# TERRESTRIAL INVERTEBRATE COMMUNITIES: THE EFFECTS OF SUCCESSIONAL AGE, HABITAT STRUCTURE AND SEASONALITY.
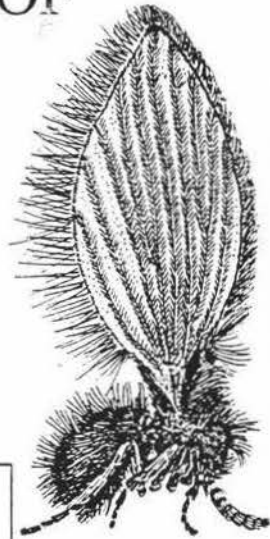
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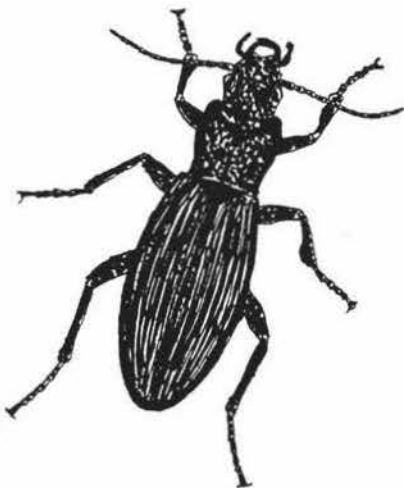OF THE REQUIREMENTS FOR
THE DEGREE OF MASTER OF SCIENCE
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# ABSTRACT

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Ground dwelling invertebrate communities at five sites of successional vegetation of increasing age, were sampled with pitfall traps between December 1992 and January 1994. Species richness peaked in mid successional manuka and late successional broadleaf/podocarp habitats. Individual abundance was highest in early and mid sere sites. Increased habitat heterogeneity and complexity in mid succession may have elevated species richness above that of early sere sites. Furthermore, as manuka is a native plant with a wide geographical range, this may also have contributed to the higher species richness at the Manuka and Broadleaf/Podocarp forest sites. In contrast, the number of guilds per site was highest in the climax forest, and again probably relates to high habitat heterogeneity, complexity and plant diversity at these sites.

Invertebrate faunae associated with wooden block refuges placed in the five successional habitats were collected in late November 1993 after nine months. The invertebrate assemblages associated with these blocks yielded similar patterns to those collected with pitfall sampling, with highest diversity and abundance in mid succession. Availability and spacing of alternative natural refuges again seems most likely to have influenced these patterns.

Predator abundance was highest in the Pasture and declined as habitat age increased. However, predator diversity peaked in mid and late succession, declining again in the climax Podocarp forest. Competitive exclusion in the climax forest and an inability for native species to colonise exotic pasture, seem most likely to have limited predator species richness at these sites. In contrast, predation pressure, as assessed with caterpillar (*Galleria mellonella*) baits, increased along the successional gradient. Peak predation intensity in late succession is attributed to the larger size and greater effectiveness of predators occurring in these habitats.

In summary, invertebrate community structure clearly changed along the successional gradient; species richness peaked in habitats of intermediate age, the number of guilds increased to peak in late succession, while the number of invertebrates declined. Predation intensity also increased with successional age, however, there was no clear relationship between predation levels, predator abundance or predator diversity.

# CHAPTER ONE

## *GENERAL INTRODUCTION*

# INTRODUCTION

Succession as defined by Begon *et al.* (1990) is the non-seasonal, directional and continuous pattern of colonisation and extinction at a site by species and populations.

It is well established (Brown 1991, Lawton 1986, Lawton & McGarvin 1986, Lawton 1983, Southwood *et al.* 1979) that habitat structure, which encompasses habitat heterogeneity (horizontal structures) and complexity (vertical structures), changes with successional age. Changes in habitat structure, coupled with changes in vegetational diversity, are in turn associated with changes in the composition of the invertebrate communities within successional habitats (i.e. species abundance, richness, evenness, guild structure and predation pressure), as resources (i.e. web attachment sites, oviposition sites, food, refuges from predators) change and increase (Andow 1991, Brown & Southwood 1987).

Intensity of arthropod predation is predicted to be low in early successional habitats, with highest levels occurring in late succession (Lovei & Brown 1993). If predator abundance increases with successional age (Price 1991) and predation levels in a community are related to this (Krebs 1986) predation intensity should increase with habitat age, however few studies have tested this concept. Recently Abrams (1993) suggested that as prey are able to conceal themselves from predators to differing degrees (particularly as habitat structure increases), predation levels may not necessarily correspond directly to the number or diversity of predators occurring in a habitat.

The aim of this work is to determine how the structure of ground active invertebrate communities change with the successional age of their habitats. As habitat heterogeneity is likely to be one factor associated with successional changes in the vegetation and invertebrate communities, the impact of this was examined using artificial refuges to increase habitat heterogeneity in each of the five successional stages. Finally the interaction between predation levels and the predator assemblages, in relation to successional age, was examined using live caterpillar prey items.

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# CHAPTER TWO

## *STUDY SITES*

# DESCRIPTION OF STUDY SITES

The five study sites were located within a 5 km radius (40°70'S, 175°52'E) in pastoral hill country (Plate 2.1) in the northern Wairarapa (Fig. 2.1). The area was heavily forested by 350,000 acres (Bagnall 1976) of dense podocarp/mixed hardwood forest until the 1880's. The northern Wairarapa is characterised by high rainfall (1400-1700 mm per year), an annual temperature average between 12-12.5 °C (Bremner 1994), limestone outcrops deposited in the Miocene era (Ewen Fordyce pers. comm.) and 'central yellow brown earth' soil type. Winters are cold and wet, and moderate westerly winds occur during the equinox. Sites were chosen from a survey of successional vegetation types in the Pahiatua/Eketahuna area, using McQueen's (1991) study of successional southern Wairarapa vegetation as a guide.

## SITE 1.

Site one is a 20 year old English grass species pasture (Table 2.1), that had not been cultivated since 1972. The site is located at 300 m a.s.l., was of a level grade and occupies an area of 1.6 ha (Plate 2.2). The soil is a friable silty clay loam (20-30 cm deep) over a clay subsoil of moderately high fertility (Bremner 1994). The soil was acidic (pH 5.25), with moderate nitrogen (5.84 mg/g) and high phosphate levels (0.72 mg/g). The site is rotationally grazed by sheep, yielding a structurally simple habitat with few refuges suitable for colonisation by larger invertebrate species.



Plate 2.1. The study area is predominantly pastoral hill country with remnants of successional vegetation.
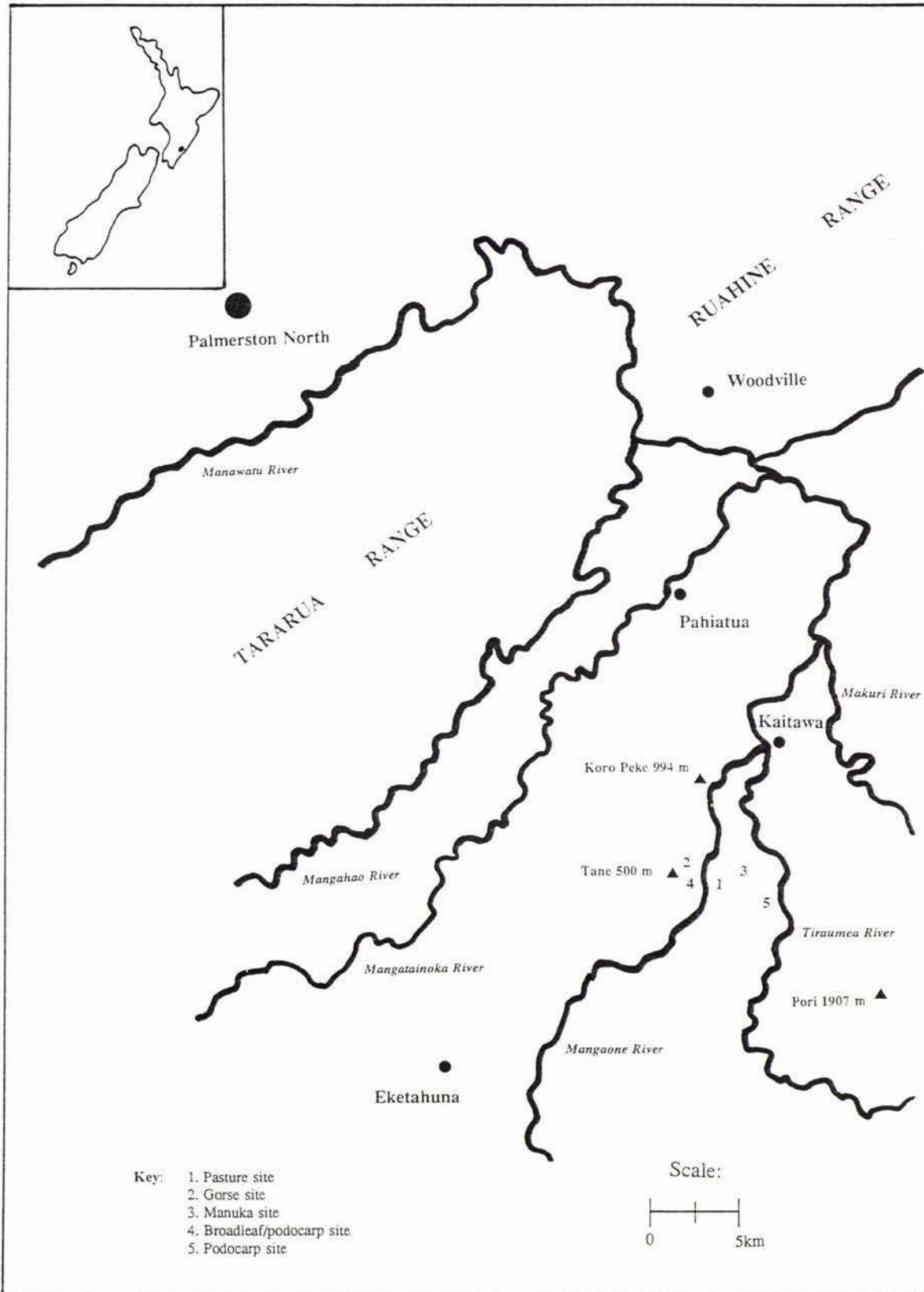
Figure 2.1. Location of study sites in the northern Wairarapa, North Island, New Zealand.

Plate 2.2. Pasture site.

## SITE 2.

The second study site is a stand of 25 year old (J. McLauchlan pers. comm.) 3 m high gorse (*Ulex europaeus*) (Plate 2.3). Gorse is a common early successional plant in the area and the site had previously been pasture since approximately 1891 (Anon 1990) and dense forest prior to that. Site two was situated at 305 m a.s.l., covering approximately 1 ha. The habitat has only two structural levels; a sparse ground cover of thistle and fern (Table 2.1) with a deep gorse litter (Table 2.2) and a monoculture shrub layer of gorse (Plate 2.3). The soil is dry even after high rainfall events, but similar in type to that of the Pasture site, the pH level was 5.30, nitrogen was 5.18 (mg/g) and phosphate levels were 0.41 (mg/g).



Plate 2.3. The Gorse site, showing understorey of deep litter and few species of ground cover vegetation.

## SITE 3

The mid successional Manuka site is approximately 40 years old (Plate 2.4). The area was originally heavy podocarp forest, which was cleared around the late 1890's. A secondary growth forest was cleared in about 1939, the area being returned to pastoral production. However, the site was allowed to revert to native vegetation about 10 years later. This site occupies a higher altitude (480 m a.s.l.) and rainfall area (Table 2.3) than the other study sites and the vegetation extends over 200 ha. It has a manuka (*Leptospernum scoparium*) canopy, fern and tree fern understorey and a ground cover of fern and grass (Table 2.1). The soil is a light clay hill loam, over a complex subsoil over a limestone base (Bremner 1994). Soil analysis showed the area to have a pH 5.30, a low nitrogen level of 3.85 (mg/g) and a low phosphate level of 0.47 (mg/g). The area is periodically stocked with sheep at low grazing intensities in winter. Ground level refuges are provided by fallen manuka branch debris and longer rank grass lengths (Plate 2.4).

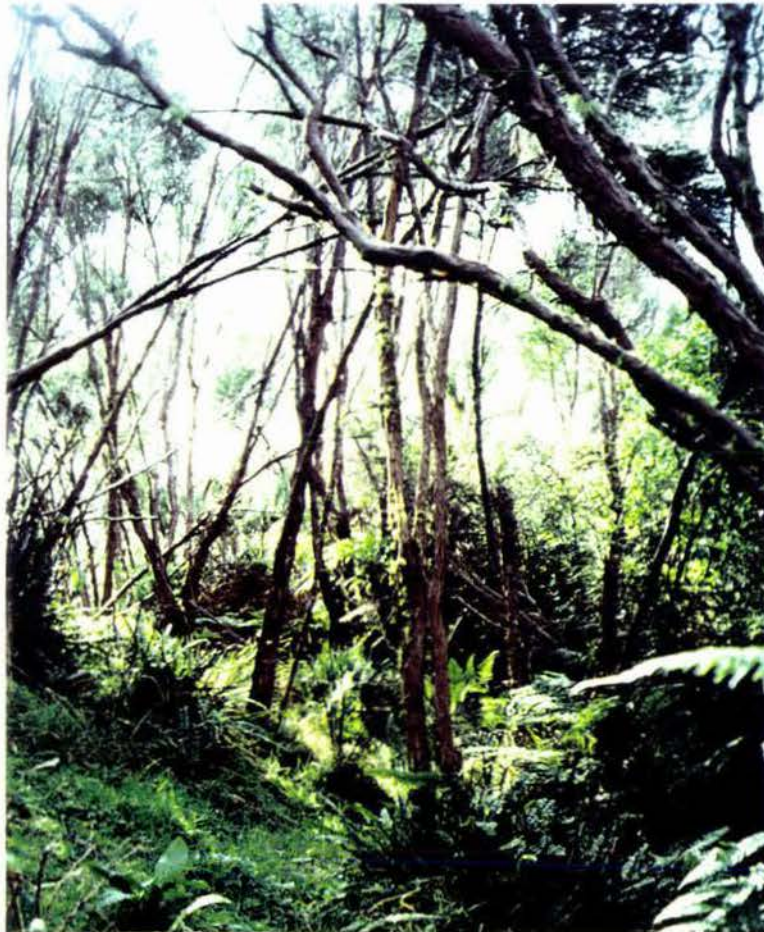Plate 2.4. Manuka site with an 8 m high sub-canopy.

## SITE 4.

The Broadleaf/Podocarp forest site is predominantly a secondary growth forest, situated near the Mangaone Stream, at an altitude of 305 m a.s.l., covering an area of 4.16 ha (Plate 2.5). All totara (*Podocarpus totara*) hardwoods and the majority of rimu (*Dacrydium cupressinum*) and kahikatea (*Podocarpus dacrydioides*) trees were

removed in the 1890's (Adcock 1973). The area also appears to have been burned at this time. Some larger individuals survived but the majority of the vegetation is 100 year old tawa *(Beilschmiedia tawa)* and kahikatea forest. There is a deep leaf litter (Table 2.2) and branch/log debris which may act as refuges for ground dwelling invertebrates (Plate 2.6). It has a spartan shrub layer of mainly kahikatea seedlings and tree fern, and a low density of ground cover species. The site has no sub canopy, a dense canopy and two emergent layer individuals (Table 2.1). The soil chemistry was again similar to that of the Pasture site, with the addition of a humus layer, pH was 5.55, nitrogen and phosphate levels were comparatively high at 8.57 (mg/g) and 0.83 (mg/g) respectively.



Plate 2.5. Broadleaf/Podocarp forest remnant, canopy level trees are between 15 and 25 m high.



Plate 2.6. Broadleaf/Podocarp forest understorey, illustrating habitat heterogeneity of log/branch debri.

**SITE 5.**

The late successional forest site is a remnant of mature podocarp forest on the banks of the Tiraumea River, at 320 m a.s.l. and occupying an area of 6.25 ha (Plate 2.7). The forest was protected by a council reserve covenant early this century (Anon 1990). The site has all forest layers present, with many emergent rimu, kahikatea and hinau (*Elaeocarpus dentatus*) over a canopy layer of tawa and pukatea (*Laurelia novae-zelandiae*). Canopy trees also have a variety of associated epiphytes increasing the structural diversity of the habitat. There is a dense and diverse shrub layer with a ground cover of native grass, fern and seedlings (Plate 2.8). The leaf litter layer is more shallow than that of the Broadleaf/Podocarp forest (Table 2.2) and it has fewer natural log debri refuges. However, alternative refuges under loose bark and epiphyte layers create a greater level of vertical architectural complexity. The soil structure is a silt loam, with a complex subsoil over a clay base. The pH was 5.55, with moderate levels of nitrogen 6.19 (mg/g) and phosphate 0.66 (mg/g).

Table 2.1. Vegetation species diversity and structural levels present at each site.

**Pasture**
   Groundcover: white clover (*Trifollium repens*), rye grass (*Lolium prenneae*)
      Yorkshire fog (*Holcus lanatus*), browntop (*Agrotis capillaris*).
**Gorse**
   Groundcover: gorse spine litter, ladder fern, winged thistle (*Carduus tenuiflorus*).
   Shrub layer: gorse (*Ulex europaeus*).
**Manuka**
   Groundcover: white clover, browntop, native grasses, hydrocotalae
      (*Hydrocotalae moschata*), fern (*Paesia scaberula*), ladder fern.
   Shrub layer: silver fern (*Alsophila tricolor*), mahoe (*Melicytus ramiflorus*).
   Sub canopy: manuka (*Leptospermum scoparium*).
**Broadleaf/Podocarp Forest**
   Groundcover: deep leaf litter, fallen logs, sparse ladder fern, hydrocotalae,
      titoki (*Alectryon excelsus)* seedlings, some kahikatea seedlings
      (*Dacrycarpus dacrydioides*), fern (*Phmatosonis scandens*).
   Shrub layer: sparse silver fern and small kahikatea, *Copropsoma rotundafolia*.
   Sub canopy: nil
   Canopy: predominantly tawa (*Beilschmiedia tawa*), some kahikatea, pukatea
      (*Laurelia novae-zelandiae*) and titoki.
   Emergent layer: a rimu (*Dacrydium cupressinum*), kahikatea.
**Podocarp Forest**
   Groundcover: leaf litter, fallen logs, dense seedlings, hen & chicken
      fern (*Asplenium bulbitenum*), forest oat grass (*Microleana anniacea*),
      hook grass (*Uncinia sp*), moss.
   Shrub layer:seedlings of canopy trees, coprosoma (*Coprosoma rotundafolia*),
      tree nettle (*Urtica ferox*), rangiora (*Bracyglottis repanda*), tree fern.
   Canopy: pukatea, hinau (*Eaocarpus dentatus*), mahoe, tawa.
   Emergent layer: rimu, kahikatea, matai, miro (*Prumnopitys ferruginea*) and
      tawa.

Plate 2.7. Podocarp forest site, illustrating 15-25 m canopy level trees and 40-50 m emergent level species.



Plate 2.8. Late successional Podocarp forest understorey, illustrating the dense ground cover vegetation.

Table 2.2. Leaf litter depths and grass lengths recorded monthly between January 1993 and January 1994, at the five study sites.

| | Average grass length (cm) | |
| --- | --- | --- |
| | Pasture | Manuka |
| Jan 1993 | - | - |
| Feb | 11.8 | 11.2 |
| Mar | 4.65 | 7.6 |
| Apr | 12.88 | 18 |
| May | 4.2 | 8.35 |
| June | 2.61 | 3.95 |
| July | 2.07 | 2.75 |
| Aug | 1.4 | 12.5 |
| Sept | 2.5 | 2.25 |
| Oct | 2.3 | 2.1 |
| Nov | 2.22 | 3.21 |
| Dec | 2.9 | 5.35 |
| Jan 1994 | 10.3 | 12.9 |

| | Average leaf litter depth (cm) | | |
| --- | --- | --- | --- |
| | Gorse | Broadleaf/Podocarp Forest | Podocarp Forest |
| Jan 1993 | - | - | - |
| Feb | - | 4.8 | 2.6 |
| Mar | 4.2 | 4 | 2.2 |
| Apr | 3.2 | 2.6 | 2.6 |
| May | 5.04 | 2.3 | 1.5 |
| Jun | 4.2 | 2.2 | 1.89 |
| Jul | 2.3 | 1.9 | 1.0 |
| Aug | 2.7 | 1.82 | 1.18 |
| Sept | 2.34 | 1.9 | 1.24 |
| Oct | 2.1 | 1.1 | 1.48 |
| Nov | 3.55 | 1.33 | 1.4 |
| Dec | 2.4 | 2.1 | 1.97 |
| Jan 1994 | 5.1 | 1.94 | 2.76 |

Table 2.3. Monthly rainfall and temperature measurements recorded between January 1993 and January 1994, at the five study sites.

| | Monthly rainfall (mm) | | | | |
| --- | --- | --- | --- | --- | --- |
| | Pasture | Gorse | Manuka | Broadleaf/ Podocarp Forest | Podocarp Forest |
| Jan 1993 | - | - | - | - | - |
| Feb | 78 | - | 80 | 35 | 47 |
| Mar | 55.4 | 50.1 | 55.3 | 32.1 | - |
| Apr | 132.4 | 90 | 298 | 80 | 61.5 |
| May | 56 | 23.5 | 230 | 23.5 | 26 |
| Jun | 93.5 | 60 | 241 | 60 | 67 |
| Jul | 100 | 33.5 | 124.5 | 50 | 66.5 |
| Aug | 30.5 | 58.7 | 59.5 | 25 | 21.5 |
| Sep | 65 | 23.5 | 102.5 | 25 | 35 |
| Oct | 69.5 | 30 | 103 | 40 | 35.5 |
| Nov | 90 | 34 | 109 | 30 | 49.5 |
| Dec | 176.5 | 88 | 276 | 85 | 117 |
| Jan 1994 | 55.5 | 30 | 80.5 | 28 | - |

| | Monthly ground temperature range (°C) | | | | |
| --- | --- | --- | --- | --- | --- |
| | Pasture | Gorse | Manuka | Broadleaf/ Podocarp Forest | Podocarp Forest |
| Jan 1993 | - | - | - | - | - |
| Feb | 9-49 | - | 7-37 | 6-23 | 8-39 |
| Mar | 4.5-55 | 4-30 | 1-39 | 5-24 | 3-24 |
| Apr | 6-44 | 4-25 | 6-35 | 4-19 | 4.5-24 |
| May | 3-40 | 4-13 | 4-31 | 4-13 | 3-9 |
| Jun | 2.5-30 | 3-12 | 2.5-25 | 2-11 | 3-13 |
| Jul | 1-26 | 0.5-14.5 | 0-17 | 0-10 | -1-12 |
| Aug | 0-29 | -0.5-14 | 0-23 | 0.5-15 | 0.5-12 |
| Sep | 0-33 | -1.5-14 | -0.5-30 | 0-10 | 2-11 |
| Oct | -1-45 | 0-23 | 1-26.5 | 0.5-21 | 0.5-11 |
| Nov | 6.5-4.5 | 4.5-33.5 | 14.5-40 | 11-22 | 9-25 |
| Dec | 4-45 | 1.5-36 | 3-39 | 4.5-26 | 4-30 |
| Jan 1994 | 6-46 | 5-40 | 3-45 | 5-29 | 5-23 |

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# CHAPTER THREE

## THE EFFECT OF
## HABITAT STRUCTURE AND
## SEASON ON THE GROUND ACTIVE
## INVERTEBRATE COMMUNITIES
## OF NEW ZEALAND
## SUCCESSIONAL VEGETATION

## ABSTRACT

Ground dwelling invertebrate communities at five sites of increasing successional age were sampled between December 1992 and January 1994. Species diversity peaked in mid and late successional forest. Total abundance peaked in early and mid succession, principally because of high numbers of Collembola, mites and hymenopteran parasitoids. Dominance was highest, and species diversity lowest in early succession sites. The number of trophic guilds increased with the successional age of the habitats, perhaps because plant diversity and hence resource availability increased. Of the five environmental variables examined, mean monthly rainfall and grass minimum tempera-ture were most strongly correlated with invertebrate activity.

**Key words**: ground invertebrate communities, succession, habitat structure, diversity, seasonality, New Zealand.

## INTRODUCTION

Habitat age can determine the degree of structural diversity present in an environ-ment, which can in turn influence the type of invertebrate communities which occupy these habitats (Lawton 1983, Southwood *et al.* 1979). Structural diversity encom-passes two components of habitat structure; horizontal structure or habitat heteroge-neity and vertical structure or habitat complexity, both of which are likely to increase with the successional age of the habitat (Brown 1991). These have been shown to promote changes in density (Brown & Southwood 1987, Edwards-Jones & Brown 1993), species richness (Denno & Roderick 1991, Lawton 1983, Leather 1986, Murdoch *et al.* 1972, Southwood *et al.* 1979, Uetz 1991), evenness (Murdoch *et al.* 1972), abundance (Brown & Southwood 1987, Southwood *et al.* 1982) and guild structure (Brown & Southwood 1987, Hendrix *et al.* 1988) in the resident inverte-brate communities. Price (1991) has attempted a synthesis of these papers, with some general predictions about the response of invertebrate communities to successional

change; these include greater species richness, an increase in evenness and a decrease in individual abundance as the age of the habitat increases.

Furthermore, habitat structure can moderate the effect of seasonal influences, such as weather, which can also effect the activity and abundance of the invertebrate fauna within these habitats (Thomas *et al.* 1992). Activity levels in a number of New Zealand forest invertebrate species are associated with temperature fluctuations. Moeed and Meads (1985, 1986, 1987) found temperature range to be the most important influence on invertebrate community composition in a New Zealand Podocarp forest. Munro and Death (1994) also found a significant correlation between the activity of predatory invertebrates and rainfall levels in a number of forest and pasture habitats. Other variables associated with season and the successional age of a habitat, such as grass length and leaf litter depth have also been shown to influence the invertebrate communities living within them (Plowman 1979, Uetz 1975, 1979).

This study examines the ground active invertebrate communities in five habitats (Pasture, Gorse, Manuka shrubland, Broadleaf/Podocarp and Podocarp forests) of increasing successional age. The aim is to establish whether successional age, structural diversity, seasonality or some combination of these has the greatest influence on patterns of species richness, abundance and guild structure among the invertebrate communities in these habitats.

## METHODS

*Invertebrate Sampling*

Ground active invertebrates were sampled at 30 day intervals between December 1992 and January 1994 by pitfall trapping. While it is acknowledged that pitfall trapping has some limitations (Greenslade 1960), it is still an effective method for sampling ground active species, although it assesses a combination of abundance and activity rather than abundance *per se* (Topping & Sunderland 1992). Therefore, the use of the term abundance in this study refers to a measure of activity and abundance, rather than abundance. Preliminary trials using other methods of sampling

(quadrate sampling, D-Vac and sweep netting) found pitfall sampling was the best method for obtaining a diversity of species of different sizes and activity patterns (Death & Munro unpublished data).

Five replicate traps of cylindrical plastic containers (11 cm diameter and 10 cm deep) were placed at each site at 10 m intervals along a 50 m transect. Traps were dug in level with the surrounding ground and filled with 300 ml of 70% ethylene glycol and a few drops of detergent to break the surface tension of the fluid. Galvanised iron covers (20 cm by 20 cm) were raised 3 cm above the ground over the pitfalls to prevent rain entering. Samples were sieved to 500 $u$m with an Endecott sieve and placed in 70% ethanol prior to sorting. Samples were processed using the morphospecies method of Beatty and Oliver (1994). Samples were hand sorted and enumerated as morphospecies using a 10x compound microscope and reference collection compiled during the study. This collection was subsequently checked by experts, to confirm taxonomic accuracy. Certain groups such as Diptera were identified to order rather than morphospecies, as their association with ground active invertebrate communities is predicted to be transient (Brown & Southwood 1987).

*Environmental variables*

Total rainfall (mm), temperature maximums and minimums (°C) and 20 replicate measurements of leaf litter depth and grass length were taken monthly at each site. Two soil core samples (each consisting of five 25 cm$^2$ replicates) were taken to determine soil pH, total nitrogen and total phosphate concentrations at each site. Availability of potential log and branch refuges at ground level was determined by counting the number of such structures (larger than 5 cm diameter) along a 50 m by 10 m transect at each site in February 1994. Environmental variables for each site are presented in Table 3.1.

Table 3.1. Environmental variables sampled in the five successional study sites, between December 1992 and January 1994.

| Site | Temperature Range °C | Total Rainfall (mm) | Grass Length (cm) | Leaf Litter (cm) | Log/branch Debris (m²) | pH | Total N (mg/g) | Total P (mg/g) |
|------|------|------|------|------|------|------|------|------|
| Pasture | -1-9 | 1002 | 2.1-6.9 | nil | 0/0 | 5.25 | 5.84 | 0.72 |
| Gorse | -1-23 | 1002 | nil | 3.5-5.2 | 1/19 | 5.30 | 5.18 | 0.41 |
| Manuka | -0.5-35 | 1759 | 2.3-13.4 | nil | 1/25 | 5.30 | 3.85 | 0.47 |
| Broad/Pod | 0.8-18 | 1002 | nil | 1.6-3 | 1/12.5 | 5.55 | 8.57 | 0.83 |
| Podocarp | -1-19 | 720 | nil | 1.5-2.6 | 1/13.8 | 5.55 | 6.19 | 0.66 |

*Data analysis*

Diversity was assessed using the Margalefs (Clifford & Stephenson 1975) and Berger-Parker (Berger & Parker 1970) diversity indices. Margalefs index is given by:

$$D_{MG}=(S-1)/\ln N$$

and measures species richness.

The Berger-Parker dominance index is given by:

$$D_{BP}=N_{max}/N$$

and measures species equitability.

Guild structure was determined using information on the ecology of invertebrate species and families from Insects of Australia Vol 1 and 2 (CSIRO 1991) and the Fauna of New Zealand series (DSIR 1982-1985). The guilds were defined following Brown and Southwood (1987) as predator, parasitoid, scavenger, phytophage, detritivore, saphrophagous, fungi, scavenger/predators (ants) and mould/fungi feeders. Differences in guild structure between sites and seasons were assessed using relative abundances for each of the functional feeding groups.

Site and seasonal differences were assessed with a mixed model (SITES fixed and MONTHS random) two way analysis of variance (ANOVA) using the GLM procedure of SAS (SAS 1985) with SITE*MONTH as the appropriate error term for testing site effects (Sokal & Rohlf 1981). Data were log transformed (x+1) to remove heteroscedasity where appropriate. The Bonferroni *a posterio* means test was used to evaluate significant site differences. Environmental data were correlated with biological data, using Pearsons correlation coefficient and the CORR procedure of SAS (SAS 1985). Ordination and classification were carried out using the PATN multivariate statistics package (Belbin 1993). Cluster analysis was performed with the Bray-Curtis dissimilarity index (Bray & Curtis 1957), and the flexible UPGMA clustering algorithm. The Bray-Curtis distance measurement was chosen because of its power in exploring patterns in ecological data (Beals 1984). DECORANA (detrended correspondence analysis) was used for the ordination analysis because of the inherent nonlinearities in ecological data.

# RESULTS

*Diversity patterns*

A total of 48,118 individuals were collected in the samples, from which 562 inverte-
brate morphospecies were identified. Of this, 152 species were Coleoptera, 103
hymenopteran parasitoids, 103 species of Araneae and 52 Acari species.

Total number of species and Margalefs index (Fig. 3.1) both indicate that mid
successional habitats had the highest species richness. Significant differences in spe-
cies number ($F_{4,46}=28.63$, $P<0.001$) and Margalefs index ($F_{4,46}=30.57$, $P<0.001$)
occurred between all site combinations except Manuka and Broadleaf/Podocarp forest
and Gorse and Podocarp forest.
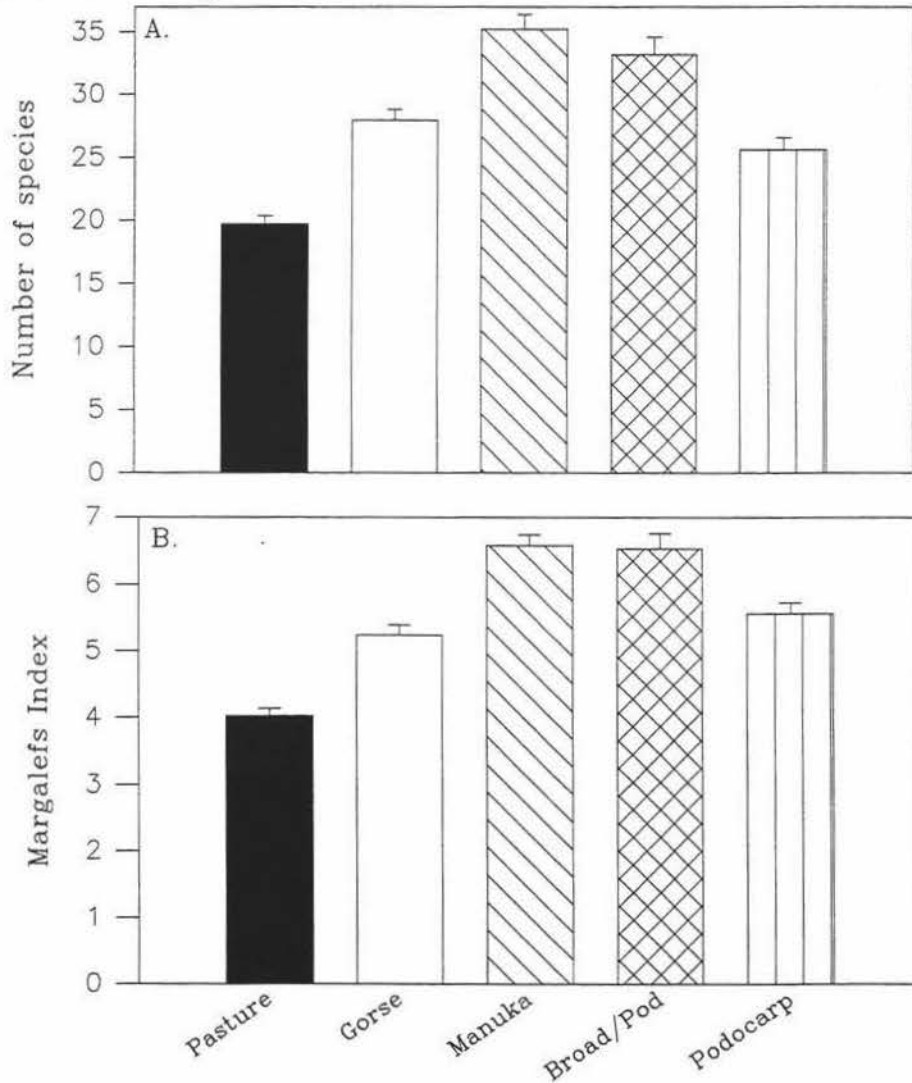


Sites of increasing successional age

Figure 3.1. A. Mean number of invertebrate species and B. Margalefs Index of species richness for
invertebrates collected between December 1992 and January 1994, in habitats of
increasing successional age.

Both indices indicated significant seasonal differences, $(F_{12,252}=23.75, P<0.001)$ and $(F_{12,252}=15.88, P<0.001)$, for species number and Margalefs index respectively, with the most notable decline occurring in winter (Fig. 3.2). However, there was also a significant interaction between site and season $(F_{46,252}=6.61, P<0.001, F_{46,252}=2.85, P<0.001)$ for species number and Margalefs species richness respectively, such that seasonal influences were different at different sites.

The mean number of total individuals trapped at each site between December 1992 and January 1994 is plotted in Fig.3.3. Mean abundance was greatest in the early successional and mid successional habitats $(F_{4,46}=7.00, P<0.001)$. As with species richness there was a marked seasonal decline in winter $(F_{12,252}=24, P<0.001)$ (Fig. 3.4), although again seasonal effects differed between sites $(F_{46,252}=4.22, P<0.001)$.
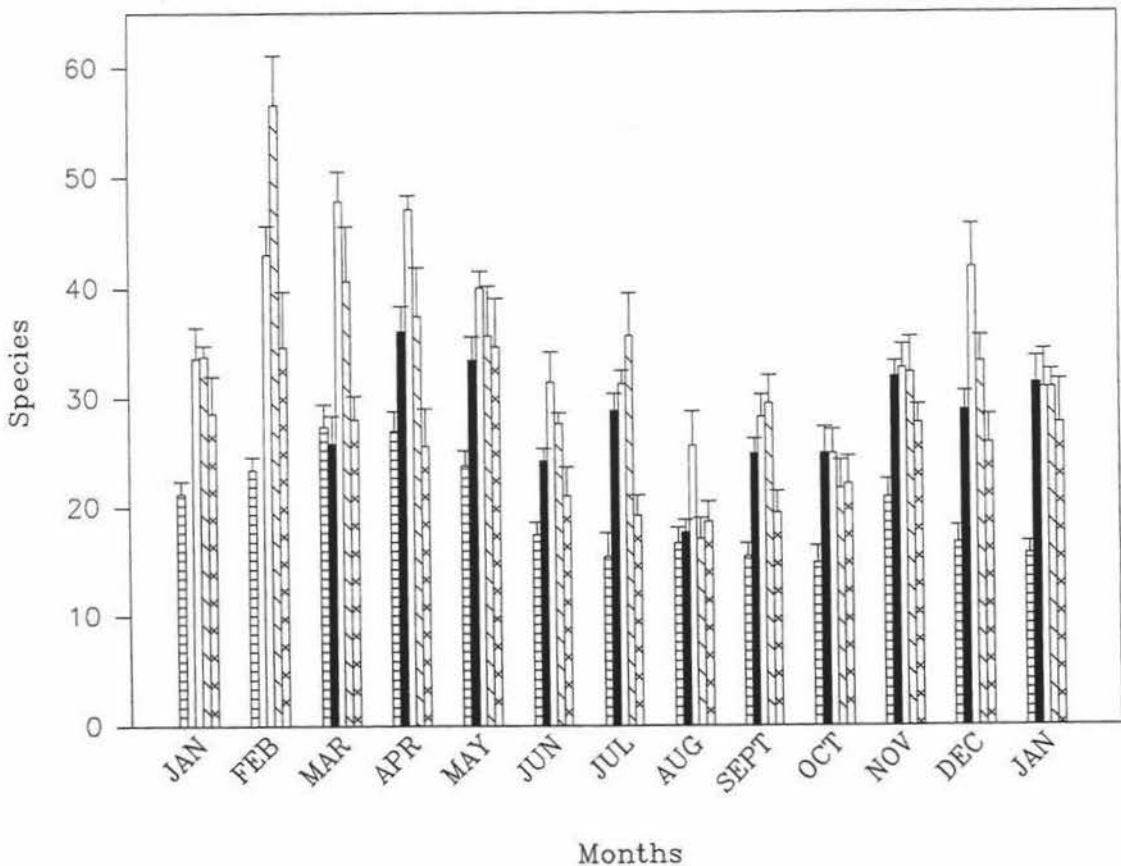


Figure 3.2. Mean number of species collected per site in each of 13 months between December 1992 and January 1994, in habitats of increasing successional age. Sites are represented as:
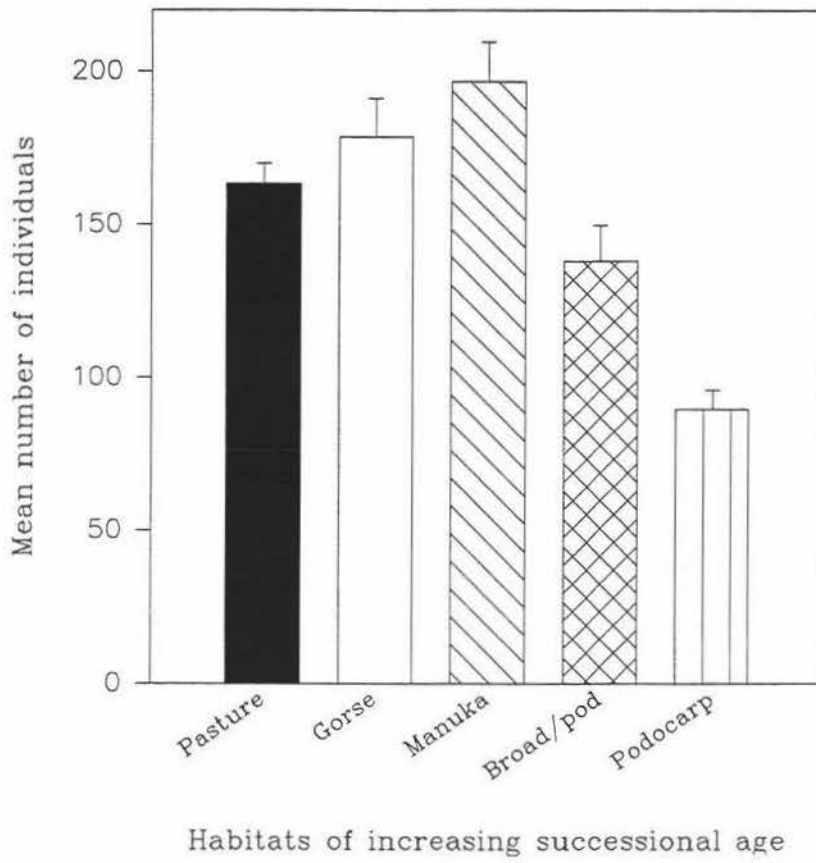Pasture ⊞  Gorse ■  Manuka ☐  Broadleaf/Podocarp ⊠
Podocarp ⊠

Figure 3.3. Mean number of individuals collected per site between December 1992 and January

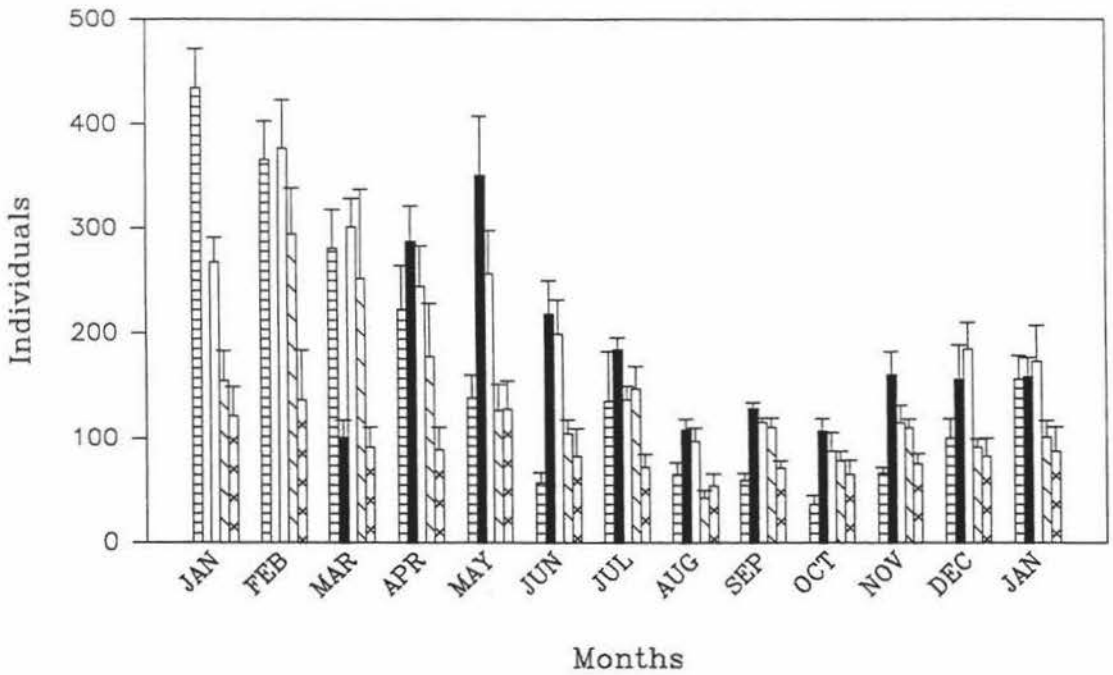1994, in sites of increasing successional age.



Figure 3.4. Mean number of individuals per site in each of 13 months between December

1992 and January 1994, in sites of increasing successional age. Sites are shown as: Pasture

Gorse    Manuka    Broadleaf/Podocarp    and Podocarp

Not surprisingly total abundance did correlate positively, though weakly, with monthly measures of rainfall and minimum temperatures (Table 3.2). However, they did not correlate with leaf litter depth or grass length.

Table 3.2. Pearson correlation coefficients between total abundance and monthly measurements of environmental variables taken at each of the study sites.

|  | Grass length | Leaf litter | Rainfall | Temperature |
|---|---|---|---|---|
| Correlation r coefficients | 0.10 | 0.10 | 0.31 | 0.20 |
| Significance | $P$=0.301 | $P$=0.398 | $P$<0.001 | $P$<0.001 |
| Number  n | 290 | 290 | 290 | 290 |

The two early successional habitats had communities which were most heavily dominated numerically by a single taxon ($F_{4,46}$=7.91, $P$<0.001) (Fig. 3.5). Isotomatidae Collembola dominated in the Gorse and Diptera dominated in the Pasture. Dominance levels also changed with season ($F_{12,252}$=3.92, $P$<0.001) although seasonal responses differed between sites $(F_{46,252}$=5.07, $P$<0.001).
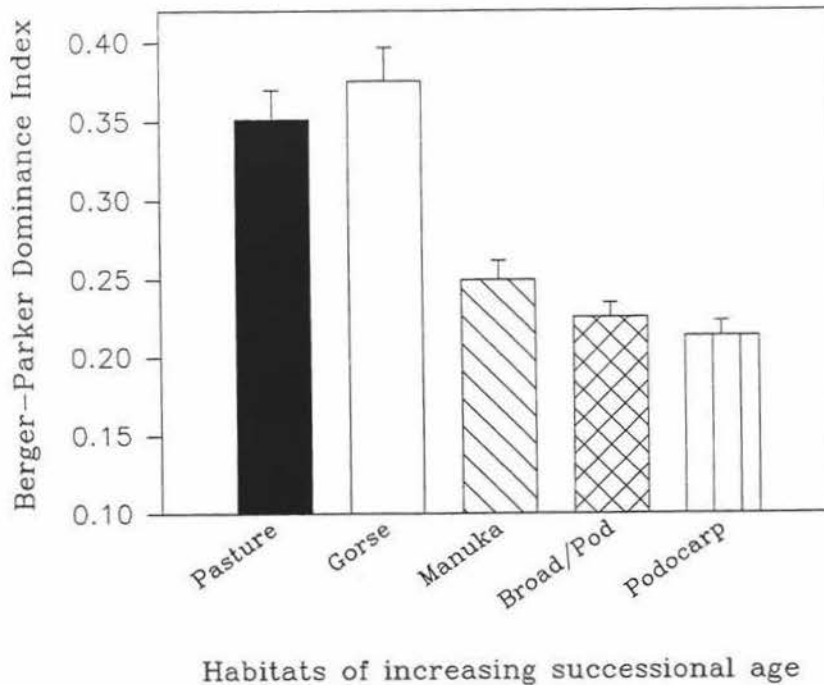


Figure 3.5. Mean Berger-Parker Dominance Index values for invertebrate communities collected between December 1992 and January 1994, in habitats of increasing successional age.

*Guild structure*

Mean relative abundance of the nine most common guilds are presented in Fig. 3.6. The number of guilds increases to peak in late succession ($F_{4,46}$=35.82, $P$<0.001). All the communities were numerically dominated by detritivores (55-65% of the community), except that of the Pasture site. Relative abundance of this group did not change seasonally at the sites with leaf litter (Gorse, Broadleaf/Podocarp and Podocarp forests), however, the grass based Pasture and Manuka experienced a low mean abundance of detritivores in winter ($F_{12,252}$=3.93, $P$<0.001). Overall detritivore abundance was significantly different between sites ($F_{4,46}$=8.21, $P$<0.001).
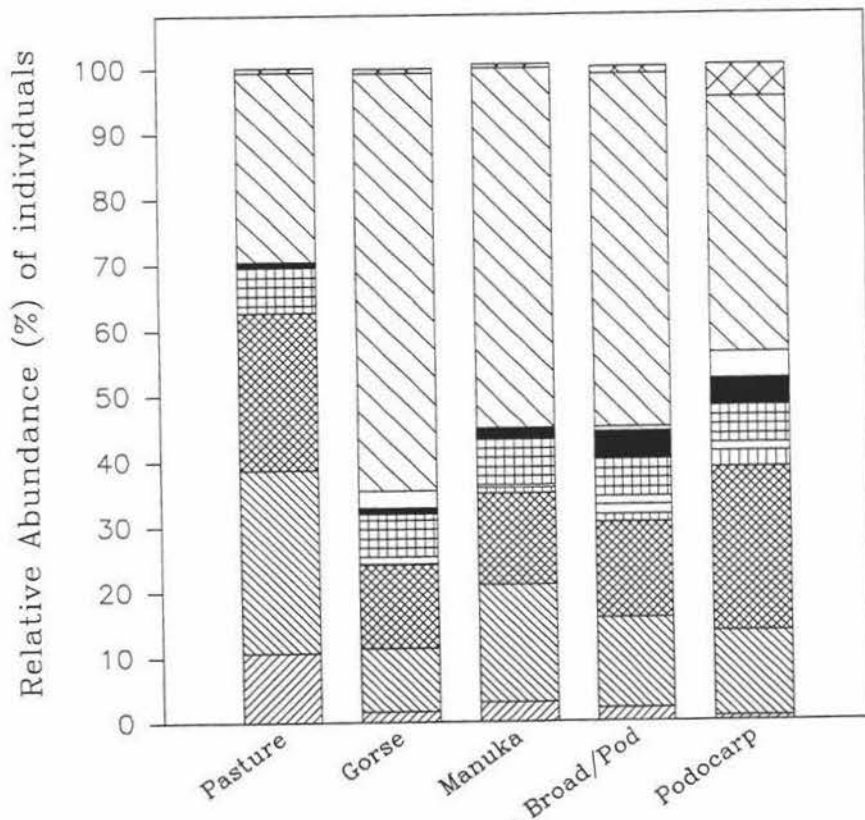


Figure 3.6. Mean relative abundance of the 9 most common feeding guilds collected between December 1992 and January 1994, in habitats of increasing successional age, are represented by:

Parasitoid [image]    Scavenger [image]    Predator [image]    Scavenger/Predator (ant) [image]

Mould/Fungi [image]    Phytophage [image]    Fungi [image]    Saphrophagous [image]

Detritivore [image]    Other [image]

Scavenger and predator guilds were the next most abundant groups. Mean predator abundance was greatest in the Pasture and Manuka sites, decreasing with increasing successional age ($F_{4,46}$=5.36, $P<0.001$). However, the relative abundance of predators was greatest at the Pasture (22%) and Podocarp forest (25%) site. Abundance of predators peaked in spring in the Pasture, autumn and spring in Manuka and Broadleaf/Podocarp forest habitats and autumn in the Gorse and Podocarp forest. Abundance was lowest in summer in this guild at all sites ($F_{12,252}$=5.74, $P<0.001$). Scavengers were most abundant in the Pasture habitat (20%) ($F_{4,252}$=5.97, $P<0.001$) and seasonally most common in summer for early and mid successional seres and spring in latter successional forest (Broadleaf/Podocarp and Podocarp) ($F_{12,252}$=2.94, $P<0.05$).

Parasitoids peaked in relative abundance in the Pasture habitat (10%) ($F_{4,46}$=15.93, $P<0.001$). In contrast, fungivore individuals (mostly Coleoptera) became more numerous as successional age increased, peaking in the late successional Broadleaf/Podocarp forest with a decline in the Podocarp forest ($F_{4,46}$=4.69, $P<0.005$). Seasonally fungivore abundance was highest in all sites in summer ($F_{12,252}$=5.09, $P<0.001$).

*Community structure*

DECORANA split the samples into two broad groups (Fig. 3.7); all the pasture samples and all the remaining sites. In most cases all seasonal samples from each site were closest to each other indicating site rather than season was most important in determining community structure. Axis 2 graded from the late successional sites (Broadleaf/Podocarp and Podocarp forest) at one end, to the mid successional sites (Gorse and Manuka) at the other, although there was no clear division in the centre. Axis 3 served to group the Manuka samples more closely, but did not change the overall pattern.

Taxa positively associated with axis 1 (i.e., those associated with the Pasture sites) included 4 species of Linyphiidae, 1 Lycosidae, 3 Staphylinidae, the small carabid *Clivina vagans* and lepidopteran larvae of the genus Wiseana (Table 3.3).
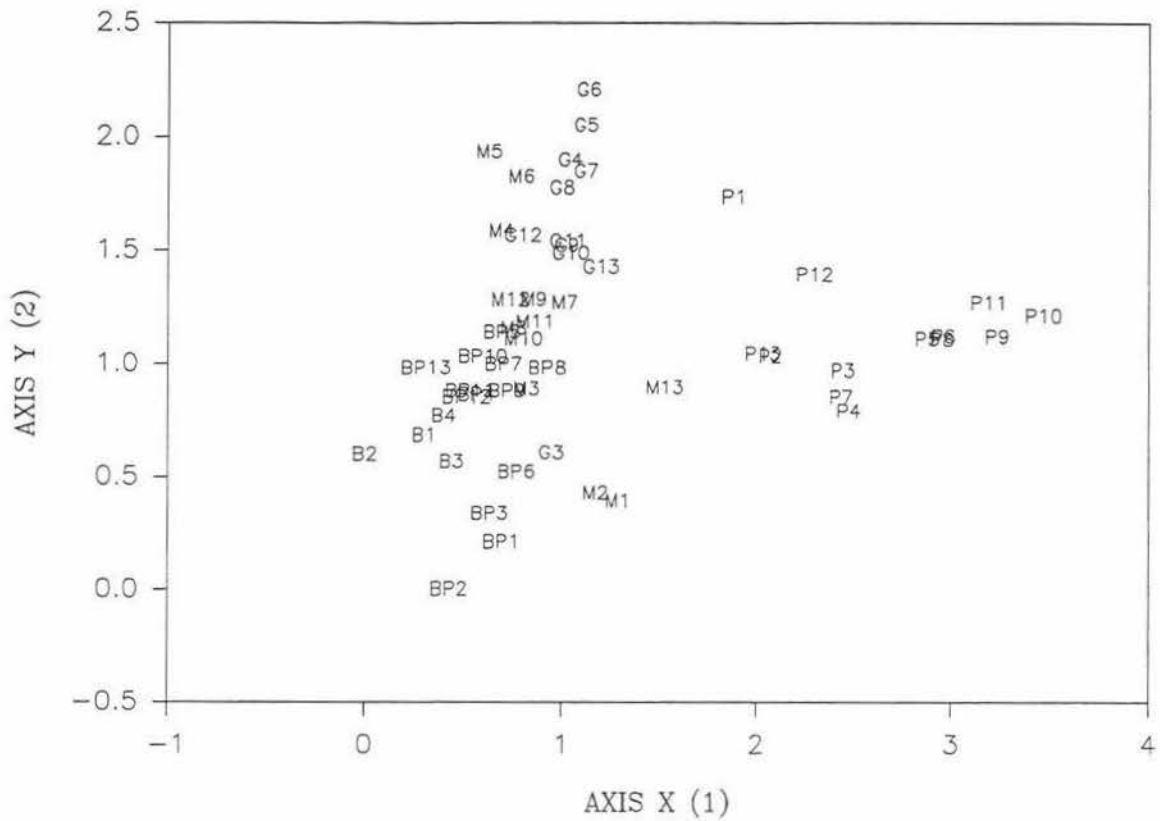
Figure 3.7. Axis 1 as a function of axis 2, for a DECORANA analysis of community structure for the 13
seasonal samples per site, collected between December 1992 and January 1994. Sites are coded
as; P=Pasture, G=Gorse, M=Manuka, BP=Broadleaf/Podocarp and B=Podocarp.

Table 3.3. Taxa significantly correlated with the three main DECORANA axes. Taxa are
listed, in declining order of importance.

| Axis 1<br>Positive axis association | Axis 2 | Axis 3 |
| --- | --- | --- |
| Linyphiidae *sp.3* | Isotomatidae *sp.* | Araneae *sp.14* |
| Linyphiidae *sp.1* | *Placamostethus planiusculus* | *Trichopria sp.2* |
| Formicidae *sp.7* | *Paracmotemnus sp.1* | *Trichopria sp.1* |
| *Deroceras reticulum* | | Acari *sp.31* |
| Acari *sp.26* | | Hemiptera *sp.2* |
| | | *Anagroidea sp.* |

| Axis 1<br>Negative axis association | Axis 2 | Axis 3 |
| --- | --- | --- |
| Amphipoda *sp.* | Sminthuridae *sp.* | Rhaiphophoridae *sp.1* |
| Formicidae *sp.2* | *Recyntus sp.* | *Micrambina sp.* |
| *Cycloma lawsona* | *Spaerothorax sp.* | Acari *sp 1* |
| *Melanophthalmus sp.* | Staphylinidae larvae *sp.1* | *Micrambina sp.* |
| Acari *sp 1* | *Cycloma lawsona* | |
| | Formicidae *sp.2* | |
| | *Melanophthalmus sp.* | |

Positive taxon associations with axis 2 (the Gorse and Manuka sites) included: 3 species of coleopteran larvae, 1 Scarabaeidae and 2 hymenopteran parasitoids. Negative associations along this axis (late successional forest sites) involved 2 Araneae species, 1 Formicidae and 1 species of Coccinelidae larvae.

Although the cluster analysis again split all the pasture samples from the rest, it differed from the DECORANA in that it delineated the samples from the other four sites into four distinct groups representing each site (Fig. 3.8). Again the Gorse and Manuka communities were most closely related and the Broadleaf/Podocarp and Podocarp sites were similarly closest to each other.

Within each site group there was some evidence of seasonal groupings. Most notably summer samples from both 1993 and 1994 were grouped together, particularly at the less structurally complex sites. Habitat differences are clearly the most important influences on community structure, however, within each site season was also an important determinant of community structure.
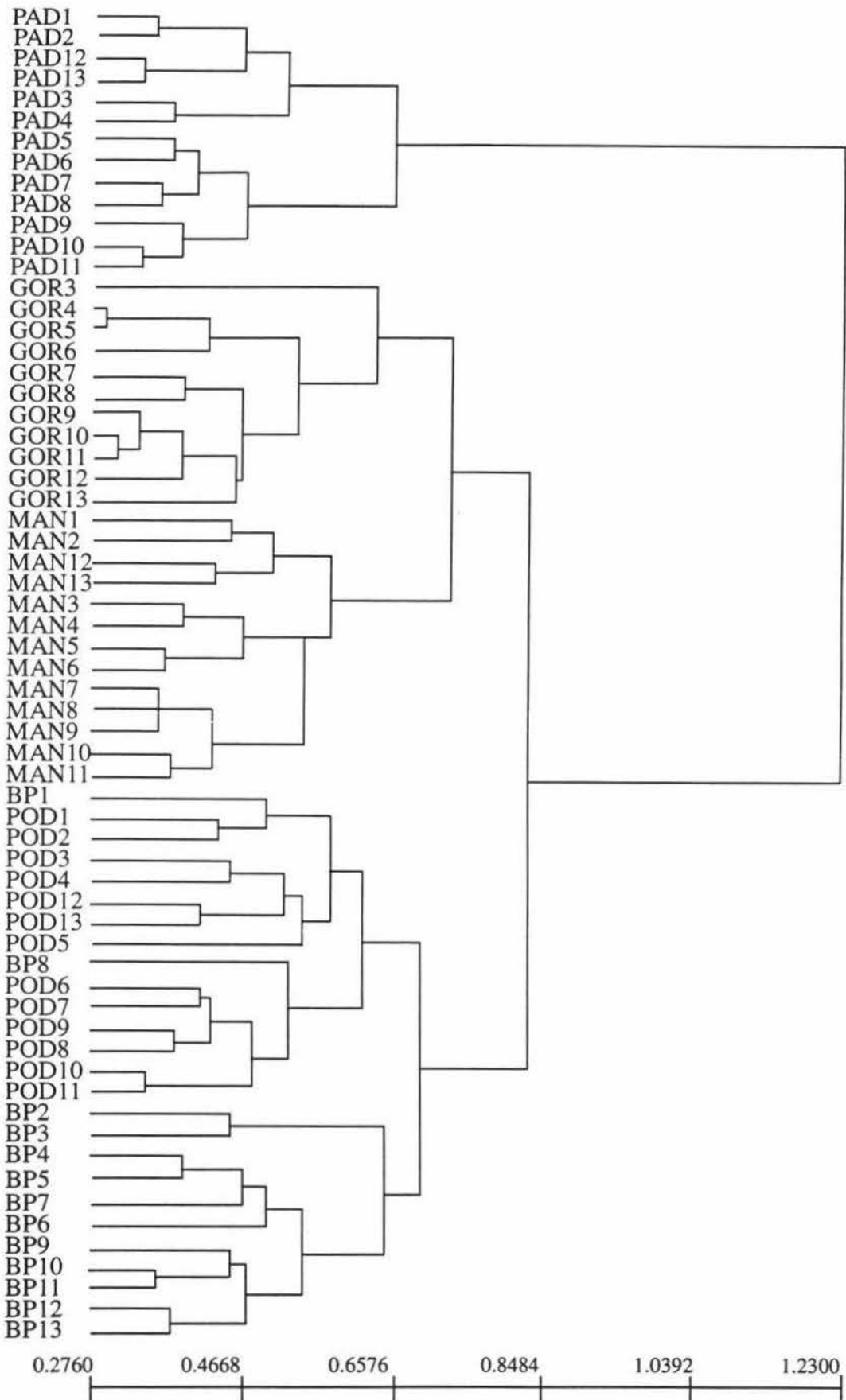
Figure 3.8. Dendrogram of 13 seasonal samples collected at the study sites between December 1992 and January 1994. Sites are: PAD = Pasture, GOR = Gorse, MAN = Manuka, BP = Broadleaf/Podocarp and POD = Podocarp forest.

## DISCUSSION

*Community diversity*

Taxon richness was highest in the mid successional Manuka and late successional Broadleaf/Podocarp forests. Increased habitat heterogeneity associated with increased successional age has been found before to be the most important factor responsible for an increase in species number with succession (Brown 1991, Lawton 1983). Measurements of habitat heterogeneity (i.e. available log and branch debris) were high in the Broadleaf/Podocarp forest (Table 3.1) and habitat complexity, i.e. increasing diversity and levels of vegetation, also increased in this and the Manuka site (Table 2.1.)

Leather (1986) and Strong *et al.* (1984) concluded that a combination of plant range and architecture were the two most important determinants of species diversity in plant insect communities. Species area effects may therefore also have been an important determinant of diversity in the Manuka shrubland. Manuka has become one of the most common successional native trees in the North Island and is found throughout New Zealand on land cleared of mature forest up to 1000 m in altitude (Salmon 1980). Lawton and McGarvin (1986) found greater phytophage diversity on plants with a wider geographic range and similarly Moran *et al.* (1994), found locally abundant trees to have the highest number of insects associated with them. Gorse and pasture species also have a wide geographic range in New Zealand, but because they are predominantly introduced plants it seems likely that there are fewer insect species able to inhabit them (Andow 1993). Diversity was consequently low in the Gorse and Pasture sites. In contrast to gorse and pasture, manuka is a native, and it seems likely that this has also contributed to the increased diversity, at least above that of the Gorse and Pasture sites. Native plants have been shown to support a greater diversity of invertebrates than exotics in other studies (e.g., Southwood *et al.* 1982).

Similarly, reduced species richness in the Pasture may have been the result of a combination of factors. The early successional stage of the Pasture meant habitat heterogeneity and complexity were both low. Grazing at this site further reduces structural complexity (Morris 1981), which can in turn reduce insect diversity (Brown 1991).

Pasture plant species are also predominantly exotic and the number of native inverte-
brates inhabiting these plants is consequently quite low (Cameron & Butcher 1979).

Low diversity in the climax Podocarp forest is less easy to explain. This site has
the greatest levels of habitat heterogeneity and complexity. Lower numbers of species
found in this habitat may be the result of competitive exclusion, particularly amongst
the predator guild (Niemela 1993, Raynor & Uetz 1993). Only one species of
Carabidae occurred at this site compared to 3-4 species in the Gorse, Manuka and
Broadleaf/Podocarp forests (Munro & Death 1994). Predation pressure was also
highest in this habitat (Chapt. 5) and may have led to reduced prey diversity by ex-
cluding certain species or by increasing interspecific competition for resources such as
enemy free space (Jeffries & Lawton 1984, 1985, Holt 1984).

As expected communities became more even as successional age increased,
with fewer individuals spread over a greater number of species per site. It has long
been held that monocultures are more heavily dominated and less diverse than
polycultures or native vegetation (Paoletti 1992). The early successional Pasture and
mid successional Gorse habitats with low plant diversity, clearly had the most domi-
nated communities. Brown and Southwood (1987) also found that the dominance of
phytophages declined as succession progressed. A similat trend occurred in my study,
although in this case scavengers and detritivores, the dominants in Pasture and Gorse,
respectively declined through the successional stages.

*Total abundance*

Total abundance of individuals was highest in the mid and early successional
sites: Manuka, Gorse and Pasture. Rapid nutrient release and cycling known to occur
in early successional plants (Vitousek *et al.* 1987) may have lead to greater productiv-
ity which in turn supported more individuals, although this was not reflected in the
soil samples.

Low predation pressure at these sites may have also contributed to the high
abundance in early and mid successional habitats (Chapt. 4). Although predator
species richness was highest at the Manuka site, the relative abundance of predators

was low. Certainly the high abundance of many pest species in New Zealand pasture can be attributed to their release from predation pressure in a new country.

High abundance in the early and mid successional sites may also be affected by the predominance of small individuals at these sites. Collembola, small parasitoids and mites were the most abundant individuals in all three habitats, declining in abundance in the late successional sites. Several authors (Morse *et al.* 1988, Lawton 1986, Blackburn *et al.* 1993) have shown that an area can support a greater number of small, rather than large, individuals.

*Seasonality and abundance*

Both rainfall and temperature were positively associated with activity although; temperature is more likely to be the proximate cause, high rainfall was simply a result of seasonal patterns associated with temperature change. Other New Zealand studies (Moeed & Meads 1985) have also found peaks in activity in the warm wet months of autumn. Grass length and leaf litter depths were not significant determinants of abundance in these communities as a whole, although predator abundance at these study sites (Munro & Death 1994) and species richness in other studies (Thomas *et al.* 1992, Uetz 1975, Hagstrum 1970) have been shown to be influenced by changing grass length and leaf litter depths.

*Guild structure*

Most common feeding guilds were represented in all habitats. However, the number of guilds increased with structural age, perhaps because of the increased diversity of vertical and horizontal structures. Associated with this, food resources, oviposition sites, overwintering sites and enemy free space also increased (Brown 1991, Brown & Southwood 1987 and Heong *et al.* 1991). All communities were detritivore based, with scavengers and predators the next most abundant guilds. Mean abundance of predators was highest in the Pasture and Manuka sites (Munro & Death 1994), however, their relative abundance was also high in the late successional Podocarp forest. Scavengers, predominantly Diptera, were the most dominant in the

Pasture community, perhaps because of high numbers of coprophagous or dung breeding individuals.

Mean parasitoid abundance peaked in the early successional pasture site, while species richness was highest in mid succession. Brown and Southwood (1987) also found relative abundance of parasitoids was highest in early succession. The increased ability of prey to conceal themselves because of greater habitat heterogeneity, such as that found in late succession, may explain the reduction in parasitoid diversity along the successional gradient (Hawkins 1988).

*Community structure*

Analysis of overall invertebrate community structure yielded very similar patterns to those of the refuge block assemblages from the same habitats (Chapt. 4). The Pasture consistently separated from the other habitats, the mid successional Gorse and Manuka habitats grouped together, and the late successional Broadleaf/Podocarp and Podocarp forests were also most closely related. From the refuge block study (Chapt. 4) it seems differences in the degree of structural heterogeneity between these habitats are the most likely cause of the distinction between these communities (Lawton 1986), although many of the factors discussed above with respect to diversity patterns, may also be important. Within each site seasonality, independent of which year, also seemed to be a major determinant of invertebrate community structure.

In conclusion, the increasing structural diversity associated with increasing successional age seemed to promote species richness up to a certain point. There is some evidence however, that species richness in late succession sites may be limited by competition. The number of guilds present was greatest in late succession, again probably because of increased habitat structure and floral diversity. In contrast, individual abundance peaked in early and mid successional habitats probably because of reduced predation pressure and the number of small species present.

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# CHAPTER FOUR

## COLONISATION OF ARTIFICIAL REFUGES IN SUCCESSIONAL VEGETATION BY GROUND DWELLING MACROINVERTEBRATES

## ABSTRACT

Colonisation by ground active invertebrates of wooden block refuges was examined
in a range of successional habitats within New Zealand farmland. After nine months
colonisation appeared to be complete. Collection of block assemblages at this time
indicated that species richness and individual abundance was greatest under blocks in
habitats of mid successional age. Habitat heterogeneity, such as the availability of
alternative natural refuges was highest in late successional habitats and may explain
the lower abundance and diversity of invertebrates found under experimental refuges
at these sites. In contrast, early successional habitats such as pasture appeared to
have few natural refuges, but also had fewer individuals available to colonise artifi-
cial refuges, thus abundance under these refuges was also low. It seems likely that
the availability and spacing of natural refuges and the number of individuals poten-
tially available for colonisation in a habitat dictate the degree to which refuges are
colonised.

**Key words:** succession, terrestrial invertebrate communities, refugia, colonisation.

## INTRODUCTION

Succession is the non-seasonal, directional and continuous pattern of colonisation
and extinction at a site by species and populations (Begon *et al.* 1990). Successional
processes and mechanisms have been extensively reviewed and modelled by a
number of authors (e.g. Horn 1974, Connell & Slayter 1977, Peet & Christiensen
1980). However, most of these papers have emphasised the dynamics in the
vegetational communities with little reference to animals associated with the vegeta-
tion. Despite this, successional changes in herbivorous (Brown 1985, Brown &
Hyman 1986, Godfrey 1985), predatory (Hurd & Fagan 1992, Gibson *et al.* 1992)
and parasitoid (Hawkins 1988, Hawkins *et al.* 1993) invertebrate assemblages asso-
ciated with successional vegetation development have been well documented.

Several factors have been proposed to explain these patterns, however, it is still
unclear which if any is more important (Brown 1991). From island biogeographic
theory (McArthur & Wilson 1967) successional age will in itself be important, the
longer a habitat has been in existence the more time species will have to colonise it.
However, as habitat age increases, habitat structure also changes, both horizontally

and vertically (Brown 1991). Although it is difficult to test for age effects *per se*, both habitat heterogeneity and habitat complexity have been shown to influence invertebrate communities (Southwood *et al.* 1979, Lawton 1983, Uetz 1991, Hurd & Fagan 1992, Brown & Southwood 1987).

In contrast to the aforementioned patterns, Munro and Death (1994) and Munro (Chapt. 3) examined ground-dwelling invertebrate assemblages in five habitats of increasing successional age and found that diversity peaked at sites of mid successional age. However, successional age, spatial heterogeneity and habitat complexity all differ between the habitats. One of the major contributors to habitat heterogeneity in these habitats is the availability of suitable refugia such as fallen logs, which can in turn affect the variety of species found in a habitat (Moeed & Meads 1987). In this study I investigated whether invertebrates colonise artificial refuges when they are provided in these habitats and if so, whether these assemblages are influenced by the availability of alternative refuges.

## METHODS

Physical and vegetation characteristics of the study sites were measured as outlined in Chapter 3 and are listed in Table 4.1. Artificial refuges of untreated wooden blocks (*Pinus radiata*) (30 cm by 2.5 cm) were placed at each study site for nine months from March 1993 to November 1993. Each block had three grooves routered 2 cm deep in the undersurface, a central groove 2.5 cm wide and two 1 cm wide grooves on either side. Five replicate blocks were placed at each site at 10 m intervals along a 50 m transect.

Blocks were inspected visually after 2 weeks and subsequently at monthly intervals. Visual inspection involved recording to the lowest possible taxonomic unit the number of species and individuals found under and attached to the refuge blocks. The blocks were then returned to their original position.

After nine months, the blocks and 2 cm of soil directly below the blocks was collected by cutting a trench around the block to free the turf or tree roots and then pushing a wide shovel 2 cm under the block. Each sample and the associated blocks were placed in Berlesse funnels for nine days, with a 40 watt bulb providing the heat source. Invertebrates were collected below the sample in 300 ml of ethylene glycol. Individuals were sieved to 500 $um$, hand sorted and identified to morpho species using a 10x compound microscope as outlined in Chapter 3.

*Data analysis*

Similarly data were analysed as described in Chapter 3, except that in this case patterns in community structure were also examined using TWINSPAN (two way indicator species) performed with the PC-ORD multivariate statistics package (McCune 1987).

Table 4.1. Physical and vegetation characteristics of study sites measured between March and November 1993. Sites are listed in order of increasing successional age.

| Site | Total rainfall (mm) | Average temperature range °C | Average litter depth (cm) | Average grass length (cm) | Habitat heterogeneity (log/branch debri) |
|---|---|---|---|---|---|
| Pasture | 692.3 mm | 1.2-46°C | nil | 2.10-6.98cm$^g$ | absent |
| Gorse | 403.3 mm | 1.0-23°C | 3.5-5.3 cm | nil | 1/19 m$^2$ |
| Manuka | 1322.6 mm | 0.8-35°C | nil | 2.4-13.4 cm$^g$ | 1/25 m$^2$ |
| Broad/Pod | 365.6 mm | 0.8-18°C | 1.6-3.0 cm | nil | 1/12.5 m$^2$ |
| Podocarp | 362.5 mm | 0.8-19°C | 1.5-2.6 cm | nil | 1/13.8m$^2$ |

$^g$ = site grazed periodically by sheep.

| | Groundcover | Shrublayer | Sub-canopy | Canopy level | Emergent level |
|---|---|---|---|---|---|
| Pasture | grass | absent | absent | absent | absent |
| Gorse | leaf litter, fern | gorse | absent | absent | absent |
| Manuka | grass, fern | manuka | manuka tree (F: Mytacea) | absent | absent |
| Broad/Pod forest | leaf litter, fern | tree fern seedlings | absent | native conifer & evergreens (F: Araucariaceae) | absent |
| Podocarp forest | leaf litter, fern, native grass | shrubs seedlings | juveniles of canopy species | native conifer trees (F: Podocarpaceae) | native conifer |

## RESULTS

*Diversity patterns*

The number of species colonising the refuge blocks increased rapidly in the first two months after the blocks were put out. They then increased more slowly at the grass sites (Pasture and Manuka) before declining in November, or fluctuated about this level at sites with leaf litter (Gorse, Broadleaf/Podocarp and Podocarp forests) (Fig. 4.1). Increase in the total number of individuals, in contrast, did not follow any consistent trend (Fig. 4.2), although numbers at the grassy sites increased through to August at the Pasture site and June at the Manuka site, before declining again.
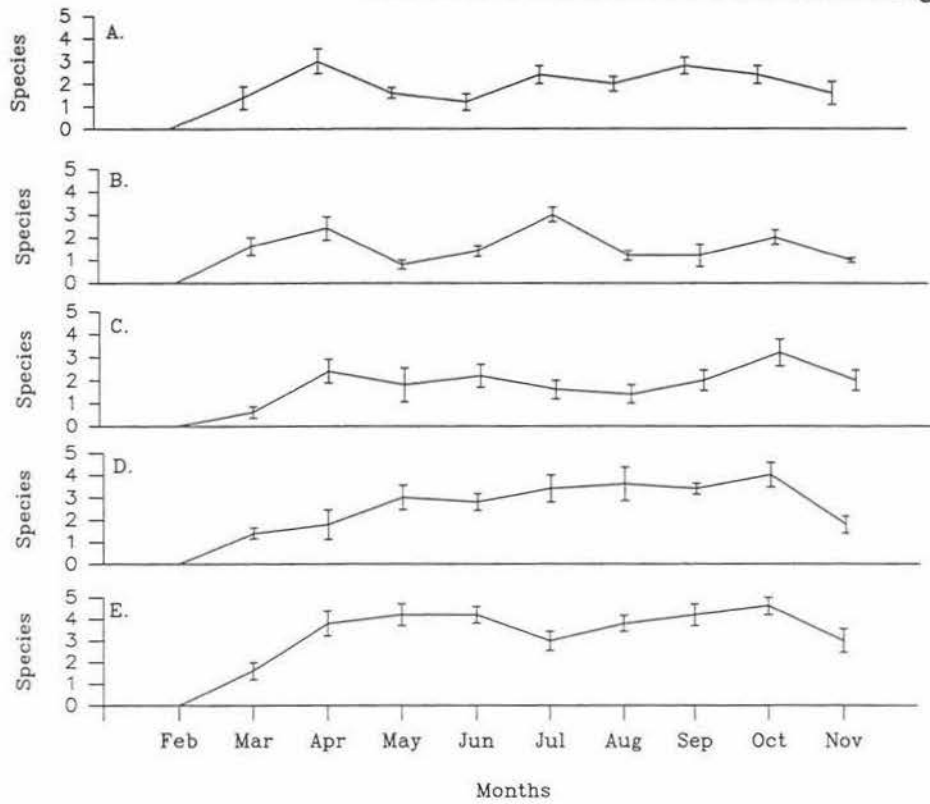
Figure 4.1. Number of species colonising refuge blocks between March and November 1993. Study sites are; **A.** Gorse, **B.** Broadleaf/Podocarp, **C.** Podocarp, **D.** Pasture, **E.** Manuka.
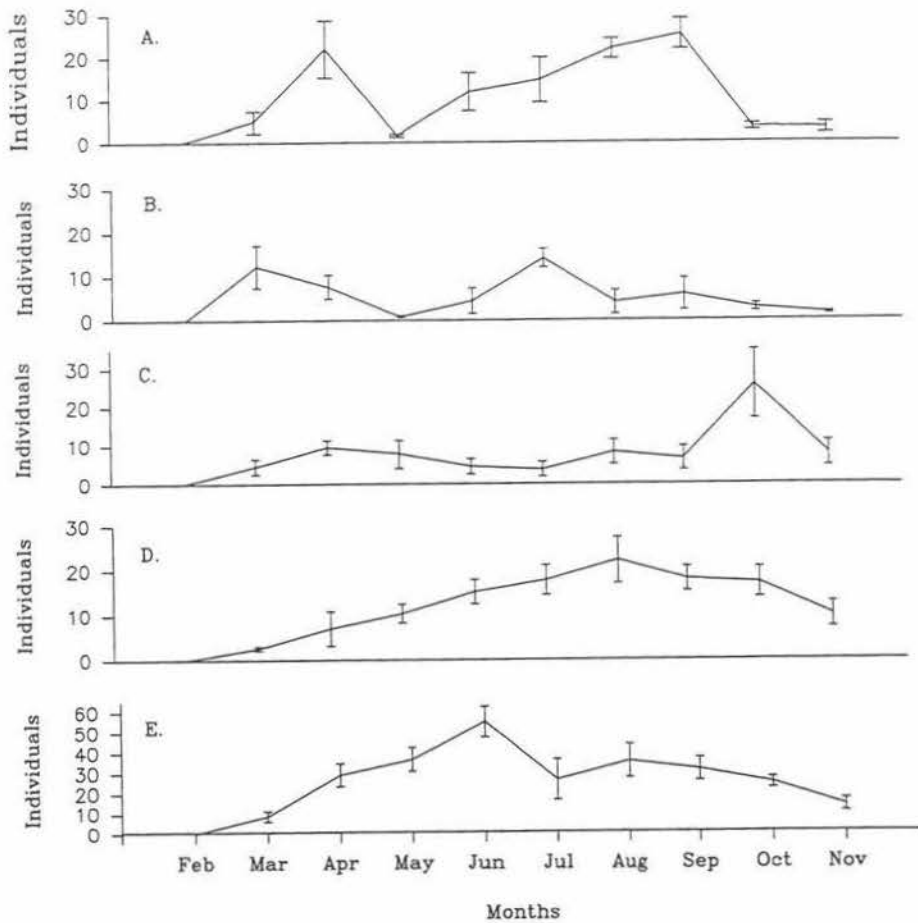


Figure 4.2. Number of individuals colonising refuge blocks between March and November 1993. Study sites are; **A.** Gorse, **B.** Broadleaf/Podocarp, **C.** Podocarp, **D.** Pasture, **E.** Manuka.

Total number of individuals collected in block assemblages at the end of the nine months was greatest in habitats of mid successional age (Gorse and Manuka). These sites had significantly more individuals ($F_{4,20}$=2.98, $P$=0.046) than early or late successional sites (Fig. 4.3). Of the 157 species recorded from the collected samples, species number (Fig. 4.4) was also greatest ($F_{4,20}$=28.47, $P$<0.001) in the Manuka, Broadleaf/Podocarp and Podocarp forests. Margalefs index for the block assemblages was also significantly greater ($F_{4,20}$=54.16, $P$<0.001) for the mid to late successional sites. In contrast, numerical dominance of site assemblages declined with increasing successional age ($F_{4,20}$=6.08, $P$<0.001) (Fig. 4.5). Pasture was the most highly dominated assemblage with high numbers of earthworms, while the two late successional forest sites displayed the greatest equitability.
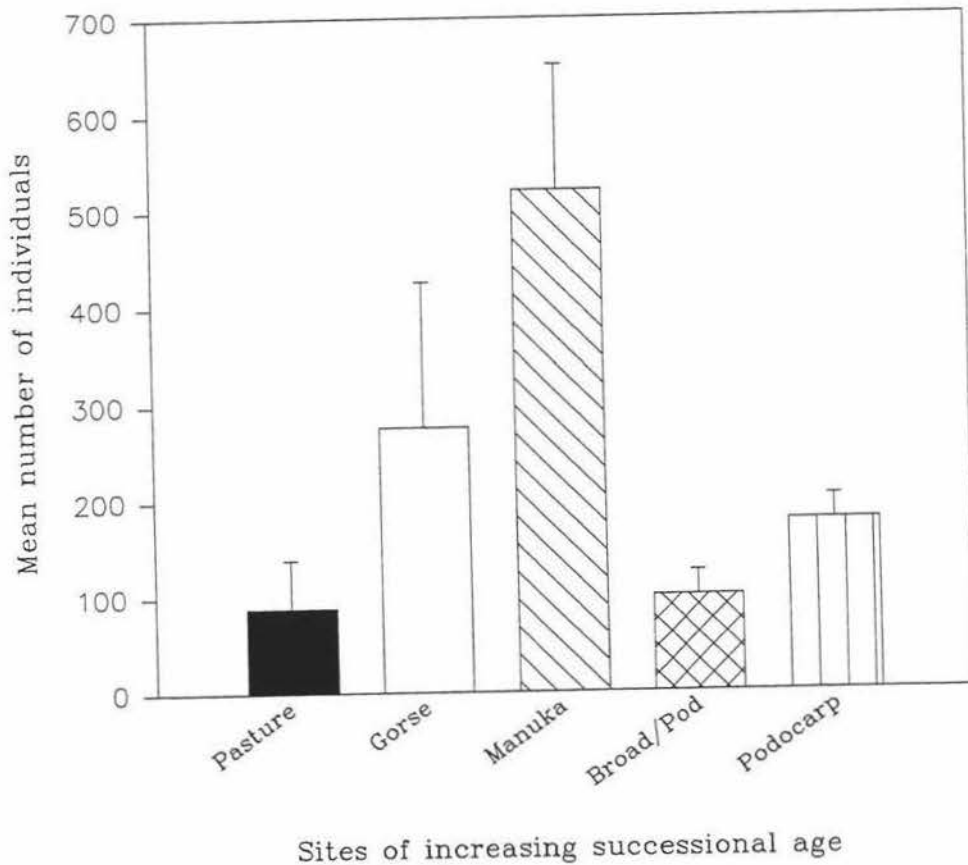
Figure 4.3. The number of individuals collected under refuge blocks at study sites after 9 months of colonisation (by Berlesse extraction).
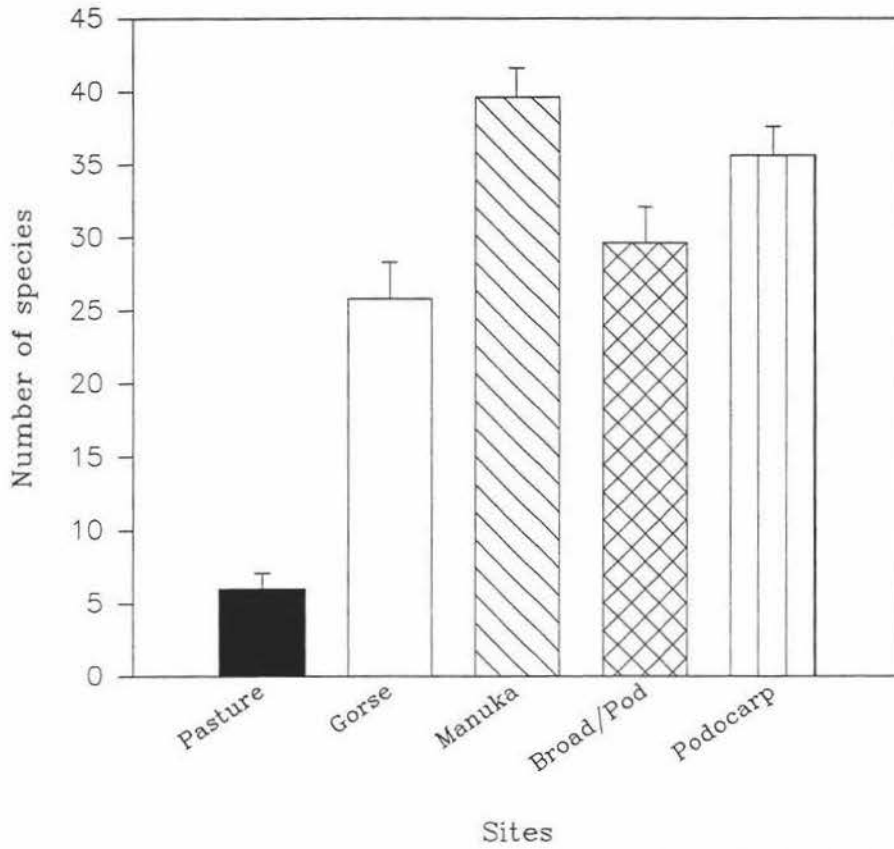
Figure 4.4. The number of species collected under refuge blocks at the study sites after 9 months of
colonisation (by Berlesse extraction).
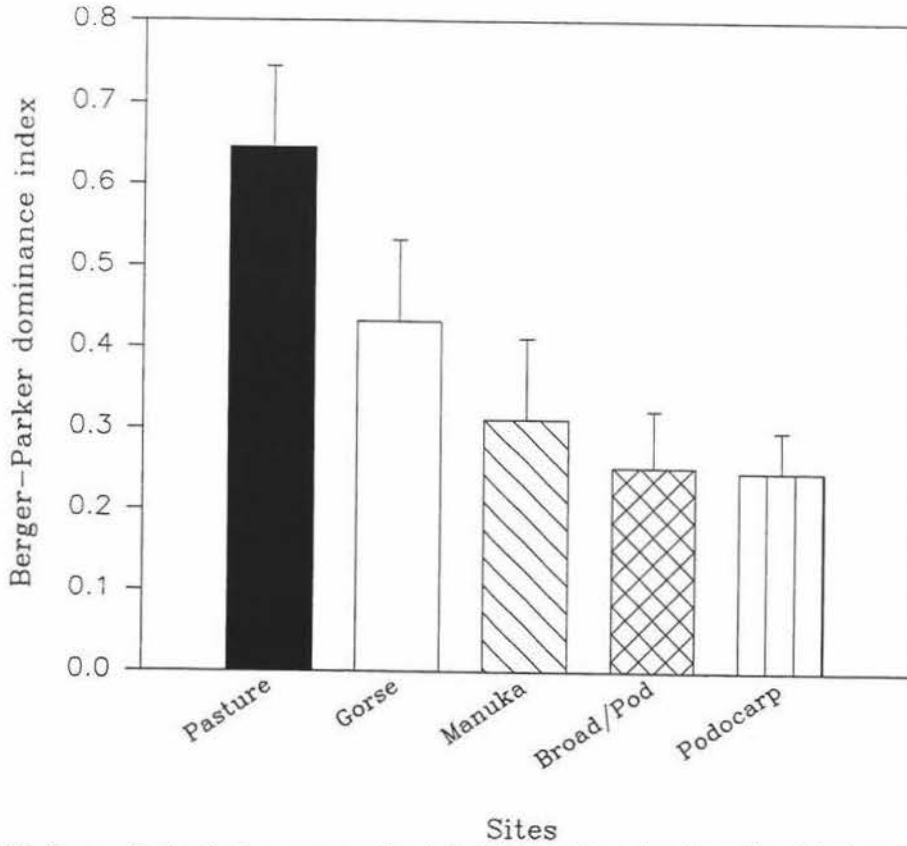


Figure 4.5. Berger-Parker Index measures for individuals collected under refuge blocks at the study
sites after a 9 month colonisation period.

*Guild and taxonomic structure*

Guild structure of collected invertebrates is plotted in Fig. 4.6. The relative abundance of predatory individuals increased with habitat age to peak at 28% in the late successional Broadleaf/Podocarp site ($F_{4,20}$=3.08, $P$<0.05), declining again in the mature Podocarp forest. Detritivores were the most abundant feeding group in all sites and no difference in the number of detritivores per site was detected ($F_{4,20}$=2.17, $P$>0.05). However, this group's relative abundance was particularly high in early successional habitats, making up 80% and 90% for Pasture and Gorse assemblages, respectively. Phytophagous individuals were rare; however, most phytophage individuals ($F_{4,20}$=23.66, $P$<0.001) occurred in the Pasture and Manuka assemblages, both sites with a grass ground cover. Hymenopteran parasitoids were most abundant in mid succession ($F_{4,20}$=15.90, $P$<0.001).



Habitats of increasing successional age.
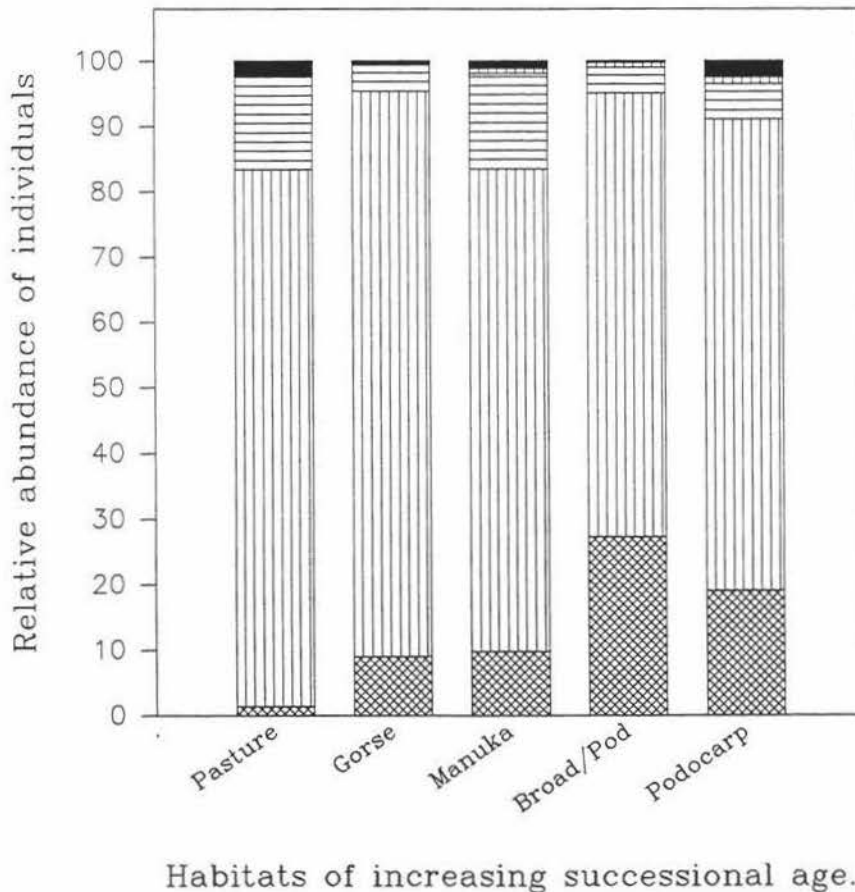
Figure 4.6. The relative abundance of individuals from the five most common feeding guilds, found to colonise the refuge blocks after a 9 month period, collected by Berlesse extraction. Guilds are represented as:  predator ▨  detritivore ⵤⵤⵤ   phytophage ▤   parasitoid ▦ and  scavenger ■
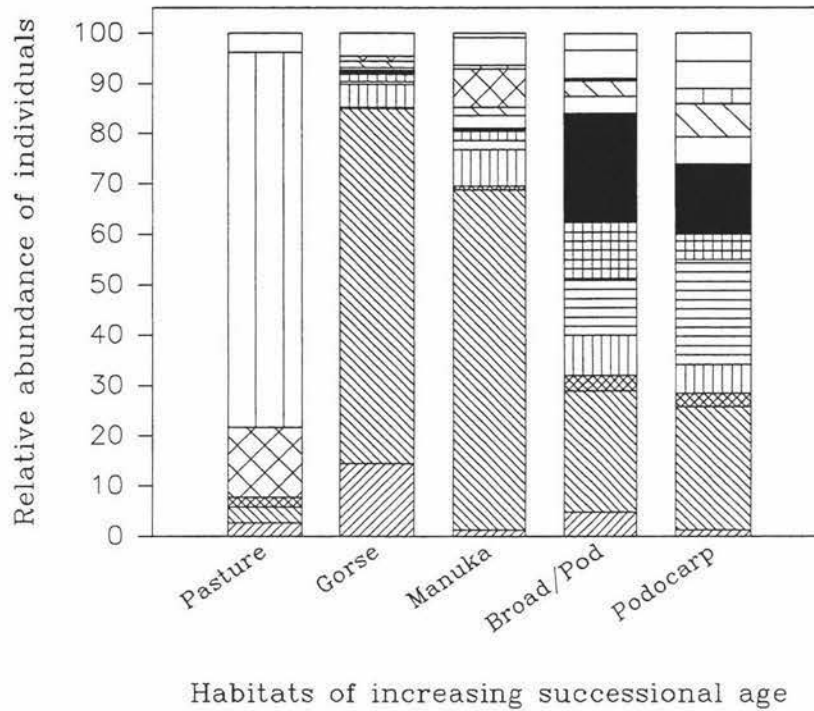
Habitats of increasing successional age

Figure 4.7. The relative abundance of individuals under refuge blocks from the most common taxo-
nomic groups, collected after a 9 month colonisation period at each of the study sites, are shown as:

Collembola ▨    Acari ▧    Araneae ▨    Coleoptera ▥    Amphipoda ▤

Chilopoda ▦    Opilion ◹    Diplopoda ■    Hemiptera ⧖    Hymenoptera ▭

Annelida ▯    Other ▭

Relative abundance of individuals in the 11 most common orders are compared
between sites in Fig. 4.7. In all but one site the most abundant group was mites
comprising between 24% and 70% of assemblages, except in the Pasture where they
were rare. The pasture refuges in contrast were dominated by earthworms compris-
ing 74% of all individuals found. Collembola were abundant in the Gorse, with
Coleoptera and Amphipoda absent from the Pasture samples, but increasing in abun-
dance with successional age.

*Assemblage structure*

Axis scores for detrended correspondence analysis (DECORANA) of assem-
blage structure for refuges in the five sites are plotted in Fig 4.8. Axis 1 of the ordi-
nation separated Pasture communities from the other sites, whereas axis 2 split sites
into two broad groups approximately corresponding to increasing vegetation age and
structural diversity of the habitats. Gorse and Manuka, both mid successional sites
with low habitat heterogeneity and complexity, were closely grouped at the upper
end of axis 2, with the two older forest sites (Broadleaf/Podocarp and Podocarp)
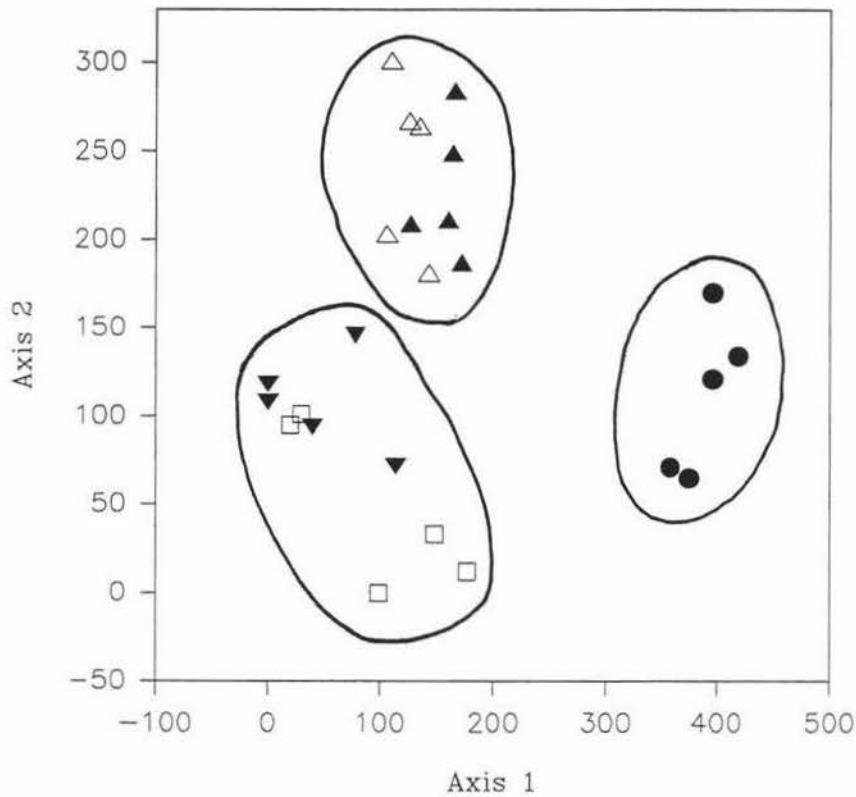grouped at the other end.

Figure 4.8. Axis 1 as a function of axis 2, for a DECORANA analysis of community structure for refuge block samples collected in November 1993. Sites are represented as: Pasture ● Gorse ▲     Manuka △     Broadleaf/Podocarp ▼     and Podocarp □

Taxa associated with axis 1 include a number of introduced species found at the Pasture site including: an earthworm (*Lumbricidae rubellus*), slug (*Deroceras reticulatum*) and two Hemiptera (Table 4.2). Axis 2 which split mid and late successional habitats from one another was positively associated with a variety of native taxa including: three predatory beetles, a Carabidae (*Selenochilus sp.*), a Coccinelidae (*Rhyzobius rarus*) and a Scydmaenidae; 2 small hymenopteran parasitoids, a Diapriidae (*Spilomicus sp 5*) and a Platygastridae; 1 Formicidae ( Sub Family: Formicinae), a mite (Oribatei), a spider (*Cambridgea sp 6)* and an Opilion (Order: Laniatores).

Table 4.2. Species associated with the three main DECORANA axes. Taxa are
listed in declinig order of importance.

| Axis 1 | Axis 2 | Axis 3 |
|---|---|---|
| Coleopteran larvae *sp.33* | Scymainidae *sp.6* | Araneae *sp.86* |
| *Lumbricus rubellus* | Spilomicrus *sp.5* | Oribatei *sp.8A* |
| Pulmonata | Araneae *sp.22* | Diapriidae *sp.4* |
| Trombiliformes *sp.24* | *Selenochilus sp.* | Armidillus sp. |
| Araneae juvenile | Formicidae *sp.2* | *Baens* sp. |
| Araneae *sp.67* | Opilion *sp.15* | *Panyolytomyia taurangi* |
| Aphididae *sp.2* | Diplopoda *sp.4* | *Brachyglutinae sp.2* |
| Hemiptera *sp.31* | Oribatei *sp.20* | *Brachyglutinae sp.2* |
| Trombiformes *sp.15* | *Platygastridae sp.5* | Geometridae *sp.2* |
| Geometridae lavae *sp.4* | *Rhyzobius rarus* | Opilion *sp.1* |

Cluster analysis of refuge block assemblages from each habitat revealed a
similar pattern with three broad groups: Pasture, Gorse and Manuka, and Broadleaf/
Podocarp and Podocarp forests (Fig. 4.9). Interestingly, replicate five from the Gorse
site proved to be an outlier to this analysis, perhaps because of greater heterogeneity
in ground cover near this block.

TWINSPAN was used to examine whether key taxa were associated with site
differences (Fig. 4.10). Again the first division separated pasture samples from the
other sites using earthworms as indicator taxa. The second division separated the
Gorse and Manuka sites from the two forest sites based on the presence of oribatid
mites and amphipods, respectively. Finally, at division 3 the presence of aphids and
Collembola respectively split the Manuka and Gorse sites. In the forest site group all
Podocarp forest replicates and two Broadleaf/Podocarp replicates were separated
from the remaining Broadleaf/Podocarp blocks. The former group had a millipede (sp.
*B*), oribatid mite and amphipods as indicator species and the latter group was com-
bined because of the presence of a different millipede (sp. *D*), a centipede and a
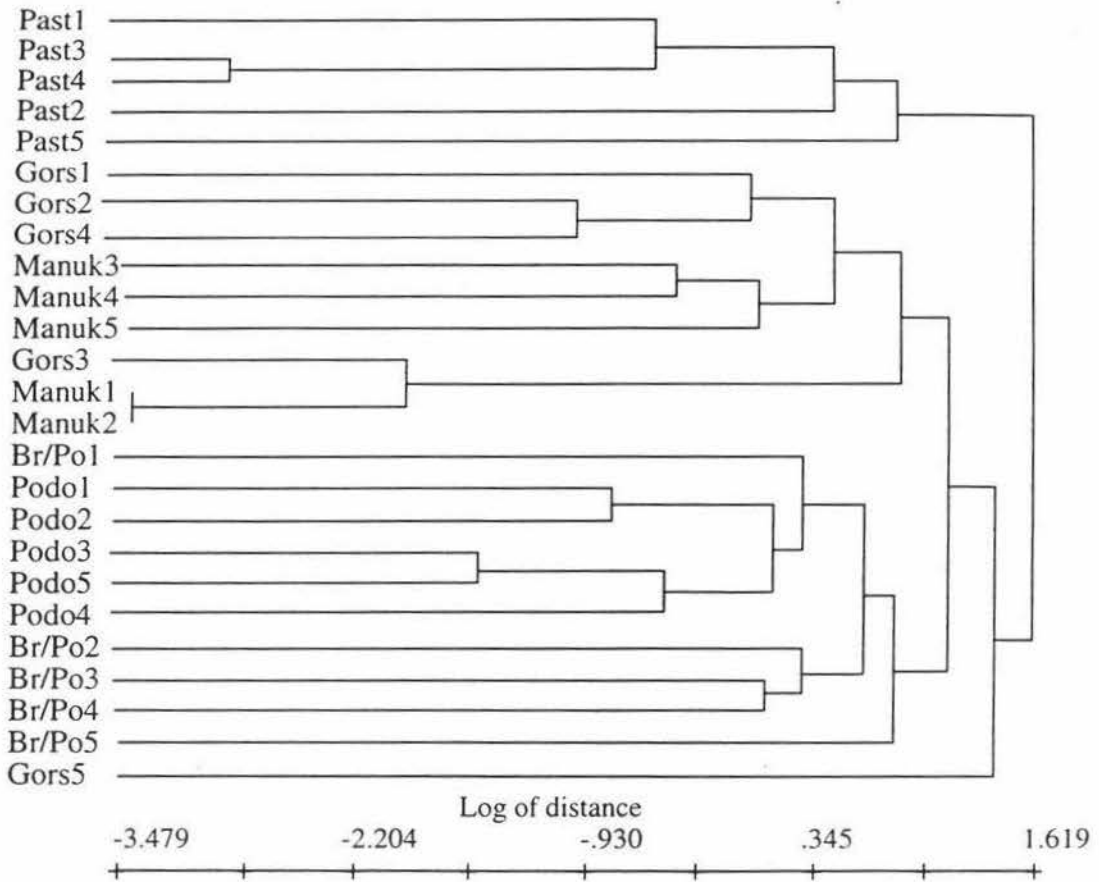Poduridae collembolan species.

Figure 4.9. Dendrogram of refuge block samples collected in November 1993 from the five successional sites. Study sites are: **Past** = Pasture, **Gors** = Gorse, **Manuk** = Manuka, **Br/Po** = Broadleaf/Podocarp forest and **Podo** = Podocarp forest. Numbers 1 - 5 represent replicates from each site.
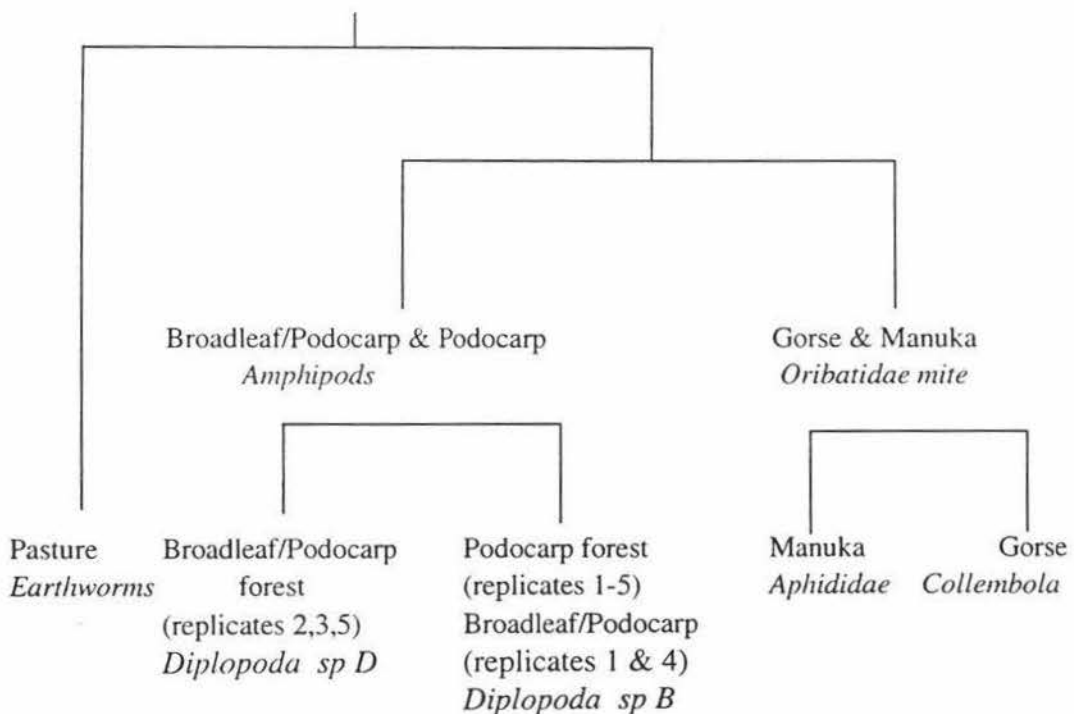


Figure 4.10. TWINSPAN analysis of refuge block samples collected in late November 1993. Habitats are divided according to the presence of key indicator species (in italics).

## DISCUSSION

*Diversity patterns*

Species richness and individual abundance under artificial refuges was greatest in the mid successional Manuka habitat. Numerical dominance however, was highest in the Pasture habitat with earthworms being the most abundant taxa. Low predator diversity but high abundance was also a feature of this habitat (Munro & Death 1994), possibly because few species are adapted to exotic grassland. In fact the majority of species at this site were introduced taxa such as Opiliones, earthworms and Carabidae. Low habitat complexity associated with pasture may also contribute to the low species richness both in this habitat (Chapt. 3) and under the refuge blocks (Rushton *et al.* 1990). Habitat complexity may be further reduced by grazing, which can in turn lower species richness and increase dominance (Gibson *et al.* 1992). In contrast, total number of individuals under the blocks was markedly higher in the mid successional Gorse and Manuka habitats and probably relates to the lower habitat heterogeneity, while greater availability of alternative refuges in the Broadleaf/Podocarp and Podocarp forest sites may have resulted in low colonisation in these sites (Bohnsack 1991).

*Guild structure*

Not surprisingly the numerically dominant guild in the block assemblages was that of detritivorous feeders. Brown (1991) found decomposer abundance to be closely correlated to leaf litter depth, and Gorse in this study had both the greatest litter depth and highest relative abundance of decomposers. The predator guild was the second largest group with highest numbers in the mid successional habitats, a trend also consistent with Brown and Southwood (1987). This may be explained by the greater availability of web attachment sites and diurnal refuges in the late succession sites. However, low predator numbers in the late successional Podocarp forest may be due to competitive exclusion between species in the predator guild (Niemela 1993). This point is supported by the occurrence of only one species of Carabidae (*Megadromas capito*) in the late successional forest, compared to four species regularly found in the Gorse, Manuka and Broadleaf/Podocarp sites (Munro & Death 1994). A decline in spider species abundance in late succession could also be related to highest primary productivity being associated with the forest canopy (Hurd & Fagan 1992), yeilding high numbers of herbivores at canopy level and hence, less prey available at ground level. The number of guilds colonising block refuges increased with time, both for passive reasons and because some, such as the predator

guild, require other guilds in order to persist ( Heong *et al.* 1991).

*Overall community structure*

Examination of overall community structure using multivariate methods revealed three broad community groups roughly corresponding to habitats of increasing successional age. These were the Pasture, Gorse and Manuka, and the two forest sites.

The most common taxa at the Pasture site (slugs, earthworms) were not found in any other site and were primarily introduced species common in exotic grassland (Cameron & Butcher 1973). It appears that habitat characteristics at this site e.g. exotic vegetation, intensive grazing by sheep, lack of diurnal refuges and other structures necessary for prey capture or predator avoidance, were not suitable for native species colonisation. Gorse and Manuka, both mid successional habitats, are . structurally less diverse and have monocultural vegetation canopies. They consequently share a number of detritivorous and predatory species despite the fact that the dominant vegetation type at one site is exotic while at the other it is native. However, the lack of more specialised species, such as those occurring in late succession e.g. fungal feeding Coleoptera and sedentary mygalomorph spiders, was probably because the appropriate food sources and habitat structures do not occur in mid succession. Both late successional forest sites had high degrees of habitat complexity evidenced by the vertical vegetation levels present and high habitat heterogeneity, with more log/branch debris and a greater diversity of ground level vegetation. Refuges such as subcortical areas under bark were also more numerous in mature trees (Baehr 1990 & Hanski 1991). Consequently fewer individuals were found under refuges in late succession, probably because of alternative natural refuges at ground level and in vertical vegetation structures.

In conclusion, increased habitat heterogeneity and habitat complexity, associated with increased successional age and the availability of alternative natural microhabitats, influenced the pattern of colonisation by invertebrates of artificial refugia. In habitats with fewer individuals, such as early succession, the potential number of individuals was low and consequently levels of colonisation were also low. In comparison the potential number of individuals was high in late succession, but low colonisation was attributed to the greater density of alternative refuges. Diversity and abundance was highest under refuges in mid successional sites, probably because of the low availability of natural refuges and high abundance of invertebrates in these sites.

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# CHAPTER FIVE

# *THE EFFECT OF HABITAT AGE ON THE INTENSITY OF PREDATION IN GROUND DWELLING INVERTEBRATE COMMUNITIES*

## ABSTRACT

Predation pressure by arthropod predators in five habitats of differing successional age, was evaluated using live lepidopteran baits. Predators in late successional forest were most effective at removing these baits, with predation intensity lowest in early succession. Predation levels were not correlated with predator abundance or diversity. Seasonal patterns in predation pressure were correlated with grass minimum temperature in all habitats. Predator abundance was highest in Pasture and declined as successional age increased. In contrast predator diversity was greatest in mid successional Manuka and late successional Broadleaf/Podocarp forest.

**Key words**: predation pressure, succession, arthropod predators.

## INTRODUCTION

In a recent attempt to develop a theoretical framework for terrestrial invertebrate communities, Price (1991) predicted that the degree of predation occurring in successional seres will increase with habitat age. However, little work has been conducted on the effect of succession *per se* on the relationship between predator and prey assemblages to support this contention. A number of studies have however, looked at the effects of increasing complexity and diversity of habitats (Winder *et al.* 1994, Hurd & Eisenberg 1990, Trujillo-Arriaga & Altieri 1990, Southerton 1984, Speight & Lawton 1976). One exception is the recent study by Lovei and Brown (1993) who examined predator impact in successional grasslands. Again however, few studies have examined changes in predation pressure through a range of successional habitats culminating in mature forest.

Invertebrate communities, particularly the predator assemblages in the five successional study sites were examined in Chapt. 3. The findings of this work showed predator abundance and diversity to be low in mature forest, possibly as a consequence of competition. Whereas in early succession, the low habitat heterogeneity of exotic grassland limited the predator guild to mostly introduced species, with high predator diversity and abundance occurring in mid to late successional sites. It seems likely to expect therefore that predation would be high in these habitats, as most models predict that predation rates on prey are proportional to predator density, though there is little experimental data to back this up (Abrams 1993).

The aim of the present study is to test predation levels within five successional habitat stages from grassland to mature forest. Quantification of the resident predator assemblages associated with these habitats and seasonal effects are also explored to examine their relationship with the intensity of predation pressure.

## METHODS

### Experiment 1

Predation trials conducted monthly between May and December 1993 used *Galleria mellonella* caterpillars as live prey baits. Predation levels were assessed at five sites of differing successional age: Pasture, Gorse, Manuka shrubland, Broadleaf/ Podocarp forest and Podocarp forest.

Caterpillars were secured alive with cotton thread behind the last pair of prolegs. This method restrained 96% of *G.mellonella*. Caterpillars that did escape could easily be distinguished from those taken by predators, because of gut residue left on the cotton by predators, compared to a clean cut of the cotton by escaping caterpillars. *G. mellonella* species were chosen as suitable prey items because they survived periods of being tethered, reducing the confounding factor of death by causes other than predation.

Cotton secured around the abdomen extended 10 cm before being taped to a galvanised iron lid (20 x 20 cm) raised 3 cm above the ground. Caterpillars were thus restrained from escape, but not immobilised. Therefore predators such as spiders which use both visual and vibratory cues (Uetz 1992) were not excluded; however, bird and mice predation was prevented. Caterpillars were taped in groups of five (at 4 cm intervals) along the lids. Six replicate lids were placed 10 m apart along a 50 m transect in each of the 5 sites. Thirty baits per site were left for a 24 hour period.

Predation level was assessed by scoring each caterpillar between 1 and 5 depending on the degree to which they were consumed. These scores correspond to:

    0 = no damage

    1 = bait pierced, but not consumed

    2 = bait 1/4 consumed

    3 = bait 1/2 consumed

    4 = bait 3/4 consumed

    5 = bait completely removed

*Experiment 2*

To assess the effects of bait size on the measurement of predation pressure, I conducted three trials with two bait sizes: 15 large (20 mm x 4 mm) and 15 small (10 mm x 2 mm) caterpillars per site. Experimental design was similar to experiment 1, however, in this case two lids had five small caterpillars and five large caterpillars in a block 1 m apart.

*Predator guild*

The predator guild was sampled as outlined in Chapt. 3. However, predator data used in conjunction with the predation experiment included only that from May to December.

*Data analysis*

Differences in predation levels between the five sites were explored using a mixed model ANOVA design and the GLM procedure of SAS (SAS 1985). Data were analysed in two forms; one with the predation score ranging from 0-5 and the other with baits classified as damaged or not, irrespective of the degree of damage. Spearman rank correlation was used to examine the relationship between predation levels and various biotic and abiotic characteristics (Table. 5.1).
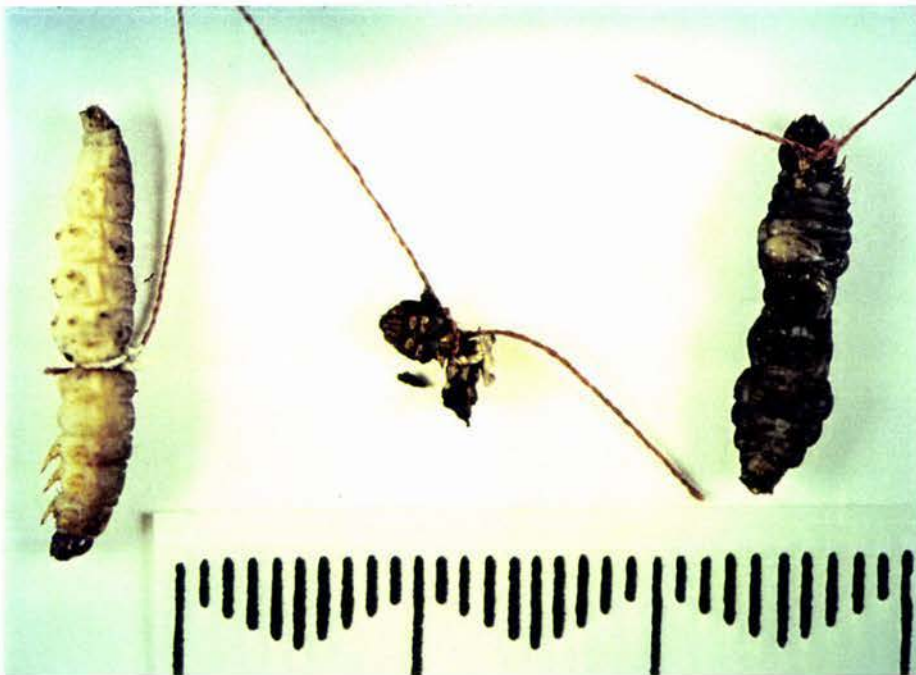


Plate 5.1. *Galleria mellonella* prey items showing Carabidae predation (centre) and spider damage (right). Lab experiments using representatives from four arthropod predator groups were used to determine the characteristic predation pattern of each group.

Plate 5.2. *Galleria mellonella* prey item being investigated by a flatworm and a mite, during a field trial.

## RESULTS

*Predation pressure*

Analysis of predation data using the 0-5 damage score system ($F_{4,28}$=94.25, $P$<0.001) and kill / no kill score ($F_{4,28}$=94.48, $P$<0.001) both indicated significant site differences. Predation levels were also significantly different between months ($F_{7,1151}$=31.47, $P$<0.001), in months with higher minimum temperatures (May, June, October, November and December) having the highest predation levels (Fig. 5.1). In contrast, active abundance in the predator guild was highest in May, declining to low levels in the following months and lacking the rise in activity in Spring that occurred in the predation data (Fig. 5.2). Although again temperature was significantly correlated with predator activity (rs=0.21, $P$<0.001) (Fig. 5.3). Data from experiment 2, found both prey sizes were taken in equal abundance (Fig. 5.4) ($F_{1,436}$=3.36, $P$=0.06) in all sites.
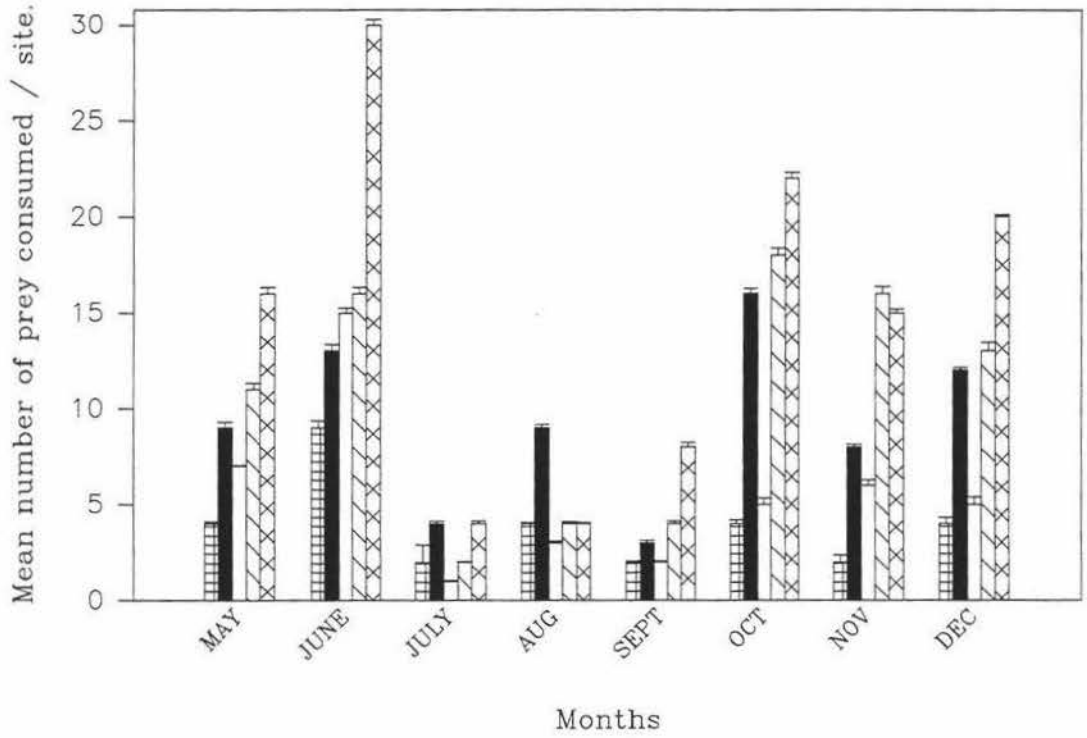
Figure 5.1. Seasonal trends in predation intensity recorded between May and December 1993, in habitats of increasing successional age. Pasture ⊞  Gorse ■  Manuka ☐
Broadleaf/Podocarp ◥  Podocarp ⊠
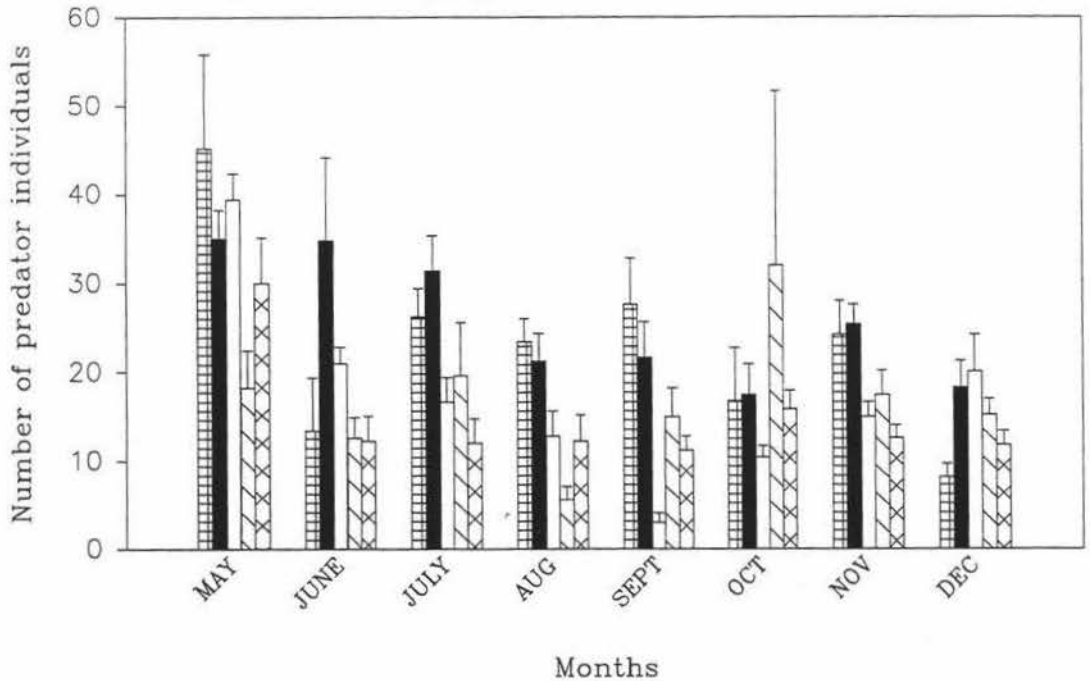


Figure 5.2.  Mean number of predatory individuals collected in pitfall traps between May and December 1993, in five habitats of increasing age. Pasture ⊞ Gorse ■ Manuka ☐
Broadleaf/Podocarp ◥ Podocarp forest ⊠
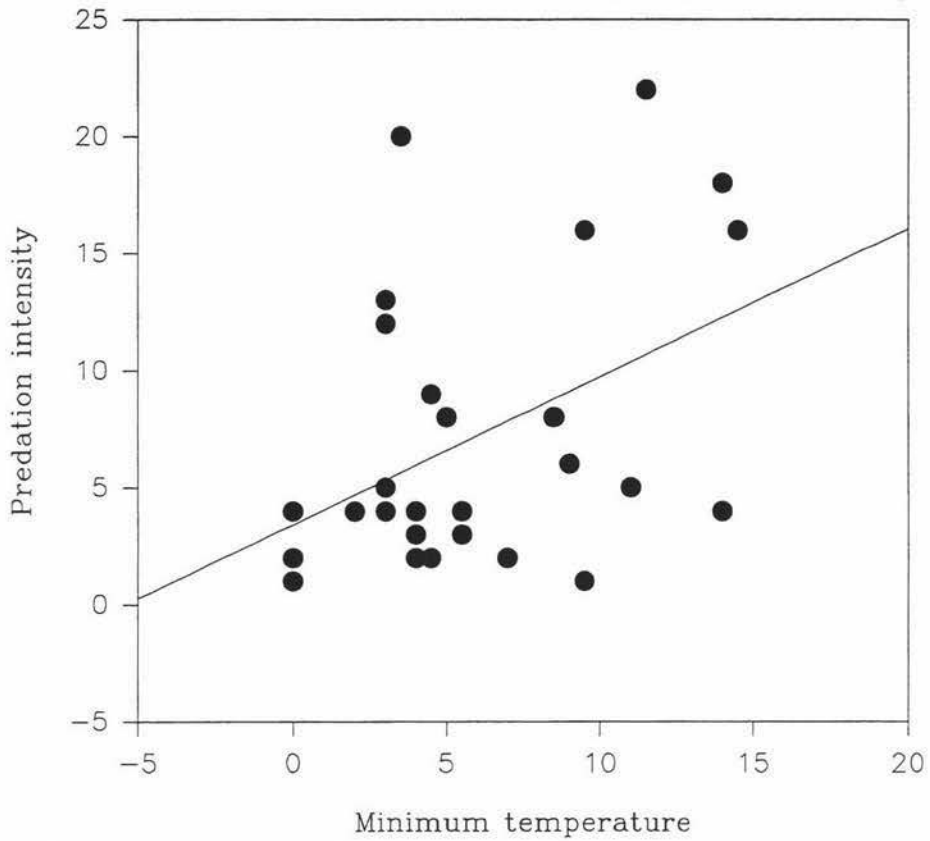
Figure 5.3. Correlation between predation intensity and the minimum temperature recorded during each predation trial (rs=0.21, *P*<0.001).
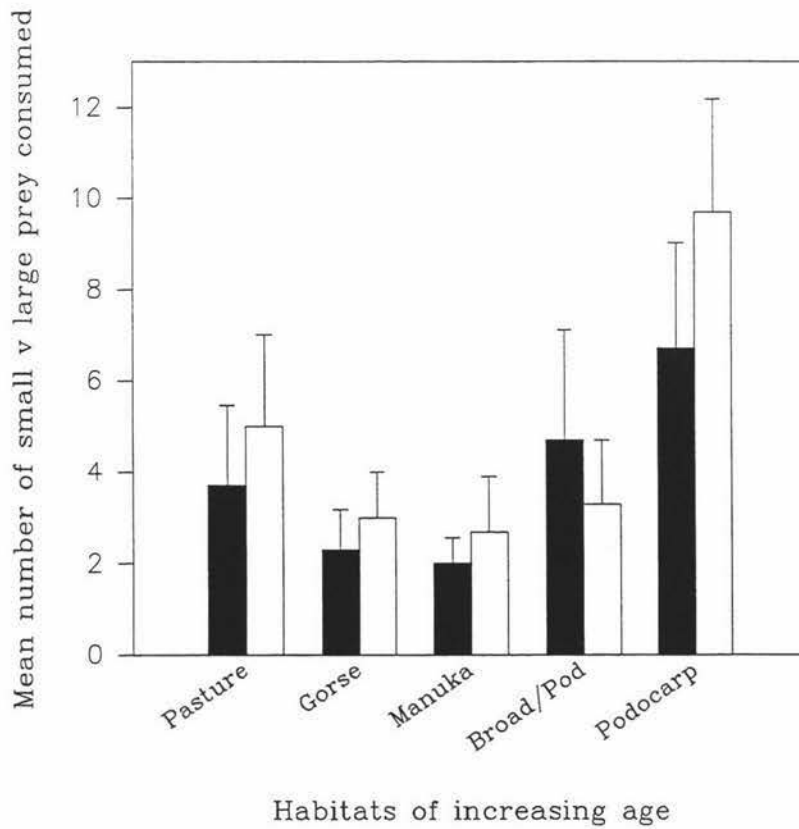


Figure 5.4. Mean number of large and small *Galleria mellonella* caterpillars preyed upon by arthropod predators, during three trials conducted at weekly intervals between February and March 1994. Prey sizes are represented as: large prey ■ and small prey ▢

Mean predation levels were highest in mid successional Gorse and late successional Broadleaf/Podocarp and Podocarp forests (Fig. 5.5) and lowest in the Pasture and Manuka. Surprisingly, this pattern was the reverse of that for total predator abundances in these sites, with a negative correlation (rs=0.13, $P$=0.98) between abundance and predation intensity.
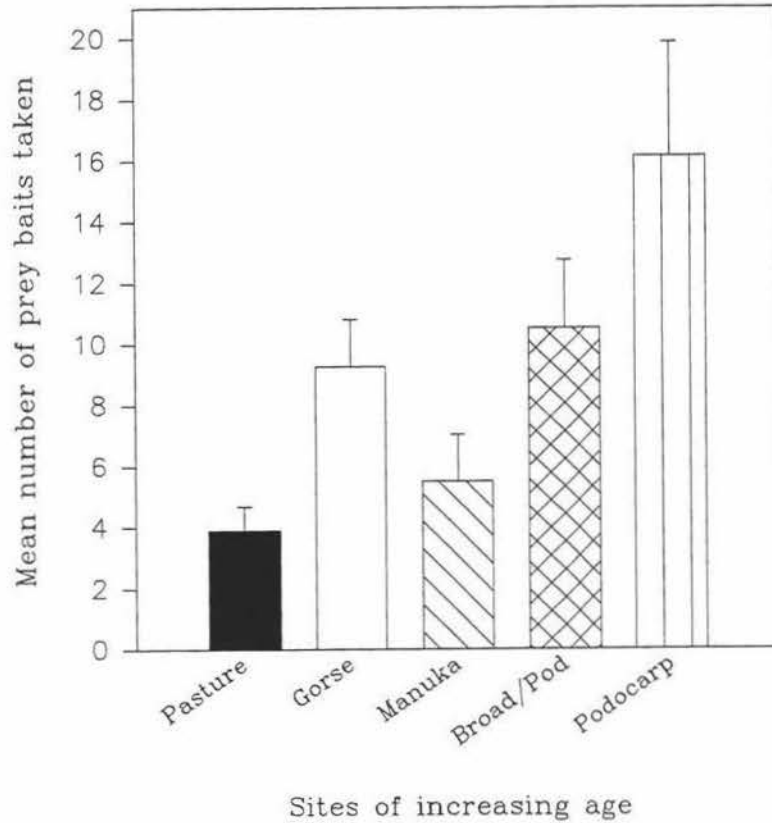


Figure 5.5. Mean intensity of predation on Galleria mellonella baits by arthropod predators between May and December 1993, at each of the five successional sites.

*Predator assemblage structure*

Investigation of the predator guilds found at the five study sites, showed predation levels were not correlated with Margalefs species richness ($P$=0.59), species number ($P$=0.76) (Fig. 5.6), relative predator abundance ($P$=0.63) (Fig 5.7) or mean predator abundance ($P$=0.82) (Fig. 5.8). Correlation coefficients are presented in Table 5.1.

Whereas relative predator abundance (as a percentage of the whole community), between May and December, was highest in the early successional Pasture and mid successional Gorse and Manuka, predation was found to be highest in the mid successional Gorse and late successional forests. Furthermore no relationship could be found between the relative abundance of predatory order or family and predation intensity in the communities of the five study sites (Fig. 5.9).
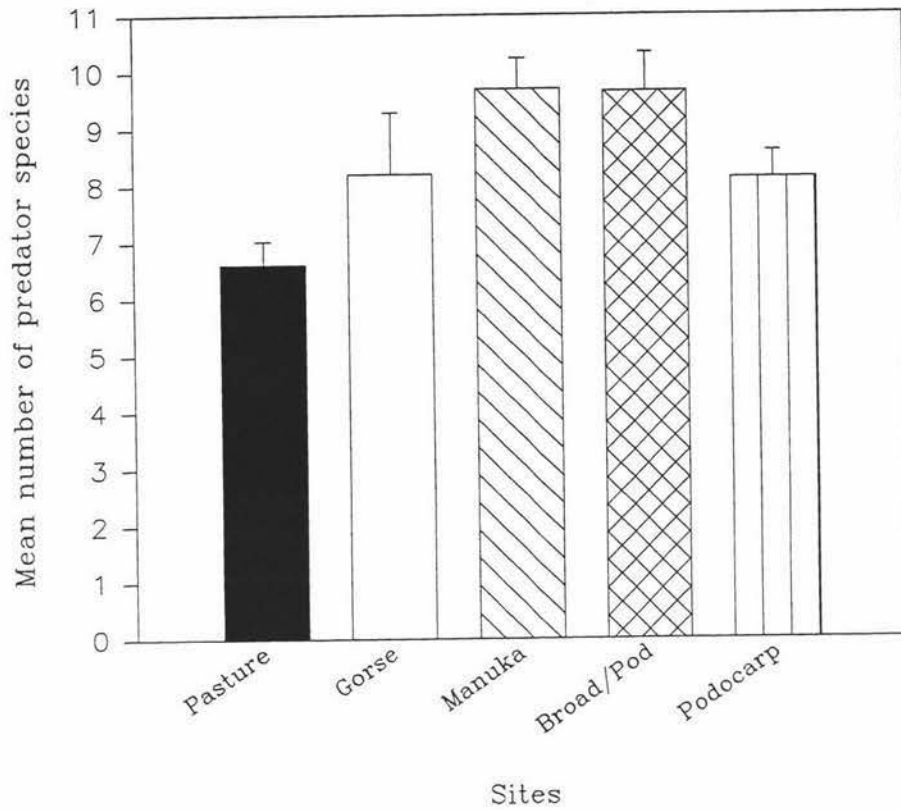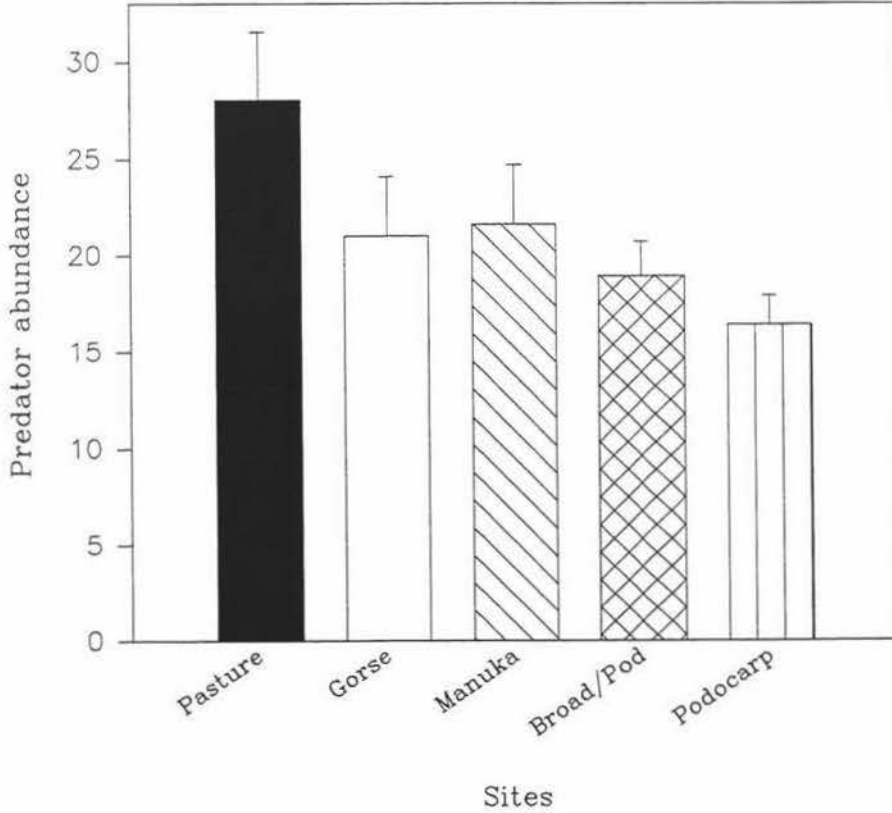
Figure 5.6. Mean number of predator species collected between May and December 1993, in the
five successional sites.

Table 5.1. Correlation coefficients between predation rates and the predator assem-
blage in sites of increasing successional age, between May and December 1994.

| | Predator abundance | Predator spp number | Margalefs spp richness | Carabidae abundance | Predator relative abundance | Minimum temperature |
|---|---|---|---|---|---|---|
| Predation rate (r) | 0.01 | 0.07 | 0.1 | 0.07 | 0.13 | 0.45 |
| Significance | $P=0.98$ | $P=0.63$ | $P=0.51$ | $P=0.63$ | $P=0.40$ | $P<0.01$ |
| Number (n) | 40 | 40 | 40 | 40 | 40 | 40 |

Of the predator guilds in the sites with high predation levels: the Gorse assem-
blage was dominated by Staphylinidae and spiders, the late successional forests as-
semblages by Araneae, Staphylinidae and Opiliones, and the Manuka assemblage by
spiders and staphylinids (Fig. 5.9.).
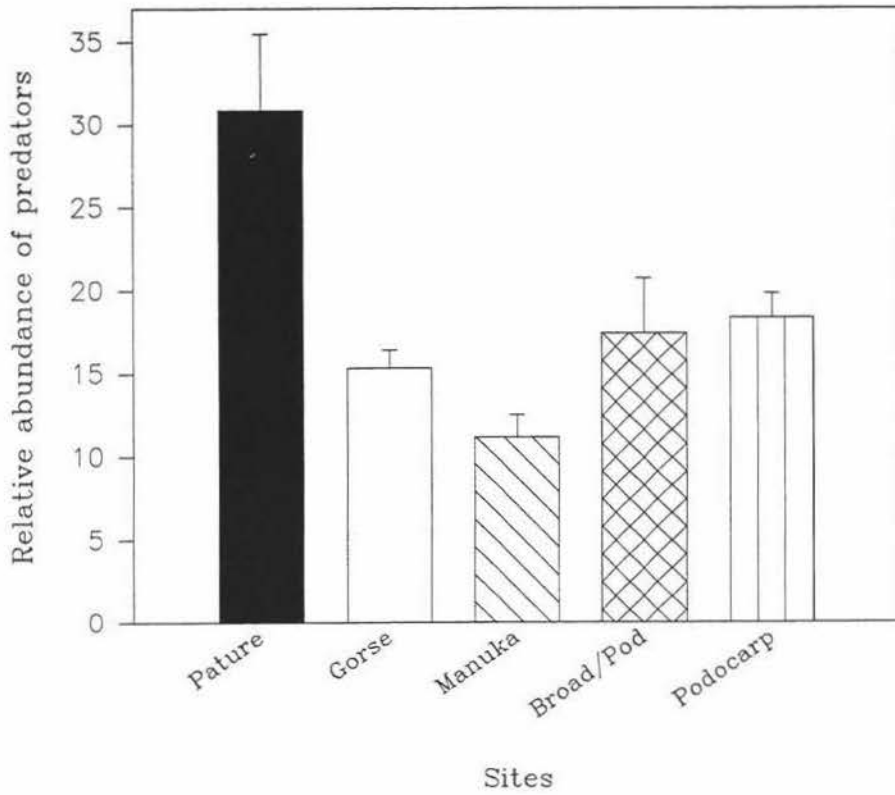
Sites

Figure 5.7. Mean relative abundance of predatory individuals (as a % of community) collected between May and December 1993, in the five successional sites.



Sites

Figure 5.8. Mean number of predatory individuals, collected between May and December 1993, in the five successional sites.
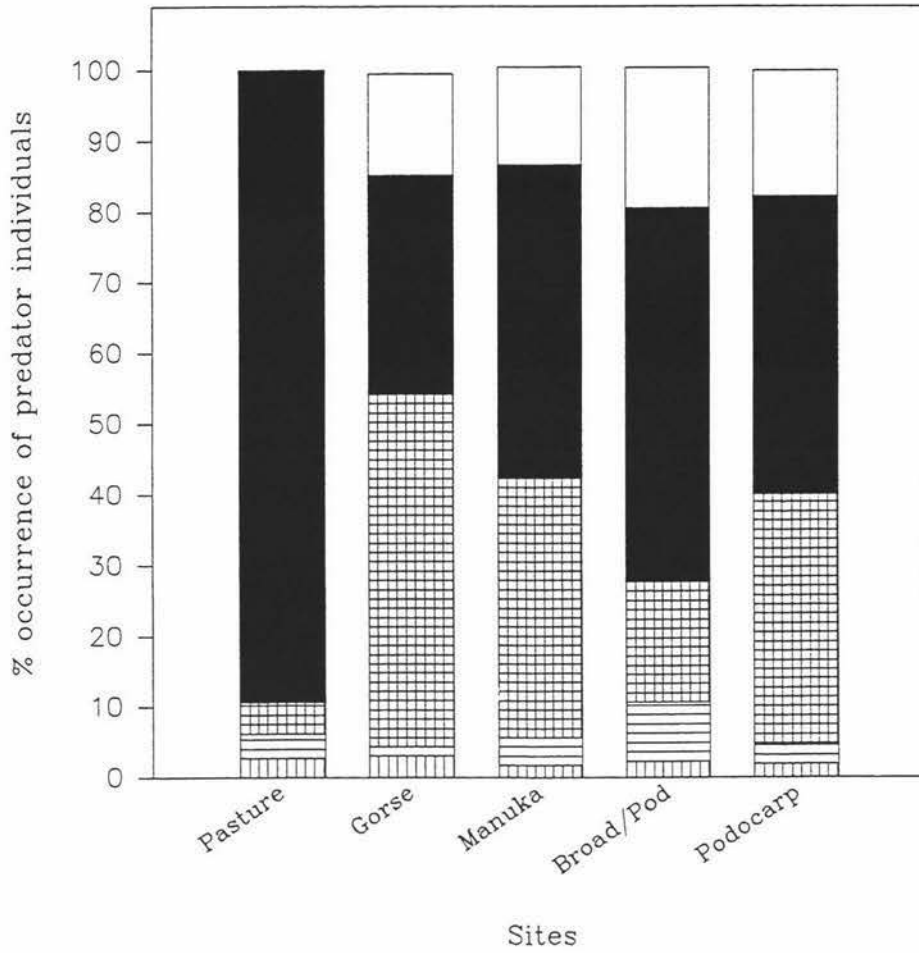
Figure 5.9. Mean relative abundance (%) of individuals from the five most common predatory families/orders, represented as: Carabidae ▯ Formicidae ▤ Staphylinidae ▦ Araneae ■ Opilion ▯

## DISCUSSION

*Predation and succession*

The pattern of increasing predation pressure with increasing successional age recorded at the study sites, conforms with the predictions of Southwood and Comins (1976), Southwood (1981) and Price (1991), that predation levels will be low in early succession and highest in late succession. Low levels of predation pressure recorded at mid successional sites is also consistent with Lovei and Brown (1993) who recorded low predation levels in mid succession, in their case in grassland. However, lowest predation intensity in the present study was recorded in early successional Pasture, in contrast to their findings.

The lack of a relationship between predation levels, and predator abundance or diversity is surprising. However, as indicated by Abrams (1993) predation rates are not necessarily related to predator density, because predator avoidance behaviour and increased habitat heterogeneity may provide shelter for prey from predation. Predation rates and predator density may not, therefore, always assume a linear relationship.

It appears that differences in predation levels at the sites may be governed by differences in habitat suitability, which in turn affect the size distribution of predators in these habitats rather than the abundance or diversity. Early successional grassland recorded the lowest predation levels, but highest predator abundance. However, predator abundance there was largely a result of high numbers of small *Linyphiidae* spiders, with none of the larger native species found at the forest sites. Similarly, Manuka, although a native plant, and again with high predator abundance, also had assemblages where the majority of species were small and predation pressure was low. Gorse, on the other hand, although an exotic habitat, had a higher structural diversity allowing more large native species to inhabit it i.e. Carabidae, Opiliones and *Cambridgea* (a large spider species). As a consequence predation levels were higher. High predation levels in the late successional forests may also be attributed to predators in these habitats being more effective because of their size, although predator abundance in these habitats was low.

High numbers of prey were taken in the warmer autumn and spring in all sites except Pasture and Manuka, when daily minimum temperatures were higher than those in winter. Predation in the Pasture and Manuka sites peaked in June, but lacked the rise in spring that occurred at the other sites. Temperature fluctuations nor predator abundance could explain the low spring predation in these habitats.

However, during the spring, grazing occurred at the Pasture and Manuka sites. Stock grazing in spring was found to be correlated with declines in the predator assemblages in these sites (Munro & Death 1994), and other authors have found a similar decline amongst the predator guild, due to changes in habitat heterogeneity because of grazing or grass cutting (Hutchinson & King 1980, Morris & Rispin 1987, Rushton *al.* 1990). It seems likely therefore, that grazng may be responsible for the low predation levels in spring.

In conclusion, predation was found to be highest in the late successional forest habitats and may be a result of the larger, more effective, native predator species occurring in these sites. Occurrence of large predators seems to be related to higher levels of habitat heterogeneity, which are a feature of late successional vegetation. Conversely, the lack of appropriate structures to encourage large predator inhabitation of early and mid successional sites, resulted in the of low predation intensity in these sites. Therefore terrestrial arthropod predation levels may not always be related to the obvious characteristics of a predator assemblage such as abundance and diversity, as is predicted by the current models of predation.

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# CHAPTER SIX

## SYNTHESIS

## THESIS SYNTHESIS

The community patterns obtained from both pitfall and refuge sampling largely conformed to those outlined in other studies. Brown (1991), Lawton (1983) and Southwood *et al.* (1979) all found diversity to increase with increasing habitat heterogeneity and complexity. However, in contrast to their work, diversity declined in the climax forest.

The predation experiment supported the findings of the theoretical work of Abrams (1993), that predation levels are not necessarily related to the density, abundance or species richness of the predator assemblage in any particular habitat. The only biotic or abiotic variable measured in this study, that correlated with predation intensity in the five successional habitats, was temperature.

However, the finding that predation intensity is greater in the later successional vegetation remnants, offers some support for the contention that these habitats may act as reservoirs of natural enemies in agroecosystems. Further research to establish the degree of benefit from native predators in such remnants will need to be directed towards: their degree of mobility (e.g. their ability to move from forest remnants); predator adaptability to refuges in farmland (e.g. the type of refuges required to enable colonisation); and the level of predation exerted by different species of predator, rather than the whole assemblage and the impact of this on pest populations.

From the biodiversity perspective of conservation, remnants of successional vegetation are of value for the retention of a wide variety of invertebrates, and the vertical (i.e. trophic level linkages) and horizontal interactions (i.e. interspecific competition on the same trophic level) associated with invertebrate communities in these habitats. It is therefore, interesting to find that even vegetation that has not yet reached a mature successional stage, such as mid successional manuka, is of value in preserving diversity, although community interactions may not be as tightly developed as in mature forest. Mid successional vegetation in this study was found to harbour both new (a new genus of the millipede of the family Delodesmidae) and rare (an apomorphic hymenopteran parasitoid of the family Diapriidae, *Idiotypa sp 28*) species. The size of forest remnant considered of conservation value has hitherto been defined by criteria developed for vertebrate and plant species preservation. The present study has shown small areas (5-10 h) of vegetation contain high invertebrate species richness. Areas of successional vegetation that are small or early in the successional sequence may therefore, be of value for maintaining invertebrate diversity.

In conclusion, this work found that diversity levels do not always increase in a linear way with succession, although community functioning does seem to increase with successional age. It has also produced support for the argument that predation levels can not always be correlated with the obvious characteristics of predator assemblages, such as abundance and species number. Finally, this is one of the first studies in New Zealand to highlight the possible links between forest conservation and agriculture, via the use of native arthropod natural enemies. Also, (to the best of my knowledge), this is the first study to examine terrestrial invertebrate communities along a successional gradient in New Zealand vegetation.

# ACKNOWLEDGEMENTS

# ACKNOWLEDGEMENTS

# APPENDICES

# FOREST REMNANTS: THEIR POTENTIAL AS A SOURCE OF NATURAL ENEMIES IN AGRICULTURE.

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## SUMMARY

Some schools of ecological theory predict that predator species abundance will be greater in patches of more mature habitat than in earlier successional habitats such as pasture. To examine this, ground active invertebrates were sampled by pitfall trapping between December 1992 and January 1994 in five habitats of increasing successional age; pasture, gorse, manuka, regenerating podocarp and a mature podocarp remnant in the Northern Wairarapa. Diversity of predators increased through early successional sites, peaked in mid successional stages, and declined in later successional sites. Individual predator numbers were highest in the pasture and declined through habitats of increasing succession in most months.

**Keywords:** natural enemies, forest reserves, ecological theory.

## INTRODUCTION

Both theoretical (Murdoch et al. 1985) and empirical work (Winder et al. 1994) indicates that polyphagous arthropod predators can achieve significant levels of control of insect pests within agroecosystems. However, most studies investigating generalist predators in agriculture have relied on manipulating the habitat, eg. field margin refuges and intercropping to increase entomophage abundance within agroecosystems (Dennis & Fry 1992; Herzog and Funderbunk 1986; Letourneau 1990).

Current economic trends in extensively managed pastoral systems have seen a concentration of resources into more productive land, encouraging the retirement of erosion prone and major weed problem areas. Conservation efforts by the government and private landowners have also seen many remnants of native vegetation set aside. Studies of predator assemblages in pasture, crop and orchard habitats from both overseas (Reichart & Lockley 1984; Adams 1984) and in New Zealand (Death unpublished data) indicate that spiders, opiliones, centipedes, and carabids may be the potentially important predators in such systems. These are the same invertebrate predators that can be very common in retired land and native forest remnants (Butcher and Emberson 1981) and are potentially important in agricultural systems. If forest reserves do harbour more natural enemies which have the capacity to move into neighbouring agricultural land, they may offer a ready source of predators for exploitation in agroecosystems.

Price (1991) in a recent review of forces important in structuring insect communities suggested that predator diversity and abundance should increase as habitat age and complexity increases. In this study we examine the potential of such retired land to act as reservoirs of beneficial entomophages and whether or not this potential increases with successional age of the remnant as predicted by Price.

## METHODS

The study sites were located within a 5 km radius in pastoral farmland within the northern Wairarapa. Dominant vegetation types found at the study sites roughly correspond to habitats of increasing successional age found in the Wairarapa (McQueen 1991). Thus vegetation in order of increasing successional age were: pasture (20 years since last cultivated), gorse (25 years old), manuka (30-40 years old), regenerating broadleaf/podocarp

forest (100 years since cleared by fire) and mature podocarp forest. Biotic and abiotic characteristics of the study sites are given in Table 1.

**Table 1. Biotic and abiotic characteristics of study sites recorded between December 1992 and January 1994.**

| Site | Annual rainfall (mm) | Grass minimum temperature °C | Area (ha) | Dominant vegetation | Leaf litter (cm) |
|------|------|------|------|------|------|
| Pasture | 1002 | -1 9 | 1.6 | white clover ryegrass | nil |
| Gorse | 1002 | -1 6 | 1.0 | gorse | 3-15 |
| Manuka | 1759 | -.5 14 | 200 | manuka,mahoe silver fern | nil |
| Broadleaf/ podocarp | 1002 | 0 11 | 4.16 | tawa,titoki pukatea,kahikatea | 2-5 |
| Podocarp | 720 | -1 11 | 6.25 | rimu,tawa,matai kahikatea | 1-4 |

Ground active invertebrates were sampled at monthly intervals between December 1992 and January 1994 by pitfall trapping. Although pitfall traps measure a combination of activity and density, predator activity is more likely to reflect predation rates than density per se (Abrams 1993) and this in turn is more likely to reflect their potential in pest control. Five replicate traps (plastic containers, 11 cm diameter and 10 cm deep) were sunk level with the surrounding ground at each site approximately 10 m apart along a 50 m transect. Traps were filled with 300 ml of 70% ethylene glycol and a few drops of detergent to break surface tension, and covered with galvanised iron covers (20 cm by 20 cm) raised 3 cm above the traps to prevent rain entering. Samples were sieved to 500 ìm, sorted, and enumerated as RTUs (recognisable taxonomic units) under x10 magnification. The RTUs were subsequently identified to family. Statistical analysis was performed with the GLM procedure of SAS (SAS 1985), using log transformed data.

## RESULTS
Of the predatory species collected the greatest diversity was recorded amongst spiders (85 species), staphylinids (27 species), harvestman (15 species) and predacious coleopteran larvae (15 species). A smaller number of other predatory species were also collected including Carabidae, ants, centipedes, pseudoscorpions and Reduviidae. Some species of spiders, staphylinids, carabids and opiliones were restricted to only one habitat. However, all other species were found at a number of sites.

Site differences in both predator species richness and abundance were highly significant (Table 2). The largest differences occurred at either end of the successional spectrum with species richness lowest in both the early (i.e. pasture) and late successional stages (i.e. mature podocarp). Maximum diversity occurred in the gorse, manuka and broadleaf/ podocarp habitats. In contrast the number of predatory arthropods was highest in the pasture and declined through increasing successional stages.

Abundance (Fig 1) and diversity (Fig 2) of predators also changed seasonally at the study sites, with the lowest number of individuals and species recorded in the winter months. Differences between the sites in species richness were consistent across seasons although there was a significant interaction between site and season in the abundance data (Table 2). This was a result of very low numbers of insects in the pasture between June and December, in contrast to the other sites during this period. Greater availability of microhabitat refuges (eg. logs, rank grass & leaf litter) from low winter temperatures in later successional habitats may in part explain the reduced abundance in the pasture throughout winter.
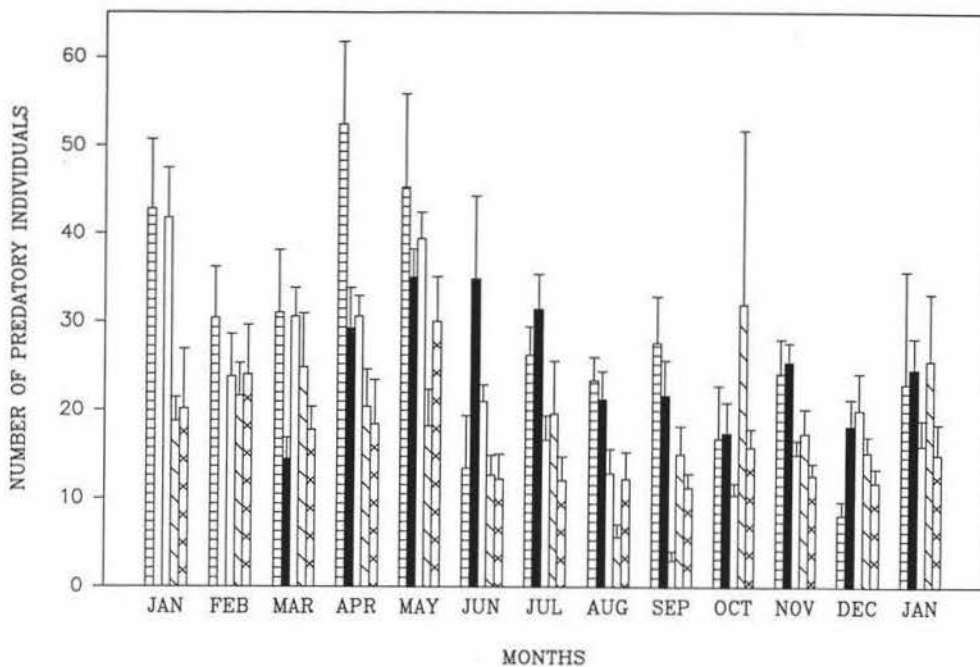
**Figure 1:** Number of individual predators in habitats of increasing successional age between December 1992 and January 1994. Sites are represented by: Pasture ▦   Gorse ■   Manuka ▭   Broadleaf/Podocarp ◺   Podocarp ⊠



**Figure 2:** Predatory species found in habitats of increasing successional age between December 1992 and January 1994. Sites are represented by: Pasture ▦   Gorse ■   Manuka ▭   Broadleaf/Podocarp ◺   Podocarp ⊠
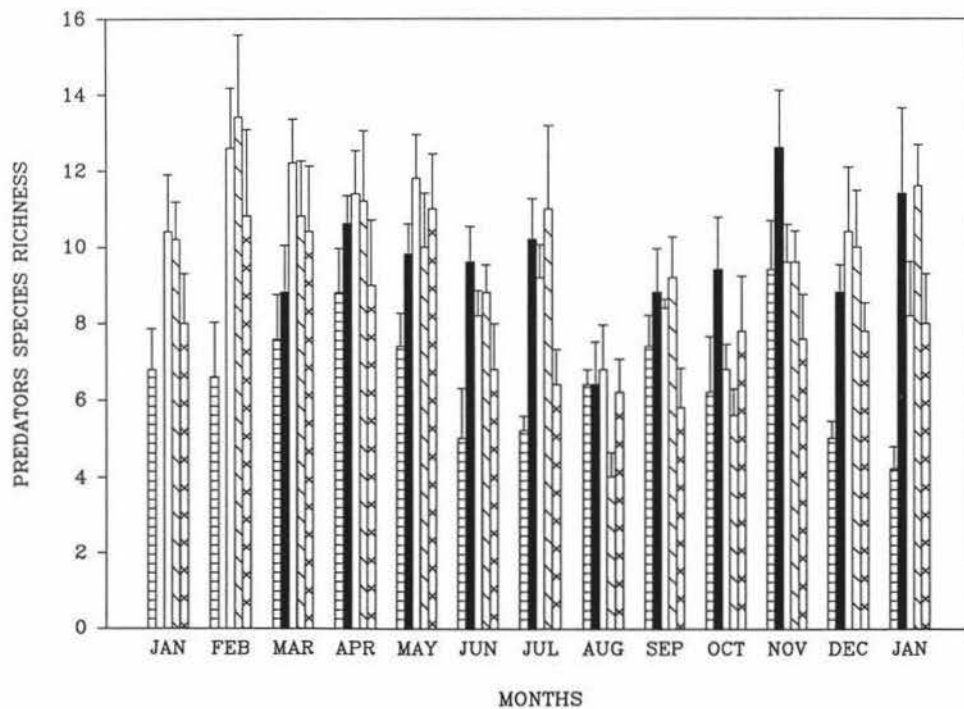
**Table 2. Mean abundance and diversity of predators pitfall trapped, per site and per month, and results of Analysis of Variance.**

|  | Sites | | Seasons | | |
|---|---|---|---|---|---|
|  | No./site[1] | Std Error | Month | No. individuals/ month[2] | No. Species/ month |
| **Species** | | | | | |
| Pasture | 1.817 | 0.240 | Jan | 30.9 | 2.441 |
| Gorse | 2.772 | 0.327 | Feb | 29.95 | 3.123 |
| Manuka | 2.879 | 0.278 | Mar | 23.73 | 2.927 |
| Broadleaf | 3.090 | 0.318 | Apr | 30.20 | 2.144 |
| Podocarp | 2.518 | 0.347 | May | 33.56 | 2.693 |
|  | | | Jun | 18.80 | 2.450 |
| **Individuals** | | | Jul | 21.16 | 2.500 |
| Pasture | 28.04 | 3.944 | Aug | 15.04 | 1.985 |
| Gorse | 24.83 | 2.862 | Sep | 78.40 | 2.518 |
| Manuka | 21.62 | 6.304 | Oct | 18.48 | 2.379 |
| Broadleaf | 18.98 | 5.069 | Nov | 18.95 | 3.010 |
| Podocarp | 16.40 | 3.375 | Dec | 14.68 | 2.787 |
|  | | | Jan | 20.84 | 2.176 |

| Analysis of Variance | F | df | P |
|---|---|---|---|
| **No. of species** | | | |
| Site | 15.78 | 4 | <0.001 |
| Season | 6.39 | 12 | <0.001 |
| Site Season interaction | 1.32 | 46 | 0.09 |
| Error | | 252 | |
| **No. of individuals** | | | |
| Site | 13.85 | 4 | <0.001 |
| Season | 9.19 | 12 | <0.001 |
| Site Season interaction | 1.90 | 46 | 0.001 |
| Error | | 252 | |

[1]  Mean number trapped over 13 months

[2]  Mean from all sites

## DISCUSSION

The peak in invertebrate predator diversity in patches of mid-successional age corresponds to that found by Brown and Southwood (1987) in successional grasslands, and fits within the framework of general ecological theory (Petraitis et al. 1989), although not within the predictions of Price (1991) for invertebrate communities. In contrast, individual predator abundance was found to decrease as the age and complexity of the habitat increased. Thus early successional sites were characterised by high numbers but low diversity of predators such that one or two species were very abundant (liniphid and lycosid spiders in this case). Later successional sites showed concomitant declines in total number of predators and in the very late stages a decline in diversity.

The decline in predator diversity in the climax forest may be the result of competitive exclusion between predators which has not had time to reach completion in the earlier stages of succession. Studies of ground beetles (Carabidae) have shown interspecific competition can be important in structuring carabid assemblages (Niemela 1993). This seems to be the case in our study with only one species of carabid (*Megadromus capito*) in the late succession forest compared to 3-4 species (*Mecodema simplex, Holcapsis oedicnema,*

*Plocamostethus pleniusculus)* found in mid successional sites.

In contrast to the predictions of Price (1991), it seems that reserves of mid-successional age offer the greatest potential source of predator diversity although pasture has the highest density of predatory species. Whether the species found in pasture are those species most effective in controlling pasture pest species, or if species found in some of the vegetation refuges are more effective, is currently being evaluated. Furthermore, if such a relationship is established the capacity for predators in these systems to migrate into the pasture to feed on pest species requires investigation. However, it does seem that vegetation remnants of mid-successional age do offer considerable potential as sources of an array of predators that may be useful in agroecosystems.

## ACKNOWLEDGEMENTS

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# LIST OF TAXA

* morphospecies identifed only to family or genus level

## COLEOPTERA

**Anobiidae**
1 species*

**Anthicidae**
*Anthicus pellucidipes*

**Apionidae**
*Apion ulicis*

**Byrrhidae**
2 species*

**Carabidae**

| | | |
|---|---|---|
| *Megadromas capito* | *Plocamostethus planiusculus* | *Mecodema simplex* |
| *Holcapsis oedicnema* | *Clivina vagans* | *Ctenognathus sp.* |
| *Selenochilus ruficornis* | *Zolus astratus* | *Demetrida nasuta* |
| *Holcapsis vagepunetata* | *Notogonum lawsoni* | *Neocicindela parryi* |

**Cerambycidae**

| | | |
|---|---|---|
| *Oemona hirta* | *Nodulosoma sp.* | *Ptinosoma sp.* |

**Chrysomelidae**

| | |
|---|---|
| *Adoxia sp.* | 1 species* |

**Clambidae**
*Spaerothorax sp.*

**Cleridae**
*Phymatophaea sp.*

**Coccinellidae**

| | |
|---|---|
| *Rhyzobius rarus* | 2 species* |

**Colydiidae**

*Enarsus bakewelli*      *Pycnomerus sp.*        *Recyntus sp.*
*Protarphius sp.*        *Bitoma rugosa*         2 species*

**Corylophidae**

*Anisomeristes sp.*      *Holopsis sp 1*         *Holopsis sp 2*
*Holopsis sp 3*

**Cryptophagidae**

*Picrotus thoracicus*    *Micrambina sp 1*       *Micrambina sp 2*

**Cucujidae**

*Brontopriscus pleuralis*

**Curculionidae**

*Clypeolus sp.*          *Omoeacallus crisioides*  *Phrynixus sp.*
*Pactola demissa*        *Brchyolus sp.*         *Praeolepra sp.*
*Listronatus bonariensis*  2 species*

**Elateridae**

*Conoderus exsul*        *Agrypnus variablis*    *Betarmonoides frontalis*

**Erotylidae**

*Cryptodacne sp 1*       *Cryptodacne sp 2*

**Helodidae**

*Cyphon sp 1*            *Cyphon sp 2*

**Histeridae**

*Parepieris sp 1*        *Parepieris sp 2*

**Hydrophilidae**

*Cycloma lawsona*        *Tormissus magnulus*    *Dactylosternum sp.*

**Lathridiidae**

*Aridius nodifer*        *Lithostygnus sp.*      *Melanophthalmus sp.*
*Bicava variegata*       *Bicava sp 1*           *Encicmus sp.*
2 species*

**Leiodidae**

Subfamily : Cholevinae

*Inocatops concinnus*      *Paracatops lugubris*      1 species*

Subfamily : Coloninae

*Colon hirtale*

Subfamily : Leiodinae

*Agaricaldes sp.*      *Zeadolops sp.*


**Lucanidae**

*Lissotes reticulatus*      *Lissotes stewarti*


**Melandryidae**

*Hylobia sp 1*      *Hylobia sp 2*      *Lyparochis sp 1*

*Lyparochis sp 2*      *Lyparochis sp 3*


**Merophysiidae**

*Holoparamecus tenuis*


**Mordellidae**

*Stenomordellaria neglecta*


**Mycetophagidae**

*Triphyllus hispidellus*      *Triphyllus sp 1*      *Triphyllus sp 2*


**Nemonychidae**

*Rhinorhynchus rufulus*


**Nitidulidae**

*Epurea sp.*      *Omosita discoidea*      *Soronia hystrix*


**Oedemeridae**

*Thelyphassa brouni*


**Pselaphidae**

Subfamily : Brachyglutinae 4 species*

Subfamily : Euplectinae 2 species*

Subfamily : Faroninae      *Stenosagoa sp.*

Subfamily : Pselaphinae

*Pselaphophus sp 1*      *Pselaphophus sp 2*      *Pselaphus pauper*

Subfamily : Tyrinae 1 species*

**Ptiliidae**
*Notoptenidium lawsoni*

**Salpingidae**
*Salpingus sp1*            *Salpingus sp 2*

**Scaphidiidae**
2 species*

**Scarabaeidae**
*Pyronata festiva*          *Saphobius sp.*

**Scymaenidae**
1 species*

**Staphylinidae**
Subfamily : Aleocharinae
*Falagria concinna*          *Oligota masculina*            *Tramiathaea*
*cornigera*
*Atheta sp.*                12 species*
Subfamily : Ossoriinae
*Paratrochus sp.*            *Anotylus sp 1*                *Anotylus sp 2*
Subfamily : Paederinae 1 species*
Subfamily : Proteininae
*Silphotelus nitidus*
Subfamily : Staphylininae 1 species*
*Quedius sp 1*              *Quedius sp 2*                *Philonthus sp.*
Subfamily : Tachyporinae
*Sepedophilus sp.*           *Tachyporus sp.*
Subfamily : Euaesthetinae
*Agnosthaetus sp.*

**Tenebrionidae**
*Kaszabadelium aucklandicum*

**Zopheridae**
*Syrphetodes marginatus*

# HYMENOPTERA

**Aphelinidae**

*Pteroptix sp.*            *Aphytis sp.*

**Braconidae**

Subfamily : Alysiinae

3 species*                *Spilomicrus sp.*

Subfamily : Aphidiinae

4 species*

Subfamily : Doryctinae

1 species*

Subfamily : Euphorinae

1 species*

Subfamily : Microgastrinae

1 species*

Subfamily : Rogadinae

2 species*

**Charipidae**

1 species*

**Diapriidae**

Subfamily : Ambositrinae

*Diphoropria sinuosa*      *Pantolytomyia taurangi*      *Pantolytomyia*
*flocculosa*

Subfamily : Belytinae

*Stylachista sp 1*         *Stylachista sp 2*            *Stylachista sp 3*

Subfamily : Diapriinae

*Spilomicrus sp 1*         *Trichopria sp 1*             *Genus D* undecribed

*Paramesius sp 1*          *Entomacis sp 1*              *Spilimicrus sp 4*

*Entomacris sp 2*          *Paramesius sp 2*             *Spilomicrus sp 5*

*Entomacris sp 3*          *Corynopria sp.*              *Malvina sp.*

*Trichopria sp 2*          *Idiotypa sp.*

**Encyrtidae**

1 species*                 *Odiaglyptus biformis*

**Eucoilidae**

*Kleidotoma sp 1*          *Heaxacola sp.*               *Kleidotoma sp 2*

**Eulophidae**
5 species*

**Formicidae** (winged)
Subfamily : Ponerinae
*Mesoponera castaneicolor*

**Ichneumonidae**
Subfamily : Tersilochinae
1 species* and 4 species*

**Meagaspilidae**
4 species*

**Mymaridae**

| | | |
|---|---|---|
| *Austalomymar sp 1* | *Australomymar sp 2* | *Mymar pulchellum* |
| *Arescon sp.* | *Anagroidea sp 1* | *Entomacis sp.* |
| *Anagroidea sp 2* | *Paracmotemnus sp.* | *Australomymar sp 3* |
| *Polynema sp.* | *Stethynium sp.* | 1 species* |

**Pompilidae**

| | | |
|---|---|---|
| *Sphictostethus fingax* | *Spictostethus nitidus* | *Diphoropria sinuosa* |
| *Priocnemis morachus* | *Priocnemis carbonaris* | |

**Pteromalidae**

| | |
|---|---|
| *Dipareta sp.* | 2 species* |

**Scelionidae**
Subfamily : Scelioninae

| | | |
|---|---|---|
| *Baens sp.* | *Holoteleia sp.* | *Idris sp 1* |
| *Idris sp 2* | | |

Subfamily : Teleasinae

| | |
|---|---|
| *Trimoris sp 1* | *Trimoris sp 2* |

**Trichogrammatidae**
*Trichogramma sp.*

# CHILOPODA

*Lamyches enarginalys*          *Paralamyctes validus*

# DIPLOPODA

**Dalodesmidae**
*sp 3.* (new genus & new species)  *Icosidesmus wheeleri*          *Pseudoprionopeltid sp*

**Schedotrigonidae**
*Schedotrigona sp.*

**Polyzoniidae**
Siphonethus sp.