = time(1) : (time(ntimes)-time(1))/(ntimes-1) : time(ntimes);
charci = interp1( time, charci, discretetimes ) ;

%-------------------------------Call the Simulation For Loop----------------------------------
for w = 0.1:0.1:0.9,
par= [0.007 0.0470 0.014  w  0.02 -0.9000]
lsfun(par, time, data)
error = ans
plot(time, data, time, data+error)
%axis([-600, 0, 0, 10])
hold on
end;
```

References

Matlab Users Guide for Sun Workstations (Matlab 1991) and optimisation toolbox manual (Grace 1992).

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Errata

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