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Epiphyte ecology in urban forests: community assembly, traits, ecophysiology and the role of tree ferns

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Hannah Catherine Rogers



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In loving memory of my grandmothers,

Aldyth Pearson and Rosalie Rigden

Abstract

Vascular epiphytes are a conspicuous feature of New Zealand's temperate rainforests. Epiphytes contribute to ecosystem functioning by increasing species diversity, enhancing habitat heterogeneity, and influencing ecosystem processes such as primary production and the cycling of water and nutrients. However, research on epiphytes in temperate regions remains limited compared to tropical regions, especially in urban environments. This thesis addresses key research gaps in our understanding of urban epiphyte communities by reporting results from four interconnected studies. Collectively, these advance our knowledge of the biology and ecology of indigenous epiphytes in two warm temperate cities on North Island, New Zealand.

In the first study, tree ferns were shown to augment native species richness in urban plant communities. Ground ferns and vascular epiphyte diversity were significantly higher in plots with tree ferns, illustrating strong facilitative effects. In contrast, light-demanding seedlings, saplings and trees were less frequent in plots with tree ferns, suggesting competitive interactions between these plant groups. Nonetheless, tree ferns can accelerate ecological restoration by increasing native plant diversity and providing an established canopy that helps suppress light-demanding invasive plant species. Community structure also differed significantly among site types in Hamilton: tree ferns increased total basal area, whereas restored sites supported more diverse tree and shrub communities. Associated shade-tolerant species, such as *Schefflera digitata*, suggest that enrichment planting of extant tree fern stands with such species may encourage a successional pathway towards conifer-broadleaved forest.

The second study investigated trait matching between epiphytes and host species. Root and rhizome characteristics among 10 epiphyte species showed varying associations with specific host preferences—either favouring tree ferns, woody trees, or exhibiting generalist tendencies. Species mainly associated with tree ferns had longer, more abundant rhizome hairs, while generalist epiphytes had wider rhizomes, longer roots, and longer, more abundant rhizome scales. Links revealed between epiphyte traits and host preferences suggest that biotic filters (e.g., host availability) may exert a greater effect on epiphyte assemblages than stochastic processes (e.g., dispersal limitation).

To better understand epiphyte tolerance to water and light availability, the third study involved an *ex-situ* greenhouse experiment. This revealed distinct physiological responses of four epiphytic ferns to water and light availability, which were associated with epiphyte microhabitat preferences. During a 12-week simulated drought, the species most closely associated with tree ferns (*Asplenium polyodon*) exhibited a rapid decline in photosynthetic capacity (A_{max}). The generalist *Pyrrosia elaeagnifolia* was drought-resistant, maintaining A_{max} and stomatal conductance (g_s). Unexpectedly, the generalist *Lecanopteris pustulata* was not drought-resistant, exhibiting significant declines in A_{max} and g_s. *Asplenium flaccidum* (associated with tree ferns in urban settings) was drought-avoidant, with low but constant A_{max} and g_s. Light environments mimicking two distinct host microhabitats (tree ferns and woody trees) revealed greater shade tolerance in *A. polyodon* than *P. elaeagnifolia*, as indicated by predawn F_v/F_m. High light conditions exacerbated plant drought stress, as shown by reduced recovery compared with plants under low light.

Finally, epiphyte community data were revisited to explicitly test the influence of environmental predictors on obligate epiphyte diversity in constrained (i.e., urban forests) and unconstrained (i.e., non-urban forests) host communities. Obligate epiphyte communities in urban forests were more homogeneous than in non-urban forests, supporting fewer epiphytic shrubs, lycophytes and orchids. SEMs showed that urban epiphyte richness was indirectly influenced by forest age and tree fern basal area, and directly positively influenced by relative humidity stability and *Dicksonia squarrosa* basal area. In non-urban forests, epiphyte richness was positively associated with tree fern and woody tree basal areas. Epiphyte richness increased with host species richness and was influenced by host assemblage composition. Tree fern basal area positively influenced epiphyte richness in urban forests, although woody tree basal area had a negative relationship, which may reflect a lack of high-quality host species.

This research has expanded our understanding of epiphyte communities in temperate cities and how host assemblages, morphological and physiological traits, and environmental conditions influence them. It also provides a basis for implementing ecological restoration of diverse host assemblages that provide sheltered, damp habitat suitable for epiphytes. Future long-term studies on a wider range of species will be needed to build upon this research.

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Table of Contents

Abstract ..... **i**
Acknowledgements ..... **iii**
Table of Contents ..... **v**
List of Figures ..... **viii**
List of Tables ..... **ix**
List of Appendices ..... **x**
Chapter 1. Introduction **1**
1.1. Background 1
1.1.1. Tree ferns in urban plant communities 2
1.1.2. Epiphyte traits and community structure 4
1.1.3. Physiological responses of epiphytes in relation to microhabitat preferences 5
1.1.4. Environmental determinants of epiphyte diversity 6
1.2. Thesis overview 8
References 11
Chapter 2. Tree ferns augment native plant richness and influence composition in urban plant communities **17**
Abstract 17
2.1. Introduction 17
2.2. Materials and methods 19
2.2.1. Study area 19
2.2.2. Site selection 20
2.2.3. Vegetation survey 22
2.2.4. Data analysis 23
2.3. Results 26
2.3.1. Plant abundances and richness 26
2.3.2. Community composition 31
2.3.3. Community structure 33
2.3.4. Environmental predictors of plant communities 35
2.4. Discussion 37
2.4.1. Community assembly and succession 37
2.4.2. Study limitations 38
2.4.3. Implications for urban ecological restoration 39
2.5. Conclusions 40
References 41
Chapter 3. Trait matching contributes to epiphyte host preferences in New Zealand urban forests **46**

Abstract 46
3.1. Introduction 46
3.2. Materials and methods 49
3.2.1. Study sites 49
3.2.2. Field data collection 50
3.2.3. Trait data collection 51
3.2.4. Data analysis 52
3.3. Results 55
3.3.1. Epiphyte metacommunities 55
3.3.2. Epiphyte networks 57
3.3.3. Functional traits influencing attachment mechanisms and host preferences 59
3.4. Discussion 61
3.4.1. Epiphyte host preferences 61
3.4.2. Functional traits 63
3.4.3. Attachment mechanisms 64
3.5. Conclusions 64
References 66
Chapter 4. Physiological responses of four epiphytic ferns to water and light availability 71
Abstract 71
4.1. Introduction 71
4.2. Materials and methods 74
4.2.1. Experimental design 74
4.2.2. Epiphyte species 75
4.2.3. Data collection 77
4.2.4. Data analysis 79
4.3. Results 80
4.3.1. Experiment results 80
4.3.2. Drought recovery responses 83
4.3.3. Frond mortality 85
4.3.4. Water potential 86
4.3.5. Isotope analysis 87
4.4. Discussion 88
4.4.1. Factors shaping epiphyte communities 88
4.4.2. Epiphyte drought responses and recovery 88
4.4.3. Light responses 89
4.4.4. Water-use efficiency and nutrient acquisition 90

4.5. Conclusions 91
References 92
Chapter 5. Microclimate stability and tree ferns enhance obligate epiphyte richness 96
Abstract 96
5.1. Introduction 96
5.2. Materials and methods 99
5.2.1. Study areas 99
5.2.2. Data collection 100
5.2.3. Data analysis 103
5.3. Results 105
5.3.1. Epiphyte communities of urban and non-urban forests 105
5.3.2. Host species composition effect on epiphyte richness 106
5.3.3. Environmental predictors of epiphyte richness 107
5.3.4. Causal pathway analysis of urban epiphyte richness 108
5.4. Discussion 112
5.4.1. Epiphyte communities of urban and non-urban forests 112
5.4.2. Host species composition effect on epiphyte richness 113
5.4.3. Environmental predictors of epiphyte richness 114
5.4.4. Causal pathway analysis of urban epiphyte richness 115
5.5. Conclusions 116
References 117
Chapter 6. Synthesis 122
6.1. Discussion 122
6.1.1. Tree ferns in urban plant communities 122
6.1.2. Epiphyte traits and community structure 123
6.1.3. Physiological responses of epiphytes in relation to microhabitat preferences 124
6.1.4. Environmental determinants of epiphyte diversity 125
6.2. Research applications 126
6.3. Recommendations for further research 127
6.4. Conclusions 127
References 129
Supplementary Materials 132
Chapter 2 132
Chapter 3 139
Chapter 4 147
Chapter 5 151

List of Figures

Chapter 1

Fig. 1. The four main interconnected chapters of the thesis 8

Chapter 2

Figure 1. Site locations in Hamilton, North Island, New Zealand 21
Figure 2. Example sites of the four site types based on restoration status 22
Figure 3. Mean rarefied native vascular plant species richness. 28
Figure 4. Nonmetric multidimensional scaling (NMDS) ordination 33
Figure 5. Tree and tree fern basal areas (m^2 ha^{-1}) of vegetation plots 34

Chapter 3

Fig. 1 Study sites (dots) where epiphyte and host species data were collected 50
Fig. 2 Rhizome and roots of the 10 measured epiphyte species 52
Fig. 3 Native obligate epiphyte composition on tree ferns 56
Fig. 4 Epiphyte-host relationships of twelve lowland epiphyte species 58
Fig. 5 Epiphyte root and rhizome trait associations with host preferences 59

Chapter 4

Fig. 1. Predicted gradient of epiphyte host preferences 76
Fig. 2. Mean ± SE of photosynthetic capacity (a), stomatal conductance (b) 83
Fig. 3. Photosynthetic capacity (A_{max}), stomatal conductance (g_s) a 85
Fig. 4. Estimated frond water potential (ψ) of epiphytes 86

Chapter 5

Fig. 1. *A priori* structural equation model (SEM) 99
Fig. 2. Study sites of non-urban vegetation plots. 100
Fig. 3. Epiphyte community composition of urban vegetation plots 106
Fig. 4. Bivariate relationships influencing obligate epiphyte richness 108
Fig. 5. Final SEMs illustrating drivers of obligate epiphyte species richness 110

List of Tables

Chapter 2

Table 1. Mean (± standard deviation) native, exotic and total plant abundances 27

Table 2. Generalised linear model results testing the effect of tree fern presence.....29

Table 3. Mean (± standard deviation) native species abundance, richness.....31

Table 4. Generalised linear model results investigating environmental predictors 35

Chapter 3

Table 1. Host assemblages surveyed in the present study and by Bryan (2011) 51

Table 2. Mean (± SD) values of the morphological traits measured.....60

Chapter 4

Table 1. Linear mixed effects model results for photosynthetic capacity (A_{max}) 82

Table 2. Mean (± SE) stable isotope values for the four epiphytic fern species. 87

Chapter 5

Table 1. Mean ± SE obligate epiphyte richness, forest age, tree fern basal area 101

Table 2. Mean ± SD of epiphyte richness, mean relative humidity 103

Table 3. Final results for the first SEM testing causal pathways of epiphyte 111

Table 4. Final results for the second SEM testing causal pathways.....111

List of Appendices

Chapter 2

Figure A1. Rarefaction and extrapolation curves for each plot 132

Figure A2. Redundancy analysis (RDA) of the effect of restoration..... 133

Figure S1. Vegetation plot design (200 m^2)..... 134

Figure S2. Variation partitioning of the effects of tree fern basal area..... 134

Table B1. Pairwise comparisons of vascular plant communities..... 135

Table B2. Indicator species associated with three of our site types 135

Table B3. Scientific names associated with the six-letter species codes 135

Table S1. Site age and history of the sixteen vegetation plots. 137

Table S2. Pairwise comparisons of native vascular plant communities..... 138

Table S3. Three leading dominant trees or tree ferns..... 138

Chapter 3

Fig. S1. Urban epiphyte-host network using binary presence/absence 139

Fig. S2. Compositional differences of epiphyte assemblages 140

Fig. S3. Epiphyte root and rhizome trait correlation heat map..... 141

Table S1. Site information for the 32 sites assessed 141

Table S2. Mantel Test results for each dataset. 142

Table S3. Epiphyte species allocated to the three groups. 143

Table S4. Null model results (using 'Econullnetr' R package)..... 143

Table S5. Indicator species of three host types 144

Table S6. Scientific names associated with the six-letter codes 144

Table S7. Linear mixed effects model results. 146

Chapter 4

Fig. S1. Mean ± SE of A_{max} (a), g_s (b) and F_v/F_m (c) of the epiphytic ferns. 147

Fig. S2. Mean frond mortality ± SE of the four epiphytic ferns..... 148

Fig. S3. Volumetric soil moisture against predawn frond water potential (ψ_{wpd})..... 148

Table S1. Pairwise comparisons of species A_{max} between Week 2 and Week 12. 149

Table S2. Pairwise comparisons of the g_s of plants..... 150

Table S3. Pairwise comparisons of predawn F_v/F_m..... 150

Table S4. Recovery linear mixed effects model results for photosynthesis..... 150

Table S5. Analysis of variance (ANOVA) results comparing $\delta^{13}C$ 151

Chapter 5

Fig S1. Daily mean temperature recorded at the Ruakura climate station.....151
Fig S2. Daily mean rainfall recorded at the Ruakura climate station. 152
Fig S3. Rarefaction curves illustrating sampling effort for obligate epiphyte.....153
Fig S4. Daily relative humidity data from the gully (green symbols) 153
Table S1. List of obligate (i.e., holo-epiphyte) and hemi-epiphyte species 154
Table S2. Daily temperature statistics for Hamilton and New Plymouth 155
Table S3. Daily rainfall statistics for Hamilton and New Plymouth.....156

Chapter 1. Introduction

The present chapter (Chapter 1) provides an overview of relevant research (more detailed literature reviews are found within each of the main chapters), presents the main research question for each chapter, and outlines the thesis contents.

1.1. Background

Vascular epiphytes (i.e., plants that grow on other plants for structural support) make up approximately 10% of plant species globally (Zotz et al., 2021). Epiphytes contribute to ecosystem processes by modifying nutrient and water fluxes, but the magnitude of these effects differs across ecosystems (Nadkarni, 1986; Zotz, 2016). For example, large nest epiphytes retain water and accumulate leaf litter, forming canopy soil and creating microhabitats that other epiphytes can colonise (Chen et al., 2019). The relationship between an epiphyte and its host species is commensal, although epiphytes may exhibit nutritional piracy (e.g., intercepting minerals) or structural piracy by physically impairing hosts with heavy loads (Strong, 1977; Benzing and Seemann, 1978). Epiphytes may also alter the host tree microclimate by buffering temperature fluctuations and reducing moisture loss (Stanton et al., 2014).

While epiphytes are generally associated with tropical regions, the diversity and biomass of epiphytes in New Zealand's temperate rainforests are comparable to some tropical forests (Hofstede et al., 2001). Vascular epiphytes make up almost 3% of New Zealand's indigenous flora (Kirby, 2016). The taxonomic spectrum of New Zealand's epiphytic flora, like temperate forests in Chile and montane forests in the Himalayas, is dominated by ferns (Zotz, 2005). For example, more than two-thirds of the native epiphytic flora are ferns. Other life forms of the native epiphytic flora are orchids (15%), shrubs and trees (11%), nests (3%), and succulents (3%). Prominent threats to vascular epiphytes in New Zealand include diminished bird populations that constrain seed dispersal, skewed sex ratios of dioecious species, browsing by invasive possums (*Trichosurus vulpecula*), and habitat loss (Myron et al., 2021).

In cities, lower epiphyte diversity likely results from fragmented forests with homogeneous host assemblages and a scarcity of large hosts (Taylor and Burns, 2015a; Gallego et al., 2025). Fragmented forest patches also have stronger edge effects, leading to warm, dry microclimates that may encourage homogeneous, drought-tolerant plant communities (Alvim

et al., 2021; Gallego et al., 2025). Urban heat island effects may also lead to warmer, drier microclimates unfavourable for epiphytes (Rooke-Devoy, 2023). Epiphytes are sensitive to changes in forest structure, making them useful indicators of ecological integrity and microclimate stability. Hence, knowledge of epiphyte communities in modified urban environments will help inform conservation and restoration projects.

Ecological restoration activities facilitate the recovery of degraded ecosystems (Clewell et al., 2004). This practice presents particular challenges in modified urban environments subject to ongoing anthropogenic disturbances. Nevertheless, there is an increasing urgency to protect and restore indigenous biodiversity in cities, given the numerous ecosystem services it provides (Klaus and Kiehl, 2021). Restoration projects often follow bespoke objectives, although restoring the full suite of species naturally occurring prior to disturbance is a broadly shared goal (Noreika et al., 2020). While trees and shrubs are often the focus of forest restoration, projects with long-term objectives of restoring the full range of species must also consider other life forms, such as epiphytes (Gómez-Aparicio, 2009; Reid et al., 2016). Furthermore, understanding how different pioneer plant communities influence successional trajectories and community assembly can help maximise native diversity in ecological restoration. The restoration of late-successional plant groups, such as epiphytes, requires ecological knowledge of their environmental tolerances and interactions with host species (Oishi and Doei, 2015).

1.1.1. Tree ferns in urban plant communities

Urban forest patches face ongoing human disturbances, which can lead to novel plant assemblages dominated by invasive species (Stewart et al., 2004). Vegetation in warm temperate cities can range from native forest remnants to recombinant plant assemblages. Recombinant or novel plant assemblages often support a high proportion of exotic plants, but in warm temperate cities, these communities can also support naturally colonising native tree ferns (Rogers and Clarkson, 2025). Early arriving tree ferns can host diverse vascular epiphyte communities and play an important functional role in New Zealand's rainforests (Brock et al., 2018a). However, research on how tree ferns influence community assembly is limited in urban settings.

Pioneer plant communities have a critical role in ecological succession and community assembly (Dávila-Hernández et al., 2025). In New Zealand's temperate rainforests, tree ferns are ubiquitous and can form important pioneer communities (Brock et al., 2018a). Tree ferns have been shown to act as ecological filters, altering community composition by inhibiting or facilitating the regeneration of other plants (Chau et al., 2013). For example, they modify community assembly with megaphylls that cast deep shade and form thick, slowly decomposing leaf litter (McKelvey, 1953; Forbes et al., 2016). Priority effects that result in tree ferns colonising first may trigger a positive feedback loop that prevents other species from establishing (Walker et al., 2010; Weidlich et al., 2021). Invasive tree ferns can also promote the dispersal and establishment of exotic epiphytes (Riefner and Smith, 2019). However, tree ferns provide numerous ecosystem services, including assisting soil development and bank stabilisation (Walker et al., 2010). In addition, tree ferns are important hosts of vascular epiphytes (Brock and Burns, 2021), and they occasionally provide major regeneration sites for angiosperm trees such as *Pterophylla racemosa* (Coomes et al., 2005).

Limited research has examined successional pathways following pioneer tree fern communities in New Zealand, although Blaschke (1988) suggested that broadleaved scrub develops 35–50 years after disturbance, a general pathway supported by Brock et al. (2018a) and Silvester (1964). Forest communities dominated by the pioneer tree fern *Cyathea medullaris* with an understory of *C. dealbata* were shown to influence community assembly towards shade-tolerant species (Brock et al., 2018a). In comparison, Brock et al. (2018b) showed that community assembly following the dominance of the light-demanding angiosperm *Kunzea robusta* facilitated higher abundances of less shade-tolerant species. Knowledge of tree fern ecology, including their competitive or facilitative interactions with different plant groups, will help inform their appropriate management in ecological restoration.

Ecological restoration practitioners focus on restoring pioneer trees and shrubs (i.e., light-demanding angiosperm and conifer species). Meanwhile, tree ferns are largely overlooked in restoration projects despite being important pioneers of conifer-broadleaved forests (Wyse et al., 2018). Extant tree fern stands may accelerate restoration progress by providing a well-established native canopy, a primary objective in ecological restoration. A developed canopy suppresses light-demanding invasive plants that compete with native species (Martin et al., 2009). While restoration projects primarily focus on woody pioneer species, understanding

the role of tree ferns in urban environments will present opportunities for ecological restoration.

1.1.2. Epiphyte traits and community structure

A key goal in ecology is to understand the role of stochastic versus deterministic processes in structuring plant communities (Kraft and Ackerly, 2014). Neutral theory suggests that stochastic processes (e.g., ecological drift and chance colonisation) are entirely responsible for community structure (Hubbell, 2011). From a deterministic perspective, niche theory argues that environmental filters, biotic interactions and interspecific trade-offs govern community assembly (Chase and Myers, 2011). Evidence for both stochastic and deterministic processes governing epiphyte community structure has been found (Taylor and Burns, 2015b; Mendieta-Leiva et al., 2022). For example, Janzen et al. (2020) found indistinguishable patterns between those observed and those generated by near-neutral models. Furthermore, both neutral and niche-based processes have been found to simultaneously influence epiphyte community structure (Francisco et al., 2021).

Non-random epiphyte-host interactions, including epiphyte host preferences, support niche theory, in which environmental filters (e.g., functional traits) determine community assembly (Lavorel and Garnier, 2002). Epiphyte host preferences refer to the strength of relationships between an epiphyte and host species. Strict host-specificity is rare, in which an epiphyte species occurs exclusively on a single host species. However, a certain host bias is ubiquitous, with epiphytes exhibiting preferences for only a few host species, or a single 'host type' based on host traits (Callaway et al., 2002; Wagner et al., 2015). Host preferences may therefore be visualised along a continuum, ranging from host-specific epiphytes to generalist epiphytes that grow on many host species.

Research on epiphyte host preferences has focused on the role of host traits (Hirata et al., 2009; Wagner and Zotz, 2020). Smooth or unstable, flaking bark may deter epiphyte colonisation, while rough yet stable bark is more conducive to epiphytes (Wyse and Burns, 2011). In a cloud forest in Mexico, epiphyte preferences for tree ferns were attributed to their thicker root mantle and greater water retention than angiosperms (Mehltreter et al., 2005). Host species architecture, size and age can also significantly influence epiphyte communities (Hirata et al., 2009). However, epiphyte functional traits likely also contribute to host

preferences (Wagner et al., 2015). Functional traits impact the performance and environmental tolerance of species, which may partially explain species interactions and distributional patterns (Kearney et al., 2010). For example, epiphyte traits such as root length and the presence of velamen and/or trichomes may facilitate epiphyte attachment by enhancing the surface area of epiphyte roots and rhizomes (Wang et al., 2021; Tay et al., 2023). The ability to entangle rhizomes or roots around entire stems or branches may enable epiphytes to establish on hosts with flaking bark (Benzing, 1978). Additionally, leaf traits associated with water relations, such as succulence, $\delta^{13}C$ and $\delta^{15}N$, have been shown to vary with microclimate conditions (Gotsch et al., 2022). Trait matching between epiphyte and host species was observed in a lowland forest in Panama; however, this phenomenon was limited to the tree crowns and was not evident on the host stems (Wagner et al., 2021). Further investigation into mechanisms underpinning trait matching, such as epiphyte functional traits, will deepen our understanding of factors contributing to non-random epiphyte-host interactions.

1.1.3. Physiological responses of epiphytes in relation to microhabitat preferences

Similar to the functional role of morphological traits, plant responses to environmental change (i.e., their ecophysiology) can influence plant community structure (Harrison et al., 2010; Gotsch et al., 2015; Einzmann et al., 2015). Epiphyte tolerance to major abiotic conditions may partially explain their preferences for certain hosts or microhabitats. For example, a study in Brazil found that the abundance of specialist epiphytes partially depended on suitable host traits (Elias et al., 2021). In contrast, generalist epiphytes appear to be well adapted to harsh abiotic conditions in human-modified environments (de Lima et al., 2025). On individual hosts, the vertical stratification of epiphytes has been examined using Johansson zones (Zotz, 2007; Sanger and Kirkpatrick, 2017). Vertical distributional patterns are mainly attributed to changes in natural ‘zones’ of environmental conditions, namely relative humidity and radiation (Johansson, 1974). Host microhabitats that differ significantly in their abiotic conditions (e.g., water and light availability) and bark characteristics can support distinct epiphyte communities (Moran et al., 2003).

Water is considered the main abiotic limitation to the growth and survival of vascular epiphytes (Zotz and Hietz, 2001). Without access to terrestrial soil resources, epiphytes rely on regular rainfall or stable, humid environments. Drought causes significant plant stress,

limiting growth and photosynthetic activity, and, in extreme cases, leads to death (Ferguson et al., 2022). Epiphytes utilise various drought strategies to minimise stress, including drought tolerance (maintaining metabolic functions), drought avoidance (e.g., shedding leaves to minimise transpiration), and poikilohydry (i.e., no regulation of water content). While some drought strategies may be more advantageous in certain environments, boundaries between them are not obvious because they are not mutually exclusive (Zhang et al., 2016).

Light is another major evolutionary driver of epiphytes (Kluge et al., 1989). Growing in the canopy, with increased light levels, can be advantageous, although well-lit environments can cause photoinhibition in shade-tolerant epiphytes (Williams et al., 2020). Epiphytes can exhibit habitat partitioning or vertical stratification on host species in response to gradients in light and humidity (Sanger and Kirkpatrick, 2017). Epiphyte species growing in shaded, damp host microhabitats may be less drought-resistant and more susceptible to photoinhibition than those associated with well-lit, drier microhabitats. For example, tree ferns can cast deep shade; they have been shown to limit the photosynthetically active radiation (PAR) at 1.4 m above the forest floor to approximately 1% in New Zealand (Coomes et al., 2005). In comparison, light availability under podocarp-broadleaf stands in New Zealand can be 1.9% and more than 4% under *Nothofagus* forest (Lusk and Carr, 2024).

Nutrient acquisition can also limit epiphyte growth and survival (Benzing, 1990). Stable isotope studies suggest that plants mainly acquiring nitrogen from the atmosphere (via N-fixing bacteria) exhibit more depleted ^{15}N than plants obtaining nitrogen from leaf litter (Watts and Watkins, 2021). Associated with water availability, epiphytes acquire nutrients from rainfall or organic matter that accumulates in the canopy (Zotz and Hietz, 2001). PAR availability also affects gas exchange and, therefore, plant nutrient status. Hence, interactive effects among these key resources (water, light and nutrients) contribute to plant physiological functioning (Salazar-Tortosa et al., 2018). Understanding the tolerance of epiphytes to essential resources (e.g., water, light and nutrient availability) will contribute to our knowledge of factors influencing their distributional patterns.

1.1.4. Environmental determinants of epiphyte diversity

The structural dependence of epiphytes makes them particularly vulnerable to environmental change (Benzing, 1998). Global trends in epiphyte diversity show a sharp decline in richness with increasing distance from the equator as tropical rainforest and precipitation decline (Gentry and Dodson, 1987; Taylor et al., 2022). Regional predictors of epiphyte diversity include climate and disturbance events that alter forest structure and host assemblages (Bartels and Chen, 2012). Rainfall and elevation are often positively correlated with epiphyte richness, although these relationships are not always linear (Wolf and Flamenco-S, 2003; Cardelús et al., 2006). Large-scale natural disturbance events, such as wildfires, also significantly affect epiphyte communities by altering forest structure (Bartels and Chen, 2012).

At a local scale, forest age, microclimate conditions, and host assemblages influence epiphyte diversity (Ding et al., 2016; Toivonen et al., 2017; Oswaldo et al., 2022). On individual trees, gradients of air temperature, vapour pressure deficits and relative humidity can shape epiphyte communities (Cardelús and Chazdon, 2005). Large trees that provide structural heterogeneity influence epiphyte composition with differences in canopy cover, branch diameter and moss depth (Woods et al., 2019). The association of epiphytes with stable microclimates makes them useful bioindicators for conservation and restoration, particularly in modified urban forests (Jarquin-Pacheco et al., 2025).

Epiphytes are structurally dependent on other plants, so their establishment and survival are reliant on suitable host microhabitats. High-quality host species (i.e., those that host diverse epiphyte assemblages) may be characterised as providing structurally heterogeneous substrates with increased moisture retention. In contrast, poor host species may have thin, smooth or peeling bark that can deter epiphytes from establishing (Vergara-Torres et al., 2010). Although factors influencing epiphyte diversity on individual hosts have been well studied, comparatively less is known about these relationships using plot-based methodology or at a regional scale.

Host assemblages influence epiphyte communities by determining the availability and quality of epiphyte habitat. Both host species diversity and density should positively correlate with epiphyte diversity by increasing habitat heterogeneity and providing a greater establishment surface area (Bartels and Chen, 2012; Woods et al., 2019). The occurrence of clumped epiphyte assemblages (e.g., where one large host supports most epiphytes within a forest plot)

suggests that the presence and density of suitable hosts may be more important than host species richness (Grubb et al., 1963; Zotz and Schultz, 2008). It also suggests that forest density alone is not sufficient as an indicator of epiphyte diversity because forests dominated by poor host species will likely support depauperate epiphyte communities.

1.2. Thesis overview

This thesis presents original research on the ecology of vascular epiphytes and their host species in urban forests, with a focus on tree ferns. The aim of the research was to determine and quantify key processes structuring epiphyte communities in Hamilton and New Plymouth, two North Island cities in New Zealand. Understanding the key processes driving plant community assembly will contribute to our knowledge of indigenous epiphytes in New Zealand and help inform restoration projects aimed at reinstating the full suite of species. Ecological research in urban environments is lacking in New Zealand, and this research was designed to help fill this gap (Fig. 1).



Fig. 1. The four main interconnected chapters of the thesis. Epiphyte ecology was studied at a range of scales, from broad community analyses (Chapter 2) to fine-scale analysis of morphological traits (Chapter 3), plant physiological responses to water and light availability (Chapter 4), and environmental predictors of obligate epiphyte richness1 in urban and non-urban forests (Chapter 5).

This thesis comprises six chapters: one has been published (Chapter 2), and three have been submitted to scientific journals or are being prepared for submission. Hence, minor differences in style, grammar, or formatting occur between chapters due to individual journal requirements. The main goal of this research was to determine key abiotic and biotic factors influencing epiphyte communities in urban environments with special regard to the New Zealand context. Each of the four main chapters poses an overarching research question that contributes to this goal.

Chapter 2: *How do tree ferns influence native plant richness and composition in urban plant communities?*

Chapter 2 investigates how tree fern presence influences urban native plant communities in Hamilton, New Zealand. Native species richness was assessed using plant groups such as trees and shrubs, ground ferns and vascular epiphytes. In addition, community composition was examined using multivariate analysis, and structural analyses were undertaken using basal area measurements of trees, shrubs, and tree ferns. This research is published as: Rogers, H. C., Burdon, F. J., & Clarkson, B. D. (2025). Tree ferns augment native plant richness and influence composition in urban plant communities. *Forests*, *16*(9), 1498.

Chapter 3: *Does trait matching between epiphyte root and rhizome traits and host types partially explain host preferences in urban settings?*

Chapter 3 examines how epiphyte traits contribute to attachment mechanisms and host preferences in urban forests. First, epiphyte host preferences were assessed using metacommunity and network analyses. Morphological traits that may contribute to host preferences, including rhizome diameter, hair and scale abundance, hair and scale length, and standard root length, were then measured for 10 species. This chapter has been submitted to *Plant Ecology* titled ‘Trait matching contributes to epiphyte host preferences in New Zealand urban forests’.

Chapter 4: *How do the physiological responses of four epiphytic ferns to water and light availability influence their microhabitat and host preferences?*

Chapter 4 tests the effects of water and light availability on the physiological performance of four epiphytic ferns exhibiting preferences for tree ferns or woody

trees. A three-month *ex-situ* experiment was conducted using a fully crossed factorial design (2 × 2) based on water availability (no water, watered) and light levels mimicking the tree fern microhabitat (low light) or woody tree microhabitat (high light). Weekly measurements were made of gas exchange, chlorophyll fluorescence, plant growth and frond water potentials. This chapter has been submitted to *Flora* titled 'Physiological responses of four epiphytic ferns to water and light availability'.

Chapter 5: *What are the key environmental predictors of obligate epiphyte diversity in urban and non-urban forests?*

Chapter 5 assesses environmental predictors of obligate epiphyte richness and composition in urban and non-urban forests. A structural equation model (SEM) was completed using species observational data and microclimate data at the plot level for plant communities in Hamilton and New Plymouth. In addition, abiotic and biotic factors influencing epiphyte richness were assessed for non-urban forest plots. This chapter is in preparation for journal submission.

Chapter 6 provides a synthesis of the research and its contribution to tree fern and vascular epiphyte biology and ecology. The chapter then discusses the implications of this research and its potential application in urban ecological restoration projects. Finally, research topics and questions that require further attention to fully disentangle mechanisms underpinning epiphyte-host relationships are provided.

References

Alvim, F. S., Furtado, S. G., & Menini Neto, L. (2021). Are vascular epiphytes in urban green areas subject to the homogenization of biodiversity? A case study in the Brazilian Atlantic Forest. *Urban Ecosystems*, *24*(4), 701–713.

Bartels, S. F., & Chen, H. Y. (2012). Mechanisms regulating epiphytic plant diversity. *Critical Reviews in Plant Sciences*, *31*(5), 391–400.

Benzing, D. H. (1978). Germination and early establishment of *Tillandsia circinnata* Schlecht. (Bromeliaceae) on some of its hosts and other supports in southern Florida. *Selbyana*, *5*(1), 95–106.

Benzing, D. H. (1998). Vulnerabilities of tropical forests to climate change: the significance of resident epiphytes. *Climatic Change*, *39*(2), 519–540.

Benzing, D. H. (1990). Vascular epiphytes. General biology and related biota. Cambridge: Cambridge University Press.

Benzing, D. H., & Seemann, J. (1978). Nutritional piracy and host decline: a new perspective on the epiphyte-host relationship. *Selbyana*, *2*(2/3), 133–148.

Blaschke, P. M. (1988). *Vegetation and landscape dynamics in eastern Taranaki hill country* (PhD Thesis, Open Access Te Herenga Waka-Victoria University of Wellington).

Brock, J. M., & Burns, B. R. (2021). Patterns of woody plant epiphytism on tree ferns in New Zealand. *New Zealand Journal of Ecology*, *45*(1), 1–10.

Brock, J. M., Perry, G. L., Lee, W. G., Schwendenmann, L., & Burns, B. R. (2018a). Pioneer tree ferns influence community assembly in northern New Zealand forests. *New Zealand Journal of Ecology*, *42*(1), 18–30.

Brock, J. M., Perry, G. L., Burkhardt, T., & Burns, B. R. (2018b). Forest seedling community response to understorey filtering by tree ferns. *Journal of Vegetation Science*, *29*(5), 887–897.

Callaway, R. M., Reinhart, K. O., Moore, G. W., Moore, D. J., & Pennings, S. C. (2002). Epiphyte host preferences and host traits: mechanisms for species-specific interactions. *Oecologia*, *132*(2), 221–230.

Cardelús, C. L., & Chazdon, R. L. (2005). Inner-crown microenvironments of two emergent tree species in a lowland wet forest. *Biotropica: The Journal of Biology and Conservation*, *37*(2), 238–244.

Cardelús, C. L., Colwell, R. K., & Watkins Jr, J. E. (2006). Vascular epiphyte distribution patterns: explaining the mid-elevation richness peak. *Journal of Ecology*, 144–156.

Chase, J. M., & Myers, J. A. (2011). Disentangling the importance of ecological niches from stochastic processes across scales. *Philosophical transactions of the Royal Society B: Biological sciences*, *366*(1576), 2351–2363.

Chau, M. M., Walker, L. R., & Mehltreter, K. (2013). An invasive tree fern alters soil and plant nutrient dynamics in Hawaii. *Biological invasions*, *15*(2), 355–370.

Chen, L. C., Wang, L. J., Martin, C. E., & Lin, T. C. (2019). Mediation of stemflow water and nutrient availabilities by epiphytes growing above other epiphytes in a subtropical forest. *Ecohydrology*, *12*(7), e2140.

Clewell, A., Aronson, J., & Winterhalder, K. (2004). *The SER International Primer on Ecological Restoration.* Society for Ecological Restoration International Science & Policy Working Group.

Coomes, D. A., Allen, R. B., Bentley, W. A., Burrows, L. E., Canham, C. D., Fagan, L., Forsyth, D. M., Gaxiola-Alcantar, A., Parfitt, R. L., Ruscoe, W. A., Wardle, D. A., Wilson, D. J., & Wright, E. F. (2005). The hare, the tortoise and the crocodile: the ecology of angiosperm dominance, conifer persistence and fern filtering. *Journal of Ecology*, *93*(5), 918–935.

Dávila-Hernández, G., Meave, J. A., Muñoz, R., & Gonzalez, E. J. (2025). A flash in the pan? The population dynamics of a dominant pioneer species in tropical dry forest succession. *Population Ecology*, *67*(1), 32–44.

de Lima, M. M., Demetrio, G. R., de Sousa Nogueira, E. M., Tiburcio, I. C. S., & Moura, F. (2025). The role of the ouricuri palm (*Syagrus coronata* (Mart.) Becc.) in supporting epiphyte biodiversity in traditional Caatinga agricultural systems. *Journal of Arid Environments*, *231*, 105471.

Ding, Y., Liu, G., Zang, R., Zhang, J., Lu, X., & Huang, J. (2016). Distribution of vascular epiphytes along a tropical elevational gradient: disentangling abiotic and biotic determinants. *Scientific Reports*, *6*(1), 19706.

Einzmann, H. J., Beyschlag, J., Hofhansl, F., Wanek, W., & Zotz, G. (2015). Host tree phenology affects vascular epiphytes at the physiological, demographic and community level. *AoB plants*, *7*, plu073.

Elias, J. P., Mortara, S. R., Nunes-Freitas, A. F., van den Berg, E., & Ramos, F. N. (2021). Host tree traits in pasture areas affect forest and pasture specialist epiphyte species differently. *American Journal of Botany*, *108*(4), 598–606.

Ferguson, B. N., Gotsch, S. G., Williams, C. B., Wilson, H., Barnes, C. N., Dawson, T. E., & Nadkarni, N. M. (2022). Variation in cloud immersion, not precipitation, drives leaf trait plasticity and water relations in vascular epiphytes during an extreme drought. *American Journal of Botany*, *109*(4), 550–563.

Forbes, A. S., Norton, D. A., & Carswell, F. E. (2016). Tree fern competition reduces indigenous forest tree seedling growth within exotic Pinus radiata plantations. *Forest Ecology and Management*, *359*, 1–10.

Francisco, T. M., Couto, D. R., Garbin, M. L., Misaki, F., & Ruiz-Miranda, C. R. (2021). Role of spatial and environmental factors in structuring vascular epiphyte communities in two neotropical ecosystems. *Perspectives in Plant Ecology, Evolution and Systematics*, *51*, 125621.

Gallego, Y. A., Carmona-Higuita, M. J., & Benavides, A. M. (2025). Urban trees as biodiversity scaffolds: patterns and drivers of epiphyte diversity in a tropical city. *Urban Ecosystems*, *28*(6), 238.

Gentry, A. H., & Dodson, C. H. (1987). Diversity and biogeography of neotropical vascular epiphytes. *Annals of the Missouri Botanical Garden*, *74*(2), 205–233.

Gómez-Aparicio, L. (2009). The role of plant interactions in the restoration of degraded ecosystems: a meta-analysis across life-forms and ecosystems. *Journal of Ecology*, *97*(6), 1202–1214.

Gotsch, S. G., Nadkarni, N., Darby, A., Glunk, A., Dix, M., Davidson, K., & Dawson, T. E. (2015). Life in the treetops: ecophysiological strategies of canopy epiphytes in a tropical montane cloud forest. *Ecological Monographs*, *85*(3), 393–412.

Gotsch, S. G., Williams, C. B., Bicaba, R., Cruz-de Hoyos, R., Darby, A., Davidson, K., Dix, M., Duarte, A., Glunk, A., Green, L., Ferguson, B., Muñoz-Elizondo, K., Murray, J.G., Picado-Fallas, I., Naesborg, R., Dawson, T.E., & Nadkarni, N. (2022). Trade-offs between succulent and non-succulent epiphytes underlie variation in drought tolerance and avoidance. *Oecologia*, *198*(3), 645–661.

Grubb, P. J., Lloyd, J. R., Pennington, T. D., & Whitmore, T. C. (1963). A comparison of montane and lowland rain forest in Ecuador I. The forest structure, physiognomy, and floristics. *The Journal of Ecology*, 567–601.

Harrison, S. P., Prentice, I. C., Barboni, D., Kohfeld, K. E., Ni, J., & Sutra, J. P. (2010). Ecophysiological and bioclimatic foundations for a global plant functional classification. *Journal of Vegetation Science*, *21*(2), 300–317.

Hirata, A., Kamijo, T., & Saito, S. (2009). Host trait preferences and distribution of vascular epiphytes in a warm-temperate forest. *Plant Ecology*, *201*(1), 247–254.

Hofstede, R. G., Dickinson, K. J., & Mark, A. F. (2001). Distribution, abundance and biomass of epiphyte-lianoid communities in a New Zealand lowland *Nothofagus*-podocarp temperate rain forest: tropical comparisons. *Journal of Biogeography*, *28*(8), 1033–1049.

Hubbell, S. P. (2011). The unified neutral theory of biodiversity and biogeography. In *The unified neutral theory of biodiversity and biogeography*. Princeton University Press.

Janzen, T., Zotz, G., & Etienne, R. S. (2020). Community structure of vascular epiphytes: a neutral perspective. *Oikos*, *129*(6), 853–867.

Jarquin-Pacheco, M. B., Armenta-Montero, S., Contreras-López, J., & Carvajal-Hernández, C. I. (2025). Urban forests as habitats for vascular epiphytes and allied terrestrial plants. *Urban Ecosystems*, *28*(4), 150.

Johansson, D. (1974). Ecology of vascular epiphytes in West African rain forest. *Acta Phytogeographica Suecica*. 59: 1–136.

Kearney, M., Simpson, S. J., Raubenheimer, D., & Helmuth, B. (2010). Modelling the ecological niche from functional traits. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1557), 3469–3483.

Kirby, C. L. (2016). Field guide to New Zealand's epiphytes, vines & mistletoes. Hamilton, New Zealand: The Environmental Research Institute, University of Waikato.

Klaus, V. H., & Kiehl, K. (2021). A conceptual framework for urban ecological restoration and rehabilitation. *Basic and Applied Ecology*, *52*, 82–94.

Kluge, M., Avadhani, P. N., & Goh, C. J. (1989). Gas exchange and water relations in epiphytic tropical ferns. In *Vascular plants as epiphytes: Evolution and ecophysiology* (pp. 87–108). Berlin, Heidelberg: Springer Berlin Heidelberg.

Kraft, N. J., & Ackerly, D. D. (2014). Assembly of plant communities. *Ecology and the Environment*, *8*, 67–88.

Lavorel, S., & Garnier, E. (2002). Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional Ecology*, *16*(5), 545–556.

Lusk, C. H., & Carr, M. A. (2024). Canopy structure and understorey light availability in Nothofagus and podocarp-broadleaf stands in a New Zealand forest. *New Zealand Journal of Botany*, *62*(4), 549–559.

Martin, P. H., Canham, C. D., & Marks, P. L. (2009). Why forests appear resistant to exotic plant invasions: intentional introductions, stand dynamics, and the role of shade tolerance. *Frontiers in Ecology and the Environment*, *7*(3), 142–149.

McKelvey, P. J. (1953). Forest colonisation after recent volcanicity at West Taupo. 435–448.

Mehltreter, K., Flores-Palacios, A., & García-Franco, J. G. (2005). Host preferences of low-trunk vascular epiphytes in a cloud forest of Veracruz, Mexico. *Journal of Tropical Ecology*, *21*(6), 651–660.

Mendieta-Leiva, G., Buckley, H. L., & Zotz, G. (2022). Directional changes over time in the species composition of tropical vascular epiphyte assemblages. *Journal of Ecology*, *110*(3), 553–568.

Moran, R. C., Klimas, S., & Carlsen, M. (2003). Low-trunk epiphytic ferns on tree ferns versus angiosperms in Costa Rica. *Biotropica*, *35*(1), 48–56.

Myron, K. J., Clarkson, B. D., & Gemmill, C. E. (2021). Biological flora of New Zealand 16: *Pittosporum kirkii* Hook. f. ex Kirk, Kirk's kōhūhū, thick-leaved kohukohu. *New Zealand Journal of Botany*, *59*(1), 112–136.

Nadkarni, N. M. (1986). The nutritional effects of epiphytes on host trees with special reference to alteration of precipitation chemistry. *Selbyana*, 44–51.

Noreika, N., Pärtel, M., & Öckinger, E. (2020). Community completeness as a measure of restoration success: multiple-study comparisons across ecosystems and ecological groups. *Biodiversity and Conservation*, *29*(13), 3807–3827.

Oishi, Y., & Doei, H. (2015). Changes in epiphyte diversity in declining forests: implications for conservation and restoration. *Landscape and Ecological Engineering*, *11*(2), 283–291.

Oswaldo, J., Hugo, C., Wilmer, T., Ismael, P., Wilson, Q., & Omar, C. (2022). Successional forests stages influence the composition and diversity of vascular epiphytes communities from Andean Montane Forests. *Ecological Indicators*, *143*, 109366.

Reid, J. L., Chaves-Fallas, J. M., Holl, K. D., & Zahawi, R. A. (2016). Tropical forest restoration enriches vascular epiphyte recovery. *Applied Vegetation Science*, *19*(3), 508–517.

Riefner, R. E., & Smith, A. R. (2019). New and noteworthy epiphytic ferns from the urban forests of Coastal Southern California, USA. *Phytologia*, *101*(1), 81–112.

Rogers, H. C., & Clarkson, B. D. (2025). Epiphyte-host relationships of remnant and recombinant urban ecosystems in Hamilton, New Zealand: the importance of *Dicksonia squarrosa* (G. Forst.) Sw., whekī. *New Zealand Journal of Botany*, *63*(1), 150–159.

Rooke-Devoy, T. H. (2023). Diversity and conservation of urban epiphytes in central Auckland. MSc Thesis, University of Auckland.

Salazar-Tortosa, D., Castro, J., Villar-Salvador, P., Viñegla, B., Matías, L., Michelsen, A., ... & Querejeta, J. I. (2018). The "isohydric trap": A proposed feedback between water shortage, stomatal regulation, and nutrient acquisition drives differential growth and survival of European pines under climatic dryness. *Global Change Biology*. 24(9), 4069–4083.

Sanger, J. C., & Kirkpatrick, J. B. (2017). Fine partitioning of epiphyte habitat within Johansson zones in tropical Australian rain forest trees. *Biotropica*, *49*(1), 27–34.

Silvester, W. B. (1964). Forest regeneration problems in the Hunua Range, Auckland. *Proceedings of the New Zealand Ecological Society*, 11, 1–5.

Stanton, D. E., Huallpa Chávez, J., Villegas, L., Villasante, F., Armesto, J., Hedin, L. O., & Horn, H. (2014). Epiphytes improve host plant water use by microenvironment modification. *Functional Ecology*, *28*(5), 1274–1283.

Stewart, G. H., Ignatieva, M. E., Meurk, C. D., & Earl, R. D. (2004). The re-emergence of indigenous forest in an urban environment, Christchurch, New Zealand. *Urban Forestry & Urban Greening*, *2*(3), 149–158.

Strong Jr, D.R. (1977). Epiphyte loads, tree falls, and perennial forest disruption: a mechanism for maintaining higher tree species richness in the tropics without animals. *Journal of Biogeography*, 215–218.

Tay, J. Y., Zotz, G., & Einzmann, H. J. (2023). Smoothing out the misconceptions of the role of bark roughness in vascular epiphyte attachment. *New Phytologist*, *238*(3), 983–994.

Taylor, A., & Burns, K. (2015a). Plant composition patterns inside an endemic birds' nest fern (*Asplenium goudeyi*) on Lord Howe Island: effects of fern size, fern isolation and plant dispersal abilities. *Journal of Tropical Ecology*, *31*(5), 413–421.

Taylor, A., & Burns, K. (2015b). Epiphyte community development throughout tree ontogeny: an island ontogeny framework. *Journal of Vegetation Science*, *26*(5), 902–910. https://doi.org/10.1111/jvs.12289.

Taylor, A., Zotz, G., Weigelt, P., Cai, L., Karger, D. N., König, C., & Kreft, H. (2022). Vascular epiphytes contribute disproportionately to global centres of plant diversity. *Global Ecology and Biogeography*, *31*(1), 62–74.

Toivonen, J. M., Suominen, L., Gonzales-Inca, C. A., Trujillo Paucar, G., & Jones, M. M. (2017). Environmental drivers of vascular and non-vascular epiphyte abundance in tropical pre-montane cloud forests in Northern Peru. *Journal of Vegetation Science*, *28*(6), 1198–1208.

Vergara-Torres, C. A., Pacheco-Álvarez, M. C., & Flores-Palacios, A. (2010). Host preference and host limitation of vascular epiphytes in a tropical dry forest of central Mexico. *Journal of Tropical Ecology*, *26*(6), 563–570.

Wagner, K., & Zotz, G. (2020). Including dynamics in the equation: Tree growth rates and host specificity of vascular epiphytes. *Journal of Ecology*, *108*(2), 761–773.

Wagner, K., Mendieta-Leiva, G., & Zotz, G. (2015). Host specificity in vascular epiphytes: a review of methodology, empirical evidence and potential mechanisms. *AoB plants*, *7*, plu092.

Wagner, K., Wanek, W., & Zotz, G. (2021). Functional traits of a rainforest vascular epiphyte community: trait covariation and indications for host specificity. *Diversity*, *13*(2), 97.

Walker, L.R.; Sharpe, J.M. (2010). Ferns; disturbance and succession. (2010). In Fern Ecology; Cambridge University Press: New York, NY, USA, pp. 177–219.

Wang, X., Shen, C., Meng, P., Tan, G., & Lv, L. (2021). Analysis and review of trichomes in plants. *BMC Plant Biology*, *21*(1), 70.

Watts, J.L., & Watkins, Jr, J.E., 2021. Crossing the divide: An exploration of functional traits in ferns that grow across terrestrial, epipetric, and epiphytic habitats. *American Fern Journal*, 111(4), 308–326.

Weidlich, E. W., Nelson, C. R., Maron, J. L., Callaway, R. M., Delory, B. M., & Temperton, V. M. (2021). Priority effects and ecological restoration. *Restoration Ecology*, *29*(1), e13317.

Williams, C.B., Murray, J.G., Glunk, A., Dawson, T.E., Nadkarni, N.M., & Gotsch, S.G. (2020). Vascular epiphytes show low physiological resistance and high recovery capacity to episodic, short-term drought in Monteverde, Costa Rica. *Functional Ecology*. 34(8), 1537–1550.

Wolf, J. H., & Flamenco-S, A. (2003). Patterns in species richness and distribution of vascular epiphytes in Chiapas, Mexico. *Journal of Biogeography*, *30*(11), 1689–1707.

Woods, C. L., Nevins, L. M., & Didier, E. J. (2019). Structural heterogeneity of trees influences epiphyte distributions in a northern temperate rainforest. *Journal of Vegetation Science*, *30*(6), 1134–1142.

Wyse, S. V., & Burns, B. R. (2011). Do host bark traits influence trunk epiphyte communities?. *New Zealand Journal of Ecology*, 296–301.

Wyse, S. V., Wilmshurst, J. M., Burns, B. R., & Perry, G. L. (2018). New Zealand forest dynamics: a review of past and present vegetation responses to disturbance, and development of conceptual forest models. *New Zealand Journal of Ecology*, *42*(2), 87–106.

Zhang, W., Hu, H., & Zhang, S. B. (2016). Divergent adaptive strategies by two co-occurring epiphytic orchids to water stress: escape or avoidance?. *Frontiers in Plant Science*, *7*, 588.

Zotz, G. (2005). Vascular epiphytes in the temperate zones–a review. *Plant Ecology*, *176*(2), 173–183.

Zotz, G. (2007). Johansson revisited: the spatial structure of epiphyte assemblages. *Journal of Vegetation Science*, *18*(1), 123–130.

Zotz, G. (2016). Epiphyte communities. In Plants on Plants–The Biology of Vascular Epiphytes. Cham: Springer International Publishing, pp 167–202

Zotz, G., & Hietz, P. (2001). The physiological ecology of vascular epiphytes: current knowledge, open questions. *Journal of Experimental Botany*, *52*(364), 2067–2078.

Zotz, G., & Schultz, S. (2008). The vascular epiphytes of a lowland forest in Panama—species composition and spatial structure. *Plant Ecology*, *195*(1), 131–141.

Zotz, G., Weigelt, P., Kessler, M., Kreft, H., & Taylor, A. (2021). EpiList 1.0: a global checklist of vascular epiphytes. *Ecology* 102(6):e03326.

Chapter 2. Tree ferns augment native plant richness and influence composition in urban plant communities

Abstract

Tree ferns are ubiquitous in New Zealand forests, but there is limited knowledge of their role in urban plant communities and potential use in restoration. We assessed sixteen sites by measuring 200 m^2 plots to investigate how tree ferns influence vascular plant composition in Hamilton, North Island, New Zealand. The sixteen plots were assigned to four site type combinations based on restoration status (restored or unrestored) and tree fern presence, each with four plots. Average native plant species richness was higher at sites with tree ferns (36 ± 16; $S = 68$) than sites without (19 ± 14; $S = 41$), with more diverse ground fern and epiphyte assemblages. Higher native plant richness at restored sites (34 ± 18; $S = 62$) compared to unrestored sites (20 ± 14; $S = 44$) was partially attributed to increased plant abundances. Multivariate analyses revealed differences in plant community composition among our site types. Angiosperms and conifers were less prevalent in plots with tree ferns, suggesting competitive relationships among these groups. However, tree ferns were associated with some shade-tolerant trees, such as *Schefflera digitata*. Indicator species of sites with tree ferns were mainly ground ferns and epiphytes (e.g., *Blechnum parrisiae* and *Trichomanes venosum*), whereas species with high fidelity to sites without tree ferns were pioneer trees and shrubs (e.g., *Pittosporum eugenioides*). Community structure analysis revealed that total basal areas were highest at unrestored sites with tree ferns, but restored sites had more diverse tree communities. Environmental predictors which correlated significantly with the compositional differences among our site types were tree fern basal area and restoration age. Our results highlight the need to reconsider the potential of tree ferns in current restoration practice. Tree ferns were found to augment native plant diversity in our study, indicating their potential to enhance urban ecological restoration projects in New Zealand.

2.1. Introduction

Forests support a significant portion of global biodiversity and provide myriad ecosystem services. However, global forest loss is still high, mainly driven by agricultural and urban development [1,2]. Urban expansion places significant pressure on biodiversity via habitat loss and modification [3], but urban ecological restoration presents a unique nature-based solution to combat biodiversity loss and climate change [4,5]. As the number of urban

restoration projects rises internationally [6], there is a growing need to contribute to current knowledge of urban plant community composition and assembly. Pioneer species play a critical role in ecological succession and community assembly, influencing the successional pathway and 'climax' community [7,8]. Early arriving plants also impact the functional diversity of ecosystems [9] and the number of colonizing species via community competition [10]. Understanding how pioneers influence community composition is vital for successful restoration, allowing restoration practitioners to mimic natural succession and assist the recovery of disturbed ecosystems to support a fuller assemblage of species.

In New Zealand, restoration practitioners concentrate on restoring pioneer trees and shrubs [11], which we refer to as light-demanding angiosperm and conifer species first planted at restoration projects. In contrast, we are unaware of any urban restoration projects where tree ferns have been planted, despite also being important pioneers of conifer-broadleaved forests [12]. Tree ferns can act as ecological filters, either inhibiting or facilitating the regeneration of other plants [13–15]. When forming extensive thickets, tree ferns may arrest succession, restricting the arrival of pioneer angiosperms and conifers via shading effects and slow-decomposing fronds. For example, tree ferns suppressed podocarp regeneration in exotic [16] and indigenous forests [17–20]. A stand of *Cyathea dealbata* also restricted angiosperm establishment in secondary forests on the Coromandel Peninsula [21].

Previous research indicates that tree ferns can also accelerate successional processes [22]. For example, they contribute to soil development, provide slope stabilisation and are excellent phorophytes [23–25]. Tree ferns enhance habitat heterogeneity, influencing nutrient, light and water cycles via their megaphylls and providing substrate conducive to epiphyte establishment [26]. Furthermore, tree ferns can provide an important regeneration niche for angiosperms, mediating competition with conifers [27]. A study in the Waitutu Ecological District found that 60% of mature *Pterophylla racemosa* (a native angiosperm tree) regenerated epiphytically on tree ferns [13]. Tree fern stands may also provide more suitable habitat for shade-tolerant species than pioneer trees. For example, *Cyathea medullaris*-dominated forest supported more shade-tolerant species than *Kunzea ericoides* forest [28]. Furthermore, extant tree ferns may advance restoration by decades by providing a native canopy (a primary goal in ecological restoration) from the outset of projects. Common pioneer species planted in restoration projects, such as *Leptospermum scoparium* and *Kunzea ericoides*, may take twenty years to reach a height of 7 m [29].

Research on community assembly and successional pathways following tree ferns is scarce. However, gullies and topographic depressions with early colonising tree ferns (e.g., *Dicksonia squarrosa* and *Cyathea medullaris*) may encourage broadleaved scrub 35-50 years after disturbance, *Beilschmiedia tawa* forest after 150-350 years and *Metrosideros robusta–Dacrydium cupressinum–B. tawa* forest after 400 years [30]. In Hamilton urban environments, successional pathways have diverged from natural forest trajectories due to the range of anthropogenic disturbances that influence plant communities. Images show grey willow-dominated forest containing *Dicksonia squarrosa* established in some gullies more than 20 years after livestock grazing ceased when land was subdivided for housing development [31]. Although tree ferns form important pioneer communities of conifer-broadleaved forests in New Zealand, there is limited information on how these species influence urban plant communities.

We present results from one of the first studies on urban tree fern communities in New Zealand; most research on tree ferns has focused on non-urban forests after natural rather than anthropogenic disturbance. The aim of this study was to investigate how tree ferns influence urban plant communities and identify environmental variables contributing to community composition. We tested three hypotheses: (1) tree fern presence significantly affects vascular plant community composition at sites not actively restored by augmenting ground fern and epiphyte richness, (2) actively restored sites support richer, more abundant pioneer tree and shrub assemblages, and (3) tree fern basal area and restoration age are important environmental predictors of compositional differences among our site types. Better understanding how tree ferns impact diversity and composition in urban plant communities will help guide ecological restoration activities.

2.2. Materials and methods

2.2.1. Study area

Indigenous vegetation cover is low in New Zealand's major urban centres, ranging from <1 to 8.9% [32]. Urban forests support novel plant communities with a high prevalence of exotic species [33]. Research on restoring urban forests has focused on forest remnants or reconstructing native ecosystems using landforms to guide plantings [34,35]. With a focus on planting pioneer trees, there has been little research on existing pioneer tree ferns.

Practitioners have also overlooked tree ferns and the native species they support; blanket clearance of exotic trees, a common approach, is unfavourable to existing native plants, including tree ferns [36].

Hamilton is a small city (approximately 11,000 ha) located in the central North Island, New Zealand (37°46′59.99″S, 175°16′59.99″E). New Zealand has been identified as one of 25 world biodiversity hotspots for conservation priorities [37]. Hamilton lies within the Hamilton Ecological District [38]. Hamilton has a warm temperate climate with a mean annual temperature of 13.7°C and a mean annual precipitation of 1,190 mm [39]. There is approximately 267 ha (2.5%) of native-dominant vegetation in Hamilton (HCC unpublished database). Hamilton's natural vegetation is concentrated in gullies that form intricate networks throughout the city. The gullies formed 15,000 years ago via spring sapping when the Waikato River changed course, undermining banks, trapping sediment and creating a network of streams. Before human arrival, gully floors were dominated by semi-swamp species like *Dacrycarpus dacrydioides* (kahikatea), *Laurelia novae-zelandiae* (pukatea) and *Syzygium maire* (waiwaka) [34]. As rural land in Hamilton was converted to urban subdivisions, grey willow (*Salix cinerea*) rapidly became the dominant tree in the gullies. Compared to small, drained kahikatea remnants in Hamilton, the gullies, with their developed canopy, higher humidity, and abundant tree ferns, may support more diverse native understory communities [40]. Hamilton's gullies can also support rich assemblages of locally uncommon life forms, including epiphytes [41].

2.2.2. Site selection

After an extensive survey of gullies and reserves in Hamilton, sixteen sites were selected (Figure 1). We adopted a fully crossed factorial design to investigate how tree fern presence influences urban plant communities while considering the impact of active plantings on these communities using restoration status. Our site types consisted of four categories: restored sites with tree ferns (n = 4), unrestored sites with tree ferns (n = 4), restored sites without tree ferns (n = 4) and unrestored sites without tree ferns (n = 4). Restored sites had been planted with native trees and shrubs (native tree basal area > 7 m^2 ha^{-1}), and unrestored sites had not been planted (< 3 m^2 ha^{-1}). Sites with tree ferns had at least 12 individuals in a plot, and those without had three or fewer (see Figure 2 for site type examples). The thresholds used to

determine site type were adopted as feasible targets for the study sites, enabling a comparison between sites with and without tree ferns.

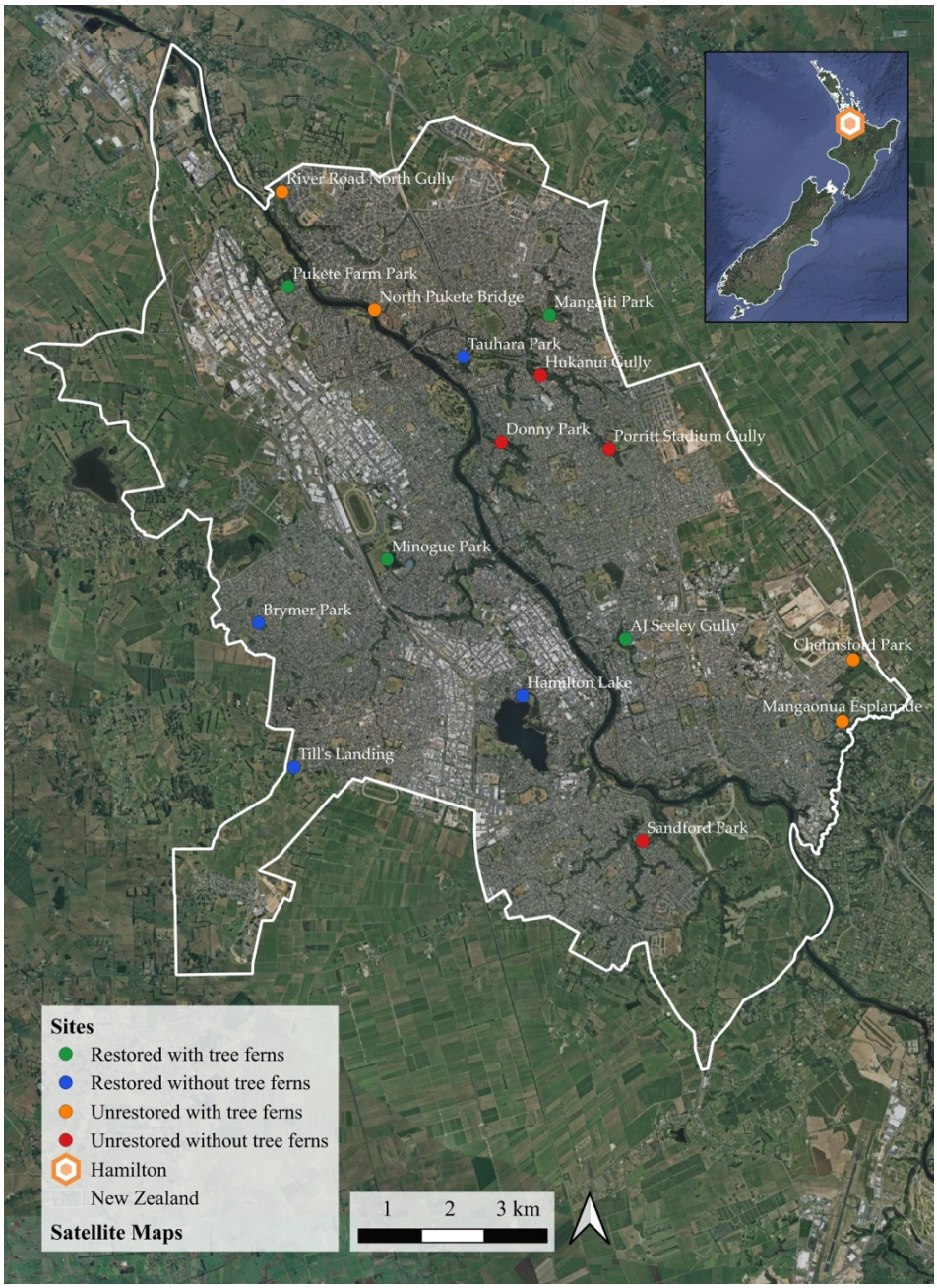


Figure 1. Site locations in Hamilton, North Island, New Zealand. Each dot represents a site where one 20 × 10 m vegetation plot was assessed, and the colour denotes the site type (i.e., green dots are restored sites with tree ferns, blue dots are restored sites without tree ferns, orange dots are unrestored sites with tree ferns, and red dots are unrestored sites without tree ferns). A map of New Zealand is also provided, indicating the study location (Hamilton), near the centre of the North Island.



Figure 2. Example sites of the four site types based on restoration status (restored, unrestored) and the presence of tree ferns (with, without).

Restoration age (i.e., time since native plantings began) guided site selection and was sourced from an unpublished Hamilton City Council restoration database and verified by tree cores [42] (see Table S1, Supplementary Materials). Tree fern basal areas at sites with tree ferns (dominated by *Dicksonia squarrosa*) were similar to those recorded in younger (<80 yr) podocarp-broadleaf forests on central North Island [19]. Soil types at our sites ranged from Kirikiriroa gritty silt loam, Te Kowhai silt loam, Tamahana silt loam, Kainui silt loam, Waikato loamy sand to Hamilton clay loam and Kaipaki peaty loam (Manaaki Whenua unpublished database). All four site types had the two major soil types (Kirikiriroa gritty silt loam and Tamahana silt loam).

2.2.3. Vegetation survey

A single vegetation plot (20 × 10 m) was measured at each site following a method developed by the People, Cities and Nature (PCaN) research programme and used in establishing a permanent plot network of 97 plots in nine cities across New Zealand [43]. Four permanent vegetation plots (200 m^2) were selected from the PCaN plot network in Hamilton (n = 9) that met the restored sites without tree ferns site type requirements. The

remaining twelve sites that met the requirements of the other three site types (i.e., not in the PCaN plot network) were selected separately; specific plot locations were identified using a random number generator. Our plots were half the area of the nationally developed forest methodology [44] because of the limited patch size and extent of vegetation in the urban context (Figure S1, Supplementary Materials).

Each plot was split into eight 25 m^2 subplots, and measurements were made for ground cover, ground ferns, woody plants (trees and shrubs), tree ferns and epiphytes. Ground cover (%) per subplot was estimated visually using standard categories (i.e., herbaceous cover, leaf litter and sticks, moss and bare ground). Ground ferns were counted per subplot. For woody species, data were collected separately for seedlings (< 1.35 m tall), saplings (> 1.35 m tall but < 2.5 cm diameter at breast height, DBH), and trees (woody species > 2.5 cm DBH). Tree ferns were counted per subplot; we only recorded tree fern diameters for individuals with a DBH greater than 2.5 cm. Vascular epiphyte measurements included abundance (count) and host species. Nomenclature follows the Flora of New Zealand [45].

In addition, variables that could influence the study communities were recorded, specifically canopy cover (using the %Cover CanopySurveying application), slope (using a SUUNTO PM-5 clinometer), canopy height (with a Haglöf Vertex IV Hypsometer) and geographical coordinates. A tree core from the largest individual was collected from each plot to estimate the maximum age and verify previously documented restoration ages (Table S1). Distance from the patch edge (i.e., between the plot and vegetation margin) was determined using the Near geoprocessing tool in ArcGIS Pro (a geographic information system).

2.2.4. Data analysis

We compared compositional differences among our four site types (i.e., unrestored sites with tree ferns, unrestored sites without tree ferns, restored sites with tree ferns and restored sites without tree ferns) and investigated environmental variables influencing these differences using a range of statistical approaches. Data were analysed and visualised in R version 4.2.2 [46]. Unless specified, all multivariate analyses used the “vegan” R package [47].

2.2.4.1. Community analysis

We investigated the influence of our site types on plant richness to test our first two hypotheses (i.e., tree ferns augment native plant richness, and restored sites hold more speciose and diverse plant communities). To account for differences in plant abundances, we estimated rarefied species richness for each plot and plant group (i.e., seedlings, saplings, trees, ground ferns and epiphytes) using a sample-size-based rarefaction and extrapolation (R/E) sampling curve approach with the "iNEXT" (v. 3.0.0) R package [48]. Rarefaction curves were extrapolated to a higher number of individual plants for total native species richness (n = 200) than for exotic richness and individual plant groups (n = 50). The different approaches were explained by the lower abundances of the latter groups, requiring a smaller number of individuals to standardise richness (Figure A1).

We then fitted generalised linear models (GLMs) with restoration age as a covariate to test the influence of tree fern presence and restoration status on species abundances and richness of different plant groups (i.e., native and exotic plant species, and individual plant groups, including seedlings, saplings, trees, ground ferns and epiphytes). We compared GLM results using raw (i.e., unrarefied) and rarefied species richness but present results for the latter, as rarefaction accounts for the influence of plant abundances on richness responses [48]. The GLMs using count data responses were fitted with a log link function, assuming a Poisson distribution. We tested the multivariate models for multicollinearity using the variance inflation factor (VIF); all models had acceptable VIF values below 5. We compared models with and without the interaction term using a likelihood ratio test to determine if there were interactive effects between restoration status and tree fern presence. Where there was no statistically significant influence of the interaction, we present the additive model results. Post-hoc comparisons were tested using a least-squares means approach with Tukey's correction for multiplicity via the "lsmeans" package in R [49]. In the written results, we state the 95% confidence interval for the parameter estimates of the GLMs and post-hoc tests in addition to the statistical significance at alpha = 0.05.

To assess how tree fern presence and restoration status influence plant community composition, we used permutational multivariate analysis of variance (PERMANOVA) with abundance data for native and exotic species combined and native species alone. The PERMANOVA tests were performed using the "adonis2" function in the "vegan" R package [47]. Community composition data were first Hellinger transformed to simultaneously minimise the effects of vastly different total abundances and account for rare species [50].

The transformed community data using the Bray-Curtis dissimilarity were then analysed with PERMANOVA to test if plant community composition differed among our four site types [51]. Each PERMANOVA model included restoration age as a covariate. To determine which plant species were influential in the PERMANOVA results, we used the "indicspecies" R package to identify indicator species with high fidelity to our site types [52]. A nonmetric multidimensional scaling (NMDS) ordination using the "metaMDS" function was used to visualise plant communities in each site type and help interpret the PERMANOVA results. Convex hulls were drawn around the four site types, and indicator species and the 10 most abundant species (i.e., counts of species ranked by dominance) were plotted using their axes scores.

We used basal areas (as an indicator of biomass) to test our first two hypotheses further regarding the influence of tree fern presence and restoration status on vascular plant communities. We fitted four GLMs (each assuming a Gaussian distribution) to investigate differences in total, native tree, exotic tree and tree fern basal areas among the site types with restoration age as a covariate. Model predictors in the GLMs had acceptable variance inflation factor (VIF) values <5. Post-hoc differences were tested using a least-squares means approach with Tukey's correction for multiplicity. We also tested compositional differences in species basal areas among the site types using PERMANOVA, but do not present the results as they reiterate the same compositional differences among our site types found using species abundances.

2.2.4.2. Environmental variable analysis

To test our third hypothesis, we investigated the influence of potential environmental predictors on plant community responses, including species richness and community composition. Six GLMs were fitted to identify potential environmental predictors of richness for total native species and each plant group (i.e., seedlings, saplings, trees, ground ferns and epiphytes) using a log link function and assuming a Poisson distribution for count data. The 10 environmental predictors we considered were average slope, canopy cover, restoration age, maximum tree age, maximum canopy height, distance to the patch edge, the total plant basal area, as well as the basal area of tree ferns, native trees and exotic trees. We assessed the normality of environmental predictors using Shapiro-Wilk tests and log-transformed predictors to reduce skewness. Environmental predictors were then standardised (i.e., centred on the mean and scaled to unit variance) using the "decostand" function in the vegan R

package. Rarefied richness integers were used for all models to account for differences in plant abundances across site types. The "step" R function was used to forward select important environmental predictors (from our 10 predictors) of our univariate responses for each model.

To consider potential environmental and spatial predictors of overall plant community composition and account for potential spatial autocorrelation, a distance-based redundancy analysis (dbRDA) using the Bray-Curtis dissimilarity [53] was conducted on the Hellinger-transformed community data. The same 10 log-transformed and standardised environmental predictors used for the univariate GLMs were considered for the dbRDA.

In our initial model fitting for the dbRDA, we also considered spatial structuring of plant communities (e.g., distance-decay relationships). The spatial structuring of plant community data using geographic coordinates for sites was assessed using a principal coordinates of neighbour matrices (PCNM) approach [54]. PCNM descriptors (or axes) may help describe processes structuring communities at different spatial scales [55]. PCNM axes were generated from site coordinates using the "pcnm" R function in the "vegan" package. The PCNM axes were used in the initial model selection procedure for the dbRDA, but none were selected, and they were not considered further.

To avoid overfitting the dbRDA model and select only influential predictors explaining variation in plant community composition, we used a forward stepwise procedure using the "ordistep" function [56]. Two predictors were selected for the final dbRDA model: tree fern basal area and restoration age. Variation partitioning was then undertaken to assess the relative contribution of tree fern basal area and restoration age to variation in community composition (Figure S2, Supplementary Materials). The significance of each independent variation component was permutation-tested using 1,000 randomizations [57]. We used the "capscale" (dbRDA) and "varpart" (variation partitioning) functions for these constrained multivariate analyses.

2.3. Results

2.3.1. Plant abundances and richness

More than 6,000 individuals of 155 native vascular plant species were recorded across 16 sites (Table 1). Generalised linear model (GLM) results showed significant differences in

plant abundances and species richness with tree fern presence and restoration status (Table 2). Native plant abundances were significantly affected by the interaction between tree fern presence and restoration status ($F_{1,11}$ = 12.0, P < 0.01). Post-hoc results revealed that native plant abundances were higher at restored sites without tree ferns when compared to their unrestored equivalents (z = 2.7, P < 0.01), but unrestored sites with tree ferns had higher native abundances than the restored sites (z = -9.7, P < 0.001). Restored sites without tree ferns had higher native abundances than those with tree ferns (z = 6.3, P < 0.001), whereas the opposite was observed at unrestored sites with tree ferns, which had higher abundances than unrestored sites without tree ferns (z = -35.6, P < 0.001).

Table 1. Mean (± standard deviation) native, exotic and total plant abundances, richness and rarefied richness at the four site types based on restoration status (restored, unrestored) and tree fern presence (with, without). The mean total (i.e., tree fern, native and exotic tree) basal areas (m^2/ha) per site type are also presented.

Group	Variable	Unrestored with Mean ± SD	Unrestored without Mean ± SD	Restored with Mean ± SD	Restored without Mean ± SD
Native	Abundance	659.5 ± 449.3	61.5 ± 50.0	295.0 ± 82.0	351.8 ± 186.9
	Richness	32.8 ± 3.8	8.5 ± 5.8	38.5 ± 23.3	29.5 ± 12.5
	Rarefied richness	20.2 ± 1.4	6.7 ± 5.0	20.0 ± 4.5	16.1 ± 1.1
Exotic	Abundance	40.8 ± 25.0	132.3 ± 125.8	16.5 ± 25.2	54.8 ± 49.3
	Richness	7.0 ± 1.4	7.3 ± 4.0	3.5 ± 1.7	8.0 ± 3.4
	Rarefied richness	4.4 ± 2.4	4.6 ± 2.9	2.1 ± 1.6	6.5 ± 3.4
Total	Abundance	700.3 ± 465.9	193.8 ± 169.3	311.5 ± 66.4	406.5 ± 195.2
	Richness	39.8 ± 5.0	15.8 ± 7.9	42.0 ± 22.7	37.5 ± 14.0
	Rarefied richness	24.3 ± 2.3	13.0 ± 2.8	22.5 ± 5.2	22.1 ± 3.8
	Basal area	25.7 ± 12.2	9.0 ± 6.8	18.5 ± 3.3	18.4 ± 3.4

Native plant abundances appeared to partially affect native species richness, which was higher at restored sites whether tree ferns were present (z = -5.1, P < 0.001) or absent (z = -3.2, P < 0.01). However, after accounting for differences in native plant abundances through rarefaction, the GLM revealed that the interaction between tree fern presence and restoration

status had a significant effect on plant richness ($F_{1,11} = 8.4$, $P < 0.05$; see Figure 3). Tree fern presence positively influenced rarefied native plant richness at unrestored sites ($z = -4.0$, $P < 0.001$), but this influence was not statistically significant at restored sites ($z = -1.0$, $P = 0.3$). In contrast, restoration status positively affected native species richness at sites without tree ferns ($z = 2.9$, $P < 0.01$), but did not have a significant influence at sites with tree ferns ($z = -0.04$, $P = 1.0$).

Exotic plant abundances were significantly lower at sites with tree ferns ($F_{1,12} = 6.6$, $P < 0.05$) but did not vary with restoration status ($F_{1,12} = 2.4$, $P = 0.2$). Furthermore, rarefied exotic species richness was not significantly influenced by tree fern presence ($F_{1,12} = 2.1$, $P = 0.2$) or restoration status ($F_{1,12} = 0.4$, $P = 0.5$).

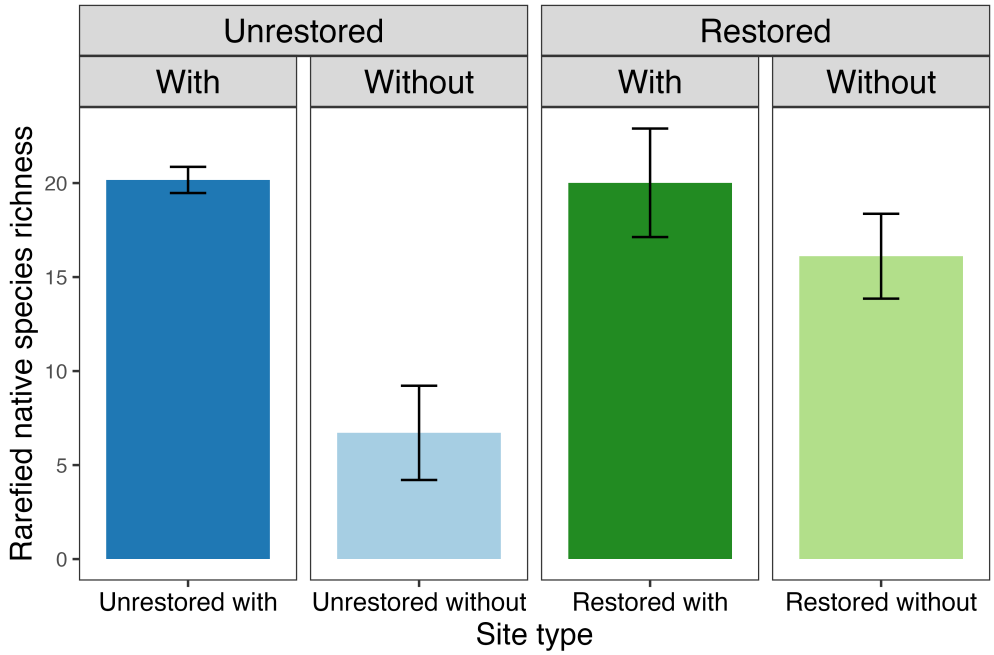


Figure 3. Mean rarefied native vascular plant species richness for the four site types based on restoration status (restored, unrestored) and the presence of tree ferns (with, without). Error bars represent one standard error.

The abundances and species richness of native plant groups differed across site types (Tables 2 and 3). Seedling abundances were not significantly influenced by tree fern presence ($F_{1,12} = 0.2$, $P = 0.7$) or restoration status ($F_{1,12} = 0.02$, $P = 0.9$). Rarefied native seedling richness was significantly influenced by the interaction between tree fern presence and restoration status ($F_{1,11} = 5.6$, $P < 0.05$). Post-hoc results showed that tree ferns negatively affected

rarefied seedling richness at restored sites (z = 2.1, P < 0.05) but had no significant effect at unrestored sites (z = -1.3, P = 0.2). Furthermore, restoration status did not significantly influence rarefied seedling richness when tree ferns were present (z = -1.7, P = 0.1) or absent (z = -1.1, P = 0.3).

Native sapling abundances were not significantly influenced by tree fern presence (z = 0.04, P = 0.8) or restoration status (z = 2.1, P = 0.1). Rarefied native sapling richness was significantly influenced by the interaction between tree fern presence and restoration status ($F_{1,11}$ = 6.9, P < 0.05). Sapling richness was positively affected by tree fern presence at unrestored sites (z = -2.4, P < 0.05) but not at restored sites (z = 0.9, P = 0.4). In comparison, restoration status did not significantly influence rarefied sapling richness when tree ferns were present (z = -1.5, P = 0.2) or absent (z = -0.6, P = 0.8).

Native tree abundances (i.e., woody trees excluding tree ferns) were significantly higher at restored sites ($F_{1,12}$ = 5.6, P < 0.05) but were not affected by tree fern presence ($F_{1,12}$ = 0.9, P = 0.7). There was no statistically significant difference in rarefied tree species richness with tree fern presence ($F_{1,12}$ = 0.3, P = 0.6) or restoration status ($F_{1,12}$ = 0.04, P = 0.8).

Table 2. Generalised linear model results testing the effect of tree fern presence and restoration status on total native abundances, rarefied species richness, as well as abundance and rarefied richness of seedlings, ground ferns and epiphytes. Incidence rate ratios with 95% confidence intervals (CI) are provided. Statistically significant *P*-values at α = 0.05 are in bold. See Supplementary Materials, Table S2 for GLM results for total exotic plants, native sapling and tree abundances and richness.

Model	Predictors	Incidence Rate Ratio	95% CI	*P*-value
Total native abundances	(Intercept)	294.83	119.39 – 679.37	**<0.001**
	Tree ferns [Yes]	0.76	0.28 – 1.93	0.571
	Status [Unrestored]	0.42	0.01 – 14.98	0.633
	Restoration age [log(x) + 1]	1.49	0.35 – 6.51	0.584
	Tree ferns [Yes] × Status [Unrestored]	14.12	2.92 – 108.85	**0.003**
Rarefied native species richness	(Intercept)	13.10	8.65 – 19.45	**<0.001**
	Tree ferns [Yes]	1.10	0.71 – 1.71	0.663

(n = 200)	Status [Unrestored]	1.18	0.27 – 5.17	0.825
	Restoration age [log(x) + 1]	1.60	0.87 – 2.97	0.133
	Tree ferns [Yes] × Status [Unrestored]	2.72	1.38 – 5.55	**0.005**
Rarefied	(Intercept)	4.53	2.46 – 8.00	**<0.001**
seedling	Tree ferns [Yes]	0.47	0.22 – 0.93	**0.037**
richness	Status [Unrestored]	2.72	0.25 – 33.83	0.420
(n = 50)	Restoration age [log(x) + 1]	3.00	1.10 – 8.78	**0.036**
	Tree ferns [Yes] × Status [Unrestored]	3.89	1.26 – 13.07	**0.021**
Ground fern	(Intercept)	12.67	2.26 – 49.91	**0.001**
abundances	Tree ferns [Yes]	7.45	2.47 – 33.96	**0.002**
	Status [Unrestored]	0.15	0.00 – 8.77	0.368
	Restoration age [log(x) + 1]	0.38	0.05 – 2.02	0.288
Rarefied	(Intercept)	0.99	0.41 – 2.14	0.974
ground fern	Tree ferns [Yes]	3.98	2.24 – 7.60	**<0.001**
richness	Status [Unrestored]	1.42	0.12 – 16.66	0.776
(n = 50)	Restoration age [log1p]	0.95	0.34 – 2.54	0.922
Native epiphyte	(Intercept)	15.28	0.03 – 493.91	0.211
abundances	Tree ferns [Yes]	6.77	0.80 – 401.85	0.156
	Status [Unrestored]	3.35	0.00 – 22.29 x 10^6	0.850
	Restoration age [log(x) + 1]	0.89	0.00 – 252.60	0.963
Rarefied native	(Intercept)	0.62	0.18 – 1.77	0.411
epiphyte	Tree ferns [Yes]	5.40	2.42 – 14.23	**<0.001**
richness	Status [Unrestored]	10.21	0.59 – 229.80	0.123
(n = 50)	Restoration age [log(x) + 1]	2.25	0.72 – 7.26	0.163

Ground fern abundance was significantly higher at sites with tree ferns ($F_{1,12}$ = 15.1, P < 0.01) but did not differ with restoration status ($F_{1,12}$ = 1.3, P = 0.4). Likewise, rarefied ground fern richness was strongly positively influenced by tree fern presence ($F_{1,12}$ = 24.7, P < 0.001) but was not significantly affected by restoration status ($F_{1,12}$ = 0.01, P = 0.8). While neither tree ferns nor restoration status had a statistically significant effect on epiphyte abundance at the α = 0.05 level, tree ferns were associated with increased epiphyte abundance ($F_{1,12}$ = 3.3, P = 0.9). Furthermore, rarefied native epiphyte richness was significantly higher at sites with tree ferns ($F_{1,12}$ = 13.2, P < 0.001) but was not affected by restoration status ($F_{1,12}$ = 2.5, P = 0.1).

Table 3. Mean (± standard deviation) native species abundance, richness and rarefied richness for each plant group and site type. Our plant groups were tree ferns, seedlings, saplings, trees, ground ferns and epiphytes. Site types were based on restoration status (restored, unrestored) and tree fern presence (with, without). The mean tree fern basal areas (m^2 ha^{-1}) per site type are also presented.

Plant group	Variable	Unrestored with Mean ± SD	Unrestored without Mean ± SD	Restored with Mean ± SD	Restored without Mean ± SD
Tree ferns	Abundance	68.8 ± 33.9	0.8 ± 1.5	25.0 ± 12.1	0.5 ± 1.0
	Richness	2.3 ± 1.3	0.3 ± 0.5	2.3 ± 1.0	0.3 ± 0.5
	Rarefied richness	2.1 ± 1.3	1 ± 0.0	2.3 ± 1.0	1 ± 0.0
	Basal area	21.1 ± 10.5	0.2 ± 0.4	6.1 ± 1.5	0.0 ± 0.0
Seedlings	Abundance	24.3 ± 4.0	7.3 ± 11.3	101.5 ± 100.9	125.0 ± 144.7
	Richness	3.5 ± 1.0	1.3 ± 1.3	7.8 ± 6.6	9.3 ± 5.6
	Rarefied richness	3.2 ± 1.2	1.8 ± 1.5	4.9 ± 3.3	7.4 ± 3.2
Saplings	Abundance	23.8 ± 12.2	15.3 ± 16.5	72.5 ± 34.4	79.5 ± 40.3
	Richness	5.3 ± 3.1	1.5 ± 0.6	11.0 ± 8.8	7.8 ± 2.9
	Rarefied richness	4.5 ± 2.7	1.5 ± 0.6	5.5 ± 3.1	6.0 ± 1.6
Trees	Abundance	59.8 ± 21.0	6.0 ± 7.1	33.3 ± 9.4	30.5 ± 9.7
	Richness	4.3 ± 1.3	2.3 ± 2.9	8.0 ± 2.9	9.5 ± 4.5
	Rarefied richness	3.1 ± 0.6	2.7 ± 2.3	6.3 ± 3.2	7.7 ± 3.4
Ground ferns	Abundance	75.8 ± 53.9	14.3 ± 22.0	58.3 ± 45.7	4.8 ± 5.0
	Richness	6.3 ± 1.0	2.0 ± 1.4	5.8 ± 3.8	1.8 ± 1.5
	Rarefied richness	5.9 ± 1.5	1.8 ± 1.3	4.0 ± 1.4	0.8 ± 1.0
Epiphytes	Abundance	486.5 ± 376.0	7.3 ± 10.4	39.5 ± 36.2	70.8 ± 131.1
	Richness	13.5 ± 3.3	1.5 ± 1.7	6.0 ± 5.5	1.3 ± 1.5
	Rarefied richness	8.6 ± 1.9	1.0 ± 1.4	5.5 ± 5.1	1.4 ± 1.1

2.3.2. Community composition

Distinct plant communities were associated with our site types, further supporting our first two hypotheses. Our permutational multivariate analysis of variance (PERMANOVA) models found significant differences in total vascular plant composition (native and exotic species) across all pairwise comparisons except for between restored sites with and without tree ferns (see Figure 4 and Table B1). Native plant composition also differed significantly among five of the six pairwise comparisons across all levels of our factorial design (Table S3, Supplementary Materials).

Abundant species (i.e., the 10 most dominant species overall) at restored sites were *Dacrycarpus dacrydioides, Melicytus ramiflorus, Hoheria populnea* and *Pyrrosia elaeagnifolia*. In contrast, abundant species at sites with tree ferns were *Deparia petersenii, Tmesipteris lanceolata* and *T. elongata.* Three abundant species were associated with sites without tree ferns, which were *Coprosma robusta* and two exotic species (*Hedera helix* and *Ligustrum sinense*).

Indicator species analysis identified 12 species for three site types (Table B2). Unrestored sites with tree ferns were associated with the most indicator species (8), including ground ferns (*Blechnum minus*), tree ferns (*Dicksonia squarrosa*), epiphytic ferns (*Tmesipteris elongata*, *T. lanceolata*, *Trichomanes venosum*, *Rumohra adiantiformis* and *Hymenophyllum flabellatum*) and one exotic herb (*Myosotis sylvatica*). No indicator species were associated with unrestored sites without tree ferns, likely because of their depauperate assemblages. Species with high fidelity to restored sites with tree ferns were *Blechnum parrisiae* and *Cyathea medullaris*. In comparison, indicator species of restored sites without tree ferns were *Pittosporum eugenioides* and *P. tenuifolium*.

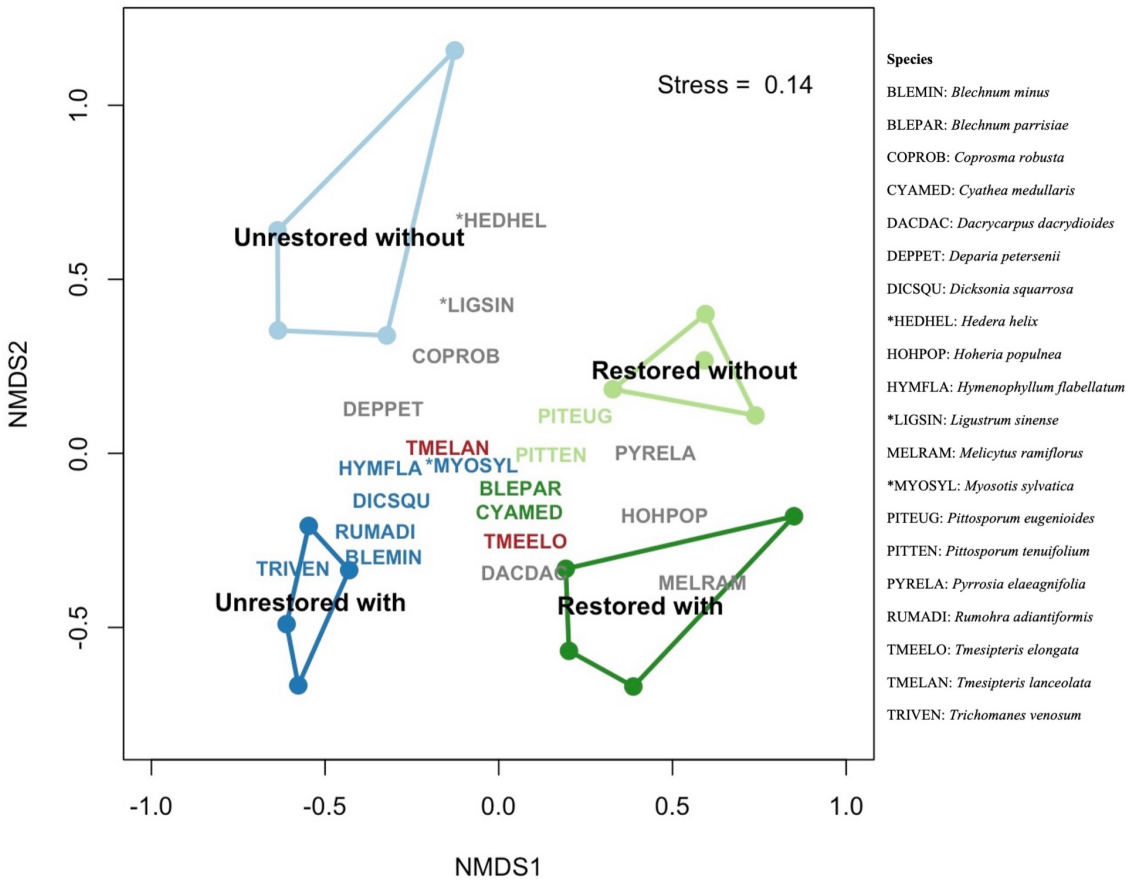


Figure 4. Nonmetric multidimensional scaling (NMDS) ordination of plant community composition by abundances. Convex hulls are drawn around the four site types: restored with tree ferns (dark green), restored without tree ferns (light green), unrestored with tree ferns (dark blue) and unrestored without tree ferns (light blue). The ordination had a 'fair' stress score of 0.14. Coloured dots represent the sites, and six-letter codes represent indicator or abundant species (see legend for scientific names). An asterisk denotes an exotic species. Species colours represent indicator species of the site types: restored with tree ferns (dark green), restored without tree ferns (light green) and unrestored with tree ferns (dark blue). Species in grey are eight of the most abundant species, and species in red (2) represent indicators of unrestored sites with tree ferns that are also abundant species. The 10 most abundant species accounted for 62% of the mean relative abundance.

2.3.3. Community structure

We investigated differences in plant community structure among our site types using the basal area of stems greater than 2.5 cm DBH (see Supplementary Materials, Table S4 for complete model statistics). GLMs revealed that total basal area (native trees, exotic trees and

tree ferns) was significantly higher at sites with tree ferns ($F_{1,12}$ = 8.1, P < 0.05) but did not differ with restoration status ($F_{1,12}$ = 0.002, P = 1.0). Native tree basal area was significantly higher at restored sites ($F_{1,12}$ = 8.4, P < 0.05) but did not vary significantly with tree fern presence ($F_{1,12}$ = 0.7, P = 0.7). Furthermore, tree fern basal area was significantly higher at sites with tree ferns ($F_{1,12}$ = 17.2, P < 0.01), but restoration status had no significant effect ($F_{1,12}$ = 0.4, P = 0.5). Finally, exotic tree basal area did not vary significantly with tree fern presence ($F_{1,12}$ = 3.8, P = 0.1) or restoration status ($F_{1,12}$ = 1.0, P = 0.3).

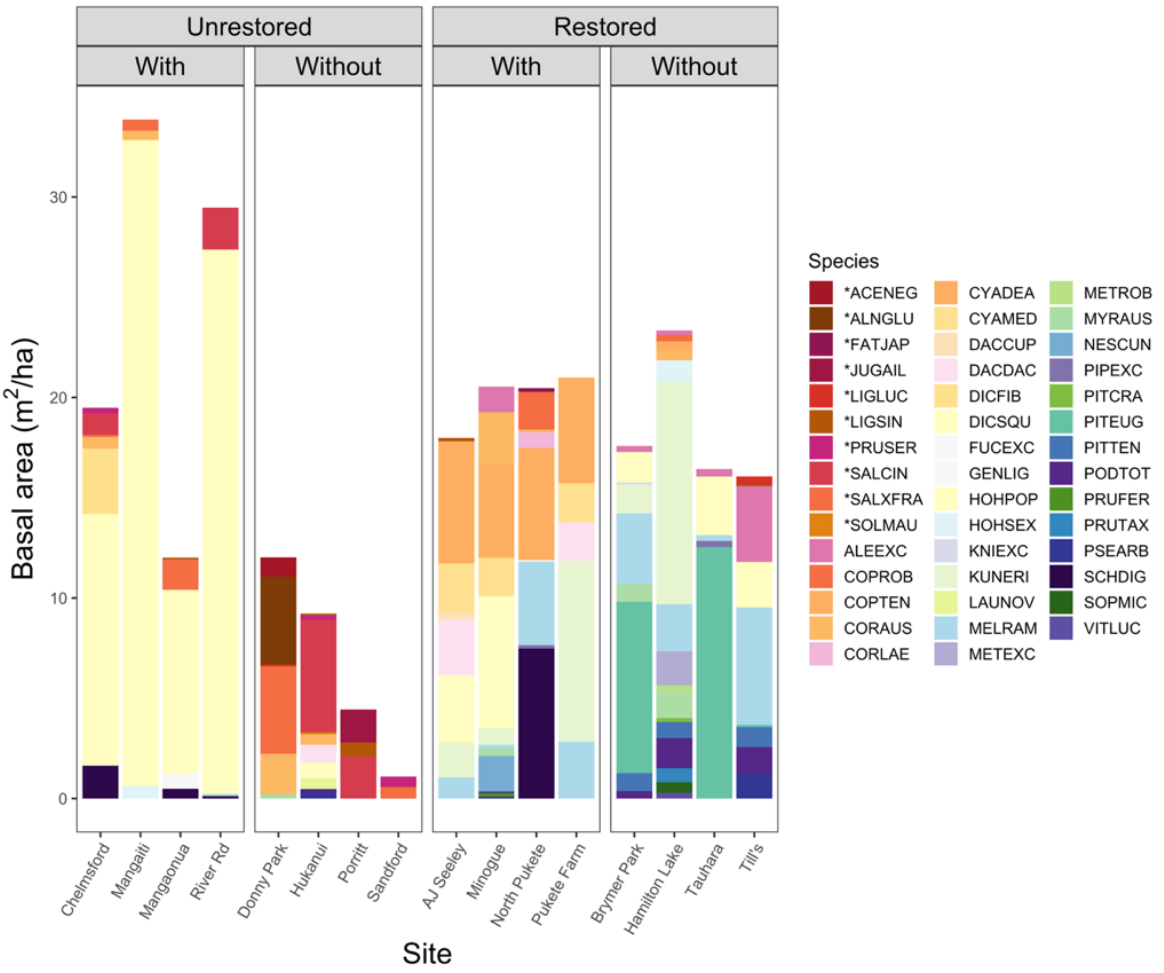


Figure 5. Tree and tree fern basal areas (m^2 ha^{-1}) of vegetation plots measured in Hamilton, New Zealand. The 16 plots were assigned to our four site types based on restoration status (restored, unrestored) and the presence of tree ferns (with, without). An asterisk denotes an exotic species. Scientific and common names associated with the six-letter species codes are provided in Table B3.

Figure 5 shows the basal areas for individual plant species across sites. Unrestored sites with tree ferns had the highest average basal area (25.7 ± 12.2 m^2 ha^{-1}), dominated by *Dicksonia squarrosa* (82%). Unrestored sites without tree ferns had the lowest average basal area (9.0 ± 6.8 m^2 ha^{-1}), with only a few exotic trees, such as *Salix cinerea* and *Alnus glutinosa* (Table S5, Supplementary Materials). Basal areas were more similar among restored sites, whether tree ferns were present (18.5 ± 3.3 m^2 ha^{-1}) or absent (18.4 ± 3.4 m^2 ha^{-1}). While unrestored sites with tree ferns were dominated by *D. squarrosa* (light yellow bars), restored sites with tree ferns had higher basal areas of *Cyathea dealbata* and *C. medullaris* (orange bars).

2.3.4. Environmental predictors of plant communities

We examined potential environmental predictors of individual plant groups and total native species richness across our site types. GLM results identified environmental predictors correlated with plant community composition (Table 4). Rarefied native richness (Table 4) was positively influenced by tree fern basal area (z = 4.4, P < 0.001) and restoration age (z = 4.4, P < 0.001) but negatively influenced by maximum canopy height (z = -3.0, P < 0.01) and average slope (z = -1.6, P = 0.1). Rarefied exotic species richness was negatively associated with tree fern basal area, but the relationship was not statistically significant at an alpha level of 0.05 (z = -1.6, P = 0.1, Table 4).

Table 4. Generalised linear model results investigating environmental predictors of native rarefied richness, exotic rarefied richness, and rarefied richness per plant group (i.e., seedling, sapling, tree, ground fern and epiphyte richness). Environmental predictors were standardised (i.e., centred on the mean and scaled to unit variance). Incidence rate ratios with 95% confidence intervals (CI) are provided. Statistically significant *P*-values at α = 0.05 are in bold.

Model	Predictors	Incidence Rate Ratio	95% CI	*P*-value
Rarefied native richness (n = 200)	(Intercept)	14.46	12.58 – 16.49	**<0.001**
	Tree fern basal area	1.37	1.19 – 1.58	**<0.001**
	Restoration age	1.58	1.29 – 1.94	**<0.001**
	Maximum canopy height	0.75	0.62 – 0.91	**0.003**
	Average slope	0.88	0.75 – 1.03	0.108

Rarefied exotic richness (n = 50)	(Intercept)	4.30	3.35 – 5.40	**<0.001**
	Tree fern basal area	0.82	0.63 – 1.05	0.117
Rarefied native seedling richness (n = 50)	(Intercept)	3.91	2.97 – 5.02	**<0.001**
	Restoration age	1.64	1.27 – 2.16	**<0.001**
Rarefied native sapling richness (n = 50)	(Intercept)	3.84	2.89 – 4.96	**<0.001**
	Restoration age	2.15	1.46 – 3.25	**<0.001**
	Tree fern basal area	1.20	0.91 – 1.58	0.194
	Maximum canopy height	0.63	0.43 – 0.90	**0.014**
	Average slope	0.71	0.50 – 0.96	**0.037**
Rarefied native tree richness (n = 50)	(Intercept)	4.41	3.41 – 5.57	**<0.001**
	Restoration age	1.82	1.37 – 2.44	**<0.001**
	Maximum tree age	0.78	0.60 – 1.02	0.065
Rarefied ground fern richness (n = 50)	(Intercept)	2.59	1.81 – 3.53	**<0.001**
	Tree fern basal area	1.89	1.40 – 2.61	**<0.001**
Rarefied native epiphyte richness (n = 50)	(Intercept)	2.96	2.09 – 4.01	**<0.001**
	Tree fern basal area	2.35	1.77 – 3.20	**<0.001**

Environmental predictors influencing rarefied native species richness differed among individual plant groups. Table 4 shows that restoration age positively affected seedling (z = 3.7, $P < 0.001$) and tree species richness (z = 4.1, $P < 0.001$). Native sapling species richness (Table 4) was also positively influenced by restoration age (z = 3.8, $P < 0.001$) but was negatively influenced by maximum height (z = -2.5, $P < 0.05$) and average slope (z = -2.1, $P < 0.05$). Although not statistically significant at an alpha level of 0.05, tree fern basal area had a positive relationship with rarefied native sapling richness (Table 4). Table 4 also shows strong positive relationships between tree fern basal area with rarefied ground fern (z = 4.0, $P < 0.001$) and epiphyte richness (z = 5.7, $P < 0.001$).

Our distance-based redundancy analysis (dbRDA) found significant correlations between tree fern basal area and restoration age with differences in plant community composition by abundances across sites (Figure A2). Variation partitioning revealed the amount of variation (R^2 = 0.29) in plant community composition explained by tree fern basal area and restoration

age, with slightly more variation explained independently by tree fern basal area ($F_{1,13} = 3.2$, $P < 0.01$, $R^2 = 0.15$) than restoration age ($F_{1,13} = 3.3$, $P < 0.01$, $R^2 = 0.14$). There was no shared variation explained by these two environmental variables.

2.4. Discussion

We identified distinct plant communities associated with restoration status and tree fern presence. Higher native plant richness at restored sites without tree ferns was partially driven by increased plant abundances, with more diverse woody pioneer communities. In contrast, the presence of tree ferns at unrestored sites supported higher native species richness with more diverse epiphyte and ground fern assemblages. Most epiphyte species (approximately 90%) were on tree ferns, and 65% of ground ferns only occurred in plots with tree ferns. Tree ferns provide a thick root mantle and fibrous substrate with high moisture retention that is conducive to epiphyte establishment [58]. Hence, tree ferns appear to augment native species richness by providing suitable habitat for these groups. These results highlight the strong association between tree ferns, epiphytes, and ground ferns, three functionally diverse plant groups that contribute to ecosystem processes [59,60]. Additionally, increased basal areas (i.e., an indicator of biomass) at our sites with tree ferns showed the significant effect that tree ferns can have on plant community structure and composition. Our results therefore show that the presence of tree ferns can enhance native species richness and the functioning of urban ecosystems via richer epiphyte and ground fern assemblages.

2.4.1. Community assembly and succession

We found a range of differences in plant composition among our site types, suggesting that early-arriving tree ferns significantly impact plant community composition and assembly [23]. The most abundant tree fern at unrestored sites was *Dicksonia squarrosa*, while *Cyathea medullaris* and *C. dealbata* were more abundant at restored sites. Restored sites with tree ferns also had fewer native seedlings, saplings and trees (i.e., angiosperms and conifers), signalling competitive relationships among these groups, which is consistent with previous research [61]. Where priority effects lead to tree ferns establishing first, a positive feedback loop may prevent other species from establishing and occasionally inhibit successional processes [14,62,63]. Our results suggest that tree ferns do not inhibit some shade-tolerant species, and with the natural or assisted arrival of these species, may assist the successional pathway towards conifer-broadleaved forest.

In urban restoration, enrichment planting (i.e., planting late-successional species in the understory of pioneer communities) is critical for replacing short-lived pioneers with long-lived species [35]. Little to no enrichment planting has been undertaken at our restored sites, and few late successional species were recorded in any of our site types. Species such as *Dacrydium cupressinum*, *Alectryon excelsus* and *Hedycarya arborea* have been sparsely planted at some restored sites.

We did not directly investigate successional pathways using remeasurement of tree fern communities over time; however, community composition on our chronosequence may signal potential pathways. Tree ferns are primarily considered mid-late successional species, although species including *Dicksonia squarrosa* and *Cyathea medullaris* can dominate early successional stages. Higher native sapling species richness at our unrestored sites with tree ferns suggests that tree ferns may assist species regeneration. Furthermore, our sites with tree ferns supported some shade-tolerant broadleaf species (e.g., *Schefflera digitata*), which aligns with a previous study where tree ferns did not inhibit shade-tolerant species [28]. Putative pathways following these communities include the development of a broadleaf understory after 40 years and conifer-broadleaved forest after 80-100 years [12,30,64].

2.4.2. Study limitations

Whilst our results suggest that tree ferns can act as ecological filters, thereby altering plant community composition, our study has some limitations. First, our statistical power was limited by the sites available that met the criteria for site selection (i.e., n = 4 per site type; Table S1), which could have reduced our ability to statistically identify differences (i.e., increased chance of Type II errors); however, in many cases, our analyses detected significant (α=0.05) differences among the treatments. Second, species richness is expected to increase with time. Although we controlled for plot restoration age (i.e., time since native planting began) in our statistical analyses as a covariate, the age of sites dominated by tree ferns was difficult to verify because, unlike woody species we dated, they do not have annual growth rings. Third, our study design was a mensurative experiment, and sites with tree ferns may be confounded by other variables. While our results signal the importance of retaining extant tree ferns, experimentally planting them at restoration sites and observing long-term

successional trajectories would provide additional insights into their role in shaping community composition.

2.4.3. Implications for urban ecological restoration

Standard restoration practice focuses on restoring pioneer trees and shrubs, such as *Leptospermum scoparium* and *Kunzea ericoides*, without recognising the ecological value of pioneer tree ferns. Pioneer trees are favoured because they are easily sourced and affordable. In contrast, ferns are rarely available from restoration nurseries. Pioneer trees also grow faster than tree ferns. In two decades, *Kunzea ericoides* can reach 7 m in height [29], compared to *Cyathea medullaris* (2.3 m) and *Dicksonia squarrosa* (1 m) [65].

Our results highlight the need to protect extant tree ferns as they can augment native species richness and enhance opportunities for urban restoration projects. Although monospecific colonies can arrest succession [14], we found tree fern communities to support higher native species richness, providing habitat for ground ferns and epiphytes, both poorly represented functional groups in urban forests [66,67]. Extant tree fern stands also provide the advantage of a native-dominated canopy from the outset of restoration projects. Establishing and maintaining a canopy is critical to the success of ecological restoration projects [68]. A developed canopy slows the establishment and growth of light-demanding invasive plants that compete with native species [69]. However, a canopy can take several decades to reinstate, requiring ongoing labour to release native trees from exotic species that persist in high light levels. Our sites with tree ferns were associated with reduced exotic species abundance. Therefore, using extant tree ferns rather than replacing them with pioneer trees could advance restoration progress.

A bespoke approach, planting pioneers best suited to the site conditions, should be employed in urban restoration. Determining which pioneer species are appropriate for a site should be guided by their ecology (e.g., growth strategy and habitat). *Kunzea ericoides* and *Leptospermum scoparium* generally colonise drier sites [28], and tree ferns occur on hillslopes and gullies or depressions. Dense stoloniferous thickets of *Dicksonia squarrosa* may restrict tree regeneration but support diverse epiphyte communities. These stands may require manipulation (i.e., reducing the cover or density of dominant canopy species to increase diversity) to prevent monospecific self-perpetuating thickets and allow tree

regeneration or enrichment planting without diminishing epiphyte diversity. In contrast, monopodial *Cyathea medullaris* and *C. dealbata* may require less thinning. Studies manipulating tree fern stands have primarily included binary treatment groups [16] or frond thinning trials [61], but there is a lack of long-term research measuring community composition along a gradient of tree fern densities.

We identified some potential environmental predictors of our distinct plant communities, including restoration age and tree fern basal area. Slope and maximum canopy height also negatively affected native species richness, possibly due to reduced soil moisture on steeper sites and inadequate enrichment planting beneath tall pioneer trees. Furthermore, tree fern basal areas positively influenced native epiphyte and ground fern species richness and was negatively affected exotic species richness.

2.5. Conclusions

In conclusion, our results highlight the ecological value of extant tree ferns in augmenting native species richness, supporting functional groups like ground ferns and epiphytes, and potentially suppressing exotic species by providing an early canopy. Incorporating pioneer tree ferns into restoration practice will encourage the diversification of plant communities and the range of species and life forms they support. Tree fern basal area and restoration age significantly contributed to our distinct plant communities, but further research on epiphyte functional traits and environmental drivers is necessary to better understand epiphyte-host and epiphyte-environment relationships. Long-term quantitative research on how tree fern density influences community composition is also needed to determine thresholds for maximising indigenous plant diversity in urban ecosystems. Overall, our study suggests a need to reconsider current restoration practices that often overlook or remove tree ferns in favour of faster-growing pioneer trees.

References

1. Heino, M.; Kummu, M.; Makkonen, M.; Mulligan, M.; Verburg, P.H.; Jalava, M.; Räsänen, T.A. Forest loss in protected areas and intact forest landscapes: a global analysis. *PloS One* **2015**, *10*(10), 0138918.
2. Curtis, P.G.; Slay, C.M.; Harris, N.L.; Tyukavina, A.; Hansen, M.C. Classifying drivers of global forest loss. *Science* **2018**, *361*(6407), 1108–1111.
3. Güneralp, B.; Seto, K.C. Futures of global urban expansion: uncertainties and implications for biodiversity conservation. *Environmental Research Letters* **2013**, *8*(1), 014025.
4. Roeland, S.; Moretti, M.; Amorim, J.H.; Branquinho, C.; Fares, S.; Morelli, F.; Calfapietra, C. Towards an integrative approach to evaluate the environmental ecosystem services provided by urban forest. *Journal of Forestry Research* **2019**, *30*, 1981–1996.
5. Lepczyk, C.A.; Aronson, M.F.; La Sorte FA. Cities as sanctuaries. *Frontiers in Ecology and the Environment* **2023**, *21*(5), 251–259.
6. United Nations Environment Programme. On World Cities Day, UNEP announces 19 cities to restore nature's rightful place in urban areas. Available online: www.unep.org/technical-highlight/world-cities-day-unep-announces-19-cities-restore-natures-rightful-place-urban (accessed on 9 September 2024).
7. Chazdon, R.L. Chance and determinism in tropical forest succession. *Tropical Forest Community Ecology* **2008**, *1*, 384–408.
8. Dávila-Hernández, G.; Meave, J.A.; Muñoz, R.; González, E.J. A flash in the pan? The population dynamics of a dominant pioneer species in tropical dry forest succession. *Population Ecology* **2024,** *67*(1), 32–44.
9. St. Martin, P.; Mallik, A. U. Alternate successional pathway yields alternate pattern of functional diversity. *Journal of Vegetation Science* **2019**, *30*(3), 461–470.
10. Cadotte, M. W. The interacting influences of competition, composition and diversity determine successional community change. *Journal of Ecology* **2023**, *111*(8), 1670–1680.
11. Laughlin, D. C.; Clarkson, B. D. Tree seedling survival depends on canopy age, cover and initial composition: trade-offs in forest restoration enrichment planting. *Ecological Restoration* **2018**, *36*(1), 52–61.
12. Wyse, S.V.; Wilmshurst, J.M.; Burns, B.R.; Perry, G.L. New Zealand forest dynamics: a review of past and present vegetation responses to disturbance; and development of conceptual forest models. *New Zealand Journal of Ecology* **2018**, *42*(2), 87–106.
13. Coomes, D.A.; Allen. R.B.; Bentley, W.A.; Burrows, L.E.; Canham, C.D.; Fagan, L.; Wright, E.F. The hare; the tortoise and the crocodile: the ecology of angiosperm dominance; conifer persistence and fern filtering. *Journal of Ecology* **2005**, *93*(5), 918–935.
14. Walker, L.R.; Landau, F.H.; Velazquez, E.; Shiels, A.B.; Sparrow, A.D. Early successional woody plants facilitate and ferns inhibit forest development on Puerto Rican landslides. *Journal of Ecology* **2010**, *98*(3) 625–635.
15. Chau, M.M.; Walker, L.R.; Mehltreter, K. An invasive tree fern alters soil and plant nutrient dynamics in Hawaii. *Biological Invasions* **2013**, *15*, 355–370.

16. Forbes, A.S.; Norton, D.A.; Carswell, F.E. Tree fern competition reduces indigenous forest tree seedling growth within exotic Pinus radiata plantations. *Forest Ecology and Management* **2016**, *359*: 1–10.
17. McKelvey, P.J. Forest colonisation after recent volcanicity at West Taupo. *New Zealand Journal Forest* **1953**, 6, 435–438.
18. Wardle, P. The kahikatea (*Dacrycarpus dacrydioides*) forest of south Westland. *In Proceedings of New Zealand Ecological Society* **1974**, *21*, 62–71.
19. Smale, M.C.; Beveridge, A.E.; Pardy, G.F.; Steward, G.A. Selective logging in podocarp/tawa forest at Pureora and Whirinaki. *New Zealand Journal of Forestry Science* **1987**, *17*, 29–50.
20. Norton, D.A. Seedling and sapling distribution patterns in a coastal podocarp forest; Hokitika Ecological District; New Zealand. *New Zealand Journal of Botany* **1991**, *29*(4), 463–466.
21. Burns, B.R.; Smale, M.C. Changes in structure and composition over fifteen years in a secondary kauri (*Agathis australis*)-tanekaha (*Phyllocladus trichomanoides*) forest stand; Coromandel Peninsula; New Zealand. *New Zealand Journal of Botany* **1990**, *28*(2), 141–158.
22. Donoghue, S.; Turner, P. A. A review of Australian tree fern ecology in forest communities. *Austral Ecology* **2022**, *47*(2), 145–165.
23. Moran, R.C.; Klimas, S.; Carlsen, M. Low-trunk epiphytic ferns on tree ferns versus angiosperms in Costa Rica. *Biotropica* **2003**, *35*(1), 48–56.
24. Walker, L.R.; Sharpe, J.M. Ferns; disturbance and succession. In Fern Ecology. Cambridge University Press: New York, United States of America, 2010; pp. 177–219.
25. Wagner, K.; Mendieta-Leiva, G.; Zotz, G. Host specificity in vascular epiphytes: a review of methodology; empirical evidence and potential mechanisms. *AoB plants* **2015**, *7*, plu092.
26. Negrão, R.; Sampaio-e-Silva, T.; Kortz, A.R.; Magurran, A.; Matos, D.M. An endangered tree fern increases beta-diversity at a fine scale in the Atlantic Forest Ecosystem. *Flora* **2017**, *1*(234), 1–6.
27. Brock, J.M.; Morales, N.S.; Burns, B.R.; Perry, G.L. The hare; tortoise and crocodile revisited: Tree fern facilitation of conifer persistence and angiosperm growth in simulated forests. *Journal of Ecology* **2020**. *108*(3), 969–981.
28. Brock, J.M.; Perry, G.L.; Lee, W.G.; Schwendenmann, L.; Burns, B.R. Pioneer tree ferns influence community assembly in northern New Zealand forests. *New Zealand Journal of Ecology* **2018**. *42*(1), 18–30.
29. Boffa Miskell Limited. The manuka and kanuka plantation guide. Available online: www.trc.govt.nz/assets/Documents/Guidelines/Land-infosheets/Manuka-plantation-guide-landcare-April2017.pdf (accessed on 9 September 2024).
30. Blaschke, P.M. Vegetation and landscape dynamics in eastern Taranaki hill country. PhD Thesis, Victoria University, Wellington, 1988.
31. McLeary, W. H. A study of the gully systems of the Waikato Basin with particular reference to those in and surrounding the City of Hamilton: a research study. Diploma dissertation, University of Canterbury, Christchurch, 1972.

32. Clarkson, B. D.; Kirby, C. L. Ecological restoration in urban environments in New Zealand. *Ecological Management & Restoration* **2016**, *17*(3), 180–190.
33. Stewart, G.H.; Ignatieva, M.E.; Meurk, C.D.; Earl, R.D. The re-emergence of indigenous forest in an urban environment; Christchurch; New Zealand. *Urban Forestry & Urban Greening* **2004**, *2*(3), 149–158.
34. Clarkson, B.D.; Bylsma, R.J. Restoration planting in urban environments. *Indigena* **2016**, (May), 7–10.
35. Wallace, K.J.; Clarkson, B.D. Urban forest restoration ecology: a review from Hamilton; New Zealand. *Journal of the Royal Society of New Zealand* **2019**, *49*(3), 347-369.
36. Clarkson, B.D.; McGowan, R.; Downs, T.M. In *Proceedings of the Hamilton Gullies Workshop,* University of Waikato, Hamilton, New Zealand, 29–30 April 2000.
37. Myers, N.; Mittermeier, R. A.; Mittermeier, C. G.; Da Fonseca, G. A.; Kent, J. Biodiversity hotspots for conservation priorities. *Nature* **2000**, *403*(6772), 853–858.
38. McEwen, W. M. *Ecological regions and districts of New Zealand;* Department of Conservation: Wellington, New Zealand, 1987.
39. National Institute of Water and Atmospheric Research (NIWA). Climate data and activities, Available online: https://niwa.co.nz/education-and-training/schools/resources/climate (accessed on 23 July 2024).
40. Rogers, H.C.; Clarkson, B.D. Restoration strategies for three *Dacrycarpus dacrydioides* (A. Rich.) de Laub.; kahikatea remnants in Hamilton City; New Zealand. *Forests* **2022**, *13*(10), 1633.
41. Rogers, H.C.; Clarkson, B.D. Epiphyte-host relationships of remnant and recombinant urban ecosystems in Hamilton; New Zealand: the importance of *Dicksonia squarrosa* (G. Forst.) Sw.; whekī. *New Zealand Journal of Botany* **2025**, *63*(1), 150-159.
42. MacKay, D.B.; Wehi, P.M.; Clarkson, B.D. Evaluating restoration success in urban forest plantings in Hamilton; New Zealand. *Urban Habitats* **2011**, *6*(1).
43. Planting a lasting urban forest. Available online: www.peoplecitiesnature.co.nz/publications (accessed on 19 December 2024).
44. Hurst, J.M.; Allen, R.B. Lincoln; NZ.: Manaaki Whenua-Landcare Research. A permanent plot method for monitoring indigenous forests: field protocols. Available online: https://nvs.landcareresearch.co.nz/Content/PermanentPlot_FieldProtocols.pdf (accessed on 16 February 2024).
45. Breitwieser, I.; Heenan, P.J. 2023. Flora of New Zealand Online. Available online: www.nzflora.info (accessed on 9 September 2024).
46. R Core Team. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing; Vienna; Austria. Available online: www.R-project.org (accessed on 23 February 2025).
47. Oksanen, J.; Simpson, G.L.; Blanchet, F.G.; Kindt, R.; Legendre, P.; Minchin, P.R.; O'Hara, R.B.; Solymos, P.; Stevens, M.H.; Szoecs, E.; Wagner, H. Vegan: Community Ecology Package. R package version 2.6–4. Available online: http://CRAN.R-project.org/package=vegan (accessed on 13 September 2024).
48. Hsieh, T.C.; Ma, K.; Chao, A. iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). *Methods in Ecology and Evolution* **2016**, *7*(12), 1451–6.

49. Lenth, R.V. Least-squares means: the R package lsmeans. *Journal of Statistical Software* **2016**, *69*, 1–33.
50. Legendre, P.; Gallagher, E.D. Ecologically meaningful transformations for ordination of species data. *Oecologia* **2001**, *129*, 271–280.
51. Ricotta, C.; Podani, J. On some properties of the Bray-Curtis dissimilarity and their ecological meaning. *Ecological Complexity* **2017**, *31*, 201–205.
52. De Cáceres, M.; Jansen, F.; De Caceres, M.M. Package 'indicspecies'. *Indicators* **2016**, 8(1), 29.
53. Legendre, P.; Anderson, M.J. Distance-based redundancy analysis: testing multispecies responses in multifactorial ecological experiments. *Ecological Monographs* **1999**, *69*(1), 1–24.
54. Borcard, D.; Legendre, P. All-scale spatial analysis of ecological data by means of principal coordinates of neighbour matrices. *Ecological Modelling* **2002**, *153*(1-2), 51–68.
55. Borcard, D.; Legendre, P.; Avois-Jacquet, C.; Tuomisto, H. Dissecting the spatial structure of ecological data at multiple scales. *Ecology* **2004**, *85*(7), 1826–1832.
56. Blanchet, F.G.; Legendre, P.; Borcard, D. Forward selection of explanatory variables. *Ecology* **2008**. *89*(9), 2623–2632.
57. Peres-Neto, P.R.; Jackson, D.A.; Somers, K.M. Giving meaningful interpretation to ordination axes: assessing loading significance in principal component analysis. *Ecology* **2003**, *84*(9), 2347–63.
58. Mehltreter, K.; Flores-Palacios, A.; García-Franco, J. G. Host preferences of low-trunk vascular epiphytes in a cloud forest of Veracruz, Mexico. *Journal of Tropical Ecology* **2005**, *21*(6), 651-660.
59. Spicer, M.E.; Woods, C.L. A case for studying biotic interactions in epiphyte ecology and evolution. Perspectives in Plant Ecology; *Evolution and Systematics* **2022**, *54*, 125658.
60. Azevedo-Schmidt, L.; Currano, E.D.; Dunn, R.E.; Gjieli, E.; Pittermann, J.; Sessa, E.; Gill, J.L. Ferns as facilitators of community recovery following biotic upheaval. BioScience 2024, 74(5), 322–332.
61. Brock, J.M.; Perry, G.L.; Burkhardt, T.; Burns, B.R. Forest seedling community response to understorey filtering by tree ferns. Journal of Vegetation Science 2018, 29(5), 887–897.
62. Weidlich, E.W.; Nelson, C.R.; Maron, J.L.; Callaway, R.M.; Delory, B.M.; Temperton, V.M. Priority effects and ecological restoration. Restoration Ecology 2021, 29(1), e13317.
63. van Breugel, M.; Bongers, F.; Norden, N.; Meave, J.A.; Amissah, L.; Chanthorn, W.; Dent, D.H. Feedback loops drive ecological succession: towards a unified conceptual framework. Biological Reviews 2024, 99(3): 9282011949.
64. Clarkson, B. D. Ecological restoration in Hamilton City. Royal New Zealand Institute of Horticulture. Proceedings of Greening the City, Christchurch, New Zealand. 2005.
65. Bystriakova, N.; Bader, M.; Coomes, D.A. Long-term tree fern dynamics linked to disturbance and shade tolerance. Journal of Vegetation Science 2011, 22(1), 72–84.
66. Landeros-López, J. G.; Krömer, T.; Gómez-Díaz, J. A.; Velázquez-Rosas, N.; Carvajal-Hernández, C. I. Influence of Microclimatic Variations on Morphological Traits of Ferns in Urban Forests of Central Veracruz, Mexico. Plants 2025, 14(11), 1732.

67. Jarquin-Pacheco, M. B.; Armenta-Montero, S.; Contreras-López, J.; Carvajal-Hernández, C. I. Urban forests as habitats for vascular epiphytes and allied terrestrial plants. Urban Ecosystems 2025, 28(4), 1–13.
68. Auckland Council. Te Haumanu Taiao - Pānuitia Ngā Aratohu; 2024. Available online: https://www.tiakitamakimakaurau.nz/protect-and-restore-our-environment/te-haumanu-taiao-restoring-natural-environment/te-haumanu-taiao-guide/ (accessed on 29 August 2025).
69. Martin, P.H.; Canham, C.D.; Marks, P.L. Why forests appear resistant to exotic plant invasions: intentional introductions; stand dynamics; and the role of shade tolerance. Frontiers in Ecology and the Environment 2009, 7(3), 142–149.

Chapter 3. Trait matching contributes to epiphyte host preferences in New Zealand urban forests

Abstract

Ecologists have studied factors shaping the structure of epiphyte communities for decades, focusing on host traits and microclimate conditions. Here, we investigated how epiphyte traits influence host preferences in urban environments. We assessed vascular epiphyte metacommunities at a fine scale and networks at a broad scale using data from 32 sites in two New Zealand cities: Hamilton and New Plymouth. Host preferences were measured using three host types (tree ferns, angiosperm trees, and conifer trees) to reflect host functional syndromes and account for biogeographical variation in host species distributions. We measured rhizome and root traits of 10 epiphyte species hypothesised to influence attachment mechanisms and host preferences. Epiphyte metacommunities differed significantly among host types, and host preferences were identified using interaction network analyses. Stronger host preferences in Hamilton than New Plymouth suggest deterministic processes have a greater effect on epiphyte assemblages in cities with younger vegetation and less stable microclimates. Trait analyses revealed that epiphytes with preferences for tree ferns had more abundant and longer rhizome hairs, while generalist epiphytes had wider rhizomes, longer roots, and longer, more abundant rhizome scales. Attachment mechanisms differed with host preferences. Epiphytes with preferences for tree ferns primarily used an interlocking mechanism, whereas species mainly on woody hosts used adhesion, and generalists employed both mechanisms. Our results suggest that epiphyte traits contribute to the non-random structure of urban epiphyte assemblages, with trait matching supporting host preferences in urban settings.

3.1. Introduction

The processes underpinning community structure are of key interest to ecologists (Kraft and Ackerly 2014), and the relative importance of ecological determinism (e.g., niches) versus neutral theory (e.g., stochasticity) remains a controversial topic in ecology. Neutral theory argues that communities are structured entirely by stochastic processes, such as ecological drift, chance colonisation and random extinction (Hubbell 2011). In contrast, niche theory suggests that community structure results from environmental filtering, biotic interactions, and interspecific trade-offs (Chase and Myers 2011). Understanding the stochastic and

deterministic factors that shape patterns of biodiversity is crucial for the conservation and restoration of plant communities in modified landscapes such as cities (Swan et al. 2021).

Functional traits are closely linked to the niche concept as they contribute to the performance of species and, therefore, tolerance of environmental conditions (Kearney et al. 2010). They are the morphological, physiological, and phenological characteristics that affect plant performance, including growth, reproduction, and survival (Violle et al. 2007). Plant functional traits rarely evolve in isolation; rather, they reflect integrated trait syndromes – sets of traits shaped by abiotic and biotic factors (Hietz et al. 2022). Functional traits help describe mechanistically how plants interact with their environment and other species (e.g., trait matching), thus helping us better understand what drives patterns of biodiversity (Schellenberger Costa et al. 2018; Wagner et al. 2021).

Vascular epiphytes (i.e., plants that perch upon other plants for structural support) make up approximately 10% of plant species globally (Zotz et al. 2021). While commonly associated with tropical regions, the diversity and biomass of epiphytes in temperate rainforests, such as those in New Zealand and Chile, are comparable to many tropical forests (Hofstede et al. 2001; Zotz 2005). Several studies have identified random epiphyte-host interactions in support of neutral processes structuring epiphyte communities (Burns 2008; Burns and Zotz 2010; Janzen et al. 2020). However, the effect of moisture availability on epiphyte distributions at a larger scale (Mendieta-Leiva et al. 2020) and epiphyte host preferences at a local scale (Wagner et al. 2015) suggest that deterministic processes also shape epiphyte communities.

Epiphyte host preferences describe how strongly an epiphyte species is associated with a particular host species (Wagner et al. 2015). While strict host-specificity (i.e., an epiphyte growing exclusively on one host species) is rare, many epiphytes exhibit host preferences, occurring on only a few host species (Callaway et al. 2002). In contrast, generalist epiphytes grow on multiple host species in different habitats. Research on factors underpinning host preferences has concentrated on host traits in tropical rainforests (Wagner and Zotz 2020). While host preferences are generally assessed using host species, broader host types can reveal trait matching between epiphytes and host substrate characteristics (e.g., fibrous substrate of tree ferns versus fissured or smooth bark of angiosperm and conifer trees). For

example, epiphytes exhibited host preferences for tree ferns in tropical cloud forests of Costa Rica (Moran et al. 2003) and Mexico (Mehltreter et al. 2005).

Despite receiving less attention than host traits, epiphyte traits are also functionally important, directly impacting how epiphytes adhere to host species. Traits influencing epiphyte attachment likely include rhizome and/or root length (Benzing 1978), the spongy velamen (Benzing 1973; Tay et al. 2023), and the presence or abundance of trichomes, which increase the attachment surface area (Wang et al. 2021; Tay et al. 2023). Recognised attachment mechanisms include mechanical interlocking, in which roots and hairs grow into small bark anomalies, and adhesion, in which a glue-like substance facilitates epiphyte attachment (Tay et al. 2021). Trait matching between epiphyte and host species is implicitly deterministic and may reveal factors supporting species interactions (Wagner et al. 2015; Wagner et al. 2021), particularly in fragmented and degraded landscapes such as cities, where host assemblages are less diverse (Gallego et al. 2025).

Urban epiphyte research has highlighted the negative impact of anthropogenic disturbances on epiphyte diversity, with fewer large, old hosts and warmer, less humid microclimates (Martins et al. 2020; Alvim et al. 2021). Constrained host assemblages may encourage homogeneous epiphyte communities, dominated by generalist species (Nitta et al. 2020; Jarquin-Pacheco et al. 2025). Research in New Zealand cities has highlighted the impact of host assemblages (Rogers et al. 2025), drier microclimates, host bark type, and isolation from other seed sources on urban epiphyte communities (Bryan 2011). Another New Zealand study identified urban epiphytes with host preferences for a tree fern (*Dicksonia squarrosa*), while generalists were strongly associated with woody hosts (Rogers and Clarkson 2025). However, to the best of our knowledge, this study is the first to examine how vascular epiphyte traits influence host preferences and the structure of urban epiphyte assemblages.

We assessed epiphyte-host interactions at the metacommunity and network level. Epiphyte metacommunities are epiphyte communities on an individual host tree linked by dispersal within and across sites (Burns 2008). In comparison, networks describe associations between epiphyte and host species. First, we used observations at the individual host level from field surveys (i.e., epiphyte count data) in two urban centres to investigate variation in epiphyte assemblages explained by key host characteristics. We then examined epiphyte-host interactions at a broad scale using iNaturalist records from lowland environments on New

Zealand's North Island. Finally, to better understand the mechanisms driving urban epiphyte-host interactions, we measured six epiphyte attachment traits. We focused on two hypotheses: H1) tree ferns host distinct epiphyte assemblages compared to woody hosts in urban environments (i.e., implying deterministic processes leading to non-random associations), and H2) epiphyte root and rhizome traits and attachment mechanisms influence host preferences (i.e., leading to trait matching).

3.2. Materials and methods

3.2.1. Study sites

For analyses involving field data from vegetation surveys, we used 32 urban sites in Hamilton (n = 24) and New Plymouth (n = 8) located on North Island, New Zealand (Fig. 1). New Zealand's major urban centres support a low proportion of native-dominant vegetation cover, ranging from <1 to 8.9% (Clarkson and Kirby 2016). Furthermore, urban plant communities often consist of younger, smaller, isolated vegetation patches (Stewart et al. 2004; MacKay et al. 2011), which likely constrain epiphyte diversity.

Hamilton is a city of approximately 11,000 ha in the centre of the North Island (37°46′59.99″S, 175°16′59.99″E). With a warm temperate climate, Hamilton has a mean annual temperature of 13.7 °C and a mean annual precipitation of 1,190 mm (National Institute of Water and Atmospheric Research 2020). New Plymouth is a smaller city (approximately 7,500 ha) on the west coast of the North Island (39°03′28.11″S, 174°04′27.62″E). New Plymouth has a mean annual temperature of 14 °C and a mean annual precipitation of 1,400 mm (Taranaki Regional Council 2022).



Fig. 1 Study sites (dots) where epiphyte and host species data were collected in Hamilton (left) and New Plymouth (right). The map of New Zealand (centre) shows the location of Hamilton (orange symbol) and New Plymouth (blue symbol) on the North Island

New Plymouth has a more diverse epiphytic flora than Hamilton (Supplementary Information, Table S1), attributed to higher annual rainfall and older, more diverse vegetation and host assemblages (Wallace et al. 2017; HCC unpublished database).

3.2.2. Field data collection

We collected epiphyte-host data from 32 urban study sites within continuous tracts of vegetation across two New Zealand cities (Hamilton and New Plymouth). Contiguous vegetation patches support cooler, more stable microclimates compared to isolated street trees (Jiao et al. 2017), and thus should minimise environmental heterogeneity affecting epiphyte communities. Data were compiled at the individual host level from site vegetation surveys (Bryan 2011; PCaN 2024). Fourteen sites across both cities were sampled in 2023/2024. Eighteen sites across both cities were sampled in 2009/2010. The time elapsed between the two surveys meant we focused on differences in each dataset separately when analysing

epiphyte metacommunities. Because the sites surveyed in each study differed, the host species composition also varied between the two datasets (Table 1).

Table 1. Host assemblages surveyed in the present study and by Bryan (2011). This information includes host abundances for the three host types (tree ferns, angiosperm trees, and conifer trees), as well as total host abundance and host species richness. The percentage contribution of each host type to the total hosts measured in each dataset is also provided

	Present study	**Bryan (2011)**
Angiosperm trees	50 (18%)	135 (76%)
Conifer trees	2 (1%)	33 (18%)
Tree ferns	218 (81%)	10 (6%)
Total host abundance	270	178
Host species richness	19	24

The starting location for each site survey was randomly determined (Bryan 2011; PCaN 2024). Host species (i.e., woody trees and shrubs and tree ferns > 2.5 cm DBH) were identified, counted and measured for DBH, and vascular epiphytes were identified and counted. Binoculars assisted epiphyte identification on taller host species, and epiphytes not identified to species level (n = 34) were excluded from analysis. The species nomenclature follows Breitwieser and Heenan (2023).

Almost 5,000 obligate epiphytes (28 species) on 448 individual hosts (31 species) were recorded at the study sites. We focused on native obligate vascular epiphytes (hereafter, epiphytes); data on facultative and accidental epiphytes were excluded. Obligate epiphytes or holo-epiphytes were defined as species that occur almost exclusively on other plants (Burns 2010).

3.2.3. Trait data collection

We measured epiphyte root and rhizome traits of 10 epiphyte species (Fig. 2). Species selection was based on host preferences identified from network analyses (see "Data analysis" below for further details). The 10 epiphyte species were nine ferns and one orchid. Two orchids with host preferences for woody hosts (i.e., *Drymoanthus adversus* (Hook.f.) Dockrill and *Bulbophyllum pygmaeum* (Sm.) Lindl.) were not measured because they are rare

in Hamilton. Epiphyte samples were collected at four publicly accessible gullies with permission from Hamilton City Council.



Fig. 2 Rhizome and roots of the 10 measured epiphyte species. First row, left to right: *Pyrrosia elaeagnifolia*, *Lecanopteris pustulata*, *Earina mucronata*, *Asplenium flaccidum* and *Asplenium polyodon*. Second row, left to right: *Arthropteris tenella, Lecanopteris scandens*, *Tmesipteris lanceolata* (on tree fern substrate), *Trichomanes venosum* and *Hymenophyllum flabellatum* (on tree fern substrate)

We measured root and rhizome traits of 30 samples per epiphyte species. The number of individual plants measured per species varied based on growth form or rarity. Samples of *Earina mucronata* were collected entirely from one individual plant because it is locally uncommon in Hamilton. Samples were standardised to 1 centimetre of rhizome and its connected roots, attached to petri dishes, and measured using an Olympus SZH10 Stereo Microscope with a 0.1 mm lens. Samples with roots longer than 10 mm were measured with a standard ruler.

Six traits were measured: rhizome diameter, hair and scale abundance (using visual estimates of % cover), maximum hair and scale length, and standard root length (i.e., the sum of root lengths over a predetermined rhizome length). We measured maximum plant length (i.e., maximum frond or leaf length from the rhizome) to account for plant size in our analyses.

3.2.4. Data analysis

Statistical analyses were completed in R version 4.2.2 (R Core Team 2023) to test our hypotheses.

3.2.4.1. Metacommunity analysis

To test H1, we assessed epiphyte assemblages on three host types at the metacommunity scale (i.e., epiphyte assemblages on individual hosts) in two New Zealand cities. We compiled data from two datasets (Table 1). Our decision to assess host preferences at the host type scale was supported by the low specialisation scores of austral epiphyte networks, which suggest that epiphytes in southern regions are associated with specific host traits rather than host species (Taylor et al. 2016). Using host types also helped minimise potential biogeographical effects on epiphyte-host interactions across the two cities studied.

Multivariate analyses used the 'vegan' R package (Oksanen et al. 2013). Permutational multivariate analysis of variance (PERMANOVA) used Hellinger-transformed data with the Bray-Curtis dissimilarity. Our first PERMANOVA model compared the effects of city, dataset and host type (accounting for the nested design of sites within cities) using the 'adonis2' R function (McArdle and Anderson 2001). After detecting a significant interactive effect among city, dataset and host type, we used PERMANOVA models for each city and focused on differences in each dataset individually.

We visualised differences in epiphyte metacommunities among the host types using non-metric multidimensional scaling (NMDS). To understand which epiphyte species contributed to differences among host types, indicator species analysis was performed using the 'indicspecies' R package (De Cáceres et al. 2016). Species showing strong congruence with the host types, based on permutation test significance ($\alpha = 0.05$), and abundant species (i.e., the 10 most dominant species overall) not identified as indicator species were overlain on the NMDS plot to illustrate prominent epiphyte species (Fig. 3). We completed four additional NMDS plots, separating the data by city and dataset (Supplementary Information, Fig. S2).

To assess spatial autocorrelation (e.g., dispersal limitation, mass effects) in epiphyte community composition for each dataset and city within each dataset, we completed Mantel tests using the Bray-Curtis dissimilarity and geographic distances (based on site coordinates). We found no evidence for spatial structuring (i.e., dispersal limitation driving epiphyte community composition) at the site level in our datasets (Supplementary Information, Table S2).

Finally, we used the “capscale” (db-RDA) and “varpart” (variation partitioning) R functions to assess the variation explained by host type, dataset and city. Each independent variation component was tested for statistical significance using 1,000 random permutations (Peres-Neto et al. 2003).

3.2.4.2. Network analysis

At the network level, we conducted exploratory analysis of lowland epiphyte-host interactions at a broad scale. Epiphyte observations were downloaded on 5 November 2025 from iNaturalist (New Zealand), a versatile global citizen science platform providing open-access species observation data and increasingly used in biodiversity research (Mason et al. 2025). Approximately 1,730 (73%) of the observations downloaded were made by two of the authors (H.R. and B.C.).

The iNaturalist data were refined to include only research-grade observations specifying both the epiphyte and host species from the North Island, New Zealand. Observations were then limited to <450 m a.s.l. with a positional accuracy of <50 m. We then chose high-quality host species (i.e., with ≥ 10 epiphyte records) to construct a bipartite network with the bipartite R package (Dormann et al. 2008) and visualise the host-epiphyte interactions (Fig. 4). The interaction network supported our selection of 12 epiphyte species exhibiting preferences for one of three host groups: tree ferns, woody trees, or a generalist habit (four per group; see Supplementary Information, Table S3). These data from a broader geographic area helped identify epiphyte host preferences unconstrained by host assemblages.

Null model testing further supported the selected 12 epiphyte species by assessing the strength of epiphyte-host interactions using presence/absence data from our 32 urban sites (Supplementary Information, Table S4). A null modelling approach helps inform the degree of determinism in networks by providing estimates of expected interaction strengths against which the observed values can be compared. We used 100 model iterations with the “econullnetr” R package to test the randomness of observed interactions (Vaughan et al. 2018) and visualised these urban networks in a bipartite plot (Supplementary Information, Fig. S1).

3.2.4.3. Trait analysis

To investigate how epiphyte root and rhizome traits influenced the host preferences, we used linear mixed-effects models (LMEs) and principal components analysis (PCA). These analyses helped test H2 (epiphyte root and rhizome traits and attachment mechanisms influence host preferences). We first used four LMEs to examine how epiphyte rhizome diameter, standard root length, and scale abundance and length vary with host preferences. Maximum plant length was included as a covariate. Rhizome hair abundance and length were not assessed because they were only associated with epiphytes on tree ferns. The normality of the predictors was assessed using Shapiro-Wilk tests; we log-transformed and standardised all five epiphyte traits. Our models accounted for variation in species within each host group with epiphyte species as a fixed effect. The random effect of individual plant sampled accounted for non-independent trait measurements. Post-hoc tests used the "emmeans" R package (Lenth 2016).

PCA investigated epiphyte traits linked to host preferences (Abdi and Williams 2010). We removed hair abundance, scale length, and maximum plant length because they were highly correlated with other traits ($r > 0.7$). A correlation heatmap using the "pheatmap" R package (Kolde 2015) illustrated correlated root and rhizome traits (Supplementary Information, Fig. S3).

3.3. Results

3.3.1. Epiphyte metacommunities

When examining epiphyte metacommunities, we found that tree ferns supported distinct communities compared to woody hosts (Fig. 3). PERMANOVA showed a significant interactive effect between host type and dataset in Hamilton ($F_{2,298} = 3.2$, $P < 0.05$, $R^2 = 0.01$) and New Plymouth ($F_{1,103} = 4.3$, $P < 0.05$, $R^2 = 0.03$).

In Hamilton, the present study found significant differences in epiphyte community composition on tree ferns compared to angiosperm trees ($F_{1,225} = 60.1$, $P < 0.01$, $R^2 = 0.21$), but no significant difference between tree ferns and conifers ($F_{1,197} = 3.2$, $P = 0.5$, $R^2 = 0.02$) or angiosperm and conifer trees ($F_{1,30} = 3.3$, $P = 1.0$, $R^2 = 0.10$). Data collected by Bryan (2011) in Hamilton revealed significantly different epiphyte assemblages on tree ferns and conifer trees ($F_{1,36} = 22.8$, $P < 0.05$, $R^2 = 0.39$). There was no significant difference in

epiphyte assemblages between tree ferns and angiosperm trees ($F_{1,69} = 12.0$, $P = 0.2$, $R^2 = 0.15$) or angiosperms and conifer trees ($F_{1,95} = 2.8$, $P = 0.1$, $R^2 = 0.03$).

In New Plymouth, the present study found a significant difference in epiphyte assemblages on tree ferns and angiosperms ($F_{1,37} = 5.8$, $P < 0.01$, $R^2 = 0.14$). No conifers were surveyed in New Plymouth for the present study. The Bryan (2011) dataset showed differences in epiphyte assemblages on tree ferns compared to angiosperm trees in New Plymouth ($F_{1,72} = 4.6$, $P < 0.01$, $R^2 = 0.06$). However, Bryan's (2011) New Plymouth data showed no significant differences in epiphyte assemblages between tree ferns and conifer trees ($F_{1,3} = 2.7$, $P = 0.2$, $R^2 = 0.47$) or angiosperm and conifer trees ($F_{1,69} = 1.0$, $P = 0.5$, $R^2 = 0.02$).

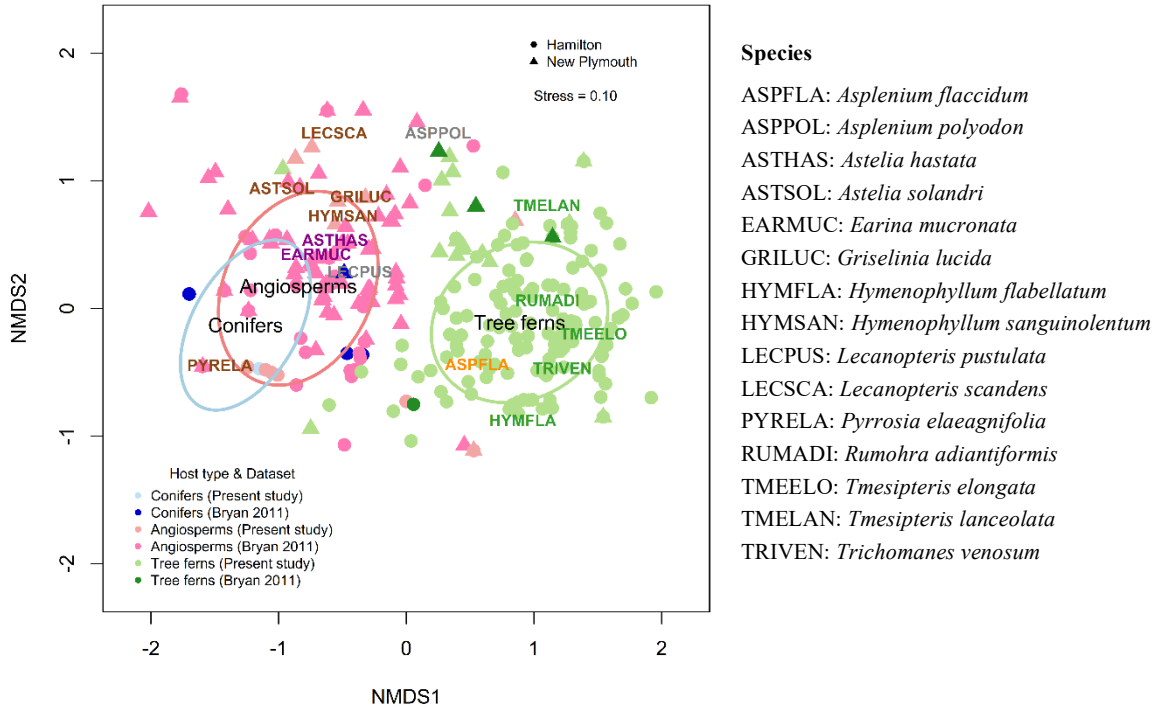


Fig. 3 Native obligate epiphyte composition on tree ferns (green symbols), angiosperm trees (pink symbols), and conifer trees (blue symbols). Circles denote hosts measured in Hamilton and triangles represent hosts measured in New Plymouth. Darker shaded symbols are hosts measured by Bryan (2011), and lighter shaded symbols are hosts measured in the present study. Ellipses associated with host type represent one standard deviation. Six-letter codes denote indicator species or abundant species. Green codes represent indicator species of tree ferns (5), purple codes represent species associated with angiosperm trees (2), brown codes represent species associated with both angiosperm and conifer trees (5), and orange codes

denote indicator species of tree ferns and conifer trees (1). Grey codes represent abundant species (i.e., the 10 most dominant species) not selected as indicator species (2). Stress = 0.10

We identified indicator species for one or two host types (Supplementary Information, Table S5). The five species associated with tree ferns were all ferns: *Hymenophyllum flabellatum*, *Rumohra adiantiformis* (G.Forst.) Ching, *Tmesipteris elongata*, *T. lanceolata* and *Trichomanes venosum*. Three of these species were used for trait analyses. Indicator species of angiosperm trees were the nest epiphyte *Astelia hastata* Colenso, and the fern *Arthropteris tenella,* with the latter used for trait analyses. The five indicator species of both angiosperm and conifer trees were the ferns *Pyrrosia elaeagnifolia* and *Lecanopteris scandens* (G.Forst.) Perrie & Brownsey*,* and *Hymenophyllum sanguinolentum* (G.Forst.) Sw.*,* the nest epiphyte *Astelia solandri* A.Cunn. and the shrub *Griselinia lucida* (J.R.Forst. & G.Forst.) G.Forst. Two of these species were used for trait analyses.

Variation partitioning of epiphyte community composition revealed the total amount (R^2 = 25.7%) explained by the three explanatory variables (host type, dataset and city). More variation was independently explained by host type ($F_{2,441}$ = 15.1, P < 0.01, R^2 = 6.1%) than by city ($F_{1,441}$ = 26.2, P < 0.01, R^2 = 5.4%) or dataset ($F_{1,441}$ = 14.1, P < 0.01, R^2 = 2.8%). The shared variation between host type and dataset was relatively large (R^2 = 10%), with host type and city explaining less variation (R^2 = 0.5%). The three predictors combined explained a small amount of variation (R^2 = 0.9%). Overall, host type explained 17.5% of the variation in epiphyte community composition.

3.3.2. Epiphyte networks

Certain epiphyte-host interactions were either stronger or weaker than null model expectations (Supplementary Information, Table S4). The ferns *Tmesipteris lanceolata* P.A.Dang., *Trichomanes venosum* R.Br. and *Hymenophyllum flabellatum* Labill. showed preferences for the tree ferns *Cyathea medullaris* (G.Forst.) Sw. and *Dicksonia squarrosa* (G.Forst.) Sw. In contrast, the orchids *Drymoanthus adversus* and *Bulbophyllum pygmaeum* and the fern *Arthropteris tenella* (G.Forst.) J.Sm. showed stronger associations with woody hosts like *Alectryon excelsus* Gaertn.*, Knightia excelsa* R.Br. and *Dacrycarpus dacrydioides* (A.Rich.) de Laub. Generalist epiphytes with stronger links than null model expectations to multiple host types were the ferns *Asplenium flaccidum* G.Forst.*, Lecanopteris pustulata*

(G.Forst.) Perrie & Brownsey and *Pyrrosia elaeagnifolia* (Bory) Hovenkamp and the orchid *Earina mucronata* Lindl. Fig. 4 shows epiphytes displaying a generalist habit or host preferences for tree ferns or woody hosts.

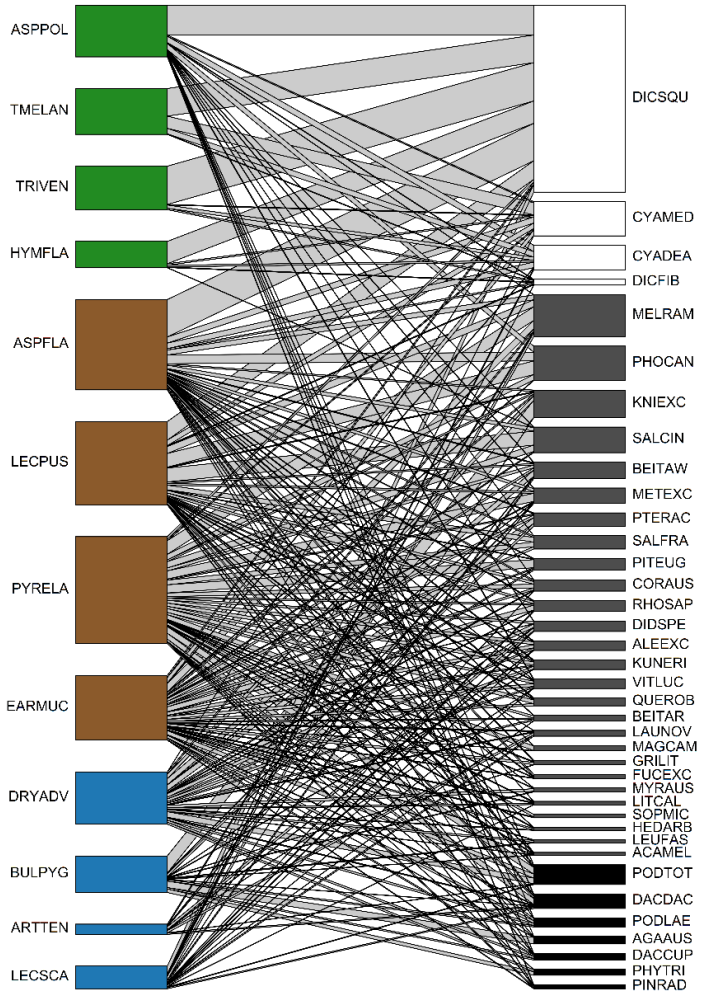


Fig. 4 Epiphyte-host relationships of twelve lowland epiphyte species. Six-letter codes on the left represent epiphyte species, and on the right represent host species. Epiphyte box colours correspond with host preferences: species with preferences for tree ferns (green), woody hosts (blue) or species with generalist tendencies (brown). Host box colours symbolise tree ferns (white), angiosperm trees (dark grey) and conifers (black). The width of each link (between an epiphyte and host) is relative to the number of records for that relationship. Research-grade observations < 450 m a.s.l. with positional accuracy < 50 m were obtained from iNaturalist NZ. Host species selected had ≥ 10 epiphyte records (scientific names associated with six-letter codes and the number of observations per species are provided in Supplementary Information, Table S6)

3.3.3. Functional traits influencing attachment mechanisms and host preferences

Epiphyte root and rhizome traits were correlated with host preferences (Fig. 5). Traits positively associated with a generalist habit were rhizome diameter, standard root length and maximum plant length (Table 2). Epiphytes associated with woody hosts were also positively correlated with rhizome diameter. In contrast, epiphytes with preferences for tree ferns were associated with longer and more abundant rhizome hairs.

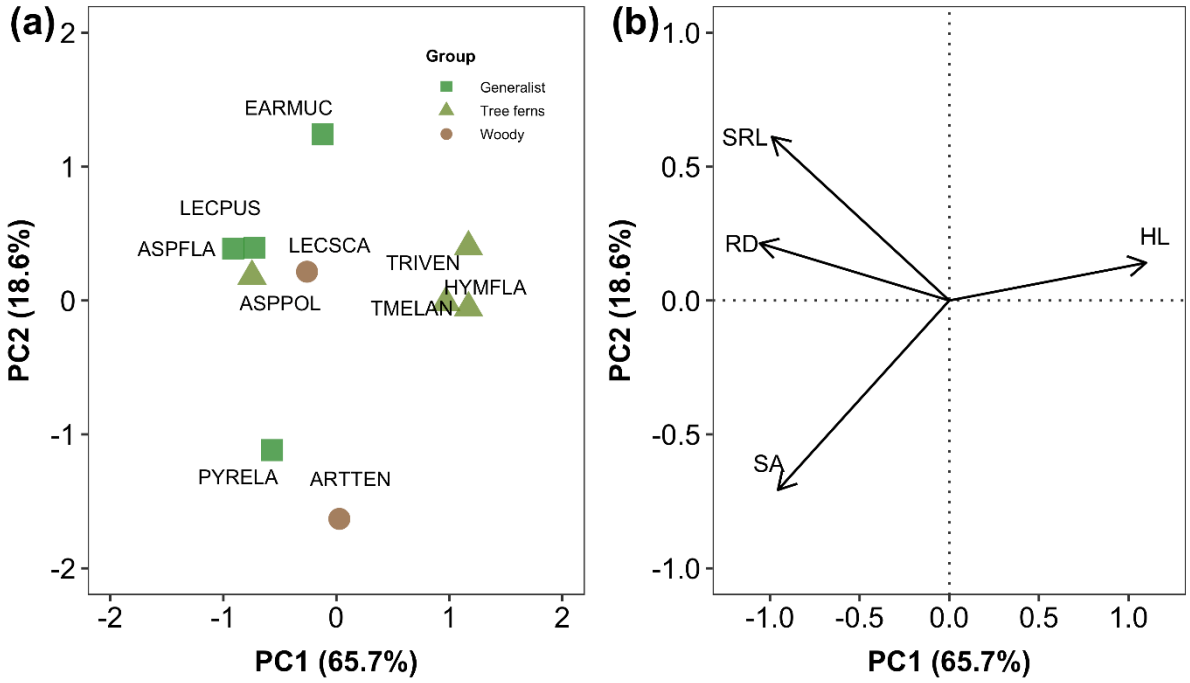


Fig. 5 Epiphyte root and rhizome trait associations with host preferences (i.e., epiphytes with preferences for tree ferns, woody hosts, or exhibiting a generalist habit) using principal components analysis (PCA). PC species scores are presented on the left (a), and loadings are on the right (b). Symbols denote epiphyte groups (green squares: generalists; yellow triangles: preferences for tree ferns; brown circles: preferences for woody hosts). Six-letter codes represent the scientific species name (see Table 2). Traits influencing epiphyte host preferences (in Euclidean space) are presented on the right: standard root length (SRL), rhizome diameter (RD), scale abundance (SA), and hair length (HL). Trait data were log-transformed and standardised (i.e., centred on the mean and scaled to unit variance), and highly correlated traits ($r > 0.7$) were excluded

Table 2. Mean (± SD) morphological traits of the 10 epiphytic species, measured from 30 rhizome samples per species. Each epiphyte species was assigned either an adhesion, interlocking or combined (i.e., using adhesion and interlocking) attachment mechanism based on the compatibility of these traits with its observed host preferences. Measured traits were the maximum plant length, rhizome diameter, standard root length, scale abundance, scale length, rhizome hair abundance and length. Blank cells indicate traits structurally absent in that species rather than unmeasured

Group	Species	Proposed attachment mechanism	Max. plant length (cm)	Rhizome diameter (mm)	Standard root length (cm)	Rhizome scale abundance (%)	Scale length (mm)	Rhizome hair abundance (%)	Hair length (mm)
Generalist	*Asplenium flaccidum*	Interlocking	37.1 ± 20.0	8.8 ± 3.2	36.3 ± 29.7	59.2 ± 16.0	4.4 ± 2.2		
Generalist	*Earina mucronata*	Combined	35.0 ± 0.0	2.0 ± 0.3	8.1 ± 5.3				
Generalist	*Lecanopteris pustulata*	Combined	17.9 ± 1.7	7.7 ± 1.3	6.7 ± 5.5	47.8 ± 10.2	2.5 ± 0.6		
Generalist	*Pyrrosia elaeagnifolia*	Combined	6.8 ± 3.3	1.2 ± 0.3	2.0 ± 3.0	91.7 ± 11.3	1.8 ± 0.8		
Tree ferns	*Asplenium polyodon*	Interlocking	28.4 ± 8.6	6.2 ± 2.2	8.3 ± 6.6	56.5 ± 22.3	2.8 ± 1.4		
Tree ferns	*Hymenophyllum flabellatum*	Interlocking	6.1 ± 1.5	0.4 ± 0.1	0.01 ± 0.01			24.8 ± 17.1	0.4 ± 0.2
Tree ferns	*Tmesipteris lanceolata*	Interlocking	5.6 ± 1.8	0.9 ± 0.3				35.0 ± 16.6	0.4 ± 0.2
Tree ferns	*Trichomanes venosum*	Interlocking	2.4 ± 0.6	0.2 ± 0.1	0.003 ± 0.003			66.7 ± 17.9	0.1 ± 0.0
Woody	*Arthropteris tenella*	Adhesion	10.3 ± 0.8	1.8 ± 0.4		60.3 ± 23.8	1.2 ± 0.3		
Woody	*Lecanopteris scandens*	Adhesion	13.7 ± 2.9	1.7 ± 0.4	1.9 ± 1.9	35.5 ± 17.5	1.6 ± 0.4		

After accounting for maximum plant length and epiphyte species as fixed effects, the LMEs revealed statistically significant differences in epiphyte rhizome diameter, standard root length (SRL), and scale abundance and length with host preferences (Supplementary Information, Table S7). Rhizome hairs were observed only on epiphytes with preferences for tree ferns, so comparisons of hair length or abundance could not be made across the groups.

Generalist species had wider rhizomes than epiphytes with preferences for tree ferns (t = 16.35, $P < 0.001$) and woody hosts (t = 10.44, $P < 0.001$). Epiphytes associated with woody hosts also had wider rhizomes than epiphytes associated with tree ferns (t = 10.95, P <

0.001). Generalists had higher SRL than the epiphytes associated with tree ferns ($t = 3.62$, $P < 0.01$) and woody hosts ($t = 5.25$, $P < 0.001$). There was no significant difference in SRL between epiphytes associated with tree ferns or woody hosts ($t = 1.11$, $P = 0.52$).

In addition, rhizome scale abundance was significantly higher on generalists than on epiphytes with preferences for tree ferns ($t = 3.39$, $P < 0.01$) or woody hosts ($t = 3.49$, $P < 0.01$). Scale abundance did not vary significantly between epiphytes associated with tree ferns and those associated with woody hosts ($t = -0.85$, $P = 0.68$). Finally, epiphytes associated with woody hosts had shorter scales than generalists ($t = 7.28$, $P < 0.001$) and epiphytes mainly on tree ferns ($t = 2.60$, $P < 0.05$). However, scale length did not vary significantly between generalists and epiphytes with preferences for tree ferns ($t = 1.63$, $P = 0.24$).

3.4. Discussion

Our results suggest that deterministic processes, mediated by epiphyte root and rhizome traits, have a key role in structuring urban epiphyte assemblages through attachment mechanisms and host preferences. The apparent determinism of epiphyte-host associations in urban forests highlights the importance of examining epiphyte traits and biotic interactions with hosts to better understand key factors shaping epiphyte communities.

3.4.1. Epiphyte host preferences

We found evidence for non-random epiphyte preferences using three host types in two urban settings. Analysis at this wider level (i.e., among host types) is useful for assessing the influence of host characteristics on epiphyte assemblages. For example, tree ferns have a structurally complex substrate with high moisture retention (Moran et al. 2003), while angiosperm and conifer trees can have smooth, fissured or flaky bark; these differences influence epiphyte communities (Wyse and Burns 2011). The use of host types may have increased our ability to detect strong host preferences. Previous work has shown that host bias is more apparent in environments where hosts have unrestricted ranges (Wagner et al. 2015). This result differs from our study, in which urban vegetation patches that are less diverse than non-urban forest, so specialised epiphytes might have been affected by the absence of preferred hosts.

Our results suggest that constrained host assemblages may shape epiphyte communities in urban settings by favouring epiphytes with particular traits suited to the available hosts. This result contradicts previous research that found epiphyte networks were stochastically structured in undisturbed forests (Taylor et al. 2016). In our study, epiphyte composition at the metacommunity level varied significantly among tree ferns, angiosperm trees, and conifer trees with no evidence for spatial structuring (e.g., dispersal limitation, mass effects). Tree ferns and angiosperm trees hosted distinct epiphyte assemblages, likely reflecting differences in host characteristics that affect epiphyte colonisation. Conifer trees supported less distinct epiphyte assemblages, partially overlapping with those of angiosperm trees, although this pattern may be due to limited sampling of conifer hosts in this study. Overlapping host traits associated with the woody host types (angiosperm trees and conifer trees) may partly explain the greater similarity in their epiphyte assemblages compared to tree ferns.

Differences in the strength of relationships between host types and epiphyte assemblages for the two cities suggest that deterministic processes (e.g., trait matching) may have a stronger effect on epiphyte assemblages in younger vegetation with less stable microclimates. In Hamilton, host type (associated with host characteristics) had a stronger influence on epiphyte assemblages than in New Plymouth. Our analyses showed greater variance explained in epiphyte assemblage composition when comparing tree ferns and angiosperm trees in Hamilton (R^2 = 21%) than in New Plymouth (R^2 = 14%). These differences may result from variation in local climate, host assemblages and vegetation age. Hamilton has a drier climate, less diverse host assemblages, and younger vegetation than New Plymouth (Bryan 2011). Research in dry tropical forests of Mexico has also found stronger host preferences with epiphytes constrained by host assemblages and microclimate conditions (Vergara-Torres et al. 2010; de la Rosa-Manzano et al. 2014).

Epiphyte preferences for tree ferns may reflect overlapping habitat preferences for cool, humid environments, and the suitability of tree fern substrate for epiphyte colonisation. In contrast, epiphytes strongly associated with angiosperm and conifer host species were largely generalists, suggesting their greater tolerance to environmental conditions. Although environmental conditions were not measured in this study, our results reinforce the importance of tree ferns in these urban settings (Rogers and Clarkson 2025; Rogers et al. 2025), where host assemblages are generally younger and more depauperate than those in non-urban forest. While tree ferns provide a reduced surface area for epiphyte establishment

compared to woody hosts at maturity, they may act as important ‘stepping stones’ for epiphyte dispersal (Taylor and Burns 2015). However, further research on environmental drivers, including physiological experiments assessing epiphyte responses to varying microclimate conditions, is needed to establish the relative importance of environmental factors versus species traits in shaping epiphyte assemblages.

3.4.2. Functional traits

Functional traits affect species performance, and in the case of epiphytes, signal how well they have adapted to living in the canopy. Epiphyte root and rhizome traits are multifunctional, contributing to epiphyte attachment mechanisms and physiological processes, such as the storage and/or absorption of water and nutrients (Mehltreter et al. 2022). Nevertheless, measuring attachment traits is useful for investigating mechanisms such as multi-stage epiphyte adherence. Anecdotal evidence suggests that epiphytes that entangle roots around whole stems or branches establish more successfully on hosts with flaking bark (Benzing 1978). In addition, fern roots may display thigmotropism, adjusting the direction of growth and developing hairs in response to contact with substrate (Pearson 1969). Epiphyte traits enhancing the surface area for attachment include trichomes (e.g., hairs and scales) and the velamen – a specialised, uni- to multiseriate rhizodermis found in many orchids (Tay et al. 2024).

In our study, epiphyte traits associated with generalist species included longer, more abundant rhizome scales. While the function of scales in epiphytic orchids and ferns requires further testing (Benzing and Pridgeon 1983; Benzing 2012), in bromeliads, their role in water and nutrient uptake was established early (Schimper 1888). These appendages may enhance species performance, allowing epiphytes to occupy a broader ecological niche and tolerate a wider range of environmental conditions. In comparison, traits positively correlated with epiphytes mainly on tree ferns were rhizome hair abundance and length. Therefore, species with a hairy, extensive root system may indicate an epiphyte that establishes on hosts with fibrous substrate, weaving among asperities and occasionally penetrating the bark surface. Hairs can facilitate water and nutrient uptake, and hair dimorphism (i.e., changes in hair shape and structure) may enable epiphytes to adapt to substrate characteristics (Pearson 1969).

We focused on variation among species; intraspecific trait variation by substrate type requires further investigation. We examined biological traits relating to epiphyte attachment mechanisms; ecological traits were not measured. Morphological traits can signal species that have successfully adopted the epiphytic lifestyle, but eco-physiological experiments growing epiphytes on different host substrates are needed to fully elucidate these interactions. Other traits (e.g., leaf traits) also likely influence epiphyte-host interactions. For example, species with thicker, succulent leaves may be better associated with more exposed microhabitats on deciduous trees.

3.4.3. Attachment mechanisms

Attachment mechanisms exist along a continuum; however, adhesion and interlocking mechanisms are easily discerned and ecologically useful (Tay and Zotz 2023). We found epiphytes with preferences for woody hosts used an adhesion mechanism, whereas those mainly on tree ferns used an interlocking mechanism. Generalists appear to utilise both mechanisms (i.e., a combined mechanism) with long (occasionally wide), creeping rhizomes and abundant scales or 'suckers'.

An adhesion mechanism was used by the epiphytes with preferences for woody host species. Some angiosperm and conifer trees have rugose, deeply fissured bark that facilitates epiphyte colonisation, but species with hard, smooth bark can hinder epiphyte establishment (Spicer et al. 2022). Therefore, epiphytes with preferences for woody trees (particularly for smooth-barked host species) require a robust attachment mechanism, which may be achieved by producing a glue-like substance that adheres the velamen or rhizome to the host.

Epiphytes with host preferences for tree ferns appear to use an interlocking attachment mechanism with thin or erect rhizomes and creeping roots covered in fine hairs. The species strongly associated with tree ferns in our study were ferns of ancient lineage that either lack true roots (e.g., *Tmesipteris lanceolata*) or have fine, creeping rhizomes and branching roots (e.g., *Hymenophyllum flabellatum*). The traits of these epiphytes best match those of tree ferns, which provide a fibrous substrate with high moisture retention.

3.5. Conclusions

Our study is among the first to examine links between epiphyte traits, attachment mechanisms and host preferences in urban forests. While epiphyte communities in non-urban forests have exhibited stochastic structuring, our results suggest that epiphyte-host interactions are partially determined by epiphyte traits in modified urban settings. These differences likely reflect trait compatibility between epiphytes and their hosts, which can be more pronounced in urban environments with limited host assemblages and increased environmental heterogeneity (e.g., less stable microclimates). Our research emphasises the need to protect and diversify host assemblages in urban ecological restoration projects. Further research is needed to elucidate the independent roles of environmental factors and other functional traits that affect epiphyte-host interactions.

References

Abdi H, Williams LJ (2010) Principal component analysis. Wiley interdisciplinary reviews: computational statistics. 2(4):433–459. https://doi.org/10.1002/wics.101

Alvim FS, Furtado SG, Menini Neto L (2021) Are vascular epiphytes in urban green areas subject to the homogenisation of biodiversity? A case study in the Brazilian Atlantic Forest. Urban Ecosystems 24(4):701–713. https://doi.org/10.1007/s11252-020-01070-7

Benzing DH (1973) Mineral nutrition and related phenomena in Bromeliaceae and Orchidaceae. The Quarterly Review of Biology 48(2):277–290. https://doi.org/10.1086/407590

Benzing DH (1978) Germination and early establishment of *Tillandsia circinnata* Schlecht. (Bromeliaceae) on some of its hosts and other supports in southern Florida. Selbyana, 5(1):95–106.

Benzing DH, Pridgeon AM (1983) Foliar trichomes of Pleurothallidinae (Orchidaceae): functional significance. American Journal of Botany 70:173–180. https://doi.org/10.1002/j.1537-2197.1983.tb07856.x

Benzing DH (2012) Air plants. Cornell University, Ithaca, NY

Breitwieser I, Heenan PJ (2023) Flora of New Zealand. www.nzflora.info. Accessed 10 February 2026.

Bryan C (2011) Ecology of vascular epiphytes in urban forests with special reference to the shrub epiphyte *Griselinia lucida*. MSc Thesis, the University of Waikato.

Burns KC (2008) Meta-community structure of vascular epiphytes in a temperate rainforest. Botany 86(11):1252–1259. https://doi.org/10.1139/B08-084

Burns KC (2010) How arboreal are epiphytes? A null model for Benzing's classifications. New Zealand Journal of Botany 48(3-4):185–191. https://doi.org/10.1080/0028825X.2010.503775

Burns KC, Zotz G (2010) A hierarchical framework for investigating epiphyte assemblages: networks, meta-communities, and scale. Ecology 91(2):377–385. https://doi.org/10.1890/08-2004.1

Callaway RM, Reinhart KO, Moore GW, Moore DJ, Pennings SC (2002) Epiphyte host preferences and host traits: mechanisms for species-specific interactions. Oecologia 132:221–230. https://doi.org/10.1007/s00442-002-0943-3

Chase JM, Myers JA (2011) Disentangling the importance of ecological niches from stochastic processes across scales. Philosophical transactions of the Royal Society B: Biological sciences 366(1576):2351–2363. https://doi.org/10.1098/rstb.2011.0063

Clarkson BD, Kirby CL (2016) Ecological restoration in urban environments in New Zealand. Ecol. Manag. Restor. 17:180–190. https://doi.org/10.1111/emr.12229

De Cáceres M, Jansen F, De Caceres MM (2016) Package 'indicspecies'. indicators 8(1).

de la Rosa-Manzano E, Andrade JL, Zotz G, Reyes-García C (2014) Epiphytic orchids in tropical dry forests of Yucatan, Mexico–Species occurrence, abundance and correlations with host tree characteristics and environmental conditions. Flora-Morphology, Distribution, Functional Ecology of Plants 209(2):100–109. https://doi.org/10.1016/j.flora.2013.12.002

Dormann CF, Gruber B, Fründ J (2008) Introducing the bipartite package: analysing ecological networks. Interaction 1(0.2413793):8-11.
Gallego YA, Carmona-Higuita MJ, Benavides AM (2025) Urban trees as biodiversity scaffolds: patterns and drivers of epiphyte diversity in a tropical city. Urban Ecosystems 28(6):238. https://doi.org/10.1007/s11252-025-01824-1
Hietz P, Wagner K, Nunes Ramos F, Cabral JS, Agudelo C, Benavides AM, Zotz G (2022) Putting vascular epiphytes on the traits map. Journal of Ecology 110(2):340–358. https://doi.org/10.1111/1365-2745.13802
Hofstede RG, Dickinson KJ, Mark AF (2001) Distribution, abundance and biomass of epiphyte-lianoid communities in a New Zealand lowland *Nothofagus*-podocarp temperate rain forest: tropical comparisons. Journal of Biogeography 28(8):1033–1049. https://doi.org/10.1046/j.1365-2699.2001.00613.x
Hubbell SP (2011) The unified neutral theory of biodiversity and biogeography. Vol 32. Princeton University Press. https://doi.org/10.1515/9781400837526
Janzen T, Zotz G, Etienne RS (2020) Community structure of vascular epiphytes: a neutral perspective. Oikos 129(6):853–867. https://doi.org/10.1111/oik.06537
Jarquin-Pacheco MB, Armenta-Montero S, Contreras-López J, Carvajal-Hernández CI (2025) Urban forests as habitats for vascular epiphytes and allied terrestrial plants. Urban Ecosystems 28(4):1–13. https://doi.org/10.1007/s11252-025-01756-w
Jiao M, Zhou W, Zheng Z, Wang J, Qian Y (2017) Patch size of trees affects its cooling effectiveness: A perspective from shading and transpiration processes. Agricultural and Forest Meteorology 247:293–299. https://doi.org/10.1016/j.agrformet.2017.08.013
Kearney M, Simpson SJ, Raubenheimer D, Helmuth B (2010) Modelling the ecological niche from functional traits. Philosophical Transactions of the Royal Society B: Biological Sciences 365(1557):3469–3483. https://doi.org/10.1098/rstb.2010.0034
Kolde R (2015) Package 'pheatmap' R package. 1(7):790. https://github.com/raivokolde/pheatmap
Kraft NJ, Ackerly DD (2014) Assembly of plant communities. In: Ecology and the Environment (pp. 1-18). Springer, New York, pp 1–18.
Lenth RV (2016) Least-squares means: The R package lsmeans. Journal of Statistical Software 69:1–33. https://doi.org/10.18637/jss.v069.i01MacKay DB, Wehi PM, Clarkson BD (2011) Evaluating restoration success in urban forest plantings in Hamilton, New Zealand. Urban Habitats 6(1). www.urbanhabitats.org/v06n01/hamilton_full.html
Martins PLSS, Furtado SG, Menini Neto L (2020) Could epiphytes be xenophobic? Evaluating the use of native versus exotic phorophytes by the vascular epiphytic community in an urban environment. Community Ecology 21(1):91–101. https://doi.org/10.1007/s42974-020-00001-y
Mason BM, Mesaglio T, Barratt Heitmann J, Chandler M, Chowdhury S, Gorta SBZ, Callaghan CT (2025) iNaturalist accelerates biodiversity research. BioScience:biaf104. https://doi.org/10.1093/biosci/biaf104
McArdle BH, Anderson MJ (2001). Fitting multivariate models to community data: a comment on distance-based redundancy analysis. Ecology 82(1):290–297. https://doi.org/10.1890/0012-9658(2001)082[0290:FMMTCD]2.0.CO;2

Mehltreter K, Flores-Palacios A, García-Franco JG (2005) Host preferences of low-trunk vascular epiphytes in a cloud forest of Veracruz, Mexico. Journal of Tropical Ecology 21(6):651–660. https://doi.org/10.1017/S0266467405002683

Mehltreter K, Wachter H, Trabi C, Testo W, Sundue M, Jansen S (2022) Hydathodes in ferns: their phylogenetic distribution, structure and function. Annals of Botany 130(3):331–344. https://doi.org/10.1093/aob/mcac076

Mendieta-Leiva G, Porada P, Bader MY (2020) Interactions of epiphytes with precipitation partitioning. In: Precipitation partitioning by vegetation: A global synthesis. Cham: Springer International Publishing, pp 133–146.

Moran RC, Klimas S, Carlsen M (2003) Low-trunk epiphytic ferns on tree ferns versus angiosperms in Costa Rica. Biotropica 35(1):48–56. https://doi.org/10.1111/j.1744-7429.2003.tb00261.x

Nitta JH, Watkins Jr JE, Davis C (2020) Life in the canopy: community trait assessments reveal substantial functional diversity among fern epiphytes. New Phytologist 227(6):1885–1899. https://doi.org/10.1111/nph.16607

Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'hara RB, Simpson GL, Solymos P, Stevens MH, Wagner H, Oksanen MJ (2013). Package 'vegan'. Community Ecology Package 2(9):1–295.

Pearson HM (1969) Rhizoids and root hairs of ferns. American Fern Journal 59(3): 107–122. https://doi.org/10.2307/1545990

People, Cities and Nature Programme, PCaN (2024) Planting a Lasting Urban Forest. www.peoplecitiesnature.co.nz/publications. Accessed on 10 February 2026.

Peres-Neto PR, Jackson DA, Somers KM (2003) Giving meaningful interpretation to ordination axes: Assessing loading significance in principal component analysis. Ecology 84:2347–2363. https://doi.org/10.1890/00-0634

R Core Team (2023) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. www.R-project.org.

Rogers HC, Burdon FJ, Clarkson BD (2025) Tree Ferns Augment Native Plant Richness and Influence Composition in Urban Plant Communities. Forests 16(9):1498. https://doi.org/10.3390/f16091498

Rogers HC, Clarkson BD (2025) Epiphyte-host relationships of remnant and recombinant urban ecosystems in Hamilton, New Zealand: the importance of *Dicksonia squarrosa* (G. Forst.) Sw., whekī. New Zealand Journal of Botany 63(1):150–159. https://doi.org/10.1080/0028825X.2023.2245776

Schellenberger Costa D, Zotz G, Hemp A, Kleyer M (2018) Trait patterns of epiphytes compared to other plant life-forms along a tropical elevation gradient. Functional Ecology 32(8):2073–2084. https://doi.org/10.1111/1365-2435.13121

Schimper AFW (1888) Die epiphytische Vegetation Amerikas, vol 2, Botanische Mitteilungen aus den Tropen. Gustav Fischer, Jena

Spicer ME, Ortega J, Carson WP (2022) Substrate texture and natural removal processes mediate vascular epiphyte establishment: Experimental evidence from a Panamanian cloud forest. The Journal of the Torrey Botanical Society 149(1):86–97. https://doi.org/10.3159/TORREY-D-21-00038.1

Stewart GH, Ignatieva ME, Meurk CD, Earl RD (2004) The re-emergence of indigenous forest in an urban environment, Christchurch, New Zealand. Urban Forestry & Urban Greening 2(3):149–158. https://doi.org/10.1078/1618-8667-00031

Swan CM, Brown B, Borowy D, Cavender-Bares J, Jeliazkov A, Knapp S, Lososová Z, Padullés Cubino J, Pavoine S, Ricotta C, Sol D (2021) A framework for understanding how biodiversity patterns unfold across multiple spatial scales in urban ecosystems. Ecosphere 12(7):e03650. https://doi.org/10.1002/ecs2.3650

Taranaki Regional Council. (2022). Our place: Taranaki State of Environment 2022. Retrieved 12 June 2026, from: https://www.trc.govt.nz/council/plans-and-reports/monitoring-reports/state-of-the-environment-report-2022

Tay JY, Zotz G, Einzmann HJ (2023) Smoothing out the misconceptions of the role of bark roughness in vascular epiphyte attachment. New Phytologist 238(3):983–994. https://doi.org/10.1111/nph.18811

Tay JY, Zotz G, Gorb SN, Einzmann HJ (2021) Getting a grip on the adhesion mechanism of epiphytic orchids–evidence from histology and cryo-scanning electron microscopy. Frontiers in Forests and Global Change 4:764357. https://doi.org/10.3389/ffgc.2021.764357

Tay J, Werner JC, Zotz G (2024) Morphological diversity of the velamen radicum in the genus *Anthurium* (Araceae). Plant Biology 26:679–690.

Taylor A, Burns K (2015) Epiphyte community development throughout tree ontogeny: an island ontogeny framework. Journal of Vegetation Science 26(5):902–910. https://doi.org/10.1111/jvs.12289

Taylor A, Saldaña A, Zotz G, Kirby C, Díaz I, Burns K (2016) Composition patterns and network structure of epiphyte–host interactions in Chilean and New Zealand temperate forests. New Zealand Journal of Botany 54(2):204–222. https://doi.org/10.1080/0028825X.2016.1147471

Vaughan IP, Gotelli NJ., Memmott J, Pearson CE, Woodward G, Symondson WO (2018) econullnetr: An r package using null models to analyse the structure of ecological networks and identify resource selection. Methods in Ecology and Evolution 9(3):728–733. https://doi.org/10.1111/2041-210X.12907

Vergara-Torres CA, Pacheco-Álvarez MC, Flores-Palacios A (2010) Host preference and host limitation of vascular epiphytes in a tropical dry forest of central Mexico. Journal of Tropical Ecology 26(6):563–570. https://doi:10.1017/S0266467410000349

Violle C, Navas ML, Vile D, Kazakou E, Fortunel C, Hummel I, Garnier E (2007) Let the concept of trait be functional! Oikos 116(5):882–892. https://doi.org/10.1111/j.0030-1299.2007.15559.x

Wagner K, Mendieta-Leiva G, Zotz G (2015) Host specificity in vascular epiphytes: a review of methodology, empirical evidence and potential mechanisms. AoB plants 7:plu092. https://doi.org/10.1093/aobpla/plu092

Wagner K, Wanek W, Zotz G (2021) Functional traits of a rainforest vascular epiphyte community: trait covariation and indications for host specificity. Diversity 13(2):97. https://doi.org/10.3390/d13020097

Wagner K, Zotz G (2020) Including dynamics in the equation: Tree growth rates and host specificity of vascular epiphytes. Journal of Ecology 108(2):761–773. https://doi.org/10.1111/1365-2745.13333

Wallace KJ, Laughlin DC, Clarkson BD (2017) Exotic weeds and fluctuating microclimate can constrain native plant regeneration in urban forest restoration. Ecological Applications 27(4):1268–1279. https://doi.org/10.1002/eap.1520

Wang X, Shen C, Meng P, Tan GL (2021) Analysis and review of trichomes in plants. BMC Plant Biology 21:1–11. https://doi.org/10.1186/s12870-021-02840-x

Wyse SV, Burns BR (2011) Do host bark traits influence trunk epiphyte communities? New Zealand Journal of Ecology:296–301.

Zotz G (2005) Vascular epiphytes in the temperate zones–a review. Plant Ecology 176:173–183. https://doi.org/10.1007/s11258-004-0066-5

Zotz G, Weigelt P, Kessler M, Kreft H, Taylor A (2021) EpiList 1.0: a global checklist of vascular epiphytes. Ecology 102(6):e03326. https://doi.org/10.1002/ecy.3326

Chapter 4. Physiological responses of four epiphytic ferns to water and light availability

Abstract

Drought severely impacts plants by restricting water availability, leading to reduced growth, physiological stress, and potential death. Epiphytic ferns, particularly those relying on tree fern hosts in drier urban forests, may be susceptible to drought with limited access to water. High light can exacerbate drought stress and contribute to epiphyte habitat partitioning. We investigated the physiological responses of four epiphytic ferns (two species often growing on tree ferns and two generalists) to drought and light availability. A three-month ex-situ drought experiment was conducted using a fully crossed factorial design based on water availability (watered, drought) and light availability (low, high). Species responses were measured using photosynthesis, chlorophyll fluorescence, frond water potentials and mortality, and stable isotope analysis. Water scarcity had a stronger negative effect on epiphyte performance than light availability. The generalist *Pyrrosia elaeagnifolia* was the most drought-resistant species, although responses did not strictly follow microhabitat preferences. *Asplenium polyodon*, which is closely associated with tree ferns, rapidly declined in photosynthetic capacity under drought stress and exhibited photoinhibition under drought and high light. Contrary to expectations, the generalist *Lecanopteris pustulata* showed rapid declines in physiological responses under drought, and *A. flaccidum* exhibited drought avoidance. Our results suggest that species such as *A. polyodon* are vulnerable to increasing drought events and require damp, cool microhabitats to maintain metabolic function. Habitat overlap between drought-sensitive epiphytes and hosts such as tree ferns underscores the need to conserve and enhance both plant groups in ecological restoration projects, particularly in modified urban forests.

4.1. Introduction

Drought can influence plant health by inhibiting photosynthetic activity and growth (Ferguson et al., 2022). While some plants have evolved to tolerate or avoid drought, species responses differ substantially. Species drought responses contribute to distributional patterns and community assembly, which have consequences for conservation and restoration (Zirbel et al., 2017). Structurally dependent plants (i.e., epiphytes) are particularly susceptible to drought because they lack a connection to the ground and rely on regular rainfall or stable, humid environments (e.g., occult precipitation). Understanding how epiphyte species perform

under different environmental conditions (i.e., their ecophysiology) is necessary to elucidate drivers of epiphyte microhabitat and host preferences.

Strict epiphyte host specificity (i.e., an epiphyte growing exclusively on one host species) is rare, but epiphytes can exhibit host preferences (Callaway et al., 2002). A previous study found non-random epiphyte-host interactions in two cities on North Island, New Zealand (Rogers et al., 2026, under review). Trait matching between epiphyte roots and rhizomes and host substrates may partially explain host preferences. However, understanding how plant communities are shaped by species environmental tolerance is necessary to appropriately manage them in ecological restoration projects.

Preferences for certain hosts or microhabitats may reflect an epiphyte's environmental tolerance. For example, generalists occurring on many hosts may exhibit greater environmental tolerance and have wider niches than specialist epiphytes (Elias et al., 2021). Links between epiphyte host preferences and environmental tolerance may be partially explained by differences in host substrate and light environments between distinct host types (e.g., tree ferns and woody hosts). Tree ferns provide a sheltered epiphyte microhabitat and structurally complex substrate that retain moisture and have megaphylls that cast deep shade (Moran et al., 2003). Partitioning of epiphytes by microhabitat (e.g., generalists versus species associated with tree ferns) may reveal differences in species tolerance to major abiotic factors structuring epiphyte assemblages, such as water and light availability.

Water scarcity is arguably the most important abiotic constraint of the epiphytic habitat (Zotz and Hietz, 2001). Epiphyte diversity is therefore closely associated with regional-scale rainfall patterns (Gentry and Dodson, 1987). Yet at a finer scale, epiphytes can persist in dry, well-lit microhabitats. Under drought conditions, epiphytic ferns can maintain photochemical efficiency, as indicated by the ratio of variable to maximum fluorescence (F_v/F_m), and occasionally exhibit greater water-use efficiency than terrestrial species (Campany et al., 2021). Adopting a drought avoidance strategy likely assists epiphytes in water-scarce environments, where species exhibit high water-use efficiency by minimising water loss via transpiration (Campany et al., 2021). Some epiphytic orchids escape drought by shedding their leaves to minimise transpiration (Zhang et al., 2016). Epiphytes can, however, exhibit drought tolerance (maintaining metabolic functions during drought), while *Hymenophyllum* species are poikilohydric and cannot regulate their water content (Aros-Mualin and Kessler,

2024). In water-scarce environments, epiphyte communities may be drastically reshaped with impacts cascading to ecosystem functions (McDermott, 2024).

Light gradients can lead to strong partitioning of species between well-lit canopy microhabitats and deep shade near the forest floor (Sanger and Kirkpatrick, 2017). Light environments influence epiphyte size and phenology; under high light, epiphytes may reduce growth and reproduction to minimise photodamage and water loss via transpiration (Cervantes et al., 2005). Canopy epiphytes in exposed, well-lit locations may exhibit Crassulacean acid metabolism (CAM), minimising water loss by fixing carbon at night (Lambers et al., 2008). However, high light environments (associated with higher vapour-pressure deficit and temperature) may negatively affect epiphyte drought resistance and diminish post-drought recovery (Williams et al., 2020).

Nutrient acquisition can also impair vascular epiphyte performance (Benzing, 1990). Epiphytes acquire nutrients from atmospheric sources (e.g., rainfall) or from organic matter in the canopy (Zotz and Hietz, 2001). Stable isotope analysis can reveal the interactive effects of water scarcity, light environments, and nutrition on plant survival and performance (Salazar-Tortosa et al., 2018). $\delta^{15}N$ indicates plant nitrogen sources, where plants mainly obtaining nitrogen from the atmosphere (via N-fixing bacteria) are more depleted in ^{15}N than plants acquiring nitrogen from leaf litter (Watts and Watkins, 2021). Foliar delta carbon-13 ($\delta^{13}C$) is a long-term measure of intrinsic water-use efficiency, which is strongly affected by stomatal activity and photosynthetic capacity (Seibt et al., 2008). In addition, both light environments and leaf nitrogen concentrations influence gas exchange and, therefore, plant drought responses.

Physiology research on vascular epiphytes in temperate regions is limited (Zotz and Hietz, 2001). In New Zealand, research has highlighted the potential for biotic interactions with host species to shape epiphyte communities, but questions remain about how abiotic conditions influence both host and epiphyte assemblages (Rogers et al., 2025; Rogers et al., 2026, under review). An early study on water relations in New Zealand plants found that *Lecanopteris pustulata* exhibited drought avoidance and low tolerance with high values of water content at turgor loss (Bannister, 1986). Drought experiments on specialised epiphytic shrubs showed that *Pittosporum cornifolium* exhibited a drought tolerance strategy, whereas *P. kirkii* and *Griselinia lucida* employed drought postponement (Bryan, 2011; Myron, 2012). Less

attention has been given to temperate epiphytic ferns (Anderson, 2021). However, desiccation tolerance (restored metabolic functions upon rehydration) was observed in the filmy fern *Hymenophyllum sanguinolentum*; the fern exhibited responses comparable to European species (Proctor, 2012). Additionally, the decline in photochemical efficiency of the epiphytic fern *Notogrammitis billardierei* after 10 days without water demonstrated its drought sensitivity (Taylor and Burns, 2016).

Here, we present results from one of the first *ex-situ* physiology experiments on epiphytic ferns that exhibit preferences for tree ferns or a woody host microhabitat. The aim of this study was to investigate how epiphyte responses to drought and light availability differ with microhabitat preferences and degree of specialisation. We tested two hypotheses: H1) epiphytes associated with tree ferns are less drought-resistant, less water use efficient, and exhibit lower drought recovery than generalist epiphytes, and H2) epiphytes associated with tree ferns are more susceptible to photoinhibition and frond mortality under high light than generalist species.

4.2. Materials and methods

We conducted an *ex-situ* glasshouse experiment on the University of Waikato campus in Hamilton, New Zealand. The experiment involved four epiphytic fern species exposed to different combinations of water and light availability. The "drought" phase of the experiment started on 10 July 2025 and concluded when approximately 50% of the plants in the high light, drought treatment had lost half their foliage (at 12 weeks). In the "drought recovery" phase of the experiment, responses (following the watering of all plants) were measured for an additional two weeks after the drought phase of the experiment concluded.

4.2.1. Experimental design

The experiment used a fully crossed factorial design (2 × 2) based on water and light availability. The four treatment groups were (1) drought, high light; (2) drought, low light; (3) watered, high light; and (4) watered, low light. Five plants of each of the four epiphyte species were randomly allocated to each group (i.e., a total of 80 individual plants used in the experiment). The epiphytic ferns were grown in a University of Waikato shade house in 2.5 L pots of potting mix (Fern Factor, Christchurch, New Zealand) between August 2024 and July 2025 (11 months). One week before the experiment started, plants were acclimatised by

transferring them into a glasshouse (where the experiment took place), with automated temperature, humidity and ventilation control. Plants in the watered treatments were watered to field capacity once a week, and those in drought treatments did not receive water during the 12-week simulated drought.

Before starting the experiment, the light environment of the two distinct epiphyte microhabitats, tree fern stems (low light) and woody trees (high light), was quantified in a nearby forest reserve. *In-situ* canopy openness was measured for each microhabitat using an LAI-2200C Plant Canopy Analyser. Mean diffuse non-interceptance of the woody tree microhabitat was 12.7% (n = 11), and 1.6% (n = 11) in the lower light tree fern microhabitat. A combination of overhead shade screens and neutral-density shade cloth was then used to create light environments in the glasshouse, resulting in similar reductions in total daily irradiance compared to an unshaded environment.

During the experiment, the four treatment blocks were moved weekly around the glasshouse to minimise the confounding effect of position and any underlying environmental gradients. A Ridder Synopta 2 climate regulation system recorded a mean daily temperature of approximately 15 °C (10-20 °C), and a mean daily relative humidity of 78% (70-90%). Temperature and relative humidity settings were determined from data collected in a nearby forest reserve with abundant epiphytes. Automated misting was used to increase humidity without wetting the plants. Instantaneous photosynthetic photon flux density (PPFD) for the low and high light treatments was compared with open-sky measurements using a spectrometer (LI-180, LI-COR Inc., Nebraska) when establishing the shade treatments. During the experiment, quantum sensors (LI-190, LI-COR Inc.) connected to a datalogger (CR10X, Campbell Scientific, Utah) and calibrated against the spectrometer recorded PPFD continuously across the four treatment groups (logging every 10 seconds, saving 15-minute averages). Unobstructed hourly solar irradiance was obtained from a nearby weather station for comparison (Ruakura EWS, DataHub, Earth Sciences New Zealand 2025). Average PPFD for the 12-week experiment was 3.4 mol m^{-2} day^{-1} for the high light treatments, and 0.8 mol m^{-2} day^{-1} for the low light treatments, corresponding to 15% and 3% of unobstructed PPFD for the two light treatments, respectively.

4.2.2. Epiphyte species

Individuals of four epiphytic fern species were collected from Mangaonua Gully, Hamilton (37.7826° S, 175.2528° E) in August 2024. Previous network analyses of urban epiphyte–host interactions (Rogers et al., 2026, under review) informed the selection of species with either stronger preferences for tree ferns (*Asplenium polyodon* G.Forst. and *A. flaccidum* G.Forst.) or woody host species (*Pyrrosia elaeagnifolia* (Bory) Hovenkamp and *Lecanopteris* pustulata (G.Forst.) Perrie & Brownsey). These preferences for distinct microhabitats may reflect the physiological requirements of the epiphytes for water and light (Fig. 1). The species nomenclature follows Perrie and Brownsey (2024).

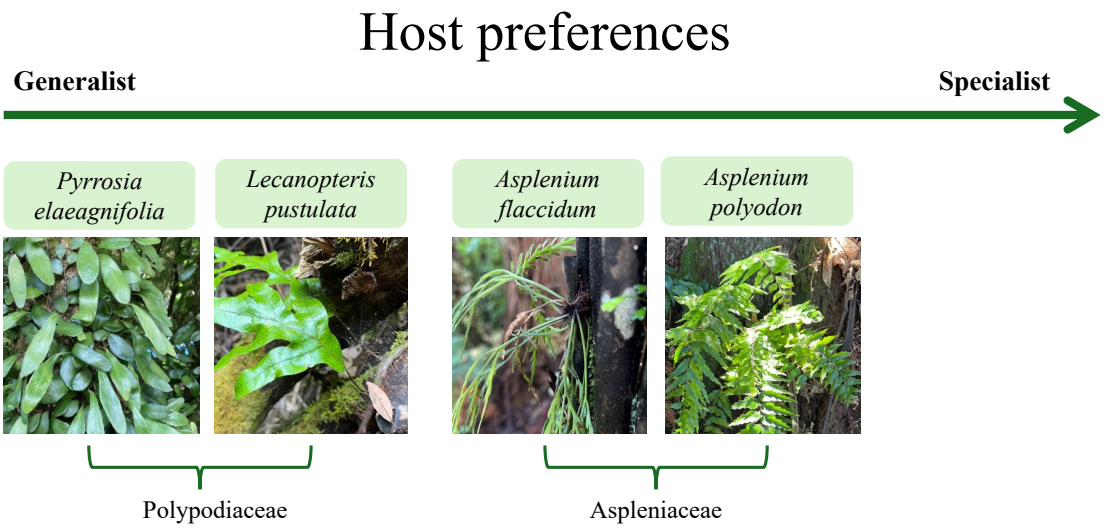


Fig. 1. Predicted gradient of epiphyte host preferences for the four fern species. *Pyrrosia elaeagnifolia* and *Lecanopteris pustulata* exhibit a generalist habit, whereas *Asplenium flaccidum* and *A. polyodon* are more closely associated with tree ferns when growing in urban settings.

Variation in the morphological traits of the four species likely impacts their ecophysiology (Gotsch et al., 2022). *Asplenium polyodon* and *A. flaccidum* have short, erect rhizomes with fine, hairy roots spreading laterally, often interlocking with tree fern adventitious roots that surround the caudex. *Asplenium flaccidum* has thick, long, drooping fronds, whereas *A. polyodon* has large, thin fronds. The generalist species *P. elaeagnifolia* and *L. pustulata* have extensive creeping rhizomes covered in scales. *Pyrrosia elaeagnifolia* has relatively small but succulent, coriaceous fronds covered in stellate hairs, whereas *L. pustulata* has large, deeply pinnatifid, glabrous fronds.

4.2.3. Data collection

Several physiological and ecological indicators of performance were measured at the individual plant level in response to drought and light availability. Gas exchange, chlorophyll fluorescence and frond water potential techniques were used during the experiment. Separately from the experiment, we collected frond samples of the four species during the wet and dry seasons for stable isotope analyses to compare species water-use efficiency and nutrient status.

4.2.3.1. Gas exchange

Photosynthetic capacity (A_{max}) and stomatal conductance (g_s) were measured weekly using a portable photosynthesis system (LI-6800XT, LI-COR Biosciences, Lincoln, NE, USA). The photosynthesis system was acclimated to the glasshouse for 30 minutes before measurements began. Preliminary light response curves were completed for each species to determine that a PPFD of 800 µmol m^{-2} s^{-1} was sufficient to saturate photosynthesis and record the A_{max} of all species. During regular weekly measurements of Amax, plants were acclimated to a PPFD of approximately 800 µmol m^{-2} s^{-1} under an LED grow light (4Seasons Helios 720 EVO+) for at least 15 minutes. This procedure minimised the effects of variable natural light and avoided extended delays while the stomata opened, allowing the plants to reach steady-state rates of photosynthesis and transpiration before measurements were taken using the photosynthesis system.

Chamber conditions were regulated at a PPFD of 800 µmol m^{-2} s^{-1}, a flow rate of 300 µmol s^{-1}, CO_2 of 420 µmol mol^{-1}, 60% relative humidity (maintaining vapour-pressure deficit between 0.5-1.0 kPa), and an air temperature of 18 °C. Each week, three of five plants per species and treatment group were haphazardly selected, and one fully expanded mature frond was measured on each (n = 48). Each frond was placed in a 6 cm^2 LED chamber for measurement. Frond area in the chamber was measured by photographing the samples and estimating frond areas using ImageJ software (Schneider et al., 2012).

4.2.3.2. Chlorophyll fluorescence

The maximum potential quantum efficiency of PSII (F_v/F_m) was determined using a pulse amplitude modulated chlorophyll fluorometer (MINI-PAM, Walz, Effeltrich, Germany). Weekly predawn (i.e., dark-adapted) F_v/F_m was measured as an indicator of plant stress under

the water and light treatments (Anderson, 2023). Shade-tolerant plants are expected to show declining F_v/F_m (an indicator of photoinhibition) under water stress and in high light environments (Riaño and Briones, 2013). We measured three haphazardly selected leaves per species and group (n = 48) using a fluorometer frond clip equipped with an internal thermocouple.

4.2.3.3. Frond mortality and water potentials

Weekly frond counts (live and dead), pot weights, and volumetric water content (measured with a HydroSense II soil moisture probe) were recorded for all plants to monitor how species responded to drought stress. To evaluate the relationship between soil moisture and plant water potentials, we measured frond water potentials (ψ) for all four species using additional plants not used in the experiment (Supplementary Materials, Fig. S3). Fronds of individual plants were measured at various pot weights for predawn ψ, alongside the potting mix volumetric water content and pot weight. Measurements were made using a pressure chamber (Model 1505D, PMS Instrument Co.) following the methods of Boyer and Kramer (1995) and Scholander et al. (1965). Fronds were cut at the stipe base with a razor blade, wrapped in a plastic bag to minimise transpiration and placed in the pressure chamber. A reading was taken once water emerged from the freshly cut stipe. During the experiment, pot weight of each plant (n = 80) was recorded weekly to estimate frond water potentials.

4.2.3.4. Isotope analysis

Independent of the *ex-situ* experiment, stable isotope analysis was performed on the four species using samples collected from nearby forest reserves. We used isotope analysis to compare species water-use efficiency ($\delta^{13}C$) and nutrient acquisition ($\delta^{15}N$). Samples from four individual plants were collected in summer after a dry period (February 2025), and in winter (July 2025), when it was wet (n = 4). Each sample consisted of 2-4 recently developed fronds. Fronds were oven-dried at 60 °C for 24 hours, finely crushed, accurately weighed to 4 mg, encapsulated in 8 mm (H) × 5 mm (W) tin capsules with an approximate volume of 160 µL, and analysed at the Lincoln University Stable Isotope Laboratory, Christchurch, New Zealand. Isotopes were analysed using a Sercon 20-22 IRMS instrument (Crewe, Cheshire, United Kingdom). International reference materials USGS-40 and USGS-41 were used for calibration of isotopic and elemental values, and EDTA-OAS (Ethylenediaminetetraacetic acid organic analytical standard) was used to assess analytical accuracy. All isotope and elemental values were within accepted reference ranges.

4.2.4. Data analysis

Statistical analyses to test our two hypotheses were completed in R version 4.4.2 (R Core Team 2024). We used linear mixed-effects models (LMEs) for A_{max} and g_s to compare species between Week 2 and Week 12 of the 'drought' phase. Species F_v/F_m between the same weeks were compared using generalised linear mixed models (GLMMs) assuming a beta distribution with a logit link function (Brooks et al., 2017). First, we fit three global models (one per response) with fixed categorical variables of species, time (i.e., Week 2 versus Week 12), light and water treatments. Sample (i.e., unique plant ID) was included as a random effect in all models to account for the non-independence of repeated measures. The models compared plant responses between Week 2 (the first complete week of measurements) and Week 12 (the final week of the drought phase) to capture maximum temporal variation. The best model was determined using log-likelihood ratio tests in the "buildmer" R package (Voeten, 2021). Interaction terms among species, time, light, and water treatments are reported for significant likelihood-ratio tests; otherwise, we present additive model results.

In addition, models for each response (A_{max}, g_s and F_v/F_m) were used to assess how epiphytes in the drought treatments responded to rewatering during the recovery phase between Weeks 12 and 14. Weekly frond mortality (the proportion of dead fronds to the total count) among species and over time was also assessed using a generalised linear model with a binomial distribution. Pairwise comparisons of species responses for all models were made using the "emmeans" R package with Tukey's correction for multiplicity (Lenth, 2016).

To visualise changes over time in response to treatments (e.g., temporal drought effects) for the three physiological endpoints, generalised additive mixed models (GAMMs) were fitted with sample (i.e., unique plant ID) as a random effect using the "mgcv" R package (Wood, 2017). We fit GAMMs for each species and response variable for both watered and drought treatments (i.e., six plots); light treatment groups were amalgamated based on water treatments as water had a stronger effect on the responses over time (Table 1). The GAMMs used a natural cubic spline with a basis dimension k = 4 to capture nonlinearity while avoiding overfitting. The GAMMs complemented the linear mixed-effects models and

highlighted the nonlinearity of responses over time in response to changing stress levels, particularly after rewatering (i.e., the recovery phase).

To characterise changes in frond water potential across the four species during the experiment, a soil moisture release curve was constructed using the ψ measurements and pot weights recorded on plants not included in the main experiment. First, we calculated the soil volumetric water content (θ) using Eq. 1, where M_w is the mass of water (weight of potting mix – dry weight), and V_t is the total soil volume.

$$\text{Eq. 1.} \quad \theta = \frac{M_w}{V_t}$$

Second, we fitted a log-log curve (Eq. 2) following Campbell (1974) to θ and ψ measurements for the four species (n = 54), where ψ_e is the air entry potential, and b is an empirical slope parameter.

$$\text{Eq. 2.} \quad \psi = \psi_e \left(\frac{\theta}{\theta_s}\right)^{-b}$$

The results suggested the four species exhibited the same relationship between predawn ψ and pot weight (Supplementary Materials, Fig. S3). Finally, Eq. 2 was used to estimate ψ from pot weights during the experiment, with multiple regression used to assess the effects of time (Weeks 2–12), species, and light and water treatments on estimated ψ. We log-transformed ψ to meet linear model assumptions.

Analysis of variance (ANOVA) compared $\delta^{13}C$, $\delta^{15}N$, and total nitrogen among the four species with season as a fixed effect. Non-normal variables detected from Shapiro-Wilk tests were log-transformed (i.e., total N). The models detected no significant interactions between species and season, so we present the additive model results. Pairwise comparisons were performed using the "lsmeans" R package (Lenth, 2016) and the Benjamini-Hochberg method (Haynes, 2013) to control false positives and increase power.

4.3. Results

4.3.1. Experiment results

Epiphyte species associated with tree ferns (hereafter tree fern specialists) were less drought-resistant than generalists, exhibiting greater declines in A_{max} and g_s under the simulated drought. High light also caused a greater decline in F_v/F_m of tree fern specialists, especially under drought conditions, indicating their greater shade tolerance compared to generalist species (Fig. 2). A_{max} was significantly influenced by the interaction between water treatments and time (Table 1), suggesting that drought effects strengthened over time. Significant interactions between species and time, and among species, time, and light indicated species-specific responses over time that also depended on light availability. Furthermore, the significant interactive effect of water and light treatments on A_{max} suggests stronger negative effects of drought under high light conditions (Fig. 2).

Tree fern specialist epiphytes had lower A_{max} during the simulated drought than the generalists (Table 1). Species pairwise comparisons within each level of time and light treatments showed that under low light *A. flaccidum* had significantly lower A_{max} than *L. pustulata* at Week 2 (estimate: -1.8, $P < 0.05$). Under low light, *P. elaeagnifolia* exhibited higher A_{max} than *A. flaccidum* (estimate: -1.9, $P < 0.05$), *A. polyodon* (estimate: -2.5, $P < 0.001$) and *L. pustulata* (estimate: -3.0, $P < 0.001$) by Week 12. Under high light, *A. flaccidum* had significantly lower A_{max} than *L. pustulata* (estimate: -2.1, $P < 0.01$) and *P. elaeagnifolia* (estimate: -2.0, $P < 0.01$) at Week 2. There were no significant differences in the A_{max} of species under high light at Week 12 (see full pairwise comparison results in Supplementary Materials, Tables S1–S3).

Stomatal conductance (g_s) was significantly influenced by the interaction between water and time (Table 1), suggesting stronger drought effects over time. A significant interaction between species and time also indicated differences in species responses over time (i.e., with increasing stress). Pairwise comparisons within each level of time showed that water treatments did not significantly affect g_s at Week 2 (estimate: 0.01, $P = 0.07$), but plants under drought stress had significantly lower g_s by Week 12 (estimate: 0.04, $P < 0.001$). At Week 2, *A. flaccidum* exhibited significantly lower g_s than *A. polyodon* (estimate: -3.8, $P < 0.01$) and *L. pustulata* (estimate: -3.7, $P < 0.01$). However, stomatal conductance did not differ significantly among species at Week 12.

Table 1. Linear mixed effects model results for photosynthetic capacity (A_{max}) and stomatal conductance (g_s), and generalised linear mixed model results for photochemical efficiency (F_v/F_m). Predictors for each model were water treatments, species, time (i.e., Week 2 versus Week 12), and light treatments, and statistically significant interactions. *F*-values (for the LMEs) or χ^2 (for GLMM) and *P*-values are provided for each categorical predictor. Statistically significant p-values at the α=0.05 level are in boldface.

Predictor(s)	A_{max}		g_s		F_v/F_m	
	F	***P*-value**	***F***	***P*-value**	χ^2	***P*-value**
Water	1.13	0.29	3.50	0.06	0.32	0.57
Species	3.62	**<0.05**	6.16	**<0.001**	15.53	**<0.01**
Time	3.90	**0.05**	2.89	0.09	0.01	0.91
Light	1.23	0.27	0.40	0.53	0.14	0.71
Water ×Time	28.69	**<0.001**	13.33	**<0.001**	1.03	0.31
Species × Time	7.71	**<0.001**	2.83	**<0.05**		
Light × Time	0.69	0.41			0.014	0.91
Water × Light	8.77	**<0.01**			0.28	0.60
Species × Light	0.99	0.40				
Species × Time × Light	3.96	**<0.05**				
Water ×Time × Light					5.15	**<0.05**

Predawn F_v/F_m declined significantly in all species under drought and high light, but not under low light (significant interaction among time, water and light treatments; Table 1). As expected, F_v/F_m did not differ significantly during the experiment for plants in the watered, low light treatment (estimate: 0.02, $P = 0.9$) or the watered, high light treatment (estimate: 0.05, $P = 0.8$). One of the specialist species (*A. polyodon*) had significantly lower F_v/F_m than the two generalist epiphytes *P. elaeagnifolia* (estimate: -0.6, $P < 0.001$) and *L. pustulata* (estimate: -0.4, $P = 0.05$). There were no significant differences in F_v/F_m between *A. polyodon* and *A. flaccidum* (estimate: -0.3, $P = 0.1$), *A. flaccidum* and *L. pustulata* (estimate: -0.05, $P = 1.0$), *A. flaccidum* and *P. elaeagnifolia* (estimate: -0.3, $P = 0.3$) or *L. pustulata* and *P. elaeagnifolia* (estimate: -0.2, $P = 0.5$).

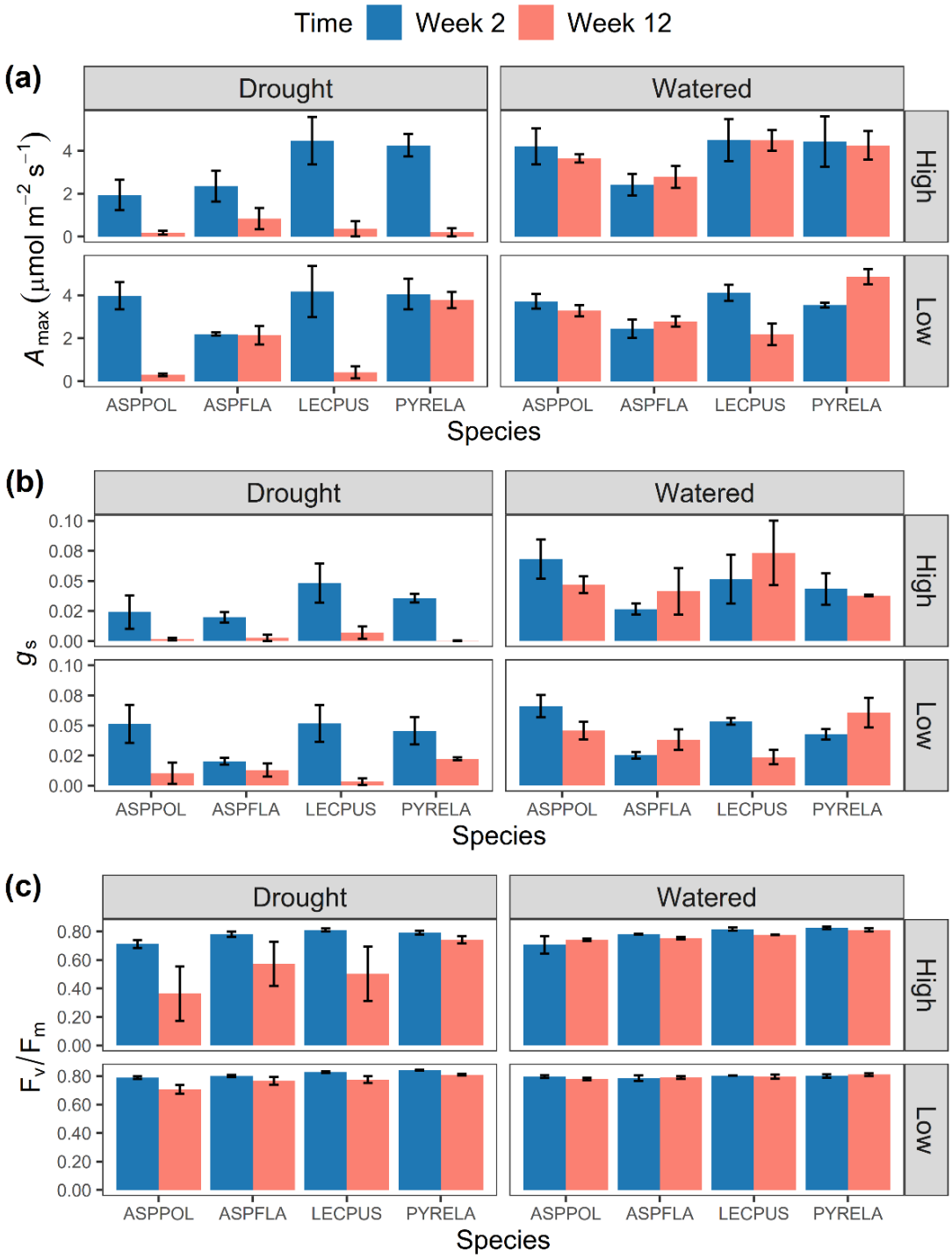


Fig. 2. Mean ± SE of photosynthetic capacity (a), stomatal conductance (b) and predawn F_v/F_m (c) of the epiphytic ferns within the four treatment groups for Week 2 and Week 12 of the experiment. Treatments were based on water (drought, watered) and light (high, low).

4.3.2. Drought recovery responses

A_{max} recovery during the drought recovery phase (Weeks 12-14) was significantly affected by interactions between species and time ($F_{3,14} = 4.61$, $P < 0.05$), and species and light

treatments ($F_{3,32} = 4.37$, $P < 0.05$). An interaction among species, time, and light also significantly influenced A_{max} recovery ($F_{3,15} = 6.8$, $P < 0.01$). See Supplementary Materials, Fig. S1 for species recovery bar plots and Table S4 for recovery LME model results.

During the recovery phase (between Weeks 12 and 14), A_{max} of the species most negatively affected by the simulated drought (*A. polyodon* and *L. pustulata*) recovered significantly more for those under low light than those under high light. For example, *P. elaeagnifolia* had significantly higher A_{max} than *A. polyodon* (estimate: -3.2, $P < 0.001$) and *L. pustulata* at Week 12 (estimate: -3.2, $P < 0.001$). Yet by Week 14, there were no significant differences between species under low light. Under high light, there were no significant differences in the A_{max} of species at Week 12. However, *P. elaeagnifolia* had significantly higher A_{max} than *A. flaccidum* by Week 14 (estimate: -2.2, $P < 0.05$), *A. polyodon* (estimate: -2.4, $P < 0.05$), and *L. pustulata* (estimate: -2.1, $P < 0.05$).

The g_s of plants in the drought treatment recovered significantly ($F_{1,27} = 14.6$, $P < 0.001$). However, the recovery of g_s did not differ significantly between species ($F_{3,23} = 1.7$, $P = 0.2$) or light treatments ($F_{1,23} = 2.3$, $P = 0.1$).

Recovery of F_v/F_m differed significantly with species ($\chi^2 = 9.6$, $P < 0.05$) and plants under high light recovered more (after a greater decline during the simulated drought) than plants under low light conditions ($\chi^2 = 18.4$, $P < 0.001$). There were no individual effects of time ($\chi^2 = 0.04$, $P = 0.9$), but an interaction between time and light significantly influenced F_v/F_m recovery ($\chi^2 = 9.0$, $P < 0.01$). After a greater decline in F_v/F_m during the simulated drought, the tree fern specialist *A. polyodon* recovered more than *P. elaeagnifolia* during the recovery phase (estimate: 0.9, $P < 0.05$). There were no other statistically significant pairwise comparisons between the species.

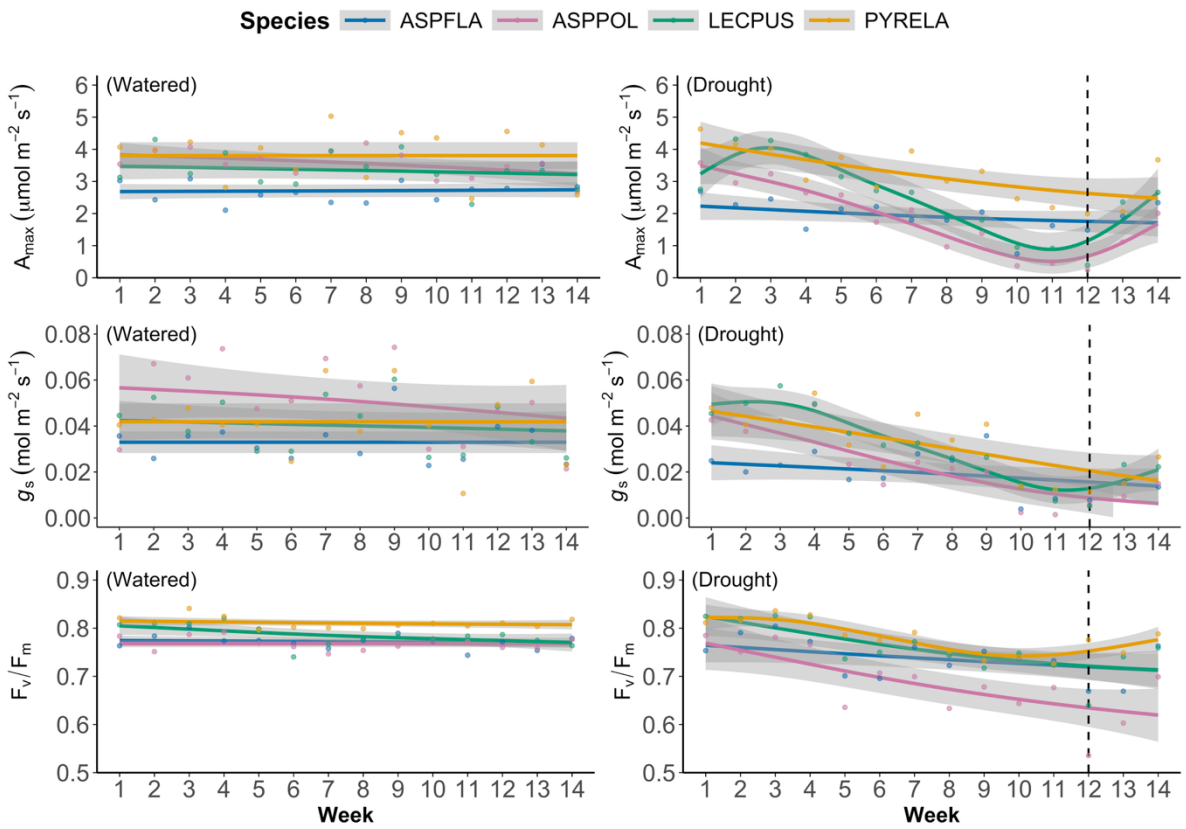


Fig. 3. Photosynthetic capacity (A_{max}), stomatal conductance (g_s) and maximum quantum efficiency of photosystem II (F_v/F_m) of the four epiphytic ferns in the watered (left) and drought (right) treatments. Dots represent the weekly mean values for each species, and the grey zones represent 95% confidence intervals of the generalised additive models (GAMs). Colours denote the four species: blue (*Asplenium flaccidum*), pink (*Asplenium polyodon*), green (*Lecanopteris pustulata*) and orange (*Pyrrosia elaeagnifolia*). The dotted line at Week 12 marks the end of the drought and the start of the recovery phase.

Fig. 3 illustrates the temporal variation in the physiological responses of the four epiphytic fern species to drought conditions, and their recovery during the drought recovery phase (Weeks 12-14). Plants under drought stress showed declining A_{max}, g_s, and predawn F_v/F_m. The GAMs explained significant proportions of deviance in A_{max} (49.8%), g_s (48.2%), and F_v/F_m (48.9%).

4.3.3. Frond mortality

Species frond mortality differed significantly ($\chi^2_3 = 42.2$, $P < 0.001$), and frond mortality increased over time ($\chi^2_1 = 98.5$, $P < 0.001$). Tree fern specialists had significantly lower frond mortality than generalist species (Supplementary Materials, Fig. S2). *Lecanopteris pustulata*

had higher frond mortality than *A. polyodon* (estimate: 0.98, $P < 0.01$) and *A. flaccidum* (estimate: 1.4, $P < 0.001$). Likewise, *P. elaeagnifolia* showed higher frond mortality than *A. polyodon* (estimate: 0.86, $P < 0.01$) and *A. flaccidum* (estimate: 1.28, $P < 0.001$). Frond mortality did not differ significantly between *L. pustulata* and *P. elaeagnifolia* (estimate: 0.12, $P = 0.90$), or between *A. flaccidum* and *A. polyodon* (estimate: -0.42, $P = 0.68$).

4.3.4. Water potential

Estimated frond water potential (ψ) of plants in the drought experiment differed significantly among treatment groups and over time (Fig. 4). Multiple linear regression showed that predicted ψ differed significantly over time ($F_{1,128} = 39.6$, $P < 0.001$), between water treatments ($F_{1,128} = 95.1$, $P < 0.001$), and light treatments ($F_{1,128} = 6.0$, $P < 0.05$). However, ψ did not differ significantly among the four species ($F_{3,128} = 0.2$, $P = 0.9$), suggesting similar drying rates under drought conditions. Pairwise comparisons revealed significantly lower ψ in Week 12 than Week 2 (estimate: -0.5, $P < 0.001$). Frond water potential was also significantly lower in drought treatments than watered treatments (estimate: 0.8, $P < 0.001$), and lower under high light than low light (estimate: -0.2, $P < 0.05$).

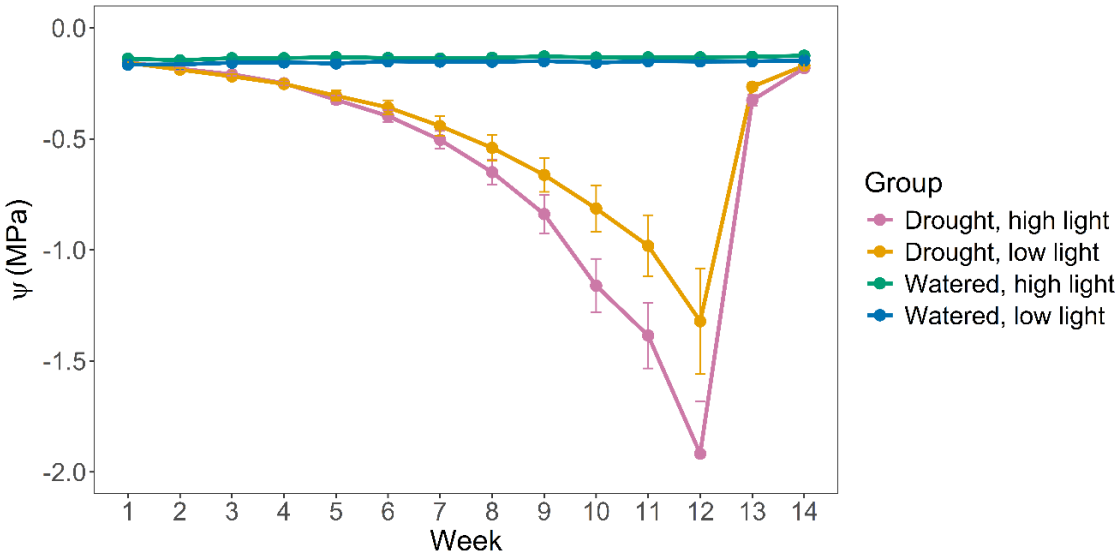


Fig. 4. Estimated frond water potential (ψ) of epiphytes in the four treatment groups during the simulated drought (between Weeks 1 and 12) and recovery phase (between Weeks 12 and 14). Points represent the mean ψ per week and group, and error bars represent the standard error. Colours denote treatment groups: pink (drought, high light), yellow (drought, low light), green (watered, high light), and blue (watered, low light).

4.3.5. Isotope analysis

Stable isotope analysis revealed differences among the four epiphytic ferns (Table 2). Foliar $\delta^{13}C$ differed significantly among species ($F_{3,27} = 12.8$, $P < 0.0001$) and was higher (indicating greater WUE) during the dry season ($F_{1,27} = 6.4$, $P < 0.05$). *Asplenium flaccidum* had significantly lower (more negative) $\delta^{13}C$ than *P. elaeagnifolia* (estimate: 4.4, $P < 0.001$), *L. pustulata* (estimate: 3.2, $P < 0.001$) and *A. polyodon* (estimate: 1.9, $P < 0.05$). *Pyrrosia elaeagnifolia* was more water-use efficient with higher (less negative) $\delta^{13}C$ than *A. polyodon* (estimate: 2.5, $P < 0.01$). However, $\delta^{13}C$ did not differ significantly between *L. pustulata* and *P. elaeagnifolia* (estimate: -1.2, $P = 0.11$) or *L. pustulata* and *A. polyodon* ($P = 0.76$). See Supplementary Materials, Table S5, for ANOVA results comparing isotopes among species and seasons.

$\delta^{15}N$ also varied significantly with species ($F_{3,27} = 6.0$, $P < 0.01$) and season ($F_{1,27} = 14.2$, $P < 0.001$). *Asplenium flaccidum* had significantly lower $\delta^{15}N$ than *P. elaeagnifolia* (estimate: 3.1, $P < 0.05$) and *L. pustulata* (estimate: 2.8, $P < 0.05$). Likewise, *A. polyodon* had significantly lower $\delta^{15}N$ than *P. elaeagnifolia* (estimate: 2.6, $P < 0.05$) and *L. pustulata* (estimate: 2.3, $P < 0.05$). There was no significant difference in $\delta^{15}N$ between *P. elaeagnifolia* and *L. pustulata* (estimate: 0.3, $P = 0.75$) or *A. flaccidum* and *A. polyodon* (estimate: 0.5, $P = 0.69$).

Table 2. Mean ± SE (n = 4) stable isotope values for the four epiphytic fern species and two seasons.

Season	Species	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	Total N (%)
Dry (February)	ASPPOL	-29.03±0.57	0.38±0.53	1.06±0.03
	ASPFLA	-30.86±0.42	-0.11±0.26	0.86±0.04
	LECPUS	-28.61±0.15	4.64±0.29	0.98±0.04
	PYRELA	-26.97±0.50	3.31±0.16	0.81±0.03
Wet (July)	ASPPOL	-30.99±0.29	-0.92±0.71	1.99±0.05
	ASPFLA	-32.92±0.24	-1.46±0.31	1.14±0.05
	LECPUS	-28.86±0.15	-0.54±0.51	1.18±0.05
	PYRELA	-28.02±0.45	1.39±0.37	1.55±0.05

Differences in total nitrogen were detected among species ($F_{3,27} = 7.1$, $P < 0.01$) and between seasons ($F_{1,27} = 49.2$, $P < 0.001$). *Asplenium polyodon* showed higher total nitrogen than *A. flaccidum* (estimate: 0.4, $P < 0.01$), *L. pustulata* (estimate: 0.3, $P < 0.01$) and *P. elaeagnifolia* (estimate: 0.3, $P < 0.05$). However, total nitrogen did not vary significantly between *A. flaccidum* and *L. pustulata* (estimate: -0.1, $P = 0.4$), *A. flaccidum* and *P. elaeagnifolia* (estimate: -0.1, $P = 0.2$), or *L. pustulata* and *P. elaeagnifolia* (estimate: -0.05, $P = 0.6$).

4.4. Discussion

During the 12-week simulated drought, epiphytic ferns in this *ex-situ* experiment showed declines in photosynthetic capacity, stomatal conductance, and photochemical efficiency. Over time, drought conditions affected epiphyte physiological responses more strongly than light availability. In support of H1, the generalist *P. elaeagnifolia* (perhaps the most widely distributed vascular epiphyte in New Zealand) exhibited greater drought resistance under low and high light conditions than the other species that exhibit preferences for more shaded, damp microhabitats. H2 was supported by photoinhibition exhibited in *A. polyodon*, the species most closely associated with the tree fern microhabitat. However, the generalist species *L. pustulata* was no more drought-resistant than the *Asplenium* species, and *A. flaccidum* did not exhibit photoinhibition under high light.

4.4.1. Factors shaping epiphyte communities

Previous research identified epiphyte host preferences in two cities on the North Island, New Zealand (Rogers et al., 2026, under review). Network analysis showed non-random interactions, suggesting that deterministic processes play a key role in the structure of urban epiphyte communities. Host species that persist in modified urban environments and provide a suitable establishment surface for epiphytes can augment epiphyte diversity (Rogers et al., 2025). Constrained host assemblages and less stable microclimates in highly modified urban plant communities may strengthen epiphyte-host interactions. Trait matching between epiphyte root and rhizome traits and host substrate characteristics may contribute to microhabitat preferences, although species ecophysiology also likely plays an important role.

4.4.2. Epiphyte drought responses and recovery

We hypothesised that epiphyte drought responses contribute to patterns of epiphyte-host interactions in urban settings. Generalist epiphytes growing on a wider range of hosts and

environments were therefore predicted to exhibit greater drought resistance than species associated with the damp, cool tree fern microhabitat. We found evidence of higher drought resistance in the generalist *P. elaeagnifolia*, which maintained A_{max} and F_v/F_m under drought stress. However, *L. pustulata* was more susceptible to drought stress, rapidly declining in A_{max} after approximately three weeks without water. Upon rehydration, recovery of *P. elaeagnifolia* was modest, reflecting minimal physiological decline during the drought, whereas *L. pustulata* recovered significantly under both low and high light treatments.

The epiphyte most closely associated with tree ferns (*A. polyodon*) was least tolerant of water scarcity and high light, rapidly closing its stomata and reducing photosynthetic capacity under drought to minimise water loss. In contrast, *A. flaccidum* was least responsive to drought conditions or light treatments, maintaining consistently low A_{max} and g_s and stable F_v/F_m. The limited physiological response of *A. flaccidum* to drought suggests that it is a conservative species that limits water loss via low stomatal conductance, and its maintenance of water content (i.e., lack of water stress) is expressed through minimal changes in F_v/F_m.

Contrary to H2, frond mortality was higher under drought conditions for generalist epiphytes than for the species associated with the tree fern microhabitat. Generalist species (e.g., *P. elaeagnifolia* and *L. pustulata*) may shed fronds after a certain period of water stress to minimise lamina surface area and escape drought effects. Increased growth rates of generalist species may also contribute to higher frond mortality (e.g., via higher frond turnover) than those with preferences for cool, damp microhabitats. For example, *A. flaccidum* has thick, coriaceous fronds that exhibit low photosynthetic capacity, which may result in lower frond mortality. Epiphytic orchids may be forced to shed leaves under drought stress or may exhibit leaf shedding to avoid drought (Zhang et al., 2016), although we are unaware of any research demonstrating that epiphytic ferns utilise this strategy. Other morphological traits not assessed here that likely affect species drought responses include total frond area and lamina succulence (Ferguson et al., 2022).

4.4.3. Light responses

On average, species maximum rates of CO_2 uptake (A_{max}) were 2.3 μmol m^{-2} s^{-1} (*Asplenium flaccidum*), 2.6 μmol m^{-2} s^{-1} *(A. polyodon),* 2.9 μmol m^{-2} s^{-1} *(Lecanopteris pustulata),* and 3.5 μmol m^{-2} s^{-1} (*Pyrrosia elaeagnifolia*). These values are similar to the average A_{max} measured

in >80 other epiphytic species (3 μmol m^{-2} s^{-1}; Zotz, 2016). While individual effects of light treatments did not significantly influence A_{max} or g_s during the experiment, species recovery of A_{max} varied significantly between light treatments. Significant interactive effects between light and water treatments support previous research that photoinhibition caused by high light is especially severe when combined with drought conditions (Hietz and Briones, 2001). Strong temporal trends illustrated increasingly negative effects of this interaction over time.

Photochemical efficiency in *A. polyodon* was most negatively affected by high light, which did not fully recover during the recovery phase. The other species associated with tree ferns (*Asplenium flaccidum*) did not exhibit photoinhibition under either low or high light treatments. Furthermore, *P. elaeagnifolia* and *L. pustulata* did not exhibit significant photoinhibition under high light, suggesting greater light tolerance. Observed photoinhibition in *A. polyodon* supports H2 that species closely associated with tree ferns are more susceptible to photoinhibition under high light than generalists. However, the limited response of *A. flaccidum* suggests that it is more tolerant of light environments and has a weaker association with the tree fern microhabitat. Further research monitoring epiphyte performance on their preferred hosts (and natural substrate) is needed to better understand how species physiology influences epiphyte-host relationships.

4.4.4. Water-use efficiency and nutrient acquisition

Foliar $\delta^{13}C$ indicates a plant's intrinsic water-use efficiency; higher (less negative) $\delta^{13}C$ suggests greater water-use efficiency (Pate, 2001). In support of H1, $\delta^{13}C$ increased from tree fern specialists to generalist epiphytes, suggesting tree fern specialists are less water-use efficient. The four species also exhibited higher $\delta^{13}C$ in the dry season than in the wet season, indicating higher WUE with reduced water availability. None of the species appear to use crassulacean acid metabolism ($\delta^{13}C$ higher than -20‰), but *P. elaeagnifolia* showed the highest WUE. Mean $\delta^{13}C$ values of *P. elaeagnifolia* in the dry season (-27.0) were comparable to the tropical epiphytes measured by Kluge et al. (1989), including *Asplenium nidus* (-26.3), *Pyrrosia adnascens* (-25.7) and *Nephrolepis acutifolia* (-25.7).

The main nutrient sources of plants can be inferred from $\delta^{15}N$ analysis. In epiphytes, lower foliar $\delta^{15}N$ values have been linked to a greater reliance on nitrogen from atmospheric deposition, whereas higher $\delta^{15}N$ values suggest nitrogen is mainly sourced from the host

substrate or canopy soil (Hietz et al., 2002), although differences in isotopic fractionation during nitrogen uptake can also contribute to these differences (Wania et al., 2002). Significantly lower δ^{15}N values in *A. flaccidum* and *A. polyodon* than in *P. elaeagnifolia* and *L. pustulata* suggest that the former rely more on atmospheric nitrogen. However, drought stress can significantly impact N isotope discrimination via photosynthesis (Wania et al., 2002). Higher δ^{15}N of some species (e.g., *L. pustulata*) may therefore reflect greater reductions in photosynthesis under drought conditions. Differences in host substrate nutrient composition (tree ferns versus woody hosts) may also influence these results. Further research measuring δ^{15}N of both epiphytes and host substrate is needed.

Low total nitrogen content in fronds may result from morphological variation among species rather than poor nitrogen supply (Hietz et al., 1999). Although total nitrogen was significantly higher in *A. polyodon* than in the other three epiphytic ferns, this result may reflect reduced lamina succulence compared to *A. flaccidum*, *P. elaeagnifolia* and *L. pustulata,* which have water-storing tissue that can reduce protein concentrations.

4.5. Conclusions

We found significant differences in the drought responses of four epiphytic ferns, associated with their microhabitat and host preferences. In urban environments, these relationships may be strengthened by unstable microclimates and constrained host assemblages. Although ferns are generally considered shade plants, some species occur in well-lit environments with fluctuating humidity. This study highlights the variation in environmental tolerance and ecophysiology of epiphytic ferns, which may influence the structure of epiphyte communities. Research on other species and taxonomic groups, and *in-situ* measurements, are required to fully elucidate how abiotic conditions shape epiphyte communities. Protecting and restoring suitable microhabitats and hosts, such as tree ferns, is crucial for epiphyte diversity as drought events increase.

References

Anderson, O.R., 2021. Physiological ecology of ferns: Biodiversity and conservation perspectives. Int. J. Biodivers. Conserv. 13(2), 49–63. https://doi.org/10.5897/IJBC2021.1482.

Anderson, O.R., 2023. Photophysiology, dark respiration and leaf desiccation resilience of the fern *Adiantum capillus-veneris* L. J. Ecol. Nat. Environ. 15, 1–8. https://doi.org/10.5897/JENE2023.0947.

Aros-Mualin, D., Kessler, M., 2024. Untangling poikilohydry and desiccation tolerance: evolutionary and macroecological drivers in ferns. Ann. Bot. 134(7), 1139–1150. https://doi.org/10.1093/aob/mcae167.

Bannister, P., 1986. Drought resistance, water potential and water content in some New Zealand plants. Flora. 178(1), 23–40.

Benzing, D.H., 1990. Vascular epiphytes. General biology and related biota. Cambridge: Cambridge University Press.

Boyer, J., Kramer, P.J., 1995. Measuring the water status of plants and soils. San Diego: Academic Press.

Brooks, M.E., Kristensen, K., Van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Mächler, M., Bolker, B.M., 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalised linear mixed modeling. The R Journal, 9(2), 378–400. https://doi.org/10.32614/ RJ-2017-066.

Bryan, C.L., 2011. Ecology of vascular epiphytes in urban forests with special reference to the shrub epiphyte *Griselinia lucida*. MSc Thesis, University of Waikato.

Callaway, R.M., Reinhart, K.O., Moore, G.W., Moore, D.J., Pennings, S.C., 2002. Epiphyte host preferences and host traits: mechanisms for species-specific interactions. Oecologia. 132, 221–230. https://doi.org/10.1007/s00442-002-0943-3.

Campany, C.E., Pittermann, J., Baer, A., Holmlund, H., Schuettpelz, E., Mehltreter, K., Watkins, J.E., 2021. Leaf water relations in epiphytic ferns are driven by drought avoidance rather than tolerance mechanisms. Plant Cell Environ. 44(6), 1741–1755. https://doi.org/10.1111/pce.14042.

Campbell, G.S., 1974. A simple method for determining unsaturated conductivity from moisture retention data. Soil Sci. 117, 311–314.

Cervantes, S.E., Graham, E.A., Andrade, J.L., 2005. Light microhabitats, growth and photosynthesis of an epiphytic bromeliad in a tropical dry forest. Plant Ecol. 179(1), 107–118. https://doi.org/10.1007/s11258-004-5802-3.

Earth Sciences New Zealand. 2025 Climate station data (hourly): Station Hamilton, Ruakura 2 EWS. https://data.niwa.co.nz/products/climate-station-hourly/files/67d606c5256f92dc33a2283f (accessed 13 March 2026).

Elias, J.P., Mortara, S.R., Nunes-Freitas, A.F., van den Berg, E., Ramos, F.N., 2021. Host tree traits in pasture areas affect forest and pasture specialist epiphyte species differently. Am. J. Bot. 108(4), 598–606. https://doi.org/10.1002/ajb2.1634.

Ferguson, B.N., Gotsch, S.G., Williams, C.B., Wilson, H., Barnes, C.N., Dawson, T.E., Nadkarni, N.M., 2022. Variation in cloud immersion, not precipitation, drives leaf trait

plasticity and water relations in vascular epiphytes during an extreme drought. Am. J. Bot. 109(4), 550–563. https://doi.org/10.1002/ajb2.1833.

Gentry, A.H., Dodson, C.H. 1987. Diversity and biogeography of neotropical vascular epiphytes. Ann. Missouri Bot. Gard. 74(2), 205–233. https://doi.org/10.2307/2399395.

Gotsch, S.G., Williams, C.B., Bicaba, R., Cruz-de Hoyos, R., Darby, A., Davidson, K., Nadkarni, N., 2022. Trade-offs between succulent and non-succulent epiphytes underlie variation in drought tolerance and avoidance. Oecologia. 198(3), 645–661. https://doi.org/10.1007/s00442-022-05140-9.

Haynes, W., 2013. Benjamini–Hochberg Method. In: Dubitzky, W., Wolkenhauer, O., Cho, KH., Yokota, H. (eds) Encyclopaedia of Systems Biology. Springer, New York, NY. https://doi.org/10.1007/978-1-4419-9863-7_1215.

Hietz, P, Briones, O., 2001. Photosynthesis, chlorophyll fluorescence and within-canopy distribution of epiphytic ferns in a Mexican cloud forest. Plant Biology. 3, 279–287. https://doi.org/10.1055/s-2001-15198.

Hietz, P., Wanek, W., Popp, M., 1999. Stable isotopic composition of carbon and nitrogen and nitrogen content in vascular epiphytes along an altitudinal transect. Plant Cell Environ. 22(11), 1435–1443. https://doi.org/10.1046/j.1365-3040.1999.00502.x.

Hietz, P., Wanek, W., Wania, R., Nadkarni, N.M., 2002. Nitrogen-15 natural abundance in a montane cloud forest canopy as an indicator of nitrogen cycling and epiphyte nutrition. Oecologia. 131(3), 350–355. https://doi.org/10.1007/s00442-002-0896-6

Kluge, M., Avadhani, P.N., Goh, C.J., 1989. Gas exchange and water relations in epiphytic tropical ferns. In Vascular Plants as Epiphytes: Evolution and Ecophysiology (pp. 87–108). Berlin, Heidelberg: Springer Berlin Heidelberg. https://doi.org/10.1007/978-3-642-74465-5_4.

Kluge, M., Avadhani, P.N., Goh, C.J., 1989. Gas exchange and water relations in epiphytic tropical ferns. In: Lüttge, U. (Eds.), Vascular Plants as Epiphytes: Evolution and Ecophysiology, pp. 87–108. Springer Berlin Heidelberg. https://doi.org/10.1007/978-3-642-74465-5_4.

Lambers, H., Chapin, F.S., Pons, T.L., 2008. Plant Physiological Ecology (Vol. 2, No. 1, pp. 11–99). New York: Springer.

Lenth, R.V., 2016. Least-squares means: the R package lsmeans. J. Stat. Softw. 69, 1-33. https://doi.org/10.18637/jss.v069.i01.

McDermott, A., 2024. Climate change is drying out canopy plants—that could mean less water for the entire rainforest. Proc. Natl. Acad. Sci. 121, e2415456121.

Moran, R.C., Klimas, S., Carlsen, M., 2003. Low-trunk epiphytic ferns on tree ferns versus angiosperms in Costa Rica. Biotropica. 35(1), 48–56. https://doi.org/10.1111/j.1744-7429.2003.tb00261.x.

Myron, K.J., 2012. *Pittosporum kirkii*: autecology of an endemic shrub epiphyte. MSc Thesis, University of Waikato.

Pate, J.S., 2001. Carbon isotope discrimination and plant water-use efficiency. In: Unkovich, M., Pate, J., McNeill, A., Gibbs, J. (Eds.), Stable isotope techniques in the study of biological processes and functioning of ecosystems (Vol. 40, pp. 19–36). Kluwer, Boston.

Perrie, L., Brownsey, P., 2024. Identification guide to the ferns and lycophytes of Aotearoa New Zealand. Te Papa Press.

Proctor, M.C., 2012. Light and desiccation responses of some Hymenophyllaceae (filmy ferns) from Trinidad, Venezuela and New Zealand: poikilohydry in a light-limited but low evaporation ecological niche. Ann. Bot. 109, 1019–1026. https://doi.org/10.1093/aob/mcs012.

R Core Team., 2024. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. www.R-project.org.

Riaño, K., Briones, O., 2013. Leaf physiological response to light environment of three tree fern species in a Mexican cloud forest. J. Trop. Ecol. 29(3), 217–228. doi:10.1017/S0266467413000230.

Rogers, H.C., Burdon, F. J., Clarkson, B.D., 2025. Tree ferns augment native plant richness and influence composition in urban plant communities. Forests. 16(9), 1498. https://doi.org/10.3390/f16091498.

Salazar-Tortosa, D., Castro, J., Villar-Salvador, P., Viñegla, B., Matías, L., Michelsen, A., ... & Querejeta, J. I. 2018. The "isohydric trap": A proposed feedback between water shortage, stomatal regulation, and nutrient acquisition drives differential growth and survival of European pines under climatic dryness. Global Change Biology. 24(9), 4069–4083. https://doi.org/10.1111/gcb.14311

Sanger, J.C., Kirkpatrick, J.B., 2017. The distribution of vascular epiphytes over gradients of light and humidity in north-east Australian rainforest. Austral Ecology. 42(8), 976–983. https://doi.org/10.1111/aec.12526.

Schneider, C.A., Rasband, W.S., Eliceiri, K.W., 2012. NIH Image to ImageJ: 25 years of image analysis. Nature Methods. 9(7), 671–675. doi:10.1038/nmeth.2089

Scholander, P.F., Bradstreet, E.D., Hemmingsen, E.A., Hammel, H.T., 1965. Sap Pressure in Vascular Plants: Negative hydrostatic pressure can be measured in plants. Science. 148(3668), 339–346. https://doi.org/10.1126/science.148.3668.339.

Seibt, U., Rajabi, A., Griffiths, H., Berry, J.A., 2008. Carbon isotopes and water use efficiency: sense and sensitivity. Oecologia. 155(3), 441–454. https://doi.org/10.1007/s00442-007-0932-7.

Taylor, A., Burns, K., 2016. Radial distributions of air plants: a comparison between epiphytes and mistletoes. Ecology. 97(4), 819–825. https://doi.org/10.1890/15-1322.1.

Voeten, C.C., 2021. Package 'buildmer'. Computer software]. https://cran. r-project. org/web/packages/buildmer/index. html.

Wania, R., Hietz, P., Wanek, W., 2002. Natural 15N abundance of epiphytes depends on the position within the forest canopy: source signals and isotope fractionation. Plant Cell Environ. 25(4), 581–589. https://doi.org/10.1046/j.1365-3040.2002.00836.x.

Watts, J.L., Watkins, Jr, J.E., 2021. Crossing the divide: An exploration of functional traits in ferns that grow across terrestrial, epipetric, and epiphytic habitats. Am. Fern J. 111(4), 308–326. https://doi.org/10.1640/0002-8444-111.4.308.

Williams, C.B., Murray, J.G., Glunk, A., Dawson, T.E., Nadkarni, N.M., Gotsch, S.G., 2020. Vascular epiphytes show low physiological resistance and high recovery capacity to episodic, short-term drought in Monteverde, Costa Rica. Functional Ecology. 34(8), 1537–1550. https://doi.org/10.1111/1365-2435.13613.

Wood, S.N, 2017. Generalised additive models: an introduction with R. chapman and hall/CRC.

Zhang, W., Hu, H., Zhang, S.B., 2016. Divergent adaptive strategies by two co-occurring epiphytic orchids to water stress: escape or avoidance? Front. Plant Sci. 7, 588. https://doi.org/10.3389/fpls.2016.00588.

Zirbel, C.R., Bassett, T., Grman, E., Brudvig, L.A., 2017. Plant functional traits and environmental conditions shape community assembly and ecosystem functioning during restoration. J. Appl. Ecol. 54(4), 1070–1079. https://doi.org/10.1111/1365-2664.12885.

Zotz, G. 2016. Physiological ecology. In Plants on Plants–The Biology of Vascular Epiphytes. Cham: Springer International Publishing, pp 95–137.

Zotz, G., Hietz, P., 2001. The physiological ecology of vascular epiphytes: current knowledge, open questions. J. Exp. Bot. 52(364), 2067–2078. https://doi.org/10.1093/jexbot/52.364.2067.

Chapter 5. Microclimate stability and tree ferns enhance obligate epiphyte richness

Abstract

Human impacts on the environment pose threats to indigenous biodiversity, particularly vascular epiphytes – structurally dependent plants that are susceptible to environmental change. How disturbance affects epiphyte diversity is unclear because direct environmental effects are difficult to disentangle from indirect effects via host assemblages. We compared key environmental predictors of obligate epiphyte richness in lowland urban and non-urban forests. Species data and a year of microclimate data were collected for urban forest plots, and plant and macroclimate non-urban data were from national repositories for vegetation surveys and environmental geospatial layers. Urban epiphyte communities were less diverse with fewer epiphytic shrubs, lycophytes, and orchids than higher elevation non-urban plots, partly explained by elevation. Tree fern basal area positively influenced epiphyte richness in urban and non-urban forests, whereas woody tree basal area positively influenced non-urban richness but negatively influenced urban richness. Elevation, mean annual temperature, precipitation and humidity did not significantly influence non-urban epiphyte richness. Structural equation modelling showed that *Dicksonia squarrosa* basal area and relative humidity stability had direct positive effects on obligate epiphyte richness in urban forests. Our results underscore the role of tree ferns as hosts across the urban-rural gradient in our North Island, New Zealand study areas. Epiphyte diversity increased with microclimate stability and the availability of suitable host species, highlighting key ecological constraints to be addressed by urban restoration projects.

5.1. Introduction

Vascular epiphytes are structurally dependent non-parasitic plants that contribute disproportionately to plant diversity in tropical and temperate rainforests (Taylor et al. 2022). Their strong reliance on atmospheric sources of water and nutrients makes them sensitive to environmental change. Global patterns show epiphyte species richness declining with increasing latitude, as tropical rainforests and precipitation decline (Taylor et al. 2022). Epiphytes can make up approximately 50% of the vascular flora in tropical rainforests (Kelly et al. 2004). Temperate regions support a less diverse epiphytic flora, although montane forests in the Himalayas and rainforests of Chile and New Zealand are comparable to many tropical rainforests (Zotz 2005). Given the sensitivity of epiphytes to environmental change,

they can serve as useful indicators for conservation and restoration, particularly in modified urban environments (Krömer et al. 2025).

Landscape processes hypothesised or shown to influence epiphyte richness include rainfall (Cardelús et al. 2006), temperature (Taylor et al. 2021), elevation (Wolf and Flamenco-S 2003), and days of cloud cover (Taylor et al. 2022). Areas with high rainfall are usually more conducive to epiphytes, although this relationship is not strictly linear (Wolf and Flamenco-S 2003). Precipitation generally increases with elevation, yet epiphyte richness often peaks at mid-elevations in cloud forests (Cardelús et al. 2006). In addition, natural disturbance events such as wildfire severely impact epiphyte communities by altering forest structure and host composition at the landscape scale (Bartels and Chen 2012).

Forest structure and host composition determine epiphyte habitat availability and quality. Tall forests with diverse host assemblages are expected to support higher epiphyte diversity, as they provide a range of substrates for epiphyte colonisation (Burns 1995; Bartels and Chen 2012; Woods et al. 2019). Differences in host traits, architecture and life histories increase habitat heterogeneity by creating gradients in light, humidity, and temperature (Sanger and Kirkpatrick 2017). Nevertheless, some species are poor hosts, often with smooth or flaky bark that can deter epiphyte establishment (Zotz 2016). Clumped epiphyte distributions may result from the presence of suitable, large host species (Grubb et al. 1963; Nieder et al. 2000; Zotz and Schultz 2008). Therefore, the increased prevalence of suitable host species may be more important for epiphyte richness in vegetation plots than host species richness.

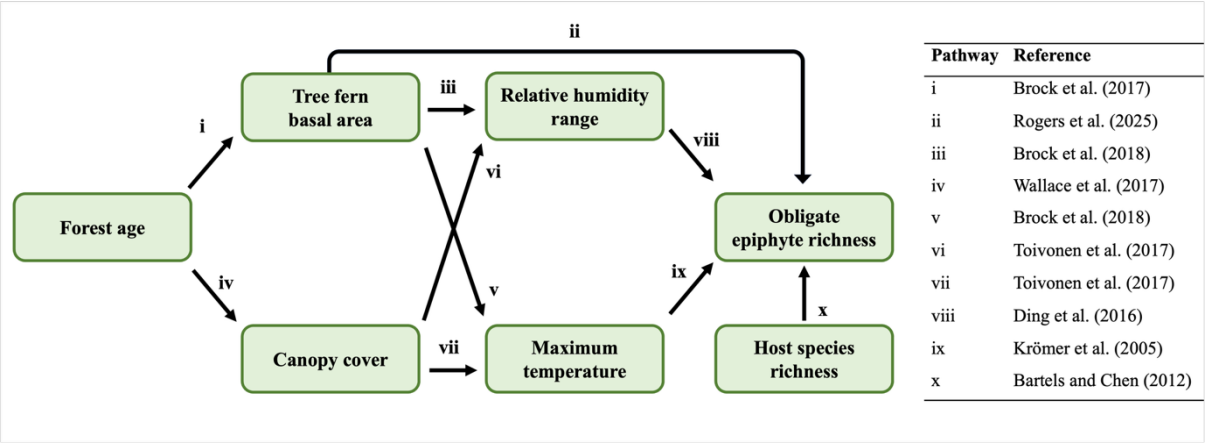
Tree basal area has been positively correlated with epiphyte species richness and abundance (Ding et al. 2016). However, the effect of tree fern basal area on epiphyte richness has received less attention. Tree ferns are ubiquitous and are often excellent hosts due to their structurally complex root mantles with high moisture retention and megaphylls that provide a sheltered microhabitat for epiphytes. In New Zealand urban forests, tree ferns were found to host more diverse vascular epiphyte assemblages than woody angiosperm trees (Rogers et al. 2025) – a result also found in non-urban forests of Costa Rica (Moran et al. 2003). Overlapping habitats of tree ferns and epiphytes may strengthen these relationships (Roberts et al. 2005).

Stands of trees that host epiphytes form an epiphyte metacommunity where local factors and dispersal determine community composition (Rogers et al. 2026, under review). Abiotic factors influencing epiphyte communities on individual trees include air temperature, vapour pressure deficit (Cardelús and Chazdon 2005) and microhabitat characteristics (Sanger and Kirkpatrick 2017). At the stand level, forest age positively influences epiphyte richness and density, as microclimates tend to be more stable in late-successional communities (Oswaldo et al. 2022). Water scarcity is possibly the most significant abiotic constraint of vascular epiphytes (Zotz and Hietz 2001); consequently, relative humidity can considerably regulate their occurrence (Ding et al. 2016). Elevated temperatures may exacerbate drought stress in epiphytes (Toivonen et al. 2017; Williams et al. 2020), and the urban heat island effect associated with densely populated human settlements may hinder the establishment of viable epiphyte populations (Mondragón and Mora-Flores 2023).

Land-use practices impact epiphyte communities by altering abiotic and biotic conditions. Urban forests subject to ongoing forest clearance due to land development tend to support less diverse and more homogeneous epiphyte communities. This phenomenon is primarily attributed to smaller, fragmented vegetation patches and less stable microclimates in urban settings (Adhikari et al. 2015; Gallego et al. 2025). Drought-tolerant species have been shown to dominate urban epiphyte communities compared with old-growth forests (Einzmann et al. 2016). A North Island New Zealand study found that urban forests supported only approximately 55% of the regional epiphyte species pool, a pattern that correlated with warmer, drier microclimates (Bryan 2011). However, research on key environmental predictors of urban and non-urban epiphyte diversity is limited, particularly in temperate regions (Krömer et al. 2025).

Previous research has described differences between epiphyte communities in non-urban and urban environments (Bryan 2011) and demonstrated that humidity and tree basal area positively influence urban epiphyte richness and density (Wallace et al. 2017). Here, we investigated environmental factors structuring obligate epiphyte communities at local and regional scales, focusing on the role of tree ferns. Three hypotheses were tested: (H1) urban forests support less diverse and more homogeneous epiphyte communities compared to non-urban forests; (H2) host species richness and composition (using basal areas) contribute to differences between urban and non-urban epiphyte communities; and (H3) urban epiphyte richness increases with habitat quality (i.e., forest age, the availability of preferred hosts such

as tree ferns, and microclimate stability). To evaluate these non-exclusive and potentially interacting drivers, we used a causal network approach (Fig. 1), guided by key references documenting pathways that influence urban plant communities.



Pathway	Reference
i	Brock et al. (2017)
ii	Rogers et al. (2025)
iii	Brock et al. (2018)
iv	Wallace et al. (2017)
v	Brock et al. (2018)
vi	Toivonen et al. (2017)
vii	Toivonen et al. (2017)
viii	Ding et al. (2016)
ix	Krömer et al. (2005)
x	Bartels and Chen (2012)

Fig. 1. *A priori* structural equation model (SEM) hypothesising environmental factors underpinning obligate epiphyte richness in urban forests. Each pathway is supported by references shown in the figure.

5.2. Materials and methods

5.2.1. Study areas

The central North Island of New Zealand has a warm temperate climate. New Plymouth is a small coastal city with a mean annual temperature of 14 °C, an average annual rainfall of 1,400 mm and an annual average of 8 ground frost days (Taranaki Regional Council 2022; NIWA 2020). Hamilton is in the central North Island, with a mean annual temperature of 13.7 °C, an annual rainfall of 1,190 mm and an annual average of 46 ground frost days (NIWA 2020). New Zealand's major urban centres have low indigenous vegetation cover, ranging from less than 1% to 9% (Clarkson and Kirby 2016). Hamilton has less native-dominated vegetation (~2.5%) than New Plymouth (~8.9%).

To compare urban and non-urban epiphyte communities dominated by trees and shrubs (hereafter, forests for simplicity), we collected data from two North Island cities and from National Vegetation Survey (NVS) plots in numerous forest parks. Urban forests are often associated with younger, more fragmented, and less diverse plant communities than non-urban forests (MacKay et al. 2011). However, urban forests can support assemblages dominated by stress-tolerant species, and comparisons with contiguous non-urban forests are

needed to identify distributional gaps in species and inform conservation strategies (Jarquin-Pacheco et al. 2025; Gallego et al. 2025).

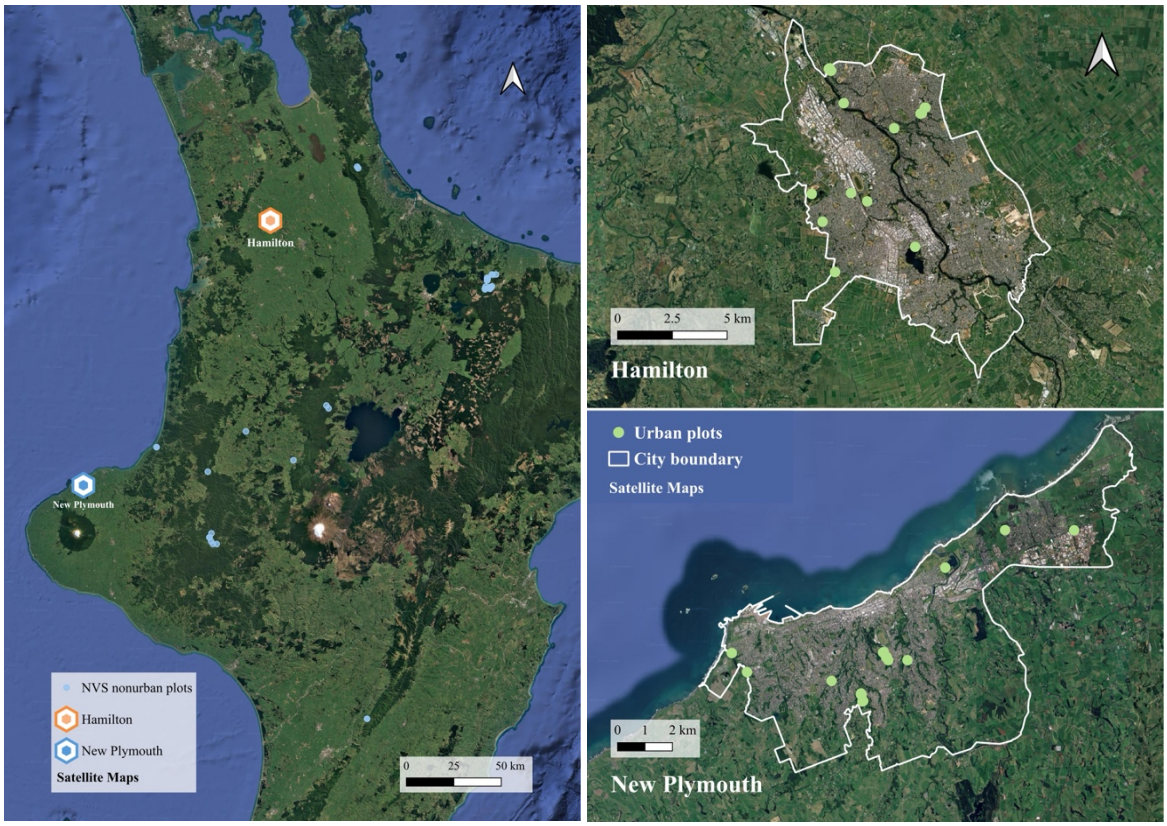


Fig. 2. Study sites of non-urban vegetation plots from the National Vegetation Survey (NVS) (left; blue dots; n = 34), and urban plots are represented by green dots in Hamilton (top right; n = 20) and New Plymouth (bottom right; n = 21).

The NVS plots used in this study ranged in latitude from -37.5 (Kaimai-Mamaku Forest Park) to -40.2 (Ruahine Forest Park), within protected forest parks on the North Island (Fig. 2). These NVS plots were designated as “non-urban” forest plots because they were situated in contiguous forest with a minimum area of 350 ha. Conversely, the urban forest plots were in forest patches ranging from 0.1 to 30 ha.

5.2.2. Data collection

Vegetation surveys were conducted in two cities on the North Island of New Zealand. A total of 41 plots were measured in Hamilton and New Plymouth. We aggregated two datasets to capture two distinct landforms in the cities and a wider range of site ages and microclimates that likely influence epiphyte species richness (Table 1). Topographic depressions (e.g.,

gullies) can provide microclimate buffering by reducing wind and solar radiation exposure (McNichol et al. 2024; Jucker et al. 2018). Hence, plots for the two datasets were classified as either measured in gullies (i.e., topographic depressions) or in smaller, flat reserves with less stable microclimates. Eighteen 200 m^2 plots (20 × 10 m) were surveyed in reserves following a method developed by the People, Cities and Nature research programme (PCaN 2024). Another 23 plots were measured in gullies using a 3 m radius (28 m^2).

For each vegetation plot survey, we identified and counted vascular epiphyte and host species, and recorded host species DBH (diameter at breast height, 1.35 m). We focused on native obligate and hemi-epiphytes in this study (hereafter, epiphytes); facultative and accidental epiphytes were excluded from the analyses. Obligate or holo-epiphytes are species that occur almost exclusively on other plants, while hemi-epiphytes usually germinate in the canopy and send their roots to the forest floor (Burns 2010; Kirby 2016). Epiphytes used in our analyses are listed in Supplementary Materials, Table S1. The species nomenclature follows Breitwieser and Heenan (2023).

A temporal gap exists between the measurement periods of our datasets (2017 and 2024), although similar annual temperatures and rainfall during these years suggest it had a negligible effect on the microclimate data collected (NIWA 2017; NIWA 2024). The mean annual temperature was comparable in New Plymouth in 2017 (14.2 °C) and 2024 (14.1 °C), and in Hamilton in 2017 (14.5 °C) and 2024 (14.4 °C). Total annual rainfall was similar in New Plymouth in 2017 (1,253 mm; 203 days of rainfall) and 2024 (1,086 mm; 203 days of rainfall), although rainfall was considerably higher in Hamilton in 2017 (1,381 mm; 168 days of rainfall) than in 2024 (842 mm; 150 days of rainfall). See the full comparisons for temperature and rainfall in Supplementary Materials, Figs. S1–2; Tables S2–S3.

Table 1. Mean ± SE obligate epiphyte richness, forest age, tree fern basal area and daily range in relative humidity for the two datasets per city assessed in the SEM.

City	Dataset	Year	n	Obligate epiphyte richness	Forest age (yrs)	Tree fern basal area (m^2 ha^{-1})	Relative humidity range (%)
Hamilton	Gullies	2024	11	5.6 ± 1.0	31 ± 11	41.6 ± 6.9	31.3 ± 1.4
Hamilton	Reserves	2017	9	0.1 ± 0.1	17 ± 10	5.4 ± 5.4	59.3 ± 1.1
New Plymouth	Gullies	2024	12	3.8 ± 0.8	90 ± 10	22.8 ± 8.1	29.5 ± 1.2
New Plymouth	Reserves	2017	9	0.6 ± 0.4	19 ± 11	1.4 ± 1.0	49.8 ± 1.5

There is ongoing debate regarding the influence of plot shape on plant richness; however, plot shape is considered to have a minimal effect on richness when sampled within a single vegetation type, such as our forest plots (Keeley and Fotheringham 2005; Güler et al. 2016). Nevertheless, to standardise epiphyte and host species richness for differences in plot area, we used the species-area relationship (SAR) power-law:

$$S = cA^z$$

where S represents species richness, c represents small-scale richness (e.g., per 1 m^2), A is the area, and z is the accumulation coefficient (i.e., the rate at which species richness increases with sampled area). We determined z for the 200 m^2 plots using the linear form of the SAR and applied the resulting multipliers to the smaller 28 m^2 plots (1.43) and the 400 m^2 plots (0.89) to adjust species richness for comparison. The SAR is considered one of the oldest and closest approximations to an ecological law (Arrhenius 1921; Lomolino 2000), offering a simple yet effective approach for comparing vegetation surveys across different plot sizes (Barandun et al. 2026). Epiphyte richness has been shown to scale with host size (Flores-Palacios and García-Franco 2006; Wang et al. 2017), so it is expected to follow a power law function similar to the universal SAR. Using predicted species richness for the 200 m^2 plots, we scaled the richness of the 23 smaller urban plots and the larger 400 m^2 non-urban plots to enable comparison in our models.

We selected ecologically relevant variables hypothesised to explain variation in epiphyte richness. Hourly measurements of relative humidity and temperature were systematically recorded at the 41 plots for a year using HOBO (Honest Observer by Onset, Bourne, Massachusetts, United States of America) data loggers, placed on a tree nearest to the plot centre at DBH. Additional data collected at each plot included canopy cover (using the %Cover CanopySurveying application) and vegetation age (i.e., years since active plantings commenced) obtained from unpublished databases (MacKay 2006; Wallace 2017; HCC 2021).

National Vegetation Survey (NVS) data from non-urban forests enabled a comparison with the urban epiphyte communities (Table 2). We selected NVS plots from the North Island that measured vascular epiphytes and DBH of trees and tree ferns with DBH ≥ 2.5 cm. As some plots were spatially clustered, a random selection of one plot per unique geographic

coordinate (n = 34) was made using the "delete duplicate geometries" tool in QGIS (a geographic information system) to ensure spatial independence. We further refined the data to include only plots below 600 m a.s.l., which approximates the altitudinal transition from lowland to upland forest in the Waikato region (Clarkson 2002). The 20 × 20 m NVS plots followed nationally developed methodology (Hurst and Allen 2007). Tree fern and woody tree basal areas were calculated using DBH measurements. Environmental variables hypothesised to influence epiphyte richness were extracted from NZEnvDS (McCarthy et al. 2021) for each plot using the "sample raster file" tool in QGIS. These variables were elevation, mean annual temperature, mean annual humidity, and total annual precipitation.

Table 2. Mean ± SD of epiphyte richness, mean relative humidity, elevation, host richness, and tree fern and woody tree basal area in urban and non-urban forest plots. Climate data were obtained from NZEnvDS.

	Urban (n = 41)	**Non-urban (n = 34)**
Obligate epiphyte richness	2.8 ± 3.2	8.8 ± 5.9
Mean annual relative humidity (%)	80.2 ± 1.2	81.3 ± 1.3
Total annual precipitation (mm)	1,473 ± 193	2,038 ± 302
Mean annual temperature (°C)	13.7 ± 0.1	11.9 ± 0.7
Elevation (m)	42 ± 18	336 ± 137
Host species richness	1.7 ± 1.8	9.0 ± 4.7
Tree fern basal area (m^2 ha^{-1})	19.3 ± 25.6	8.3 ± 11.7
Woody tree basal area (m^2 ha^{-1})	15.6 ± 15.7	46.8 ± 23.3

5.2.3. Data analysis

Statistical analyses were completed in R version 4.4.2 (R Core Team 2024). A comparison of epiphyte community composition between urban and non-urban plots was conducted with PERMANOVA using the "adonis2" function in the "vegan" R package (Oksanen et al. 2013). Community dissimilarity was evaluated using the Jaccard index on a binary (presence-absence) matrix to account for sparse data. The PERMANOVA model accounted for datasets as a blocking factor and elevation as a covariate. To visualise the differences in epiphyte community composition, we used nonmetric multidimensional scaling (NMDS). Indicator species of urban and non-urban forests were identified using the "indicspecies" R package and overlaid on the ordination. Furthermore, a rarefaction and extrapolation curve using the

"iNEXT" R package (Hsieh et al. 2016) helped confirm increased species richness in non-urban plots after accounting for sampling effort (Supplementary Materials, Fig. S3).

To determine the range in relative humidity (i.e., humidity stability) from data collected at each vegetation plot, which we expected to influence obligate epiphyte richness, we first calculated daily mean values. For each plot, we then calculated the minimum and maximum relative humidity (from the mean values) and determined the range by subtracting the former from the latter (Supplementary Materials, Fig. S4).

Linear mixed-effects models (LMMs) were fit using the "lme4" R package (Bates et al. 2015) to assess 12 bivariate relationships influencing urban epiphyte richness. Our models included city as a fixed effect and site as a random effect to account for the nested study design. Fig. 4 presents urban bivariate relationships using generalised linear models (GLMs) and generalised additive models (GAMs). In addition, we fitted six GLMs with Gamma distributions to examine environmental drivers of epiphyte richness in non-urban forests. Likelihood-ratio tests were used for the six non-urban GLMs.

Prior to structural equation modelling (SEM), the linearity of all relationships for the urban data was examined using regression diagnostics. Two SEMs were then completed to explain obligate epiphyte richness using the 'piecewiseSEM' R package (Lefcheck 2016). The first SEM included total tree fern basal areas, and the second model focused on the effect of *Dicksonia squarrosa* basal area on epiphyte richness. We completed the second model to test the direct effects of *D. squarrosa,* the species most dominant in the gully systems, which may provide a substrate more conducive to epiphytes. In contrast, species such as *Cyathea dealbata* can occur in drier environments on vegetation patch edges in urban settings. Constituent LMMs were used in the SEM with city as a fixed effect and site as a random effect. Fisher's C statistic determined model fit, with well-fit models yielding small *C* statistics and P values > 0.05.

For the first SEM, the most parsimonious model of obligate epiphyte richness in urban forests was obtained by removing nonsignificant pathways (α=0.05) from the *a priori* global model that did not fit the data well and indicated missing paths (Fisher's $C = 79.5$, df = 12, $P < 0.0001$; Fig. 1). To improve model fit, we excluded maximum daily temperature from the model, as it was highly correlated with relative humidity. We then removed the

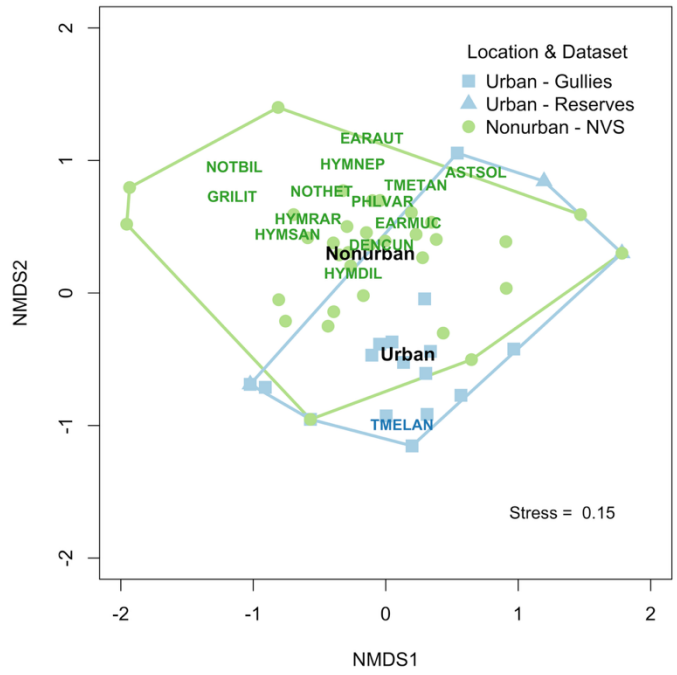
nonsignificant pathway between tree fern basal area and epiphyte richness. Additionally, forest age did not significantly affect tree fern basal area, but tree fern basal area significantly influenced canopy cover, so we adjusted these pathways accordingly. As a final step, we added a correlated error term between tree fern basal area and the range in relative humidity to account for the bidirectional relationship. For the second SEM, we used the improved model fit from the first SEM but replaced total tree fern basal areas with *Dicksonia squarrosa* basal area (the most prominent tree fern species in the gullies).

5.3. Results

A total of 46 obligate epiphyte species were recorded across all plots. Non-urban plots (n = 34; 1.4 ha) had 45 species, and urban plots (n = 41; 0.43 ha) had 16 species. The 46 species included ferns (32), lycophytes (1), nests (3), orchids (5), and shrubs (5). Epiphytic ferns dominated both urban and non-urban plots, although no lycophytes and only one of the five epiphytic shrubs (*Griselinia lucida*) were recorded in the urban plots. The only species exclusively in urban plots was *Arthropteris tenella*. After accounting for differences in plot area, non-urban plots had an average of 9 species, compared with 3 in urban plots. Likewise, the average host species richness was higher in non-urban plots (9) than in urban plots (2).

5.3.1. Epiphyte communities of urban and non-urban forests

Epiphyte community composition differed significantly between the urban and non-urban vegetation plots ($F_{1,52} = 5.2$, $P < 0.01$) and with elevation ($F_{1,52} = 2.0$, $P < 0.01$). Some overlap existed in ordination space between urban and non-urban plots (Fig. 3), although urban epiphyte communities were comparatively less diverse. Furthermore, urban reserves supported lower diversity than urban gullies, with minimal variation in epiphyte composition (Fig. 3). The only indicator species of urban forests was the epiphytic fern *Tmesipteris lanceolata*. The 13 indicator species associated with non-urban forests were seven ferns: *Hymenophyllum dilatatum*, *H. nephrophyllum*, *H. rarum*, *H. sanguinolentum, Notogrammitis billardierei*, *N. heterophylla*, *Tmesipteris tannensis*; one nest *Astelia solandri*; three orchids *Dendrobium cunninghamii, Earina autumnalis* and *E. mucronata*; one lycophyte *Phlegmariurus varius*; and one tree *Griselinia littoralis*.



Indicator species

ASTSOL: *Astelia solandri*

DENCUN: *Dendrobium cunninghamii*

EARAUT: *Earina autumnalis*

EARMUC: *Earina mucronata*

GRILIT: *Griselinia littoralis*

HYMDIL: *Hymenophyllum dilatatum*

HYMNEP: *Hymenophyllum nephrophyllum*

HYMRAR: *Hymenophyllum rarum*

HYMSAN: *Hymenophyllum sanguinolentum*

NOTBIL: *Notogrammitis billardierei*

NOTHET: *Notogrammitis heterophylla*

PHLVAR: *Phlegmariurus varius*

TMELAN: *Tmesipteris lanceolata*

TMETAN: *Tmesipteris tannensis*

Fig. 3. Epiphyte community composition of urban vegetation plots (blue symbols) and non-urban (green symbols) using nonmetric multidimensional scaling (NMDS). Datasets are represented by shapes: gullies (square), reserves (triangle), and NVS (circles). Convex hulls are drawn around the two locations or forest types. The ordination achieved a "fair" stress score of 0.15. Six-letter codes represent indicator species of urban (blue) and non-urban (green) epiphyte communities.

5.3.2. Host species composition effect on epiphyte richness

Host species richness was positively associated with epiphyte richness in urban ($F_{1,39}$ = 17.8, P < 0.001, D^2 = 65.8%) and non-urban plots ($F_{1,32}$ = 3.9, P < 0.05, D^2 = 8.9%). Tree fern basal area also positively influenced epiphyte richness in urban ($F_{1,39}$ = 7.7, P < 0.01, D^2 = 44.2%) and non-urban plots ($F_{1,32}$ = 6.1, P < 0.05, D^2 = 13.7%). Woody tree basal area had inconsistent effects on epiphyte richness – with a negative effect in urban plots ($F_{1,39}$ = 6.4, P < 0.05, R^2 = 14.5%) and a positive effect in non-urban plots ($F_{1,32}$ = 5.9, P < 0.05, D^2 = 13.2%).

Average plot basal areas (m^2 ha^{-1}) highlighted the dominance of tree ferns in urban plots, including *Dicksonia squarrosa* (13.3), *Cyathea cunninghamii* (2.2), and *C. medullaris* (2.2). In comparison, the most prominent woody trees were *Dacrycarpus dacrydioides* (2.0), *Cordyline australis* (1.9), *Pittosporum eugenioides* (1.7), and *Melicytus ramiflorus* (1.4).

Non-urban plots were dominated by woody tree species, such as *Pterophylla racemosa* (9.3), *Beilschmiedia tawa* (4.8), and *M. ramiflorus* (4.4); prominent tree fern species were *Cyathea smithii* (3.9), *C. dealbata* (2.4), and *D. squarrosa* (1.1).

5.3.3. Environmental predictors of epiphyte richness

LMMs showed that urban epiphyte richness was negatively influenced by the mean daily range in relative humidity ($F_{1,39} = 50.3$, $P < 0.001$, $R^2 = 56.5\%$) and the mean daily temperature ($F_{1,39} = 38.5$, $P < 0.001$, $R^2 = 49.1\%$). Epiphyte richness increased with *D. squarrosa* (whekī) basal area ($F_{1,31} = 27.1$, $P < 0.001$, $R^2 = 44.3\%$) and canopy cover ($F_{1,39} = 28.2$, $P < 0.001$, $R^2 = 42.4\%$).

Indirect relationships influencing epiphyte richness included the positive effects of tree fern basal area ($F_{1,39} = 10.3$, $P < 0.01$, $R^2 = 17.8\%$) and *D. squarrosa* (whekī) basal area on canopy cover ($F_{1,28} = 12.1$, $P < 0.01$, $R^2 = 23.2\%$). Likewise, forest age positively influenced canopy cover ($F_{1,39} = 48.9$, $P < 0.001$, $R^2 = 56.7\%$) and negatively influenced the range of relative humidity ($F_{1,39} = 17.6$, $P < 0.001$, $R^2 = 51.3\%$).

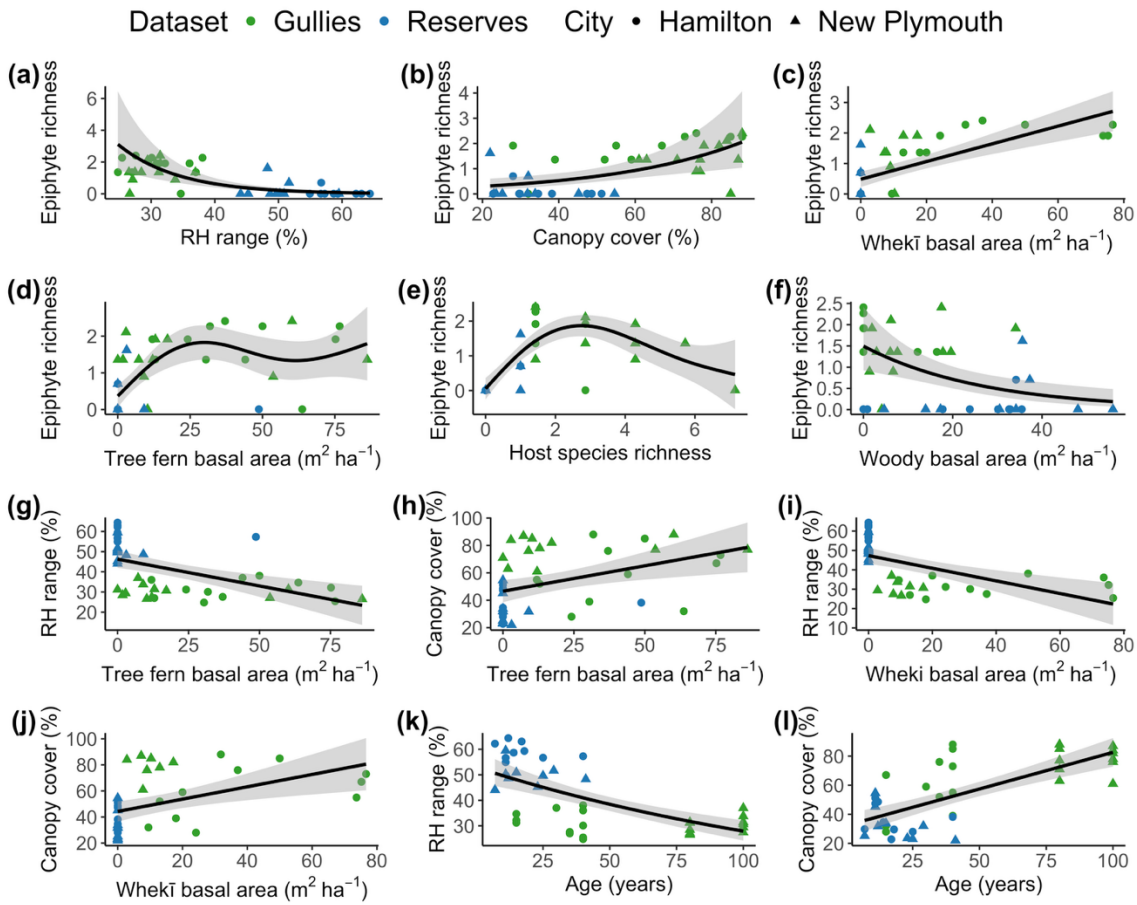


Fig. 4. Bivariate relationships influencing obligate epiphyte richness in urban environments. Symbol shapes and colours represent the cities and datasets: green circles (Hamilton gullies), green triangles (New Plymouth gullies), blue circles (Hamilton reserves), and blue triangles (New Plymouth reserves). Generalised additive models (GAMs) were used to predict epiphyte richness from tree fern basal area (d) and host species richness (e); the remaining relationships were fitted using generalised linear models (GLMs). Grey ribbons represent the 95% confidence intervals.

Non-urban generalised linear models (GLMs) revealed that epiphyte richness was not significantly influenced by mean annual temperature ($F_{1,32}$ = 0.6, P = 0.5, D^2 = 1.4%) or elevation *(*$F_{1,32}$ = 1.8, P = 0.2, D^2 = 4.6%). Furthermore, neither mean annual humidity ($F_{1,32}$ = 2.5, P = 0.1, D^2 = 5.4%) nor total annual precipitation ($F_{1,32}$ = 1.7, P = 0.2, D^2 = 3.5%) significantly influenced epiphyte richness. Limited variation in humidity (80–84%) and precipitation (1,350–2,400 mm) at the non-urban plots may have led to nonsignificant relationships with epiphyte richness.

5.3.4. Causal pathway analysis of urban epiphyte richness

The final SEM, including total tree fern basal area, fit the data well (Fisher's $C = 8.5$, df = 8, $P = 0.4$; Fig. 5) and explained 61% of the variation in epiphyte species richness. The SEM indicates that epiphyte richness increases with relative humidity stability (i.e., a smaller range) and with greater canopy cover. Forest age had an indirect positive effect on epiphyte richness by enhancing relative humidity stability and increasing canopy cover. While tree fern basal area positively influenced canopy cover, a bidirectional relationship with relative humidity was apparent in the data, though not statistically significant (Table 3). There were no correlated paths between forest age and tree fern basal areas, or humidity stability and canopy cover. Differences between the two cities were negligible, with no statistically significant effects on the SEM variables (Fig. 5).

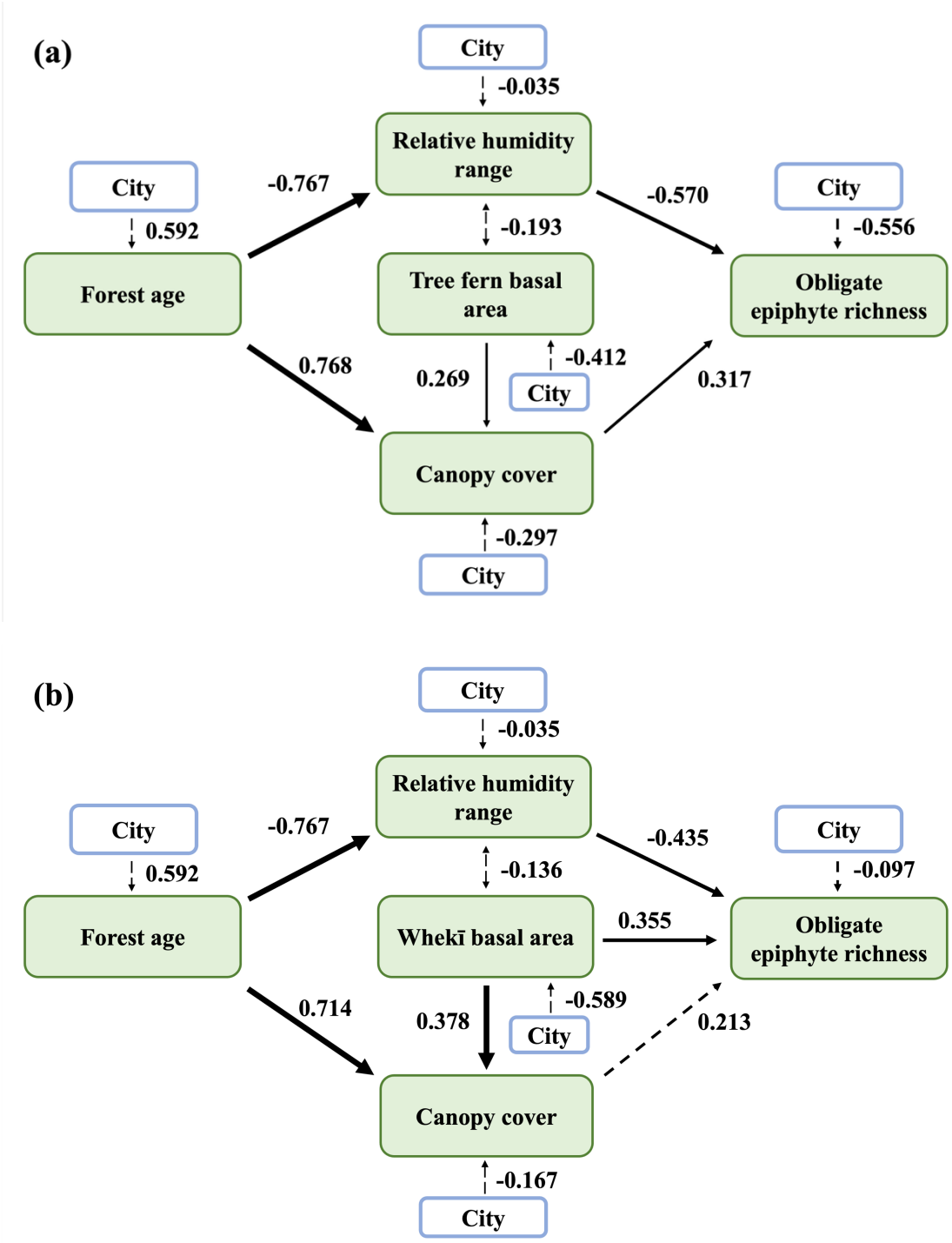


Fig. 5. Final SEMs illustrating drivers of obligate epiphyte species richness using data from Hamilton and New Plymouth, two cities on the North Island, New Zealand. The first model tested the effects of tree fern basal area (a), and the second tested the effects of whekī (*Dicksonia squarrosa*) basal area (b) on epiphyte richness. Linear mixed-effects models with site as a random effect were fit for each relationship. Arrow width is proportional to the standardised path coefficients. Dashed arrows represent nonsignificant relationships, and blue boxes represent city effects on each variable.

Table 3. Final results for the first SEM testing causal pathways of obligate epiphyte richness. Statistically significant *P*-values at the α=0.05 level are in bold. Caution should be taken when interpreting estimates of categorical predictors (i.e., city) that represent multiple contrasts.

Response	Predictor	Estimate	Standard estimate	SE	df	P-value	R^2
Epiphyte richness	Relative humidity range	-0.04	-0.57	0.009	31	**<0.001**	0.61
	Canopy cover	0.01	0.32	0.005	36	**<0.05**	
	City	-0.39	-0.56		1	0.054	
Relative humidity range	Forest age	-0.30	-0.77	0.070	23	**<0.001**	0.51
	City	-0.45	-0.04		1	0.787	
Canopy cover	Forest age	0.53	0.71	0.086	18	**<0.0001**	0.62
	Tree fern BA	0.24	0.27	0.095	33	**<0.05**	
	City	-6.75	-0.30		1	0.256	
Forest age	City	19.46	0.59		1	0.075	0.12
Tree fern BA	City	-10.54	-0.41		1	0.245	0.04
~Tree fern BA	~ Relative humidity range	-0.19	-0.19		41	0.117	

Table 4. Final results for the second SEM testing causal pathways focused on the effect of whekī (*Dicksonia squarrosa*) basal areas on obligate epiphyte richness. Statistically significant *P*-values at the α=0.05 level are in bold. Caution should be taken when interpreting estimates of categorical predictors (i.e., city) that represent multiple contrasts.

Response	Predictor	Estimate	Standard estimate	SE	df	P-value	R^2
Epiphyte richness	Relative humidity range	-0.030	-0.435	0.010	31	**<0.01**	0.66
	Canopy cover	0.008	0.213	0.005	26	0.157	
	Whekī BA	0.014	0.355	0.006	29	**<0.05**	
	City	-6.13	-0.097		1	0.664	
Relative humidity range	Forest age	-0.303	-0.767	0.072	23	**<0.001**	0.51
	City	-0.451	-0.035		1	0.913	
Canopy cover	Forest age	0.494	0.714	0.087	12.513	**<0.001**	0.65
	Whekī BA	0.387	0.378	0.121	30.392	**<0.01**	
	City	-3.14	-0.167		1	0.528	
Forest age	City	19.5	0.592		1	0.075	0.12
Whekī BA	City	-15.7	-0.589		1	**<0.05**	0.14
~Tree fern BA	~ Relative humidity range	-0.136	-0.136		41	0.202	

The second SEM, testing the effect of *D. squarrosa* basal area on epiphyte richness, also fit the model well (Fisher's $C = 3.6$, df = 6, $P = 0.7$; Fig. 5), explaining slightly more variation in epiphyte richness than the first SEM (66%). Replacing tree fern basal area with *D. squarrosa* basal area made the effect of canopy cover on epiphyte richness nonsignificant (Table 4). Compared to the first SEM, this model showed both a significant direct effect of *D. squarrosa* on obligate epiphyte richness and indirect (although not significant) effects via its influence on canopy cover.

5.4. Discussion

Abiotic and biotic factors play important roles in structuring plant communities (Götzenberger et al. 2012). The structural dependence of vascular epiphytes makes them vulnerable to changes in microclimate and host assemblages (Hietz 1999). Our results supported H1: urban epiphyte communities were less diverse and compositionally distinct from non-urban communities, with only approximately one-third of the richness recorded in the non-urban plots. In support of H2, we found that differences in host species richness and composition (using basal areas) between urban and non-urban forests influenced the epiphyte communities. Host species richness and tree fern basal area were positively correlated with obligate epiphyte species richness in both urban and non-urban forest stands. The influence of woody tree basal area was inconsistent: it negatively influenced urban epiphyte richness but positively influenced non-urban epiphyte richness. Support for H3 (that habitat quality drives urban epiphyte richness) was found from the causal pathway analysis where stable humidity and *Dicksonia squarrosa* basal area increased epiphyte richness. These results highlight both the indirect effects of vegetation age and the direct role of microclimate conditions and host assemblages for providing suitable epiphyte habitat.

5.4.1. Epiphyte communities of urban and non-urban forests

Urban forests generally support limited reservoirs of epiphyte diversity attributed to their altered biophysical conditions (Jarquin-Pacheco et al. 2025). The average and total obligate epiphyte richness of our urban plots was approximately one-third of the richness of non-urban plots. Whilst the epiphyte communities in the larger non-urban forest patches were more diverse, the difference in the average elevation (approximately 300 m) should be considered when interpreting these results. Non-urban plots at higher elevations likely experience increased rainfall and cooler temperatures. A series of hierarchical environmental

filters, from regional to local urban species pools, likely determines community assembly (Keddy 1992). Climate and biogeography are important at regional scales, while species traits (e.g., dispersal mechanisms and physiological constraints) are pertinent at local scales (Aronson et al. 2016). These processes acting at different spatial scales likely shape epiphyte community composition and help determine the realised diversity observed within plots.

Compositional analyses showed that ferns dominated epiphyte assemblages at both urban and non-urban plots. Unlike tropical regions, the taxonomic spectrum of temperate epiphyte communities is dominated by ferns and fern allies (Zotz 2005). Nonetheless, life forms such as shrubs, lycophytes and orchids form a significant component of New Zealand's epiphytic flora but were largely absent from the urban plots. Species not recorded in the urban plots that are naturally absent from Hamilton (but only uncommon in New Plymouth) were the shrubs *Brachyglottis kirkii* and *Pittosporum cornifolium*, the tree *Metrosideros robusta*, and the orchids *Dendrobium cunninghamii* and *Bulbophyllum pygmaeum*. Fragmentation and possum browsing may be implicated for the shrubs (Cowan et al. 1997), whilst wind-dispersed lycophytes and orchids may be limited by unsuitable habitat in younger urban forests (Adhikari et al. 2015; Rogers and Clarkson 2025).

5.4.2. Host species composition effect on epiphyte richness

Host species richness had a significant positive effect on epiphyte richness in urban and non-urban forests. However, the urban data demonstrated a hump-shaped relationship; epiphyte richness declined when plots included more than four host species. One possible explanation for this result is the dominance of the high-quality host *Dicksonia squarrosa* in some plots, which, when forming a dense monospecific stand, may inhibit the colonisation of other host species. Other measured plots with increased host richness but lacking high-quality species such as *D. squarrosa* may have contributed to lower epiphyte richness.

Host compositional analysis using basal areas accentuates the role of tree ferns in enhancing epiphyte richness across both forest types. Woody tree basal area had an inconsistent relationship with epiphyte richness: it negatively influenced urban epiphyte richness but positively affected non-urban epiphyte richness. The negative effect of woody tree basal areas in urban sites may result from unfavourable environmental conditions (e.g., drier, less stable microclimates), and a lack of high-quality hosts. An urban study in Mexico found that

woody cover positively influenced bromeliad richness but not overall epiphyte communities (Aoki-Gonçalves et al. 2023). Hence, woody hosts may only enhance the diversity of a certain group of epiphytes.

Host quality, here defined as the mean epiphyte richness recorded on a host species, was highest in the urban plots for the tree ferns *C. medullaris* (4 species) and *D. squarrosa* (3), and the angiosperm trees *Beilschmiedia tawa* (4 species), *Laurelia novae-zelandiae* (4) and *Alectryon excelsus* (4). Higher densities of high-quality tree fern host species may account for the positive effect of tree fern basal areas on epiphyte richness. Meanwhile, the high basal areas of poor woody host species such as *D. dacrydioides* and *P. eugenioides* likely underpin the negative relationship between woody tree basal area and epiphyte richness in urban forests.

In undisturbed forests, epiphyte diversity generally increases with the size of individual hosts (Flores-Palacios and García-Franco 2006; Shen et al. 2022). At a larger scale, but in support of increased habitat availability leading to richer epiphyte communities, we found a positive relationship between plot woody tree basal area and epiphyte species richness in the non-urban plots.

5.4.3. Environmental predictors of epiphyte richness

We attempted to minimise the effects of elevation in our comparison between urban and non-urban epiphyte communities by limiting the non-urban plots to < 600 m a.s.l. (Table 2), which had a 60 m elevational overlap. However, richer epiphyte communities at higher elevation non-urban plots may be partially driven by environmental factors. For example, sites at higher elevations generally experience higher precipitation and cooler temperatures, which can impact epiphyte communities. Additional comparisons of urban and non-urban epiphyte communities at similar elevations are therefore necessary to disentangle the role of biotic and abiotic factors on epiphyte richness.

Relative humidity range had a strong negative effect on urban epiphyte richness, highlighting the importance of stable microclimates for epiphyte communities. Temperature negatively influenced urban epiphyte richness but had no significant effect on non-urban epiphyte richness. While the impact of temperature on epiphytes in temperate regions remains poorly

understood (Zotz 2005), these relationships may reflect the negative effect of warmer temperatures in urban forests that intensify epiphyte drought stress. Still, a higher-resolution climate dataset for non-urban plots may further reveal the effect of temperature.

5.4.4. Causal pathway analysis of urban epiphyte richness

The SEMs showed that forest age and tree fern basal area were significant indirect predictors of obligate epiphyte richness in the urban forest plots. Contrary to *a priori expectations*, forest age did not significantly affect tree fern basal area, possibly because tree ferns occur across successional stages and can persist for more than 250 years (Brock et al. 2016). However, increasing forest age positively influenced relative humidity stability and higher tree fern basal areas led to increased canopy cover, thereby enhancing obligate epiphyte richness. The importance of stable humidity and forest age aligns with previous research (Wallace et al. 2017).

The first SEM showed no direct effects of total tree fern basal area on epiphyte richness, which we hypothesised was the result of plots dominated by species such as *Cyathea dealbata*, which can occur in drier habitats on vegetation patch edges. Hence, the second SEM focused on *D. squarrosa* basal area to test the effects of this tree fern host that can dominate gully floors. The second SEM found a direct positive effect of *D. squarrosa* basal area on epiphyte richness. This result likely reflects greater habitat overlap between epiphytes and *D. squarrosa* than other tree fern species measured in this study. However, it may also reflect other characteristics of *D. squarrosa* that are more conducive to epiphytes than *Cyathea* species.

A bidirectional relationship between tree fern basal area and humidity stability in our study suggests that while sites with stable humidity likely aid tree fern establishment, tree ferns may likewise contribute to microclimate stability via shading effects. Disentangling the directionality of this relationship requires additional measurements in a range of ecological contexts. Humid habitats are often necessary for tree fern establishment, regeneration and physiological performance (Hunt et al. 2002; Riaño and Briones 2015). Topographic depressions (e.g., gullies) in urban settings that retain high humidity should, therefore, be more conducive to tree ferns than topographically uniform vegetation patches. Nonetheless,

tree ferns cast deep shade (Coomes et al. 2005), which may contribute to stable microclimate conditions.

While the SEM identified some key environmental predictors of urban epiphyte richness, the effects of forest patch size, shape, connectivity, and plant dispersal limitations require further attention. In addition, although climate station data show minimal differences in rainfall and temperature between the two measurement years (2017 and 2024), our results may be confounded by temporal effects. Future studies that employ uniform plot methodologies across urban-rural gradients in a shorter time span are necessary to confirm the primary factors influencing epiphyte diversity in temperate regions.

5.5. Conclusions

We identified compositional differences between urban and non-urban obligate epiphyte communities, as well as key environmental predictors of epiphyte richness. Poorly represented life forms and lower epiphyte diversity in urban forests are likely attributable to younger, fragmented plant communities with unstable microclimates. This study emphasises the importance of mature forests, stable microclimates, and the availability of high-quality hosts (e.g., *Dicksonia squarrosa*) for epiphyte richness. Long-term protection of forest remnants in cities is therefore critical for the protection and enhancement of indigenous epiphyte diversity as well as efforts to expand, buffer and reconnect them by restoration planting. To aid macroecological investigations of epiphytic plant communities, high-resolution regional climate data are necessary to further disentangle environmental predictors of epiphyte richness across natural and anthropogenic gradients, such as urban-rural transitions.

References

Adhikari YP, Fischer A, Pauleit S (2015) Sustainable conservation perspectives for epiphytic orchids in the central Himalayas, Nepal. Appl Ecol Environ Res 13(3), 753–767. https://doi.org/10.15666/aeer/1303_753767

Aoki-Gonçalves F, Pena JC, Toledo-Aceves T, MacGregor-Fors I (2023) Urban epiphytes: Bromeliad diversity in a green cover gradient across a Neotropical streetscape. Urban For. Urban Green. 83:127901. https://doi.org/10.1016/j.ufug.2023.127901

Aronson MFJ, Nilon CH, Lepczyk CA, Parker TS, Warren PS, Cilliers SS, Goddard MA, Hahs AK, Herzog C, Katti M, La Sorte FA, Williams NSG, Zipperer W (2016) Hierarchical filters determine community assembly of urban species pools. Ecology 97:2952–2963. https://doi.org/10.1002/ecy.1535

Arrhenius O (1921) Species and area. J Ecol 9(1):95–99. https://doi.org/10.2307/2255763

Barandun M, Pauler CM, Lüscher G, Guisan A, Knop E, Schneider MK (2026) Scaling species richness: When vegetation surveys don't match in plot area. J Ecol 114(1):e70232. https://doi.org/10.1111/1365-2745.70232

Bartels SF, Chen HY (2012) Mechanisms regulating epiphytic plant diversity. Critical Crit. Rev. Plant Sci. 31(5):391–400. https://doi.org/10.1080/07352689.2012.680349

Bates D, Maechler M, Bolker B, Walker S, Christensen RHB, Singmann H, Dai B, Grothendieck G, Green P, Bolker MB (2015) Package 'lme4'. convergence 12(1):2.

Breitwieser I, Heenan PJ (2023) Flora of New Zealand Online. www.nzflora.info. Accessed 28 May 2026

Brock JM, Perry GL, Lee WG, Burns BR (2016) Tree fern ecology in New Zealand: A model for southern temperate rainforests. For Ecol Manage 375:112–126. https://doi.org/10.1016/j.foreco.2016.05.030

Burns, BR (1995) Environmental correlates of species richness at Waipoua Forest sanctuary, New Zealand. NZ J E:153–162.

Burns KC (2010) How arboreal are epiphytes? A null model for Benzing's classifications. NZ J Bot 48(3-4):185–191. https://doi.org/10.1080/0028825X.2010.503775

Bryan CL (2011) Ecology of vascular epiphytes in urban forests with special reference to the shrub epiphyte *Griselinia lucida*. Thesis, University of Waikato

Cardelús CL, Chazdon RL (2005) Inner-crown microenvironments of two emergent tree species in a lowland wet forest 1. Biotropica 37(2):238–244. https://doi.org/10.1111/j.1744-7429.2005.00032.x

Cardelús CL, Colwell RK, Watkins Jr JE (2006) Vascular epiphyte distribution patterns: explaining the mid-elevation richness peak. J Ecol: 144–156. https://www.jstor.org/stable/3599617

Clarkson BD (2002) Upland forests and special open habitats. In: The botany of the Waikato, 1st edn. The Waikato Botanical Society Inc, Hamilton, New Zealand, pp 82–90.

Clarkson BD, Kirby CL (2016). Ecological restoration in urban environments in New Zealand. Ecol Manage & Restor 17(3):180–190.

Coomes DA, Allen RB, Bentley WA, Burrows LE, Canham CD, Fagan L, Forsyth DM, Gaxiola-Alcantar A, Parfitt RL, Ruscoe WA, Wardle DA, Wilson DJ, Wright EF (2005) The hare, the tortoise and the crocodile: the ecology of angiosperm dominance,

conifer persistence and fern filtering. J Ecol 93(5):918–935. https://doi.org/10.1111/j.1365-2745.2005.01012.x
Cowan PE, Chilvers BL, Efford MG, McElrea GJ (1997) Effects of possum browsing on northern rata, Orongorongo Valley, Wellington, New Zealand. J Roy Soc New Zeal 27(2):173–179. https://doi.org/10.1080/03014223.1997.9517530
Ding Y, Liu G, Zang R, Zhang J, Lu X, Huang J (2016) Distribution of vascular epiphytes along a tropical elevational gradient: disentangling abiotic and biotic determinants. Sci Rep 6(1):19706. https://doi.org/10.1038/srep19706
Einzmann HJR, Doecke L, Zotz G (2016) Epiphytes in human settlements in rural Panama. Plant Ecol Divers 9(3):277–287. https://doi.org/10.1080/17550874.2016.1177127
Flores-Palacios A, García-Franco JG (2006) The relationship between tree size and epiphyte species richness: testing four different hypotheses. J Biogeogr 33(2):323–330. https://doi.org/10.1111/j.1365-2699.2005.01382.x
Gallego YA, Carmona-Higuita MJ, Benavides AM (2025) Urban trees as biodiversity scaffolds: patterns and drivers of epiphyte diversity in a tropical city. Urban Ecosyst 28(6):238. https://doi.org/10.1007/s11252-025-01824-1
Götzenberger L, de Bello F, Bråthen KA, Davison J, Dubuis A, Guisan A, Leps J, Lindborg R, Moora M, Pärtel M, Pellissier L, Pottier J, Vittoz P, Kobel K, Zobel M (2012) Ecological assembly rules in plant communities—approaches, patterns and prospects. Biological Reviews 87(1):11–127. https://doi.org/10.1111/j.1469-185X.2011.00187.x
Grubb PJ, Lloyd JR., Pennington TD, Whitmore TC (1963) A comparison of montane and lowland rain forest in Ecuador I. The forest structure, physiognomy, and floristics. J Ecol:567–601. https://doi.org/10.2307/2257748
Güler B, Jentsch A, Apostolova I, Bartha S, Bloor JM, Campetella G, ... Dengler J (2016). How plot shape and spatial arrangement affect plant species richness counts: implications for sampling design and rarefaction analyses. J. Veg. Sci. 27(4):692–703. https://doi.org/10.1111/jvs.12411
Hietz P (1999) Diversity and conservation of epiphytes in a changing environment. Pure Appl Chem 70(11):1–11.
Hsieh TC, Ma K, Chao A (2016) iNEXT: An R package for rarefaction and extrapolation of species diversity (Hill numbers). Methods Ecol Evol 7:1451–1456. https://doi.org/10.1111/2041-210X.12613
Hunt MA, Davidson NJ, Unwin GL, Close DC (2002) Ecophysiology of the soft tree fern, *Dicksonia antarctica* Labill. Austral Ecology 27(4):360–368. https://doi.org/10.1046/j.1442-9993.2002.01190.x
Hurst JM, Allen RB. (2007) Lincoln; NZ.: Manaaki Whenua-Landcare Research. A permanent plot method for monitoring indigenous forests: field protocols. https://nvs.landcareresearch.co.nz/Content/PermanentPlot_FieldProtocols.pdf Accessed 05 November 2026
Jarquin-Pacheco MB, Armenta-Montero S, Contreras-López J, Carvajal-Hernández CI (2025) Urban forests as habitats for vascular epiphytes and allied terrestrial plants Urban Ecosyst 28(4):150. https://doi.org/10.1007/s11252-025-01756-w

Jucker T, Hardwick SR, Both S, Elias DM, Ewers RM, Milodowski DT, ... & Coomes DA (2018) Canopy structure and topography jointly constrain the microclimate of human-modified tropical landscapes. Glob Change Biol 24(11):5243–5258. https://doi.org/10.1111/gcb.14415

Keddy PA (1992) Assembly and response rules: two goals for predictive community ecology. J Veg Sci 3: 157–164. https://doi.org/10.2307/3235676

Keeley JE, Fotheringham CJ (2005) Plot shape effects on plant species diversity measurements. J. Veg. Sci. 16(2):249–256. https://doi.org/10.1111/j.1654-1103.2005.tb02362.x

Kelly DL, O'Donovan G, Feehan J, Murphy S, Drangeid SO, Marcano-Berti L (2004) The epiphyte communities of a montane rain forest in the Andes of Venezuela: patterns in the distribution of the flora. J Trop Ecol 20(6):643–666. doi:10.1017/S0266467404001671

Kirby CL(2016) Field Guide to New Zealand's Epiphytes, Vines & Mistletoes. Hamilton, New Zealand: The Environmental Research Institute, University of Waikato.

Krömer T, Einzmann HJ, Mendieta-Leiva G, Zotz G (2025) Impact of land-use change on vascular epiphytes: a review. Plants 14(8):1188. https://doi.org/10.3390/plants14081188

Lefcheck JS (2016) piecewiseSEM: Piecewise structural equation modelling in R for ecology, evolution, and systematics. Methods Ecol Evol 7(5):573–579. https://doi.org/10.1111/2041-210X.12512

Lomolino MV (2000) Ecology's most general, yet protean pattern: the species-area relationship. J Biogeogr 27: 17–26. https://doi.org/10.1046/j.1365-2699.2000.00377.x

MacKay DB (2006) Ecology of restored gully forest patches in Hamilton Ecological District. Thesis, University of Waikato

MacKay DB, Wehi PM, Clarkson BD (2011) Evaluating restoration success in urban forest plantings in Hamilton, New Zealand. Urban Habitats 6(1).

McCarthy JK, Leathwick JR, Roudier P, Barringer JR, Etherington TR, Morgan FJ, Odgers NP, Price RH, Wiser SK, Richardson SJ (2021) New Zealand environmental data stack (NZEnvDS). N Z J Ecol 45(2):1–8. https://www.jstor.org/stable/48621886

McNichol BH, Wang R, Hefner A, Helzer C, McMahon SM, Russo SE (2024) Topography-driven microclimate gradients shape forest structure, diversity, and composition in a temperate refugial forest. Plant-Environ Interact 5(3):e10153. https://doi.org/10.1002/pei3.10153

Mondragón D, Mora-Flores MP (2023) First steps to study the demography of vascular epiphytes in cities. Braz J Biol 84:e270998. https://doi.org/10.1590/1519-6984.270998

Moran RC, Klimas S, Carlsen M (2003) Low-trunk epiphytic ferns on tree ferns versus angiosperms in Costa Rica. Biotropica 35(1):48–56. https://doi.org/10.1111/j.1744-7429.2003.tb00261.x

National Institute of Water and Atmospheric Research (NIWA) (2017) Annual climate summary 2017. https://niwa.co.nz/climate-and-weather/annual/annual-climate-summary-2024. Accessed 5 May 2026

National Institute of Water and Atmospheric Research (NIWA) (2020). Climate data and activities. https://niwa.co.nz/climate-and-weather/climate-data-and-activities. Accessed 05 May 2026

National Institute of Water and Atmospheric Research (NIWA) (2024). Annual climate summary 2024. https://niwa.co.nz/climate-and-weather/annual/annual-climate-summary-2024. Accessed 5 May 2026

Nieder J, Engwald S, Klawun M, Barthlott W (2000) Spatial distribution of vascular epiphytes (including Hemiepiphytes) in a Lowland Amazonian Rain Forest (Surumoni Crane Plot) of Southern Venezuela 1. Biotropica 32(3):385–396. https://doi.org/10.1111/j.1744-7429.2000.tb00485.x

Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'hara RB, Simpson GL, Solymos P, Stevens MH, Wagner H, Oksanen MJ (2013) Package 'vegan'. Community Ecology Package 2(9):1–295.

Oswaldo J, Hugo C, Wilmer T, Ismael P, Wilson Q, Omar C (2022) Successional forests stages influence the composition and diversity of vascular epiphytes communities from Andean Montane Forests. Ecol Indic 143:109366. https://doi.org/10.1016/j.ecolind.2022.109366

People, Cities and Nature (PCaN) (2024) Planting a Lasting Urban Forest. www.peoplecitiesnature.co.nz/publications. Accessed 2 June 2026.

R Core Team (2024) R: A Language and Environment for Statistical Computing_. R Foundation for Statistical Computing, Vienna, Austria. www.R-project.org

Riaño K, Briones O (2015) Sensitivity of three tree ferns during their first phase of life to the variation of solar radiation and water availability in a Mexican cloud forest. A J Bot 102(9):1472–1481. https://doi.org/10.3732/ajb.1500228

Roberts NR, Dalton PJ, Jordan GJ (2005). Epiphytic ferns and bryophytes of Tasmanian tree-ferns: a comparison of diversity and composition between two host species. Austral Ecol 30(2):154. https://doi.org/10.1111/j.1442-9993.2005.01440.x

Rogers HC, Clarkson BD (2025) Epiphyte-host relationships of remnant and recombinant urban ecosystems in Hamilton, New Zealand: the importance of *Dicksonia squarrosa* (G. Forst.) Sw., whekī. NZ J Bot 63(1):150–159. https://doi.org/10.1080/0028825X.2023.2245776

Rogers HC, Burdon FJ, Clarkson BD (2025) Tree Ferns Augment Native Plant Richness and Influence Composition in Urban Plant Communities. Forests 16(9):1498. https://doi.org/10.3390/f16091498

Sanger JC, Kirkpatrick JB (2017) The distribution of vascular epiphytes over gradients of light and humidity in north-east Australian rainforest. Austral Ecol 42(8):976–983. https://doi.org/10.1111/aec.12526

Shen T, Song, L, Collart F, Guisan A, Su Y, Hu HX, Wu Y, Dong JL, Vanderpoorten A (2022) What makes a good phorophyte? Predicting occupancy, species richness and abundance of vascular epiphytes in a lowland seasonal tropical forest. Front For Glob Change 5:1007473. https://doi.org/10.3389/ffgc.2022.1007473

Taranaki Regional Council. (2022). Our place: Taranaki State of Environment 2022. https://www.trc.govt.nz/council/plans-and-reports/monitoring-reports/state-of-the-environment-report-2022. Accessed 05 November 2026

Taylor A, Keppel G, Weigelt P, Zotz G, Kreft H (2021) Functional traits are key to understanding orchid diversity on islands. Ecography 44(5):703–714. https://doi.org/10.1111/ecog.05410

Taylor A, Zotz G, Weigelt P, Cai L, Karger DN, König C, Kreft H (2022) Vascular epiphytes contribute disproportionately to global centres of plant diversity. Glob Ecol Biogeogr 31(1):62–74. https://doi.org/10.1111/geb.13411

Toivonen JM, Suominen L, Gonzales-Inca CA, Trujillo Paucar G, Jones MM (2017) Environmental drivers of vascular and non-vascular epiphyte abundance in tropical pre-montane cloud forests in Northern Peru. J Veg Sci 28(6):1198–1208. https://doi.org/10.1111/jvs.12577

Wallace KJ (2017) Urban restoration ecology: Investigating environmental change, ecological function, and enrichment planting. Thesis, University of Waikato

Wallace KJ, Laughlin DC, Clarkson BD (2017) Exotic weeds and fluctuating microclimate can constrain native plant regeneration in urban forest restoration. Ecol App 27(4):1268–1279. https://doi.org/10.1002/eap.1520

Wang Q, Guan WB, Wong MHG, Ranjitkar S, Sun WN, Pan Y, ... & Shen LX (2017) Tree size predicts vascular epiphytic richness of traditional cultivated tea plantations in Southwestern China Glob Ecol Conserv 10:147–153. https://doi.org/10.1016/j.gecco.2017.03.002

Williams CB, Murray JG, Glunk A, Dawson TE, Nadkarni NM, Gotsch SG (2020) Vascular epiphytes show low physiological resistance and high recovery capacity to episodic, short-term drought in Monteverde, Costa Rica. Funct. Ecol. 34(8):1537–1550. https://doi.org/10.1111/1365-2435.13613

Wolf JH, Flamenco-S, A (2003) Patterns in species richness and distribution of vascular epiphytes in Chiapas, Mexico. J Biogeogr 30(11):1689–1707. https://doi.org/10.1046/j.1365-2699.2003.00902.x

Woods CL, Nevins LM, Didier EJ (2019) Structural heterogeneity of trees influences epiphyte distributions in a northern temperate rainforest. J Veg Sci 30(6):1134–1142. https://doi.org/10.1111/jvs.12797

Zotz G, Hietz P (2001) The physiological ecology of vascular epiphytes: current knowledge, open questions. Jour Exper Bot 52(364):2067–2078. https://doi.org/10.1093/jexbot/52.364.2067

Zotz G (2005) Vascular epiphytes in the temperate zones–a review. Plant Ecol 176(2):173–183. https://doi.org/10.1007/s11258-004-0066-5

Zotz G, Schultz S (2008) The vascular epiphytes of a lowland forest in Panama—species composition and spatial structure. Plant Ecol 195(1):131–141. https://doi.org/10.1007/s11258-007-9310-0

Zotz G. (2016) Epiphyte communities. In Plants on Plants–The Biology of Vascular Epiphytes. Cham: Springer International Publishing, pp 167–202

Chapter 6. Synthesis

6.1. Discussion

This thesis helps fill knowledge gaps on the ecology of vascular epiphytes and host assemblages in New Zealand urban forests through four interconnected research strands. The analyses range in scale from individual epiphyte biology to community assemblage and regional comparisons of epiphyte diversity. This breadth of approach has significantly advanced understanding of the ecology of indigenous vascular epiphytes in New Zealand urban forest communities.

In Chapter 2, tree ferns were shown to augment native plant species richness by enhancing ground fern and epiphyte richness in urban plant communities. The high proportion of vascular epiphytes hosted by tree ferns underscores the importance of these hosts, which often occur in cool, sheltered microhabitats within predominantly warm, dry urban environments. Factors contributing to epiphyte-host interactions and host preferences were then revealed, including epiphyte root and rhizome traits (Chapter 3) and epiphyte physiological responses to water and light availability (Chapter 4). Finally, environmental predictors of obligate epiphyte richness were identified in urban and non-urban forests (Chapter 5).

6.1.1. Tree ferns in urban plant communities

The role of tree ferns in urban plant communities in New Zealand was quantified for the first time (Chapter 2). As observed in non-urban forest studies, tree ferns acted as ecological filters in Hamilton, exerting a significant influence on community assembly (Turner et al., 2012; Brock et al., 2018). Tree ferns augmented native plant diversity, primarily by increasing ground fern species richness (65% of species were exclusively in plots with tree ferns) and vascular epiphyte richness (90% of species were recorded on tree ferns). Tree ferns facilitate epiphyte richness by providing a suitable establishment surface. Overlapping habitats may also contribute to their positive association with ground ferns in our study. Additionally, tree ferns may reduce competition and modify the local environment through shading effects.

Plant community structure and composition also differed with the presence of tree ferns – plots with tree ferns had higher total basal areas, dominated by tree ferns with occasional shade-tolerant angiosperm trees. Plots with tree ferns also had fewer light-demanding angiosperm and conifer tree species, consistent with other research showing competitive relationships among these groups (Coomes et al., 2005; Forbes et al., 2016). However, tree fern basal area was positively (though not significantly) associated with native sapling richness, which may be partly explained by the presence of shade-tolerant species absent in plots without tree ferns, such as *Schefflera digitata, Fuchsia excorticata* and *Laurelia novae-zelandiae*.

Restoration age (i.e., time since active plantings at a site) positively influenced the richness of native seedling, sapling, and tree species (Wallace et al., 2017). However, restoration age independently explained slightly less variation in plant community composition than tree fern basal area. This result confirms the strong influence of tree ferns on Hamilton plant communities, thereby warranting further research in other cities in New Zealand and internationally.

6.1.2. Epiphyte traits and community structure

A novel approach to examining the mechanisms underlying epiphyte-host interactions—specifically through the measurement of epiphyte root and rhizome traits—provided evidence of deterministic structuring for the first time in New Zealand cities (Chapter 3). A central goal of ecology is to understand the influence of stochastic and deterministic processes on community structure (Connor and Simberloff, 1979; Hubbell, 2011). Inconsistent trends show that stochastic processes (e.g., dispersal constraints) influence community structure at a biogeographic level (Taylor and Burns, 2015; Janzen et al., 2020) or suggest that both processes simultaneously influence epiphyte community structure (Francisco et al., 2021). However, deterministic processes may exert stronger effects than stochastic processes at a local scale in tree crowns (Wagner et al., 2021) and in disturbed forests (Köster et al., 2009; Werner and Gradstein, 2009; Dislich and Mantovani, 2016).

In support of niche theory, this study identified different epiphyte metacommunities on tree ferns than on woody hosts, with no evidence of spatial structuring. These relationships were partially explained by trait matching between epiphyte root and rhizome traits and broad host

types (based on bark or substrate type. Specifically, epiphytes exhibiting a preference for tree ferns had more abundant and longer rhizome hairs; species predominantly associated with woody hosts had shorter rhizome scales; and generalist epiphytes had wider rhizomes, longer roots, and longer and more abundant scales. Furthermore, the stronger host preferences observed in Hamilton, which has less diverse host assemblages than New Plymouth, suggest that deterministic processes have a greater influence on epiphyte community structure in cities with younger, more fragmented vegetation.

6.1.3. Physiological responses of epiphytes in relation to microhabitat preferences

In Chapter 4, links were identified between epiphyte physiological responses to water and light availability and their microhabitat preferences. These results support those of Chapter 3, suggesting that deterministic processes (e.g., environmental filters) can significantly influence the structure of urban epiphyte communities. This study provides new insights into the ecophysiology of four New Zealand epiphytic ferns; the only previous research on the water relations of any of these species was conducted in 1986 (Bannister, 1986). Drought conditions severely affected *Asplenium polyodon*, the species most closely associated with the tree fern microhabitat, resulting in rapid declines in photosynthetic capacity (A_{max}) and stomatal conductance (g_s). In contrast, the generalist species *Pyrrosia elaeagnifolia*, which often grows on woody trees, demonstrated drought resistance. The other generalist, *Lecanopteris pustulata*, unexpectedly did not exhibit drought resistance, demonstrating steeper declines in gas exchange than *P. elaeagnifolia*. Finally, *A. flaccidum*, which is associated with tree ferns in urban settings, employed drought avoidance, maintaining low yet consistent Amax and gs.

In water-scarce environments, drought resistance or avoidance likely contributes to the success of species such as *P. elaeagnifolia* and *A. flaccidum* (Campany et al., 2021). In contrast, drought-sensitive species like *A. polyodon* may be restricted to cool, damp habitats. While *P. elaeagnifolia* showed higher water-use efficiency based on $\delta^{13}C$, it did not exhibit Crassulacean acid metabolism (CAM), as found in other *Pyrrosia* species internationally (Winter et al., 1986; Chiang et al., 2013).

Light treatments mimicking two distinct epiphyte microhabitats—tree ferns, characterised by low-light conditions, and woody trees, characterised by high-light conditions—revealed

interspecific variation in light tolerance. For example, *A. polyodon* exhibited photoinhibition under high light, as indicated by a decline in predawn F_v/F_m (the maximum potential quantum efficiency of Photosystem II), whereas *P. elaeagnifolia* tolerated elevated light levels. These results are consistent with previous research suggesting that generalist epiphytes dominate disturbed habitats because they tolerate more exposed and drier microclimates than specialist epiphytes (Elias et al., 2021).

6.1.4. Environmental determinants of epiphyte diversity

Finally, environmental predictors of obligate epiphyte diversity were determined for urban and non-urban forests at a regional scale (Chapter 5). Significant differences in the epiphyte community composition were found between urban and non-urban forests. Urban epiphyte communities were less diverse, supporting a limited pool of species found across the central North Island of New Zealand. The scarcity of specialist shrub and nest epiphytes in the measured urban plots aligns with other research that suggests that epiphyte communities are generally homogeneous in human-modified systems (Alvim et al., 2021; Jarquin-Pacheco et al., 2025; Menini Neto et al., 2025). However, because the non-urban plots were, on average, 300 m higher in elevation than the urban forest, this study cannot disentangle the relative contributions of abiotic and biotic differences, and comparisons with contiguous lowland forest are necessary.

Consistent with the view that epiphytes are primarily constrained by water availability (Zotz and Hietz, 2001), humidity stability was a significant predictor of obligate epiphyte richness in cities. In non-urban forests, elevation, precipitation, temperature, and humidity did not significantly influence epiphyte richness; however, these results may reflect the lower-resolution data available at this scale. At the individual-host level, size and age have consistently been shown to positively influence epiphyte diversity (Flores-Palacios and García-Franco, 2006; Wagner and Zotz, 2020; Donoghue and Turner, 2022). The present study identified a significant effect of host composition, measured using basal area, on epiphyte diversity, consistent with previous research (Oishi and Doei, 2015). This study quantified, for the first time at the plot level, the effect of host basal area using two host types, tree ferns and woody hosts—on epiphyte richness. Tree fern basal area positively influenced obligate epiphyte richness in both urban and non-urban plots, consistent with international and national research highlighting the importance of tree ferns as hosts

(Mehltreter et al., 2005; Gaxiola et al., 2008; Brock and Burns, 2021). In contrast, woody tree basal area positively affected epiphyte richness in non-urban plots but negatively affected it in urban plots. This latter finding may indicate either a lack of mature, high-quality host species in urban forests or a reduced role of woody trees relative to tree ferns in these communities.

6.2. Research applications

This research has identified the following recommendations for the management of tree ferns and vascular epiphytes in urban ecological restoration projects:

- Extant tree fern stands should be protected and enhanced to diversify pioneer communities and augment native species richness. Planting shade-tolerant trees that naturally occur with tree ferns, such as *Schefflera digitata* in this research and *Laurelia novae-zelandiae*, as documented by Bystriakova et al. (2011), will encourage sites to follow the natural successional trajectory. However, manipulating tree fern stands (i.e., reducing the density of dominant canopy species to increase diversity) or, less severely, removing megaphyll leaf litter may help establish light-demanding angiosperms and conifers.
- Vegetated sites near water bodies (e.g., lakes or streams) or within landform depressions (e.g., gullies) offer opportunities to maintain and enhance tree fern and epiphyte diversity, as they retain moisture and provide cool, sheltered habitat.
- The colonisation and survival of epiphyte species sensitive to environmental change require sufficiently large, mature host species and host assemblages that provide stable microclimates. While urban environments generally contain few old-growth forest remnants or mature trees, protecting these habitats is critical for epiphyte diversity. Restoration projects should ensure the long-term protection and planting (to assist regeneration) of suitable host species to ensure the persistence of viable epiphyte populations in urban forests.
- Indicator species can guide the prioritisation of urban forest patches for conservation and restoration. These species can indicate progress towards established restoration goals. For instance, the presence of locally uncommon, hygrophilous epiphyte species that are largely found growing on tree ferns in urban forests signals biodiversity opportunities. Changes in the frequency and distributions of indicator species also indicate changes in the trend and condition of urban forests.

6.3. Recommendations for further research

- Long-term experiments assessing community composition across a gradient of tree fern densities (e.g., basal areas) are needed. These data are necessary to confirm the facilitative effects of tree ferns on ground ferns and epiphytes reported in Chapter 2, and to determine the density threshold at which tree ferns hinder tree regeneration and potentially arrest successional processes.
- Traits of additional epiphyte species, other than the 10 measured in Chapter 3, should be assessed to determine the entire range of variation in New Zealand's epiphytic flora contributing to epiphyte-host relationships. Simultaneous measurement of epiphyte root and leaf traits, along with host substrate traits, would better determine the degree of trait matching between epiphytes and host species.
- Physiological measurements of a wider range of epiphyte species growing on their natural host substrates (i.e., in-situ measurements) are essential to confirm the relationships identified in Chapter 4 and to further elucidate the relationships between epiphyte performance and microhabitat preferences. Further research is also required to compare the physical and chemical properties of tree ferns and woody trees that influence epiphyte establishment, including water retention. Understanding epiphyte species tolerance to environmental conditions will help disentangle factors structuring epiphyte communities in disturbed and undisturbed forests.
- Greater plot replication, using standardised methodology along an urban–non-urban gradient, is needed to further establish key environmental predictors of obligate epiphyte richness at the regional level. Microclimate data from existing permanent vegetation plots (e.g., NVS plots) would complement species occurrence data and enable further investigation of the factors shaping epiphyte communities.
- Trials monitoring the success rates of transplanting tree ferns and epiphytes will help identify opportunities for restoration projects to accelerate the establishment of these focal plant groups.

6.4. Conclusions

In conclusion, this thesis advances our understanding of epiphyte-host interactions in temperate cities in New Zealand. Epiphytes can serve as useful bioindicators of forest structural complexity and integrity in human-disturbed environments, given their dependence

on suitable host species and their association with stable microclimates. Knowledge of epiphyte ecology can therefore inform the management of plant communities, helping to minimise further losses in epiphyte diversity in urban settings. This research has provided early insights into the factors contributing to epiphyte-host interactions in urban temperate environments. Trait complementarity and niche overlap between epiphytes and broad host types supported non-random interactions, which were likely strengthened by constrained host assemblages and less stable microclimates in urban forests. For example, the root and rhizome traits of more specialised epiphytes, including fine rhizomes with fewer scales, appear to restrict certain drought-sensitive species to tree ferns in urban environments. Tree ferns can support diverse epiphyte assemblages because they provide a structurally complex substrate conducive to epiphyte establishment. Nevertheless, the niche overlap between tree ferns and shade-tolerant, drought-sensitive epiphytes suggests that abiotic and biotic factors jointly influence epiphyte community structure. As cities warm and drought events become more frequent, protecting habitats suitable for epiphytes vulnerable to microclimatic change will be essential to maintaining and enhancing indigenous plant diversity in urban forests.

References

Alvim, F. S., Furtado, S. G., & Menini Neto, L. (2021). Are vascular epiphytes in urban green areas subject to the homogenization of biodiversity? A case study in the Brazilian Atlantic Forest. *Urban Ecosystems*, *24*(4), 701–713.

Bannister, P. (1986). Drought resistance, water potential and water content in some New Zealand plants. *Flora*, *178*(1), 23–40.

Brock, J. M., Perry, G. L., Lee, W. G., Schwendenmann, L., & Burns, B. R. (2018). Pioneer tree ferns influence community assembly in northern New Zealand forests. *New Zealand Journal of Ecology*, *42*(1), 18–30.

Brock, J. M., & Burns, B. R. (2021). Patterns of woody plant epiphytism on tree ferns in New Zealand. *New Zealand Journal of Ecology*, *45*(1), 1–10.

Bystriakova, N., Bader, M., & Coomes, D. A. (2011). Long-term tree fern dynamics linked to disturbance and shade tolerance. *Journal of Vegetation Science*, *22*(1), 72–84.

Campany, C. E., Pittermann, J., Baer, A., Holmlund, H., Schuettpelz, E., Mehltreter, K., & Watkins, J. E. (2021). Leaf water relations in epiphytic ferns are driven by drought avoidance rather than tolerance mechanisms. *Plant, Cell & Environment*, 44(6), 1741–1755.

Chiang, J. M., Lin, T. C., Luo, Y. C., Chang, C. T., Cheng, J. Y., & Martin, C. E. (2013). Relationships among rainfall, leaf hydrenchyma, and Crassulacean acid metabolism in *Pyrrosia lanceolata* (L.) Fraw. (Polypodiaceae) in central Taiwan. *Flora-Morphology, Distribution, Functional Ecology of Plants*, *208*(5-6), 343–350.

Connor, E. F., & Simberloff, D. (1979). The assembly of species communities: chance or competition? *Ecology*, *60*(6), 1132–1140.

Coomes, D. A., Allen, R. B., Bentley, W. A., Burrows, L. E., Canham, C. D., Fagan, L., Forsyth DM, Gaxiola-Alcantar AU, Parfitt, R.L., Ruscoe, W.A., Wardle, D.A., & Wright, E. E. (2005). The hare, the tortoise and the crocodile: the ecology of angiosperm dominance, conifer persistence and fern filtering. *Journal of Ecology*, *93*(5), 918–935.

Dislich, R., & Mantovani, W. (2016). Vascular epiphyte assemblages in a Brazilian Atlantic Forest fragment: investigating the effect of host tree features. *Plant Ecology*, *217*(1), 1–12.

Donoghue, S., & Turner, P. A. (2022). A review of Australian tree fern ecology in forest communities. *Austral Ecology*, *47*(2), 145–165.

Elias, J. P., Mortara, S. R., Nunes-Freitas, A. F., van den Berg, E., & Ramos, F. N. (2021). Host tree traits in pasture areas affect forest and pasture specialist epiphyte species differently. *American Journal of Botany*, *108*(4), 598–606.

Flores-Palacios, A., & García-Franco, J. G. (2006). The relationship between tree size and epiphyte species richness: testing four different hypotheses. *Journal of Biogeography*, *33*(2), 323–330.

Forbes, A. S., Norton, D. A., & Carswell, F. E. (2016). Tree fern competition reduces indigenous forest tree seedling growth within exotic Pinus radiata plantations. *Forest Ecology and Management*, *359*, 1–10.

Francisco, T. M., Couto, D. R., Garbin, M. L., Misaki, F., & Ruiz-Miranda, C. R. (2021). Role of spatial and environmental factors in structuring vascular epiphyte communities in two neotropical ecosystems. *Perspectives in Plant Ecology, Evolution and Systematics*, *51*, 125621.

Gaxiola, A., Burrows, L. E., & Coomes, D. A. (2008). Tree fern trunks facilitate seedling regeneration in a productive lowland temperate rain forest. *Oecologia*, *155*(2), 325–335.

Hubbell, S. P. (2011). The unified neutral theory of biodiversity and biogeography. In *The unified neutral theory of biodiversity and biogeography*. Princeton University Press.

Janzen, T., Zotz, G., & Etienne, R. S. (2020). Community structure of vascular epiphytes: a neutral perspective. *Oikos*, *129*(6), 853–867.

Jarquin-Pacheco, M. B., Armenta-Montero, S., Contreras-López, J., & Carvajal-Hernández, C. I. (2025). Urban forests as habitats for vascular epiphytes and allied terrestrial plants. *Urban Ecosystems*, *28*(4), 150.

Köster, N., Friedrich, K., Nieder, J., & Barthlott, W. (2009). Conservation of epiphyte diversity in an Andean landscape transformed by human land use. *Conservation Biology*, *23*(4), 911–919.

Mehltreter, K., Flores-Palacios, A., & García-Franco, J. G. (2005). Host preferences of low-trunk vascular epiphytes in a cloud forest of Veracruz, Mexico. *Journal of Tropical Ecology*, *21*(6), 651–660.

Menini Neto, L., Carvalho, L. P., de Macêdo Mello, R., & Furtado, S. G. (2025). The city in the clouds: vascular epiphytes in Brazil's highest urban area are highly influenced by the surrounding vegetation. *Community Ecology*, *26*(2), 395–409.

Oishi, Y., & Doei, H. (2015). Changes in epiphyte diversity in declining forests: implications for conservation and restoration. Landscape and Ecological Engineering, 11(2), 283-291.

Taylor, A., & Burns, K. (2015). Plant composition patterns inside an endemic birds' nest fern (*Asplenium goudeyi*) on Lord Howe Island: effects of fern size, fern isolation and plant dispersal abilities. *Journal of Tropical Ecology*, *31*(5), 413–421.

Turner, B. L., Wells, A., Andersen, K. M., & Condron, L. M. (2012). Patterns of tree community composition along a coastal dune chronosequence in lowland temperate rain forest in New Zealand. *Plant Ecology*, *213*(10), 1525–1541.

Wagner, K., & Zotz, G. (2020). Including dynamics in the equation: Tree growth rates and host specificity of vascular epiphytes. *Journal of Ecology*, *108*(2), 761–773.

Wagner, K., Wanek, W., & Zotz, G. (2021). Functional traits of a rainforest vascular epiphyte community: trait covariation and indications for host specificity. *Diversity*, *13*(2), 97.

Wallace, K. J., Laughlin, D. C., & Clarkson, B. D. (2017). Exotic weeds and fluctuating microclimate can constrain native plant regeneration in urban forest restoration. *Ecological Applications*, *27*(4), 1268–1279.

Werner, F. A., & Gradstein, S. R. (2009). Diversity of dry forest epiphytes along a gradient of human disturbance in the tropical Andes. *Journal of Vegetation Science*, *20*(1), 59–68.

Winter, K., Osmond, C. B., & Hubick, K. T. (1986). Crassulacean acid metabolism in the shade. Studies on an epiphytic fern, *Pyrrosia longifolia*, and other rainforest species from Australia. *Oecologia*, *68*(2), 224–230.

Zotz, G., & Hietz, P. (2001). The physiological ecology of vascular epiphytes: current knowledge, open questions. *Journal of Experimental Botany*, *52*(364), 2067–2078.

Supplementary Materials

Chapter 2

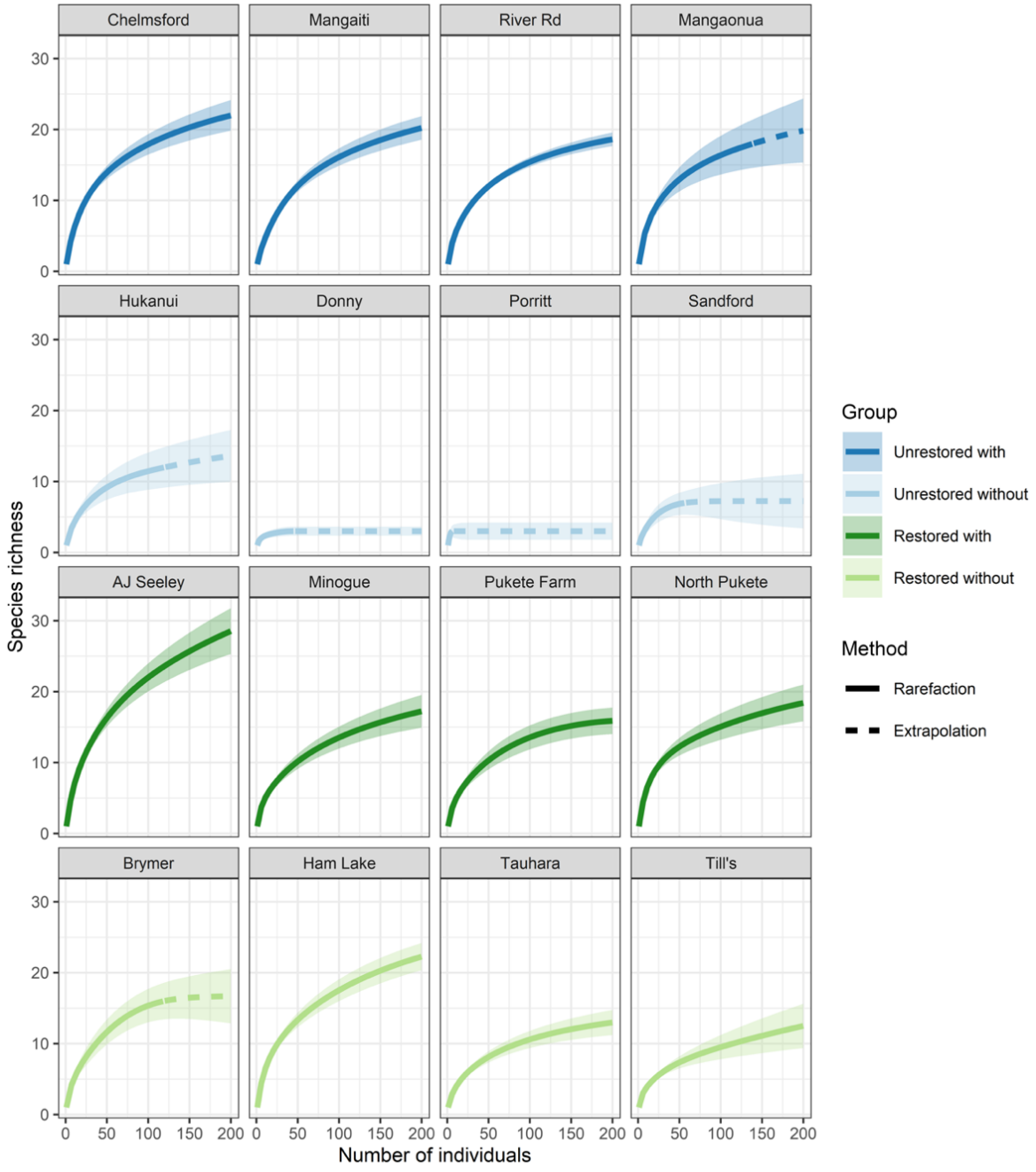


Figure A1. Rarefaction and extrapolation curves for each plot. Data were extrapolated to 200 individuals to investigate whether sampling intensity satisfied the expected native species richness. Colours represent the four study groups: unrestored with tree ferns (dark blue), unrestored without (light blue), restored with (dark green) and restored without (light green).

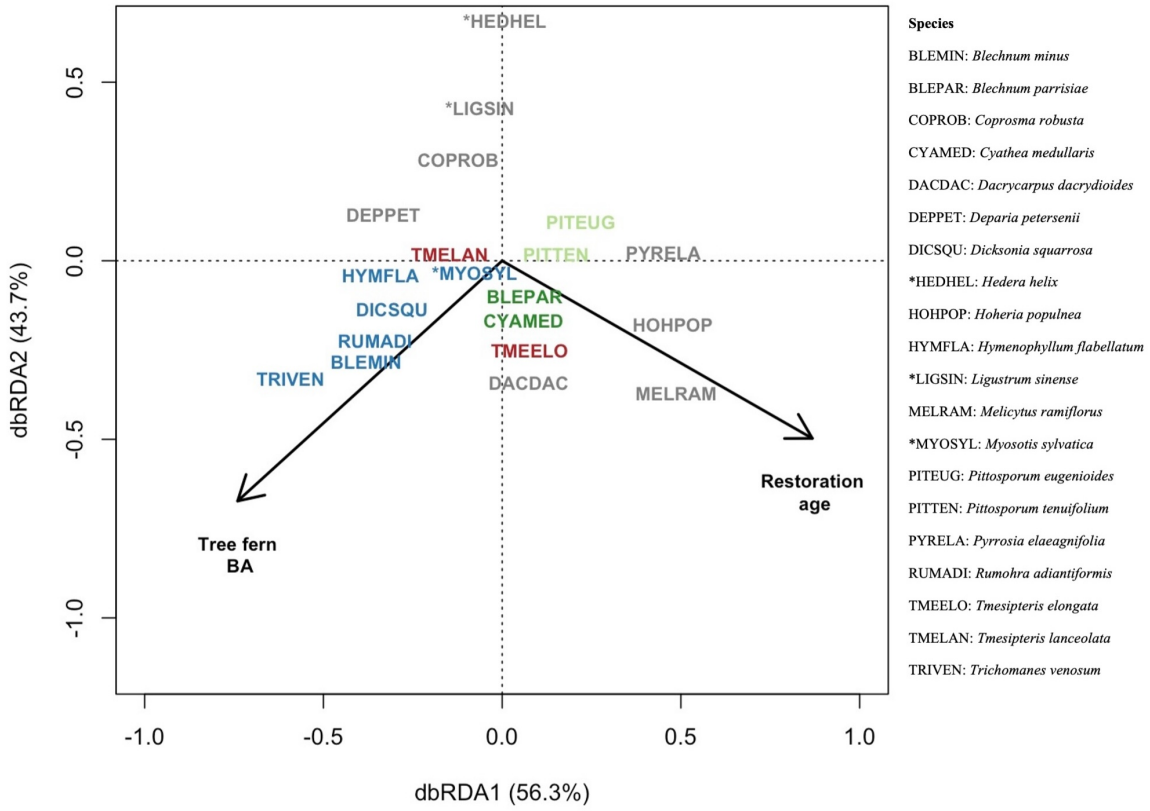


Figure A2. Redundancy analysis (RDA) of the effect of restoration age and tree fern basal area (BA) on influential species (six-letter codes). Our study groups were based on restoration status (restored, unrestored) and the presence of tree ferns (with, without). Species colours represent indicator species of the study groups: restored sites with tree ferns (dark green), restored sites without tree ferns (light green) and unrestored sites with tree ferns (dark blue). Species in grey are eight of the most abundant species, and red species (2) represent indicator species of unrestored sites with tree ferns that are also abundant species. These 10 most abundant species accounted for 62% of the mean relative abundance. An asterisk denotes exotic species.

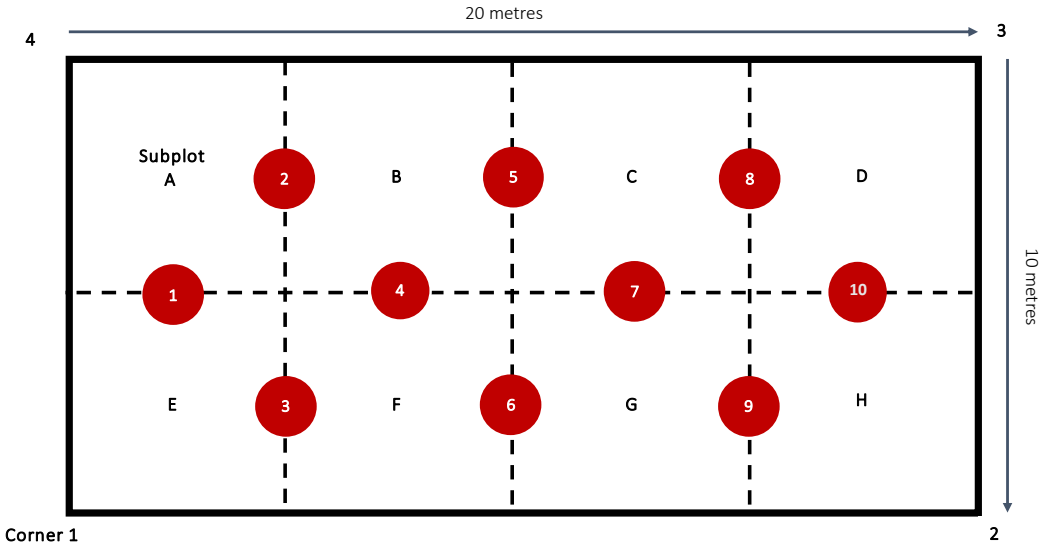


Figure S1. Vegetation plot design (200 m^2). Seedlings were measured in 10 circular seedling subplots (represented by numbers; 1.5 m radius), and ground ferns, groundcover, saplings, trees and epiphytes were measured per square subplot (represented by letters; 25 m^2).

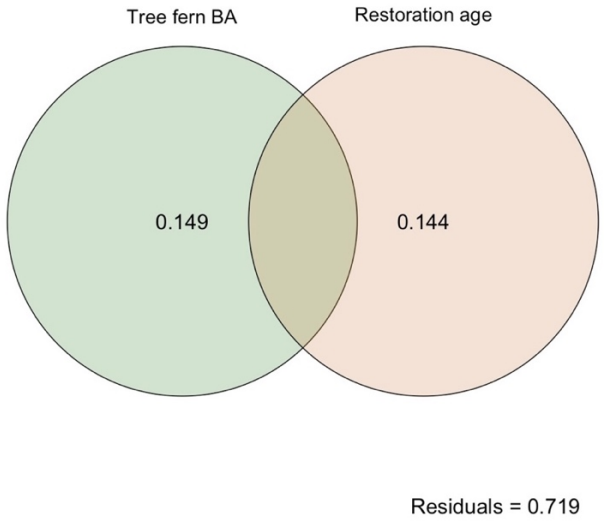


Figure S2. Variation partitioning of the effects of tree fern basal area and restoration age on community composition. Spatial predictors were removed as they did not have a significant influence on community structure.

Table B1. Pairwise comparisons of vascular plant communities (native and exotic abundances) among the four site types using permutational multivariate analysis of variance (PERMANOVA) and accounting for restoration age (i.e., years since native plantings started) as a covariate.

Group 1	**Group 2**	***F*-value**	***R*^{2}**	***P*-value**
Unrestored without	Restored with	2.23	0.47	< 0.05
Unrestored without	Restored without	2.25	0.47	< 0.05
Unrestored with	Restored with	2.58	0.51	< 0.05
Unrestored with	Unrestored without	4.61	0.43	< 0.05
Unrestored with	Restored without	4.68	0.65	< 0.05
Restored with	Restored without	0.87	0.13	0.68

Table B2. Indicator species associated with three of our site types. Indicator values represent the strength of the relationship between the species abundances and the site type; values closer to 1 signal stronger associations. An asterisk denotes an exotic species.

Site type	**Species**	**Indicator value**	***P*-value**
Unrestored sites with tree ferns	*Tmesipteris elongata*	1.00	< 0.01
	Tmesipteris lanceolata	0.92	< 0.01
	Trichomanes venosum	0.96	< 0.01
	Blechnum minus	0.93	< 0.01
	Rumohra adiantiformis	0.87	< 0.05
	Dicksonia squarrosa	0.89	< 0.01
	Hymenophyllum flabellatum	0.87	< 0.05
	**Myosotis sylvatica*	0.87	< 0.05
Restored sites with tree ferns	*Blechnum parrisiae*	0.87	< 0.05
	Cyathea medullaris	0.87	< 0.05
Restored sites without tree ferns	*Pittosporum eugenioides*	0.97	< 0.01
	Pittosporum tenuifolium	0.80	< 0.05

Table B3. Scientific names associated with the six-letter species codes presented in the trees and tree fern basal area facet plot (see Figure 5). Common and family names are also provided.

Status	**Six-letter code**	**Scientific name**	**Common name**	**Family**
Exotic	ACENEG	*Acer negundo*	Box elder	Sapindaceae

	ALNGLU	*Alnus glutinosa*	Alder	Betulaceae
	FATJAP	*Fatsia japonica*	Fatsia	Araliaceae
	JUGAIL	*Juglans ailantifolia*	Japanese walnut	Juglandaceae
	LIGLUC	*Ligustrum lucidum*	Tree privet	Oleaceae
	LIGSIN	*Ligustrum sinense*	Chinese privet	Oleaceae
	PRUSER	*Prunus serrulata*	Japanese cherry	Rosaceae
	SALCIN	*Salix cinerea*	Grey willow	Salicaceae
	SALXFRA	*Salix ×fragilis*	Crack willow	Salicaceae
	SOLMAU	*Solanum mauritianum*	Woolly nightshade	Solanaceae
	ALEEXC	*Alectryon excelsus*	Tītoki	Sapindaceae
	COPROB	*Coprosma robusta*	Karamū	Rubiaceae
	COPTEN	*Coprosma tenuicaulis*	Hukihuki	Rubiaceae
	CORAUS	*Cordyline australis*	Tī kōuka	Asparagaceae
	CORLAE	*Corynocarpus laevigatus*	Karaka	Corynocarpaceae
	CYADEA	*Cyathea dealbata*	Ponga	Cyatheaceae
	CYAMED	*Cyathea medullaris*	Mamaku	Cyatheaceae
	DACCUP	*Dacrydium cupressinum*	Rimu	Podocarpaceae
	DACDAC	*Dacrycarpus dacrydioides*	Kahikatea	Podocarpaceae
	DICFIB	*Dicksonia fibrosa*	Whekī-ponga	Dicksoniaceae
	DICSQU	*Dicksonia squarrosa*	Whekī	Dicksoniaceae
	FUCEXC	*Fuchsia excorticata*	Kōtukutuku	Onagraceae
	GENLIG	*Geniostoma ligustrifolium*	Hangehange	Loganiaceae
	HOHPOP	*Hoheria populnea*	Houhere	Malvaceae
	HOHSEX	*Hoheria sextylosa*	Houhere	Malvaceae
	KNIEXC	*Knightia excelsa*	Rewarewa	Proteaceae
	KUNERI	*Kunzea ericoides*	Kānuka	Myrtaceae
Native	LAUNOV	*Laurelia novae-zelandiae*	Pukatea	Atherospermataceae
	MELRAM	*Melicytus ramiflorus*	Māhoe	Violaceae
	METEXC	*Metrosideros excelsa*	Pōhutukawa	Myrtaceae
	METROB	*Metrosideros robusta*	Northern rātā	Myrtaceae
	MYRAUS	*Myrsine australis*	Red mapou	Primulaceae
	NESCUN	*Nestegis cunninghamii*	Black maire	Oleaceae
	PIPEXC	*Piper excelsum*	Kawakawa	Piperaceae
	PITCRA	*Pittosporum crassifolium*	Karo	Pittosporaceae
	PITEUG	*Pittosporum eugenioides*	Tarata	Pittosporaceae
	PITTEN	*Pittosporum tenuifolium*	Kōhūhū	Pittosporaceae
	PODTOT	*Podocarpus totara*	Tōtara	Podocarpaceae
	PRUFER	*Prumnopitys ferruginea*	Miro	Podocarpaceae
	PRUTAX	*Prumnopitys taxifolia*	Matai	Podocarpaceae
	PSEARB	*Pseudopanax arboreus*	Whauwhaupaku	Araliaceae
	SCHDIG	*Schefflera digitata*	Patē	Araliaceae
	SOPMIC	*Sophora microphylla*	Kōwhai	Fabaceae
	VITLUC	*Vitex lucens*	Pūriri	Lamiaceae

Table S1. Site age and history of the sixteen vegetation plots. Restoration age refers to the time since native plantings began at a site (unpublished Hamilton City Council restoration database; Mackay et al. 2011). Maximum age is based on tree cores of the largest tree in each plot. Site history information is from Downs et al. (2000).

Study group	Plot	Restoration age	Maximum age	Site history/management
Restored with tree ferns	AJ Seeley Gully	52	35	*Dacrycarpus dacrydioides* forest planted > 50 years ago. *Cyathea dealbata* and *C. medullaris* were prominent in the understory.
	Minogue Park	33	9	Surrounded by *Dacrycarpus dacrydioides* forest planted 33 years ago and dominated by *Hoheria populnea* with some *Cyathea medullaris*.
	Pukete Farm Park	15	15	Adjacent to an *Agathis australis* grove planted approximately 15 years ago. Canopy of *Kunzea ericoides* with *Cyathea medullaris* and *C. dealbata* in the understory.
	North Pukete	21	21	Riverside vegetation supporting *Melicytus ramiflorus, Cyathea medullaris* and *C. dealbata*. Plantings took place approximately 20 years ago.
Restored without tree ferns	Brymer Park	23	16	Canopy of native pioneer trees, such as *Pittosporum eugenioides* and *Melicytus ramiflorus*.
	Hamilton Lake	21	13	*Podocarpus totara* forest was planted approximately 21 years ago. Some understory species were planted, but many are naturally regenerating.
	Tauhara Park	25	24	A stand of *Pittosporum eugenioides* planted 25 years ago, with native understory species.
	Till's Landing	18	18	*Pittosporum eugenioides* forest with *Melicytus ramiflorus* and *Pseudopanax arboreus.*
Unrestored with tree ferns	Chelmsford Park	NA	9	A canopy of the exotic tree *Salix cinerea* with occasional *Prunus serrulata*. *Dicksonia squarrosa* was prominent in the understory.
	Mangaiti Gully	NA	11	A stand of *Dicksonia squarrosa* with scarce native trees. *Carex geminata* was also prominent in the damp semi-swamp areas.
	River Road Gully	NA	15	*Salix cinerea* forest with *Dicksonia squarrosa* and occasional *Fuchsia excorticata*.
	Mangaonua Gully	NA	6	Edge of a *Dicksonia squarrosa* stand with occasional *Schefflera digitata* and *Coprosma robusta*.
Unrestored without tree ferns	Hukanui Gully	NA	12	*Salix cinerea* forest with other prominent exotic trees such as *Ligustrum sinense* and *L. lucidum.*
	Donny Park	NA	13	Exotic canopy of *Alnus glutinosa* and *Salix ×fragilis* with low native species richness.
	Porritt Stadium	NA	17	An exotic canopy of *Juglans ailantifolia* and *Salix cinerea*. *Tradescantia fluminensis* formed dense ground cover, preventing tree regeneration.
	Sandford Park	NA	7	Exotic canopy of trees such as *Salix ×fragilis* and *Prunus serrulata*. Groundcover was mainly *Tradescantia fluminensis* and *Hedera helix*.

Downs TM, Clarkson BD, Beard CM. 2000. Key Ecological Sites of Hamilton City, CBER Contract Report No. 5., Hamilton, Centre for Biodiversity and Ecology Research (University of Waikato).

Table S2. Pairwise comparisons of native vascular plant communities among the four site types using permutational multivariate analysis of variance (PERMANOVA) with restoration age (i.e., years since native plantings started) as a covariate. Data were Hellinger-transformed.

Group 1	Group 2	*F*-value	R^2	*P*-value
Unrestored without	Restored with	2.47	0.50	< 0.05
Unrestored without	Restored without	2.96	0.54	< 0.05
Unrestored with	Restored with	2.85	0.53	< 0.05
Unrestored with	Unrestored without	4.86	0.45	< 0.05
Unrestored with	Restored without	5.53	0.69	< 0.01
Restored with	Restored without	1.37	0.35	0.15

Table S3. Three leading dominant trees or tree ferns for each site type based on the average basal area presented with the standard deviation. An asterisk denotes an exotic species.

Group	Species	Life form	Average basal area (m^2 ha^{-1})
Unrestored sites with tree ferns	*Dicksonia squarrosa*	Tree fern	20.28±11.20
	**Salix cinerea*	Tree	0.79±1.00
	Dicksonia fibrosa	Tree fern	0.73±1.50
Unrestored sites without tree ferns	**Salix cinerea*	Tree	1.93±2.70
	**Alnus glutinosa*	Tree	1.10±2.19
	**Salix ×fragilis*	Tree	1.07±1.86
Restored sites with tree ferns	*Cyathea dealbata*	Tree fern	5.38±0.60
	Kunzea ericoides	Tree	2.90±3.60
	Melicytus ramiflorus	Tree	2.06±1.50
Restored sites without tree ferns	*Pittosporum eugenioides*	Tree	5.30±5.43
	Kunzea ericoides	Tree	3.13±4.63
	Melicytus ramiflorus	Tree	3.00±2.01

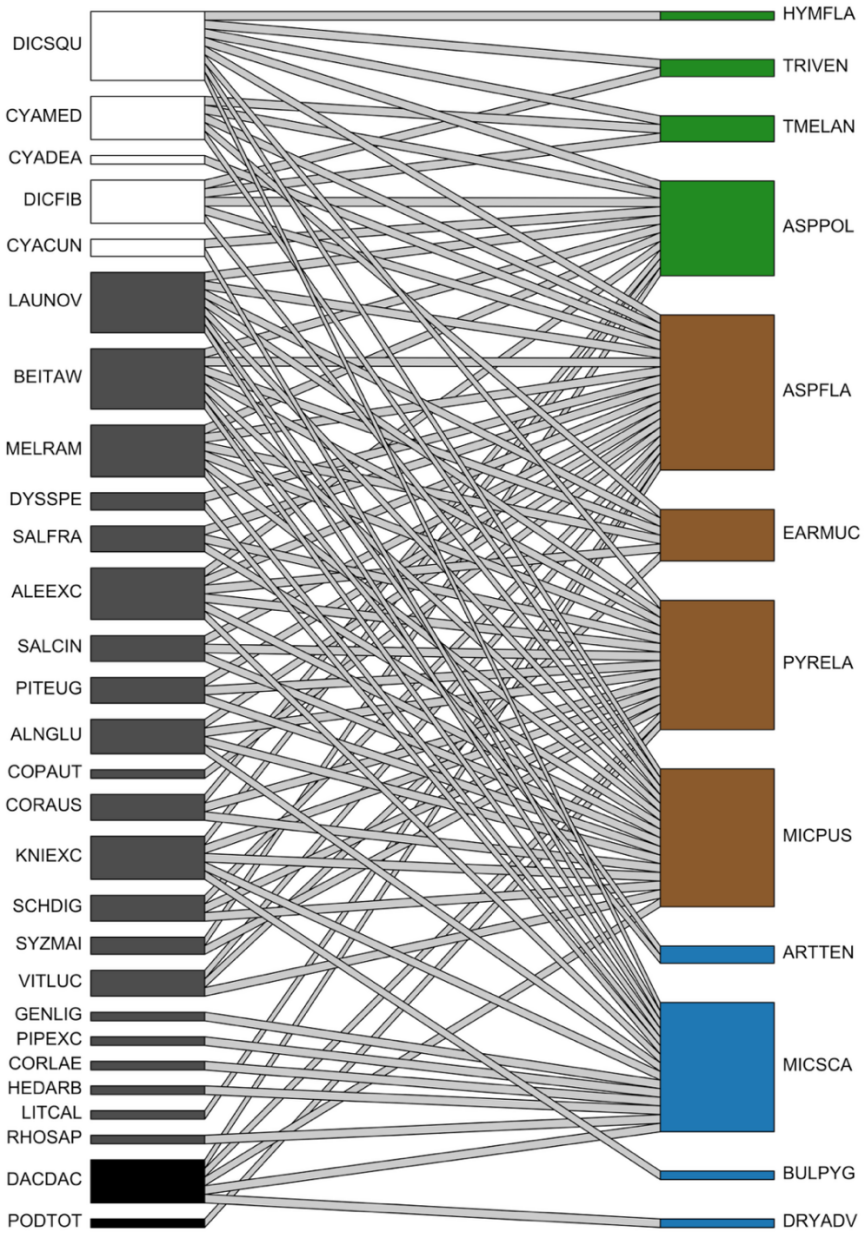


Fig. S1. Urban epiphyte-host network using binary presence/absence data from the 32 urban sites. The bipartite plot illustrates the strength of relationships. Full network analysis results using null model analysis are provided in Table S3.

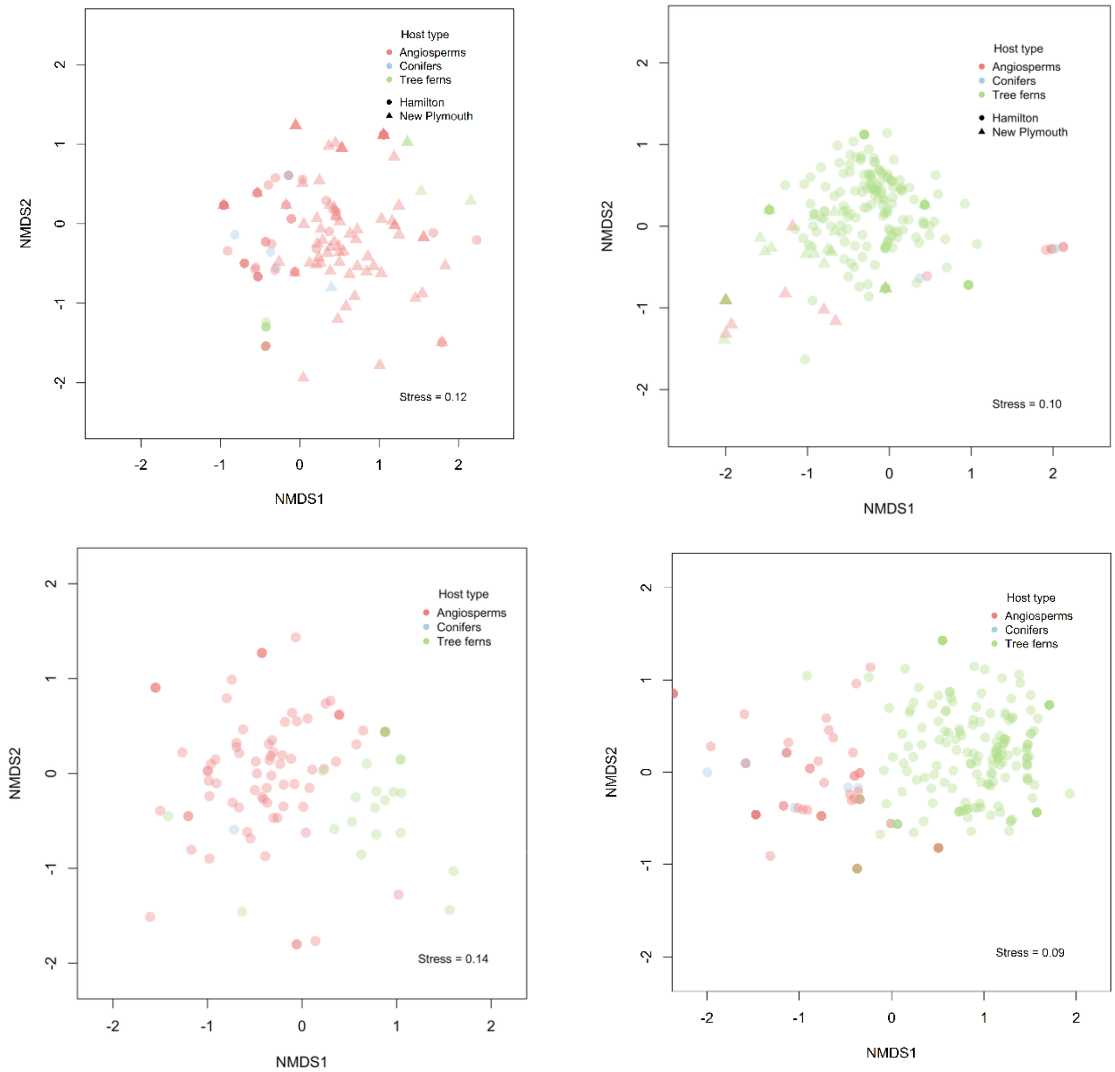


Fig. S2. Compositional differences of epiphyte assemblages on individual hosts using non-metric multidimensional scaling (NMDS). The top two plots are the full dataset split into data from Bryan (2011) on the left and the present study on the right. Triangles denote hosts measured in New Plymouth, and circles represent hosts measured in Hamilton. Colours represent the three host types: tree ferns (green), angiosperm trees (pink), and conifer trees (blue). Stress scores were *fair* for both the Bryan (2011) ordination (0.12) and the present study (0.10). The bottom two plots show the full dataset split by the two cities: New Plymouth (left) and Hamilton (right). Stress scores were *fair* for New Plymouth (0.09) and Hamilton (0.14).

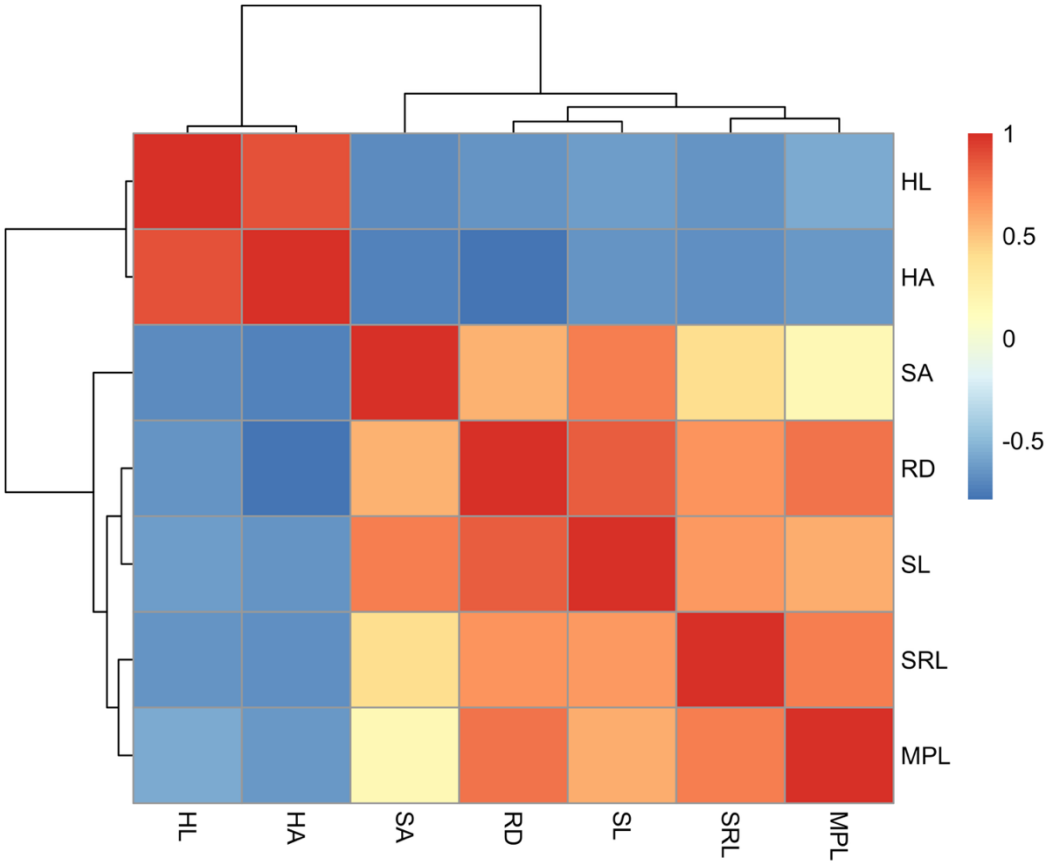


Fig. S3. Epiphyte root and rhizome trait correlation heat map. Codes denote traits: hair length (HL), hair abundance (HA), scale abundance (SA), rhizome diameter (RD), scale length (SL), standard root length (SRL) and maximum plant length (MPL). SRL, HL, HA and RD were log-transformed, and all traits were standardised (i.e., centred on the mean and scaled to unit variance).

Table S1. Site information for the 32 sites assessed in Hamilton and New Plymouth. The city, site, restoration age (i.e., the time since plantings began), native obligate epiphyte richness and abundance, and host richness and abundance are provided per site. Hamilton site restoration ages were sourced from an unpublished Hamilton City Council (HCC) database, and New Plymouth site ages were from Bryan (2011). Sites with a restoration age of 0 have not been actively restored.

City	Site	Restoration age	Obligate epiphyte richness	Obligate epiphyte abundance	Host richness	Host abundance
Hamilton	AJ Seeley	52	5	31	6	5
Hamilton	Ashmore Court	25-100	1	1	1	1
Hamilton	Berkley	100+	1	4	1	5
Hamilton	Braithwaite	25-100	1	4	1	4
Hamilton	Chelmsford	0	8	331	5	34

Hamilton	Claudelands	100+	6	51	7	10
Hamilton	Hammond	100+	9	41	5	19
Hamilton	Hillcrest	100+	2	3	1	5
Hamilton	Hudson	15-25	2	2	1	1
Hamilton	Hukanui	0	3	22	1	1
Hamilton	Mangaiti	13	9	762	2	41
Hamilton	Mangakotukutuku	May-15	3	7	1	4
Hamilton	Mangaonua	0	7	31	2	5
Hamilton	Mooney	100+	1	3	1	3
Hamilton	North Pukete	0	3	67	4	4
Hamilton	Onukutara	May-15	2	4	1	3
Hamilton	Pukete East	25-100	4	28	3	5
Hamilton	Pukete Farm	15	2	7	2	1
Hamilton	Ranfurly	15-25	1	1	1	1
Hamilton	River Rd	0	9	1,793	2	47
Hamilton	Sandford	0	3	7	2	1
Hamilton	St Andrews	15-25	1	1	1	1
Hamilton	Tauhara	25	1	1	1	1
Hamilton	Tauhara River	25-100	4	12	5	5
New Plymouth	Budley	100+	10	38	5	5
New Plymouth	Huatoki	50-100	14	89	4	5
New Plymouth	Huatoki North	50-100	7	305	4	5
New Plymouth	Huatoki South	50-100	8	173	5	6
New Plymouth	Pukekura North	25-100	3	156	6	12
New Plymouth	Pukekura South	25-100	11	173	8	6
New Plymouth	Ratapihipihi	100+	17	175	11	11
New Plymouth	Te Henui	15-100	10	18	2	5
Total			**28**	**4341**	**31**	**262**

Table S2. Mantel Test results for each dataset and separately for each city within the datasets using 999 permutations. Epiphyte community dissimilarity was calculated using the Bray-Curtis index, and geographic distance was based on site coordinates.

Data	**Mantel statistic r**	**P-value**
Present study	0.021	0.332
Bryan (2011)	0.101	0.154
Present study, Hamilton	0.040	0.290
Present study, New Plymouth	-0.258	0.542
Bryan (2011), Hamilton	0.071	0.348
Bryan (2011), New Plymouth	0.024	0.417

Table S3. Epiphyte species allocated to the three groups (i.e., generalist epiphytes and epiphytes with preferences for tree ferns or woody hosts). The twelve epiphyte species were from six families and consisted of nine ferns and three orchids.

Group	Species	Family	Class
Tree ferns	*Asplenium polyodon*	Aspleniaceae	Fern
	Hymenophyllum flabellatum	Hymenophyllaceae	Fern
	Tmesipteris lanceolata	Psilotaceae	Fern
	Trichomanes venosum	Hymenophyllaceae	Fern
Generalists	*Asplenium flaccidum*	Aspleniaceae	Fern
	Earina mucronata	Orchidaceae	Orchid
	Lecanopteris pustulata	Polypodiaceae	Fern
	Pyrrosia elaeagnifolia	Polypodiaceae	Fern
Woody hosts	*Arthropteris tenella*	Tectariaceae	Fern
	Bulbophyllum pygmaeum	Orchidaceae	Orchid
	Drymoanthus adversus	Orchidaceae	Orchid
	Lecanopteris scandens	Polypodiaceae	Fern

Table S4. Null model results (using 'Econullnetr' R package) testing the strength of epiphyte-host relationships using presence/absence data of epiphyte records on host species at the site level (n = 32). One hundred null models compared the observed with the expected number of interactions to determine whether each relationship was weaker or stronger than expected. Statistically significant interactions involving the 12 study species are presented. A lower and upper 95% confidence interval and standard effect sizes (SES) are presented for each interaction.

Epiphyte species	Host species	Observed	Null	Lower 95 CI	Upper 95 CI	Test	SES
Arthropteris tenella	*Laurelia novae-zelandiae*	3	1.1	0.0	2.0	Stronger	2.57
Asplenium flaccidum	*Cyathea medullaris*	1	2.8	1.2	3.8	Weaker	-2.28
Asplenium flaccidum	*Dicksonia fibrosa*	4	2.3	2.0	3.0	Stronger	3.52
Asplenium flaccidum	*Dicksonia squarrosa*	12	8.9	7.2	10.8	Stronger	2.59
Asplenium flaccidum	*Knightia excelsa*	0	1.3	1.0	2.0	Weaker	-2.69
Asplenium flaccidum	*Salix × fragilis*	1	2.0	2.0	2.0	Weaker	NA
Asplenium flaccidum	*Salix cinerea*	2	1.1	1.0	1.8	Stronger	2.85
Asplenium polyodon	*Cyathea medullaris*	0	1.3	1.0	2.0	Weaker	-2.69
Asplenium polyodon	*Dicksonia squarrosa*	11	7.2	6.0	8.8	Stronger	3.68
Asplenium polyodon	*Salix × fragilis*	0	1.0	1.0	1.0	Weaker	NA
Bulbophyllum pygmaeum	*Knightia excelsa*	2	0.3	0.0	1.8	Stronger	2.52
Earina mucronata	*Dacrycarpus dacrydioides*	0	1.5	1.0	2.0	Weaker	-2.85
Earina mucronata	*Knightia excelsa*	0	1.1	0.2	2.0	Weaker	-1.94
Earina mucronata	*Laurelia novae-zelandiae*	6	4.4	4.0	5.8	Stronger	2.29
Hymenophyllum flabellatum	*Dicksonia squarrosa*	5	3.2	2.0	4.0	Stronger	2.28
Lecanopteris pustulata	*Dicksonia fibrosa*	3	1.8	1.0	2.8	Stronger	1.90

Lecanopteris pustulata	*Melicytus ramiflorus*	5	2.5	1.0	4.0	Stronger	1.97
Lecanopteris pustulata	*Salix cinerea*	2	0.6	0.0	1.0	Stronger	2.71
Lecanopteris scandens	*Alectryon excelsus*	4	2.8	1.5	3.0	Stronger	1.90
Lecanopteris scandens	*Coprosma autumnalis*	0	2.1	1.2	3.0	Weaker	-3.70
Lecanopteris scandens	*Dacrycarpus dacrydioides*	1	1.9	1.2	2.0	Weaker	-2.85
Lecanopteris scandens	*Dicksonia squarrosa*	5	3.8	3.0	4.0	Stronger	2.85
Lecanopteris scandens	*Melicytus ramiflorus*	5	3.1	2.0	4.8	Stronger	2.17
Lecanopteris scandens	*Salix × fragilis*	0	1.0	1.0	1.0	Weaker	NA
Lecanopteris scandens	*Vitex lucens*	0	1.4	0.2	2.0	Weaker	-2.00
Pyrrosia elaeagnifolia	*Alectryon excelsus*	6	3.1	2.0	4.0	Stronger	3.31
Pyrrosia elaeagnifolia	*Laurelia novae-zelandiae*	7	5.9	5.0	6.8	Stronger	1.94
Pyrrosia elaeagnifolia	*Salix cinerea*	2	0.6	0.0	1.0	Stronger	2.71
Tmesipteris lanceolata	*Cyathea medullaris*	4	1.2	0.0	3.0	Stronger	2.47
Tmesipteris lanceolata	*Dicksonia squarrosa*	11	8.1	7.0	9.0	Stronger	3.31
Trichomanes venosum	*Dicksonia squarrosa*	12	8.0	7.0	9.8	Stronger	4.24
Trichomanes venosum	*Salix × fragilis*	0	1.0	1.0	1.0	Weaker	NA

Table S5. Indicator species of three host types (tree ferns, angiosperm trees and conifer trees). Indicator values denote the strength of the relationship between the epiphyte species and the group; higher values signal stronger relationships. Data were from the present study and Bryan (2011).

Group	**Species**	**Indicator value**	***P* value**
Tree ferns	*Hymenophyllum flabellatum*	0.210	<0.05
	Rumohra adiantiformis	0.289	<0.05
	Tmesipteris elongata	0.701	<0.01
	Tmesipteris lanceolata	0.549	<0.01
	Trichomanes venosum	0.776	<0.01
Angiosperm trees	*Astelia hastata*	0.499	<0.01
	Earina mucronata	0.368	<0.05
Angiosperm trees & conifer trees	*Pyrrosia elaeagnifolia*	0.802	< 0.01
	Lecanopteris scandens	0.533	< 0.01
	Astelia solandri	0.316	< 0.05
	Griselinia lucida	0.261	< 0.05
	Hymenophyllum sanguinolentum	0.254	< 0.05
Conifer trees & tree ferns	*Asplenium flaccidum*	0.581	<0.01

Table S6. Scientific names associated with the six-letter codes presented on Fig. 4. The number of iNaturalist NZ epiphyte observations (November 2025) for each species is also provided.

Group	**Six-letter code**	**Scientific name**	**No. of observations**
Epiphyte species	ASPPOL	*Asplenium polyodon*	177

	TMELAN	*Tmesipteris lanceolata*	158
	TRIVEN	*Trichomanes venosum*	150
	HYMFLA	*Hymenophyllum flabellatum*	91
	ASPFLA	*Asplenium flaccidum*	311
	MICPUS	*Lecanopteris pustulata*	287
	PYRELA	*Pyrrosia elaeagnifolia*	369
	EARMUC	*Earina mucronata*	223
	DRYADV	*Drymoanthus adversus*	180
	BULPYG	*Bulbophyllum pygmaeum*	126
	ARTTEN	*Arthropteris tenella*	35
	MICSCA	*Lecanopteris scandens*	78
Host species	DICSQU	*Dicksonia squarrosa*	643
	CYAMED	*Cyathea medullaris*	118
	CYADEA	*Cyathea dealbata*	85
	DICFIB	*Dicksonia fibrosa*	20
	MELRAM	*Melicytus ramiflorus*	145
	PHOCAN	*Phoenix canariensis*	119
	KNIEXC	*Knightia excelsa*	95
	SALCIN	*Salix cinerea*	88
	BEITAW	*Beilschmiedia tawa*	57
	METEXC	*Metrosideros excelsa*	53
	PTERAC	*Pterophylla racemosa*	46
	SALFRA	*Salix fragilis*	46
	PITEUG	*Pittosporum eugenioides*	41
	CORAUS	*Cordyline australis*	39
	RHOSAP	*Rhopalostylis sapida*	38
	DIDSPE	*Didymocheton spectabilis*	36
	ALEEXC	*Alectryon excelsus*	33
	KUNERI	*Kunzea ericoides*	33
	VITLUC	*Vitex lucens*	33
	QUEROB	*Quercus robur*	27
	BEITAR	*Beilschmiedia taraire*	20
	LAUNOV	*Laurelia novae-zelandiae*	20
	MAGCAM	*Magnolia campbellii*	18
	GRILIT	*Grisiliena littoralis*	16
	FUCEXC	*Fuchsia excorticata*	14
	MYRAUS	*Myrsine australis*	14
	LITCAL	*Litsea calicaris*	12
	SOPMIC	*Sophora microphylla*	12
	HEDARB	*Hedycarya arborea*	11
	LEUFAS	*Leucopogon fasciculatus*	11
	ACAMEL	*Acacia melanoxylon*	10
	PODTOT	*Podocarpus totara*	68
	DACDAC	*Dacrycarpus dacrydioides*	50
	PODLAE	*Podocarpus laetus*	31
	AGAAUS	*Agathis australis*	26
	DACCUP	*Dacrydium cupressinum*	23
	PHYTRI	*Phyllocladus trichomanoides*	20
	PINRAD	*Pinus radiata*	14

Table S7. Linear mixed effects model results testing the effect of host category on rhizome diameter, standard root length (SRL), scale abundance and scale length. Response variables were log-transformed and standardised (i.e., centred on the mean and scaled to unit variance). The models accounted for plant size (maximum plant length) and epiphyte species as fixed effects. Plant identity was accounted for as a random effect.

Model (response)	Predictors	Estimates	CI	P-value
Rhizome diameter	(Intercept)	-0.13	-0.26 – 0.00	0.054
	Host category [tree ferns]	-1.09	-1.21 – -0.97	**<0.001**
	Host category [woody trees]	0.20	0.09 – 0.31	**<0.001**
	Maximum plant length	0.28	0.20 – 0.36	**<0.001**
	Epiphyte [ASPFLA]	1.12	0.94 – 1.31	**<0.001**
	Epiphyte [ASPPOL]	1.97	1.73 – 2.21	**<0.001**
	Epiphyte [EARMUC]	-0.15	-0.35 – 0.06	0.172
	Epiphyte [HYMFLA]	0.28	0.16 – 0.41	**<0.001**
	Epiphyte [LECPUS]	1.28	1.14 – 1.42	**<0.001**
	Epiphyte [LECSCA]	-0.13	-0.23 – -0.02	**<0.05**
	Epiphyte [TMELAN]	0.88	0.74 – 1.02	**<0.001**
SRL	(Intercept)	0.31	-0.01 – 0.63	0.058
	Host category [tree ferns]	-0.44	-1.06 – 0.18	0.162
	Host category [woody trees]	-0.65	-0.99 – -0.31	**<0.001**
	Maximum plant length	0.67	0.47 – 0.86	**<0.001**
	Epiphyte [ASPPOL]	0.09	-0.51 – 0.68	0.774
	Epiphyte [EARMUC]	-0.28	-0.59 – 0.03	0.072
	Epiphyte [HYMFLA]	-0.34	-0.64 – -0.04	**<0.05**
	Epiphyte [LECPUS]	0.06	-0.24 – 0.37	0.681
	Epiphyte [PYRELA]	-0.06	-0.52 – 0.40	0.812
Scale abundance	(Intercept)	1.28	0.84 – 1.71	**<0.001**
	Host category [tree ferns]	-1.82	-2.58 – -1.07	**<0.001**
	Host category [woody trees]	-1.01	-1.48 – -0.55	**<0.001**
	Maximum plant length	0.40	0.04 – 0.75	**<0.05**
	Epiphyte [ASPFLA]	-1.60	-2.40 – -0.80	**<0.001**
	Epiphyte [LECPUS]	-1.54	-2.13 – -0.94	**<0.001**
	Epiphyte [LECSCA]	1.15	-1.59 – -0.71	**<0.001**
Scale length	(Intercept)	-0.12	-0.54 – 0.30	0.564
	Host category [tree ferns]	0.06	-0.61 – 0.74	0.852
	Host category [woody trees]	-0.82	-1.22 – -0.41	**<0.001**
	Maximum plant length	0.29	-0.03 – 0.61	0.074
	Epiphyte [ASPFLA]	0.85	0.13 – 1.57	**<0.05**
	Epiphyte [LECPUS]	0.34	-0.18 – 0.86	0.195
	Epiphyte [LECSCA]	0.47	0.09 – 0.84	**<0.05**

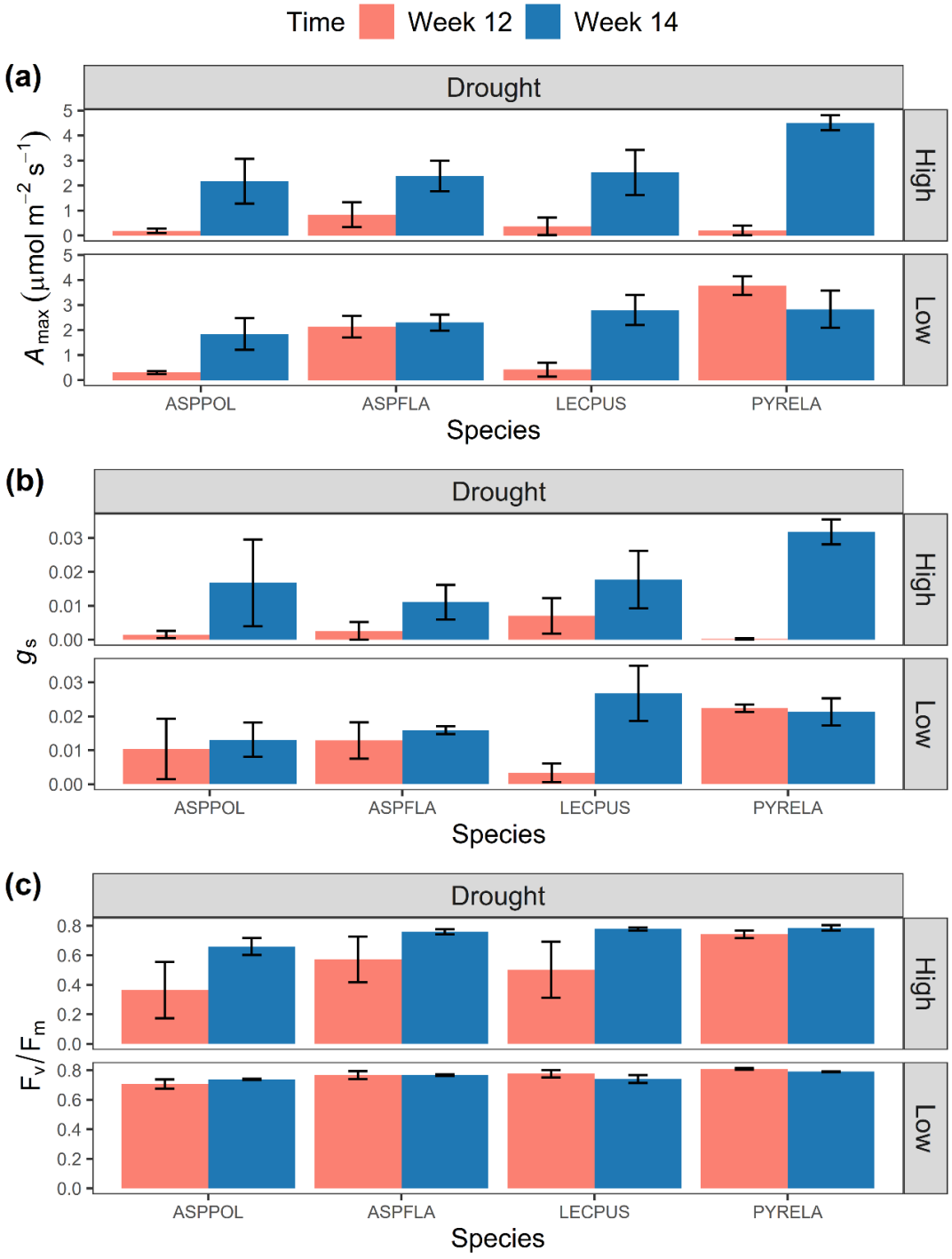


Fig. S1. Mean ± SE (n = 3) of A_{max} (a), g_s (b) and F_v/F_m (c) of each epiphytic ferns during the recovery phase (Week 12-14) when plants that were in the drought treatments were rewatered.

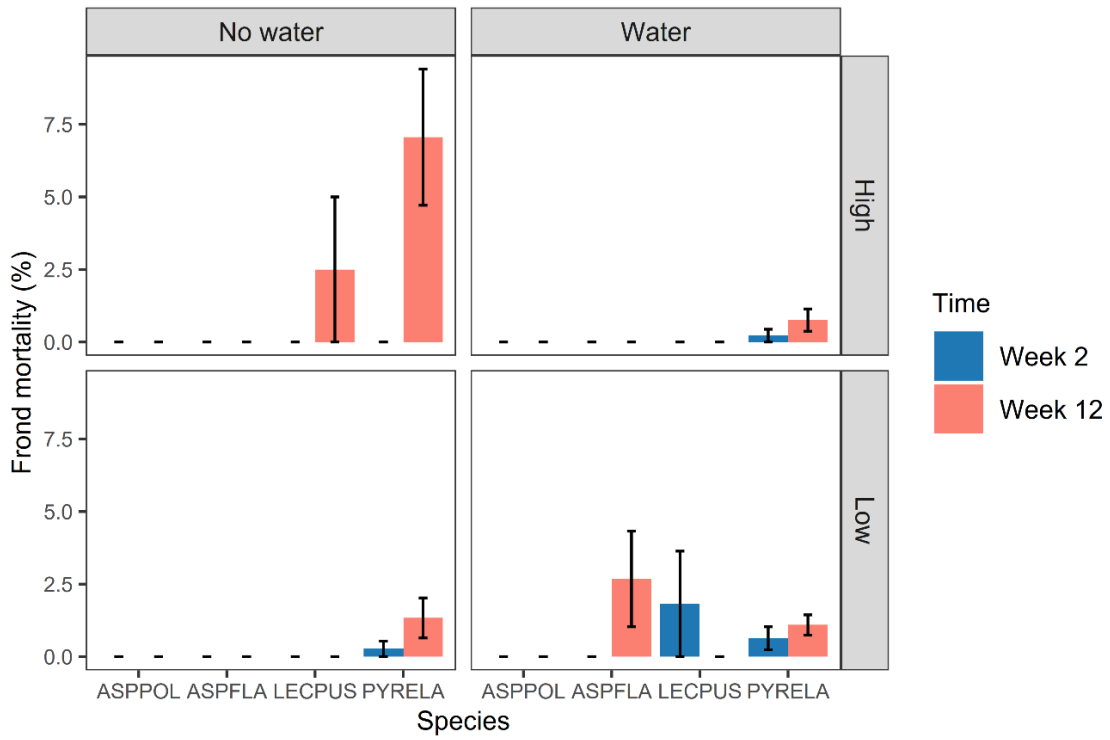


Fig. S2. Mean frond mortality ± SE (n = 5) of the four epiphytic ferns in each treatment group at Week 2 (blue bars) and Week 12 (pink bars) of the simulated drought. ASPPOL: *Asplenium polyodon* (specialist), ASPFLA: *Asplenium flaccidum* (specialist), LECPUS: *Lecanopteris pustulata* (generalist), and PYRELA: *Pyrrosia elaeagnifolia* (generalist).

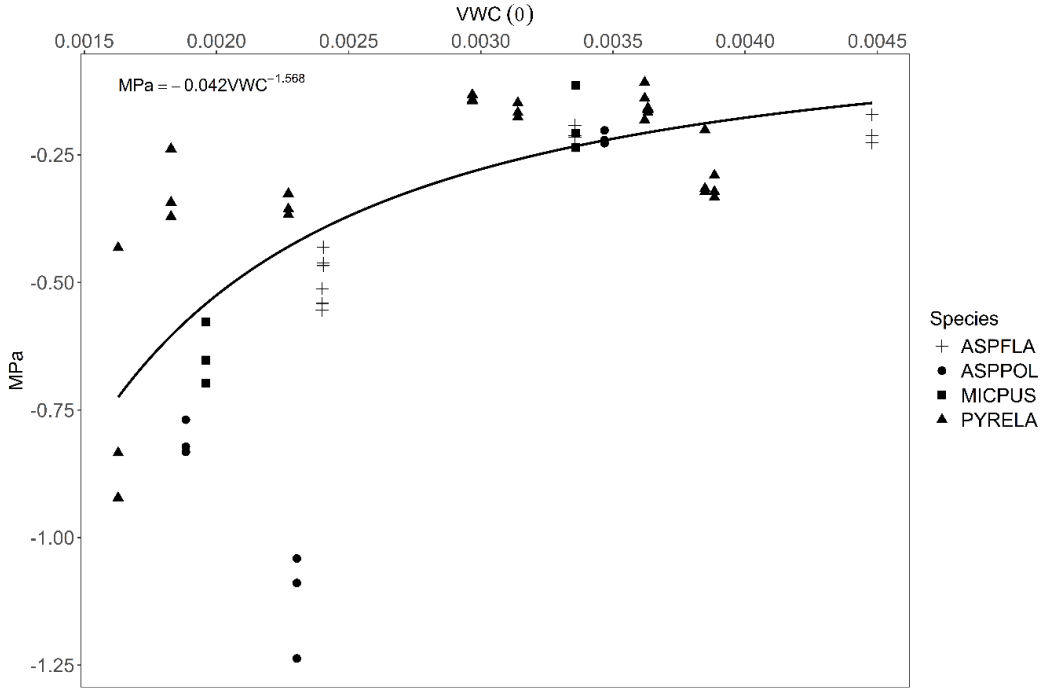


Fig. S3. Volumetric soil moisture against predawn frond water potential (ψ_{wpd}) for plants not included in the drought experiment. Symbols represent the species: ASPFLA: *Asplenium*

flaccidum (cross), ASPPOL: *Asplenium polyodon* (circle), LECPUS: *Lecanopteris pustulata* (square) and PYRELA: *Pyrrosia elaeagnifolia* (triangle).

Table S1. Pairwise comparisons of species A_{max} between Week 2 and Week 12, and under low or high light. For each contrast, the estimate, standard error, degrees of freedom, *t*-value and *P*-value are provided. Statistically significant *P*-values at the α=0.05 level are in boldface.

Week, Light	Contrast	Estimate	SE	df	*t*	*P*-value
Week 2, low light	ASPFLA–ASPPOL	-1.53	0.60	77	-2.54	0.06
	ASPFLA–LECPUS	-1.80	0.60	77	-2.99	**<0.05**
	ASPFLA–PYRELA	-1.45	0.60	77	-2.41	0.08
	ASPPOL–LECPUS	-0.27	0.60	77	-0.45	0.97
	ASPPOL–PYRELA	0.08	0.60	77	0.14	1.00
	LECPUS–PYRELA	0.35	0.60	77	0.58	0.94
Week 12, low light	ASPFLA–ASPPOL	0.67	0.60	77	1.11	0.68
	ASPFLA–LECPUS	1.13	0.60	77	1.88	0.25
	ASPFLA–PYRELA	-1.88	0.60	77	-3.12	**<0.05**
	ASPPOL–LECPUS	0.46	0.60	77	0.77	0.87
	ASPPOL–PYRELA	-2.55	0.60	77	-4.23	**<0.001**
	LECPUS–PYRELA	-3.01	0.60	77	-5.00	<0.001
Week 2, high light	ASPFLA–ASPPOL	-0.68	0.60	77	-1.13	0.67
	ASPFLA–LECPUS	-2.10	0.60	77	-3.49	**<0.01**
	ASPFLA–PYRELA	-1.96	0.60	77	-3.25	**<0.01**
	ASPPOL–LECPUS	-1.43	0.60	77	-2.37	0.09
	ASPPOL–PYRELA	-1.28	0.60	77	-2.13	0.15
	LECPUS–PYRELA	0.15	0.60	77	0.24	1.00
Week 12, high light	ASPFLA–ASPPOL	-0.08	0.60	77	-0.13	1.00
	ASPFLA–LECPUS	-0.63	0.60	77	-1.04	0.73
	ASPFLA–PYRELA	-0.40	0.60	77	-0.67	0.91
	ASPPOL–LECPUS	-0.55	0.60	77	-0.92	0.80
	ASPPOL–PYRELA	-0.33	0.60	77	-0.54	0.95
	LECPUS–PYRELA	0.23	0.60	77	0.37	0.98

Table S2. Pairwise comparisons of the g_s of plants in the two water treatments and over time (Week 2 versus Week 12). Statistically significant *P*-values are in boldface.

Water treatment, week	Estimate	SE	df	*t*	*P*-value
Drought, Week 2	0.010	0.006	85	1.870	0.065
Drought, Week 12	0.038	-.006	85	6.847	<0.0001

Table S3. Pairwise comparisons of predawn F_v/F_m over time (Week 2 versus Week 12), and between water and light treatments. Statistically significant *P*-values are in boldface.

Week, water treatment, light	Estimate	SE	*z*	*P*-value
Week 2/Week 12, drought, high light	1.135	0.167	6.799	<0.0001
Week 2/Week 12, drought, low light	0.287	0.187	1.531	0.126
Week 2/Week 12, watered, high light	0.051	0.181	0.285	0.776
Week 2/Week 12, watered, low light	0.021	0.184	0.113	0.910

Table S4. Recovery linear mixed effects model results for photosynthetic capacity (A_{max}) and stomatal conductance (g_s), and generalised linear mixed model results for photochemical efficiency (F_v/F_m). Models included only drought-treatment plants (i.e., unwatered). Predictors for each model were species, time (i.e., Week 12 versus Week 14), and light treatments, and significant interactions. F-values (for the LMEs) or χ^2 (for GLMM) and *P*-values are provided for each explanatory variable. Statistically significant *P*-values are in boldface.

Predictor(s)	A_{max} (recovery)		g_s (recovery)		F_v/F_m (recovery)	
	F	*P*-value	*F*	*P*-value	χ^2	*P*-value
Species	8.52	<0.001	1.67	0.20	9.61	<0.05
Time	0.15	0.71	14.61	<0.001	0.04	0.85
Light	2.46	0.13	2.33	0.14	18.44	<0.001
Species × Time	4.61	<0.05			8.97	<0.01
Light × Time	1.39	0.25				
Species × Light	4.37	<0.05				
Species × Time × Light	6.83	<0.01				

Table S5. Analysis of variance (ANOVA) results comparing $\delta^{13}C$, $\delta^{15}N$ and total nitrogen among species and seasons. Statistically significant *P*-values are in boldface.

Response	Predictor	*F*	*P*-value	R^2
$\delta^{13}C$	Species	12.826	<0.0001	0.569
	Season	6.441	<0.05	
$\delta^{15}N$	Species	6.049	<0.01	0.478
	Season	14.204	<0.001	
Total N	Species	1.778	0.194	0.22
	Season	4.031	0.063	

Chapter 5

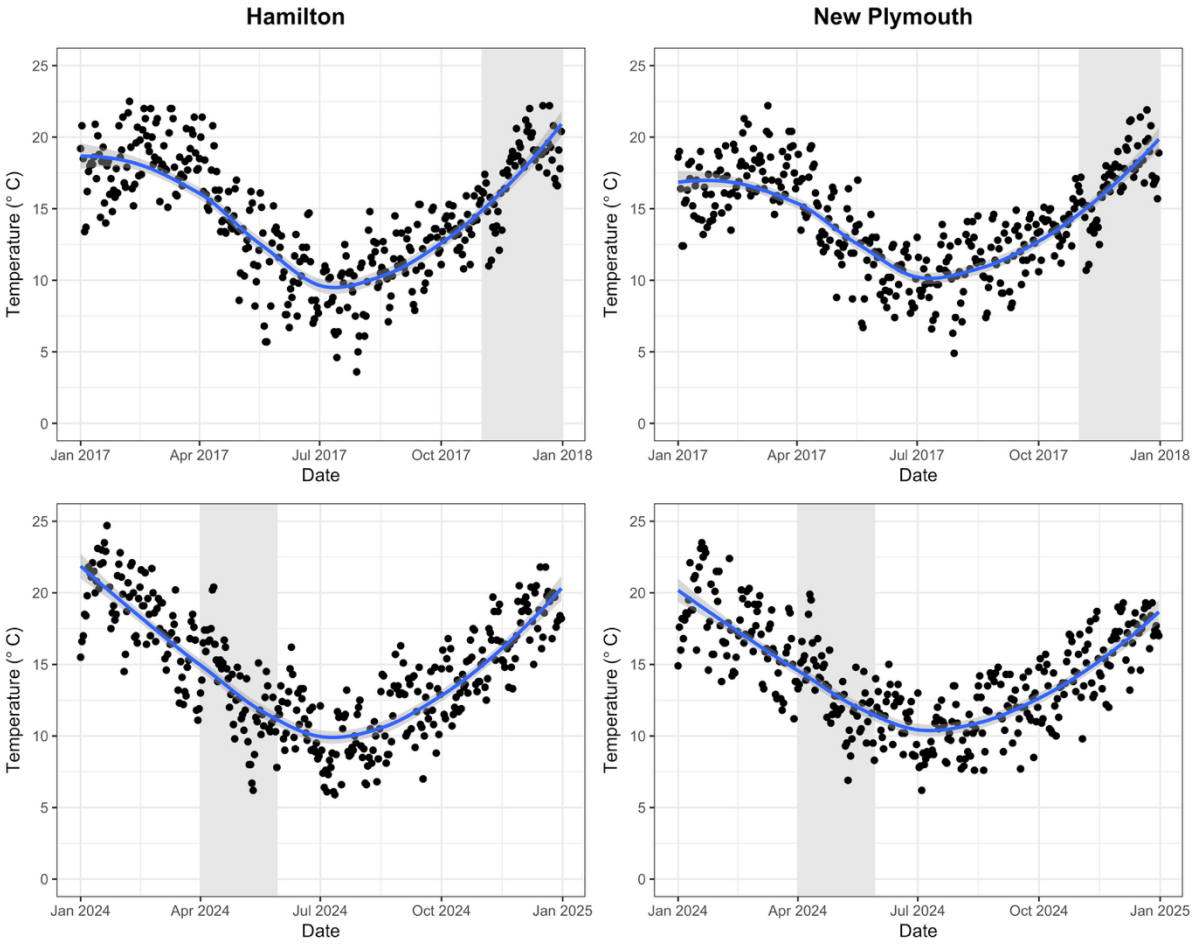


Fig S1. Daily mean temperature recorded at the Ruakura climate station in Hamilton, 2017 (top left) and 2024 (bottom left), and at the airport in New Plymouth, 2017 (top right) and 2024 (bottom right). Data were obtained from the NIWA national climate database. Grey ribbons represent the period the vegetation surveys were conducted.

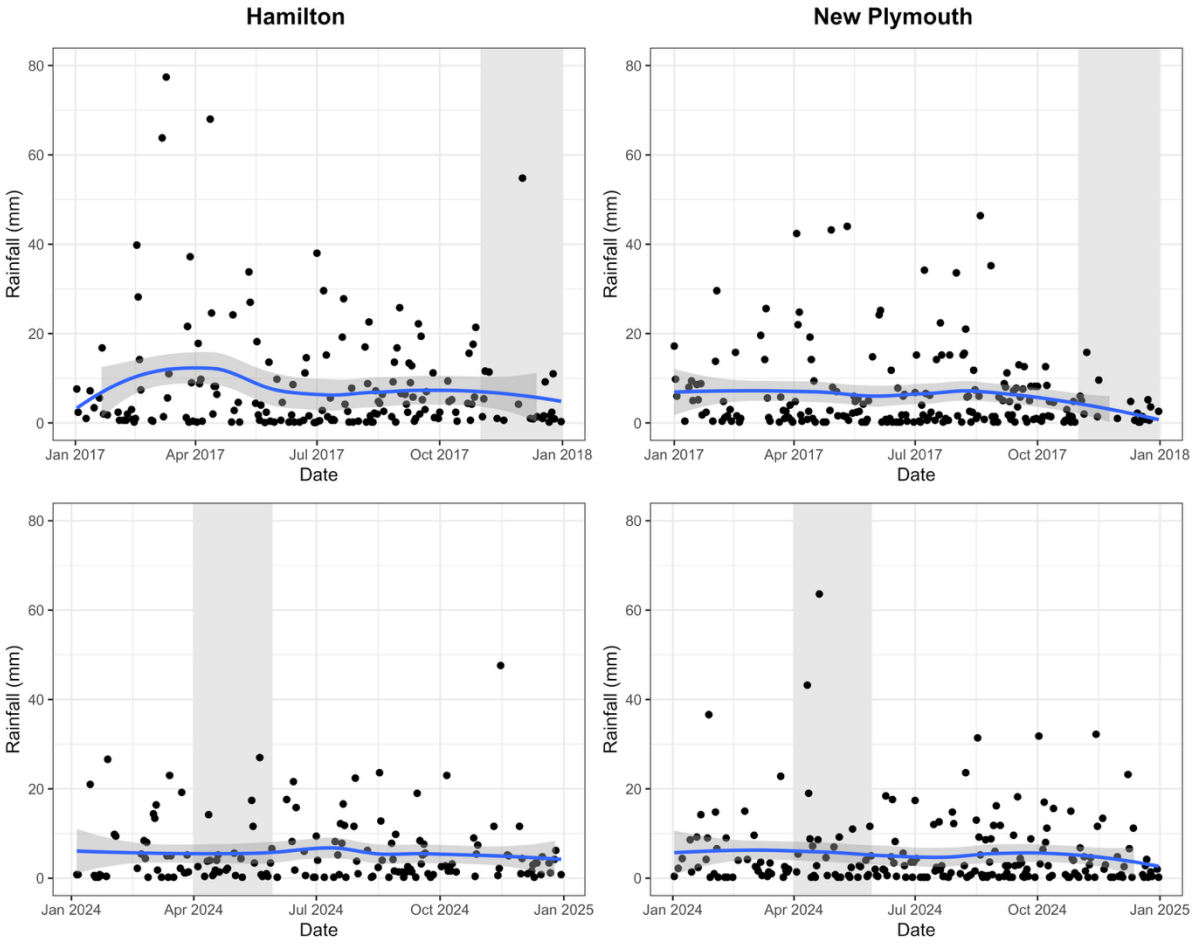


Fig S2. Daily mean rainfall recorded at the Ruakura climate station in Hamilton, 2017 (top left) and 2024 (bottom left), and at the airport climate station in New Plymouth, 2017 (top right) and 2024 (bottom right). Data were obtained from the NIWA national climate database. Grey ribbons represent the period the vegetation surveys were conducted.

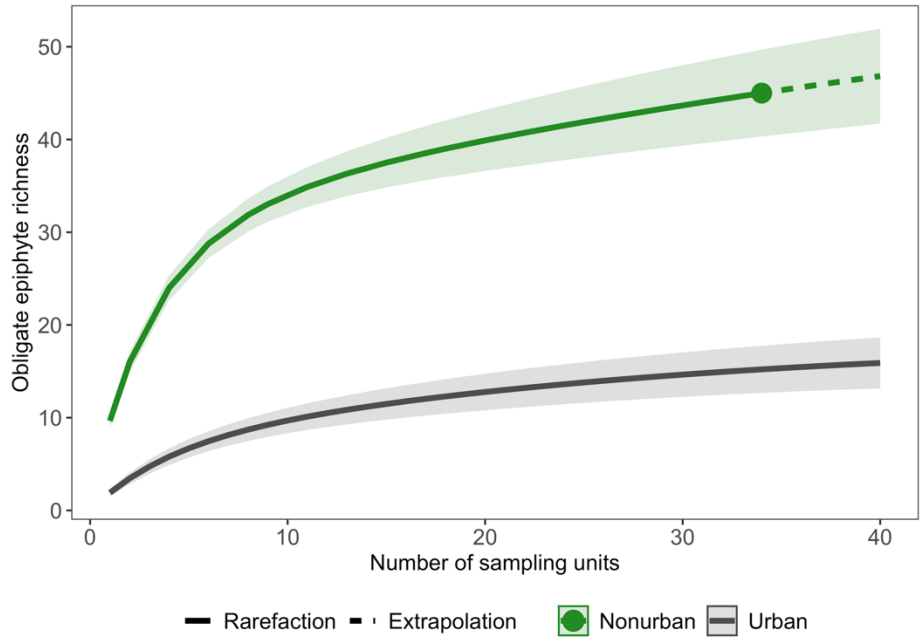


Fig S3. Rarefaction curves illustrating sampling effort for obligate epiphyte species richness with the number of plots for the non-urban dataset (green line) and urban dataset (grey line). The number of plots was extrapolated to n = 40 in the non-urban dataset to enable comparison with the urban dataset.

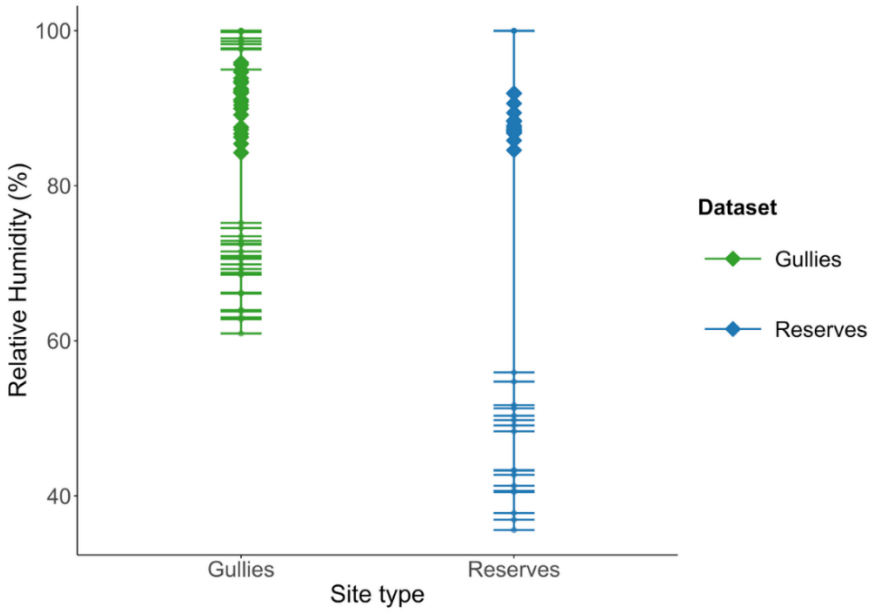


Fig S4. Daily relative humidity data from the gully (green symbols) and reserve (blue symbols) vegetation plots. Mean daily relative humidity values are represented by diamonds, while smaller circles represent minimum or maximum values. The gully sites occurred within topographic depressions with less microclimatic variation, whereas the reserve vegetation plots were on flat, smaller patches of vegetation.

Table S1. List of obligate (i.e., holo-epiphyte) and hemi-epiphyte species used in this study. The list was adapted from Kirby (2016).

Epiphyte species	Life form	Classification
Abrodictyum caudatum	Ferns & fern allies	Obligate
Arthropteris tenella		Obligate
Asplenium flaccidum		Obligate
Asplenium polyodon		Obligate
Davallia tasmanii		Obligate
Hymenophyllum armstrongii		Obligate
Hymenophyllum bivalve		Obligate
Hymenophyllum demissum		Obligate
Hymenophyllum dilatatum		Obligate
Hymenophyllum flabellatum		Obligate
Hymenophyllum flexuosum		Obligate
Hymenophyllum frankliniae		Obligate
Hymenophyllum lyallii		Obligate
Hymenophyllum malingii		Obligate
Hymenophyllum minimum		Obligate
Hymenophyllum multifidum		Obligate
Hymenophyllum nephrophyllum		Obligate
Hymenophyllum peltatum		Obligate
Hymenophyllum pluviatile		Obligate
Hymenophyllum pulcherrimum		Obligate
Hymenophyllum rarum		Obligate
Hymenophyllum revolutum		Obligate
Hymenophyllum rufescens		Obligate
Hymenophyllum sanguinolentum		Obligate
Hymenophyllum scabrum		Obligate
Hymenophyllum villosum		Obligate
Loxogramme dictyopteris		Obligate
Lecanopteris novae-zealandiae		Obligate
Lecanopteris pustulata		Obligate
Notogrammitis angustifolia		Obligate
Notogrammitis billardierei		Obligate
Notogrammitis heterophylla		Obligate
Notogrammitis pseudociliata		Obligate
Notogrammitis rawlingsii		Obligate
Phlegmariurus billardierei		Obligate
Phlegmariurus varius		Obligate
Psilotum nudum		Obligate
Pyrrosia elaeagnifolia		Obligate
Rumohra adiantiformis		Obligate
Tmesipteris elongata		Obligate
Tmesipteris lanceolata		Obligate
Tmesipteris sigmatifolia		Obligate
Tmesipteris tannensis		Obligate
Tmesipteris horomaka		Obligate

Trichomanes venosum		Obligate
Astelia hastata	Nests	Obligate
Astelia microsperma		Obligate
Astelia solandri		Obligate
Bulbophyllum pygmaeum	Orchids	Obligate
Bulbophyllum tuberculatum		Obligate
Dendrobium cunninghamii		Obligate
Drymoanthus adversus		Obligate
Drymoanthus flavus		Obligate
Earina aestivalis		Obligate
Earina autumnalis		Obligate
Earina mucronata		Obligate
Pterostylis silvicultrix		Obligate
Taeniophyllum norfolkianum		Obligate
Brachyglottis kirkii	Shrubs/trees	Obligate
Griselinia littoralis		Non-strangling hemiepiphyte
Griselinia lucida		Non-strangling hemiepiphyte
Metrosideros bartlettii		Strangling hemiepiphyte
Metrosideros robusta		Strangling hemiepiphyte
Pittosporum cornifolium		Obligate
Pittosporum kirkii		Obligate
Peperomia blanda	Succulents	Obligate
Peperomia tetraphylla		Obligate
Peperomia urvilleana		Obligate

Table S2. Daily temperature statistics for Hamilton and New Plymouth in 2017 and 2024.

City	**Daily temperature**	**2017**	**2024**
Hamilton	Mean	14.5	14.4
	Median	14.6	14.3
	SD	4.2	4.2
	Minimum	3.6	5.9
	Maximum	22.5	24.7
New Plymouth	Mean	14.2	14.1
	Median	14.2	13.8
	SD	3.5	3.5
	Minimum	4.9	6.2
	Maximum	22.2	23.5

Table S3. Daily rainfall statistics for Hamilton and New Plymouth in 2017 and 2024.

City	Daily rainfall	2017	2024
Hamilton	Mean	8.2	5.6
	Median	3.2	3.1
	SD	12.5	7.2
	Minimum	0.1	0.2
	Maximum	77.4	47.6
	Total	1381	842
	Rain days (n)	168	150
New Plymouth	Mean	6.2	5.4
	Median	2.4	2.4
	SD	8.8	8.2
	Minimum	0.2	0.2
	Maximum	46.4	63.6
	Total	1253	1086
	Rain days (n)	203	203

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Co-Authorship Form

School of Graduate Research
The University of Waikato
Private Bag 3105
Hamilton 3240, New Zealand
Phone +64 7 838 5096
Email: SGR@waikato.ac.nz
Website: http://www.waikato.ac.nz/students/research-degree

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Tree ferns augment native plant richness and influence composition in urban plant communities. Published in Forests

Nature of contribution by PhD candidate	Study design, data collection and analyses, writing – draft and final version
Extent of contribution by PhD candidate (%)	95%

CO-AUTHORS

Name	Nature of Contribution
Bruce D. Clarkson	Study design, funding, draft revisions
Frank J. Burdon	Data analyses, draft revisions

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The undersigned hereby certify that:
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- that the candidate wrote all or the majority of the text.

Name	Signature	Date
Bruce Dudley Clarkson	[redacted]	11/06/2026
Francis John Burdon		11/06/2026

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School of Graduate Research
The University of Waikato
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Hamilton 3240, New Zealand
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Epiphyte traits influence host preferences and urban epiphyte assemblages

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Extent of contribution by PhD candidate (%)	95%

CO-AUTHORS

Name	Nature of Contribution
Bruce D. Clarkson	Study design, funding, draft revisions
Frank J. Burden	Data analyses, draft revisions
Catherine L. Kirby	Data collection, draft revisions

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- that the candidate wrote all or the majority of the text.

Name	Signature	Date
Bruce Dudley Clarkson	[redacted]	11/06/2026
Francis John Burden		11/06/2026
Catherine L. Kirby		11/6/26

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School of Graduate Research
The University of Waikato
Private Bag 3105
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Phone +64 7 838 5096
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Physiological responses of four epiphytic ferns to water and light availability

Nature of contribution by PhD candidate	Study design, data collection and analyses, writing – draft and final version
Extent of contribution by PhD candidate (%)	95%

CO-AUTHORS

Name	Nature of Contribution
Bruce D. Clarkson	Study design, funding, draft revisions
Mike J. Clearwater	Study design, draft revisions
Frank J. Burdon	Data analyses, draft revisions

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- that the candidate wrote all or the majority of the text.

Name	Signature	Date
Bruce Dudley Clarkson	[redacted]	11/06/2026
Francis John Burdon		11/06/2026
Michael John Clearwater		12/6/2026

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Co-Authorship Form

School of Graduate Research
The University of Waikato
Private Bag 3105
Hamilton 3240, New Zealand
Phone +64 7 838 5096
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Microclimate stability and tree fern density enhance obligate epiphyte richness

Nature of contribution by PhD candidate	Study design, data collection and analyses, writing – draft and final version.
Extent of contribution by PhD candidate (%)	95%

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