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ISLAND BIOGEOGRAPHY:

A STUDY OF HABITAT ISLANDS OF MOUNTAIN BEECH FOREST

(Nothofagus solandri, var. cliffortioides)

IN TONGARIRO NATIONAL PARK

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A thesis presented in partial  
fulfilment of the requirement for the degree  
of Master of Science in Zoology at  
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## Abstract.

MacArthur and Wilson's (1967) model for island biogeography is examined, particularly with regard to the proposed species-area relationship. The first chapter includes a consideration of the theoretical background.

Nine habitat islands and corresponding mainland regions of similar area were selected. All the sites possess a canopy of mountain beech trees, (Nothofagus solandri var. cliffortioides), and are located in the western segment of Tongariro National Park. Plants and litter animals were sampled from within these sites to determine the possible relationship between species and area.

Forest plant species numbers as well as proportions, assessed using a modification of the Point-centred quarter method, revealed a statistically significant species-area relationship.

Litter Crustacea collected in one thousandth of a square metre core samples, and removed from cores by wet extraction, show a gradation in habitat preference, hence a species-area relationship cannot be determined.

A wide range of animals collected in pitfall traps appear also not to produce a significant species-area relationship. Possible reasons for the obscurity of such a relationship are considered.

An overall assessment of the information gathered in the light of island biogeographic theory is presented, and some more recent thought on the causal explanations for the species-area relationship are discussed.

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## CHAPTER 1 : INTRODUCTION

### Section 1      The Background Theory;                   A Literature Review.

Analysis of island biota, and the theories and implications which have followed, is a facet of science which is some twenty years old.

In 1962 Preston defined the relationship between the number of species on an island and the area of that island. He claimed that the number of species of a given taxon found on an island is related to the area of the island to the power of  $z$ , multiplied by a further factor dependant upon the taxon, the biogeographic region, and the population density.  $z$  relates to the relative abundance of a species, and although it varies among taxa it can be approximated by assuming that species abundance forms a lognormal distribution.

The species-area relationship Preston presented is more simply described by Diamond (1971), who also draws the relationship of distance between island and mainland into his description: "The number of species on islands increases with island area but decreases with island distance from the mainland. .... Thus small remote islands should reach equilibrium at a lower number of species than large islands near the mainland. Similar principles may apply to island-like mainland situations,....."

In 1967 R. H. MacArthur and E. O. Wilson published their classic work The Theory of Island Biogeography, and it is appropriate briefly to examine the major concepts, especially those relating to the present study. An island is defined as a "visibly discrete object that can be labelled with a name and its resident population identified thereby." The biological processes of dispersal, invasion, competition, adaptation and extinction are all important in island ecology.

In considering the species-area relationship, MacArthur and Wilson reiterate the relationship described by Preston, adding that the number of species on a given island is approximately related to the area of that island according to the formula  $S = CA^2$ , where  $S$  is the number of species in the island fauna,  $A$  is the area of the island, and  $C$  is a factor dependant upon population density, as well as the innate diversity of a given taxon.

MacArthur and Wilson further suggest that if a graph is plotted of the absolute number of individuals per species (abscissa) against the number of species falling into each abundance class (ordinate), the curve described will be skewed strongly away from the lower values; that is there are more rare species than common species. A description is also given of a theoretical curve for the number of individuals, (as opposed to species), found in the various species abundance classes. An equation for the total number of organisms ( $J$ ) in a taxon on a given island is presented; the value of  $J$  increases linearly with the area of the island, (provided climate and topography are uniform). i.e.  $J = pA$ , where

$p$  is the density of individual organisms, and  
 $A$  is the area of the island.

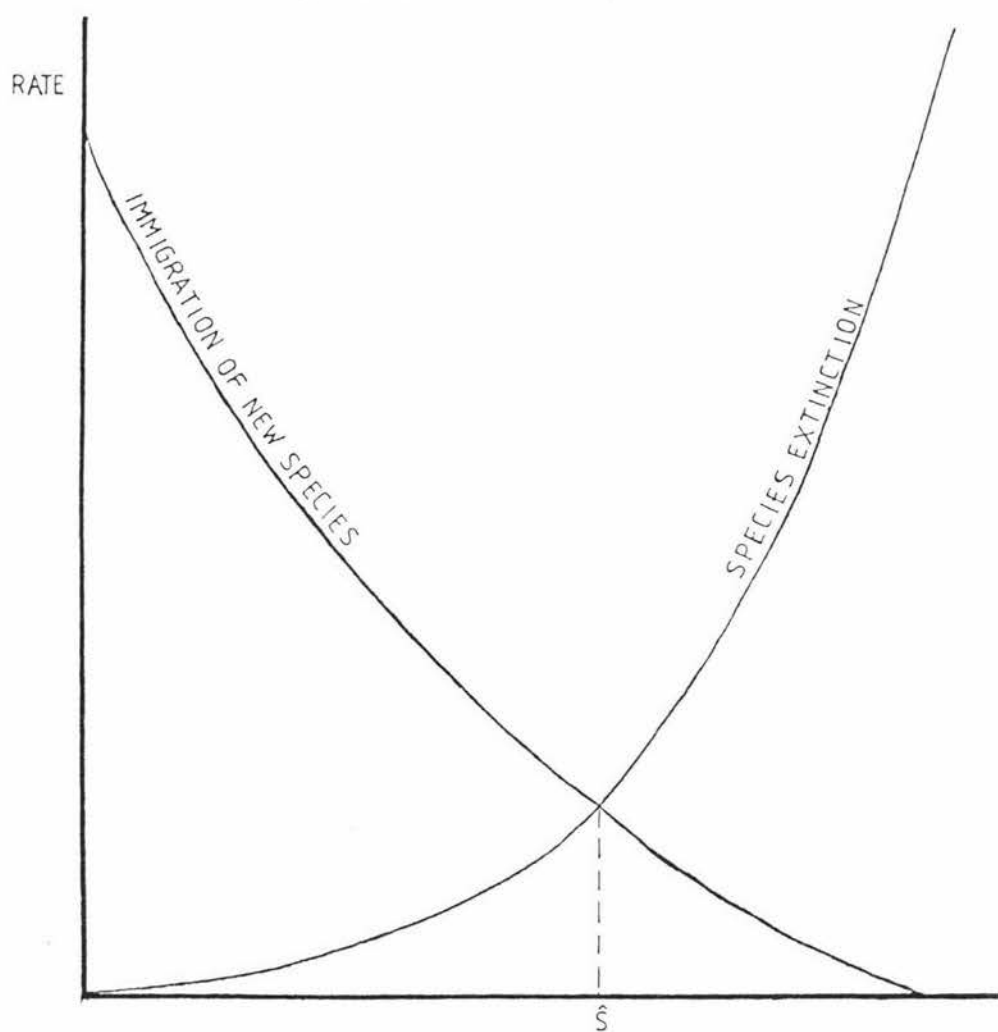
Mainland sampling areas are also taken into consideration. A mainland sampling area of similar size to an island will carry a greater number of species, because more species persist close at hand, hence there is a higher immigration rate of transient species into a small mainland area. As such an area is enlarged it becomes a more complete sample. As islands become larger there is an increasing heterogeneity of habitats, allowing more species to coexist.

The concept of species equilibrium is described; in many cases immigration is balanced by extinction, and hence a state of equilibrium exists. Rates of immigration and extinction vary with the number of species present (see figure 1, between pp 3 and 4)

Immigration describes a falling curve because as more new species become established, fewer immigrants will belong to new species. More rapidly dispersing species will become established first, causing a swift initial drop in immigration rate, whilst the later arrival of slow colonists will drop the overall rate by an even diminishing degree.

The extinction curve rises since the more species there are present, the more likely it is that any given one will become extinct, due to a smaller than average population size acting through both ecological and genetical accident. It is exponential because the combination of diminishing population size, and the increasing probability of interference

FIGURE 1. EQUILIBRIUM MODEL OF THE BIOTA OF A SINGLE ISLAND. (After MacArthur and Wilson, 1967.)



NUMBER OF SPECIES PRESENT

$\hat{S}$  is the equilibrium species number.

amongst species will have an accelerating detrimental effect.

As alterations in the curves are made the equilibrium point will be shifted; if immigration is reduced or extinction increased, the equilibrium will occur at a point with fewer species. This implies that if the area of the island is reduced, or its isolation increased, it will equilibrate with fewer species.

Several further points are made: the non-equilibrium hypothesis states that distant islands have taken longer to colonize because of low immigration rates. Chaining or clustering of islands affects immigration rates, significantly increasing them. This phenomenon also reduces the slope of the species-area curve. In the case of some small islands, turnover rate in the biota may be so rapid that the extinction rate is not area dependant. In these islands, an increase in area does not result in an increase in species number.

Since the publication of The Theory of Island Biogeography numerous authors have attempted to demonstrate the validity of the concepts involved, and some have sought to apply them to conservation.

Wilson and Simberloff (1969), and Simberloff and Wilson (1969) have written on the recolonization of defaunated islands, placing emphasis on a dynamic equilibrium between immigration and extinction. If over saturation occurs, equilibrium rapidly re-establishes. The authors attempted to successfully illustrate this.

Both Brown (1971) and Willis (1974)

have considered individual aspects of a community in relation to island biogeography. Brown worked with small mammals on montane islands, which he concluded were relict populations, not representing equilibria between rates of colonization and extinction. Willis studied birds on the Barro Colorado islands, and suggests that small size and isolation of islands plays an important role in extinctions.

Diamond has become increasingly interested in the conservation aspects of biogeography. As a consequence of differences in seasonality and hence in bird vagility, in 1971 he concluded that a tropical island would have an avifaunal immigration rate half that of a temperate island of identical age and isolation. He later (1972) states that relaxation time is dependant upon rate of immigration and extinction. Land bridge islands of decreasing area approach oceanic islands in species composition and diversity, due to increased extinction rate and relaxation times. Here he begins to apply the theories to a national park situation, suggesting that a large continuous area is more useful as a park than a number of small broken reserves. In 1975 he defined suitable shapes for reserves, circular being considered the optimal since it reduces dispersal distances. A small reserve has higher extinction rates.

Terburgh (1974) offers prescriptions for different groups of animals. He claims that animals on the highest trophic level, migratory species, colonial nesting species, widespread species with poor dispersal and colonization abilities, and endemics of oceanic

islands are extinction prone. Each of these groups should be treated according to its own requirements: "Large reserves are needed to preserve natural vegetation formations, animals at the top of the trophic pyramid, and widespread species with sedentary habits or poor colonizing ability. Endemics or rare habitat types can frequently be protected with a relatively small investment of land." He thus proposes that extinction in some groups is not solely dependant upon the dynamics of an equilibrium, but is also related to the pressures of human population.

May (1975) too has written relating biogeography to the design of wildlife preserves. He highlights the problems of park management in terms of idealized reserve shape and size; "many scattered parks have over a single park the advantage that all eggs are not in one basket." and "dynamic features of natural populations can create management problems when even a very large area is enclosed."

Simberloff and Abele (1976) counter Diamond's (1972) suggestion of a large continuous area being most effective as a reserve. They state that this concept can be "incorrect under a variety of biologically feasible conditions." They made an island into an archipelago by digging one metre wide channels through it, in an attempt to invalidate Diamond's theory. They find that a cluster of small areas has more species than a single large area in this isolated experiment.

Diamond, (1976), Terburgh, (1976) and Whitcomb et al (1976) have all responded critically to the work of Simberloff and Abele. Diamond (1976) states that some habitats only exist on

large islands; for example species with seasonally or spatially patchy food supplies must integrate resources over large areas. Species which exist at low densities, when they become extinct on an island rarely recolonize, and have a low probability of occurrence at equilibrium, except on large islands. Some areas of locally high resource production may be important hedges against extinction, but may constitute only a fraction of breeding territories. The criticisms of Terburgh (1976) and Whitcombe et al (1976) differ in detail, but are essentially similar.

These considerations provide a background to the project. The basic relationships between size, distance from the mainland, and species diversity and proportions are of especial interest, because island biogeography is now seen to have strong conservational overtones. The topic selected attempts to evaluate the basic hypothesis and the practical implications that are involved in island biogeography, by examining aspects of some habitat islands in a continuous land mass.

## Section 2      Study Aims.

### 2.    1.    General.

The objective of this study is to examine nine habitat islands of indigenous New Zealand mountain beech forest (Nothofagus solandri, var. cliffortioides) in Tongariro National Park, in terms of island biogeographic theory. The habitat islands range in size from ten square metres to 9,225 square metres, (from one to in excess of 600 trees), and are to be compared with what can be considered mainland regions of mountain beech forest of equivalent area.

### 2.    2.    Basic questions arising from island biogeographic theory.

- A Is the species-area relationship described by MacArthur and Wilson (1967) applicable to these habitat islands of indigenous forest?
- B How do the numbers of species present in an island relate to the distance of the island from the mainland?
- C If the actual number of species present does not differ between islands, are there significant differences in the proportions of the species present, or in the actual numbers representing a particular species?
- D If differences between sites are not apparent, what are the possible reasons?

### 2.    3.    Parameters to be determined.

- A Whether the influence of altitude, history and habitat variation are negligible (Gilpin and Diamond, 1976).

- B The area of the islands.
- C The distance of each island from its respective mainland.
- D The length of time over which the island has been separated from its mainland.
- E The numbers of species, and proportions of flora and fauna within the islands and mainlands.
- F The species of plants and animals found in the 'sea' around the sites, and their degree of overlap with site species.

### Section 3      The Study Area.

#### 3.    1.    Description of the region.

The region in which the sites are situated consists of mountain beech forest (Nothofagus solandri var. cliffortioides), interspersed with areas of subalpine scrub and tussock grassland. Tongariro National Park is an area of high rainfall and montane climate; the normal annual rainfall is 2914mm. (1941 - 1970) and the normal annual temperature is 7.2°C (1941 - 1970), (New Zealand Meteorological Service). The soil comprises recent volcanic ash whilst the underlying rock is sedimentary with some volcanic intrusions.

#### 3.    2.    Selection of sites.

Sites for the study were selected on the basis of their similarity of structure. In all sites the forest canopy is primarily composed of mountain beech (Nothofagus solandri var. cliffortioides), with mountain celery pine (Phyllocladus alpinus) being the secondary

canopy tree. Occasionally Hall's totara (Podocarpus hallii) and mountain cedar (Libocedrus bidwillii) occur in the canopy. The subcanopy includes broad leaf (Griselinia littoralis), three finger (Neopanax simplex), mountain five finger (Neopanax colensoi) and a number of Coprosma species, (C. foetidissima, C. tenuifolia, C. pseudocuneata, C. microcarpa, C. colensoi, C. australis, and several hybrids), as well as pepperwood (Pseudowintera colorata), Myrsine divaricata, Pokaka (Elaeocarpus hookerianus) and Putaputaweta (Carpodetus serratus). The understory consists of several groups: the small shrubs Cyathodes juniperina, C. fasciculata, Gaultheria antipoda, G. paniculata; the ferns, of which the filmy ferns, (Hymenophyllum spp.), are most numerous, and the herbs, bush flax, (Astelia nervosa), being prominent. Numerous juveniles of canopy and subcanopy trees and shrubs are also found on the forest floor. Plates I to VI (between pp. 10 and 11) illustrate some forest plants and indicate the density of subcanopy growth.

The position of sites is also thought to be important; all sites are situated in the western region of the Park, with an altitudinal range between 890 and 1220 metres. None of the sites are riparian; sites located beside streams may have an abnormally high immigration rate, and are hence avoided.

### 3. 3. Access to and distribution of sites.

Access to the sites is either directly from the road (State Highways 47 and 48), or from Park tracks; the Ridge track, the Mangatipopo track and the Taranaki Falls track. Sites shown in figure 2, (between pp. 11 and 12 ),

Plate I

Dense mainland forest subcanopy and undergrowth;  
Coprosma spp. at rear, Neopanax colensoi (juvenile)  
and Astelia nervosa in the foreground.

Plate II

Dense forest growth; Myrsine divaricata in the  
background, Astelia nervosa in the foreground.



Plate III

Plants on the forest floor; Coprosma spp. and  
Astelia nervosa.

Plate IV

Small shrubs on the floor of Site 8 island;  
Neopanax simplex (juvenile), Gaultheria spp. and  
Hebe venustula.

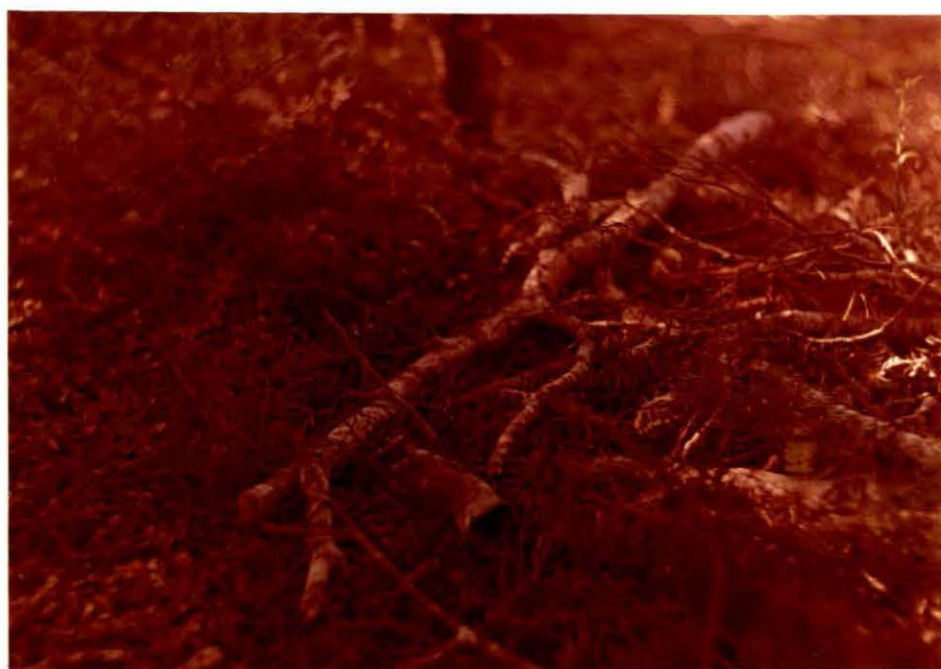


Plate V

Sparse juvenile plants on the floor of Site 9 island; Neobanax simplex, Griselinia littoralis and Coprosma spp.

Plate VI

Litter on the floor of Site 8 island; in contrast to the mainland forest, few plants are visible.



are numbered in size sequence, from the largest to the smallest. The sites numbered on the map (figure 2) are illustrated in plates VII to XIV (between pp. 11 and 12 ).

### 3. 4. Fulfilling the parameters.

- A The effect of altitudinal difference between the highest and lowest sites is assumed to be negligible, since the same forest type exists at both altitudes.

The sites are all on the western side of Mt. Ruapehu, and are hence subject to similar climatic regimes.

Information on the history of the sites can be obtained by examining the age structure of the mountain beech stands; if the age structure of canopies are similar, it can be presumed that the sites have undergone similar histories.

Wardle (1980) states that the diameter growth rate of mountain beech under standard conditions is fairly constant throughout life. Growth rate does however vary greatly between sites; the average ring width being 0.8 mm., but trees at high altitude or on poor soils may have a ring width of only 0.2 mm.

Since growth rate is evidently constant, it is possible to estimate the age structure of the nine sites and their respective mainlands using girth measurements; these measurements were converted to diameter for statistical purposes. Measurements were taken at breast height where possible, they were otherwise taken below the lowest branch. Twenty or all trees (whichever was the least) in each site were measured

FIGURE 2. MAP SHOWING LOCATION OF SITES IN TONGARIRO NATIONAL PARK.

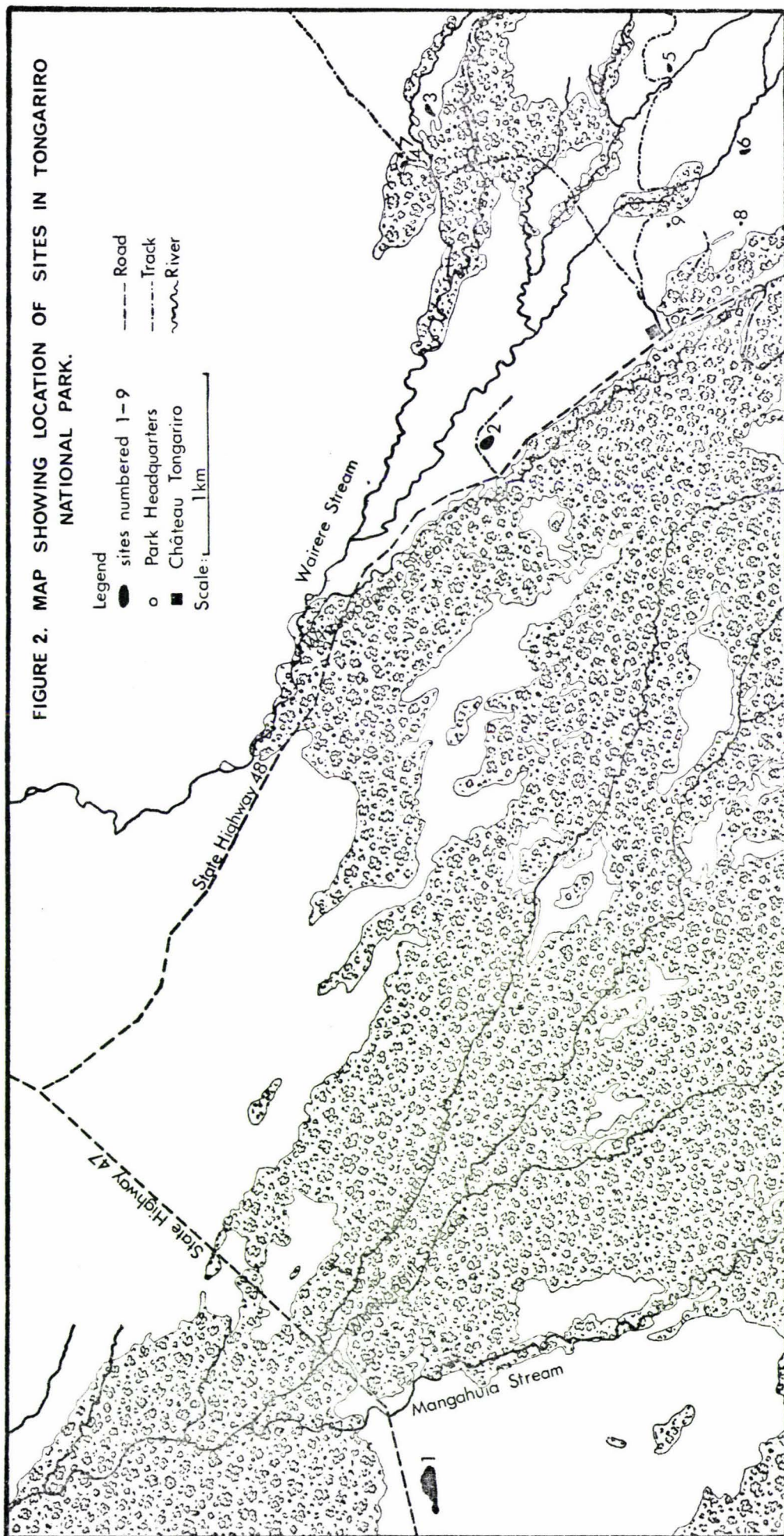


Plate VII

Site 1 island.

Plate VIII

Site 2 island.



Plate IX

Site 3 island.

Plate X

Site 4 island at left, Site 7 island at right.



Plate XI  
Site 5 island.

Plate XII  
Site 6 island



Plate XIII

Left hand arrow; Site 6 island.

Central arrow; Site 9 island.

Right hand arrow; Site 8 island.

Plate XIV

Site 8 island.



as part of the sampling procedure described in Chapter 2, Section 1. 2.

Graphs representing the diameter structure of island-mainland pairs are shown in figure 3, (between pp. 12 and 13 ), the x axis denotes ranking sequence. The graphs alone suggest that the age structure for island-mainland pairs resemble each other, and it can be seen that all the sites follow a similar trend.

Mountain beech forest structure seldom forms a truly normal distribution (Wardle, 1980), thus to verify the similarity in structure of island-mainland pairs the data are tested statistically using the non-parametric Kolmogorov-Smirnov two sample test for small samples (Siegel, 1956). Five centimetre diameter classes (Skipworth, 1981) are used in order to perform this test. In the two tailed test used, the greatest absolute difference between numbers of trees falling into each class determines the level of significance. In all of the seven pairs tested, (two of the pairs cannot be tested because there is only a single tree in each site, and mainland trees of similar size were selected for comparison), there is no significant difference; there is a less than five per cent chance of the two sets of data coming from populations with different distributions. (Appendix I, p. 81.)

- B The area of the islands was determined using aerial photographs of the region.

FIGURE 3. DIAMETER STRUCTURE OF TREES IN ISLAND  
MAINLAND PAIRS.

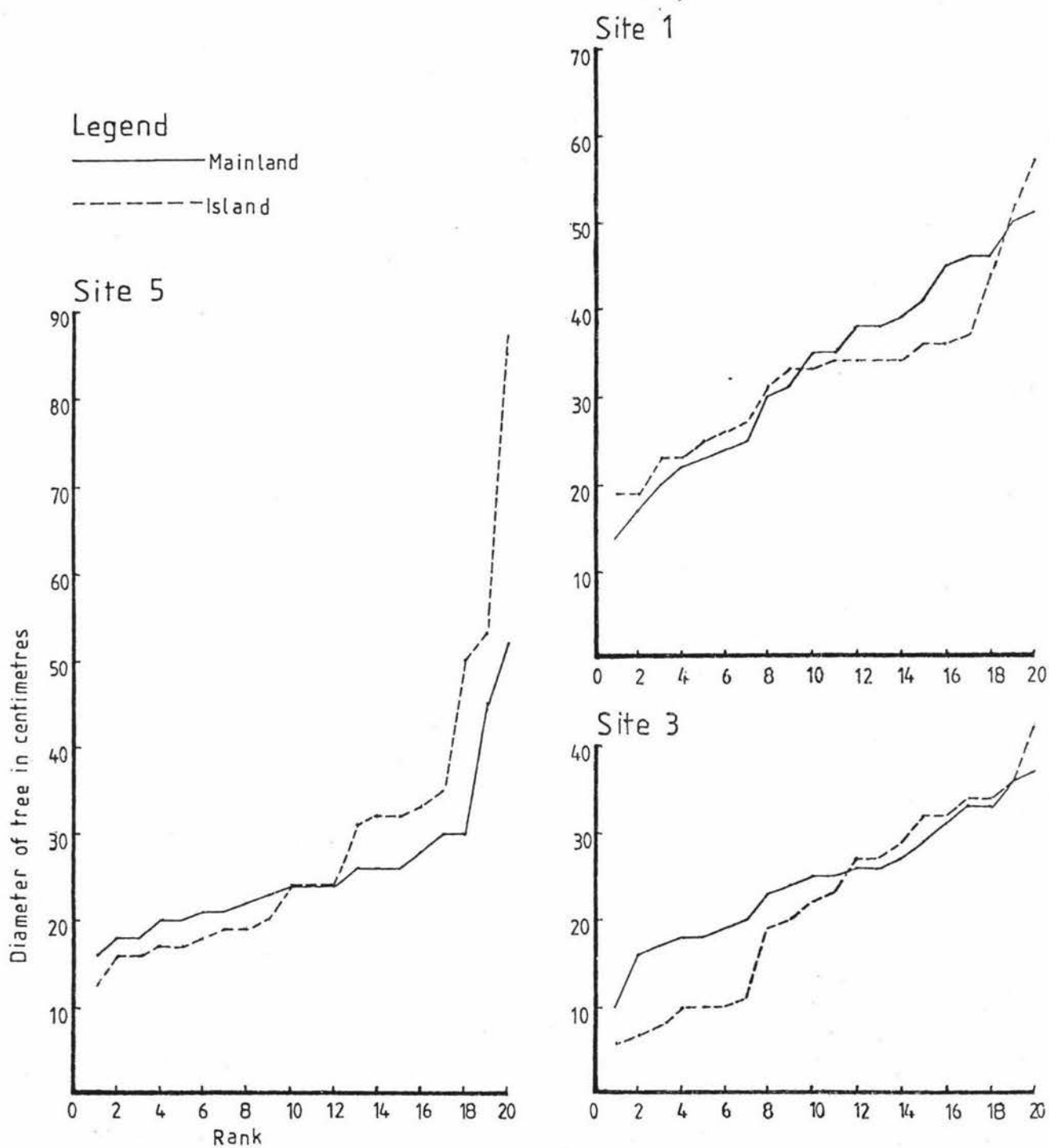
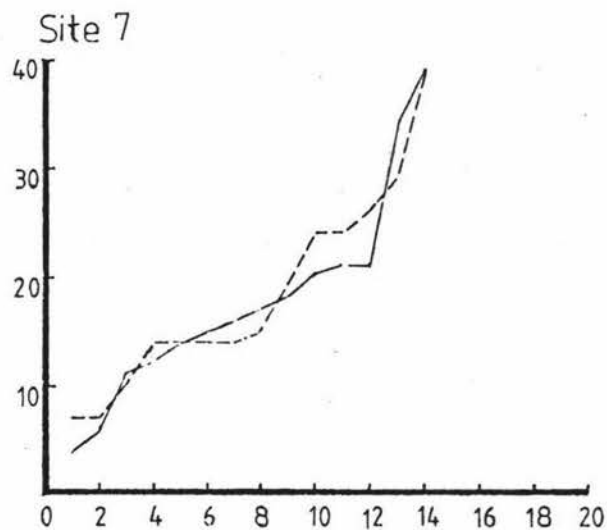
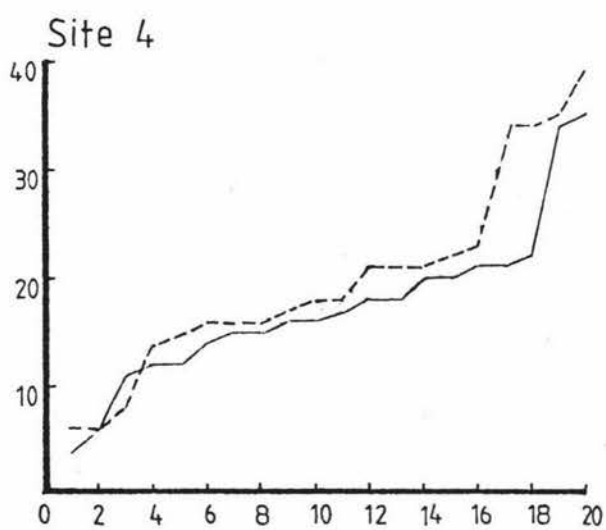
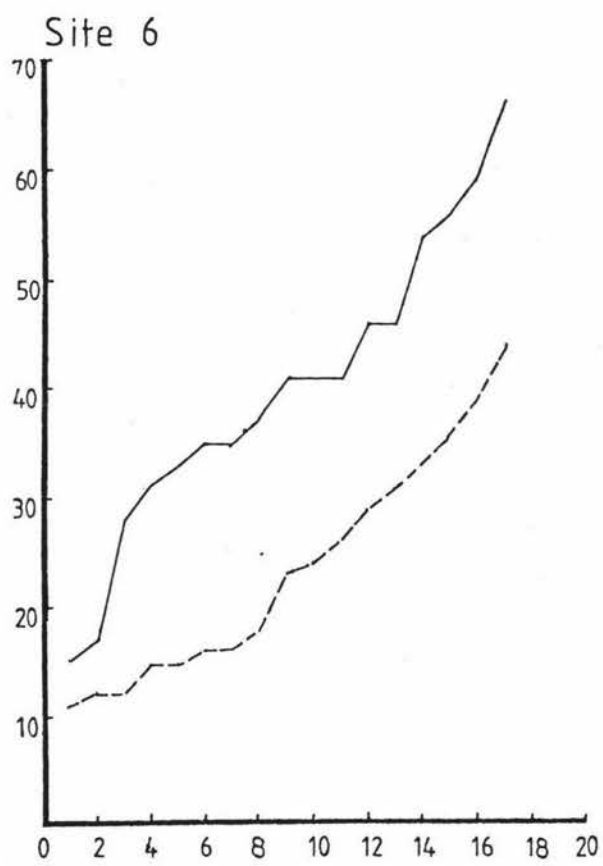
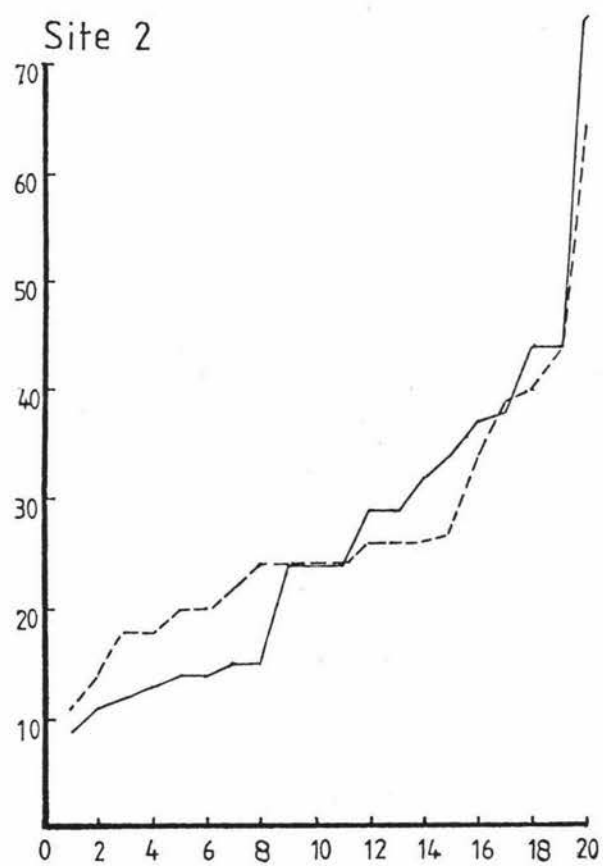


FIGURE 3. (Continued.)



A dissecting microscope was set up in conjunction with a camera lucida, and because the outline of each island was not absolutely clear it was traced ten times. The linear scale of the drawings relative to the aerial photograph was noted. The islands were then cut out and weighed, as were ten pieces of paper four centimetres square in area. The mean weight for each island was calculated and divided by the mean weight of one centimetre square, giving a mean value for the area of each of the paper islands in square centimetres. These values were then divided by the square of the linear scale relating the paper cut out to the aerial photograph, to obtain the actual area occupied by the island on the photograph. A known distance on the ground was compared with the same distance on the aerial photograph, (measured using a calibrated eyepiece micrometer), to determine the linear scale of the photograph. The square of the linear scale thus obtained was then multiplied by the areas of the islands on the aerial photograph in order to ascertain the actual ground areas. The area of the islands and their area relative to the smallest island are presented in Table I (between pp. 13 and 14 ).

- C The distance of each island from its mainland was obtained by using a calibrated eyepiece micrometer to make measurements from the aerial photograph. The measurements were then multiplied by the linear scale relating distance on the photograph to distance on the ground,

TABLE I Site area and distance relationships.

Site	Area of island (metres <sup>2</sup> )	Area relative to area of smallest island (expressed in multiples of the area of the smallest island)	Distance of island from its corresponding mainland (metres)	Island-mainland distance relative to shortest island-mainland distance (expressed in multiples of the shortest island-mainland distance)	Number of trees in the island
1	9,225	951	175	12	In excess of 600
2	2,049	211	137	9	597
3	519	54	45	3	75
4	268	28	15	1	61
5	195	20	296	20	33
6	110	11	215	14	17
7	51	5	42	3	14
8	33	3	60	4	1
9	10	1	27	2	1

(calculated for 3.4.B.). The distance of each island from its mainland and the distance relative to the smallest island-mainland distance are also presented in Table I (between pp. 13 and 14 ). The number of trees in each site is included in this table.

- D The length of time of separation of the island from its mainland is difficult to determine, although in several cases some inferences can be made: both site 8 and site 6 may well have been separated from their mainlands by the occurrence of slips. Site 9 (a single tree) probably represents the establishment of a seedling in isolation, hence the age of this site is directly related to the age of the tree. This, assuming bands of 0.8 mm., is approximately 195 years.
- E comprises the main body of the work and will be considered in the following chapters. F is examined in association with E.

## CHAPTER 2 : PLANTS

## Section 1      Methods

## 1.    1.    Plant Reference Collection.

A consideration of the flora involves identification of forest plants; a reference collection was constructed in order to ensure that this was carried out correctly and consistently. The text used in checking the identity was Flora of New Zealand, Volume I, H. H. Allan (1961), and Volume II, L. B. Moore and E. Edgar (1970), in conjunction with Atkinson's species list (1971). Some of the Coprosma spp. at Ruapehu do not conform to species described in the literature, Dr. Atkinson (in litt.), has examined and provided information on these, but here they are simply identified as Coprosma A and B.

## 1.    2.    Plant sampling procedure.

The selection of any particular sampling method involves a consideration of its field efficiency; i.e., the time required in the field to obtain an adequate level of accuracy. Lindsey, Barton and Mikes (1958) have compared a number of forest sampling methods with reference to these constraints. All the methods discussed sample for density as well as proportions of species, however, density was not required for this study, and the technique was appropriately adjusted. The procedure adopted is a modification of the

Point-centred quarter sampling method, (Cottam, Curtis and Hale 1953, and Cottam and Curtis 1956).

The adapted sampling method obtains not only the actual number of species occurring in island-mainland pairs, but also the proportion of each species present. The plants are divided into four groups for examination; trees, shrubs, ferns and herbs. Trees are catagorized as being greater than two metres in height, whilst shrubs, including juveniles, are classed as being less than two metres in height. The shrubs correspond to Raunkiaer's (1934, 1937) Nanophanerophytes and to Atkinson's (1975) lower understory. Herbs are taken to be all the remaining plants on the forest floor, with the exception of ferns, mosses, lichens and liverworts, but including such plants as orchids, bush flax (Astelia nervosa), Celmesia and Ourisia spp.

With plant catagories established, a compass direction was selected using random number tables, and a random distance paced in that direction in order to obtain a point from which to work. The identity of the ten nearest individuals were recorded for each of the groups defined above. Girth of the nearest beech tree was also noted, and the data used in construction of the age structure graphs in Chapter 1, Section 3. 4., figure 3 (between pp. 12 and 13). For each site (island and mainland), twenty such samples were taken, providing a total sample of 200 plants from each group per site.

## Section 2. Results.

### 2. 1. The exclusion of non-forest plants.

Habitat islands are not as discrete as those isolated by water, in that they are surrounded by substrate not substantially different from their own. This similarity allows some species of plants and animals to inhabit areas both inside and outside the forest. Elimination of outside plant species encroaching upon the forest is important for comparison of absolute numbers of plant species in island-mainland pairs. Such intruders do not represent true forest species, and hence exaggerate the numbers found, particularly in small islands.

Sampling outside the sites was used to determine the non-forest plants, in conjunction with observations substantiated by habitat descriptions in the literature (Cokayne, 1908, Dobbie and Crookes 1951, Stevenson 1954, Allan 1961, Poole and Adams 1963, Salmon 1968, Moore and Edgar 1970, Mark and Adams 1973).

A chi-squared test comparing all inside and outside plant species found in both islands and mainlands shows that there are fewer outside plant species in mainlands than would be expected; O/E ratio 0.42, and more outside plant species in islands than would be expected; O/E ratio 1.43. (Table II, between pp. 17 and 18 )

Table II. Chi-squared analysis of inside and outside plant species found in both islands and mainlands.

		Mainland	Island
Observed:	Total inside plant species	59	56
	Total outside plant species	6	29
Expected:	Total inside plant species	49.8	65.1
	Total outside plant species	15.1	19.8
O/E Ratio:	Inside plant species	1.17	0.86
	Outside plant species	0.42	1.43

Chi-squared = 11.399,  $P < 0.05$

These figures suggest that outside plant species will represent a disruptive factor in subsequent tests and hence should be discarded.

Tests carried out on individual sites for separate plant groups indicate that there are insufficient plant species in the majority of cases to obtain viable chi-squared values.

## 2. 2. Presence or absence of all species in all sites.

Appendix II (p. 85 ) lists the presence or absence of species in each group for all sites, (including the non-forest species discussed in Section 2. 1.). Island-mainland pairs are arranged in sequence of decreasing size.

In general, large islands and mainlands have a greater number of species than do small islands and their mainlands. For example, in the shrub category, site 1, the largest site, has a total of 19 forest shrubs in both island and mainland, whereas site 9, the smallest site contains a total of 9 forest shrubs in the island and 13 in the mainland.

With decreasing island size, the difference between the number of forest species in the island and its corresponding mainland increases; islands having fewer species than mainlands of equivalent size e.g. In large areas, such as site 1 similar numbers of tree species are found in both island and mainland, the island supports 12 species, and the mainland 13. In smaller sites islands support far fewer tree species than their corresponding mainlands; in site 8 there is only 1 tree species in the island, but 8 in the mainland, and similarly in site 9 there are only 2 tree species in the

island, but 6 in the mainland.

A trend towards a larger number of non-forest plants in smaller islands is also indicated; site 1 island contains only 3 non-forest shrub species, whereas site 8 island contains 13 non-forest shrub species.

2. 3. Chi-squared analysis of the total number of plant species in each site.

The first two columns of Table III (between pp. 19 and 20 ) show the total number of species of plant for all groups combined, with sites in order of decreasing area. The remaining two columns convey the observed/expected values for a chi-squared test carried out on the figures in the first two columns. This table is compiled using data from Appendix II. Although the test is not significant at the 5% level, the data suggest that O/E ratios are lower for small islands (e.g., site 9 island has an O/E ratio of only 0.79); that is, small islands carry fewer plant species than would normally be expected. The difference between island-mainland ratios for large islands is small in most cases, (e.g., sites 1, 2, 4 and 5), indicating their high level of similarity. Small island-mainland pairs have larger differences between their ratios, (e.g., site 9), demonstrating their reduced level of similarity.

Chi-squared tests were also performed on plant species numbers for all the separate groups, however, only the shrub category produced a viable result, but the table was not significant at the 5% level. The remaining groups; trees, ferns and herbs gave expected values of which 20% were less than 5, rendering the test invalid. However, all groups followed the same general



trend demonstrated by the total species number,

Figure 4, (between pp. 20 and 21 ), illustrates the total species number for each site, both island and mainland, plotted against the log of the area of that site.

Points on the species versus log area graph are assumed to be linear on the basis of the work of Whitehead and Jones (1968), Gilpin and Diamond (1976), and Greig-Smith (1964) states: "The approximately linear form of the species-log-area curve over the ranges of area normally met with does..... mean that the slope of the line can usefully be used as an empirical measure of the relative species diversity of communities".

The lines on the graph are based on linear regression analysis, Model I; least squares, (Sokal and Rohlf, 1973). The F ratios for these lines are significant for the island at the 1% level, (F ratio = 152.13), and for the mainland at the 5% level, (F ratio = 9.74).

The mainland line slopes more steeply than that for the island, indicating that increasing species number in sites is related to the increasing area of sites, and also that the species number for a mainland of a given area would be expected to be greater than that for an island of similar area. The species-area relationship (MacArthur and Wilson, 1967) holds for the plants in this particular study.

Figure 5, (between pp. 20 and 21 ), plots the total species number for each site both island and mainland, against the distance between mainland and island. These data were tested using linear regression analysis, however

FIGURE 4. SPECIES-LOG AREA GRAPH FOR PLANTS.

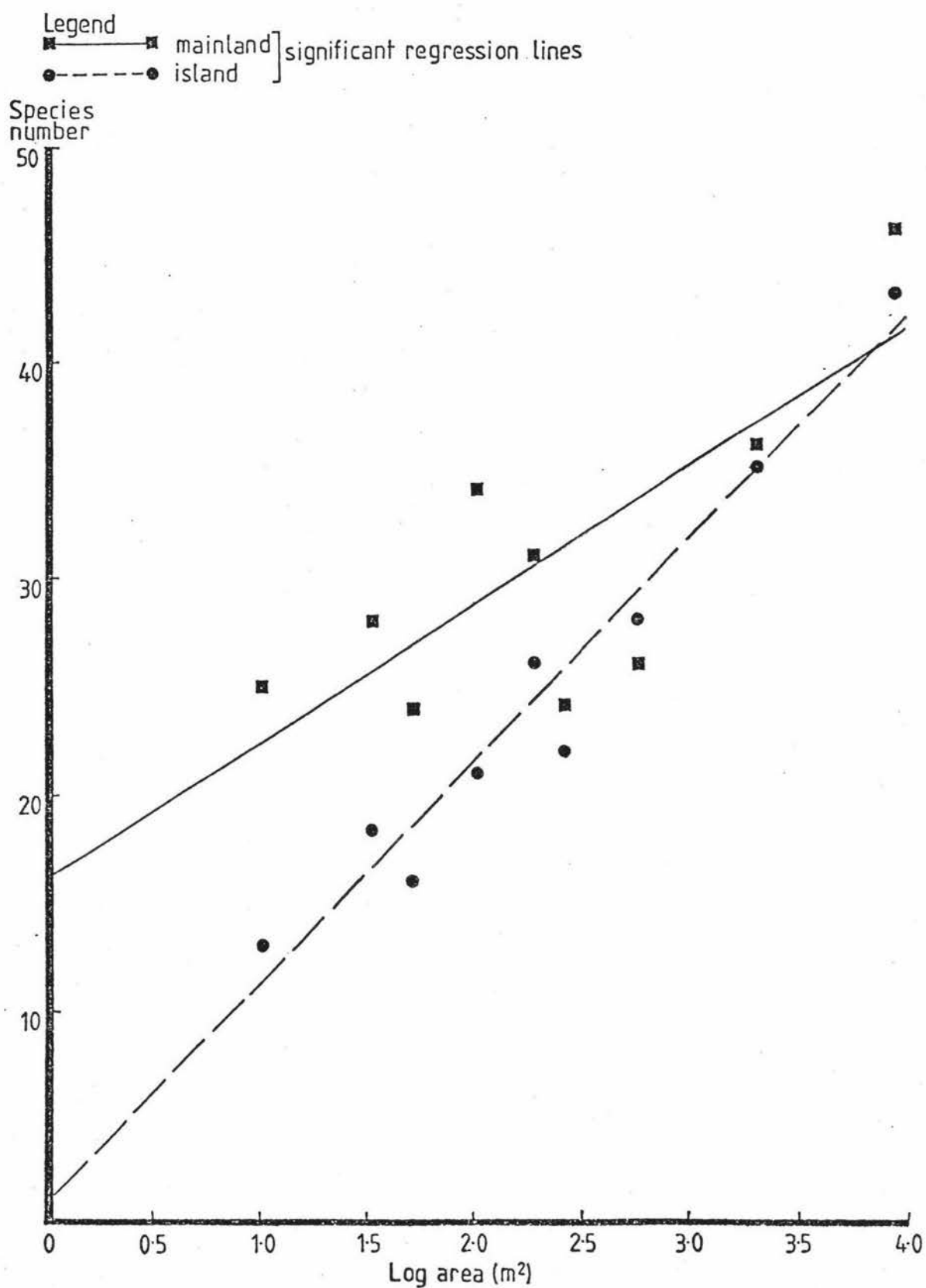
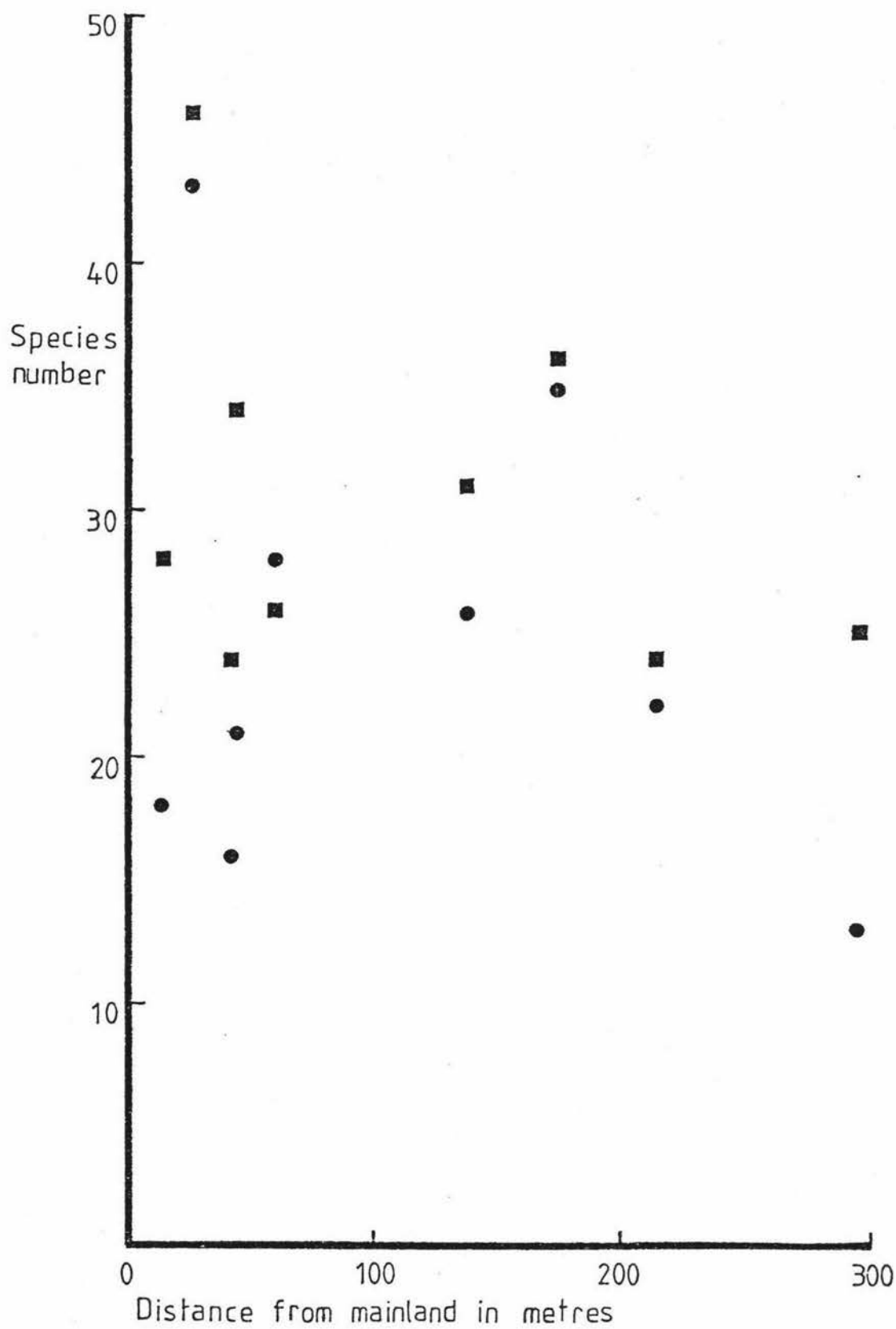


FIGURE 5. SPECIES-DISTANCE GRAPH FOR PLANTS.



Legend. (No significant regression lines.)

■ mainland

● island

Neither mainland nor island produced significant lines at the 5% level. The area-distance relationship (MacArthur and Wilson, 1967) does not therefore appear to apply to plant species in this study.

2. 4. Jaccard's coefficient of community.

Table IV, (between pp. 21 and 22 ), presents Jaccard's coefficient of community for each group in all sites, as well as for the total number of species in all sites. Data from Appendix II is used in the construction of table IV.

Jaccard's (1912) coefficient of community is an index of similarity between two communities which is independent of the number of species within that community. The formula as defined by Jaccard (1912) is:

$$\text{coefficient of community} = \frac{\text{Number of species common to the two districts} \times 100}{\text{Total number of species in the two districts}}$$

Greig-Smith, (1964), states that comparisons of plant species lists are valuable to the plant geographer, e.g., in comparing the floras of different islands, and recommends Jaccard's coefficient of community as one such comparative measure. Application of this formula to both flora and fauna is also advocated by Koch, (1957), and Muller-Dombois and Ellenburg (1974).

The percentage of community similarity between islands and their corresponding mainlands derived using Jaccard's index, shows a general decline in smaller islands, i.e., smaller islands have less plants in common with their mainlands than do larger islands, conforming with island biogeographic theory. For example,

Table IV Jaccard's coefficient of community  
for plant species.

	Plant Group:				
	Trees	Shrubs	Ferns	Herbs	Total plant species
Site 1	63%	73%	71%	67%	75%
Site 2	58%	55%	57%	33%	51%
Site 3	60%	73%	100%	100%	85%
Site 4	50%	80%	67%	67%	76%
Site 5	25%	63%	50%	67%	59%
Site 6	18%	67%	40%	67%	65%
Site 7	40%	67%	67%	50%	65%
Site 8	13%	69%	100%	25%	64%
Site 9	33%	69%	25%	33%	52%

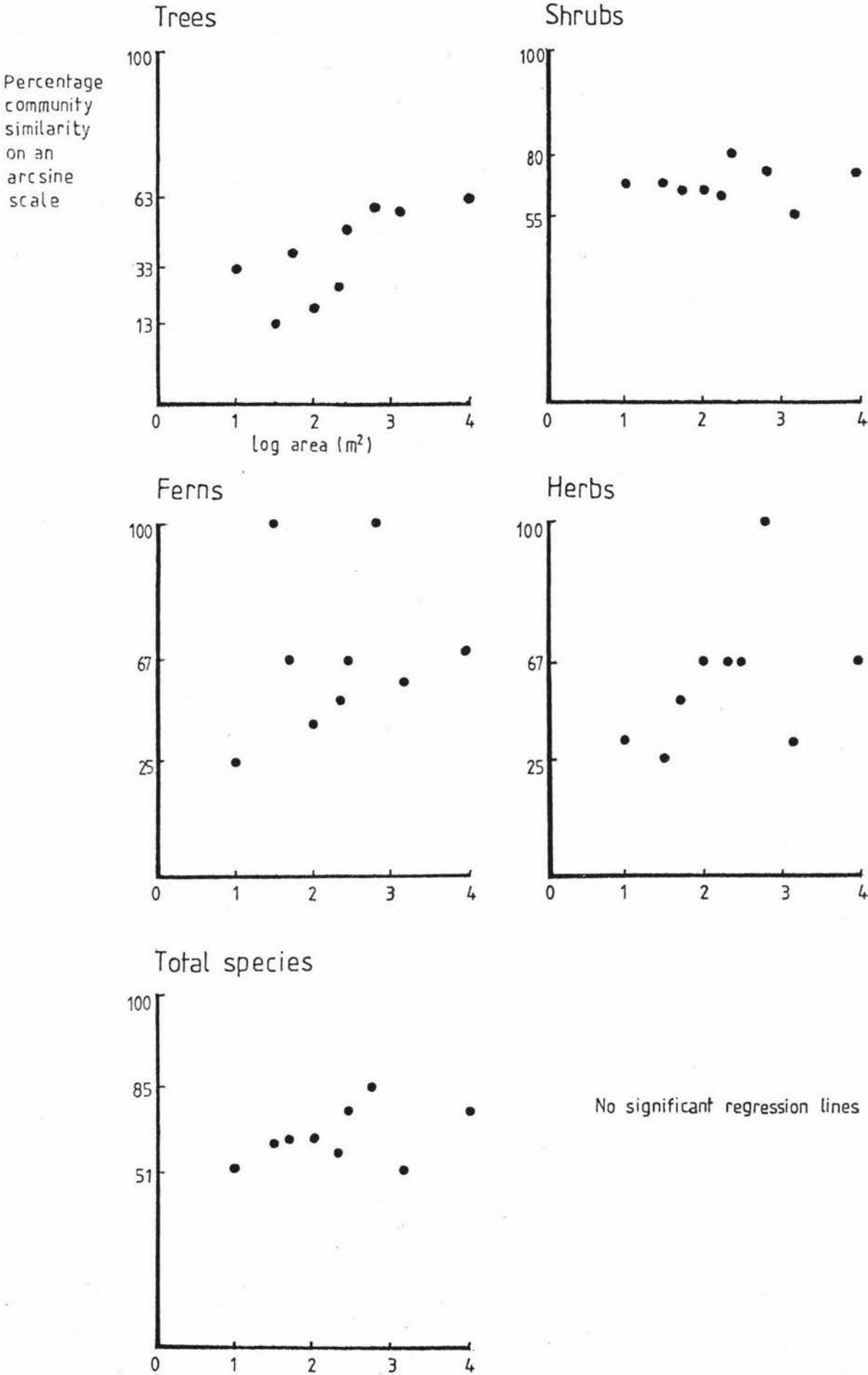
in site 1, the largest site, 63% of the tree species are found in both island and mainland, whereas in site 9 the smallest site, only 33% of tree species are common to both island and mainland.

A relationship between island size and Jaccard's coefficient of community is much more apparent than one between distance from the mainland and the coefficient in this particular study. Although none of the graphs in figure 6 (between pp. 22 and 23 ) can be shown to be significant using linear regression analysis, there is an apparent tendency towards increasing community similarity with increased area.

## 2. 5. Proportions of all species in all sites

Appendix III, (p. 95 ), shows the proportions, (expressed as a percentage), of all species in all sites (including non-forest species), listed in order of decreasing site area. The species proportions are obtained by the method described in Section 1. 2. (p. 15 ), and are reduced to a percentage value from a total sample of 200 plants in each group for every site. The tables indicate that, in a number of cases, the proportion of plants belonging to a single species differs considerably between an island and its corresponding mainland. e.g., Nothofagus solandri, mountain beech, comprises 96.5% of the tree species in site 6 island, but only 11.0% of the tree species in site 6 mainland. Also, Neopanax simplex, three finger, constitutes only 1.0% of the shrub species in site 5 island, but 20.5% of the shrub species in site 5 mainland. Numerous other such examples may be found in the tables.

FIGURE 6. JACCARD'S COEFFICIENT OF COMMUNITY FOR PLANTS.  
(Plotted against log area.)



Frequently, the smaller the island, the greater the proportion of non-forest plants found within it. For example, site 1 island contains no non-forest shrubs, but smaller sites such as site 6 island and site 7 island have respectively 26.5% and 52.0% non-forest shrubs as part of their composition.

## 2. 6. Spearman-Rank correlation test.

Table V, (between pp. 23 and 24 ), presents the Spearman-Rank correlation values (Seigel, 1956), for proportions of species in all groups at all sites. Information from Appendix III is used to produce table V.

The non-parametric Spearman-Rank correlation coefficient allows comparison of frequencies of plants of the same species in island-mainland pairs. The null hypothesis maintains that the two variables are unrelated.

In the tree category, the tests indicate that even if island-mainland pairs contain similar numbers of species, the proportions of these species in each site are not related, (except in the case of site 2, a large site, which might be expected to be approaching mainland species composition).

The shrubs show a greater degree of relationship between island-mainland pairs in terms of species proportions, although smaller sites exhibit a lesser degree of relationship to their mainlands than do large sites. e.g., large sites 1 island and mainland, and 2 island and mainland are related, (5% and 1% levels of significance respectively), whereas small sites 8 island and mainland, and 9 island and mainland are unrelated. Shrubs appear to possess a greater degree of similarity in species

Table V Speerman-Rank correlation values.

	Trees			Shrubs			Ferns			Herbs		
	$r_s$	N	correl- ation	$r_s$	N	correl- ation	$r_s$	N	correl- ation	$r_s$	N	correl- ation
Site 1	0.330	13	unrelated	0.538	19	related $P < 0.05$	0.084	11	unrelated	-	-	-
Site 2	0.634	14	related $P < 0.05$	0.803	21	related $P < 0.01$	0.097	7	unrelated	0.800	4	unrelated
Site 3	0.391	10	unrelated	0.555	15	related $P < 0.05$	-	-	-	-	-	-
Site 4	0.535	6	unrelated	0.758	15	related $P < 0.01$	-	-	-	-	-	-
Site 5	0.179	12	unrelated	0.288	19	unrelated	0.800	4	unrelated	-	-	-
Site 6	0.018	12	unrelated	0.491	18	related $P < 0.05$	0.475	5	unrelated	-	-	-
Site 7	0.649	6	unrelated	0.558	15	related $P < 0.05$	-	-	-	-	-	-
Site 8	0.426	7	unrelated	0.391	17	unrelated	-	-	-	-	-	-
Site 9	0.131	7	unrelated	0.017	13	unrelated	-	-	-	-	-	-

where  $r_s$  = Speerman-Rank correlation coefficient.  
and N = number of sample pairs.

composition between island and mainland in smaller sites than do trees: it is possible that shrubs have been able to reach a stable equilibrium on medium sized islands, (e.g., in sites 3, 4, 6 and 7 shrub species in islands and corresponding mainlands are related), whereas trees have only been able to do so on the larger islands, (e.g., in site 2, tree species in the island and its corresponding mainland are related).

In most cases, both herbs and ferns had less than four species pairs available for testing, and use of the Spearman-Rank test was not possible. However in all cases tested the island and mainland species proportions were unrelated, this may suggest that the various understory species each require specific conditions for growth, (e.g., a deep litter layer, low light intensity, or a narrowly defined microclimate), although it is difficult to make inferences from a small number of tests. (An attempt was made to use a chi-squared test values to complete the table, however the frequency of zero and very low values was high, and the test had to be abandoned.)

## 2. 7. Ellenburg's frequency coefficient of community similarity

Table VI, (between pp. 24 and 25 ), gives the frequency coefficient of community similarity (Ellenburg, 1956) for each group in all sites. Appendix III contains the information necessary for the reproduction of table VI.

Ellenburg (1956) modified Jaccard's coefficient of community to allow the use of percentage biomass in the formula. The use of percentage frequency in the formula is also

Table VI      Ellenburg's frequency coefficient  
of community similarity for plants.

	Plant Group			
	Trees	Shrubs	Ferns	Herbs
Site 1	82%	93%	78%	98%
Site 2	91%	90%	93%	99%
Site 3	90%	81%	90%	100%
Site 4	92%	98%	100%	100%
Site 5	81%	84%	93%	97%
Site 6	42%	88%	84%	98%
Site 7	96%	69%	61%	0%
Site 8	47%	79%	91%	75%
Site 9	44%	69%	89%	95%

appropriate (Muller-Dombois and Ellenburg, 1974).

Ellenburg's formula can be stated thus:

$$\text{Frequency coefficient of community similarity} = \frac{(M_c \div 2)}{M_a + M_b + (M_c \div 2)} \times 100$$

Where  $M_c$  = the sum of the percentage frequency, (or biomass), of species common to both groups.

$M_a$  = the sum of the percentage frequency, (or biomass), of species restricted to the first stand.

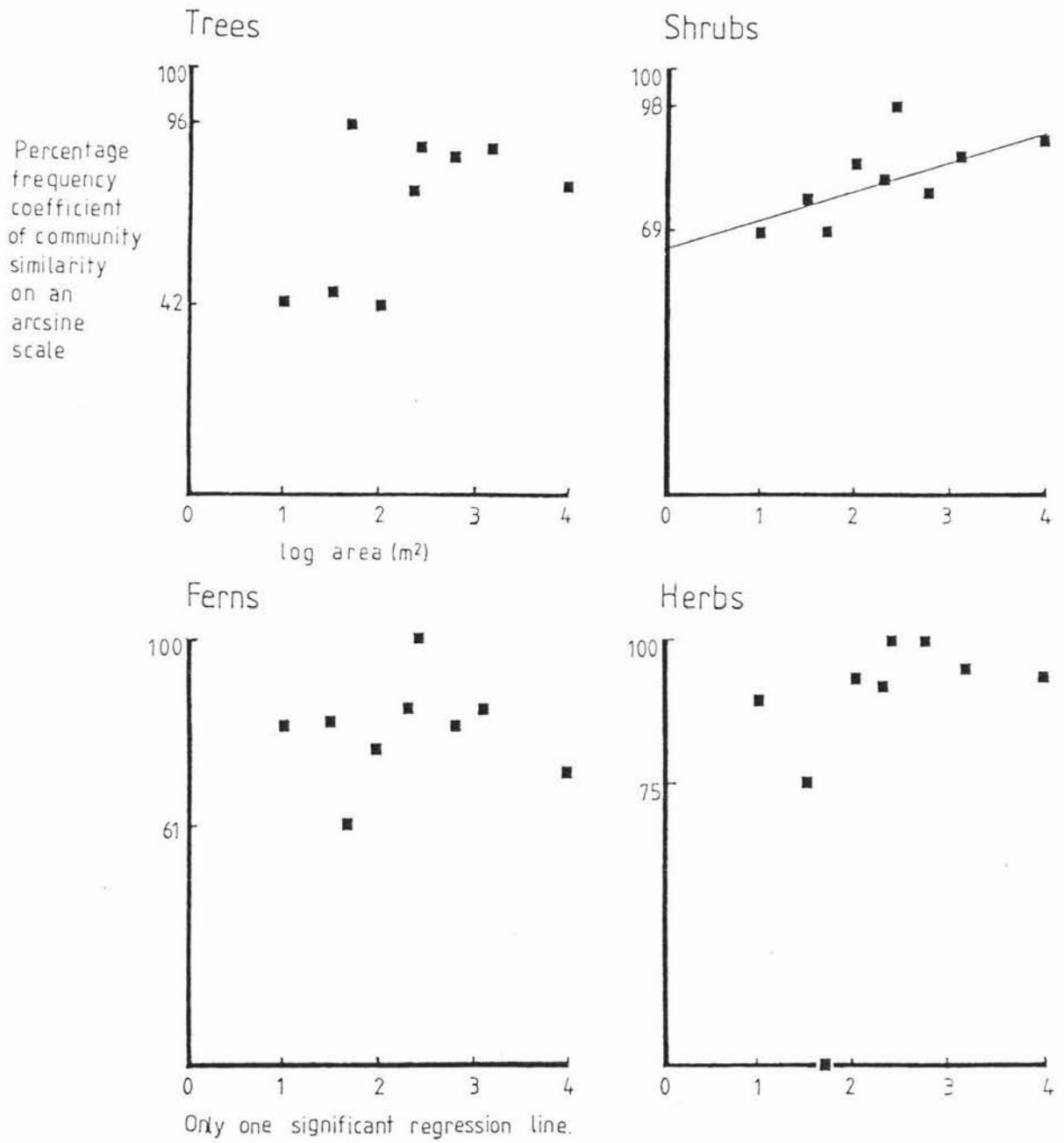
$M_b$  = the sum of the percentage frequency, (or biomass), of species restricted to the second stand.

In the equation, division by two of the sum of the frequency values  $M_c$  allows equal weight to be given to both common and unique species.

Gleason, (1920), applied quantitative values directly to Jaccard's formula, however, this gives double weight to common species relative to unique ones. In an island biogeographic consideration this would be inappropriate, since rare species are relatively important in indicating differences between islands and their mainlands, as well as inter island differences.

Table VI (between pp. 24 and 25 ), and the graphs in figure 7, (between pp. 25 and 26 ), illustrate a general trend towards increasing community similarity on the basis of percentage frequency with increased area. (e.g., Trees in site 1 show an 82% frequency coefficient of community similarity, whereas

FIGURE 7. ELLENBURG'S FREQUENCY COEFFICIENT OF COMMUNITY SIMILARITY FOR PLANTS. (Plotted against log area.)



trees in site 9 show only a 44% frequency coefficient of community similarity. Also shrubs in site 1 show a 93% coefficient of community similarity whereas shrubs in site 9 show only a 69% frequency coefficient of community similarity.) The tendency towards increasing community similarity with increased area concurs with that demonstrated using Jaccard's coefficient of community, which is dependant upon species number alone, (Table IV and figure 6).

The results presented in this chapter will be discussed at length in Chapter 5.

## CHAPTER 3 : LITTER CRUSTACEA.

### Section 1 Methods.

#### 1. 1. Background.

The Crustacean Orders Amphipoda and Isopoda form a large proportion of the leaf mould fauna of New Zealand, (Hurley, 1950). The terrestrial Crustacea considered herein, (Amphipoda, Isopoda, Copepoda and Ostracoda), are primarily located in the circum-Pacific region; Hurley for example describes the terrestrial Amphipoda, all belonging to the Family Talitridae, as being "limited to countries bordering the Indian and Pacific Oceans, and to the Pacific islands."

Attention has been focused on the New Zealand terrestrial Crustacea because of their limited distribution and their importance in the litter fauna. The preference for moist litter displayed by most terrestrial Crustacea suggests that many of these animals are forest species.

Enchytraeidae, Acari, and Nematoda were also present in large numbers in the cores, however their cosmopolitan distribution, (McColl, 1977), as well as the difficulties involved in identification, have precluded them from consideration.

#### 1. 2. Sampling Procedure.

The size of the sample unit, and the

number of units collected must be adequate to provide a reasonable estimate of population density, (standard error not more than 5% of the mean). In selecting a suitably sized sample unit, the dimensions of the animals must be taken into account, as well as the size of the study area, and its vulnerability to destructive sampling. Transport, labour and the availability of laboratory facilities are also of significance, (J. Springett, pers. comm.).

With regard to the factors outlined above, samples of one thousandth of a square metre, ( $10\text{ cm}^2$ ), in surface area were collected using a cylindrical corer.

The total litter horizon was sampled in each case, although the volume of litter differed with variation in the litter depth between sites; hence population densities are conventionally expressed as numbers per unit surface area (J. Springett, pers. comm.)

Microhabitat variation was avoided by sampling at an arbitrary distance of 0.3 metres from the base of a beech tree, at the South-East aspect. Thirty such samples were taken from each site in one sampling session. Sites with fifteen to thirty trees were sampled at 0.3 and 0.6 metres from the base of the tree. Measurements for one such site were recorded in pairwise fashion and tested for any possible relationship between the two data sets. Using the chi-squared test a significant difference was found between cores taken at 0.3 and 0.6 metres from the base of the tree, and it is obvious from the tables that this difference is not a consistent one, suggesting that the two data sets are not related. (Appendix IV p. 100.)

Sites with less than fifteen trees were sampled by defining transects lying South-East/North-West, cores being taken at 0.3 metre intervals along these transects. Transects were a minimum of 1 metre apart, and sufficient were used to obtain thirty samples. As a further precaution against environmental patchiness, an attempt was made to ensure that there was a minimum of slope at the base of trees beneath which samples were taken.

Each site was visited three times to minimize seasonal differences in the results, and where possible, island-mainland pairs were sampled during the same field expedition. A set of thirty cores was taken between each island-mainland pair to establish the degree of similarity between forest and subalpine scrub habitat types.

1. 3. Extraction method, equipment and procedure.

1. 3. 1. Method.

The collected cores were taken to the laboratory and animals removed during the following two days. Cores and extracted animals were stored at 5°C.

A behavioural method of separation was employed; namely the wet funnel extractor. Macfaydyen, (1957), states that where a heated funnel filled with water is used, (Boermann 1917, Overgaard 1948), "The aquatic component of the soil fauna swims out into the water and then sinks as a result of the high temperature", and "this extraction procedure is often highly efficient."

### 1. 3. 2. Equipment.

Multiple funnel apparatus was utilized; the equipment is illustrated in Plate XV (between pp. 30 and 31 ). A diagrammatic representation of an individual unit is shown in Figure 8 (between pp. 30 and 31 ). A maximum of 32 samples can be processed at any one time using this equipment.

### 1. 3. 3. Procedure.

The procedure for setting up the extractor was as follows: initially collecting vials were fitted into a rubber extension at the base of each funnel. Funnels were then placed in the rack and filled to the brim with cold water. Litter core samples were individually transferred to 50 mesh sieves, (aperture size 0.3 mm.), and gently lowered into the water filled funnels. Shade rings were positioned over the funnels and the lights, (25 Watt bulbs), were lowered until they were level with the top of the shade rings. The samples were subjected to an increasing heat and light intensity over a three hour period: the lights were switched on, and the simmerstat set at half for the first 30 minutes, following this the simmerstat was set to full. 120 minutes after the bulbs were lit, they were lowered to just above the soil surface. A further 60 minutes completed the extraction, and the lights were switched off, collecting vials removed, and funnels allowed to drain.

### 1. 4. Examination of samples.

Examination of samples was carried out as soon as possible, but where necessary samples could be stored at 5°C for up to four days without any adverse effect on counting (J. Springett, pers. comm.). Chapman (1961) states that "the

Plate XV

Wet funnel extraction apparatus.

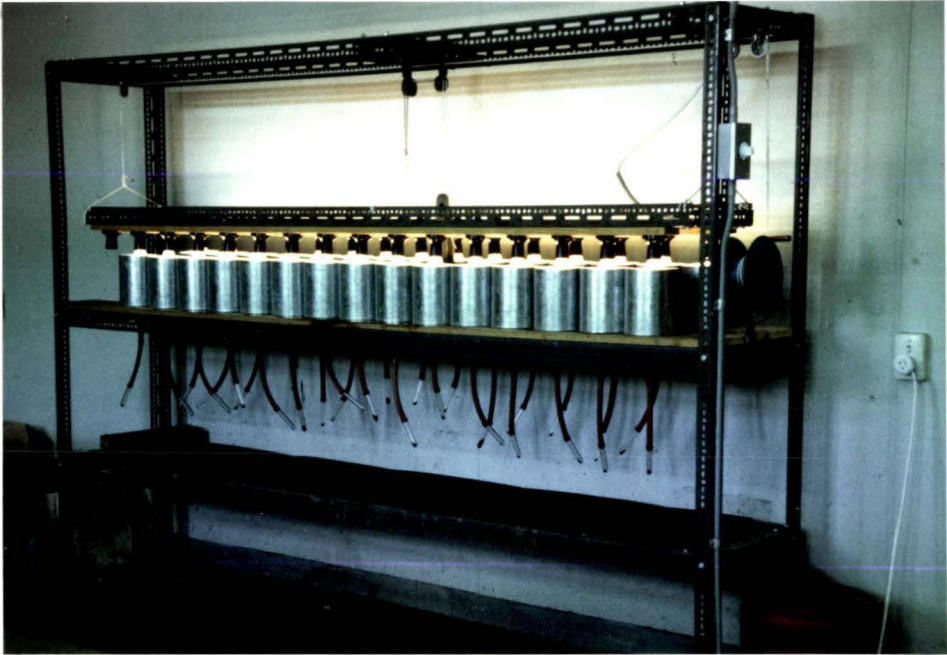
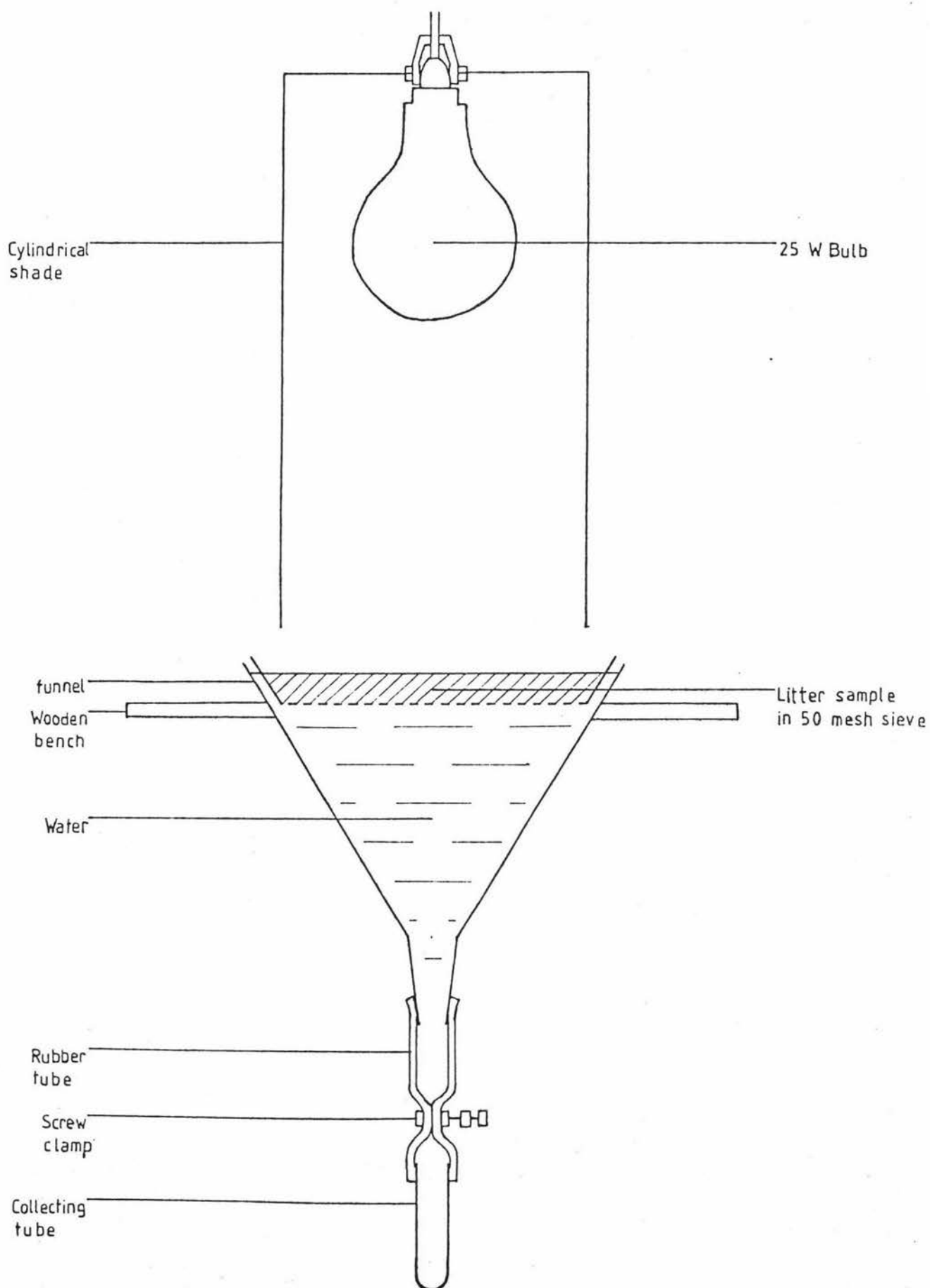


FIGURE 8. WET FUNNEL EXTRACTION APPARATUS.

(After Burges and Raw 1967.)



ostracods could survive for up to a fortnight completely immersed in water".

Samples were examined under a binocular dissecting microscope, (x 120). Each sample was placed in a petri dish marked with a grid of 1 cm by 1 cm squares, and every field was counted, following the grid sequence. The total number of each type of animal per core was then recorded.

1. 5. Identification and brief habitat description.

1. 5. 1. Mesocypris audax (Ostracoda)

Mesocypris audax is the sole terrestrial representative of the Subclass Ostracoda to be found in New Zealand, (Chapman, 1960 and 1961), Harding, (1953), documented the only other known terrestrial species; Mesocypris terrestris, from Africa. Both belong to the Subfamily Cypinae.

The New Zealand terrestrial ostracod Mesocypris audax ranges in length from 0.55 to 1.10 mm, its shell is yellowish green in colour. The valves of the shell are moderately hairy, the left being slightly larger than the right. A detailed description of the holotype was given by Chapman, (1961).

The ostracods are found in native forest leaf mould ranging widely in vegetation type and altitude. Where they occur, they do so in large numbers; Chapman, (1961), stated that "20 to 30 may be obtained from a few handfuls of litter", and interestingly, she also noted "Harpacticoid copepods are very numerous in this habitat....."

In their natural habitat, they are capable of surviving climatic extremes; hairs on the valves enabling them to conserve water in dry conditions, "Animals have survived (and

bred) for over 6 months in a glass dish lined with moist filter paper, with fragments of humus for food." (Chapman, 1961.)

Well chewed plant remains in faecal pellets suggest that the animal's diet consists of decaying plant remains which have been broken down into small pieces, alternatively they may feed upon fungi or diatoms growing on the organic debris, (Chapman, 1961).

Reproduction is considered to be parthogenetic; no males have yet been located. Animals with well developed eggs are found from September to May, these hatch within the mother's shell, and young are seen in mid September, (Chapman, 1961).

1. 5. 2. Trichoniscus phormianus (Isopoda)

The Suborder Isopoda belongs to the Order Pericarida of the Subclass Malacostraca. The terrestrial isopods possess pleopods modified for air breathing, and belong to the Tribe Oniscoidea (Hurley, 1961). A key to this Tribe has been constructed (Hurley, 1958): the isopod collected in this study has been identified as Trichoniscus phormianus using this key.

The animal is approximately 4.00 mm in length, it is dorso-ventrally compressed, has seven pairs of legs and can readily be identified by the sculpturing on its back.

1. 5. 3. Bryocamptus stouti and Goniocyclops silvestris (Copepoda)

The two animals collected in this study belonging to the Subclass Copepoda have been identified as Bryocamptus stouti and Goniobyclops silvestris on the basis of information set out

by Harding, (1958). Both the animals described by Harding (1958), were found in beech (Nothofagus truncata) forest litter.

The copepods are cylindrical in shape; the trunk is composed of ten segments comprising thorax and abdomen, (Barnes, 1974). The Bryocamptus stouti female is 0.60 mm in length and the male 0.55 mm. Goniocyclops silvestris is approximately 0.40 mm in length.

## Section 2 Results.

## 2. 1. Habitat preferences.

Soil and litter form a continuous habitat for Crustacea between island and mainland, hence there is incomplete isolation of sites. Because of this habitat continuity it is not possible to eliminate non-forest animals, instead it is only possible to identify the habitat preferences of individual species.

A chi-squared test comparing total numbers of animals of the various species found in both forest, (island and mainland combined), and non-forest situations was performed. The results of this test are shown in Table VII below.

Table VII Observed  
Expected values for the chi-squared comparison of total numbers of animals found in forest and non-forest regions.

	<u>Bryocamptus</u> <u>stouti</u>	<u>Goniocyclops</u> <u>silvestris</u>	<u>Tricho-</u> <u>niscus</u> <u>phormianus</u>	<u>Ostracoda</u> ( <u>Mesocypris</u> <u>audax</u> & the unidentified Ostracod)
Forest	1.00	1.00	0.95	0.98
Non- Forest	0.66	0.79	11.30	3.26

Chi-squared = 238.47,  $P < 0.001$

(The observed values used in calculation of this table are presented in Appendix V, p. )

The high values for Trichoniscus  
phormianus (11.30) and for the ostracods (3.26)

in non-forest conditions indicate that they have an overall preference for non-forest areas. The two copepod species can be considered to be primarily forest animals.

Table VIII below presents the observed/expected table for a chi-squared test performed on the total data for islands and non-forest areas.

Table VIII      Observed  
                  Expected values for the chi-squared  
                  comparison of total numbers of  
                  animals found in island and non-forest  
                  regions.

	<u>Bryocamptus</u> <u>stouti</u>	<u>Goniocyclops</u> <u>silvestris</u>	<u>Tricho-</u> <u>niscus</u> <u>phormianus</u>	<u>Mesocypris</u> <u>audax</u>
Island	1.00	1.00	0.88	1.01
Non- Forest	0.87	0.64	10.05	0.20

Chi-squared = 175.96,  $P < 0.001$

(The observed values used in calculation of this table are presented in Appendix V p.      ).

Tables VII and VIII indicate that animals exhibit a graduation in habitat preference. Bryocamptus stouti prefers the island to the non-forest region, (difference in O/E ratio = 0.13), with less difference than the forest to the outside region, (difference in O/E ratio = 0.34), suggesting that this copepod has a slight preference for the mainland over the island. This tendency can be illustrated thus:

Bryocamptus stouti

Mainland       $\xleftarrow{\text{preference}}$       island       $\xleftarrow{\text{preference}}$       outside

Strong preference for forest  
over non-forest

It therefore appears that Bryocamptus stouti is primarily a forest dwelling species with a slight preference for mainland over island. The optimal habitat of Goniocyclops silvestris appears to be the island; the difference in O/E ratio between island and non-forest (0.36) is greater than the difference between forest and non-forest (0.21). This preference can be illustrated thus:

Goniocyclops silvestris

Mainland       $\xrightarrow{\text{preference}}$       island       $\xleftarrow{\text{preference}}$       outside

Trichoniscus phormianus shows a marked preference for non-forest over forest (difference in O/E ratio = 10.35), its preference for non-forest over island is only slightly smaller, (difference in O/E ratio = 9.17) indicating that it is primarily a non-forest species. This marked preference for non-forest regions can be illustrated thus:

Trichoniscus phormianus

Mainland       $\xrightarrow{\text{preference}}$       island       $\xrightarrow{\text{preference}}$       outside

A chi-squared test was carried out on total data for each of the two ostracods, that is Mesocypris audax, and an unknown species which occurred rarely, however the test was invalid as 10% of the values were less than 5; expected tables

suggest but do not prove that the unknown animal is an outside species.

Mesocypris audax appears to be better suited to the island habitat. Although not shown separately in the forest/non-forest comparison, Mesocypris audax shows a slight preference for island over mainland in the test outlined in the previous paragraph. (This test is not significant, therefore the relationship is not an absolute one.) Table VIII ( page 35 ) shows the preference of Mesocypris audax for islands over non-forest areas, (difference in O/E ratio = 0.81). These preferences can be illustrated thus:

Mesocypris audax

Mainland       $\xrightarrow{\text{preference}}$       island       $\xleftarrow{\text{preference}}$       outside

2. 2. Raw data; total, mean and range.

The information presented in Appendices V to VII (pp. 102 to 104 ) represents a summary of the raw data. All the tables in Appendices V to VII are set out similarly; sites are arranged in descending order of island size, and values are given for the various Crustacean species collected. Appendix V gives the total number of animals found in 90 cores (this material is used for calculations in Appendices VI, VII and Table IX between pp. 37 and 38 ) Appendix VI shows the mean number of animals found per core, and Table IX indicates the calculated mean numbers per square metre.

Appendices V, VI and Table IX all suggest similar trends. In most cases, both copepod species and Mesocypris audax occur in

Table IX. Calculated mean number of animals per square metre.

	<u>Bryocamptus</u> <u>stouti</u>	<u>Goniocyclops</u> <u>silvestris</u>	<u>Tricho-</u> <u>niscus</u> <u>phormianus</u>	<u>Mesocypris</u> <u>audax</u>	Ostracod (unknown species)
Site 1:					
Island	7,356	1,480	233	6,500	156
Mainland	11,000	1,722	344	7,667	6,889
Non-forest	0	0	200	33	500
Site 2:					
Island	10,088	1,000	222	0	11
Mainland	6,811	378	267	0	11
Non-forest	1,666	67	67	0	200
Site 3:					
Island	5,167	656	256	0	11
Mainland	12,389	989	367	0	0
Non-forest	0	0	33	0	0
Site 4:					
Island	11,878	944	200	11	0
Mainland	7,589	322	444	0	0
Non-forest	0	0	0	0	0
Site 5:					
Island	12,300	367	367	0	0
Mainland	37,778	733	200	0	0
Non-forest	67	0	0	0	0
Site 6:					
Island	244	33	67	0	0
Mainland	33,133	811	322	0	0
Non-forest	367	0	133	0	0
Site 7:					
Island	2,944	1,456	33	11	0
Mainland	8,400	378	211	0	0
Non-forest	0	0	33	0	0
Site 8:					
Island	2,633	22	44	0	0
Mainland	40,478	1,156	222	0	67
Non-forest	0	0	167	0	0
Site 9:					
Island	11,244	200	200	0	100
Mainland	6,133	544	67	0	0
Non-forest	67	67	67	0	0
Overall mean numbers per square metre for sites 1 to 9:					
Island	7,340	684	177	725	31
Mainland	18,190	781	272	859	78
Non-forest	240	15	78	4	78

greatest numbers in the mainlands, islands carry less of these animals, and sub-alpine scrub (non-forest) regions contain relatively few such animals; exceptions being where islands are large and mainland-like for example, site 1 mainland supports 11,000 Bryocamptus stouti 1,722 Goniocyclops silvestris and 7,667 Mesocypris audax per metre square, whereas its island supports only 7,356 Bryocamptus stouti, 1,480 Goniocyclops silvestris, and 6,500 Mesocypris audax per metre square, (between site 1 island and mainland, only 30 Mesocypris audax per square metre were found). An exception to this generalization exists in site 2, where the island is large, and approaches mainland conditions, the island contains 10,088 Bryocamptus stouti per metre square, but the mainland has only 6,811 animals per metre square of the same species. The trend followed by the two copepods and Mesocypris audax indicates that they may primarily be forest dwellers. The isopod appears more flexible in its habitat preferences, existing in both forest and non-forest areas, although in reduced numbers in non-forest regions. (e.g. Site 6 island has 67 isopods per metre square, the mainland 322 per metre square, and between the sites there are 60 isopods per metre square.)

The mean of numbers of animals per metre square for all nine sites shown at the bottom of Table IX (p. 37 and 38) indicates that for all species the mean number of animals per metre square found in mainlands is higher than that found in islands.

Appendix VII outlines the range of numbers of animals per core. Cores which did not contain animals of the various species

considered were taken in all sites, resulting in a wide range in numbers of animals per core. Despite this range, in the smaller sites 5 to 9, the maximum number of Bryocamptus stouti in mainlands is higher than that in islands, concurring with the pattern shown by mean numbers of animals per metre square for these sites. The maximum number of animals per core seems in general to imitate the trend set by the mean numbers of animals per metre square in each site.

## 2. 3. Island - mainland comparison.

Table X (between pp. 39 and 40 ) illustrates the observed/expected ratios and the chi-squared values for tests performed on the data for individual sites. The data used in these tests have been adjusted in some cases in order to avoid using values of less than 1, and 10% of values less than 5, which render the test invalid. All the values on the table for individual islands and the value for the sum of the islands are significant, with the exception of site 6.

From Table X it can be seen that the copepod Bryocamptus stouti shows only one marked difference between island and mainland O/E ratios and this occurs in one of the smaller sites, site 7, (O/E difference = 0.32) where the island has fewer animals than the mainland. All other sites appear to have relatively similar numbers of animals in both island and mainland. It is possible that in general Bryocamptus stouti, once established in an island, is capable of fairly rapid population increase to an equilibrium level, irrespective of island size and distance from the mainland.

Table X  $\frac{\text{observed}}{\text{expected}}$  values for chi-squared tests performed on data for individual sites

	<u>Bryocamptus</u> <u>stouti</u>	<u>Goniocyclops</u> <u>silvestris</u>	<u>Tricho-</u> <u>niscus</u> <u>phormianus</u>	<u>Mesocypris</u> <u>audax</u>	Ostracod (unknown species)	chi-squared value and significance level
Site 1:						
Island	0.94	1.08	0.97	1.08	0.45	chi-squared = 28.25
Mainland	1.03	0.93	1.01	0.93	1.40	P < 0.001
Site 2:						
Island	0.99	1.19	0.77			chi-squared = 10.97
Mainland	1.01	0.70	1.34			P < 0.01
Site 3:						
Island	0.96	1.28	1.31			chi-squared = 8.93
Mainland	1.01	0.87	0.86			P < 0.05
Site 4:						
Island	1.00	1.21	0.52			chi-squared = 28.87
Mainland	0.99	0.66	1.74			P < 0.001
Site 5:						
Island	0.97	1.30	2.53			chi-squared = 44.17
Mainland	1.00	0.89	0.48			P < 0.001
Site 6:						
Island	0.99	0.66	2.27			chi-squared = 4.85
Mainland	1.00	1.02	0.90			(Not significant)
Site 7:						
Island	0.78	2.39	0.48			chi-squared = 188.96
Mainland	1.10	0.31	1.25			P < 0.001
Site 8:						
Island	1.00	0.31	2.75			chi-squared = 8.00
Mainland	0.99	1.04	0.88			P < 0.05
Site 9:						
Island	1.01	0.43	1.14			chi-squared = 42.81
Mainland	0.96	1.98	0.74			P < 0.001
Overall values for sites 1 to 9 combined:						
Island	0.93	1.51	1.27	1.48	0.94	chi-squared = 326.80
Mainland	1.02	0.77	0.87	0.78	1.02	P < 0.001

It appears from the total O/E ratio for Goniocyclops silvestris given in table X that it is an aggressive island colonizer, (O/E ratio for islands is 1.51 whereas that for mainlands is only 0.77). Larger islands 2, 3, 4 and 5 as well as smaller island 7 follow the same trend as that set by the total. In these island sites the copepod may be showing an initial population increase, whereas the mainland animals may have declined somewhat to an equilibrium; or Goniocyclops silvestris may simply prefer the type of habitat found in these islands. Islands 6, 8 and 9 show a reverse trend; this may indicate that for initial population development a certain size of island is necessary, or that these small islands resemble non-forest regions in the habitat they offer this copepod.

The total values in table X indicate that Trichoniscus phormianus is generally found in larger numbers in islands than in mainlands, although in individual samples preference appears to be highly variable. An unknown micro-habitat preference may account for this variability, rather than the size of the island or its distance from the corresponding mainland. Since the isopod shows a marked preference for non-forest areas, (Section 2. 1. p. 34 ), it will be readily available to colonize forest areas which fulfil its habitat requirements. For the two ostracod species no general trends can be identified as these animals only occur in significant numbers in one site in each case. Mesocypris audax is present only in site 1 where it appears to favour the island situation slightly, an analysis of island/mainland totals support this. Site 1 island seems to be mainland-like in its

performance.

Total values for the unknown ostracod species show no real preference for island over mainland, however in site 1 there is a marked preference for the mainland; tests in Section 2. 1. (p. 34 ) suggest that this animal is primarily a non-forest dweller.

The results presented in this chapter will be further considered in Chapter 5, Discussion.

## CHAPTER 4 : PITFALL TRAP ANIMALS

### Section 1     Methods.

#### 1.    1.    Background.

Pitfall traps provide a simple means of collecting surface-active animals. This method avoids capturing large numbers of flying insects; an advantage in a study where animals with a high dispersal ability are to be avoided, their presence in a site not necessarily indicating residence.

A further beneficial aspect of this procedure is that in comparison with other sampling methods (e.g. hand sorting), trapping does not disturb the habitat unduly. This is particularly important in small sites where habitat disruption in the initial sampling may severely modify the results of a further sampling.

The numbers of animals caught in pitfall traps provide a measure of activity levels, and it is considered (McColl, 1975), that these levels are closely related to population density. In this study it is assumed that numbers of animals trapped give a reasonable indication of the population density of animals found in the sites.

#### 1.    2.    Sampling procedure

The trapping method adopted largely follows that described by H. P. McColl (1975). The traps consist of plastic containers 10cm in

diameter and 12cm deep, set into the ground so that the rims are slightly below the litter surface. 40 to 50ml of 8% formalin is placed in each container; the formalin acts as a preservative, and prevents escape or cannibalism (J. Springett, pers. comm.). The suitability of formalin as a preservative with respect to its influence as an attractant or a repellent has been considered, however, it was used consistently throughout the study, and any resulting bias should be uniform. To prevent excessive accumulation of leaf litter or rain water in the traps, roofs consisting of lightweight nylon with four bamboo legs were placed over the containers, (Plate XVI between pp. 43 and 44).

Traps were set for 14 day periods, with one exception in winter, where heavy snow prevented access to the sites. A set of 30 traps allowed 15 traps to be positioned in an island and its corresponding mainland for each 14 day interval.

H. P. McColl (1975), whose work was carried out on the floor of a Nothofagus truncata forest states "Climatic conditions on the forest floor were never extreme, and activity was maintained by many groups throughout the year", it would thus appear that seasonal variability plays only a minor role in the data collected, however, seasonal effects were taken into account in planning the sampling regime: the paired sampling of an island and its corresponding mainland ensures the absence of seasonal effects when examining island-mainland pairs. As a further precaution against seasonal variation, and in order to allow meaningful inter-island comparison, two sample sets were taken from each site, several months intervening between visits.

Plate XVI

Pitfall trap.



This results in data from a total of 30 traps for each site being available for analysis, as well as providing samples of animals which may have been present at different times of the year, and allowing sites to recover from the initial sampling. (The latter being particularly important in sites such as 7, 8 and 9, where traps are distributed over a small area.)

Traps were laid out on transects within the sites; this, in combination with red and orange roofs, allowed relatively easy retrieval of traps. The length of the transects varied according to the size of the site; transects stretched from end to end of island sites, and a similar sized transect was employed in the corresponding mainland. Transects were placed at different positions within the sites for each of the two samplings. In very small sites, traps were spread throughout the whole area of the site at as great a distance from each other as possible. A total of 30 traps were placed outside sites in order to ascertain the type of animals found in non-forest areas.

On collection samples were transferred from the traps into smaller receptacles and stacked in P.V.C. downpiping tubes in order to maintain containers in an upright position, and to separate samples from different sites. These tubes were then placed in packs for transport back to the laboratory.

#### 1. 3. Sorting and counting.

The contents of each trap was sorted individually to remove debris, and the total number of animals of each species, for 15 traps was recorded. Trap results were combined because numbers of animals from individual traps

proved to be too low for statistical treatment.

The animals for each set of 15 traps were stored in appropriately labelled containers in 70% ethanol and 3% glycerol (J. Springett, pers. comm.). Type specimens were retained separately in small vials containing the same solution.

#### 1. 4. Identification.

Type specimens were sorted into groups for statistical analysis; the majority of species were grouped into Orders, the lowest level of organization used in tabulation was Family. Classification was carried out using a key set out by Oldroyd (1958).

In the majority of instances, specific identification of animals was not possible; in a number of examples suitable keys were not available, and frequently animals have not been named at the specific level (e.g. Johns' 1962 and 1964 papers on Diplopoda include a number of unnamed species). Identification of the Coleoptera at either a specific or generic level has been carried out by Dr. M. J. Meads (pers. comm.). Division of the Diplopoda into Families and the Chilopoda into Orders was effected with the help of D. M. Mill, using keys constructed by Johns (1962), and Cloudsley-Thompson (1958). Further identification has been prevented by the constraints mentioned above, as well as by the limited time available.

## Section 2. Results.

### 2. 1. Non-forest animals.

In chapter 2, Section 2. 1. (p. 17) it was possible to exclude plants which could be identified as non-forest species on the basis of sampling performed outside the sites, supported by habitat descriptions in the literature.

Whilst plants can be readily separated in this manner, forest and subalpine scrub boundaries being reasonably well defined, the division of animals into forest and non-forest categories cannot be as easily exacted. Chapter 3, Section 2. 1. (p. 34) describes the habitat preferences of the various Crustacean species, habitat continuity rendering elimination of non-forest species impossible. Similarly it is inappropriate to ignore animals collected in pitfall traps in non-forest regions.

The result of chi-squared analysis comparing all forest and non-forest animal species found in both islands and mainlands is not significant at the 5% level, (Appendix VIII p. 105). Table XI (between pp. 46 and 47) has been constructed using data in Appendix IX (p. 106) and shows the absolute total number of species found in each site, as well as the number of species in each group, excluding all species found in non-forest areas. A chi-squared test performed on this data was not significant at the 5% level. Removal of non-forest species from the data should reduce the number of species found in islands, where non-forest species are most likely to encroach. Table XI however shows that although sites 5, 6, 7, and 8 are small sites, contrary to what is expected,

Table XI Total animal species in taxonomic groups  
excluding non-forest species.

Legend

I = Island  
M = Mainland

Site number	1I	1M	2I	2M	3I	3M	4I	4M	5I	5M	6I	6M	7I	7M	8I	8M	9I	9M
Hemiptera	4	3	0	2	0	0	0	2	0	0	5	3	0	0	3	2	3	1
Coleoptera	21	17	6	13	7	6	6	5	8	6	15	10	9	7	12	14	10	11
Curculionidae	2	1	0	1	0	0	2	1	0	0	2	1	1	0	2	5	2	2
Trichoptera	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0
Diptera	7	9	6	9	8	10	9	11	0	9	14	10	6	5	14	6	4	11
Lepidoptera	3	4	2	1	1	3	2	1	5	3	5	3	1	1	2	2	0	1
Hymenoptera	5	2	1	1	3	1	2	2	7	1	5	0	1	0	2	4	0	4
Orthoptera	2	1	0	0	1	0	1	0	1	0	1	1	0	1	0	0	0	0
Acari	2	1	0	1	0	1	1	0	2	1	2	1	1	0	2	1	1	1
Phalangida	2	2	2	1	1	1	2	1	2	0	1	2	1	1	0	2	1	2
Araneae	9	9	5	6	5	9	7	5	9	4	6	10	9	9	7	6	7	8
Diplopoda	8	9	7	6	3	5	5	6	7	5	5	4	3	3	4	3	2	5
Chilopoda	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Gastropoda	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0
Oligochaeta	1	1	3	1	0	2	2	2	0	1	1	1	1	0	2	1	1	2
Turbellaria	1	1	1	1	0	0	1	1	0	0	1	1	0	1	1	1	0	0
Total species	67	61	33	43	29	40	41	39	41	30	63	47	33	29	51	47	32	49
Expected values (chi-squared)	64	64	38	38	35	34	40	40	36	35	55	55	31	31	49	49	41	40
O/E values (chi-squared)	1.05	0.95	0.87	1.13	0.83	1.18	1.03	0.98	1.14	0.86	1.15	0.85	1.06	0.94	1.04	0.96	0.78	1.23

Chi-squared = 11.93 P > 0.05 (not significant)

islands in all these sites contain more species than their mainlands. From this evaluation it can be inferred that species collected outside sites are not exclusively non-forest dwellers, and therefore they cannot be ignored.

Animals collected in pitfall traps may display a range of habitat preferences, for example, animals found outside sites may optimally exist in island conditions, but infrequently be found in mainland and non-forest regions; similarly, species sampled from any of the various areas may not necessarily be restricted to them, or be living under the most favourable conditions.

2. 2. Number of species and absolute numbers of animals found in each group in all sites.

Appendix IX (p. 106 ) presents the numbers of animals of each species in all sites. Tables XII and XIII (between pp. 47 and 48) have been drawn from the figures in Appendix IX. Sites in the tables are arranged in order of decreasing area.

The values for the absolute total number of species in each group (Table XII) do not follow an obvious trend of declining species number with decreasing island size. However, very large islands appear to be mainland-like in the number of species they support, (for example site 1 island contains 103 species, whilst the mainland contains 92 species), differing from very small islands which sustain fewer species than their corresponding mainlands, (e.g. site 9 island contains only 60 species, whereas the mainland contains 82 species).

Table XII Total animal species in taxonomic groups including non-forest species.

Legend

I = Island

M = Mainland

O = Outside forest

Site number	1I	1M	2I	2M	3I	3M	4I	4M	5I	5M	6I	6M	7I	7M	8I	8M	9I	9M	O
Colembola	3	3	3	3	3	3	3	3	3	3	3	3	2	3	3	3	3	3	3
Hemiptera	4	3	0	2	0	0	0	2	0	0	6	3	0	0	5	3	3	1	1
Coleoptera	30	27	12	20	14	13	18	11	15	12	30	20	17	18	22	24	17	20	22
Curculionidae	2	1	0	1	0	0	3	1	0	1	3	1	2	0	2	5	3	2	2
Trichoptera	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0
Diptera	9	10	8	9	10	12	9	12	7	11	15	10	8	5	15	6	4	11	1
Lepidoptera	3	4	2	1	1	3	2	1	5	3	5	3	1	1	2	2	0	1	1
Hymenoptera	7	3	2	2	5	1	3	3	9	1	7	1	2	1	3	2	0	5	3
Blattodea	0	1	0	0	1	1	1	1	1	0	1	1	1	1	1	0	0	0	1
Orthoptera	4	2	1	2	2	1	2	2	3	0	3	2	0	2	2	2	1	1	4
Crustacea	2	2	2	2	2	2	2	1	1	2	2	2	1	1	2	2	2	2	2
Acari	4	3	1	2	2	3	2	1	3	2	5	3	2	1	5	3	3	3	3
Phalangida	4	4	4	3	4	3	4	5	4	3	5	4	2	3	3	5	3	6	4
Pseudo-scorpionida	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Araneae	18	15	12	9	12	15	13	10	17	9	15	17	14	18	16	13	15	16	15
Diplopoda	10	10	8	8	5	6	7	7	8	5	7	5	4	5	6	4	3	7	2
Chilopoda	1	1	0	1	1	0	0	0	0	0	1	0	0	0	0	0	2	2	2
Gastropoda	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0	0	0	0
Oligochaeta	1	2	4	2	1	3	3	3	0	2	2	2	1	0	2	2	1	2	1
Turbellaria	1	1	1	1	0	0	1	1	0	0	1	1	0	1	1	1	0	0	0
Total species	103	92	60	68	63	68	74	66	76	54	111	78	57	61	90	77	60	82	68

Table XIII Total number of animals including non-forest species.

## Legend

I = Island

M = Mainland

O = Outside forest

Site number		1	2	3	4	5	6	7	8	9	0.
Colembola	I	134	5647	2266	4304	3139	1462	1999	903	1734	850
	M	1293	6698	2113	4009	2036	1761	3003	2755	2950	
Hemiptera	I	4	0	0	0	0	8	0	6	3	1
	M	7	2	0	2	0	11	0	3	1	
Coleoptera	I	146	55	48	63	45	193	44	86	36	62
	M	225	87	35	29	62	143	61	122	94	
Curculionidae	I	2	0	0	6	0	26	16	3	3	52
	M	2	1	0	1	2	1	0	5	3	
Trichoptera	I	0	0	0	2	0	0	0	0	0	0
	M	0	0	2	12	0	0	0	0	0	
Diptera	I	55	17	17	34	19	63	61	20	14	1
	M	18	44	25	80	18	21	9	22	35	
Lepidoptera	I	5	2	4	3	7	6	3	279	0	1
	M	7	1	3	2	3	3	1	3	2	
Hymenoptera	I	23	21	15	12	23	80	18	23	0	104
	M	5	4	2	7	2	1	2	26	15	
Blattodea	I	0	0	4	2	6	15	4	7	0	12
	M	1	0	1	1	0	1	1	0	0	
Orthoptera	I	4	2	6	8	18	44	0	27	1	9
	M	5	6	4	3	0	2	4	12	2	
Crustacea	I	165	117	28	35	6	28	19	31	8	73
	M	97	74	33	32	27	76	61	57	30	
Acari	I	15	7	3	6	7	14	2	7	3	28
	M	6	4	12	20	8	6	5	22	7	
Phalangida	I	37	16	15	15	16	27	9	12	3	15
	M	12	16	9	20	15	10	9	14	13	
Pseudo- scorpionida	I	0	0	0	0	0	0	0	0	0	1
	M	0	0	0	0	0	0	0	0	0	
Araneae	I	82	83	67	105	108	143	124	73	149	73
	M	63	50	56	73	56	106	72	103	61	
Diplopoda	I	51	18	11	10	37	25	5	14	5	8
	M	46	24	16	10	25	21	13	8	23	
Chilopoda	I	1	0	1	0	0	1	0	0	2	2
	M	2	1	0	0	0	0	0	0	3	
Gastropoda	I	0	0	0	0	0	0	0	0	0	0
	M	0	0	1	2	0	0	1	0	0	
Oligochaeta	I	3	12	1	14	0	7	1	11	2	3
	M	6	6	7	6	3	18	0	8	6	
Turbellaria	I	2	1	0	1	0	1	0	1	0	0
	M	1	1	0	3	0	3	2	2	0	
Total animals	I	1909	5998	2486	4620	3431	2143	2305	1503	1963	1295
	M	1796	7019	2319	4312	2257	2184	3244	3162	3245	

Figure 9A (between pp. 48 and 49) plots the species number against the log of the island area for both island and mainland, sites 1 to 9. F ratios from regression analysis of both island and mainland data are not significant at the 5% level, hence regression lines cannot be drawn. Figure 9B (between pp. 48 and 49) represents the species number plotted against the distance between each island and its corresponding mainland, again F ratios from regression analysis of these data are not significant at the 5% level, thus regression lines cannot be plotted. Neither a species-area nor a species-distance relationship is apparent for animals collected in pitfall traps.

Contrary to expectations, the absolute total number of animals for each site, listed in table XIII, indicates that with decreasing site size, there is no marked decline in the total number of animals found in an island. However, sites 7, 8 and 9 contain noticeably fewer animals than their corresponding mainlands, (Site 7 island has 2305 animals, whilst the mainland has 3244 animals; Site 8 island has 1503 animals, whilst the mainland has 3162 animals; Site 9 island has 1963 animals whilst the mainland has 3245 animals), suggesting that a difference in the total number of animals a site can support exists within some smaller island-mainland pairs.

Regression analysis comparing total number of animals in each site with log of area of islands and mainlands is not significant at the 5% level. Total number of animals and distance between an island and its corresponding mainland were also compared using regression

FIGURE 9A. SPECIES-LOG AREA GRAPH FOR ANIMALS.

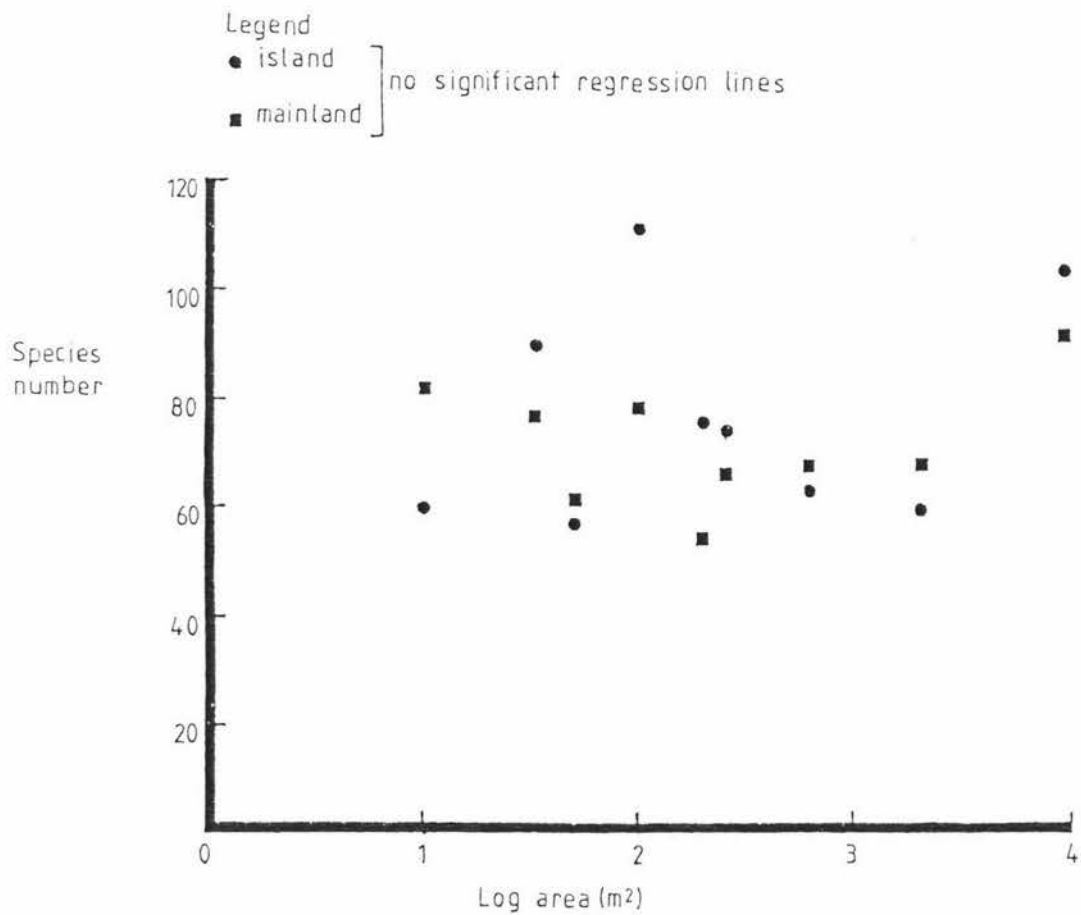
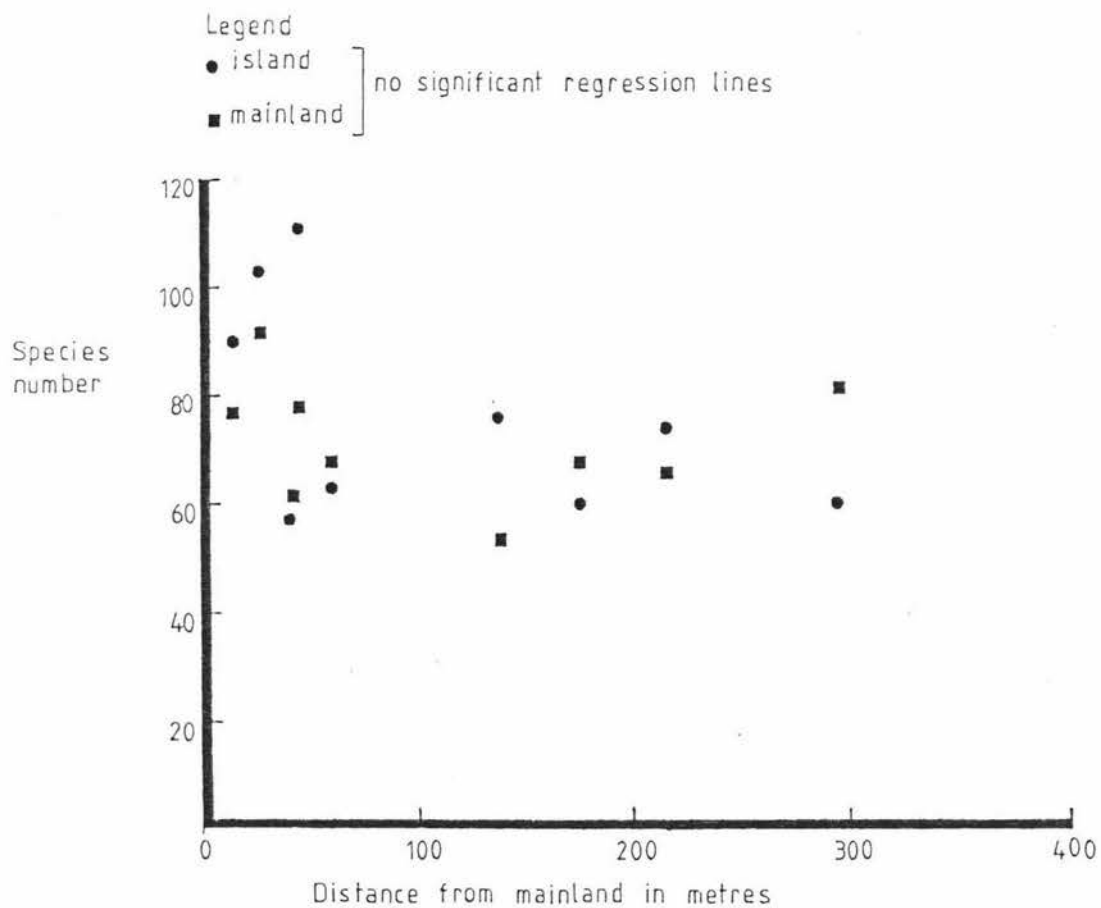


FIGURE 9B. SPECIES-DISTANCE GRAPH FOR ANIMALS.



analysis, and again the F ratios were not significant at the 5% level.

2. 3. Chi-squared analysis of species numbers and numbers of individuals.

Chi-squared tests were executed on data presented in Tables XII and XIII (between pp. 47 and 48 ), this included analysis of individual groups, as well as absolute totals, for both species number, and number of individuals.

None of the tests performed in material from Table XII were significant at the 5% level, that is species numbers found in paired islands and mainlands appeared unrelated.

Chi-squared analysis of numbers of individuals found in island-mainland pairs were significant for several groups (Colembola, Coleoptera, Diptera, Acari, Phalangida, Araneae Diplopoda and Crustacea), as well as for the absolute total number of individuals. Table XIV (between pp. 49 and 50 ) presents the ratio of observed/expected for each of these significant chi-squared tests.

The O/E ratios for Colembola indicate that more animals than would be expected are found in the large islands and less than would be expected are found in the small islands, (large sites 1 to 5 respectively have O/E ratios of 1.09, 0.99, 1.12, 1.12 and 1.31, while small sites 6 to 9 respectively have O/E ratios of 0.98, 0.86, 0.53 and 0.80). The Coleoptera follow a similar trend, with fewer animals (O/E = 0.61) than would be expected in site 9. Diptera demonstrate a marked difference between very large and very small islands; site 1 island contains more animals than would be

Table XIV Observed values for significant chi-squared  
Expected analyses of numbers of animals in  
Island-mainland pairs.

Legend

I = Island  
M = Mainland

Colembola

Site Number	I	M
1.	1.09	0.92
2.	0.99	1.00
3.	1.12	0.89
4.	1.12	0.89
5.	1.31	0.73
6.	0.98	1.01
7.	0.86	1.11
8.	0.53	1.39
9.	0.80	1.16

Chi-squared = 1529.5  
P < 0.001

Coleoptera

Site Number	I	M
1.	0.86	1.11
2.	0.85	1.11
3.	1.25	0.78
4.	1.49	0.58
5.	0.93	1.05
6.	1.25	0.78
7.	0.93	1.05
8.	0.91	1.07
9.	0.61	1.31

Chi-squared = 67.8  
P < 0.001

Diptera

Site Number	I	M
1.	1.42	0.53
2.	0.54	1.49
3.	0.79	1.22
4.	0.57	1.46
5.	1.00	1.02
6.	1.41	0.53
7.	1.64	0.28
8.	0.93	1.07
9.	0.56	1.48

Chi-squared = 111.8  
P < 0.001

Crustacea

Site Number	I	M
1.	1.32	0.70
2.	1.28	0.74
3.	0.98	1.01
4.	1.08	0.92
5.	0.41	1.52
6.	0.57	1.37
7.	0.51	1.43
8.	0.75	1.21
9.	0.47	1.47

Chi-squared = 97.6  
P < 0.001

Table XIV (continued).

Acari			Phalangida		
Site Number	I	M	Site Number	I	M
1.	1.41	0.60	1.	1.33	0.57
2.	1.21	0.79	2.	0.92	1.10
3.	0.47	1.49	3.	1.07	0.89
4.	0.51	1.46	4.	0.79	1.26
5.	1.02	0.97	5.	0.95	1.06
6.	1.46	0.55	6.	1.27	0.64
7.	1.02	1.02	7.	0.94	1.07
8.	0.98	1.01	8.	0.85	1.17
9.	0.44	1.52	9.	0.39	1.77
Chi-squared = 26.0 P < 0.01			Chi-squared = 21.2 P < 0.01		
Araneae			Diplopoda		
Site Number	I	M	Site Number	I	M
1.	0.95	1.06	1.	1.07	0.93
2.	1.04	0.93	2.	0.90	1.08
3.	0.92	1.10	3.	0.87	1.11
4.	0.99	1.00	4.	1.02	1.02
5.	1.10	0.84	5.	1.21	0.80
6.	0.97	1.04	6.	1.09	0.90
7.	1.06	0.90	7.	0.62	1.35
8.	0.70	1.43	8.	1.26	0.75
9.	1.19	0.72	9.	0.40	1.56
Chi-squared = 39.5 P < 0.001			Chi-squared = 17.4 P < 0.05		
Total animals					
Site Number	I	M			
1.	1.09	0.91			
2.	0.97	1.02			
3.	1.09	0.91			
4.	1.09	0.91			
5.	1.27	0.75			
6.	1.05	0.95			
7.	0.88	1.10			
8.	0.68	1.28			
9.	0.79	1.17			
Chi-squared = 1227.7      P < 0.001					

expected ( $O/E = 1.42$ ) and site 9 island supports fewer animals than would be expected ( $O/E = 0.56$ ).  $O/E$  ratios for the remaining sites show considerable variation, which may be related to both the dispersal ability of Diptera, and some seasonality in sampling. A difference between very large and very small islands can also be noted in the Acari; large islands such as site 1 have a greater number of animals than would be expected ( $O/E = 1.41$ ) and small sites, for example site 9, have fewer animals than would be expected ( $O/E = 0.44$ ). This trend also applies to the Phalangida (Site 1,  $O/E = 1.33$ ; Site 9,  $O/E = 0.39$ ), the Diplopoda (Site 1,  $O/E = 1.07$ ; Site 9  $O/E = 0.40$ ), and the Crustacea (Site 1,  $O/E = 1.32$ , Site 9,  $O/E = 0.47$ ). The Araneae appear to be reasonably evenly distributed throughout the sites; in general their ability to succeed in a site does not appear to be determined by the size of the site.

The analysis of the absolute total number of animals confirms the general trend set by the groups Diptera, Acari, Phalangida, Diplopoda and Crustacea; larger sites have slightly more animals than would be expected, (Site 1,  $O/E$  ratio = 1.09, Site 3  $O/E = 1.09$ , Site 4,  $O/E$  ratio = 1.09, Site 5,  $O/E$  ratio = 1.27, Site 6,  $O/E$  ratio = 1.05, the exception being Site 2 with an  $O/E$  ratio of 0.97), whilst smaller sites have fewer animals than would be expected, (Site 7, to 9  $O/E$  ratios are respectively; 0.88, 0.68 and 0.79).

## 2. 4. Jaccard's coefficient of community.

Table XV (between pp. 50 and 51) presents Jaccard's coefficient of community for each group in all sites, as well as for the total number of species in all sites. Appendix IX

Table XV Jaccard's coefficient of community  
for animal species.

Site number	1	2	3	4	5	6	7	8	9
Colembola	100%	100%	100%	100%	100%	100%	67%	100%	100%
Hemiptera	0%	0%	0%	0%	0%	0%	0%	40%	33%
Coleoptera	33%	35%	23%	26%	13%	43%	35%	28%	23%
Curculionidae	0%	0%	0%	33%	0%	0%	0%	40%	0%
Trichoptera	0%	0%	0%	100%	0%	0%	0%	0%	0%
Diptera	13%	33%	18%	43%	15%	25%	20%	5%	25%
Lepidoptera	20%	50%	33%	50%	14%	14%	100%	0%	0%
Hymenoptera	43%	33%	20%	67%	11%	14%	50%	25%	0%
Blattodea	0%	0%	100%	100%	0%	100%	100%	0%	0%
Orthoptera	20%	50%	0%	33%	0%	25%	0%	100%	100%
Crustacea	100%	100%	100%	50%	50%	100%	100%	100%	100%
Acari	75%	50%	67%	50%	25%	60%	50%	33%	50%
Phalangida	60%	75%	40%	50%	40%	50%	67%	33%	50%
Araneae	38%	24%	42%	35%	47%	29%	33%	45%	43%
Diplopoda	54%	45%	38%	56%	44%	50%	29%	67%	43%
Chilopoda	0%	0%	0%	0%	0%	0%	0%	0%	33%
Oligochaeta	50%	50%	33%	100%	0%	100%	0%	33%	50%
Turbellaria	100%	100%	0%	100%	0%	100%	0%	100%	0%
Total animal species	35%	40%	33%	44%	25%	35%	34%	34%	34%

provides the data necessary for construction of Table XV. The formula for Jaccard's coefficient of community is given in Chapter 2, Section 2. 4. (p. 21 ); it is a measure of the similarity between two communities which is independent of the number of species within that community.

The values for the total percentage community similarity between islands and their corresponding mainlands, derived using Jaccard's index, do not show a decline with decreasing island size as would be expected. Sites 2 and 4 do however have larger coefficients of community than the smaller sites, (Site 2 coefficient = 40%, Site 4 coefficient = 44%), indicating a slight tendency for larger islands to show a greater similarity to their corresponding mainlands than do smaller islands to their mainlands.

Figure 10 (between pp. 51 and 52) shows values for Jaccard's coefficient of community plotted against log area, F ratios from regression analysis are not significant for any of these graphs.

## 2. 5. Ellenburg's frequency coefficient of community similarity.

Information presented in Appendix IX (p. 106 ) has been utilized to obtain Ellenburg's frequency coefficient of community similarity for all groups (Table XVI, between pp. 51 and 52 ). The formula for Ellenburg's frequency coefficient of community similarity is set out in Chapter 2, Section 2. 7. (p. 24).

In several groups, the value for the frequency coefficient of community similarity is high in large sites such as Site 1, and low

FIGURE 10. JACCARD'S COEFFICIENT OF COMMUNITY FOR ANIMALS.  
(Plotted against log area.)

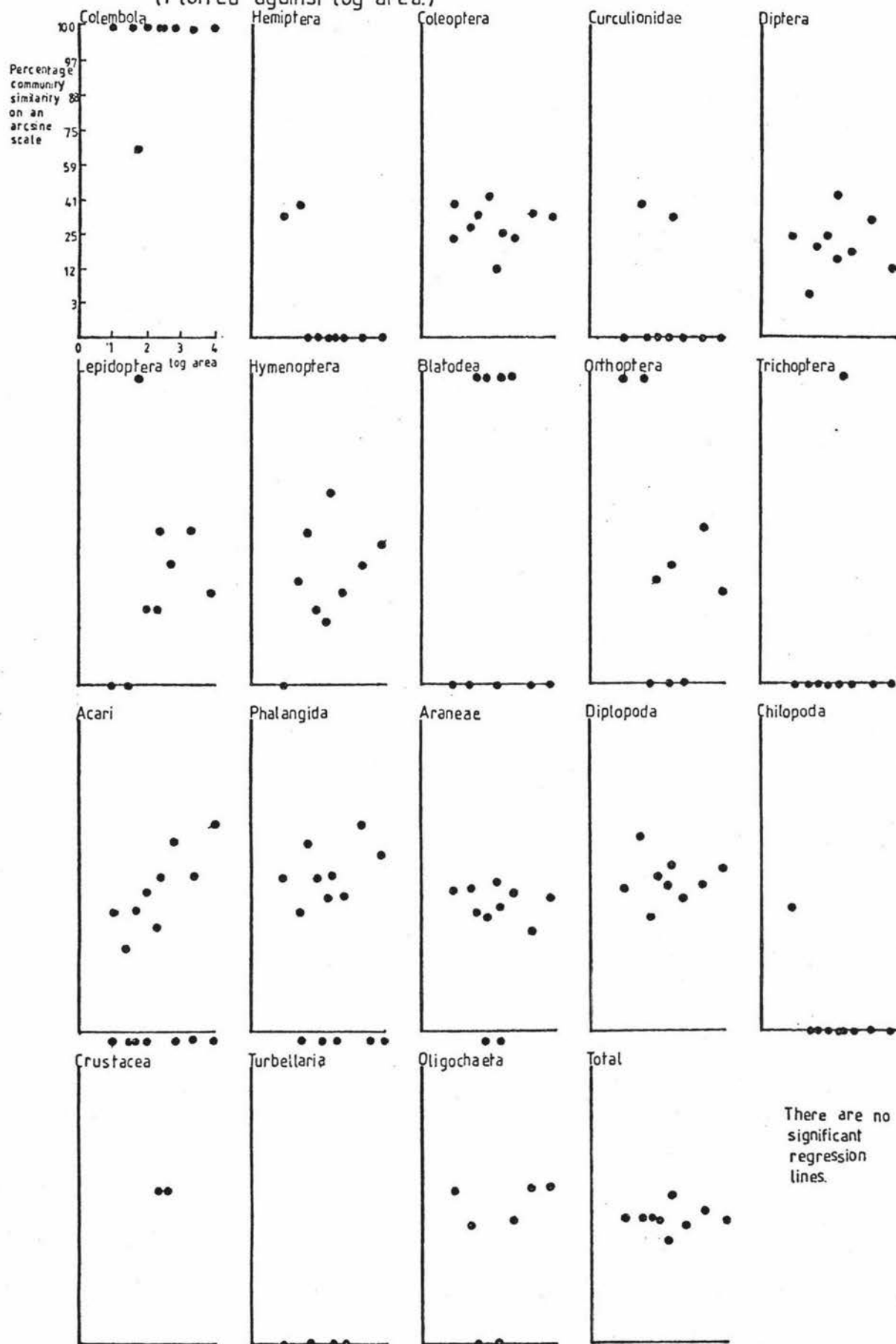


Table XVI Ellenburg's frequency coefficient of community similarity for animal species.

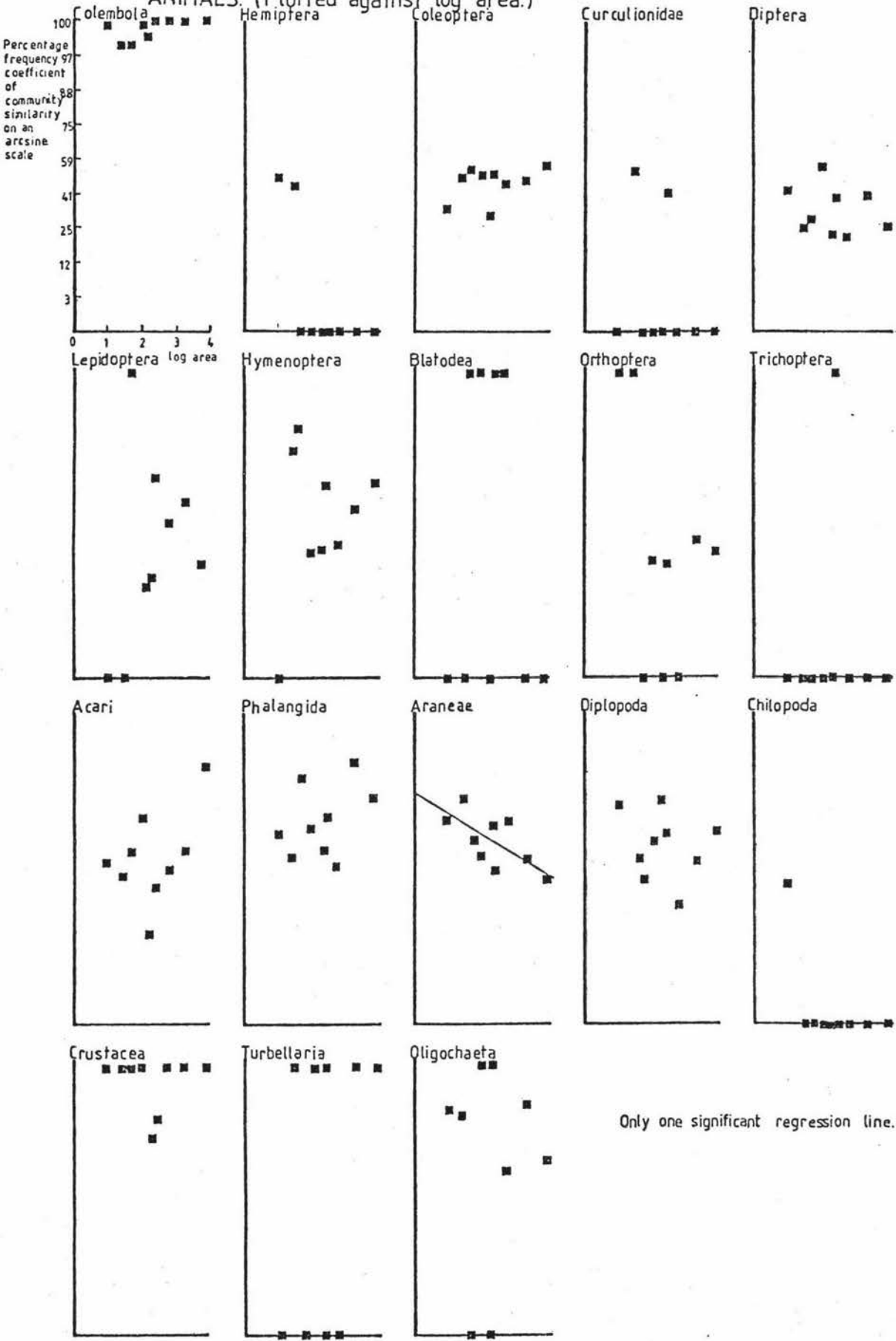
Site number	1	2	3	4	5	6	7	8	9
Colembola	100%	100%	100%	100%	99.5%	100%	99%	99%	100%
Hemiptera	0%	0%	0%	0%	0%	0%	0%	46.4%	50.2%
Coleoptera	55.5%	49.4%	46.5%	51.7%	31.8%	52.4%	54.9%	50.6%	34.9%
Curculionidae	0%	0%	0%	41.3%	0%	0%	0%	53.9%	0%
Trichoptera	0%	0%	0%	100%	0%	0%	0%	0%	0%
Diptera	26.5%	41.5%	22.3%	39.2%	23.2%	55.3%	29.2%	26.4%	43.4%
Lepidoptera	28.6%	60%	50.2%	71.7%	23.8%	19.8%	100%	0%	0%
Hymenoptera	69.7%	56.9%	38%	68.9%	36.4%	33.8%	89.6%	84.3%	0%
Blattodea	0%	0%	100%	100%	0%	100%	100%	0%	0%
Orthoptera	35.6%	41.3%	0%	29.9%	0%	31.2%	0%	100%	100%
Crustacea	100%	100%	100%	91.4%	86.1%	100%	100%	100%	100%
Acari	93.2%	60%	49.8%	41.3%	20.9%	75.3%	60%	45.8%	52.5%
Phalangida	81.9%	94.2%	51.3%	75.4%	59.7%	70.2%	89.6%	54.9%	67.4%
Araneae	44.7%	54.7%	73.3%	50.2%	72%	56.6%	65.6%	81.7%	75.3%
Diplopoda	68.9%	53.6%	32.2%	66.7%	81.9%	63.4%	43.6%	55.6%	80.8%
Chilopoda	0%	0%	0%	0%	0%	0%	0%	0%	41.3%
Oligochaeta	60%	85%	55.2%	100%	0%	100%	0%	81%	84.3%
Turbellaria	100%	100%	0%	100%	0%	100%	0%	100%	0%

in small sites such as Site 9, (e.g. Acari, Site 1 = 93.2%, Site 9 = 52.5%; Phalangida, Site 1 = 81.9%, Site 9 = 67.4%), suggesting an association between decreasing island size, and a decline in community similarity.

Ellenburg's frequency coefficient of community similarity is plotted against log area in Figure 11 (between pp. 52 and 53). Only one F ratio from regression analysis is significant at the 5% level; the F ratio for Araneae = 7.00. The slope of the regression line indicates that there is decreasing community similarity with increasing island size, a reversal of the expected trend. Araneae may be best suited to lightly forested regions, accounting for this relationship.

Material presented in this chapter will be examined further in Chapter 5, Discussion.

FIGURE 11. ELLENBURG'S FREQUENCY COEFFICIENT OF COMMUNITY SIMILARITY FOR ANIMALS. (Plotted against log area.)



Only one significant regression line.

## CHAPTER 5: DISCUSSION

The fundamental questions raised by island biogeographic theory, as outlined in Chapter 1, Section 2. 2. (p. 8 ), are considered here in detail for each group within the study. This includes an appraisal of species-area and species-distance relationships, as well as species proportions. Additionally, some recent views on possible causal explanations for the species- area relationship, conservation and competition are presented.

### Section 1 Plants

Consideration of the plant data initially involves the definition and elimination of non-forest species. Chi-squared analysis strongly supports the exclusion of non-forest plants, allowing an assessment which is presumed to be more realistic. An examination of the raw information reveals that a large number of non-forest plants are found in the smaller islands.

The species-area relationship (MacArthur and Wilson, 1967) is in general supported by the data. The unworked data shows large islands and mainlands to have more species than small islands and mainlands. Moreover, the difference between the number of forest species in an island and its corresponding mainland increases with

decreasing site size, islands supporting fewer species than mainlands. Chi-squared analysis of the total number of plant species, (not significant at the 5% level), suggests that small islands carry fewer plant species than would be expected, agreeing with the pattern noted for the unanalysed information.

The graph of number of species plotted against log area for each site, (Figure 4, between pp. 20 and 21 ), presents major evidence in support of a species-area relationship for plants in this study. The lines for both island and mainland are significant under linear regression analysis. Because of the importance of the species-area relationship, it seems appropriate here to examine its mathematical background and graphical representation.

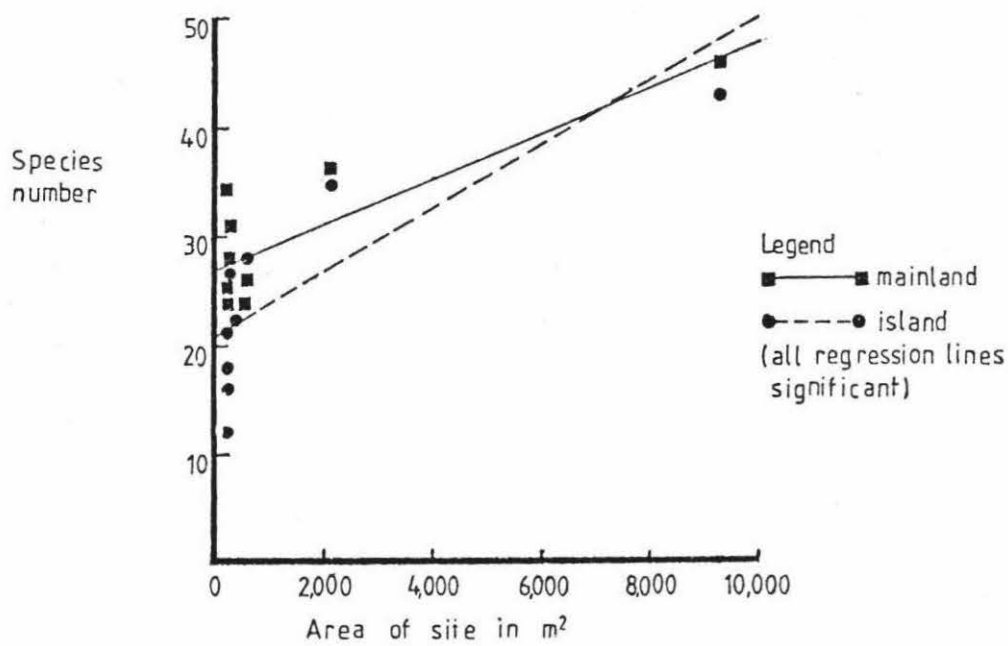
The species-area model has been examined mathematically in a variety of ways, (see Connor and McCoy, 1979). The species-area relationship can be expressed as the function  $S = kA^z$ , where  $S$  is the number of species,  $A$  is the area of the island and  $k$  and  $z$  are constants;  $z$  being the slope of the species-area graph and  $k$  being the  $y$  intercept on the graph. (For further discussion of this function see Chapter 1, Section 1 p. This function is often approximated by the double logarithmic or power function (Arrhenius, 1921);  $\log S = \log k + z \log A$ . Gleason (1922) noted that the equation presented by Arrhenius gave impossibly high estimates of species numbers when applied to large areas; he therefore proposed the exponential relationship:  $S = \log k + z \log A$ .

Connor and McCoy (1979) test the possible graphical relationships, (log species number versus log area; species number versus log area; log

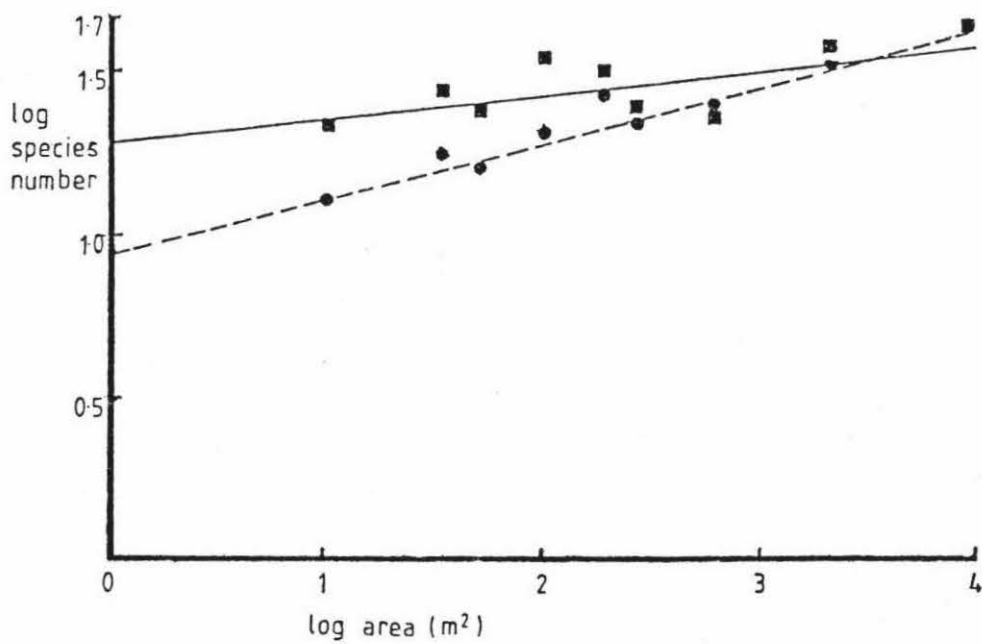
species number versus area and species number versus area), in an attempt to find the model giving the best statistical fit. The premises for transforming independent or dependent variables in regression analysis are: "to transform a curvilinear relationship into a linear one, and to normalize the residuals and make them homoscedastic" (Sokal and Rohlf 1969). The model which produces a linear relationship and reduces the deviation of points around the regression line is categorized as the best model. It is found that the power function and the untransformed models provide good fits most frequently, Connor and McCoy (1979) advocate "continued use of the power function and other linear models because of the relative ease with which they can be compared, and their past and present usage". They do however warn that approximating models with the power function may mask valuable biological information, and it therefore seems most appropriate to utilize the model giving the best statistical fit. Further, one may expect the power function model to fit studies with relatively large area ranges better, as a consequence of higher species number. The apparent lineation of the relationship between species number and area (untransformed) may be the result of sampling a narrow range of areas.

The debate over the presentation of the species-area relationship has necessitated inclusion of graphs of species versus area and log species versus log area (Figure 12A and B between pp. 55 and 56 ), as well as their significance under regression analysis, for comparison with the species-log area graph, Fig. 4. (between pp. 20 and 21 ) included in Chapter 2. From regression analysis, F ratios for all the graphs in both figures 4 and 12A and B

FIGURE 12. A. SPECIES-AREA GRAPH FOR PLANTS.



B. LOG SPECIES-LOG AREA GRAPH FOR PLANTS.



are significant; the critical value at the 5% level being 5.59 and at the 1% level 12.20. F ratios for the species-area graph are 15.12 and 20.01 for island and mainland respectively; for the species-log area graph values are 152.13 and 9.74; and for the log-species-log area graph 155.16 and 8.28. Despite the similar F ratios for the species-log area and the log species-log area graphs, figure 4 appears to be the most appropriate model in the light of the above discussion; the total number of species under examination is not large, and thus the power function graph may obscure some information. The lineation of the spp-area graph may be an artefact of the narrow range of areas sampled.

The constants  $z$  and  $k$  in the equation  $S = kA^z$  can be inferred from the slope parameter and the intercept parameter of the power function, (log species versus log area graph), (MacArthur and Wilson, 1967). Connor and McCoy (1969) challenge this view stating "published predictions and interpretations concerning both the slope and the intercept parameters are not supported by the available evidence", and they are "skeptical that any biological significance can be attached to these parameters and recommend that they be viewed as fitted constants devoid of specific biological meanings."

Despite this dispute it seems useful to present the slope of the log/log graph for comparison with the predicted figures. Preston (1962) stated that the slope of the log/log graph for isolated areas (i.e. islands) would fall between 0.20 and 0.40. MacArthur and Wilson (1967) hypothesised that the slope for island sites

would be between 0.20 and 0.35, and they also conclude that the slope of the log/log graph will be between 0.12 and 0.17 for non-isolated area. An explanation for the difference in slope between island and mainland is given by Galli et al. (1976); habitat islands differ from parcels of habitat within a mainland, in that parcels of habitat receive species enrichment from adjoining terrain, and this is minimized in the case of islands, which also provide an edge effect. Experimentally determined values may fall outside the theoretical range, for example Johnson et al. (1968) produced a slope of 0.472 for islands and 0.158 for mainlands.

The figures in this instance for the slope of the log/log graph are 0.175 and 0.078 for island and mainland respectively. Both these values are consistently lower than predicted; the island value being 0.025 less than the lowest forecast, and the mainland value being 0.042 smaller. It may be hypothesised that habitat islands have a higher immigration rate of transient species than do islands isolated by water, resulting in a reduced slope for the log species-log area graph.

No regularly occurring value is apparent for the intercept parameter; MacArthur and Wilson (1967) proposed that the species intercept may be affected by local environmental conditions or other factors. Heatwole (1975) suggests we abandon attempts to attach biological significance to the y intercept, and instead turn our attention to the x or area intercept, which he believes to be an indication of the "minimal area" necessary to support a breeding

population of the particular taxon studied. A study performed by Usher (1979) on nature reserves in Yorkshire indicates that the coefficients  $c$  and  $z$  are dynamic and can change with time, having significant implications for conservation policies.

The  $y$  or species intercepts for the log species-log area graph are 0.955 (9.02 species) and 1.294 (19.68 species) for island and mainland respectively. The harsh montane environment may restrict species diversity, as well as population density, accounting for the relatively low species intercept found for this study. MacArthur and Wilson (1967) state that this value "clearly should be less in those regions where quality of the environment is poorer and the total number of organisms in the taxon smaller".

Jaccard's coefficient of community and Ellenburg's frequency coefficient of community similarity both serve to emphasize the species-area relationship. Jaccard's (1912) coefficient of community shows that small islands have less plants in common with their respective mainlands than do large islands. Ellenburg's (1956) frequency coefficient of community likewise demonstrates a general trend towards increasing community similarity, on the basis of percentage frequency, with increased area.

Examination of species proportions reveals that there is a large difference in the proportions of plants between islands and their associated mainlands in many cases. Spearman-Rank correlation tests applied to this information disclose that proportions of trees

in island-mainland pairs are only related in very large sites. Shrubs show a greater degree of relationship between island and mainland, particularly in larger sites. Where it is possible to test ferns and herbs, they appear unrelated. One possible explanation is that an equilibrium situation may only prevail on very large islands for trees, and on medium sized islands for shrubs, given that mainland species are at equilibrium.

None of the data support a species-distance relationship, perhaps because the sites are all too close to their mainlands for such a relationship to exist. The reduced barrier to dispersal between a habitat island and its mainland, when compared with an island surrounded by water, may contribute largely to the absence of a species-distance relationship: animals will continually reach islands from the mainland, however island size alone will limit their success.

One predominant question arises from the demonstration of a species-area relationship within the plants; if it were possible to divide plants into dispersal groups, would a pattern emerge entailing the occurrence of rapidly dispersing (*r* selected) species on small islands, similar to that observed by Whitehead and Jones (1968)? (*r* selection is defined by MacArthur and Wilson, 1967, as: "selection favouring a higher population growth rate and higher productivity. This form of selection will come to the fore during the colonization episode, or in species which are frequently engaged in colonizing episodes".)

## Section 2    Litter Crustacea.

The low species diversity of the litter Crustacea, combined with the presence of a continuous litter substrate between island and mainland, has necessitated a different approach to these animals.

Attempts to eliminate non-forest species are inappropriate where litter provides a continuous habitat between mainland and island, instead habitat preferences have been studied. Analysis shows that some species optimally inhabit the mainland (Bryocamptus stouti), whilst others prefer the island situation (Goniocyclops silvestris and Mesocypris audax), and still others appear to be primarily non-forest dwellers (Trichoniscus phormianus and the unknown ostracod). This tendency towards habitat preference, as opposed to habitat restriction, presents complications in the examination of possible species-area relationships. There will not be a direct relationship between island size and numbers of species, or between island size and numbers of animals per square metre, when the assumption that all the species involved optimally inhabit mainland forest breaks down. Nevertheless, it remains possible to draw some conclusions from the results. Examination of the mean number of animals per metre square for each species shows that in all sites the mean number of animals found in mainlands is higher than that found in islands, suggesting that the mainland environment may be able to sustain a greater Crustacean biomass. Litter depth may be instrumental in determining the biomass of Crustacea a site is able to support; a study

of Acari performed by Stanton and Tepedino (1977) demonstrated such a relationship.

It seems probable that the species composition of a site is more closely related to the carrying capacity of the site and to the interactions between Crustacean species, than to any sort of species-area relationship.

### Section 3 Pitfall trap animals.

Habitat continuity precludes the elimination of non-forest species collected in pitfall traps. Statistical analysis does not support the separation of species found in traps placed outside the sites from the total data. A habitat preference situation similar to that demonstrated for litter Crustacea may well exist for pitfall trap animals.

The pitfall trap data do not confirm a species-area or a species-distance relationship; plots of species number against log area, and against distance from the mainland, are not significant at the 5% level, (regression analysis). The small distance between an island and its corresponding mainland may account for the lack of a species-distance relationship, (see Section 1 of this chapter, p. 59 ). A difference in the number of species supported by an island and its corresponding mainland is apparent in the extreme case of a very small site, similarly a decline in the absolute total number of animals can be noted for very small islands, suggesting that a partially obscured species-area relationship may occur. Chi-squared tests carried out

on the total number of animals in taxonomic groups (Colembola, Diptera, Acari, Phalangida, Diplopoda and Crustacea) more animals than expected are found in large island sites, whilst less than expected occur in small island sites, again indicating a possible species-area relationship. However the occurrence of some groups (e.g. Araneae) does not appear to be dependent upon the size of the site.

Whilst giving a reasonable estimate of the number of species in sites, pitfall traps will not accurately represent species proportions; relatively high numbers of actively dispersing species will be collected, and predators may be attracted to traps by the presence of their prey. An examination of species proportions using pitfall trap material was thus considered invalid.

Frequency of occurrence in traps has been used in the determination of Ellenburg's frequency coefficient of community similarity; this coefficient indicates percentage similarity in the frequency of animals occurring in pitfall traps, rather than absolute proportions of species within sites.

A tendency towards an association between island size and declining community similarity is manifested in both Jaccard's coefficient of community and Ellenburg's frequency coefficient of community similarity, supporting a semi-hidden species-area relationship.

The total absence of a species-area relationship is not unheard of; a study of large mammals on East African reserves (Miller and Harris, 1977) demonstrates no relation between the number of species and area. There are

numerous possible explanations for the concealment of a species-area relationship for pitfall trap animals, these can be broadly classed in terms of:

1. Feeding relationships.
2. Colonization and survival abilities.
3. Habitat requirements.
4. Species packing.
5. Individual taxonomic differences.
6. Sampling procedure.

Each of these is discussed in the following sections.

### 3. 1. Feeding relationships.

A consideration of the number of species per site, as well as the total number of animals collected in traps in each site, may be insufficient to demonstrate a relationship between species and area.

Feeding relationships may play an important role in the species-area relationship. Rey and McCoy (1979) suggest the division of animals into two groups, herbivores and predators/ parasites. They predict that predators will exist in high numbers in the mainland and low numbers in an island. Increasingly large islands may be expected to support progressively larger numbers of predator species. With increasing distance from the mainland there will be greater dominance by herbivores. Simberloff (1976) also suggests predators and parasites are likely to suffer extinction with decreased area. The animals trapped in this study are insufficiently known to infer accurately feeding relationships, however, if it were possible to categorize animals as herbivores and predators, a more

obvious species-area relationship could emerge.

A measure of the biomass as opposed to the total number of animals obtained may indicate that progressively larger islands support an increasingly large biomass, lending support to any demonstrable species-area relationship.

### 3. 2. Colonization and survival abilities.

The ability to colonize a site and survive in it is important in determining a species-area relationship.

The colonization and survival abilities of animals collected in pitfall traps may be highly variable, Simberloff (1976) emphasises this stating "three of these species, the nonballooning spider Ariadna arthuri, the polyxenid millipede Lophoproctinus bartschi, and the oniscid isopod Rhyscotus sp., combine poor dispersal ability with extremely good persistence once present. This contrasts with several spiders.....and bugs which seem to be adept at reaching islands but are quite likely to be extinguished once there."

It seems possible that a large number of species with high dispersal ability but poor capacity to persist in a site, (r selected), and a small number of species with low dispersal ability but good survival ability, (K selected, defined by MacArthur and Wilson 1967 as "Selection favouring a more efficient utilization of resources,"), may be trapped. Bias would thus arise in the overall results, and prevent a species-area relationship from becoming apparent.

In assessing animals collected in traps

the assumption is made that animals found in the traps are able to survive and reproduce within the habitat from which they have been sampled.

Although pitfall trapping would appear to be a satisfactory method of obtaining information regarding animals existing in a particular site, as opposed to other forms of trapping (Chapter 4 p. 42 ), the assumptions made regarding survival and reproduction remain contestable.

The question of whether the animals collected are propagules arises for mobile species, (animals), whereas for non-mobile species, (plants), the sampling technique employed selects only established propagules (Chapter 2 Section 1. 2. p. 15) MacArthur and Wilson (1967) define a propagule as "The minimal number of individuals of a species capable of successfully colonizing a habitable island. A single mated female, an adult female and a male, or a whole social group may be propagules providing they are the minimal unit required".

The capacity to reproduce is an important criterion in deciding which animals are relevant to the habitat and are likely to survive, yet it has been pointed out that this data would be "almost impossible to obtain" (Rey and McCoy, 1979). The presence of animals in pitfall traps which are unable to survive if restricted to the habitat from which they are collected could well be of major importance in obliterating any species-area relationship present.

### 3. 3. Habitat requirements.

Habitat requirements may vary radically between species; subtle variations in microhabitat

between sites may result in different species establishing. For example Mader and Mühlenberg (1981) in a study of carbid species found that the species composition in a small forest island had little similarity with that of the larger forest or surrounding fields; only two large forest species were caught in the small forest island.

The plant community present in a site may also perform a role in the species present; Root (1973) found that insects on plants were organised into component communities with few connections between these units.

### 3. 4. Species packing.

MacArthur (1972) indicated that similar habitats with closely packed species may be occupied by very different numbers of species, otherwise, where species are not closely packed, similar habitats should have similar species with only slight differences in abundance. If species were found to be closely packed in beech forest islands, then similar habitats could contain different numbers of species, accounting for the lack of a species-area relationship.

### 3. 5. Individual taxonomic differences.

Authors have invoked different explanations for the distributions of various animal taxa in their studies: Goldstein (1974) suggested that marginal habitat was the explanation for the low populations on small islands, rather than low immigration rate into distant sites. Stanton and Tepedino (1977) find that mite species diversity is a function of the amount of litter present and microclimatic predictability. Mühlenberg et al. (1977, two papers) study both spiders and ants on some Seychelles islands and

propose different explanations for the distributions of each of these groups: immigration and extinction rates, as well as a greater spectrum of resources being available on larger islands, explains the correlation between the number of species and area of the site for spiders. There is no significant correlation between the number of species, island size and the available resources, in the case of the ants. Instead, the diversity and number of ant species does not vary considerably between different habitats; correlation between niche breadth and relative abundance of ant species appears to explain the pattern observed.

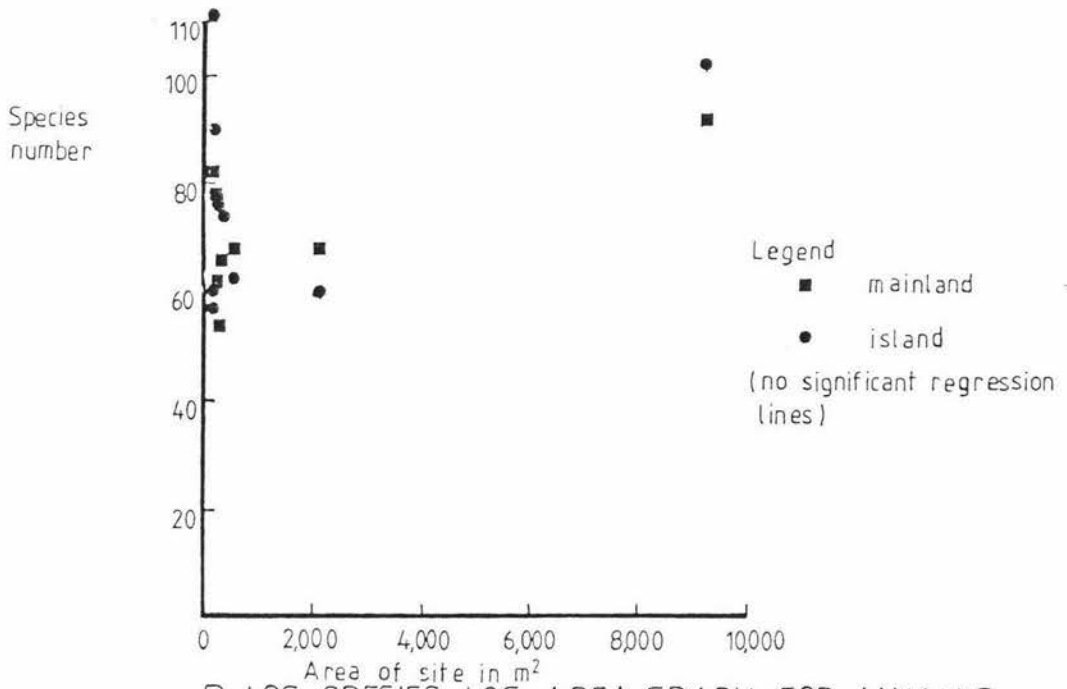
The wide range of explanations for the varied distributions of animals belonging to different taxonomic groups indicates that no single hypothesis will be adequate to explain the diverse relationships between the groups. Each taxon may be entitled to an individual explanation of its distribution, dependent upon characteristics of the group itself, and the particular situation in which it occurs.

### 3. 6. Sampling procedure.

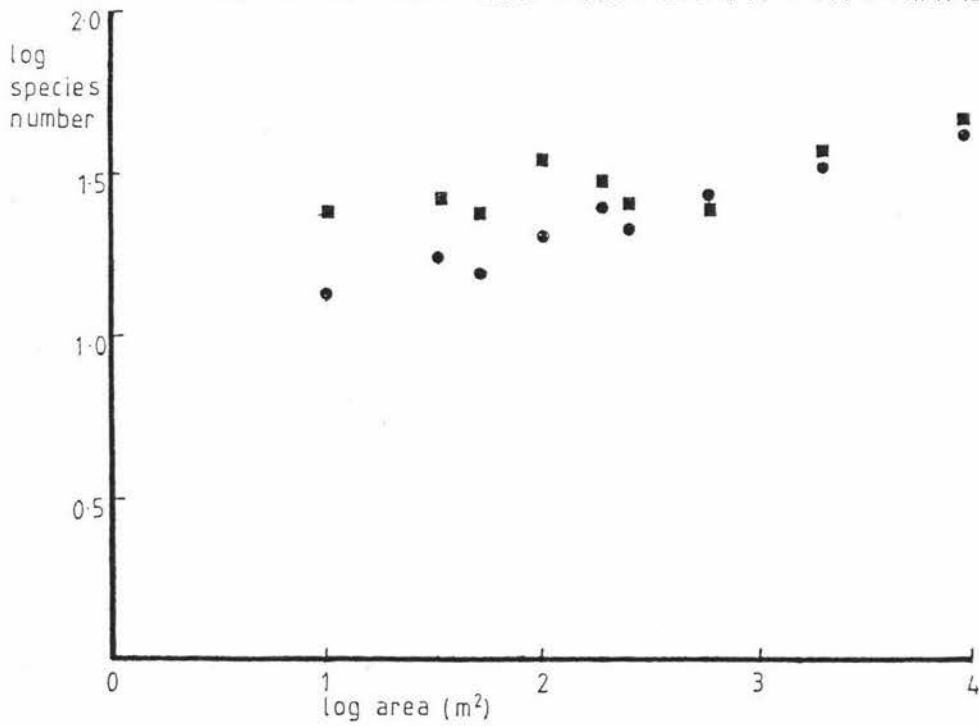
A further possible explanation for the reduced species-area relationship for pitfall trap animals should be entertained; although a large number of samples were taken, this quantity may still have been insufficient to overcome the seasonal effects, hence obscuring any species-area relationship.

(Figures 13 A and B, between pp. 67 and 68, plot the species-area and the log species-log area graphs for animals; neither are significant under regression analysis.)

FIGURE 13. A. SPECIES-AREA GRAPH FOR ANIMALS.



B. LOG SPECIES-LOG AREA GRAPH FOR ANIMALS.



## Section 4 Combined plant and animal data.

Table XVII below gives the total number of species, plant and animal, found in both islands and mainlands.

Table XVII Total number of species, both plant and animal, found in islands and mainlands.

Site Number	1	2	3	4	5	6	7	8	9
Number of species in island	146	95	91	96	102	132	73	108	73
Number of species in mainland	138	104	94	90	85	112	85	105	107

With the exception of the species-area relationship for the mainland, none of the three types of presentation (species/area, species/log area and log species/log area, Figure 14 A, B and C, between pp. 68 and 69 ) were significant at the 5% level under regression analysis. It may reasonably be assumed that the lineation of the species-area graph for the mainland can be attributed to the narrow range of areas sampled, thus no overall species-area relationship is apparent.

In order to elucidate the lack of a significant species-area relationship for the total data, the Pearson product-moment correlation coefficient was determined for a comparison of plant and animal data. The correlation coefficient is not significant at the 5% level, (coefficient = 0.276, and the critical value for 7 degrees of freedom is 0.666), showing that

D. SPECIES LOG AREA GRAPH FOR ALL SPECIES.

log area (m <sup>2</sup> )	Species number (Circles)	Species number (Squares)
1.0	75	110
1.5	110	108
1.8	75	85
2.0	135	112
2.2	105	85
2.4	95	90
2.8	90	95
3.3	95	105
4.0	145	140

Figure 1 is a scatter plot showing the relationship between log species number (Y-axis) and log area (m²) (X-axis) for all species. The Y-axis ranges from 0 to 2.5, and the X-axis ranges from 0 to 4. Data points are categorized by location: mainland (squares) and island (circles). A legend indicates that only one significant regression line is shown. The data points are clustered around a log species number of 2.0, with log area values ranging from approximately 1.0 to 4.0.

there is no relationship between the number of plant species in a site and the number of animal species also found there.

However, this does not rule out a relationship between some plant and animal species in the various sites. Dynamic coevolution between host plants and associated animals, involving reciprocal adaptations between herbivores and plants, is believed to be important in an examination of species-area relationships, (Strong, 1979).

Several further factors which may influence the general species composition of sites should be noted.

The importance of edge effects in habitat islands should not be overlooked; in very small islands edge effects may play a major role in influencing the populations of plants and animals present. Variation in microclimate at the edge of a site can result in the establishment of non-forest plant species and their associates. Gilbert(1980) states that the increased environmental heterogeneity found at the edge of small islands can have a major effect upon species composition.

Although the assumption is made that the factors of altitude, history and climate are all constant, and attempts have been made to ensure this is the case as far as is possible, it is difficult to find a natural situation complying with all factors (Strong, 1979). Minor variations in the factors may be sufficient to disrupt any species-area patterns.

The large number of possible reasons for a species-area relationship not being

apparent, presented here and in section 3 of this chapter, serve to emphasize the importance of the presentation of non significant data urged by Connor and McCoy (1979); "such examples are as informative about the species-area relationship as are significant positive correlations". Any number of the explanations given may be important in this particular study.

Section 5    Possible causal explanations for  
the species-area relationship.

Although the existence of a species-area relationship in many situations is generally indisputable, (although Kuris et al., 1980, have questioned even this), the theoretical basis for the relationship remains a point of argument.

The most prominent underlying causal relationship is the equilibrium hypothesis, sometimes known as the area- per se hypothesis, proposed by MacArthur and Wilson (1967). This theory explains species number as a function of immigration and extinction rates. Although support for this hypothesis comes from a number of studies, many authors (e.g. Gilbert, 1980, Strong, 1979, and Lawton et al. 1981) believe acceptance of the MacArthur and Wilson (1967) theory occurred before sufficient evidence had accumulated in support of it.

Gilbert (1980) states that Simberloff and Wilson (1969) provided the only irrefutable evidence in favour of the theory, and Simberloff (1976) himself remonstrates strongly in support of the equilibrium hypothesis: "Habitat diversity differences are not a sufficient explanation of the widely observed effect of area upon species number". Other recent work confirming the equilibrium theory includes that of Wallace (1975) whose simulation experiment using *Drosophila* shows that the species number on an island is determined by those that arrive minus those that are lost; and Dritschilo et al. (1975)

who draw the analogy between mites on mice and species equilibrium numbers of island faunas. Lassen's (1975) work on fresh water snails lends strong support to the idea of a dynamic equilibrium, and Abele and Patton (1976) have also demonstrated the feasibility of this hypothesis.

Amongst those who believe that causal relationships should not be invoked from demonstration of the species-area relationship is Gilbert (1980); the presence of a relationship does not necessarily imply the existence of a dynamic equilibrium. He also remarks that equilibrium theory was accepted before there was sufficient evidence to demonstrate its validity. Other authors are in agreement with this view-point; Strong (1979) says "there is no reason to interpret the species-area relationship as a justification for the equilibrium model, or vice versa because the relationships are neither uniquely predicted by it, nor do they corroborate in a more than trivial way." Also Lawton et al. (1981) state that "species-area relationships are empirical patterns; to find them or to look for them in no way implies acceptance of the MacArthur-Wilson theory of island biogeography (MacArthur and Wilson, 1967)".

Another very reasonable possibility for an explanation for the species-area relationship is the "habitat diversity hypothesis", (Williams, 1964), in which as the size of the area sampled is increased, new habitats with their associated species are encountered, culminating in increased species number with area. Support for the concept of increasing habitat heterogeneity ultimately resulting in the species-area relationship comes from several authors. Goeden (1979) finds that for reefs,

sites with the greatest habitat diversity tend to have the greatest absolute number of species, however he concedes that it is difficult to extrapolate to other cases, since large environmental differences are involved. Goldstein (1974) indicated that niche segregation and community structure were important controlling factors in the species-area relationship. Other authors who have demonstrated a positive correlation between species number and number of habitats include Abele (1974), Harman (1972) and Dexter (1972).

Connor and McCoy (1979) advocate an alternative to the area per se and habitat diversity hypotheses in the form of the null hypothesis; "under this hypothesis the correlation between species number and area is viewed solely as a sampling phenomenon, rather than the result of biological processes such as diversification through specialized habitat utilization or the balancing of species immigrations and extinctions." Through passive sampling from the species pool, larger areas will receive effectively larger samples than smaller areas and ultimately contain more species. Osman (1977) shows that passive sampling is probably very important in determining the number of species found on different sized boulders in the subtidal zone.

Other suggested mechanisms differ according to circumstances. Work on strand islands carried out by Whitehead and Jones (1968) showed that species number on small islands is limited almost exclusively by island ecology. From an assessment of foliage height, diversity and cover, Galli et al. (1976) infer habitat differences to be minimal, instead they attribute observed increase in bird species richness to

progressive encountering of different minimum areas, breeding and feeding territories being capable of predicting this pattern. Immigration-related processes appear almost entirely responsible for initiating a relatively stable species-area relationship in the work of Schoener and Schoener (1981). Strong (1979) suggests "pseudoturnover" may be created by repeatedly immigrating or vagrant species in some situations, accounting partially for the species-area relationship.

Each of the three major mechanisms is probably important in determining the relationship between species number and area in one or another species assemblage, although it is "difficult to assess their proportional contribution in any particular study," (Connor and McCoy, 1979). They believe that most studies have failed to eliminate the alternative hypotheses; "to conclude that habitat diversity alone is the cause of the species-area relationship one must not only demonstrate the effects of such diversity on numbers of species, but also the lack of any relationship between extinction probabilities and area. On the other hand, to conclude that area alone can influence the number of species one must identify a species-area effect in a truly homogeneous habitat.....the reasons underlying ideal diversity patterns can be elucidated only by sound biological examination and experimentation, not by the invocation of currently accepted dogma". Gilbert (1980) also places emphasis upon the inability of a single theory to fit all situations, due to the large degree of variation in different circumstances.

This brief review outlines the range of possible mechanisms for the species-area

relationship; many of these mechanisms may be involved in an explanation of the obvious species area-relationship for plants, and the partial species-area relationship for animals seen in this study. It would appear futile to suggest a monopoly of any one particular causal explanation, without clear evidence against the others.

## Section 6 Species co-occurrence on islands.

Recently, the role of competition in species co-occurrence on islands has come under scrutiny. Diamond (1975) proposes several assembly rules for bird communities; these indicate patterns of permitted and forbidden combinations of species able to co-exist as resident populations on islands. He believes that such patterns can be explained by interspecific competition for resources, over exploitation strategies, differences among dispersal rates, and low transition probabilities between "permissible combinations".

The assembly rules are challenged by Connor and Simberloff (1979), who make a strong argument for competitive exclusion by observed active replacement of one species by another.

Evidence in support of interspecific competition is given by Diamond and Gilpin (1982): ecologically similar species frequently inhabit separate close islands, "interspecific fighting, overlap in diet, niche shifts in habitat and abundance correlated with presence or absence of competitors, failed invasions of species on islands occupied by competitors, decline in abundance of species following a successful invasion by a competitor, and evolution of character displacement within historical times following successful invasions".

A method of analysis allowing comparison of co-existing species has been devised by Gilpin and Diamond (1982). Using this method they show that there is far more non-randomness to the overall pattern of species

co-existence within a guild than would be expected. The reasons for such a non-random distribution are "related to species habitat preferences, endemism, competition, geographical origins and distributional strategies".

It appears that a complex range of factors are important in species co-occurrence on islands, and it is possible that many of these may be involved in the distribution of species within sites examined in this study.

## Section 7 Conservation and reserve size.

Within the context of conservation, disagreement has arisen over the suitability of differing reserve sizes. Simberloff and Abele (1976) propose that several small refuges may preserve more species than a single large refuge under a number of biologically feasible conditions. Diamond (1976), Terborgh (1976) and Whitcomb et al. (1976) criticise this stand-point on several grounds; a small refuge may not preserve species which require a minimum area or population size for survival; small refuges are less likely to preserve all trophic levels; extinction proceeds more rapidly in small refuges, and fragmentation of an available refuge area is an irreversible strategy. Cole (1981) shows that where islands contain only a very small fragment of the total species pool, more species occur in small broken areas, however this is inappropriate for permanent refuges where attempts are made to preserve a large portion of the species pool. He concludes that in general larger refuges or islands preserve more species than a series of small refuges of equivalent total area.

Perhaps the real reason for disagreement is a quantitative as opposed to a qualitative examination of species in small areas. In studies such as those of Wilson and Simberloff (1969), Simberloff and Wilson (1969), Simberloff (1969) and Simberloff (1976) a large number of different species may be present in different sites. These will largely represent r-selected species, however the species referred

to by Diamond (1977) and others are primarily k-selected which, although they may not amount to such a large total number of species, are qualitatively important from a conservation aspect. This is exemplified in the work of Jarvinen and Ulfstand (1980) who note that in Denmark, Sweden, Norway and Finland an average of 2.8 r-selected species and 0.6 k-selected species constitute successful colonists per decade.

Williamson (1975) reinforces the need for sufficiently large native reserves remarking that "if a reserve is intended to maintain 'central' species, then its effective size is smaller than its apparent area, since edge species will frequently be different from those at the centre of the reserve".

It is difficult to predict a suitable minimum size for a beech forest nature reserve using the information collected, since pitfall trap animals appear to differ between island and mainland even in very large sites. However, it seems likely on the basis of the data gathered, that an area of approximately 9,225 m<sup>2</sup> (the size of Site 1), would be sufficiently large to preserve a full compliment of species.

## Section 8 Conclusion.

From this study, the species-area relationship, described by MacArthur and Wilson (1967), is apparent for plants in habitat islands of indigenous beech forest. Habitat continuity restricts examination of litter Crustacea to an assessment of habitat preference. A possible species-area relationship for pitfall trap animals is obscured by a number of proposed factors.

Neither plants nor animals in this study conform to a species-distance relationship; it seems probable that the habitat between island and mainland, as well as the relatively small island-mainland distance, does not provide a sufficient barrier to dispersal.

An explanation of the possible relations is enhanced by information provided by species proportions and numbers of individuals.

Appendix I Age structure of trees in island-mainland pairs (Kilmogorov-Smirnov two sample test).

Legend

I = Island

M = Mainland

A total of 20 trees in each site were sampled. For significance at the 5% level an absolute difference in tree numbers of 9 is required, where  $N = 20$ .

Site 1.

Diameter class (cm)	Number of trees in each diameter class		Absolute difference in number of trees
	I	M	
10-14	1	0	1
15-19	1	2	1
20-24	4	2	2
25-29	1	3	2
30-34	2	7	5
35-39	5	3	2
40-44	1	1	0
45-49	3	0	3
50-54	2	1	1
55-59	0	1	1

Greatest absolute difference in tree numbers = 5  
(not significant)

Site 2.

Diameter class (cm)	Number of trees in each diameter class		Absolute difference in number of trees
	I	M	
5-9	0	1	1
10-14	2	5	3
15-19	2	2	0
20-24	7	3	4
25-29	4	2	2
30-34	1	2	1
35-39	1	2	1
40-44	2	2	0
45-49	0	0	0
50-54	0	0	0
55-59	0	0	0
60-64	1	0	1
65-69	0	0	0
70-74	0	1	1

Greatest absolute difference in tree numbers = 4  
(not significant)

## Site 3.

Diameter class (cm)	Number of trees in each diameter class		Absolute difference in number of trees
	I	M	
5-9	3	0	3
10-14	4	1	3
15-19	1	5	4
20-24	3	3	0
25-29	3	6	3
30-34	4	3	1
35-39	1	2	1
40-44	0	0	0
45-49	0	0	0
50-54	0	0	0
55-59	1	0	1

Greatest absolute difference in tree numbers = 4  
(not significant)

## Site 4.

Diameter class (cm)	Number of trees in each diameter class		Absolute difference in number of trees
	I	M	
10-14	1	0	1
15-19	7	3	4
20-24	4	9	5
25-29	0	4	4
30-34	4	2	2
35-39	1	0	1
40-44	0	0	0
45-49	0	1	1
50-54	2	1	1
55-59	0	0	0

Greatest absolute difference in tree numbers = 5  
(not significant)

## Site 5

Diameter class (cm)	Number of trees in each diameter class		Absolute difference in number of trees
	I	M	
5-9	1	2	1
10-14	8	4	4
15-19	5	7	2
20-24	2	5	3
25-29	1	0	1
30-34	1	1	0
35-39	0	1	1
40-44	1	0	1
45-49	0	0	0
50-54	0	0	0
55-59	0	0	0
60-64	1	0	1

Greatest absolute difference in tree numbers = 4  
(not significant)

## Site 6

Diameter class (cm)	Number of trees in each diameter class		Absolute difference in number of trees
	I	M	
10-14	0	5	3
15-19	1	5	4
20-24	0	2	2
25-29	1	2	1
30-34	2	2	0
35-39	3	2	1
40-44	3	1	2
45-49	3	0	3
50-54	1	0	1
55-59	2	0	2
60-64	1	0	1

Greatest absolute difference in tree numbers = 4  
(not significant)

Diameter class (cm)	Number of trees in each diameter class		Absolute difference in number of trees
	I	M	
0- 4	0	2	2
5- 9	2	0	2
10-14	5	5	0
15-19	2	4	2
20-24	2	3	1
25-29	2	0	2
30-34	0	0	0
35-39	1	0	1
40-44	0	0	0

Greatest absolute difference in tree numbers = 2  
(not significant)

Appendix II. Species presence/absence.  
(Forest and non-forest species).

Legend

I = Island  
M = Mainland  
X = Species presence

TREES

Forest species.

Site number	1	1	2	2	3	3	4	4	5	5	6	6	7	7	8	8	9	9
	I	M	I	M	I	M	I	M	I	M	I	M	I	M	I	M	I	M
<u>Nothofagus solandri</u>	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
<u>Phyllocladus alpinus</u>	X	X	X	X	X	X	X	X	X	X	X	X	X	X			X	X
<u>Coprosma foetidissima</u>			X	X	X	X	X		X	X	X		X		X		X	X
<u>Neopanax simplex</u>	X	X	X		X	X	X	X		X				X		X		
<u>Myrsine divaricata</u>	X	X	X	X	X	X	X			X		X						
<u>Coprosma A</u>	X	X	X			X				X		X				X		
<u>Coprosma pseudocuneata</u>					X	X			X	X		X		X		X		
<u>Coprosma tenuifolia</u>	X	X	X	X						X		X						X
<u>Neopanax colensoi</u>	X		X	X						X		X				X		
<u>Griselinia littoralis</u>	X	X	X	X	X	X	X			X		X				X		
<u>Podocarpus hallii</u>	X	X					X					X						X
<u>Coprosma colensoi</u>					X	X				X								
<u>Coprosma microcarpa</u>		X		X		X												
<u>Libocedrus bidwillii</u>										X		X						



SHRUBS  
Forest species.

Site number	1 I	1 M	2 I	2 M	3 I	3 M	4 I	4 M	5 I	5 M	6 I	6 M	7 I	7 M	8 I	8 M	9 I	9 M
<u>Nothofagus solandri</u>	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
<u>Phyllocladus alpinus</u>	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
<u>Neopanax simplex</u>	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
<u>Cyathodes juniperina</u>	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X		X
<u>Myrsine divaricata</u>	X	X	X	X	X	X	X	X	X	X	X	X			X	X	X	X
<u>Griselinia littoralis</u>	X	X	X	X	X	X	X	X			X	X	X	X	X	X	X	X
<u>Neopanax colensoi</u>	X	X	X	X	X	X	X	X	X	X	X	X	X	X			X	X
<u>Coprosma foetidissima</u>	X	X	X	X	X	X	X	X	X	X	X	X			X	X	X	X
<u>Coprosma microcarpa</u>	X	X	X	X	X	X	X	X	X	X	X	X			X	X	X	X
<u>Coprosma pseudocuneata</u>				X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
<u>Coprosma A</u>	X	X	X	X	X	X			X	X	X	X			X	X	X	X
<u>Coprosma colensoi</u>	X	X		X	X				X	X	X	X			X	X	X	X
<u>Coprosma tenuifolia</u>	X	X	X	X		X			X	X	X	X						X
<u>Gaultheria antipoda</u>		X		X	X		X	X	X		X		X	X	X			
<u>Podocarpus hallii</u>	X	X			X		X	X	X		X	X	X	X				
<u>Coprosma B</u>				X			X			X		X	X		X	X		
<u>Cyathodes fasciculata</u>	X	X		X			X	X						X		X		

SHRUBS (continued)  
Forest species.

Site number	1 I	1 M	2 I	2 M	3 I	3 M	4 I	4 M	5 I	5 M	6 I	6 M	7 I	7 M	8 I	8 M	9 I	9 M
<u>Carpodetus</u> <u>serratus</u>	X	X		X								X						X
<u>Elaeocarpus</u> <u>hookerianus</u>	X		X						X									
<u>Coprosma</u> <u>linariifolia</u>				X					X									
<u>Pseudowintera</u> <u>colorata</u>	X	X																
<u>Libocedrus</u> <u>bidwillii</u>												X						
<u>Rubus</u> <u>schmidelioides</u>	X			X														
<u>Coprosma</u> <u>australis</u>			X															
<u>Pseudopanax</u> <u>crassifolium</u>	X																	
<u>Pittosporum</u> <u>kirkii</u>				X														
<u>Olearia</u> <u>arborescens</u>																X		
<u>Aristotelia</u> <u>serrata</u>			X															
<u>Coprosma</u> <u>linariifolia</u> <u>x tenuifolia</u>				X														

Non-forest species.

<u>Olearia</u> <u>nummularifolia</u>							X	X	X		X		X	X	X	X	X	
<u>Hebe</u> <u>venustula</u>							X		X		X				X	X	X	

SHRUBS (continued)  
Non-forest species.

Site number	1 I	1 M	2 I	2 M	3 I	3 M	4 I	4 M	5 I	5 M	6 I	6 M	7 I	7 M	8 I	8 M	9 I	9 M
<u>Myrsine</u> <u>nummularia</u>					X		X		X		X		X		X			
<u>Dracophyllum</u> <u>recurvum</u>							X		X		X		X		X		X	
<u>Cassinia</u> <u>vauvilliersii</u>							X	X	X		X			X				
<u>Dracophyllum</u> <u>filifolium</u>		X							X		X				X		X	
<u>Leptospermum</u> <u>scoparium</u>									X		X				X			
<u>Cyathodes</u> <u>colensoi</u>													X		X		X	
<u>Calluna</u> <u>vulgaris</u>		X		X														
<u>Gaultheria</u> <u>paniculata</u>							X						X					
<u>Epacris</u> <u>alpina</u>													X					
<u>Hebe</u> <u>stricta</u>				X														
<u>Hebe stricta</u> <u>x venultula</u>															X			
<u>Hebe</u> <u>tetragona</u>															X			
<u>Coprosma</u> <u>cheesmanii</u>															X			
<u>Cyathodes</u> <u>empetrifolia</u>															X			
<u>Pimelea</u> <u>microphylla</u>															X			

SHRUBS (continued)  
Non-forest species.

Site number	1 I	1 M	2 I	2 M	3 I	3 M	4 I	4 M	5 I	5 M	6 I	6 M	7 I	7 M	8 I	8 M	9 I	9 M
<u>Aciphylla</u> <u>squarrosa</u>		X																
<u>Dacrydium</u> <u>laxifolium</u>											X				X			

Total shrubs

Site number	1	2	3	4	5	6	7	8	9
Total island forest species	19	16	14	13	17	15	11	13	9
Total mainland forest species	19	18	12	14	14	15	14	14	13
Total island non-forest species	3	2	1	6	7	8	6	13	5
Total mainland non-forest species	0	0	0	2	0	0	2	2	0

HERBS  
Forest species.

Site number	1	1	2	2	3	3	4	4	5	5	6	6	7	7	8	8	9	9
	I	M	I	M	I	M	I	M	I	M	I	M	I	M	I	M	I	M
<u>Astelia</u> <u>nervosa</u>	X	X	X	X	X	X	X	X	X	X	X	X			X	X	X	X
<u>Lagenophora</u> <u>petiolata</u>	X		X		X	X	X	X	X	X	X	X	X	X		X		X
<u>Ourisia</u> sp.	X	X	X	X									X			X		
<u>Luzuriaga</u> <u>parviflora</u>					X	X	X	X		X								
<u>Pterostylis</u> sp.			X															
<u>Gastrodia</u> <u>cunninghamii</u>			X															

Non-forest species.

<u>Anisotome</u> <u>aromatica</u>						X	X	X		X		X	X	X	X	X		
<u>Celmesia</u> <u>spectabilis</u>						X	X	X		X		X	X		X	X		
<u>Helychrysum</u> <u>filicaulle</u>															X		X	
<u>Calorophus</u> <u>minor</u>																X		
<u>Luzula</u> <u>migrata</u>										X								

Total herbs

Site number	1	2	3	4	5	6	7	8	9
Total island forest species	3	5	3	3	2	2	1	1	1
Total mainland forest species	2	3	3	2	3	3	2	3	2

## HERBS (continued)

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Total herbs									
Site number	1	2	3	4	5	6	7	8	9
Total island non-forest species	0	0	0	2	3	2	2	3	3
Total mainland non-forest species	0	0	0	2	0	0	2	2	0

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Appendix III Species proportions expressed as a percentage.  
(Forest and non-forest species).

### Legend

I = Island

I = Island  
M = Mainland

TREES  
Forest species.

[illegible]



## Non-forest species.

Site number	1I	1M	2I	2M	3I	3M	4I	4M	5I	5M	6I	6M	7I	7M	8I	8M	9I	9M
<u>Olearia</u> <u>nummularifolia</u>	0	0	0	0	0	0	1	0	15	0	1	0	5	1	0	3	3	0
<u>Hebe</u> <u>venustula</u> .	0	0	0	0	0	0	0.5	0	35	0	8	0	3	0	35	2	3	0
<u>Myrsine</u> <u>nummularia</u>	0	0	0	0	0.5	0	3	0	4	0	8	0	3	0	0	0	0	0
<u>Dracophyllum</u> <u>recurvum</u>	0	0	0	0	0	0	1	0	15	0	3	0	2	0	0.5	0	25	0
<u>Cassinia</u> <u>vauvilliersii</u>	0	0	0	0	0	0	0.5	3	1	0	4	0	0	1	1	0	0	0
<u>Dracophyllum</u> <u>filifolium</u>	0	0	0	0	0	0	0	0	0.5	0	0.5	0	0	0	25	0	85	0
<u>Lentospermum</u> <u>scoparium</u>	0	0	0	0	0	0	0	0	4	0	2	0	0	0	2	0	0	0
<u>Cyathodes</u> <u>colensoi</u>	0	0	0	0	0	0	0	0	0	0	0	0	9	0	75	0	1	0
<u>Gaultheria</u> <u>paniculata</u>	0	0	0	0	0	0	4.5	0	0	0	0	0	9	0	0	0	0	0
<u>Epacris</u> <u>albina</u>	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
<u>Hebe</u> <u>stricta</u>	0	0	0.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<u>Hebe stricta</u> <u>x venustula</u>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.5	0	0	0
<u>Hebe</u> <u>tetragona</u>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0

## Total shrubs.

Total forest species	100	100	99.5	100	99.5	100	89.5	87	84	100	73.5	100	68	98	81.5	95	82	100
Total non-forest species	0	0	0.5	0	0.5	0	10.5	3	16	0	26.5	0	32	2	18.5	5	18	0

FERNS  
Forest species.

Site number	1I	1M	2I	2M	3I	3M	4I	4M	5I	5M	6I	6M	7I	7M	8I	8M	9I	9M
<u>Hymenophyllum</u> <u>spp.</u>	66	72	695	815	81	92	83	88	755	815	50	74	33	65	25	97	14	935
<u>Grammitis</u> <u>billardieri</u>	75	2	3	7	8	8	35	12	5	13	8	45	15	2	0	2	0	35
<u>Gleichenia</u> <u>cunninghamii</u>	0	0	35	5	11	0	0	0	0	55	0	105	0	33	4	0	0	0
<u>Blechnum</u> <u>penna-marina</u>	0	05	10	0	0	0	0	0	0	0	2	75	0	0	0	0	0	3
<u>Polystichum</u> <u>vestitum</u>	105	0	5	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
<u>Blechnum</u> <u>capense</u>	0	25	0	0	0	0	0	0	0	0	0	35	0	0	0	0	0	0
<u>Asplenium</u> <u>flaccidum</u>	3	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<u>Grammitis</u> <u>heterophylla</u>	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<u>Blechnum</u> <u>discolor</u>	0	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<u>Blechnum</u> <u>membranaceum</u>	0	55	0	15	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<u>Histiopteris</u> <u>incisa</u>	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<u>Todea</u> <u>hymenophylloides</u>	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<u>Blechnum</u> <u>fluviatile</u>	0	05	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Non-forest species.

<u>Gleichenia</u> <u>dicarpa</u>	0	0	0	0	0	0	125	0	185	0	40	0	64	0	705	0	86	0
<u>Lycopodium</u> <u>fastigiatum</u>	0	0	9	0	0	0	1	0	0	0	0	0	15	0	0	1	0	0
<u>Lycopodium</u> <u>scariosum</u>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	05	0	0	0

Total ferns

Total forest species	100	100	91	100	100	100	865	100	815	100	60	100	345	100	29	99	14	100
Total non-forest species	0	0	9	0	0	0	135	0	185	0	40	0	655	0	71	1	86	0

## HERBS

## Forest species.

Site number	1I	1M	2I	2M	3I	3M	4I	4M	5I	5M	6I	6M	7I	7M	8I	8M	9I	9M
<u>Astelia nervosa</u>	995	985	78	915	76	92	315	945	35	88	535	655	0	785	445	475	86	95
<u>Lagenophora petiolata</u>	05	0	21	25	23	4	11	55	645	95	4	33	15	0	0	135	0	5
<u>Ourisia</u> sp.	0	15	1	45	0	0	0	0	0	0	0	15	0	0	0	15	0	0
<u>Luzuriaga parviflora</u>	0	0	0	15	1	4	05	0	0	25	0	0	0	0	0	0	0	0

## Non-forest species.

<u>Anisotome aromatica</u>	0	0	0	0	0	0	475	0	45	0	27	0	7	2	7	35	15	0
<u>Celmesia spectabilis</u>	0	0	0	0	0	0	95	0	27	0	155	0	285	195	485	25	125	0
<u>Luzula migrata</u>	0	0	0	0	0	0	0	0	05	0	0	0	0	0	0	0	0	0

## Total herbs

## Total forest species

100 100 100 100 100 100 43 100 68 100 575 100 15 785 445 94 86 100

## Total non-forest species

0 0 0 0 0 0 57 0 32 0 425 0 985 215 555 6 14 0

Appendix IV. Paired litter cores sampled  
at 0.3 m and 0.6m from the tree  
base (Chi-squared analysis).

Pair number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Number of <u>Bryocamptus</u> <u>stouti</u> 0.3 m from tree base	4	2	3	1	1	13	2	4	1	1	6	24	13	0	0
Number of <u>B. stouti</u> 0.6 m from tree base	0	4	4	8	0	17	1	11	16	6	1	0	0	1	0

Only 6 out of the 15 values above were of  
sufficient size for analysis.

Table of O/E ratios for  
chi-squared test performed on  
these 6 values:

Pair number		
4	0.32	1.73
6	0.86	1.14
8	0.57	1.45
9	0.17	1.89
12	1.88	0.04
13	1.85	0.07

Chi-squared = 51.121 for 5 degrees of freedom  
therefore significant at the 5% level.

The remaining values were lumped in two groups;  
those where the number of animals 0.3m from  
the base of the tree was larger, and those where  
the number of animals 0.6m from the base of the  
tree was greater.

Number of animals at 0.3m greater			Number of animals at 0.6m greater		
Pair number			Pair number		
1	4	0	2	2	4
5	1	0	3	3	4
7	2	1	10	1	6
11	6	1	14	0	1
Totals					
	13	2		6	15

Table of O/E values for chi-squared test including lumped values.

Pair number		
	4	0.32 1.73
	6	0.86 1.14
	8	0.57 1.46
	9	0.16 1.90
	12	1.88 0.04
	13	1.84 0.08
No. animals at 0.3m greater	1.60	0.34
No. animals at 0.6m greater	0.59	1.44

Chi-squared = 60.751 for 7 degrees of freedom  
therefore significant at the 5% level.

There is a significant difference in the number of animals collected at 0.3 and 0.6m from the base of a tree, and O/E ratios show that this difference is not a consistent one. This suggests that the number of animals collected in paired cores 0.3 and 0.6m from the base of a tree will be independant of eachother.

## Appendix V. Total number of animals (90 cores)

	<u><i>Hyocamptus</i></u> <u><i>stouti</i></u>	<u><i>Goniocyclops</i></u> <u><i>silvestris</i></u>	<u><i>Tricho-</i></u> <u><i>niscus</i></u> <u><i>phormianus</i></u>	<u><i>Mesocycpris</i></u> <u><i>audax</i></u>	Ostracod (unknown species)
Site 1:					
Island	662	133	21	585	14
Mainland	990	155	31	690	62
Non-forest	0	0	6	1	15
Forest					
(island + mainland)	1,652	288	52	1,275	76
Site 2:					
Island	908	90	20	0	1
Mainland	613	34	24	0	1
Non-forest	50	2	2	0	6
Forest					
(island + mainland)	1,521	124	44	0	2
Site 3:					
Island	465	59	23	0	1
Mainland	1,115	89	33	0	0
Non-forest	0	0	1	0	0
Forest					
(island + mainland)	1,580	148	56	0	1
Site 4:					
Island	1,069	85	18	1	0
Mainland	683	29	40	0	0
Non-forest	0	0	0	0	0
Forest					
(island + mainland)	1,752	114	58	1	0
Site 5:					
Island	1,107	33	33	0	0
Mainland	3,400	66	18	0	0
Non-forest	2	0	0	0	0
Forest					
(island + mainland)	4,507	99	51	0	0
Site 6:					
Island	220	3	6	0	0
Mainland	2,982	73	29	0	0
Non-forest	11	0	4	0	0
Forest					
(island + mainland)	3,202	76	35	0	0
Site 7:					
Island	265	131	3	1	0
Mainland	756	34	19	0	0
Non-forest	0	0	1	0	0
Forest					
(island + mainland)	1,021	165	22	1	0
Site 8:					
Island	237	2	4	0	0
Mainland	3,643	104	20	0	6
Non-forest	0	0	5	0	0
Forest					
(island + mainland)	3,880	106	24	0	6
Site 9:					
Island	1,012	18	18	0	9
Mainland	552	49	6	0	0
Non-forest	2	2	2	0	0
Forest					
(island + mainland)	1,564	67	24	0	9
Sum of values for sites 1 to 9:					
Island	5,945	554	143	587	25
Mainland	14,734	633	220	696	63
Non-forest	65	4	21	1	21
Forest					
(island + mainland)	20,679	1,187	363	1,283	88

Appendix VI. Mean number of animals per core.

	<u>Brvocatptus</u> <u>stouti</u>	<u>Goniocyclons</u> <u>silvestris</u>	<u>Tricho-</u> <u>niscus</u> <u>phormianus</u>	<u>Mesocoryis</u> <u>audax</u>	Ostracod (unknown species)
Site 1:					
Island	7.36	1.48	0.23	6.50	0.16
Mainland	11.00	1.72	0.34	7.67	0.69
Non-forest	0	0	0.20	0.03	0.50
Site 2:					
Island	10.09	1.00	0.22	0	0.01
Mainland	6.81	0.38	0.27	0	0.01
Non-forest	1.67	0.07	0.07	0	0.20
Site 3:					
Island	5.17	0.66	0.26	0	0.01
Mainland	12.39	0.99	0.37	0	0
Non-forest	0	0	0.03	0	0
Site 4:					
Island	11.88	0.94	0.20	0.01	0
Mainland	7.59	0.32	0.44	0	0
Non-forest	0	0	0	0	0
Site 5:					
Island	12.30	0.37	0.37	0	0
Mainland	37.78	0.73	0.20	0	0
Non-forest	0.07	0	0	0	0
Site 6:					
Island	2.44	0.03	0.07	0	0
Mainland	33.13	0.81	0.32	0	0
Non-forest	0.37	0	0.13	0	0
Site 7:					
Island	2.94	1.46	0.03	0.01	0
Mainland	8.40	0.38	0.21	0	0
Non-forest	0	0	0.03	0	0
Site 8:					
Island	2.63	0.02	0.04	0	0
Mainland	40.48	1.16	0.22	0	0.07
Non-forest	0	0	0.17	0	0
Site 9:					
Island	11.24	0.20	0.20	0	0.10
Mainland	6.13	0.54	0.07	0	0
Non-forest	0.07	0.07	0.07	0	0
Overall mean for sites 1 to 9:					
Island	7.34	0.68	0.18	0.72	0.05
Mainland	18.19	0.78	0.27	0.86	0.08
Non-forest	0.08	0.005	0.03	0.001	0.03

Appendix VII. Range of number of animals per core.

	<u>Bryocamotus</u> <u>stouti</u>	<u>Goniocyclops</u> <u>silvestris</u>	<u>Tricho-</u> <u>niscus</u> <u>phormianus</u>	<u>Mesocyparis</u> <u>audax</u>	Ostracod (unknown species)
Site 1:					
Island	0-59	0-17	0-2	0-200	0-2
Mainland	0-84	0-26	0-4	0-301	0-13
Site 2:					
Island	0-133	0-10	0-3	0	0-1
Mainland	0-78	0-4	0-2	0	0-1
Site 3:					
Island	0-65	0-8	0-3	0	0-1
Mainland	0-163	0-12	0-5	0	0
Site 4:					
Island	0-168	0-32	0-2	0-1	0
Mainland	0-98	0-4	0-4	0	0
Site 5:					
Island	0-200	0-17	0-9	0	0
Mainland	0-274	0-7	0-3	0	0
Site 6:					
Island	0-63	0-1	0-1	0	0
Mainland	0-311	0-7	0-3	0	0
Site 7:					
Island	0-24	0-17	0-2	0-1	0
Mainland	0-126	0-3	0-2	0	0
Site 8:					
Island	0-45	0-1	0-1	0	0
Mainland	0-300	0-9	0-2	0	0-4
Site 9:					
Island	0-99	0-6	0-2	0	0-2
Mainland	0-97	0-7	0-2	0	0
Maximum range:					
Island	0-200	0-32	0-9	0-200	0-2
Mainland	0-311	0-26	0-5	0-301	0-13

Appendix VIII      Chi-squared analysis of all forest  
and non-forest animal species  
found in both islands and mainlands.

		Mainland Island	
Observed:	Total forest animal species	151	174
	Total non-forest animal species	57	55
Expected:	Total forest animal species	155	170
	Total non-forest animal species	53	59
O/E Ratio:	Total forest animal species	0.97	1.02
	Total non-forest animal species	1.08	0.93

Chi-squared = 0.729     $P > 0.05$  (not significant)

Appendix IX Numbers of animals of each species,  
(arranged in taxonomic groups).

Legend

I = Island  
M = Mainland  
O = Outside forest

Site number	1I	1M	2I	2M	3I	3M	4I	4M	5I	5M	6I	6M	7I	7M	8I	8M	9I	9M	0
<b>Order</b>																			
<b>Colembola</b>																			
sp.1.	1232	1152	5496	6646	2202	2044	4244	3955	3037	2017	1387	1708	1839	832	2929	2706	1605	2897	760
sp.2.	11	11	96	38	23	30	11	36	5	12	22	25	0	33	12	5	10	20	3
sp.3.	71	130	55	14	41	39	49	18	97	7	53	28	160	41	59	44	119	33	87
<b>Order</b>																			
<b>Hemiptera</b>																			
sp.1.	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	1
sp.2.	0	0	0	0	0	0	0	0	0	0	3	0	0	0	2	1	0	0	0
sp.3.	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
sp.4.	0	5	0	1	0	0	0	0	0	0	0	7	0	0	1	0	0	0	0
sp.5.	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
sp.6.	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
sp.7.	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0
sp.8.	0	1	0	1	0	0	0	1	0	0	1	0	0	0	0	0	1	1	0
sp.9.	1	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0
sp.10.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0
sp.11.	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
sp.12.	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
sp.13.	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
sp.14.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
sp.15.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
<b>Order</b>																			
<b>Coleoptera</b>																			
sp.1.	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<u>Odontria</u> sp.1	1	2	1	1	2	0	0	0	1	1	3	0	0	0	1	0	0	1	0
sp.2.	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
sp.3.	0	0	0	0	0	1	0	0	4	0	5	0	0	0	0	0	1	0	0
sp.4.	0	0	0	0	1	0	2	1	0	0	6	1	8	3	2	2	2	1	1
Family																			
Staphy- linidae A	15	5	4	2	0	4	1	0	19	0	1	14	1	0	1	10	0	6	0
Family																			
Staphy- linidae B	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	12	0	0	0
sp.5.	5	0	0	0	0	1	0	1	0	0	4	0	0	0	0	0	1	0	0
sp.6.	6	0	0	0	2	0	0	0	1	0	0	0	1	2	0	0	0	0	0
Family																			
Colydiidae A	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	3	1	3	0
Family																			
Colydiidae B	3	4	2	1	0	0	1	0	0	0	7	2	0	3	0	1	2	0	1
Family																			
Colydiidae C	0	1	0	1	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0
sp.7.	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
sp.8.	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
sp.9.	0	2	0	1	0	2	0	0	1	0	4	1	0	0	0	0	0	2	0

Site number	1I	1N	2I	2M	3I	3M	4I	4M	5I	5M	6I	6M	7I	7M	8I	8M	9I	9M	O
Order																			
Coleoptera (continued)																			
sp.10.	13	5	5	7	4	2	5	3	0	2	15	0	1	4	0	2	0	12	1
sp.11.	8	7	2	8	3	9	7	5	1	2	9	5	4	5	4	11	0	6	1
sp.12.	30	48	0	23	1	0	1	0	0	0	0	17	0	1	3	13	0	0	0
sp.13.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
sp.14.	11	0	0	0	0	0	0	0	0	0	1	0	0	0	0	3	0	0	1
sp.15.	0	0	1	0	2	0	0	0	0	0	0	1	0	0	0	1	0	0	0
sp.16.	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
sp.17.	0	3	0	0	0	0	3	0	2	0	6	0	2	0	0	0	3	0	2
sp.18.	0	0	1	6	0	1	0	0	0	0	2	0	0	0	0	3	0	3	0
sp.19.	0	16	0	0	0	0	0	0	0	0	4	0	0	0	0	1	0	3	0
sp.20.	5	0	0	4	0	0	3	0	0	0	2	2	0	0	0	0	0	1	0
sp.21.	1	13	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0
sp.22.	1	0	0	1	0	0	0	0	0	1	2	0	0	0	0	1	1	0	0
sp.23.	3	0	0	0	0	0	0	0	0	1	4	0	0	0	0	1	0	1	0
sp.24.	0	0	0	0	0	0	0	0	0	2	1	1	0	0	1	0	0	0	0
sp.25.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
sp.26.	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
sp.27.	0	0	0	7	0	0	6	0	2	0	0	0	0	0	1	0	1	0	0
sp.28.	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
sp.29.	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
sp.30.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Scopodes sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Family Carabidae A	0	0	0	0	6	1	4	0	0	1	0	0	0	1	1	3	0	11	1
Zelus femoralis	0	1	1	5	0	1	10	4	0	0	7	2	7	2	10	1	3	8	5
sp.31.	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
sp.32.	0	2	0	1	1	0	0	2	0	0	0	1	0	0	0	0	0	0	0
sp.33.	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
sp.34.	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0
sp.35.	0	0	2	2	0	0	0	0	0	1	0	1	0	2	14	3	0	0	0

Site number	1I	1M	2I	2M	3I	3M	4I	4M	5I	5M	6I	6M	7I	7M	8I	8M	9I	9M	0
Order Coleoptera (continued).																			
sp.39.	0	0	0	0	0	0	0	0	0	0	1	0	0	2	0	0	0	0	4
<u>Mecodema</u> <u>occonori</u>	0	0	0	0	0	0	3	0	3	0	10	3	0	3	2	0	3	4	5
<u>Anchomenus</u> <u>novae</u> <u>Zealandae</u>	0	0	0	0	0	0	0	0	2	1	44	0	0	0	0	20	0	0	3
sp.40.	1	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
sp.41.	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
sp.42.	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	4	0	0
sp.43.	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
sp.44.	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
sp.45.	1	0	0	0	5	0	0	0	3	0	0	0	3	2	0	0	0	0	1
<u>Holcaspis</u> sp. A	0	1	0	0	0	0	0	0	2	0	1	0	1	0	0	3	1	2	0
<u>Holcaspis</u> sp. B	6	3	3	0	5	3	1	0	1	0	7	10	1	0	5	0	2	1	3
<u>Megadromis</u> <u>virgil</u>	0	0	0	4	0	0	2	6	0	1	1	15	4	4	3	4	0	0	3
sp.46.	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
sp.47.	3	0	0	0	0	0	0	0	0	0	2	1	1	0	0	0	0	0	0
Larval Coleoptera																			
sp.48.	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
sp.49.	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0
sp.50.	0	0	0	4	2	0	0	0	0	0	0	0	1	0	1	0	0	0	0
sp.51.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
sp.52.	2	0	0	4	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
sp.53.	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
sp.54.	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
sp.55.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
sp.56.	0	0	0	1	0	1	1	0	0	0	2	1	0	0	1	0	0	1	1
Family Curculionidae																			
sp.1.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
sp.2.	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	1	0	0	0
sp.3.	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
sp.4.	0	0	0	0	0	0	4	0	0	2	24	0	15	0	0	0	1	0	50
sp.5.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
sp.6.	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0
sp.7.	0	0	0	1	0	0	1	0	0	0	0	1	0	0	2	1	0	1	0
sp.8.	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0
sp.9.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
sp.10.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0

Site number	1I	1N	2I	2N	3I	3M	4I	4M	5I	5M	6I	6M	7I	7M	8I	8M	9I	9M	0
Family Curculionidae (continued).																			
sp.11.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
sp.12.	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Order Trichoptera																			
sp.1.	0	0	0	0	0	2	2	12	0	0	0	0	0	0	0	0	0	0	0
Order Diptera																			
sp.1.	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0
sp.2.	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
sp.3.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
sp.4.	0	1	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0
sp.5.	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
sp.6.	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0
sp.7.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
sp.8.	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
sp.9.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
sp.10.	0	0	0	0	0	0	0	0	0	0	2	0	0	1	0	0	0	0	0
sp.11.	0	2	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
sp.12.	7	1	0	0	0	0	0	0	0	0	0	2	0	0	1	0	0	0	0
sp.13.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0
sp.14.	1	0	0	1	0	2	4	1	0	1	2	4	0	0	0	0	0	0	0
sp.15.	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	2	0
sp.16.	0	0	0	2	0	0	6	1	0	0	1	0	1	1	0	3	1	2	0
sp.17.	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0
sp.18.	2	0	0	0	0	0	0	0	0	0	1	3	0	0	0	0	0	0	0
sp.19.	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0
sp.20.	0	0	0	1	0	0	0	0	0	0	5	0	0	0	0	2	5	5	0
sp.21.	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0
sp.22.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0
sp.23.	4	5	1	5	4	6	13	14	10	0	39	6	33	2	1	12	7	10	0
sp.24.	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	2	0	5	0
sp.25.	0	0	0	0	1	0	1	1	0	0	1	1	1	0	0	0	0	0	0
sp.26.	0	0	0	0	0	2	0	0	1	6	1	0	0	0	1	0	1	0	0
sp.27.	0	1	0	0	3	0	0	8	0	0	0	0	0	0	2	0	0	0	0



Site number	1I	1M	2I	2M	3I	3M	4I	4M	5I	5M	6I	6M	7I	7M	8I	8M	9I	9M	0
Family Formicidae (continued).																			
sp.9.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0
sp.10.	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0
sp.11.	0	0	0	0	2	0	1	2	1	2	0	0	0	0	0	1	0	0	0
sp.12.	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Family Vespidae																			
sp.13.	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	2
sp.14.	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
sp.15.	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
sp.16.	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Order Blattodea																			
sp.1.	0	1	0	0	4	1	2	1	6	0	15	1	4	1	7	0	0	0	12
Order Orthoptera Family Rhaphidophoridae																			
sp.1.	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
sp.2.	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
sp.3.	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
sp.4.	1	4	2	1	0	4	2	2	8	0	20	1	0	1	22	9	1	2	6
Family Stenopelmatidae																			
<u>Hemiandrus</u>																			
<u>fulcifer</u>	1	0	0	5	5	0	0	1	9	0	22	0	0	0	5	3	0	0	1
sp.5.	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
sp.6.	0	1	0	0	0	0	6	0	1	0	2	0	0	3	0	0	0	0	0
Family Gryllidae																			
sp.7.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
sp.8.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Class Crustacea																			
<u>Orchestia</u>																			
<u>lesliensis</u>	139	86	114	67	27	30	32	32	6	23	23	69	19	61	30	53	7	27	60
(Suborder Amphipoda)																			
<u>Trichoniscus</u>																			
<u>phormianus</u>	26	11	3	7	1	3	3	0	0	4	5	7	0	0	1	4	1	3	13
(Suborder Isopoda)																			
Order Acari																			
sp.1.	5	2	0	0	0	0	0	0	0	7	3	1	0	0	1	11	1	0	5
sp.2.	7	1	7	2	1	1	1	20	0	0	6	4	1	5	3	4	1	1	1
sp.3.	0	0	0	0	0	0	0	0	1	0	1	0	1	0	1	0	0	0	0
sp.4.	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
sp.5.	2	3	0	2	0	8	5	0	4	1	1	1	0	0	0	7	1	4	0
sp.6.	0	0	0	0	2	3	0	0	2	0	3	0	0	0	1	0	0	2	22

Site number	1I	1M	2I	2M	3I	3M	4I	4M	5I	5M	6I	6M	7I	7M	8I	8M	9I	9M	0
Order Phalangida																			
sp.1.	0	0	0	0	0	0	0	1	0	0	3	0	0	0	5	2	1	1	4
sp.2.	0	2	0	0	6	4	8	4	5	0	6	1	0	0	0	0	0	1	0
sp.3.	0	0	0	0	1	0	0	2	0	1	1	0	0	1	2	0	0	1	5
sp.4.	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
sp.5.	1	1	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0
sp.6.	25	6	5	1	2	0	1	11	3	1	4	3	0	0	0	2	0	3	4
sp.7.	0	0	1	1	0	0	0	0	0	0	0	2	0	0	0	3	1	1	0
sp.8.	10	3	9	15	6	1	4	2	6	13	13	4	7	7	5	6	1	6	2
sp.9.	0	0	1	0	0	0	2	0	2	0	0	0	2	1	0	1	0	0	0

## Order Pseudoscorpionida

sp.1.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
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## Order Araneae

<u>Miturga</u> sp.	5	2	2	1	3	4	8	5	4	3	7	6	3	10	3	1	6	3	0
sp.1.	12	0	7	5	8	1	9	1	19	10	10	28	4	6	12	18	60	7	11
sp.2.	17	3	1	2	5	3	0	4	8	2	37	28	7	8	22	34	28	5	11
sp.3.	2	0	0	0	0	0	3	0	0	0	0	0	8	0	0	0	0	0	0
sp.4.	0	0	4	0	0	4	0	13	2	4	4	2	6	1	0	0	1	2	0
sp.5.	0	0	0	11	17	16	7	2	33	10	43	4	10	0	0	0	11	1	0
sp.6.	0	0	0	0	0	0	20	0	8	0	5	0	60	9	0	0	0	0	8
sp.7.	7	11	52	25	24	17	40	35	6	18	0	16	15	18	9	21	10	21	0
sp.8.	2	1	0	0	0	1	0	0	0	0	0	0	0	0	0	4	0	0	0
sp.9.	9	0	0	0	2	0	3	0	0	0	9	0	0	2	0	0	0	0	5
sp.10.	1	0	0	2	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0
sp.11.	0	0	2	0	0	0	1	0	4	2	7	0	2	0	5	5	4	3	0
sp.12.	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
sp.13.	0	0	2	0	0	0	0	3	0	0	0	0	0	1	0	0	0	0	0
sp.14.	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
sp.15.	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
sp.16.	0	20	4	0	1	0	2	1	2	0	4	0	0	4	0	2	6	3	2
sp.17.	0	0	0	0	0	0	0	0	0	0	0	4	0	2	7	5	0	0	1
sp.18.	3	15	6	0	0	1	0	0	5	0	2	3	0	1	2	5	0	3	3
sp.19.	2	0	0	0	0	1	2	0	0	0	1	0	0	0	1	0	0	1	0
sp.20.	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0
sp.21.	0	1	0	0	0	0	0	0	2	0	0	0	1	0	2	0	0	0	0
sp.22.	0	0	0	0	0	1	0	2	0	0	0	1	0	1	0	0	0	0	0
sp.23.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0
sp.24.	0	1	0	0	1	1	0	0	0	0	0	0	1	3	0	0	3	0	0
sp.25.	0	0	0	2	0	0	2	0	0	0	0	0	3	1	0	0	1	0	0
sp.26.	2	0	0	0	1	3	1	7	3	4	8	1	0	2	2	5	6	5	2



Site number	1I	1M	2I	2M	3I	3M	4I	4M	5I	5M	6I	6M	7I	7M	8I	8M	9I	9M	0
Subclass Diplopoda (continued).																			
Family Sphaerotheridae																			
sp.16.	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Family Schedotrigonidae																			
sp.17.	7	4	0	1	0	5	1	1	1	1	2	0	1	0	1	2	0	3	0
Subclass Chilopoda																			
Order Scolopendromorpha																			
sp.1.	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
sp.2.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
sp.3.	1	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1
Order Geophilomorpha																			
sp.4.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	1
Class Gastropoda																			
sp.1.	0	0	0	0	0	1	0	2	0	0	0	0	0	1	0	0	0	0	0
Class Oligochaeta																			
sp.1.	0	3	2	1	1	3	4	1	0	2	3	3	0	0	0	1	0	0	3
sp.2.	3	3	8	5	0	2	6	3	0	1	4	15	0	0	10	7	2	5	0
sp.3.	0	0	1	0	0	2	4	2	0	0	0	0	1	0	1	0	0	1	0
sp.4.	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Class Turbellaria																			
<u>Geonemertes</u>																			
spp.	2	1	1	1	0	0	1	3	0	0	1	3	0	2	1	2	0	0	0

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