Community Ecology of Epiphytes and other Arboreal Plants in the New Zealand Eco-region

By

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A thesis submitted to the Victoria University of Wellington

In fulfilment of the requirements for the degree of

Doctor of Philosophy

Victoria University of Wellington

(2021)

This thesis was conducted under the supervision of

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" The trunks of tree-ferns are very often laden with epiphytal vegetation; and it is in no mean spirit of martyrdom and self-mortification that they thus lend a hand to their weaker brethren – indeed, the tree fern, covered with epiphytes all up its trunk appears at the top with its spreading crown of luxuriant fronds, serene and beautiful as ever. "

– Airini Pope

(1926)

List of Papers

Chapter 2 – **Dawes, T.N.**, and Burns, K.C., 2020. Facultative hemiepiphytism as a recruitment strategy in small-seeded tree species. J Veg Sci.; 31: 1102–1113. https://doi.org/10.1111/jvs.12924

Chapter 3 – **Dawes, T.N.**, Community assembly of epiphytes and climbers on a host tree fern species (*'in preparation'*)

Chapter 4 – **Dawes, T.N.**, and Burns, K.C., A keystone fungus radically alters the structure of a New Zealand epiphyte community (Submitted for consideration and under review at *Oecologia*).

Chapter 5 – **Dawes, T.N.**, Hutton, I. and Burns, K.C., 2021. Spatial ecology and host diversity of three arboreal plants from Lord Howe Island. Australian Journal of Botany, 68(6), pp.458-465. https://doi.org/10.1071/BT20017

Chapters 2 and 5 are published, Chapter 4 is submitted for publication and under review, Chapter 3 manuscript is 'in preparation' pending a submission. Following encouragement from my supervisor, Chapter 3 of my thesis will be submitted as a sole-author paper. In Chapters 2, 4 and 5, pronouns have been changed from 'we' to 'I', and from 'our' to 'my', for comparability.

General Abstract

Epiphytes and other structurally-dependent plants have a spatial ecology and community structure intrinsically linked to that of the host trees in the forest, unlike fully terrestrial plants. Understanding of the ecological implications of this from a theoretical perspective is in its infancy. New Zealand's south temperate rainforest, whilst not as species rich as tropical forests, hosts one of the richest temperate epiphyte floras. Our understanding of the ecological processes structuring the epiphyte communities of New Zealand forests is however lacking. Here, I present four key studies seeking to add to our knowledge of epiphyte community structure, host specificity and spatial ecology in the New Zealand eco-region.

First, I tested if seed size determined the likelihood of woody plant species occurring epiphytically on tree ferns (their arboreality) – Chapter 2. Arboreality was negatively related to seed size, with only smaller-seeded species commonly occurring on tree ferns. However, the effect of seed size reduced in later life history stages, as expected. These small-seeded species, most notably *Weinmannia racemosa*, appear to be utilising an alternative recruitment strategy by establishing epiphytically on the tree fern trunks.

Second, on *Cyathea dealbata* host tree ferns, I tested patterns of species accumulation, metacommunity network structure, and differences in vertical stratification (Chapter 3). Epiphytes and climbers followed a species accumulation model of succession between tree ferns of different sizes and between older and younger portions of the tree fern. The metacommunity network showed patterns of species co-occurrence and nestedness consistent with null expectations. Epiphytes of different habits and different

dispersal syndromes show different vertical profiles of occurrence, with bird-dispersed species occurring more often near the top of the tree fern than other taxa.

To understand an unusual pattern in epiphyte between-host structuring, I quantified the relationship between epiphytic plant and sooty mould assemblages in New Zealand montane beech forest (Chapter 4). Due to the presence of host specific scale insects, the sooty mould was limited to two of three co-dominant canopy tree species. On these two host species, epiphyte richness was significantly reduced. The host size-richness relationship in these two species was also removed, with species composition significantly altered compared to the mould free host species. My results are consistent with the sooty mould amensally excluding the epiphytes and it can be considered as a part of a keystone species complex (with the host beeches and scale insects). This produces a strong pattern of parallel host specificity otherwise not seen in epiphyte assemblages.

Lastly, I compared the differences in spatial niche and host species diversity between three arboreal plants, with divergent ecophysiology, on Lord Howe Island (Chapter 5). These focal species were a dwarf mistletoe, an epiphytic orchid and an epiphytic fern. The mistletoe was restricted to thinner branches, and had a significantly different niche to both epiphyte taxa. The host diversity of the mistletoe and orchid both differed significantly from null model expectations. However, the epiphytic fern (*Platycerium bifurcatum*) had a host diversity consistent with null expectations.

Taken together, these studies increase our understanding of epiphyte community assembly in New Zealand and provide a platform to encourage further work in this field. They also provide results that expand understanding of spatial patterns between host and up vertical clines.

Acknowledgements

Huge amounts of thanks go to the whole of the School of Biological Sciences, who have provided a great research home from when I first arrived in Wellington in 2017 to my thesis hand-in and beyond. There have been so many characters and friendly faces giving the department so much life, especially the wonderful Mary Murray! The SBS mixers and Friday drinks have always been much needed throughout the PhD journey.

Thanks so much to all of my flatties through the years, for all the friendship and support. Special thanks to the 7 St. Michael's crew for providing a stable home-life through the first half of my PhD, and so many wonderful flat dinners. Huge appreciation for the 21 St. Michael's gang for getting me through the 2020 rollercoaster, with fond memories of the lockdown walks. Thanks so much to the Rakau crew for helping me stumble over the finish line and for tolerating my hand-in breakdown.

My deepest gratitude go to all my friends who have helped make life in Wellington enjoyable throughout. Special thanks to Yvan, Zeineb, Tom O, Annemieke, and everyone too numerous to list who have made it so fun. Thanks to Regan for helping read sections of writing on the last night of thesis writing and assisting in the hours before my hand-in. Thanks to Tom Timberlake for the years of friendship, and for reading my application to Victoria, without which I might not have ended up here!

Finally, the biggest thanks and acknowledgements to all my family, who have supported me throughout my studies and PhD research. Especially huge thanks to my dad who has been really supportive, especially whilst not being able to visit in 2020 as planned. Special thanks to my amazing mum, who has always supported me so much over the years!

Contents

Chapter 1 – General Introduction

Introduction to Epiphytes and other Arboreal Plants

Forests, especially rainforests, have a high three-dimensional structural complexity creating a broad range of habitats within the canopy (Lowman and Rinker, 2004). The rise of these heterogeneous angiosperm-dominated forest canopies has led to the diversification of many specialised guilds of organisms over the last 100 million years (Benton, 2010), including key canopy-forming plant taxa (e.g. Davis et al., 2005, Wang et al., 2009) and many habitat-dependent organisms (e.g. ants – Moreau et al., 2006, e.g. amphibians – Roelants et al., 2007). This includes the diversification of key canopy plant taxa (e.g. epiphytic liverworts – Feldberg et al., 2014, e.g. epiphytic ferns – Schuettpelz and Pryer, 2009, Watkins Jr. and Cardelús, 2012), for which the exploration of novel habitats may have driven this ecological change (Sundue et al., 2015). Thus in extant forests, a vast diversity of 'arboreal' plants inhabit the three-dimensional habitat mosaic in forest canopies (Benzing, 1995). Vascular epiphytes – the most speciose group of these structurally dependent plants – account for over 9% of the vascular plant flora (Gentry and Dodson, 1987, Zotz, 2013b).

Epiphytes share forest canopies with a number of other guilds of structurally dependent plants, including hemiepiphytes, climbing plants, and mistletoes, all of which have a distinct ecophysiology. Epiphytes are defined herein as plants (or other sessile organisms) growing upon a host plant for the duration of its life, not parasitising host water or nutrients, and unconnected to terrestrial soil. This definition and terminology in this section follows Moffett (2000), who discusses in-depth the issue of defining an epiphyte. Hemiepiphytes, in contrast, germinate epiphytically but secondarily produce a rooted connection to terrestrial soil (Moffett, 2000, Zotz, 2013a). Climbers (vines and lianas) germinate on the forest floor and then climb up a host tree, with woody climbers often referred to as lianas. Likewise, nomadic vines (previously "secondary hemiepiphytes") germinate on the forest floor and climb up host trees, but with the capacity to secondarily lose and re-establish connection with the forest floor soil (Zotz, 2013a) – a group largely ignored in the

present thesis. Mistletoes, also unlike epiphytes, are arboreal hemiparasites that parasitise the xylem of host trees branches.

Whilst these may seem trivial distinctions in terminology, the physiological differences in these guilds of arboreal plants are fundamental to their ecology. Epiphytes are necessarily limited in their acquisition of water and micronutrients to a greater or lesser extent throughout their life (Zotz and Hietz, 2001, Laube and Zotz, 2003). Contrast this with hemiepiphytes, which are only similarly limited during establishment (Putz and Holbrook, 1986), or climbers, which are not limited in this regard. Conversely, climbers, as soil-rooted species, have to compete with terrestrial trees for soil water (Schnitzer et al., 2005, De Deurwaerder et al., 2018). Likewise, vascular and non-vascular epiphytes are usually considered separately given the significant differences in their physiology, which can lead to very different ecological patterns (Affeld et al., 2008). Another area of distinction is whether epiphytes are obligate (almost always an epiphyte), facultative (sometimes an epiphyte) or accidental (typically terrestrial but does occur epiphytically) in their fidelity to the epiphytic habit (Benzing, 2004, Burns, 2010). These distinctions are especially pertinent to this thesis because, although the primary focus is on obligate epiphytes, I seek to make comparisons between epiphytes and other groups, as well as studying facultative, accidental, and non-vascular epiphytes. Chapter 2 includes facultative and accidental epiphytes and hemiepiphytes, chapter 3 includes both epiphytes and climbers, chapter 4 includes both non-vascular and vascular epiphytes, and chapter 5 includes both epiphytes and mistletoes. However, the focus in this introduction shall remain on vascular epiphytes as a common thread.

Succession in Epiphytes

It has long been recognised that succession seems to occur in epiphyte communities (Dudgeon, 1923), with extensive documentation in epiphytic lichens (Stone, 1989, Lyons et al., 2000, Ellis and Ellis, 2013). Successional patterns are closely linked to tree age and succession appears to

differs across a climatic gradient (Ellis and Coppins, 2006). Within trees, successional patterns also relate to branch age (Stone, 1989).

In vascular epiphyte assemblages, species richness increases with host tree size (Hietz-Seifert et al., 1996, Burns and Dawson, 2005, Flores-Palacios and García-Franco, 2006) and thus also age (Zotz and Vollrath, 2003). Epiphyte species accumulation has also been linked to tree ontogeny, following an island ontogeny model (Taylor and Burns, 2015a). Different host species have a different average point of first epiphyte establishment and subsequent rate of species accumulation (Taylor and Burns, 2015a). Species accumulation likely begins with rapid species accumulation, before switching to a second phase of low species richness increase but high increase in species abundances (Spruch et al., 2019).

Where temporal changes have actually been mapped in an epiphyte community, epiphyte individuals accumulate over time (Laube and Zotz, 2006a, Einzmann et al., 2021), and do not appear to reach a saturation point (Einzmann and Zotz, 2017). Assemblages on individual trees appear highly dynamic (Laube and Zotz, 2006a), yet community composition becomes more similar between host trees over time (Einzmann et al., 2021). However, so-called pioneer species appear able to persist in the community until tree death (Laube and Zotz, 2006a). Given that host trees appear to never reach a stable climax community of epiphytes, and that community replacement of pioneer taxa does not occur, the argument has been made that epiphyte communities do not undergo true succession (Laube and Zotz, 2006a), at least in the sense of terrestrial plant communities (Cowles, 1899, Clements, 1916). Woods' species accumulation model of primary succession in vascular epiphytes attempts to reconcile these differences. At the level of the entire tree, species accumulate over time from early-colonising to late-colonising species (Woods, 2017 – Fig. 1a). Whilst within the inner crown, a more typical replacement model of succession occurs, early colonising species in smaller trees are sequentially replaced by later colonising species in this zone in larger individuals (Woods, 2017 – Fig. 1b). This model provides a framework to quantify successional patterns moving forward.

<u>Community Assembly in Epiphytes</u>

Understanding community assembly has been central to plant ecology and theoretical ecology, with long-standing debate between competitive structure (Diamond, 1975) and stochastic processes (Connor and Simberloff, 1979) driving this field of enquiry. Neutral theory (Hubbell, 2001) and traits-based models of community assembly (Ackerly and Cornwell, 2007) are two key frameworks that taken up this mantle, as well as attempts to reconcile a conceptual synthesis of community ecology (Vellend, 2010). Whilst the spatially structured communities of epiphytes and other arboreal plants have largely suffered from a paucity of theory compared to terrestrial community assembly (Kitching, 2006, Zotz, 2016b). However, beyond the species accumulation model of succession, a number of further theoretical frameworks have attempted to address this. Trait-based community assembly, for example, has begun to be applied to epiphytes (Petter et al., 2016, Wagner et al., 2021), indicating the potential importance of trait-environment interaction in determining species spatial structure. The importance of traits for epiphyte spatial ecology has been suggested extensively by previous ecophysiological work (e.g. Zotz and Andrade, 1998, Zotz and Hietz, 2001). Conversely, Janzen et al. (2020) have produced a neutral model to test epiphyte communities against neutral theory, demonstrating speciation as the major process deviating from chance expectations, with the neutral model otherwise characterising observed data well. This approach will likely present further insights into the processes behind observed patterns.

The theoretical approach that has been furthest advanced in recent years is that of network analysis. Analysing epiphyte host species networks by means of network theory (Burns, 2007) and comparing observed networks to randomised networks (following Gotelli, 2000) has enabled hypothesis testing of community-wide patterns. Many epiphyte-host networks exhibit the property of nestedness (Burns, 2007, Silva et al., 2010, Piazzon et al., 2011, Francisco et al., 2018a). This could be due to facilitation by early colonising or 'nest' epiphytes (Taylor et al., 2016) or be due to null explanations such as the range of host tree diameter distributions (Zhao et al., 2015, Zotarelli et al.,

2018). Equally, not all epiphyte-host networks show nestedness (Taylor et al., 2016). Contrary to nestedness, some epiphyte networks show negative co-occurrence patterns (Burns and Zotz, 2010), which may be indicative of segregation between hosts, although this pattern is more rarely reported (Taylor et al., 2016). Factors such as host size distribution and host traits (e.g. bark texture and wood density) have also been shown to structure network topology (Sáyago et al., 2013). The meta-network framework of Burns and Zotz (2010), builds upon this approach by distinguishing epiphyte-host species networks from epiphyte-host individual networks based upon a single host species (which they refer to as a metacommunity network). This allows for network analysis to be conducted at both a coarse-scale and fine-scale with respect to epiphyte-host interaction matrices. Early evidence suggests metacommunity or host-individual networks are considerably less structured than host species networks (Burns, 2008, Burns and Zotz, 2010), although these have received considerably less attention.

Host specificity in Epiphyte Communities

Host specificity patterns are one of the most heavily studied aspects of horizontal (i.e. between host individual) community structure in epiphytes (dating back to Schimper, 1888, see Zotz, 2016b). The emerging patterns indicate that epiphytes typically are able to utilise a broad range of host species (following review by Wagner et al., 2015). This is to be expected due to the commensalistic nature of the interaction between epiphytes and their hosts, which would be unlikely to drive host-epibiont co-evolution. However, epiphytes do often occur more commonly on certain hosts (Callaway et al., 2002, Vergara-Torres et al., 2010), showing between host structure at the community level (Einzmann et al., 2015). This commonality of host bias, coupled with broad host range, leads to an overall of pattern that epiphytes are "neither host-specific nor random" in distribution (Laube and Zotz, 2006b). A diverse range of possible mechanisms and host traits have been implicated in host biases in epiphytes. Some of the key traits implicated include bark texture/rugosity (Wyse and Burns, 2011), bark chemistry (Frei and Dodson, 1972), bark persistence

(López-Villalobos et al., 2008), substrate water content (Callaway et al., 2002, Mehltreter et al., 2005), substrate water-retention capacity (Castro Hernández et al., 1999), branch longevity (Cortés-Anzúres et al., 2017), crown architecture (Aguirre et al., 2010), and host tree phenology (Einzmann et al., 2015). Regardless of species specific mechanisms, host specificity may lead to broad-scale patterns across the community (Wagner et al., 2021). This might especially be the case where certain host species are overall 'better quality' phorophytes (Toledo-Aceves et al., 2017), whilst others are universally poor, for example due to bark shedding (López-Villalobos et al., 2008).

Thesis Overview

New Zealand has one of the richest epiphyte floras of the temperate regions (Dickinson et al., 1993, Hofstede et al., 2001, Zotz, 2005), with a considerable history of detailed description (Oliver, 1930, Robertson, 1964, Dawson, 1988). Furthermore, the New Zealand rainforest resembles tropical rainforests in physical structure (Dawson and Sneddon, 1969), making it an ideal study system for epiphyte ecology. This dissertation aims to utilise key case studies from the New Zealand eco-region to further our understanding of the community structure of epiphytes and other arboreal plants. Data chapters are arranged as manuscripts that are either published or in review, leading to some crossover with the general introduction and discussion sections.

Chapter 2 quantifies the tendency of woody plants to occur epiphytically, as the degree of 'arboreality', by surveying tree ferns and paired forest floor plots. Woody plants more likely to occur epiphytically have a high arboreality, and are facultative epiphytes and hemiepiphytes. I then test the hypothesis that there is a relationship between seed size and arboreality. This introduces the idea of a key trait filtering taxa from the epiphytic community.

In Chapter 3, I explore epiphyte and climber community assembly on the host tree fern *Cyathea dealbata*. First, I quantify patterns of species accumulation between tree ferns of different sizes, and between younger and older sections within tree ferns. Second, I analyse the structure of the single-host metacommunity matrix, comparing co-occurrence and nestedness to null model

expectations. Finally, I analyse whether differences guilds of epiphyte and climber exhibited

different vertical profiles, as well as whether wind and bird dispersed epiphytes exhibit different

vertical profiles.

Focusing on the predominantly non-vascular epiphyte community of New Zealand's

montane beech forest, Chapter 4 assesses the effect of an amensalist sooty mould on between-host

community structure. I quantify the difference in mould cover between host beech species. I then

assess how epiphyte richness, host size-richness relationship and species composition vary between

host species with and without extensive mould cover. Additionally, I consider whether the sooty

mould can be consider a part of keystone species complex. This chapter highlights how an unusual

interaction with an epiphytic mould can radically alter typical between-host epiphyte community

structure and community-wide patterns of host specificity.

Chapter 5 was conducted on the subtropical Lord Howe Island. Using three focal arboreal

plant species with very different water acquisition strategies, I compare within-tree spatial niche and

host specificity. I test for differences in relative height on host plant and branch diameter, as two key

axes of spatial niche. A null model is then generated from an inventory of forest tree composition,

which can be repeatedly subsampled to generate an expected host richness or Shannon diversity. I

compare the observed host richness and diversity to an expected distribution to assess whether host

specificity matches chance expectations.

Chapter 2 – Facultative hemiepiphytism as a recruitment strategy in small-seeded tree species

Abstract

Shade-tolerant tree species often produce larger seeds with greater energetic resources to cope with light limitation. On the other hand, shade-intolerant species often produce smaller seeds with greater dispersal potential to colonise lighter, more-disturbed areas of forest. I test the hypothesis that small-seeded species utilise an alternative recruitment strategy in a New Zealand rainforest by establishing epiphytically on the trunks of tree ferns. To assess whether small-seeded tree species rely on tree fern epiphytism for recruitment I quantified relative abundances of both epiphytic and terrestrial subpopulations in 14 woody plant species across a range of seed sizes. I used a paired study design where I surveyed all 3727 woody plants occurring on 322 tree ferns and in matching forest floor plots of equivalent area. Using a linear model, I then assessed the relationship between species' seed size and their epiphytic tendency (arboreality). Arboreality scores differed both between species and between life history stages. Seed size predicted arboreality regardless of life history stage, with small-seeded species more likely to occur arboreally than larger-seeded ones. However, the effect of seed size decreased predictably in later life history stages. Seed size also predicted arboreality when the model was re-run using subsets of data restricted to common understorey tree ferns. Interspecific differences in the epiphytic establishment of New Zealand tree species are pronounced, with only smaller-seeded species able to use this regeneration niche. Small-seeded species, especially *Weinmannia racemosa*, appear to be utilising an alternative recruitment strategy by establishing epiphytically on tree fern trunks.

<u>Introduction</u>

Seed size varies considerably across species globally (more than 11.5 orders of magnitude from smallest to largest), and within plant communities (Moles et al., 2005). Variation in seed size can have important effects on key aspects of plant ecology, particularly recruitment dynamics (Jakobsson and Eriksson, 2000, Burke and Grime, 1996, Rees et al., 2001). Seed mass influences key seedling attributes such as growth rates (Augspurger, 1984), mortality and environmental tolerances, and these in turn impact the environmental conditions within which species can germinate and survive (Leishman et al., 2000). Thus, seed size can have important effects on plant recruitment and plant community structure.

Larger-seeded species have greater energetic provisioning, allowing them to germinate and establish in the light-limited environment of the forest understorey (Foster and Janson, 1985, Westoby et al., 1992, Leishman and Westoby, 1994). Conversely, small seeds have fewer energetic resources for the establishment of the germinating seedling and therefore these species are often shade-intolerant. Therefore, small-seeded species have trouble recruiting in the understorey of closed-canopy forests and tend to recruit in light gaps or disturbed areas (Pearson et al., 2002). Small seeds are produced in larger numbers and therefore have a better dispersal probability (Turnbull et al., 1999, Moles and Westoby, 2006), increasing their chances of arriving in a light gap or other area of disturbance in the forest. Plant species exist on a recruitment continuum from relatively undisturbed forest with low light and high moisture to more disturbed canopy with higher light and lower moisture retention (Brokaw, 1987, Denslow, 1987, Rüger et al., 2018). Seed size closely correlates with this disturbance regime continuum (Westoby et al., 1992, Osunkoya et al., 1994, Hewitt, 1998). Partitioning of species regeneration niches along this continuum is a potentially vital mechanism for maintaining tree species richness and their competitive co-existence (Grubb, 1977, Silvertown, 2004, Paoli et al., 2006).

Tree ferns are an important component of southern temperate rainforests and a key functional group in terms of the dynamics of the forest vegetation (Brock et al., 2016, Brock et al.,

2019), for instance pioneer tree ferns can influence community assembly (Brock et al., 2018b). In some circumstances, shading by tree ferns acts as an important recruitment filter for tree species (Coomes et al., 2005, Brock et al., 2018a). The surfaces of tree fern trunks can also provide ideal substrate for many epiphyte and climber species (Pope, 1926, Moran et al., 2003), including epiphytic seedlings of woody plants (Gaxiola et al., 2008). Some tree species preferentially establish on elevated microsites more generally (Lusk and Kelly, 2003). Adult trees that have recruited epiphytically on tree fern trunks have been documented (Newton and Healey, 1989, Derroire et al., 2007) , where large roots extend down the side of the tree fern and make contact with the soil (Pope, 1926). Some species even produce girdling roots that fuse to form a pseudotrunk around the tree fern below the point of initial attachment and these species can outlive the host tree fern (Pope, 1926). These species are facultative or accidental hemiepiphytes. Herein, I use the term hemiepiphyte (a species which germinates epiphytically before making a soil-rooted connection later in its life) in the sense of Zotz (2013a), Zotz (2016b), who follows Moffett in defining the term as equivalent to the previously used 'primary hemiepiphyte' without the need for such a qualifier (Moffett, 2000). Individuals that reach this strangling stage can then survive as a terrestrially-rooted tree upon the death of the host tree fern, including the New Zealand species *Weinmannia racemosa* (Wardle and MacRae, 1966, Gaxiola et al., 2008). However, it is unclear how common this recruitment pathway is in New Zealand forests and whether individuals recruiting hemiepiphytically frequently contribute to free-standing adults in the population (although see Dawson and Sneddon, 1969, Beveridge, 1973, Dawson, 1988 who hint at its commonality).

Here I investigate the role tree ferns play in the establishment of small-seeded rainforest trees. Specifically I address two key questions: 1) Are individuals of different tree species more likely to establish on tree fern trunks than on the forest floor? 2) Does seed size predict the relative likelihood of tree species to occur epiphytically on tree ferns (henceforth termed 'arboreality')?

Methods

Study Site

My study site, Kaitoke Regional Park (41° 3' S, 175° 11' E) is a 2,860 ha area of both primary old-growth and secondary successional native temperate rainforest located in the Greater Wellington region, lower North Island New Zealand (Fig. 2.1). Kaitoke covers part of the southern foothills of the Tararua ranges, much of which is inaccessible. Major topographic features are the southern ridge (created by the Wellington faultline), which marks the change from lowland to hill country, and the Hutt River, which has formed the valley to the north of this ridge. The major bedrock in the regional park is greywacke, with alluvial deposits occurring in some riverine and flatter parts of the park (Greater Wellington Regional Council, 2007, hereafter abbreviated to GWRC). A range of soil types exist within Kaitoke; a majority of land cover consisting of brown earth soils (GWRC 2007). Annual rainfall in the park is c.2000 mm, with a mean annual temperature of 10.5°C in Kaitoke's valleys (GWRC 2007).

The park's vegetation consists of a mixture of broadleaf-podocarp and beech (Nothofagaceae) forest, including sizeable areas of mature broadleaf forest. In addition, there are areas of successional scrub and forest along the southern ridge of the park. The canopy is varied in structure with *Weinmannia racemosa* (Cunoniaceae) and *Elaeocarpus dentatus* (Elaeocarpaceae) being the most common canopy species in broadleaf dominated areas; *Knightia excelsa* (Proteaceae), *Beilschmiedia tawa* (Lauraceae), *Prumnopitys ferruginea* (Podocarpaceae) and *Laurelia novae-zelandiae* (Atherospermataceae) are also major canopy components. Large emergent conifers of the Podocarpaceae, chiefly *Dacrydium cupressinum* and *Dacrycarpus dacrydioides*, and the emergent tree-forming hemiepiphyte *Metrosideros robusta* (Myrtaceae) occur in mature areas of the forest. *Hedycarya arborea* (Monimiaceae), *Melicytus ramiflorus* (Violaceae), *Coprosma grandifolia* (Rubiaceae), *Pseudopanax arboreus* (Araliaceae) and *Pseudopanax crassifolius* are important subcanopy trees, along with the large shrub *Geniostoma ligustrifolium* (Loganiaceae). The other major subcanopy components are the tree ferns that are the focus of this study, with three

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species *Cyathea dealbata* (Cyatheaceae), *Cyathea smithii* and *Dicksonia squarrosa* (Dicksoniaceae)

most commonly occurring. A fourth species of tree fern – *Cyathea medullaris*, a tall, light-loving

pioneer species (Brock et al., 2018b) – often persists in the subcanopy; with two locally rare species

(*Cyathea cunninghamii* and *Dicksonia fibrosa*) giving a total of six tree fern species at the site.

Nomenclature follows the latest editions of the Checklist of the New Zealand Flora for seed plants

(Schönberger et al., 2019a) and ferns (Schönberger et al., 2019b) respectively.

Field Surveying

To elucidate the differences in species' arboreality (relative likelihood of occurring on a tree

fern compared to the forest floor) I used a paired study design, with each sampling unit consisting of

a tree fern-forest floor plot pair. I sampled as many tree ferns (and associated plots) as possible on a

variety of tracks/areas in broadleaf-podocarp rainforest dominated areas of Kaitoke Regional Park in

order to encompass as much of the heterogeneity of the forest as was practicable. This included

sampling tree ferns up to 30m off track and sampling from narrow hiking trails to reduce the impact

of any possible edge effect (such as in Williams-Linera, 1992) on my data. Tree fern sampling

included individuals of broad range of heights and reflected the approximate prevalence of each

species of tree fern, although some species of fern were preferentially sampled to enable

comparison between tree fern species. Tree ferns also had to be > 1.2m tall to be included in the

survey, as younger tree ferns rarely have epiphytic plants growing on them until they reach

approximately this stature. Most importantly, the presence/absence of plants growing epiphytically

or hemiepiphytically on tree ferns was ignored when selecting tree ferns to avoid biasing the results.

The surface of each tree fern trunk was conceptualised as the side of a cylinder so that the

paired plot could be constructed of an approximately equivalent surface area, thereby controlling for

the effect of substrate area (Fig. 2.2). Height of the tree fern crown (to the nearest 0.1m) and

circumference at breast height (to the nearest cm) of each tree fern were measured (as required for

the surface area of a cylinder). When measuring the height of tree ferns over 2.2 metres (height of

an outstretched arm), fern height was calculated using a clinometer, or in cases of poor visual access an estimate was made based on previously measured nearby plants. The tree fern's circumference was then used to measure out the short edge (width) of a rectangular forest floor plot and tree fern height as the long edge (length) – as per figure 2.2. Forest floor plots were carried out 1 metre from the tree fern (to avoid the transition zone of spreading root lattice at the ferns base and the area of the heaviest macro-litter accumulation) and in one of two ways dependent on tree fern density:

(1) In dense tree fern groves, systematic sampling was implemented in order to avoid spatial pseudoreplication of the forest floor, from plots overlapping one another, by having plots directed at a consistent angle approximately perpendicular to the track.

(2) In more open forest with a sparse tree fern subcanopy, the direction of the forest floor plot was established using a random number generator, with a second direction generated when other tree ferns, plots from other tree ferns (again to avoid spatial pseudoreplication) or trails were present.

I recorded all tree and shrub individuals, including saplings and seedlings, growing on the tree fern and in the associated forest floor plot. I recorded the species identity (identified primarily using Dawson and Lucas, 2012) and the height of each individual woody plant, to allow me to assess the changing prevalence of epiphytism on tree ferns over the tree's ontogeny. The height of epiphytic individuals on tree ferns was measured from the point of attachment upwards/outwards to the most-distal part of the stem. In soil-rooted adults, where an obvious root connection or partial trunk reaches the ground, the height was recorded from the ground. In the genus *Nestegis*, it was not possible to reliably identify the thin-leaved juveniles (to c. 1 metre tall) to species and all appeared to be a single morphospecies. Hence, these species were treated as '*Nestegis* sp.' in my data.

From this vegetation survey, I constructed population pyramids (split into terrestrial and epiphytic subpopulations) showing the size class structure of each species in order to show how arboreality changes with tree ontogeny. This was only done where a minimum of fifty individuals of a species were recorded in the survey, these species with 50+ individuals becoming my focal species

for all subsequent analyses. The size class boundaries were defined based upon the height tiers from the Recce method of describing New Zealand vegetation (Hurst and Allen, 2007), with all plants >12m (both tiers 1 & 2 From Hurst & Allen) forming the largest size class. Furthermore, the definitions of terms 'seedling', 'sapling' and 'adult' from herein match the smallest (0 – 0.3 m), second smallest (0.31 – 2 m) and a pool of the data from the three largest (≥ 2.01 m) size classes respectively. Additionally, binomial tests were carried out to determine if the numbers of terrestrial and epiphytic individuals of each species within each size class were significantly different from one another. To account for multiple comparisons, statistically conservative Bonferroni corrections were applied to the p-values, within each size class (a test family of 14).

Investigating the Relationship between Seed Size and Arboreality

In order to quantify the extent to which species incorporate tree ferns as a part of their regeneration niche, I calculated an 'arboreality score' as the ratio of arboreal to terrestrial abundance – one was added to both the numerator and denominator to correct for zero values. Arboreality was then calculated for the seedling, sapling and adult size classes. Note that 'adults' were the pool of the largest three size classes in order to encapsulate a meaningful number of individuals.

Given that physical size is hypothesised to filter which seeds can accumulate on the surface of the tree fern, I measured seed size (i.e. length, width) as opposed to seed mass for my analyses. Seeds were collected between December 2018 and March 2019. Fruits were collected from multiple individuals, and seeds were measured from multiple fruits. 26 to 80 seeds were measured per species (Table 2.1). Sufficient measurements of four species could not be collected in the field and in this instance values were derived from Webb and Simpson (2001). Measurements of all species were checked for consistency with these literature values (Webb and Simpson, 2001) when both measures were available. Seed length was measured as the longest length along the largest axis of the seed. In *Knightia* and *Laurelia*, a large wing or awn was present as part of or attached to the seed

– these were ignored for seed length (detailed in Table 2.1). Seed width was recorded as the longest axis perpendicular to seed length. Some seeds were not radially symmetrical, and so for larger seeds a third dimension of a depth value was recorded; width was assumed equal to depth for smaller ± spheroid seeds. For all seed measurements, the species average was used.

In order to assess the role of seed size in predicting species arboreality, I ran a linear model assessing the effect of seed length on arboreality with tree's size class as a random factor. Each datapoint in the model represents a specific size class (seedling, sapling or adult) for a given species. Both the seed size metric and arboreality score were log-transformed using the natural logarithm (ln) in this and all subsequent models due to values of these variables being spread across multiple orders of magnitude. The model was initially run with an interaction term present, which was then removed when this was found to be not significant. Furthermore, equivalent linear models using literature-derived seed lengths, seed width and seed depth (as alternatives to seed length) were also carried out to check that my findings were robust to differences in the seed size metric used. Additionally, due to multiple models being run, p-values were adjusted using a Bonferroni correction to reduce the risk type I errors, with a test family of 8 for the 4 size classes for models both with and without interaction terms.

To identify how any effect of seed size changes across size classes, linear regressions of seed size against arboreality, for each of the seedling, sapling and adult size classes, were also carried out. Additionally, my initial linear models were rerun twice, using subsets of my main dataset with only data from each of the two commonest understory tree fern species (*Cyathea dealbata* and *C. smithii*). Like my prior analyses, data were natural log transformed and post-hoc Bonferroni corrections applied. All analyses were carried out in the R environment (R Core Team, 2020) and plots were created using the 'ggplot2' package (Wickham, 2016), with the 'gridExtra' package (Auguie, 2017) used in assembling figure 2.3.

<u>Results</u>

I surveyed 322 tree ferns (of 5 species) and paired forest floor plots, which contained a total of 4007 woody plant individuals, 3727 identifiable to species. The majority of unidentified taxa were very young seedlings with only cotyledons, damaged plants or young seedlings later identified as non-focal taxa (e.g. climbers). Of the 3727 individuals identified, 1154 were found growing epiphytically and 2573 were growing on the forest floor. The surveyed individuals belonged to 36 species (including the *Nestegis* sp. morphospecies), with 25 of these occurring epiphytically at least once (Appendix 2.1). Across the survey, fifty individuals or more were recorded for 14 taxa; only these taxa with >= 50 individuals were used in the analyses. Five species recruited epiphytically in the > 2m size class, including older, soil-rooted individuals remaining either structurally dependent on the host or developing into free-standing trees. Three further species had epiphytic 'saplings' (0.31 – 2m size class). One species (*Geniostoma ligustrifolium*) was even observed fruiting whilst growing epiphytically in this sapling class (Appendix 2.2).

Species had different size-class structures between the terrestrial and arboreal subpopulations (Fig. 2.3). Seven species were significantly more likely to occur on the forest floor in all three size categories (or lacked data for adults as in *Nestegis* sp.; Fig. 2.3), as in typical terrestrial recruitment. Conversely, one species was more likely to be arboreal in two out of three size categories; showing a preference for arboreal establishment. Three species showed no significant difference between arboreal and terrestrial abundance, whilst the remaining three taxa exhibited an intermediate result (Fig. 2.3).

Seed length significantly predicted the tendency of species to occur arboreally on tree ferns (Linear Model, F = 22.60, *p* = 0.0002). Species with smaller seeds had a higher arboreality score (Fig. 2.4). However, this was not significantly determined by tree ontogeny (i.e. size class, F = 0.29, *p* = 1.00) and there was no significant interaction between size class and seed length (F = 2.07, *p* = 1.00). This finding was robust to the use of alternative seed size metrics in the model (Table 2.2).

Despite seed length predicting arboreality irrespective of size class, analysing each size class separately with linear regressions yielded reduced explanatory power of seed size over tree ontogeny (Seedlings: R^2 = 0.60, p = 0.003; Saplings: R^2 = 0.28, p = 0.12; Adults: R^2 = 0.10, p = 0.62; Fig. 2.5). This trend was also consistent across other seed size metrics (Table 2.3).

When the dataset was restricted to just the two commonest tree fern species – *Cyathea dealbata* (n = 133) and *C. smithii* (n = 91) – and the linear model rerun, the results were broadly consistent (Table 2.4). The slight variation in these results can likely be accounted for by the reduction in sample size from the overall dataset leading to reduced accuracy of the arboreality scores.

Discussion

Although most species were less likely to occur on tree ferns than the forest floor, *Weinmannia racemosa* and *Pseudopanax arboreus* were more likely to occur on tree ferns in most size classes, representing examples where epiphytic establishment on tree ferns appears to be a viable recruitment strategy. Seed size is negatively correlated with arboreality and seed size is sufficient to predict the degree of arboreality, with only smaller-seeded species able to exploit epiphytic establishment as a recruitment strategy. Decreased seed size increases the relative likelihood of species establishing upon tree fern trunks as a substrate. Hence, my results suggest that shade-intolerant small-seeded species utilise epiphytism as an escape from the heavy shade of the forest floor (consistent with the results of Gaxiola et al. 2008), providing recruitment opportunities that are otherwise somewhat limited in mature forest.

Explaining the relationship between seed size and arboreality

In addition to any possible filtering at the dispersal phase, I hypothesise that the mechanism underpinning the relationship between seed size and arboreality is the physical filtering of larger seeds, which are not able to lodge in the surface of the tree fern as easily. The surface of a tree fern

trunk consists of a root mantle, persistent frond stipes and often hairs and scales around the stipe bases (Dawson, 1988). This root mantle is thicker than and retains more water than the bark of angiosperm trees, making tree fern trunks ideal hosts for epiphytes (Mehltreter et al., 2005, Moran et al., 2003). However crucially, the root mantle also creates a mesh of nooks and crevices within which seeds can lodge. Larger seeds cannot lodge in this mesh, even if they sometimes catch on the outside or lodge behind stipe bases higher up the trunk. This factor presumably creates the pattern of smaller-seeded species being more likely to occur arboreally on tree ferns, even if the work does not experimentally examine this physical filtering process.

Seed size strongly predicts arboreality, whilst tree ontogeny or interaction with tree ontogeny does not. However, the results from analysing seedling, sapling and adult arboreality separately indicate that the signal of this pattern is strong at the seedling stage and subsequently fades through ontogeny. Later demographic filters – i.e. other traits – then influence the post-germination survival of both epiphytic and terrestrial individuals reducing the signal of the seed size pattern. Post-germination survival of epiphytic individuals is expected to be low given that epiphyte assemblages have been shown to have high mortality rates (Zuleta et al., 2016) and high turnover of individuals (Laube and Zotz, 2006a). The traits influencing these mortality rates could include root traits such as plasticity of rooting architecture (Pope, 1926, Fry et al., 2018, Liu et al., 2014) and drought-resistance/desiccation-tolerance related traits such as leaf mass per unit area. Desiccation is a key driver of mortality amongst epiphytes (Zuleta et al., 2016); however, recent evidence has questioned the importance of drought-resistance for accidental epiphytes as they tend to occur in substrates with high water-storage capacity (Hoeber et al., 2020). This may be true in my study given the high water-storage capacity of tree fern trunks (Mehltreter et al., 2005). However overall, my sampling approach does not allow for the most robust understanding of the patterns in later life history stages partly due these issues of high mortality and turnover.

Seed Size and Regeneration Niche

The same small-seeded species that typically germinate on tree ferns are also the species associated with light gaps, more-disturbed and lighter areas of the forest (Appendix 2.3). These small-seeded species are usually excluded beneath a closed-canopy, consistent with small-seeded species elsewhere (e.g. Foster and Janson, 1985, Westoby et al., 1992). I have shown that these small-seeded species use tree fern trunks as an elevated establishment surface, escaping light competition at ground level. Although the link between seed size and successional stage has been questioned (Hammond and Brown, 1995), my data does at least seem to support the link between seed size and understorey light conditions.

A key species from my study, *Weinmannia racemosa*, had one of the smallest seed sizes and had the highest arboreality of any species and its regeneration niche is consistent with these lighter understorey conditions. *W. racemosa* regenerates in earlier successional forest, lighter forest (Smale et al., 1997) and light gaps (Lusk and Ogden, 1992). It has one of the fastest growth rates in New Zealand's broadleaf-podocarp rainforest (Lusk and Ogden, 1992, Wardle and MacRae, 1966) and grows fastest as a sapling (Lusk and Ogden, 1992) to allow it to colonise these light gaps and disturbed forests. This is offset by the fact this species appears to have a shorter lifespan than other New Zealand rainforest trees (Lusk and Ogden, 1992). Also consistent with my results, regeneration of *W. racemosa* in closed-canopy forest without fallen logs is rare (Stewart, 1986) and regeneration is more generally ineffective in mature forest (Smale and Kimberley, 1993). Consequently, regeneration on tree ferns seems far more important for *W. racemosa* than for any other species.

Facultative Hemiepiphytism and Accidental Epiphytism

Frequently, the surface of tree fern trunks and the forest floor are not clearly distinct. Tree fern trunks tend to transition from vertical trunk to horizontal ground through a more broadly spreading base of root lattice, sometimes with additional build-up of detritus around the base. Other microhabitats around the forest understorey can also be considered intermediary between being

epiphytic on a tree fern and the forest floor, including elevated microsites such as trunks of fallen

trees, rotting logs and stumps. These elevated microsites also tend to be preferentially utilised by

seedlings of smaller-seeded tree species (Lusk and Kelly, 2003, Christie and Armesto, 2003),

including *W. racemosa*, which has also been shown to prefer elevated microsites (Bellingham and

Richardson, 2006, Stewart and Veblen, 1982, Wardle and MacRae, 1966). A spectrum of terrestrial

to arboreal establishment sites helps explain the facultative nature of tree fern epiphytism and

hemiepiphytism.

Epiphytism is an ecological condition that exists on a spectrum (Burns, 2010), and as such

the number of plant species which utilise either facultative or accidental epiphytism to some extent

may be severely underestimated (Zotz and List, 2003). Recent evidence concurs that accidental

epiphytism appears to be more widespread than previously thought, including in temperate regions

(Hoeber et al., 2019, Zotz, 2005, Hofstede et al., 2001). Furthermore, the arboreality score (used

with a survey approach controlling for substrate area) is an easily-applicable way of quantifying the

degree to which species occur epiphytically. Accidental epiphytes are also known to relatively

frequently reach reproductive maturity (Sharp, 1957, Hoeber et al., 2019).

It is important to clarify that my focal species include both facultative epiphytes and

facultative hemiepiphytes, as well as including both facultative and accidental epiphytes as per

classifications by Benzing and others (Benzing, 1990, Burns, 2010, Zotz, 2016b). Based on

observation of whether individuals put down roots or not, landscape-level abundance and my

quantitative data I clarify the nature of epiphytism and hemiepiphytism for each species

(summarised in Appendix 2.4). *Weinmannia racemosa* and *Pseudopanax arboreus* are facultative

hemiepiphytes. Although *Melicytus ramiflorus* was relatively abundant epiphytically in the survey, it

is very common terrestrially at a landscape level (especially in earlier-successional habitat) so it is

better described as both an accidental hemiepiphyte and accidental epiphyte (as opposed to

facultative) as these phenomena are rare in relative terms in this species. *Coprosma grandifolia* and

Geniostoma ligustrifolium are both facultative epiphytes, although *C. grandifolia* was once observed

making a terrestrially-rooted connection so could simultaneously be described as an accidental hemiepiphyte. All the other species are best described as typically terrestrial and then as accidental epiphytes where necessary as every species (except *Nestegis* sp.) was recorded epiphytically on one or more instances, although this was exceedingly rare for *Hedycarya arborea* and *Elaeocarpus dentatus* (Appendix 2.4) – these species are also never hemiepiphytes in any sense.

Role of Tree Fern Species

Analyses restricted to particular host tree fern species yielded similar results to the full analyses, even considering the reduced number of field replicates. This indicates that patterns of arboreality do not differ significantly between host tree fern species, particularly in congeners of a similar ecological niche. This concurs with general principles of epiphyte ecology that even if certain host species are preferentially inhabited by epiphytes (host bias), species are still physically capable of utilising a broad range of hosts (Wagner et al., 2015). Given that I am considering facultatively epiphytic plants, host range is expected to be suitably broad.

However, I cannot rule out particular species having differences in host bias. Although *Cyathea dealbata* and *Cyathea smithii* have broadly similar ecological niches, some of the other ferns less represented in the survey tend to occur in different environmental conditions, especially with regards to shade-tolerance (Bystriakova et al., 2011). For example, *Cyathea medullaris* is often a pioneer species in early successional scrub and forest with occasional persistence in mature forest (Brock et al., 2018b). In this case, the differing regeneration niche of this tree fern may interact with the arboreality of tree species. Mature individuals of this tree fern lack persistent frond stipes and tend to have a smooth, weathered surface above around 1m in height which is typically uninhabitable by most woody epiphytes and hemiepiphytes. One species which has very small seeds and was rarely recorded as growing epiphytically in my survey – *Brachyglottis repanda* – is often epiphytic on the large root-latticed base of *Cyathea medullaris* in more open early successional forest and scrub (*unpubl. data*). Therefore, there remains scope for species-specific differences in

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host tree fern use across the wider landscape, especially between different habitat types. However, where tree ferns provide a suitable establishment surface for woody epiphytes and hemiepiphytes, the species that generally establish epiphytically are small-seeded.

The Role of Dispersal

Dispersal is an important process influencing accidental epiphytism and facultative hemiepiphytism on tree ferns. Currently, many New Zealand tree species experience increased dispersal limitation due to the extinction of much of the avifauna at a local or national level (Kelly et al., 2010). Increased dispersal limitation will reduce seed rain of endozoochorous species, which account for just over 60% of the focal species in my study, and therefore consequently may reduce overall seedling abundance. Large-seeded species may also be disproportionately affected by increased dispersal limitation (Wotton and Kelly, 2011). However, the site does have active predator control, meaning the invasive mammalian predators that drive these avifaunal extinctions in New Zealand (e.g. Innes et al., 2010) should have a reduced impact on native bird abundance locally (O'Donnell and Hoare, 2012). Additionally, an increase in dispersal limitation leading to an overrepresentation of anemochorous species should not impact my overall conclusions given that the relative abundance in the community is not a factor in my analyses. Therefore, it remains to be seen how increased dispersal limitation and differences in dispersal syndrome may influence assemblages of accidental epiphytes and facultative hemiepiphytes. However, clues from obligate epiphytes elsewhere suggest high levels of dispersal limitation may be an important factor in species abundance (Ackerman et al., 1996, Mondragón and Calvo-Irabien, 2006, Victoriano-Romero et al., 2017), especially within forest interiors (Cascante-Marín et al., 2009).

Study Limitations

Firstly, because tree ferns were the sampling replicates, my sample only included a small number of adults, limiting my ability to draw conclusions about the adult population. The analyses

offer some insights, however, understanding the landscape-wide impact of tree fern based

recruitment may require another approach that does not control for substrate area.

The second area of limitation was the difficulty of controlling for the many biotic and abiotic

variables than can influence seedling abundance and community composition. Whole areas of the

literature tackle the influence of such factors on seedling abundance, composition and survival (e.g.

Clark et al., 1998, Denslow and Guzman G., 2000, Moles and Westoby, 2004, Lawes et al., 2005). My

approach to dealing with this multitude of variables was to sample across the heterogeneity of the

forest with a relatively large sample size. A model taking into account plot-level differences in

moisture level, canopy shading and other similar variables would unlikely have givenme as clear

patterns. Future experimental work may be needed to fill this niche.

However, the issue of tree fern shading may be an especially pertinent factor given the

results of Brock et al. (2018a) indicate that tree fern crown shading represses forest floor seedling

abundance. Whilst shading reduces abundance, their results do not indicate that it alters community

composition; therefore, seedling abundance of all species may be similarly suppressed on the forest

floor. In which case, all species would have an inflated arboreality score based on lower abundance

of seedlings near tree ferns. Conversely, tree ferns may also shade their own trunk to a similar

degree to the forest floor around them, making any effect of tree fern shading on my data

somewhat uncertain. Additionally, as outlined in my methods, the plots were carried out beginning

at one metre away from the tree fern, thus avoiding the worst hit area of shading and macro-litter

fall.

Another possible risk is that patchy dispersal may have led to aggregated seedling

distributions (with many individuals on the same tree fern) increasing sampling artefacts. As

discussed earlier, further research that integrates the process of dispersal may counter this potential

issue.

Whilst these limitations may have had a marginal impact upon the results, the central result

of seed size correlating with arboreality is clear enough to withstand some margin of error. Thus, my

overall conclusion that facultative hemiepiphytes and accidental epiphytes tend to be small-seeded species appears sufficiently robust.

Global Applicability and Future Work

Despite the limited spatial scale of my study, I know that tree fern based regeneration occurs elsewhere in New Zealand in different forest types (Gaxiola et al., 2008) and also occurs in other southern temperate forests, such as Tasmania (Bowkett, 2011). There is also evidence that similar regenerative processes may also occur across a range of tropical forests globally where tree ferns are a major constituent, such as in Brazil (Negrão et al., 2017), Jamaica (Newton and Healey, 1989) and La Réunion Island (Derroire et al., 2007). Beyond facultative hemiepiphytism on tree ferns, similar processes of facultative hemiepiphytic regeneration may occur using other types of host plants including possible north temperate analogues, such as a case from Canada of facultatively hemiepiphytic conifers using another conifer species as a host (Burns, 2008). However, it appears that high humidity/rainfall are fundamentally important in driving the incidence of facultative hemiepiphytism globally, with oceanic islands and other high rainfall areas comprising the examples cited in the section thus far. At a regional scale in Wellington, other sites with slightly lower annual rainfall (Map 5 - GWRC 2007) have markedly lower incidences of facultative hemiepiphytism on tree ferns (*pers. obs.*).

More generally, the ecophysiological mechanisms underpinning patterns in arboreality need further enquiry. It would be of particular interest to understand the possible role of phenotypic plasticity in determining species adult arboreality. Some species of facultative hemiepiphyte show remarkably different morphology between hemiepiphytic and terrestrial individuals – for example *Weinmannia racemosa* and *Pseudopanax arboreus* (observed as part of this study) or *Tsuga heterophylla* (Burns, 2008). Hemiepiphytic individuals can have roots spreading from all directions from the point of attachment, typically lateral roots wrap around the trunk and occasionally roots travel vertically up the tree fern trunk (Pope, 1926); effectively these are neutrally and negatively

geotropic roots, which would not occur in terrestrial individuals. Hence, I can hypothesise that

plasticity in rooting morphology is important for being able to grow hemiepiphytically.

Phylogeny also appears to play a role in the likelihood that species are able to grow as

hemiepiphytes, with key taxa from this study reappearing in different areas of the globe – including

other species in the genus *Weinmannia* (Lawton, 1992, Derroire et al., 2007) and other species in the

family Araliaceae (Williams-Linera, 1992, Lawton, 1992, Feild and Dawson, 1998). Thus, plasticity in

growth form or life history, such as facultative epiphytism, demonstrates phylogenetic constraint, a

potentially interesting avenue for understanding repeated patterns in evolutionary ecology.

Conclusions

Overall results demonstrate that several New Zealand tree species – most notably

Weinmannia racemosa and *Pseudopanax arboreus* – are more likely to regenerate on tree ferns than

on the forest floor. Furthermore, seed size predicts the tendency for individuals of a given species to

occur arboreally, with small-seeded species occurring more often on tree ferns than larger-seeded

ones. This in turn supports my overall hypothesis that small-seeded tree species exploit tree ferns as

an alternative recruitment strategy in southern temperate rainforest.

Figure 2.1 – A map showing location of my study site, Kaitoke Regional Park (indicated by the black star). Its location is shown within the Wellington region (grey map with scale bar) and the location of the Wellington region within New Zealand (line drawn map inset to the left).
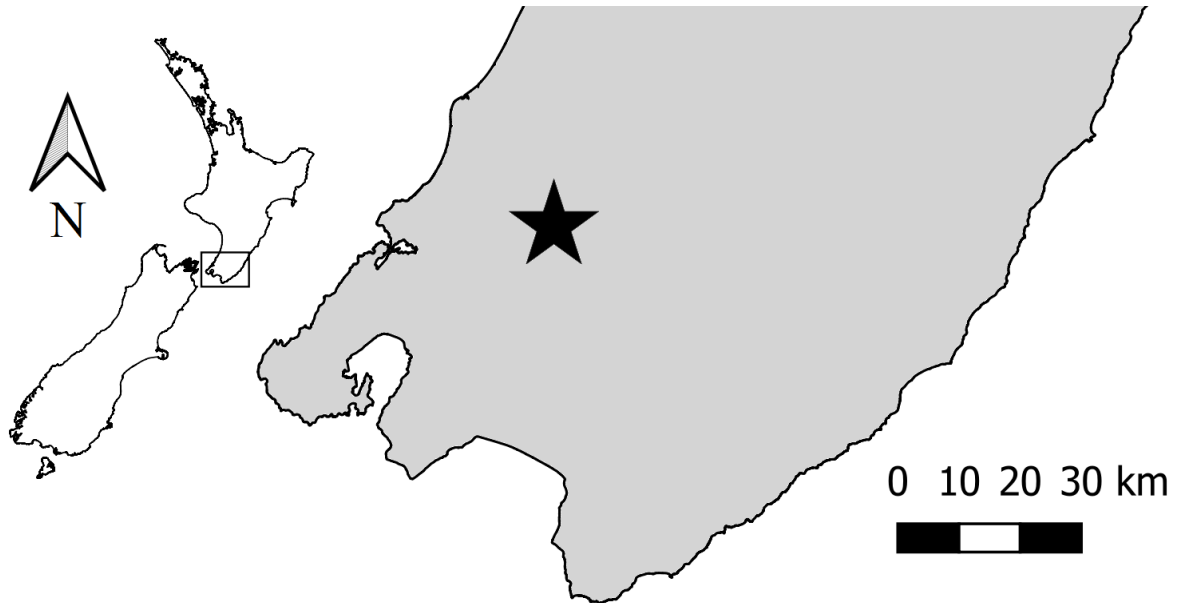
Figure 2.2 – A graphic representation of the field study design for chapter 2. Tree fern surface area was estimated by treating the tree fern caudex as a cylinder, and creating a forest floor plot of equivalent area as shown.
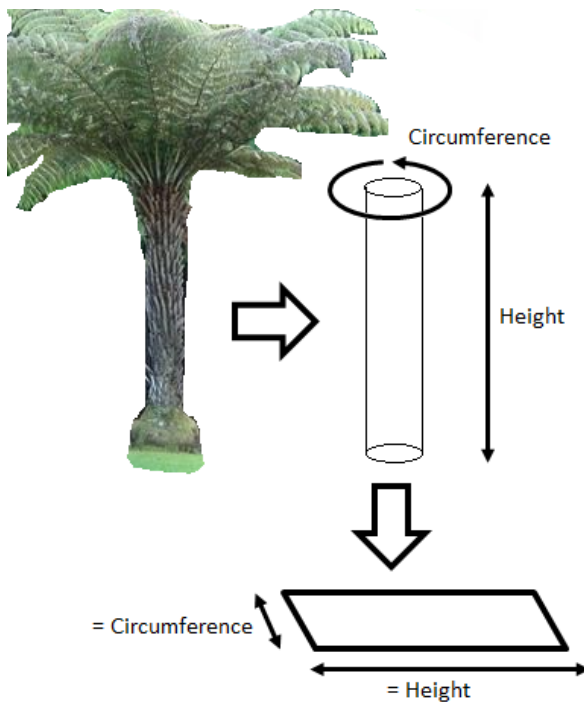
Figure 2.3 – Population pyramids showing the size-class structure of the fourteen most abundant species in the dataset (min 50 individuals). The pyramids are divided into terrestrial/forest floor (black, left) and epiphytic/tree fern (grey, right) subpopulations. The frequency of individuals are along the horizontal axis with the size classes up the vertical axis. The three size classes are seedlings (0 – 0.3m), saplings (0.31 – 2m) and adults (>2.01m). Asterisks indicate the significance levels from the results of binomial testing (post-Bonferroni correction), with asterisks to the left of or within black bars indicating that species and size class is more likely to occur terrestrially and those on the right or within the grey bars indicating those more likely to occur epiphytically. (* represents $p <$ 0.05, ** represents $p <$ 0.01, *** represents $p <$ 0.001)
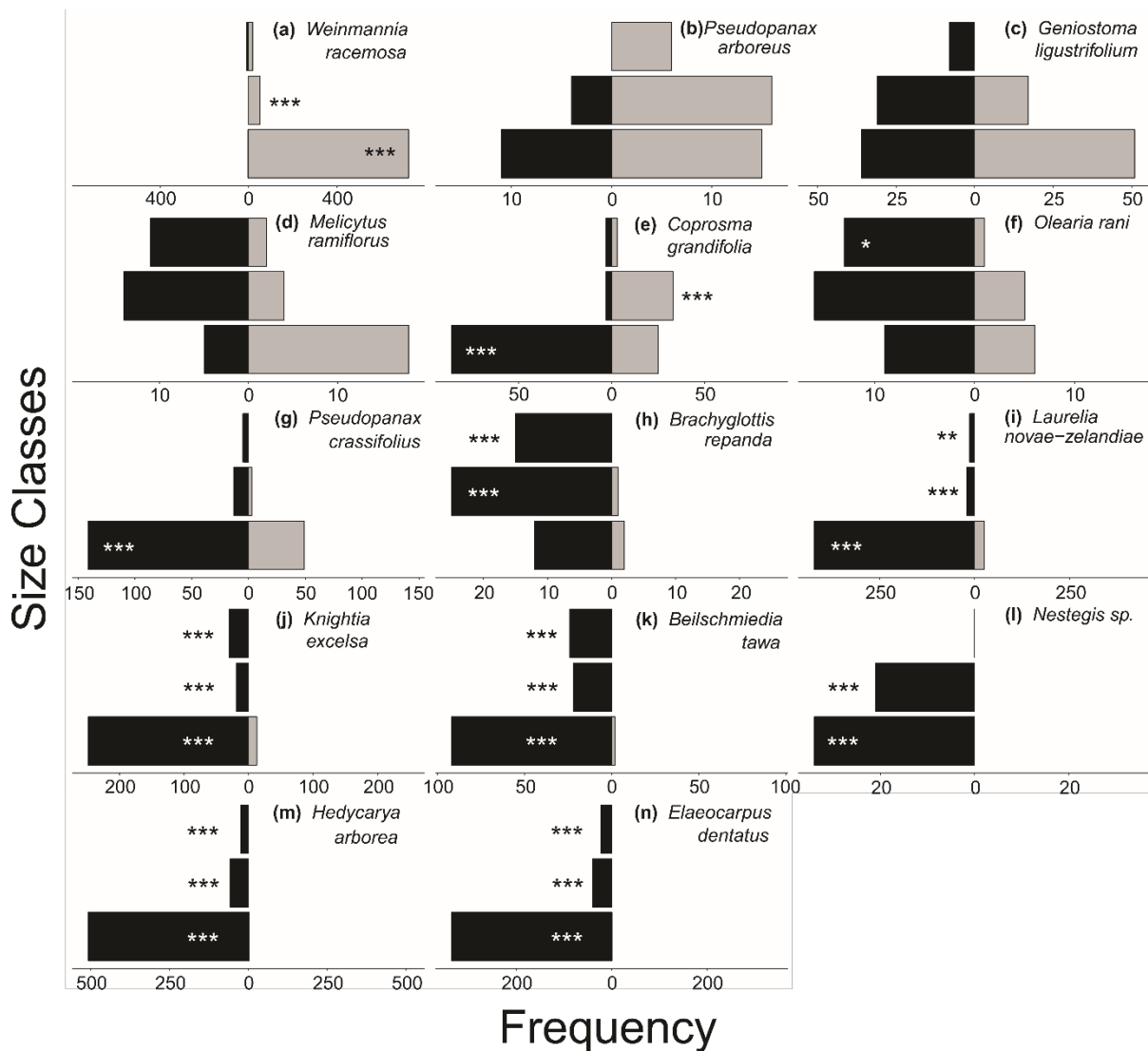
Figure 2.4 – A scatterplot of seed length against arboreality. Each point represents a species at particular size class/life history stage (seedling, sapling, adult). Both seed length and arboreality score are natural logarithm transformed.

Figure 2.5 – Linear regressions of the relationship between seed length and arboreality at each of the seedling (a), sapling (b) and adult size (c) classes. Both variables are natural logarithm transformed. The grey bands represents the 95% confidence interval around each regression line.
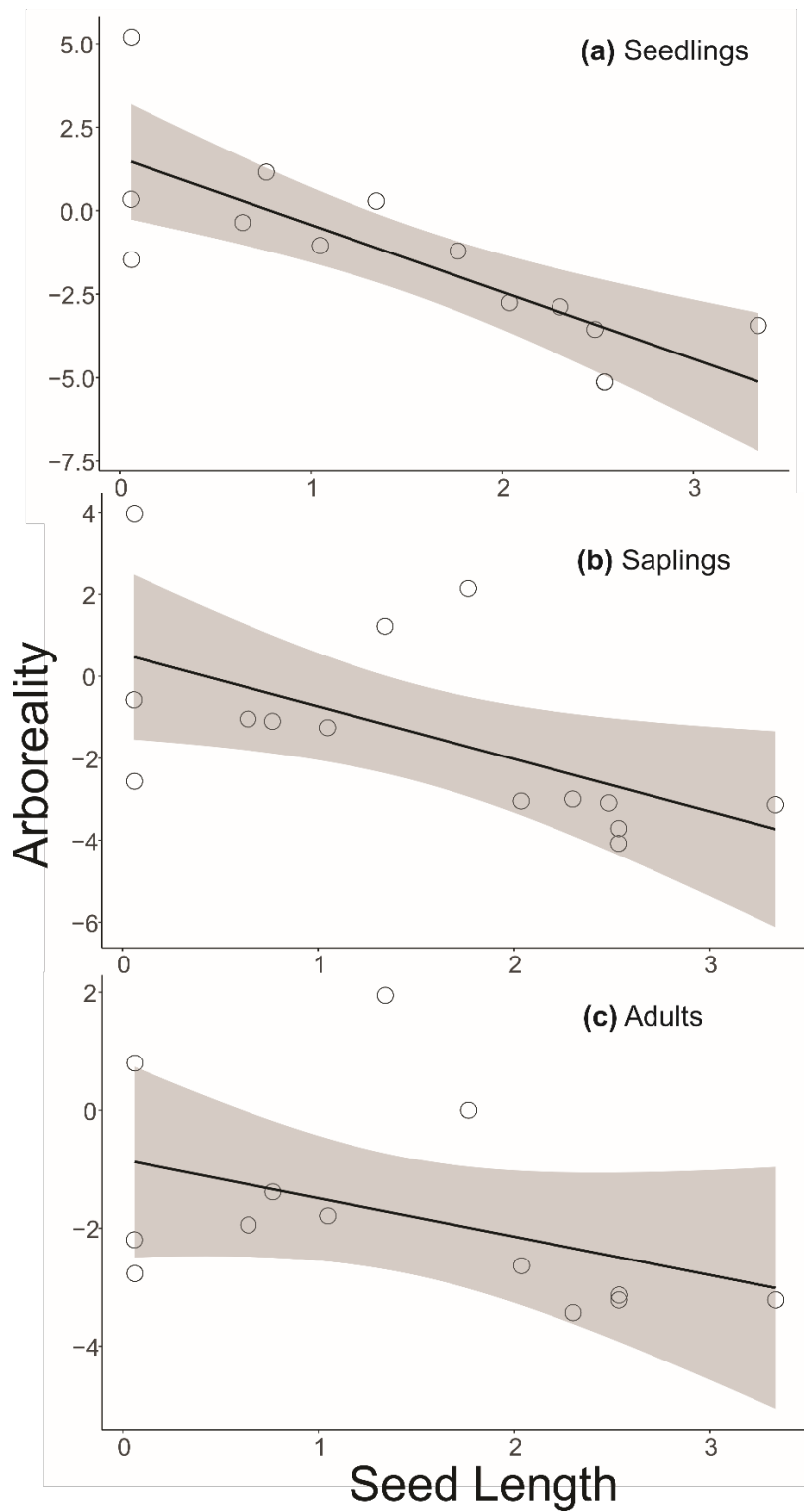
1   **Table 2.1** – A table containing sample sizes and source information for all the seed size data included in my analyses. The Data Source column indicates the
2   species for which literature data were used – in which case seed data was extracted from descriptions in Webb & Simpson (2001). The seed length,
3   literature length, seed width and depth all report values in millimetres (mm). Measured values are means and also standard deviation show the standard
4   deviation around the mean. Literature derived values do not have an associated standard deviation; note that this includes the four cases where seed data
5   is entirely literature derived. Where seed depth was assumed to be equal to seed width, this column is left blank for those species. The final column gives
6   the dispersal syndrome of each species. All reported values are rounded to 1 decimal place.

Species	Data Source	Seeds Measured (# Indiv.)	Seed Length	Seed length (Lit.)	Seed width	Seed depth	Dispersal Syndrome
Beilschmiedia tawa	Field Measurements	26 (6)	28.2 ± 4.3	26	12.2 ± 1.1	11.4 ± 1.0	Endozoochory
Brachyglottis repanda	Field Measurements	40 (4)	1.1 ± 0.1	1.4	0.2 ± 0.1		Anemochory
Coprosma grandifolia	Field Measurements	80 (8)	5.9 ± 0.5	6.3	3.72 ± 0.26	2.1 ± 0.2	Endozoochory
Elaeocarpus dentatus	Field Measurements	50 (5)	12.6 ± 1.2	13	8.3 ± 0.9	7.6 ± 0.9	Endozoochory
Geniostoma ligustrifolium	Field Measurements	60 (6)	1.1 ± 0.1	1.2	0.7 ± 0.1		Endozoochory
Hedycarya arborea	Field Measurements	9 (2)	12.6 ± 0.8	11.5	8.4 ± 0.4	7.1 ± 0.3	Endozoochory
Knightia excelsa *	Webb & Simpson	N/A	10	10	4.4		Anemochory
Laurelia novae-zelandiae	Field Measurements	40 (4+)	7.7 ± 0.9	17.5	2.3 ± 0.4	1.2 ± 0.3	Anemochory
Melicytus ramiflorus	Field Measurements	70 (7)	2.2 ± 0.2	2	1.4 ± 0.1		Endozoochory
Nestegis sp.†	Webb & Simpson	N/A	12	12	6		Endozoochory
Olearia rani ‡	Webb & Simpson	N/A	1.9	1.9	0.5		Anemochory
Pseudopanax arboreus	Field Measurements	70 (7)	3.8 ± 0.3	3.7	2.5 ± 0.2	1.7 ± 0.1	Endozoochory
Pseudopanax crassifolius	Webb & Simpson	N/A	2.9	2.9	1.7		Endozoochory
Weinmannia racemosa	Field Measurements	43 (6)	1.1 ± 0.1	1.4	0.4 ± 0.0		Anemochory

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8   * - *Knightia excelsa* has an unusual fruiting phenology (nearly 1 year to mature) and dispersal method (follicle splits to release winged wind-dispersed seed).
9   This made seed collection very difficult logistically.

10   † - Given the uncertainty on which species of *Nestegis* sp. is represented in the forest floor juvenile community and the fact that no adults were
11   encountered when accessible areas of the site were searched, literature data had to be used in this case.

12   ‡ - *Olearia rani* is reported to flower only once every three years. There are reports of flowering in November 2017 in the area and no flowering/fruiting
13   was observed in the austral summer of 2018/2019 when I collected seeds for measurement.

Table 2.2 – A table showing the results of each of the linear models assessing the effect of seed size on species arboreality with plant size class (seedling, sapling and adult) as a random factor. Each linear model was also run with an interaction term in the model. The initial linear model using seed length was also rerun using a variety of seed size measurements. Seed length was the initial seed metric used, followed by seed length from the literature, seed width and seed depth (replacing width where available) for comparison. Arboreality and seed size metrics are natural logarithm transformed in all cases. All *p*-values have had a Bonferroni correction applied to them.

Seed Size Metric	Influence of Seed Size		Influence of plant Size Class		Interaction Term	
	F value	p-value	F value	p-value	F value	*p*-value
Seed Length	23.91	<0.001	0.30	1.00	2.07	1.00
Lit. Seed Length	23.74	<0.001	0.29	1.00	1.93	1.00
Seed Width	15.66	0.003	0.24	1.00	1.93	1.00
Seed Depth	18.19	0.001	0.27	1.00	1.63	1.00

Table 2.3 – A table showing the full results of regressions between seed size and each seedling, sapling and adult arboreality, using multiple seed size metrics. All axes are natural logarithm transformed. The results for each seedling, sapling and adult arboreality are remarkably consistent in explanatory power (R^2 value) and in model significance (p-value), regardless of seed metric used. Within each, size class, a Bonferroni correction has been applied to p-values.

Seed metric (x)	Size class of Arboreality (y)	R^2	Slope	Intercept	p-value
Seed Length	Seedlings	0.60	-2.01	1.58	0.003
Lit. Seed Length	Seedlings	0.58	-2.00	1.75	0.004
Seed Width	Seedlings	0.51	-1.63	-0.20	0.010
Seed Depth	Seedlings	0.50	-1.67	-0.40	0.011
Seed Length	Saplings	0.28	-1.28	0.54	0.12
Lit. Seed Length	Saplings	0.29	-1.30	0.69	0.11
Seed Width	Saplings	0.18	-0.94	-0.67	0.30
Seed Depth	Saplings	0.23	-1.06	-072	0.19
Seed Length	Adults	0.10	-0.65	-0.84	0.62
Lit. Seed Length	Adults	0.11	-0.68	-0.74	0.56
Seed Width	Adults	0.01	-0.41	-1.49	1.00
Seed Depth	Adults	0.06	-0.53	-1.49	0.83

Table 2.4 – A table showing the results of the linear model comparable to the main analysis (in table 2.2) but now with a subset of the data restricted to just the common understory tree ferns *Cyathea dealbata* and *Cyathea smithii* respectively as the host. As in Table 2.2, each linear model was carried out for all seed size metrics. *P*-values have had a Bonferroni correction applied with analyses for each host tree fern species as a test family.

Host Tree Fern	Seed Size Metric	Influence of Seed Size		Influence of Size Class		Interaction Term	
		F value	p-value	F value	p-value	F value	p-value
Cyathea dealbata	Seed Length	17.14	0.002	<0.01	1.00	1.24	1.00
	Lit. Seed Length	16.23	0.002	0.02	1.00	1.01	1.00
	Seed Width	11.54	0.014	<0.01	1.00	1.23	1.00
	Seed Depth	14.78	0.004	<0.01	1.00	0.95	1.00
Cyathea smithii	Seed Length	15.87	0.003	1.26	0.30	2.92	0.54
	Lit. Seed Length	17.40	0.002	1.32	0.28	3.31	0.38
	Seed Width	10.91	0.018	1.15	0.33	2.72	0.64
	Seed Depth	11.52	0.014	1.13	0.34	2.07	1.00

Chapter 3 – Community assembly of epiphytes and climbers on a host tree fern species

Abstract

Community assembly of structurally-dependent plants, such as epiphytes and climbers, is poorly understood. The emerging meta-network framework has become a popular approach to address this theory deficit. However, almost all work in this area focuses on understanding epiphyte-host species networks, whilst single-host metacommunity networks have received little attention. Tree ferns make good hosts for subcanopy epiphytes, with their simple shape and monopodial growth also making them ideal to test patterns of species accumulation and vertical structuring. Hence, I aimed to test 1) the species accumulation model of epiphyte succession, 2) patterns of co-occurrence and nestedness in a single-host metacommunity matrix, 3) differences in vertical occurrence of different epiphyte and climber groups, on the host tree fern *Cyathea dealbata*. Epiphytes and climbers on *C. dealbata* fit the species accumulation model of succession both between hosts and different aged sections of a given host. The epiphyte and climber metacommunity matrix is mostly randomly structured with no evidence for any departure from null expectations in co-occurrence patterns or nestedness. Despite this lack of matrix structure, different habits of epiphytes and climbers occupied vertical space differently, as did wind and bird dispersed epiphytes. Thus, I conclude that epiphytes on *C. dealbata* have a stochastic or Gleasonian horizontal structure, coupled with a vertical structure that varies between arboreal plants of different habit and dispersal syndrome, possibly mediated by variation in microhabitat tolerance.

Introduction

Assembly of vascular epiphyte communities is poorly characterised, especially with regards to a theoretical framework (Kitching, 2006, Zotz, 2016b). Descriptions of the succession of epiphyte communities have long been central to the thinking of how epiphyte communities develop over time (Dudgeon, 1923, Stone, 1989). Empirical evidence of a lack of community turnover, with a continued accumulation of epiphytes even in mature forests (Flores-Palacios and García-Franco, 2006, Laube and Zotz, 2006a, Einzmann and Zotz, 2017), has led to the replacement of these traditional terrestrial successional models with an empirically-validated species accumulation model of succession for epiphytes (Woods, 2017). Other theoretical frameworks have then built upon these species accumulation models, including the conceptualisation of host trees as islands with host tree ontogeny linked to species accumulation (Taylor and Burns, 2015a, Spruch et al., 2019). Recent work has also more explicitly tackled community assembly from both neutral (Janzen et al., 2020) and traits-based perspectives (Petter et al., 2016, Wagner et al., 2021), indicating that neutral processes and the trait-environment interactions play a role in community structure.

Community assembly of climbing plants, such as lianas, is similarly poorly understood (Schnitzer and Bongers, 2002). Like epiphytes, they rely structurally on host trees and as such the assembly patterns of epiphytes and climbers may be similar (Malizia, 2003). Conversely, the soil-rooted nature of climbers may lead to very different assembly patterns to other arboreal plants (Blick and Burns, 2009). Interactions between epiphytic and climbing plants may also alter the way their communities are structured, although currently this has not been tested (Zotz, 2016b). At the network scale, there is evidence that host-climber networks are less nested and less clearly structured than epiphytes (Blick and Burns, 2009).

A key emerging framework for analysing structurally dependent plants is a network-based approach (Burns, 2007). The meta-network framework (Burns and Zotz, 2010) builds on this idea by separating epiphyte species host species networks (as 'networks' *sensu stricto*) from epiphyte species host individual network – as epiphyte metacommunities. Much progress has been on made

characterising epiphyte species host species networks (e.g. Silva et al., 2010, Sáyago et al., 2013, Taylor et al., 2016), with many epiphyte-host species networks showing patterns of nestedness (e.g. Piazzon et al., 2011, Ceballos et al., 2016, Zotarelli et al., 2018, Francisco et al., 2018a, Naranjo et al., 2019). Results for climber-host species networks are a little less clear with each of significant nestedness (Sfair et al., 2010), neutral nestedness (Addo-Fordjour et al., 2016) and so-called "anti-nestedness", or compartmentalisation, (Addo-Fordjour and Afram, 2021) all reported. However, comparatively few studies have assessed metacommunity networks in epiphytes (Burns, 2008) or climbers (Blick and Burns, 2011), in the sense of Burns and Zotz (2010). Zhao et al. (2015) used a matrix of host individuals, but of many different host species, unlike the host-specific meta-communities of Burns and Zotz (2010), thus potentially confounding the host-epiphyte interactions with metacommunity structure. Pincheira-Ulbrich et al. (2018) use a traditional metacommunity concept (e.g. Leibold et al., 2004) with forest fragments and epiphyte species to construct their matrix, thus is not conceptually comparable to an epiphyte-species-host-individuals matrix. Despite the far more limited usage of single-host metacommunity networks compared to epiphyte-host species networks, metacommunity networks may have some potential advantages. Whilst epiphyte-host species networks are clearly optimal for elucidating patterns associated with host specificity, host-individual based networks may be better for quantifying physical co-occurrences between epiphyte or climber species – aggregation or segregation. This more direct measure of physical aggregation/segregation may better allow potential testing for community-wide interspecific interactions in arboreal plants, such as competition or facilitation.

Tree ferns act as a particularly good host to many epiphytes (Pope, 1926, Moran et al., 2003), possibly due to the higher levels of water retention in their caudex compared to most angiosperm tree trunks (Mehltreter et al., 2005). In terms of their physical structure, they are also simpler hosts than most angiosperms, lacking a complex branching architecture and often being of a smaller stature. Thus, subcanopy/understorey tree ferns effectively offer only the lowest two Johansson zones – base-of-tree and trunk (*sensu* Johansson, 1974). This may potentially explain why

certain common members of the obligate epiphyte community are missing (e.g. orchids, shrub epiphytes in New Zealand), whilst epiphytic ferns (Roberts et al., 2005), and facultative and accidental epiphytes are more common than they otherwise would be (Pope, 1926, Brock and Burns, 2021b). Tree ferns also host only a small subset of liana richness, albeit including a few abundant species in New Zealand. Despite hosting a potentially skewed subset of the epiphyte and liana community, their simple shape means that tree ferns are an ideal model system for studying the community assembly patterns of structurally dependent arboreal plants. Tree fern height is a reasonable proxy for tree fern age given their monopodial growth (Brock et al., 2019). Similarly, the lowest portion of the tree fern caudex is the oldest part of the plant, whilst the highest portion is the youngest part of the tree fern. This also makes them a great study system for understanding the vertical structuring of the community.

I therefore attempted to address the following research questions, using the tree fern host *Cyathea dealbata* (ponga / silver fern) as a model system:

(1) Does the pattern of species accumulation with tree fern height differ between epiphytes and climbers?

(2) Is there a pattern of species accumulation from the highest (youngest) portion of the tree fern to the lowest (oldest) portion, and again does this differ between epiphytes and climbers?

(3) Does the epiphyte and climber meta-community show a significant pattern of co-occurrence (negative or positive) compared to chance expectations? Furthermore, do different subsets of the meta-community show different patterns to the overall matrix?

(4) Similarly, does the epiphyte and climber meta-community, or any of the major meta-community subsets, show a significant difference in nestedness compared to chance expectations?

(5) Do different epiphyte and climber groups show differences in vertical space occupation?

Methods

Study Site

Field surveying was carried out in Kaitoke Regional Park (41° 3' S, 175° 11' E). Vegetation in

Kaitoke is dominated by a mixture of broadleaf-podocarp rainforest and southern beech

(Nothofagaceae) forest. The broadleaf forest in the park has a structure similar to tropical rainforest

(Dawson and Sneddon, 1969), with tree ferns forming a major subcanopy component. The three

commonest tree fern species are *Cyathea dealbata* (Cyatheaceae), *Cyathea smithii* and *Dicksonia*

squarrosa (Dicksoniaceae). For a full description of the site (including physical geography) and the

vegetation composition of the broadleaf forest areas see Chapter 2.

Field Surveying

In order to characterise community composition of epiphytes and climbers on tree ferns, I

surveyed tree ferns of the species *Cyathea dealbata* (commonly known as ponga or silver fern).

Surveying was restricted to a single host species to avoid the effect of host species in the data and to

assess an epiphyte species host individual meta-community matrix (sensu Burns and Zotz, 2010). *C.*

dealbata was chosen as the most suitable focal host for my study as it is a subcanopy component of

mature forest (unlike the early successional *C. medullaris* – Brock et al. (2018b)), that does not form

clonal groves (as in *D. squarrosa*) and lacks a persistent 'frond skirt' (as in *C. smithii*). Frond skirts

have been hypothesised to be an adaptation to exclude epiphytes and climbers (Page and Brownsey,

1986), although this is disputed (Brock and Burns, 2021a), hence why a host species without a

persistent frond skirt was chosen. A frond skirt may also alter vertical structuring of the community.

Additionally, *C. dealbata* also typically has the straightest caudex with a largely vertically uniform

diameter. Tree fern individuals less than 1.5m in height were not sampled as these lack epiphytes

and climbers. Individuals directly on trails were also excluded. For each tree fern sampled, its height

in metres was recorded to the nearest 0.05m.

Epiphyte and climber composition was recorded for not only each tree fern, but for each vertical quartile of each tree fern (Fig. 3.1). This also allowed for assessment of how the community colonises the tree fern over time, with the base of the tree fern representing the oldest part of the fern and the top representing the youngest portion. The lowest (and oldest) part of the trunk was designated as quartile 1 (Q1), whilst the highest (and also youngest) part was designated as quartile 4 (Q4) – Fig. 3.1. Epiphytes and climbers were recorded as presence/absence data, due to the difficulty determining and separating out individuals for many taxa, especially the climbers, filmy ferns and other rhizomatously spreading ferns.

The common twining liana *Ripogonum scandens* (commonly known as Supplejack) was ignored. It does not fit well within a discrete host trees model, given that the stems of this species spread extensively through the forest (including aerially curling upwards without a host, hanging between hosts, and travelling more or less horizontally through the understorey). For consistency, another less abundant twining climber was also excluded (*Parsonsia* – with only a couple of encountered individuals). During the surveying, *Tmesipteris elongata* and *Tmesipteris tannensis* were encountered. However, a majority of *Tmesipteris* individuals lacked mature synangia and weren't reliably identified to species, hence were treated as *Tmesipteris* sp. for the purposes of this study.

A difficult to identify group, filmy ferns were identified using Brownsey and Perrie (2016) and (Kirby, 2014). Nomenclature was checked against the online Checklist of the New Zealand Flora – for ferns and lycophytes (Schönberger et al., 2019b); for seed plants (Schönberger et al., 2019a).

Plant Habit Classification

Species occurring on the tree fern were classified as either climbers or epiphytes (in a broad sense) for the purposes of my richness analyses. Epiphyte species were further split into four subcategories (summarised in Appendix 3), for use in my co-occurrence analyses and analysis of vertical profile. These four categories were filmy ferns (Hymenophyllaceae), non-woody obligate epiphytes, non-woody facultative and accidental epiphytes, and woody epiphytes.

Filmy ferns have a distinctively thin frond lamina (only a single cell layer thick), and thus show a strong preference for high moisture environments. They also all spread rhizomatously up and down the tree fern caudex. Most are obligate epiphytes (and lithophytes), although some are facultative epiphytes (notably *Hymenophyllum demissum* which is also common on the forest floor). For these reasons, it is logical to expect filmy ferns to have a more similar spatial ecology to one another compared to other epiphytes, and treat them as a distinct category.

In both the woody epiphyte and 'non-woody facultative and accidental epiphyte' groups, facultative and accidental epiphytes were grouped together for analyses, due to the difficulty in categorising this distinction. Woody facultative hemiepiphytes were also included within woody epiphytes as they are epiphytic in the first phase of their life and likely have similar dispersal limitations, which is a key relevant factor in community assembly processes.

Analyses – Richness

In order to assess differences in species accumulation on tree ferns of different heights (as a proxy for age) between epiphytes and climbers, I conducted two general linear models (with a Poisson method to account for the use of count data) of how height affects richness – one for epiphyte richness and another for climber richness. A third model using overall arboreal richness was also calculated for comparison. To also assess how epiphytes and climbers differentially colonise the vertical sections of the tree ferns, I carried out three general linear models (also based on a Poisson distribution) of how richness varies between vertical quartiles of the tree fern – again, one for each of epiphyte, climber and overall richness.

Analyses – Co-occurrence patterns and Nestedness

In order to analyse patterns of co-occurrence in the community, I used a null model approach following Gotelli (2000) and a meta-community framework following Burns and Zotz (2010). The meta-community matrix consisted of epiphyte/climber species as columns, tree fern

individuals as rows, and cells populated with binary presence-absence data. Given that rare species can disproportionately distort matrix properties (Blüthgen et al., 2008), species occurring on less than three tree ferns were removed from the matrix. To quantify the co-occurrence pattern in this matrix, I used the C-score (Stone and Roberts, 1990), which is usually considered more appropriate than most similar measures (Gotelli, 2000). This was calculated using the R function 'C.score' (in the package 'bipartite') and using a normalised version of the score (i.e. values constrained between 0 and 1). Note that normalised C-scores of 1 indicate a totally checkerboarded composition (i.e. complete negative co-occurrence) whilst a normalised C of 0 indicates no checkerboardedness (i.e. complete positive co-occurrence). I then generated 10,000 randomised matrices using the R function 'permatfull' (package 'vegan'). The randomised matrices had constrained column and row totals, which correspond to arboreal species abundance, and richness of taxa per tree fern, respectively. The matrices were generated using a 'quasi-swap' algorithm, which is a form of non-sequential swapping algorithm, meaning the generated matrices are independent from one another (Miklós and Podani, 2004). Given the use of a non-sequential swapping algorithm, 10,000 null matrices should suffice for an unbiased distribution of expected values (Lehsten and Harmand, 2006). I then compared the observed C-score with the distribution of expected C-scores. A p-value was generated as a proportion of expected values greater than the observed value, thereby also generating the p-values by direct comparison (as advocated for in Veech, 2012). This is analogous to two separate one-tailed tests, with p-values outside the bounds of $0.05 < p < 0.95$ (following Gotelli, 2000) being less or more checkerboarded (respectively) than null expectations.

Given recent suggestion that co-occurrence analyses are best restricted to small numbers of similar species (Presley et al., 2019), five additional models were run on five sub-compartments of the matrix (similar to Blick and Burns, 2011). These sub-compartments related to the five habit classes defined earlier – climbers, filmy ferns, non-woody holoepiphytes, non-woody facultative and accidental epiphytes, and woody epiphytes. The null model conducted for each sub-compartment was methodologically identical to the procedure used on the overall matrix. Following the 6 analyses

(for the overall matrix and the 5 sub-compartments), Hochberg corrections (at n=6) were applied to each *p*-value to account for multiple tests (Hochberg, 1988). For the test of greater checkerboardedness than chance, Hochberg corrections could be applied to 1-*p* as a separate test family (although note that these results were all non-significant prior to correction rendering this step unnecessary).

Following the null model for co-occurrence, a similar null model was run testing for meta-community nestedness. This null model was run using the same 10,000 null matrices. It thus importantly also maintained row and column totals (Ulrich and Gotelli, 2007) and used matrices generated by means of a non-sequential swapping algorithm. As a metric for nestedness, I used the Nestedness metric based on Overlap and Decreasing Fill (NODF; Almeida-Neto et al., 2008). Observed NODF was calculated for the meta-community matrix and then expected NODF calculated from each of the 10,000 null matrices. This process was repeated for the 5 matrix sub-compartments, as per the co-occurrence null model. A similar Hochberg correction was also subsequently applied.

Analyses – Differences in Vertical Profile

When assessing the vertical profile of epiphytes and climbers, species occurring on ≥8 tree ferns were deemed to have sufficient data to be representative of that species' vertical occurrence patterns on *C. dealbata* and were included in this analysis. For each species, the number of times it was recorded in each vertical quartile across the 170 surveyed tree ferns was tabulated as their occurrence. To remove the effect of differences in abundance between species, raw occurrence for each quartile was then divided by the total number of tree ferns that the species occurred on, giving a normalised occurrence for each quartile. This was organised as a matrix with species as rows, each of the four vertical quartiles as a column, and each cell containing the normalised occurrence. In order to assess differences in overall vertical profile between the 5 arboreal plant habit categories (climbers, filmy ferns, obligate epiphytes, facultative epiphytes, woody epiphytes), I conducted a

permutational multivariate analysis of variance (PERMANOVA). For the PERMANOVA, the matrix of species normalised occurrence by vertical quartile was converted to a distance matrix using a Bray-Curtis dissimilarity metric. The PERMANOVA was then conducted using the R function 'adonis' (the 'vegan' package), with 9999 permutations.

Likewise, to visualise these differences in vertical composition between epiphyte and climber taxa, I carried out a non-metric multidimensional scaling (NMDS) analysis. The NMDS used the same Bray-Curtis distance matrix used in the PERMANOVA. NMDS was then calculated from this distance matrix (using the R function 'metaMDS' in the 'vegan' package), fitting the points to two dimensions. Species were then coloured by the five habit categories of arboreal plant on the NMDS ordination plot.

To also assess any potential differences in vertical profile between epiphytes with different dispersal syndromes, I repeated both the PERMANOVA and NMDS. For these analyses, the climbers were removed from the occurrence matrix, as climbers do not disperse directly onto the tree fern but climb onto it from the forest floor. The two groupings of the PERMANOVA were now wind-dispersed and bird-dispersed epiphyte species. These same two groups were plotted onto the NMDS ordination plot.

Software and Packages

All analyses were carried out in R version 4.0.3 (R Core Team, 2020) using the R studio interface v.1.1.423 (RStudio Team, 2016). The packages 'openxlsx' v.4.2.2 (Schauberger and Walker, 2020), 'ggplot2' v.3.3.2 (Wickham, 2016), 'reshape2' v.1.4.4 (Wickham, 2007), 'gridExtra' v. 2.3 (Auguie, 2017), 'vegan' v. 2.5-6 (Oksanen et al., 2019) and 'bipartite' v.2.15 (Dormann et al., 2008) were used in scripts importing, analysing, and plotting the data.

Results

I surveyed 170 tree ferns, which had 50 species of vascular plant growing dependently upon them (analytically these were treated as 49 species with the merging of the two *Tmesipteris* sp.). Of these, 6 species were soil-rooted climbers, including 3 eudicot lianas, 1 climbing monocot, and 2 climbing ferns. 8 of the recorded species were filmy ferns (Hymenophyllaceae) which were mostly obligate epiphytes. 9 other taxa were obligate epiphytes (including an oft lithophytic species), consisting of 1 lycophyte, 6 ferns (including *Tmesipteris* sp.) and 2 monocots in the genus *Astelia*. A further 7 fern species were recorded as in the 'non-woody facultative and accidental epiphytes' group. Woody epiphytes, including 11 accidental epiphytes, 3 facultative epiphytes, 4 facultative hemiepiphytes and one obligate hemiepiphyte, totalled 19 species – many in low numbers.

Of the overall 49 taxa recorded, 37 occurred on ≥3 tree ferns (and were therefore included in co-occurrence and nestedness analyses), whilst only 24 taxa occurred on ≥8 tree ferns (and thus were included in the vertical gradient analyses). Each tree fern individual hosted between 1 and 15 epiphyte and climber species. Tree fern individuals also varied between 1.6 and 7.6 metres tall.

Epiphyte richness was significantly positively related to tree fern height ($p = 1.45 \times 10^{-14}$; Fig. 3.2b). Despite the relatively low richness of climbers, climber richness was also positively linked to tree fern height ($p = 0.0016$; Fig. 3.2c). Although, the richness relationship for climbers has a larger standard error (0.045) than that for epiphytes (0.029). Given epiphytes and climbers have a similar size-richness relationships, this is reflected in the accumulation of overall arboreal richness with tree fern height ($p = 9.3 \times 10^{-13}$; Fig. 3.2a). As well as increasing with tree fern size, arboreal richness also increases down the vertical profile of the tree fern to the oldest quartile at the base (Fig. 3.3a), with a significant difference in richness between vertical quartiles ($p < 2.2 \times 10^{-16}$). Epiphyte richness is significantly different between the vertical quartiles of the tree fern ($p < 2.2 \times 10^{-16}$), with the lowest quartile – Q1 – having a much higher mean richness (2.46) than Q4 (0.60; Fig. 3.3b). Richness is also significantly different between vertical quartiles for climbers ($p < 2.2 \times 10^{-16}$; Fig. 3.3c), and mean

richness is also higher in Q1 (1.82) than Q4 (0.76), though the difference in richness between the base and the top of the tree fern is not as great as that seen in epiphytes (Fig. 3.3).

The overall epiphyte and climber meta-community had a C-score consistent with chance expectations from the null model (Fig. 3.4a; p = 0.761). Each epiphyte sub-compartment of the matrix also had C-scores consistent with chance randomisation within the null model constraints (Figs. 3.4 c-f; filmy ferns – p = 0.287; corrected p = 0.761 for each non-woody obligate epiphytes, non-woody fac.-acc. epiphytes, and woody epiphytes – NB: Hochberg corrections lead to multiple p-values being the same). The C-score for the climber sub-compartment of the matrix was also consistent with null expectations following Hochberg correction, although had a marginally lower C-score than chance expectations prior to this adjustment (Fig. 3.4b; corrected p = 0.200, raw p = 0.033).

The overall epiphyte and climber meta-community matrix had a NODF value consistent with chance expectations of the null model (Fig. 3.5a; p = 0.875). The filmy fern matrix sub-compartment was less nested than null expectations (Fig. 3.5c; p = 0.0072). Climbers (Fig. 3.5b; p = 0.875) and the other epiphyte matrix sub-compartments were as nested as chance expectations (Figs. 3.5 d-f; p = 0.875 for both non-woody obligate epiphytes and woody epiphytes; p = 0.831 for non-woody fac.-acc. epiphytes), with observed NODF values matching expectations.

The five different habit categories of epiphytes and climbers had significantly different vertical profiles (Fig. 3.6a; PERMANOVA: Habit – F = 4.82, R^2 = 0.50, p = 10^{-4}). Species' vertical profiles ordinated to two dimensions with a low stress score for the NMDS (0.134), indicating a robust 2D representation of the data. Climbers, filmy ferns and accidental epiphytes were most likely to occur in the lowest quartile (Q1) and were steadily less likely to occur higher up, with facultative epiphytes absent in Q4 (Fig. 3.7 a, b, d). Obligate epiphytes were most common in Q2 and Q3 (Fig. 3.7 c), whilst woody epiphytes were most common in Q1 and Q4 (Fig. 3.7 e) – making woody epiphytes the only group where Q4 was not the quartile with lowest occurrence (Fig. 3.7).

Wind-dispersed and bird-dispersed epiphytes had significantly different vertical profiles (Fig. 3.5b; PERMANOVA: Dispersal Syndrome – $F = 6.00$, $R^2 = 0.26$, $p = 0.0034$). Epiphyte species' vertical profiles also ordinated to two dimensions with a low stress score for the NMDS (0.112). Wind-dispersed epiphytes occurred most commonly in the lowest quartiles of the tree fern (Fig. 3.8 a), compared to bird-dispersed epiphytes which had more or less equiprobable occurrences across all four vertical quartiles (Fig. 3.8 b).

Discussion

I demonstrate a pattern of species accumulation with tree fern height consistent with previously reported patterns (Laube and Zotz, 2006a, Einzmann and Zotz, 2017). However, epiphytes and climbers did not differ appreciably in their species accumulation patterns (question 1). Likewise, both epiphytes and climbers accumulate on the lower portions of the tree fern compared to the younger portions higher up the tree fern (question 2). The epiphyte and climber metacommunity demonstrates no evidence of either positive or negative co-occurrence patterns, and neither do the key sub-compartments of the matrix (question 3). Similarly, there is only limited evidence of differences in nestedness to chance expectations, with the overall matrix and four key sub-compartments matching the null distribution (question 4) – although the filmy ferns are less nested than chance expectations. Epiphytes and climbers, as well as different types of epiphytes, showed differences in their vertical profile, as did epiphytes of different dispersal syndromes (question 5). These patterns allow me to clearly elucidate key structuring processes, or lack thereof for some aspects, in the epiphyte and climber single-host metacommunity on the tree fern *Cyathea dealbata*.

The Species Accumulation Model of Succession

My findings of species accumulation are in keeping with Woods' (2017) accumulation model of primary succession, when applied at the scale of whole phorophyte individuals. However, my within zone results are slightly divergent from Woods (2017), as within zone patterns of succession

do not follow a replacement model. Each portion of the tree fern appears to follow an accumulation model, with richness related to relative age of that section. However this discrepancy is easy to reconcile, as tree fern hosts lack the architectural complexity of angiosperm host trees, with the entire subcanopy tree fern equivalent to the lowest two Johansson zones in a canopy tree (*sensu* Johansson, 1974). Thus, tree ferns, as more structurally simple hosts, are well described by the species accumulation model of succession at the level of the whole host, but lack the within crown species replacement model of succession due to the paucity of habitat variation. It will be interesting to see if other structurally simple hosts such as palms, or other tree fern taxa, follow a similar modification of Woods' (2017) model – although the results of Zotz and Vollrath (2003) indicate this may be the case.

Gleasonian Metacommunity Structure

Our results match previous results which indicate that single-host epiphyte metacommunities lack structure and match chance expectations for both co-occurrence and nestedness (Burns, 2008, Burns and Zotz, 2010), as do most single-host metacommunities for lianas (Blick and Burns, 2011). These somewhat random patterns of metacommunity assembly support Henry Gleason's 'individualistic concept of plant associations' (Gleason, 1926) and the importance of stochasticity in structuring epiphyte and climber assemblages. An alternate modelling approach has yielded some differences in community structure from neutral models (Janzen et al., 2020); however the key difference from neutral was speciation – a process largely beyond the consideration of my network model. Crucially, the results of Janzen et al. (2020) are also consistent within a Gleasonian view, given Gleason's focus on the importance of the role of 'environmental selection' on each species.

A key corollary of this Gleasonian view of single-host metacommunity assembly is that species interactions seem to, at least in *C. dealbata* hosts, play a limited role in structuring the community. Indeed, there is limited empirical evidence documenting epiphyte-epiphyte and

epiphyte-liana interactions (Zotz, 2016b), including facilitation interactions (Francisco et al., 2018b).

Facilitation, in particular, might be expected given the stress-gradient hypothesis (Bertness and

Callaway, 1994, Callaway and Walker, 1997, Maestre et al., 2009). However, tree ferns may

represent one of the least water-stressed phorophyte types (Mehltreter et al., 2005).

The notable exception to this Gleasonian metacommunity structure is that of the filmy ferns,

which show a less nested structure than by chance expectations. Whether this result represents a

statistical artefact or is due to the unique ecophysiology of the Hymenophyllacaeae (Dubuisson et

al., 2003, Parra et al., 2009) remains to be seen. A qualitative assessment of the metacommunity

matrix indicates a possibility that the filmy ferns may show slight compartmentalisation (Appendix

4). Two common species (*Hymenophyllum flabellatum* and *H. revolutum*) often co-occur, whilst the

two commonest species (*Trichomanes venosum* and *H. demissum*) often occur in the absence of any

other filmy ferns, and the rarest species happened to almost never co-occur with *T. venosum*.

Almeida-Neto et al. (2007) demonstrate that poorly filled matrices with high turnover can result in

less nestedness than chance expectation as a statistical artefact, without a particular ecological

process driving this result. However, in this case (at 0.2), the filmy fern subcompartment has the

median matrix fill of the five subcompartments so is the not worst matrix subcompartment in terms

of fill.

Metacommunity and Network Scales

Epiphyte host species networks are consistently more structured (e.g. Sáyago et al., 2013)

than single-host metacommunity networks (Burns, 2008). Even in the few cases where both have

been analysed in the same system, the host species based networks show clearer deterministic

structure (Burns and Zotz, 2010, Blick and Burns, 2011). These different network scales show distinct

patterns, and these clearly reflect different biological relationships. Epiphyte-host species networks

are determined by epiphyte-host interactions (Sáyago et al., 2013, Cortés-Anzúres et al., 2020).

Whereas, single-host metacommunities by definition ignore the effect of host species. Thus, these

metacommunity matrices are more reflective of patterning or interactions between epiphytic or climbing taxa – this could be either positive/negative co-occurrences due to abiotic requirements, or direct interactions such as facilitation or competition. As yet, however, there is little evidence for these patterns when excluding the role of host species.

Vertical Community Structure

The indication that different habits of epiphyte and climber have differences in vertical profile seems somewhat counter to the overall pattern of species accumulation. Even though tree ferns only reach the subcanopy of the forest, there is still a substantial vertical gradient in abiotic conditions (Petter et al., 2016). Therefore, given how sensitive epiphytes are to microhabitat conditions (Woods et al., 2015), this gradient in abiotic conditions is likely to affect establishment. Indeed, the regeneration niche of different epiphyte species has been shown to vary vertically (Wagner et al., 2013). Woody epiphytes, especially the bird dispersed species, are the group most commonly occurring in the highest portion of the tree fern, potentially due to being better able to resist desiccation in the more exposed drier conditions further up towards the canopy. Filmy ferns, on the other hand, are especially desiccation sensitive and so have been shown to be more prevalent closer to the forest floor (Zotz and Büche, 2000, Saldaña et al., 2014).

The Role of Dispersal

Beyond the broad importance of dispersal for epiphytes and climbers to colonise novel host trees, dispersal syndrome appears to play a role in the vertical structuring the community. Brock has recently demonstrated that amongst woody facultative and accidental epiphytes, endozoochorous species have on average a higher vertical distribution than anemochorous species (Unpublished conference talk - Brock, 2018). Given my results (Fig. 3.7), it seems that this difference in vertical profile between wind-dispersed and bird-dispersed epiphytes is broader than just the woody taxa. Given the age gradient of the tree fern, the declining occurrence rate up the tree fern in wind-

dispersed epiphytes matches the expectation from species accumulation models. The vertical profile of bird-dispersed epiphytes contravenes expectations. Birds may perch or forage on the tops of the tree ferns skewing their distribution towards the tops of the tree ferns. Or as suggested earlier, the larger seeds may provide greater energetic resources early in establishment. However, whether dispersal syndrome plays a role in spatial structuring of epiphytes on other types of phorophyte remains an open question.

The high stochasticity and largely random matrix structure in this study may also be somewhat reflective of dispersal limitation in epiphytes at a community-wide scale (as indicated by Janzen et al., 2020). Indeed, empirical evidence for dispersal limitation has been shown in multiple epiphyte taxa (Mondragón and Calvo-Irabien, 2006, Cascante-Marín et al., 2009, Victoriano-Romero et al., 2017). Although, dispersal limitation does not appear to be strong enough to lead to a distribution that is more aggregated or segregated than by chance, with the possible exception of the aberrant low nestedness result of the filmy ferns.

Conclusion

In conclusion, I demonstrate that both epiphyte and climber richness increase with tree fern size and increase from the younger to the older portions of the tree fern. These results are consistent with the species accumulation model of succession in epiphytes. Furthermore, the epiphyte and climber matrix, as well as most subcompartments, have co-occurrence and nestedness levels consistent with null expectations. This indicates that within a single host species, the epiphyte and climber metacommunity is stochastically assembled. Different epiphyte and climber groups do, however, tend to colonise different portions of *C. dealbata* caudices at different rates. Wind and bird dispersed epiphytes also have very different vertical profiles. Taken together, these results indicate horizontal patterns of epiphytes and climbers on *C. dealbata* hosts are largely random, whilst vertical patterning differs between habit groups and dispersal syndromes, despite an overall pattern of species accumulation over time.
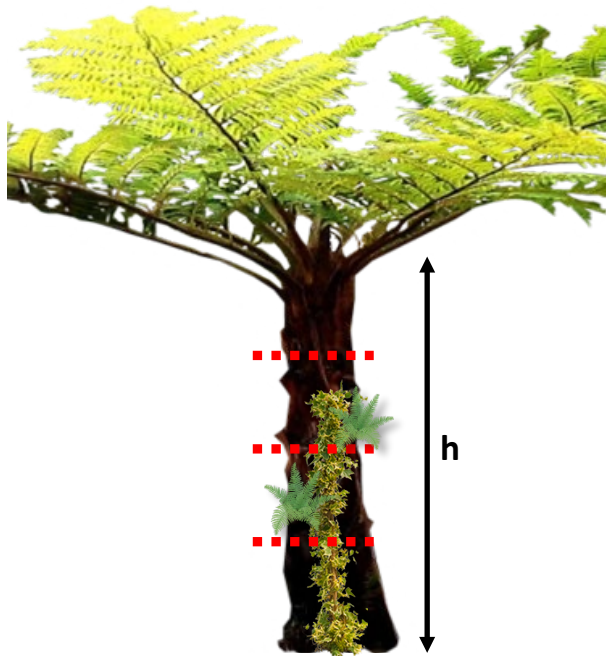
Figure 3.1 – A graphic representation of the field study design for chapter 3. This shows the height (h) of the tree fern measured to the crown, with the 4 vertical quartiles of the tree fern (as divided by the dotted red lines) relative to the overall height. The stylised epiphyte species is present in in quartiles 2 and 3 (Q2 + Q3), while the stylised climber is present in quartiles 1 to 3 (Q1-3) on the tree fern.
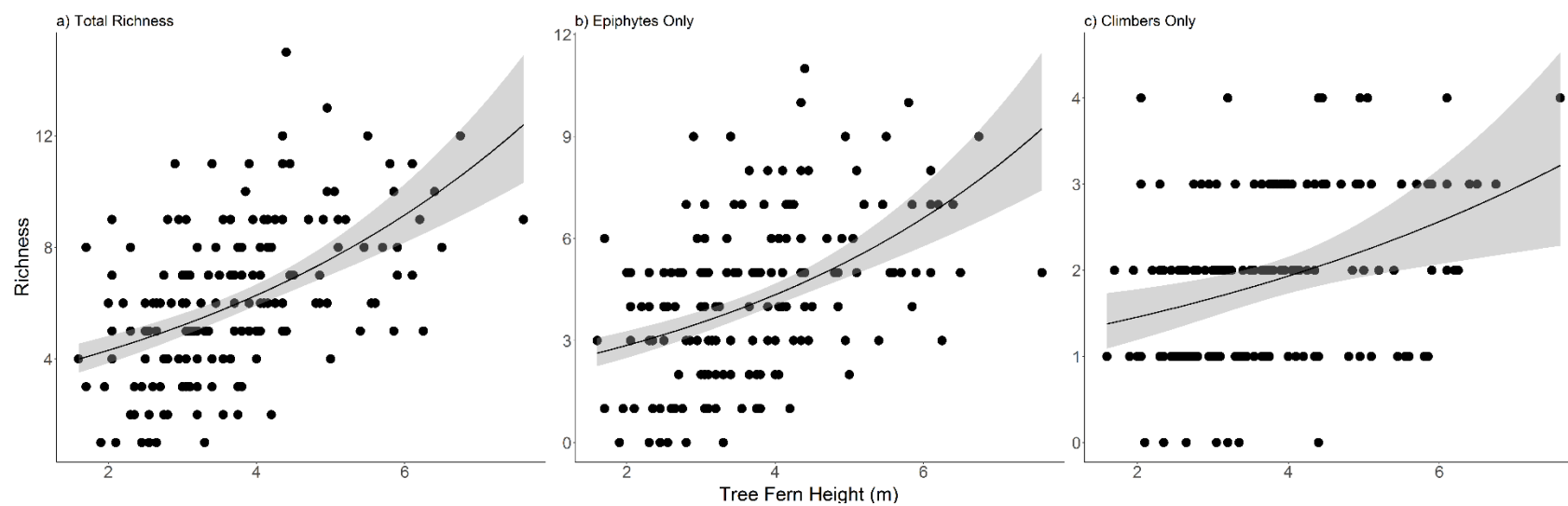
Figure 3.2 – Poisson linear models of how tree fern height predicts **a)** total arboreal richness, **b)** epiphyte richness, and **c)** climber richness, each with a Poisson regression line with standard error.
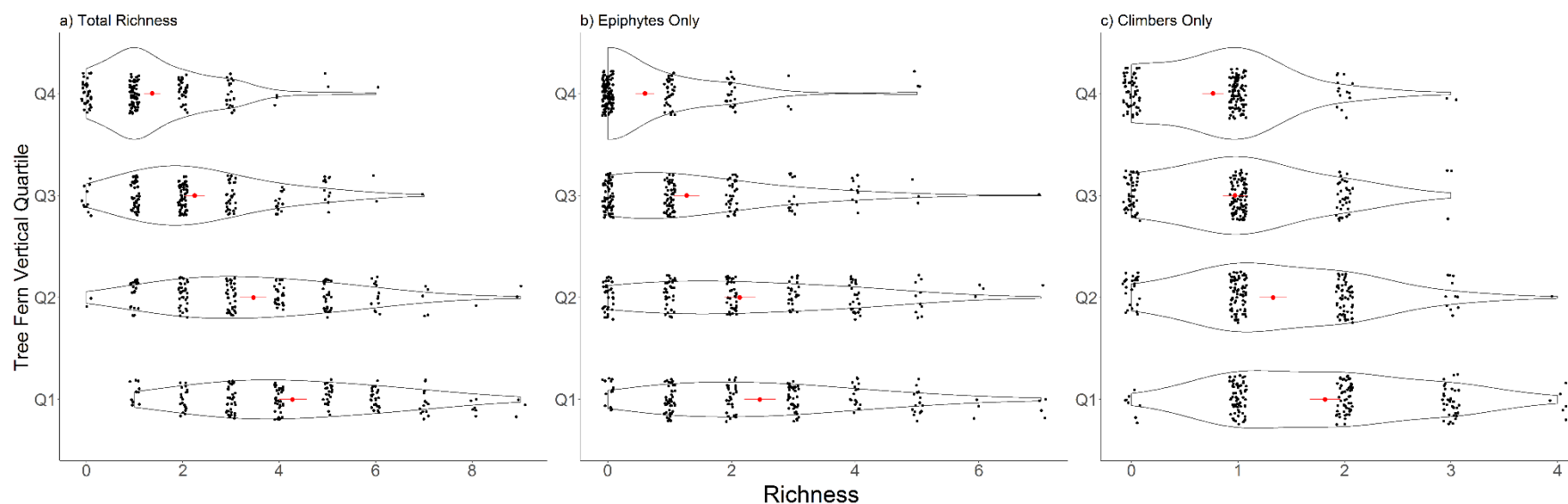
Figure 3.3 – Dot and violin plots of richness by vertical quartile, plot **a)** showing total richness, **b)** epiphyte richness, and **c)** climber richness. For each plot, Q1 represents the lowest portion of the tree fern, whilst Q4 the highest portion. The axes have been flipped such that the dependent variable – vertical quartile – is on the y-axis to match the vertical stratification of the tree fern itself (as illustrated in Fig. 3.1). The red point represents the mean and range bars the 95% confidence interval (calculated by two times the standard error).
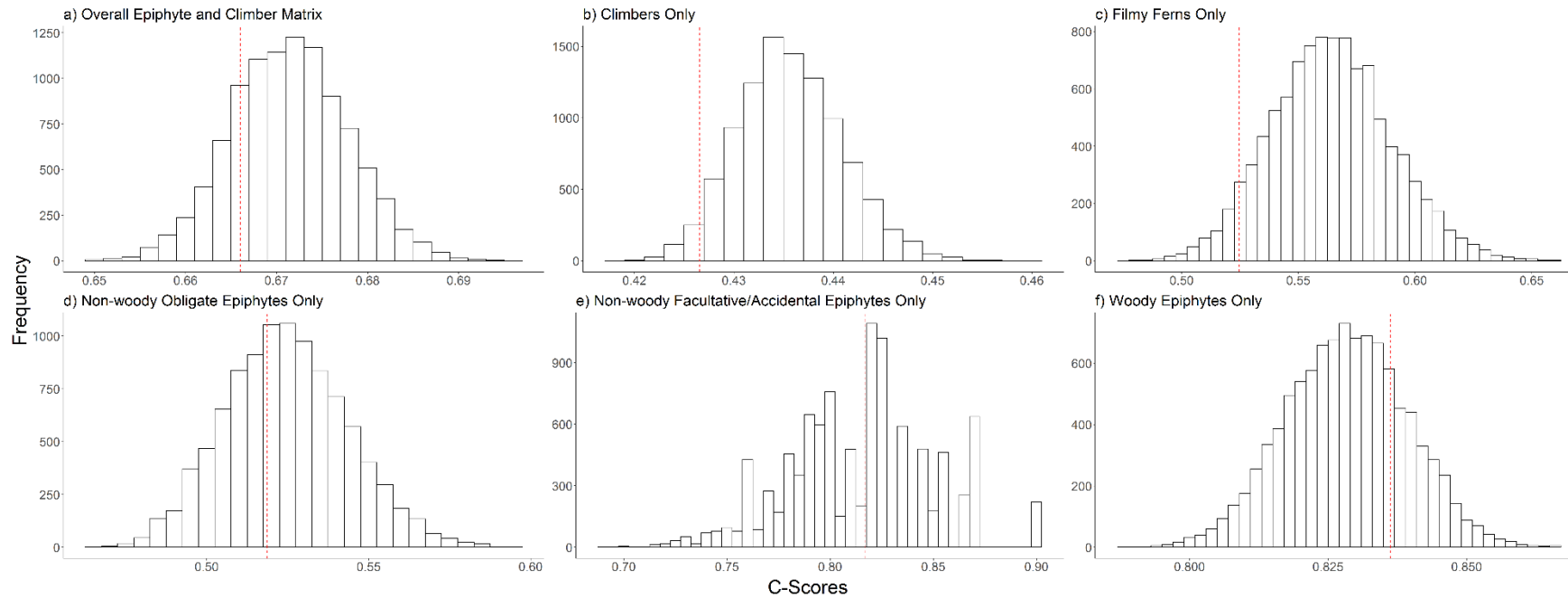
Figure 3.4 – Distributions of expected C-scores from the null models for **a)** the overall matrix, **b)** the climber sub-compartment, **c)** the filmy ferns, **d)** the non-woody obligate epiphytes, **e)** the non-woody facultative-accidental epiphytes, and **f)** the woody epiphytes. On each plot, the observed C-scores is marked with a red dotted line.
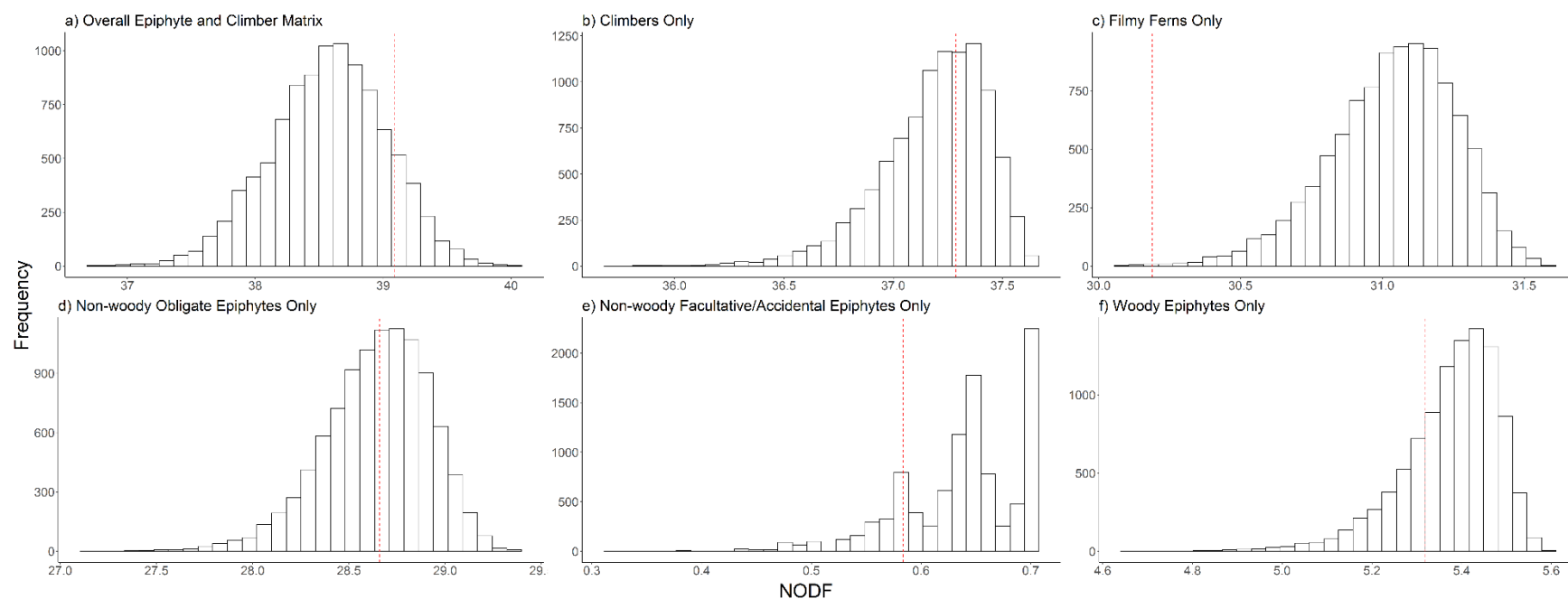
Figure 3.5 – Distributions of expected nestedness (NODF) from the null models for **a)** the overall matrix, **b)** the climbers only, **c)** the filmy ferns, **d)** the non-woody obligate epiphytes, **e)** the non-woody facultative-accidental epiphytes, and **f)** the woody epiphytes. On each plot, the observed NODF value is marked with a red dotted line.
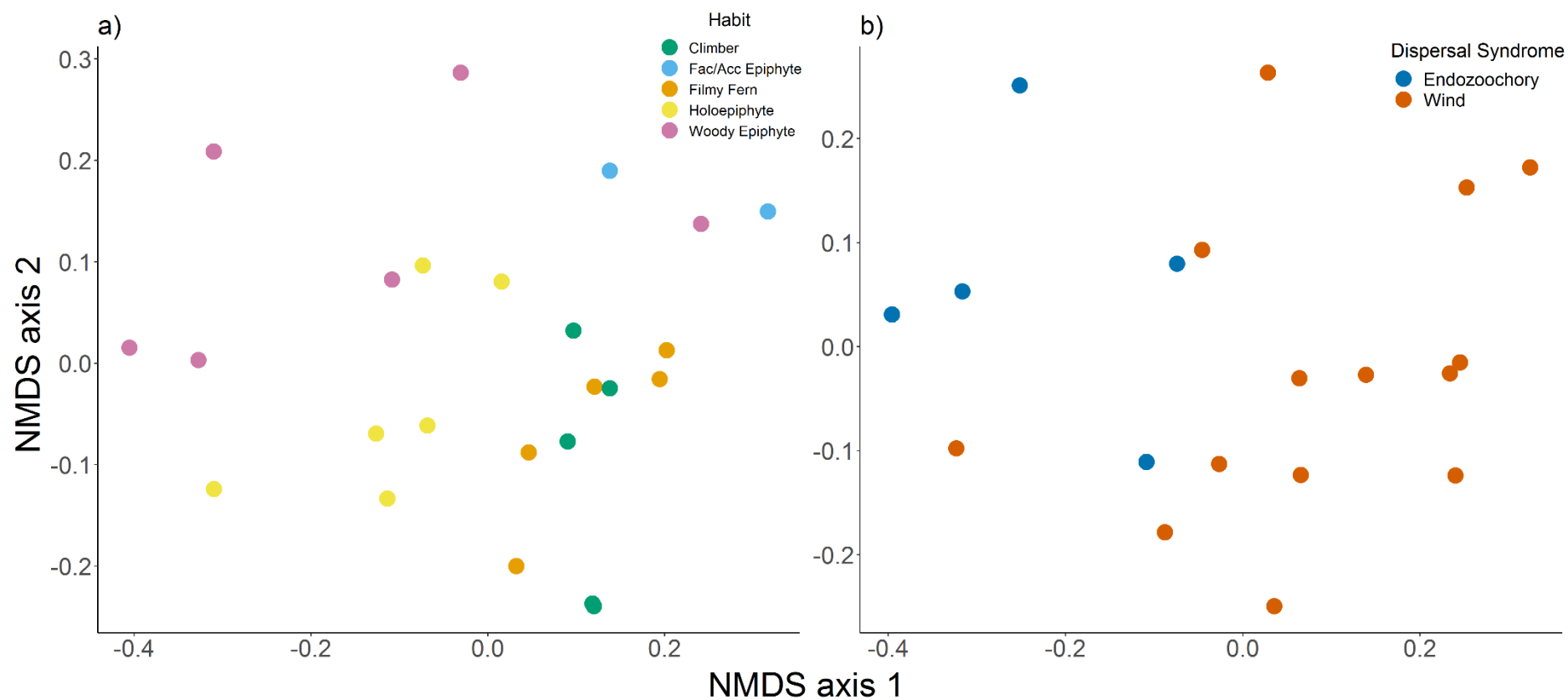
Figure 3.6 – A non-metric multidimensional scaling (NMDS) ordination based on the vertical profile of the each epiphyte and climber species. Coloured by **a)** their habit and **b)** their dispersal syndrome (for epiphytes only).
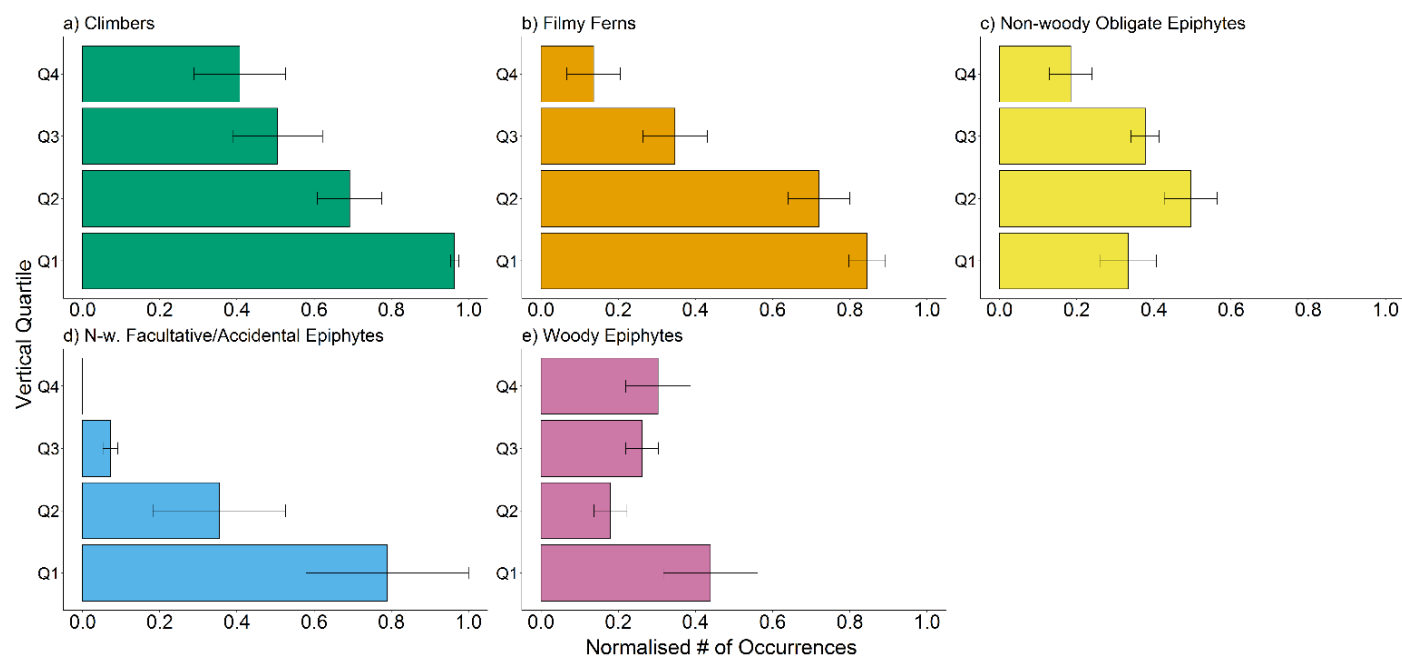
Figure 3.7 – Bar graphs showing the mean and standard error of the normalised number of occurrences by vertical quartile. Species were grouped by habit with overall mean in that habit plotted – with **a)** Climbers, **b)** Filmy Ferns, **c)** Non-woody obligate epiphytes, **d)** Non-woody facultative and accidental epiphytes, and **e)** woody epiphytes.
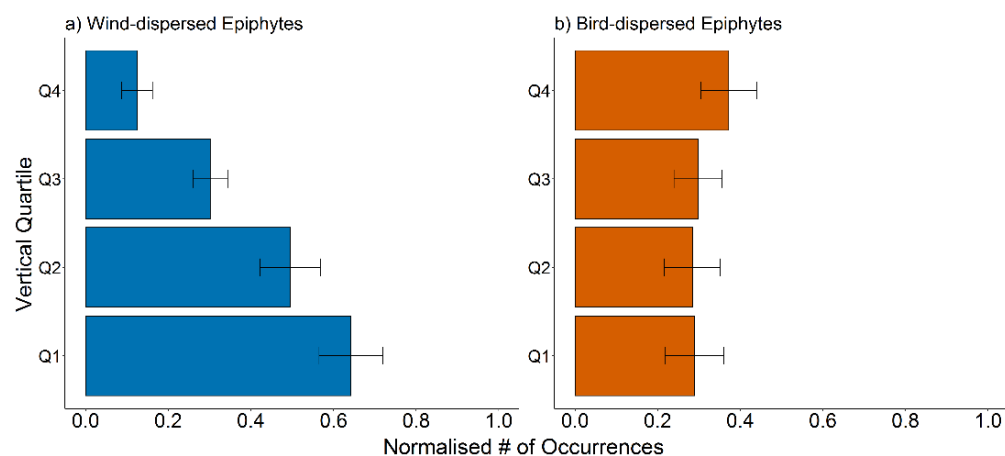
Figure 3.8 – Bar graphs showing the between species mean and standard error of the normalised number of occurrences of epiphytes by vertical quartile.

Species were grouped by dispersal syndrome, with **a)** showing the wind-dispersed epiphytes, and **b)** showing the bird-dispersed epiphytes.

Chapter 4 – A keystone fungus radically alters the structure

of a New Zealand epiphyte community

Abstract

Epiphyte communities typically show only weak host specificity, with epiphytes utilising a broad range of host species. Community-wide strongly host specific distributions do not occur in epiphytes. Similarly, amensalist interactions are underreported in the ecological literature, with any interactions between epiphytic taxa broadly unreported. Here I characterise an unusual forest system (New Zealand montane beech forest) where an amensalist sooty mould excludes other epiphytes and thereby radically alters the structure of the epiphyte community. I surveyed the low-trunk epiphyte assemblages on the three co-dominant canopy beech species, also recording the percentage cover of sooty mould; allowing me to characterise the interaction between the sooty mould cover, host identity and epiphyte richness. I show that *Lophozonia menziesii* is the only beech completely lacking sooty mould cover and has a significantly higher epiphyte richness than the other beech species, with sooty mould cover explaining differences each host species' epiphyte richness. The other two host species also lack a host size-epiphyte richness relationship and show an altered epiphyte species composition. The results are consistent with the sooty mould amensally (or asymmetrically competitively) excluding other epiphytes. I conclude that the major effect of the sooty mould on the ecological community (along with the beech scale insects) may act as a keystone species complex.

Introduction

Understanding how epiphyte communities are structured is one of the key outstanding avenues of study in the field of epiphyte ecology (Zotz, 2016b, Janzen et al., 2020). The primary avenue of tackling this problem has been from the perspective of host specificity, which has developed an increasingly extensive literature (Wagner et al., 2015). Host specificity in epiphyte-host interactions has long been hypothesised to provide spatial structure to epiphyte communities (Schimper, 1888, Zotz, 2016b). Epiphyte species almost never show strict host specificity to a single host species (Migenis and Ackerman, 1993), but tend to utilise a broad range of hosts (Wagner et al., 2015). However, within this broad pool of host species, epiphyte species often occur disproportionately on certain hosts (Callaway et al., 2002, Vergara-Torres et al., 2010). Then across whole epiphyte communities, the exact host trait-matching and degrees of specificity varies between epiphyte taxa to build community-level patterns (Wagner et al., 2021). Certain host characters, such as bark texture (Wyse and Burns, 2011), crown architecture (Aguirre et al., 2010) and phenology (Einzmann et al., 2015), can mechanistically explain these patterns to some degree. Clear and consistent taxonomic differences in host specificity have not been properly elucidated, and they are often not pronounced when present. However, non-vascular epiphytes (chiefly lichens and bryophytes) appear to show especially low host specificity (Schmitt and Slack, 1990). They also have a different spatial community structure more generally (Affeld et al., 2008) and have distributions more strongly determined by microhabitat conditions (Holz et al., 2002) than by host identity. Overall, a broad pattern of "neither host-specific nor random" (Laube and Zotz, 2006b) appears to hold across most epiphyte communities (both vascular and non-vascular) from the tropics to the temperate regions. Certainly, strong community-wide specialisation to a particular host species has not been documented (although see discussion of "good" and "bad" hosts in Toledo-Aceves et al., 2017).

Something which can fundamentally determine community structure in certain ecosystems is the role of dominant (Power et al., 1996) or keystone (Paine, 1969) species. Dominant species

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have a high abundance or biomass and thus exert a significant impact on community structure (Power et al., 1996), whilst keystone species lack this high abundance/biomass yet have a disproportionately strong impact on community structure. Many examples of dominant or keystone species, especially pertaining to the regulation of trophic interactions (e.g. Hebblewhite et al., 2005) and by means of ecosystem engineering (Jones et al., 1994), have been documented – despite growing controversy of overuse/misuse of the keystone concept (Cottee-Jones and Whittaker, 2012). However, the discussion of dominant and keystone species has not been considered with respect to epiphyte communities. In the most basic sense canopy trees act as 'dominant species' collectively in the way they create habitat for the entire epiphyte meta-community. Similarly, canopy emergent trees have been previously considered 'keystone ecological structures' (Lindenmayer et al., 2014). The only suggestion of 'keystone epiphytes' comes from tank bromeliads (Talaga et al., 2015, Svensk et al., 2020), which act as ecosystem engineers by housing aquatic invertebrate communities in their phytotelmata (Kitching, 2001). Epiphytes acting as a keystone for the other epiphytes have not been documented. More broadly, epiphyte-epiphyte interactions in general have not been adequately documented (Zotz, 2016b), and are thus described by some as failing to meet the true definition of an ecological community (Mendieta-Leiva and Zotz, 2015) – although this point remains up for debate.

Amensalism (first coined by Haskell, 1949) is defined as any interaction where one organism is harmed or negatively impacted and the other is unaffected (Brewer, 1994, p. 246), it can be thought of as a 0/- interaction. Amongst the extensive research into ecological interactions, amensalist interactions have been largely ignored (Townsend et al., 2002). Additionally, amensalism may be more important than previously thought in stabilising community structure (Dodds, 1997, Mougi, 2016). However, amensalist interactions have not been shown in the context of having the disproportionate effects of a keystone species or interaction. Considering amensalism in an epiphyte context can also highlight the breadth of ecological interactions that may have been overlooked in epiphyte communities.

Sooty moulds are a diverse group of fungi with a consistent gross morphology of forming black colonies of mycelia (Chomnunti et al., 2014). They grow in some New Zealand beech forests more profusely than anywhere else in the world (Hughes, 1972, 1976). These heterotrophic organisms subsist upon honeydew secretions (Hughes, 1976) and it is the vast honeydew secretions of beech scale insects (*Ultracoelostoma* sp.) that allow the profusion of these organisms in beech forest (Beggs et al., 2005). Often considered epiphytes themselves (e.g. Crous et al., 2009), sooty moulds appear to negatively impact other groups of epiphytic organisms (e.g. lichens - see Buckley, 2011). The abundance of beech scale insect and the prevalence of sooty moulds are not consistent between beech species, being rare or absent from silver beech [*Lophozonia menziesii*] (Wardle, 1984, Dawes & Burns pers. obs.). However, the details of how the sooty mould structures epiphyte communities, especially with respect to the host specificity, has not yet been fully elucidated. To what extent this case represents an amensalist keystone interaction for the epiphyte community is also a crucial discussion point of this study.

Therefore, I ask the following research questions, in order to further elucidate the interaction between sooty moulds and epiphyte communities:

(1) Does sooty mould cover vary between host tree species?

(2) Does epiphyte richness vary between host tree species?

(3) Therefore, does sooty mould cover determine epiphyte richness by mediating the host species-epiphyte richness relationship?

(4) Does epiphyte composition vary between host species?

(5) Does the typical host size-epiphyte richness relationship also vary between host species?

Methods

Study Site

My study was carried out on the northern shores of Lake Rotoiti (41° 48' S, 172° 50' E), in Nelson Lakes National Park, South Island, New Zealand (Fig. 4.1a). The lake shore is c.635m above

sea level and situated in a glacially-formed valley. The vegetation consists of montane beech forest

dominated by three canopy tree species – silver beech (*Lophozonia menziesii*; Fig. 4.1b), mountain

beech (*Fuscospora cliffortioides*; Fig. 4.1c) and red beech (*Fuscospora fusca*; Fig. 4.1d). Nomenclature

for the three host beech species follows Heenan and Smissen (2013). The site has a high prevalence

of sooty beech scale insects (*Ultracoelostoma* spp.) infecting the red and mountain beech – the

authors did not observe a single scale insect on silver beech (although it supposedly may occur in

some instances). Extensive sooty mould communities thrive on the honeydew excreted by these

insects (Fig. 4.1e). Whilst morphologically and ecologically uniform, sooty moulds at the site have

been shown to be phylogenetically diverse (Dhami et al., 2013). A species rich community of

bryophyte and lichen epiphytes occurs on the site, including a conspicuous element of pendent

macrolichens (Simpson, 1977, Galloway and Simpson, 1978). By contrast, the vascular epiphyte

communities at the site are somewhat depauperate by New Zealand standards (e.g. Burns and

Dawson, 2005), with only three common epiphytic fern species present (*Asplenium flaccidum*,

Notogrammitis billardierei and *Hymenophyllum multifidum*) – although this is more typical of

epiphyte communities in other temperate regions (Zotz, 2005). For additional descriptions of the

forest at the site see Taylor and Burns (2016) and for description of scale insects at the site see

Wardhaugh and Didham (2005, 2006).

Taxonomic Approach, Scope and Limitations

Given the diverse range of taxa that occur epiphytically at the site, and the taxonomic

difficulties associated with their identification, certain restrictions on taxonomic scope were applied

to my study. Firstly, of the major lichen morphologies, crustose and leprose lichens were excluded

given the difficulty in accurately identifying these species in the field and the typical requirement for

light microscopy, chemical spot-testing and thin layer chromatography (as in for e.g. Ellis and

Coppins, 2007). For similar reasons, epiphytic algae were also deemed outside my remit. Given my

focus is primarily on photosynthetic epiphytes, and non-lichenised fungi may be saprophytic on the

host trees bark, these were also excluded (although these were found to be rare on living trees anyway). Liverworts represent a lineage of plants that are especially difficult to identify without microscopy and significant specialist expertise – hence I took an approach of estimating the morphospecies richness of these organisms in the field but did not identify them to 'true' scientific taxa. Ferns with only three common species in different families were always identified to species. Mosses and macrolichens (foliose and fruticose lichens) were identified to genus and, where obvious and distinct morphospecies were present in a genus, to species. Some exceptions were made to accommodate the lead researcher's inexperience with these taxa, for example so-called 'jelly lichens' were recorded as belonging to '*Collema*/*Leptogium* sp.', which was justified given this group occurred at low abundances (typically 1-2 individuals per host tree) and usually require microscopy to identify to either genus. Additionally, where lichen species were borderline in their morphological grouping, such as some squamulose lichens (e.g. *Psoroma* sp.), I chose to be inclusive as far as possible. However, in all cases conservatism was applied to all taxonomic decisions to avoid inaccuracy in the dataset (e.g. classify as *Pannaria* sp. rather than to potentially misidentify to species). For full details of taxonomic and surveying decisions see Appendix 5. In summary, my survey encompassed ferns, mosses, foliose and fruticose lichens, and an estimate of liverwort morphospecies richness, whilst excluding crustose and leprose lichens, epiphytic algae and non-lichenised fungi. Although this taxonomic approach has some potential limitations, my dataset should still be scientifically robust and offer a strong starting point for bryologists and lichenologists to reappraise and build upon this work in the future. For lichen identification I primarily used 'New Zealand's Foliose Lichens: An Illustrated Key' (Malcolm et al., 2011) and 'Lichens of New Zealand: An Introductory Illustrated Guide' (Knight, 2014), whilst for mosses I primarily used 'New Zealand Mosses - An Illustrated Key' (Malcolm et al., n.d.). Nomenclature was checked for consistency against Schönberger et al. (2019b) for ferns, Gibb et al. (2020) for mosses and Galloway (2007) for lichens.

Field Surveying

Field surveying was completed in September 2020 under Department of Conservation (DOC) permit number '83759-FLO'. I surveyed 60 trees of each of the three canopy dominant tree species on/near trails to the east of Lake Rotoiti's Kerr Bay, restricted to < c. 20m elevation above the lake shore to avoid a confounding effect of an elevational gradient. Surveying was restricted to potential host trees with a diameter at breast height (DBH; at c. 1.3m high) above 10cm, thus excluding saplings. For each surveyed tree, the host species identity, DBH (in centimetres) and an estimate of sooty mould cover were recorded. Sooty mould cover on the low trunk was estimated by recording the presence/absence of sooty mould at 10 points spaced at 10cm intervals vertically downward from breast height on 4 different sides of the tree. The count of 'present' sooty mould (out of 40) was then multiplied by 2.5 to get an estimate of percentage cover. Finally, a survey of all low-trunk epiphytes was carried out. All epiphytic individuals found from the base of the tree to c. 2.5 metres high were included, except any individuals occurring on lateral branches (as these were absent at this height for most trees). I recorded the species, genus or morphospecies of each epiphytic taxon within the taxonomic scope (as defined above), to a consistent degree for each taxon, and repeated on each host tree. Hence, the survey yielded presence-absence data for each taxon on each host individual. During surveying, specimens were collected of bryophyte and lichen taxa for identification outside of the field where necessary – this was done as sparingly as possible and in compliance with DOC permit-holder requirements.

Data Analyses

In order to quantify the differences in sooty mould cover between host tree species I carried out an analysis-of-variance (ANOVA) of sooty mould cover with each host species as a group. Similarly, an ANOVA of total epiphyte richness between the three host species was carried out. For both ANOVAs, post-hoc Tukey HSD pairwise tests were also carried out between host species. To more directly assess the relationship between sooty mould cover and epiphyte richness, I also

carried out a linear model assessing how both mould cover and host species affect epiphyte

richness, including a possible interaction term. For all analyses of species richness, I analysed the

data both including and excluding my estimates of liverwort morphotaxon richness. As these did not

differ appreciably, the analyses containing liverwort morphotaxon richness are reported herein.

To assess whether the three host species also host a different composition of epiphyte

species, I used non-metric multi-dimensional scaling (NMDS) to visualise the dispersion of individuals

in ordination space. I used a presence-absence matrix of epiphyte species on host individuals as raw

data. Host individuals hosting two or fewer epiphyte taxa were removed from the matrix for this

analysis to eliminate individuals with a very limited epiphyte community. Likewise, the handful of

epiphytes not identified to a consistent morphotaxon were also removed, as well as the liverwort

morphotaxa richness estimate. I then calculated a Bray-Curtis dissimilarity metric to construct the

distance matrix (note that a Bray-Curtis metric with presence-absence data is also equivalent to a

Sorenson-Dice metric). The main NMDS analysis fitted the points to two dimensions, although an

additional NMDS was run which fitted the points to three dimensions to assess the effect on the

stress value. In addition to the NMDS, I carried out a permutational multivariate analysis of variance

(PERMANOVA) using the 'adonis' R function (from the 'vegan' package), to test for differences in

group centroids between the three host species. I also used the R function 'betadisper' (also from

'vegan') to test for differences in mean distance to the centroid between the three host species. This

analysis allowed me to assess the degree of variability of species composition in each of the three

host species. Note that both of these analyses use the raw Bray-Curtis dissimilarity matrix, as

opposed to the NMDS output.

To test if typical host-size-epiphyte-richness relationships were impacted by sooty mould, I

calculated linear models of DBH against epiphyte richness for each host species, and compared the

results.

All analyses were carried out in R version 4.0.3 (R Core Team, 2020) using the R studio

interface v.1.1.423 (RStudio Team, 2016). The packages 'openxlsx' v.4.2.2 (Schauberger and Walker,

2020), 'ggplot2' v.3.3.2 (Wickham, 2016), 'plyr' v.1.8.6 (Wickham, 2011), 'forcats' v.0.5.0 (Wickham, 2020), 'vegan' v. 2.5-6 (Oksanen et al., 2019) and 'gridExtra' v. 2.3 (Auguie, 2017) were used in scripts for importing and analysing the data and plotting the figures.

Results

The dataset consisted of a sample size of n = 60 for both red and silver beech, and n = 57 for the mountain beech (data from three mountain beech host individuals were removed from the dataset due to missing or incomplete field data). Across all 177 host individuals, I recorded a total of 44 putative epiphyte taxa, comprised of 26 lichens, 15 mosses and 3 ferns. Host individuals supported between zero and 25 epiphyte taxa (including liverwort morphospecies). A full list of the taxa recorded during surveying is included in Appendix 5, with notes on taxonomic delimitation and ID included. Whilst most taxa were not separated below genus level, *Pseudocyphellaria* spp. showed vast morphological diversity representing what I assessed to be at least seven true species, which were treated as separate morphospecies. *Menegazzia* (with 3), *Nephroma* (2), *Sticta* (2) and *Hypnum* (2) were also treated as more than one taxon per genus.

Mean sooty mould cover was lowest in *L. menziesii* (at 0.8% ± 3.1) and much higher in *F. cliffortioides* and *F. fusca* (88.5% ± 16.1 and 74.9% ± 27.0 respectively). Thus, sooty mould cover was significantly different between the three host species (F = 395.4, df = 2, $p < 2 \times 10^{-16}$; Fig. 4.2b) and between each post-hoc pairwise species comparison (*F. fusca-F. cliffortioides* $p \approx 0.0002$, other pairs: $p < 10^{-7}$). Mean epiphyte richness (totalled across all taxa) was highest in *L. menziesii* (at 17.3 ± 3.10 standard deviations) and much lower in *F. cliffortioides* and *F. fusca* (4.18 ± 4.64 and 1.98 ± 2.49 respectively). Thus, epiphyte richness was significantly different between the three host species (F = 333.1, df = 2, $p < 2 \times 10^{-16}$; Fig. 4.2a) and between each post-hoc pairwise species comparison (*F. fusca-F. cliffortioides* $p \approx 0.0026$, other pairs: $p < 10^{-7}$).

Additionally, in a linear model assessing the effect of both host species and sooty mould cover, both host species ($p < 2.2 \times 10^{-16}$) and mould cover ($p < 8 \times 10^{-15}$) significantly affect epiphyte

richness (Fig. 4.3). The interaction term between the two factors was also significant ($p < 4.3 \times 10^{-8}$), indicating a difference in the slope of the relationship in each of the host species.

Non-metric multidimensional scaling analysis fitted to two dimensions (shown in Figure 4.4) produced a stable solution with a stress value of 0.215, an acceptable score for two dimensions. Rerunning the NMDS analysis fitting the points to three-dimensional space also produced a stable solution and reduces the stress score to 0.157. However, the two dimensional solution is presented here for ease of interpretation, which is justifiable given the only limited reduction in stress between the 2D and 3D solutions. Epiphytic species composition of the three host species was significantly different as indicated by differences in the group centroids (PERMANOVA: $F = 19.95$, $R^2 = 0.29$, $p = 0.001$). In addition, analysis of average dispersion from the group centroid indicates that *L. menziesii* has significantly lower mean distance to centroid than either *Fuscospora* species (F = 36.1, df = 2, $p < 1.8 \times 10^{-12}$; Fig. 4.5).

In addition to the differences in epiphyte richness and composition between host species, there is also a difference in the slope of the host size-richness relationship. *Lophozonia menziesii* exhibits a significant positive relationship between DBH and epiphyte richness (*Adj. R²* = 0.18, *p* = 0.00048; Fig. 4.6a), whilst neither *Fuscospora* species does (*F. cliffortioides*: *p* = 0.68; *F. fusca*: *p* = 0.19; Fig. 4.6b-c).

Discussion

My results confirm that both sooty mould cover and epiphyte richness vary between the host beech species (research questions 1 and 2), with sooty mould cover significantly lower in *L. menziesii* and epiphyte richness significantly higher in *L. menziesii*. The combined analysis also confirms that both sooty mould cover, host species and the interaction of these two factors determine epiphyte species richness (Q3), with the expected negative relationship between mould cover and epiphyte richness central to this (as shown in Fig. 4.3). The changes in epiphyte richness

between hosts is accompanied by changes to the host size-richness relationships and overall species composition (Q's 5 and 4 respectively).

Explaining the differences in epiphyte assemblages between host species

The near-total absence of sooty mould cover from *L. menziesii* matches the lack of beech scale insect infestation on this species. The extensive scale insect infection on *Fuscospora cliffortioides* and *F. fusca* leads to this extensive mould cover, as the moulds feed on the secreted honeydew. The mould in turn excludes the epiphytic lichens, bryophytes and ferns, although the exact mechanism is not clear. The sooty mould appears able to grow over lichens and mosses (Dawes pers. obs.; also noted by Buckley, 2011) and thus may physically smother them, depriving them of light and/or preventing gas exchange. They may also exert an allelopathic effect and chemically inhibit the growth of other organisms, analogous to that reported in the bark of some 'poor' host trees of epiphytes (Valencia-Díaz et al., 2010, Harshani et al., 2014). Although the chemistry of sooty moulds are very poorly known (Chomnunti et al., 2014), they are known to influence accumulation of polycyclic aromatic hydrocarbons (PAHs) (Jouraeva et al., 2006) and metal ions (Aragão et al., 2012), and have been reported to produce antibacterial compounds (Herath et al., 2012). The allelopathy hypothesis nonetheless complements a more plausible mechanism of physical exclusion by the moulds. Exclusionary chemistry may, however, play a role in the host specificity of the beech scale insects themselves, with chemicals in the bark of the trees mediating the host-parasite interaction in some way.

Sooty Moulds as Amensalists

This exclusion by the sooty moulds appears to represent amensalism (a 0/- interaction). To be considered an amensalist, the focal organism must negatively impact another interacting organism, whilst be unaffected by this other organism. In the absence of sooty mould, epiphyte richness is relatively high, dropping to low or zero on the beeches where sooty mould is abundant –

consistent with sooty mould excluding other epiphytes. This fits with the first criterion of a demonstrable negative impact of the sooty mould on the epiphyte community. There is also no indication that the epiphytes impact the mould in any way, in apparent consistency with the second of these criteria. On *Lophozonia menziesii*, it is the lack of a honeydew food source that excludes the mould rather than any action of the epiphytes themselves. Ideally, experimental evidence would be needed to confirm the lack of impact of any of the epiphyte community on the sooty moulds. Conversely, evidence of a negative impact of epiphytic lichens and plants on sooty mould would surely be required to indicate that this interaction is competitive (other than by evoking "the ghost of competition past" sensu Connell, 1980). However beyond traditional symmetrical competition, asymmetric competition remains another plausible hypothesis for the role of the sooty moulds in this system. Indeed, amensalism is merely the extreme form of asymmetric competition (Lawton and Hassell, 1981). A hypothesis of asymmetric competition in this instance would posit that the epiphytes have a small or negligible negative effect on the sooty mould, as opposed to absolutely zero in a strictly amensalist interaction.

Sooty Moulds as possible Keystone Assemblages

It is clear from my results that the sooty mould assemblage at the site exerts a significant effect on the remaining epiphyte community. It thus fulfils the first criterion of a keystone species. Whether this effect is disproportionate to sooty mould abundance is more debatable. Sooty moulds clearly have a high abundance in the ecosystem, especially in terms of surface cover, and potentially also a significant biomass (Wardhaugh and Didham, 2006). In this sense they could potentially be considered a dominant species instead. The other issue with considering sooty mould as a keystone species is that beech scale insects are already considered a keystone species (Beggs et al., 2005, Beggs and Wardle, 2006). This is because not only do they support the sooty moulds themselves, but they also support vastly increased abundances of native birds (Gaze and Cloud, 1983) and invasive wasps (Moller and Tilley, 1989), whilst structuring native arthropod communities (Didham, 1993,

Ewers, 2002). Although the moulds themselves also appear to play a role in affecting invertebrate assemblages (Collier, 1990). On the other hand, both the beech scale insect and sooty mould could be considered a 'keystone species complex' (sensu Daily et al., 1993, Hermosillo-Núñez et al., 2018). Given that sooty moulds are an assemblage of similar species anyway (Hughes, 1976, Dhami et al., 2013), they could only be considered be a part of an extended keystone concept (sensu Mouquet et al., 2013), rather than a keystone species in the strict sense. Regardless of whether sooty moulds neatly fit into a particular keystone concept, these organisms are clearly of central importance of structuring the epiphyte community at my study site.

Sooty Moulds as Epiphytes

It is also key to note that sooty moulds themselves can be considered epiphytes dependent on definition. Epiphytes are typically defined as plants which are structurally supported by a host plant without nutritionally parasitising this host or relying on a physiological connection to water and nutrients from the soil (e.g. Benzing, 1990, Zotz, 2016b). Sooty moulds fulfil all these major criteria (although they are obviously not a plant). They also do not appear to be saprophytic on the host tree's bark, as they already have access to a copious supply of honeydew secretion to feed off. In a stricter case, one might limit the definition of epiphyte to photosynthetic organisms (i.e. plants, algae, lichens) and use a broader term such as 'epibiota' to refer to sooty moulds. However, Moffett (2000, 2001) argues for an inclusive use of the term for all sessile organisms including fungi and here I agree the term epiphyte is suitable for sooty moulds. It must therefore be noted that the sooty mould assemblage is a subset of the broader epiphyte community (or strictly epiphyte assemblage *sensu* Mendieta-Leiva and Zotz, 2015).

Host Specificity in the epiphyte community

The crucial corollary of this exclusionary role of sooty mould is the unusual structure of the epiphyte community between the three co-dominant host tree species. The sooty moulds densely

coat the two *Fuscospora* species, whilst the other epiphyte taxa are largely restricted to *L. menziesii*

and exhibit a high richness on this host species. Thus the sooty mould assemblage shows a strong

host bias towards *Fuscospora* spp. Conversely, the other epiphytic taxa are largely restricted to *L.*

menziesii, and if they are present on the other two host species, they are much less frequent. In this

case a strong host bias to *L. menziesii*. What is striking is the community level coordination in host

specificity. With some minor exceptions, each species of epiphytic plant and lichen in this system

occurs preferentially on *L. menziesii*. Notably, not a single epiphytic fern individual was recorded on

either *Fuscospora* (see host occurrence data in Appendix 5). This greater species richness on *L.*

menziesii is also likely matched by equivalent community-wide and within-species increases in

abundance and percentage cover – with many moss species especially growing in thick mats or

clumps (Dawes *pers. obs.*). Further work incorporating changes in abundance would likely increase

the strength of the host specificity patterns observed.

Epiphytic plants generally show a lesser degree of host specificity than other organisms

(Wagner et al., 2015) which may be under co-evolutionary selection pressures such phytophagous

insects (Jaenike, 1990). However, this is not quite the case in this system. Epiphyte host specificity is

mediated by the mould distribution between hosts which is in turn determined by the beech scale

insect host specificity. Given that beech scale insects are phytophagous insects, it is therefore

interesting that epiphyte host specificity patterns are closer to those of phytophagous insects (e.g.

Jaenike, 1990). Especially comparable is a case reported from a three co-dominant host tree system

where a majority of species are restricted to a single host (Morrow, 1977), although in this instance

the insect assemblage does not have a common favoured host.

Role of Host DBH and demography

One downstream effect of sooty mould exclusion is the absence of any host size epiphyte

richness relationship on *Fuscospora cliffortioides* and *F. fusca* hosts. The mould exclusion prevents

epiphyte species accumulation as it would typically occur (e.g. Einzmann and Zotz, 2017, Einzmann

et al., 2021), with epiphytes occurring too sporadically on hosts of all sizes. Another facet of this, is the subtle differences in the pattern seen on *F. cliffortioides* and *F. fusca* hosts. Paradoxically, *F. cliffortioides* hosts a slightly greater mean epiphyte richness than *F. fusca*, but also a greater mean sooty mould cover. The best apparent explanation can be found by examining the DBH-mould cover relationships, considering the differences in size class distribution between the two host taxa and considering the bark morphology in larger older trees. In both *Fuscospora* species, sooty mould cover decreases with increased DBH (Fig. 4.7). This is due to the reduction in scale insect infection with increased host size, with scale insects failing to penetrate the thick bark of mature host trees (Wardhaugh et al., 2006). Meanwhile, there are fewer large *F. cliffortioides* in the community compared to *F. fusca*, as *F. fusca* has a higher adult survivorship and greater longevity (Stewart and Rose, 1990, Ogden et al., 1996). *F. cliffortioides* had a greater abundance of younger trees at the site (Dawes *pers*. *obs*.) seemingly with a lower adult survivorship and longevity (Ogden et al., 1996 Table 3.5). Thus, no *F. cliffortioides* individuals >60cm in diameter were surveyed, compared to 2 and 11 for *L. menziesii* and *F. fusca* respectively. The presence of large *F. fusca* trees lacking sooty mould explains the lower mean sooty mould cover in this host species. However, these large trees with reduced sooty mould cover retain the characteristically low epiphyte richness of younger *F. fusca* (see Fig. 4.5c). This may be due to the splintering rugose bark texture (Fig. 4.8) or potentially due to lingering allelopathic chemicals on the bark from previous sooty mould occupation. Why the epiphyte richness is slightly higher on *F. cliffortioides* than *F. fusca* is a little harder to explain, and may be related to incomplete colonisation by sooty moulds on some of these younger trees. However, the overall indication is that host tree demography may play a minor role in structuring the epiphyte community.

Context and Applicability

The patterns and interactions documented in this study must of course be placed within a certain context. For example, Power et al. (1996) stress the importance of context dependency in

the nature of keystone species or species complexes. Whilst sooty moulds are clearly of significant ecological importance in this system, Hughes (1976) describes sooty moulds in New Zealand beech forests as more prevalent than anywhere else, and this seems certainly true comparative to all other temperate ecosystems. Even within New Zealand, this phenomenon is somewhat restricted. Beech scale insect are only especially abundant in low-to-mid elevation beech forest of northern South Island (Morales et al., 1988). Hence, I can qualify that sooty moulds appear to form a keystone complex with beech scale insects largely in northern South Island New Zealand where the two organisms coexist in greater abundance and exerting disproportionate influence on the surrounding ecological community. Despite this context dependency, this case study still has wider ecological applicability for our understanding of the role of amensalist interactions, keystone complexes and epiphyte-epiphyte interactions in forest communities. I provide empirical evidence that apparently amensalist (or asymmetrically competitive) interactions can be important in spatially structuring species assemblages. I also show how these disproportionately significant interactions can alter typical patterns of host specificity amongst the epiphyte assemblage.

Conclusions

Here I demonstrate that extensive sooty mould assemblages in New Zealand montane beech forests exclude all other groups within the epiphyte community. This creates a stronger host specificity in the epiphyte community than expected in most epiphyte systems. Therefore, sooty moulds can be thought of an amensalist and potentially also a component of a keystone species complex, along with the beech scale insects on which they depend. Overall, this study hints at the broader possibility of interspecific epiphyte interactions, even in more 'typical' systems.

Figure 4.1 – Photographs showing the study site, the three host species of beech tree and a sooty mould coating. **a)** Southern beech forest extending from the shores of Lake Rotoiti up to the slopes of the Saint Arnaud range in Nelson Lakes National Park, South Island, New Zealand. **b)** Image of the trunk of an example silver beech (*Lophozonia menziesii*), along with equivalent images of **c)** mountain beech (*Fuscospora cliffortioides*) and **d)** red beech (*F. fusca*). Note that the colour coding of labels b-d matches the colour scheme used in all subsequent figures in this chapter. **e)** A close up image of sooty mould coated bark, with many anal filaments of sooty beech scale insect also visible.
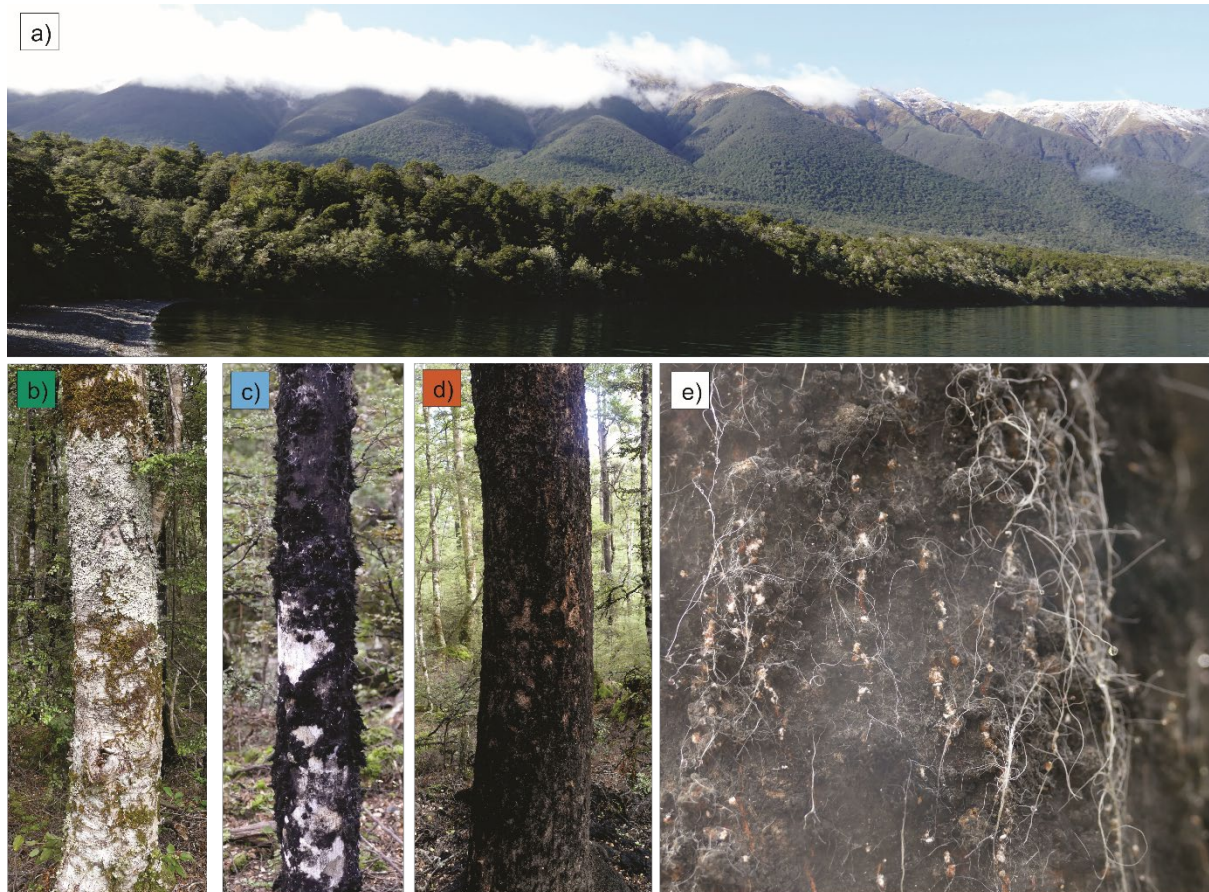
Figure 4.2 – Boxplots showing the variation in **a)** epiphyte richness and **b)** sooty mould cover (as a %) between the three host beech species – silver beech (*Lophozonia menziesii*; blue-green), mountain beech (*Fuscospora cliffortioides*; pale blue) and red beech (*F. fusca*; vermilion).
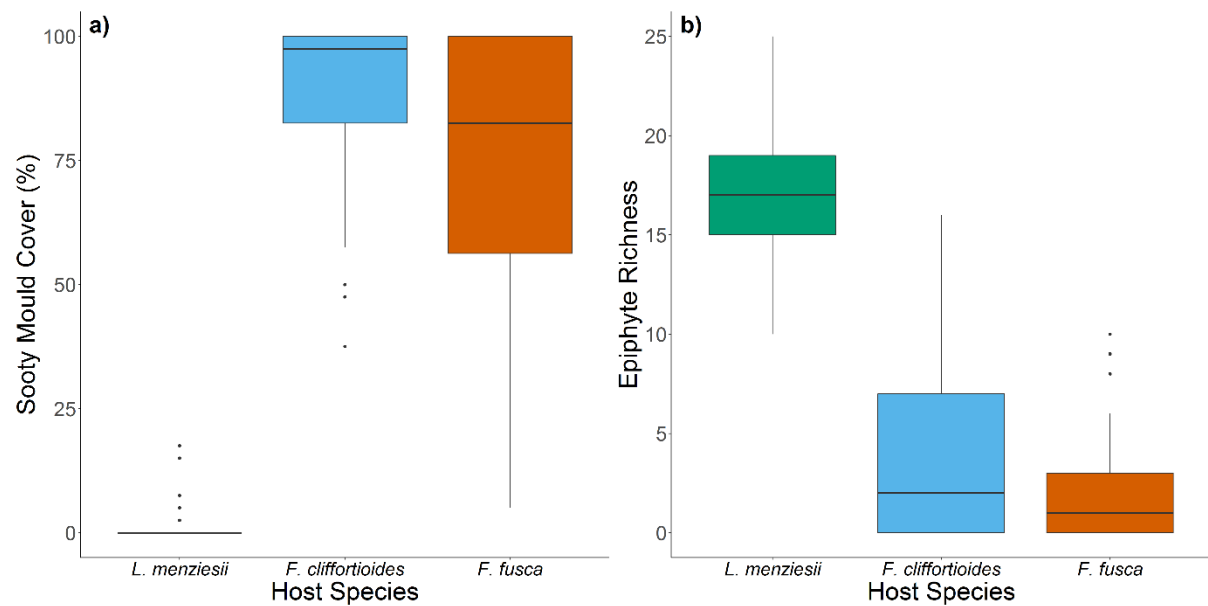
Figure 4.3 – A scatterplot showing the negative relationship between sooty mould cover (as a %) and epiphyte richness.
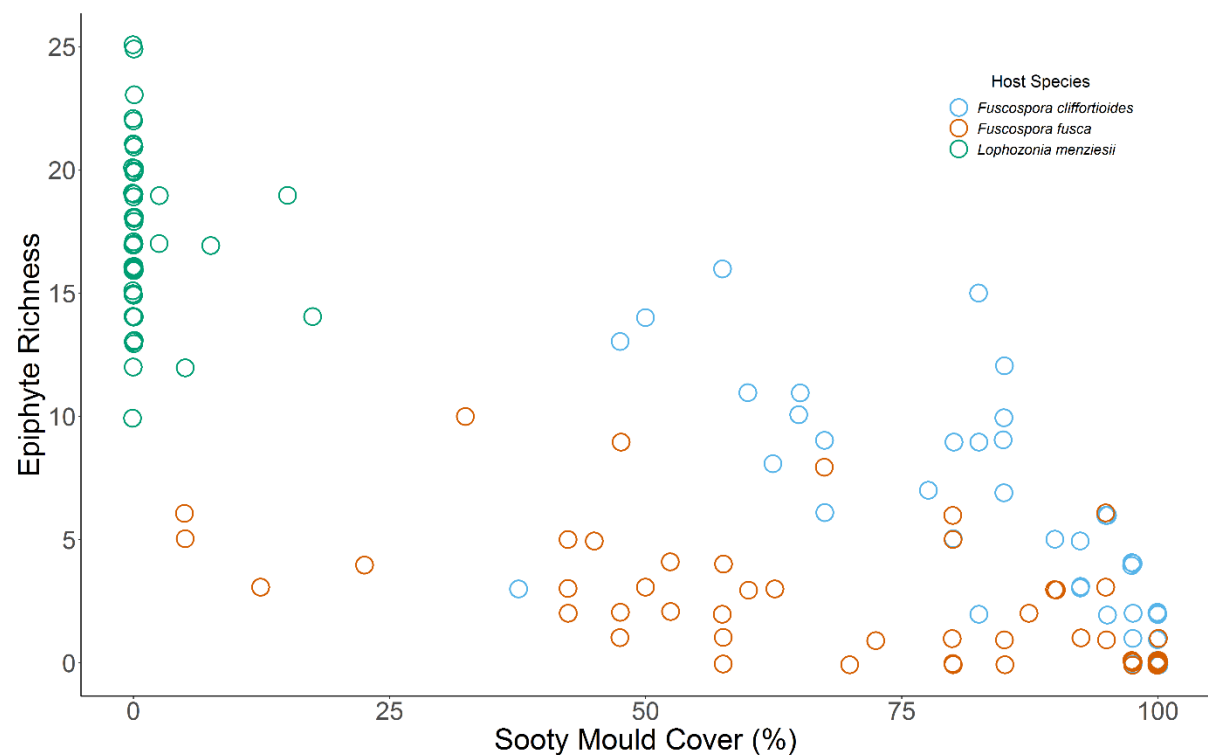
Figure 4.4 – A plot of a non-metric multi-dimensional scaling (NMDS) analysis of differences in epiphyte species composition between host individuals. Host individuals are coloured by host species, with a similarly coloured 95% confidence ellipse for each host species – *Lophozonia menziesii* is blue-green, *Fuscospora cliffortioides* is pale blue, and *F. fusca* is vermilion.
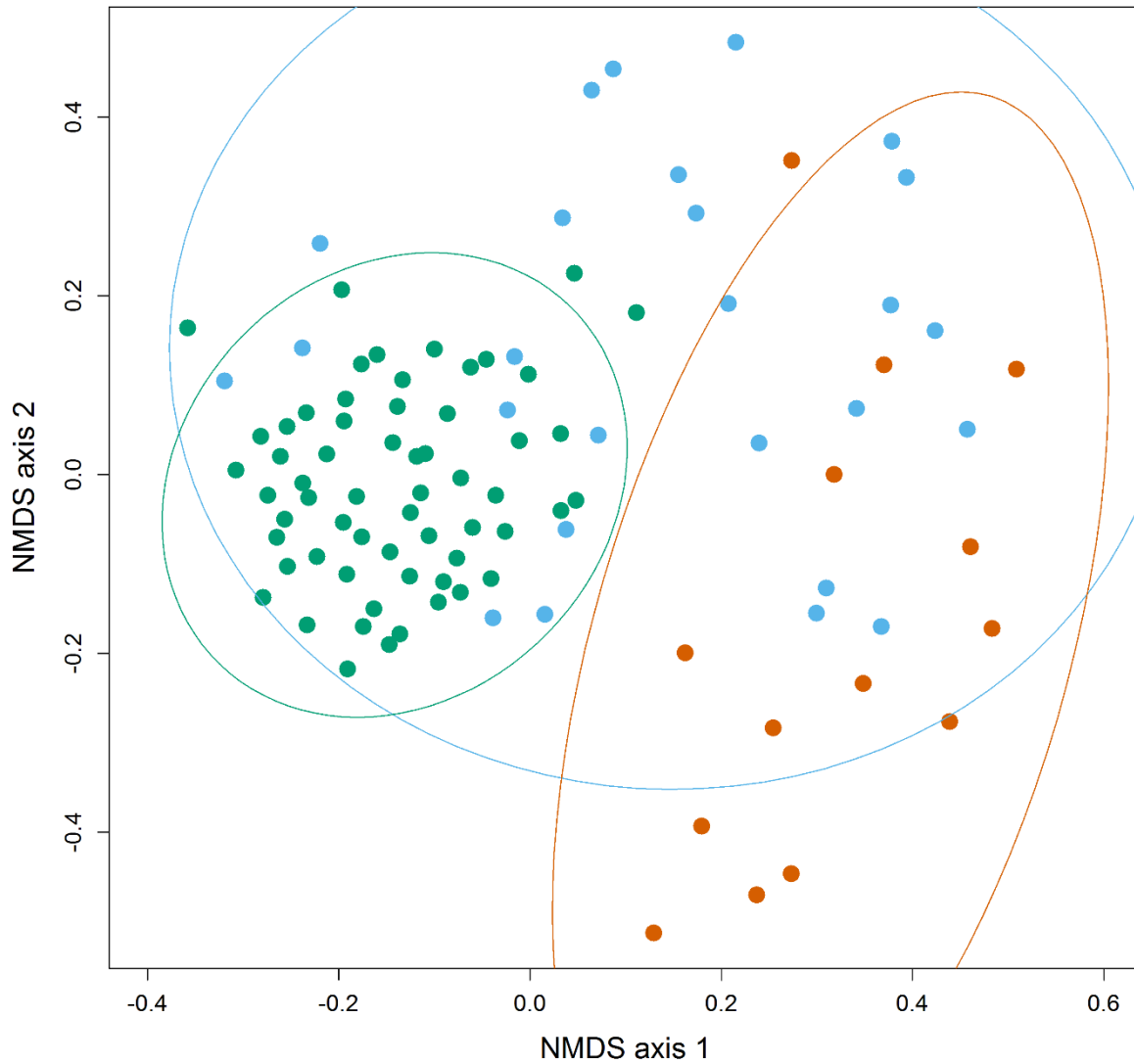
Figure 4.5 – Boxplots of the distance from the group centroid for each individual of each of the three host species. Results of Tukey HSD pairwise comparisons are summarised as letters above the boxplots, with the species indicated by the letter B (*F. cliffortioides* and *F. fusca*) not being significantly different from one another, but different from *L. menziesii*.
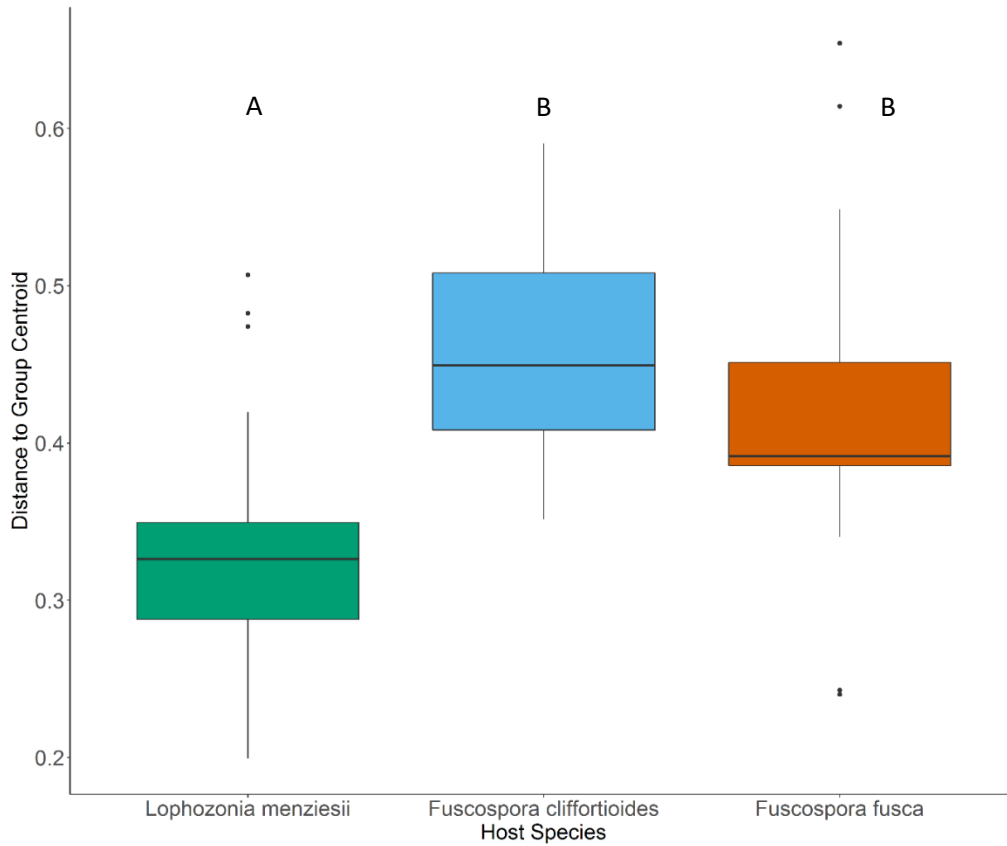
Figure 4.6 – Scatterplots of diameter at breast height (DBH; in cm) – a proxy of tree size – plotted against epiphyte richness for **a)** Silver Beech (*Lophozonia menziesii*), **b)** Mountain beech (*Fuscospora cliffortioides*) and **c)** Red beech (*F. fusca*). Note that a regression line is plotted on panel **a)** which is the only graph to exhibit a positive DBH-richness relationship.
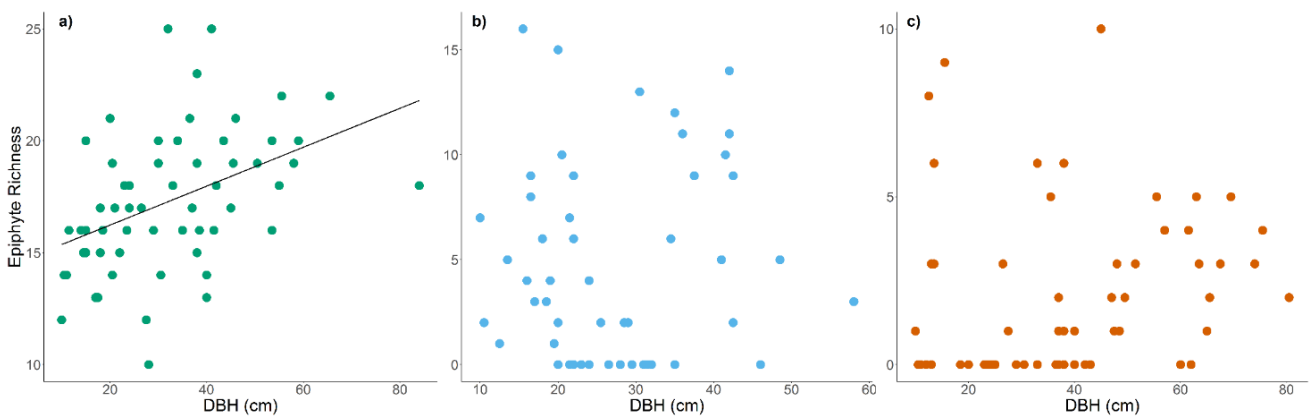
Figure 4.7 – A scatterplot showing the relationships between host diameter at breast height (DBH) and sooty mould cover (as a %). Host Species are coloured following the key – *F. cliffortioides* is coloured pale blue, *F. fusca* vermilion and *L. menziesii* is coloured blue-green.

Figure 4.8 – A photograph showing the bark of a large mature individual of *Fuscospora fusca*. The bark is fissured in texture and that small fragments of the outer bark are flaking off the surface.
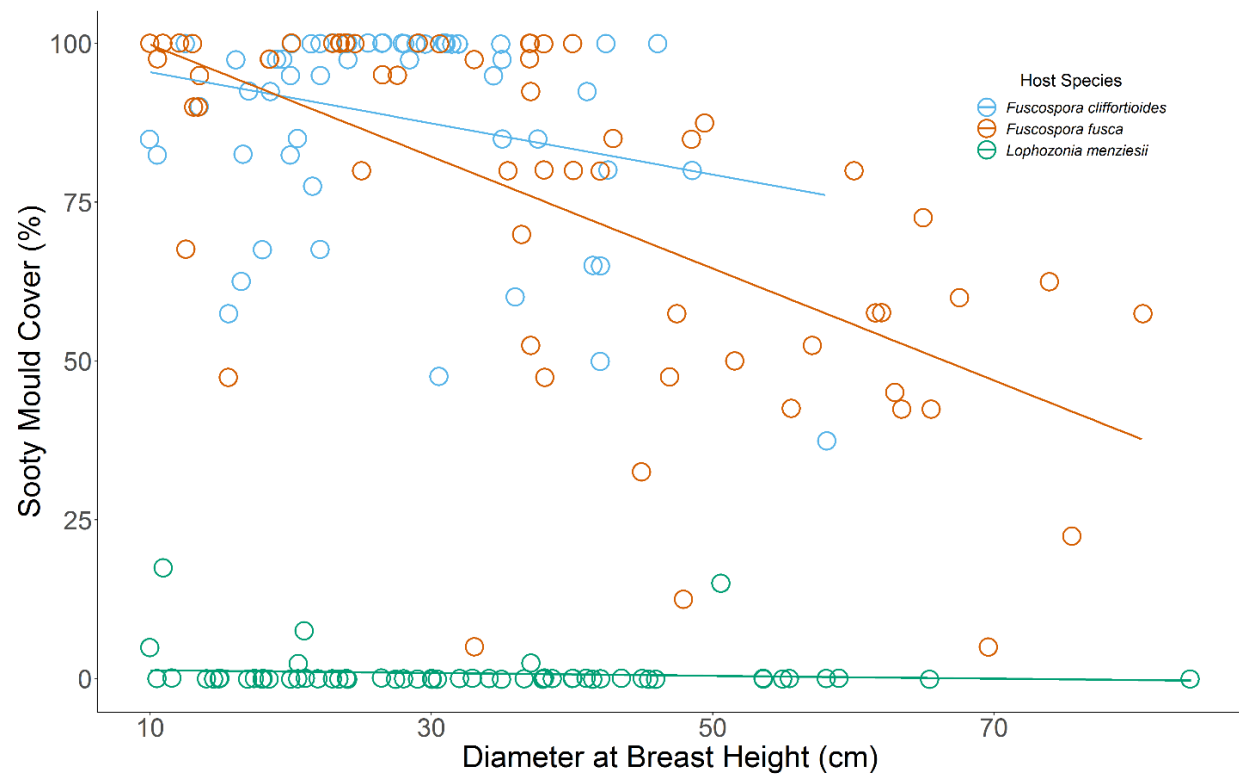
Chapter 5 – Spatial ecology and host diversity of three arboreal plants from Lord Howe Island

Abstract

In canopy ecology, it has long been understood that different guilds of arboreal plants have different spatial distributions and degrees of host specificity. Here, I present a case study looking at how within-crown spatial niche and host specificity vary between three very different morphologies of arboreal plant on Lord Howe Island, interpreting these in terms of different water acquisition strategies. I quantify within-crown spatial niche and created a null model to test host specificity in three species with very different water acquisition strategies (a mistletoe, an orchid and a detritus-collecting fern). The mistletoe had a greater host specificity than the two epiphyte species, and was restricted to thinner branches. The fern occurred further from the outer crown than the other species including on the trunks of host trees, and was the only species to show no indication of host specificity. Differences in distribution are consistent with differences in water acquisition strategy, providing an initial link between traits and spatial distribution, a potentially fruitful avenue of future research.

<u>Introduction</u>

Arboreal plants constitute at least 13% of global vascular plant richness (Zotz, 2013b, Gentry, 1991, Watson, 2004), with epiphytes alone contributing ≥9% (Zotz, 2013b), and form a crucial component of the ecological functions in the forest canopy (Gotsch et al., 2016). Arboreal plant communities have a unique spatial structure driven by the physical dependence upon host trees (Zotz and Schultz, 2008), with host tree identity also playing an important role in community spatial structuring (e.g. Hirata et al., 2009, Vergara-Torres et al., 2010, Wagner et al., 2015, Norton and De Lange, 1999). Absence of access to a terrestrial water source is also fundamental to the ecological and evolutionary strategies of arboreal plants (Zotz and Hietz, 2001). Variations in adaptation to water limitation in arboreal plants can then influence their spatial ecology (Hietz and Briones, 1998).

The vast majority of plants rely on soil as a reservoir of water and nutrients. Being unable to access this reservoir in the soil, arboreal plants are placed under a distinct water and nutrient stress (Zotz and Hietz, 2001). Water and nutrients can be ephemeral resources for these plants, hence mechanisms to acquire, store and manage water and nutrient relations are of vital importance. Arboreal plants display a diverse range of adaptations to cope with these stresses by acquiring and storing these resources (Zotz, 2016b).

A number of major strategies of water and micronutrient acquisition have evolved in arboreal plants; the major guilds of which are parasites, epiphytes, hemiepiphytes, climbing plants and nomadic vines (Moffett, 2000, Zotz, 2013a). The two contrasting strategies of parasitism and epiphytism are especially distinct ecologically. Arboreal ectoparasitic plants, primarily mistletoes, have roots that penetrate the host tree bark in structures known as haustoria allowing parasitic acquisition of water and micronutrients from the host. Epiphytes, on the other hand, live commensalistically on the host tree without a direct physiological connection or nutritional parasitism upon the host. Consequently, epiphytes exhibit a broad range of adaptations to acquire and store rainfall, atmospheric humidity and environmental micronutrients, such as those occurring in canopy detritus. One especially prominent group is the epiphytic orchids, which have roots

sheathed in a velamen radicum – succulent spongy tissue which facilitates water and nutrient uptake and storage (Zotz and Winkler, 2013). For orchids, mycorrhizae may also play an important role in micro-nutrient uptake (Brundrett, 2009, Otero et al., 2007). Another key group are the humus-accumulating epiphytes, which utilise some form of litter-collecting morphology to store detritus that can also hold water (Karasawa and Hijii, 2006). Hence, arboreal plants have an array of strategies, from parasitic water acquisition, to water uptake by specialist tissues, to utilising an external water storage source.

Different guilds of arboreal plants can have very different spatial patterns. Spatial patterns of arboreal plant communities can occur at the stand-level and above, at the level of the individual host tree or at the level of the within-tree zonation (Mendieta-Leiva and Zotz, 2015). Within-tree spatial ecology is usually conceptualised using Johansson zones (following Johansson, 1974), which consist of different structural zones within the tree from low-trunk to outermost twigs. Different epiphyte taxa may have differential preference for varying branch sizes, vertical positions within the crown of the tree and relative proximal-distal distributions with respect to the centre of the crown, amongst other variables. This within-tree spatial variation need not be confined within the Johansson zone framework, with quantitative approaches illustrating a finer-scale spatial patterning and allowing the teasing apart different axes of spatial variation (Zotz, 2007, Sanger and Kirkpatrick, 2017).

Different guilds of arboreal plants may also be different in their interaction with host trees including all facets of host specificity – both in host range and bias (Wagner et al., 2015). Mistletoes tend to have greater host specificity than epiphytes, due to haustorium formation being somewhat specialised to certain host species (Okubamichael et al., 2011). Although host specificity is highly variable between mistletoe taxa, generalist mistletoes are not totally unrestricted and still show host preference (Norton and Carpenter, 1998). Meanwhile, epiphytes are considered to be host generalist in the majority of instances, albeit commonly showing some host bias as well (Wagner et

al., 2015 and references therein). However, there is not sufficient evidence as to how epiphyte host specificity may vary between ecological subgroups of epiphytes.

For this paper, I define the term host specificity in a relatively broad manner to mean the tendency of an arboreal plant to occur on a particular set of host trees. Most importantly, I relate the idea of host specificity to ideas of host richness and host diversity. A species that has a high host specificity has a low host tree diversity, and vice versa. Additionally, the separate facets of host specificity (*sensu* Wagner et al. 2015) of basic host specificity and structural host specificity are inversely related to the ideas of host richness and evenness. High basic host specificity is equivalent to low host richness (or low host range), whilst high structural host specificity is equivalent to a low host evenness (or a high host bias). I make these conceptual equivalences clear now, as I use the parameters of host richness and Shannon diversity (which incorporates both richness and evenness) in the model – rather than a measure of host specificity *per se*.

Null models have become increasingly important tools in ecology (Gotelli and Graves, 1996), especially since the advent of neutral theory (Hubbell, 2001) which has placed stochastic processes in the spotlight of ecological enquiry. Equally, by comparing what I would expect by chance to real-world ecological observations I can test for signals of deterministic processes. However, null models have been rarely employed in epiphyte and mistletoe ecology (although see Janzen et al., 2020). Where null models have been utilised, they tend to be limited to the context of network analyses (Burns, 2007, Burns, 2008) and involve matrix reshuffling methods which do not account for potential host species which are not recorded in field surveying.

On the subtropical Lord Howe Island, the lowland forest has three relatively common arboreal plant taxa each with distinctive adaptations to the water limitation of living in the forest canopy. These three focal species include a dwarf mistletoe, an epiphytic orchid and a detritus-collecting elkhorn fern. I set out to test whether these species are distributed differently within host trees and whether host diversity matches null expectations. I also ask whether differences in distribution are interpretable considering the distinct differences in water acquisition strategy.

<u>Methods</u>

Study Site

My study area was on the subtropical Lord Howe Island (31° 33' S, 159° 05' E); a volcanic island 6.9 million years in age and <15 km² in area, 600km east of Port Macquarie, New South Wales, Australia (see also previous descriptions in Savolainen et al., 2006, Taylor and Burns, 2015b). The study was conducted in lowland forest in two areas: one in the north and one in the centre of the island. The area in the north consisted of more-exposed, wind-truncated, drier forest. The survey area in the centre of the island consisted of more typical lowland, subtropical rainforest.

Study Species

To compare different arboreal plant ecological strategies, I looked at three focal taxa (Fig. 5.1): *Korthalsella sp.* (Santalaceae), *Dendrobium macropus* subsp. *howeanum* (Orchidaceae) and *Platycerium bifurcatum* (Polypodiaceae). *Korthalsella* is a dwarf mistletoe that acquires its water and micronutrients by parasitising the xylem of its host. *Dendrobium* and *Platycerium* are both epiphytes that live commensally on their host and thus acquire their water from the environment – i.e. rainfall, humidity. However, *Dendrobium* and *Platycerium* both have different water storage strategies. *Dendrobium* is an epiphytic orchid with roots sheathed in a velamen radicum to assist water and micronutrient uptake (Zotz and Winkler, 2013) and a stem which stores water for times of drought (Hutton *pers. obs.*). *Platycerium* is a fern that acts as a 'nest epiphyte' by accumulating fallen detritus from the surrounding canopy and by forming a spongy substrate from older decomposing fronds in the nest (see descriptions in Oliwa et al., 2016, Oliwa et al., 2017); the accumulated detritus and spongy substrate act as an external water and micronutrient store for the plant (Zona and Christenhusz, 2015). In summary, I looked at an ectoparasite with parasitic water and micronutrient acquisition (*Korthalsella*), an epiphyte with specialised internalised water storage (*Dendrobium*) and an epiphyte with an external water store (*Platycerium*).

Field Sampling

In the two survey areas, I searched extensively for epiphytes and mistletoes to sample. In order for each surveyed individual to be an independent sample, a maximum of one individual per host tree was recorded; thus reducing the impact of high dispersal limitation on my results. To avoid bias, this was arbitrarily the first individual observed. For each arboreal plant, three measurements were recorded:

1.) Diameter of branch (or trunk).

2.) Height of the plants anchoring point above ground.

3.) Height of the host tree.

Where plants were attached to the primary trunk of the host tree, this trunk diameter was the recorded as 'branch diameter'. The third measure was gathered to standardise height above ground relative to the height of the host tree. Relative height on the host tree was calculated as a ratio of height above ground to height of the host tree (i.e. measure 2 above divided by measure 3). The identity of the host species was also recorded for every individual.

Analysing differences in Spatial Niche

In order to assess the difference in spatial niche between the three arboreal plants, two linear models (analysis of variance, ANOVA) were conducted. The first assessed if branch diameter differed significantly between species. Branch diameter was always ln-transformed as *Korthalsella* occurred on branches an order of magnitude smaller than the other species. The second model assessed if relative height on host tree differed between the three species. Branch diameter was plotted against relative height on host tree to visualise this spatial niche separation.

Constructing a Null Model to test for evidence of host specificity

If arboreal plants exhibit zero host specificity of any kind, I would expect them to occur on a random selection of host trees and for host tree diversity to reflect that of the background tree species diversity in the forest. In order to assess whether arboreal plants are non-randomly distributed between host tree species, I built a null model, which simulated a scenario of trees being populated by arboreal plants at random. This allowed me to compare observed host richness and diversity to a random chance-expectation of a host richness and diversity. To build the null model I compiled a forest inventory, which was a representative sample of trees from the forest. During field sampling, I did this by stopping at 30 random points on the trail in each of the two survey areas and recorded the identity of the five nearest trees. This gave a total of 300 trees (30 x 2 x 5 = 300), of 23 potential host tree species, to populate a virtual forest. This randomised host composition was a random subsample of this virtual forest (without repeat sampling of individual trees) of the same sample size of the observed sampling. The species richness and a Shannon's diversity index were calculated for this random subsample. This subsampling procedure was repeated 1000 times, giving 1000 values of richness and Shannon diversity for random subsets of the forest trees. Hence, my null hypothesis is that observed richness and Shannon diversity will fall within the frequency distribution of these 1000 simulated richness and Shannon diversity values from the forest inventory. To test this, host species richness and Shannon diversity were calculated for the observed samples of each arboreal plant species (using the same individuals recorded for the spatial niche analysis) and compared to the distribution of the 1000 simulated values. This comparison was performed by means of a z-test, which assesses difference from the mean of expected distribution as a normal distribution. This gaveme a probability that the observed host diversity was the same as the null expectation.

In addition to this null model, binomial tests were used on the raw data to assess whether particular tree species were over- or under-represented as host species. This was done in order to assess whether differences between the composition of each possible host species reflected overall

host diversity. A binomial test was carried out for each combination of arboreal plant and potential host tree. For each binomial test, the 'expected probability' was the proportional occurrence of each tree species in the forest inventory. The 'number of successes' was the number of times that tree was a host for the respective arboreal plant in the observed dataset. The 'number of comparisons' was the number of arboreal plants surveyed.

All analyses were carried out in R version 3.4.2 (R Core Team, 2020) using R studio v. 1.1.423 (RStudio Team, 2016). The packages 'openxlsx' v. 4.1.0 (Schauberger and Walker, 2020), 'ggplot2' v. 3.0.0 (Wickham, 2016) and 'vegan' v. 2.5-4 (Oksanen et al., 2019) were also used in coding these analyses and for graphing figures.

Results

Field surveying recorded details of 112 arboreal plants, 45 each of *Dendrobium macropus* and *Platycerium bifurcatum*, whilst only 22 individuals of *Korthalsella* were encountered (on separate host individuals). *Korthalsella* was recorded on 2 host species, whilst *Dendrobium* and *Platycerium* occurred on 7 and 14 species respectively.

Korthalsella occurred on significantly smaller branches than both *Dendrobium* and *Platycerium* (F = 519.84, df = 109, $p < 2.2 \times 10^{-16}$, ln-transformed data). Mean relative height on host tree was significantly different between the three species (F = 14.193, df = 109, p=3.327 x 10^{-6}), although any difference between *Platycerium* and *Dendrobium* could be at due to unequal variances (0.045 and 0.019 respectively). The difference in spatial niche between the three species can be visualised as in Figure 5.2.

Korthalsella and *Dendrobium* have a lower host species richness than expected by chance (Fig. 5.3; p = 4.88 x 10^{-7}, p = 1.40 x 10^{-5} respectively). Both species also have a lower host Shannon diversity than expected by chance (p = 5.03 x 10^{-13} and p = 9.66 x 10^{-5} respectively). On the other hand, *Platycerium* has a host richness and Shannon diversity within the expectations of the simulated null model (Richness: p = 0.91; Shannon diversity: p = 0.41; Table 5.1).

Binomial testing shows that one of the two host species of *Korthalsella* (*Drypetes deplanchei*) was over-represented in its observed host composition compared to chance expectation (as determined by its background abundance in the forest) (Table 5.2). Three host species for both *Dendrobium* (*Elaeodendron curtipendulum*, *Guioa coriacea* and *Syzygium fullagarii*) and *Platycerium* (*E. curtipendulum*, *Lagunaria patersonia* and *S. fullagarii*) were also overrepresented compared to chance expectations. One host species for *Platycerium* (*Ficus macrophylla*) was recorded once as a host tree but not in the forest inventory, so could not be directly compared with a null expectation, but was likely also overrepresented compared to chance.

Discussion

The three arboreal plant species have very different within-crown distributions, host richness and host preference. The patterns exhibited by the three plants are consistent with their vastly divergent ecophysiology; with *Korthalsella* restricted to certain hosts and the upper part of host trees, while the epiphyte species are more broadly distributed in the canopy.

The mistletoe occurred on thinner branches, which would typically be in the outer parts of trees and in smaller trees. Given that mistletoes are less limited in water acquisition than epiphytes, access to light becomes their ecological priority (and *Korthalsella* was most common in the shorter-stature forest, especially more open areas). Smaller branches will have thinner bark by allometric scaling (Bertram, 1989), so may also be easier for the haustoria to penetrate. The small stature of *Korthalsella* may further limit it to smaller host branches. Both epiphyte species exhibit noticeable canopy niche differentiation from *Korthalsella*, but less clear differences between one another, as would be expected given the differences between the mistletoe and epiphyte guilds. The larger branch diameter requirements in the epiphytes may represent a need for sturdier point of attachment due to a lack of physiological connection to the host (as in mistletoe haustoria). Some difference in spatial niche does exist between the two epiphytes, with *Platycerium* more commonly occurring at lower heights beneath the canopy including on the trunks of trees. One explanation for

Platycerium occurring at lower heights is its apparent ability to colonise vertical surfaces, possibly due to its formation of a large colony. Another explanation is that the vertical stratification of epiphytes could be due to differences in water sensitivity in the regeneration phase (Wagner et al., 2013). My observed spatial patterns of arboreal plants also fit with previous ideas of epiphytes being divided into Johansson zones (Johansson, 1974), without the need for such qualitative canopy divisions (as per Zotz, 2007).

As expected in an ectoparasite, *Korthalsella* exhibits a narrow host range, far outside chance expectations. Nutritional parasitism may require physiological adaptation to circumvent specific hosts 'immune' response (such as the response documented in Hegenauer et al., 2016), necessitating a more limited host pool. Conversely, *Korthalsella* host richness may have been significantly underestimated in my study given the small sample size, the fact that it also parasitises at least one vine species (*pers. obs.*) and because host generalist mistletoes can be host specialist at local scales (Okubamichael et al., 2016). One explanation for *Dendrobium* having a lower host diversity is that, unlike *Platycerium*, *Dendrobium* does not appear to utilise vertical surfaces and therefore certain structural classes of hosts; for example, it was unrecorded on arborescent monocots and smaller subcanopy trees. Palms, for example, generally host a lower richness of epiphytes than branched dicots (Aguirre et al., 2010). *Platycerium*, meanwhile, had a host diversity matching chance expectations. Its ability to occur on the vertical trunk of the tree and lower in the tree's crown appear to enable a wider host diversity, including the palm *Howea belmoreana*, the stilt-palm *Pandanus forsteri* and slender trees such as *Sophora howinsula*.

Beyond overall host richness and diversity, interesting patterns in host species composition occurred. The main host of *Korthalsella* (*Drypetes deplanchei*) was overrepresented in the host composition compared to chance expectations, which is consistent with the low host Shannon diversity. *D. deplanchei* was the most common potential host tree in the forest (esp. the wind-truncated, lighter areas of the forest) and therefore a good host to utilise due to its abundance (Norton and Carpenter, 1998). *Dendrobium* and *Platycerium* both had hosts overrepresented

compared to the chance expectation. These included some of the largest host tree species in the forest, most notably *Syzygium fullagarii*, the largest tree in the island's lowland rainforest. Larger trees have a greater surface area, with more chance of propagules landing on them, and are likely to be older, giving more time for successful dispersal (Flores-Palacios and García-Franco, 2006, Taylor and Burns, 2015a); tree growth rates may also be a factor (Wagner and Zotz, 2020). Larger individuals of the species *Elaeodendron curtipendulum* have a distinctly rugose bark; a trait commonly associated with good host species for epiphytes (Wyse and Burns, 2011). Hence, other selectively neutral processes of ecology not accounted for in my model may explain some of the overrepresented host species. However, the overrepresentation of some host species for *Platycerium* coupled with an overall host richness and diversity matching chance expectation creates somewhat of a paradox. The simplest explanation to this is that the vast majority of hosts were recorded at levels not statistically significantly different from chance and the minority of overrepresented hosts have limited impact upon overall host richness and diversity. Equally, the overrepresented species may be offset by all other species being slightly underrepresented (if not statistically significantly so), with no overall difference in host diversity.

My null model is a simple one and thus has a number of assumptions underlying it. The most fundamental aspect of the model is that nothing of the physical characteristics of the tree species are taken into account. Biologically, the null expectation might still suggest that the average surface area or age of each potential host be accounted for. Under this scenario, typically larger or older species would be expected to house more epiphytes. However, the binomial testing complements the null model, in that it allows us to identify key phorophyte taxa to which this may apply (e.g. *Syzygium fullagarii*). I hope the basic model used in this study highlights the potential utility of more complex null models for understanding epiphyte and mistletoe ecology.

My study has clear limitations imposed; it is based upon a relatively small sample size and just three focal species, potentially creating an artefactual result. Additionally, whilst I quantified spatial niche and host relations of the three species, I did not quantify traits of these species. Further

work in the link between morphology and ecological niche may prove fruitful. However, the

theoretical points arising from this case study involving three interesting taxa remain relevant to our

understanding of the spatial ecology of different guilds of arboreal plants.

This study suggests that ecophysiological traits are potentially important in constraining the

spatial ecology of arboreal plant species. I expect many of these to relate to the water and

micronutrient relations of the different kinds of plant. This study also indicates a possible future

direction of understanding epiphyte community assemblage from a trait-based perspective. It may

be promising for epiphyte researchers to investigate how traits structure the spatial ecology of

epiphyte assemblages.

In conclusion, the differences in spatial ecology and host specificity in the three arboreal

plant species are consistent with the limitations imposed by the differences in water and

micronutrient acquisition and storage strategies that they exhibit. I then hypothesise that the

smaller differences between more similar species of arboreal plant may contribute to finer-scale

community assembly processes.

Table 5.1 – A table summarising the results of comparison between the distributions of expected values and the observed values.

Species	Diversity Metric	Model comparison p-value	*p*-value from Z-test
Korthalsella	Species Richness	0***	4.88×10^{-7} ***
"	Shannon Diversity	0***	5.03×10^{-13} ***
Dendrobium	Species Richness	0***	1.40×10^{-5} ***
"	Shannon Diversity	0.004***	9.66×10^{-5} ***
Platycerium	Species Richness	0.684	0.91
"	Shannon Diversity	0.402	0.41

Table 5.2 – A table showing the numbers of possible hosts identified in my forest inventory and the actual observed host composition for the three arboreal plant species. Blank cells indicate zero values. Asterisks (*) indicate where the number of recorded host individuals differs from the expected probability (relative abundance in the forest inventory): *** $p < 0.001$, ** $0.001 < p < 0.01$, * $0.01 < p < 0.05$.

Species	Forest Inventory	Arboreal plant host species composition		
		Korthalsella	Dendrobium	Platycerium
Atractocarpus stipularis	2			
Baloghia inophylla	7			
Celtis conferta	2			
Chionanthus quadristamineus	1			
Coprosma putida	2			
Cryptocarya triplinervis	12	1		1
Dodonaea viscosa	26		2	1
Drypetes deplanchei	115	21***	23	12
Dysoxylum pachyphyllum	6			3
Elaeodendron curtipendulum	12		8***	6**
Ficus macrophylla				1
Guioa coriacea	4		5**	1
Howea belmoreana	21			2
Lagunaria patersonia	4		2	3*
Myoporum insulare	1			
Myrsine platystigma	5			
Olea paniculata	22			2
Pandanus forsteri	10			4
Polyscias cissodendron	8			
Sarcomelicope simplicifolia	1		1	1
Sophora howinsula	8			1
Syzygium fullagarii	6		4*	7***
Xylosma maidenii	20			
Zygogynum howeanum	5			
Totals:	300	22	45	45

Figure 5.1 – Photographs showing the habit of the three focal species of arboreal plant. A) A number of individuals of *Korthalsella sp.* growing on a host *Drypetes deplanchei* in stunted dry forest in front of a backdrop of Lord Howe island's volcanic plateaux. B) *Dendrobium macropus* is an epiphytic orchid with scrambling roots emanating from its point of attachment to the host, sheathed in a velamen radicum. C) *Platycerium bifurcatum* is an epiphytic fern, which grows in a colony that forms a 'rubbish-bin' or tank morphology that collects detritus that in turn stores water.

Figure 5.2 – Cartesian plot showing the within-crown spatial niche of each individual of the three focal arboreal plant species. Note that the branch diameter (x-axis) is natural logarithm transformed and the relative height on the host plant (y-axis) is a proportion.
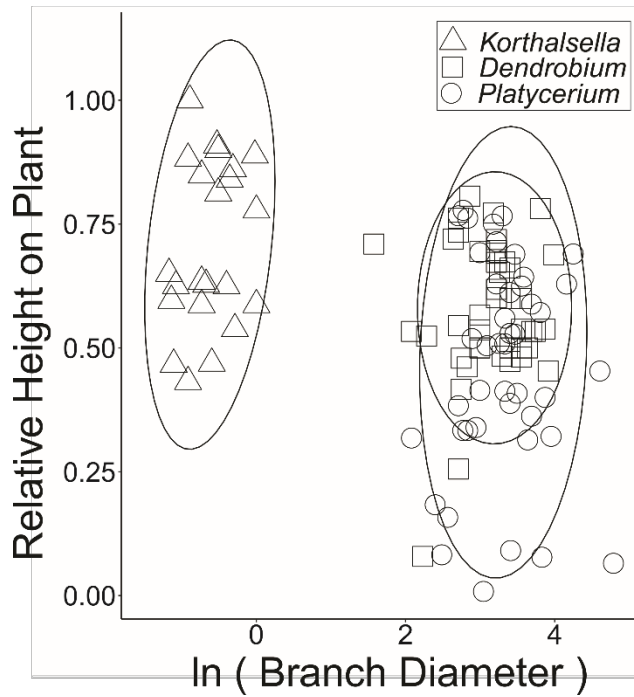
Figure 5.3 – Histograms of expected frequencies of host Shannon diversity generated from the null model with observed host diversity for each of three species marked by a red dashed line. **A)** *Korthalsella* – the mistletoe. **B)** *Dendrobium* – the orchid. **C)** *Platycerium* – the fern with a tank-like morphology. **NB:** Note than the bin-width is always 0.1, but the graph for *Korthalsella* has a different x-axis due to its lower observed value and different distribution of expected values.
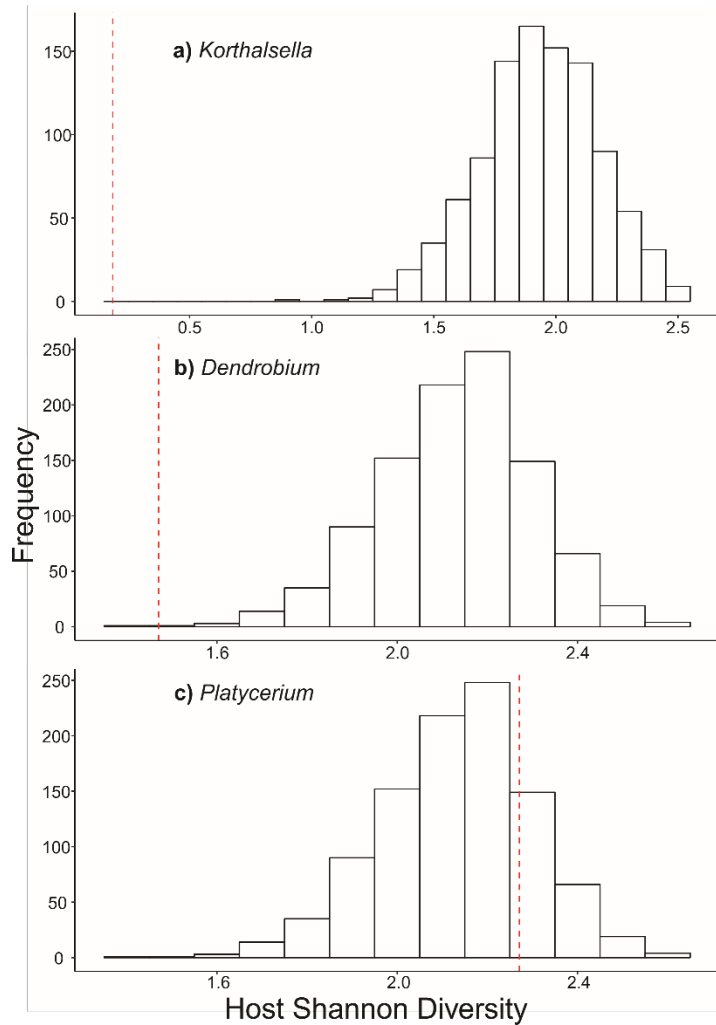
Chapter 6 – General Discussion

This thesis presents key findings on the community ecology, host specificity and spatial ecology of epiphytes and other arboreal plants in the New Zealand eco-region. I show that in woody plants, small-seeded species are more likely to occur growing epiphytically compared to larger-seed species (Chapter 2), re-emphasising the importance of small seed size to the epiphyte syndrome. Epiphytes and climbers on tree ferns fit the species accumulation model of succession, both between hosts of varying size, and between the younger and older portions within tree ferns (Chapter 3). The epiphyte and climber metacommunity matrix fits with randomised expectations under my null model conditions, both in co-occurrence and nestedness patterns (Chapter 3). However, the vertical patterns of occurrence were different between different habits of epiphyte and climber, as well as between different wind and bird dispersed epiphytes (Chapter 3). I demonstrate that, as part of a keystone species complex, sooty mould excludes epiphytes from *Fuscospora* hosts but not *Lophozonia menziesii*, creating a pattern of parallel host specificity (Chapter 4). Within-crown spatial niche is clearly different between three arboreal plant species, each with a radically different ecophysiology (a mistletoe, an epiphytic orchid, and an epiphytic fern; Chapter 5). Whilst the mistletoe and epiphytic orchid are significantly more host specific than null expectations, the epiphytic fern had a host diversity matching chance expectations (chapter 5) – indicating that some epiphytes show very little host bias. Taken together, these results help build a picture of epiphyte community structure in New Zealand forests and contribute to broader knowledge of epiphyte community assembly.

The Role of Dispersal in structuring arboreal plant communities

Under attempts to derive a unified synthesis of community ecology, dispersal has been recognised as one of the four most fundamental processes underpinning all of ecology (Vellend, 2010). Certain key approaches such as metacommunity frameworks especially emphasise the importance of dispersal (Vellend, 2010). Evidence suggests that dispersal may be one of the most

important processes for epiphytes, which is logical given the spatially discreet nature of host trees in a forest. The findings of this thesis reinforce these facts (e.g. Chapter 2).

Dispersal propagule size may pose a crucial filter to species being epiphytic or not (Chapter 2), with larger seeds more often excluded from the arboreal environment. Smaller diaspores may also have a greater dispersal ability (Westoby et al., 1996) or at least the greater volume of seeds provide better odds of successful dispersal to a suitable microsite on a new host. Dispersal syndrome also plays a key role structuring epiphyte assemblages, with animal-dispersed taxa underrepresented when compared to terrestrial plants (Zotz, 2016b). Bird-dispersed species on tree ferns also appear to have a very different pattern of vertical incidence than wind-dispersed species (Chapter 3), whilst this remains to be explored in other types of host. The overall pattern of random within-host community structure is consistent with the stochastic nature of dispersal (Chapter 3), with chance arrival on novel hosts a key factor. Similarly, some epiphyte species also show a random between-host distribution (e.g. *Platycerium bifurcatum* – Chapter 5). Whilst other non-random distributions between hosts are likely structured by post-dispersal establishment, including germination (Mondragón and Calvo-Irabien, 2006) and post-germination survival (Zotz, 2004, Toledo-Aceves and Wolf, 2008). Dispersal limitation may also be a factor in structuring epiphyte assemblages (Cascante-Marín et al., 2009), including between-host structure (Victoriano-Romero et al., 2017). Bird-dispersed species may suffer a greater degree of dispersal limitation than other dispersal syndromes, especially in a New Zealand context (see Kelly et al., 2010). In mistletoes, dispersal limitation may be even greater than in epiphytes (Rawsthorne et al., 2011), due to the more limited host pool that they are able to utilise (as in Chapter 5; see also Okubamichael et al., 2016). Some have questioned whether dispersal is a truly stochastic or neutral process (Lowe and McPeek, 2014), and certainly for bird dispersal this may be the case. Birds may prefer certain host trees for foraging (especially frugivores), for example. Indeed, birds may prefer the tops of larger tree ferns as perches or forage sites compared to smaller ones (one possible explanation for the curious vertical profile of bird-dispersed epiphytes in Chapter 3).

The Role of Host Species for Epiphytes

Interactions between epiphytes and their host can shape community structure (Wagner et al., 2015, Wagner and Zotz, 2020). Different epiphyte taxa can show different degrees of host specificity (Chapter 5). Epiphytes with different growth forms and ecophysiologies may be restricted to utilising certain host pools. For example, the orchid *Dendrobium macropus* preferentially inhabits larger horizontal branches, compared to vertical trunks on which it struggles to grow, meaning it was never recorded on palms and more-slender subcanopy trees (Chapter 5). Likewise in New Zealand forests, epiphytes with a scrambling morphology generally only occur in the outer (*Pyrrosia elaeagnifolia*) or middle crown (e.g. *Earina* sp. orchids) in larger angiosperm hosts. Thus, these epiphytes are also absent from palms and tree ferns (both were completely absent from my data for Chapter 3). Conversely, the high water retention of tree fern caudices (Mehltreter et al., 2005) means that tree ferns support facultative and accidental epiphytes that are rarely present on other hosts (chapters 2 and 3) – outside of branch crotches at least (as per Hoeber and Zotz, 2021). Therefore, this thesis also emphasises the distinct ecological role of tree fern phorophytes in the New Zealand temperate rainforest.

Beyond differences in host structural class, epiphytes can show preference for host species. For example, *Brachyglottis repanda* occurs more frequently epiphytically on the earlier successional tree fern *Cyathea medullaris* compared to understory *C. dealbata* or *C. smithii*, likely due to the higher light levels suiting its regeneration niche (reported in chapter 2 discussion). Matching similar literature findings from angiosperm hosts, with epiphytes showing preference for hosts with rugose bark (Wyse and Burns, 2011), bark persistence (López-Villalobos et al., 2008), and branch longevity (Cortés-Anzúres et al., 2017), amongst other traits (see chapter 1 discussion of host specificity). However, the most striking example of this is a whole community of epiphytic ferns, bryophytes and lichens showing parallel host specificity to *Lophozonia menziesii* host trees (Chapter 4). The interaction between host trees and another taxon (in this case a host specific insect parasite) can

indirectly modulate epiphyte host availability. Whilst a somewhat extreme case study, this finding highlights the potential for keystone interactions to structure species assemblages; even in epiphytes where keystone interactions have not been previously reported.

Conclusions and Future Work

Understanding of community assembly processes in epiphytes, including the role of traits, is still in its infancy. This thesis shows that seed size can predict the likelihood species are to occur arboreally on tree ferns (Chapter 2). Larger seed species are highly unlikely to occur as facultative epiphytes or hemiepiphytes, whilst small-seeded species occur epiphytically more often. How seed size or other dispersal traits shapes epiphyte community structure is a key direction in future research. Future work understanding post-dispersal establishment, including traits linked to seedling survival, will help improve our understanding of the trait-environment interactions central to the epiphyte syndrome (*sensu* Zotz, 2016a). Furthermore, building a more complete picture of global patterns of facultative and accidental epiphytism will improve knowledge of the drivers behind adaptation to the epiphytic habit.

Chapter 3 makes three key findings about the assembly of epiphytes and climbers on a tree fern host species. Firstly, both between tree ferns of different heights and between different aged sections of a tree fern, epiphytes and climbers both follow a species accumulation model of succession. Reaffirming this increasingly established pattern in angiosperm hosts (e.g. Burns and Dawson, 2005, Flores-Palacios and García-Franco, 2006, Woods, 2017) for tree fern phorophytes. Secondly, between host individuals there is no metacommunity network structure. Co-occurrence and nestedness patterns matched chance expectations. I conclude that this indicates a broadly random community structure, consistent with Gleasonian views of ecology (see Gleason, 1926). Exploring the metacommunity structure in many host species will be needed to support the generality of this conclusion, although it is consistent similar networks in (Burns, 2008, Burns and Zotz, 2010). Finally in chapter 3, I demonstrated that epiphytes and climbers with different habits

and dispersal syndromes showed differences in vertical profile on the tree fern. This finding

contrasts with the central role of stochasticity in the previous two findings and indicates that traits

may play a role in finer-scale community structure. Future work may extend this finding by analysing

how dispersal syndrome shapes within-host spatial patterns in other structural classes of host.

Experimentation may seek to elucidate potential mechanisms underpinning this pattern. More

generally, quantifying the relative contributions of stochastic and more deterministic elements of

community assembly will be aid in producing a more unified understanding of epiphyte

communities.

In New Zealand montane beech forests, sooty mould assemblages smother two of the three

co-dominant host trees, significantly suppressing epiphyte richness, removing the host-size richness

relationship, and altering species composition (Chapter 4). This leads to a highly unusual pattern of

strong parallel host specificity across the epiphyte community. I conclude that the exclusionary

interaction of the sooty mould is likely amensalist in its nature and that it structures the epiphyte

community in a manner consistent with being a keystone assemblage. Alternately, the sooty mould,

beech scale insect, and host beeches could be considered a keystone species complex (*sensu* Daily et

al., 1993) structuring the beech forest ecosystem, including the epiphytes. In either interpretation,

interactions structuring an epiphyte community have not previously been reported. This case study

of atypical community structure highlights the potential for otherwise poorly documented species

interactions to be more widespread in epiphyte assemblages. Further work may better elucidate

this, and other, epiphyte-epiphyte interactions with experimental approaches.

Chapter 5 shows that arboreal plants of different growth forms and with different

ecophysiologies exhibit different spatial niches, and show different degrees of host specificity.

Mistletoes inhabit a very different spatial niche to most epiphytes by exclusively occupying the

thinner outer branches, due to the difficulty in haustorium penetration through thicker bark, taken

together with the scaling law between branch size and bark thickness (of Bertram, 1989). Both the

mistletoe and epiphytic orchid show a host diversity significantly lower than null model

expectations, indicative of some degree of host specificity. Meanwhile, the epiphytic elkhorn fern

(*Platycerium bifurcatum*) has a host diversity matching chance expectations – indicating an absence

of host specificity. Future work should seek to better understand how growth form and

ecophysiological traits, such as water acquisition and storage, relate to spatial ecology or host

specificity, especially at a broader ecological scale. This study also highlights the potential for more

widespread use of very simple null modelling approaches as a key tool for testing host specificity,

and more broadly, in epiphyte ecology.

Appendices

<u>Appendix 1 - Glossary</u>

The following glossary presents a (non-comprehensive) list of key terms used in this thesis and the definition of these terms, especially highlighting where usage may differ from broader use in ecology (e.g. metacommunity), or how terms relate to similar terms (e.g. holoepiphyte vs hemiepiphyte). The terms are grouped into three broad topics – Epiphyte Ecology and General Botany; General Ecology; and Statistics and Networks – and then alphabetised within each topic.

Epiphyte Ecology and General Botany

Accidental Epiphyte – a typically terrestrial species of plant, such as a tree or shrub, that occasionally germinates epiphytically, usually with limited survival past the juvenile phase.

Arboreal plant – any plant that lives some of its life in the forest canopy and/or dependent on a host plant. This term is inclusive of epiphytes, hemiepiphytes, climbers and mistletoes.

Arboreality – the tendency of a plant to occur epiphytically compared to terrestrially, once surface area is accounted for. This value is calculated as epiphytic abundance (plus one), divided by terrestrial abundance (plus one).

Caudex – the main axis of a plant. Typically used herein to refer to the 'trunk' of a tree fern, which is not a true trunk nor true stem. The caudex of a tree fern consists of an erect rhizome, surrounded by a mantle of both persistent frond stipes and a lattices of roots.

Climber – any plant germinating on the ground which climbs up a host plant or tree, inclusive of the terms vine and liana.

Epibiont (pl. **Epibiota**) – any organism living on the surface of another organism.

Epiphyte – any plant or lichen species that grows commensally on the surface of another host plant without any soil-rooted connection or nutritional parasitism of the host.

Facultative epiphyte – any plant species that can grow either epiphytically or terrestrially.

Filmy Fern – any fern of the family Hymenophyllaceae, which are distinctive in having a lamina only one cell thick.

Haustorium (pl. **Haustoria**) – a specialised root of a mistletoe or other parasitic plant that penetrates the vascular tissue of the host plant.

Hemiepiphyte – a plant species that germinates epiphytically and then subsequently produces a root down to the soil below. Hemiepiphytes include species which can form girdling roots and form a pseudo-trunk around their host and outlive it after its death.

Holoepiphyte – a true epiphyte, in contrast to a hemiepiphyte.

Liana – a climbing plant with a woody stem.

Mistletoe – a plant that is an aerial ectoparasite (i.e. external parasite) of another plant, and that is still capable of photosynthesis.

Nest epiphyte – an epiphyte that has erect leaves which aid in the accumulation of canopy detritus, which in turn facilitates the retention of water and micronutrients.

Obligate Epiphyte – a plant species that always or nearly always grows epiphytically.

Phorophyte – the host plant of an epiphyte.

Phytotelmata – a water-filled cavity of a land plant, especially of an epiphytic plant.

Velamen radicum – the layer of spongy epidermal tissue that sheaths the roots of orchids and some other monocots.

Vine – a non-woody climbing plant.

General Ecology

Amensalism – an interaction in which one interacting species is detrimentally affected, whilst there is no or negligible effect on the other.

Anemochory – of a seed or fruit, dispersed by wind.

Assemblage – a collection of species of a related group in a particular location. This term has term has been suggested in an epiphyte context given that, strictly, epiphytes cannot be a true community without inclusion of all of the other species in the forest (see Mendieta-Leiva & Zotz 2015). However, the term 'epiphyte community' is still widely used in place of 'epiphyte assemblage' for ease of communication.

Commensalism – an interaction in which one interacting species benefits but there is no or negligible effect on the other species. This describes the interaction between an epiphyte and its host tree (the epiphyte benefits from the structural support, the host is largely unaffected).

Endozoochory – of a seed or fruit, dispersed by animals internally. In a New Zealand context, this is primarily birds.

Keystone interaction – a species interaction which disproportionately influences overall community structure.

Keystone species complex – a collection of species which collectively disproportionately influence community structure.

Morphospecies – a putative species defined in the field by macro-morphology.

Morphotaxon – a taxonomic entity (of any rank) defined in the field by macro-morphology.

Statistics and Networks

Co-occurrence – the degree to which species coexist in the same location, such as epiphytes on the same host individual or species. Co-occurrence can be negative of positive, where positive co-occurrence is when species pairs have a tendency to coexist, with negative co-occurrence the opposite.

C-score – (short for 'checkerboard score') a measure of the randomness of species occurrences in a system, with a high c-score indicating a highly non-random checkerboard pattern.

Checkerboardedness – the degree to which a matrix or network shows a checkerboard pattern, where a checkerboard pattern indicates negative co-occurrence between species.

Metacommunity – a set of interacting communities linked by dispersal. In an epiphyte context a subtly different use is employed: a set of host-individual based epiphyte assemblages linked by dispersal (each host tree contains one assemblage).

Metacommunity network – (in an epiphyte context) a network describing the interaction between epiphyte species and host individuals.

Meta-network framework – the framework proposed by Burns & Zotz (2010) whereby two scales of network exist. One scale (the network scale) looks at the interactions between epiphyte species and host tree species, whilst the other (metacommunity scale) looks at the interaction between epiphyte species and host individuals (of the same species).

Negative co-occurrence – the tendency of species pairs not to coexist with one another in an ecological system. Negative co-occurrence can occur across a system, with many species tending to not co-occur. Extreme negative co-occurrence in a system would look like a checkerboard. Thus, with regards to a network or matrix, checkerboardedness has a broadly similar meaning to negative co-occurrence.

Nestedness – a measure of order in an ecological system, especially one which can be quantified by a bipartite network. A system is nested when species with few interaction partners interact with a subset of interaction partners of species with many partners. In an epiphyte context, this means rarer epiphytes occurring on few hosts occur on a subset of the hosts that common epiphytes occur on.

NODF – a widely used nestedness metric for a binary matrgix following Almeida-Neto et al. (2008) – short for 'Nestedness metric based on Overlap and Decreasing Fill'.

PERMANOVA – PERmutational Multivariate ANalysis Of VAriance.

Appendix 2

Four supplementary tables for chapter 2. All data in appendix 2 refers to the species from chapter 2.

Appendix 2.1

A summary of the abundance of all species encountered during field surveying, grouped into two groups: a group containing the 14 species included in the analyses (i.e. meeting the 50 individuals threshold) and another group containing the remaining species. The species included in the analysis are above the dividing line. Species within each group are ordered by epiphytic abundance. All values of abundance are raw totals pooled from the entire survey, irrespective of size class or host tree fern.

Species	Epiphytic Abundance	Terrestrial Abundance	Overall Abundance
Weinmannia racemosa	795	11	806
Geniostoma ligustrifolium	68	75	143
Coprosma grandifolia	61	92	153
Pseudopanax crassifolius	52	159	211
Pseudopanax arboreus	37	15	52
Laurelia novae-zelandiae	26	455	481
Melicytus ramiflorus	24	30	54
Knightia excelsa	13	297	310
Olearia rani	12	38	50
Brachyglottis repanda	3	52	55
Hedycarya arborea	2	590	592
Beilschmiedia tawa	2	138	140
Elaeocarpus dentatus	1	398	399
Nestegis sp.	0	55	55
Griselinia littoralis	13	1	14
Coprosma lucida	12	15	27
Schefflera digitata	7	17	24
Carpodetus serratus	6	22	28
Leucopogon fasciculatus	4	4	8
Coprosma foetidissima	4	2	6
Raukaua edgerleyi	4	0	4
Prumnopitys ferruginea	2	27	29
Dacrydium cupressinum	2	4	6
Griselinia lucida	2	0	2
Aristotelia serrata	1	4	5
Coprosma rhamnoides	1	3	4
Myrsine salicina	0	23	23
Pseudowintera axillaris	0	20	20
Piper excelsum	0	6	6
Prumnopitys taxifolia	0	6	6
Dacrycarpus dacrydioides	0	4	4
Myrsine australis	0	3	3
Lophomyrtus bullata	0	2	2
Pennantia corymbosa	0	2	2
Raukaua anomalus	0	2	2
Fuscospora truncata	0	1	1

Appendix 2.2

Table summarising the sizes of the tallest recorded epiphytic/hemiepiphytic individuals of each of species (in metres) and providing comments on observations of reproductive biology (i.e. flowering or fruiting). Measurements for free-standing hemiepiphytically-recruited individuals are included but indicated by an asterisk (*), with the measurement for the tallest epiphytic/hemiepiphytic individual (with extant host) given afterwards. N/A indicates a taxon was never recorded as an epiphytically occurring individual. Comments on reproductive biology indicate specific heights where fruiting individuals were encountered in the survey, otherwise general observations of fruiting epiphytic/hemiepiphytic individuals at the site are also recalled.

Species	Tallest Epiphytic Individual Recorded (m)	Comments on Observations of Reproductive Biology
Beilschmiedia tawa	0.3	
Brachyglottis repanda	1.04	
Coprosma grandifolia	5.5	Fruiting epiphytic individuals recorded in the survey of heights 1.5 and 3 metres tall.
Elaeocarpus dentatus	0.26	
Geniostoma ligustrifolium	1.4	Individuals from at least tall 0.51m metres recorded with at least one unripe fruiting capsule.
Hedycarya arborea	0.05	
Knightia excelsa	0.08	
Laurelia novae-zelandiae	0.07	
Melicytus ramiflorus	9*, 1.6	
Nestegis sp.	N/A	
Olearia rani	5	
Pseudopanax arboreus	7	Fruiting observed in hemiepiphytic adults.
Pseudopanax crassifolius	1.7	
Weinmannia racemosa	12*, 10	Fruiting observed in hemiepiphytic adults.

Appendix 2.3

A comparison between seedling arboreality and the typical establishment conditions of the 14 focal tree species from chapter 2. Seedling arboreality is the ratio of arboreal to terrestrial abundance for individuals of the size class ≤ 30 cm in height. Typical establishment conditions are based on field observations and literature descriptions. Species are then ordered by seedling arboreality.

Species	Seedling Arboreality	Establishment Conditions*†‡
Weinmannia racemosa	5.20	Successional Scrub and Forest, Open-Canopy Forest
Melicytus ramiflorus	1.15	Successional Scrub
Geniostoma ligustrifolium	0.34	Light Gaps
Pseudopanax arboreus	0.29	Successional Scrub and Forest
Olearia rani	-0.36	Successional Forest, Open-Canopy Forest
Pseudopanax crassifolius	-1.04	Light Gaps, Open-Canopy Forest
Coprosma grandifolia	-1.21	Light Gaps, Forest Edges
Brachyglottis repanda	-1.47	Light Gaps, Successional Forest
Laurelia novae-zelandiae	-2.75	Closed-Canopy Forest
Knightia excelsa	-2.88	Light Gaps, Successional and Closed-Canopy Forest
Beilschmiedia tawa	-3.43	Closed-Canopy Forest
Nestegis sp.	-3.56	Closed-Canopy Forest
Elaeocarpus dentatus	-5.13	Closed-Canopy Forest
Hedycarya arborea	-5.13	Closed-Canopy Forest

* Closed-Canopy Forest refers to mature broadleaf-podocarp rainforest in New Zealand.
† Open-Canopy Forest refers to other forest types in New Zealand such as Beech (Nothofagaceae) forest or *Weinmannia*-dominated areas in association with beech forest, both of which occur in Kaitoke.
‡ Light Gaps refers to disturbed canopy areas in mature broadleaf-podocarp (or to a lesser extent successional) forest.

Appendix 2.4

A table summarising the qualitative degree of epiphytism/hemiepiphytism exhibited by each species recorded and which terms are appropriate for each species. Plants are categorised as facultative or accidental epiphytes and as accidental or facultative hemiepiphytes. I follow the consensus in common usage (Benzing 1990, Burns 2010, Zotz 2016) in using the term 'accidental' epiphyte as opposed to the perhaps more intuitive 'occasional' epiphyte of Moffett (2000).

Species	Degree of Epiphytism
Weinmannia racemosa	Facultative Hemiepiphyte
Pseudopanax arboreus	Facultative Hemiepiphyte
Geniostoma ligustrifolium	Facultative Epiphyte
Melicytus ramiflorus	Typically Terrestrial; Accidental Epiphyte*; Accidental Hemiepiphyte*
Coprosma grandifolia	Facultative Epiphyte; Accidental Hemiepiphyte†
Olearia rani	Typically Terrestrial; Accidental Epiphyte; Accidental Hemiepiphyte‡
Pseudopanax crassifolius	Typically Terrestrial; Accidental Epiphyte
Brachyglottis repanda	Typically Terrestrial; Accidental Epiphyte¥
Laurelia novae-zelandiae	Typically Terrestrial; Accidental Epiphyte
Knightia excelsa	Typically Terrestrial; Accidental Epiphyte
Beilschmiedia tawa	Typically Terrestrial; Rare as an Accidental Epiphyte
Nestegis sp.	Terrestrial; No evidence of accidental epiphytism recorded.
Hedycarya arborea	Typically Terrestrial; Rare as an Accidental Epiphyte
Elaeocarpus dentatus	Typically Terrestrial; Rare as an Accidental Epiphyte

* Note that *Melicytus ramiflorus* occurs somewhat frequently epiphytically on tree ferns as a seedling or young sapling. Additionally, two adult individuals with multiple trunks and a hollow base were deemed to have established epiphytically, with subsequent death of the host. However, given that this is one of the commonest species establishing terrestrially in early successional forest, becoming a canopy dominant in mid-succesional forest, its relative abundance epiphytically or hemiepiphytically is likely far lower than indicated by my survey data (with adults nearly as common as seedlings due to focus on closed-canopy forest). Although it must also be noted that following Moffett 2000, it might be better described as an 'occasional' hemiepiphyte rather than 'accidental' as these rare hemiepiphytically-established individuals are likely to be reproductive.

† *Coprosma grandifolia* commonly occurs epiphytically on tree ferns (including reproductive individuals). However, this species rarely produces sufficient rooting to make terrestrial connection, but one large hemiepiphytic individual in our survey appeared to have made a terrestrially rooted connection.

‡ The sole *Olearia rani* found growing hemiepiphytically had germinated <20cm from the base of the tree fern trunk so was easily able to establish terrestrial rooting. Hemiepiphytic establishment in this species is otherwise rare.

¥ Alternatively, other unpublished data suggests *Brachyglottis repanda* may be sufficiently common on *Cyathea medullaris* in earlier successional habitat to be referred to as a facultative epiphyte.

Appendix 3

A table listing the taxa recorded during field surveying for chapter 3. Reported for each species are the higher taxonomic group (lycophyte, fern, conifer, monocot, magnoliid, eudicot), habit classifications, dispersal syndrome, and the number of tree fern individuals each species was recorded on [#] (out of a possible 170). Comments on habit classification or ID are provided where relevant. Non-woody ± obligate epiphytes are recorded as 'Obligate Epiphyte' for brevity. Likewise non-woody facultative and accidental epiphytes are abbreviated to 'Fac/Acc Epiphyte', with all species being best described as accidental epiphytes except *Asplenium oblongifolium* which is a facultative epiphyte – noted in the comments. Species are ordered by habit (specific), and within that by higher taxon, and then alphabetically.

Species	Higher Taxon	Habit - Broad	Habit - Specific	Dispersal Synd.	Comments	#
Blechnum filiforme	Fern	Climber	Climber	Wind		60
Microsorum scandens	Fern	Climber	Climber	Wind		2
Freycinetia banksii	Monocot	Climber	Climber	Endozoochory		40
Metrosideros diffusa	Eudicot	Climber	Climber	Wind		98
Metrosideros fulgens	Eudicot	Climber	Climber	Wind		60
Metrosideros perforata	Eudicot	Climber	Climber	Wind		60
Hymenophyllum demissum	Fern	Epiphyte *s. l.*	Filmy Fern	Wind	A facultative epiphyte, by far the commonest filmy fern on the forest floor (as well as on tree ferns) and therefore occasionally spreading rhizomatously onto the base the tree fern. However, likely mostly epiphytic germination.	84
Hymenophyllum dilatatum	Fern	Epiphyte *s. l.*	Filmy Fern	Wind		4
Hymenophyllum flabellatum	Fern	Epiphyte *s. l.*	Filmy Fern	Wind		59
Hymenophyllum multifidum	Fern	Epiphyte *s. l.*	Filmy Fern	Wind		5
Hymenophyllum nephrophyllum	Fern	Epiphyte *s. l.*	Filmy Fern	Wind	A facultative epiphyte.	8
Hymenophyllum rarum	Fern	Epiphyte *s. l.*	Filmy Fern	Wind		5
Hymenophyllum revolutum	Fern	Epiphyte *s. l.*	Filmy Fern	Wind		43
Trichomanes venosum	Fern	Epiphyte *s. l.*	Filmy Fern	Wind		64
Phlegmariurus varius	Lycophyte	Epiphyte *s. l.*	Obligate Epiphyte	Wind		1
Asplenium flaccidum	Fern	Epiphyte *s. l.*	Obligate Epiphyte	Wind		60

Species	Group	Type	Sub-type	Dispersal	Notes	Count
Asplenium polyodon	Fern	Epiphyte *s. l.*	Obligate Epiphyte	Wind		84
Microsorum pustulatum	Fern	Epiphyte *s. l.*	Obligate Epiphyte	Wind	Sometimes treated as a climber (e.g. Blick & Burns 2011) and other times an epiphyte (e.g. Kirby 2014). It usually germinates epiphytically, but when it does occur terrestrially its rhizomes can climb up host trees. However, here I follow Kirby (2014) and classify it as an epiphyte.	14
Notogrammitis billardierei	Fern	Epiphyte *s. l.*	Obligate Epiphyte	Wind		5
Rumohra adiantiformis	Fern	Epiphyte *s. l.*	Obligate Epiphyte	Wind		16
Tmesipteris sp.	Fern	Epiphyte *s. l.*	Obligate Epiphyte	Wind	Combination of *T. elongata*, *T. tannensis* and unidentified *Tmesipteris* specimens, due to a lack of certainty of species ID of the many infertile specimens.	20
Astelia hastata	Monocot	Epiphyte *s. l.*	Obligate Epiphyte	Endozoochory		1
Astelia solandri	Monocot	Epiphyte *s. l.*	Obligate Epiphyte	Endozoochory		68
Asplenium bulbiferum	Fern	Epiphyte *s. l.*	Fac/Acc Epiphyte	Wind		11
Asplenium oblongifolium	Fern	Epiphyte *s. l.*	Fac/Acc Epiphyte	Wind	Facultative epiphyte.	19
Blechnum discolor	Fern	Epiphyte *s. l.*	Fac/Acc Epiphyte	Wind		2
Dicksonia squarrosa	Fern	Epiphyte *s. l.*	Fac/Acc Epiphyte	Wind	A case of one tree fern species occurring epiphytically on another tree fern species. Rare recorded in the literature.	1
Lastreopsis hispida	Fern	Epiphyte *s. l.*	Fac/Acc Epiphyte	Wind		3
Leptopteris hymenophylloides	Fern	Epiphyte *s. l.*	Fac/Acc Epiphyte	Wind		4
Lindsaea trichomanoides	Fern	Epiphyte *s. l.*	Fac/Acc Epiphyte	Wind		1
Dacrydium cupressinum	Conifer	Epiphyte *s. l.*	Woody Epiphyte	Endozoochory		5
Beilschmiedia tawa	Magnoliid	Epiphyte *s. l.*	Woody Epiphyte	Endozoochory		1
Hedycarya arborea	Magnoliid	Epiphyte *s. l.*	Woody Epiphyte	Endozoochory		3
Laurelia novae-zelandiae	Magnoliid	Epiphyte *s. l.*	Woody Epiphyte	Wind		3
Coprosma grandifolia	Eudicot	Epiphyte *s. l.*	Woody Epiphyte	Endozoochory		23
Coprosma lucida	Eudicot	Epiphyte *s. l.*	Woody Epiphyte	Endozoochory		3
Elaeocarpus dentatus	Eudicot	Epiphyte *s. l.*	Woody Epiphyte	Endozoochory		8
Geniostoma ligustrifolium	Eudicot	Epiphyte *s. l.*	Woody Epiphyte	Endozoochory		5

Species						Count
Griselinia littoralis	Eudicot	Epiphyte *s. l.*	Woody Epiphyte	Endozoochory	Possible issue ID'ing at least one *Griselinia* seedling. When very young (<20cm tall) they can be difficult to reliably ID to species.	3
Griselinia lucida	Eudicot	Epiphyte *s. l.*	Woody Epiphyte	Endozoochory		1
Knightia excelsa	Eudicot	Epiphyte *s. l.*	Woody Epiphyte	Wind		9
Leucopogon fasciculatus	Eudicot	Epiphyte *s. l.*	Woody Epiphyte	Endozoochory		5
Melicytus ramiflorus	Eudicot	Epiphyte *s. l.*	Woody Epiphyte	Endozoochory		1
Olearia rani	Eudicot	Epiphyte *s. l.*	Woody Epiphyte	Wind		2
Pseudopanax arboreus	Eudicot	Epiphyte *s. l.*	Woody Epiphyte	Endozoochory		10
Pseudopanax crassifolius	Eudicot	Epiphyte *s. l.*	Woody Epiphyte	Endozoochory		8
Raukaua edgerleyi	Eudicot	Epiphyte *s. l.*	Woody Epiphyte	Endozoochory		1
Schefflera digitata	Eudicot	Epiphyte *s. l.*	Woody Epiphyte	Endozoochory		2
Weinmannia racemosa	Eudicot	Epiphyte *s. l.*	Woody Epiphyte	Wind		43

Appendix 4

A plot showing the matrix fill of the filmy fern subcompartment of my community matrix from chapter 3. Rows represent filmy fern species, columns host tree fern individuals, black boxes represent presences, and white boxes absences. The filmy fern taxa are (top to bottom): *Trichomanes venosum*, *Hymenophyllum dilatatum*, *Hymenophyllum flabellatum*, *Hymenophyllum revolutum*, *Hymenophyllum demissum*, *Hymenophyllum multifidum*, *Hymenophyllum rarum*, and *Hymenophyllum nephrophyllum*.
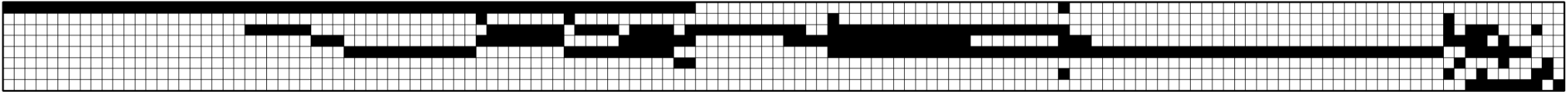
Appendix 5

A table listing the taxa recorded in surveying for chapter 4, with the family and higher order grouping also given (with lichens further subdivided into fruticose and foliose morphologies). Notes are provided to clarify any taxonomic issues, surveying or identification decisions, and the likelihood that the taxon represents a 'true' scientific species. The number of host individuals occupied of each of the three host species are given in the final three columns (L.m. = *Lophozonia menziesii*; F.c. = *Fuscospora cliffortioides*; F.f. = *Fuscospora fusca*). This gives an indication of both the bias in host distribution and of how common the taxon was in the surveyed area.

* - Psoroma sp. is a squamulose lichen, which is here treated as a subgroup of foliose lichens for simplicity.

Taxon	Family	Broad Grouping	Notes (Taxonomic, ID, Surveying etc.)	*L.m.*	*F.c.*	*F.f.*
Usnea sp.	Parmeliaceae	Fruticose Lichen	A morphologically variable genus (including within species) that is difficult to identify to species purely based on morphology.	30	30	18
Cladonia sp.	Cladoniaceae	Fruticose Lichen		18	3	8
Bunodophoron sp.	Sphaerophoraceae	Fruticose/Foliose Lichen	Possibly 2 (or maybe more) species in this genus at the field site. However, it was not easy to separate out consistently distinct morphospecies.	29	6	15
Sticta latifrons	Lobariaceae	Foliose Lichen		4	0	0
Sticta cf. *martinii*	Lobariaceae	Foliose Lichen		2	0	0
Pseudocyphellaria billardierei	Lobariaceae	Foliose Lichen	Initially misidentified as 'probable *Pseudocyphellaria rufovirescens* but with black apothecia' due to the similarity in thallus branching pattern.	10	7	0
Pseudocyphellaria faveolata	Lobariaceae	Foliose Lichen	At least one seemingly clear specimen. Either locally uncommon in the surveyed area or under-recorded.	1	2	0
Pseudocyphellaria homoeophylla	Lobariaceae	Foliose Lichen		37	4	0
Pseudocyphellaria glabra	Lobariaceae	Foliose Lichen	Can be morphologically variable, so may have some missed pseudocryptic species.	38	5	2
Pseudocyphellaria cf. *colensoi*	Lobariaceae	Foliose Lichen	Potentially more than one 'true' species. However, a more or less consistent pale green large *Pseudocyphellaria* with yellow soredia seemed to fit best as *P. colensoi*.	14	11	1

Taxon	Family	Type	Notes			
Pseudocyphellaria cf. *multifida*	Lobariaceae	Foliose Lichen	One seemingly clear specimen. Either locally uncommon in the surveyed area or under-recorded. Potentially confused with *P. glabra* during field surveying and thus underrepresented in the data.	1	1	0
Pseudocyphellaria cf. *gretae*	Lobariaceae	Foliose Lichen		5	2	0
Lobaria adscripta	Lobariaceae	Foliose Lichen		41	12	0
Nephroma australe	Nephromataceae	Foliose Lichen		19	7	2
Nephroma sp. 'cyano'	Nephromataceae	Foliose Lichen	In the field, there appeared to be a single species of *Nephroma* with a cyanobacterial photobiont. Initially suspected to be *N. rufum*, on inspection of packet samples *Nephroma plumbeum* var. *isidiatum* may be a better fit.	20	5	0
Menegazzia nothofagi	Parmeliaceae	Foliose Lichen		7	3	1
Menegazzia cf. *subpertusa*	Parmeliaceae	Foliose Lichen		0	3	0
Menegazzia cf. *pertransita*	Parmeliaceae	Foliose Lichen	May have inadvertently been treated as somewhat of a dustbin taxon for "more typical" *Menegazzia* specimens that lacked the features of *M. nothfagi* or *N. subpertusa*. Could potentially include more than one 'true' species.	14	6	7
Hypogymnia subphysodes	Parmeliaceae	Foliose Lichen		5	1	2
?*Pannoparmelia angustata*	Parmeliaceae	Foliose Lichen	This taxon appeared consistent. It looked superficially like *Pannoparmelia angustata*, but didn't appear to have an obvious black 'hypothallus' as this species supposedly has. It did have a black underside and rhizines, so could be this researcher's inexperience with this structure that is confused here. Alternatively, this taxon this could be a totally different species such as one of the Pannariaceae.	4	5	0
Parmelia cf. *tenuirima*	Parmeliaceae	Foliose Lichen	A large (and seemingly morphologically consistent) species of the genus *Parmelia* was a common feature of the epiphyte flora and *P. tenuirima* seems a close match.	19	2	3
Pannaria sp.	Pannariaceae	Foliose Lichen	At least one large individual fitted with *P. sphinctrina*, but a broader variation of morphologies existed, including smaller and harder to ID specimens. Quite possibly multiple 'true' species.	18	2	0

Psoroma sp.	Pannariaceae	Foliose Lichen*	Some specimens that fit well with *Psoroma asperellum*. However, with difficulty in being certain for many of the smaller/poorer specimens, conservatism was applied and '*Psoroma* sp.' used.	31	8	1
UnID sp. "Perithecioid Sub-crust."	-	Foliose/Crustose Lichen	This species was primarily crustose in habit but often had up-curled foliose lobes of the more distal portions of the thallus, hence it was included in the survey. This unidentified taxon had black perithecioid reproductive structures and a distinctive dark-olive-green colouration.	16	0	0
Collema/*Leptogium* sp.	Collemataceae	Foliose Lichen	a.k.a. 'Jelly Lichens' – these are taxonomically tricky group that can be hard to reliably determine to one of these two closely related genera without microscopy. In my survey, they rarely occurred as more than 1 or 2 individuals on a host tree, so any missed pseudocryptic diversity is unlikely to significantly alter the results for this taxon.	13	1	0
Peltigera sp.	Peltigeraceae	Foliose Lichen	Only 1 individual surveyed, thus definitely just 1 species.	0	1	0
Weymouthia cochlearifolia	Lembophyllaceae	Moss		6	0	0
Lembophyllum sp.	Lembophyllaceae	Moss	Only 2 NZ species, so limited scope for missed diversity.	9	0	0
Lepyrodon australis	Lepyrodontaceae	Moss		24	4	0
Macromitrium sp.	Orthotrichaceae	Moss	*Macromitrium* sp. have a distinctive scrambling form that spreads around host tree trunks. However, more established individuals form dense clumps. These two forms mean that morphological intraspecific variation in can be as great as any interspecific variation. Hence, I conservatively didn't identify Macromitrium beyond genus level.	59	19	2

Species	Family	Type	Notes			
Glyphothecium sciuroides	Ptychomniaceae	Moss	One of the commonest morphospecies during surveying, occurring in relatively high abundance. It was not ID'd in the field but was a consistent taxon. Initially, this was identified as *Cyrtopus setosus* based on sporophyte position, but leaf shape was wrong and so this ID was corrected to *G. sciuroides* – it seems unlikely (based on consistent appearance) that multiple taxa were present and intermixed.	56	8	2
Thuidiopsis furfurosa	Thuidiaceae	Moss		29	9	0
Hypnum chrysogaster	Hypnaceae	Moss		38	13	17
Hypnum cupressiforme var. filiforme	Hypnaceae	Moss	Some very clear individuals appear to be this distinctly filiform variety of *Hypnum*. However, other "UnID'd filiform moss" was recorded that were less as unidentified.	17	0	0
Papillaria flavolimbata	Meteoriaceae	Moss	*P. flavolimbata* has a distinct habit and overall appearance, but also had filiform spreading strands (± leafless to the naked eye). These spreading strands could have contributed to the records of "UnID'd filiform moss" on a handful of host individuals.	17	0	0
Wijkia extenuata	Sematophyllaceae	Moss	Not a taxon that was separated out in the field. However, appeared in a number of specimen packets and fitted with *Wijkia*. Either locally uncommon epiphytically or under-recorded in this survey.	3	0	0
Dicranoloma sp.	Dicranaceae	Moss	From the early parts of surveying treated as a single taxon (most likely *D. menziesii*). Later a clump of a very distinctly larger *Dicranoloma* (maybe *D. robustum*) was recorded. However, for consistency, this whole genus was kept as a single morphotaxon, but seems likely that the vast majority was probably *D. menziesii* anyway.	58	9	4
Mesotus celatus	Dicranaceae	Moss		54	1	0
Holomitrium perichaetiale	Dicranaceae	Moss		1	0	0
UnID sp. "Little Tufty"	-	Moss		22	2	1
UnID sp. "Cuppy"	-	Moss		5	0	0

Hymenophyllum multifidum	Hymenophyllaceae	Fern	A putative species list from the area lists only 2 other *Hymenophyllum* species, but all examined fronds appeared to be *H. multifidum*. Although another taxon could conceivably have been present in low numbers given the sometimes subtle differences between *Hymenophyllum* species.	11	0	0
Notogrammitis billardierei	Polypodiaceae	Fern	Whilst *Notogrammitis* can also seem pseudocryptic without experience of the group, there was no indication of more than one species.	26	0	0
Asplenium flaccidum	Aspleniaceae	Fern		5	0	0

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