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2657

A Dynamical Systems Framework for Modelling Plant Community Organisation

By

Anthony Owen Cole

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at Massey University

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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.

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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.
$(3) \Leftrightarrow \left\lvert \frac{df}{dN}\Big\vert_{\overline{N}} \right\rvert \prec 1$	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).
$M_{(n,m)} = \sum_{i=0}^{n}\sum_{j=0}^{n} P_{cmij}\binom{n}{i} b^i(1-b)^{n-i}\binom{n}{j} d^{n-j}(1-d)^j$	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.
$N_{t+1} = N_t + r_1N_t\frac{(K_1 - N_t - \alpha M_t)}{K_1}$ $M_{t+1} = M_t + r_2M_t\frac{(K_2 - M_t - \beta N_t)}{K_2}$	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.