Spiders as Surrogate Species in Ecological Monitoring, Habitat Classification and Reserve Selection

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ADDITIONS AND CORRECTIONS

Page 12: (Phil Servid, pers comm) dated 2001.

Page 20: (Phil Servid, pers comm) dated 2000.

Page 41: Plant nomenclature follows Allan (1961), Connor & Edgar (1987), and Edgar & Connor (2000).

Page 45: Table 3.1. Replace *Beilschmedia* with *Beilschmiedia*, and *Eleocarpus* with *Elaeocarpus*.

Page 45: PHI sampling was carried out during March 1999, immediately after the spider sampling was completed.

Page 46: Random placement of pitfall traps and beating quadrats was effected by haphazardly throwing an object into the 400 m^2 sampling area.

Page 47, Table 3.2: For leaf dimensions ≥ should replace >

Page 53, Caption to Figure 3.5: Cluster analysis used abundance data

Page 54, Figure 3.4: Eigenvalues for DCA ordinations

Axis	(a)	(b)	(c)
1	0.81	0.63	0.58
2	0.19	0.24	0.22
3	0.11	0.03	0.02

Page 57, Table 3.4: Taxa are ordered according to the range of the successional gradient occupied. Figures are the total number of each taxon recorded at each site over the entire sampling period.

Page 65, para 4, line 1: Replace "individual" with "individuals"

Page 65: References to litter characteristics are based on unstructured personal observations.

Page 72, Table 4.1 caption: Delete reference to plant species richness (this is presented in Table 4.2)

Page 75: Replace "indentification" with "identification".

Page 79, Table 4.2: Black beech (*Nothofagus solandri*) add var. *solandri*. Replace *Sophia* with *Sophora*.

Page 85, Figure 4.5 caption: Replace "complimentarity" with "complementarity".

Additional References

Allan, H.H. 1961. Flora of New Zealand Vol. 1. Department of Science and Industrial Research, Government Printer, Wellington N.Z.

Connor, H.E.; Edgar, E. 1987. Name changes in the indigenous New Zealand Flora, 1960 - 1986 and Nomina Nova IV, 1983 - 1983. *New Zealand Journal of Botany*, 25: 115-170.

Edgar, E.; Connor, H.E. 2000. Flora of New Zealand, Vol V. Manaaki Whenua Press, Lincoln, N.Z.

G.M.I. Coombe, April 2002.

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ABSTRACT

ABSTRACT

The use of invertebrates in the monitoring of terrestrial ecosystems was investigated using spiders as a focal group. In a review of previous literature, spiders were found to meet the majority of criteria required of suitable ecological indicators, including high diversity and abundance, a widespread distribution, easy sampling and sorting, relatively low random fluctuation in population sizes and community composition, a range of dispersal abilities, measurable response to habitat change and representation of other taxa. The main weaknesses of spiders as ecological indicators were the lack of taxonomic expertise and sparse knowledge of baseline biology. However, these disadvantages could be rectified and it was concluded that spiders are suitable for further investigation as ecological indicators, involving field trials and hypothesis testing.

The spider communities in the litter, herb and shrub layer of eight sites representing four habitat types within a forest successional series were sampled in Pouiatoa State Forest in Northern Taranaki. There were no distinct trends in spider richness or abundance across the successional series. However, spider species and family composition both reflected the successional stage from which they were taken. Site classifications using DCA and cluster analysis were similar when using either plant or spider data. Spider communities demonstrated potential for use in habitat classification of terrestrial ecosystems.

Spiders and seven other ground-active invertebrate groups were sampled with pitfall traps from fourteen forest remnants within the Rangitikei Ecological Region to test whether spiders were able to act as indicators of plant and invertebrate diversity. Within-site richness (α-diversity) of spiders was strongly correlated with that of all other invertebrates combined, but spiders were not good predictors of between-site richness (β-diversity) of all other invertebrates. Correlation between the α- and β-diversities of plants and invertebrates were low, indicating that maximising plant diversity in reserve selection might not maximise invertebrate diversity. It is recommended that ground-active invertebrates be included in surveys of potential forest reserves.

Spiders are a useful surrogate group for invertebrate communities and could be more widely used in the assessment, monitoring and management of terrestrial ecosystems.

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I would like to thank the tireless technicians, Cathy Lake and Tracey Harris, for hunting up all the right gear and gallons of 70% ethanol. Special thanks also to Barbara, Erica and Jodie for immense (and undervalued) logistical support, and to Dawn for the crash course in ArcView. Also thanks to The Department of Conservation, Forest and Bird and Stu Langridge for access to sites, and to Alex for helping with the fun job of laying pitfalls. And another big thank you to Phil Sirvid for his helpful comments on early drafts of Chapter 2.

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CHAPTER ONE

General Introduction

GENERAL INTRODUCTION

Invertebrates and Ecological Monitoring

Biodiversity is recognized as having enormous economic value, both directly as a resource for human use (Kunin and Lawton 1996) and indirectly as a vital component of ecosystem functioning and sustainability (Lawton 1994, Tilman *et al* 1996, Nijs and Roy 2000). There are also aesthetic and ethical aspects inherent in the maintenance of undisturbed natural systems and high levels of habitat, taxonomic and genetic diversity. However, human-induced habitat change and degradation of both environmental and biotic systems has lead to drastic declines in species numbers world-wide (Stork 1997). Arresting this decline requires knowledge of ecosystem function and how ecosystems respond to disturbance. This enables measures to be implemented minimising deleterious impacts on native communities, and allow for sustainable landscape development incorporating both economic and conservation interests. Extensive surveys and monitoring of the flora and fauna within endangered ecosystems is required to achieve this purpose.

Invertebrates represent the greatest proportion of terrestrial biodiversity (Stork 1997) and are vital components in many ecosystem processes (Kajak 1997, Schowalter 2000, Whitford 2000). However, general information about biology, ecology, distribution and taxonomy is scarce for many species (Oliver and Beattie 1996a, New 1999, Hooper *et al* 2000). The combination of high species numbers, small body size, complex interactions within communities, and poor biological and taxonomic knowledge mean that the ecological monitoring of invertebrates is often difficult. There is generally too little time, money and expertise available to enable all species to be catalogued, even on small regional scales (Disney 1986). Consequently, invertebrates have been underrepresented in conservation programmes and disturbance impact studies, especially in comparison to less diverse groups more amenable to sampling or with greater public appeal, such as large vertebrates or plants (e.g. Hilty and Merenlender 2000).

Surrogate Species

A surrogate is a single species or a group of species used as a proxy measure of ecosystem conditions that cannot be measured directly due to time and cost restraints, or lack of suitable methods, expertise or knowledge (Landres *et al* 1988, McGeoch 1998, Caro and O'Doherty 1999, Hilty and Merenlender 2000). These ecosystem conditions could be the biotic and abiotic components, such as species richness, species composition, soil quality and microclimate; functioning and processes, including nutrient turnover and energy dynamics; or conservation value, including complementarity, naturalness and presence of target taxa. There are three main uses for surrogate species: detection and monitoring of disturbance in ecosystems; providing information on ecological processes; and addressing conservation questions, including the selection of areas for protection, and monitoring of conservation techniques.

There are four main types of surrogate species: environmental indicators, ecological indicators, biodiversity indicators and umbrella species (McGeoch 1998, Caro and O'Doherty 1999). *Environmental indicators* are species that are used to detect the presence, or gauge the degree, of disturbance in an ecosystem. They are used as proxy instruments for measuring environmental conditions, particularly in relation to human-produced pollution (McGeoch 1998). The most common examples of this type are species that accumulate toxins in their tissues, but it also includes species whose presence or absence from a site indicates the presence of a particular pollutant, or those that show a measurable change in their biology or morphology in response to disturbance. *Ecological indicators* are selected to demonstrate the impact on the remaining flora and fauna within the community, and therefore act more as a surrogate for that community rather than for the disturbance itself (McGeoch 1998). Ecological indicators can play an important role in understanding the impacts of disturbance of biota, and thus aid in management and conservation of disturbed systems (e.g. Rodríguez *et al* 1998). *Biodiversity indicators* are a group of species whose diversity correlates with the diversity of other higher taxa in a habitat or a group of habitats. They can be used to identify sites of high species richness (α-diversity) or a set of sites that when combined maximizes the species diversity across a landscape (β-diversity), and therefore can play an important role in the selection of sites for conservation. As an α-diversity indicator, the hotspots for the taxa selected (those sites where their richness is highest) should coincide with the hotspots of other taxa. For the β-diversity indicators, the selection of sites that maximizes their richness across the landscape should also maximise the richness of other taxa. There has been a great volume of literature devoted to testing and discussing the utility of biodiversity indicators involving many faunal and floral groups, with mixed results and conclusions (Vane-Wright *et al* 1991, Prendergast *et al* 1993, Sætersdal *et al* 1993, Gaston 1996, Gaston and Williams 1996, Howard *et al* 1998, Kerr *et al* 2000). *Umbrella species* are those whose habitat is specifically managed to maintain viable populations of the umbrella, and in doing so simultaneously conserves a large part of the habitat for other, sympatric species (Caro and O'Doherty 1999). The most obvious examples of this type of surrogate in New Zealand are the various kiwi species (*Apteryx* spp.), which are the focus of intensive conservation involving the protection of large stretches of native forest and removal of introduced predators. Both of these measures will simultaneously benefit other native species present within the same habitat. Umbrella species are usually the specific targets for conservation in this way, and as such hold intrinsic value in themselves. Environmental, ecological and biodiversity indicators, on the other hand, do not necessarily have to be conservation targets, though it has been suggested that they should be of some economic importance (Hilty and Merenlender 2000).

The surrogate species concept provides a method by which invertebrates can be viably incorporated into ecological monitoring programmes. With debate about the degree to which invertebrate communities are represented by plant or vertebrate surrogates still ongoing (e.g. Oliver *et al* 1998, Panzer and Schwartz 1998), various terrestrial invertebrate groups are now recognised as potentially useful surrogate species including ants (Majer and Beeston 1996, Oliver *et al* 2000), beetles (Hutcheson *et al* 1999), braconid wasps (Lewis and Whitfield 1999), butterflies (Kerr *et al* 2000), and tiger beetles (Rodríguez *et al* 1998). In New Zealand, the use of invertebrate surrogates has been restricted mainly to detection of pollution in aquatic environments (e.g. Boothroyd and Stark 2000, Scarsbrook *et al* 2000). In contrast, there has been relatively little attention given to the utility of terrestrial invertebrate surrogates in ecological monitoring and reserve selection, or to whether current conservation strategies are adept at protecting invertebrate diversity (but see Hutcheson *et al* 1999).

Introduction to Spiders

Spiders comprise the order Araneae in the class Arachnida, a class that also includes scorpions, mites, harvestmen and seven other orders. They are characterized by having two main body parts, the cephalothorax, to which are attached eight walking legs, eyes, pedipalps and chelicerae, and the abdomen, the posterior of which are attached the silk-producing spinnerets. Spider species exhibit a wide variety of life histories and morphologies, though all feed on other animals, with the great majority being generalist predators utilising a diverse range of prey types (Moulder and Reichle 1972, Turnbull 1973, Eberhard 1990, Nyffeler *et al* 1994). The devotion to a single feeding strategy makes spiders unique among other diverse invertebrates orders, such as the Diptera and

Coleoptera, which exhibit a range of trophic habits (Coddington and Levi 1991), and makes them one of the most important predator guilds in a wide variety of habitats. Spiders have been shown to influence many ecosystem functions, such as energy dynamics (Moulder and Reichle 1972), litter decomposition (Kajak 1997) and plant productivity (Carter and Rypstra 1995). They have also been investigated as biocontrol agents in agroecosystems, with accumulating evidence that despite being generalist predators, spiders can be effective at reducing invertebrate pest numbers and thus reducing crop damage (see Riechert and Lockley 1984 for a review; see also Riechert and Bishop 1990, Carter and Rypstra 1995 for additional experimental evidence). There has been little work on using spiders as environmental or ecological indicators, outside a few agriculture and grassland studies (e.g. Pristavko and Zhukovets 1988, Marc *et al* 1999) and those involving detection and monitoring of industrial pollutants (Clausen 1986, Maelfait 1996, Cárcamo *et al* 1998), though New (1999) discusses the potential for spiders as a focal group in general invertebrate conservation.

Thesis structure

Chapter 2 analyses how spiders conform to *a priori* criteria for suitable ecological indicators based on previously published literature. Chapter 3 establishes whether spider communities can be used to distinguish between habitat types along a successional gradient, and thus be useful in habitat classification in New Zealand. Chapter 4 investigates how well spider and other ground-active invertebrate diversity is correlated with plant diversity, determines whether any particular invertebrate group sampled shows potential as biodiversity indicators for all other invertebrates, and discusses the findings in the light of current reserve selection procedure in New Zealand. Chapter 5 reviews the findings of the previous chapters with respect to ecological monitoring in New Zealand.

CHAPTER TWO

Spider Communities as Ecological Indicators in Terrestrial Ecosystems

2.1 THE ROLE AND USES OF ECOLOGICAL INDICATORS

The main role of an ecological indicator is to demonstrate a measurable response, through a change in individual, population or community parameters, to an alteration in habitat conditions that represents to some extent the response of other, unsampled taxa within the community (McGeoch 1998). In many cases, the habitat change under investigation is the result of anthropogenic disturbance. There are three main types of human induced disturbance on communities, each of which can affect a number of habitat parameters: habitat fragmentation, foreign species invasion and direct human actions.

Habitat fragmentation involves the breaking up of previously continuous habitat, mainly via vegetation clearance, leaving isolated remnants interspersed with other vegetation types in a modified landscape. A common form of fragmentation has been the removal of forest to make way for farmland or cropland. Fragmentation can alter the microclimate of forest remnants by modifying solar, wind and hydrological regimes, which in turn can affect many other community processes such as litter decomposition, susceptibility to foreign species invasion, tree dieback and soil erosion (Saunders *et al* 1991 and references therein, Murcia 1995, Didham *et al* 1996). Small or isolated remnants also run the risk of local extinction of species due to reduction in population sizes and immigration rates, altering community composition (Saunders *et al* 1991).

Foreign species invasion is the accidental or deliberate introduction by humans of a non-native species into a habitat, and has been a common disturbance within New Zealand ecosystems (Vitousek *et al* 1997). The selective predation of certain species (O'Donnell 1996, Toft and Rees 1998), competitive displacement (Leathwick *et al* 1983) and habitat modification (Towns *et al* 1997 and refs therein) can all affect community composition. One of the most destructive invasions is that of a large grazer or browser into an ecosystem. They can effect plant composition and architecture through selective herbivory (Allen *et al* 1984, Parkes 1993), both of which will have flow on effects to invertebrates that rely on plants for food or shelter (Morris 2000). Browsers and grazers can also modify other aspects of the habitat, including the chemical, physical and infiltration properties of the soil, near ground and soil microclimate, and increasing the invasibility of a forest patch for foreign plant species (Yates *et al* 2000).

The third disturbance type are the results of direct human actions within the habitat itself, which includes the input of fertilizers and pesticides, ploughing, burning, cropping, harvesting and selective grazing in agricultural landscapes (Paoletti and Sommaggio 1996, Morris 2000). In forest habitats, human actions can include selective logging, direct exploitation of species through hunting, implementation of fire regimes and influx of pollutants from adjacent habitats (Bromham *et al* 1999, Caro and O'Doherty 1999).

Ecological indicators can be used to demonstrate the impact of these disturbances on the biota of an ecosystem. In doing so they provide information that can either be used in the development of management strategies minimizing such impacts, or used to assess the success of these strategies.

2.2 CRITERIA FOR ECOLOGICAL INDICATORS

The characteristics of a suitable ecological indicator will depend on the situation being monitored and what information is required to address management objectives (McGeoch 1998). Many authors however have offered a basic set of criteria that are likely to be important in the majority of situations, and these are summarized in Table 2.1. The eight criteria presented here are orientated mainly towards the use of a group of terrestrial invertebrates as bioindicators, but most are also applicable to single species and vertebrates. These criteria can be divided into three categories: logistic (relating to the cost efficiency of the monitoring programme), biological (relating to the inherent qualities within the group) and ecological (relating to the relationship between the indicator group and other non-target taxa).

Identification to species usually increases the amount of information contained within a sample (Hutcheson 1990, Spurgeon *et al* 1996). Therefore the bioindicator group should be taxonomically well-known, enabling easy identification and reducing the chances of species misidentification. Part of the reason for the use of bioindicators is that measuring the whole community is prohibitively expensive and time-consuming. Therefore, sampling and sorting of bioindicators also needs to be easily achieved, reducing monitoring costs (Caro and O'Doherty 1999).

A high degree of knowledge of baseline biology (e.g. life history, physiological tolerances) allows the pathways through which bioindicators show response to

Table 2.1: Suggested criteria for ecological indicator groups (summarized from Gibson *et al* 1992a, McGeoch 1998, Caro and O'Doherty 1999, Hilty and Merenlender 2000)

Category	Criteria
Logistic	1. Taxonomically well-known, high level of expertise available for identification
	2. Easily sampled and sorted
	3. Baseline biology known
Biological	4. Abundant, diverse and widespread
	5. Low random fluctuations in population numbers and community turnover
	6. A range of dispersal abilities
Ecological	7. Well defined response to habitat change
	8. Representative of other taxa and/or ecosystem processes

disturbance to be elucidated (McGeoch 1998, Caro and O'Doherty 1999). On a pure bioindicatory level, where it is solely the nature of the response that is important, rather than the causal factors behind it, this may be an unnecessary criterion for already established bioindicators. However, it becomes important during the selection process, as it enables predictions to be made, suggesting those taxa most likely to prove useful in the monitoring programme at hand and reducing the chances of time being wasted testing unsuitable groups (McGeoch 1998).

The indicator group needs to be numerically abundant to ensure that samples are large enough for meaningful statistical analysis and so the group is easy to monitor (Caro and O'Doherty 1999).

High diversity increases the number of ecological niches covered by the group, increasing the potential response range (Kremen *et al* 1994). A widespread distribution allows for the extrapolation and cross-comparison of results over a greater area and number of sites (McGeoch 1998, Caro and O'Doherty 1999, Hilty and Merenlender 2000).

Random changes in species abundance and composition may obscure responses to disturbance or give misleading results (Gruttke and Kornacker 1995), so a low level of unpredictable community change is desirable (Hilty and Merenlender 2000).

Some authors have suggested that low mobility is an important attribute in a bioindicator. This reduces its ability to avoid disturbance (Hilty and Merenlender 2000 and references therein), and provides evidence that a site is able to support a permanent population of the indicator (Bromham *et al* 1999). It is then likely that the group is representative of the habitat being sampled rather than just a chance collection of vagrants (Spurgeon *et al* 1996). However, in the analysis of habitat restoration success, which is part of ecological indication, an important community measure is the recolonisation of species associated with pre-disturbance conditions (Keesing and Wratten 1998, Reay and Norton 1999). In addition, disturbance can attract species to a habitat that are not usual members of the community (Lewis and Whitfield 1999). More mobile species will provide faster and more robust results in this respect, given that the absence of a poor disperser from a site may not be due to unfavorable habitat conditions, but rather an inability to migrate there. For an indicator group to be used in a variety of contexts therefore, it is desirable that the member species exhibit a variety of dispersal capabilities, and that these are well known.

The most important criterion for the indicator group is that there be a clear, predictable response to change within their habitat. This would involve a measurable change in community parameters, such as the richness, composition or relative abundance of species, families or guilds, which can be correlated with the manner or degree of disturbance. This response also needs to represent the response of at least some other taxa, and not be peculiar to the faunal group being monitored.

One further criterion for bioindicators proposed by some authors is specialization of species at lower taxonomic levels, though the importance of this has been debated. Specialist species are potentially more likely to respond, and respond faster, to changes in habitat conditions than habitat generalists. Generalists utilize a range of niches and could conceivably switch resources in response to disturbance, remaining unaffected (Hilty and Merenlender 2000). Conversely, due to the narrow niche breadth they occupy, specialists are likely to represent the ecological response of only a few species (Landres *et al* 1988), whereas habitat generalists are more likely to be representative of a greater range of taxa. The reason why this criterion was not included here is that there is confusion over the scale at which specialization is important (Hughes 2000). Also, specialization does not necessarily mean there will be a response to a particular disturbance (MacNally *et al* 2000, Owens and Bennett 2000) and generalists can exhibit response to habitat change

(Seamon and Adler 1996). Therefore, information on habitat specificity may not accurately predict whether a particular species will respond to ecosystem perturbation.

2.3 HOW SPIDERS FIT THE CRITERIA

2.2.1 Taxonomy and Identification

A lack of taxonomic clarity is an important factor behind the relative absence of terrestrial invertebrates in bioindication and conservation evaluation studies compared to vascular plants and vertebrates (Oliver and Beattie 1996a), and this is especially true of spiders (e.g. Cárcamo *et al* 1998). Lack of taxonomic expertise, complicated identification methods and a large proportion of undescribed species all discourage programmes based on spider communities. However, these undeniable disadvantages should not necessarily preclude spiders from being investigated as potential bioindicators.

Species identification

Spider identification is based on comparative morphology, with molecular techniques yet to come into widespread use. The most common method for distinguishing species is by examination of the genitalia, namely the female copulatory structures (epigynum) and the male palpi. Differences in genitalia reflect a reproductive barrier between similar species and their dimensions are generally less variable than other body parts (Coddington and Levi 1991). Despite its diagnostic power, the use of genitalia is time-consuming, given the often minute differences that distinguish species and that the epigynum is only fully observable after dissection. Other morphological characters are used in the identification of families and superfamilies, including the presence or absence of trichobothria (fine hairs on the legs) and book lungs; the number and arrangement of the eyes and spinnerets; the position of the legs (prograde or laterigrade); and the number of claws at the end of the tarsus (2 or 3). These synapomorphies are based around a relatively stable family-level phylogeny proposed by Coddington and Levi (1991) that, despite subsequent work redefining certain phylogenetic relationships (e.g. Griswold *et al* 1997, Schütt 2000), remains a solid foundation from which systematic araneologists can work.

Because species identification requires adult specimens, one of the main disadvantages when identifying spiders is that if juveniles dominate the sample (e.g. Mason *et al* 1997), a large proportion of the individuals will be unnamed at the species level (e.g. Visser *et al* 1999).

Species inventory

The spider fauna from some regions of the world are better known than others. The spiders of Britain and Japan are thought to be almost completely catalogued, whereas it is estimated that only 20% of the total number of species present in Australia have been named (Coddington and Levi 1991, New 1999). In New Zealand, the figure is somewhere between 30-45 %, with 1100 named species (Phil Sirvid, pers. comm., Te Papa Museum, Wellington) from an estimated fauna of between 2500 and 3600 species (Platnick 1992, Forster and Forster 1999).

There are many obstacles to descriptive taxonomy in spiders slowing the progress of complete species inventory. Sexual dimorphism is common in spiders, as is variation between individuals of a species. In the past there has been difficulty in communication between researchers (Coddington and Levi 1991), leading to a large number of species being given different names by different researchers (synonyms). Recently, taxonomic revisions of spider families have started to provide a degree of structure in the inventory of spiders. By presenting data for all species they cover and identifying synonyms, such studies provide a platform from which future taxonomic descriptions can work, and many are illustrated in a manner aiding the identification of species by non-specialists (Coddington and Levi 1991). Another valuable resource is a web site (Platnick 2001) that regularly updates the discovery of new species, and identifies synonyms as they become known, though it does not yet provide descriptions.

Taxonomic expertise

There are very few paid professional spider taxonomists worldwide, reflecting a lack of employment opportunities in the field (Coddington and Levi 1991). This limits the advancement in both the knowledge of spider phylogeny and the description of new spider species, as well as hampering the work of nonsystematic araneologists who require identification and taxonomic advice. Currently there are no paid full-time professional systematic araneologists in New Zealand (Phil Sirvid, pers. comm), with all of the experts capable of identifying a large set of spider taxa being employed in jobs that leave little time for taxonomic work. There are spider collections accessible to researchers in the museums of Auckland, Wellington, Christchurch and Otago. However, simply matching taxa to a previously described individual is a time consuming method of identification.

The lack of experts available for identification purposes should not deter the investigation of spiders as potential bioindicators, however. If spiders prove to be suitable organisms to gauge habitat conditions, and there develops a high demand for their use as bioindicators, then increased demand for the species identification and description may attract more scientists into spider taxonomy. Indeed the almost fully described spider faunas of Britain and Japan demonstrate that it is possible to achieve complete and usable spider taxonomy for a region the size of New Zealand.

Identification by non-specialists

To some extent, non-specialists need to be involved in the identification of terrestrial invertebrates. Not only does it increase the overall expertise as the non-specialists become more proficient, but it will also allow taxonomists to concentrate on describing and revising species if they are able to spend less time identifying known species for other workers (Do *et al* 1999). These advantages are counterbalanced by the increase in the chances of misidentification, which can have major effects on measures of diversity and evenness (Hengeveld 1996), and the increase in man-hours required to identify a large group of spiders or other invertebrates by non-specialists.

At present there are no up-to-date keys readily available for the identification to species of New Zealand spiders. The Otago Museum Bulletin series consisting of Forster (1967), Forster and Wilton (1968), Forster (1970), Forster and Wilton (1973), Forster and Blest (1979) and Forster *et al* (1988) all contain species descriptions and keys for a range of families. However, Forster (1967), the only published key for New Zealand spider families is badly out of date, with large parts of it rendered inaccurate by later volumes in the series. Vink (1995) has produced a more up-to-date (albeit unpublished) key for identification to family by the non-specialist, enabling all but three (Desidae, Amaurobiidae and Amphinectidae) to be established by external morphology. A similar key for species would seem to remain some way off.

The use of computers to scan digital images of spider genetalia and provide an accurate species identification is still in its infancy, though preliminary results are encouraging (Do *et al* 1999). This technology may yet play an important role in not just spider identification, but terrestrial invertebrates in general (Weeks and Gaston 1997).

In the absence of comprehensive, user-friendly keys, the identification of spiders to morphospecies remains the most viable option for the non-specialist when dealing with community samples. This is where untrained individuals categorize specimens on the basis of external morphology into substitute taxonomic units (Oliver and Beattie 1996a). Representative specimens of each unit, or morphospecies, can be forwarded to a taxonomist to check the validity of the divisions made, and subsequently correct for cases of splitting (one actual species represented by more than one morphospecies) and lumping (one morphospecies representing more than one actual species). The main advantage of this technique is that non-specialists become more familiar with the spider community, recognizing previously encountered morphs and learning the actual species identity once checked and named by a taxonomist. Taxonomists also need not sort through the whole collection of spiders, but rather just a few representatives of each morphospecies.

Variations of this technique have been widely used in New Zealand with Coleoptera communities (Hutcheson 1990, Hutcheson and Kimberley 1999, Harris and Burns 2000) and hold great potential for use with spider communities, as demonstrated by Oliver and Beattie (1996a). In their study, lumping, which is more difficult to amend than splitting, was a rare occurrence for spiders, and analysis using uncorrected morphospecies and actual species data produced very similar results for site richness and classification.

Morphospecies may not be so useful in long-term monitoring activities, as they have to be assigned exactly the same way over the monitoring period (McGeoch 1998). A great deal of information has to be learned by anyone coming into the project halfway through to be able to assign specimens to the correct morphospecies. Unfortunately, this is more or less the same as having to identify to species, and in the absence of even rudimentary keys, becomes potentially as time-consuming.

Another option for the non-specialist when dealing with a large spider sample is to only identify to families for data analysis. The morphological features used to define families are easier for a novice to learn than those for species, and many juvenile specimens that cannot be determined to species can be identified to family, increasing the size of the data set. The use of families as the basic taxonomic level is common in spider studies (e.g. Mason 1992, Halaj *et al* 1997, Bromham *et al* 1999) and can be as informative as species when comparing communities (Oliver and Beattie 1996a, Chapter 3). Nevertheless, this provides a potential stopgap method while taxonomic expertise grows and up-to-date keys are developed. As more people begin to work with the group, the base of scientific knowledge should gradually increase, both in terms of taxonomy and species description, and natural history of individual species.

2.2.2 Sampling

There are many methods available in the collection of spiders from the field, each with associated advantages and disadvantages. What follows is a brief description of some of the most common spider sampling techniques (see Duelli *et al* 1999 for a detailed review of the invertebrate sampling methods available in agricultural systems).

Absolute sampling

Absolute sampling involves the physical removal of a part of the habitat, usually in the form of branch, litter or turf samples. These are then taken back to the laboratory where directional light and/or heat force the spiders to leave the sample. This method is the most reliable estimate of spider density and community composition, but it is also one of the most time-consuming and is inherently destructive to the habitat being sampled (Morris 2000). Clipping and bagging of branches can produce a large number of individuals, but with litter samples the collection can be quite small, possibly because hunting spiders take to other refuges, such as fallen logs, when not actively foraging (Forster and Forster 1999). Dobyns (1997), for example, found a total of only 45 spiders in thirteen 1-m^2 litter samples. However, of the 18 species caught in his study, 3 were not found during the concurrent 144 man-hours spent on handsearches, illustrating the ability of absolute sampling in collecting covert species.

Visual search

Direct searching of microhabitats within a sample plot and subsequent hand collection of spiders is useful for the sampling of cryptic or rare species that may be overlooked in other sampling methods (Turnbull 1973), and is thus is a good estimator of species richness. It is often used for the sampling of web-building spiders, as the spider webs are readily apparent and can be used as a surrogate measure of population density (e.g. Rypstra 1986, Miyashita *et al* 1998). This method is laborious, particularly when sampling species that do not build webs, requiring a significant amount of time to be spent in the field. For studies that require a number of sites to be sampled over a long time period, this becomes a significant disadvantage. In addition, Dobyns (1997) reported that using the beating method (see below) on forest undergrowth provides a similar estimate of taxonomic composition to a more time-consuming hand-search. Potential sources of bias in this method include selective sampling of some microhabitats, different abilities of different searchers, searcher avoidance by spiders, difficulty in extracting mygalomorphs from tunnels, variation in success with time of day, and over- or under-representation of clumped populations (Turnbull 1973, Uetz 1977, Dobyns 1997).

Pitfall traps

The most common method for sampling ground-active spiders is pitfall trapping (Hurd and Fagan 1992, Rushton and Eyre 1992, Usher *et al* 1993, Gruttke and Kornacker 1995, Mabelis 1996, Muzika and Twery 1997, Topping and Lövei 1997, Cárcamo *et al* 1998). In its simplest form, a pitfall trap is a vessel, dug into the ground, the edge flush with the soil surface, and a raised cover placed overhead to keep out rain and debris. The vessel is either left empty and checked regularly for live trapping, or filled with a non-evaporating liquid, usually ethylene glycol, which kills the invertebrates and preserves them until they are collected from the field. Habitat structure (Melbourne 1999), pitfall size (Brennan *et al* 1999), preservative type (Hurd and Fagan 1992) and weather conditions (Honék 1988) can all influence pitfall catch. The greatest source of bias is in the differential trappability of individuals, which is a function of density, activity levels and pitfall avoidance/escape ability (Turnbull 1973, Uetz 1977). Trappability can vary both between species, producing relative abundance patterns skewed towards more active species and those less able to avoid or escape pitfalls (McColl 1975, Topping 1993); and within species, producing sex ratios biased towards males (e.g. Moeed and Meads 1985, Kajak and Lukasiewicz 1994, Mabelis 1996) and age ratios biased towards adults (e.g. Topping and Sunderland 1992, Maelfait 1996, Buddle *et al* 2000). Due to their very nature, pitfalls are unable to sample arboreal spiders in their true proportion in the field, though often at least a few specimens of this group of spiders are collected with this method.

The continued popularity of pitfall trapping indicates the benefits inherent in the method. As they can be constructed out of a variety of simple materials, and the preservative reused, pitfall traps are inexpensive for widespread sampling. Outside the initial set-up, little effort is required on the part of the collector, which reduces man-hours in the field and provides an excellent sample size to sampling effort ratio. Pitfall sampling is a continuous sampling method, sampling day and night and through seasons, thus eliminating problems with spot sampling in time (Topping and Sunderland 1992), and it tends to target adult spiders over juveniles, which aids in species identification.

Pitfall traps are best suited for the study of dispersal and patrolling in spiders. Here the usual criticisms are not at odds with the goals of the study, as it is the relative activity within a certain area that is under investigation (Bishop and Riechert 1990, Kajak and Lukasiewicz 1994). However, pitfalls are still of use in bioindication work because they can identify differences in spider communities both between sites subject to differing disturbance levels, and within the same habitat over time after the addition or removal of a disturbance. This assumes that under similar conditions the probability of capture per individual of a species is the same (Mabelis 1996), and therefore any disparity in pitfall catches should therefore reflect a change in either in the actual spider community or a change in trappability as a result of the disturbance. In the second case, a distinct and measurable change in the trappability of certain species can be, in effect, a bioindicatory trait in itself.

Beating

This method consists of the shaking or beating of vegetation to dislodge spiders so that they fall onto a dropcloth placed on the ground beneath the vegetation canopy. The spiders can then be transferred from the dropcloth, most commonly via use of a small aspirator, into a preservative (or kept live) and taken back to the lab for identification. This sampling method will naturally be biased towards individuals that are easily dislodged from the vegetation, and this can vary both between species and within species (Costello and Daane 1995, Marc and Canard 1997). However, it has been shown beating provides an accurate estimate of the species composition (Costello and Daane 1997, Dobyns 1997) and density (Ehmann and MacMahon 1996) on shrubs, vines and other mid-strata plants, though beatings are obviously not suitable for the sampling of litter, grass or forest canopy dwelling spiders. Beating is one of the few methods that can target spiders, as the collector can selectively vacuum spiders from the dropcloth and ignore other invertebrates, though this can be time-consuming if there is a large number of invertebrates dislodged. Costello and Daane (1997) have modified this technique by placing a cloth funnel directly under vineyard foliage during the beating process, and it outperformed the traditional dropcloth in both density and species composition estimation relative to the absolute sampling control.

Suction sampling

Suction sampling is commonly used in grassland and other habitats with low vegetation (e.g. a salt marsh; Döbel *et al* 1990). The suction sampler vacuums the invertebrates from the vegetation and into a sampling bag, using a nozzle of set size placed flat on the ground. Generally, only the invertebrates within the nozzle area will be collected, which means that the resulting sample will provide a good estimate of density. There are sources of error, however, associated with this method. Efficiency of suction sampling decreases with increasingly tall or complex vegetation, such as tussock (Dennis *et al* 1998), and invertebrates can be sucked in from just outside the nozzle, leading to oversampling (Samu *et al* 1997). Gardner *et al* (1995) has modified this method for use in the ground litter of forests, with a filter to keep out the leaves.

Knock-down fogging, trunk traps and flight interception traps.

These three methods all provide a means to sample invertebrates resident in forest canopies. Knock-down fogging involves the application of an insecticide to the canopy, with interception nets or even upside-down umbrellas positioned underneath to collect falling invertebrates (e.g. Richardson *et al* 1999, Majer *et al* 2000). This technique can collect a large number of individuals, but it is relatively resource-intensive and therefore quite expensive, as well as potentially environmentally destructive. There may also be bias associated with the positioning of the collection devices under the tree, due to non-random distribution of arthropods within the canopy (Richardson *et al* 1999).

A trunk trap consists of a netting girdle that circles the trunk of a large tree, and guides invertebrates walking either up or down the trunk into a collection tray containing a preservative (e.g. Moeed and Meads 1983). Trunk trap collection is subject to the same bias as pitfall traps, given the similarity in concept. With the possibility that the local spider population in individual trees is depleted by constant trapping (Moeed and Meads 1983), it is not recommended that trunk traps be left for long periods of time on the same tree.

In its simplest form, a flight interception trap consist of two vertical panes of clear glass or PVC with plastic funnels at both the top and bottom to collect invertebrates that either fall or climb following impact with the glass. Though this method primarily samples flying invertebrates (Coleoptera, Diptera and Hymenoptera in particular), it is also capable of collecting a significant number of spiders, as shown by the 70 spider morphospecies caught in the canopies of three tree species by McWilliam and Death (1998).

Summary

The best overall sampling technique for spiders depends on the habitat being sampled, the parameter being measured (abundance, species richness, species composition) and time and money available. Absolute sampling is the most accurate method for estimating spider density in pasture and forest branches, but has limited use on the forest floor, where the habitat is more complex. Suction sampling can give a good estimation of population abundance in low growing vegetation, and beatings are suitable for estimating species composition on shrubs and vines in much less time than it takes for either absolute sampling or visual searches. Pitfall traps remain the most time and cost efficient method of sampling the ground-active spider community, though the potential for bias means that it is unwise to use this method to measure absolute abundance. For an estimation of total species richness, especially in complex habitats such as forests, it is suggested that a combination of sampling techniques, which together sample all of the microhabitats present, be used (e.g. pitfalls traps, beatings and flight intercept traps, as well as a supplementary visual search). There remain a number of options available in sampling the spider community, most of which are able to collect individuals in relatively high numbers. Therefore a suitable sampling strategy can be designed for use in any ecological monitoring project.

2.2.3 Baseline biology

There have been a number of international publications reviewing the general biology of spiders (Turnbull 1973, Wise 1993, Foelix 1996), life cycles (Marc *et al* 1999), and foraging ecology (Riechert and Lockley 1984, Nyffeler *et al* 1994). In New Zealand, papers describing the habits of individual species constitute the greatest percentage of spider biology literature. This work has tended to skew towards the Salticidae (e.g. Forster 1977, Jackson *et al* 1990), the katipo and Australian redback (e.g. Smith 1971, Forster 1992) and mygalomorphs (e.g. Laing 1973), with very little on cursorial hunting spiders and vagrants (but see Pollard and Jackson 1982), especially forest dwelling species. Forster and Forster (1973) produced the first attempt to synthesize general spider biology in New Zealand, which has since been updated (Forster and Forster 1999). While this provides a useful introduction to the habits of a number of the most common and conspicuous native species, a great deal of basic information for the majority of species remains to be learned. The lack of information on the autoecology of individual species is not restricted to New Zealand (Marc *et al* 1999), but this explains some of the reticence in using spiders for large scale monitoring projects in this country.

2.2.4 Distribution, diversity and abundance

Spiders are a truly global order, with representatives found within almost every conceivable environment, with the exception of the deep lakes and oceans (Turnbull 1973 and references therein). Distribution within New Zealand is equally widespread, with spiders found in pasture, tussock, shrubland, all types of forest, swampland, dry riverbeds and lake edges, the seashore and sand dunes, houses and other buildings, alpine zones, caves and off-shore islands (Forster and Forster 1999). Therefore, their presence in any given terrestrial community is assured. Spiders are well distributed within these habitats, inhabiting numerous microhabitats. For example, forest spiders can be found in the leaf litter, on undergrowth foliage, in the canopy, under the bark of trees, under rocks, on lichen, in holes in trunks and branches, in and under rotting logs and in the soil (Forster and Forster 1999).

It is the high diversity of the Araneae that enables them to inhabit so many different habitats and microniches. The 40,000 or so named species places spiders as the seventh most speciose order on the planet, behind the Coleoptera, Hymenoptera, Lepidoptera, Diptera, Hemiptera and Acari (Coddington and Levi 1991). At a higher taxonomic level, the 3450 genera and 108 families worldwide (Platnick 2001) also represent a high level of diversity. In New Zealand, there are 1100 named spider species from 55 families and 268 genera (Phil Sirvid, pers. comm.).

There can be a great range in species richness from site to site, even from similar habitat types. This is illustrated in Table 2.2, where the number of species found in forests around the world ranged between 14 and 144, though not all microhabitats were accessed, and the numbers are certain to be underestimates. The New Zealand examples, of which there are admittedly few, have a narrower range of 20 in Court's (1984) survey of forest litter on the Hen and Chicken Islands to 70 in the canopies of three tree species in lowland podocarp forest (McWilliam and Death 1998). The family richness is less variable, ranging between 8 and 34 families per site (Table 2.2). One of the features of spider assemblages is that there can be a high number of species in homogenous, even monotypic, plant communities (e.g. 134 species in three peanut fields, Agnew and Smith 1989; 62-90 species in *Calluna* heathland, Maelfait *et al* 1990).

Despite the total reliance on predation as a trophic strategy, spider species exhibit a wide variety of foraging methods. Guilds, which group together families that forage in similar fashion, may be used in the comparison of sites and analysis of data. These guilds can range from the simple division between spiders that use webs to catch their prey and those that do not (e.g. Döbel *et al* 1990, Costello and Daane 1995) to several smaller divisions, such as the jumping spiders (Salticidae), ambushers (Thomisidae), runners (Philodromidae), nocturnal hunters (Clubionidae and Anyphaenidae), orb-weavers (Araneidae, Tetragnathidae and Uloboridae), cobweb spiders (Theridiidae), sheet-web spiders (Linyphiidae) and hackle-band weavers (Dictynidae) used by Halaj *et al* (2000b). The number of potential guilds allows flexibility in how a community can be analysed, with the taxonomic level at which the spider community is to be monitored (species, genera, family or guild) able to be chosen to suit the objectives of the study.

Spider abundance varies from habitat to habitat and site to site. Turnbull (1973) calculated an average density of 130.8 individuals per square metre from studies encompassing a number of different habitats; the range, however, was large (0.64-842/m^2). The abundance of spiders on foliage is can range between 5-20/m^2 (Mason 1992 and references therein, Mason *et al* 1997, Halaj *et al* 2000b), though Polis and Hurd (1995) report up to 200/m^3 in cacti on small islands in the Gulf of California.

Densities like these make spiders one of the most abundant terrestrial arthropod groups (Moulder and Reichle 1972, Olszak *et al* 1992b, Kajak and Lukasiewicz 1994, Gunnarsson 1996, Kajak 1997). One caveat to this is that the individuals are not shared equally among species, but rather a few numerically dominant species and a number of rare ones characterize most spider communities (Turnbull 1973, Dobyns 1997). Therefore it is often difficult to conclude whether species that are rare in samples (i.e. 1-2 individuals only) are just naturally rare in that habitat or vagrants who happen to have dispersed in but are unlikely to survive and reproduce there. It is also difficult to compare the presence/absence of rare species in samples between sites, because their absence from a particular sample may be by chance and thus does not necessarily mean absence from the site. However, the high diversity of spiders provides resolution to the data set in this

Table 2.2: Range of species and family richness in forest sites.

Forest type[a]	Strata sampled	Species (Families)	Country	Reference
Preclimax sweet gum and poplar (1)	litter (pitfall)	11 (9)	United States	Hurd and Fagan (1992)
Climax beech, oak and maple (1)		14 (8)		
Coastal (1)	litter	20 (ns)	New Zealand	Court (1984)
Douglas and grand fir (1)	canopy	26 (13)	United States	Mason *et al* (1997)
Metrosideros (1)	litter, ground, understorey foliage	31 (19)	New Zealand	Court (1982)
Zelkova and *Castanopsis* spp. (7)	understorey foliage	34[b] (9)	Japan	Miyashita *et al* (1998)
Oak and dogwood (10)		59[b] (9)		
Beech, oak and spruce (1)	litter (pitfall)	66 (ns)	Germany	Brüning (1991)
Northern rata, totara and tawa (3)	canopy	70[c] (ns)	New Zealand	McWilliam And Death (1998)
Oak and white birch woodlots (22)	litter (pitfall)	81 (ns)	Netherlands	Mabelis (1996)
Hardwood (1)	litter, ground, understorey foliage	92 (20)	United States	Dobyns (1997)
Coniferous, deciduous or mixed (28)	litter (pitfall)	97 (ns)	England	Usher *et al* (1993)
Oak, hickory and pine (1)	litter (pitfall)	120 (17)	United States	Martinat *et al* (1993)
Eucalyptus spp. (1)[d]	litter (pitfall and litter sampling)	Total: 121 (31) Per forest type: 27-59 (ns)	Australia	Oliver and Beattie (1996a)
Oak-mixed hardwood (5)	litter (pitfall)	144 (24)	United States	Muzika and Twery (1997)

[a] the number in parentheses represents the number of separate forests or woodlots sampled. [b] web spiders only.
[c] morphospecies. [d] incorporating four different vegetation assemblages (dry, moist, grassy and rain forest).
ns = not specified

regard and should dampen the effects of such occurrences when the community is treated as a whole.

2.2.5 Population and community fluctuation

Spider populations are subject to annual variations in abundance and community composition (Moulder and Reichle 1972, Agnew and Smith 1989, Bishop and Riechert 1990, Olszak *et al* 1992a, Muzika and Twery 1997), as are most other terrestrial invertebrates (Moeed and Meads 1985, Neumann 1991, Ponsard *et al* 2000). This variation can be attributed to a combination of seasonal macroclimate change (temperature, rainfall, humidity etc.) affecting activity, migration and mortality levels (Moulder and Riechle 1972 and references therein, Turnbull 1973) and the divergent life-histories of species causing differential peaks in population throughout the year (Uetz 1977, Canard 1990, Mabelis 1996). Detailed knowledge of individual species reproductive cycles and physiological tolerances should enable the prediction of natural fluctuations. It is possible to identify certain species that are indicators for season (i.e. those that are only present or abundant during certain times of the year), and therefore establish temporal guilds (Bell *et al* 1999), which could be incorporated into a monitoring programme. There are, however, confounding factors that can prohibit a simple standardization of seasonal fluctuation. Habitats are inherently dynamic and thus ecological parameters can change over time as in succession, making the habitat more favorable for some species and less favorable for others as years pass (Brown 1991, McIver *et al* 1992). Even climax communities will have variations in niche and resource type and availability between years as canopy dieback or wind throw causes mini-successions to occur (Frelich and Reich 1995). Unseasonable weather conditions will affect spider communities and confound comparisons between years at the same site (e.g. Gunnarsson 1996), though spider community composition has been shown to vary less in relatively stable habitats than other invertebrate groups (Gibson *et al* 1992a). Community fluctuation can also depend on the scale at which the community is analyzed. Canard (1990), in a survey of heathland spiders in France, found that though species composition was subject to temporal and spatial change over the course of sampling, functional group composition was generally more stable. Some level of population or community fluctuation will be unavoidable, however, as one of the characteristics of a good bioindicator, response to ecosystem change, is also a characteristic that ensures some degree of temporal fluctuation.

One component that can be avoided in the selection process for ecological indicators is the tendency for populations to go through boom/bust cycles. Some spider populations demonstrate self-limiting dynamics, where intraspecific competition for territorial space keeps numbers at a stable level below that where food supply becomes important (Riechert 1974, Riechert and Hedrick 1990). Therefore, even though they can exhibit numerical responses to changes in prey density (see 2.2.7 below), spiders are unlikely to exhibit a large density increase in response to greatly increased prey levels (Riechert and Lockley 1984) or a following population crash to very low numbers (but see Polis *et al* 1998).

2.2.6 Dispersal ability

Spiders are often among the first invertebrate colonizers of new habitat patches (Gruttke and Kornacker 1995, Spiller *et al* 1998). This is primarily the result of ballooning, a dispersal process where spiders, usually as juveniles, expel silk into the air and are picked up by wind currents, allowing vast distances of up to several hundred kilometres to be traveled (Turnbull 1973, Marc *et al* 1999). Ballooning in juveniles avoids overcrowding and thus competition and cannibalism following hatching (Turnbull 1973). Members of Linyphiidae, Lycosidae and Araneidae are the most common ballooners (Crawford *et al* 1995, Marc *et al* 1999), though the practice is widespread among other families (Turnbull 1973, Agnew and Smith 1989, Bishop and Riechert 1990). Only members of Linyphiidae regularly balloon as adults, though adult specimens from other families are sometimes found in low numbers (Agnew and Smith 1989). Native New Zealand spiders are not generally as predisposed to ballooning as spiders overseas, but it is still assumed that juvenile spiders do employ this technique (Forster and Forster 1999). Ballooning spiders have the potential to quickly locate all available habitat patches in a fragmented landscape (Burel and Baudry 1995, Mrzljak and Wiegleb 2000). Indeed, colonization of agroecosystems by spiders is thought to be primarily via aerial travel from distant sites (Bishop and Riechert 1990).

The other main method of dispersal employed by spiders is walking, though distances traveled in this way are often quite small, especially for web-building spiders (Marc *et al* 1999). There also appears to be a low propensity for spiders to disperse by this method between adjacent habitats with great physiognomic differences, such as between grassland and forest patches (Kajak and Lucasiewicz 1994) or gardens and forest patches (Bishop and Riechert 1990). Therefore, species that have minimal ballooning ability may be more susceptible to the effects of habitat fragmentation. Low dispersal rates have been observed or inferred for mygalomorphs (e.g. Pedersen and Loeschcke 2001) and other large forest species (e.g. Mabelis 1996). The difference in dispersal abilities between spider species allows compositional differences to develop between highly disturbed ecosystems, which are dominated by species with a high dispersal rate, and more stable systems, where species with a lower mobility are able to accumulate and predominate (Marc *et al* 1999 and references therein).

2.2.7 Response to Habitat Variables

Foliage structure

Spiders rely on specific structural components of the habitat for web-attachment, foraging, communication, refuges for egg laying and protection from predators (Turnbull 1973, Forster and Forster 1999) and may therefore be affected by a change in habitat structure. The importance of vegetation structure to the spider community in grassland has been well documented, with abundance and richness generally lower in less complex habitats (Halaj et al 2000a, Morris 2000). Experimental manipulations in shrubs and trees, involving the tying or clipping of branches to create variations in foliage density and architecture, produce similar results. The total number of spiders generally increases with increasing habitat density and complexity (Hatley and MacMahon 1980, Robinson 1981, Gunnarsson 1990, Brandt and Lubin 1998, Halaj et al 2000b), as does species richness (Hatley and MacMahon 1980, Brandt and Lubin 1998, Halaj et al 2000b) and body size (Gunnarsson 1996, Halaj et al 2000b). However, these trends are not consistent on every occasion. Gunnarsson (1990) found no difference in body sizes between control stands of spruce and stands subject to partial removal of needles, and Gunnarsson (1996) found the relationship between needle and spider density to be inconsistent in the same habitat; on both occasions it appears that bird predation may have a mitigating effect on the vegetation-spider relationship.

Despite the general increase in spider density and diversity with increasing habitat density and complexity, differential responses are observable in different species, families and guilds that are often comparable from study to study. Hatley and MacMahon (1980) tied, clipped or left untouched the branches of several sagebrush shrubs and found that nocturnal hunters (a guild grouping the families Gnaphosidae, Clubionidae and Anyphaenidae) were more abundant in vegetation-dense shrubs; the same guild (minus Gnaphosidae) also reached highest densities in the tied (and thus dense) Douglas-fir branches of Halaj *et al* (2000b). Both sets of authors suggest that the observed trend is the result of increased refuges available for these spiders in dense vegetation. The agile hunters (Salticidae and Oxyopidae) were the only guild to prefer clipped to tied shrubs in Hatley and MacMahon's (1980) study. This observation is supported by the patterns shown by two salticid species in the artificial habitat units constructed by Robinson (1981), both of which preferred open habitat structures. Halaj *et al* (2000b) found that relative abundance of Salticidae did not significantly differ between tied, control and thinned branches, but was greatly reduced on branches that had all needles removed. Both Hatley and MacMahon (1980) and Robinson (1981) suggested that dense vegetation might inhibit the foraging strategy of salticids, which is based around good eyesight over medium to long distances, and a stalk-and-leap capture method (Forster and Forster 1999). Complete removal of needles may make the salticids more visible to both potential prey and predators, and thus represent decreased habitat quality.

Hatley and MacMahon (1980) found higher abundance of web-building spiders in tied sagebrush branches than clipped. The guild was dominated by small spiders of the family Theridiidae, of which individual species have demonstrated clear preferences for dense vegetation elsewhere (Robinson 1981, Chapter 3). Halaj *et al* (2000b) separated the web-spiders into four guilds – the orb-web spiders (Araneidae, Tetragnathidae and Uloboridae), the sheet-web spiders (Linyphiidae), the cob-web spiders (Theridiidae) and the hackle-band weavers (Dictynidae) – and found that orb-web spiders were the dominant group when needle-density was reduced, but sheet-web spiders (Linyphiidae) became dominant in control and tied branches. Individual species of the family Araneidae are known to select web sites according to habitat structure (e.g. McNett and Rypstra 2000). It appears that the larger web-building species, characteristic of this family, require more widely spaced attachment points for their webs, hence an increased abundance in less-dense habitats. The smaller webs of Theridiidae and Linyphiidae are conversely more suited to the close arrangement of many web attachment points (e.g. Schaefer 1978).

The species, family and guild patterns exhibited in the above manipulations reflect those observed within natural habitats. The findings of Halaj *et al* (2000b) are similar to observational and correlative studies of tree species that naturally differ in floristic diversity and density. Docherty and Leather (1997) compared the spider fauna between lodgepole pine and the structurally more complex scots pine stands in Scotland and discovered that both abundance and richness was higher in scots pine canopies (see also Rypstra 1986, Mason *et al* 1997, Visser *et al* 1999). On a finer scale, partitioning of space within a single tree can also occur. Web-building guilds partition apple trees according to structural attributes (Marc and Canard 1997): orb-web spiders were found between large branches, frame-web spiders (Theridiidae and Dictynidae) at the end of small branches, sheet-web spiders (Linyphiidae) between leaves near the base of the tree and tubular-web species (Segestriidae) under bark on the tree trunk. It appears that the relationship between the entire spider community and vegetation structure is relatively constant over a range of scales and locations, though species composition may influence the manner and degree to which guilds respond to structural changes (Robinson 1981).

Litter structure

The richness and abundance of the ground dwelling spider community tends to increase with increasing depth and/or complexity of litter where it occurs, as suggested by many correlative studies (Döbel *et al* 1990, Uetz 1991 and references therein). Bultman and Uetz (1984) compared the arthropod community in both natural and artificial (made from chalandered vinyl) litter that varied in complexity. Small spider (primarily linyphiid) abundance was positively correlated with litter depth and/or complexity, though this trend was reversed during one of the sampling months. Larger spiders were also generally more abundant in deep, complex litter though again this trend was reversed in one of the sampling months. The authors suggest that this supports the findings of Uetz (1979), who discovered that litter structure is only important during the middle part of summer, with prey density and microclimate having a greater effect on the spider community during early and late summer respectively. It has been suggested that it is litter that is the limiting resource for the spider community in forest stands (Hurd and Fagan 1992).

As with foliage-dwelling spiders, individual species and families of ground spiders exhibit different preferences in their choice of habitat type. For example, many Lycosidae species are more abundant in thin, compressed litter (Uetz and Unzicker 1976, Uetz 1977, 1979, 1991). Additionally, Uetz (1979) reported that the relative abundance of the two nocturnal hunting families Clubionidae and Gnaphosidae, and the ambushing family Thomisidae, increases with litter depth and complexity. Ingham and Samways (1996) found that members of Clubionidae and Thomisidae were more abundant where litter was deep and complex in South African forest patches. In much the same fashion as the response of foliage spiders to plant density or architecture, these observations are tied to the foraging and reproductive habits of the individual species, families and guilds. For example, many members of the Thomisidae employ a sit-and-wait foraging strategy (Forster and Forster 1999) that benefits from the presence of refuges, which are more abundant in deep, complex litter.

Microclimate

Spider species have physiological tolerances that allow them to function best within a certain range of environmental conditions (e.g. Moulder and Reichle 1972, Li 1995, Barghusen *et al* 1997, Rossolimo *et al* 1997) and reproductive success can be linked to the thermal environment (Marc *et al* 1999). The macroclimate of the region will determine the range and nature of the species present in the regional pool (Bell *et al* 1999). The microclimates present within a single habitat, which are a function of the prevailing macroclimate and the modifying influence of resident plant species (Turnbull 1973), may influence what subset of species from the regional pool are able to successfully maintain populations at that site, and which ones are numerically dominant (e.g. Canard 1990, Bell *et al* 1999). The importance of microclimate to the habitat selection of individual spider species has been demonstrated (Turnbull 1973, Wise 1993, Ruzicka *et al* 1995, Yanez and Floater 2000), and it may also be the causal factor behind other apparent relationships. Often the association observed between habitat structure and spider distribution is actually a response by the spider to the microclimates associated with the different physical structures (Uetz 1991 and references therein).

Changes in microclimate are also likely to affect other invertebrate taxa that are prey, predators or competitors to spiders (Cloudley-Thompson 1962), and therefore it is difficult to establish the extent of the direct influence of microclimate on the spider community. Indeed, species in general are not guaranteed to be present everywhere that their environmental tolerance range exists due to other factors that may confound microclimate influence (e.g. Davis *et al* 1998). If microclimate does determine the range of species that could potentially survive at a particular site, then the combined influences of habitat structure, prey, predation and competition may determine exactly which species from within that range are present at that site.

Prey

Much of the interest in spider-prey interactions has been focused on the ability of the spider community to suppress invertebrate pest populations as a means of biocontrol (e.g.

Riechert and Lockley 1984, Riechert and Bishop 1990, Carter and Rypstra 1995, Marc *et al* 1999). Inherent to their success in this capacity is the requirement for some form of numerical response to an increase in prey density, either through increased reproduction or aggregation (Riechert and Lockley 1984). Both field and experimental studies have demonstrated an increase in spider density with increasing prey density for both ground spiders (Riechert 1974, Chen and Wise 1999) and web spiders (Wise 1975, Polis *et al* 1998). Evidence also suggests that spiders will abandon sites were food abundance is low (Riechert and Lockley 1984 and references therein). Food shortages are common in natural spider populations (Wise 1993), and spiders in general exhibit a number of adaptive traits associated with these shortages (Riechert and Lockley 1984). Food is not a limiting resource in all cases, however (Riechert and Cady 1983, Döbel *et al* 1990, Spence *et al* 1996, Halaj *et al* 1997). In many of these instances, particularly involving web-building spiders, habitat structure proved to be a more important regulator of population density. McNett and Rypstra (2000) concluded that large orb-web spiders base primary habitat selection on structural attributes, but feeding success, which would be linked to prey abundance, determines how long they remain there. The relative importance of food density and habitat structure may be intrinsically related; where food is abundant, habitat space may become limiting and vice-versa (e.g. Mason *et al* 1997). There is also evidence that the significance of prey density to spider populations can vary depending on the time of year (Uetz 1979).

The generalist feeding nature of most spider species (Nyffeler *et al* 1994) means that the taxonomic composition of the spider community is less likely to vary with change in the abundance and composition of prey, except possibly in the rare cases of prey-specific spiders. Uetz (1979) did however report evidence of prey abundance partially affecting spider richness in leaf litter. The most likely way for species composition to change as a result of prey density variation is indirectly through competition. Reduction in food may increase competition between species and lead to competitive exclusion; or, conversely, an increase in prey abundance may decrease competition and allow the coexistence of more species through specialization. Evidence for competition between spiders is mixed however (see below).

Predators

The influence of predation on individual spiders can be inferred by avoidance behaviour (Bremner *et al* 1989, Riechert and Hedrick 1990, Riechert and Hall 2000) and the evolutionary influence can be assumed from the cryptic colouring of many species (Forster and Forster 1999). Experimental studies have confirmed that predators can have an effect on the spider community. Dial and Roughgarden (1995) removed lizards from the canopy of tropical rain forest and found that orb-web spiders increased in abundance following the removal. Leaf spiders greater than 2mm long also increased in abundance, though those less than 2mm long showed no effect. Differential effects of predation depending on spider size have been noted elsewhere. Gunnarsson (1996) reported how spider body size is significantly larger on spruce branches where bird predation is excluded compared to control branches, supporting the findings of Askenmo *et al* (1977) within the same habitat.

One of the most comprehensively studied spider-predator systems is that involving web spiders and lizards on islands in the Bahamas. Observational studies show that lizard-free islands have greater abundances and diversity of spiders than those containing lizards (Schoener and Toft 1983, Toft and Schoener 1983). Consequent experimental studies identified the causal factors behind these patterns: lizards reduce short-term spider survivorship (Spiller and Schoener 1988) and food consumption (Spiller and Schoener 1990); directly reduce spider density (Schoener and Spiller 1987) and diversity by removal of rare species (Schoener and Spiller 1996, Spiller and Schoener 1998); and prohibit immigration onto islands (Schoener and Spiller 1995). There is also evidence that the lizards affect the spider community through competition for food (see below). Strong predatory effects are not seen in all spider populations. Eleven species of small vertebrate predators (reptiles, amphibians and mammals) were removed from experimental plots on the floor of a maple-oak forest by Wise and Chen (1999b), yet there was no resultant effect on the density of a resident wolf spider population.

Schoener and Spiller (1996) introduced lizards onto previously lizard-free islands to simulate the effects of foreign species invasion; spider density and diversity were quickly reduced to the levels found on nearby islands that naturally contained lizards. Other experiments involving introduced predators on native spider fauna are scarce. Toft and Rees (1998) report how the introduced wasp *Vespula vulgaris* lowers the probability of orb-web spider survival in New Zealand beech forest. However, the spider species used in the experiment was an introduced species, *Eriophora pustulosa*, which is not usually found in the forest interior.

Predation of spiders by spiders is also common in natural communities, with intraspecific predation (cannibalism) potentially a significant cause of death in ground spiders (Wagner and Wise 1996, 1997). However, as reviewed in Marc *et al* (1999), the evidence for the importance of cannibalism in spiders is mixed, and worthy of further research. Interspecific predation is more commonly encountered (Jackson 1992, Wise and Chen 1999a), but the importance of this in the structuring of spider communities is also unclear.

Competitors

Given that many species have a wide potential ecological range, it would be expected that spiders would be subject to considerable interspecific competition. Wise (1993) reviewed the evidence for competition between spider species and concluded that it is weak, and indeed, in some instances, competition is not in evidence even where niches overlap considerably (e.g. Riechert and Cady 1983). Space and food segregation (Uetz 1977, Robinson 1981, Spiller 1984, Moring and Stewart 1994, Jedlickova 1996), temporal partitioning (Uetz 1977, Spiller 1984), and intraspecific territoriality (Riechert 1974, Riechert and Cady 1983) have all been suggested as ways spiders avoid competition and allow coexistence. Of course, in the "ghost of competition past" paradigm (Connell 1980), all of these things are potentially the evolutionary outcomes of competition. Given that the debate still continues on whether it is important in spider communities, very little can be concluded on how interspecific competition may affect spider community response to disturbance. Riechert and Lockley (1984) suggest that competition may limit the ability of spider communities to increase their density in response to food levels.

In comparison to intraorder competition, there has been little work done on the effects of competition between spiders and other taxa, with most studies investigating competition from ants or lizards. There does not appear to be any general rule governing the influence of ants on the spider community. Correlative evidence from a forest floor habitat suggests a colony of red wood ants (*Formica polyctena*) has no effect on the abundance or composition of either the ground-active or the web-building spider fauna in the vicinity (Brüning 1991), and ant removal had no significant density effects on spiders in white birch canopies (Karhu 1998). Halaj *et al* (1997), however, removed the ant fauna (mostly *Camponotus laevigatus*) from Douglas-fir canopy and reports that while neither the abundance of web-building spiders nor the overall composition or diversity of the community were affected, abundance of hunting spiders from the families Salticidae, Anyphaenidae and Oxyopidae did increase in ant-free canopies. The authors suggest that this is the result of interference competition (rather than predation or competition for food) between ants and the spiders, as suggested by regular observations of spider avoidance behaviour in the presence of ants.

Predatory effects of lizards generally confound their competitive effects on spider communities. Spiller and Schoener (1990) presented the results of an experimental lizard removal experiment, where density of all web spiders were up to three times higher in lizard-free plots. The presence of lizards reduced the abundance of some arthropods contained in the diet of the most common web-spider species, *Metepeira datona*, which in turn reduced food consumption and had a negative effect on female spider body size and fecundity. The relationship between the lizards and *M. datona* appeared to switch from predator/prey when the spiders are young, to a mixture of predator/prey and competition when the spiders are adults.

2.2.8 Response to Disturbance and Representation of Other Taxa: Examples from Forest Habitats

Given the nature of most disturbances, a number of habitat features important to the spider community can be affected simultaneously. The degree to which the spider community will respond depends on how the disturbance in question affects each of these features. Spider community parameters in relation to habitat composition and quality in grasslands, croplands and heathlands has been documented and reviewed extensively (Warren *et al* 1987, Gibson *et al* 1992b, Rushton and Eyre 1992, Dennis *et al* 1998, Halaj *et al* 2000a, Sunderland and Samu 2000) with some authors suggesting their use as monitoring tools within these habitats (Pristavko and Zhukovets 1988, Maelfait *et al* 1990, Gibson *et al* 1992a, Rushton and Eyre 1992, Pozzi *et al* 1998). Less is known of the response of forest spider communities to disturbance. Below is a brief summary of some of the results of disturbance within this habitat type on the invertebrate community, and spiders in particular.

Fragmentation

Two studies have explicitly investigated the effect of forest fragmentation on the spider community. Mabelis (1996) sampled the ground spider fauna in a number of oak/birch/beech woodlots in the Netherlands. There was a greater total number of species found in larger woodlots, but no relationship between species density (the number of species per unit area) and forest patch size. This, plus the random distribution among the woodlots of many of the species found, suggests that forest fragmentation has little effect on the majority of the spider fauna. However, one species, the large agelenid *Coelotus terrestris*, demonstrated a significantly non-random distribution pattern, suggesting a relatively poor dispersal capability and thus, the authors suggest, would be affected by fragmentation. A second species, *Gonatium rubellum*, was also distributed non-randomly, which is somewhat surprising given that it is a member of the Linyphiidae, a family well known for good dispersal capabilities.

The second study, Miyashita *et al* (1998), investigated the response of web spiders to fragmentation in oak-dogwood and *Zelkova-Castanopsis* forest in Japan. Like Mabelis (1996), they found total species richness increased with fragment area, but the regression between species density and fragment area was also significantly positive. The relationship between species density and area was positive for the whole data set, but when separated by region, it was significant for Yokohama fragments but not Tokyo fragments. The authors also suggest that it is mainly when the difference in isolation is large that there is an effect when comparing spider communities. Large species of the family Araneidae appeared more susceptible to forest fragmentation, with proportionally fewer species in small fragments, whereas the proportion of small Theridiidae species in the community actually increased with decreasing fragment size. Spider population density within the fragments seemed to fit a saturation curve, with density dropping markedly in areas less than a hectare in size. Abensperg-Traun *et al* (1996) also found the abundance of ground spiders (excluding myglamorphs) was affected by remnant area in eucalypt woodland in Australia. Total spider density and diversity also decreased from isolated 10-hectare patches to 1-hectare patches to single trees of scots pine in the survey undertaken by Ozanne *et al* (2000).

Neither of these two main surveys measured the response of other arthropod taxa, though Miyashita *et al* (1998) do suggest that the abundance of large flying arthropods may be lower in smaller fragments, based on previous research. The results of other studies have indicated a general trend of decreasing abundance and diversity in the invertebrate fauna as patch size decreases, though the response of different groups often differs and consequently alters community structure (e.g. Ingham and Samways 1996, Bolger *et al* 2000, Ozanne *et al* 2000, Gibbs and Stanton 2001). For example, the abundance and diversity of spiders and the abundance of carabids and cockroaches tended to increase in the smaller buckwheat patches sampled by Bolger *et al* (2000), whereas fly diversity and abundance, and mite and bristletail abundance, all increased with increasing patch size. It is therefore difficult to generalise effects on the biota given the wide range of impacts fragmentation can have on an ecosystem (Saunders *et al* 1991).

Browsing

Mygalomorph spiders were one of only three invertebrate groups to be negatively affected by intensive sheep and cattle grazing in the survey of eucalypt woodlands in Australia by Abensperg-Traun *et al* (1996). The authors suggest that it is the requirement for permanent burrows that leads to their great reduction in numbers due to soil compaction in heavily grazed remnants. Some groups, including lycosid spiders and a mixture of detritivores and omnivores, were found to be more abundant under moderate grazing intensity. Beetles as a group were significantly more abundant and diverse in areas of highest grazing, a trend not matched by any spider group, though spider species richness was not reported. Bromham *et al* (1999), who surveyed another series of eucalypt woodlands in Australia, reported that the diversity of spider families (species richness not calculated) was highest in ungrazed woodland, following the same pattern as invertebrate order diversity. Total invertebrate abundance was much lower in ungrazed sites than grazed but this was almost entirely attributable to the response of ants. A number of smaller orders actually increased their abundance in ungrazed patches. Spiders were only slightly more abundant in the absence of grazing, though the families Amauribiidae and Zodaridae were significantly more abundant, and wolf spiders (Lycosidae) least abundant, in the presence of grazing.

These two examples illustrate how grazing can affect disparate groups of invertebrates, but to different degrees and in different directions (see also Suominen *et al* 1999). Spider communities also appear to have members that respond differently to the disturbance because some of the consequences of browsing, such as reduction of foliage density or litter compaction, will actually benefit some guilds in comparison to others (see 2.2.7).

Direct management

Almost five times more invertebrates were reported on the branches of Norway spruce in natural forest than in nearby managed forests subject to selective logging and thinning in northern Sweden (Pettersson *et al* 1995). All twelve orders sampled from the canopy were more abundant in the natural forests, including spiders. In fact, both all spider and large spider abundance, along with the number of invertebrate orders and individuals, were all higher in natural forests at all locations. The authors relate the effects to branch size and lichen abundance, both of which are higher in natural forest, due to increased age of the trees. In a follow-up paper, Pettersson (1996) demonstrated that spider richness and diversity was also highest in natural, lichen-rich forests, suggesting that this is a result of the decreased habitat density and/or complexity in managed forests.

The ground-active and understory spider fauna can be influenced by forestry practice. In a study of Oregon coniferous forest, McIver *et al* (1992) found that there were clear changes in the guild structure of the litter spider community with increasing successional age following clear-cutting. Diurnal pursuit species, consisting of a number of lycosid species, dominated the catch early after disturbance (3-7 year old stands), but reduced in importance with increasing successional age, with sheet-web (Linyphiidae), funnel-web and trapdoor spiders becoming proportionally more dominant. Highest lycosid abundance in young stands following harvesting has also been reported in the boreal forests of Alberta, Canada (Buddle *et al* 2000), with web-building spiders becoming more dominant in older forests. Broadly similar trends in spider community composition have been demonstrated in other managed forests (Pajunen *et al* 1995, Junker *et al* 2000). McIver *et al* (1992) relate the effects of successional age on spider communities in part to prey abundance and composition (along with microclimate and litter development), which suggests that spiders can indicate the response of other invertebrates in this system. Patterns in spider community composition along forest successional gradients following clear-cutting have also been shown to be similar to those of carabid beetles (Niemelä *et al* 1996). Litter spiders have been suggested as bioindicators for the quality of the forest floor habitat after logging in situations where analysis of understory plant composition is not appropriate (McIver *et al* 1992).

River regulation leading to changes in flow and channel morphology can affect riparian vegetation and the resident ground-active invertebrate communities. Ellis *et al* (2001) experimentally flooded an area of forest on the banks of the Rio Grande, New Mexico, and found that though inundation produced changes in the community composition of all invertebrates, all insects, all beetles and carabids, there was no significant differences in the spider or ant communities before or after flooding. These results are contrary to those found by Bell *et al* (1999), who reported distinct spider assemblages from areas subjected to regular flooding compared to those that are not subject to any flooding, within single forest patches in Western Europe. In that study, spider community composition only reflected whether a site was flooded or not; sites that were only rarely flooded were not significantly different to those that were frequently inundated. It is unclear whether the control sites used by Ellis *et al* (2001) as a comparison to the experimentally flooded and naturally flooded sites are permanently dry. In addition, it has been shown that spider populations can escape flooding by migration to higher ground or tree trunks (Höfer 1990). This may reduce the ability to detect differences in community composition following one-off or infrequent flooding events, such as those investigated by Ellis *et al* (2001). There still remains great scope for the further investigation into riparian communities that can be affected by river management.

Spiders have been used in estimating the success of native forest restoration. In a project involving the planting of native trees in areas of grassland in the Port Hills of New Zealand, Reay and Norton (1999) reported a strong association between spider community composition and site age. This indicated that the restoration was able to provide conditions that allowed for recolonisation by indigenous invertebrate fauna, though the study did not report any particular species that may act as indicators for the restoration of native forest.

The construction of roads through otherwise continuous stretches of forest has been shown to affect the composition of invertebrate communities. Haskell (2000) investigated this in the Cherokee National Forest in Tennessee, and reported that the overall abundance and richness of the invertebrate fauna decreased with increasing proximity to unpaved roads. Of the sixteen taxa measured, fourteen exhibited a decrease in abundance close to roads, and spiders were one of the four groups (along with Chilopoda, Acarina and Coleoptera) for which this decrease was significant. It is suggested that these patterns are related to the effect of the roads on the leaf litter depth.

Spider communities can exhibit clear succession patterns following fire in forests. Members of the family Lycosidae increasing in abundance post-fire and members of the Linyphiidae decreasing in abundance, and only recovering 15-30 years following the fire, in a similar manner to succession following clear-cutting (Buddle *et al* 2000). Forest fires can have contrasting results on different taxa in a community. Following an uncontrolled fire in a mountain ash forest in Australia, spider, mite, Diptera, Collembola and wasp abundance were unaffected, but beetle and ant abundance significantly increased, and pseudoscorpions, harvestmen and amphipods showed population suppression for up to a year after the fire (Neumann 1991). However, long-term use of fire control may have a greater effect on the litter-dwelling invertebrate fauna than one-off fires. York (1999) reported a significant reduction in numbers for many inverterbrate groups in coastal eucalypt forest subject to repeated low-intensity burning compared to unburnt forest. Some taxa, including spiders that were unaffected or facilitated in Neumann's (1991) survey following a single fire, showed declines in areas of repeated fires. Similarly, Springett (1976) also found that all bar one of eleven invertebrate groups were more abundant in unburnt than regularly burnt eucalypt forests in Western Australia, with spiders between two and three times more abundant. In addition, overall species diversity was twice as high in the unburnt forests. Some species were found either in burnt or unburnt forest but not both, and spiders were one of the groups that had representative species for both situations. The likely reason for the negative response shown by these invertebrate groups to fire, as suggested by both Springett (1976) and York (1999), lies in the destruction and simplification of the litter layer. Interestingly, a study of the spider community in *Spartina pectinata* wetlands in the USA showed that the spider abundance was significantly higher in annually burnt wetlands than those that remained unburnt (Johnson 1995). This appeared to parallel the increase in abundance of potential prey at the burnt sites, possibly as a result of increased productivity following fire. There seems to be a great range of response possible in invertebrate communities depending on the habitat type and fire frequency.

2.4 CONCLUSION

Biogeographical and ecological history determines the distribution and niche occupied by a taxonomic group within a region (Pearson and Carroll 1998), and local processes such as competition, predation and climatic variability will help determine community abundance and structure on a smaller scale (e.g. Polis and Hurd 1995, Spiller and Schoener 1995, Bell *et al* 1999). With the enormous heterogeneity of environments, species life histories and disturbances present globally, the conclusion that there will never be a single group of taxa able to act as reliable ecological indicators in every situation is not unexpected. Faunal responses to disturbance are not consistent from site to site or region to region, as indicated by the examples discussed above. The criteria presented here are intended as a guide in selecting a shortlist of suitable taxa from the particular region where monitoring is required, a list that may differ from those of other regions, countries or continents. From this set of potential indicators, preliminary surveys can then be carried out to establish which one is the most useful in the context of the disturbance being investigated.

Spiders suggest themselves as likely candidates in these preliminary surveys for a number of reasons. They are abundant, diverse and widespread, present in almost every terrestrial habitat. They can be readily sampled using a variety of methods that can be tailored for the objectives of the project. Though they do demonstrate seasonal fluctuations in species abundance and composition, spider communities are relatively stable in comparison with other invertebrate groups and, apart from a few exceptional cases, not subject to severe boom-bust cycles. As a group they exhibit a variety of dispersal strategies, enabling their use in a variety of situations, from indicating restoration success to investigation of habitat fragmentation effects. Spiders have demonstrated responses to the experimental manipulation of several environmental factors that may be affected by disturbance, including vegetation and litter structure, prey density, predation levels and competition effects, in addition to having individual species show preferences for certain microclimatic conditions. Most important of all, spider communities have shown distinct responses to disturbance in a range of habitats and regions. Such responses are nearly always representative of at least a subset of other invertebrate taxa.

There are two important caveats attached to the use of spider communities as ecological indicators. Firstly, taxonomic knowledge is limited in many regions of the world. A combination of many undescribed species and a lack of spider taxonomists combine to restrict the use spiders in widespread monitoring schemes outside countries, such as Britain, where the fauna is more well known and reliable methods for identification to species by non-specialists are available. Secondly, there is still a lot to learn in terms of basic biology for many species worldwide. Predictions cannot be made on how the resident spider fauna may respond to a local disturbance, nor are the species most likely to be sensitive to disturbance able to be established beforehand. It is important to note that neither of these disadvantages are inherent to spiders as a group, but rather reflect current scientific priorities and can be rectified with increased interest, support and funding. This may be more forthcoming should spiders, or any invertebrate group, prove to be useful in ecological monitoring as surrogate species.

CHAPTER THREE

Spider Community Composition Across a Successional Gradient

3.1 INTRODUCTION

Secondary succession is the process of recolonisation of an area by vegetation following disturbance, with a directional turnover of plant species producing a series of distinct community types known as seral stages (Archibold 1995, Barbour *et al* 1999). In addition to plant species composition, other community attributes such as plant diversity (Odum 1969), plant biomass, cover, density and height (Barbour *et al* 1999) and habitat heterogeneity and complexity (Brown 1991) will differ between seral stages. The abundance, diversity and composition of resident terrestrial invertebrate communities also vary along the plant successional gradient (Southwood *et al* 1979, Munro 1995, Tscharntke and Greiler 1995).

Spiders as a group are strongly influenced by habitat structure (Hatley and MacMahon 1980, Robinson 1981, Uetz 1991), and to a lesser extent by prey abundance (Riechert and Lockley 1984) and microclimate (Turnbull 1973), and should therefore also be expected to exhibit divergent community attributes between seral stages. Hutcheson *et al* (1999) state that for any invertebrate group to be useful in ecological monitoring, it needs to have communities characteristic of specific vegetation types. Certainly, any group that fails to exhibit measurable differences between vastly divergent plant communities is unlikely to show a response to changes within the same habitat, an important criterion in ecological indication. Individual spider species may not exhibit a high degree of habitat specificity, with many found in a range of habitat types, but differences in spider community structure can be detected between habitats (Turnbull 1973, Bell *et al* 1999). Variation in the spider community between seral stages has been documented, but parameters such as species and family richness, abundance and composition do not necessarily follow a linear trend with successional age, nor do patterns necessarily correspond between different successional series (Bultman *et al* 1982, Gibson *et al* 1992b, Hurd and Fagan 1992, McIver *et al* 1992, Van der Merwe *et al* 1996). In New Zealand there is a lack of both spider community surveys across successional gradients and detailed ecological knowledge of native spider species. Therefore it is unknown to what degree or direction native spider abundance, diversity and composition varies with successional age of a habitat, and whether certain species are restricted to particular habitat types enabling distinct spider communities to be associated with seral stages.

The aim of this study is to describe the spider community across a typical New Zealand native shrubland-forest succession; describe the relationship between the plant community and spider composition and diversity; and to investigate the ability of the spider community to discriminate between different seral stages.

3.2. METHODS

3.2.1 Study Sites

All sampling took place in Pouiatoa State Forest (NZMS 260 Q19 395335), located approximately 40km east of New Plymouth, New Zealand (Fig. 3.1). Covering 3612 hectares of steep, dissected Urenui siltstone hill country, Pouiatoa consists of both primary and seral habitat types, with tawa forest/manuka-treefern scrub (47% of the area) and tawa-kamahi-hinau-rewarewa forest (37%) the dominant forest types (Bayfield *et al* 1991). Like most of the forests in the region, Pouiatoa contains a number of pest species, with feral goats (*Capra hircus*) and brush-tailed possums (*Trichosurus vulpecula*) present in very high numbers in and around the periphery of the forest. Sheep and cattle from adjacent grazing land are also occasionally present, mainly in the mixed manuka habitat occurring along much of the border between the native forest and pasture.

Four habitat types were selected along the south-east side of Pouiatoa forest: young manuka/kanuka scrub (MAN), advanced manuka/kanuka forest (ADM), mixed broadleaf/podocarp forest with no understorey (BNF) and mixed broadleaf/podocarp forest with an understorey of shrubs and saplings (N). Each type was selected for its distinct plant species assemblage and/or habitat structure (Table 3.1, Plates 3.1, 3.2). MAN, ADM and N represent stages in the vegetative succession from exotic pasture to climax native forest, and BNF represents an architectural variation of N induced by higher densities of browsing mammals.

Two representative areas were selected for each habitat type, giving a total of eight sampling sites (Fig 3.1). The paired sites (e.g. MAN1 and MAN2) were not located within the same continuous stretch of that vegetation type, but were separated from each other by other vegetation types, including grazed pastures. At each site, vegetation and spider sampling took place within a single 20m x 20m plot. The size of the plot was chosen to match the upper limit of Allen's (1992) estimation of the plot size required for the reconnaissance method of vegetation sampling on single landforms, where plant

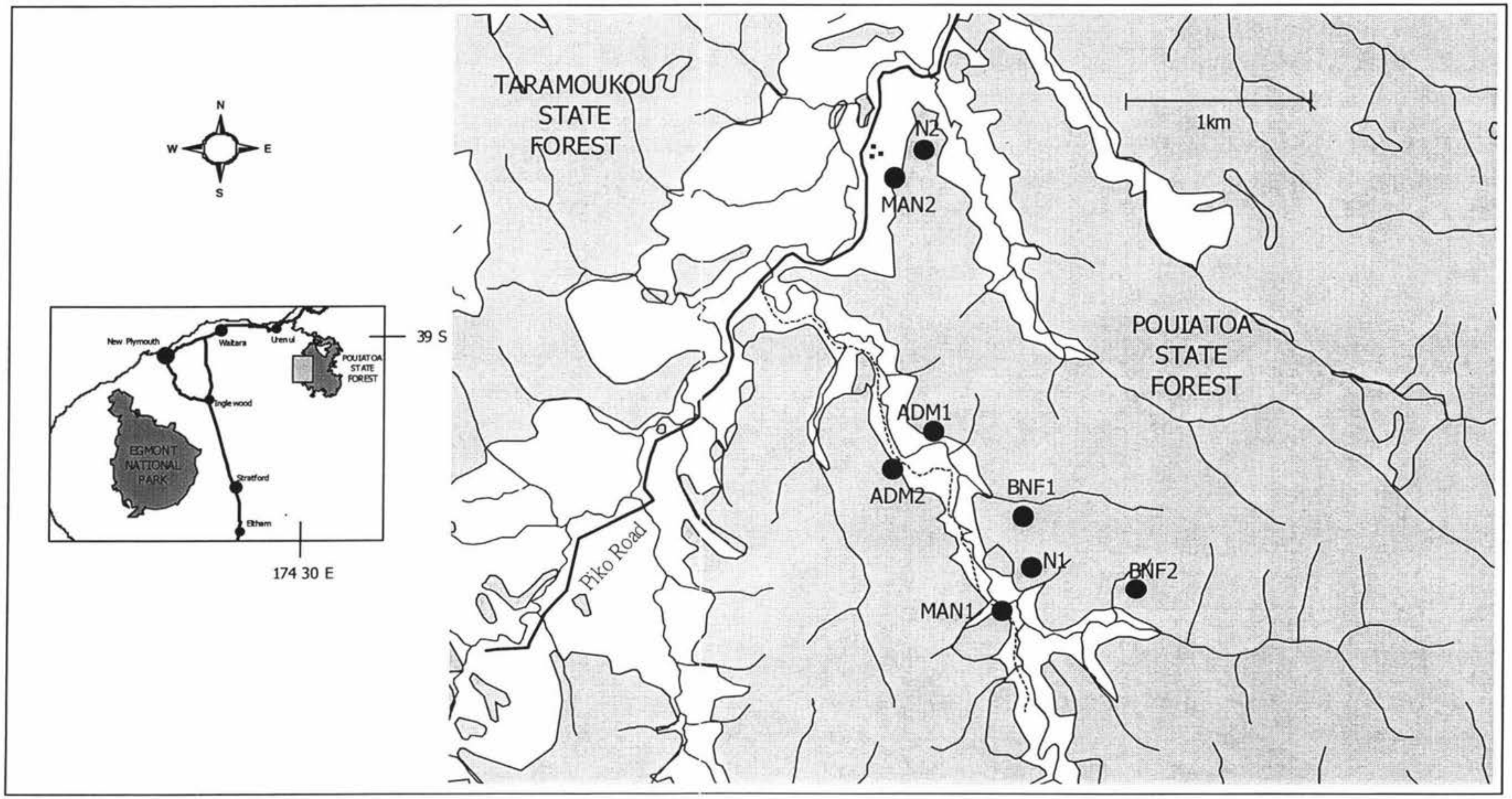


Fig. 3.1: Location of the eight study sites in Pouiatoa State Forest, northern Taranaki, New Zealand

Plate 3.1: A young manuka site (MAN, top) and an advanced manuka site (ADM, bottom) from a forest succession surveyed in Pouiatoa State Forest, northern Taranaki.

Plate 3.2: A browsed native forest site (BNF, top) and an unbrowsed native forest site (N, bottom) from a forest succession surveyed in Pouiatoa State Forest, northern Taranaki.

Table 3.1: Description of the four habitat types along a successional gradient from native shrubland to forest.

Habitat Type Code	Details
MAN	Habitat description: young mixed manuka/kanuka up to 3 metres tall, overtopping grass and ground ferns. Common plant species: manuka (*Leptospermum scoparium*), kanuka (*Kunzea ericoides*), ring fern (*Paesia scaberula*), bracken (*Pteridium esculentum*), browntop (*Agrostis capillaris*)
ADM	Habitat description: very sparse 8 metre high kanuka trees, overtopping moderately dense layer of tree fern and a number of woody shrubs and saplings. Common plant species: manuka, kanuka, wheki (*Dicksonia squarrosa*), shining spleenwort (*Asplenium oblongifolium*), kiwakiwa (*Blechnum fluviatile*), rangiora (*Brachyglottis repanda*), hangehange (*Geniostoma rupestre*), heketare (*Olearia rani)*
BNF	Habitat description: mixed podocarp/broadleaved forest, with relatively closed canopy layer and very little shrub or sapling growth, possibly the result of goat browse. Little herb or ground fern growth. Common plant species: tawa (*Beilschmedia tawa*), miro (*Prumnopitys ferruginea*), rimu (*Dacrydium cupressinum*), *Cyathea smithii*, hinau (*Eleocarpus dentatus*), rewarewa (*Knightia excelsa*), mahoe (*Melicytus ramiflorus*), silver fern (*Cyathea dealbata*)
N	Habitat description: mixed podocarp/broadleaved native forest, with a variable canopy cover ranging from relatively closed to ragged and open in places. Moderate shrub and sapling growth, with little evidence of goat browse. Common plant species: tawa, miro, rimu, hinau, rewarewa, mahoe, rangiora, heketare, wheki, silver fern, *Blechnum discolor*, supplejack (*Ripogonum scandens*)

species are recorded until new species are rarely encountered. At all native forest sites (BNF and N), the plots were set about 40 metres from the border between the forest and adjacent habitat to standardize any edge effect between the sites.

3.2.2 Vegetation Sampling

Vegetation diversity and structure was sampled using the point-height intercept method. Twenty-five sampling pins were randomly placed within the 400m^2 sampling area. Following Gardner *et al* (1995), three different pins were used at each point. At each sampling point, a 2m pin was placed vertically and the plant species and structures touching within 10 cm height intervals recorded. A 5m pin was then placed on the same point, and the species and structures touching within each 50cm height interval between 2 metres and 5 metres off the ground were recorded. Finally, a 10m pin was erected and all the touches between 5m and 10m recorded at 1m intervals. At the native forest sites, the canopy reached beyond 10 metres in height, so above this height the touches per metre interval was estimated visually, using binoculars.

Plant species richness for each site was calculated as the number of species that touched at least one of the twenty-five sampling pins. *Species composition* was calculated by giving each species an abundance score equal to the number of pins touched by that species. The maximum abundance score for an individual species at a single site was therefore 25. Both species richness and composition were calculated at three levels: for all vegetation sampled in the plot, for vegetation sampled within three metres from the ground only (0-3m height interval) and for vegetation sampled over 3 metres from the ground (>3m height interval). Vertical distribution of plant material was plotted as the total number of touches (irrespective of species or architecture type) per height interval for all samplings pins combined per site. *Plant density* was calculated as the total number of touches below 3 metres on the sampling pins. This height limit was used because it was only from within the 0-3 metre band of vegetation from which spiders were collected. *Architectural richness* was measured, in a similar fashion to species richness, as the number of architectural types touching at least one of the 25 sampling pins. These types, based mainly on leaf shape and size, are listed in Table 3.2. Architectural richness was calculated for the 0-3m and >3m vegetation tiers, as well as for all vegetation.

3.2.3 Spider Sampling

Five pitfall traps were randomly placed within each 400m^2 sampling area for a period of six weeks, from mid-January to late February 1999. Each pitfall had a diameter of 102mm and set flush with the ground, with a 20cm by 20cm iron cover placed 5cm above the pitfall to intercept rain and falling debris. 50% ethyl glycol was used as the preservative in the pitfalls, and upon collection the spider specimens were transferred into 70% ethanol. In addition, hand searching and beatings were done as a supplement to the pitfall trapping. A 5 x 5 metre plot was marked out within the 400 m^2 sampling area, where hand searching took place. Two hours were spent searching all habitats within the 25m^2 area for spiders. Hand searching took place at the same time of day at each site, from 4:00pm to 6:30pm. All spiders collected were preserved in 70% ethanol.

Another 5 x 5m square was set out for the beatings. All vegetation contained therein was given ten shakes by hand above a white sheet acting as a drop cloth. All spiders that fell

Table 3.2: Categories used in the analysis of plant architectural richness (modified from Gardner *et al* 1995).

Architectural types	
Moss	Lanceolate/elliptic leaf (<4cm long)
Grass/sedge leaf	Lanceolate/elliptic leaf (>4cm long)
Grass seed stem	Oval/ovate leaf (<4cm long)
Clover leaf	Oval/ovate leaf (>4cm long)
Cone/seed capsule	Oval/ovate leaf ciliate (>4cm long)
Loose bark	Linear leaf (>4cm long)
Woody branch (<1cm diameter)	Oblanceolate leaf serrated (>4cm long)
Woody branch (1-2cm diameter)	Oblanceolate leaf non-serrated (>4cm long)
Woody branch (>2cm diameter)	Obovate leaf (>4cm long)
Live tripinnate fern frond	Oblong leaf (>4cm long)
Dead tripinnate fern frond	Ovate leaf (>4cm long)
Live bipinnate fern frond	Litter
Dead bipinnate fern frond	

onto the cloth were preserved in 70% ethanol. There was no time limit set for this method, rather it continued until all the vegetation reachable by hand was shaken.

Spiders were sorted first into a reference collection of morphospecies (Oliver and Beattie 1996a), which were then forwarded to an experienced taxonomist to correct cases of splitting or lumping. Most of the juvenile specimens could not be identified further than family; these were excluded from measures of species richness and composition, but retained for analysis of family composition and overall abundance.

3.2.4 Data Analysis

The relationships between measures of the spider community (total species richness, species richness by sampling strategy, spider abundance and individual family abundance) and plant community variables (species richness, plant density and architecture diversity) across the eight sites were investigated with Pearson correlations, using Bonferroni corrected probabilities. Spider species and family abundances were $\log_{10}(x+1)$ transformed to reduce the influence of extremely abundant species or samples. Differences in community composition between the eight sites were investigated for both the plant and spider species assemblages using the Bray-Curtis measure of dissimilarity, given by the equation:

$$D_{ih} = \frac{\sum_{j=1}^{p} | a_{ij} - a_{hj} |}{\sum_{j=1}^{p} a_{ij} + \sum_{j=1}^{p} a_{hj}}$$

where D_{ih} = dissimilarity between sites *i* and *h*, a_{ij} = the abundance of species *j* at site *i*, and a_{hj} = the abundance of species *j* at site *h*. Scores range from 0 (identical communities) to 1 (no shared species). Bray-Curtis measures of dissimilarity using log-transformed abundance data have been shown to be one of the best measures of successional trends in invertebrate communities (Huhta 1979).

Ordinations of the sites using plant species, plant architecture, spider species and spider family composition were performed using detrended correspondence analysis (DCA), using PC-ORD ver. 4 (McCune and Mefford 1999). Cluster analysis was performed using the Relative Sorenson distance measure and Group Average linking. For both the DCA and cluster analyses, $\log_{10}(x + 1)$ transformed abundance data were used in the analysis of spider species composition. For spider family composition, the abundance of each family was converted to a percentage of the total number of spiders collected (relative abundance) for use in the analysis.

3.3 RESULTS

3.3.1 Plant Communities

The most number of plant species (16) were found at N1 and, in general, the four forest sites, BNF1, BNF2, N1 and N2, had the highest overall plant species richness, due to high number of species found above 3 metres (Fig. 3.2a). However, ADM2, with a high diversity of young woody species in the 0-3m height tier was the second most species-rich site overall. The young manuka sites contained the fewest plant species, with 9 found at MAN1 and 7 found at MAN2.

Overall architectural richness (Fig. 3.2b) showed considerable variation even within the same habitat type. The greatest richness of architecture types was in two forest sites BNF2 and N1. The high overall richness at BNF2 was the result of a diverse canopy rather than understorey. Architectural richness below 3 metres had a positive relationship with plant species richness below 3 metres ($r = 0.71$, $p < 0.05$) but not for all height categories combined ($r = 0.59$, $p > 0.10$).

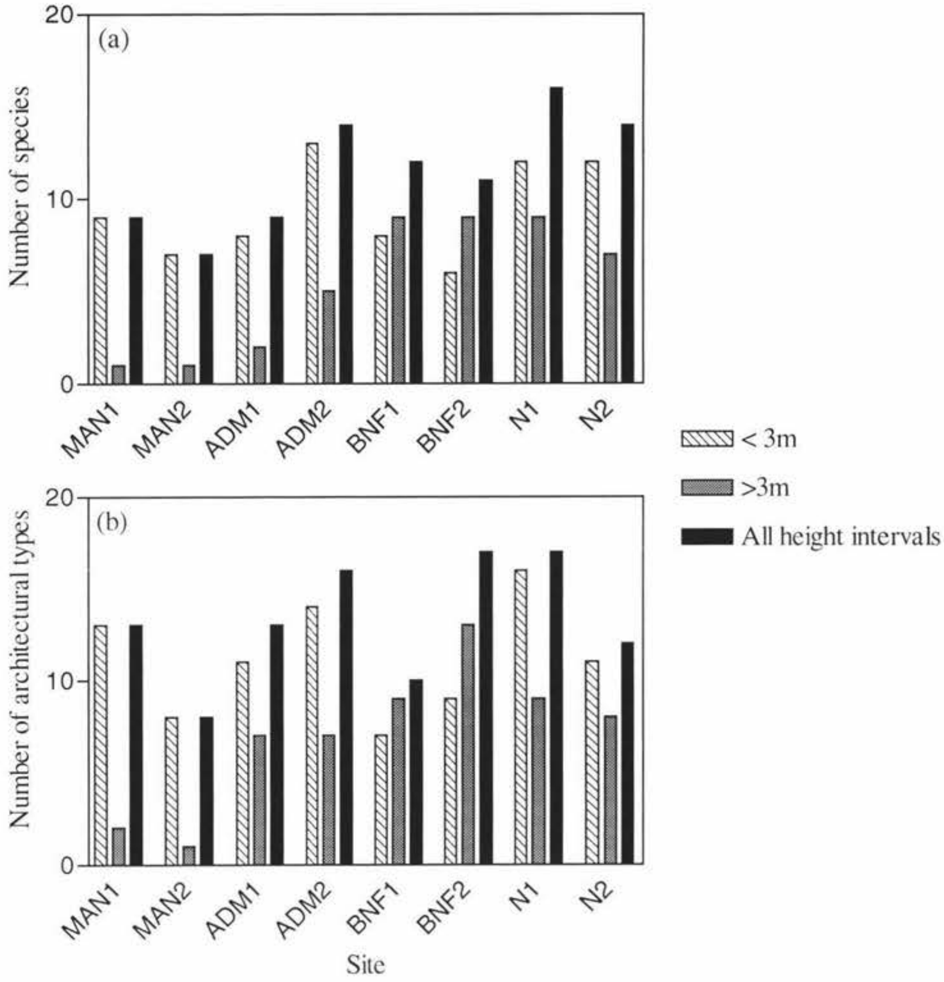


Fig. 3.2: (a) Plant species richness, and (b) plant architectural richness, of eight study sites representing four habitat types along a successional gradient, as measured between 0-3 metres above the ground, above 3 metres, and both intervals combined.

Vertical distribution of the vegetation was noticeably different between habitat types (Fig. 3.3). A dense understorey characterizes the two MAN sites, with the presence of grasses, ferns and manuka giving a high number of touches within the 0-3 metre height interval. The same band of vegetation was less dense in the advanced manuka stands; small broadleaf saplings and fern fronds from the canopy of *D. squarrosa* replace the manuka shrubs. Unlike the young manuka stands, vegetation is present more than six metres above the ground, in the form of a sparse but distinct canopy of kanuka foliage.

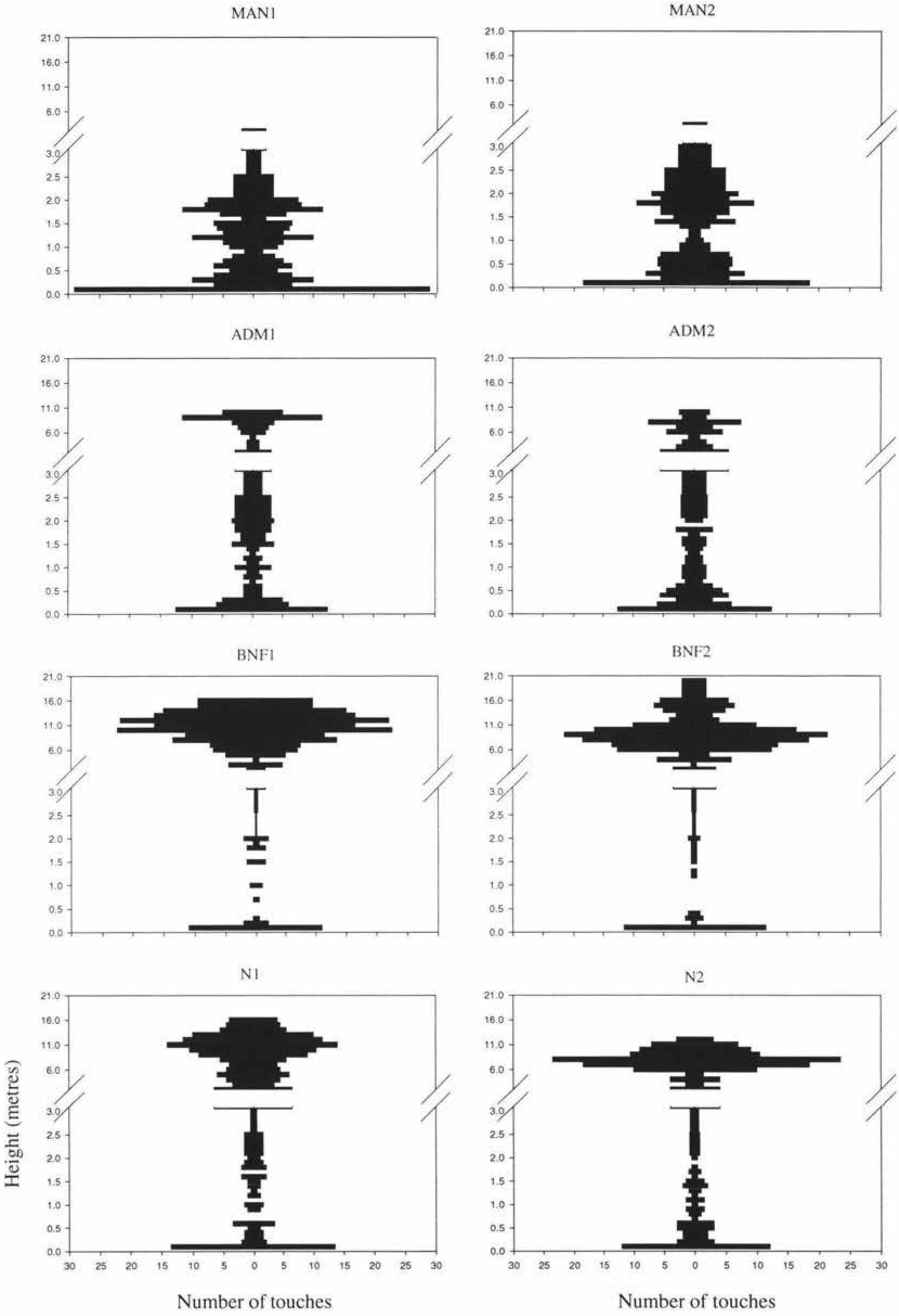


Figure 3.3: Vegetation height profiles of eight sites representing four habitat types along a successional gradient.

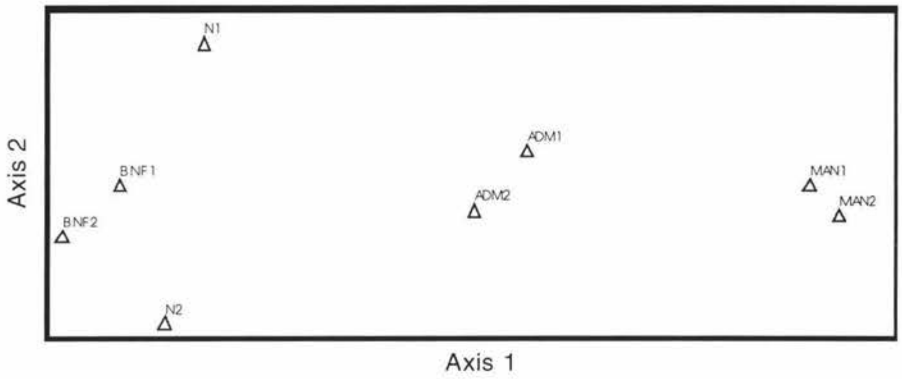
The browsed native forest sites were comprised of relatively closed canopies over a very sparse shrub and sapling layer and little vegetation ground cover. The density of vegetation between 0 and 50cm was low, and between 50cm and 3m a number of height intervals had no vegetation recorded within them. The greatest percentage of the vegetation was restricted to the canopy. The N sites had a greater amount of shrubs, saplings and ground vegetation present in the 0 – 3m band than the BNF sites.

The DCA ordination of plant species composition separated the MAN sites, ADM sites and four forest sites along Axis 1 (Fig 3.4a). Manuka abundance was positively correlated with this axis, whereas several of the forest species, including tawa, rewarewa and miro were negative correlates. There was no clear separation of the forest types along either axis.

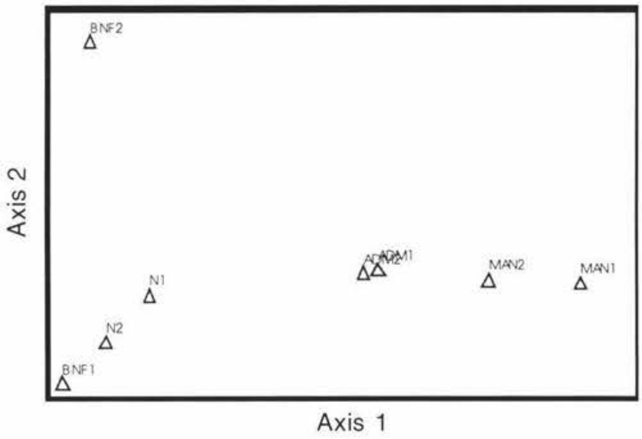
The ordination based on overall architectural composition produced comparable results to that of the plant species, with the three groups along Axis 1 remaining the same (Fig. 3.4b). Along Axis 2, BNF2 is separated from the other three forest sites due to the large abundance of miro leaves in the canopy providing a unique architectural variation. Architectural composition under three metres produces an ordination separating the two MAN sites from the other six along Axis 1 on a gradient of increasing small lanceolate/elliptic leaf density (Fig. 3.4c). On Axis 2, the ADM, N and BNF sites are separated on a gradient of decreasing tripinnate fern frond (*D. squarrosa* and *Cyathea* spp.) and large leaf (heketare, rangiora and hangehange) abundance.

Cluster analysis of the three plant community attributes produced similar groupings of sites to DCA ordination (Fig. 3.5). In all cases, the paired sites of both MAN and ADM cluster together, though the BNF and N sites only become distinct from each other based on plant architecture below three metres (Fig. 3.5c). In addition, the ADM sites group with the MAN sites for both plant species and total architecture (Fig. 3.5a &b) but in terms of plant architecture under three metres, the ADM sites are more similar to the forest sites (Fig. 3.5c).

(a) plant species



(b) plant architecture (all)



(c) plant architecture (<3m)

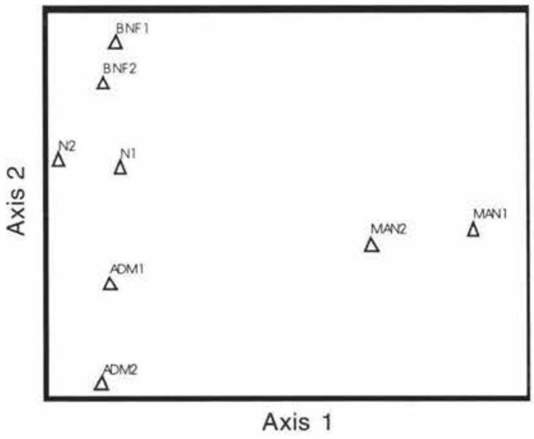
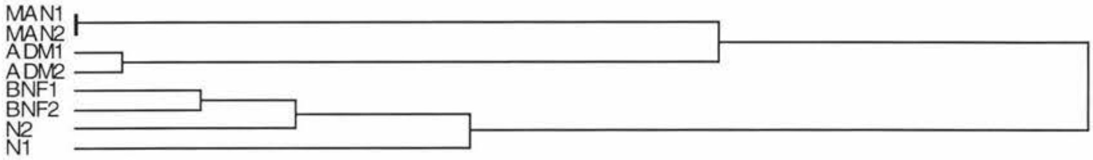
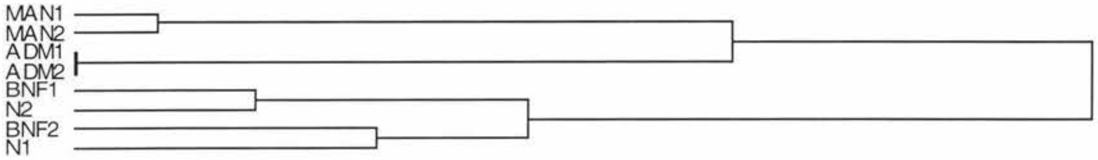


Fig. 3.4: DCA ordinations of eight study sites representing four habitat types along a successional gradient, based on (a) plant species; (b) total plant architecture; and (c) architectural composition within the 0-3m vegetation band.

(a) plant species



(b) plant architecture (all)



(c) plant architecture (<3m)

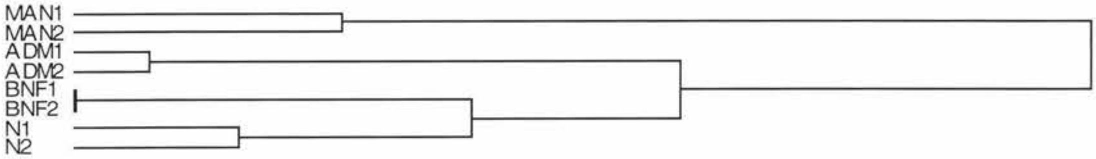


Fig. 3.5: Cluster dendograms of eight study sites representing four habitat types across a successional gradient as grouped by: (a) plant species composition; (b) total plant architectural composition; and (c) architectural composition within the 0-3m vegetation band.

3.3.2 Spider Communities

In total, 1003 spiders were caught over the sampling period, representing at least 46 species from 22 families. It is likely that this is an underestimate of the actual richness of the spiders collected, as 604 (60.2%) of the individuals were unable to be determined to a recognizable taxonomic level. Of these unidentified individuals, 47.5% were juveniles from the family Miturgidae, and 15.6% were juvenile Lycosidae.

There was no pattern of absolute abundance across habitat types (Fig. 3.6a). The total number of spiders caught for the three sampling techniques combined was relatively similar between all sites, except for higher abundance in ADM1 and N2. Handsearch sampling collected a very similar number of spiders across all sites, though this number was small, ranging between 15 and 25 individuals only. Pitfall sampling collected the most spiders at all sites.

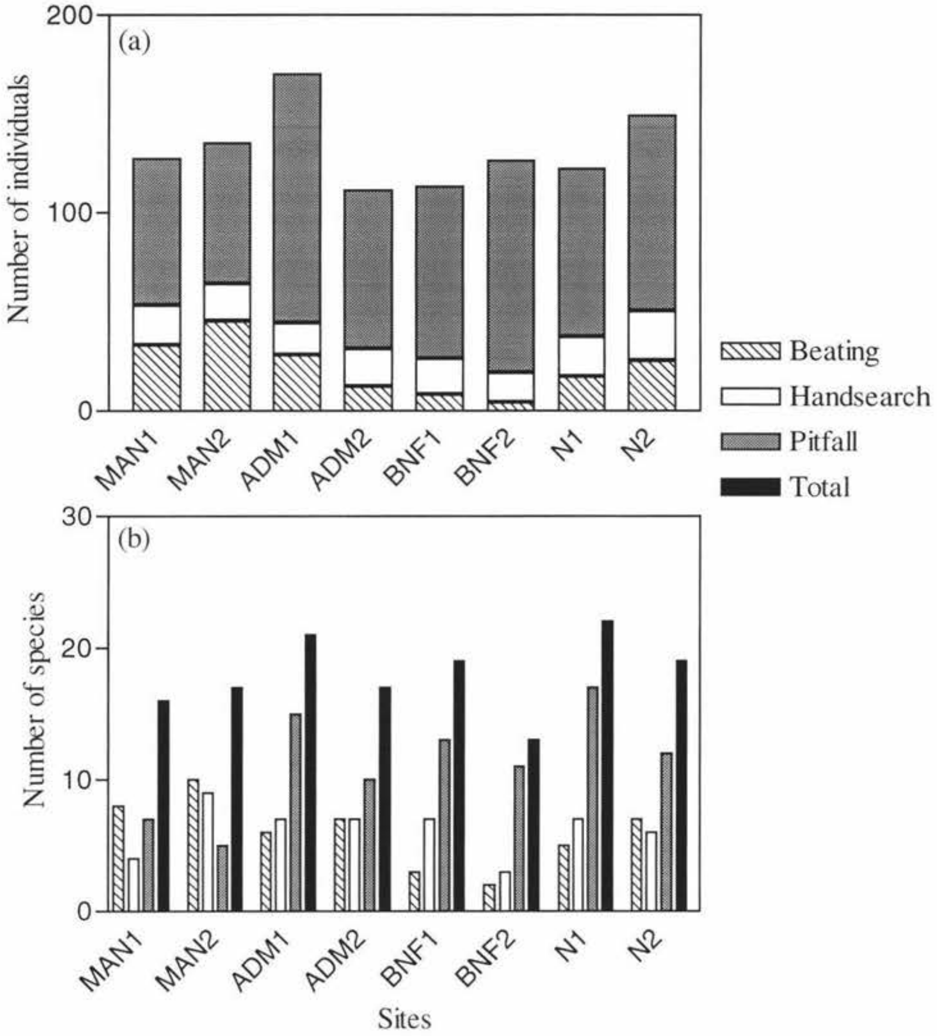


Fig. 3.6: (a) Spider abundance and (b) spider species richness by collection method from eight study sites representing four habitat types along a successional gradient.

The abundance of spiders collected using the beating method was positively correlated with plant density in the 0-3 metre height stratum ($r = 0.83$, $p < 0.05$), but the abundance of pitfall-trapped spiders had a negative association with plant density below three metres, though this was not significant ($r = -0.62$; $p > 0.10$).

The highest spider species richness was found at N1 and ADM1 and the lowest at BNF2 (Figure 3.6b); however, there were no clear trend in species richness between habitat types. Pitfall sampling collected the most species of all methods at the ADM, BNF and N sites, but not at the MAN sites, where beatings produced a greater number of species. Richness of the beating samples was positively correlated with plant density in the 0-3m

Table 3.3: Correlations between spider species richness and plant community parameters along a successional gradient. (- = not calculated).

Spider richness	Plant species (<3m)	Plant species (all)	Plant architecture (<3m)	Plant architecture (all)	Plant density (<3m)	Plant density (all)
Beating	0.35	-	0.18	-	0.84	-
Pitfall	0.14	0.65	0.34	0.48	-0.73	-0.16
Handsearch	0.24	-	-0.08	-	0.16	-
TOTAL	0.38	0.37	0.35	-0.09	-0.17	-0.27

tier ($r = 0.84$, $p < 0.01$; Table 3.3). Pitfall spider richness, in contrast, had a negative correlation with plant density ($r = -0.73$, $p < 0.05$). However, when all three sampling methods are combined, there is no relationship between spider richness and plant density ($r = -0.17$, $p > 0.5$). There were no significant relationships between spider richness and either plant architecture or plant species richness, though the richness of pitfall-trapped spiders was moderately associated with overall plant richness ($r = 0.65$, $p > 0.05$; Table 3.3).

Overall, 89.8% of the spiders identifiable to family level were from one of seven families – Miturgidae (37.2%), Lycosidae (19.2%), Theridiidae (9.7%), Amphinectidae (7.8%), Salticidae (7.3%), Thomisidae (4.6%) and Agelenidae (3.2%) – with 15 other families contributing only 11.2% of the individuals. Two sites, BNF1 and N1, each contained 14 families, with two sites, ADM2 and BNF2, having the lowest family richness with 10 each. There was variation in the relative abundances of the seven most common families between sites and habitat types (Fig. 3.7).

Amphinectidae, which was represented by only one species (*Paramamoea incerta*), increased in relative abundance along the successional gradient, being the least abundant in the MAN sites and reaching a peak at the BNF sites. There was a negative correlation between the abundance of Amphinectidae and plant density below 3 metres in height ($r = -0.88$, $p < 0.01$). In contrast, the family of sheet-web spiders, Theridiidae, was most abundant in MAN1 and MAN2, but least in BNF1 and BNF2 (Fig 3.7). There was a positive association between the absolute abundance of this family and plant density below 3 metres ($r = 0.91$, $p < 0.01$). No other family showed any significant positive relationship with plant density.

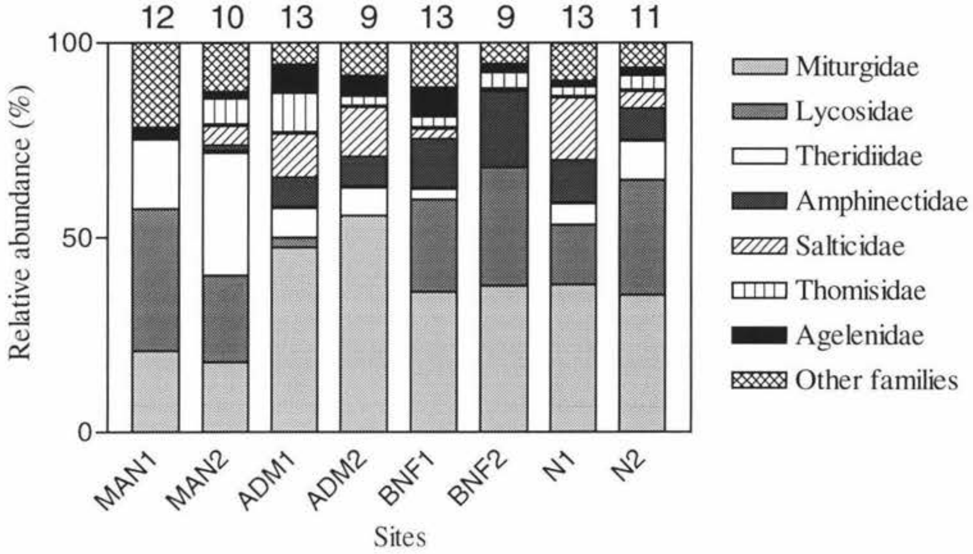


Fig. 3.7: Relative abundance of the seven most abundant spider families from eight study sites representing four habitat types across a successional gradient. The figure above each column is the number of families found at that site. Other families include: Anapidae, Araneidae, Clubionidae, Cycloctenidae, Gnaphosidae, Hahniidae, Huttonidae, Malkaridae, Mimetidae, Neolanidae, Nicodamidae, Orsolobidae, Stiphiidae, Tetraganthidae and Zodariidae.

Miturgidae had a consistent representation within the four forest sites, ranging between 35 and 38% (Fig. 3.7). Relative abundance was lowest at the MAN sites but peaked in the ADM sites, providing upwards of 55% of the individuals identified. This maximum coincided with the heavy reduction in the abundance of Lycosidae, which ranged from 15-37% at the other sites, but was represented by only four juvenile individuals in ADM1 and absent entirely from ADM2. The distribution of the two unnamed lycosid species collected indicates some degree of habitat specificity: one was found only in the four forest sites, the other only at the two young manuka sites (Table 3.4).

Four species were found within at least one site of each habitat type, with three (*Aorangia* sp., Malkaridae sp. and *Paramamoea incerta*) generally forest-floor species (Table 3.4). Another forest-floor species, the miturgid *Ulidon* sp. was abundant in the ADM, BNF and N sites, but absent from the MAN sites. Young manuka had the most number of species missing that were present within all other habitat types (five), but also had the most number of species found nowhere else (nine), with four of these found at both MAN1 and MAN2. Most of the species restricted to one habitat type or site were found only in low taxa

Table 3.4: Distribution of spider species across eight sites representing four habitat types along a successional gradient.

	MAN1	MAN2	ADM1	ADM2	BNF1	BNF2	N1	N2	TOTAL
Aorangia sp.	2	1	11	5	7	2	1	2	31
Stiphidiidae sp.	6	1	1	3	-	1	2	-	14
Malkaridae sp.	6	-	1	1	1	-	3	2	14
Paramamoea incerta	-	1	11	8	12	21	11	10	74
Dipoena sp.	-	3	-	2	-	-	-	8	13
Hypodrassodes maoricus	6	-	-	-	1	-	1	-	8
Megadictyna thilenii	-	-	2	-	2	2	1	1	8
Sidymella angularis	-	-	4	1	2	1	1	2	11
Sidymella sp.	-	-	1	-	-	2	-	1	4
Trite auricoma	-	-	4	4	1	-	5	-	14
Ulidon sp1.	-	-	10	6	5	11	10	3	45
Theridiidae sp.	1	4	3	1	-	-	-	-	9
Amphinecta sp.	-	-	1	-	-	1	-	-	2
Clubiona pecularis	-	-	1	2	1	-	-	-	4
Cycloctenus centralis	-	-	3	-	-	-	-	1	4
Phoroncidia sp.	-	-	1	-	-	-	-	1	2
Eriphora pustulosa	-	-	-	-	1	1	-	1	3
Lycosidae sp1.	-	-	-	-	16	6	4	26	52
Lycosidae sp2.	15	11	-	-	-	-	-	-	26
Episinus conifera	10	10	-	-	-	-	-	-	20
Nanometa sp.	2	2	-	-	-	-	-	-	4
Euryopsis sp1.	1	1	-	-	-	-	-	-	2
Zodariidae sp.	-	-	-	-	1	1	-	-	2
Euryopsis sp2.	-	-	-	-	-	-	1	1	2
Salticidae sp3.	-	-	-	-	-	-	1	1	2
Novakiella trituberculosa	2	-	-	-	-	-	-	-	2
Mimetus sp.	1	-	-	-	-	-	-	-	1
Colaraneae viriditas	1	-	-	-	-	-	-	-	1
Diaea sp.	-	4	-	-	-	-	-	-	4
Cyclosa trilobata	-	2	-	-	-	-	-	-	2
Artoria sp.	-	-	2	-	-	-	-	-	2
Argyrodes sp.	-	-	1	-	-	-	-	-	1
Hahniidae sp.	-	-	1	-	-	-	-	-	1
Salticidae sp4.	-	-	1	-	-	-	-	-	1
Ulidon sp3.	-	-	-	1	-	-	-	-	1
Cambridgea sp.	-	-	-	2	-	-	-	-	2
Cycloctenus sp.	-	-	-	1	-	-	-	-	1
Salticidae sp1.	-	-	-	1	-	-	-	-	1
Episinus sp.	-	-	-	-	2	-	-	-	2
Arcaearanea sp.	-	-	-	-	1	-	-	-	1
Neolama dalmasi	-	-	-	-	1	-	-	-	1
Salticidae sp2.	-	-	-	-	1	-	-	-	1
Duripelta borealis	-	-	-	-	-	-	1	-	1
Huttonia sp.	-	-	-	-	-	-	1	-	1
Theridion zantholabio	-	-	-	-	-	-	1	-	1
Novanapis spinipes	-	-	-	-	-	-	-	1	1

numbers; the 28 such species contributing only 19.5% of the total number of identified individuals.

The spider community tended to have a narrower range of dissimilarity scores than the plant community when comparing between habitat types (Table 3.5). This was particularly marked when comparing the BNF and N sites, where the range for plants was 0.39 to 0.62, but for the spiders it was only 0.39 to 0.45. The young manuka sites were the most dissimilar from other sites for both plants (range 0.62-1.00) and spiders (0.73-0.91). The dissimilarity scores of the plant community confirm the intermediate position in the gradient of the ADM sites, having a medium overlap with both the MAN (0.62-0.73) and the two N sites (0.56-0.72). The lack of shrubs and saplings in the BNF sites resulted in high dissimilarity scores with the ADM sites (0.77-1.0). The spider community in advanced manuka tended to be more similar to the forest sites (0.44-0.58) than the young manuka sites (0.73-0.83). The taxonomic overlap for spiders of the four forest sites was consistent (0.39-0.45).

The similarity between sites tends to decrease the further apart on the successional gradient they are, for both plants and spiders. Dissimilarity measures for the spider community were positively correlated with those of the plant community (Fig. 3.8).

Table 3.5: Bray-Curtis dissimilarity scores for eight study sites representing four habitat types across a successional gradient. The values above the diagonal are for the plant communities, the values below for the spider communities. Figures in bold are comparisons between sites of the same habitat type.

	MAN1	*MAN2*	*ADM1*	*ADM2*	*BNF1*	*BNF2*	*N1*	*N2*
MAN1		**0.25**	0.62	0.69	0.94	1.00	0.95	0.95
MAN2	**0.52**		0.67	0.73	0.94	1.00	0.90	0.91
ADM1	0.83	0.80		**0.34**	0.81	1.00	0.71	0.72
ADM2	0.75	0.73	**0.43**		0.77	0.89	0.72	0.56
BNF1	0.85	0.91	0.44	0.50		**0.41**	0.39	0.40
BNF2	0.87	0.84	0.43	0.57	**0.35**		0.62	0.48
N1	0.76	0.86	0.45	0.49	0.45	0.39		**0.48**
N2	0.86	0.81	0.53	0.58	0.39	0.44	**0.44**	

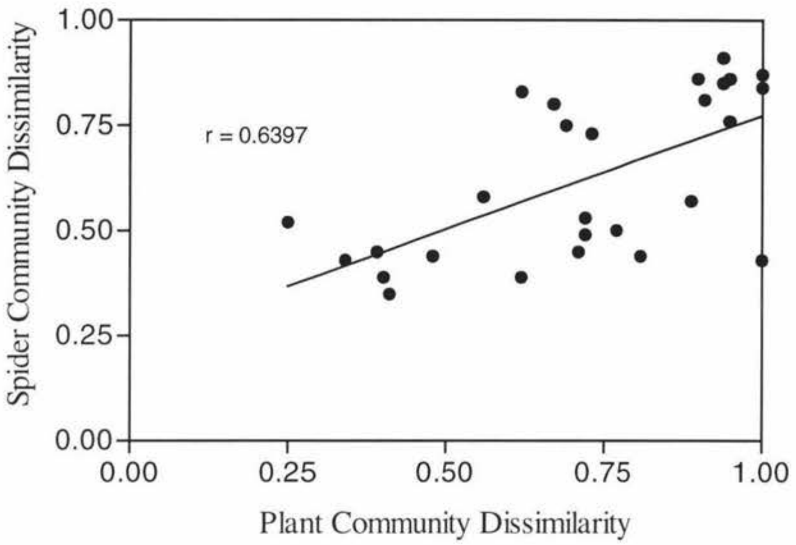
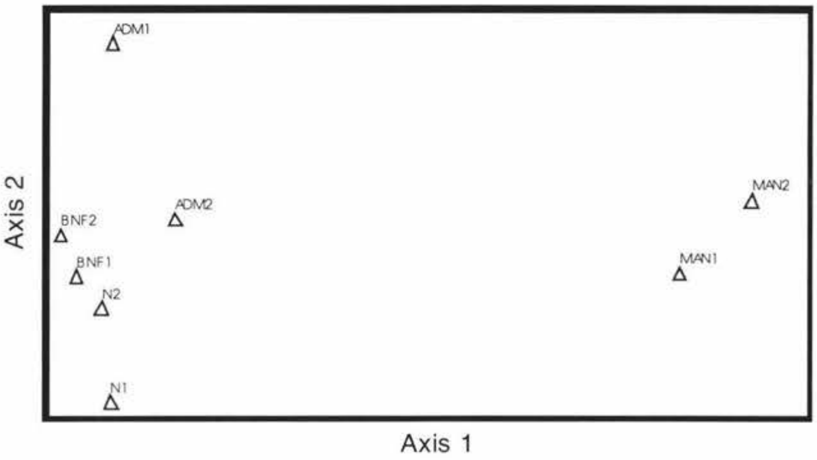


Figure 3.8: Correlation of Bray-Curtis dissimilarity scores between the plant and spider communities of eight sites, representing four habitat types across a successional gradient.

DCA analysis of the spider communities based on species composition (Fig. 3.9a) separated the two MAN sites from the others along Axis 1. The ADM sites were not clearly defined from the forest sites along this axis as for the ordination using plant attributes (Fig. 3.4a & b). Taxa positively correlated with Axis 1 included *Episinus conifera* and Lycosidae sp2, while those negatively correlated included *Megadictyna thilenii*, Uliodon sp1, Lycosidae sp1 and *Paramamoea incerta*. The ADM, BNF and N sites tend to separate from each other along Axis 2, with N1 and N2 near the base and BNF1 and BNF2 near the center. Both *Paramamoea incerta* and Theridiidae sp. were positively associated with this axis.

Using the relative abundance of spider families (Fig. 3.9b), sites were divided into three main groups, one containing the MAN sites; one containing the ADM sites and N1; and the other containing the BNF sites and N2. This result is similar to that obtained by the plant species ordination (Fig. 3.4a) in terms of the site groups obtained. The only point of difference for the site groupings is with N1 joining with the ADM sites in the spider family analysis rather than with the other forest sites. The families Tetragnathidae, Lycosidae, Theridiidae and Araneidae were all positively associated with axis 1, with Miturgidae negatively associated. For axis 2, Nicodamidae was a positive, and Salticidae and Stiphidiidae negative, associates.

(a) spider species



(b) spider families

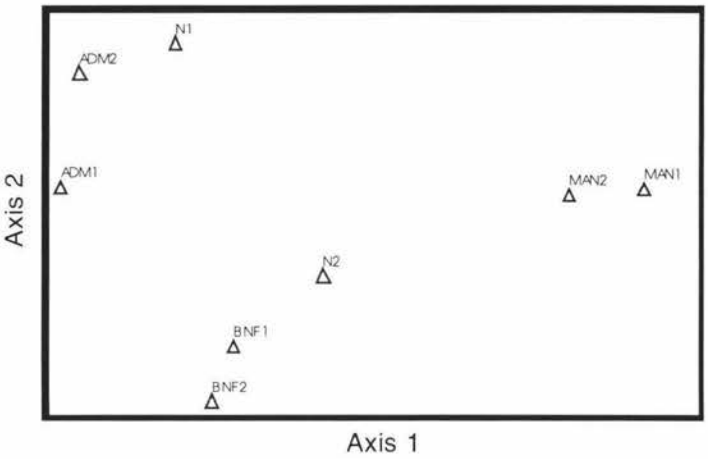
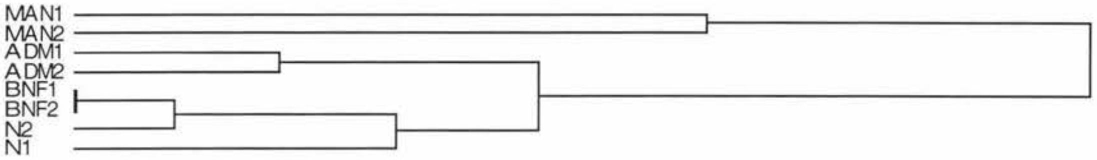


Fig. 3.9: DCA ordination of eight study sites representing four habitat types across a successional gradient, using (a) log(x+1) abundance of spider species and (b) relative abundance of spider families.

Cluster analyses of the spider community demonstrated a clear similarity between habitat classification using plants and those using spiders. The cluster dendogram based on spider species composition (Fig. 3.10a) is comparable to that created using plant species composition (Fig. 3.5a). The MAN sites are paired together, as are the ADM sites, and the four forest sites form a nested arrangement with the BNF sites paired together. The main difference between the two cluster diagrams is that the ADM sites group with the forest sites rather than the MAN sites. Family relative abundance (Fig. 3.10b) gives the same result as for species composition in terms of group divisions and internal branch structure.

(a) spider species



(b) spider families

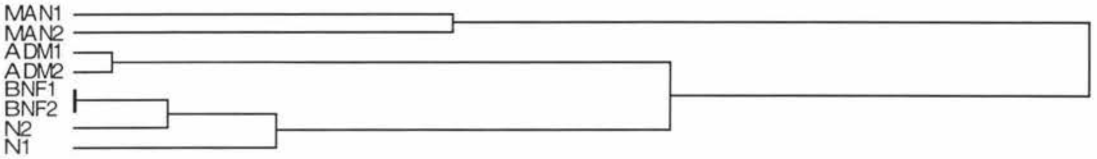


Fig 3.10: Cluster dendograms of the eight study sites representing four habitat types across a successional gradient as grouped by: (a) log(x+1) abundance of spider species, and (b) relative abundance of spider families.

3.4 DISCUSSION

3.4.1 Richness and Abundance of Foliage Spiders

The abundance and richness of those spiders collected using the beating method was greatest at the young manuka stage and lowest at the browsed native forest sites. Under this collection strategy, the sites with high plant density below 3 metres had a greater amount of vegetation shaken, increasing the actual plant area sampled even though the plot size remained constant from site to site. Following general individual-area theory (Connor *et al* 2000), there should be a greater total number of spiders collected from vegetation-dense plots. Plant density below 3 metres, which was maximal at the two MAN sites and minimal at the BNF sites, was the only significant correlate with foliage spider abundance. Previous studies have demonstrated a positive correlation between foliage density and absolute spider abundance on a range of spatial scales. Gunnarsson (1990) and Halaj *et al* (2000b) found this pattern on individually manipulated branches of Norwegian spruce and Douglas-fir respectively, Hatley and MacMahon (1980) within whole sage shrubs and Rypstra (1986) within temperate, subtropical and tropical forest communities. On occasions, other limiting factors can reduce the importance of available habitat space to spider communities. The influence of bird predation on spruce-dwelling spider communities has been shown to obscure the effects of needle density (Gunnarsson

1996). The correlation between foliage density and spider abundance in the present study suggests that there is no other limiting factor, such as severe predation or extreme macroclimate, keeping spider populations below the level at which available habitat space is important.

The greater proportion of unexplored habitat (i.e. vegetation over 3m) within the advanced manuka and forest sites, suggests that there were more individuals left to be found at these sites. No conclusion can therefore be made on canopy spider abundance across the gradient, except that it is likely to be a function of vegetation density/biomass.

Foliage spider richness was also correlated with plant density (Table 3.3). Species richness is expected to increase with sampling area due to the greater the number of individuals collected and the greater variety of microhabitats expected to be included in the sample. However, neither foliage spider richness nor plant density was correlated with plant species or architectural richness, despite architecture having a proven influence on foliage spider communities in experimental manipulations (Hatley and MacMahon 1980, Robinson 1981). The lack of correlation here suggests that either vegetation structure effects operate on a scale different to that measured, or that there are factors other than structural diversity affecting foliage spider richness. Manuka habitat has been shown to contain a high abundance and diversity of invertebrates (Munro 1995), potentially providing a greater variety of prey and therefore enabling the coexistence of a number of spider species. Additionally, plant-dense sites may provide a greater variety of microclimates, something that is known to strongly influence the site selection of web spiders (Turnbull 1973, Uetz 1991).

The vertical stratification of vegetation, characteristic of increased successional age (Brown 1991), should increase the number of microhabitats available for use by web spiders (Greenstone 1984). Yet in this successional system, the native forest sites do not provide an increased abundance or diversity of microhabitats for foliage spiders below 3 metres. Browsing by introduced ungulates has been shown to reduce the density of understorey vegetation (Allen *et al* 1984), so the presence of goats in the study area may be indirectly reducing spider diversity in the undergrowth. Gibson *et al* (1999a, b) have shown that sheep grazing decreases diversity and abundance of the spider fauna in a grassland.

It would be expected that there would be more undiscovered species in the forest sites than in the young manuka sites, based on the proportion of unexplored habitat. Seventy spider morphospecies were caught in flight intercept traps in the canopies of eighteen trees representing three species (rata, tawa and totara) from three lowland forest reserves in the Manawatu-Wanganui region (McWilliam and Death 1998). This suggests the presence of a number of unsampled species from the canopy within the BNF and N sites, with the potential to thus make overall foliage spider diversity increase with increasing successional age in this system, as predicted by successional theory (Odum 1969).

3.4.2 Abundance and Richness of Cursorial Spiders

Abundance of ground-active spiders (i.e. those from pitfall traps) in this survey showed no change across the successional gradient from young manuka/kanuka stands to broadleaf/podocarp forest. This is in contrast to other studies that have demonstrated a decrease in cursorial spider abundance from younger to older woody plant assemblages (Hurd and Fagan 1992, Munro 1995). Species richness, on the other hand, was lower at the youngest successional stage (MAN) than at any of the other three habitat types. Cursorial spider species richness can increase with increasing successional age (Bultman *et al* 1982, Mrzljak and Wiegleb 2000), but not in all studies. A large reduction in species diversity of up to 50% has been observed between young herbaceous communities and older, woody stages further along the succession pathway (Hurd and Fagan 1992). These authors proposed that lower numbers of ground dwelling prey in older communities, due to the shift of most primary production to the canopy, reduces ground spider species richness. The results of Munro (1995), one of the few studies of ground-dwelling terrestrial invertebrates across a successional gradient in New Zealand, supports this theory; abundance of total invertebrates and species richness of the predator guild were significantly lower in native forest sites compared to manuka and pasture. However, the structure and composition of the manuka site in her study was equivalent to the ADM sites sampled here, rather than the young, dense shrub vegetation of the MAN sites. A three-metre high gorse stand in Munro's (1995) study was found to contain less predator species than the manuka or forest sites. Although gorse is an introduced species and has different leaf architecture to manuka, the overall habitat type (monotypic dense shrub layer, sparse ground cover of ferns, dry soil and litter) is similar to that of the MAN sites. Therefore it is possible that the microclimatic conditions characteristic of this stage in the successional series reduces the diversity of both arthropod predators as a whole, and spiders in particular.

There was no readily apparent relationship between cursorial spider richness and the plant attributes measured. While there was a moderately negative relationship between plant density and spider species richness, pitfall-trapped spiders were not significantly influenced by the taxonomic or architectural diversity of the plant community (Table 3.3). This is not surprising given that ground-hunting spiders do not require the presence of particular types of vegetation support for web construction. The abundance and diversity of cursorial spiders can be influenced by a number of other components of habitat structure, including litter depth and complexity, and the occurrence of logs or crevices, for retreats, predator avoidance and egg-laying (Chapter 2). Uetz (1991) found spider abundance and diversity to be lowest in shallow, structurally simple litter. The MAN sites were characterized by having a thin litter layer consisting of mostly one leaf type, another potential explanation as to why this habitat type was relatively species-poor compared to the others. Despite the dissimilarity in the kind of litter between advanced manuka sites (very thick layers of dead fern fronds) and forest sites (moderately deep (1-5cm) litter consisting of leaves from canopy trees), there were no significant overall abundance or richness differences in the spider communities. Differences in species and family composition between ADM and forest sites are apparent (see below), suggesting that these litter types may favour divergent species assemblages without necessarily differing in overall diversity or abundance.

Diversity of habitat refuges may contribute to the differences in species richness between sites. In general, the forest sites contained more woody debris than either the MAN or ADM sites (as Munro 1995 found); and the forest and ADM sites both contained more vegetation overhangs and crevices than young manuka sites. Quantification of this habitat data is needed to determine its significance to the diversity of the cursorial spider fauna along the successional series.

3.4.3 Spider Family and Species Composition

Despite the lack of diversity or abundance gradients, some compositional elements of the spider community did vary with habitat type. The relative abundance of Theridiidae was greatest where the plant density (below 3m) was highest, meaning that the importance of this family is much greater within the young manuka stand than any other habitat type. In fact, it is the theridiid response to plant density that accounts for the positive response of the whole foliage spider community, as no other family exhibited any correlation with the amount of vegetation present at a site. Salticidae, for example, had the lowest relative abundance within the MAN and BNF habitat types (Fig. 3.7), which are at opposite ends of the plant density spectrum. This family is known for a stalk and run foraging behaviour based on good eyesight over medium-to-long distances (Forster and Forster 1999), and it is therefore possible that dense foliage, such as that offered by manuka, does not suit this strategy of prey capture (Hatley and MacMahon 1980); whereas at the BNF sites it may be simply the lack of foraging sites, rather than the poor-quality of those sites, that contributes to low salticid density.

Paramamoea incerta, the only representative of the family Amphinectidae, was proportionally more abundant during the later stages of succession, peaking at the browsed native forest sites. This suggests a preference for deep, complex litter and relatively open ground. Very little is known about this family, with most of the species thought to be nocturnal hunters (Forster and Wilton 1973). Other known nocturnal hunting families, Gnaphosidae and Clubionidae, were only caught in low numbers.

Lycosidae (wolf spiders) are known to prefer to forage in open areas of shallow, relatively compressed litter (Uetz 1977, 1991). In the present study, there was little difference in the relative abundance of this family between the sparse litter of the MAN habitat type and the deeper, more complex litter of the forest sites (BNF and N). There was, however, a large decrease in the abundance of lycosids within the ADM sites, suggesting that the very thick cover of dead fern fronds does not offer a suitable habitat for this family.

Despite the Lycosidae contributing a consistent proportion of the individuals at all sites except ADM1 and ADM2, the two species in this family showed no overlap in their distribution along the successional gradient (Table 3.4). Though the difficulty in identifying juvenile spiders means that this observation cannot be conclusive, such habitat specificity is not without precedent in wolf spiders (e.g. Hurd and Fagan 1992)

Forty-six percent of the spider species identified were found at only one site, and 61% were found within only one habitat type (Table 3.4). In comparison, 68% of species collected by Hurd and Fagan (1992) were found at only one of the four habitat types surveyed, and in a survey of a French agricultural landscape, 40% of species were found in only one of the three habitats sampled, grassland, scrubland and woodland (Burel and

Baudry 1995). Such figures would suggest that there is a large degree of habitat specificity in spider species; however, as with the other studies, most of the species restricted to one habitat type here were rare. The only habitat-restricted species to have more than 5 adult specimens collected were Lycosidae sp2 and the theridiid *Episinus conifera*. It is difficult to make conclusions about the habitat preferences of rare species, as they may have been missing from a collection merely because their low-density populations were overlooked in the sampling process. Unfortunately, this is an unavoidable consequence of random sampling of communities that consist of a few common species and a large number of rare ones (e.g. Dobyns 1997, Harris and Burns 2000). Given this possible source of bias, only three species can be confidently attributed as a habitat specialists in this system, *Episinus conifera* (MAN), Lycosidae sp2 (MAN), Lycosidae sp1 (forest), though both *Ulidon* sp. and *Paramamoea incerta* show a marked preference for ADM and forest sites. Evidence of spider species with strong habitat preferences is common in other studies (e.g. Maelfait *et al* 1990, Bell *et al* 1999).

3.4.4 Community Classification

Spider community dissimilarity was significantly correlated with plant community dissimilarity (Table 3.5, Fig. 3.8), suggesting at least some congruence between the spider and plant communities, or rather, the spider community and habitat type. Congruence between spider and plant communities as measured by cluster analysis, and to a lesser extent by ordination, was relatively high; consistent inter-site relationships are observed from both sets of data. Harris and Burns (2000) compared the classification of 10 plots by both vegetation and beetle species composition using 'two-way indicator species analysis' (TWINSPAN) and found that the resulting dendograms were very similar. The results achieved in the present study are interesting, given the debate that continues on the utility of basing conservation decisions on plant community attributes, assuming that this acts as a suitable surrogate for the invertebrate fauna (see Chapter 4 for further discussion).

The spider community exhibited an ability to classify the sites according to the predetermined habitat type. Habitat classification by terrestrial invertebrates in New Zealand has been chiefly restricted to the use of Coleoptera, with a number of examples of beetle community composition discriminating between broad habitat types (Hutcheson 1990, Crisp *et al* 1998, Harris and Burns 2000). There may be a limit to the scale at which beetles are useful in habitat classification; Hutcheson and Kimberley (1999) found distinct differences between heathland, wetland, shrubland and forest sites, but the beetle community was unable to discriminate between two types of shrubland characterized by different dominant plant species. Each of the successional stages investigated here (young manuka, advanced manuka and native forest) appear to have a characteristic spider fauna. There have been no comparable studies involving New Zealand spider communities other than that by Topping and Lovei (1997) who compared the spider faunas of pasture and native tussock and found considerable differences in species composition. The results presented here provide initial evidence that spiders meet one of the criteria offered by Hutcheson *et al* (1999) for a biodiversity indicator species, that of having communities characteristic of distinct vegetation assemblages. Any group that demonstrates this ability can potentially play a role in, among other things, evaluation of restoration success, where the arrival of species characteristic of the native community being reestablished can be monitored. The good dispersal abilities of spiders (Marc *et al* 1999) would make them especially useful in this capacity. The spider communities also demonstrated an ability to distinguish between the BNF and N sites (Fig. 3.10), which indicates potential for fine-scale ecological monitoring of disturbance, though this requires further testing under experimental conditions.

It is interesting to note the performance of family relative abundance in classifying the sites into their habitat type. It is generally assumed that the use of higher taxonomic levels will reduce the information present in a data set, and thus the resolution of site classification (Hutcheson 1990). Families, though, are commonly used as the basic units of measurement in many spider studies, mainly because of the time-consuming and difficult nature of identifying to species (e.g. Mason 1992). Here, however, there was no loss of resolution in the use of family data; it produced a very similar cluster dendogram to that based on log-transformed species data. This could be because the differences between the habitat types (in particular between MAN, ADM and the forest sites) were large enough to measurably affect general foraging strategies or web-type, rather than acting solely on the more narrow niches occupied by individual species. It is possible that analysis of guild structure may be as useful as either family or species composition, though a lack of basic ecological information on spider species can restrict such an application. Still, family composition shows promise as a surrogate for species composition, at least until taxonomic expertise is widely available for confident species identification.

3.4.5 Conclusion

The congruence between spiders and plants is probably the result of both indirect and direct causal factors. A particular species of plant will provide a unique structural arrangement of web attachment points or foraging locales that will differentially favor some spider species over others. In addition, the presence of certain plant species may also modify important aspects of the spider's environment, such as microclimate (shade, temperature, wind stress etc.) and prey composition or availability. One of the main theories on the mechanics of succession is that plant species modify their environment to facilitate the invasion of other species characteristic of the next successional stage (Odum 1969). Logically, this facilitation effect could also extend to the invertebrate communities found there. Experimental manipulations are required to determine the relative importance of these habitat components to the spider community as a whole, and to certain groups that are poorly understood (e.g. Amphinectidae). Spiders have been investigated internationally as potential indicators of a community's response to finer-scale changes in vegetation structure than those investigated here (see Chapter 2). This study demonstrates that New Zealand spider communities do have potential for use in medium to broad scale habitat classification, and that they warrant further investigation of their usefulness at finer scales.

CHAPTER FOUR

Spiders as Indicators of Ground Invertebrate α- and β-Diversity in Forest Remnants

4.1 INTRODUCTION

Human-induced habitat modification has fragmented many native communities in all countries around the globe, leading to a select number of natural areas distributed through a highly modified landscape. In ideal circumstances, protection would be afforded to all of these remnant areas. However, limited capital and labour resources, and increasing anthropogenic land-use pressures, mean that only a subset of these sites can be preserved and maintained. Therefore, in order to maximise conservation potential, criteria need to be established in order to prioritise sites and ensure that the 'best' ones are selected first. Physical attributes such as size, shape and isolation have been proposed as criteria for site selection, based on island biogeographic and species-area theory (Diamond 1975, Usher 1991), though often the most suitable sites based on theory are not necessarily the most practical (Ogle 1989). Recently, actual measurement of species diversity has begun to take precedence over simple size-and-shape considerations. Identification and utility of hotspots (those areas with highest within-site diversity, or α-diversity), complementarity (a set of sites that maximise total landscape or β-diversity) and the systematic and phylogenetic affinities of the species contained within and between areas have all generated a great deal of literature (Vane-Wright *et al* 1991, Prendergast *et al* 1993, Faith and Walker 1996, Howard *et al* 1998, Pearson and Carroll 1998, Virolainen *et al* 2000).

The best-informed conservation decisions will be made where full and accurate species lists are available for each area under consideration. However, such detailed information is not always possible, due to poor taxonomy and prohibitive costs (Disney 1986). A possible solution is the use of biodiversity indicators to predict either the α-diversity (within-site richness) or the β-diversity (between-site complementarity) of other taxa. There is conflicting evidence as to whether congruence in the diversity patterns between taxa amounts to anything more than isolated occurrences (Gaston 1996), but there have been enough instances to suggest that biodiversity indicators can be of potential use in reserve selection (Howard *et al* 1998, Pearson and Carroll 1998, Virolainen *et al* 2000). If such congruence exists, surrogate species or indicator groups can provide a suitable means to maximise overall diversity while minimising the land area required for protection (Reyers *et al* 2000).

Vegetation has long been used as a surrogate for biodiversity in conservation planning in many parts of the world, with sites perceived and prioritised according to the resident plant community (Noss 1987, Hutcheson *et al* 1999). However, there is some concern that vegetation communities do not accurately represent the resident faunal community, particularly in the case of terrestrial invertebrates and some authors have suggested that these be included in conservation surveys (Rykken *et al* 1997, Oliver *et al* 1998, Hutcheson *et al* 1999). In New Zealand, the Protected Natural Areas (PNA) programme is the primary system for reserve evaluation, with site selection based mainly on a combination of physical features, including size, shape and buffering, and attributes of the plant community, including diversity, representativeness and naturalness (Kelly and Park 1986). Paralleling the global situation, taxonomic, ecological and biogeographic information on native New Zealand invertebrates is sparse (Hutcheson *et al* 1999), and there has been little attempt to investigate whether the vegetation-based PNA programme is conserving a satisfactory percentage of these species. Logistics have also prevented greater use of invertebrates in conservation planning. Lawton *et al* (1998) report how the sampling, sorting and identification of invertebrates can take 3-120 times longer than vertebrates (but see Oliver *et al* 1998). Of all taxa, therefore, invertebrates may benefit the most from the discovery of a suitable biodiversity indicator. As a group, spiders suggest themselves as ideal subjects for investigation as biodiversity indicators. They are abundant, widespread and diverse, easily sampled and amenable to rapid biodiversity assessment techniques such as sorting to morphospecies (Chapter 2), characteristics of good biodiversity indicators (McGeoch 1998).

The aim of this study is to provide a survey of the ground-active invertebrate community in New Zealand lowland forest patches and to test for congruence between spider α- and β-diversity with that of other invertebrate groups. If so, it would suggest spiders as potential biodiversity indicators for the invertebrate community as a whole. Additionally, the degree to which plant and invertebrate diversity are correlated within these sites will be investigated to establish whether selecting areas based on β-diversity, or complementarity, of the plant community will maximise the β-diversity of the invertebrate community.

4.2. METHODS

4.2.1 Study Sites

The Rangitikei Ecological Region, defined for the purposes of the PNA programme, is approximately 388,200 hectares in size, consisting of rolling hill country, cliffs, gorges and river terraces. Extensive clearance since the 1870's of the once continuous mixed broadleaf-podocarp forest has left a series of forest remnants with a combined area of 20,000 hectares scattered around the region (Lake and Whaley 1995).

Fourteen forest sites were selected from around the central part of the Rangitikei Ecological region (Fig. 4.1) after a preliminary walk-through of several potential sites to establish approximate plant richness and composition attributes. The sites selected ranged in size from 5 to 80 hectares and in altitude from 60 to 540 metres (Table 4.1), and were chosen to represent a range of forest types within the region. Most of the fourteen sites are currently under the protection of either the Department of Conservation or The Royal Forest and Bird Protection Society of New Zealand. The exceptions are Bird Grove Bush and North End Base Bush, which are located on private land. All sites are within 50 kilometres of each other, with the closest two sites being Bird Grove Bush and Sutherland's Scenic Reserve, 1.5 km apart (Fig. 4.1).

Table 4.1: Location, size, altitude and plant species richness of the fourteen study sites.

	Grid Reference NZMS 260	Size	Altitude	Plot Topography[a]
Apiti Scenic Reserve	T22 590367	32ha	540m	F
Bird Grove Bush	S22 111423	10ha	180m	F, M, S
Bruce Park Scenic Reserve	S22 262352	14ha	240m	M
C. L. Pemberton Memorial Reserve	T22 594436	5ha	480m	F, M, S
Mangaweka Scenic Reserve	T22 480513	32ha	380m	M, S
Maungakaretu Scenic Reserve	S22 229505	29ha	280m	F, M, S
McPherson's Bush	S22 094379	10ha	60m	F, M
North End Base Bush	T22 585567	25ha	380m	F
Pukeroa Scenic Reserve	S22 229528	8ha	180m	F
Rahui Bush Reserve	T22 318324	20ha	140m	F
Simpsons Scenic Reserve	T22 321418	36ha	300m	F, M
Sutherland's Bush	S22 123417	60ha	80m	F
Taihape Scenic Reserve	T21 509669	80ha	400m	F
Vinegar Hill Reserve	T22 356377	20ha	180m	F

[a] F = flat ground, M = medium slope, S = steep slope. See text for details.

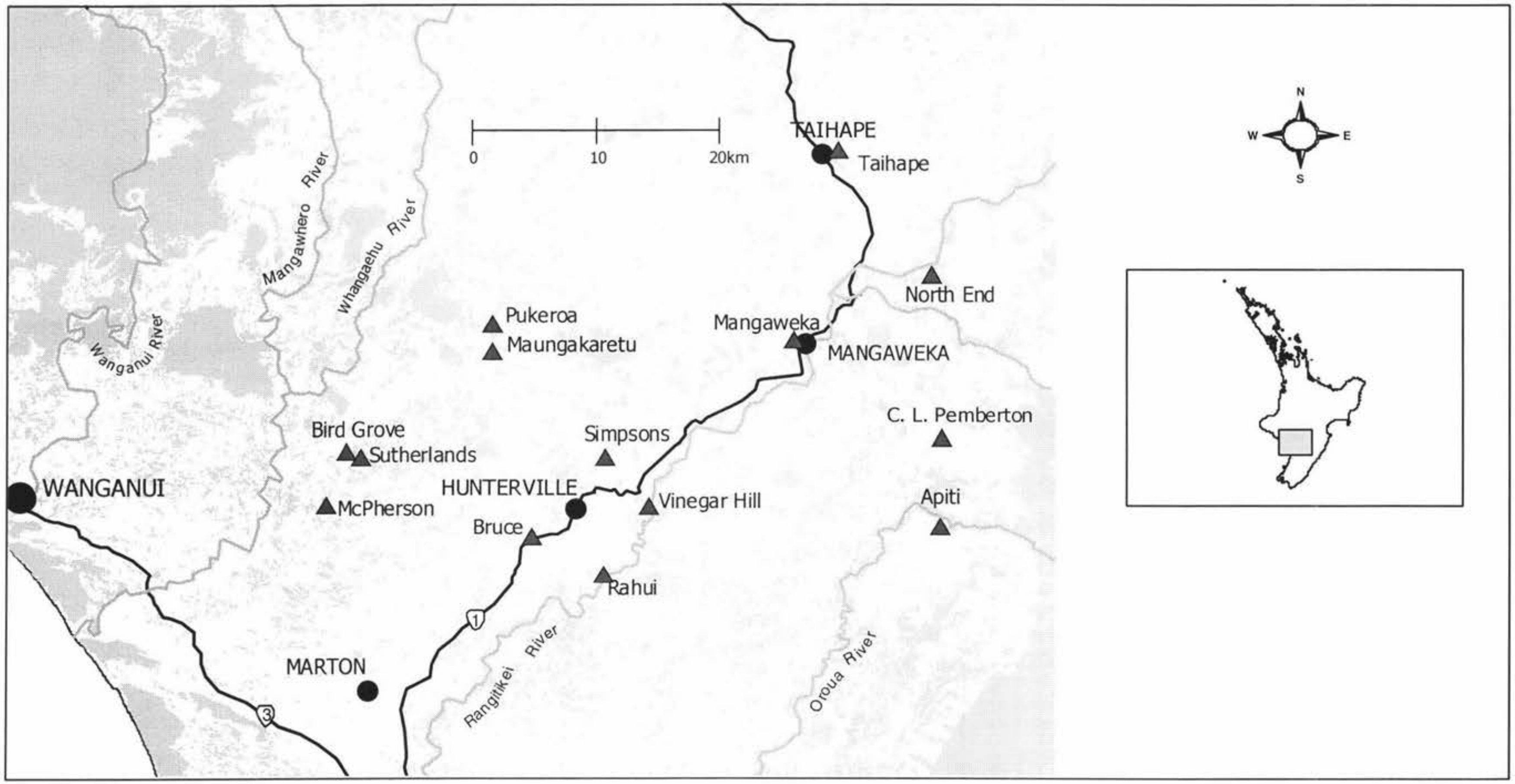


Fig. 4.1: Location of the fourteen study sites within the Rangitikei Ecological Region, New Zealand

4.2.2 Invertebrate Sampling

Invertebrate sampling took place continuously from November 1999 to March 2000 inclusive, using pitfall traps. The disadvantages of using pitfalls for invertebrate sampling have been well documented, but they still provide the most efficient and cost-effective method for sampling a number of sites over a significant period of time (see Chapter 2 for discussion). At each site, a transect 50 metres long was laid down approximately 40 metres in from, and perpendicular to, the forest edge. The transect was positioned randomly within the forest patch, except to avoid a gap in the canopy or unusual topographic feature that did not represent the site as a whole (e.g. man-made drains, walking tracks). Five metres to either side of the transect, a row of five pitfall traps were set at 10 metre intervals (Fig. 4.2). Each pitfall trap consisted of a plastic container (upper diameter 102mm, lower diameter 86mm and height 99mm) dug into the ground so that the upper rim was flush with the soil surface, and covered by a metal "roof" to keep out rain water and falling debris.

A mixture of 50% ethylene glycol and 50% water was used as a preservative. Pitfalls to the left of the transect, labelled 1-5, remained in the same position for the duration of sampling. Pitfalls to the right of the transect, labelled 6-10, were moved five metres to the right (i.e. further away from the transect) after each sampling month (Fig. 4.2). This sampling design was used to test whether there was any difference in catch rates between moved and fixed pitfalls, such as due to local depletion of invertebrate populations or attraction of invertebrates to new traps (the "digging-in effect"). Sites were visited at the end of each month and the invertebrates sieved out and transferred into 70% ethanol. During December, a number of sites were inaccessible due to flooding of access roads, so the invertebrates went uncollected, and the pitfalls unmoved until the following month, at all sites.

Eight invertebrate groups were sorted into morphospecies based on external morphological characteristics, a technique proven to be an accurate method for the estimation of invertebrate species richness (Oliver and Beattie 1996a, Kerr *et al* 2000). These groups were ground beetles (Coleoptera: Carabidae), other beetles (Coleoptera,

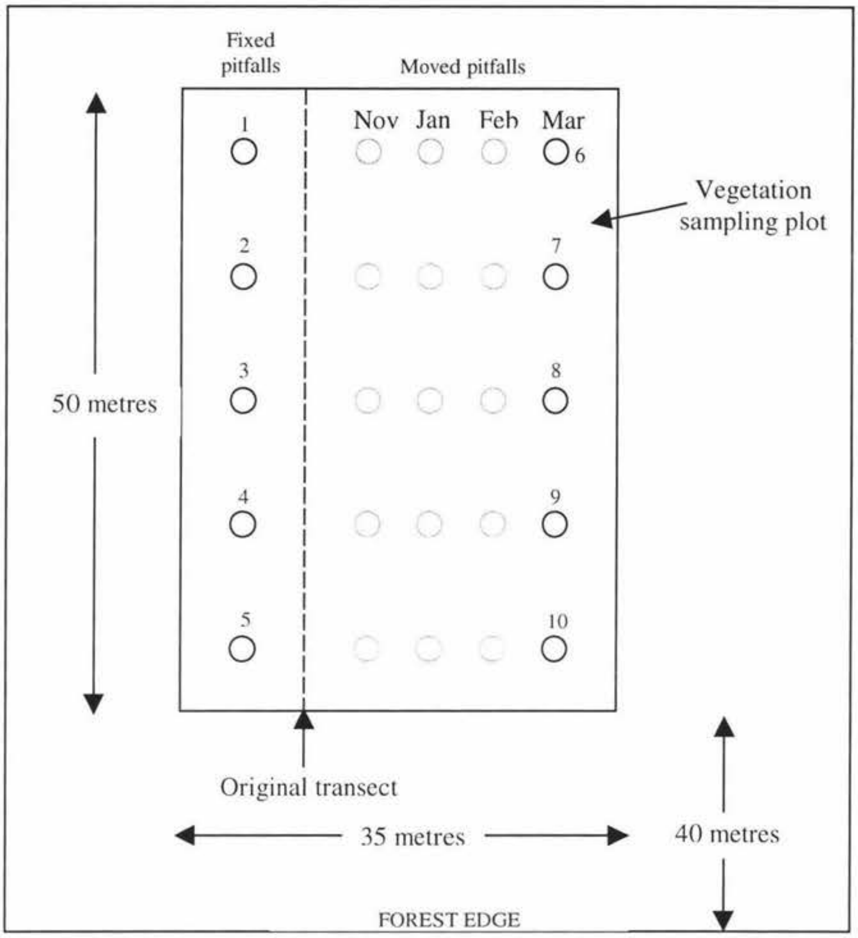


Figure 4.2: Orientation of pitfalls used in the sampling of fourteen forest sites in the Rangitikei Ecological Region. Pitfalls and distance from forest edge not drawn to scale. See text for details.

excluding Carabidae), flies (Diptera), bees and wasps (Hymenoptera, excluding Formicidae), bugs (Hemiptera), spiders (Araneae), mites (Acari) and harvestmen (Opiliones). Representatives of the morphospecies of spiders, carabids, beetles, flies, wasps and bugs were sent to expert taxonomists for confirmation and indentification where possible. Mites and harvestmen remained as morphospecies.

4.2.3 Vegetation Richness and Basal Area

Plant species richness of each site was recorded in a plot set up around the pitfalls at the end of the five months of invertebrate sampling (Fig. 4.2). A count of all plant species present in the plot, excluding epiphytes, was done by a systematic walk-through of the plot until no new species were found. All stems >2cm in diameter (at breast height) present in the plot were counted by species, and the diameter recorded to enable calculation of basal area per species.

4.2.4 Statistical Analysis

α-Diversity Associations

Species richness was measured as the total number of species captured per site over all five months of sampling. Species richness was then compared with that of the plant community, individual invertebrate groups, and all invertebrates combined using Pearson correlations. All invertebrate species richness was also compared to total remnant area and altitude. When correlating the richness of individual invertebrate taxa with combined invertebrate richness, the latter (referred to as 'other invertebrate richness') was calculated after the removal of the particular group being compared. Differences in the richness and absolute abundance between fixed and moved pitfall traps were analysed with paired t-tests for both individual pitfall data and for pooled data (i.e. the combined data from the five moved pitfalls compared with the combined data from the fixed pitfall traps) by site. For the analysis of the individual pitfall traps, the traps were paired 1 & 6, 2 & 7, 3 & 8, 4 & 9 and 5 & 10 (Fig. 4.2).

β-Diversity Associations

Two measures of β-diversity were calculated for different uses. The first was a simple complementarity equation based on species presence/absence at two sites:

$$\text{Complementarity} = (a + b)/(a + b + c)$$

where a = the number of species found at Site A but not Site B; b = the number of species found at Site B but not Site A; and c = the number of species found at both Site A and B. A value of 0 represents identical species composition, whereas a value of 1 indicates no shared species. Every paired combination of the fourteen sites was used (a total of 91 combinations), and an average complementarity score based on these was calculated for each individual invertebrate group and all invertebrates combined. Because two random samples from within the same community would still be expected to exhibit some degree of complementarity (Niemelä *et al* 1996), this observed average complementarity was compared with that of random samples from a single regional pool. To do this, data from all sites were pooled to create the theoretical regional community. Fourteen samples were then redrawn from the regional pool to match the total abundance and number of species of the real data for each site and complementarity scores calculated between the samples. This was repeated 10,000 times using a program written in Visual Basic, and the average complementarity scores from this were compared to the observed complementarity scores between the fourteen sites for all individual invertebrate groups and all invertebrates combined.

The second β-diversity calculation used was the Bray-Curtis measure of community dissimilarity. This is a similar equation to the complementarity one presented above, except that it also incorporates abundance data:

$$D_{ih} = \frac{\sum_{j=1}^{p} \left| a_{ij} - a_{hj} \right|}{\sum_{j=1}^{p} a_{ij} + \sum_{j=1}^{p} a_{hj}}$$

where D_{ih} = dissimilarity between sites *i* and *h*, a_{ij} = the abundance of species *j* at site *i*, and a_{hj} = the abundance of species *j* at site *h*. Scores range from 0 (identical communities) to 1 (no shared species).

Community dissimilarity was calculated between each site-pair based on the $\log_{10}(x+1)$ transformed abundance data for all invertebrate taxa separately and the $\log_{10}(x+1)$ transformed basal area data for the plant community. Basal area data characterised the dominant canopy and sub-canopy species only and thus approximates PNA assessments of forest type. The congruence between dissimilarity measures of the individual invertebrate groups and plants was quantified using a Mantel test and a Monte Carlo test with 1000 randomizations to test the significance (PC-ORD Ver. 4). Individual invertebrate group dissimilarity between sites was also tested against the community dissimilarity of all other invertebrates. The geographic distance between sites was compared with the Bray-Curtis dissimilarity of the invertebrate groups, all invertebrates and plants using Mantel tests.

Reserve Selection Algorithm

A simple algorithm based on complementarity was used to rank the fourteen sites separately for the eight invertebrate groups and the plant community (Howard *et al* 1998). The most species-rich site was selected first, the site with the greatest number of species not included in the first site was selected second, the site with the greatest number of species not included in the first two sites third, and so on. In the event of a tie, the site with the greatest overall diversity for that group was selected. The rankings for each site

(1 = first choice, 14 = last choice) on the eight lists generated by each of the invertebrate taxa were averaged to approximate the ideal ranking of the sites on the entire invertebrate community with each group of equal importance. The combined data for all invertebrates was also run through the algorithm to produce an 'All Invertebrate' list, where the rankings are more likely to favour the high diversity groups. Spearman Rank Correlations were used to compare site rankings derived from the individual invertebrate groups and those from Average Rank, All Invertebrates and plants.

4.3 RESULTS

4.3.1 Plant Richness and Forest Canopy Composition

Plant richness ranged from 21 species observed at Vinegar Hill to 47 at Mangaweka, with an average of 33 species per plot (Table 4.2). Tawa (*Beilschmiedia tawa*), titoki (*Alectryon excelsus*) and mahoe (*Melicytus ramiflorus*) were the dominant canopy species at most sites, with the exceptions of the four northeastern sites, Apiti, C. L. Pemberton, North End and Taihape, where tawa and titoki were entirely absent. The most common emergent species across all sites were matai (*Prumnopitys taxifolia*) and kahikatea (*Dacrycarpus dacrydioides*), with the occasional rimu (*Dacrydium cupressinum*). Totara (*Podocarpus totara*) was the dominant emergent at two sites, North End and Taihape.

4.3.2 Invertebrate Richness

In the five months of sampling, a total of 18,062 individuals and 495 species or morphospecies were collected from the eight invertebrate groups, with an average of 111 species per site. Overall invertebrate richness was highest at Apiti Scenic Reserve, which contained 170 species, 35 more than the next most species-rich site, Sutherlands (Fig. 4.3). Lowest overall richness was found at Pukeroa and Maungakaretu with 79 and 80 species respectively. There was no significant correlation between invertebrate richness and patch-area ($r = 0.29$, $p > 0.1$), nor between invertebrate richness and altitude ($r = 0.32$, $p > 0.1$).

Spiders were represented by 63 species within 30 families, from a total of 1950 spiders caught during the sampling period (Table 4.3). This made the Araneae the third-most species-rich, and third-most abundant, group. Three mainly cursorial families, Miturgidae, Amphinectidae and Lycosidae, made up 86.7% of all the individuals

Table 4.2: Plant species richness and dominant tree canopy species present in 50 x 35m plots at fourteen forest sites in the Rangitikei Ecological Region.

	Species Richness	Emergents	Canopy/subcanopy
Apiti	37	Rewarewa (*Knightia excelsa*)	Five-finger (*Pseudocarpus arboreus*), mahoe, hinau (*Elaeocarpus dentatus*)
Bird Grove	26	Pukatea (*Laurelia novae-zelandiae*)	Tawa, titoki, mahoe
Bruce	31	Rimu	Tawa, titoki, mahoe
C. L. Pemberton	32	Red beech (*Nothofagus fusca*), black beech (*Nothofagus solandri*)	Rimu, hinau
Mangaweka	47	Miro (*Prumnopitys ferruginea*), kowhai (*Sophia microphyllum*)	Tawa, titoki, mahoe, white maire (*Nestegis lanceolatus*), five-finger
Maungakaretu	30		Tawa, titoki, mahoe
McPherson	29	Rimu, matai	Tawa, titoki, pukatea, mahoe
North End	39	Totara, matai	Mahoe, lemonwood (*Pittosporum eugenioides*)
Pukeroa	28	Pukatea, kahikatea, matai	Tawa, titoki, kahikatea, pukatea, mahoe
Rahui	35	Pukatea, kahikatea, matai	Tawa, titoki, kahikatea, pukatea, mahoe
Simpsons	42	Rimu, kahikatea, matai	Mahoe, white maire, five-finger
Sutherlands	38	Kahikatea	Tawa, titoki, mahoe, kahikatea
Taihape	27	Totara, kahikatea, matai	Mahoe, *Coprosma grandifolia*
Vinegar	21	Rewarewa	Tawa, titoki, pukatea, mahoe

collected, though for the Miturgidae and Lycosidae many of these were juvenile specimens. The most abundant species were an amphinectid from the genus *Amphinecta* (25% of all identified adult spiders), an unnamed lycosid (14%), the miturgid *Ulidon* sp1 (8%) and a member of Synotaxidae, *Meringa* sp. (7%). For species lists of spiders, carabids, beetles, flies and wasps, see the Appendix.

Flies were the most abundant group sampled overall, though the abundance of carabids and other beetles combined meant that the Coleoptera were the most abundant order (Table 4.3). Flies were the most species-rich group, with 135 species collected; however, 78% of all flies caught were from three species, *Megaselia* sp. (Phoridae; 43% of all flies), *Tricimba tinctipennis* (Chloropidae; 24%) and *Calliphora stygia* (Calliphoridae; 11%).

Spider species richness was highest at Apiti, with 26 species recorded, and lowest at Pukeroa, with only 8 collected (Table 4.3). Apiti was also the most-species rich site for

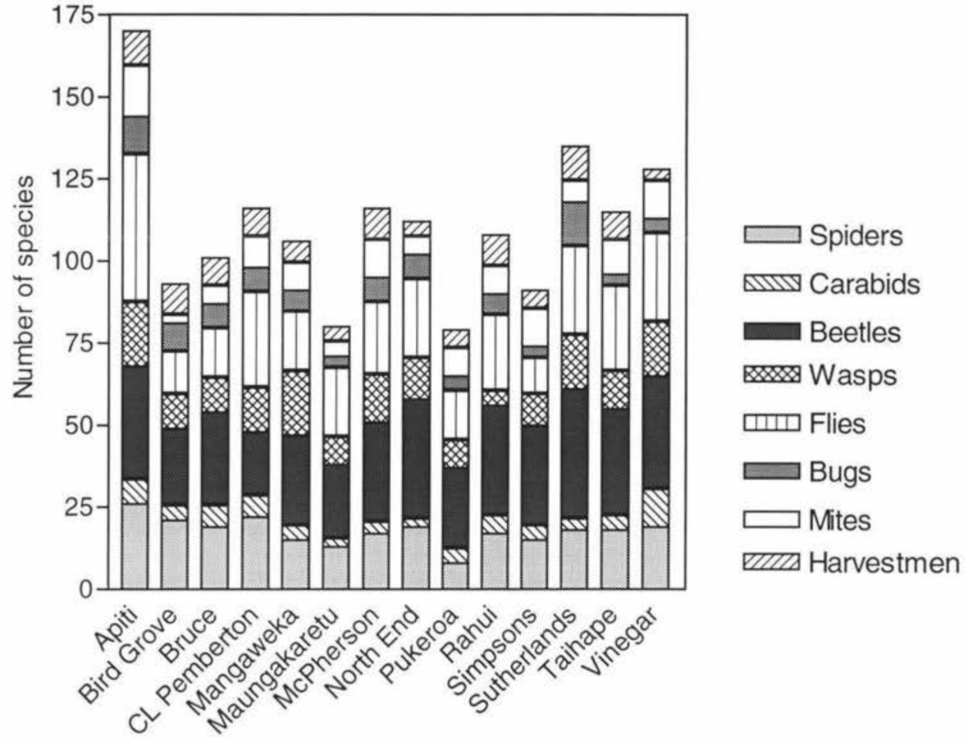


Figure 4.3: Species richness of eight invertebrate groups collected by pitfall from fourteen forest sites in the Rangatikei Ecological Region.

Table 4.3: Summary of abundance, species richness and family richness for the eight invertebrate groups sampled over all fourteen forest sites in the Rangitikei Ecological Region.

	No. of individuals	Species	Families	Species hotspot (number of spp.)	Species coldspot (number of spp.)
Spiders	1950	63	30	Apiti (26)	Pukeroa (8)
Carabids	1186	23	1	Vinegar Hill (12)	Maungakaretu, North End (3)
Beetles	5462	105	38	Sutherlands (39)	C.L. Pemberton (19)
Wasps	714	63	13	Apiti, Mangaweka (20)	Rahui (5)
Flies	6539	135	33	Apiti (45)	Simpsons (11)
Bugs	734	29	12	Sutherlands (13)	Maungakaretu, Simpsons, Taihape (3)
Mites	824	46	-	Apiti (16)	Bird Grove (3)
Harvestmen	653	30	-	Apiti, Sutherlands (10)	Vinegar (3)

four other invertebrate groups, with Sutherland's the most species-rich site for three groups. There was a greater range of sites (nine in total) representing cold-spots for individual invertebrate groups. Only Simpsons and Maungakaretu were the least species-rich site for more than one invertebrate group.

Spiders demonstrated no differences in species richness or abundance between fixed and moved pitfalls (Table 4.4). However, five other invertebrate groups did exhibit some differences. Moved pitfalls contained significantly more species of carabids, beetles, mites and harvestmen per trap than unmoved traps. The only group to demonstrate the opposite effect were wasps, with unmoved pitfalls containing more species per trap. When the data were combined by site, only the carabids and wasps showed significant effects. Both groups had a greater number of species in the moved pitfalls, a reverse for wasp richness from the results gained when the pitfalls were analysed separately. Only the carabids and the beetles showed any significant differences in abundance, with both showing an increased catch in those pitfall traps that were moved monthly.

4.3.3 α-Diversity Congruence

The majority of within-site correlations of species richness among invertebrate taxa were positive (25 out of 28). There were several moderately strong associations; however none were significant with Bonferroni correction for multiple tests (Table 4.5). The strongest correlation for spider richness was with the flies ($r = 0.65$). Spiders and flies tended to have the strongest associations with other invertebrate taxa, both with three correlations above 0.5 and averages of 0.44 and 0.47 respectively. Neither the carabids nor the beetles

Table 4.4: Results of paired t-tests comparing invertebrate abundance and richness between moved and unmoved pitfall traps. "Pitfall" refers to analysis of pitfalls separately (n = 70); "Site" refers to analysis of pitfalls grouped by site (n = 14).

Invertebrate group		Richness	Abundance
Spiders	Pitfall	NS	NS
	Site	NS	NS
Carabids	Pitfall	* (M>U)	* (M>U)
	Site	* (M>U)	NS
Beetles	Pitfall	** (M>U)	* (M>U)
	Site	NS	NS
Wasps	Pitfall	*** (U>M)	NS
	Site	* (M>U)	NS
Flies	Pitfall	NS	NS
	Site	NS	NS
Bugs	Pitfall	NS	NS
	Site	NS	NS
Mites	Pitfall	* (M>U)	NS
	Site	NS	NS
Harvestmen	Pitfall	** (M>U)	NS
	Site	NS	NS

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$
NS = Not Significant
M = Moved, U = Unmoved

Table 4.5: Pearson correlation coefficients for the congruence between taxa in absolute species richness per site. Harv. = harvestmen. All correlations have Bonferonni p values of > 0.05.

	Carabids	**Beetles**	**Wasps**	**Flies**	**Bugs**	**Mites**	**Harv.**	**Plants**
Spiders	0.40	0.24	0.46	0.65	0.58	0.25	0.51	0.01
Carabids		0.10	0.30	0.36	-0.02	0.48	-0.08	-0.41
Beetles			0.29	0.38	0.39	0.30	0.14	-0.09
Wasps				0.54	0.49	0.42	0.13	0.19
Flies					0.48	0.57	0.33	0.03
Bugs						-0.02	0.70	0.17
Mites							0.11	0.07
Harv.								-0.02

had particularly strong relationships with other invertebrate groups, with correlation coefficients all below 0.5. The strongest single association was between harvestmen and bugs (r = 0.70). Plant richness was poorly associated with the richness of invertebrate groups, with a range of –0.09 to 0.17 for seven of the eight groups, and a moderately negative correlation (r = -0.41) with the carabids.

Correlations between individual invertebrate groups and the richness of all other invertebrate groups combined were not significant, though all were positive (Fig. 4.4). Spiders demonstrated the second strongest correlation (r = 0.67), behind that of the flies (r = 0.75). Two other groups, the wasps and the bugs, also had Pearson correlation coefficients over 0.5. Plant richness had no relationship with the richness of all invertebrates combined (r = 0.02, p > 0.9).

4.4.3 β-Diversity Congruence and Site Ranking

Community congruence between taxa

Bray-Curtis dissimilarity of the spider community between sites demonstrated low congruence with other invertebrate groups. Correlation coefficients from the Mantel test ranged between –0.01 and 0.28 (Table 4.6). Similarly low congruence was found among other invertebrate groups with the strongest single correlation, between flies and wasps, only 0.45. No single invertebrate group demonstrated a strongly positive association with all other invertebrates combined. Spiders had one of the lowest correlations with all other invertebrates, with a correlation coefficient of only 0.24.

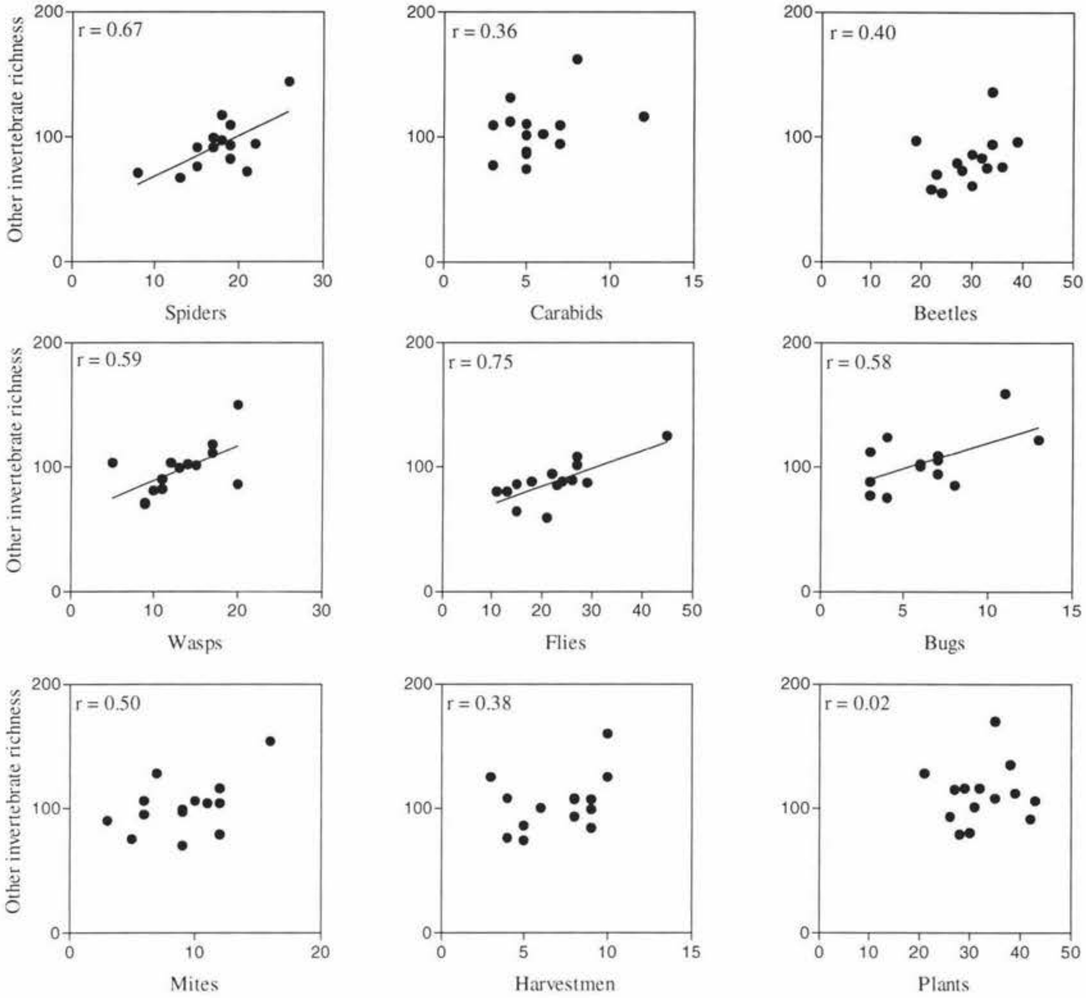


Figure 4.4: Correlations between species richness of individual taxa versus all other invertebrates across fourteen forest sites. r = Pearson correlation coefficient.

The plant community had only weak associations with invertebrate groups, ranging from 0.03 to 0.31, the strongest relationships being with spiders and carabids (Table 4.6). The strongest relationships between community dissimilarity and geographic distance were with plants and spiders. These community differences tended to increase with distance, though the correlation coefficients were low and none were significant.

Table 4.6: Correlations between Bray-Curtis dissimilarity matrices of invertebrate groups, all invertebrates, plants and geographic distance using Mantel test. All correlations have a p-value > 0.05 with Bonferroni correction. Harv = harvestmen. All = all other invertebrates.

	Carabids	Beetles	Wasps	Flies	Bugs	Mites	Harv.	Plants	All.	Distance
Spiders	0.21	0.12	0.28	0.15	-0.01	0.03	0.09	0.31	0.24	0.37
Carabids		0.26	0.12	0.22	0.34	0.15	0.21	0.31	0.42	0.06
Beetles			0.07	0.25	-0.07	-0.18	-0.01	0.22	0.17	0.10
Wasps				0.45	0.06	0.06	0.08	0.20	0.35	0.29
Flies					0.16	-0.03	0.31	0.14	0.43	0.16
Bugs						0.30	0.39	0.09	0.25	0.07
Mites							0.40	0.03	0.12	0.01
Harv.								0.18	0.37	0.13
Plants									0.35	0.43
All										0.27

Complementarity scores

The range of between-site complementarity scores for invertebrate taxa sampled was relatively narrow (Fig. 4.5), with only the lower diversity invertebrate taxa (carabids, bugs and harvestmen) exhibiting a difference of over 0.5 between the highest and lowest scores. The scores for all invertebrates combined were particularly clumped, with a range of only 0.62 to 0.80, an indication that no pair of sites were especially similar in total invertebrate composition. Spiders had the lowest mean complementarity score of any invertebrate group (0.65) and mites the highest (0.78).

For all taxa, observed average species complementarity was significantly greater than expected from random sampling a single community ($p < 0.0001$; Table 4.7), indicating that there were differences in species presence/absence between sites that cannot be accounted for by random sampling from a homogenous fauna.

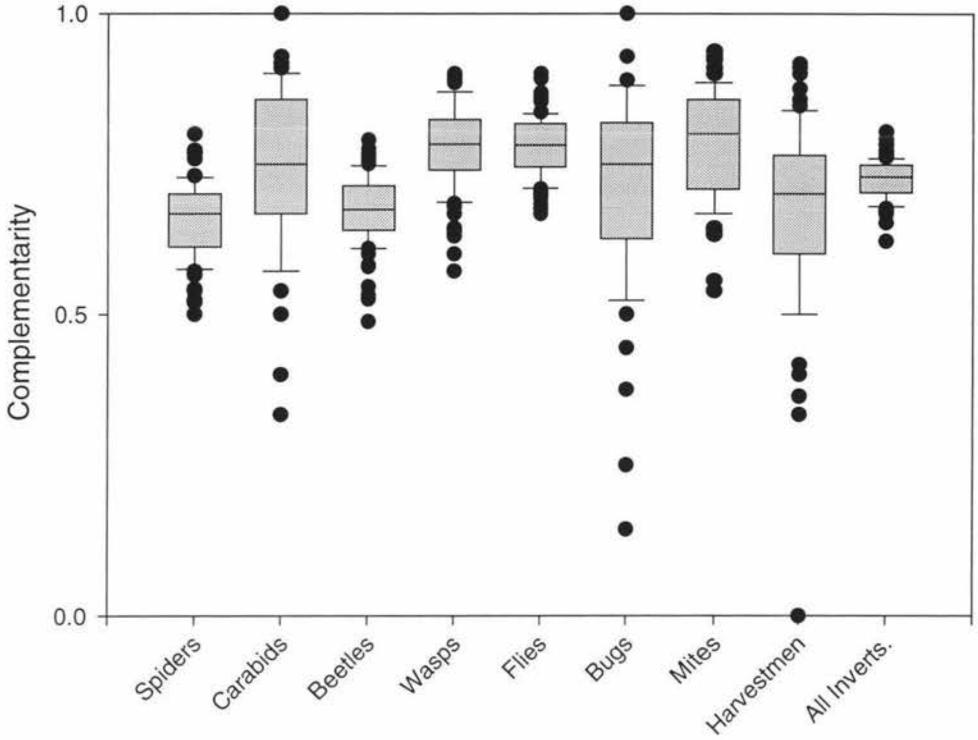


Figure 4.5: Range of pairwise complimentarity scores for plants and invertebrate groups at fourteen forest sites in the Rangitikei Ecological Region. Complementarity of 1.0 = no species in common.

Priority site ranking

When the Average Rank list was calculated, Apiti was placed first and Maungakaretu last (Table 4.8a). The geographically closest neighbour to Apiti, C. L. Pemberton, was ranked in second place, followed by Sutherlands and three sites tied for fourth. Similarly, the geographic neighbours, Maungakaretu and Pukeroa, were ranked last and second-to-last on the Average Rank list. When the entire invertebrate data set was run through the complementarity algorithm, the resultant list (All Invertebrates) was similar to that for Average Rank (Spearman rank correlation = 0.83), though only four sites held the same rank on the two lists (Table 4.8a). Plants were poor surrogates for the entire invertebrate community, with rank correlations of –0.04 and 0.04 with Average Rank and All Invertebrates respectively.

Table 4.7: Differences between observed mean complementarity between sites and randomised mean complementarity between sites for eight invertebrate taxa.

	Observed mean complementarity	Random mean complementarity	P-value
Spiders	0.65	0.52	$p < 0.0001$
Carabids	0.74	0.39	$p < 0.0001$
Beetles	0.67	0.49	$p < 0.0001$
Flies	0.78	0.65	$p < 0.0001$
Wasps	0.77	0.66	$p < 0.0001$
Bugs	0.72	0.60	$p < 0.0001$
Mites	0.78	0.60	$p < 0.0001$
Harvestmen	0.67	0.55	$p < 0.0001$

Priority area lists generated by the complementarity algorithm have a wide variation in site rankings across individual invertebrate taxa (Table 4.8b). Eight of the fourteen sites have a difference of over ten places between their highest and lowest rank. Only two sites show some degree of consistency between taxa: Apiti was ranked either first or second for seven of the eight groups, and was fourth for beetles. At the other end of the scale, Maungakaretu was ranked in the bottom seven sites for all taxa. There were considerable differences between the site list for plants and the invertebrate taxa, reflected in low rank correlations ranging between –0.22 and 0.42.

The priority site list based on spider complementarity had only a moderate correlation with those for Average Rank and All Invertebrates (rank correlations of 0.49 and 0.36 respectively), even though the top two sites for spiders (Apiti and C. L. Pemberton) were also the top two sites for the Average Rank list. The flies demonstrated the greatest similarity in site priority with that for all invertebrates combined, with rank coefficients of 0.75 and 0.70 with the Average Rank and All Invertebrate lists respectively.

Species accumulation

Though flies had the strongest overall relationship with total invertebrate complementarity, Fig. 4.6 shows that there is little difference in the percentage of invertebrate species captured by stepwise reserve selections based on different groups. This is particularly evident for the top three sites, where there is less than 5% difference in the total number of invertebrates included for sites selected by seven of the eight invertebrate groups. The best indicator of invertebrate β-diversity depended on the

Table 4.8: Site rankings based on taxa complementarity for (a) combined invertebrate group data and plants, and (b) individual invertebrate groups, and associated Spearman Rank correlations.

(a)	Average Rank	All Invertebrates	Plants
Apiti	1	1	4
C.L. Pemberton	2	5	5
Sutherlands	3	3	6
Vinegar	4=	2	14
Taihape	4=	4	13
Rahui	4=	7	9
McPherson	7	12	8
Bruce	8	11	11
Bird Grove	9	8	3
North End	10	6	7
Mangaweka	11	10	1
Simpsons	12	9	2
Pukeroa	13	13	12
Maungakaretu	14	14	10
Rank correlations:			
- with Average Rank	-	0.83	-0.04
- with All Invertebrates		-	0.04

(b)	Spiders	Carabids	Beetles	Wasps	Flies	Bugs	Mites	Harv.
Apiti	1	2	3	4	1	2	1	2
C.L. Pemberton	2	4	14	7	2	7	6	3
Sutherlands	10	13	1	8	7	1	13	1
Vinegar	12	1	13	2	6	5	3	14
Taihape	9	10	6	9	3	9	4	6
Rahui	5	3	12	13	4	3	8	8
McPherson	6	7	11	3	11	10	5	7
Bruce	8	9	4	11	8	6	10	5
Bird Grove	4	6	7	14	13	4	11	4
North End	3	14	2	5	5	11	14	13
Mangaweka	7	12	8	1	10	12	7	11
Simpsons	13	5	5	12	14	13	2	9
Pukeroa	14	11	9	6	12	8	12	10
Maungakaretu	11	8	10	10	9	14	9	12
Rank correlations:								
- with Average Rank	0.49	0.42	-0.01	0.19	0.75	0.73	0.36	0.61
- with All Invertebrates	0.36	0.31	0.21	0.18	0.70	0.62	0.32	0.35
- with plant list	0.42	-0.02	0.27	-0.03	-0.22	-0.07	0.07	0.31

number of sites to be selected. For example, if only three sites could be chosen, harvestmen would have been the best surrogate group, whereas maximum invertebrate richness in four sites would have been best predicted by carabid richness.

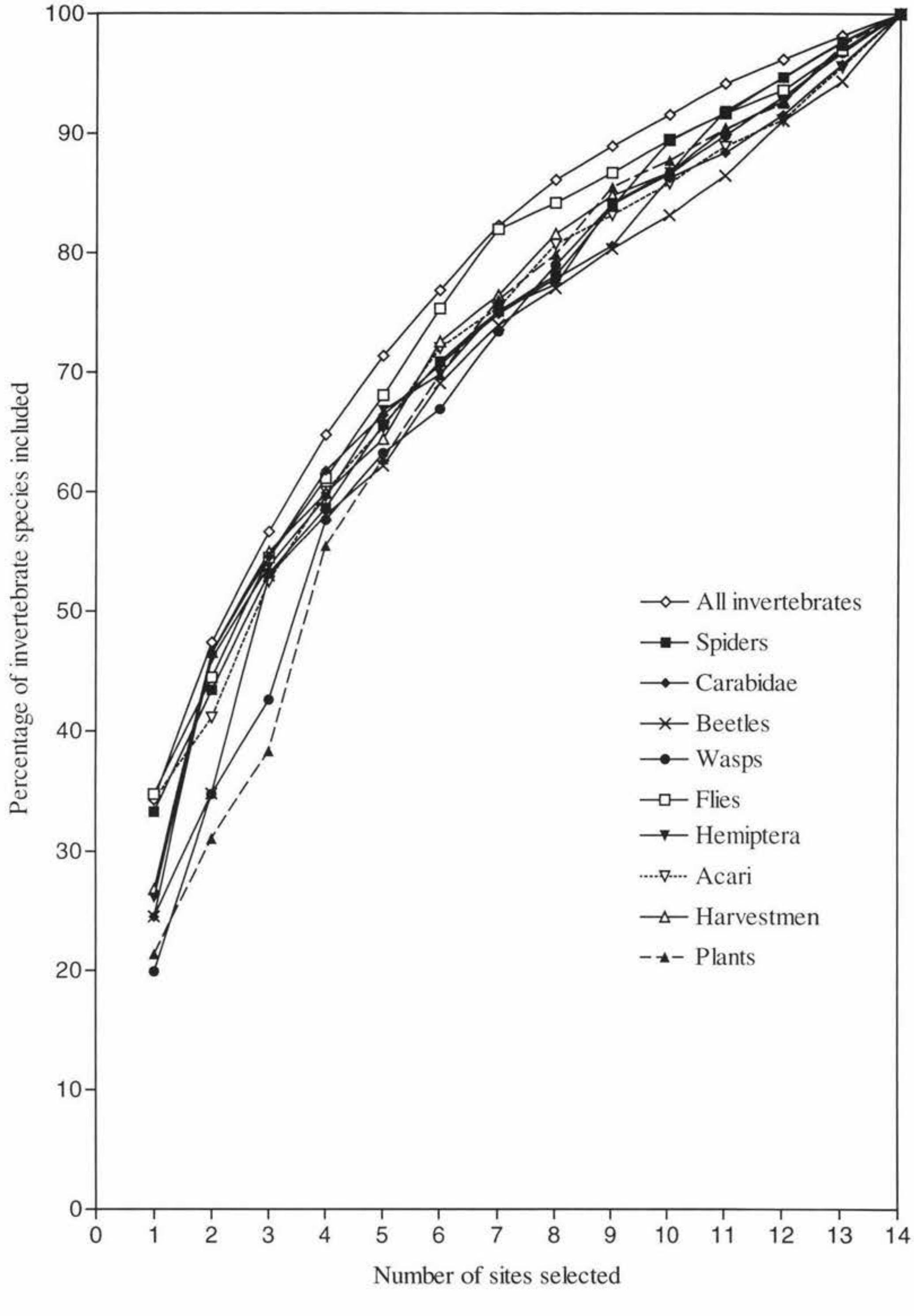


Figure 4.6: Percentage of invertebrate species included in step-wise site selection algorithm based on complementarity of individual taxa.

Spiders were not the best predictor at any threshold. Site selection using plant data encompassed fewer invertebrate species than any invertebrate group in the top 2-4 sites range, but proved to be as good as invertebrate groups when the number of sites increased above seven.

4.4 DISCUSSION

4.4.1 Congruence of Spider Richness with Other Invertebrate Groups

α-Diversity

The site with highest species richness for spiders, Apiti Scenic Reserve, was also the most species-rich for four other invertebrate groups (wasps, flies, mites and harvestmen) and all invertebrates combined (Fig. 4.3, Table 4.3). The coincidence of hotspots for different taxa has been infrequently reported (Gaston and Williams 1996, Reyers *et al* 2000, Virolainen *et al* 2000 and references therein), with overlap thought to be especially poor at smaller spatial scales (Gaston 1996). Biodiversity levels at a site such as Apiti can be the product of numerous factors, including species interactions such as competition, predation and mutualism; resource heterogeneity and productivity; as well as dispersal and extinction rates (Huston 1999, Loreau 2000). Apiti had a unique vegetation community in comparison to the others sampled, with the canopy being dominated by five-finger and hinau. It is possible that this assemblage supports a naturally higher invertebrate diversity. This site is also located in close vicinity to the Ruahine Ranges, and could therefore be receiving many immigrating species from this large neighbouring tract of forest. The other site close to the ranges, C.L. Pemberton, also had a relatively high species diversity considering its size (5ha). The actual cause of the elevated diversity levels at Apiti can only be determined with more detailed surveys. It appears though that spiders, as well as any of the four other groups which reached highest species richness at Apiti, may have potential in identifying areas of high invertebrate diversity.

Within-site richness of spiders was positively correlated with the richness of several other invertebrate groups, though none were significant (Table 4.5). Spiders also had the second strongest correlation of any invertebrate group with the richness of all other invertebrates combined (Fig. 4.4). Local richness levels are often the result of a complex interaction of several factors (e.g. Wootton 2001), and it is difficult to determine the exact mechanisms producing the general affinity between spider and all other invertebrate diversity, or among any of the invertebrate groups. This is made even more difficult by the lack of general ecological and biogeographic knowledge for many of the species recorded in this survey.

Even on the most general ecological principles, observed patterns seem contradictory. For example, it can be assumed that diversity correlation will be highest between ecologically or phylogenetically related groups (Beccaloni and Gaston 1995, Kerr *et al* 1999). However, the correlation between spiders and carabids, the only other fully predatory group sampled, is no greater than those between trophically unrelated groups, such as wasps and bugs (Table 4.5). The highest overall correlation was between harvestmen and bugs, whereas the taxonomic pairing of carabids and beetles had a very low association in species richness. It would appear that the strength of the congruence between species richness of invertebrate groups cannot be predicted based on ecological or taxonomic affinities, at least in the forest remnants sampled here.

Further surveys, and more detailed biological information on individual species, are required to determine the combination of factors setting the diversity levels within these forest remnants. Studies in Australian forests have demonstrated a lack of correlation between the α-diversity of ground-active invertebrate groups, which can be explained by contrasting habitat preferences (Oliver and Beattie 1996a, Oliver and Beattie 1996b, Oliver *et al* 2000). Because the habitat preferences for many of the New Zealand invertebrate fauna are so poorly known, it is difficult to conclude whether general affinity between the richness levels of different invertebrate groups is the result of similar habitat requirements. Other studies have demonstrated that litter depth and complexity can influence spider community diversity (Uetz 1979, 1991), and the diversity of ground dwelling invertebrates in general (Sulkava and Huhta 1998, York 1999, Hansen 2000, Haskell 2000, Krijger and Sevenster 2001). The level of congruence in diversity observed here could be the response of invertebrate groups to an independent third variable, such as leaf litter quality.

Given the highly fragmented nature of this forest system, biogeographic factors such as size, shape and isolation of individual forest patches could be expected to influence invertebrate diversity. The manner and degree to which these factors affect resident invertebrate communities, however, appears to differ from situation to situation. Bolger *et al* (2000) reported how ground spider richness and abundance increased with increasing fragment age in California buckwheat shrub habitat, and decreased with increasing fragment area. Other invertebrate groups, including flies, bugs and mites, demonstrated the opposite trend among the same fragments. The ground active forest spiders sampled by Mabelis (1996) in the Netherlands, however, had higher species diversity in larger woodlots, though sampling effort was proportional to the size of the habitat fragment. In the present study, all sampling plots were of equal size at each site and consequently there was no significant relationship between total patch size and invertebrate richness. However the higher diversity of some invertebrate groups in moved rather than unmoved pitfalls (Table 4.4) suggests that proportional sampling based on area size will produce a greater species area effect, possibly due to an increased number of microhabitats included in larger forest patches. This in turn may strengthen the species richness correlations between the invertebrate groups observed in these forest patches (see Howard *et al* 1998).

In New Zealand, richness patterns of terrestrial invertebrates are virtually unknown, even in relation to simple environmental gradients such as altitude or latitude (but see Barker and Mayhill 1999). The results obtained in the present study suggest that much can be gained from further investigations into invertebrate diversity in forest remnants.

β-Diversity

Howard *et al* (1998) found low spatial congruence in α-diversity between plants, moths, butterflies, birds and mammals in Ugandan reserves, but when complementarity scores were calculated between forests for each taxon, there were strong positive correlations in β-diversity between most taxa. In the present study, results exhibited an opposite trend. Despite the general association in α-diversity, the correlation between the Bray-Curtis dissimilarity scores between sites for spiders and other invertebrate groups were very low (Table 4.6), indicating a low degree of congruence in β-diversity patterns across the landscape. This result was not restricted to the spider community; correlations were low between all invertebrate groups. Results of previous studies indicate that congruence in β-diversity between ground-active invertebrate groups is not common (e.g. Kotze and Samways 1999, Ellis *et al* 2001).

A lack of strong complementarity congruence between spiders and other taxa could be the result of one or a combination of three things. The first is that differences in community composition between sites may be artefacts of sampling, representing the variation that is expected among random samples of the same community rather than representing actual differences between sites. However, the complementarity between sites for every group sampled was significantly higher than that expected from random sampling, suggesting that the complementarity values observed do represent actual differences between sites.

Secondly, there may be divergent patterns of resource use and microhabitat preference between the groups. Microhabitat preferences have been used to explain β-diversity trends between taxa across sites in many other studies (Ingham and Samways 1996, Paquin and Coderre 1997, Rykken *et al* 1997, Howard *et al* 1998). In a survey of the floor of conifer forests in Finland (Niemelä *et al* 1996), spider distribution was influenced by vegetation structure, carabids by litter quality and ants by soil moisture and tree-canopy composition. If these habitat features are distributed randomly with respect to each other between sites, then it may be expected that the invertebrates associated with them will be distributed randomly as well, and hence β-diversity congruence will be low. The strong congruence shown by taxa in Howard *et al* (1998) occurred in the sampling of several broad forest types, ranging from montane forests to dry savannas across a large geographical area. Abiotic conditions and other habitat features would have been quite different between these habitats, and favoured divergent faunal assemblages. In contrast, there were no strong environmental gradients in the forest remnants sampled in the present study.

Thirdly, there may be differential patterns of local extinction and dispersal between groups. Spiders are considered to be good long distance dispersers through ballooning as juveniles (Turnbull 1973, Marc *et al* 1999). Therefore many species should have the capacity to locate most if not all suitable forest patches in the landscape (Burel and Baudry 1995), and to reduce local extinction rates through regular exchange of individuals between patches. However, relatively poorly dispersing species, such as flightless carabid species (Burel and Baudry 1995), may be absent from sites where conditions are otherwise favourable due to local extinctions and subsequent inability to recolonise. Therefore, any patterns of β-diversity across a landscape that could be related to microhabitat type and distribution may be obscured by the biogeography of individual sites. Correlations between Bray-Curtis dissimilarities of the invertebrate fauna with geographic distance revealed no conclusive pattern (Table 4.6). This is probably because there are numerous other forest patches around the region that could act as stepping-stones or sources of invertebrate colonisers for the sampled sites. Despite their reputation for good dispersal, spiders were the invertebrate group that exhibited the greatest tendency to be more dissimilar between sites far apart than those nearby. However, of the eight invertebrate groups, spiders had the strongest relationship with plants, so it is possible that the observed effect of distance on spiders may in fact be a weak response to plant community composition, which also tended to be more dissimilar with increasing distance between sites. This result is unusual in itself, given that cursorial spiders would be expected to be less dependent on vegetation composition than groups with many herbivorous species, such as beetles or bugs.

Overall, β-diversity patterns in this system are likely to be the combined result of dispersal ability (or extinction susceptibility) and microhabitat preferences of the constituent species in each group. In the absence of strong habitat gradients affecting all taxa simultaneously, no clear congruence between taxa is demonstrated.

4.4.2 Congruence between Plant and Invertebrate Richness

Diversity of the plant community at a site is one of the primary criteria used for reserve selection in the Protected Natural Areas programme (Kelly and Park 1986). However, the plant community proved to be a poor predictor of α-diversity for resident ground-dwelling invertebrate communities, either as a whole or for individual taxa, in these forest patches (Table 4.5; Fig. 4.4). A number of studies that have demonstrated no correlation between plant and ground-active invertebrate richness (Gardner *et al* 1995, Oliver *et al* 1998, Watts and Gibbs 2000). While a high diversity of shrubs and trees may be expected to contribute to a greater variety of litter types to the forest floor (Hooper *et al* 2000), and thus have an indirect influence on litter depth, litter complexity, spatial heterogeneity of resources and food abundance, the link is not always apparent. Sulkava and Huhta (1998), for example, demonstrate that the litter of four tree species maintained higher invertebrate diversity when the litter of each species was kept separate but adjacent to each other (i.e. a patchy distribution), rather than mixed together, indicating the influence of plant spatial heterogeneity, rather than plant richness *per se*.

New Zealand forests contain a number of tree species that have variable leaf and growth forms (Salmon 1990), yet many ground fern species are very similar in morphology. Both of these factors would tend to blur the relationship between plant species diversity and structural diversity of the litter in the present study. In addition to this, some of the plots sampled here contained a few large podocarp individuals (i.e. matai, kahikatea), the litter of which tended to dominate the forest floor directly beneath their crown but not in other parts of the plot. This created some degree of spatial heterogeneity not observed with smaller individuals or a well-mixed canopy. In this study therefore, plant richness may not adequately represent the diversity of resources available for invertebrate use.

Correlations between the Bray-Curtis dissimilarity measures of the plant and invertebrate communities were low (Table 4.6). Microclimate and the composition and structure of the herb-layer and litter, all of which can influence distribution of invertebrates on the forest floor (Szujecki 1987), may not have been associated with the composition of the canopy and subcanopy in the forest patches sampled here. This would account for the observed low congruence between the tree and invertebrate communities. Similar results are reported when comparing vascular plant and invertebrate (represented by ants and beetles) communities in unlogged forests in New South Wales (Oliver *et al* 1998). Rykken *et al* (1997) suggested that the distribution of carabids on the forest floor in Vermont was the result of fine-scale microclimate, microhabitat or intraspecific interactions, rather than broad-scale vegetation and topographical patterns.

4.4.3 Consequences for Reserve Selection

As discussed above, plant species richness was a poor indicator of both α- and β-diversity in invertebrates. Sites selected on the basis of high plant richness would not have included those sites with a high richness of ground-dwelling invertebrates. Likewise, a step-wise selection procedure based on maximising plant diversity across the landscape would have greatly underrepresented invertebrate β-diversity for the first four sites selected.

Plant richness is not in itself of automatic conservation value (Hutcheson *et al* 1999), which is why the Protected Natural Areas programmes has plant diversity as one of several criteria to be used in assessing the conservation priorities of sites. Other criteria include representativeness, rarity, naturalness, long-term ecological viability, size and buffering from surrounding landscape (Kelly and Park 1986). The ability of reserves chosen on naturalness of plant communities or the quality or integrity of a site, to concurrently conserve 'natural' invertebrate communities was not explicitly investigated here. This is because, while it is relatively simple to identify conservable plant species and assemblages, sparse basic biological or ecological information on invertebrate species and assemblages does not permit similar categorizations to be made for the invertebrate community. For example, following standard PNA guidelines, the patch of forest sampled in Taihape Scenic Reserve would be deemed the least desirable of the fourteen sites for protection, due to low representativeness, naturalness and relatively low plant richness. Despite this, Taihape ranks as the third most species-rich site for invertebrates and fourth on the combined invertebrate lists (All Invertebrates and Average

Rank) for complementarity (Table 4.8a), which would suggest that the site represents a more important habitat for invertebrates than plants. It is unknown how many of the species that make up the relatively high invertebrate richness at Taihape are in fact "worth" conserving in the first place (e.g. whether they are regionally rare or abundant, widespread or localised, forest-restricted or transients). Therefore, the ability of plant community integrity to act as a surrogate for conservable invertebrate richness for this region cannot be adequately investigated.

Elsewhere, programmes where plant communities form the basis for reserve selection have been shown to concurrently conserve significant percentages of invertebrate diversity (Noss 1987, Panzer and Schwartz 1998). However, plant integrity measures used in the conservation of tallgrass prairie were shown to be suboptimal for the conservation of invertebrates limited to this habitat (Panzer and Schwartz 1998). Sætersdal *et al* (1993) report that a reserve system in Sweden selected on a similar basis to the PNA programme failed to conserve maximal bird diversity, and in fact was not even the best method for conserving overall plant diversity. This provides a note of caution to assessing conservation areas based on attributes of quality and health; there are some native species that are associated with areas of moderate vegetation disturbance (Crisp *et al* 1998).

Many assessments of forest communities are based solely on tree composition, and indeed this is often the case in the PNA programme (see Lake and Whaley 1995). However, the low β-diversity congruence between plant and invertebrate communities makes it possible that many invertebrate assemblages are being duplicated, or more importantly, omitted from the reserve system. Preserving distinctive vegetation systems is as valid as preserving any other taxonomic group, and as such should not be discouraged. These results, however, suggest that invertebrate communities need to be included in the survey procedure. Even if a potential reserve has a similar vegetation assemblage to a currently protected site, it should still be surveyed to determine the distinctiveness of the invertebrate community.

Unfortunately, such an invertebrate survey would be time-consuming and labour intensive. No potential surrogate groups for invertebrate β-diversity were found in this survey; invertebrate groups, including spiders, performed no better or worse than plants. The reserve selection algorithm based on complementarity demonstrated that there was little difference in the percentage of overall richness captured when selecting sites based on different invertebrate groups (Fig. 4.6). This was probably due to the generally high complementarity scores exhibited by the invertebrate groups between most site pairs. In a step-wise selection procedure, any site chosen, except the two lowest diversity sites Maungakaretu and Pukeroa, was likely to contribute a large number of previously unrepresented species to the overall species pool. It is possible that with the addition of more sites to the selection procedure there may be a greater range in complementarity between individual sites, and thus more variation in the indicator ability of individual taxa. It is also possible that the removal of transient species from the data set, if they could be identified, may enable better characterisation of the forest-living invertebrate community. As it stands now, no one group acted as a good surrogate for the rest of the ground-active community. Hutcheson *et al* (1999) suggested Malaise-trapped beetles as the best invertebrate group for characterising terrestrial communities. The beetles (excluding carabids) trapped by pitfall in this study were actually one of the poorest performing groups in terms of β-diversity congruence with all other invertebrate groups (Table 4.8b). The undeniable benefits associated with working with beetles – high species richness, multi-trophism, relatively well-known taxonomy and ecology (Hutcheson *et al* 1999) – should not overshadow their actual ability to represent other invertebrate species.

There appears to be a greater potential for an invertebrate α-diversity (as opposed to β-diversity) indicator in reserve selection. Used in conjunction with the PNA programme, sites of high invertebrate diversity could be identified, allowing decisions to be made when presented with a choice between sites consisting of similar vegetation attributes. Four groups – spiders, wasps, flies and bugs – exhibit the strongest cases for further investigation (Fig. 4.4). In a review of invertebrate biodiversity indicators in New Zealand, Hutcheson *et al* (1999) do not recommend the use of Diptera due to a combination of too great an abundance in samples, increasing time and cost of sampling, and poor taxonomic knowledge. However, the examples given by the authors are from studies where sampling methods targeted flying insects (i.e. Malaise traps and window traps). In this study pitfalls sampled only those flies active at the litter level, and abundances were proportionally lower. Almost 80% of individuals captured over all sites were from one of three species, which reduced sorting and identification time even further. While there were inevitable cases of splitting and lumping in the morphospecies reference collection, accurate estimates of fly diversity using this method are possible with care. A possible disadvantage with the use of Diptera as a bioindicator is the potential for a high number of transient species in the sample, with flies having been captured in patently unfavourable habitats (Hughes *et al* 2000). This could be a factor in the patterns exhibited by this group in the present study, but only knowledge of the habitat preferences of individual species can determine to what degree. Most of the bugs caught in this study would also be expected to be transient in the litter faunal community, as herbivory is the trophic strategy of the majority of species within this group. In addition, the richness of bugs was low enough for misidentifications to have a large effect on data analysis.

Sorting and identification to morphospecies was particularly difficult for wasps due to the small size of many of the species. Wasps are a generally poorly known group in New Zealand (Hutcheson *et al* 1999), though they have demonstrated potential in ecological monitoring internationally (Lewis and Whitfield 1999). Using wasps as indicators of biodiversity in New Zealand would be reliant on a good base of expert taxonomists.

Of the four groups with the strongest correlation with overall invertebrate richness, spiders are offer themselves as potentially the most useful as α-diversity indicators. Although juveniles cannot be reliably identified, adult spider morphospecies richness has proved to be a good estimator of actual spider richness (Oliver and Beattie 1996a). There is generally low movement of species between forest patches and physiognomically dissimilar adjacent habitats (Bishop and Riechert 1990, Kajak and Lukasiewicz 1994), reducing proportion of transients likely to be in the sample. Spider abundance was moderate in the pitfall samples, thus reducing the time required for sorting and identification that can make super-abundant groups a disadvantage in ecological surveys (Hutcheson *et al* 1999).

4.4.4 Caveats

There are several important caveats to the results observed in this chapter. The richness patterns are only relevant to the scale at which they were sampled. For example, plants show distinct patterns of richness with altitude and latitude across the whole of New Zealand (Ohlemüller and Wilson 2000), and it cannot be assumed from this study that invertebrates will not show similar national patterns. It also cannot be assumed that the same patterns will be replicated in the forests of other Ecological regions in New Zealand, nor different habitats (e.g. wetlands, farmland, scrubland) within the same region. The only way to examine how well these patterns relate to other situations is for nationwide invertebrate surveys, something that is desperately required if only to increase baseline knowledge.

The richness measures represent only a sample of each site. As any conservation effort is going to be concerned with the whole area (in most cases), it would be desirable to sample the invertebrate community of the whole area, to determine full species lists. Some of the invertebrate groups may have a greater proportion of species with clumped distributions within sites than others, and thus potentially have a greater number of species left to find at a site. Also, due to the use of pitfalls in the sampling scheme, the species collected represent only a subset of the actual invertebrate fauna present at these sites. New Zealand forest canopies and trunks contain a high number of species (e.g. Moeed and Meads 1983, McWilliam and Death 1998), many of which will be unrepresented in pitfalls. These results have been interpreted only in terms of the ground-dwelling invertebrate community; any patterns exhibited here may or may not be paralleled by the canopy fauna. However, the ground invertebrate fauna is generally considered as an important component in the functioning of forest ecosystems (Moulder and Reichle 1972, Keesing and Wratten 1998), so the conservation value of this group should not be underestimated.

It is unknown how many of the invertebrate species caught are forest specialists rather than transients from adjacent habitats, and so it is also unknown whether these species require conservation as such. However, in the absence of this knowledge, it makes sense to preserve as much of the invertebrate diversity as possible until informed decisions can be made with regards to species ecology and distribution. In the pursuit of this, spiders, flies and wasps demonstrated the greatest potential as α-diversity indicators for the invertebrate community. Similar surveys of forest patches around both the Rangitikei Ecological Region and New Zealand will be able to test the generality of these results, and truly assess the utility of biodiversity indicators in reserve selection.

CHAPTER FIVE

Thesis Conclusion

THESIS CONCLUSION

Invertebrates are an important component in terrestrial ecosystems and as such require greater attention than has been currently received in New Zealand (Keesing and Wratten 1998). The surrogate species concept is relatively unexplored for terrestrial habitats in New Zealand, but the highly modified landscape with numerous disturbances, such as foreign species invasion, habitat fragmentation and anthropogenic pollution, creates numerous opportunities for the application of indicator taxa to monitor ecosystems. This study demonstrates how just one invertebrate group, the spiders, has the potential to be used to some extent in disturbance monitoring, habitat classification and reserve selection, and raises suggestions that the surrogate species concept may be of use in national management and conservation programmes.

Spiders meet several of the criteria for ecological indication in forest habitats (Chapter 2). They are easily sampled; abundant, widespread and diverse; have relatively low population fluctuations; have a range of dispersal abilities; show a response to habitat change; and can be representative of other taxa. Apart from certain logistical problems, such as unclear taxonomy and relatively sparse biological knowledge for many species, spiders would appear to be worthy of the next step in the indicator selection process, the detailed hypothesis testing advocated by McGeoch (1998). This involves explicitly testing the ability of the indicator group to respond to the disturbance being monitored in a predictable, measurable manner. Until this is done, no firm conclusions can be made regarding the ultimate utility of spiders as ecological indicators.

The spider community was able to classify broadly different habitat types along a successional gradient (Chapter 3). Though many of the species sampled were found in only small numbers, when analysed as a whole, the spider community was able to distinguish between seral stages. This ability has a number of uses in the management of ecosystems, especially in judging the success of ecosystem restoration following disturbance (Keesing and Wratten 1998, Reay and Norton 1999). Beetles have been suggested as useful for habitat classification in New Zealand (Hutcheson *et al* 1999, Hutcheson and Kimberley 2000), but these results illustrate that other groups should also be considered. The ability of spider family relative abundance data to distinguish between seral stages is also an important finding, as it suggests that sorting and identification time can be reduced in these situations by only identifying specimens to family without greatly reducing the resolution of the data set.

Spiders were one of four groups, along with flies, wasps and bugs, that showed potential as indicators of ground-active invertebrate α-diversity in forest remnants (Chapter 4), though any of the eight invertebrate groups sampled would have proved to be better indicators of total invertebrate diversity than plants. Indeed, these results suggest that invertebrate communities may not be fully represented by a system of reserves selected by plant communities. Plant diversity was a poor indicator of invertebrate diversity, both within single sites and between sites, with measures of plant community composition having a low congruence with the community composition of invertebrates. While there were no readily apparent invertebrate surrogates for overall invertebrate β-diversity, it would seem important to include invertebrates in future Protected Natural Area surveys, where at the very least the diversity of invertebrate species could be used to select between sites of similar vegetation attributes. This is not a new recommendation as a number of other studies have made similar suggestions (Keesing and Wratten 1998, Oliver *et al* 1998, Hutcheson *et al* 1999).

Overall, spiders display an ability to be an informative group in several aspects of ecological monitoring, and offer themselves for further research into all aspects of their biology and ecology. It is also advantageous that spiders are one of the few invertebrate groups that hold a degree of prominence in public awareness, which may make them more amenable to generating conservation interest given additional education on their unique features and benefit to ecosystems (New 1999).

The results and conclusions contained here are derived from a relatively short period of time in a restricted set of forest patches. However, the results and conclusions would seem to encourage further research into the surrogate species concept in New Zealand. There may be numerous other invertebrate groups that could serve as surrogates depending on the monitoring objectives, but have hitherto received little scientific attention due to the difficulties associated with sampling and identification of small-bodied, little-known taxa. It is strongly recommended that there be further studies into other groups in ecological monitoring, using proven methods such as identifying to morphospecies that allow for informative surveys in the absence of a fully described fauna. If invertebrates are incorporated into standard methodological frameworks for terrestrial monitoring, then the increase in demand for taxonomic and biological services may attract even more scientists to the field. Monitoring for conservation and management need not be constrained by the limits of scientific knowledge. Indeed, there remains a great opportunity for well-planned and constructed ecological monitoring programmes to be used to increase general scientific knowledge about the focal ecosystems and associated fauna.

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APPENDIX

APPENDIX:
Species Lists for Spiders, Beetles, Flies and Wasps Collected from Fourteen Forest Sites in the Rangitikei Ecological Region

ORDER: ARANEAE

AGELENIDAE
Orepukia geophila

AMAUROBIIDAE
Pakeha sp.

AMPHINECTIDAE
Amphinecta sp., *Aorangia ansa, Aorangia* sp., *Mamoea maorica, Maniho pumilio, Maniho vulgaris, Paramamoea incerta*

ANAPIDAE
Novanapsis spinipes, Zealanapis armata

ARANEIDAE
Arachnura feredayi

CLUBIONIDAE
Clubiona convoluta , *Clubiona peculiaris*

CYATHOLIPIDAE
Tekelloides flavonotatus

CYCLOCTENIDAE
Cycloctenus centralis, Toxopsiella perplexa, Toxopsiella sp.

GNAPHOSIDAE
Hypodrassodes maoricus, Hypodrassodes sp.

HAHNIIDAE
sp.

HEXATHELIDAE
Hexethele sp., *Porrhothele* sp.

HUTTONIIDAE
Huttonia sp.

IDIOPIDAE
Misgolas sp.

LINYPHIIDAE
Laetesia sp1., *Laetesia* sp2., *Mynoglenes* sp., *Mynogleninae?* sp.

LYCOSIDAE
Allotrochosina schauinslandii, sp. Lycosid sp 1, sp 2 ?

MALKARIDAE
sp.

MECYSMAUCHENIIDAE
Zearchaea clypeata

MICROPHOLCOMMATIDAE
Textricella sp.

MIMETIDAE
Mimetus sp.

MITURGIDAE
Uliodon sp1., *Uliodon* sp2.

NICODAMIDAE
Megadictyna thilenii

ORSOLOBIDAE
Duripelta borealis

SALTICIDAE
Trite auricoma, sp1., sp2.

SEGESTRIIDAE
Ariadna septimcincta, *Ariadna* sp.

STIPHIDIIDAE
Cambridgea foliata, *Cambridgea* sp.

SYNOTAXIDAE
Meringa sp., sp.

TETRAGNATHIDAE
Nanometa sp.

THERIDIIDAE
Achaearanea sp1., *Achaearanea* sp2., *Dipoena* sp., *Episinus conifera*, *Episinus* sp., *Euryopsis* sp1., *Euryopsis?* sp2., *Phoroncidia* sp1., *Phoroncidia* sp2., sp1., sp2.

THOMISIDAE
Diaea sp1., *Diaea* sp2., *Sidymella angularis*

ZODARIIDAE
Forsterella faceta

ORDER: COLEOPTERA

ADERIDAE
'*Xylophilus*' sp.

ANOBIIDAE
Ptinus speciosus

ANTHICIDAE
Cotes sp., *Sapintus pellucidipes*

ANTHRIBIDAE
Phymatus sp.

BELIDAE
Cyrotyphus tridens

BYRRHIDAE
Synorthus sp.

CARABIDAE
Agonum sp., *Aulacopodus puella*, *Aulacopodus* sp., *Ctenognathus adamsi*, *Dicrochile cephalotes*, *Haplanister crypticus*, *Holcaspis mordax*, *Holcapsis mucronata*, *Holcapsis cf. mucronata*, *Holcapsis sinuiventris*, *Holcapsis vagepunctata*, *Lecamomerus sharpi*, *Mecodema florae*, *Mecodema* cf. *oconnori*, *Mecodema validum*, *Megadromus capito*, *Megadromus turgidicaeps*, *Molopsida seriatopora*, *Notagonum lawsoni*, *Pentagonica vittipennis*, *Plocamostethus planiusculus*, *Tachys antarcticus*, *Zolus* sp.

CERAMBYCIDAE
Astetholea sp., *Hybolasius* sp., Lamiinae nr *Somatidia* sp., *Ptinosoma* sp.

CERYLONIDAE
Hypodacnella rubripes

CHRYSOMELIDAE
Adoxia sp., *Eucolaspis* sp., *Peniticus* sp.

CLAMBIDAE
sp.

CLERIDAE
Paupris aptera

COCCINELLIDAE
Adoxellus sp., *Harmonia antipoda*, *Rhyzobius rarus*, *Rhyzobius* sp.

CORTICARIIDAE
Aridius costatus, *Aridius nodifer*, *Lithostygnus* sp., *Melanophthalma* sp

CORYLOPHIDAE
Holopsis sp., *Sericoderus* sp.

CRYPTOPHAGIDAE
Atomaria lewisi, *Micrambina* sp., *Thortus* sp.

CURCULIONIDAE
Agacalles sp., *Brachyolus punctatus*, *Exomesites* sp., *Geochus* sp., *Lyperobates* sp., *Nestrius* sp., *Oreda notata*, *Rhopalomerus* sp., *Scelodolichus* sp., Brachycerinae spp., Cossoninae spp., Cryptorhynchini spp., Curculionini spp., Molytini spp., sp.

ELATERIDAE
Agrypnus variabilis, *Conoderus exsul*, '*Ctenicera*' sp., *Ochosternus zealandicus*, sp.

EROTYLIDAE
Cryptodacne sp.

HISTERIDAE
Parepierus sp.

HYDROPHILIDAE
Cercyon sp., *Cyloma guttulatus*, *Cyloma lawsonus*, *Exydrus gibbosus*, *Tormissus linsi*

LEIODIDAE
Inocatops sp., *Mesocolon* sp., *Paracatops* sp.

LUCANIDAE
Paralissotes stewarti

MELANDRYIDAE
Hylobia sp., sp.

MYCETOPHAGIDAE
Triphyllus sp.

NEMONYCHIDAE
Rhinorhynchus rufulus

NITIDULAE
Epuraea imperialis, *Epuraea* sp., *Omosita colon*

OEDEMERIDAE
Thelphassa nemoralis

PHLOEOSTICHIDAE
Priasilpha obscura

PTILIIDAE
Notoptenidium sp.

SALPINGIDAE
Salpingus sp.

SCARABAEIDAE
Costelytra zealandicum, *Saphobius* sp1., *Saphobius* sp2.

SCIRTIDAE
sp.

SCRAPTIIDAE
Nothotelus sp.

SCYDMAENIDAE
sp.

STAPHYLINIDAE
Anotylus sp., *Brouniellum* sp., *Eupines* sp., *Hamotulus* sp., *Falagria* sp., *Quedius* sp., *Sepedophilus* sp., *Silphotelus nitidus,* Aleocharinae sp., Omaliinae sp., Scaphidiinae sp., Staphylininae sp.

TENEBRIONIDAE
Archaeoglenes costipennis, *Artystona rugiceps*, *Menimus* sp., *Mimopeus opaculus*, *Omedes substriatus*

ULODIDAE
Brouniphylax sp., *Syrphetodes marginatus*

ZOPHERIDAE
Pristoderus bakewellii, *Pycnomerus* sp., sp.

ORDER: DIPTERA

ANISOPODIDAE
Sylvicola notata

BIBIONIDAE
Dilophus sp.

CALLIPHORIDAE
Calliphora stygia, Calliphora vicia, Chrysomya rufifacies, Pollenia pernix, Pollenia sp1., *Pollenia* sp2.,*Pollenia* sp3., *Pollenia* sp4., *Xenocalliphora clara, Xenocalliphora neozelandica, Xenocalliphora* sp.

CECIDOMYIIDAE
Lestremia sp., sp.

CERATOPOGONIDAE
Forcipomyia, Paradasyhelea

CHIRONOMIDAE
sp1., sp2.

CHLOROPIDAE
Tricimba tinctipennis

DITOMYIIDAE
Nervijuncta sp.

DOLICHOPODIDAE
Achalcus sp., *Chrysotimus* sp., *Micropygus* sp., *Micropygus vagans, Parentia fuscata, Parentia restricta, Parentia* sp.

DROSOPHILIDAE
Drosophila busckii, Drosophila kirki, Drosophila sp., sp.

EMPIDIDAE
Abocciputa pilosa

EPHYDRIDAE
Hydrellia tritici

HELEOMYZIDAE
Allophylina albitarsis, Allophylopsis bivittata , Allophylopsis scutellata, Fenwickia caudata, Fenwickia claripennis, Fenwickia nuda, Fenwickia sp., *Xeneura picata*

HELOSCIOMYZIDAE
Scordalus femorata

KEROPLATIDAE
Chiasmoneura fenestrata, Neoplatyura brookesi, Neoplatyura sp., *Pyrtaula punctifusa*

LAUXANIIDAE
Sapromyza neozelandica, Sapromyza simillima

MUSCIDAE
Calliphoroides antennatis, Idiohelina sp.

MYCETOPHILIDAE
Allodia fragilis, Anomalomyia guttata, Austrosynapha sp., *Morganiella fusca, Morganiella* sp., *Mycetophila colorata, Mycetophila fagi, Mycetophila filicornis, Mycetophila solitaria, Mycetophila submarshalli, Mycetophila subspinigera, Mycetophila vulgaris, Mycetophila* sp., *Tetragoneura flexa, Tetragoneura fusca, Tetragoneura oblique, Tetragoneura spinipes, Zygomia bifasciata, Zygomyia flavicoxa, Zygomyia immaculate, Zygomyia* sp.

PALLOPTERIDAE
Maorina bimacula

PHORIDAE
Abaristophora sp., Beckerinini sp1., Beckerinini sp2., Bothroprosopa sp., *Megaselia* sp1., *Megaselia* sp2., *Megaselia* sp3., *Palpocrates* sp., Phorinae sp., sp.

PSEUDOPOMYZIDAE
Pseudopomyza flavitarsis

PSYCHODIDAE
Psychoda harrisi, Trichomyia sp.

SARCOPHAGIDAE
Oxysarcodexia varia

SCATOPSIDAE
Anapausis sp., *Coboldia fuscipes*

SCIARIIDAE
Ctenosciara constrictans, Ctenosciara rufulenta, Ctenosciara xanthonota, Ctenosciara sp., sp1., sp2., sp3., sp4., sp5., sp6.

SCIOMYZIDAE
Neolimnia obscura

SIMULIIDAE
Austrosimulium sp.

SPHAEROCERIDAE
Howickia trilineata, Howickia sp., *Leptocera mediospinosa, Phthitia* sp., sp.

STRATIOMYIDAE
Australoberis refugians, Australoberis sp., Benhamyia sp., Neactina sp., Zealandoberis substituta

TABANIDAE
Dasybasis opla, Dasybasis sp.

TACHINIDAE
Pales sp., *Perrissina albiceps, Proscissio* sp., *Trigonospila brevifacies,* sp1., sp2., sp3., sp4.

TERATOMYZIDAE
Teramyza sp.

TIPULIDAE
Amphineurus bicinctus, Amphineurus hudsoni, Austrolimnophila crassipes, Austrolimnophila leucomelas, Austrolimnophila obliquata, Brevicera sp., *Gynoplistia cuprea, Leptotarsus atridorsum, Leptotarsus* sp. *Limonia unicornis, Paralimnophila skusei*

ORDER: HYMENOPTERA

BRACONIDAE
Alysiinae sp., Cotesia sp., Doryctinae sp., Rogas sp., sp.

COLLETIDAE
Hylaeus sp.

DIAPRIIDAE
Diphoropria sp1., Diphoropria sp2., Maoripria sp., Pantolytomyia sp., Archaeopria sp., Ambositrinae sp., Belytinae sp1., Belytinae sp2., Belytinae sp3., Belytinae sp4., Belytinae sp5., Belytinae sp6., Diapriinae sp1., Diapriinae sp2., Diapriinae sp3., Diapriinae sp4., Diapriinae sp5., Diapriinae sp6., Diapriinae sp7., Diapriinae sp8.Diapriinae sp9., Diapriinae sp10., Diapriinae sp11., Hemilexomyia sp., Spliomicrus sp1.Spliomicrus sp2., Spliomicrus sp3., Trichopria? sp.

EULOPHIDAE
sp.

FIGITIDAE
Anarchus sp.

ICHNEUMONIDAE
sp.

MEGASPILIDAE
Conostigmus sp., sp.

MYMARIDAE
Australomymar sp1., Australomymar sp2.

PLATYGASTERIDAE
sp.

POMPILIIDAE
Epipompilus insularis, Priocnemis monachus, Spictostethus calvus, Spictostethus nitidus

PROCTOTRUPIDAE
sp1., sp2., sp3.

PTEROMALIDAE
Cerocephalinae, Neocalosoter sp., sp.

SCELIONIDAE
Archaeoteleia sp, sp1., sp2., sp3.