Spatial complexity and microclimatic responses of epiphyte communities and their invertebrate fauna in the canopy of northern rata (*Metrosideros robusta* A. Cunn.: Myrtaceae) on the West Coast of the South Island, New Zealand

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Spatial complexity and microclimatic responses of epiphyte communities and their invertebrate fauna in the canopy of northern rata (*Metrosideros robusta* A. Cunn.: Myrtaceae) on the West Coast of the South Island, New Zealand

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Rain forest canopies are renowned for their very high biodiversity and the critical role they play in key ecological processes and their influence on global climate. Despite that New Zealand supports one of the most diverse and extensive epiphyte flora of any temperate forest system, few studies have investigated epiphyte communities and their invertebrate fauna along with factors that influence their distribution and composition. This thesis represents the first comprehensive study of entire epiphyte communities and their resident invertebrate fauna in the canopy of New Zealand's indigenous forests. The aim of this study was to determine spatial patterns of epiphyte and invertebrate species richness, abundance and community composition in relation to abiotic variables, and in particular, the responses of these communities to elevated temperature and rainfall. This study was carried out in coastal lowland podocarp-broadleaved forests at two sites on the West Coast of the South Island of New Zealand. Samples from 120 mat-forming epiphyte assemblages located on inner canopy branches of 40 northern rata (*Metrosideros robusta*) trees were studied to characterise the component flora and fauna. Additionally, biomass, branch and tree characteristics and community responses to treatments designed to elevate temperature and rainfall to simulate predicted climate change were measured.

This investigation revealed astonishing diversity and functional complexity of epiphyte and invertebrate life in this ecosystem. The 30.6 kg (dry weight) of epiphyte

material collected contained a total of 567 species, 170 epiphyte and 397 invertebrate (excluding immature specimens and mites) species, including at least 10 species new to science and many undescribed species Epiphyte communities were found to be dominated by non-vascular plants (80 % of the total species richness), particularly liverworts and invertebrate communities were dominated with respect to abundance (~ 80 % of the total individuals) by Acari, Collembola and Hymenoptera (primarily ants) and functionally by scavengers and ants.

Epiphyte and invertebrate communities were highly variable with respect to spatial patterning of species richness, abundance and composition across sites, among trees within sites and among branches within trees. Overall, a highly significant proportion, > 75 %, of the variance could be attributed to differences at the branch level, but these differences could not be explained by the environmental factors measured. There were no consistent relationships between the spatial pattern of epiphytes and invertebrates, or between vascular and non-vascular plants. However, there were significant positive correlations between epiphyte biomass and invertebrate species richness ($r = 0.472$; $p < 0.0001$) and abundance ($r = -0.395$; $p < 0.0001$), as well as non-living epiphyte biomass and scavenger species richness ($r = 0.4$; $p < 0.0001$).

Microclimatic measurements taken on epiphyte mats were also highly variable with respect to temperature and relative humidity at similar physical locations within the same tree as well as across trees within sites. There was also considerable variation in the intensity and frequency of climatic extremes, although potentially harmful climatic conditions were experienced by all the epiphyte mats for which weather variables were measured. Negative correlations existed between both epiphyte and invertebrate community composition and increased temperatures expressed as cumulative degree days above 5˚C. However, variability was such that there was no direct evidence that increased temperature and rainfall treatments had an effect on invertebrate species richness, abundance or diversity.

Northern rata host trees harbour an astonishingly diverse and complex canopy flora and fauna that is characterised by high spatial variability. Such variability highlights that to determine species distribution and community dynamics in canopy habitats in response to disturbance caused either by climate change or invasive species the structure of entire communities at different taxonomic and spatial scales, along with their responses to microclimatic factors, need to be studied. If such complexities are not taken into account, inappropriate interpretation may result in poor decisions concerning the conservation status, vulnerability and subsequent management of such unique ecosystems.

Keywords: Abundance, biomass, bryophytes, canopy, climate change, colonisation, community composition, epiphytes, guild composition, invertebrates, lichens, microclimate, New Zealand, non-vascular plants, relative humidity, species richness, temperate rain forest, temperature, vapour pressure deficit, vascular plants

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Chapter 1

General Introduction

The scientific community in New Zealand has been slow to recognise the importance of forest canopies when addressing global biodiversity and climate change issues. That is surprising for a number of reasons. First of all New Zealand has recently been recognised internationally as one of only 25 biodiversity 'hotspots' worldwide (Mittermeier *et al.*, 1999) due to its high degree of plant species endemism and exceptionally high levels of habitat loss (Myers *et al.*, 2000). A high degree of endemism is also characteristic of most New Zealand arthropod groups (Wodzicki & Wright, 1984; Klimaszewski & Watt, 1997), but only about 50% of New Zealand's insect species have been described (Emberson, 1994) and far fewer are understood ecologically (Hutcheson, 1999). The canopies of New Zealand's forests may harbour many unidentified species thereby providing additional information on the status of terrestrial biodiversity in New Zealand and contributing to global estimates. However, it is important to identify and understand the components of that diversity in this unique, and as yet still largely unknown habitat, to protect it from the threats posed by habitat loss, invasive species and now, climate change.

Canopy researchers in other parts of the world have shown that forest canopies play a critical role in forest ecosystem dynamics and form "the substrate, the buffer and the catalyst for interactions between the soil and the atmosphere" (Didham & Fagan, 2004). Most photosynthesis takes place in the upper forest canopy and it is also here where the majority of organic carbon is fixed and stored, transpiration occurs, and CO_2 is exchanged with the atmosphere (Ozanne *et al.*, 2003). Forest canopy processes also affect and regulate below ground processes and soil fertility by regulating nutrient flow to the soil through litter fall. Understanding the functional complexity of forest ecosystems and the canopy processes that drive them is fundamental to maintaining biodiversity and ecosystem services in these already vulnerable systems.

New Zealand like the rest of the world will be affected by climate change and the projections of its impacts are alarming. The New Zealand vegetation has undergone

major changes in response to past climate change (McGlone *et al.*, 1996) and major changes in the geographic range of canopy trees can be expected with future warming (Whitehead *et al.*, 1992). Consequently, distributional changes are also likely to be seen in the epiphytes and invertebrates that are dependent on these tree species, as well as changes in plant-insect interactions, forest community composition and ecosystem functioning. The response and sensitivity of the majority of species to changes in temperature and moisture regimes are largely unknown and difficult to predict, partly because the regimes themselves are difficult to predict. Prediction is difficult because of the large variability of both the New Zealand climate (due to the El Niño Southern Oscillation (ENSO) and the Interdecadal Pacific Oscillation (IPO)) as well as topography at the local scale. Nevertheless, New Zealand climate studies are important in the global context as they help verify extreme trends observed from Northern Hemisphere locations in the mid-latitudes of the sparsely monitored Southern Hemisphere (Salinger & Griffiths, 2001).

The overall aim of this PhD was to investigate the composition of mat-forming epiphyte communities and their resident invertebrate fauna to progress current knowledge and provide data to underpin more extensive studies that may address some of the issues raised above. The information provided by this study will be detailed species inventories, data concerning the functional diversity and spatial distribution of canopy species and their response to increased temperatures and rainfall under future climate-change scenarios. The sites used for this study were located in a lowland, mixed podocarp-broadleave rain forest in the northern part of the West Coast of the South Island, which is one of the most species rich and diverse regions in New Zealand (Department of Conservation, 1993). This project is a unique opportunity to provide an in-depth inventory of species in New Zealand's distinct canopy habitat that will improve our understanding of 1) the status and distribution of New Zealand's biodiversity, 2) the role of canopy communities in the functioning of forest ecosystems, and 3) its vulnerability to threats from invasive species and climate change.

The following sections review current information about forest canopies, their importance in forest ecosystems, and their vulnerability to threats from climate change. This is preceded by a brief review of existing canopy studies in New Zealand, followed by a brief outline of the contents of the five research chapters that comprise this thesis.

1.1 The role of forests

Forests play a key role in the functioning of the biosphere through processes such as carbon and water cycling, they modify the climate and architectural structure of physical environments, and they are primary producers of energy and nutrients which they provide to the other members of the ecosystem (Purves *et al.*, 1995). Forests also supply many goods and services crucial to human well-being. In recent times, forests have been greatly reduced in their extent to meet the demands of a rapidly increasing human population (Perrings *et al.*, 1995), which has led to major losses of biodiversity. New and additional pressures on forests are now arising from global climate change to which these ecosystems are predicted to be particularly vulnerable (Salinger & Griffiths, 2001).

Forests exhibit an astonishing species richness of arboreal communities (Moran & Southwood, 1982), partly because of their wide geographical distribution, but also because of their high structural complexity that provides great opportunities to species for niche diversification (Lawton, 1978). It has become apparent that forest canopies in particular, are not only important as a habitat for the majority of the Earth's species (Novotny *et al.*, 2002), but also because they contribute to the many ecological processes that drive forest ecosystems. This knowledge and the vast research potential offered by canopies has sparked considerable interest in canopy research among scientists, particularly with respect to understanding and predicting the impact of climate change on terrestrial communities (Didham, 2002).

1.2. Background of canopy research

Canopy research is a relatively new discipline but has revolutionised our understanding of biodiversity and its distribution over the past 25 years. In 1982, entomologist Terry Erwin challenged existing estimates of the number of species that live on Earth by identifying tropical forest canopies as major habitats for an exceptionally high number of arthropod species, many of which were new to science (Erwin, 1982). With this ground-breaking paper Erwin laid the foundation for future canopy research centering around global species estimates and inventories (Primack, 1998) and the concept of identification of global biodiversity hotspots by Mittermeier *et al.* (1999) almost 20 years later. It has emerged from such studies that a large proportion of the diversity in

the canopy consists of arthropods and epiphytes and that both groups contribute substantially to the dynamics of the forest ecosystems they inhabit (Nadkarni & Lowman, 1995; Watt *et al.*, 1997; Ozanne *et al.*, 2003).

Recent realisation of the importance of forest canopies and their enormous research potential has led to the development of highly sophisticated and technologically advanced canopy access techniques, including rafts and canopy cranes that have been reviewed by Moffett & Lowman (1995). These technologies have facilitated a wide range of sampling methods that were discussed by Basset *et al.* (1997). Despite major improvements in gaining access to forest canopies, difficulties remain concerning the sampling and studying of canopy insects *in situ*. Commonly-used sampling techniques, such as branch clipping and insecticide fogging, are generally biased toward certain species and may provide little information about the canopy habitat with which the organisms are closely associated. The small size of many canopy organisms and lack of taxonomic knowledge or expertise for many groups further complicates *in situ* studies and has led to a bias toward larger and more easily identifiable species, or toward low taxonomic resolution.

Nevertheless, the sophistication of canopy access techniques has led to a shift from purely descriptive toward more quantitative studies (Coxson & Nadkarni, 1995). These techniques have encouraged an increasing focus on understanding the patterns and processes that shape canopy communities (Nadkarni & Lowman, 1995) as well as the involvement of the canopy in physiological processes and the provision of ecosystem services. Ozanne *et al.* (2003) provide a synthesis of major current research projects and the latest findings regarding different aspects of canopy research including tree response to elevated CO_2 levels, plant-animal interactions and atmospheric changes. The launch of the Global Canopy Programme in 2002 was another milestone (Didham, 2002) and is aimed at integrating different access techniques, providing detailed studies of canopy processes, facilitating information sharing, and integrating researchers from different scientific fields (Lowman & Wittman, 1996) as diverse as plant physiology, conservation biology, and global atmospheric chemistry.

1.3 The role of canopy communities in forest ecosystem functioning

1.3.1 The role of the forest canopy

By definition, the forest canopy is the combination of leaves, twigs, and branches of trees, shrubs or both that form the top layer of a forest ecosystem (Moffett, 2000). The amount and spatial arrangement of these components, their morphological features, such as shape and size, and surrounding climatic factors are determinants of canopy structure. Canopy structure plays an important role in modifying climatic conditions within the canopy and at the interface of the biosphere and atmosphere, such that conditions high above the ground influence conditions on the forest floor. The canopy is a transition zone where wind energy is absorbed, radiation exchanged, rain intercepted, retained and redistributed, and biologically important compounds such as CO_2 and water vapour are exchanged (Parker, 1995). Consequently the canopy forms a gradient along which environmental conditions change, the impact being harshest on the outer canopy and declining through the lower canopy tiers toward the forest floor.

Canopy structure and complexity are related to total above ground biomass and species diversity, both of which appear to increase with architectural complexity. Hallé (1995) showed that diminishing morpho-diversity in tropical forests toward the upper canopy was related to the climatic conditions becoming harsher toward the top. Erwin (1995) also showed that gradients in light, temperature, moisture and foliage quality within canopies of individual trees affect the distribution of various arthropod species. Despite these influences there can be no doubt that in tropical and temperate rain forests one of the most important contributions to canopy complexity and biodiversity is made by epiphytes.

1.3.2 The role of epiphytes

Many forest canopies support extensive flora of vascular and non-vascular epiphytes. By definition an epiphyte is a plant that grows upon another plant but is not parasitic on it. Vascular epiphytes differ in their dependence on the tree. They include species that can live independent of the tree, or are dependent on the tree for part of their lives, or are totally restricted to the canopy (Benzing, 1995). Non-vascular epiphytes are divided into lichens, bryophytes and free-living algae and depend on the atmosphere

for water and inorganic nutrients. Unlike vascular epiphytes that are largely associated with continually high humidity habitats in low latitudes, non-vascular plants can survive long periods of drought and also thrive in areas that alternate between wet and dry conditions (Rhoades, 1995).

The composition and epiphyte load of the canopy are determined by the availability and stability of suitable substrate such as bark (and, in some cases, leaf surfaces), suspended soils, host tree characteristics such as stand age, abiotic factors, and chance establishment. Bark characteristics, for example, affected bryophyte composition of conifers in British Columbia (Kenkel & Bradfield, 1981) and lichen abundance in the southern Appalachian Mountains (Becker, 1980). With respect to host tree characteristics, Burns (1995) correlated epiphyte diversity in a New Zealand forest with old trees with typically tall canopies.

Epiphytes are an important component of many forests where they play an important role in water regulation, mineral cycling, and the provision of habitats to other organisms. For example, Benzing (1995) showed that epiphytes store water for later release and subsequent use by other vegetation, thus maintaining high humidity in the canopy during dry periods. Canopy epiphytes also serve as sinks for nutrients absorbed from the atmosphere (e.g. carbon and nitrogen) (Lowman & Wittman, 1996) and as such play an important regulatory role in nutrient conservation (Coxson & Nadkarni, 1995). Non-vascular epiphytes, for example, are adapted to hold nutrients and may moderate overall nutrient transfer by preserving surplus nutrients and slowly releasing them at times of nutrient shortage (Nadkarni, 1984a). In addition, epiphytes intercept abscised plant litter from within the canopy providing decomposition sites. Epiphytes are also a direct source of nutrition for many arboreal animals, particularly insects that may utilise pollen or nectar of flowering epiphytes or feed directly on the plant tissue. Because of their dependence on the atmosphere for nutrients (carbon, nitrogen and airborne particles) and water, many epiphytes and their associated biota have potential as bioindicators (Nadkarni & Lowman, 1995). Lichens and bryophytes, for example, are frequently used to monitor changes in air quality. Studies on epiphytes and their response to climate change may also help address some of the most important questions about the impact of global climate change on terrestrial communities (Rhoades, 1995).

Epiphytes differ substantially in structure, growth habit and function and offer a diverse range of microhabitats and microclimatic conditions. They provide a wide

range of resources such as food, camouflage, protection from predators, nesting and oviposition sites, and shelter from climatic extremes to unique communities of invertebrates. Individual epiphytic plants such as a bromeliad, for example, can constitute a variety of microhabitats ranging from fully aquatic at and near the centre of the plant to increasingly humus rich, drier sections in older more marginal leaf axils (Benzing, 1995). Such habitat diversity offers much scope for utilisation by a range of species, many of which may be specific to only one particular microhabitat on the entire plant. Other studies have also shown that there are distinct differences with respect to overall arthropod density and composition at order level between the arthropod fauna inhabiting suspended soils and leaf litter accumulating on epiphytes, and the fauna of associated ground litter (Kitching *et al.*, 1997). Besides promoting arthropod diversity, epiphytic microhabitats have been proposed to modify the climatic conditions of the surrounding area and thus permit arthropods to persist in extreme climatic conditions in the forest canopy (Benzing, 1995; Prinzing, 1997). Despite increasing knowledge, the role that epiphytes play in the determination of canopy arthropod richness remains poorly investigated and untested.

1.3.3 The role of canopy invertebrates

Canopy invertebrates, primarily insects, constitute a large proportion of global species richness and are vital to the functioning of forest ecosystems. Invertebrates are involved in nutrient cycling, plant reproduction, and are an important food source for forest birds and other vertebrates (Majer & Recher, 1988), and can often influence canopy structure by their feeding activities (Hijii et al., 2001). Invertebrates consume an astonishing variety of foods derived from plants, animals and fungi and have developed specialised feeding habits that contribute to different stages of the nutrient cycle within forest ecosystems. Scavengers and herbivores contribute substantially to the decomposition of organic matter and the release of nutrients. Herbivores are also involved in maintaining plant community composition and structure by feeding on sap and seeds and by pollination and seed dispersal (Gullan & Cranston, 2000). Invertebrates also contribute greatly to the maintenance of animal community structure within the canopy through processes such as predation and parasitism, and in some forest ecosystems, as vectors for diseases of larger animals.

Invertebrates in general have evolved traits that link them to the specific microenvironments to which they are adapted (Erwin, 1995). Many canopy studies show invertebrate distribution and overall community composition is influenced by environmental conditions and the availability and location of suitable habitats, but so far no single factors have been consistently identified as important. For example, the distribution of different arthropod groups has been shown to be associated with tree age and tree species (Schowalter, 1989) and old-growth forest characteristics (Winchester, 1997). Other studies have shown the composition and structure of dipteran (Didham, 1997) and general arthropod assemblages (Schowalter & Ganio, 1998) are related to tree species. Studies investigating the influence of canopy height on the distribution and community composition of arthropods (Schowalter & Ganio, 1998) have also produced inconsistent results.

While it is generally acknowledged that species diversity increases with habitat heterogeneity, only a few studies have looked at specific canopy microhabitats as determinants of species richness and invertebrate assemblages. Among such studies are those by Lindo & Winchester (2006), Kitching et al. (1997), Paoletti et al. (1991) and Nadkarni & Longino (1990) who found that the communities of suspended litter habitats differed substantially in their composition and abundance from communities on the forest floor. Another example is a study by Prinzing (1997) that demonstrated that lichens provided key microhabitats to Collembola living in harsh conditions on exposed tree trunks.

Because of their high sensitivity to changes in temperature and rainfall, invertebrates, particularly insects, have great potential as indicators of environmental change. Such climatic factors have a profound impact on their developmental rates, survival, and reproductive success (Gryj, 1998; Speight et al., 1999), as well as the intimate interaction and dependence of many insect species on plants.

Canopy arthropods and invertebrate communities have been shown to have a significant involvement in the ecological processes of the forest ecosystem. Because of their sheer numbers and diversity, and given their importance in the canopy system more knowledge is needed to assess the impact of climate change on this forest ecosystem as a whole. However, basic patterns in canopy invertebrate community structure remain poorly understood largely because of their taxonomic complexity (Schowalter, 1989) and the difficulties associated with in situ studies particularly in the not easily accessible canopy habitat.

1.4 Canopy research in New Zealand

Contrary to international trends in canopy research, New Zealand rain forest canopies have received little attention and remain largely unexplored. New Zealand's epiphyte fauna is one of the most diverse and extensive of any temperate forest system (Benzing, 1995; Dawson & Lucas, 2005) and has often been likened to a tropical rain forest. Indeed, a considerable component of the flora has affiliations with tropical families or genera (Dawson & Sneddon, 1969; Galloway, 2007) and epiphyte total diversity compares to or exceeds that of some tropical rain forests (Dickinson et al., 1993). Unfortunately, studies by Dickinson et al.(1993) and Hofstede et al. (2001) are the only ones that have examined entire epiphyte communities and the factors influencing their distribution and composition in the canopy. Previous epiphyte studies have mainly been carried out on aspects of the ecology of single vascular plant species, including parasitic mistletoes (Ladley & Kelly, 1996), plant physiological characteristics of different species (Jane & Green, 1985; Green et al., 1995) and their role in forest productivity (Coops et al., 1998) and have been ground-based. Distributional studies of non-vascular plants (Scott, 1966; Beever, 1984) have been restricted to easily accessible parts of tree trunks.

The composition, diversity, and spatial distribution of canopy invertebrate communities are even less understood than for epiphytes. Exceptions are studies by Didham (1992; 1997) and McWilliam & Death (1998) that highlighted the importance of canopy habitat characteristics and season, respectively, and their influence on community structure. A study by Affeld (Affeld, 2002) showed distinct differences in the composition of insect communities between canopy epiphytes and the forest floor and discovered several new species. Wardle *et al.* (2003) demonstrated that the size of arboreal habitats and host tree species affect decomposer community composition and decomposition processes. The effects of fragmentation on canopy-dwelling insects has been researched by Ewers *et al.* (2002) as part of the Hope River forest fragmentation project.

1.5 Climate change and its implications for forest ecosystems

There is little doubt that the Earth's climate is warming and that increased temperatures are already affecting terrestrial and marine ecosystems in many parts of the world.

Temperature rises similar and larger than those observed in the last 100 years have occurred in the past (UNEP, 1993; McGlone *et al.*, 1996), but the rate of warming is unprecedented in global history (Dale & Rauscher, 1994; Auckland Regional Council, 2002). Regional climate change projections for New Zealand show an increase in temperature of 0.1 to 1.4°C by 2030 and 0.2 to 4°C by 2080 (Wratt *et al.*, 2004), which would be accompanied by a 60 % increase in the annual mean westerly wind speed and lead to significant increases in rainfall in western areas of New Zealand (Hennessy *et al.*, 2007). Although the projected changes are below those predicted by global climate models (IPCC, 2001), concerns have been raised over the vulnerability of forests, which are already under considerable pressure from habitat destruction, modification and fragmentation (Salinger & Griffiths, 2001).

Higher temperatures may lead to increased invasion by exotic species adapted to warmer temperatures (IPCC, 2001). Further, plants will be affected by increasing atmospheric CO_2 concentrations that may increase the growth rates and yield of many species, which in turn may alter the competitive balance through its effect on stomatal regulation and water use (Bazzaz & McConnaughay, 1992). Additionally, increased CO_2 may modify the chemical composition of leaves and other plant parts that will affect availability of resources for herbivores (Mattson, 1980), as well as decomposition rates (Woodward, 1993), soil fertility and below-ground processes (Wolters *et al.*, 2000). Climate warming is likely to have significant effects on population dynamics, in particular the reproductive biology of species (McCarty, 2001). It may change the sex ratio of some species (Dorit *et al.*, 1991) and will change the rate of development and growth of some insects (Gullan & Cranston, 2000).

Even though the complex interactions between the biological components of ecosystems and climate are poorly understood (Orians & Soule', 2001), it is clear that changes at one level of biodiversity (genetic, species and ecosystem level) can cause changes to the other levels and result in loss of biodiversity and species extinction (UNEP, 1993). The consequences of loss of biodiversity are likely to be severe in many instances because of the role many species and populations, no matter how obscure, play in ecosystem functioning (Luck *et al.*, 2003) and provision of ecosystem services. Furthermore, the epiphytic canopy ecosystems in New Zealand rain forests are uniquely diverse and the character of whole forests could be irreparably changed if these systems were to suffer serious biodiversity loss. It is therefore crucial to identify the responses of the unique canopy species, communities and ecosystems to climate

change at regional and local scales, especially to extreme events (Salinger & Griffiths, 2001). Knowledge of how such responses vary over a range of spatial scales is essential for appropriate interpretation of observations and to make reliable predictions. But first it is essential to characterise the canopy plant and invertebrate communities at high resolution before any change occurs. Responses to changing climate can then be measured using appropriate apparatus, experimental design and controls. Climate change and human and invasive species impacts are likely to significantly disturb canopy habitats and their communities. Colonisation studies will give indications of vulnerability of communities to disturbance, their speed of recovery and the rate at which emerging habitats are utilised. Such studies will also provide information on the sources from which potential coloniser species are derived. Such data can then be used to develop informed conservation and management strategies to mitigate the direct and indirect threats of habitat change as a result of human intervention as well as climate change. Well informed decisions will be required such that biodiversity and essential ecosystem services are preserved and the unique character of our forests remains for future generations to enjoy.

1.6 Theoretical Background

Community ecology seeks to understand how patterns of species abundance, diversity and distribution are influenced by abiotic factors and species interactions (Brown, 1995). Various theories have been developed to explain existing community patterns, including: niche partitioning, disturbance, succession and equilibrium, island biogeography and, more recently, stochastic demography and dispersal.

1.6.1 Niche theory

Niche theory asserts that communities are limited membership assemblages of species that coexist in interactive equilibrium with other species in the community under strict niche partitioning of limiting resources (Hubbell, 2001). Hutchinson (1957) introduced the idea that the niche of a species is a multi-dimensional combination of factors related to a species' tolerance to various environmental conditions and resource requirements. Each species has a 'fundamental niche' that it can occupy in the absence

of competitors, but this niche is reduced to a 'realised niche' when competitors are present (Begon *et al.*, 2008). Consequently, changes in how species interact through e.g. competition, will change niche characteristics such as size, location and overlap with other species (Wiens, 1992). Studies concerned with understanding the limitations of niche overlap among species have shown high overlap among sets of a few species that differ in their ecological niche to other sets of overlapping species within the community (Wiens, 1992). Thus, the abundance of any one species in a community is strongly linked to the abundance of ecologically highly similar species (Kelly *et al.*, 2008). Indeed, the concept that communities are structured by sets of species from different ecological guilds has been especially useful when comparing communities with different species compositions (Southwood *et al.*, 1982; Stork, 1987). Even though niche theory has been challenged by the unified neutral theory (Hubbell, 2001), it nevertheless has played an important role in addressing a variety of issues, including evolutionary processes, competition and predation dynamics (Hirzel & Le Lay, 2008). It has also been useful in predicting which species can coexist, based on the concept that only species with sufficiently different niches may coexist within the same ecological community (Chase & Leibold, 2003).

1.6.2 Disturbance, succession and equilibrium theory

Natural communities are dynamic and change over time as a result of species migration, colonisation, the establishment of viable populations, and loss of species through local extinction (Begon *et al.*, 2008). Disturbance is a major cause of changing community composition and dynamics and facilitates natural selection in the evolution of life histories (Sousa, 1984). Disturbance can be of physical (e.g. fires, storms, earthquakes, flooding, drought) or biological (e.g. predation, grazing, digging by animals) nature and can cause minor to extreme changes to the composition and productivity of a community (Odum, 1969). However, the degree of change depends on the extent, magnitude and frequency of the disturbance as well as the vulnerability of organisms in the community (Sousa, 1984). Disturbances temporarily alter environmental conditions and can create new unoccupied habitats that are rapidly colonised by pioneer species. These early colonisers continue to modify their environment, and can either facilitate, prevent or not affect the establishment of

additional species (Krebs, 2001). This progressive change in community composition is termed succession.

During early succession species diversity increases as new species arrive, but in later successional stages it may decline as a result of competition and the dominance of locally superior competitors. However, whether a species is present or absent in a community is ultimately determined by a species' dispersal abilities, the existence of suitable environmental conditions and resources, and the competitive ability of other species in the community (Begon *et al.*, 2008).

Clements' (1916) classical theory of succession sees a community as highly deterministic and predictable where colonising and establishing organisms reach a stable end-point called the climax or equilibrium. This idea has been largely abandoned by modern ecologists in favour of non-equilibrium theories, based on Gleason's (1926) species-individualistic models where communities are the result of similarities in their species' requirements and tolerance, and partly chance. However, successional patterns in communities vary over different spatial and temporal scales, because natural environments and communities are not homogenous. Thus, species within a community may be differently affected by disturbance events in highly heterogeneous environments. The impact on a community is also influenced by the timing of the disturbance event. For example, a community would be overall stronger affected and over a longer period during breeding season and at times when juveniles are abundant and vulnerable, but these effects may be very localised and negligible over larger spatial scales. Also, because succession can be a rather lengthy process it is difficult to capture the entire sequence of successional changes in a community of e.g. a temperate rainforest. Thus, sampling of locations at a particular point in time will only reflect the recent ecological history of that location and be indicative of the available species pool of organisms that can persist in that environment. To understand the successional dynamics of communities, it is therefore essential to sample communities over a range of temporal and spatial scales.

1.6.3 Theory of island biogeography

The theory of island biogeography was developed by MacArthur & Wilson (1967) to explain patterns of variation in species diversity on islands. Their theory proposed that

the species richness of an island is determined by the rate of colonisation of new species and the rate of established species becoming extinct and that both are in equilibrium. Colonisation by new species is strongly influenced by the accessibility of an island in terms of its distance to the nearest species pool, such as other nearby islands or the mainland, and the dispersal abilities of species in the source pool. Generally, more isolated islands are less likely to be colonised than less isolated islands. The rate of extinction, on the other hand, is strongly linked to island size. Larger islands contain more habitat and habitat types and, thus, more resources. They thereby not only reduce the probability of extinction due to chance events, but also facilitate successful establishment of species after immigration.

Obviously, there are limits to the number of species that can exist on an island and these are generally lower on small islands than large islands. Nevertheless, in the early stages of island colonisation a large proportion of species arriving on an island will be from source pool(s) elsewhere. As more species arrive the number of species already present on the island will increase and approach the number of species available from the source pool(s), thus, leading to a drop in immigration rate (Whittaker & Fernández-Palacios, 2007). Further, the abundance of each species on an island will decrease as the number of species increases and thereby increase a species likelihood of going extinct. Once immigration and extinction rates are in equilibrium they should equal the rate of species turnover, which can be similar for islands regardless of size or degree of isolation (Whittaker & Fernández-Palacios, 2007).

Since the theory of island biogeography has emerged various studies not only have tested its validity (Diamond, 1969), but it has proved fundamental to debate in island ecology and conservation biology (Whittaker & Fernández-Palacios, 2007). Indeed, the theory has become an important tool in the creation and design of nature reserves and habitat and the estimation of extinction rates (May *et al.*, 1995). Further, island biogeography theory has been extended to any ecosystem surrounded by unlike ecosystems including forest fragments within human-modified landscapes, and also epiphyte ‘islands’ in the canopy of temperate and tropical forest systems (Ellwood *et al.*, 2002; Wardle *et al.*, 2003; Fagan *et al.*, 2006).

1.6.4 The unified neutral theory of biodiversity and biogeography

Neutral theory of biodiversity and biogeography or neutral theory is based on the theory of island biogeography, but differs in that neutrality is defined at the individual rather than species level, and thereby allows extinction rates to be predicted as a function of population size (Hubbell, 2001). It further states that species are functionally equivalent and that community changes arise as a product of drift, dispersal, and random speciation. Although it is a radical shift from traditional niche theory both are complementary (Chave, 2004). Neutral theory is concerned with species rich communities such as tropical rainforest that contain a high proportion of rare species and where niche partitioning becomes implausible to explain species coexistence (Kraft *et al.*, 2008). Unlike niche partitioning theory, neutral theory asserts that stochastic demography and dispersal are more important factors in determining community patterns and allow the coexistence of species with similar niches (Leibold, 2008). A major criticism of neutral theory relates to it's ignorance toward biological mechanisms that may contribute to niche differentiation in real communities (Brown, 2004; Chave, 2004). However, by attempting to integrate neutral and niche theory in the future, it might be possible to identify and fulfil the conditions required to apply neutral theory (Chave, 2004).

1.7 Objectives of this study

- To compile high resolution species inventories of mat-forming canopy epiphytes and their resident invertebrate fauna to characterise and examine spatial patterns of species richness, abundance and community composition.
- To examine spatial and temporal patterns in canopy microclimate and to determine relationships between microclimatic conditions and epiphyte species richness and biomass.
- To determine relationships between patterns of diversity, species richness and abundance of epiphyte communities and their resident invertebrate communities across various spatial scales.

- To experimentally test the response of canopy invertebrate communities to elevated temperatures and rainfall predicted by climate change scenarios for the West Coast of the South Island.
- To investigate the colonisation of artificial soil habitats by canopy invertebrates and the role of nearby epiphyte mats as a source of coloniser species.

1.8 Outline of Chapters 2 - 6

Chapter 2 *Characterisation of the canopy flora: Can spatial variation in epiphyte diversity and community structure be predicted from sampling vascular epiphytes alone?* Studies examining the biotic and abiotic determinants of spatial variation in epiphyte diversity have largely ignored non-vascular epiphytes despite their higher species richness in both tropical and temperate rain forests. Here, the similarity in spatial patterns of species richness, biomass and community composition across geographic regions, among trees within regions, and among branches within trees between vascular and non-vascular species is investigated. The suitability of using vascular plant diversity to estimate total epiphyte biodiversity is discussed.

Chapter 3 *Canopy microclimate: How does it influence the distribution and biomass of epiphyte communities?* The influence of microclimatic variability on canopy communities has been widely discussed, but few studies provide fine resolution data. Here, temperature, relative humidity and vapour pressure deficit were measured for inner crown epiphyte mats and the effect of microclimate on epiphyte species richness and biomass is investigated.

Chapter 4 *Characterisation of the canopy fauna: Is invertebrate community structure and its spatial variability associated with their host epiphyte communities?* The invertebrate fauna of epiphyte mats was characterised at high resolution. Epiphyte communities along with the resources they provide are highly aggregated and this should be reflected in the composition of their resident invertebrate communities. Relationships between patterns of diversity, species richness and abundance of invertebrate communities and their host epiphyte communities were examined across various spatial scales.

Chapter 5 *How do arboreal invertebrate communities respond to increased temperatures and moisture predicted under climate change?* Epiphyte mats were exposed to a range of experimentally increased temperature and rainfall treatment combinations *in situ* to investigate the effects of simulated climate change on the species richness, abundance and diversity of their resident invertebrate communities. Relationships between invertebrate community parameters and climate variables are described and the vulnerability of canopy invertebrates to climate change and aspects of their epiphytic habitat are discussed.

Chapter 6 *Colonisation: What is the contribution of epiphyte mats to the colonisation of artificial soil habitats by canopy invertebrates?* The importance of epiphyte mats as a source of coloniser species for newly available suspended soil habitats was investigated and discussed. If variation in the composition of coloniser communities across artificial soil habitat is determined by the composition of invertebrate communities in adjacent epiphyte mats, the coloniser communities should represent a subset of the epiphyte mat communities.

Chapter 7. General discussion and conclusions. This Chapter synthesises the findings of this study and will discuss their implications.

Chapter 2

Can spatial variation in epiphyte diversity and community structure be predicted from sampling vascular epiphytes alone?

Abstract

Non-vascular epiphytes have been largely ignored in studies examining the biotic and abiotic determinants of spatial variation in epiphyte diversity. The aim of this study was to test whether the spatial patterning of species richness, biomass and community composition across geographic regions, among trees within regions, and among branches within trees, is consistent between the vascular and non-vascular components of the temperate rain forest flora. This study was carried out in coastal lowland podocarp-broadleaved forests on the West Coast of the South Island of New Zealand. Single samples (30 × 25 cm) were collected from 96 epiphyte assemblages located on the inner branches of 40 northern rata (*Metrosideros robusta*) trees. For each sample, branch characteristics, such as branch height, branch diameter, branch angle, branch aspect, and minimum and maximum epiphyte mat depth, were recorded. Biomass for each individual epiphyte species was determined. Northern rata was host to a total of 157 species, comprising 32 vascular and 125 non-vascular species, with liverworts representing 41 % of all species. Within epiphyte mats, the average total organic biomass of 3.5 kg m^{-2} of branch surface area consisted largely of non-living biomass and roots. Vascular and non-vascular epiphytes showed strikingly different spatial patterns in species richness, biomass and composition between sites, among trees within sites, and among branches within trees, which could not be explained by the branch structural characteristics we measured. The two plant groups had no significant association in community composition ($r = 0.04$, $p = 0.08$). However, the species richness of vascular plant seedlings was strongly linked to the presence/absence of lichens. Non-vascular plants contributed substantially to the high species richness and

biomass recorded in this study, which was comparable to that of some tropical rain forests. High variability in community composition among epiphyte mats, and very low correlation with any of the environmental factors measured, possibly indicate high levels of stochasticity in seed or spore colonization, establishment success or community assembly among branches in these canopy communities. Although this study found some evidence that vascular plant seedling establishment was linked to the presence of lichens and the biomass of non-living components in the epiphyte mats, there was no correlation in the spatial patterning or determinants of species richness between non-vascular and vascular plants. Consequently, variation in total epiphyte biodiversity could not be predicted from the measurement of vascular plant diversity alone, which highlights the crucial importance of sampling non-vascular plants when undertaking epiphyte community studies.

2.1 Introduction

Epiphytes are characteristic of the canopies of many temperate and tropical rain forests where they contribute substantially to overall plant species diversity and biomass and are involved in crucial ecosystem processes, including water and nutrient cycling, primary productivity and CO_2 exchange (Nadkarni & Matelson, 1991; Zotz *et al.*, 1997; Richardson *et al.*, 2000a; Clark *et al.*, 2005; Fleischbein *et al.*, 2005). The majority of studies examining the biotic and abiotic determinants of spatial variation in epiphyte diversity have focused on the vascular component of the flora (monocotyledons, dicotyledons and ferns), and ignored non-vascular epiphytes (lichens, mosses and liverworts). However, a growing number of detailed inventories now suggest that non-vascular plants may often, if not always, comprise a greater component of total epiphyte richness in both tropical and temperate biomes (Cornelissen & ter Steege, 1989; ter Steege & Cornelissen, 1989; Jarman & Kantvilas, 1995; Hofstede *et al.*, 2001). Moreover, fundamental differences in the morphology, physiology, life history traits and adaptive strategies of vascular and non-vascular epiphytes result in quite different responses to environmental conditions and spatial variation in habitat structure (van Leerdam *et al.*, 1990; Rhoades, 1995; Freiberg & Freiberg, 2000). Consequently, it is questionable whether quantitative extrapolation to patterns in the diversity and spatial distribution of epiphytes, in general, is warranted

from the sampling of vascular epiphytes alone, unless there are strong biotic (facilitative or competitive) interactions between vascular and non-vascular epiphytes.

In rain forest canopies, for example, there is evidence that non-vascular epiphytes facilitate the colonization and succession of vascular epiphytes by forming a suitable substrate for vascular seedlings to establish in, and by acting as water and nutrient reservoirs (Nadkarni, 1984b; Tewari *et al.*, 1985; Benzing, 1995; Laman, 1995; Hietz *et al.*, 2002). This close interaction between non-vascular epiphytes and the initial life stages of vascular epiphytes might suggest that there is a positive association in the diversity and distribution of the two epiphyte groups. However, there have been few, if any, quantitative studies testing the degree of correlation between vascular and non-vascular epiphytes in rain forest canopies, possibly because the compilation of complete inventories involves significant logistical difficulties in canopy access, sampling small and rare species, with limited taxonomic knowledge (Flores-Palacios & García-Franco, 2001). From ground-based, terrestrial studies, though, there has been some evidence for broad positive correlations between the species richness of vascular and non-vascular plants, such as between vascular plants and mosses, and ferns and bryophytes in both tropical (Fensham & Streimann, 1997) and temperate (Pharo *et al.*, 1999) forest understories, respectively, in Australia. In other cases, no association or a negative relationship has been found between vascular and non-vascular species richness (Söderström, 1981). These conflicting data make it difficult to predict the degree of spatial association in the relative diversity and distribution of vascular and non-vascular epiphytes in forest canopies.

This study explicitly tests the degree of similarity in the spatial patterning of vascular and non-vascular epiphyte richness and biomass across multiple spatial scales in the diverse temperate rain forest flora of New Zealand. Despite the impressive diversity of the New Zealand non-vascular epiphyte flora, very few studies have investigated patterns of diversity and distribution of non-vascular epiphytes and the environmental factors influencing their relationship to vascular epiphyte communities in the forest canopy. As in other biogeographic regions, most studies documenting the distribution of canopy epiphytes in New Zealand have focused solely on vascular species, such as mistletoes (Loranthaceae) (Ladley & Kelly, 1996; Norton & de Lange, 1999; Bannister & Strong, 2001) or vines and lianas, using ground-based observations (Baars & Kelly, 1996; Baars *et al.*, 1998; Knightbridge & Ogden, 1998; Burns & Dawson, 2005). Meanwhile, studies of epiphytic bryophytes (Scott, 1966; Beever,

1984; DeLucia *et al.*, 2003) and lichens (Green *et al.*, 1995) have been restricted to easily accessible habitats such as the lower portion of tree trunks (Scott & Rowley, 1975; Setzepfand, 2001). The exceptions are studies by Dickinson *et al.* (1993) and Hofstede *et al.* (2001), which have highlighted the importance of microclimatic and structural factors (height and location on the tree, branch diameter, aspect and humus depth) in influencing epiphyte community composition and species distribution within tree crowns and between different host tree species.

The goals of this study were to undertake a comprehensive survey of vascular and non-vascular epiphytes within undisturbed rain forest canopies, and to test whether the spatial patterning of species richness, biomass and community composition across geographic regions, among trees within regions, and among branches within trees, was consistent between the vascular and non-vascular components of the flora. If the spatial determinants of non-vascular epiphyte diversity and biomass are not consistent with those of the vascular epiphyte flora, then this calls into question the ability to extrapolate regional or global measures of epiphyte richness based on sampling vascular epiphytes alone. In order to determine the degree to which the results of this study might be extrapolated across biogeographic regions, a literature survey was conducted of the relative importance of vascular and non-vascular plant species richness in rain forest canopies in a range of tropical and temperate biomes.

2.2 Methods

2.2.1 Study sites

This study was conducted at two coastal sites on the West Coast of the South Island of New Zealand: Bullock Creek (42°06′ S; 171°20′ E), Punakaiki in the Paparoa National Park, and the Heaphy Track (41°10′ S; 172°10′ E), 21 km north of Karamea in the Kahurangi National Park. Both areas have a largely undisturbed forest cover (Department of Conservation, 1996). In addition, Kahurangi National Park is a centre of biodiversity where half of New Zealand's native plants are found, many of which are endemic to this area (Department of Conservation Nelson/Marlborough Conservancy, 2001).

The maritime climate and prevailing westerly winds bring high rainfall and mild temperatures throughout the year. Punakaiki has a mean annual rainfall of 2619

mm compared with 1868 mm in Karamea (NIWA, 2007). Mean annual relative humidity is 83 %. Average daily minimum and maximum temperatures range from 13.6 - 20.6 ºC in summer (December to February) and 7.6 - 13.8 ºC in winter (June to August) in Punakaiki, and from 11.8 - 21 ºC in summer and 5.1 - 13.8 ºC in winter in Karamea. Frosts are rare (NIWA, 2007).

Both study sites support highly complex mixed lowland podocarp-broadleaved rain forest, in which our study species northern rata, *Metrosideros robusta* (Myrtaceae), is one of the dominant emergent trees, reaching heights of 35 to 40 m. Northern rata is one of 11 species in the genus *Metrosideros* that are endemic to New Zealand (Smith-Dodsworth, 1991) and it commonly starts life as an epiphyte in the canopy of large trees. It is found from the northern tip of the North Island to about 90 km south of Punakaiki, where it reaches its southern geographic limit. However, this tree species has been in serious decline because native forests have been heavily logged and converted to agriculture (Simpson, 2005). At Punakaiki, northern rata is co-dominant with several species of the Podocarpaceae family such as *Dacrydium cupressinum*, *Podocarpus totara* and *Prumnopitys taxifolia*. The main canopy layer extends up to 20 m above the ground and is largely dominated by *Weinmannia racemosa* (Cunoniaceae), but scattered individuals of *Elaeocarpus dentatus* (Elaeocarpaceae) and *Nothofagus fusca* (Fagaceae) are present on the higher slopes at Karamea. In the sub-canopy, *Dicksonia squarrosa* (Dicksoniaceae) and *Cyathea smithii* (Cyatheaceae), *Rhopalostylis sapida* (Arecaceae), *Quintinia serrata* (Escalloniaceae) and *Pseudopanax* spp. (Araliaceae) are predominant. The understorey is a thicket of impenetrable vines formed by *Freycinetia banksii* (Pandanaceae) and *Ripogonum scandens* (Smilacaceae) with the understorey trees including some individuals of *Coprosma foetidissima* (Rubiaceae), *Myrsine salicina* (Myrsinaceae) and *M. australis*. *Blechnum* (Blechnaceae) ferns and bryophytes are dominant on the forest floor in Punakaiki, but scarce in Karamea.

2.2.2 The epiphyte flora

The epiphyte flora of New Zealand's rain forests is amongst the most diverse and extensive of any temperate rain forest (Benzing, 1995; Rhoades, 1995; Dawson & Lucas, 2005). Epiphyte community composition in New Zealand is typical of most

temperate forests in that bryophytes and lichens feature prominently, while ferns and fern allies are the most species-rich representatives of the vascular flora (Zotz, 2005). Fife (1985) estimated that the New Zealand moss flora consists of about 525 species and hornworts of 15 species, while liverworts are represented by about 620 species (Glenny & Malcolm, 2005). The 1160 species of bryophytes compare to about 1706 lichen species (Galloway, 2007) and 91 vascular epiphyte species (Oliver, 1930). Of the latter, 47 species (following nomenclatural changes, (Dickinson *et al.*, 1993) qualified as typical epiphytes (being habitually epiphytic) and of these 40.2% were endemic. Tropical affinities are apparent amongst non-vascular and vascular plants alike and include several well-represented bryophyte families, such as the mosses Dicranaceae and Orthotrichaceae, the liverworts Frullaniaceae, Lejeuneaceae and Plagiochilaceae (Fife, 1985), the lichen genera *Megalospora* (Megalosporaceae), *Pseudocyphellaria* (Lobariaceae) (Galloway, 2007) and the vascular genera *Freycinetia* (Pandanaceae), *Corynocarpus* (Corynocarpaceae) and *Geniostoma* (Loganiaceae) (Dawson & Sneddon, 1969), although some of the most important tropical epiphyte taxa, such as Bromeliaceae and Araceae, are entirely absent (Zotz, 2005).

Within New Zealand, the most diverse and abundant epiphytic flora is found on the West Coast of the South Island, and epiphytes are a fundamental component of the forest canopy at both the Punakaiki and Karamea study sites. Amongst the most conspicuous species are the large nest epiphytes *Astelia solandri* and *Collospermum hastatum* (both Liliaceae), which can grow up to 2 m in height and form massive discrete clumps in, or close to, branch forks. Somewhat smaller epiphytic growth forms include pendulous orchids and drooping ferns of the family Aspleniaceae, which are often interspersed with filmy ferns (Hymenophyllaceae) and bryophytes that form patches of low-growing, mat-like branch cover.

2.2.3 Tree selection and sample collection

At the study sites, northern rata trees support abundant epiphyte communities. Hence, between April 2004 and January 2005, 20 northern rata trees were selected from an area of approximately 400 ha at each of the two study sites (Figure 2.1). Trees were considered suitable when they supported areas > 0.06 m^2 of mat-like epiphyte cover on each of at least two branches, and provided feasible access to the canopy. The majority

of trees fitted these criteria at both sites. The selected trees ranged in height from 23 to 36 m and had a stem diameter at breast height (d.b.h.) between 87 and 301 cm (mean 192.4 cm).

At each site, five of the 20 pre-selected trees were sampled on each of four separate occasions between April 2004 and April 2005. Each tree was sampled only once. On each of the four sampling occasions epiphyte community samples were collected from a total of 12 quadrats (30 x 25 cm) located on the inner branches (1.0 - 1.5 m from the main trunk) of each tree at approximately 20 m above ground. Only one epiphyte mat was sampled per branch, and either two or three branches were sampled on any given tree. Variation in the number of samples collected per tree was dictated by the design of a field experiment that took into account the patchy distribution of suitable epiphyte mats and sample processing effort without compromising the statistical analysis of the collected data. Access to the canopy was gained using single rope climbing techniques, while moveable safety lines allowed for free movement within the canopy (Winchester, 2004). To overcome sampling limitations resulting from the inaccessibility of some branches, quadrats were selected from a random subset of suitable epiphyte mats that were accessible.

Prior to the collection of epiphytes from the quadrats, the percentage foliar cover of individual plant groups (monocotyledons, lianas, ferns, bryophytes, lichens), as well as the cover of seedlings, litter and bare bark, was estimated *in situ*. Epiphytes in the quadrat samples were carefully detached from the bark with a knife and enclosed in individual plastic bags to minimize the loss of organic matter. Branch height above the ground, branch diameter, branch angle, branch aspect, and minimum and maximum epiphyte mat depth were recorded for each quadrat.

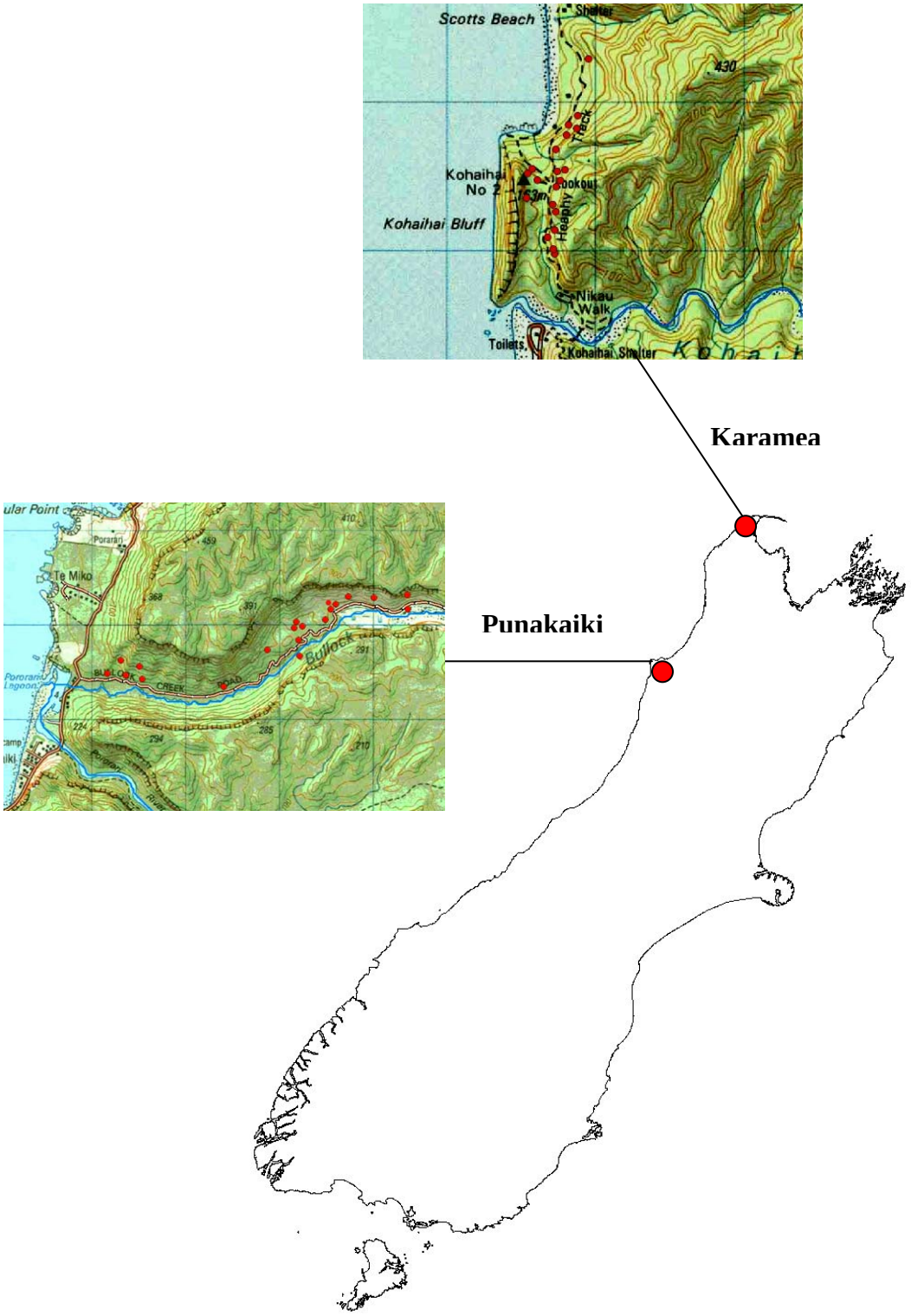


Figure 2.1 Locations of two study sites and 20 northern rata host trees within each site on the West Coast of the South Island, New Zealand

2.2.4 Processing of epiphyte material

In the laboratory, all components of each quadrat were separated, dried and weighed in order to determine the contribution of each component to the total biomass. The organic components of each quadrat were assigned to five categories: above ground tissue of individual plant species, coarse woody material (sticks, bark and seeds), fine litter, roots and soil. To separate the litter and soil from the other components, each sample was thoroughly washed over three stacked sieves of decreasing mesh size (1.7 mm, 500 µm and 75 µm mesh size). After sorting, each component was oven-dried for 72 h at 65ºC and its dry weight recorded.

All plant species were identified following the nomenclature of the Landcare Research Plant Names Database (Landcare Research, 2008, 12. Feb. 2008). Non-vascular plants were identified by expert taxonomists Peter Beveridge (mosses), Rodney Lewington (liverworts) and Barbara Polly (lichens). Reference collections are deposited in the Allan Herbarium, Landcare Research, Lincoln (CHR) and possibly Te Papa Tongarewa Herbarium (WELT).

2.2.5 Data analyses

The distribution and composition of the epiphyte communities at each study site was examined by compiling species inventories and recording the frequency of each species in the quadrats. To make valid comparisons of species richness between the two sites (Gotelli & Colwell, 2001), and assess the completeness of the inventories, sample-based rarefaction curves (with 100 random draws) were generated using EstimateS version 7.5 (Colwell, 2005). To take some account for possible bias from insufficient sampling (Magurran, 2004) two non-parametric incidence-based species richness estimators, Chao2 and ICE (Colwell, 2005), were also used to compare the species richness of major taxonomic groups between the two sites. Both estimators use presence/absence data and give minimum estimates of species richness which are based on the number of rare species found in one and two samples only (Chao2) or in 10 or fewer sampling units (ICE) (Chazdon *et al.*, 1998).

To allow comparison of epiphytic biomass with other relevant studies the biomass per quadrat surface area (750 cm^2) was converted from g cm^{-2} to kg m^{-2} of branch surface area, assuming an approximately equal distribution of epiphyte mats

among branches within the tree. These estimates are realistic given that epiphyte mats are extensive and ubiquitous on almost all branches of trees at these sites.

The similarity of total and individual plant group species composition was examined among individual quadrats within and between study sites using non-metric multidimensional scaling (NMDS) in PRIMER 5 (Clark & Warwick, 2001). Samples comprising only one species with a sole occurrence were removed from the analysis. All data were standardized as a percentage of the total biomass to account for differences in sample volumes and 4^{th} root-transformed so that rarer species made some contribution to the calculation of the similarities (Clark & Warwick, 2001). The NMDS routine was performed with 30 random restarts.

To determine how much of the variation in species richness, biomass and community composition among quadrats was due to geographic site effects, differences among individual trees, or differences among branches within trees, and to take into account the nested design of this study, we carried out a variance components analysis using the method of residual maximum likelihood (REML) (Genstat®9.1, 2006). As a measure of variance in community composition, Axis 1 of the 3-D NMDS ordination was used because this explained most for the variance among samples. The data used in the REML analyses showed no major deviations from normality, hence no transformation was required. Variance components were constrained to be non-negative. Likelihood tests were used to compare competing random models (Snell & Simpson, 1991).

To assess the correlation in spatial patterns of vascular and non-vascular plants across samples the relative biomass distribution of both plant groups was compared using a Mantel test. Matrix randomization was restricted to within sites and 10,000 permutations.

To examine the relationship between community composition and measured abiotic and biotic factors the BIO-ENV procedure in PRIMER 5 was carried out. In this procedure variation in environmental factors (branch height, branch diameter, branch angle, branch aspect, minimum and maximum epiphyte mat depth, tree, site; data were not transformed) is correlated with variation in epiphyte species distribution to identify potential determinants of epiphyte community structure. The Spearman rank coefficient was used to calculate the degree of correlation between the species and environmental data.

2.3 Results

2.3.1 Species richness

A total of 154 epiphyte species (excluding three morphospecies of unidentifiable seedlings) belonging to 51 families and 79 genera were recorded in 96 samples collected across both sites (see Appendix 1). Non-vascular species outnumbered vascular plant species by a ratio of 4:1, with 122 non-vascular species of which half were liverworts. Substantially more species (129) were found at Punakaiki than at Karamea (81), and only 51 species were shared across both sites. All epiphytes were native, and of these at least 52 species were endemic to New Zealand. Most of the epiphytes for which sufficient information was available on their growth habit were facultative or obligate epiphytes, while there were few species of lianas.

The sample-based rarefaction curves for non-vascular and vascular epiphytes showed a similar pattern at each site, in that non-vascular species richness greatly exceeded that of vascular plants (Figure 2.2). Unlike the curves for vascular plants, curves for non-vascular plants showed no sign of saturation, which indicates that not all species present at each site were recorded, despite the intense sampling effort. Identical sampling methods and similar amounts of epiphyte biomass (see below) at both sites yielded significantly more non-vascular species at Punakaiki than Karamea, as indicated by the non-overlapping 95% confidence intervals (Figure 2.2).

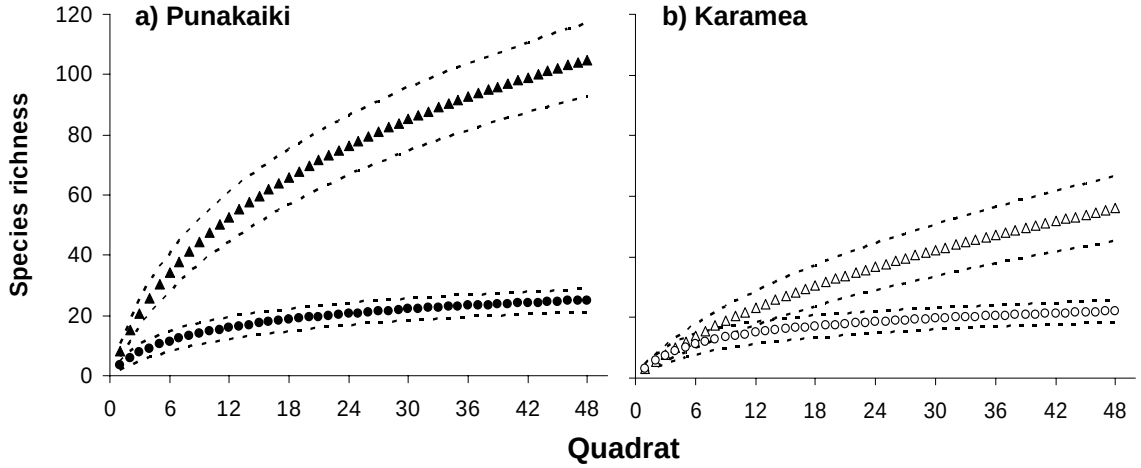


Figure 2.2 Sample-based rarefaction curves and 95% confidence intervals for non-vascular (triangles) and vascular epiphytes (circles) collected at two study sites, (a) Punakaiki and (b) Karamea.

The mean (± CI) number of epiphyte species per quadrat was 11.7 ± 0.8 at Punakaiki and 6.3 ± 0.4 at Karamea, and species from each of the major plant taxa were represented in both areas (Figure 2.3). On average, bryophytes, in particular liverworts, were the most species rich groups in quadrats at Punakaiki. Liverworts also had the highest total number of species, with about double (in Punakaiki) or triple (in Karamea) the number of species recorded for either lichens or mosses (Table 2.1). Vascular plants were represented by similar numbers of species of pteridophytes, dicotyledons and monocotyledons in quadrats at each site, but pteridophytes had the highest total species richness of the vascular plant groups.

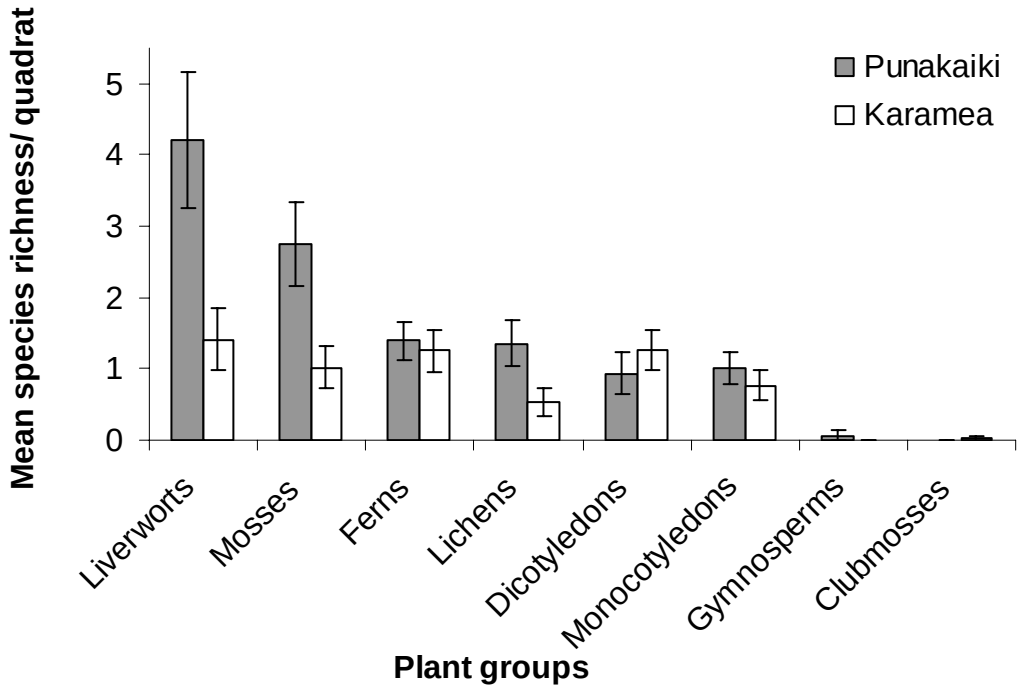


Figure 2.3 Mean (± 95% confidence intervals) number of epiphyte species per quadrat for each of the major plant taxa encountered in samples from 48 inner-canopy branches at each of the two sites.

The species richness estimators Chao2 and ICE calculated that 68.4% and 58.5% of the estimated total species present at Punakaiki and Karamea, respectively, were collected (Table 2.1). Lichens were the most undersampled group in Punakaiki with only 38.7% of the estimated number of species collected. In Karamea, the number of species of liverworts, mosses and lichens recorded each represented less than 50 % of the estimated species present. All monocotyledon and gymnosperm species in

Punakaiki and all dicotyledon species in Karamea estimated to be present were collected.

Table 2.1 Observed richness (with percent of the total in parentheses) and estimated richness (as predicted by ICE and Chao2 estimators) of epiphyte species across plant taxa for the two study sites. The percentage of the estimated species collected for each plant group was calculated by dividing the observed number of species by the mean of the ICE and Chao2 values (x 100) (Colwell, 2005). The proportion of species within each plant group shared by the two sites is given as % overlap.

	Punakaiki				Karamea				%
Plant group	**Observed**	**ICE**	**Chao2**	**% Collected**	**Observed**	**ICE**	**Chao2**	**% Collected**	**Overlap**
Monocotyledons	5 (3.9%)	5	5	100.0	5 (6.4%)	6	5	90.9	100.0
Dicotyledons	8 (6.3%)	12	13	64.0	6 (7.7%)	6	6	100.0	30.8
Gymnosperms	1 (0.8%)	1	1	100.0	0 (0.0%)	0	0	0.0	0.0
Pteridophytes	11 (8.7%)	14	13	81.5	11 (14.1%)	15	19	64.7	37.5
Liverworts	53 (41.7%)	75	74	71.1	32 (24.6%)	58	73	48.9	34.4
Mosses	26 (20.5%)	43	42	61.2	11 (14.1%)	21	29	44.0	31.0
Lichens	23 (18.1%)	51	73	37.1	13 (10.0%)	31	27	44.8	15.6
Total	**127**	**191**	**195**	**68.4**	**78**	**133**	**144**	**58.5**	

The REML variance component analyses indicated strikingly different spatial patterns in species richness for vascular and non-vascular plants. Most of the variability in species richness observed for vascular plants could be attributed to differences among branches within trees, rather than among trees or between sites, as was indicated by the very high proportion of the individual variance components, > 72 % (Table 2.2). Only monocotyledon species richness was significantly influenced by tree-level spatial variation. By contrast, there was highly significant spatial patterning in non-vascular species richness at both the tree and site levels. The species richness of liverworts, mosses and lichens all varied significantly between sites, and liverworts and mosses also showed strong variation in species richness among trees. As a consequence of the much higher relative richness of non-vascular plants, overall spatial patterning in epiphyte species richness corresponded most closely with spatial variation in non-

vascular plants, and there was little association between total epiphyte species richness and the spatial patterning of vascular species richness (Table 2.2).

Table 2.2 Variance components (± standard error, with percentage of the variance components for each plant group in parentheses) for the relative effects of site, tree and branch variation on total species richness and biomass for major plant groups. Significance levels are indicated by asterisks, as follows: *** $p < 0.001$; ** $p < 0.005$; * $p < 0.05$. The branch-level component represents the residual variance in the analysis, therefore there are no associated p-values.

	Variance components		
	Site	**Tree (site)**	**Branch (tree, site)**
Species richness			
Total	13.97 ± 20.75*** (40%)	9.10 ± 3.34*** (26%)	11.50 ± 2.17 (34%)
Monocotyledons	0.003 ± 0.03 (1%)	0.16 ± 0.09* (27%)	0.42 ± 0.08 (72%)
Dicotyledons	0.03 ± 0.08 (3%)	0.18 ± 0.14 (17%)	0.83 ± 0.16 (80%)
Pteridophytes	0.00 ± 0.03 (0%)	0.12 ± 0.13 (12%)	0.85 ± 0.16 (88%)
Liverworts	3.85 ± 5.79*** (35%)	2.96 ± 1.14** (27%)	4.25 ± 0.80 (38%)
Mosses	1.38 ± 2.09** (33%)	1.35 ± 0.46*** (33%)	1.40 ± 0.27 (34%)
Lichens	0.31 ± 0.47*** (26%)	0.02 ± 0.11 (1%)	0.87 ± 0.16 (72%)
Biomass			
Total	0.0 ± 22.9 (0%)	70.6 ± 85.6 (11%)	592.7 ± 111.1 (89%)
Monocotyledons	0.0 ± 4.3 (0%)	2.2 ± 17.0 (2%)	137.5 ± 25.7 (98%)
Dicotyledons	0.0 ± 4.9 (0%)	21.3 ± 17.9 (16%)	112.5 ± 21.1 (84%)
Pteridophytes	0.0 ± 3.1 (0%)	0.0 ± 12.6 (0%)	105.4 ± 19.6 (100%)
Liverworts	9.6 ± 21.3 (4%)	7.4 ± 30.8 (3%)	243.7 ± 45.5 (93%)
Mosses	7.1 ± 18.2 (3%)	48.5 ± 28.7 (23%)	154.7 ± 29.1 (74%)
Lichens	1.0 ± 1.9 (6%)	1.3 ± 2.1 (7%)	15.3 ± 2.9 (87%)
Ordination scores			
Total	0.04 ± 0.08 (9%)	0.21 ± 0.07*** (47%)	0.20 ± 0.04 (44%)
Monocotyledons	-0.02 ± 0.07 (3%)	0.13 ± 0.10 (25%)	0.38 ± 0.09 (72%)
Dicotyledons	-0.02 ± 0.01 (3%)	0.19 ± 0.11 (40%)	0.27 ± 0.09 (57%)
Pteridophytes	0.07 ± 0.14 (12%)	0.40 ± 0.11*** (70%)	0.10 ± 0.02 (18%)
Liverworts	-0.02 ± 0.00 (3%)	0.05 ± 0.06 (10%)	0.43 ± 0.09 (87%)
Mosses	-0.02 ± 0.01 (4%)	0.24 ± 0.10** (46%)	0.26 ± 0.06 (50%)
Lichens	-0.04 ± 0.01** (6%)	0.66 ± 0.13*** (88%)	0.05 ± 0.01 (6%)

As might be expected from the REML analysis, there was no overall correlation between Simpson's diversity of vascular and non-vascular plants ($r = 0.011$, $p = 0.937$) although within the non-vascular taxa the diversity of mosses was correlated with that of lichens ($r = 0.224$, $p < 0.03$) and of liverworts ($r = 0.28$, $p < 0.006$). Similarly, vascular plant species richness was not significantly correlated with the proportion of total biomass represented by non-vascular plants ($r = 0.189$, $p = 0.066$), even though vascular plant richness was higher in epiphyte mats with larger total biomass ($r = 0.208$, $p < 0.04$). However, the species richness of newly established vascular plant seedlings was significantly linked to the presence/absence of lichens ($z = 2.475$, $p = 0.013$).

2.3.2 Biomass

Sample quadrats at both study sites supported similar total biomass with an average dry weight of 3.48 ± 0.22 kg m^{-2} of branch surface area at Punakaiki and 3.52 ± 0.32 kg m^{-2} at Karamea (Table 2.3). On average, soil, roots and litter made up the bulk of biomass at both sites, while woody material and green living biomass of the individual plant groups contributed comparatively low biomass. Moreover, the relative distribution of biomass across the different living and non-living components of the quadrats was similar at both sites (Table 2.3). Most of the green living biomass was comprised of vascular plants, while bryophytes and lichens added only a small proportion. However, when only green living biomass was considered, quadrats at Karamea supported significantly higher vascular plant biomass (0.33 ± 0.03 kg m^{-2}) than non-vascular biomass (0.17 ± 0.04 kg m^{-2}) ($F_{(1,95)} = 7.76$, $p < 0.01$), whereas vascular (0.28 ± 0.03 kg m^{-2}) and non-vascular plant biomass (0.20 ± 0.04 kg m^{-2}) were not significantly different in epiphyte mats at Punakaiki ($F_{(1,95)} = 2.29$, $p > 0.05$). Despite this, the REML variance components analysis showed that the variance in total biomass, and in the biomass of individual plant groups, could be attributed to variation among branches within individual trees, rather than to variation between sites, for both vascular and non-vascular plants (Table 2.3).

Table 2.3 Mean epiphyte biomass per quadrat (± standard error) and distribution of living and dead biomass components for 48 quadrats at each of two study sites. Living biomass includes all plants and roots, whereas non-living biomass consists of soil, litter and woody material. For comparison, comparative data from the inner branches for two montane (Otonga and Los Cedros) and two lowland (Yasuni and Tiputini) rain forest sites in Ecuador from Freiberg & Freiberg (2000).

	Punakaiki		**Karamea**		**Otonga**		**Los Cedros**		**Yasuni**		**Tiputini**	
	(kg m^{-2})	**%**	(kg m^{-2})	**%**	(kg m^{-2})	**%**	(kg m^{-2})	**%**	(kg m^{-2})	**%**	(kg m^{-2})	**%**
Living biomass	1.45 (0.12)		1.45 (0.14)	41.1	0.87	48	2.57	43	0.76	57	0.92	50
Vascular	0.28 (0.03)	8.0	0.33 (0.03)	9.2	0.40	22	0.57	10	0.48	36	0.51	28
Monocotyledons	0.10 (0.02)	2.8	0.13 (0.03)	3.6								
Dicotyledons	0.06 (0.03)	1.6	0.09 (0.02)	2.5								
Pteridophytes	0.12 (0.02)	3.6	0.11 (0.02)	3.1								
Roots	0.98 (0.10)	28.1	0.95 (0.10)	27.0	0.19	11	0.74	12	0.27	20	0.38	20
Non-vascular	0.20 (0.04)	5.8	0.17 (0.04)	4.9	0.28	15	0.70	12	0.01	1	0.03	2
Lichens	0.03 (0.01)	0.8	0.01 (0.00)	0.1								
Bryophytes	0.18 (0.04)	5.0	0.17 (0.04)	4.8	0.28	15	0.70	12	0.01	1	0.03	2
Liverworts	0.14 (0.04)	4.1	0.07 (0.03)	2.0								
Mosses	0.03 (0.01)	0.9	0.10 (0.04)	2.8								
Non-living biomass	2.02 (0.14)	58.1	2.07 (0.25)	58.9	0.94	52	3.41	57	0.58	43	0.92	50
Litter	0.87 (0.08)	25.1	0.71 (0.09)	20.1	0.07	4	0.15	3	0.04	3	0.07	4
Soil	1.02 (0.08)	29.4	1.25 (0.18)	35.6	0.69	38	2.85	47	0.50	37	0.66	36
Total	3.48 (0.22)		3.52 (0.33)		1.81		5.98		1.34		1.84	

Although gross spatial patterning in epiphyte biomass was similar between vascular and non-vascular plants, there were striking differences in the relative distribution of rare non-vascular species among sites. Patterns in the relative rank–biomass distribution of species in epiphyte communities at the two study sites varied markedly between vascular and non-vascular plants (Figure 2.4). Whereas the relative biomass distribution of vascular plant species was very similar at the two sites, the rank–biomass curves for non-vascular plants differed greatly between sites, with

greater evenness in the relative biomass distribution among species within Punakaiki epiphyte communities (Figure 2.4).

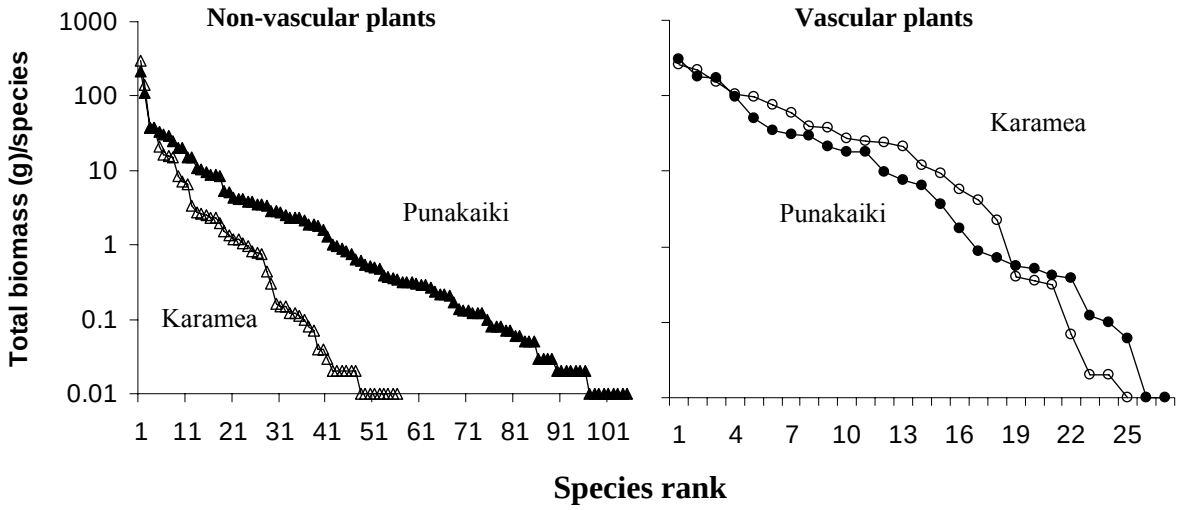


Figure 2.4 Rank-biomass distribution curves for non-vascular (triangles) and vascular plants (circles) recorded at two study sites, Punakaiki (solid) and Karamea (open). Note that the y axis is on a log scale.

Epiphyte communities at both sites were characterized by very few species with high biomass of more than 50 g per quadrat and a very large number of rare species (Figure 2.4). The 10 dominant species at each site comprised 72.3% and 79.8% of the total living above-ground biomass at Punakaiki and Karamea, respectively. Although there were a far greater number of rare non-vascular species overall, non-vascular epiphytes nevertheless contributed a relatively large proportion to the biomass of these 10 species at each site (> 30 %) including the Plagiochilaceae liverworts *Plagiochila deltoidea*, *P. radiculosa* and *Plagiochilion conjugatus*, and the mosses *Hypnum chrysogaster* (Hypnaceae) and *Leptostomum macrocarpum* (Bryaceae). Amongst the vascular species, the Orchidaceae *Earina autumnalis* and *Dendrobium cunninghamii*, the climber *Metrosideros perforata*, and the Hymenophyllaceae ferns *Hymenophyllum nephrophyllum* and *H. sanguinolentum* were the species with the highest biomass loads. Most of these species were present at both sites, but the contribution of each species to the total biomass differed.

2.3.3 Community composition

The NMDS ordination of the relative species biomass in each quadrat showed a very high degree of variation in epiphyte species composition among branches, even within the same tree. In some cases, the epiphyte species composition on two branches within the same tree was as different as that observed between trees at the two geographically separated sites. In a REML variance component analysis on NMDS axis 1 scores, overall epiphyte community composition did not vary significantly between sites, but a highly significant proportion of variance in composition was attributed to variation among trees within sites (47 %) and among individual branches (44 %) (Table 2.2). As a first indication of the degree of association in the relative spatial patterning of vascular and non-vascular plants, a Mantel test directly comparing the relative biomass distribution of vascular and non-vascular plants across samples showed there was no significant association in the community composition of the two epiphyte groups ($r = 0.04$, $p = 0.08$). The degree of dissociation in the Mantel test was not strong, though, suggesting that different taxa within both vascular and non-vascular groups might have widely varying spatial patterning in composition.

In a more detailed assessment of spatial patterning among individual epiphyte taxa, REML analyses showed that one non-vascular group, lichens, had weak but significant variation in species composition between sites (Table 2.2), and more importantly that there was strong variation in epiphyte species composition among trees for two non-vascular groups, lichens and mosses, and for one vascular group, ferns (Table 2.2). For other vascular and non-vascular groups the majority of variation in community composition occurred among branches within trees. As a result of these trends, it is evident that overall variation in epiphyte community composition will depend on the relative richness and relative biomass distribution of species within individual epiphyte classes, for which there is a low degree of association among samples.

The high degree of compositional variation among epiphyte communities within individual quadrats was difficult to explain with the range of environmental variables measured. The BIO-ENV procedure identified a combination of three variables (branch diameter, branch aspect and maximum mat depth) which maximized the grouping of the samples in ordination space, but the correlation coefficient $\rho =$

0.118 was too low to explain the dissimilarities in epiphyte community composition observed among mats.

2.4 Discussion

2.4.1 Vascular and non-vascular plants respond differently across spatial gradients

This study found striking differences in the spatial patterning of vascular and non-vascular richness, biomass and composition between sites, among trees within sites and among branches within trees. It has been suggested that differences in the biology of vascular and non-vascular plants may lead to differing patterns of diversity and distribution in the two groups (Slack, 1990; Pharo *et al.*, 1999). For example, many vascular plants need a substrate to root in that provides them with anchorage, water and nutrients. Irregular availability of water and nutrients in the substrate makes these vascular plants vulnerable to water stress. By contrast, many non-vascular plants can store substantial amounts of water in external capillary spaces amongst the leaves (Pócs, 1980; Proctor, 2000) which enables them to survive prolonged drought periods, and they have the ability to gain nutrients and rehydrate rapidly from atmospheric humidity (Rhoades, 1995; Sillett & Antoine, 2004). Different compositional and distributional patterns in vascular and non-vascular epiphytes generally also reflect the preference of non-vascular plants for cooler and wetter conditions, such as are found at higher elevations and higher latitudes, under which vascular plants decline (Gradstein & Pócs, 1989; Benzing, 1995; Rhoades, 1995).

Spatial patterns of vascular plant species richness were primarily influenced by branch-level spatial variation, in sharp contrast to the highly significant effect of tree- and site-level variation on the species richness of non-vascular plants. Overall, spatial patterning in total epiphyte species richness (vascular and non-vascular plants combined) strongly reflected that of the much more species-rich non-vascular plants, rather than reflecting spatial variation in the vascular plant groups that are commonly sampled in most studies.

Even though the spatial patterning in biomass was similar for all vascular and non-vascular plant groups in the REML analysis, the rank-biomass curves for non-vascular plants differed markedly between sites, despite similar curves for vascular

plants. A high profusion and diversity of non-vascular epiphytes is generally associated with high rainfall areas (Sillett & Antoine, 2004), and this might explain the higher average biomass per species and greater evenness of the rank-biomass plot for non-vascular epiphyte species at Punakaiki. In contrast, rank-biomass distributions for vascular epiphyte species were similar at both sites, reflecting comparable numbers of species and contributions of species to total biomass.

The lack of association in the community composition of vascular and non-vascular plants resulted from the varying spatial compositional patterns of individual epiphyte taxa, such as the ferns within the vascular epiphytes and the lichens within the non-vascular epiphytes. These patterns probably reflect the somewhat differing microhabitat requirements and consequently distributional patterns of these two taxa, compared with other taxa within their respective epiphyte groups. Unlike other vascular plants, Hymenophyllaceae fern species, for example, are highly dependent on atmospheric humidity, while lichens, in contrast to bryophytes, are generally found in drier and light environments. Consequently, both the relative species richness and relative biomass distribution of species within individual epiphyte taxa will influence overall variation in epiphyte community composition.

Overall, contrary to the findings of Pharo *et al.* (1999), these results suggest that there is no significant degree of association in the richness, biomass or community composition of vascular and non-vascular plants that would warrant the extrapolation of generalized patterns of epiphyte biodiversity from the measurement of vascular epiphytes alone. Particularly since recent evidence from both tropical and temperate biomes shows that non-vascular epiphytes represent the dominant component of epiphyte species richness in many rain forest canopies (Table 2.4), this study strongly advocates that sampling of non-vascular plants is crucial to the interpretation of variation in epiphyte community structure, a point that has previously been emphasised by Hofstede *et al.* (2001).

One of the few significant associations that was observed between vascular and non-vascular plants was an apparent increase in establishment of vascular seedlings in association with lichens. The species richness of vascular plant seedlings was significantly correlated with the presence or absence of lichens, but not of other non-vascular plants, despite the fact that lichens constituted only a small proportion of total biomass. About 71% of all lichens were foliose, nitrogen-fixing species (mostly Loberiaceae), which might be an important factor for establishing seedlings. Foliose

Table 2.4 Vascular and non-vascular total epiphyte species richness for selected tropical and temperate rain forests. [1] Holz & Gradstein (2005); [2] Cornelissen & ter Steege (1989); [3] ter Steege & Cornelissen (1989); [4] Hietz & Hietz-Seifert (1995); [5] Cardelús (2007); [6] Wolf (1993); [7] Clement *et al.* (2001); [8] Roberts *et al.*(2005); [9] Jarman & Kantvilas (1995); [10] Setzepfand (2001); [11] Hofstede *et al.* (2001); [12] this study Punakaiki; [13] this study Karamea. Where the data relate to inner branches and lower portion of the trunk (<3m in heigt) the study site is followed by (I) or (T), respectively. All other studies sampled entire trees.

	Elevation (m)	Precipitation (mm/yr)	No. of trees (sp.)	Monocots	Gymnos	Dicots	Ferns	Total vascular	Mosses	Liverworts	Lichens	Total non-vascular	Total spp.	Proportion non-vascular
Tropical rain forest														
Costa Rica[1] (I)	2900	3000	5						8	11	18	**37**		
Guyana[2] *Eperua falcata*	< 100	3860	10						10	22	12	**44**		
Guyana[2] (I) *E. grandiflora*	< 100	3860	11						13	27	8	**48**		
Guyana[2,3] (I) Walaba forest	< 100	3860	11 (2)	30		7	3	**40**	28	53	33	**114**	154	**74 %**
Guyana[2,3] (I) Mixed forest	< 100	3860	5 (5)	18		7	7	**32**	28	60	19	**107**	139	**77 %**
Mexico (I)[4]	1980	1850	36 (?)	6		4	10	**20**						
Costa Rica[5] (I) *Hyeronima* sp.	< 100	4000	4 (1)	21		8	14	**43**						
Costa Rica[5] (I) *Lecythis* sp.	< 100	4000	4 (1)	19		6	13	**38**						
Colombia[6]	1500		4 (?)						22	36	49	**107**		
Temperate rain forest														
Chile[7]	500-1200	2000-4140	7 (1)	1		8	9	**18**	5	12	15	**31**	50	**62 %**
Tasmania[8] (T)	30-580	798-1472	120 (1)				16	**16**	43	38		**81**	97	**84 %**
Tasmania[9]	220	1659-2524	1 (1)		1	9	6	**16**	16	39	76	**131**	147	**89 %**
New Zealand[10] (T)	200-800	5223-6784	48 (1)	1		3	7	**11**	29	65	57	**151**	162	**93 %**
New Zealand[11]	< 100	3455	3 (2)	11	5	25	20	**61**	35	31	28	**94**	155	**61 %**
New Zealand[12] (I) Punakaiki	< 100	2619	20 (1)	5	1	8	11	**26**	26	53	23	**102**	127	**80 %**
New Zealand[13] (I) Karamea	<100	1850	20 (1)	5		6	11	**22**	11	32	13	**56**	78	**72 %**

macrolichens, such as *Pseudocyphellaria* species, can increase the surface area of the epiphyte mat and have been shown in other studies to overgrow bryophyte species (Kantvilas & Minchin, 1989), which might provide microhabitats for seed germination or protect against potential seed predation by insects (Hawkes & Menges, 2003). It is difficult to explain why this pattern was not been observed for older vascular plants in this study, but it is possible that seedlings have a low survival rate or that successional changes in plant community composition mask this pattern.To some extent, though, these results support studies from both temperate and tropical forests in which non-vascular plants constitute the early successional species that accumulate dead organic matter, absorb and retain moisture and nutrients from the atmosphere and form the substrate for vascular plants (Kantvilas & Minchin, 1989; Nadkarni, 2000; Sillett & Antoine, 2004).

2.4.2 Why is there so much unexplained variation in the spatial distribution of epiphytes?

Differences in epiphyte composition are often a reflection of host tree characteristics such as tree d.b.h, branch diameter and branch height, aspect or location within the host tree (Tewari *et al.*, 1985; Dickinson *et al.*, 1993; Zotz, 1997; Hietz & Briones, 1998; Pentecost, 1998; Lyons *et al.*, 2000; Acebey *et al.*, 2003). Contrary to previous studies, none of these factors, either alone or in combination, explained significant variation in the observed distribution of epiphytes at our sites. It is likely that other abiotic parameters, including microsite variation in humidity, canopy cover or light conditions (van Leerdam *et al.*, 1990; Parker, 1995; Walsh, 1996), may have been more appropriate to measure as determinants of fine scale differences in community composition.The patchy distribution and rare occurrence of many species suggests that stochastic dispersal and colonization success may also be important factors shaping the composition of epiphyte communities in similar habitats in our study. Stochastic community assembly is supported by recent epiphyte community studies (Burns, 2007; Cardelús, 2007; Otero *et al.*, 2007) although aggregated spatial patterns were reported for epiphytes in other studies (Zimmerman & Olmsted, 1992; Nieder *et al.*, 2000). For most epiphyte taxa, variation in richness, biomass and composition was strongest among branches within trees, and even branches on the same tree exhibited greater differences in overall epiphyte community structure than among trees at different sites.

This may be an indication of the limited dispersal and successful colonization by wind dispersed propagules, and microscale variation in the relative abundance of propagules of each species (Wolf, 1994). In canopy habitats the chances of spores being intercepted by a suitable habitat and their ability to establish can be very low (During, 1992; Cobb *et al.*, 2001). Dispersal by vegetative reproduction can be a strong determinant of epiphyte establishment rate and success for epiphyte species, at least in some canopy and terrestrial habitats (Benzing, 1990; Kolb *et al.*, 2006), and may have been evident in a few individual mat communities that were dominated by nearly pure patches of species such as *Plagiochilion conjugatus*, *Plagiochila deltoidea*, *Leptostomum macrocarpum*, *Hymenophyllum nephrophyllum* and *Metrosideros perforata*. However, data from this study indicates that the composition of most epiphytic mat communities is likely to be the result of stochastic dispersal events.

The effect of host tree species on epiphyte communities has been widely documented (Slack, 1976; Palmer, 1986; Roberts *et al.*, 2005; Cardelús, 2007), but here an interesting new dimension is added to host-tree affinities of epiphytes that might also have given rise to unexplained variation in epiphyte composition between trees. This is perhaps one of the first intensive studies of epiphyte communities on host trees that were themselves of epiphytic origin. Northern rata often develop from seedlings establishing as epiphytes on a range of other host tree species, and while growing into freestanding trees they smother and kill the host. I suspect that northern rata trees are predisposed to 'inherit' the species pool of their host tree, and that this may impose a strong stochastic element on the epiphytic composition of northern rata. Some evidence exists for differences in the epiphytic communities on trunks of two important hosts of northern rata (the conifer *Dacrydium cupressinum* and the angiosperm *Weinmannia racemosa*) (Scott & Armstrong, 1966; Scott & Rowley, 1975) and I suspect that this may also apply to canopy branches, given the apparent differences in biological characteristics and much longer life expectancy of New Zealand conifers over angiosperms (Ogden & Stewart, 1995). Consequently, *D. cupressinum* or *W. racemosa* hosting northern rata might indirectly influence the composition of the epiphyte flora of the old-growth rata tree by providing an immediate source of arboreal plants to the epiphytically growing ratas early on in life. If that is the case, then significant tree level effects on the species richness and community composition of epiphytes (Table 2.2) may be partially explained by the

abundance of *D. cupressinum* in Punakaiki but its scarcity in Karamea, although this hypothesis remains to be tested.

2.4.3 Vascular and non-vascular epiphyte diversity in temperate and tropical rain forests

Finally, in comparative terms, it is noted that tropical rain forests are often characterized as having exceptionally high canopy epiphyte diversity (Gentry & Dodson, 1987; Benzing, 1990) and yet this study, consistent with studies by (Dickinson *et al.*, 1993; Hofstede *et al.*, 2001), found levels of epiphyte richness and biomass in a temperate rain forest that rivalled those of many tropical forests (Tables 2.3 & 2.4). Moreover, species richness is expected to increase further with greater sampling effort (as indicated by the non-asymptotic shape of the rarefaction curves and by the species richness estimators) across a wider range of tree species and microhabitats within trees (Dickinson *et al.*, 1993; Jarman & Kantvilas, 1995; Setzepfand, 2001). The major driver of this high diversity was the striking number of non-vascular epiphyte species encountered. Non-vascular epiphytes comprised more than 72 % of total species richness at the study sites, outnumbering vascular plant species by a ratio of about 4:1. A comparative assessment of vascular and non-vascular species richness across tropical and temperate biomes (Table 2.4), found that this trend is consistent in both tropical and temperate studies, but temperate forests do appear (on average) to have a higher proportion of non-vascular species (Table 2.4). Much of the observed difference between vascular and non-vascular species richness in this study was driven by the high species richness of liverworts. Across studies, the only characteristically higher diversity of any epiphyte group in tropical forests appears to be within the monocots (largely Orchidaceae, Bromeliaceae and Araceae) (Table 2.4). Clearly, non-vascular plants make a dominant contribution to overall epiphyte biodiversity in both temperate and tropical forests. If the spatial patterning of vascular and non-vascular epiphytes differs as greatly in other biogeographic regions as it does in New Zealand, then there is serious cause for concern about our ability to extrapolate regional or global estimates of epiphyte species richness from sampling vascular epiphytes alone.

2.5 Conclusions

This study has shown that northern rata trees support highly diverse and complex epiphyte communities that contain a distinct element of vascular plants, but are primarily characterized by a high number of non-vascular species, particularly liverworts. Non-vascular epiphytes are often neglected in forest canopy studies in favour of vascular plants, because of the difficulties associated with canopy access, identification of specimens and sampling logistics. While this is understandable, it is evident from the substantial contribution that non-vascular plants make to overall epiphyte biodiversity, and from the lack of congruence in the spatial association of vascular and non-vascular richness, that studies which do not include non-vascular plants provide an incomplete understanding of the structure and dynamics of canopy epiphyte communities

Supplementary plates of epiphyte mat communities

Chapter 3

The influence of canopy microclimate on the species richness and biomass of epiphytes in northern rata trees

Abstract

Microclimate is thought to be an important determinant of epiphyte distribution and community composition in canopy habitats, but few studies have taken direct micrometeorological measurements to support such conclusions. In this study temperature, relative humidity were measured and vapour pressure deficit (VPD) calculated to investigate correlations between these climatic variables and epiphyte species richness and biomass for epiphyte mats on inner canopy branches of one emergent tree species. Microclimate measurements were taken at 30 min intervals over a one year period at two study sites in a temperate rain forest on the West Coast of the South Island, New Zealand. Microclimatic differences in temperature, humidity and VPD were evident between epiphyte mats at similar growth sites from within the same tree and communities from different trees. A decline in total species richness ($r = -0.70$; $p < 0.05$), non-vascular biomass ($r = -0.63$; $p < 0.05$) and bryophyte species richness in Karamea ($r = -0.97$; $p < 0.01$) was significantly correlated with increased temperatures, expressed as degree days. VPD was an important determinant of the variability in epiphyte community composition between mats. Potentially harmful extreme climatic conditions of temperatures > 25°C, relative humidity < 70 % and VPDs < 1 kPa were experienced by all mats, but on only a few occasions over the study period. However, prolonged dry periods of up to 14 days were not uncommon and occurred at any time of year. Microclimatic conditions within the three dimensional canopy environment are variable and complex. To fully capture microclimatic variability and assess its impact on epiphyte distribution and community composition, continuous and prolonged measurements are needed at the actual

epiphyte growth site. Such information is crucial to understand the effects of changing climate on ecological processes and dynamics within a forest system.

3.1 Introduction

Crowns of emergent canopy trees form the interface between the biosphere and the atmosphere and as such are frequently exposed to high UV-radiation and wind speed and substantial fluctuations in temperature and moisture. Additionally, the outer canopy of tree crowns acts as a buffer altering the climatic conditions within the forest environment, from the canopy right down to the forest floor (Parker, 1995). Climatic changes along a vertical gradient have been well documented for several forests, showing an increase in temperature and decrease in relative humidity from the forest floor toward the canopy (Allen *et al.*, 1972; Aoki *et al.*, 1975; Szarzynski & Anhuf, 2001). This climatic variability has been strongly linked to available light levels and air flow at different heights of the forest environment, which is influenced by forest type and tree characteristics such as leaf morphology, canopy structure, branch position and branch size. Climatic patterns within the three-dimensional space of the forest canopy, on the other hand, remain poorly investigated (Parker *et al.*, 1996), mainly because it is difficult and costly to take microclimate measurements at multiple locations at great heights within the forest canopy (Walsh, 1996).

Within highly heterogeneous rain forest canopies there are a wide range of very distinct physical environments that promote a profusion of epiphyte species and biomass. In addition to the tree crowns acting as a climatic buffer, it has been suggested that epiphytes themselves moderate the climate within the forest canopy (Benzing, 1990; Parker *et al.*, 2004). However, only few studies have been carried out to test this assumption (Freiberg, 2001). Evidence that epiphytes can mitigate ambient climatic conditions and influence the canopy microclimate has come from studies by Freiberg (1997, 2001) and Stuntz *et al.* (2002a). They recorded substantially higher day-time temperatures on epiphyte-bare branches compared to temperatures at microsites next to epiphytes on the same branch. Furthermore, Stuntz *et al.* (2002a) recorded a 20% decrease in evapotranspiration in tree crowns where epiphytes were present compared with tree crowns where epiphytes were absent.

Studies of microclimatic variation in forest canopies have important ecological implications. Clearly, microclimate can influence the distribution of canopy-dwelling species (Basset, 1992; Kaspari, 1993; Freiberg, 1996; Benzing, 1998, 2004), but we still know very little about the effects of microclimate on epiphyte community composition and canopy dynamics (Cardelús & Chazdon, 2005). Such knowledge, however, is becoming increasingly important considering the reported sensitivity of many species to changing climate (Walther *et al.*, 2002; Parmesan & Yohe, 2003; Le Roux *et al.*, 2005). Non-vascular plants, shown to be important in these communities (Chapter 2), could be particularly vulnerable to increased temperatures and decreased or more infrequent rainfall (Bates et al., 2005), because they lack roots and an impermeable epidermis, making them prone to rapid desiccation. Given their demonstrated vital role in intercepting and storing large amounts of water and nutrients from the atmosphere (Pócs, 1980; Nadkarni, 1984b; Veneklaas *et al.*, 1990) and their importance as habitat for an extraordinary diversity of invertebrates, climatic changes affecting non-vascular plants could have detrimental effects on the entire canopy ecosystem.

Epiphytes are a conspicuous component of New Zealand's rain forest flora. They are major contributors to overall forest species richness and total above ground biomass, which are exceptionally high for temperate rain forests and even comparable to some species rich tropical rain forests (Hofstede *et al.*, 2001; Affeld *et al.*, 2008). While these studies have highlighted the importance of canopy microclimate in determining compositional patterns of epiphyte communities, to my knowledge, only Dickinson *et al.* (1993) have taken *in situ* microclimatic measurements from within the tree crown. To study the complete array of epiphyte communities in the crown of even a single tree is logistically challenging and requires high replication, because of the highly complex and variable composition of these communities. However, epiphyte mats are a convenient first step to study climate-epiphyte ecology, to be followed by similar studies of other epiphytic vegetation types. The main objectives of this study were to: 1) establish microclimatic profiles for epiphyte mats in the inner canopy of northern rata; 2) to investigate microclimatic variability in inner canopy habitats; and 3) to examine relationships between microclimatic and other abiotic factors and epiphyte species richness and biomass.

3.2 Methods

3.2.1 Study design and microclimatic measurements

In May 2004 six northern rata (*Metrosideros robusta*) trees were selected from two study sites, Punakaiki and Karamea, located on the West Coast of the South Island, New Zealand to measure the microclimate of 12 epiphyte mats on the inner portion of individual branches. A detailed description of the study sites' climate and vegetation, the criteria used to select suitable trees as well as canopy access techniques are given in Chapter 2. Six epiphyte mats from within the crowns of three trees at each site were randomly chosen from a set of mats that were accessible, covered a surface area of at least 30 x 25 cm, and were located about 1 m from the main trunk. Only one epiphyte mat was sampled per branch, and either one, two or three branches were sampled on any given tree. Variation in the number of samples collected per tree was dictated by the design of a field experiment (Chapter 5) that took into account the patchy distribution of suitable epiphyte mats and sample processing effort without compromising the statistical analysis of the collected data. Branch height, branch diameter, aspect, branch angle and minimum and maximum epiphyte mat depth were recorded for each epiphyte mat.

Microclimatic conditions were recorded for a total of 11 epiphyte mats. One datalogger malfunctioned during the study period so that one epiphyte mat and tree were excluded from the Karamea data set. Hobo Pro Series data loggers by Onset Computers were programmed to measure high resolution temperature and relative humidity (RH). To prevent raindrops settling on the sensors of the data loggers and interfering with the accuracy of the readings, rain shields consisting of protective, ventilated plastic containers were installed 2 cm over each data logger. One data logger was positioned in the middle of each epiphyte mat and strapped to the branch so that the sensors were in immediate proximity to the surface of the epiphytes. Microclimatic measurements were taken daily every 30 minutes for 24 hours starting 01 May 2004 and concluding 19 April 2005. During this period data collection was interrupted only briefly to download the data every three months using the software BoxCar Pro 4.3. All data loggers were calibrated prior to installation in the field. Some measurements for this study were taken from within the treatments, while other measurements were taken directly from epiphyte mats that were controls.

Once the recording of the microclimatic data finished the epiphyte mats were removed from the branches to analyse their composition and biomass. All epiphyte material was processed as outlined in Chapter 2.

3.2.2 Data analysis

Climate profiles

Annual temperature and relative humidity profiles were established for all epiphyte mats inside and outside the experimental units on the inner portion of individual branches for each of the two study sites. Mean daily temperatures and relative humidity were determined to investigate branch specific microclimatic patterns.

Microclimatic patterns for an average day during the coldest and warmest month of the year were compiled by calculating the daily means from half hourly temperature and relative humidity monthly running means for the mats at each site. Subsequently, the coldest and the hottest day of the year for a single mat were determined for each site and used to contrast daily fluctuations in temperature and relative humidity against the mean on an extreme day.

Epiphyte community composition

To examine relationships between microclimatic variability and epiphyte mat communities the composition of individual communities was characterised using biomass and species richness data from individual epiphyte mats. The Bray-Curtis similarity matrix was computed in PRIMER 5 with all data standardised to account for variability in sample volume and 4^{th} root transformed to reduce the effect of a small number of highly abundant species distorting the samples. The Bray-Curtis similarity matrix then formed the basis for computation of a non-metric multidimensional scaling (MDS) ordination, in which all samples are arranged according to their similarity with one another.

Epiphyte diversity and climate

Temperature

Relationships between total epiphyte species richness and biomass versus temperature were analysed for individual epiphyte mats. Daily temperatures were converted to

degree days (DD's) or units of physiological time often used to measure the amount of heat required by a plant or insect species to complete various developmental stages. Degree days is a biologically meaningful unit that reflects the amount of accumulated heat above a given lower temperature threshold for a 24 hour period. The lower developmental threshold temperature is known usually for important crop or pest plant species, but can vary substantially across species (Richardson, 2000). However, a 5°C threshold appears appropriate for many plant species in New Zealand and is used by NIWA for climate data summaries. In this study the commonly applied Min-Max Method proposed by Arnold (1960) was used to calculate degree days. This method uses the equation

$$DD's = \frac{(T_{\max} + T_{\min})}{2} - T_0$$

where DD's are daily degree days and T_0 is the lower temperature threshold for plant development specified as 5°C in this study. Cumulative degree days were calculated for each epiphyte mat by accumulating daily degree days over the study period, 01 May 2004 to 19 April 2005.

Relative humidity

To investigate the relationship between the atmospheric moisture conditions and epiphyte species richness and biomass, relative humidity was expressed as vapour pressure deficit (VPD). VPD is the difference between the actual amount of atmospheric moisture at a given temperature and the amount of moisture that could be present when the air is saturated at the same temperature and is generally expressed in kPa. Saturated vapour pressure $e^*(T_i)$ was calculated for each half hourly reading using the widely applied Tetens equation given by Murray (1967) for temperatures above 0°C as

$$e^*(T_i) = 0.611 \exp\left[\frac{17.27 T_i}{T_i + 237.3}\right]$$

and for temperatures below 0°C as

$$e^*(T_i) = 0.611 \exp\left[\frac{21.875 T_i}{T_i + 265.5}\right]$$

where T = temperature in °C for the *i*th time of day. Half hourly VPD was then computed as

$$VPD = e^{*}(T_i)\left[1 - \frac{RH}{100}\right]$$

where RH = relative humidity (%) at the *i*th time of day.

Diurnal differences in VPD were examined by splitting the data sets for each branch into day and night time periods. Sunrise and sunset tables provided by Land Information New Zealand (LINZ) for Greymouth and Westport were used for Punakaiki and Karamea respectively. Day time periods included VPDs calculated from measurements starting half an hour after sunrise and ending half an hour before sunset while night time periods included all VPDs calculated for the remaining times. Mean daily differences in VPD were calculated for both the day and night time period and 95% confidence intervals reported.

Correlations for epiphyte diversity and climatic factors

The relationships of both cumulative degree days and day time vapour pressure deficit with epiphyte species richness and biomass were examined for each site and both sites combined using linear regression analyses in the software package Genstat 9.1 (2006). Similar analyses were also repeated for the species richness and biomass of individual plant groups as follows: filmy ferns, mosses, liverworts, lichen and, on a broader taxonomic level, for bryophytes, non-vascular and vascular plants. There was insufficient replication in this study to run full, multivariate linear models. Instead, each variable was examined independently.

Epiphyte community composition and abiotic factors

In Chapter 2 the relationship between some physical abiotic factors and spatial variation in epiphyte community composition was investigated. However, it is also important to examine expected interactions between these factors and microclimate and possible effects on community composition. To determine to what extent the measured abiotic factors account for the observed variability in community composition within and across sites the BIO-ENV procedure in PRIMER 5 was carried out. For this purpose a similarity matrix based on Euclidean distance was computed for

the abiotic variables and subsequently matched with the Bray-Curtis similarity matrix for the biotic data. Their similarity ranks were than compared using the Spearman rank coefficient.

3.3 Results

3.3.1 Climate profiles

Average daily temperatures recorded for epiphyte mats within the rata canopy at Punakaiki and Karamea were mild throughout the year, above 10°C for 8 months of the year. There was little seasonal fluctuation, average daily temperatures for the coldest winter and warmest summer months differing by about 9.5 °C. While average temperatures showed little variability over the entire year, accumulated degree days varied considerably among epiphyte mats, up to 1082 degree days, which could have significant effects on the biology of invertebrate species. However, average temperature was 1.34°C higher ($t = 4.08$; $p < 0.01$) in Karamea than Punakaiki (Table 3.1). Despite the fact that average temperatures were lower at Punakaiki, epiphyte mats experienced the most extreme conditions at this site with temperatures dropping as low as – 0.5°C and reaching a maximum of 38.51°C nearly 8°C more than the highest temperature recorded at Karamea.

Table3.1 Comparison of canopy temperatures recorded from May 2004 to April 2005 for two field sites. Temperatures are daily averages with s.e. except for the extreme temperatures which are the actual highest and lowest values recorded over the study period.

Temperature °C	Punakaiki	Karamea
Mean	11.81 ± 0.26	13.15 ± 0.19
Mean minimum	9.09 ± 0.25	11.00 ± 0.18
Extreme minimum	- 0.5	1.90
Mean maximum	15.49 ± 0.38	16.32 ± 0.41
Extreme maximum	38.51	30.63

Annual climatic patterns

While some microclimatic measurements in this study were taken from manipulated conditions that were part of the field experiment, Figure 3.1 & 3.66 show clearly that those records are within the bounds of natural conditions recorded from unmanipulated experimental units. Individual epiphyte mats varied in mean daily temperatures, but overall followed a consistent annual pattern at both sites with temperatures being lowest in August and hottest in February (Figure 3.1a; Figure 3.2a). Variation in

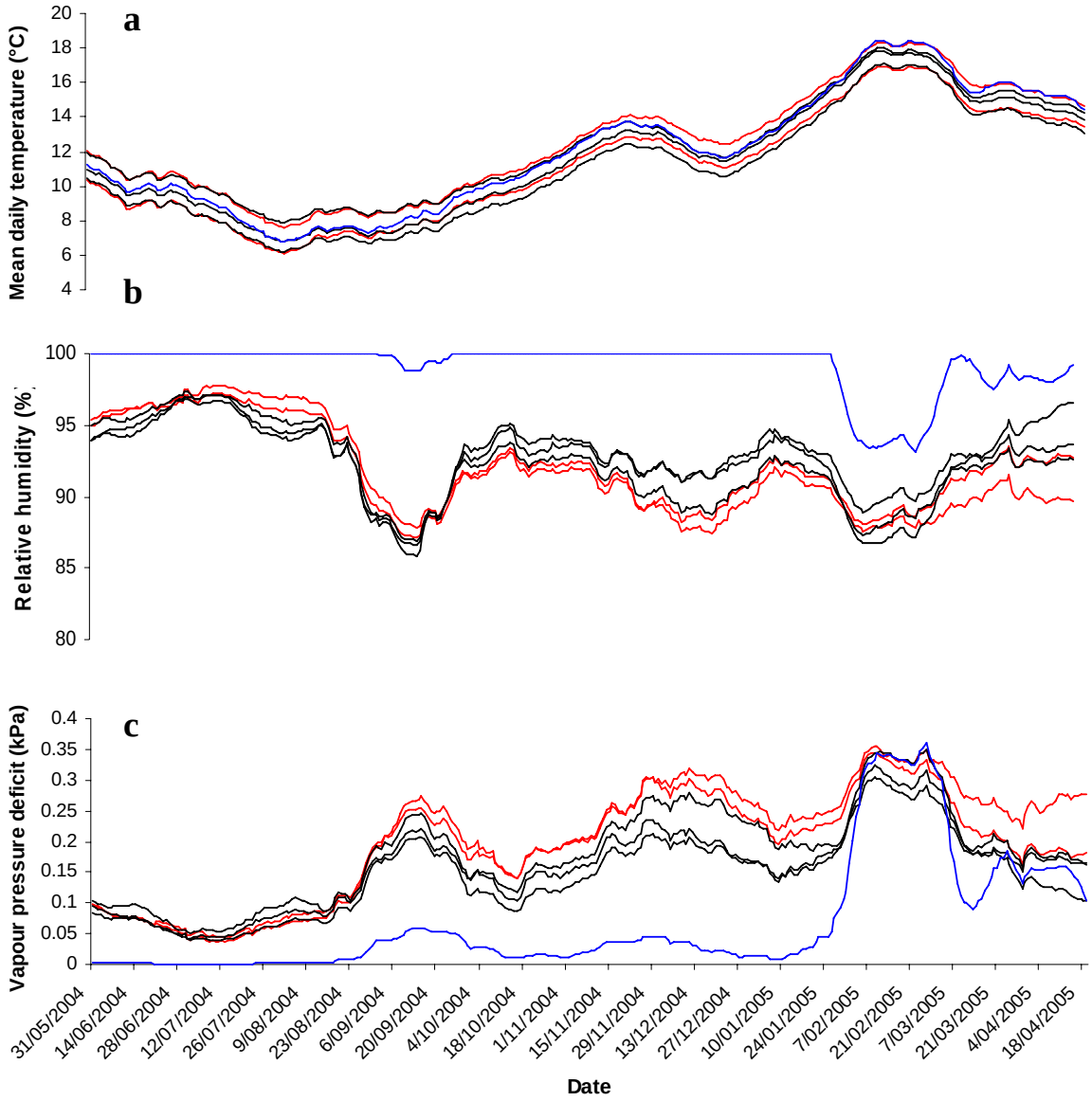


Figure 3.1 Changes in three microclimatic variables recorded over one year on individual epiphyte mats in the inner canopy of northern rata at Punakaiki. Values for temperature (a), relative humidity (b) and VPDs (c) are monthly running daily means for each branch. Branches from within the same tree have the same colour**.**

relative humidity levels at Punakaiki between mats was small where annual mean values ranged between 91.8 and 93.1% and all remained above 85% throughout the year (Figure 3.1b). The exception was one mat that had saturated humidity levels of 100 % for much of the year dropping to a 95% minimum on the hottest days of the year in February, but otherwise followed the same general trend. While relative humidity levels seemed to be little affected by temperatures, VPDs, as expected, strongly reflected changes in relative humidity. VPDs were low for the entire year, barely exceeding 0.35 kPa. The lowest VPDs, between 0.05 and 0.1 kPa, were recorded during the winter months when temperatures were lowest (Figure 3.1c). Over the winter period and early spring period (June 04 – Sep 04) there was little variation in VPD for the individual mats unlike for the rest of the sampling period. One epiphyte mat showed highly saturated humidity levels and the lowest VPD over most of the sampling period, but responded strongly to coinciding high temperatures and low relative humidity in February 2005.

Similar to Punakaiki, mean annual relative humidity at Karamea was very high for all mats, ranging between 86.8% and 100% with daily means not falling below 80%. Differences among individual epiphyte mats and within individual trees, however, were more pronounced than in Punakaiki (Figure 3.2b). Humidity levels on one branch were at saturation point for most of the year and consequently had minimal VPDs for the same period. Again, VPDs showed increased moisture deficit when relative humidity decreased. Also, during the warmer months higher VPDs coincided with high temperatures (Figure 3.2c). In general, however, VPDs were low throughout the year barely exceeding 0.35 kPa, indicating readily available moisture.

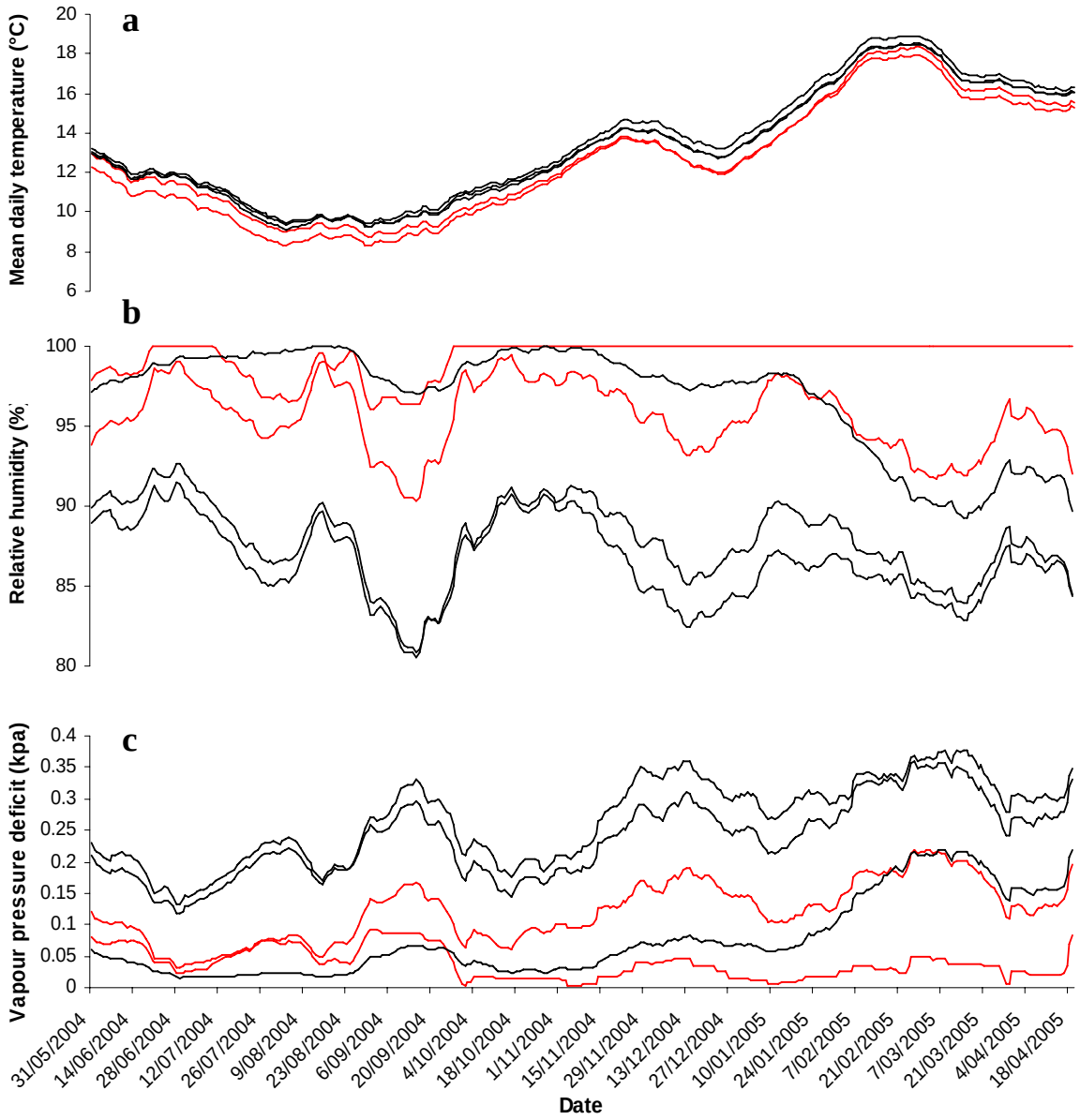


Figure3.2 Changes in microclimate recorded over one year on individual epiphyte mats in the inner canopy of northern rata at Karamea. Values for temperature (a), relative humidity (b) and VPDs (c) are monthly running daily means for each branch. Branches sampled within the same tree have the same line colour.

If average daily temperatures across all epiphyte mats are examined, daily mean temperatures fluctuated very little over a single day. However, if one examines both the warmest (February) and coldest (August) days of the year (Figure 3.3a) for individual mats average temperatures mask the extreme conditions that an epiphyte mat can experience.

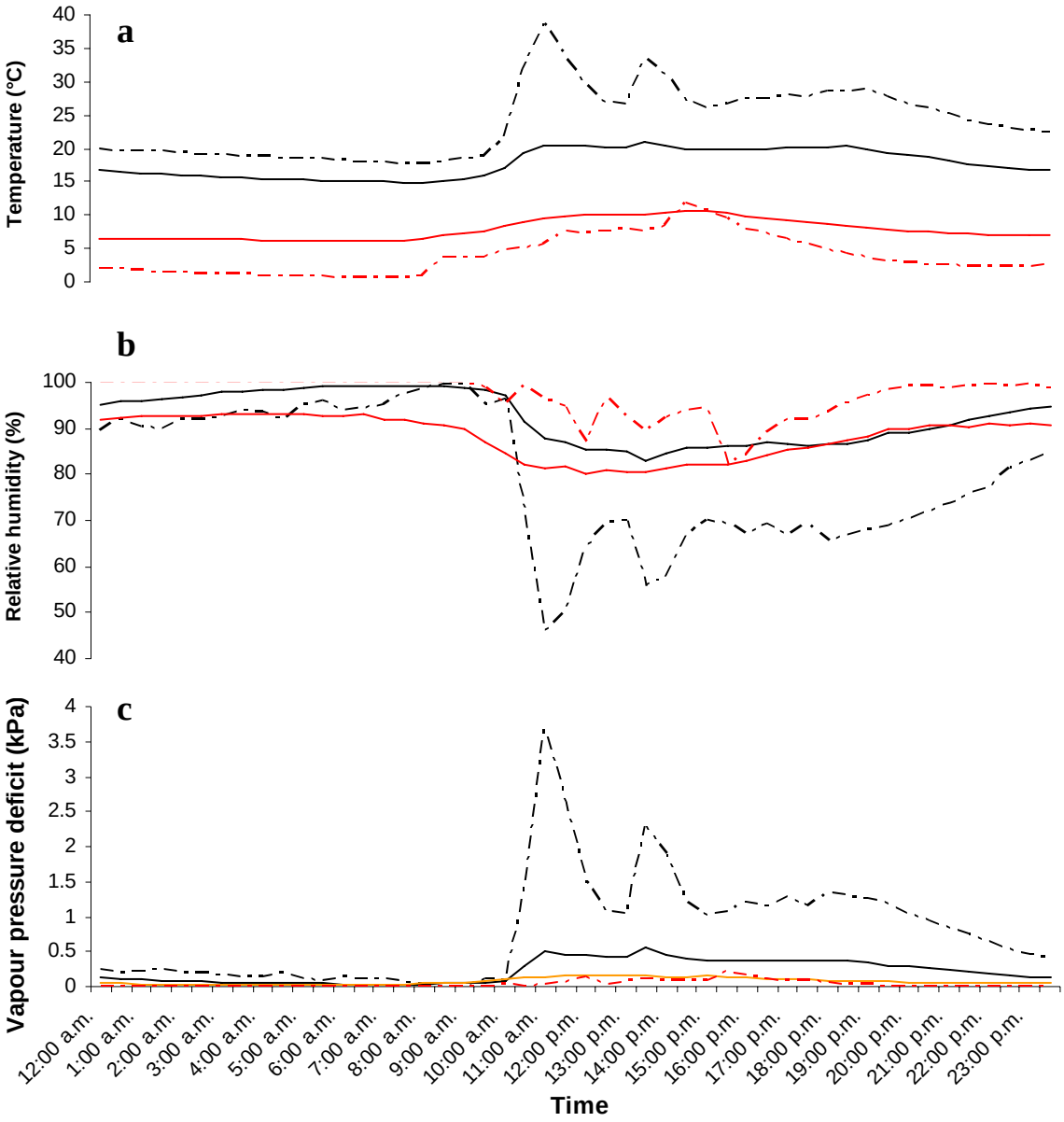


Figure 3.3 Average temperatures (a), relative humidity (b) and VPDs (c) for epiphyte mats on a single day during the hottest, February (black full lines), and one of the coldest, August (grey full lines) months of the year at Punakaiki. Broken lines show the actual climatic conditions on the coldest and hottest single day of the month and the fluctuation from the mean for the month.

Little fluctuation was also observed in relative humidity during both months with average humidity levels between 90 to 100 % and a slight drop over the midday to early afternoon period consistent with warmer temperatures for this time of day (Figure 3.3b). On the coldest day in August, following 11 days of rain, humidity was above normal for most of the day, while on the warmest day in February following 11 days

without rain, relative humidity dropped to 45% in direct response to peaking temperatures and had still only recovered slowly and not to the full extent by midnight. These climatic changes also triggered an immediate strong increase in VPD of up to 4 kPa, which decreased sharply and analogous with a drop in temperature and a simultaneous increase in relative humidity (Figure 3.3c). This very high VPD was in strong contrast to the night time VPD of below 0.5 kPa. Low average VPDs were the norm for both months staying close to 0 kPa for the entire day in August and barely exceeding 0.5 kPa for the warmest part of the day in February.

Average diurnal temperatures for the warmest and coldest month of the year in Karamea followed the same patterns observed for Punakaiki, but showed none of the dramatic fluctuations in temperatures recorded on the hottest and coldest day of the year in Punakaiki (Figure 3.4a). Mean relative humidity also fluctuated little with levels generally between 90 and 98% and reached their lowest levels when temperatures peaked during mid afternoon. On the coldest and warmest day of the year humidity levels dropped below average following 12 days with and without rain respectively (Figure 3.4b). Mean VPDs were low throughout the day in both months ranging around 0.15 kPa during the night until early morning, but increased instantly in response to rising temperatures to nearly 0.4 kPa in the late afternoon when temperatures were highest and relative humidity lowest (Figure 3.4c). The highest fluctuation in VPD was observed on the hottest day in February when the VPD abruptly rose in the early afternoon from 0 to almost 1 kPa coinciding again with the highest temperature and the lowest relative humidity of the day. The VPD on the coldest day in August showed a similar instant response to changes in temperature and relative humidity, but stayed close to the mean values for the month.

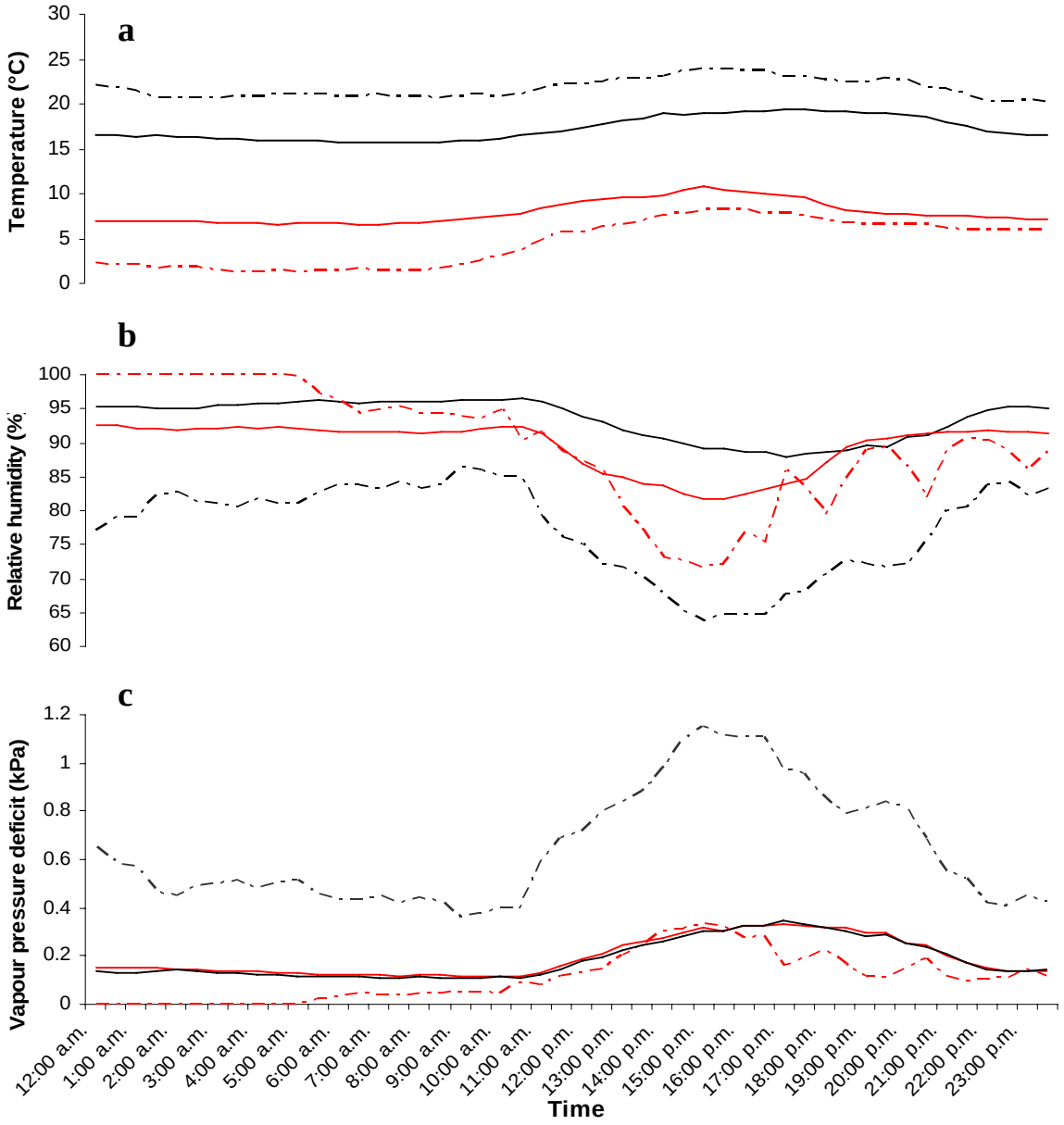


Figure 3.4 Average temperatures (a), relative humidity (b) and VPDs (c) for epiphyte mats on a single day during the hottest, February (black full lines), and coldest, August (grey full lines), months of the year at Karamea. Dotted lines show the actual climatic conditions on the coldest and hottest single day of the month and the fluctuation from the mean for the month.

Temperatures > 25°C, relative humidity < 70 % and VPDs > 1 kPa identified as being harmful to plant growth and development (Buckley *et al.*, 1980; Freiberg, 1997; León-Vargas *et al.*, 2006) were experienced by all epiphyte mats, but at varying frequencies (Figure 3.5). For example, relative humidity below 70 % was recorded on

up to 40% of days over the entire sampling period. Extreme temperatures above 25°C and VPDs over 1 kPa were measured on less than 5 and 1 % of days, respectively. The frequency of extreme conditions experienced by epiphyte mats varied within and between trees and was most apparent for relative humidity. Epiphyte mats in Karamea were less prone to lower relative humidity levels than mats in Punakaiki. Unfortunately, none of the above authors indicated how long the duration of extreme events were.

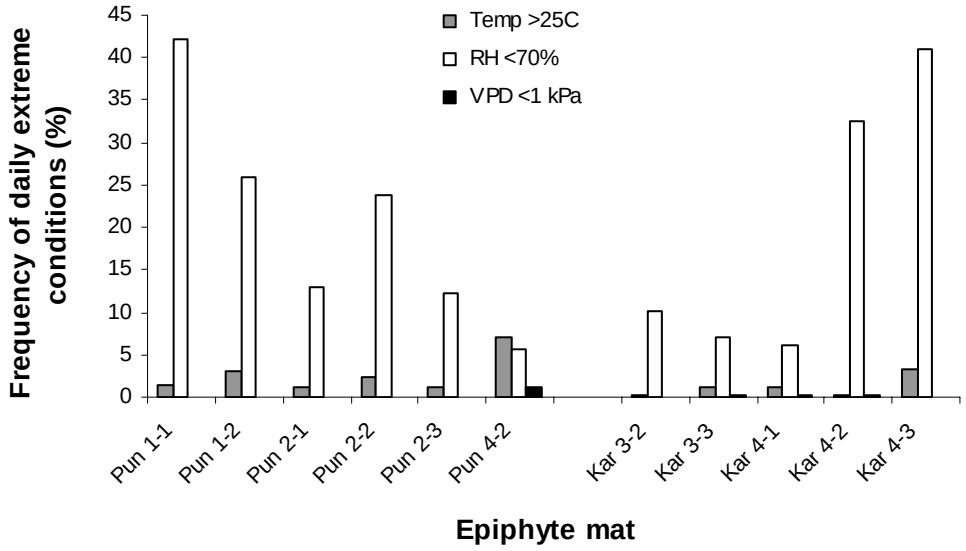


Figure 3.5 Proportion of days over the total sampling period (n = 354) with measured potentially harmful climatic conditions.

Day time mean annual VPDs in February, the hottest month of the sampling period, were higher than in August, the coldest month of the sampling period. In February, VPDs of around 0.3 kPa were recorded for all, but one, epiphyte mats, while August VPDs were around 0.2 kPa (Figure 3.6). These differences, however, were non-significant for most epiphyte mats as indicated by the overlapping confidence intervals. However, differences in VPD between the summer and winter months were significant when mats from both sites were combined ($t = - 3.32$; $p < 0.01$). In Punakaiki there was little fluctuation among epiphyte mats at both times of year, except for one mat. In Karamea, big differences in VPD were apparent between

individual mats, ranging from 0.05 kPa to 0.35 kPa, as well as for mats from within the same tree.

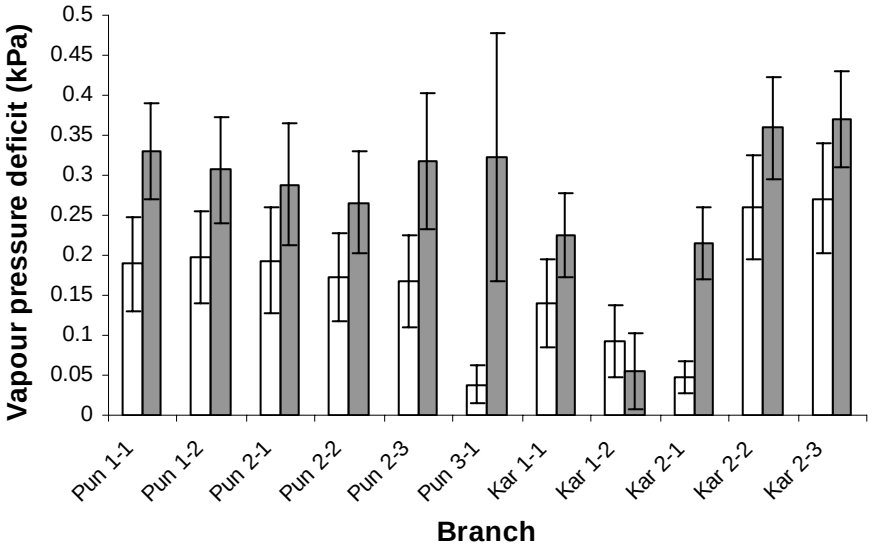


Figure 3.6 Day time mean annual vapour pressure deficit (± 95 % C.I.) for the coldest (white bars) and hottest (grey bars) months of the sampling period for individual epiphyte mats at Punakaiki (Pun) and Karamea (Kar).

A correlation analysis of relationships between climate and six abiotic factors showed no significant relationships. Although a significant relationship was identified between aspect and VPD ($R^2 = 0.45$; $p = 0.024$) for the two sites combined and showing an increase in VPD from east to west orientation of the branches, this relationship was not significant for the individual sites.

3.3.2 Epiphyte community composition

A total of 46 epiphyte species were recorded from epiphyte mats used for microclimatic measurements. These comprised 34 non-vascular and 12 vascular plant species (Appendix 2). An average of 11 species per mat was recorded in Punakaiki and 4 species in Karamea. At Punakaiki non-vascular plants comprised the most species while at Karamea mean species richness over the plant groups was similar (Figure 3.7).

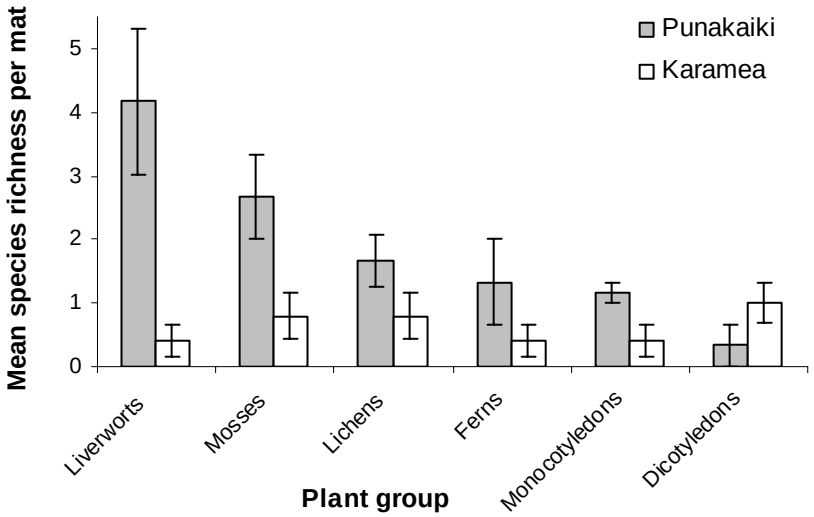


Figure 3.7 Mean number of epiphyte species per mat for two study sites with s.e.

Total biomass was very similar for both study sites with epiphyte mats in Punakaiki supporting on average 3.12 ± 0.54 kg/m^{-2} of biomass compared to 2.97 ± 0.71 kg/m^{-2} in Karamea. There was, however, much variation in the composition of the epiphyte mats across individual branches within and between trees, although roots and soil made the largest contribution to total biomass (Figure 3.8).

There was a clear division in the ordination of epiphyte communities recorded at the two study sites (Figure 3.9). The low stress value of 0.09 indicates that the representation of the ordination of samples is highly reliable (Clark & Warwick, 2001). With the exception of one epiphyte mat, all mats from the same study site were more similar to each other than to any of the mats from the other study site. Much variation was also apparent in the community composition of individual mats from within the same tree.

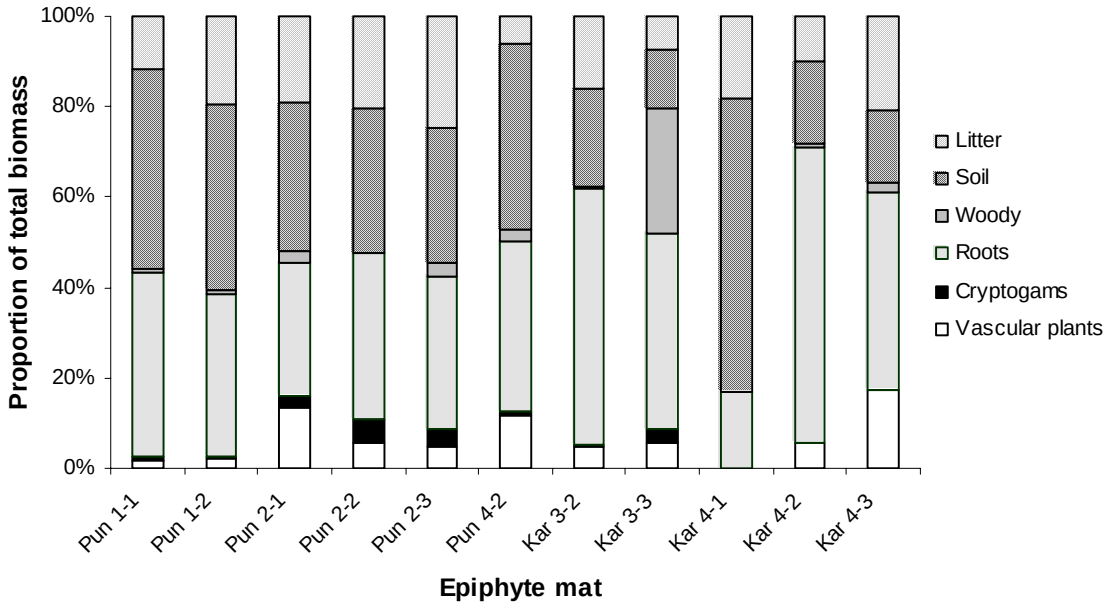


Figure 3.8 Composition of epiphyte mats showing the contribution of all living and dead components to total epiphyte mat biomass for the individual branches sampled at Punakaiki (Pun) and Karamea (Kar). Numbers and letters following each site represent the tree and individual branches within a tree respectively.

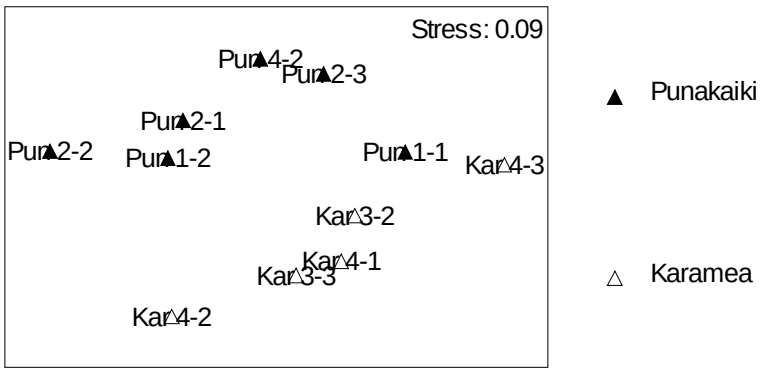


Figure 3.9 MDS plot for epiphyte communities on study branches at Punakaiki (black triangles) and Karamea (white triangles) combined. Each tree is numbered followed by a letter indicating different branches within the same tree.

3.3.3 Epiphyte community composition and abiotic factors

The BIO-ENV procedure was used to identify which abiotic factors affected overall community composition. Results from this analysis for the two study sites combined showed that 44.2% of the variation in the composition of the epiphyte communities was due to differences in mean VPD and distance to the sea. When each site was analysed separately, in Punakaiki 29.5% of the variation observed in epiphyte community composition between mats could be explained by a combination of aspect, mean annual minimum temperature and VPD. In Karamea, branch angle, minimum epiphyte mat depth and VPD were identified as significant determinants of the variability in epiphyte community composition between mats accounting for 82.5% of variance in the data.

On the finer scale, correlation analysis showed total species richness and non-vascular biomass were significantly and negatively correlated with warm temperatures, expressed as cumulative degree days, at both sites (Table 3.2 & Figure 3.10a & b). In Karamea a negative trend was also apparent for total species richness and lichen species richness, but particularly pronounced for bryophyte species richness (Figure 3.10c). Non-vascular plant species richness was also significantly negatively correlated with increasing VPDs. On the other hand, there was a positive correlation between vascular plant biomass and VPD (significant at the 10 % confidence level) at Karamea (Figure 10d). The significant negative correlation observed for filmy fern and bryophyte biomass in Punakaiki was driven by one outlying sample.

Table 3.2 Significant correlations between species richness and biomass and degree days and vapour pressure deficit for various plant groups at two study sites Punakaiki (n=6) and Karamea (n=5).

	Site	**Cumulative degree days vs.**		**Mean day time VPD vs.**	
		r	**p - value**	**r**	**p - value**
Total species richness	Both	- 0.70	< 0.05		n.s.
Non-vascular biomass	Both	- 0.63	< 0.05		n.s.
Total species richness	Karamea	- 0.93	< 0.05		n.s.
Lichen species richness	Karamea	- 0.89	< 0.05		n.s.
Bryophyte species richness	Karamea	- 0.97	< 0.01		n.s.
Non-vascular species richness	Karamea		n.s.	- 0.91	< 0.05
Vascular plant biomass	Karamea		n.s.	+ 0.81	< 0.10
Filmy fern & bryophyte biomass	Punakaiki		n.s.	- 0.95	< 0.01

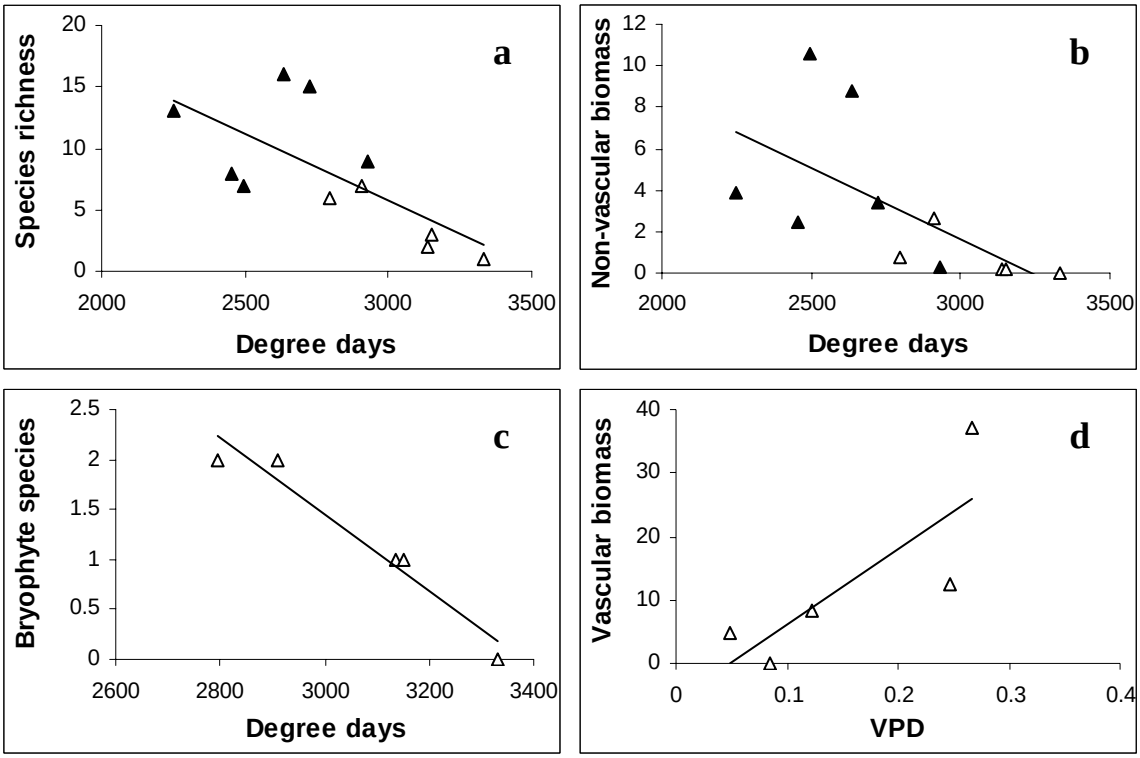


Figure 3.10 Graphic representation of significant correlation between degree days and VPD with plant community characteristics. Values for Punakaiki are represented by black triangles and values for Karamea by white triangles.

3.4 Discussion

3.4.1 Climatic variability

Climatic profiles and variation between epiphyte mats

Annual microclimatic profiles were similar for all epiphyte mats across the two study sites reflecting large scale geographical weather patterns. Seasonally fluctuating temperatures were apparent with February being the warmest and August the coldest month of year while relative humidity was on average above 85% throughout the year reflecting a fairly even distribution of rainfall. There were, however, obvious microclimatic differences in temperature, humidity and VPD between epiphyte mats from different trees and communities from within the same tree. Mean annual temperatures of mats from inner branches within the same tree varied by about 1.3°C at Punakaiki compared with 0.3°C at Karamea, while between tree differences exceeded 1.6 and 1°C at the two sites respectively. These differences are almost as large as what

is proposed by climate change scenarios. Temperatures inside the crown are thought to be influenced by the amount of solar radiation and wind speed that penetrate the canopy, but because tree crowns vary in the amount and spatial arrangement and orientation of branches, twigs, leaves and epiphytes (Parker, 1995), climatic conditions are far from homogeneous inside the canopy. A study by Cardelús & Chazdon (2005) showed that branch characteristics and epiphyte cover contributed to the poor predictability of inner crown microclimate. Increased levels of solar radiation during day time hours are usually accompanied by rising temperatures with a peak around noon. Epiphyte mats in Karamea, however, reached maximum temperatures later in the afternoon and one branch frequently reached temperatures of > 25°C between 18.30 pm and 20.30 pm in summer time. These extremes were possibly partly influenced by the west facing aspect of the branch, although, no significant relationship was found. Similarly, Dickinson *et al.* (1993) found that north facing epiphyte communities experienced 0.5 - 1°C warmer temperatures than communities on any other aspect, whereas in this study around early afternoon the reverse was true with extreme conditions recorded on the western aspect. Lower sun angles in the morning and late in the day allow sunlight to pass through horizontal gaps in the tree crown and can create temperature peaks in localised areas for a short amount of time. Whereas epiphyte mats on neighbouring branches within the same tree that may not be exposed to direct solar radiation may result in considerable temperature variations such as the 0.52 – 9.85°C range recorded in this study.

When temperatures rise, water is lost to the air through evaporation around the epiphyte mats, decreasing relative humidity. Humidity levels below 70% occurred frequently, but could change rapidly within a few hours. For example, on the hottest day relative humidity dropped as low as 45 % when the temperature was highest, but it returned to near saturation levels at night. Near saturation conditions following such a sharp decline in humidity are not uncommon in rain forests as studies by Aoki *et al.* (1975) in Malaysia and by Leigh Jr. (1999) in Panama have shown. Interestingly, preceding the hottest day was a period of 11 days without rain, but that seemed to have had little effect on the recovery of humidity levels at night in Punakaiki. Determining whether physiological processes such as respiration contribute to this rapid change or whether changes in atmospheric conditions are responsible is unknown and beyond the scope of this study. Some epiphyte mats in Karamea experienced consistently lower

relative humidity (80 – 90%) than others from within the same tree throughout the year. The canopy cover above these mats was observed to be fairly open, which would allow free air movement, higher wind speeds and turbulent mixing of air inside the canopy resulting in increased evaporation.

VPD is an "indirect measure of evaporation" (Kucera, 1954) and, as shown in this study, a useful indicator of the water loss experienced by plants. Unlike relative humidity, equal VPD is indicative of identical atmospheric moisture conditions regardless of whether temperatures are the same or not (Anderson, 1936). Mean daily VPDs fluctuated throughout the year along with changing temperatures and were at their lowest levels during the winter months when temperatures were lowest and higher during summer when temperatures were highest. However, also indicative of the complexity of the physical environment are the rapid changes brought about by atmospheric conditions. Prolonged phases of dry conditions (up to 14 days) or prolonged phases with high rainfall could equally precede periods with high VPDs. Diurnal patterns, however, revealed that all epiphyte mats were subject to very high saturation deficits (of up to 4 kPa) during the hottest part of the day, even though infrequently and for short amounts of time. As with relative humidity, VPDs generally returned to near saturation at night time consistent with patterns observed in Venezuela by Szarzynski & Anhuf (2001) and other rain forest studies summarized by Parker (1995). According to Walsh (1996) such diurnal variation occurs in response to daily patterns of plant transpiration, photosynthesis and respiration, but these in turn are strongly influenced by the amount of water available. Clearly, the frequency and intensity of moisture shortage could influence the diversity, abundance and distribution of epiphytes species in the canopy (Benzing, 1998).

3.4.2 Epiphyte community composition in relation to abiotic factors

Climate has a profound effect on species distribution in general (Woodward, 1987; Townsend *et al.,* 2000) and climatic factors explained some of the compositional variability observed for the individual epiphyte communities in this study. Temperatures as measured by physiological time (cumulative degree days) differed between epiphyte mats by up to 1082 degree days. Mats with a higher number of degree days and high VPD had significantly lower species richness and non-vascular

plant biomass at the two study sites. In Karamea, being the warmer of the two sites, the negative effects of warmer temperatures on non-vascular plant species richness was particularly evident. Temperature is one of the most important factors in a plants' life cycle, because it determines the limits within which a plant can establish, grow, reproduce and be biochemically active. Clearly, expressing temperatures in units of physiological time is a convenient tool to simplify the complex relationships between plant biology and temperature as degree days with an appropriate threshold measure only temperatures that affect plant growth. Rising temperatures increase the transpiration rate of plants, which makes non-vascular plants particularly vulnerable, because they lack roots, a cuticle and water conducting tissue (liverworts) to regulate their water loss. However, the ability of non-vascular plants to store substantial amounts of external water in external capillary spaces amongst the leaves (Proctor, 2000) protects cells from immediate damage when exposed to dry conditions. The duration of dry periods non-vascular plants can withstand without serious damage depends on the species and its water storage capacity, but also on community composition and the thickness of the accumulated humus layer (Veneklaas *et al.*, 1990). Proctor & Pence (2002) point out that most bryophyte species can withstand moderate levels of desiccation for a few days and many can survive extremely rapid desiccation in less than half an hour. While rehydration can occur within a few seconds and full recovery within a few hours the rate of recovery depends ultimately on the rate at which the desiccation occurred (Oliver *et al.*, 2005). Non-vascular plants in this study experienced short and prolonged periods of drying at any time of year despite very high and even distribution of rainfall, indicated by relative humidity above 70% for more than 90% of the time and VPDs below 1 kPa occurring less than 1%. However, previous studies use different units to investigate plant responses to dry stress. For example, León-Vargas *et al.* (2006) indicate that the metabolic processes of many bryophytes slow down when the cell water potential falls below full turgor, which is equivalent to relative humidity of 98.5 – 99.5%. At a cell relative water content of 25%, comparable to relative humidity of slightly above 95%, the plants metabolism comes to a complete standstill. Freiberg (1997), on the other hand, found stressed plants at VPDs > 1 kPa in a tropical rain forest in Costa Rica. Similarly Buckley *et al.* (1980) found that low saturation deficits caused stress in even xerophytic plants in a study in upper montane rain forests. Despite the different units used, these studies suggest that it is likely that prolonged periods of desiccation and

high accumulated temperatures as indicated by accumulated degree days could have reduced productivity, slowed down growth and resulted in the lower biomass observed for the epiphyte mats. Vascular plant biomass, however, followed the reverse trend in relation to VPD, indicating that growth conditions provided by the epiphyte mats in Karamea at least were favourable for vascular plant growth. Because vascular species are rooted in the organic substrate from which they obtain water and nutrients, water might be less of a limiting factor than for non-vascular plants at my sites.

Epiphyte communities at Karamea were in general less species rich and supported fewer non-vascular species and biomass than communities at Punakaiki. VPD combined with distance from the sea used as a measure of site differences explained 44.2% of the compositional variation between the two sites. Trees at Punakaiki were located on the flats inland from the coastline. In contrast, trees at Karamea were distributed along the coastline on higher slopes and thus were more exposed to prevailing strong westerly winds and salt spray. Air currents can affect transpiration rates by removing the boundary layer (water vapour that has accumulated at the leaf surface) of plants and can thereby accelerate water loss (Raven *et al.*, 1992). In an example given by Sveinbjörnsson & Oechel (1992) for bryophytes in Alaska wind speeds between 0.5 and 1 m s^{-1} were sufficient to directly regulate water loss from bryophyte mats on the ground. In addition, Dickinson *et al.* (1993) recorded a notably lower salt content of the air only a short distance from the coast, but similar salt concentrations for soils in the canopy and at the tree base. Although this did not seem to affect the epiphyte communities in their study, they noticed that bare patches in branch axils often coincided with saline and acidic conditions experienced in these habitats. It is possible that the drying effect of wind combined with salt spray and salt deposits create conditions that are unfavourable to seedling establishment and colonisation in some canopy habitats. Such conditions could have contributed to the lower species richness and biomass observed in Karamea.

Growing conditions as measured by microclimatic factors varied substantially for epiphyte mats from within the same tree and between different trees from within the same site affecting the community composition as was suggested by Cardelús & Chazdon (2005) from their study in Costa Rica. At both our study sites VPD was identified as one of three factors explaining some of the observed variability in epiphyte community composition. Freiberg (1996) remarked that the volume of the

humus layer and the water storage capacity and growth forms of epiphytes in the community can maintain a self-sufficient environment in drought periods and thus mitigate the effects of microclimatic extremes. Including VPD, 82.5% of the variability in epiphyte community composition at Karamea could be explained by branch angle and minimum mat depth. Levelled branches are likely to be more efficient in intercepting and retaining litter and propagules and to loose less water and nutrients from run-off than steep inclined branches. These conditions could favour the accumulation of thick layers of organic matter and facilitate seedling establishment.

3.5 Conclusion

The high variability in architectural complexity of epiphyte mat communities in this study was indicative of an equally high variation in microclimatic environments, which may have been even further enhanced by the presence of epiphytes. Microclimatic conditions varied over very short distances within the tree crown. VPD and temperature expressed as physiological time cumulative degree days were strongly correlated to the structure and composition of resident epiphyte communities, particularly non-vascular plants. The climate profiles showed that annual averages showed little seasonal variation but masked potentially harmful extreme conditions experienced by individual epiphyte mats. In order to fully appreciate variability in the canopy physical environment and its influence on the biological components it is necessary to carry out long-term micrometeorological measurements at multiple locations and directly at the epiphyte growth sites. Such information is crucial in understanding the implications of microclimate for patterns of plant distributions, ecological process and the dynamics within a forest.

Chapter 4

The influence of epiphyte diversity on the composition of resident invertebrate communities

Abstract

The influence of epiphyte diversity on the composition of invertebrate communities has been little studied despite the high abundance and diversity of both groups in many tropical and temperate forest canopies. Relationships between patterns of diversity, species richness and abundance of epiphyte communities and their resident invertebrate communities were examined across various spatial scales; among branches within a tree, among trees within regions and between two geographic regions; in lowland temperate rain forests on the West Coast of the South Island, New Zealand. Between April 2004 and January 2005, 96 samples (30 × 25 cm) were collected from individual epiphyte mats located in the crowns of 40 *Metrosideros robusta* (Myrtaceae) trees. A total of 364 invertebrate species and morphospecies were identified from 72366 adult specimens. Epiphyte mats provided habitat to a taxonomically and functionally highly diverse and abundant invertebrate fauna that was dominated in terms of abundance by Acari, Collembola and Hymenoptera (largely ants), and functionally by scavengers and ants. The overall species composition of epiphyte and invertebrate communities was highly variable among mats and no matching patterns in overall species composition and abundance were found between the two groups even when environmental variability was accounted for. However, strong positive correlations existed between the species richness of invertebrates and epiphyte mat biomass, while the species richness of herbivores was also correlated with the species richness of epiphytes. Invertebrate abundance, on the other hand, was positively correlated with epiphyte species richness, but showed a highly significant negative correlation with epiphyte mat biomass. Structural characteristics and complexity of the

epiphyte mats are clearly important for promoting high diversity and abundance of arboreal invertebrates, although responses may differ between taxonomic or functional groups depending on their resource requirements.

4.1 Introduction

Tree crowns in many temperate and tropical rain forests support an extensive flora of vascular and nonvascular epiphytes. These plants differ in structure, growth habit and function and thereby not only increase the structural complexity of the canopy, but also modify the climatic conditions of the surrounding area (Benzing, 1995; Erwin, 1995; Prinzing, 1997; Stuntz *et al.*, 2002a). An individual epiphytic plant such as a bromeliad, for example, can constitute a variety of microhabitats ranging from fully aquatic at and near the centre of the plant, to increasingly humus-rich, drier sections in older, marginal leaf axils (Benzing, 1995). Epiphytic bryophytes, on the other hand, often form dense mats that are several centimetres deep and accumulate substantial amounts of humus and leaf litter (Kitching *et al.*, 1997; Freiberg & Freiberg, 2000). Such a diversity of microhabitats and microclimatic conditions offers many niches for a multitude of invertebrate species and may at least partly explain the exceptionally high diversity of invertebrates in many forest canopies.

Epiphytes provide arboreal invertebrates with shelter from predators and climatic extremes, food and nesting sites. Lawton's (1983) resource diversity hypothesis predicts that plants that are architecturally more complex and provide a greater diversity of resources should support a greater diversity of invertebrates than structurally simple plants. Accordingly, more diverse plant communities should support a higher diversity and abundance of invertebrates, as has indeed been shown in several studies (Moeed & Meads, 1992; Crisp *et al.*, 1998). Such associations should be particularly pronounced between the diversity of plants and herbivores given that herbivores depend on plants for food (Novotny, 1993; Lowman *et al.*, 1998; Halaj *et al.*, 2000; Symstad *et al.*, 2000; Araújo *et al.*, 2006), although other studies have found no positive correlations (Feller & Mathis, 1997; Andrew *et al.*, 2003). Distinct arthropod faunas are also known from suspended soils and accumulated leaf litter associated with epiphytes in tree canopies (Nadkarni & Longino, 1990; Paoletti *et al.*, 1991; Kitching *et al.*, 1997). Often, many of these species are scavengers and are

heavily involved in the breakdown of litter and the cycling of nutrients through the wider ecosystem (Nadkarni & Longino, 1990). Variation in the depth and composition of the leaf litter and humus layers has been linked to changes in invertebrate diversity in some canopy studies (Halaj *et al.*, 2000; Stuntz *et al.*, 2002b; Yanoviak *et al.*, 2004) suggesting that positive associations may exist between scavenger diversity and the amount and type of non-living organic matter.

Despite their great abundance in many tropical and temperate forests, attempts to quantify the relationships between epiphyte and invertebrate community composition have been rare (Novotny *et al.*, 2003). The majority of the few existing studies have focused on single plant species that form discrete spatial units such as bromeliads, orchids (Dejean *et al.*, 1995; Richardson *et al.*, 2000a; Richardson *et al.*, 2000b; Stuntz *et al.*, 2002b) or bird's nest ferns (Ellwood *et al.*, 2002) while studies of invertebrates in epiphyte mats are even fewer (but see Winchester & Ring, 1999; Yanoviak *et al.*, 2003; Yanoviak *et al.*, 2004; Yanoviak *et al.*, 2006). The overall aim of this study was to increase understanding of the influence of epiphyte mat composition on the diversity of arboreal invertebrates in temperate rain forests of New Zealand. This study specifically examined 1) whether patterns in the diversity, species richness and abundance of epiphyte communities were reflected in the composition of their resident invertebrate communities across various spatial scales (among branches within a tree, among trees within regions and between two geographic regions) and seasons, and 2) whether there were relationships between resource diversity in epiphyte mats and the species richness and abundance of herbivores and scavengers in a community. It was expected that because epiphytes are generally highly aggregated in their distribution throughout the forest canopy along with the types, quality and quantity of resources they provide that such differences in resource patterning should be reflected in the distribution of canopy invertebrates.

4.2 Methods

4.2.1 Study sites

This study was conducted at two coastal sites on the West Coast of the South Island of New Zealand: at Bullock Creek (42°06′S; 171°20′E), Punakaiki in the Paparoa National Park and at the Heaphy Track (41°10′S; 172°10′E), near Karamea in the

Kahurangi National Park. Both sites are covered in largely undisturbed lowland rain forest vegetation consisting primarily of podocarp and broadleaved species that support a profusion of epiphytes and lianas. The climate is mild and very humid throughout the year with an average rainfall of approximately 2600 mm at Punakaiki and 1900 mm in Karamea. Detailed accounts of climate and vegetation of the two sites have been given in Chapter 2.

4.2.2 Tree selection and sample collection

Between April 2004 and January 2005, a total of 48 epiphyte mat samples were collected from 20 northern rata (*Metrosideros robusta*: Myrtaceae) trees at each of the two study sites over four sampling occasions. For detailed information on the biology and selection of the host tree species refer to Chapter 2. On each sampling event 12 epiphyte samples comprising 30 × 25 cm quadrats were collected from five of the 20 pre-selected trees at each site. Quadrats were located on the inner branches about 1.0 – 1.5 m from the main trunk at an average 20 m above the ground. On any given tree, either two or three quadrats were selected from a random subset of suitable and accessible epiphyte mats, but only one epiphyte mat was sampled per branch. Differences in the number of epiphyte mats sampled per tree were imposed by the design of a field experiment (Chapter 5) designed to accommodate the patchy distribution of epiphyte mats and potential difficulties in their accessibility. Single rope techniques (Winchester, 2004) were used to gain access to the canopy, while safety slings allowed for free movement between branches.

To study the interactions between epiphytes and invertebrates it was essential to sample the epiphyte habitats directly. Conventional methods such as insecticide fogging were considered unsuitable, since a considerable proportion of animals may not be captured, because they tend to remain inside funnel-shaped plants (Ellwood *et al.*, 2002) or in the thick humus layer associated with many epiphytes (Yanoviak *et al.*, 2003). Prior to collecting individual quadrat samples from the epiphyte mats the percentage foliar cover of individual plant groups, litter and bare bark was estimated. Each quadrat sample was then carefully detached from the bark and enclosed in a separate plastic bag to be transported to the lab for processing. Branch height above the

ground, branch diameter, branch angle, branch aspect, and minimum and maximum epiphyte mat depth were recorded for each quadrat.

4.2.3 Sample processing

In the laboratory invertebrates were extracted from the epiphyte material using Berlese funnels. Samples were kept in the funnels for a minimum of 3 days or until the sample material was completely dry. All invertebrates were sorted to morphospecies within higher taxa, counted and preserved in 75% ethanol. The compiled species list includes species and morphospecies and is hereafter referred to as species list. Immature specimens were quantified to order but not included in the species list. Lepidoptera larvae were the exception, in that all larval species were identified and therefore recorded in the species list. Unidentifiable specimens were grouped as 'others' and excluded from both species counts and analyses, as were Acari, which are still in the process of being identified. Specimens from most orders were sent to expert taxonomists for further identification to the lowest possible taxonomic level. Morphospecies from the few mainly minor orders for which no taxonomic expertise was available were distinguished based on morphological characteristics used in various taxonomic keys. A reference collection was deposited in the Entomology Museum at Lincoln University, Canterbury, New Zealand.

All specimens included in the species list were further quantified according to feeding guilds based on the guilds recognised by Moran & Southwood (1982) and Stork (1987). The guilds used in this study were herbivores, which were further split into chewers and sap feeders, scavengers (including dead wood, lichen and fungal feeders) and epiphyte grazers, predators, parasitoids, ants and others. Epiphyte grazers in this study consisted of Collembola and although this group is involved in the breakdown of organic matter and the cycling of nutrients, Collembola were here classified as epiphyte grazers rather than scavengers, because most species feed on micro-organisms associated with the rhizosphere and decomposing organic matter rather than decayed plant material (Greenslade, 1991). Species for which no information was available about their feeding habit or species that could be assigned to more than one guild (except ants) were classified as 'others'.

Subsequent to extracting the invertebrates, the epiphyte material from each quadrat was processed as outlined in Chapter 2.

4.2.4 Data analyses

Species inventories were compiled and frequencies of individual species in the quadrats recorded to quantify the diversity and composition of the invertebrate communities at each study site. To directly compare the species richness between the two sites and assess the completeness of the species lists, individual-based rarefaction curves were computed with an average of 50 randomisations without sample replacement in EstimateS Version 8 (Colwell, 2006). The estimated total species richness for individual invertebrate orders at each site was calculated using ACE (Abundance-based Coverage Estimator) and Chao1 estimators in EstimateS (Colwell, 2006). This programme was also used to calculate the estimated abundance-based Jaccard similarities within and between sites, which is a measure of the true number of species shared by two samples. This index is based on the probability that two individuals randomly chosen from two samples belong to a species present in both samples without necessarily being the same species. Species that are present in both samples, but were not encountered in one or both samples are taken into account by the estimator, which makes this index very useful for incompletely sampled species rich communities (Chao *et al.*, 2005).

Epiphyte community composition was further investigated using Shannon-Wiener diversity (H') and Simpson diversity (1/D) generated in PRIMER 5 (Clark & Warwick, 2001). Shannon index is most sensitive to the abundance of rare species in the community (Magurran, 1988) and, although widely used (Ludwig & Reynolds, 1988), has attracted much criticism (Hurlbert, 1971; Routledge, 1980; Lande, 1996; Magurran, 2004). This index was included here primarily for comparison with past studies. Simpson diversity is one of the most robust diversity measures and emphasises the dominant species in a community while being less sensitive to species richness (Magurran, 2004). This index captures the variance of the species abundance distribution, thus the Simpson value increases as a community becomes more even. Simpson diversity is not a pure evenness measure, but when divided by the number of species in the sample Simpson's measure of evenness (E_{1-D}) can be calculated

(Magurran, 2004). E_{1-D} is a well-performing index that is not sensitive to species richness (Smith & Wilson, 1996) and ranks minimum to maximum evenness on a scale from 0 to 1.

To examine spatial patterns of species richness, abundance, Shannon diversity and Simpson's measure of evenness between sites, among trees and branches within trees, and to take into account the unbalanced design of this study, a variance components analysis using the method of residual maximum likelihood (REML) (Genstat®9.1, 2006) was carried out. The abundance data used in the REML analyses deviated from normality and were therefore $\log_{10}$ transformed. Likelihood tests were used to compare and identify the best model from competing random models (Snell & Simpson, 1991). Different factors (site, tree and branch) were added to the model to determine whether the inclusion of any of these factors had a significant effect on the results (Johnson & Omland, 2004).

Simple linear regression was used to determine whether relationships existed between both invertebrate species richness and abundance and characteristics of the epiphyte communities (species richness, total mat biomass and green plant tissue biomass). Invertebrates were further split into guilds to determine relationships between herbivores and vascular species richness and biomass (non-vascular plants are generally a poor food source for herbivores), whereas scavengers were tested for their correlation with the non-living biomass of the epiphyte mats.

To assess the relationship between spatial patterns of invertebrates and epiphytes across samples the relative abundance distribution of the invertebrates was compared with the relative biomass distribution of the epiphytes using a Mantel test computed in the statistical package vegan in R 2.4.1. A partial Mantel-test was carried out to examine whether dissimilarities in nine environmental factors (branch height, branch diameter, branch angle, aspect, minimum and maximum epiphyte mat depth, distance between trees, tree, and site; data were not transformed) influenced the observed spatial patterns at each site. Matrix randomisation was restricted to within sites and 10,000 permutations.

4.3 Results

4.3.1 Invertebrate community composition

A total of 178641 individuals, including 72366 adult specimens, belonging to more than 364 invertebrate species (including morphospecies) and 134 families were collected from 96 epiphyte quadrats across the two study sites (Appendix 3). Epiphyte mats at both study sites supported highly abundant and species rich invertebrate communities that were comparable with respect to many of their community parameters (Table 4.1; Figure 4.1). Mean invertebrate species richness and abundance as well as mean epiphyte species richness in Punakaiki, however, were significantly higher than in Karamea (Table 4.1).

Table 4.1 Comparative measures of invertebrate community composition of epiphyte mats in the canopy of northern rata at two study sites. Standard errors are given for mean values. Significance values are results from two-sample t-tests. Epiphyte biomass is the weight of all dry organic material (d.o.m.).

	Punakaiki		**Karamea**		**p-values**
Total invertebrate abundance	93787		84854		
Mean invertebrate abundance/ 100g d.o.m.	860.69	(± 88.8)	821.78	(± 89.9)	0.76
Total invertebrate species richness	262		256		
Mean invertebrate species richness/ sample	30.48	(± 1.6)	26.27	(± 1.1)	< 0.05
Singletons	81		78		
Chao's Jaccard abundance based similarity	0.52	(± 0.008)	0.40	(± 0.009)	< 0.001
Mean Shannon (H')	1.76	(± 0.09)	1.81	(± 0.05)	0.76
Mean Simpson index (1/D)	4.22	(± 0.44)	4.92	(± 0.49)	0.29
Mean Simpson's evenness ($E_{1/D}$)	0.08	(± 0.007)	0.07	(± 0.006)	0.07
Mean epiphyte biomass (kg m^{-2})	3.48	(± 0.22)	3.52	(± 0.32)	0.77
Mean epiphyte species richness	11.70	(± 0.8)	6.30	(± 0.4)	< 0.001

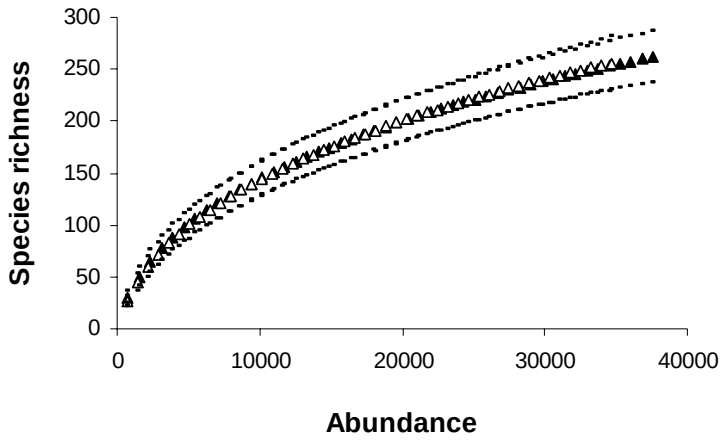


Figure 4.1 Coleman rarefaction curves (average of 50 randomisations without sample replacement ± 95 % C.I.) for invertebrates (excluding unidentified and immature specimens) collected from 48 epiphyte mats at each of two study sites, Punakaiki (solid triangles) and Karamea (open triangles).

All taxonomic groups were present at both sites except for Nematoda, which was not recorded in Karamea and Dermaptera, which was not collected in Punakaiki. Communities at both study sites varied generally little in the abundance of their invertebrate orders with Acari and Collembola comprising most individuals, around 80 % of the total (Figure 4.2). Although most taxonomic groups were more abundant in Punakaiki than Karamea, differences were only significant for Pseudoscorpiones ($t = 4.38$; $p < 0.0001$). However, Hymenoptera were more numerous in Karamea. Most orders were on average represented by less than 10 individuals.

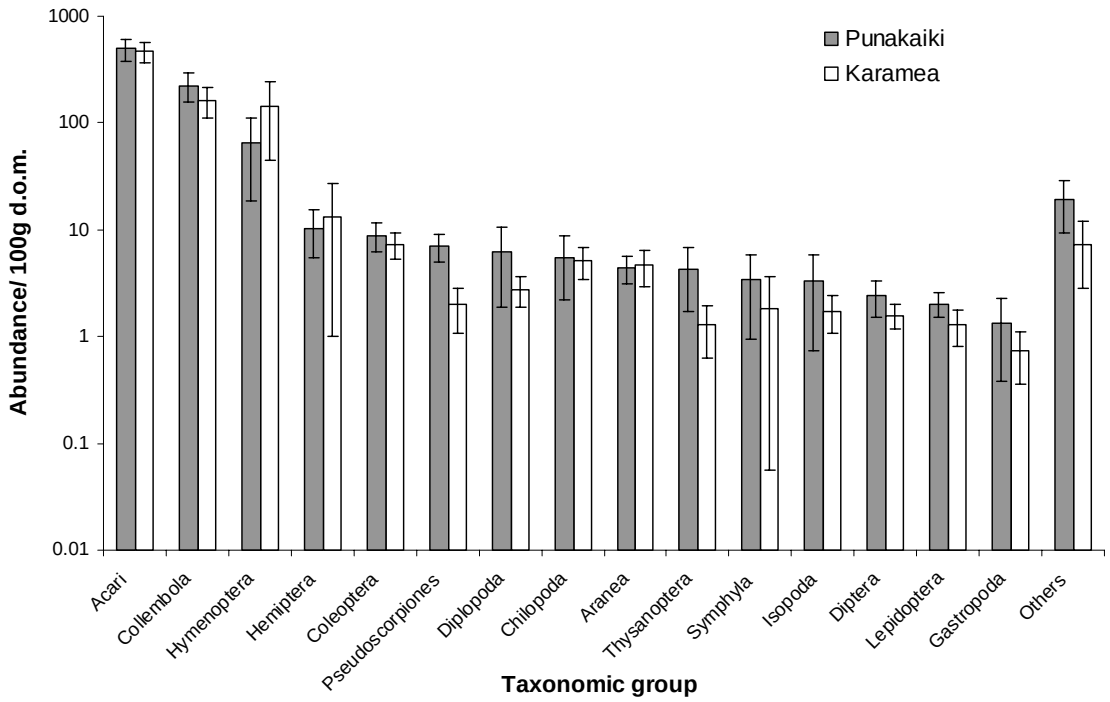


Figure 4.2 Mean invertebrate abundance (± 95% C.I.) recorded in epiphyte mats from the canopy of northern rata at two study sites Punakaiki (black bars) and Karamea (white bars). 'Others' combines the minor taxonomic groups Orthoptera, Blattodea, Psocoptera, Neuroptera, Trichoptera, Dermaptera, Amphipoda, Oligochaeta, Nematoda and Archaeognatha with a mean abundance < 1 individual and unidentified specimens.

The species richness estimators ACE and Chao1 indicate that about 69 % of the estimated total invertebrate species were collected at each of the two study sites and 42.3 % of the total species were shared between sites (Table 4.2). Of the estimated number of species collected, Thysanoptera, Psocoptera and Hymenoptera were the most undersampled orders in Punakaiki (< 50 %), and Coleoptera was the most undersampled order in Karamea (30 %). At both sites all Diplopoda, Chilopoda, Pseudoscorpiones and Isopoda (in Karamea only) species estimated to be present were collected.

Table 4.2 Observed richness (with percent of the total in parentheses) and estimated richness (as predicted by ACE and Chao1 estimators) of invertebrate species across taxa for the two study sites. The percentage of the estimated species collected for each invertebrate taxonomic group was calculated by dividing the observed number of species by the higher of the ACE or Chao1 values (x 100). The proportion of species within each invertebrate order shared by the two sites is given as % shared. Others combines all orders with ≤ 3 species.

	Punakaiki				Karamea				
Taxonomic	**Observed**	**AC**	**Chao1**	**% Collected**	**Observed**	**ACE**	**Chao1**	**% Collected**	**% Shared**
Hemiptera	44 (16.8%)	53	50	83.0	36 (14.1%)	42	42	85.7	45.5
Coleoptera	38 (14.5%)	55	50	69.1	46 (18.0%)	85	156	29.5	35.5
Hymenoptera	30 (11.5%)	65	62	46.2	24 (9.4%)	36	32	66.7	28.6
Collembola	30 (11.5%)	33	32	90.1	33 (12.9%)	39	43	76.7	57.5
Lepidoptera	26 (9.9%)	40	43	60.5	21 (8.2%)	29	27	72.4	38.2
Aranea	26 (9.9%)	36	37	70.3	26 (10.2%)	48	44	54.2	26.8
Diptera	10 (3.8%)	13	15	66.7	15 (5.9%)	22	24	62.5	38.9
Others	10 (3.8%)	11	10	90.1	12 (4.7%)	16	14	75.0	57.1
Pseudoscorpion	8 (3.1%)	8	8	100.0	7 (2.7%)	7	7	100.0	87.5
Gastropoda	8 (3.1%)	10	9	80.0	6 (2.3%)	7	6	85.7	40.0
Thysanoptera	7 (2.7%)	22	13	31.8	6 (2.3%)	8	6	75.0	44.4
Diplopoda	6 (2.3%)	6	6	100.0	4 (1.6%)	4	4	100.0	66.7
Isopoda	6 (2.3%)	9	9	66.7	7 (2.7%)	7	7	100.0	62.5
Oligochaeta	5 (1.9%)	7	6	71.4	5 (2.0%)	6	5	83.3	42.9
Psocoptera	4 (1.5%)	12	7	33.3	4 (1.6%)	8	6	50.0	33.3
Chilopoda	4 (1.5%)	4	4	100.0	4 (1.6%)	4	4	100.0	100.0
Total	**262**	**360**	**384**	**68.2**	**256**	**349**	**365**	**70.1**	**42.3**

The REML variance component analysis showed that most of the variability in community composition could be attributed to differences among branches rather than among trees or between sites (Table 4.3). The variance component values for total species richness, mean abundance/ biomass and the diversity indices were consistently high (≥ 65 %) at the branch level, although variation among trees had a significant effect on invertebrate abundance and Simpson's measure of evenness. Epiphyte species richness varied significantly on all spatial levels.

Table 4.3 Variance components (± s.e.) for the relative effects of site, tree and branch variation on total invertebrate and epiphyte species richness, abundance and diversity. Totals were calculated based on data summed over species. The asterisks indicate significance level * $p < 0.05$, ** $p < 0.001$. The branch-level component represents the residual variance in the analysis and therefore there are no associated p-values.

	Variance components						
	Site		**Tree (site)**		**Branch (tree, site)**		**Total**
Invertebrates							
Species richness	5.1 ±11.9	(4%)	21.6 ±17.0	(16%)	104.0 ±19.5	(80%)	130.7
Abundance (log_{10})/ 100g	-0.005 ±0.001	(-3%)	0.048* ±0.025	(28%)	0.128 ±0.024	(75%)	0.171
Shannon (H')	0.018 ±0.030	(11%)	0.013 ±0.019	(8%)	0.134 ±0.025	(81%)	0.165
Simpson (E1/D)	0.0000 ±0.0000	(0%)	0.0005* ±0.0003	(25%)	0.0015 ±0.0003	(75%)	0.002
Epiphytes							
Species richness	14.0** ±20.8	(40 %)	9.1** ±3.3	(26 %)	11.5 ± 2.2	(34%)	34.6
Biomass	0.0 ±22.9	(0%)	70.6 ±85.6	(11%)	592.7 ±111.1	(89%)	663.3
Shannon (H')	0.026 ±0.045	(10%)	0.051 ±0.031	(21%)	0.172 ±0.032	(69%)	0.249
Simpson (E1/D)	0.006 ±0.009	(13%)	0.009 ±0.005	(22%)	0.027 ±0.005	(65%)	0.042

4.3.2 The influence of site on guild composition

Assigning the invertebrates to feeding guilds showed that the guild composition of the invertebrate communities is remarkably similar at the two study sites. Epiphyte grazers, consisting primarily of Collembola, were by far the most abundant and species rich guild at both sites (Figure 4.3). Although ants were the second most abundant guild they contained the lowest number of species. Predators, herbivores and scavengers had a low abundance, but predators also matched the species richness of the Collembola. Of the two herbivore guilds, chewers were more species rich than the sap feeders.

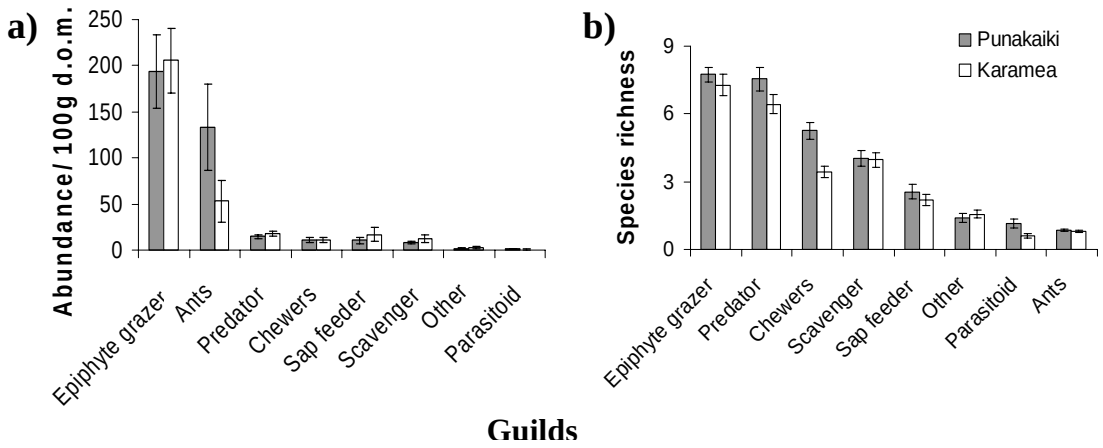


Figure 4.3 Guild composition of invertebrate communities collected from epiphyte mats in northern rata at two study sites, Punakaiki (black bars) and Karamea (white bars) by a) abundance standardised per dry organic matter (d.o.m.) weight of the epiphyte mats and b) species richness. All values are means (± s.e.).

4.3.3 Seasonal influence on invertebrate community composition

There was generally little seasonal fluctuation in invertebrate abundance across the two study sites, although seasonal patterns varied slightly (Figure 4.4). In Punakaiki a significantly lower number of invertebrates (< 400 individuals) was recorded in the winter month, July, but not in Karamea where the lowest abundance (< 550 individuals) was recorded in the spring month October. This limited seasonality is consistent with the climate data recorded from a selection of these mats over the study period (Chapter 3).

Seasonal changes were also apparent in the guild composition of the invertebrate communities, but there were no consistent patterns across the two sites. Epiphyte grazers were highly abundant throughout the year, but peaked in summer at Punakaiki and in spring at Karamea (Figure 4.5). Ant numbers in autumn and winter at Punakaiki were comparable to or exceeded the abundance of Collembola, while in spring and summer ants were significantly less abundant than in winter. At Karamea, on the other hand, ant numbers were highest in autumn and summer, with their abundance in summer significantly higher than in winter and spring. There were, however, no relationships between ant numbers and the abundance of other guilds. The two herbivore guilds were most abundant in autumn and spring at Punakaiki whereas at

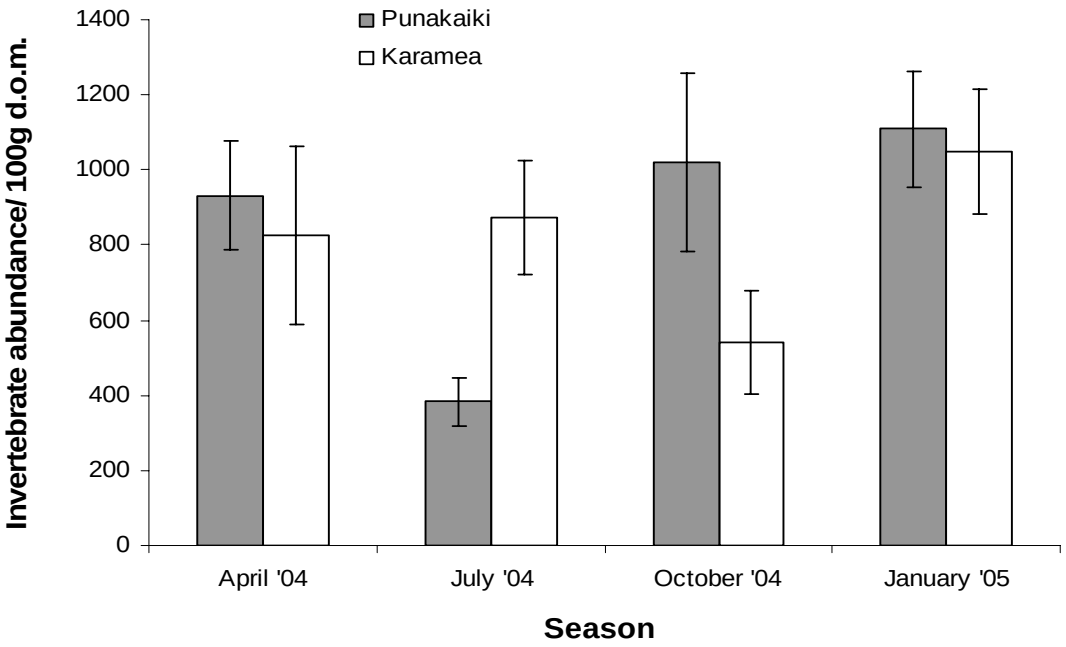


Figure 4.4 Changes in mean invertebrate abundance over four seasons for two study sites, Punakaiki (black bars) and Karamea (white bars) ± s.e.

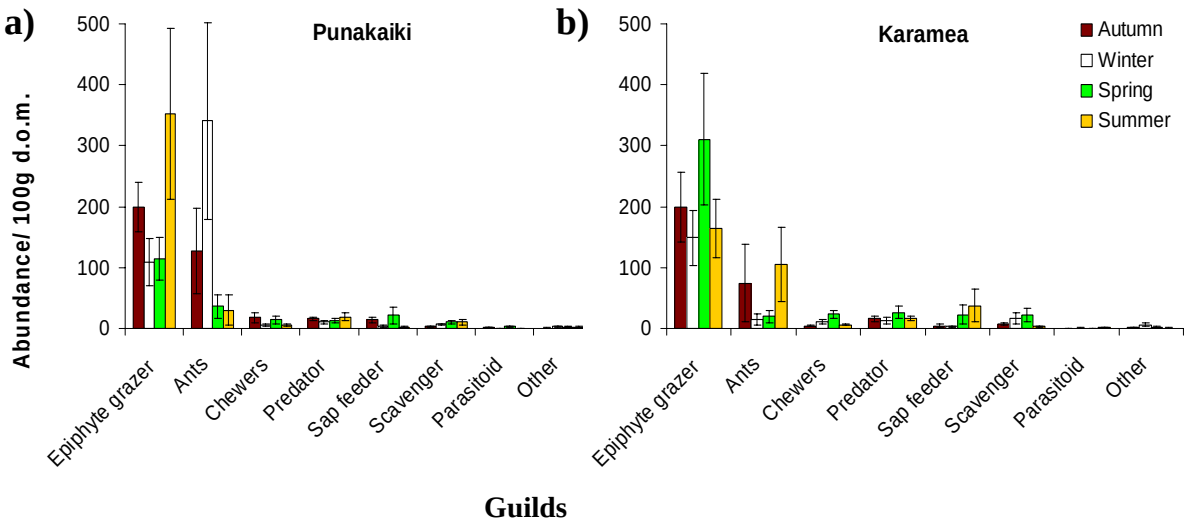


Figure 4.5 Changes in mean invertebrate abundance (± s.e.) within guilds over four seasons at two study sites a) Punakaiki and b) Karamea. Abundance was standardised by dry organic matter (d.o.m.) weight of the epiphyte mats.

Karamea the number of chewers peaked in spring and that of the sap feeders in spring and summer.

4.3.4 The influence of epiphyte mat composition

The Mantel test results showed that patterns of species similarities for invertebrates as a whole and herbivores were not correlated with epiphyte species composition. There was a weak, significant correlation at the 10 % level between herbivore and epiphyte as well as herbivore and vascular epiphyte species composition (Table 4.4). However, non-living biomass components of the epiphyte mats were not important in determining the pattern of scavenger species similarity (Table 4.4). Controlling for the effects of abiotic factors on samples within sites in the partial Mantel tests had little effect on the above relationships (Table 4.4).

Table 4.4 Results of Mantel correlations between species similarities of invertebrates and epiphyte mat components. The partial Mantel correlations control for the effect of abiotic variables within sites. Non-living material consists of soil, litter, roots and woody material such as bark, sticks and seeds.

	Explanatory factor	**Mantel r**	**p-value**	**Partial Mantel**	**p-value**
Invertebrates	Epiphytes	0.057	0.12	0.05	0.14
Herbivores	Epiphytes	0.057	0.09	0.05	0.12
Herbivores	Vascular epiphytes	0.065	0.06	0.06	0.09
Scavengers	Non-living material	0.082	0.14	0.08	0.14
Scavengers	Litter/ soil	0.074	0.19	0.07	0.20

Regression analyses showed a significant increase in both invertebrate species richness (Figure 4.6a) and abundance (Figure 4.6.b) with an increase in the total biomass of the epiphyte mats (Table 4.5). A significant positive correlation was also found for invertebrate abundance and species richness of the epiphyte communities whereas the species richness of invertebrates and epiphytes was significantly correlated at the 1 % level of significance. Herbivore species richness increased significantly with an increase in total epiphyte richness and vascular plants biomass, but herbivore abundance was not related to any of the epiphyte community characteristics. Scavenger

species richness, on the other hand, was significantly related to non-living epiphyte biomass (Figure 4.6.c), but their abundance was not (Table 4.5). However, significant nonlinear correlations (Spearman rank correlation) existed between chewer species richness and fern biomass ($p < 0.05$) as well as sap feeder species richness versus dicotyledons species richness ($p < 0.05$) and dicotyledons biomass ($p < 0.01$).

Table 4.5 Regression analysis results for total invertebrate, herbivore and scavenger guild species richness and abundance with epiphyte species richness and mat biomass components (n=96).

Correlations	**r**	**t**	**p - value**
a) Invertebrate species richness versus			
Epiphyte species richness	0.192	1.90	0.06
Total epiphyte mat biomass	0.472	5.20	< 0.0001
b) Invertebrate abundance/ 100g d.o.m. versus			
Epiphyte species richness	0.228	2.27	< 0.05
Total epiphyte mat biomass	- 0.395	- 4.17	< 0.0001
c) Herbivore species richness versus			
Epiphyte species richness	0.239	2.39	< 0.05
Vascular plant biomass	0.263	2.65	< 0.01
d) Herbivore abundance versus			
Epiphyte species richness	- 0.049	- 0.48	0.63
Green plant tissue biomass	- 0.025	- 0.24	0.81
e) Scavenger species richness versus			
Non-living epiphyte biomass	0.400	4.24	< 0.0001
f) Scavenger abundance versus			
Non-living epiphyte biomass	0.066	0.64	0.53

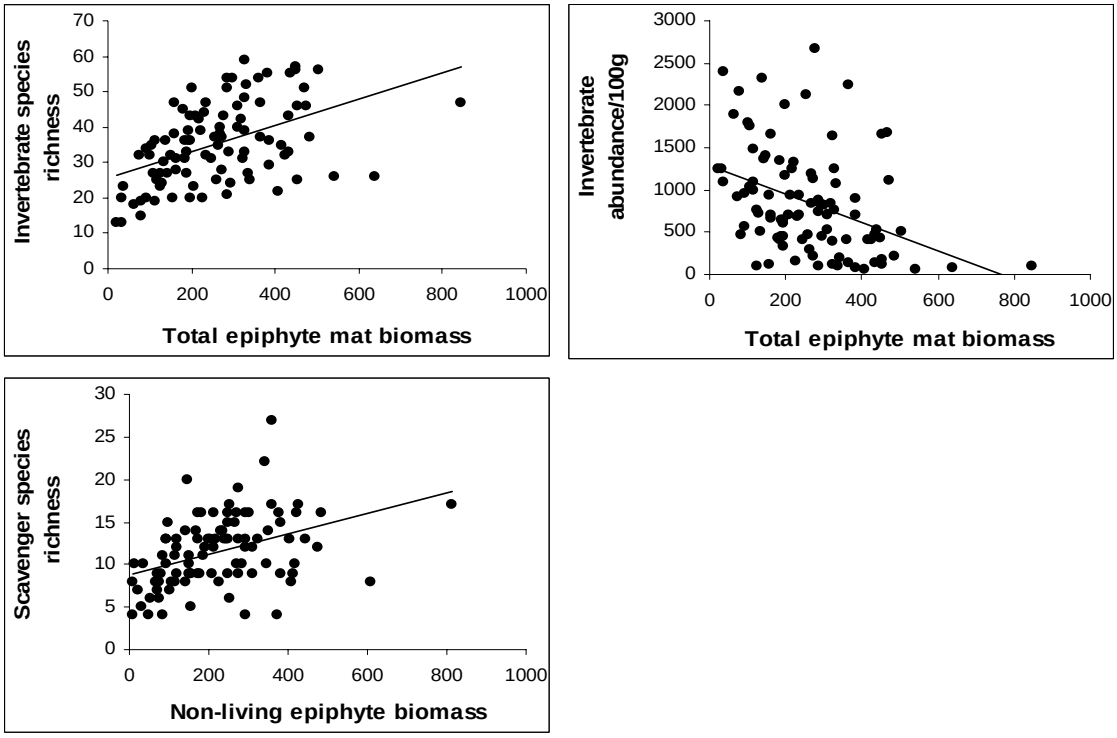


Figure 4.6 Presentation of highly significant correlations between epiphyte mat biomass and invertebrate species richness a), and invertebrate abundance b) and non-living biomass and scavenger species richness for two study sites combined.

4.4 Discussion

4.4.1 Associations between invertebrate diversity and epiphyte diversity

The absence of clear concurring patterns between the diversity of epiphytes and invertebrates in this study indicates that the interactions and dynamics within these multi-species communities are more complex than can be explained simply by epiphyte diversity. The prediction that the diversity of invertebrate communities is a function of the diversity of their respective host epiphyte communities was only partly supported by the Mantel test where a significant relationship at the 10 % level of significance was found for herbivores. This relationship remained even when differences in the environmental characteristics of the branches were taken into account. However, results from the REML analysis showed that the highly variable overall diversity of the invertebrate communities was not reflected in that of their host

epiphyte communities, suggesting that the two communities may respond to different factors. Differences in host tree and branch characteristics, microclimatic conditions and highly stochastic processes associated with dispersal, propagule colonisation and establishment success are possibly strong drivers in the community composition and diversity of canopy epiphytes (Chapter 2) and may also be responsible for their highly aggregated, island-like, distribution. Even though the distribution of canopy invertebrates may be largely driven by the type, availability and abundance of the resources provided by epiphytes (Novotny *et al.*, 2003), other factors such as species' dispersal abilities, life history traits and feeding characteristics will further influence invertebrate species richness and abundance.

Invertebrate species richness and epiphyte mat characteristics

It is expected that structurally more heterogeneous habitats generally promote higher species richness (Lawton, 1978; Tilman, 1986; Rosenzweig, 1995). This was also the case in this study, but is more complex than simply the prediction of high invertebrate diversity associated with high heterogeneity represented by high epiphyte diversity. This relationship was manifest between invertebrate species richness and the biomass of the epiphyte mats. The strong positive correlation between invertebrate species richness and epiphyte biomass is consistent with findings by Stuntz *et al.* (2002b) for single-species, epiphytic habitats. Such a relationship not only reflects an increase in resource concentration but also habitat heterogeneity through changes in different species contribution to the composition and biomass of green plant tissue as well as the depth and composition of the humus/ litter layer among epiphyte mats

In this study, most of the green tissue biomass in epiphyte mats originated from vascular epiphytes (Chapter 2) and as predicted, there was a positive correlation between the number of herbivore species and vascular plant biomass. Vascular plants are considered to be a more attractive and nutritious food source than non-vascular plants (Yanoviak *et al.*, 2004) and due to their taller size they are more conspicuous and thus easier to locate by herbivores (Lawton, 1983), although insects are more likely to use olfactory cues to locate suitable food plants. In addition, the increased leaf area of structurally complex vascular species may provide more oviposition sites, feeding sites, shelter and microhabitats, thus allowing more species to coexist and utilise available resources. Indeed, results in this study suggest that the biomass (plant surface area) and species richness of dicotyledonous plants may be a driving factor of

sap feeder (exclusively Hemiptera) species richness. Different species of dicotyledonous plants combined with their various growth stages may provide nutritiously diverse food to sap feeding species. In contrast, chewer species richness was positively correlated with fern biomass. Non-vascular plants, however, appeared to influence high herbivore species richness by increasing overall epiphyte species richness and habitat heterogeneity by adding shelter and microhabitats.

As predicted, the positive effect of increased resource diversity on species richness was also apparent in the strong correlation between scavenger species richness and the biomass of non-living organic matter in the epiphyte mats. Deeper litter/ humus layers will provide a wider range of microclimatic conditions thereby providing refuge and a buffer from microclimatic extremes and more stable climatic conditions (Villani & Wright, 1990; Rodgers & Kitching, 1998; Lindo & Winchester, 2007) in an otherwise harsh canopy environment. Such improved habitat conditions would allow more sensitive species that are usually prone to desiccation to colonise and persist in this habitat. Nutritional changes occurring in response to an increase in substrate may provide additional resources that attract a wider range of species (Wardle *et al.*, 2003).

Invertebrate abundance and epiphyte mat characteristics

Although invertebrate species richness and abundance are both influenced by habitat structure, their responses were rather different. The total number of invertebrates increased significantly with an increase in total epiphyte species richness, which may be due to the availability of a wider range of resources or the higher abundance of similar resources provided by different plant species. Such increase in resources may reduce intra- or inter-specific competition and predation pressure, which may allow populations to increase. Interestingly, invertebrate abundance decreased substantially with an increase in epiphyte mat biomass, which is contrary to the findings of Ellwood *et al.* (2002) for termite and ant abundance and bird's nest fern biomass. Scavenger abundance, on the other hand, was not correlated with the biomass of non-living organic matter. These results are difficult to explain and suggest that high quantities of resources are no substitute for quality or that many of these scavenger species are not food limited. Shortage of suitable resources or poor resource quality, that could be masked by the high biomass recorded in this study, can have detrimental effects on organisms, affecting colonisation and food web interactions (Price, 1992). Poor nutrient content and the indigestible nature of organic matter in bromeliads, for

example, has been suggested to account for the lower abundance and productivity in that system compared with *Heliconia* bracts (Richardson *et al.*, 2000b). However, such a scenario is highly unlikely to explain the observed pattern in this study as the negative relationships were consistent across sites and over the entire year.

Seasonality and invertebrate abundance

Seasonal fluctuations in invertebrate abundance were relatively minor throughout the year at both study sites suggesting that changes in the seasonal abundance of resources and climatic conditions had, in general, little effect on invertebrate numbers. However, the significantly lower number of invertebrates recorded at Punakaiki in winter is likely a reflection of the colder winter temperatures experienced at this site compared to Karamea.

Small, but often non-significant, differences in abundance were observed for the various guilds among seasons and between sites. Seasonal changes in community composition likely reflected patterns related to the life history of specific invertebrate groups or species, the seasonal availability of different foods and seasonal weather patterns. Epiphyte grazer abundance, for example, peaked in the spring and summer months when warmer and wetter conditions may enhance their and other scavenger's development and activity and thus the breakdown of organic material, whereas somewhat higher herbivore numbers coincided with spring when plants develop young and tender shoots or produce floral resources. The reasons for seasonal variation in ant abundance, however, were less conclusive and may reflect their generalist feeding habit. Alternatively, high ant numbers may have been driven by chance sampling encounters of entire colonies.

4.4.2 Scale effects on the spatial patterns of invertebrate diversity

Epiphyte mats at both study sites supported similarly diverse and highly abundant invertebrate communities that varied little in their ordinal and functional composition. Acari, Collembola, Hymenoptera (largely ants), Hemiptera and Coleoptera, dominated the communities both with respect to abundance and species richness. The proportionally high contribution of these taxonomic groups to overall community composition reflected the ranking of dominant orders with respect to species abundance and richness in forest systems worldwide. The high abundance of ants in

this study, however, was very unusual for a temperate rain forest and more reminiscent of canopy communities in tropical forests.

At the functional level, communities at both sites were characterised by an abundance of scavengers consisting primarily of Collembolan epiphyte grazers, followed by ants, whereas species richness was similarly high for scavenger, predators and the two herbivore guilds. The high abundance of scavengers in this study is typical of habitats with a substantial humus component, but also characteristic of bromeliads in tropical Puerto Rico (Richardson *et al.*, 2000b) and Panama (Stuntz *et al.*, 2002b). Community guild composition was, however, in sharp contrast to the predator-dominated communities of an orchid species in the latter study. While variation in guild composition may reflect differences in habitat type it also raises the issue of guild assignment, particularly of species whose feeding habitats are unknown as is often the case in highly diverse canopy habitats, including this one. In some cases, guild assignments of such species were inferred from known feeding habitats of closely related species or entire taxa, such as Collembola and Aranea. In other instances, species, including mites and immature specimens, were excluded from species richness and guild analysis, because their biology is poorly understood and they cover a wide range of feeding habits. Yet, other species including those that fall into more than one guild were placed into the 'others' guild. Either of these guild assignments for species with unknown feeding habit may have resulted in the misrepresentation of some guilds with regard to their abundance. While the results presented here for feeding guilds offer an incomplete picture of the invertebrate communities in this study they nevertheless give a preliminary indication of functional community structure, an aspect that is often neglected in invertebrate community studies.

The richness estimators indicate that the species lists presented for each site in this study are incomplete and that an additional 30 % or more species per site could be expected with higher sampling effort. Although the majority of individual invertebrate species were only found at one or the other site (only 42 % were shared by the two sites), Jaccard abundance-based similarity (0.95) indicates a high degree of species overlap between sites, similar to that recorded by Yanoviak *et al.* (2006) between primary and secondary forests in Costa Rica. Species overlap for samples compared between trees and branches within sites, however, was much lower with Jaccard values of 0.40 and 0.50, suggesting that communities are very variable with respect to their

species composition at a finer spatial scale. Supporting evidence comes from the variance component analysis, which showed that spatial patterns of invertebrate species richness, abundance and diversity indices were primarily influenced by spatial variation at the branch level that accounted for between 75 – 81 % of total variance, rather than by spatial variation at site or tree levels. Invertebrate abundance and Simpson's evenness were the only exceptions, as they were also significantly affected by tree level variation. High variability in climatic conditions between branches within the same tree and between trees (see Chapter 3) and the high proportion of rare species (40 %) represented by two or fewer individuals may account for some of the high variation in community characteristics observed between branches. Dispersal limitations and the clumped distribution of some species, such as the colony-forming ant *Prolasius advena*, may further help to explain the effect of tree variation on invertebrate abundance and Simpson's evenness. Alternatively, the highly variable composition of invertebrate communities may be a reflection of the distribution and composition of their epiphyte host communities and their associated resources.

4.4.3 Noteworthy discoveries

This study discovered several undescribed species in the epiphyte mat habitats. Of particular interest was the discovery of a new genus of felt scale, *Affeldococcus kathrinae*, (Hemiptera: Eriococcidae) (Henderson, 2007), new species of the genera *Acrochordonus* and *Chorizococcus* (both Hemiptera: Pseudococcidae), *Poropeza* "near" *dacrydii* (Hemiptera: Coccidae), the first New Zealand record of wingless Sciaridae (Diptera) and species of the rare Scatopsidae family (Diptera). Further new discoveries included the potentially new Yponomeutoidae sp. (Lepidoptera) and Chelagyrtodes sp. (Leiodidae: Coleoptera), two new species of the Diplopod family Dalodesmidae including one *Tongodesmus* species and a species from an unidentified Araneae family. The total number of new species is estimated to be much higher given that a large proportion, 77 %, of specimens could only be identified to genus or family level. Orders such as Hymenoptera, Diptera, Araneae and the Class Collembola were particularly difficult and identification beyond family level was impossible due to the high proportion of undescribed species and lack of taxonomic keys for these groups. These results ultimately reflect that only about 50 % of the New Zealand invertebrate

fauna has been described (Emberson, 1994) while new species are still discovered not only in ground-based terrestrial ecosystems, but now also in canopy habitats. This highlights the immense tasks and challenges faced by taxonomists and researchers incorporating the study of invertebrates in projects, but also the immense scope offered by invertebrates for exploring different aspects of their ecology and involvement in ecosystem processes.

Apart from new species, this study also recorded new distributions for various species. First arboreal distributions were recorded for the Lepidopteran genus *Mallobathra* (Psychidae) and the species *Cryptaspasma querula* (Tortricidae). In addition, a species of the cosmopolitan family Habrodesmidae (Diplopoda) has been recorded for the first time in New Zealand (Peter Johns, pers. comm. 2006). The Hemiptera species *Newsteadia gullanae* is described from Australia and has so far only been found in this study and a similar canopy study of epiphyte mats in rimu (Affeld, 2002). One of the most surprising finds was the discovery of large ant colonies comprising several hundreds to thousands of individuals of the species *Prolasius advena*. This is the first record of arboreal ant colonies for New Zealand and of a species that until now has been described as ground nesting (Don, 2007). Ants are highly abundant in the canopies of many tropical rain forests (Huxley, 1980; Stork, 1987; Floren & Linsenmair, 2005) where they often form close associations with honeydew secreting Hemipteran insects (Bach, 1991; Davidson, 1997). Although *Prolasius advena* is known to tend mealy bugs (Hodgson & Henderson, 2000) this study found no correlation in the abundance or presence/absence between the two groups.

4.4.4 Exotic species

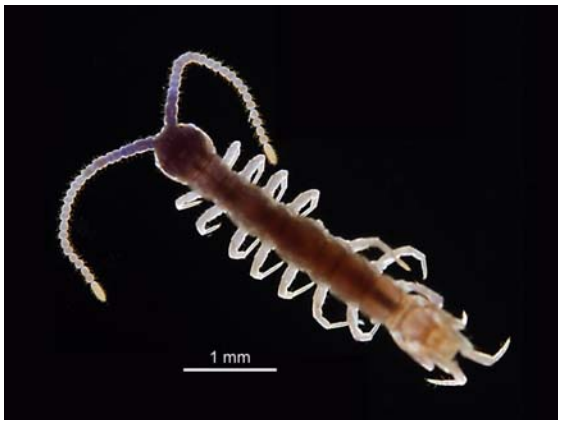
This study recorded the following confirmed introduced species: *Limothrips cerealium* (Thysanoptera: Thripidae), the nectar and pollen feeding beetles ?*Anthrenocerus australis* and *Reesa vespulae* (both Coleoptera: Dermestidae), the fungal feeding *Ephistemus globulus* and a *Cryptophagus* sp. (Stephen Thorpe, pers. comm. 2006) (both Coleoptera: Cryptophagidae) and the two Diptera species *Anthomyia punctipennis* (Anthomyiidae) and *Lonchoptera furcata* (Lonchopteridae). All species were represented by only one specimen, or one specimen per site for *L. cerealium*,

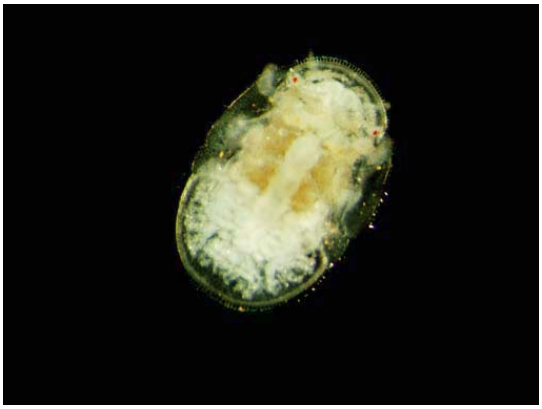
indicating that their presence might have been chance occurrences. These species may have originated from areas with human activity (farming, horticulture, gardening) located within 10 km of the vicinity of the study sites, but given their extremely low densities it is unlikely that these exotic species have become established and pose a risk to the native biodiversity found in canopy habitats. The native species *Thrips obscuratus* (Thysanoptera: Thripidae) is known to cause havoc in flower and crop production (Laurence Mound pers. comm. 2005) and was highly abundant in Punakaiki. This species swarms at certain times of year but their impact on native biodiversity is unknown.

4.5 Conclusions

This study showed that invertebrates are a very important and both taxonomically and functionally highly diverse component of epiphyte mat habitats characterised by highly abundant mites, Collembola, ants, Hemiptera and Coleoptera and functionally diverse scavengers, ants and herbivores. On the whole, spatial patterns in species composition and abundance were not consistent for epiphytes and invertebrates, which highlights the importance of studying community structure at different taxonomic and spatial scales, particularly when dealing with highly diverse and variable communities such as occur in the forest canopy. Although general patterns of invertebrate diversity may be inferred from the structural complexity of the epiphyte host community, such relationships are often very complex and varied among different guilds and species. In-depth studies of different epiphyte habitat types across a wide range of spatial scales are needed to untangle the complex interactions between the diversity of epiphytes and invertebrates and the underlying factors determining their distribution

Supplementary plates of canopy invertebrates



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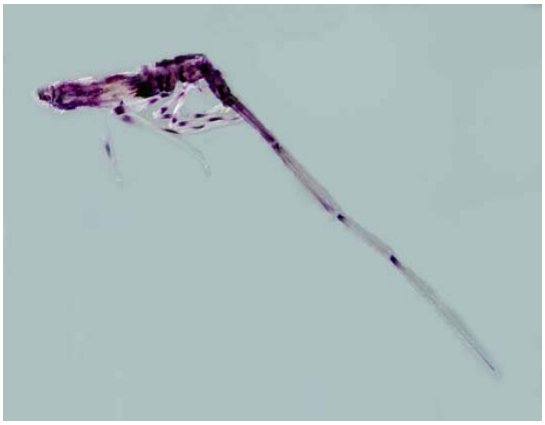


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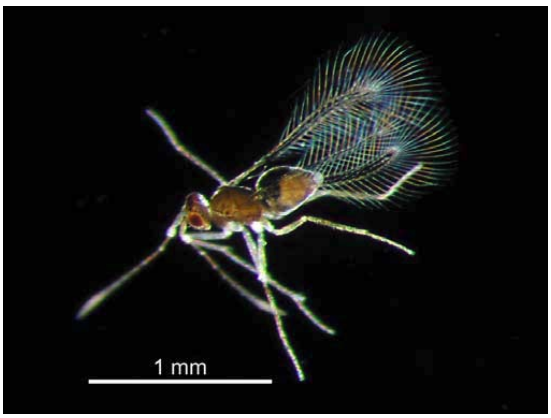
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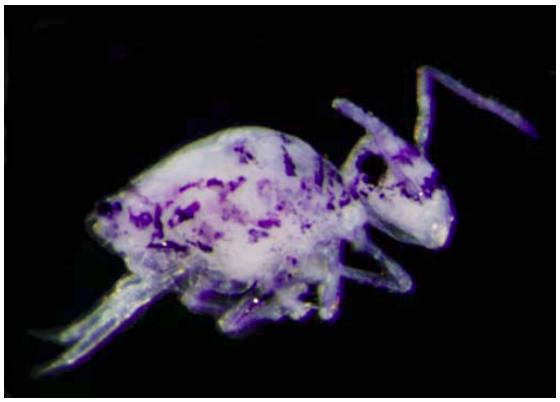


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Chapter 5

The response of arboreal invertebrate communities to increased temperatures and rainfall

Abstract

Little is known about invertebrate community responses to climate change in forest canopies. Epiphyte mat communities are potentially excellent model systems to investigate climatic responses, because they are discrete units with natural species assemblages and environmental conditions. This study attempts to investigate how the composition of invertebrate communities in epiphyte mats change in response to higher temperature and rainfall regimes, as predicted by global and regional climate models. To simulate increased temperatures and rainfall as proposed by various climate change scenarios, experimental greenhouses consisting of polycarbonate sheets were installed over epiphyte mats in the canopy of five trees at each of two study sites. Despite that treatment differences were recorded, very high variability among mats in recorded temperature and moisture meant that the treatments themselves were within the range of the control treatments. Regression analysis, however, showed significant negative associations between accumulated heat expressed as degree days and the abundance per mat of invertebrates ($r = - 0.86$; $p < 0.001$), scavengers ($r = - 0.6$; $p = 0.05$), chewers ($r = - 0.94$; $p < 0.05$ at Karamea only) and Chao-Jaccard similarity in species diversity ($r = - 0.78$; $p < 0.005$) across sites. However, potential indirect effects of epiphyte host communities are expected to further increase the vulnerability of their resident invertebrates species as the plants respond to climatic stresses in this harsh and highly variable environment.

5.1 Introduction

Rain forest canopies are renowned for their exceptionally high biodiversity and their critical role in the many key ecological processes that drive the functioning of forest ecosystems and influence global climate (Chapter 1; Ozanne *et al.*, 2003). In many parts of the world canopy ecosystems are already under enormous pressure from large scale destruction, fragmentation and degradation and now face additional stress from climate change. To date, there has been little research investigating how rain forest canopies, in particular, will be affected by climate change and what the consequences of such changes will be for canopy communities and ecosystem processes (Stork *et al.*, 2007).

Recent publications exploring the potential effects of climate change on rain forests (Coley, 1998; Stork *et al.*, 2007) indicate that elevated CO_2 levels enhance photosynthesis and plant growth where water, light and nutrients are not limiting. Further, increased CO_2 reduces the nutritional quality and palatability of foliage as leaf nitrogen levels and nitrogen-based defences (e.g. alkaloids) decrease and carbon-based defences (e.g. tannins) increase (Coley, 1998). The consequences of such changes may be substantial for canopy invertebrates which depend on epiphytes for food and may be reflected in lower abundance and species richness. Herbivores, for example, commonly increase their consumption rates to compensate for the reduced nutritional quality of CO_2 enhanced plants (Stiling & Cornelissen, 2007), which in turn increases larval developmental times and the risk of predation and parasitism due to extended feeding times (Price *et al.*, 1980), which would affect populations dynamics.

The effects of increased temperatures and changes in rainfall patterns on canopy communities may be even more profound. Reduced cloud water in tropical montane forests has been suggested to negatively affect the productivity and longevity of certain epiphytes leading potentially to subsequent compositional changes in canopy communities (Nadkarni & Solano, 2002). Changes in epiphyte species composition are likely to alter water and nutrient cycling within the forest system because of changes in the amount of atmospheric moisture and nutrients intercepted and retained by epiphytes and the composition and amount of litter accumulated. The taxonomic and functional composition of resident invertebrates may change, because some species are thought to be tightly linked to the amount and types of resources provided by epiphytes (Chapter 4). Higher temperatures and changing rainfall patterns will also directly affect

developmental and reproductive rates of invertebrates, which could have dire consequences, for example, for species-specific pollinator systems by decoupling temporal emergence/ flowering interactions (Speight *et al.*, 1999). Additionally, changing availability of resources may lead to population decline in some species with potential cascading effects in the food chain or facilitate the invasion of non-native species.

It is clear that species will respond differently and at varying rates to changes in their environment (IPCC, 1995) depending on their tolerance limits, life history traits and behavioural flexibility, but also the rate at which climatic changes occur. Further, predicted changes in regional climate may be vastly different from changes experienced on the local scale in topographically diverse areas (Chen *et al.*, 1999) and vary even further on the micro-scale such as in highly heterogeneous forest canopies (Anhuf, 2002). Some suggest that a variety of habitats and climates across different spatial scales may buffer the effects of climate change and/or provide valuable refugia that will help to maintain species assemblages (Noss, 2001), although community structure is likely to change as relative abundances of species change. However, such suggestions have remained untested in canopy habitats. To assess how canopy communities will respond to climate change studies on the relationship between the composition and structure of the communities and existing microclimatic conditions are required at a range of spatial scales. Unfortunately, there is a lack of *in situ* studies investigating community responses to climate change, particularly in canopy communities. Logistical problems in canopy access and installation of often heavy and expensive recording equipment have probably largely prevented this type of study in the past. However, *in situ* studies have the advantage over lab studies as they will measure the response of real and complex communities under natural and manipulated conditions.

In New Zealand the impact of climate change on natural ecosystems in general, has been little researched (Hennessy *et al.*, 2007). New Zealand's temperate rain forests cover extensive areas along the western side of the Southern Alps in the South Island. These forests are home to a high proportion of New Zealand's flora and fauna, many of which are endemic and threatened by introduced species, habitat modification and fragmentation, especially in the lowlands. Although the projected warming for New Zealand is less than the global average, changes in patterns of precipitation,

atmospheric and oceanic circulation, and extreme meteorological events (Auckland Regional Council, 2002) are expected to pose added risk to its already vulnerable biota. The latest report by the Intergovernmental Panel on Climate Change (IPCC) predicts an increase in temperature of 0.1 to 1.3°C by 2030 and up to 3.5°C by 2080 for the West Coast of the South Island (Hennessy *et al.*, 2007). A 60% increase in speed of the prevailing westerly winds is projected to bring more frequent and significant changes in rainfall from about -4 to up to 15 % by 2030 and increases of up to 40 % by 2080 (Hennessy *et al.*, 2007). The aim of this study was to investigate how the community composition of *in situ* communities of arboreal invertebrates in a temperate rain forest of New Zealand would change in response to higher temperature and rainfall regimes predicted under climate change. Canopy epiphyte mat communities make exceptional model systems to test community responses to climate change, because they are discrete small spatial units with natural community assemblages (Srivastava *et al.*, 2004) that are already subjected to extreme and rapidly fluctuating climatic conditions. Nevertheless, I am not aware of any studies that have directly measured the effects of climate change on canopy invertebrate communities.

5.2 Methods

5.2.1 Study sites

This study was carried out from April 2004 to April 2005 at Punakaiki (42°06′S; 171°20′E) located in Paparoa National Park and Karamea (41°10′S; 172°10′E) in Kahurangi National Park, on the West Coast of the South Island, New Zealand. Both sites have a maritime climate that results in mild temperatures and high rainfall throughout the year. Lowland podocarp-broadleaved rain forest is the characteristic vegetation with northern rata a major emergent canopy tree supporting a profusion of epiphytes, vines and lianas. Detailed descriptions of the sites, their climate and vegetation are given in Chapter 1.

5.2.2 Experimental design

In April 2004 climate experiments were established in the canopies of five northern rata trees at each of the two study sites. Twelve epiphyte mats (2 – 3 per tree) were

randomly selected from within the crowns of five trees. Mats were randomly chosen from a set of mats that were accessible, each mat covering a surface area of at least 60 x 25 cm and were located about 1 m from the main trunk (details on the selection of trees and branches are given in Chapter 1). To assess the response of invertebrate communities to different climatic treatments a quadrat sample of approximately half of the epiphyte mat (30 x 25 cm) was collected from each branch prior to applying one of four experimental treatments to the remaining area (30 x 25 cm) of the same epiphyte mat. After 12 months the post-treatment portion of the epiphyte mat was removed in April 2005 and changes in the composition of the invertebrate communities examined. In communities for which destructive sampling is essential to the effective determination of species-abundance distributions, this is as close a as possibly achievable to a before-after, control-impact (BACI) design. A BACI design was chosen because it utilises both temporal and spatial controls when the control and the impact sites (insect communities of the epiphytes) are sampled before and after the treatments. BACI is thus a statistically powerful tool, because every experimental unit has its own control (Krebs, 1999).

It is difficult to predict absolute temperature and rainfall changes, because of uncertainties of future greenhouse gas emissions, large local and regional climatic variability, insufficient fine-scale climate data as well as variation in resolution, model calculations and downscaling techniques for different climate models (Ministry for the Environment, 2001). However, a range of climate change scenarios have been developed for this century (based on CLIMPACTS HADCM2, CLIMPACTS CSIRO9 (Kenny *et al.*, 2001; Mullan *et al.*, 2001)) and NIWA Scenario 1 (Ministry for the Environment, 2001)) and formed the guidelines for this study. The treatments in this study utilised the lower and upper values of the proposed extreme events predicted by those models. In other words, a combination of increased temperatures (0.4°C and 4°C) and precipitation (4 % and 20 %) were used within a factorial design with an added control treatment.

To manipulate temperature increases each experimental unit was enclosed in a tunnel shaped, bottomless tent (“greenhouse”) open at either end to allow air circulation and free movement of insects in and out of the greenhouse (Figure 5.1). The greenhouses consisted of clear polycarbonate sheets either 0.25 mm or 0.75 mm thick. In pilot experiments these thicknesses of plastic were shown to increase temperatures

on average by 0.4°C (± 0.05) and 4°C (± 0.68) respectively. The two rainfall treatments were simulated by installing a perforated hose on the inside roof of each greenhouse, attached to a suspended rainwater catching funnel directly above the greenhouse. The funnels exceeded the size of the epiphyte mats by 4 % and 20 % to expose them to corresponding increases in naturally occurring rainfall. To reduce the risk of organic matter, particularly abscised leaves or drowned invertebrates, entering the catchments and blocking the irrigation system, the rainwater catchments were covered by a 0.5 cm x 0.5 cm mesh. Design and access restrictions meant that there were at least two replicates for each of the four treatment combinations and two controls at each site. For some treatments there were three replicates. In total 12 epiphyte mats comprised the experiment at each site.

Temperature and humidity for four treatment and two control experimental units were recorded at each study site using Hobo data loggers. Readings were taken every half hour for the 1-year treatment period. Detailed descriptions on the climate measurements are given in Chapter 3. Sample processing followed the procedures outlined in Chapter 4.

Figure 5.1 Experimental greenhouse to manipulate temperatures and rainfall on epiphyte mats

5.2.3 Data analysis

Treatment effects of temperature and rainfall increases on insect community composition (species richness, diversity, evenness, similarity and abundance) were calculated using REML (Residual Maximum Likelihood) in Genstat®9.1 (2006). This analysis accounts for the unbalanced factorial design with multiple source of error arising from, from example, variation in biotic and abiotic conditions among branches, trees or sites, in this study. The significance of the contribution of individual treatments was assessed using the Wald statistic produced by REML.

To assess the effects of the climate treatments on various community parameters Shannon and Simpson diversity indices and Simpson's measure of evenness were calculated in Primer (Clark & Warwick, 2001) and the abundance based Chao-Jaccard and Morisita-Horn indices in EstimateS (Colwell, 2006). For more details on these indices refer to Chapters 2 and 4.

Based on results from Chapter 3 Regression analysis was used to test potential correlations between accumulated heat expressed as degree days and VPDs and invertebrate community composition. Sites were correlated separately and the nested structure of mats within trees was ignored, because tree variation contributed generally little to the variability in invertebrate community composition (see REML variance component analysis Table 5.1). Where correlations followed similar trends at both sites and because site differences had little effect on the variability in invertebrate community composition (Table 5.1), mats from the two sites were combined to increase the statistical power of the analysis.

5.3 Results

The results of the REML analysis of the site, tree and branch effects on variation in community composition, ignoring treatment effects, (Table 5.1) indicated that most of the variance accounted for was at the branch level. The results of the climate change experiments showed few significant differences between any of the mean community parameters associated with the various treatment combinations of increased temperature and rainfall (Table 5.2). In fact, the temperature and rainfall treatments were found to be within the natural ranges of the control treatments. This is despite the

results of the pilot studies that indicated the desired treatment effects using the experimental greenhouses used in this study.

Table 5.1 Variance components (± standard error, with percentage of the variance components for each plant group in parentheses) for the relative effects of site, tree and branch variation on total invertebrate species richness, abundance and diversity indices. Significance levels are indicated by asterisks, as follows: *** $p < 0.001$; ** $p < 0.005$; * $p < 0.05$. The branch-level component represents the residual variance in the analysis, therefore there are no associated p-values.

	Variance components		
	Site	**Tree (site)**	**Branch (tree, site)**
Species richness	0.00 ± 23.50 (0%)	9.10 ± 51.70 (5%)	162.4 ± 69.70 (95%)
$\log_{10}$ Abundance	0.00 ± 0.04 (0%)	0.08 ± 0.07 (47%)	0.09 ± 0.04 (53%)
Shannon (logH')	0.00 ± 0.02 (0%)	0.04 ± 0.04 (36%)	0.07 ± 0.03 (64%)
Simpson (1-D)	0.00 ± 0.002 (0%)	0.002 ± 0.004 (18%)	0.009 ± 0.004 (82%)
Simpson (E1/D)	0.00 ± 0.00 (0%)	0.00 ± 0.00 (0%)	0.001 ± 0.00 (100%)
Chao-Jaccard	0.05 ± 0.08 (45%)	0.00 ± 0.02 (0%)	0.06 ± 0.02 (55%)
Morisita-Horn	0.02 ± 0.04 (25%)	0.01 ± 0.01 (12%)	0.05 ± 0.02 (63%)

Table 5.2 Estimated means (± s.e.) for increased temperature and rainfall treatment combinations on various parameters of invertebrate community composition.

	Treatment combinations				**Controls**	**Wald-test**	**p-value**
	4% Relative humidity &		20% Relative humidity &				
	0.4°C	4°C	0.4°C	4°C			
Species	38.11±6.54	41.72±6.55	43.22±6.55	44.38± 6.54	37.45± 4.63	1.20	0.88
$\log_{10}$	2.58± 0.19	2.84± 0.20	2.73± 0.20	2.98± 0.19	2.81± 0.14	3.47	0.51
Shannon	1.24± 0.16	1.13± 0.16	1.47± 0.16	1.44± 0.16	1.40± 0.12	4.90	0.35
Simpson (1-D)	0.45± 0.05	0.46± 0.05	0.61± 0.05	0.64± 0.05	0.58± 0.04	14.07	< 0.05
Simpson	0.06± 0.02	0.05± 0.02	0.07± 0.02	0.06± 0.02	0.08± 0.01	2.63	0.63
Chao-Jaccard	0.80± 0.20	0.81± 0.20	0.54± 0.20	0.89± 0.20	0.57± 0.18	7.85	0.14
Morisita-Horn	0.69± 0.15	0.42± 0.15	0.12± 0.15	0.70± 0.15	0.31± 0.13	24.88	< 0.05

Regression analysis where responses of individual epiphyte mats are related to the actual climate measurements recorded on the mats appear to be more informative. The regression analysis gave similar results to those in Chapter 3 where species responses were best reflected using cumulative degree days and VPD. Invertebrate abundance/ 100g d.o.m. was significantly and negatively correlated to cumulative degree days across both study sites at the 5 % level of significance, but also for Karamea at the 10 % significance level (Table 5.3). Similarly, lower Chao-Jaccard similarity was significantly and also negatively correlated to cumulative degree days across sites. However, the significant positive correlation between Chao-Jaccard similarity and increased VPD in Punakaiki was the result of one outlier with a low Chao-Jaccard similarity at a low VPD. Significant negative correlations were also found for the scavenger guild across both sites. Although there was a significant negative relationship between chewer abundance and degree days at Karamea this trend was not consistent at Punakaiki.

Table 5.3 Regression results for invertebrate species richness, abundance and Chao-Jaccard similarity and cumulative degree days and vapour pressure deficit (VPD) across and within study sites. The Chao-Jaccard similarity values show changes in invertebrate composition for paired mats before and after the treatments (April 2004 and April 2005).

	Site	**Cumulative degree days vs.**		**Mean day time VPD vs.**	
		r	**p - value**	**r**	**p - value**
Total species richness	Punakaiki	+ 0.603	0.206	+ 0.117	0.826
Total species richness	Karamea	- 0.692	0.195	- 0.464	0.431
Abundance/100g d.o.m.	Both	- 0.860	< 0.001	+ 0.007	0.984
Abundance/100g d.o.m.	Punakaiki	- 0.493	0.320	+ 0.347	0.501
Abundance/100g d.o.m.	Karamea	- 0.828	0.083	- 0.248	0.688
Chao-Jaccard	Both	- 0.782	< 0.005	- 0.004	0.990
Chao-Jaccard	Punakaiki	- 0.568	0.239	+ 0.836	< 0.050
Chao-Jaccard	Karamea	- 0.617	0.268	- 0.196	0.752
Scavenger	Both	- 0.601	0.050	+ 0.102	0.765
Scavenger	Punakaiki	- 0.226	0.667	+ 0.584	0.223
Scavengers	Karamea	- 0.707	0.182	- 0.188	0.763
Chewers	Punakaiki	+ 0.440	0.382	- 0.201	0.702
Chewers	Karamea	- 0.939	< 0.05	- 0.585	0.300
Predators	Punakaiki	+ 0.271	0.604	+ 0.303	0.559
Predators	Karamea	- 0.309	0.613	+ 0.063	0.920

5.4 Discussion

In Chapter 2 it was established that there was high natural climatic variability among epiphyte mats in the forest canopy consistent with studies of other rain forest canopies (Dickinson *et al.*, 1993; Freiberg, 1997; Cardelús & Chazdon, 2005). Despite best attempts to simulate predicted climate changes, temperature and humidity recorded for the treatments were within the range of those recorded for the controls (Chapter 3). Differences in the structure and density of canopy cover of the host trees and surrounding vegetation, branch aspect and wind speeds may have affected temperatures in the epiphyte mats and contributed to the recorded high climatic variability among epiphyte mats. Alternatively, the greenhouses themselves may have altered the treatment conditions by acting, for example, as wind tunnels or reduced the immigration and emigration of flying invertebrates. Thus, the mainly non-significant effects of the treatments on invertebrate species richness, abundance and diversity reported in this study may not be representative of the real temperature and moisture increases intended. Microclimatic variation among epiphyte mats was so great that the low replication and any issues regarding the accuracy of the climate experiments method prevented the detection of anything but a strong effect among treatments. This experimental setup did, however, accentuate the variability in the overall sample of mats, allowing the use of correlations to further explore the data.

Correlation analysis showed that invertebrate communities responded negatively to increased accumulated heat expressed as degree days. Extreme temperatures ranging between 0.58 and 38.5°C for individual mats and differences of up to 9°C among epiphyte mats within the same tree (Chapter 3), as recorded in this study, would require canopy residents to have adaptive mechanisms that allow them to persist and survive near to their tolerance limits. Epiphytes, for example, have developed a wide range of adaptations that allow them to collect and store water or avoid water stress (Benzing, 1987, 1995; Rhoades, 1995; Zotz & Hietz, 2001). Invertebrates, on the other hand, have the advantage of being mobile and may display a range of behavioural responses to avoid extreme temperature or moisture conditions. Conditions change over very small distances in the canopy ecosystem (Freiberg, 2001; Stuntz *et al.*, 2002a). Migration deeper into the epiphyte mats or to other parts of the branch or canopy where conditions are more favourable is an option for all but the least mobile species. This would suggest a change in species composition that could be

reflected in decreased abundance and decreased Chao-Jaccard similarity values (less similar communities) with an increase in accumulated heat and decreased moisture, as was the case in this study. Unfortunately, no data are available to define the limits of normal natural variation in species turnover of invertebrates in epiphyte mats that may have contributed to the observed patterns.

Epiphytes provide a wide range of microhabitats that can vary considerably in their microclimatic conditions. In addition, epiphytes are known to moderate canopy microclimate which further increases the microclimatic spectrum available to arboreal invertebrates. Such variety offers much scope for avoiding climatic extremes especially for the canopy's microfauna that are typically smaller than 1 mm and comprised the majority of species in this study. When heat stressed, some invertebrates move to shadier, cooler and more sheltered parts of the plants such as at the base or underside of leaves, along leaf veins, inside flower heads or seed capsules. Others, such as soil organisms may burrow deeper into the humus substrate to avoid dehydration (Villani & Wright, 1990; Rodgers & Kitching, 1998). Clearly, the presence of a wide range of microhabitats combined with the variety of behavioural responses displayed by invertebrates possibly enables many canopy residents to avoid climatic extremes in this harsh and highly variable environment.

It appears that the successful persistence of invertebrates in the canopy is tightly linked with the environment and resources provided by epiphytes and the plants ability to cope with climatic changes. Negative correlations between increased accumulated heat and the abundance of scavengers and chewers followed the same negative response also shown in Chapter 3 for epiphytes. These results indicate that invertebrate guilds are not only directly affected by climatic changes, but potentially also indirectly by the response of their host epiphyte mats to changing temperature and moisture.

Assessing the impacts of climate change on canopy epiphytes and invertebrates is further complicated by the high natural variability in community composition observed among trees within sites and among branches within trees (see also Chapters 2 & 4). Although temperature and moisture are key factors that determine where species occur and how widely they are distributed, high levels of stochasticity in dispersal, colonisation and establishment success play a major role in the composition of arboreal communities. Thus, changes in community composition on the fine spatial

scale may be attributed to climate change when in fact they are part of the natural fluctuation taking place in this dynamic environment. It is therefore important to study canopy communities over a wide range of spatial scales and over several years to understand their responses to natural climatic variation and to realistically separate these responses from the impacts of climate change.

5.5 Conclusions

While this study did not produce direct evidence of invertebrate response to climate change treatments, some results suggest a negative effect of increased temperature, as measured by degree days, on invertebrate community composition. Results were not clear for moisture effects as measured by VPD. The enormous variability in the physical environment and composition of both, epiphyte and invertebrate communities makes it difficult to assess the impact of climatic changes on canopy communities *in situ*. While increased temperature appeared to impact invertebrate communities directly and probably some guilds indirectly through their host epiphyte community, the high architectural heterogeneity of rain forest canopies is potentially a key factor that can buffer the impacts of climatic change. Epiphytes increase the structural complexity of the canopy substantially and thereby create a mosaic of habitats with varying climatic conditions, which in combination with behavioural responses would enable invertebrates to avoid and survive extreme climatic conditions and to exist in this harsh and highly variable environment. Assessing the effect of climatic changes on canopy communities requires studies that have high replication, work on different spatial scales and are carried out long-term to detect potential delayed effects on responses such as fecundity, developmental times and plant/ insect interactions.

Chapter 6

The colonisation of canopy habitats by invertebrates after disturbance

ABSTRACT

Habitat disturbance in response to climate change and/or species invasion is expected to increase in future decades. The resilience of canopy habitats and potential sources of coloniser species after disturbance is virtually unknown. While epiphytes are thought to promote and maintain high invertebrate diversity in the canopy of many rain forests, their relative role as a source of populations for the colonisation of new canopy habitats has not been directly investigated. This study determined the relative contribution of species from epiphyte mats for the colonisation of disturbed habitats by canopy invertebrates. A total of 23 branches supporting mat-forming epiphytes were selected from 10 northern rata trees (Myrtaceae: *Metrosideros robusta*). On each branch a 30 × 25mm *in situ* epiphyte sample unit was paired with a similar sized disturbed sample unit represented by an artificial soil habitat attached to the branch approximately 20 cm away. Analysis showed significant associations between the composition of herbivore, scavenger and predator guilds of the disturbed habitats and epiphyte mats, but not for overall invertebrate community composition. On average 54.7 % (± 4.27) of the total number of invertebrate species collected from the disturbed habitats were shared with their paired epiphyte mat. Most of these species were Collembola and Coleoptera and species belonging to the scavenger and predator guilds. The coloniser species in the disturbed habitats not shared with the paired epiphyte mats were primarily tiny wingless coccids (Hemiptera), Collembola, sap feeders and scavengers. These findings indicate that the composition of coloniser communities is only partly determined by the available species pool of proximate epiphyte mats and that species arriving from alternative source pools are just as important for colonising canopy habitats.

6.1 Introduction

The exceptionally high diversity of invertebrates in canopy habitats has stimulated many studies that examine compositional changes of canopy communities related to horizontal or vertical gradients, seasonality or tree species (Moran & Southwood, 1982; Basset *et al.*, 1996; Schowalter & Ganio, 1998; Wagner, 2001; Basset *et al.*, 2003; Grimbacher & Stork, 2007). Although such studies have improved our understanding of community structure in various forest canopies, factors responsible for the establishment and maintenance of high invertebrate diversity are still not fully identified or understood.

It has been suggested that epiphytes promote high invertebrate diversity (Benzing, 1990; Kitching *et al.*, 1997) by providing a variety of microhabitats, microclimatic conditions and resources for arboreal invertebrate species. Nevertheless, the relative role of epiphytes for maintaining species pools for the colonisation of newly forming or disturbed canopy habitats has been rarely investigated. Expanding tree crowns, the changing successional species composition of epiphyte communities and accumulation of organic matter on branches and in tree cavities as well as disturbance provide new opportunities for colonisation by canopy invertebrates in the highly dynamic canopy environment. The most likely sources of potential coloniser populations would be expected to be from proximate established epiphytic or suspended soil/ litter habitats within the same or neighbouring trees. Opportunistic and transient winged species frequenting the canopy may also colonise canopy habitats, at least temporarily. Despite the often high abundance and proportion of canopy specialists, particularly mites, in canopy habitats of temperate forests (Fagan *et al.*, 2006; Lindo & Winchester, 2006) canopy habitats contain invertebrate species that are shared with habitats on the forest floor. It is therefore, possible that forest floor habitats may contain additional source populations of opportunistic coloniser species. Indeed, Moeed & Mead (1983) showed that a range of ground-dwelling and flightless species, including ground beetles, earthworms, mites and Collembola, travel along tree trunks to feed or breed in the canopy of various New Zealand tree species. Ground-living invertebrate species may thus contribute to the colonisation of canopy habitats as well as dynamics within the coloniser communities.

Distance to potential source populations, the composition of the species pool and the life history traits and habitat requirements of the species present are known to

have major influences on the composition of the coloniser communities (Sousa, 1984). Epiphytic habitats are patchily distributed throughout the forest canopy and can vary substantially in their composition across branches within the same tree (Chapter 2, Cardelús, 2007). Such high variability in habitat heterogeneity and the type and amount of resources provided by the epiphytes is reflected in the taxonomic and functional composition of their resident invertebrate communities (Chapter 4). This study investigates the variation in colonisation by canopy invertebrates among disturbed habitats represented by artificial soil habitats and the relative determinants of this variation, an aspect that has not been directly investigated in canopy habitats. The relationship between variation in the composition of coloniser communities across disturbed habitats relative to the composition of invertebrate communities in adjacent epiphyte mats was determined. This relationship was examined at two study sites to establish whether any patterns were consistent across wider spatial scales.

6.2 Methods

6.2.1 Site description

This study was carried out in the coastal temperate rainforests of the West Coast of the South Island, New Zealand. Punakaiki (42°06′S; 171°20′E) is located in the Paparoa National Park and situated 150 km south of the second study site, Karamea (41°10′S; 172°10′E), which is part of the Kahurangi National Park. Both sites are characterised by a maritime climate and prevailing westerly winds resulting in mild temperatures and high rainfall throughout the year. Highly complex, mixed lowland podocarp/ broadleaved forest is the characteristic vegetation type at both sites. In these forests northern rata (*Metrosideros robusta*) and podocarp species are the dominant trees above the 20 m high dense forest canopy. The large branches of northern rata provide suitable sites for organic matter to accumulate providing substrate for epiphytes, consisting largely of conspicuous clumps of *Astelia solandri*, *Collospermum hastatum*, bryophytes, filmy ferns and orchids, to establish. The result is a mosaic of distinct, isolated, and sometimes interconnected patches of epiphyte communities of varying size and species composition. Detailed information on the climate and vegetation at the two study sites is given in Chapter 2.

6.2.2 Experimental design

In April 2004, 12 disturbed habitats represented by artificial soil substrates were attached to individual branches of five northern rata trees at each of the two study sites to study colonisation by canopy fauna. The selected trees had an average height of 30 m and mean stem diameter at breast height of 181 cm. From within each tree, two or three accessible branches that had continuous epiphyte mat cover of at least 750 cm^2 on the inner canopy section of each branch (1 – 1.5 m from the main trunk) were randomly chosen. The unequal number of branches per tree was dictated by the design of an experiment described in Chapter 5. Ultimately, three branches from each of two trees and two branches from each of three trees were utilised.

Using a paired-sample design, one soil habitat was strapped directly onto a stripped section of each branch so that it was located 20 cm from an adjacent, undisturbed epiphyte mat, but between the epiphyte mat and the outer canopy. The outer end of the branch was chosen to increase the likelihood of colonisation from the epiphyte mat rather than species migrating from the trunk or the ground. Stripping and cleaning the branch surface of any plant and soil material prior to mounting the soil habitats ensured that these sections were free of invertebrates. The artificial soil substrates consisted of plastic coated garden mesh (1 cm hole size) that was shaped into basket-like structures with a surface area of 30 cm × 25 cm, and a height of 6 cm, similar to that of the epiphyte mats. The basket height was comparable to the average depth of the humus layer of epiphyte mats at these sites. The baskets were lined with a fine plastic mesh (0.4 cm mesh size) to reduce the amount of soil lost through the mesh, but to allow small invertebrates to enter the soil from all directions. Once mounted on the branches the artificial substrates (hereafter referred to as disturbed habitats) were filled with potting mix that had earlier been defaunated by freezing at -20°C for 96 hrs. To prevent soil being blown off by wind the disturbed habitats were covered with the fine plastic mesh. The canopy was accessed using the single rope technique, which is covered in detail by Winchester (2004). Slings were used within the canopy to allow for free movement between branches. In April 2005, one year after their establishment the disturbed habitats and their adjacent epiphyte mats were removed from the canopy to analyse the composition of their invertebrate communities.

Sample processing, and the sorting and identification of species followed the procedures outlined in detail in Chapter 4.

6.2.3 Data analysis

Differences in the abundance and species richness of invertebrate orders and guilds between the two study sites were examined to determine whether site specific community patterns existed for the epiphyte mats and disturbed habitats. Since non-significant patterns were evident for the two habitat types over the study sites, the data were pooled over the sites to increase the power of subsequent statistical analysis.

A paired sample design was used in this study to control for differences in species abundance, richness and diversity between branches. Paired t-tests were used to analyse differences between the epiphyte mat and the disturbed habitats on each branch. Abundance and species richness data with a non-normal distribution were log transformed where necessary prior to analysis to normalise the data and equalise variances (Sokal & Rohlf, 1995). All paired t-tests were computed in the software package R 2.4.1.

To assess the compositional variation of invertebrate fauna in relation to habitat type across samples, the species composition of entire communities and major taxonomic groups and guilds were compared using a Mantel test. Matrix randomisations were restricted to within sites and 1000 permutations.

To assess the relative contribution of the epiphyte mats as a source of colonising invertebrate species, the number of species shared by the two habitat types was determined for each paired set of samples. General patterns of species similarities between and within the two canopy habitat types were assessed using Chao's abundance-based Jaccard index in EstimateS (Colwell, 2005). This measure accounts for species that, although present at both sites, were not detected in either one or both samples (Chao *et al.*, 2005).

6.3 Results

A total of 63,490 invertebrates were collected from epiphyte mats and disturbed habitats within the canopy. Of these, mites comprised 41,432 (65.3 %) individuals while unidentified specimens (mainly juveniles) contributed a further 754 (1.2 %) specimens. Of the remaining 21,304 specimens, 180 species were identified. As expected, invertebrates were on average significantly less abundant and species rich in the disturbed habitats compared with their neighbouring epiphyte mats for similar amounts of dry organic matter (d.o.m.) one year after establishment (Table 6.1). Differences in species richness and evenness between the two habitat types were also reflected in the significantly lower Simpson's diversity value for the disturbed habitats (Table 6.1). However, high variability in invertebrate abundance and species richness were characteristic of samples from both habitat types. Invertebrate abundance ranged from 69 to 791 individuals per sample in the disturbed habitats and from 67 to 4097 individuals in the epiphyte mats. Species richness ranged from 3 to 20 and 11 to 52 species across samples in the soil and epiphyte habitats respectively.

Table 6.1 Comparison of the composition of invertebrate communities in disturbed and undisturbed canopy habitats.after one year. Means (±s.e.) and paired-t values are based on 22 d.f.

	Disturbed habitats		**Epiphyte mats**		**Paired t-value**	**p-value**
Mean biomass of d.o.m. (g)/sample	228.7	(± 23.7)	225.7	(±19)	0.086	0.932
Total abundance	16431		47059			
Mean abundance per 100g d.o.m.	298	(± 42)	915	(±172)	3.474	< 0.01
Total species richness	60		165			
Mean species richness/ sample	11	(± 0.9)	26	(±2)	6.113	< 0.001
Total no. of families	42		82			
Mean Simpson's (1-D)/ sample	0.57	(± 0.05)	0.71	(±0.05)	2.090	< 0.05

6.3.1 Species similarity

A Mantel-test comparing the relative variation in species composition of invertebrate communities in disturbed and neighbouring epiphyte mats showed no significant correlations in the overall compositional variation of invertebrate communities

between the two habitats across and within sites (Table 6.2). However, species composition of the herbivore guild in Punakaiki and the herbivore (10% level of significance), scavenger and predator guilds in Karamea were significantly associated with the species composition of their respective guild in the paired epiphyte mats (Table 6.2). The removal of rare species (species represented by two or fewer individuals) from the Mantel-test showed a significant association in overall invertebrate composition between habitat types at the 10 % level of significance ($r = 0.226$; $p = 0.093$). However, no significant associations between any other community components of disturbed and proximate epiphyte communities over the two sites were found regardless of whether rare species were excluded.

Table 6.2 Associations in the composition of invertebrate communities between disturbed habitats and paired epiphyte mats, after one year, across branches at two study sites. A Mantel-test with 1000 permutations was used for the analysis. Unidentified specimens, including juveniles and mites, were excluded from the analyses.

	Both sites		**Punakaiki**		**Karamea**	
	r	**p-value**	**r**	**p-value**	**r**	**p-value**
Invertebrates	0.142	0.102	0.229	0.104	- 0.004	0.424
Collembolas	0.161	1	0.164	0.158	0.126	0.187
Scavengers	0.212	1	0.100	0.244	0.263	< 0.050
Herbivores	0.199	1	0.480	< 0.050	0.235	0.072
Predators	0.339	1	0.175	0.147	0.279	< 0.050

Of the 60 species collected from disturbed habitats one year after establishment, 45 species (75 %) were shared with epiphyte mats (see Appendix for detailed species list). Most of the species shared by the disturbed habitats and epiphyte mats were Collembola (22.2 % of total species) and belonged to the predator (24.4 %) and epiphyte grazer guilds (22.2 %) (Table 6.3). Between 1 and 12 (mean 6.3 ± 0.68) species representing between 14.3 % and 90.9 % (mean 54.7 % ± 4.27) of the total number of species present in the disturbed habitat were shared with the neighbouring epiphyte mat on a given branch.

Table 6.3 The number of species shared by disturbed habitats and epiphyte mats and their proportion relative to the total number of species in the disturbed substrates are shown for orders and guilds.

	Shared species	% of species total	Species only in disturbed habitats	Species richness of epiphyte mats
Orders				
Collembola	10	22.22	3	22
Coleoptera	6	13.33	3	31
Hemiptera	5	11.11	5	24
Pseudoscorpiones	4	8.90	0	8
Hymenoptera	3	6.67	0	11
Lepidoptera	3	6.67	1	11
Diptera	3	6.67	1	7
Aranea	3	6.67	0	17
Chilopoda	2	4.44	0	4
Thysanoptera	1	2.22	0	4
Blattodea	1	2.22	0	3
Diplopoda	1	2.22	1	4
Isopoda	1	2.22	0	5
Symphyla	1	2.22	0	1
Oligochaeta	1	2.22	0	4
Orthoptera	0	-	1	4
Psocoptera	0	-	0	1
Gastropoda	0	-	0	4
Amphipoda	0	-	0	1
Archaeognatha	0	-	0	1
Guilds				
Predator	11	24.45	0	41
Epiphyte grazer	10	22.22	3	22
Scavenger	8	17.78	4	26
All Scavenger	18	40.00	7	48
Chewers	6	13.33	2	30
Sap feeder	5	11.11	5	29
Parasitoid	2	4.44	0	10
Other	2	4.44	1	14
Ants	1	2.22	0	1

The average Jaccard similarity for invertebrate communities recorded in epiphyte mats (0.44 ± 0.02) exceeded that of the disturbed habitats (0.37 ± 0.02). The species similarity between disturbed habitats and the epiphyte mats was 0.39 (± 0.01).

With the exception of Orthoptera, Psocoptera, Gastropoda, Amphipoda and Archaeognatha, all taxonomic groups recorded in the epiphyte mats were also present in the disturbed substrates (Table 6.3). Acari and Collembola were the most abundant

orders in both habitats comprising 84 % of the total number of individuals in the epiphyte mats and 94 % in the disturbed habitats. The relative average abundance of Acari ($t = 2.02$; $p = 0.06$) was lower (significant at the 10% level) in the disturbed habitats, although the relative abundance of Collembola ($t = 3.97$; $p < 0.001$) and Oligochaeta ($t = 2.36$; $p < 0.05$) was significantly higher in the disturbed habitats compared with the paired epiphyte mats.

The dominance of Collembola was also reflected in the guild composition where epiphyte grazers comprised 73 % (± 5.2) in the disturbed habitats compared with 41 % (± 5.7) in the epiphyte mats ($t = 3.93$; $p < 0.001$). Except for ants ($t = 2.15$; $p < 0.05$), differences in the relative abundances of all other guilds were not significant.

6.4 Discussion

6.4.1 Epiphyte mats as determinants of coloniser community composition

Relatively few studies have investigated arboreal invertebrate communities associated with epiphytes (Stork *et al.*, 1997b) and little is known about the relative importance of these communities as a source of species populations for the colonisation of canopy habitats. In this study, coloniser communities varied substantially in their composition across disturbed habitats as was shown by the wide range in abundance, species richness and the low Jaccard similarity value among samples. The latter is indicative of little overlap in the composition of invertebrate communities for this habitat. The overall composition of disturbed habitat communities one year after establishment was found not to be associated with that of the epiphyte mats. However, closer examination at the finer community level showed significant associations between the two habitats with respect to the composition of the herbivore, scavenger and predator guilds across and within sites.

That epiphytes are an important source of invertebrate colonisers was further demonstrated by the large proportion (75 %) of all invertebrate species collected in the disturbed habitats that were shared with the epiphyte mats. This proportion dropped to an average of just over 50 % when the paired habitats on any given branch were assessed. Most shared species were relatively mobile and belonged to the most species

rich orders Collembola, Coleoptera and Hemiptera, while four orders were absent from all disturbed habitats, three of which belonged to the most species poor orders. Similarly, scavenger and predator guilds with higher total species richness in the epiphyte habitats were also better represented in the disturbed habitats. However, invertebrate community size and species richness of the epiphyte mats were not good predictors of the invertebrate community diversity in the paired disturbed habitats after one year.

Some species collected in the disturbed habitats were not found in the paired epiphyte mats and would have arrived from other, more distant sources. Such sources would include epiphyte mats from other branches within the same tree or different trees and tree species altogether given the mixed composition of the forest. Flightless species and the majority of very small species (Hemipteran coccids and Collembola) that originated from sources other than the paired epiphyte mats may have used wind as an important mode of dispersal. Alternatively, some transient and more mobile species of, for example, Collembola, Coleoptera and Orthoptera may have moved between the two habitat types given the relatively short distance. Further, many species were represented by only one individual and would therefore not have been detected in both habitats simultaneously. Rare species could potentially have influenced the results of the Mantel tests, however, their removal from the analysis made little difference to the results.

6.4.2 Colonisation

Despite that the artificial soil habitats used in this study will be quite different from those resulting from natural disturbances or processes these results indicate that the regeneration of communities could occur reasonably fast in this forest system when new habitats are provided. One year after the disturbed habitats were established in the forest canopy, on average about one third of the abundance and half the number of species recorded in the paired epiphyte mats had colonised them. Surprisingly, invertebrate abundance in the disturbed habitats exceeded that of the epiphyte mats in some instances primarily due to large numbers of Collembola and to a lesser extent, mites. Mites and Collembola were the dominant colonisers in this study and their abundance was much higher than that recorded by Wardle *et al.* (2003) for similar

sized artificial soil habitats in other broadleaved tree species in New Zealand. Apart from a possible tree species effect, the Wardle *et al.* study was conducted over only 195 days, which is likely to account for the differences between that study and what was found here. The importance of time in the colonisation process has also been highlighted in a study by Fagan *et al.* (2006) in British Columbia that assessed the colonisation of litterbags by mites over 60, 120 and 360 days. Their results showed a very high species turnover associated with the different time scales, but also a high degree of specialisation for different successional stages of litter decomposition.

Although the absolute abundance of predators, herbivore guilds and parasitoids was significantly higher in the paired epiphyte mats, the proportional contribution of the various guilds was remarkably similar between the paired habitats. The only exceptions were ants and epiphyte grazers. The high abundance of ants in the epiphyte mats can be explained by the patchy distribution of large ant colonies and the higher availability of resources such as nesting sites and nesting material, which are important factors in shaping ant communities (Floren & Linsenmair, 2005) in this habitat type. The significantly higher abundance of epiphyte grazers in the paired disturbed habitats reflects the high abundance of Collembola that are the sole component of this guild in this study. Collembola are typically soil and litter dwellers and feed on micro-organisms of the rhizosphere and decomposing organic matter (Greenslade, 1991). As such they would have found plenty of food in the disturbed habitats and their high abundance would, in turn, sustain the predator fauna for which alternative prey was very limited in this habitat. Surprisingly, the relative abundance of the two herbivore guilds was not significantly different to the paired epiphyte mats despite the lack of living plant tissue in the disturbed habitats. The majority of chewers were relatively mobile species such as Diplopods and Lepidoptera larvae and are probably visitors from the paired epiphyte mat. Alternatively, the latter may be indicative of the habitat use by Lepidoptera adults for oviposition. Sap feeders, which largely comprised scale insects, are also unlikely to have been permanent residents in the disturbed habitats considering their close association with living plants. Their presence in these habitats might have been only accidental and under the conditions provided at the time their establishment success and long term survival in the disturbed habitat would be unlikely.

Results from this study suggest that in the long-term, there may be a shift in composition from Collembola dominated communities in the disturbed habitats to mite dominated communities as indicated by the much older, established epiphyte mats. Further changes in the composition of these invertebrate communities are expected with the establishment and changing successional stages of epiphytes in the communities, including an increase in herbivores, although scavengers are likely to remain a major component of the aging communities. Clearly, to accurately document and understand continuing changes in the composition and dynamics of arboreal invertebrate communities and to assess the effect of environmental factors long term studies are needed.

6.5 Conclusion

Epiphyte mats clearly contribute the development and colonisation of arboreal soil habitats. As epiphyte communities grow and become more complex, accumulated organic matter increases in depth and develops distinct soil horizons. Pioneer epiphyte species initially provide an important substrate for other plants and invertebrates alike to establish, accumulating arboreal soils and invertebrate fauna through time eventually becoming a potential species pool for the colonisation of newly disturbed habitats. That role was reflected in the high relative proportion of invertebrate species in the disturbed habitats originating from the paired epiphyte mats after only one year. However, proximate sources of species did not totally predict coloniser composition. Other sources of species were indicated to be of similar importance. The latter findings raise questions about dispersal mechanisms and dispersal distances for most invertebrate species that are generally poorly known. All communities were characterised by highly abundant Collembola and Acari, but the relative abundance of Collembola in the disturbed habitats exceeded that of the epiphyte mats. As a result, scavengers were a major component of the invertebrate fauna in both habitat types and likely to contribute significantly to nutrient cycling within the community and the forest canopy as a whole. Because arboreal invertebrate communities affect the processes and dynamics within the forest canopy long-term samples over multiple spatial scales are essential to document how changes in the composition of these communities impact important processes.

Chapter 7

General discussion and conclusions

The aim of this PhD study was to 1) document the composition and spatial distribution of canopy epiphyte communities and their resident invertebrate fauna in northern rata, 2) examine spatial and temporal patterns in canopy microclimate and their relationships with epiphyte species richness and biomass, 3) determine relationships between patterns of diversity, species richness and abundance of epiphyte communities and their resident invertebrate communities 4) test the response of invertebrate communities to predicted increases in temperature and rainfall and 5) investigate the colonisation of artificial soil habitats by canopy invertebrates from nearby epiphyte mats.

7.1 The composition and spatial distribution of canopy communities

A highly diverse microcosm of invertebrate and epiphyte life has been revealed in this first comprehensive survey of entire epiphyte communities and their resident invertebrate fauna in the canopy of New Zealand's temperate rain forests. The 30.6 kg (dry weight) of epiphyte material harvested for this study contained 242,124 invertebrates and a total 567 species and morphospecies, including 170 epiphytes and 397 invertebrates (excluding immature specimens and mites). At least 10 invertebrate species were new to science, but this number is likely to increase given that 77 % of all species could only be identified to morphospecies because of the poor taxonomic knowledge of many invertebrate groups in New Zealand. Nearly 32 % of all species were singletons, a phenomenon that has been reported from other canopy studies (Morse *et al.*, 1988; Stork *et al.*, 1997a; Novotny & Basset, 2000). However, the collected species represented about 70 % of the total number of species estimated to be present in the sampled rata trees, which highlights the immense sampling effort that is needed to compile complete species inventories for these highly complex habitats.

The canopies of tropical rain forests are often portrayed as hotspots of epiphyte biodiversity, yet in this study epiphyte species richness (170 species) and biomass (~ 3.5 kg m^{-2}) rivals those of many tropical forests (Chapter 2). Much of the plant diversity comprised non-vascular epiphyte species (79.6 % of the total species richness), particularly liverworts. Although non-vascular plants also make a major contribution to epiphyte diversity in tropical rain forests, particularly at higher elevations (Cornelissen & ter Steege, 1989; ter Steege & Cornelissen, 1989; Wolf, 1993), they are typically associated with temperate forests. Similarly, epiphyte mat biomass and the depth of accumulated organic matter in this study exceeded that recorded in various tropical rain forests (Chapter 2). Notable differences in the composition of epiphyte mats, particularly the proportionately low green plant tissue and high litter content in this study, were indicative of higher decomposition rates in tropical rain forests.

The sheer diversity of invertebrates in tropical rain forest canopies is unsurpassed by any other terrestrial ecosystem, yet the species richness and abundance of invertebrate communities in epiphytic habitats in this study compared to or exceeded that of their tropical counterparts (Chapter 4). Around 80 % of the total individuals were Acari and Collembola, their dominance similar to patterns observed for other epiphytic habitats with a distinct humus layer in temperate and tropical rain forests. The high abundance of ant colonies in the canopy, however, was very unusual for a temperate rain forest and represents the first record of arboreally-nesting ant colonies in New Zealand. Despite similarities in guild composition and the dominance of scavengers within epiphyte habitats in tropical rain forests, guilds differed in their ordinal composition, partly reflecting differences in epiphyte habitat type.

The astounding diversity and taxonomic and functional complexity of canopy communities revealed in this study highlights the exceptional status of forest canopies in New Zealand compared with temperate rain forests elsewhere. Clearly, canopy studies in New Zealand's rain forests can provide new information on species' distributions, their ecologies and involvement in ecosystem processes but also offer much scope for discovering new species and thus should be encouraged.

7.2 Spatial patterns in species distribution and community composition

High variation in the spatial patterning of species richness, abundance and community composition across geographic regions, among trees within regions, and among branches within trees was characteristic of canopy epiphytes and invertebrates. Most of this variation, generally > 75 % of the variance, could be attributed to differences among branches within trees (Chapter 2 & 4). Nevertheless, there were inconsistencies in the spatial patterning between epiphytes and invertebrates, and also among major epiphyte plant groups, particularly vascular and non-vascular plants (Chapter 2). This high variability in community composition could not be completely explained by the environmental factors measured, confirming that patterns of species distribution and dispersal in the canopy are complex. A combination of deterministic (e.g. life history traits) and stochastic (e.g. dispersal, colonisation and establishment success) processes are likely to increase that complexity. Consequently, to assess patterns of diversity and distribution in highly variable canopy habitats studies of entire communities at different taxonomic and spatial scales are crucial.

The high within- and between-site variability in community composition demonstrates that the scale at which such studies are conducted has important implications for the interpretation of results. Inappropriate interpretation may result in poor decisions with respect to the conservation status of ecosystems and their management. For example, at the micro-scale substantial differences in species richness, abundance and community composition between epiphyte mats may be reported as a major response to environmental changes when in fact they are a reflection of the highly dynamic and variable nature of canopy communities and their environment. At the macro scale, the same results between sites give a different perspective and show that overall differences in community characteristics appeared minimal implying that on the whole, canopy communities are more robust to changes than the high variability observed on the micro-scale would suggest. Thus, while micro-scale studies could overemphasise the response of communities or species to changing environmental conditions large scale studies may fail to detect potentially harmful changes.

The high complexity of canopy communities and their environment shown in this study highlights the difficulties when assessing their vulnerability and response to

external threats. A good understanding of species composition at a high taxonomic resolution and the factors determining their distribution is therefore necessary. To detect changes in response to external factors and to progress our understanding requires large sample sizes and replication to account for the high natural variation characteristic of the canopy environment.

7.3 Implications of changing canopy microclimate for canopy species

Continuous microclimatic data sets collected *in situ* for at least 1-year and at multiple locations are rare. The continuous microclimatic data collected in this study showed that the canopy environment of northern rata trees was characterised by high microclimatic variability and climatic extremes. Substantial differences in microclimate among epiphyte mats were found at similar physical locations within the same tree and across trees within and between sites (Chapter 3). These results highlight the poor predictability of canopy microclimate (Dickinson *et al.*, 1993; Cardelús & Chazdon, 2005). Average annual temperature differences among epiphyte mats within a tree, for example, ranged between 0.5 and 9.9°C and varied by up to 1.3°C in mean annual temperature and 1082 cumulative degree days above 5°C. There was also much variation in the intensity and frequency of climatic extremes with temperatures of -0.5°C and 38.5°C, relative humidity as low as 45% and VPDs of up to 4 kPa being recorded. Most importantly, each epiphyte mat for which climatic data was available experienced conditions considered to be potentially harmful to plants (Buckley *et al.*, 1980; Freiberg, 1997; León-Vargas *et al.*, 2006).

High climatic variability and generally unquantified levels of natural climatic fluctuation in the canopy make it difficult to predict species' distributional patterns and to assess their vulnerability to climatic changes. Additional difficulties arise because of tolerance levels of different taxa. Non-vascular epiphyte species richness and biomass, for example, were negatively correlated with temperature and VPD in this study, while a positive relationship existed between vascular plant biomass and VPD (Chapter 3). These trends suggest that non-vascular species are more vulnerable to warmer and drier conditions than vascular plants probably reflecting differences in morphology, physiology, life history traits and adaptations between the two plant groups. A negative

trend was also apparent between invertebrate abundance and increasing temperature measured as cumulative degree days and indicative of species' vulnerability to climatic changes.

While epiphytes certainly provide invertebrates with shelter from frequently occurring climatic extremes, increasing temperatures in particular, may mean they become death traps for invertebrates that are unable to disperse and adjust rapidly when suitable habitats and other resources become fewer. Because of their close association with epiphytes, invertebrates may be indirectly affected by climatic changes before direct impacts become apparent. For example, the species richness of herbivores was significantly associated with that of the epiphytes and both groups responded negatively to increased temperatures. This result points to the potential detrimental impact of climatic changes on plant/ invertebrate interactions and the importance of, long-term community studies with high replication to detect any indirect or delayed effects

7.4 Epiphyte – invertebrate associations

The importance of epiphyte habitats for supporting and maintaining high invertebrate diversity in forest canopies has been widely emphasised and is also apparent in this study. Consistent with the resource hypothesis (Lawton, 1978) more complex epiphyte mats supported higher numbers of invertebrate species and individuals and influenced the guild composition of the invertebrate communities (Chapter 4). However, these correlations were negative, between epiphyte mat biomass and invertebrate and herbivore abundance suggesting that resource quantity may not be a substitute for quality. However, lack of correspondence in patterns of diversity between epiphytes and invertebrates indicated that epiphyte diversity alone cannot sufficiently explain the complex interactions and dynamics in these multi-species communities (Chapter 4).

7.5 Vulnerability of canopy communities to exotic invasion

This study highlighted that epiphyte mats are important species pools of canopy invertebrates for newly established habitats, providing on average 50 % of the total colonising invertebrate species to their paired artificial soil habitats (Chapter 6). The study of invertebrate communities in epiphyte mats and their association with

epiphytes provides information on the rate of successional processes in the colonisation of canopy habitats by invertebrates following disturbance either from climate change, human activity or invasive species.

The vulnerability of various native plant and bird species to the impacts of invasion by non-native species in undisturbed forests of New Zealand has been well documented, but little is known about non-native species impact on native invertebrates, particularly in canopy habitats. While all epiphyte species in this study were native, seven exotic insect species were identified (Chapter 4). Since each species was collected in low numbers per site, it is unlikely that these species pose an immediate threat to native canopy communities. However, the presence of such species highlights that exotic invertebrate species can penetrate deep into this native forest system and, further, that canopy habitats provide suitable conditions for exotic species that potentially could facilitate their establishment in the future.

New Zealand's forest canopies are already frequented by introduced mammals such as possums, rats, mice and stoats that threaten mistletoe populations, birds and possibly lizards and large invertebrates which occasionally form part of their diet, at least on the ground. Of all exotic insects, the aggressive introduced german and common wasps are probably the best examples of documented impact on birds and invertebrates in native forest systems of New Zealand. Many native species cannot compete with invasive species for resources and many lack defence mechanisms to deal with introduced species. The result has been the decline and local extinction of populations or entire species. Of particular concern are threats from invasive species with a well documented detrimental track record elsewhere that could potentially establish in New Zealand, such as the yellow crazy ant that by its activities has modified the character of forests on Christmas Island (O'Dowd *et al.*, 2003).

Despite enormous efforts to prevent the arrival and spread of invasive invertebrate species in New Zealand it is expected that climatic changes will alter the dynamics of exotic species that are already present and increase the risk of invasion by species from warmer regions. However, for native ecosystems many uncertainties remain concerning the consequences of exotic invasion, especially for ecosystems that are poorly understood like the forest canopy.

Monitoring programmes are therefore needed to not only detect the presence of potentially harmful species at the early stages, but also to assess their impact on keystone canopy species and the implications for entire communities. However, that

requires a good understanding of the species inhabiting forest canopies, their ecologies and interactions, compositional and distributional patterns in canopy communities, and species involvement in ecosystem processes.

7.6 Recommendations for future studies

This study clearly showed that the canopy of New Zealand's temperate rain forests provides habitat for a highly rich and diverse canopy flora and fauna that is linked by complex and many-fold associations. It also highlighted how little is known about this unique habitat. Studies of canopies and their communities may help us address a range of ecological issues related to conservation and management of biodiversity over different spatial and temporal scales, particularly in New Zealand with its exceptionally high levels of deforestation and endemism. Consequently, there is much scope for future research. The following presents possible topics derived from this study to be addressed in future investigations:

- the effect of sampling techniques on the resolution of canopy species inventories
- the role of epiphytes in the canopy water cycle and modification of canopy microclimate
- the contribution of herbivory to the accumulation of suspended organic matter and nutrient cycling
- the contribution of scavengers to the decomposition of suspended organic matter and nutrient cycling
- the vulnerability of canopy communities to threats from invasion by exotic species
- the potential of canopy species as indicators of environmental change
- testing whether epiphyte communities on host trees with epiphytic origin are predisposed by the inherited species pool of their host tree.

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APPENDIX 1

List of plant species recorded in mat-forming epiphyte communities on 20 *Metrosideros robusta* trees at each of the two study sites, Punakaiki (Pun) and Karamea (Kar). Endemic species are indicated by an asterisk*. All epiphyte species were native (no naturalized species were found). Occurrence indicates the number of samples each species was present in out of the 48 samples collected per site. Where possible epiphytes were classified into the following functional categories, according to Benzing (1989): F = facultative epiphyte, O = holo-epiphyte (obligatory), L = liana (hemi-epiphyte). Nomenclature follows the Landcare Research Plant Names Database (Landcare Research, 2008, 12. Feb. 2008)

	Occurrence		
Species	**Punakaiki**	**Karamea**	**Type**
Dicotyledons			
Araliaceae			
*Pseudopanax crassifolius**	0	2	F
Cornaceae			
*Griselinia littoralis**	6	5	F
Cunoniaceae			
*Weinmannia racemosa**	4	0	F
Myrsinaceae			
*Myrsine australis**	1	0	F
Myrtaceae			
*Metrosideros diffusa**	1	0	L
*Metrosideros fulgens**	15	20	L
*Metrosideros perforata**	13	21	L
Rubiaceae			
*Coprosma foetidissima**	2	6	F
*Coprosma lucida**	0	2	F
Winteraceae			
*Pseudowintera colorata**	1	0	F
Unidentified seedlings			
Dicotyledon sp. 'heart'	0	1	
Dicotyledon sp. 'oval'	1	2	
Dicotyledon sp. 'spiky'	1	2	
Monocotyledons			
Liliaceae			
Astelia sp.*	16	15	O
*Collospermum hastatum**	2	5	O
Orchidaceae			
*Winika cunninghamii**	7	3	O
*Earina autumnalis**	20	13	F
*Earina mucronata**	3	1	O
Gymnosperms			
Podocarpaceae			
*Dacrydium cupressinum**	3	0	F
Ferns and fern allies			
Aspleniaceae			
Asplenium flaccidum	5	0	O
Asplenium polyodon	0	2	O
*Asplenium scleroprium**	3	8	O
Grammitidaceae			
Ctenopteris heterophylla	8	0	F
*Grammitis ciliata**	0	1	O
Hymenophyllaceae			
Hymenophyllum cupressiforme	1	0	F

*Hymenophyllum demissum**	1	0	F
*Hymenophyllum dilatatum**	2	0	O
*Hymenophyllum minimum**	0	5	
*Hymenophyllum nephrophyllum **	29	13	F
Hymenophyllum rarum	2	5	F
*Hymenophyllum sanguinolentum**	10	16	F
Polypodiaceae			
Microsorum pustulatum	1	8	F
*Pyrrosia eleagnifolia**	0	1	F
Psilotaceae			
*Tmesipteris tannensis**	5	1	F
Clubmosses			
Lycopodiaceae			
Huperzia varia	0	1	F
Mosses			
Bryaceae			
Leptostomum macrocarpum	5	6	F
Dicnemonaceae			
Dicnemon calycinum	7	0	F
*Dicnemon semicryptum**	1	0	O
Dicnemon sp.	10	0	
Dicranaceae			
Dicranoloma menziesii	15	5	F
Holomitrium perichaetiale	4	1	O
Leucobryaceae			
Leucobryum candidum	2	0	F
Hypnaceae			
Hypnum chrysogaster	29	23	F
Hypnum cupressiforme var. *filiforme*	3	0	F
Lembophyllaceae			
Camptochaete sp.	1	0	O
Meteoriaceae			
Papillaria flavolimbata	1	0	O
Weymouthia cochlearifolia	13	1	F
Weymouthia sp.	1	0	
Orthotrichaceae			
*Macromitrium gracile**	14	7	O
*Macromitrium helmsii**	0	1	
*Macromitrium longipes**	1	0	O
*Macromitrium prorepens**	2	1	F
*Macromitrium retusum**	0	1	O
Macromitrium sp.	3	2	
Zygodon intermedius	1	0	F
Ptychomniaceae			
*Cladomnion ericoides**	3	0	F
Rhizogoniaceae			
Hymenodon pilifer	2	0	F
Pyrrhobryum bifarium	1	0	
Rhizogonium novae-hollandiae	1	0	
Sematophyllaceae			
Sematophyllum contiguum	2	0	F
Wijkia extenuata	7	1	F
Thuidiaceae			
Thuidium sp.	1	0	
Thuidium sparsum	1	0	
Liverworts			
Geocalycaceae			
*Chiloscyphus biciliatus**	0	2	
Chiloscyphus echinellus	1	2	
Chiloscyphus sp.	2	0	

C. sp. aff *novae zeelandiae*	1	0	
C. subporosus var. *subporosus*	0	1	
Cyanolophocolea echinella	5	0	
Heteroscyphus allodontus	1	0	
Leptoscyphus innovatus *	1	0	
Frullaniaceae			
Frullania aterrima var. *aterrima*	2	1	F
Frullania deplanata	0	1	O
*Frullania nicholsonii**	2	0	
Frullania rostrata	4	0	O
*Frullania setchellii**	1	1	
Frullania sp.	1	0	
Frullania squarrosula	1	0	O
Jungermanniaceae			
Chandonanthus squarrosus	3	0	
Cuspidatula monodon	9	0	F
Lejeuneaceae			
*Acrolejeunea allisonii**	0	1	O
Acrolejeunea securifolia subsp. *securifolia*	2	3	F
*Archilejeunea olivacea**	4	1	
Cheilolejeunea mimosa	4	1	
Cheilolejeunea sp.	0	1	
Lejeunea primordialis	1	2	
Lopholejeunea colensoi	1	0	
Lopholejeunea plicatiscypha	1	0	
*Mastigolejeunea anguiformis**	2	0	
Metalejeunea cucullata	1	3	
Nephelolejeunea hamata	0	1	O
Lepidolaenaceae			
Lepidolaena clavigera	12	6	F
Lepidolaena reticulata	2	0	
Lepidolaena taylorii	22	3	O
Lepidoziaceae			
Bazzania adnexa var. *adnexa*	5	3	F
Bazzania hochstetteri	16	4	F
Bazzania nitida	4	0	
Bazzania sp.	1	0	
Bazzania tayloriana	1	1	
*Kurzia allisonii**	0	1	
Kurzia hippuroides var. *hippuroides*	2	0	
*Lepidozia kirkii**	1	0	F
Lepidozia procera	1	0	
Telaranea tetradactyla	0	1	F
Zoopsis argentea	0	2	F
Mastigophoraceae			
Dendromastigophora flagellifera	7	0	
Metzgeriaceae			
Metzgeria crassipilus	0	1	
Metzgeria flavovirens	3	7	
Metzgeria furcata	2	4	
Metzgeria leptoneura	2	1	
Metzgeria sp.	1	0	
Schistochilaceae			
Paraschistochila tuloides	3	0	
Plagiochilaceae			
*Plagiochila caducifolia**	4	1	
Plagiochila circinalis	3	0	F
Plagiochila deltoidea	10	1	F
Plagiochila fasciculata	1	0	F
*Plagiochila gregaria**	1	0	O

Plagiochila incurvicolla	3	0	
Plagiochila lyallii	5	1	
Plagiochila radiculosa	8	1	
Plagiochilion conjugatum	13	6	F
Porellaceae			
Porella elegantula	12	3	O
Radulaceae			
Radula physoloba	3	0	F
Radula scariosa	1	0	
Radula tasmanica	1	0	
Radula uvifera	2	0	O
Lichen			
Cladoniaceae			
Cladonia confusa	10	0	
Collemataceae			
Collema sp.	5	2	
Collema subconveniens	0	1	O
Graphidaceae			
Thalloloma subvelata	1	0	O
Parmeliaceae			
Menegazzia sp.	0	1	O
Icmadophilaceae			
Siphula decumbens	1	0	F
Lobariaceae			
Pseudocyphellaria billardierei	1	0	O
*Pseudocyphellaria durietzii**	0	1	O
*Pseudocyphellaria episticta**	3	0	O
Pseudocyphellaria faveolata	1	0	O
*Pseudocyphellaria homoeophylla**	3	0	F
*Pseudocyphellaria lividofusca**	1	0	O
*Pseudocyphellaria montagnei**	0	1	O
Pseudocyphellaria multifida	3	0	
*Pseudocyphellaria rufovirescens**	0	1	O
Pseudocyphellaria sp.	5	2	
*Sticta martinii**	1	0	F
Sticta sp.	4	0	
Sticta subcaperata	0	1	O
Megalosporaceae			
*Megalospora gompholoma**	1	0	O
Pannariaceae			
Degelia durietzii	2	0	O
Psoroma sp.	2	0	
Pertusariaceae			
Ochrolechia sp.	1	0	
Pertusaria psoromica	0	2	
Pertusaria sp.	1	0	
Pertusaria truncata	1	0	O
Ramalinaceae			
Ramalina sp.	0	1	
Sphaerophoraceae			
Bunodophoron insigne	1	1	O
Bunodophoron macrocarpum	1	0	O
Bunodophoron sp.	1	1	
Unknown sp.	15	11	
Total species	**129**	**81**	
Shared species	**51**		

Benzing, D.H. (1989) Vascular epiphytism in America. *Tropical rain forest ecosystems. Biogeographical and ecological studies. Ecosystems of the World 14B* (ed. by H. Leith and M.J.A. Werger), pp. 133-154. Elsevier, Amsterdam.

Landcare Research (2008) Ngā Tipu o Aotearoa – New Zealand Plants Database. URL http://nzflora.landcareresearch.co.nz/default.aspx?NavControl=search&selected=NameSearch

APPENDIX 2

Species list of epiphytes collected from 12 inner branches in *Metrosideros robusta* at each of two study sites, Punakaiki and Karamea. The presence of each species in the number of samples collected is followed by the relative abundance (% of the total biomass) within each site. Nomenclature follows the Landcare Research Plant Names Database (Landcare Research, 2008, 12. Feb. 2008)

	Punakaiki	**Karamea**
Monocotyledons		
Astelia sp.	3 (10.39)	
Collospermum sp.		2 (17.54)
Earina autumnalis	3 (41.30)	
Earina muculatus	1 (0.42)	
Dicotyledons		
Griselinia littoralis		3 (8.27)
Metrosideros fulgens	1 (1.03)	
Metrosideros perforata	1 (1.89)	2 (59.09)
Ferns		
Asplenium flaccidum	1 (0.55)	
Ctenopteris heterophylla	1 (0.01)	
Hymenophyllum minimum		1 (7.04)
Hymenophyllum sanguinolentum	3 (3.02)	1 (2.31)
Trichomanes reniforme	3 (20.46)	
Lichens		
Brigantiaea lobulata	1 (0.01)	
Collema sp.	1 (0.01)	1 (0.09)
Indetlichen sp.1		3 (2.23)
Megalospora sp.	1 (0.36)	
Menegazzia sp.	1 (0.03)	
Pertusaria sp.	1 (0.20)	
Pseudocyphellaria episticta	1 (0.59)	
Pseudocyphellaria lindsayi	1 (0.14)	
Pseudocyphellaria sp.	2 (4.35)	
Sticta sp.	1 (0.13)	
Mosses		
Dicnemon sp.	2 (0.79)	
Dicranoloma menziesii	2 (0.01)	
Hypnum chrysogaster	5 (2.56)	3 (3.12)
Macromitrium gracile	1 (0.02)	
Macromitrium sp.	2 (0.01)	1 (0.01)
Papillaria flavo-limbata	1 (1.36)	
Weymouthia cochlearifolia	3 (0.29)	
Liverworts		
Acrobolbacea sp.	1 (0.02)	
Archilejeunea olivacea	1 (0.01)	
Bazzania hochstetteri	1 (0.01)	
Chandonanthus squarrosus	1 (1.99)	
Cheilolejeunea mimosa	2 (0.56)	
Cyanolophocolea echinella	2 (0.01)	

Lejeunea primordialis	2 (0.17)	
Lepidolaena clavigera	4 (0.28)	
Lepidolaena taylorii	1 (0.06)	
Metzgeria consanguinea	1 (0.01)	
Metzgeria furcata	2 (0.29)	
Pallavicinia lyellii		1 (0.01)
Plagiochila fasciculata	1 (0.01)	
Plagiochila lyallii	2 (0.03)	
Plagiochilion conjugatus	2 (6.43)	1 (0.28)
Porella elegantula.	1 (0.18)	
Radula physoloba	1 (0.01)	

APPENDIX 3

Species list and abundance of invertebrates collected in epiphyte mats on northern rata at two study sites, Punakaiki and Karamea. All species were assigned to one of the following guilds: chewer, sap feeder, fungivore, lichen feeder, scavenger, epiphyte grazer, predator, parasitoid, epiphyte grazer, ants and other. Other includes species with unknown or multiple feeding habits. The species status is indicated as E = endemic, I = introduced, C = cosmopolitan. Voucher specimens are deposited at the Entomology Museum at Lincoln University, Canterbury.

	Punakaiki	Karamea	Guild	Status
Coleoptera				
Anobiidae				
Ptinus speciosus	0	1	Other	E
Brentidae				
Neocyba metrosideros	1	0	Chewer	E
Byrrhidae				
Byrrhidae sp.	1	0	Chewer	E
?Cantharidae				
Amarotypus edwardsi	0	1	Predator	E
Carabidae				
Mecodema ducale	0	1	Predator	E
Platynus macropterus	0	1	Predator	E
Cerambycidae				
?*Tenebrosoma* sp.1	0	1	Chewer	E
?*Tenebrosoma* sp.2	0	1	Chewer	E
Chrysomelidae				
?*Caccomolpus* sp.	2	1	Chewer	E
Coccinellidae				
?*Adoxellus* sp.	0	7	Predator	E
Rhyzobius "small, dark"	47	27	Predator	E
Corylophidae				
Holopsis sp.1	0	4	Fungivore	E
Sericoderus sp.	6	0	Fungivore	E
Cryptophagidae				
Cryptophagus sp.	1	0	Fungivore	I
Ephistemus globulus	1	0	Fungivore	I
?*Micrambina* sp.	3	0	Fungivore	E
Paratomaria sp.	1	2	Fungivore	E
Curculionidae				
Andracalles sp.	75	27	Chewer	E

Cossoninae sp.1	0	2	Chewer	E
Curculionidae sp.	0	1	Chewer	
Euophryum sp.	1	0	Chewer	E
Geochus sp.	1	37	Chewer	E
?*Metacalles* sp.	52	14	Chewer	E
?*Microcryptorhynchus* sp.	32	36	Chewer	E
Neomycta rubra	21	0	Chewer	E
Pachyderris sp.	0	1	Chewer	E
Reyesiella sp.	0	3	Chewer	E
?*Trinodicalles* sp.	3	0	Chewer	E
Cyclaxyridae				
Cyclaxyra sp.	4	0	Fungivore	E
Dermestidae				
?*Anthrenocerus australis*	1	0	Chewer	I
Reesa vespulae	0	1	Chewer	I
Latridiidae				
Latridiidae sp.	0	6	Fungivore	E
Melandryidae				
Melandryidae sp.	0	1	Other	E
Nemonychidae				
Rhinorhynchus rufulus	1	0	Chewer	E
Nitidulidae				
?*Epuraea* sp.	0	1	Sap feeder	E
Hisparonia hystrix	1	0	Sap feeder	E
Scirtidae				
Amplectopus sp.	1	0	Chewer	E
Scirtidae sp.	4	0	Chewer	E
Scydmaenidae				
Scydmaenidae sp.	0	6	Predator	E
?*Microscydmus* sp.	187	143	Predator	E
Staphylinidae				
Aleocharinae sp.	14	3	Predator	E
Eupines sp.	0	1	Predator	E
Euplectine sp.1	152	57	Predator	E
Euplectine sp.2	2	11	Predator	E
Euplectine sp.4	39	35	Predator	E
Euplectine sp.7	1	0	Predator	E
Euplectine sp.8	0	9	Predator	E
Euplectine sp.10	0	3	Predator	E
Hamotulus sp.	4	1	Predator	E
Mesoaesthetus sp.	17	1	Predator	E
Paracorneolabium brouni	9	4	Other	E
Paratorchus sp.1	16	81	Other	E

Paratorchus sp.2	2	20	Other	E
?*Sagola* sp.1	9	5	Predator	E
?*Sagola* sp.2	2	1	Predator	E
?*Sagola* mix	2	3	Predator	E
Tenebrionidae				
Archaeoglenes costipennis	0	1	Scavenger	E
?*Cerodolus* sp.	11	1	Lichen feeder	E
Zopheridae				
Ablabus sp.	0	1	Fungivore	E
Heterargus sp.	0	1	Fungivore	E
Notocoxelus sp.	2	16	Fungivore	E
Pycnomerus sp.1	0	1	Fungivore	E
Hymenoptera				
Aphelinidae				
Aphelinidae sp.1	3	0	Parasitoid	
Aphelinidae sp.2	2	0	Parasitoid	
Aphelinidae sp.3	15	2	Parasitoid	
Braconidae				
Braconidae sp.	1	0	Parasitoid	
Ceraphronidae				
Ceraphronidae sp.1	3	0	Parasitoid	
Ceraphronidae sp.2	1	0	Parasitoid	
Ceraphronidae sp.3	1	1	Parasitoid	
Ceraphronidae sp.4	1	0	Parasitoid	
Cynipoidea				
Cynipoidea sp.	1	0	Parasitoid	
Diapriidae				
Betyla ?*eupepla*	1	0	Parasitoid	
Betyla wahine	2	0	Parasitoid	E
Entomacis sp.	1	0	Parasitoid	
Pantolytomyia taurangi	1	0	Parasitoid	E
Stylaclista sp.	1	7	Parasitoid	
Trichopria sp.	0	4	Parasitoid	
Encyrtidae				
Encyrtidae sp.	0	1	Parasitoid	
Eulophidae				
Eulophidae sp.	0	1	Parasitoid	
Formicidae				
Discothyrea antarctica	11	0	Ant	E
Huberia brouni	0	13	Ant	E
Prolasius advena	9244	14421	Ant	E
Ichneumonidae				
Ichneumonidae sp.1	0	1	Parasitoid	

Ichneumonidae sp.2	1	2	Parasitoid
Indetermined family	1	1	Parasitoid
Megaspilidae			
Lagynodes gastroleius	7	2	Parasitoid
Megaspilidae sp.1	22	0	Parasitoid
Megaspilidae sp.2	1	4	Parasitoid
Megaspilidae sp.3	0	1	Parasitoid
Megaspilidae sp.4	1	0	Parasitoid
Megaspilidae sp.5	0	1	Parasitoid
Mymaridae			
Cleruchus sp.	0	2	Parasitoid
Mymaridae sp.1	0	12	Parasitoid
Mymaridae sp.2	0	2	Parasitoid
Mymaridae sp.3	2	0	Parasitoid
Mymaridae sp.4	7	5	Parasitoid
Neserythmelus sp.	39	4	Parasitoid
Platygastridae			
Errolium sp.	3	11	Parasitoid
Platygastridae sp.1	1	0	Parasitoid
Platygastridae sp.2	1	0	Parasitoid
Platygastridae sp.3	0	1	Parasitoid
Scelionidae			
Baeus sp.	0	1	Parasitoid
Idris sp.1	2	1	Parasitoid
Idris sp.2	1	0	Parasitoid
Hemiptera			
Heteroptera			
Aleyrodidae			
white fly	1	0	Sap feeder
Aphididae			
Aphididae sp.1	0	1	Sap feeder
Aphididae sp.2	12	0	Sap feeder
Aphididae sp.3	2	8	Sap feeder
Aphididae sp.4	1	0	Sap feeder
Cicadellidae			
Cicadellidae sp.1	1	0	Sap feeder
Cicadellidae sp.2	0	1	Sap feeder
Cicadellidae sp.3	1	1	Sap feeder
Cicadellidae sp.4	1	0	Sap feeder
Enicocephalidae			
Enicocephalidae sp.	2	0	Sap feeder
Psyllidae			
Psyllidae sp.	0	1	Sap feeder

Rhyparochromidae				
Rhyparochromidae sp.	14	22	Sap feeder	
Homoptera				
Coccidae				
Coccidae sp.	1	3	Sap feeder	E
"long setae" sp.	48	8	Sap feeder	E
Coccidae “neonate” sp.	2	0	Sap feeder	E
Plumichiton flavus	0	2	Sap feeder	E
Poropeza "near" *dacrydii*/new	0	1	Sap feeder	E
Poropeza cologabata	18	0	Sap feeder	E
"short setae" sp	101	0	Sap feeder	E
Coelostomidiidae				
Coelostomidia montana	1	0	Sap feeder	E
Diaspididae				
?*Anoplaspis* sp.	5	0	Sap feeder	E
Diaspididae sp.	3	17	Sap feeder	E
Leucaspis sp.	6	6	Sap feeder	E
Eriococcidae				
Affeldococcus kathrinae	14	4	Sap feeder	E
Eriochiton sp.	2	3	Sap feeder	E
Eriochiton spinosus	0	3	Sap feeder	E
Eriococcus "near" *kamahi*	7	28	Sap feeder	E
Eriococcus abditus	121	60	Sap feeder	E
Eriococcus albatus	0	13	Sap feeder	E
?*Eriococcus albatus*	0	1	Sap feeder	E
Eriococcus “apterous” sp.	7	0	Sap feeder	E
Eriococcus “apterous” ?*elytranthae*	6	0	Sap feeder	E
Eriococcus elytranthae	196	0	Sap feeder	E
Eriococcus rata	131	39	Sap feeder	E
Eriococcus sp. 1	33	4	Sap feeder	E
Eriococcus sp. 2	9	7	Sap feeder	E
Ortheziidae				
Ortheziidae sp.	4	0	Sap feeder	E
Newsteadia gullanae	2	1	Sap feeder	
Newsteadia myersi	346	0	Sap feeder	E
Newsteadia sp.	29	2	Sap feeder	E
Phenacoleachiidae				
Phenacoleachia sp.	3	4	Sap feeder	E
Phenacoleachia zealandica	13	2	Sap feeder	E
Pseudococcidae				
?*Balanococcus* sp.	0	5	Sap feeder	E
Laminicoccus asteliae	0	3	Sap feeder	E
"Mealybug" sp.	58	659	Sap feeder	E

Pseudococcidae "neonate" sp.	1	0	Sap feeder	E
Pseudococcidae "aperous" sp.	3	0	Sap feeder	E
Pseudococcidae sp. 1	1	11	Sap feeder	E
Pseudococcidae sp. 2	48	2	Sap feeder	E
Paracoccus sp	7	56	Sap feeder	E
?*Paracoccus* sp.	86	1	Sap feeder	E
Ripersiella deboerae	2	7	Sap feeder	E
Ripersiella puhiensis	22	9	Sap feeder	E
Ripersiella sp.	0	13	Sap feeder	E
Indetermined family	1	0	Sap feeder	
Lepidoptera				
Lepidoptera adult	1	1	Nectar	
Carposinidae				
Heterocrossa ?*epomiana*	0	1	Chewer	
Geometridae				
Geometridae sp.	7	0	Chewer	
Indetermined family	31	12	Chewer	
?Nepticulidae				
?Nepticulidae sp.	1	0	Chewer	
Noctuidae				
Plusiinae sp.	0	1	Other	
Oecophoridae				
Atomotricha sp.	3	1	Chewer	
Gymnobathra sp.	2	3	Chewer	
Gymnobathra 'spotty'	0	2	Chewer	
?*Gymnobathra* sp.	1	0	Chewer	
?*Leptocroca* sp.	1	0	Chewer	
Oecophoridae sp.	11	7	Chewer	
?Oecophoridae sp.	0	12	Chewer	
Thamnosara sp.	0	1	Chewer	
Tingena sp.	84	42	Chewer	
Tingena “spotty”	0	8	Chewer	
?*Tingena* sp.	2	0	Chewer	
Trachypepla sp.	1	1	Other	
Psychidae				
Grypotheca sp.	6	2	Chewer	
Psychidae sp.	20	6	Chewer	
?Psychidae sp.	3	0	Chewer	
Mallobathra sp.	7	4	Chewer	
?*Mallobathra* sp.	3	0	Chewer	
Reductoderces sp.	38	17	Chewer	
?*Reductoderces* sp.	1	0	Chewer	
Scoriodyta sp.	9	2	Chewer	

?Pyralidae				
?Pyralidae Sp.	1	0	Chewer	
Torticidae				
?*Pyrgotis* sp.	1	0	Chewer	
Capua intractana	11	3	Chewer	
?*Cryptaspasma querula*	0	2	Chewer	
Cryptaspasma sp.	0	1	Chewer	
"*Hymenophyllum* eating" sp.	1	0	Chewer	
Pyrgotis sp.	1	0	Chewer	
Torticidae sp.	2	0	Chewer	
?Torticidae sp.	1	1	Chewer	
Diptera				
Acalyptratae				
Acalyptratae sp.	1	4	Other	
Anthomyiidae				
Anthomyia punctipennis	0	1	Other	I
Cecidomyiidae				
Cecidomyiidae sp.	17	11	Scavenger	
Ceratopogonidae				
Ceratopogonidae	1	0	Other	
Chironomidae				
Chironomidae sp.	8	6	Other	
Orthocladiinae sp.	0	4	Other	
Drosophilidae				
Drosophilidae sp.	0	1	Other	
Lonchopteridae				
Lonchopteridae sp.	4	0	Scavenger	
Lonchoptera furcata	0	6	Scavenger	I
Mycetophilidae				
Anomalomyia sp.	7	1	Other	
Psychodidae				
Psychodidae sp.	23	28	Scavenger	
Scatopsidae				
Scatopsidae sp.	2	0	Other	
Sciaridae				
Sciaridae sp. 1	37	28	Scavenger	
Sciaridae ?sp. 2	0	2	Scavenger	
"wingless" sp.	0	2	Scavenger	
Simuliidae				
Simuliidae sp.	0	1	Predator	
Sphaeroceridae				
Sphaeroceridae sp.	1	1	Other	
Tipulidae				
Tipulidae sp.	0	1	Other	

Thysanoptera			
Mesothripidae			
Mesothrips brunneus	1	0	Fungivore
Phlaeothripidae			
Baenothrips moundi	34	5	Fungivore
Lissothrips dugdalei	1	0	Fungivore
Psalidothrips sp.	1	2	Fungivore
Thripidae			
Aptinothrips rufus	0	1	Phytophagous
Frankliniella occidentalis	0	2	Phytophagous
Limothrips cerealium	1	1	Phytophagous
Thrips obscuratus	273	26	Phytophagous
Thrips obscuratus?	5	0	Phytophagous
Psocoptera			
Elipsocidae			
Sabulopsocus tractuosus	1	10	Other
Indetermined family	1	1	Other
Liposcelidae			
Liposcelis sp.	0	2	Predator
Philotarsidae			
Philotarsidae sp.	0	1	Other
Psyllipsocidae			
Dorypteryx longipennis	1	0	Other
Trogiidae			
Trogium evansorum Sm.	3	0	Other
Blattodea			
Blattidae			
Celattoblatta bulgaris	41	11	Scavenger
Celattoblatta subcorticaria	21	9	Scavenger
Blattellidae			
Parellipsidion pacachycercum	10	4	Scavenger
Orthoptera			
Indetermined family	4	3	Other
Ground weta	0	1	Other
Raphidophoridae			
Raphidophoridae sp.	0	2	Other
Dermaptera			
Anisolabididae			
Parisolabis ?nelsonensis	0	2	Predator
Trichoptera			
Leptoceridae			

Triplectides cephalotes	1	0	Scavenger
Neuroptera			
Hemerobiidae			
Micromus tasmaniae	2	1	Predator
Diplopoda			
Cambalidae			
Eumastigonus sp.	5	87	Chewer
Dalodesmidae			
Tongodesmus new	2	50	Chewer
Propolyxenus sp.	714	107	Chewer
Siphonethus sp.	1	0	Chewer
Indetermined family sp.1	4	13	Chewer
Indetermined family sp.2	6	0	Chewer
Chilopoda			
Chilenophilidae			
Zelanion sp.	358	134	Predator
Cryptopidae			
Cryptops sp.	22	22	Predator
Henicopidae			
Henicops maculatus	58	210	Predator
Paralamyotes (Haasiella) sp.	47	235	Predator
Gastropoda			
Gastropoda sp.1	50	4	Other
Gastropoda sp.2	13	44	Other
Gastropoda sp.3	13	0	Other
Gastropoda sp.4	1	0	Other
Gastropoda sp.5	73	9	Other
Gastropoda sp.6	0	3	Other
Gastropoda sp.7	4	0	Other
Gastropoda sp.8	0	26	Other
Athoracophoridae			
Athoracophorus sp.1	4	1	Chewer
Athoracophorus sp.2	1	0	Chewer
Aranea			
Araneidae			
Araneidae sp.	0	1	Predator
Clubionidae			
Clubiona sp.	15	0	Predator
Clubionidae sp.1	1	0	Predator
Desidae			
Desidae sp.	1	0	Predator
Desidae/Amaurobiidae/Amphinectidae (DAA)			

DAA sp.1	4	0	Predator
DAA sp.2	30	10	Predator
DAA sp.3	0	1	Predator
DAA sp.4	11	2	Predator
DAA sp.5	0	1	Predator
Gnaphosidae			
Gnaphosidae sp.1	1	0	Predator
Gnaphosidae sp.2	0	1	Predator
Hahniidae			
Hahniidae sp.	0	1	Predator
Hexathelidae			
Hexathelidae sp.	0	1	Predator
Mycropholcommatidae			
Mycropholcommatidae sp.	4	0	Predator
Mysmenidae			
Mysmenidae sp.1	2	19	Predator
Mysmenidae sp.2	0	2	Predator
Mysmenidae sp.3	0	1	Predator
Mysmenidae sp.4	0	3	Predator
Mysmenidae sp.5	4	5	Predator
Neolanidae/Agelenidae (NA)			
NA sp.1	4	0	Predator
NA sp.2	1	0	Predator
NA sp.3	27	20	Predator
NA sp.4	28	12	Predator
NA sp.5	2	0	Predator
NA sp.6	1	0	Predator
Opiliones			
Nuncia sp.	1	0	Predator
Opiliones sp.1	7	21	Predator
Opiliones sp.2	0	2	Predator
Opiliones sp.3	1	0	Predator
Opiliones sp.4	0	1	Predator
Salticidae			
Salticidae sp.1	4	2	Predator
Salticidae sp.2	4	1	Predator
Salticidae sp.3	2	0	Predator
Staphiidae			
Staphiidae sp.	1	0	Predator
Synotaxidae			
Synotaxidae sp.1	0	3	Predator
Synotaxidae sp.2	1	1	Predator
Thomisidae			

Diaea sp.	3	3	Predator
Sidymella sp.	0	5	Predator
Thomisidae sp.1	0	1	Predator
Thomisidae sp.2	0	1	Predator
Unknown sp.	1	0	Predator
Pseudoscorpiones			
Pseudoscorpione sp.1	66	22	Predator
Pseudoscorpione sp.2	377	33	Predator
Pseudoscorpione sp.3	275	134	Predator
Pseudoscorpione sp.4	17	10	Predator
Pseudoscorpione sp.5	5	49	Predator
Pseudoscorpione sp.6	8	6	Predator
Pseudoscorpione sp.7	23	0	Predator
Pseudoscorpione sp.8	8	2	Predator
Isopoda			
Isopoda sp.1	107	69	Scavenger
Isopoda sp.2	30	82	Scavenger
Isopoda sp.3	1	0	Scavenger
Isopoda sp.4	385	14	Scavenger
Isopoda sp.5	0	5	Scavenger
Isopoda sp.6	1	4	Scavenger
Isopoda sp.7	1	63	Scavenger
Isopoda sp.8	0	2	Scavenger
Amphipoda			
Talitridae sp.1	54	32	Scavenger
Talitridae sp.2	0	1	Scavenger
Symphyla	523	195	Scavenger
Archaeognatha	4	12	Other
Others	2503	793	Other
Oligochaeta			
Oligacheta sp.1	1	14	Scavenger
Oligacheta sp.2	0	1	Scavenger
Oligacheta sp.3	3	3	Scavenger
Oligacheta sp.4	3	22	Scavenger
Oligacheta sp.5	0	4	Scavenger
Oligacheta sp.6	1	0	Scavenger
Oligacheta sp.7	7	0	Scavenger
Nematoda	3	0	Scavenger
Collembola			
Brachystomellidae			
Brachystomellidae sp.1	1355	527	Epiphyte grazer
Brachystomellidae sp.2	30	28	Epiphyte grazer

Brachystomellidae sp.3	6	94	Epiphyte grazer
Cyphoderidae			
Cyphoderidae sp.1	66	26	Epiphyte grazer
Dicyrtomidae			
Dicyrtomidae sp.1	1	0	Epiphyte grazer
Dicyrtomidae sp.2	9	33	Epiphyte grazer
Entomobryidae			
Entomobryidae sp.1	67	253	Epiphyte grazer
Entomobryidae sp.2	0	1	Epiphyte grazer
Entomobryidae sp.3	1	0	Epiphyte grazer
Entomobryidae sp.4	8	30	Epiphyte grazer
Entomobryidae sp.5	1	1	Epiphyte grazer
Isotomidae			
Isotomidae sp.1	7684	7252	Epiphyte grazer
Isotomidae sp.2	48	127	Epiphyte grazer
Isotomidae sp.3	320	1088	Epiphyte grazer
Isotomidae sp.4	9067	4088	Epiphyte grazer
Isotomidae sp.5	323	86	Epiphyte grazer
Neanuridae			
Neanuridae sp.1	0	57	Epiphyte grazer
Neanuridae sp.2	267	870	Epiphyte grazer
Neanuridae sp.3	0	6	Epiphyte grazer
Neanuridae sp.4	32	256	Epiphyte grazer
Neanuridae sp.5	0	1	Epiphyte grazer
Onychiuridae			
Onychiuridae sp.1	686	222	Epiphyte grazer
Paronellidae			
Paronellidae sp.1	0	23	Epiphyte grazer
Paronellidae sp.2	10	0	Epiphyte grazer
Paronellidae sp.3	4	0	Epiphyte grazer
Sminthuridae			
Sminthuridae sp.1	998	167	Epiphyte grazer
Sminthuridae sp.2	1	0	Epiphyte grazer
Sminthuridae sp.3	76	128	Epiphyte grazer
Sminthuridae sp.4	4	0	Epiphyte grazer
Sminthuridae sp.5	2	7	Epiphyte grazer
Tomoceridae			
Tomoceridae sp.1	759	267	Epiphyte grazer
Tomoceridae sp.2	0	6	Epiphyte grazer
Tomoceridae sp.3	0	11	Epiphyte grazer
Tomoceridae sp.4	3	4	Epiphyte grazer
Tomoceridae sp.5	0	17	Epiphyte grazer
Tomoceridae sp.6	103	69	Epiphyte grazer

Tomoceridae sp.7	36	1	Epiphyte grazer
Indetermined sp.1	2	0	Epiphyte grazer
Indetermined sp.2	0	1	Epiphyte grazer
Indetermined sp.3	0	734	Epiphyte grazer
Acari	52308	46924	Other
Total species richness	**262**	**256**	
Total abundance	**93787**	**84854**	

APPENDIX 4

Taxonomic list of invertebrates identified in 24 artificial soil habitats and neighbouring epiphyte mats. The frequency of individual species encountered across all samples is given for both habitat types. All species were assigned to one of the following guilds: chewer, sap feeder, fungivore, lichen feeder, scavenger, epiphyte grazer, predator, parasitoid, epiphyte grazer, ants and other. Other includes species with unknown or multiple feeding habits.

	Artificial soil habitats	Epiphyte mats	Guild
Coleoptera			
Brentidae			
Neocyba metrosideros	0	1	Herbivore
?Cantharidae			
?*Cantharidae* sp.	0	1	Predator
Carabidae			
Amarotypus edwardsi	0	1	Predator
Mecodema ducale	0	1	Predator
Chrysomelidae			
Caccomolpus? sp.	0	1	Herbivore
Coccinellidae			
?*Adoxellus* sp.	0	1	Predator
Rhyzobius "small, dark"	0	2	Predator
Corylophidae			
Holopsis sp.1	0	1	Fungivore
Holopsis sp.2	0	1	Fungivore
Sericoderus sp.	1	1	Fungivore
Cryptophagidae			
?*Micrambina* sp.	0	1	Fungivore
Curculionidae			
Andracalles sp.	1	8	Herbivore
Bradypatae sp.	0	1	Herbivore
Geochus sp.	0	2	Herbivore
?*Metacalles* sp.	0	5	Herbivore
?*Microcryptorhynchus* sp.	0	1	Herbivore
Neomycta rubra	0	2	Herbivore
Nestrius sp.	0	2	Herbivore
Zeacalles sp.	0	1	Herbivore
Endomychidae			
Holoparamecus sp.	1	1	Fungivore
Nemonychidae			
Rhinorhynchus rufulus	0	1	Herbivore
Ptilidae			
?*Nellosana* sp.	3	0	Fungivore
Scydmaenidae			
Microscydmus? sp.	0	14	Predator
Staphelinidae			
Euplectine sp.1	4	6	Predator
Euplectine sp.2	2	6	Predator
Euplectine sp.6	0	1	Predator
Hamotulus sp.	0	1	Predator
Mesoaesthetus sp.	0	1	Predator
Paratorchus sp.1	0	1	Other
?*Sagola* sp.	0	2	Predator

Paracorneolabium brouni	1	3	Other
Tenebrionidae			
Artystona sp.	1	0	Lichenfeeder
?*Cerodolus* sp.	0	1	Lichenfeeder
Zopheridae			
Notocoxelus sp.	1	0	Fungivore
Hymenoptera			
Aphelinidae			
Aphelinidae sp.	0	2	Parasitoid
Cynipoidea			
Cynipoidea sp.	0	1	Parasitoid
SF Formicinae			
Prolasius advena	14	19	Scavenger
Megaspilidae			
Megaspilidae sp.	1	2	Parasitoid
Lagynodes gastroleius	0	4	Parasitoid
Mymaridae			
Mymaridae sp.	3	4	Parasitoid
Platygastridae			
Errolium sp.	0	2	Parasitoid
Platygastridae sp.	0	1	Parasitoid
Scelionidae			
Idris sp.	0	1	Parasitoid
Mirobaeus sp.	0	1	Parasitoid
Trichogrammatidae			
Trichogrammatidae sp.	0	2	Parasitoid
Hemiptera			
Aleyrodidae			
white fly	0	1	Sap feeder
Aphididae			
Aphididae sp.	0	1	Sap feeder
Cicadellidae			
Cicadellidae sp.	0	1	Sap feeder
Cicadidae			
Amphipsalta zelandica	0	1	Sap feeder
Coccidae			
Poropeza "near" *dacrydii*/new?	0	1	Sap feeder
Poropeza cologabata	0	2	Sap feeder
Diaspididae			
Diaspididae sp.	0	2	Sap feeder
Leucaspis sp.	0	2	Sap feeder
Eriococcidae			
Affeldococcus kathrinae	1	0	Sap feeder
Eriochiton sp.	1	0	Sap feeder
Eriococcus abditus	0	1	Sap feeder
Eriococcus elytranthae	0	2	Sap feeder
Eriococcus rata	6	5	Sap feeder
Eriococcus sp.1	2	0	Sap feeder
Eriococcus sp.2	0	2	Sap feeder
Ortheziidae			
Newsteadia myersi	0	3	Sap feeder
Newsteadia sp.	2	2	Sap feeder
Phenacoleachiidae			
Phenacoleachia sp.	0	1	Sap feeder
Pseudococcidae			
Balanococcus sp.	0	2	Sap feeder
?*Chorizococcus* sp./new	0	1	Sap feeder
Pseudococcidae sp./apterous	1	0	Sap feeder
Pseudococcidae sp.1	0	1	Sap feeder
Pseudococcidae sp.2	1	4	Sap feeder

Paracoccus glaucus	0	1	Sap feeder
Paracoccus sp.	2	1	Sap feeder
Ripersiella sp./apterous male	0	2	Sap feeder
Ripersiella deboerae	2	0	Sap feeder
Ripersiella puhiensis	0	3	Sap feeder
Rhyparochromidae			
Rhyparochromidae sp.	1	4	Sap feeder
Lepidoptera			
Crambidae			
Glaucocharis sp.	0	1	Herbivore
Oecophoridae			
Oecophoridae sp.	0	5	Herbivore
Thamnosara sp.	0	2	Herbivore
Tingena sp.	2	12	Herbivore
Tingena sp.'spotty'	0	1	Herbivore
Psychidae			
Psychidae sp.	0	4	Herbivore
Mallobathra sp.	0	3	Herbivore
*Reductoderce*s sp.	2	4	Herbivore
Scoriodyta sp.	0	2	Herbivore
?Pyralidae			
?Pyralidae sp.	1	0	Herbivore
Tortricidae			
?*Capua intractana*	0	3	Herbivore
Inidentified Lepidoptera family	1	2	Herbivore
Diptera			
Acalyptratae			
Acalyptratae sp.	0	1	Other
Cecidomyiidae			
Cecidomyiidae sp.	1	0	Scavenger
Chironomidae			
Orthocladiinae sp.	2	5	Other
Phoridae			
Phoridae sp.	0	1	Other
Psychodidae			
Psychodidae sp.	1	1	Scavenger
Sciaridae			
Sciaridae sp.1	2	5	Scavenger
Sciaridae sp.2?	0	1	Scavenger
Wingless sp.	0	1	Scavenger
Thysanoptera			
Phlaeothripidae			
Baenothrips moundi	0	5	Fungivore
Nesothrips sp.	0	1	Fungivore
Thripidae			
Adelphithrips sp.	0	1	Herbivore
Thrips obscuratus	3	12	Herbivore
Psocoptera			
Psyllipsocidae			
Dorypteryx longipennis	0	1	Other
Blattodea			
Blattellidae			
Parellipsidion pacachycercum	0	1	Scavenger
Blattidae			
Celattoblatta bulgaris	0	2	Scavenger
Celattoblatta subcorticaria	3	6	Scavenger
Orthoptera			
Tree weta	2	0	Other
Ground weta	0	1	Other
Raphidophoridae sp.	0	3	Other

Diplopoda			
Cambalidae			
Eumastigonus sp.	0	2	Herbivore
Dalodesmidae			
Dalodesmidae sp./new	0	2	Herbivore
Tongodesmus sp./new	0	1	Herbivore
Polyxenidae			
Propolyxenus sp.	3	12	Herbivore
Inidentified Diplopoda family	1	0	Herbivore
Chilopoda			
Chilenophilidae			
Zelanion sp.	15	17	Predator
Cryptopidae			
Cryptops sp.	0	2	Predator
Henicopidae			
Henicops maculatus	12	13	Predator
Paralamyotes (Haasiella) sp.	0	2	Predator
Gastropoda			
Gastropoda sp.1	0	9	Other
Gastropoda sp.2	0	3	Other
Gastropoda sp.3	0	1	Other
Gastropoda sp.4	0	1	Other
Araneae			
Araneidae			
Araneidae sp.	0	1	Predator
Clubionidae			
Clubionidae sp.	0	4	Predator
Desidae/Amaurobiidae/Amphinectidae			
DAA sp.1	0	3	Predator
DAA sp.2	0	8	Predator
DAA sp.3	0	2	Predator
DAA sp.4	0	1	Predator
DAA sp.5	0	1	Predator
Hexathelidae			
Hexathelidae sp.1	0	2	Predator
Mysmenidae			
Mysmenidae sp.1	0	3	Predator
Mysmenidae sp.2	0	1	Predator
Neolanidae/Agelenidae			
NA sp.1	0	3	Predator
NA sp.2	0	9	Predator
NA sp.3	0	4	Predator
Opiliones			
Opilione sp.1	1	9	Predator
Opilione sp.2	1	3	Predator
Salticidae			
Salticidae sp.	0	1	Predator
Thomisidae			
Thomisidae sp.1	3	1	Predator
Thomisidae sp.2	0	1	Predator
Pseudoscorpiones			
Pseudoscorpione sp.1	9	13	Predator
Pseudoscorpione sp.2	10	10	Predator
Pseudoscorpione sp.3	1	12	Predator
Pseudoscorpione sp.4	1	5	Predator
Pseudoscorpione sp.5	0	1	Predator
Pseudoscorpione sp.6	0	1	Predator
Pseudoscorpione sp.7	0	2	Predator
Pseudoscorpione sp.8	0	1	Predator
Isopoda			

Isopoda sp.1	0	12	Scavenger
Isopoda sp.2	1	8	Scavenger
Isopoda sp.3	0	3	Scavenger
Isopoda sp.4	0	1	Scavenger
Isopoda sp.5	0	1	Scavenger
Amphipoda	0	3	Scavenger
Symphyla	10	13	Scavenger
Archaeognatha	0	1	Other
Oligochaeta			
Oligochaeta sp.1	12	5	Scavenger
Oligochaeta sp.4	0	2	Scavenger
Oligochaeta sp.5	0	2	Scavenger
Oligochaeta sp.6	0	2	Scavenger
Collembola			
Brachystomellidae			
Brachystomellidae sp.1	0	1	Epiphyte grazer
Brachystomellidae sp.2	7	16	Epiphyte grazer
Cyphoderidae			
Cyphoderidae sp.	0	4	Epiphyte grazer
Dicyrtomidae			
Dicyrtomidae sp.	0	2	Epiphyte grazer
Entomobryidae			
Entomobryidae sp.1	9	4	Epiphyte grazer
Entomobryidae sp.2	0	2	Epiphyte grazer
Entomobryidae sp.3	1	0	Epiphyte grazer
Entomobryidae sp.4	9	9	Epiphyte grazer
Isotomidae			
Isotomidae sp.1	15	18	Epiphyte grazer
Isotomidae sp.2	15	19	Epiphyte grazer
Isotomidae sp.3	0	3	Epiphyte grazer
Isotomidae sp.4	12	4	Epiphyte grazer
Neanuridae			
Neanuridae sp.	0	5	Epiphyte grazer
Onychiuridae			
Onychiuridae sp.	5	13	Epiphyte grazer
Paronellidae			
Paronellidae sp.1	0	1	Epiphyte grazer
Paronellidae sp.2	0	1	Epiphyte grazer
Sminthuridae			
Sminthuridae sp.1	14	14	Epiphyte grazer
Sminthuridae sp.2	1	0	Epiphyte grazer
Sminthuridae sp.3	1	0	Epiphyte grazer
Sminthuridae sp.4	0	2	Epiphyte grazer
Tomoceridae			
Tomoceridae sp.1	13	19	Epiphyte grazer
Tomoceridae sp.2	2	4	Epiphyte grazer
Tomoceridae sp.3	0	3	Epiphyte grazer
Tomoceridae sp.4	0	6	Epiphyte grazer
Tomoceridae sp.5	0	1	Epiphyte grazer