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THE DISTRIBUTION OF EPIPHYTIC ASTELIA AND THEIR ROLE IN HABITAT FORMATION

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Abstract

The question of how abiotic and biotic filters contribute to community assembly across multiple scales is central to contemporary ecology. The stress-gradient hypothesis (SGH) predicts that as abiotic stress increases the net direction of biotic interactions will shift from negative (competitive) to positive (facilitative). Epiphytes are subject to stressful abiotic conditions, with light, water and nutrient-limitations across multiple scales; this makes epiphyte communities ideal taxa for studying community assembly. Moreover, epiphytes are important components of ecosystems as they create and modify habitats for a variety of other flora and fauna. Epiphyte assemblages in New Zealand are nested, which has been attributed to the high proportion of obligate, rather than facultative, epiphytes, and the presence of epiphytic Astelia spp. that trap litter, which may facilitate other vascular epiphytes. My thesis aimed to: (i) identify the abiotic conditions correlated with Astelia spp. distributions across three hierarchically nested spatial extents (regional, forest and host), (ii) assess whether the Astelia spp. exhibited niche differentiation at any of these scales, and (iii) whether Astelia spp. facilitated other vascular epiphytes.

I employed presence-only species distribution models (SDMs) to characterise the three species distributions across New Zealand. At three forest sites in northern New Zealand representing different points along environmental gradients identified as important by the SDMs, I conducted ground-based surveys to: (i) evaluate the SDMs’ predictions and (ii) assess if local-scale abiotic correlates of Astelia distributions differed from those at the regional-scale. I used drones to determine differences in radial, vertical and structural preferences in epiphytic Astelia spp. on individual hosts. In addition, I
examined the associations of other vascular epiphytes with Astelia spp. along gradients of abiotic stress among forest sites, within forest sites and on individual host trees.

I found evidence that epiphytic Astelia spp. differ in their drought-/shade-tolerance, with tolerance of low temperatures defining southern range limits. Similarly, at the host-scale niche partitioning was observed along vertical gradients of light/water stress on host trees. Other vascular epiphyte associations with Astelia spp. were species-specific and varied along gradients of light and water availability. These associations tended to be negative for ‘pioneering’ species of the epiphyte community (i.e. Pyrrosia eleagnifolia) and positive for later successional species (i.e. shrub epiphytes). These results suggest that Astelia spp. form habitat critical for the success of vascular epiphytes particularly at high abiotic stress, consistent with the SGH.
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Chapter 1 - Introduction

1.1 Community assembly

One of the key questions in ecology is how communities of organisms assemble. Community assembly is the process through which individuals in a regional pool of species colonise an area, and then via their interactions with the environment and each other to form local communities (HilleRisLambers et al. 2012). The first filter determining a species presence in a local community is its presence in the meta-community (Poff 1997; HilleRisLambers et al. 2012) (Fig. 1.1), which is defined as those species that could potentially colonise and establish in the community (Lessard et al. 2012; Fukami 2015). Given a species presence in the regional meta-community, it must then be capable of dispersing to the local habitat. If the species successfully disperses to a given habitat, to establish and reproduce it must survive the abiotic and biotic pressures of the ecosystem (HilleRisLambers et al. 2012). The members of a local community can alter the abiotic features of their environment making it more or less favourable to other species, meaning that community membership and the physical environment can change through time (Connell & Slatyer 1977; McCook 1994; HilleRisLambers et al. 2012).
Figure 1.1 – The process of community assembly at multiple scales. Each disc represents filters at a given scale through which communities assemble; (A) The pool of species present in the meta-community that could potentially disperse to a given habitat; (B) three scales at which species are subject to abiotic and biotic filters, and; (C) the abiotic and biotic filters at the local scale through which species assemble. These filters can interact with one another. The solid line represents species tolerating the abiotic and/or biotic conditions, while the dashed/dotted line represents a species only able to tolerate abiotic/biotic conditions through facilitation by another species. The dotted line between the two filters represents the interaction between abiotic and biotic elements of the environment. Each species passage through a filter depends on its successful dispersal. Adapted from the figures in Poff (1997) and HilleRisLambers et al. (2012).
When a disturbance event removes some or all the individuals in a patch of habitat the community will begin reassembling (Fukami 2015). The first barrier a species in the regional pool must overcome is dispersal (HilleRisLambers et al. 2012), which in the case of plant dispersal is influenced by dispersal mode (e.g., anemochory, zoochory, etc.) and associated propagule dispersal traits (e.g. winged seeds, etc.) (Bullock et al. 2002). In addition, each species ability to disperse to available habitat can be constrained by where it is present in the landscape (Ozinga et al. 2005). If a plant species successfully disperses to a habitat patch, then it must be able to withstand the abiotic and biotic elements associated with that patch at that time (Gleason 1926).

Abiotic factors, such as water availability, temperature and nutrient availability, influence a species success in a given environment and impose limits on whether a species can establish and persist in a given habitat (Hsiao 1973; Levitt 1980). For instance, plants that occur in deserts have developed specific physiological traits that allow them to cope with drought, while many alpine plants have adaptations that allow them to endure sub-zero temperatures that would normally lyse cells and result in death (Levitt 1980). The importance of an abiotic factor as a limit can be mediated by positive and negative interactions with other members in the local community leading to differences between fundamental and realised niches.

Biotic interactions such as competition, facilitation and predation, influence the establishment and persistence of species in an environment (Bascompte 2008; Van Dam 2008). These biotic interactions alter the physiological limits of the participants and/or the abiotic environment itself. Facilitative interactions can be either mutualistic or commensal and many exist in plant communities (Finegan 1984; Bascompte 2008). Nurse plants may facilitate other species by altering their immediate abiotic
environment, in ways which indirectly benefit their associates (Finegan 1984; Padilla & Pugnaire 2006; Fagundes Marina et al. 2018). An example of this type of facilitation is seen in *Agathis australis* which podsolizes the soil beneath its canopy through its recalcitrant litter (Wyse 2012). The acidic and nutrient-poor status of the organic soils that develop beneath *A. australis* act as a filter, with species being either positively or negatively associated with *A. australis*, effectively altering the local community (Wyse et al. 2014). Species that are thought to be more competitively adept in nutrient rich, or less acidic environments are then out-competed by species capable of tolerating these conditions.

### 1.2 Facilitation

Facilitation is the positive interaction between two species, where either one (commensalism) or both participants (mutualism) receive a net benefit (Bruno et al. 2003; Brooker et al. 2008). These interactions often result in the expansion of the realised niche of one or both participants, and in extreme cases can allow an expansion of the realised niche beyond the species fundamental niche (Brooker et al. 2008; He & Bertness 2014; Bulleri et al. 2016). In plant communities, the benefits derived from facilitative interactions can be *direct*, such as one species altering nutrient, water or thermal stressors via shading, microbial symbioses or habitat formation, or as providing refuge from herbivory, or *indirect*, such as by suppression of a mutual competitor for another species (Brooker et al. 2008). Both direct and indirect facilitative interactions can be either obligatory or facultative, i.e. whether a species depends on facilitation for survival or not. The nature of the relationship between these participants is determined

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1 Taxonomy for New Zealand species follows that provided by [www.nzpcn.org.nz](http://www.nzpcn.org.nz)
by evolutionary constraints and/or the abiotic and biotic context of the relationship (Brooker et al. 2008).

While Darwinian theory originally implied that competition is the predominant driving force behind community assembly, there is increasing evidence for the existence of commensal and mutualistic interactions among plant species (Bruno et al. 2003; Brooker et al. 2008). Plant interactions can be either positive (i.e. facilitative), negative (i.e. competitive), or neutral for the individuals involved, with the net outcome of the interactions determining where the relationship lies. The net outcome is considered because plants can compete for one resource while simultaneously ameliorating conditions (facilitation) with regards to a second. The net interaction (i.e. facilitative - competitive) between two species has been hypothesised to be at least partly determined by the strength of the abiotic stressor imposed by the environment (Pugnaire & Luque 2001; He & Bertness 2014). The so-called Stress Gradient Hypothesis (SGH) suggests that with increasing stress, the net interaction of species in a community is more likely to be facilitative in nature, as the cost of competition is less than the benefit gained from such an interaction (Bertness & Callaway 1994; Kawai & Tokeshi 2007). Some variants of the SGH suggest that the net interaction may return to competition in extremely stressful conditions (Fig. 1.2), when resources are so limited that sharing becomes untenable, while other variants suggest an asymptotic relationship (Le Roux & McGeoch 2010). However, these variants are not mutually exclusive and likely depend on the system and species being examined.
When plant communities undergo primary succession pioneer species typically form the initial cohort at a given site (Connell & Slatyer 1977; McCook 1994). The facilitative model of succession holds that these pioneer species begin to alter the abiotic conditions in the habitat patch, improving abiotic conditions by increasing moisture availability and/or nutrient availability. These alterations allow other species to colonise the site by ameliorating abiotic or biotic stressors, which later successional species often cannot tolerate (Connell & Slatyer 1977). Several ‘pioneer’ have been identified and shown to expand the realised niche of their associates (Callaway & Walker 1997; Bruno et al. 2003; Brooker et al. 2008). For example, *Metrosideros excelsa* acts as a habitat former and pioneer for much of the vascular plant life on Rangitoto.

**Figure 1.2** – Hypothetical curves of the SGH. (A) represents an asymptotic curve on facilitation with respect to stress; (B) shows a net neutral outcome with respect to high stress, and; (C) a return to competition in extremely stressful environments. Adapted from Kawai & Tokeshi (2007).
Island in the Hauraki Gulf (Clarkson 1990; Wilcox 2007; Walker et al. 2010; Clarkson et al. 2015). Once established on bare lava flows, *M. excelsa* provides shade to organisms beneath its canopy by sheltering them from temperatures that can range from 21.5 – 52°C (Wilcox 2007), stabilising the microclimate and increasing the rate of soil formation through the accumulation of humus and its own litter. The presence of these habitat formers (i.e. *M. excelsa* trees) increases local species richness by altering the realised niche space of their associates (Clarkson 1990; Walker et al. 2010; Clarkson et al. 2015). By understanding how species interact and coexist we gain insights into the core of community assembly. These insights can potentially help to inform restoration management by establishing ways to leverage natural pathways (e.g. facilitation networks) in community assembly. Moreover, understanding how communities assemble can enable us to predict how communities will respond to changes in species composition (i.e. through the introduction or loss of species; Jiang & Patel 2008) or abiotic conditions (e.g., climate change; Webb et al. 2010).

### 1.3 Epiphyte ecology

Epiphytes are a model group of species with which to examine the processes driving community assembly, particularly competition and facilitation. Epiphytes are plants that live non-parasitically on other host plants (phorophytes) and obtain nutrients in their arboreal habit from sources other than terrestrial soils or the phorophyte for at least part of their life-cycle (Benzing 2008). Epiphytes are often broadly categorised based on their life-history traits; i.e. whether the species requires a host to complete its life cycle (obligate), can occur without a host under suitable conditions (facultative), or occurs atypically as an epiphyte (occasional/ephemeral) (Benzing 2008). These plants are commonly exposed to stresses along multiple resource gradients (e.g., moisture,
nutrients) that are compressed spatially (Adibah & Ainuddin 2011), making epiphyte communities suitable for studies on community assembly and the competition-facilitation spectrum.

Epiphytes require the same basic resources as other vascular plants to establish and persist: light, water, nutrients and space. However, in epiphytic habitats the availability of these resources is similar to the conditions that pioneer species experience during primary succession. That is, epiphytes are commonly subject to high light and low nutrient conditions with transient access to water (Benzing 2008). These conditions are the result of the often-exposed positions they inhabit in the canopy, and the epiphytes more restricted access to stores of water and nutrients compared to most plants rooted in terrestrial soils (Benzing 2008).

Epiphytes commonly attain water from either rain (often via stemflow/through-fall), stores in canopy soil or directly from water vapour in the air (Parker 1983; Castro Hernández et al. 1999; Benzing 2008). While rain often carries additional nutrients with it, especially after a period of stemflow (Chuyong et al. 2004), it can be highly variable seasonally and ephemeral when it does occur (Tait et al. 2006). As rainfall is patchy in many locations with a relative paucity in the summer or dry seasons, water vapour is often the most constant source for epiphytes (Zotz & Hietz 2001; Benzing 2008). In addition, some epiphytes have specialised structures for trapping water, like birds’ nest epiphytes, which can stabilise the microclimate by slowly releasing moisture into the air (Turner & Foster, 2006) or access via roots in the case of some Astelia spp. (Oliver 1930; Zotz et al. 2017). Moreover, once canopy soil and humus have formed, plants can access the moisture stored in these accumulations.
As each phorophyte begins essentially devoid of accumulations of canopy soil or cryptogam mats, there is a lack of safe sites for the germination or persistence of many epiphytic vascular plants initially (Steege & Cornelissen 1989; Enloe et al. 2006). As such, epiphyte communities often begin with lichens or bryophytes colonising the host, which act as establishment sites themselves (Mizuno et al. 2015) or the accumulation of humus and canopy soil commences (Oliver 1930; Lyons et al. 2000; Gjerde et al. 2012). Non-vascular plants are then commonly succeeded or sequentially colonised by vascular plants such as ferns and/or fern allies, which accelerate the accumulation of humus, detritus and microbes/fauna specialised in decomposition (Oliver 1930; Dawson & Sneddon 1969; Wardle et al. 2003; Burns & Dawson 2005; Benzing 2008).

Once sufficient soil has accumulated the phorophyte is then more capable of supporting woody dicot epiphytes, which often germinate out of existing epiphytic clumps (Oliver 1930). Some epiphytes, like epiphytic Astelia spp., seem to have evolved structures (i.e. specialised leaf bases or root masses) that trap litter (Zona & Christenhusz 2015). The trapping of litter likely increases the accumulation of humus and the formation of soil, development of soil microbe communities and water storage (Oliver 1930; Wardle et al. 2003; Derraik & Heath 2005; Reyes-García et al. 2008; Orlovich et al. 2013; Killick et al. 2014; Birch 2015).

Epiphytic plants that occur in or near the base of their phorophyte would likely have more stable microclimates (Denmead & Bradley 1985; Sanger & Kirkpatrick 2017b), and thus more consistent access to water from the air and moisture condensation on the bark. Furthermore, they may be able to garner nutrients from stemflow, detritus and humus (Parker 1983), although access to both water and nutrients often comes at the cost of light (Montgomery & Chazdon 2001; Sanger & Kirkpatrick 2017b). Conversely, epiphytes occurring in the emergent tier have increased access to light but
highly variable access to water, as there are greater daily fluctuations in humidity above the canopy (Denmead & Bradley 1985; Sanger & Kirkpatrick 2017b). Due to the variability in access to water and light, epiphytic communities exhibit vertical and radial stratification across their hosts (Hofstede et al. 2001; Zotz & Hietz 2001; Fritz 2009; Parra et al. 2009; Sanger & Kirkpatrick 2017b; Taylor & Burns 2016).

As resource availability varies both vertically (Denmead & Bradley 1985; Sanger & Kirkpatrick 2017b) and radially (Kutiel 1992; Badano et al. 2005; Taylor & Burns 2016) on the host there is often a degree of niche differentiation, with epiphyte species segregating themselves along these gradients (Oliver 1930; Hofstede et al. 2001; Graham & Andrade 2004; Parra et al. 2009; Taylor & Burns 2016; Sanger & Kirkpatrick 2017b). For instance, light and moisture availabilities are often negatively associated along the vertical axis (Denmead & Bradley 1985; Dickinson et al. 1993; Sanger & Kirkpatrick 2017b). Similarly, nutrient loads and the accumulation of canopy soil/humus are higher beneath the canopy, where there is a greater interception of detritus and litter, relative to that on emergent stems (Clark & Clark 1992; Paoli et al. 2008). Moreover, in the Southern Hemisphere the northern side of the tree is exposed to more sunlight than the southern side and has less moisture availability, other controls being equal. As the extremes of these gradients can occur on a single host, epiphyte communities make ideal subjects for studies on facilitation and competition.

If epiphytes successfully complete their life-cycle then their propagules face the challenge of dispersal, with most epiphytes in New Zealand dispersing either through anemochory or zoochory (Thorsen et al. 2009). Due to their inability to successfully establish and persist on the ground, for obligate and many facultative epiphytes host trees represent ‘islands’ in a ‘sea’ of soil (Burns 2008; Taylor & Burns 2015). The nature
of their hosts and the physical separation of these communities means that they can be viewed through the lens of island biogeography (Löbel & Rydin 2009), as they commonly follow similar patterns in ontogeny to community development on islands (Taylor & Burns 2015). As each tree potentially hosts a unique epiphytic assemblage, a collection of host trees can be viewed as a meta-community, even at a local scale, providing a framework through which to study the assembly of these communities (Burns 2008; Burns & Zotz 2010).

Most research on community assembly in plants has focused on terrestrial plants, with epiphytic counterparts receiving much less attention. Moreover, much of the research on epiphyte community assembly has considered tropical ecosystems, although there is a growing body of research being conducted in southern temperate systems (Burns & Dawson 2005a; Taylor & Burns 2015; Taylor et al. 2016; Taylor & Burns 2016; Sanger & Kirkpatrick 2017a, b). Vascular epiphytes constitute 10% of vascular plants globally (Kress 1989; López-Villalobos et al. 2008; Zotz 2016), but can comprise up to 63% of the local vascular plant species richness at some sites in New Zealand (Gentry & Dodson 1987; Burns 1995). Vascular epiphytes provide resources for local fauna by providing food, water and nesting habitat (Derraik & Heath 2005; Affeld et al. 2009; Henwood et al. 2014). In addition, epiphytes can benefit their hosts by hosting predators that control potential herbivores (Hammill et al. 2014), by releasing moisture during dry periods (Turner & Foster 2006; Benzing 2008), and by fixing atmospheric nitrogen and carbon which can later decompose on the forest floor (Lowman & Wittman 1996; Benzing 2008). However, they have also been observed to host potential herbivores (Cowan 1989), suggesting that the benefits associated with them is context specific. As epiphytes constitute an important component of forest ecosystems it is important that
we develop an understanding of how these communities form, and how this process differs among ecosystems.

1.4 Epiphytic flora of New Zealand

New Zealand has a unique range of vascular epiphytes with over 100 species typically occurring epiphytically (Kirby 2016), many of which are endemic (Oliver 1930; Dawson 1988; Wardle 1991). New Zealand has high alpha diversity of epiphytes and biomass across relatively small extents (Affeld 2008). Some native phorophytes host large number of vascular epiphytes, with as many as 49 species being observed on a single phorophyte (Hofstede et al. 2001). In NZ, the ferns are the largest group of vascular epiphytes in terms of number of species. These species are spread across 16 genera, with a variety of growth forms (e.g. herbaceous vines, pendant ferns, etc.) in the 46 species, 24 of which are endemic (Kirby 2016). Of the non-endemic epiphytic ferns in New Zealand, most are thought to have dispersed from other islands and continents in the South Pacific, such as Australia, South America and southern Asia, although several may be Gondwanan relics (Moreira-Muñoz 2011; Kirby 2016). The majority of NZ’s epiphytic ferns belong to the family Hymenophyllaceae (filmy ferns) with species occurring as creeping or tufted ferns, or herbaceous vines (Kirby 2016). All of these species go through typical fern reproductive cycles, with their sporangia requiring moisture to releasing spores and these germinating to form gametophytes. These gametophytes require moisture for sperm transfer between antheridia and archegonia for fertilisation leading to fully formed fern sporophytes (Ranker & Haufler 2008; Pittermann et al. 2013). In contrast, all other vascular epiphytes in New Zealand are angiosperms which release fully formed seeds post pollination.
Of the angiosperms, the Orchidaceae contribute ten commonly epiphytic species in NZ, spread across six genera, all of which require faunal pollinators (Kirby 2016). The roots of orchids, in particular, have a whitish outer-layer, called a velamen, that can absorb and store moisture, providing a degree of drought-tolerance (Zotz & Winkler 2013; Zotz et al. 2017). Of the ten species in New Zealand all either form mat-like growth forms or tufts (e.g. *Bulbophyllum pygmaeum*), while *Earina* spp. and *Dendrobium cunninghamii* commonly form pendants that hang freely from host tree branches (Kirby 2016). A further seven species are woody-dicots, five of which form shrubs, and two of which are hemi-epiphytic tree species (*Metrosiderus robusta* and *Griselinia lucida*). Three species of *Peperomia* are succulent shrubs and three *Astelia* spp. are nest epiphytes (Kirby 2016). The remainder of the vascular epiphytes in New Zealand are either vines that establish on the forest floor and climb up, or parasitic mistletoes, neither of which are considered in this study.

The epiphyte communities that form in New Zealand have a much larger ratio of obligate to facultative vascular epiphytes than exists in northern temperate systems (Burns 2008). Taylor et al. (2016) found that New Zealand epiphyte communities show a high degree of nesting, meaning that there are a number of specialist species that appear to interact with more generalist species and this may be a result of the high proportion of obligate epiphytes. In particular, the nesting observed was attributed to the presence of a group of litter-trapping nest epiphytes that may facilitate other obligate species (Taylor 2016). These nest epiphytes are the three epiphytic species in the *Astelia* genus: *Astelia hastata*, *A. microsperma* and *A. solandri* (Birch 2015), which are thought to be habitat formers (Wardle et al. 2003). These epiphytic *Astelia* spp. are thought to facilitate other vascular epiphytes through the formation of canopy soil,
which stores moisture, or through the water reservoirs that form at the base of their leaves (Oliver 1930; Wardle et al. 2003; Killick et al. 2014; Kirby 2016).

Epiphyte community succession in New Zealand typically begins with lichens or bryophytes colonising phorophytes, and starting the accumulation of the soil, humus and moisture required for most vascular epiphytes to germinate (Oliver 1930; Dawson & Sneddon 1969b; Kirby 2016). *Pyrrosia eleagnifolia, Microsorum pustulatum* subsp. *pustulatum* and/or *Earina mucronata* are commonly the first vascular epiphytes to colonise a phorophyte due to their tolerance of dry and low nutrient conditions (Oliver 1930; Dawson & Sneddon 1969b; Kirby 2016). Moreover, as these species disperse anemochorously they can reach a wide variety of hosts (Thorsen et al. 2009). *P. eleagnifolia* is a mat-forming fern that sprawls over the host bark; this species typically forms small leathery leaves relatively tolerant of drought (Dickinson et al. 1993; Burns & Dawson 2005; Kirby 2016). *P. eleagnifolia*’s physiognomy allows soil and humus to collect between the rhizomes, which, in turn, store moisture and provide suitable locations for the establishment of vascular plants (Dickinson et al., 1993; Kirby, 2016). Mats of *P. eleagnifolia* are colonised by ferns (e.g. *Asplenium flaccidum*), orchids (e.g. *Earina* spp. or *Dendrobium cunninghamii*) or epiphytic *Astelia* spp. (Kirby 2016), although there is a degree of host specificity in these successions (Wyse & Burns 2011; Wagner et al. 2015).

1.5 New Zealand nest epiphytes (*Astelia* spp.)

The *Astelia* genus belongs to the family *Asteliaceae*, with the plants being rhizomatous tufted perennials (Birch 2015). Twenty-six *Astelia* spp. are distributed around the Austral-Pacific region, 17 of which are found in New Zealand, occupying a wide variety of habitats (Bayer et al. 1998; Birch 2015; Kirby 2016). New Zealand is known for the
large number of endemic *Astelia* spp., three of which commonly assume an epiphytic life-style (Birch 2015). The three epiphytic *Astelia* spp. are commonly known as ‘perching lilies’, due to their arboreal nature, or ‘nest epiphytes’ for their nest-like appearance (Fig 1.3).

![Image](image_url)  

**Figure 1.3** – The large green tufted plants are colonies of epiphytic *Astelia* spp., growing on a *Metrosiderous robusta*. Photo credit: author’s own.

All of these nest epiphytes are robust tufted epiphytes, with *A. hastata* and *A. solandri* often forming large colonies of individuals, otherwise known as ‘clumps’ (Moore & Edgar 1970). All three epiphytic *Astelia* spp. have leaves that are narrow, strongly keeled and overlapping at their base, forming a natural reservoir, or ‘phytotelma’,
where water and litter can collect (Oliver 1930; Moore & Edgar 1970; Killick et al. 2014). The roots of these plants commonly grow through the gap at the base of the leaves, allowing access to the water in the phytotelma during times of drought (Oliver 1930). These reservoirs are most pronounced in *A. hastata*, due to the greater width and rigidity of this species leaves, compared to the relatively narrow, drooping leaves of *A. microsperma* and *A. solandri* (Moore & Edgar 1970). Moreover, *A. hastata* and *A. microsperma* both typically grow leaves in a fan-like arrangement which *A. solandri* lacks (Moore & Edgar 1970; Kirby 2016). Early observations of epiphytic *Astelia* spp. suggested that both *A. hastata* and *A. microsperma* tended to occupy higher vertical tiers, while *A. solandri* tended to occur beneath the canopy (Dawson & Sneddon 1969). In addition, some studies have noted that *A. microsperma* tends to occur around 300 m a.s.l. or higher (Kirby 2016). All three species form dioecious inflorescences, which are often precocious but more complex in older individuals. These inflorescences are insect-pollinated and tend to have flowering times that are somewhat staggered but overlapping heavily during the summer months (Moore 1970; Moore & Edgar 1970). However, some overlap between flowering times has led to a degree of hybridisation of these species (Kirby 2016).

The fruit of epiphytic *Astelia* spp. is an important food source for the lesser short-tailed bat (*Mystacina tuberculata*, Daniel 1976) and native birds such as *Callaeas cinereus*, *Mohoua ochrocephala*, and *Hemiphaga novaeseelandiae*, and are thought to be dispersed by these species (Thorsen et al. 2009; Kirby 2016). Moreover, *Astelia* spp. provide nesting habitat for a range of birds, such as *Falco novaseelandiae* (Barea et al. 1997), *H. novaeseelandiae* and *Philesturnus rufusater* (Kirby 2016). In at least *A. hastata*, the small reservoirs at the base of each leaf provide breeding grounds for Diptera, and habitat for
threatened amphibians, such as *Leiopelma archeyi*, and threatened geckos (*Hoplodactylus* or *Naultinus* spp., Henwood *et al.* 2014). However, *Trichosurus vulpecula* has also been documented to shelter in these clumps (Cowan 1989), and they may also act as a home for rats (*Rattus* spp.), although evidence for this is largely anecdotal.

Due to the habitat forming qualities of nest epiphytes, they are thought to support several native plants. All three *Astelia* spp. are effective litter trappers and tend to accumulate large amounts of detritus, humus and water, which form soil in the canopy (Wardle *et al.* 2003; Burns & Dawson 2005; Cockayne 2011). The moisture these plants accumulate in their phytotelma may behave in the same manner as those collected by other tank epiphytes (Zona & Christenhusz 2015), in that moisture is released during dry spells, facilitating their persistence in exposed locations (Reyes-Garcia *et al.* 2008). It has long been speculated that the nest epiphytes of New Zealand facilitate other epiphytic vascular plant life through the formation of canopy soil and the provision of water (Dawson 1988). However, little empirical work has been conducted to confirm these relationships or to determine which species, and under what conditions, are associated with epiphytic *Astelia* spp.

### 1.6 Thesis overview

This thesis aims to determine the niche space and partitioning of the three epiphytic *Astelia* spp. in New Zealand and examine their possible roles in facilitating the assembly of diverse epiphytic communities in temperate rainforests. To achieve this, I will:

- Identify abiotic correlates of the nest epiphytes of the *Astelia* genus at regional, local and host-tree scales.
- Identify other epiphyte species that are likely associates of epiphytic *Astelia* spp. and suggest possible mechanisms by which *Astelia* spp. may be facilitating them.
Indirectly test the SGH through observational field work that assesses how the relationship between epiphytic *Astelia* spp. and other vascular epiphytes changes across abiotic gradients at regional, local and host scales.

My approach examines niche space at a range of spatial scales reflecting the effect of scale on ecological observation (Levin 1992; HilleRisLambers *et al*. 2012; Chave 2013). At the local scale, I also conducted sampling using a drone as a novel survey method. As such, I have included a preliminary assessment of the use of drones for surveying epiphyte communities in this thesis. The thesis is structured as follows.

Chapter one presents a literature review as an introduction, and a thesis overview.

Chapter two presents a quantitative assessment of the abiotic correlates of nest epiphyte distributions at the regional scale. I developed a Species Distribution Model (SDM) for each of *A. hastata, A. microsperma*, and *A. solandri* using the maximum entropy (MAXENT) method. Data on the presence of these three species around New Zealand were sourced from the National Vegetation Survey (NVS; [nvs.landcareresearch.co.nz](http://nvs.landcareresearch.co.nz)), while information on the abiotic predictor variables (e.g., climate variables such as precipitation and temperature, etc.) predictors came from the Land Environments of New Zealand (LENZ; [landcareresearch.co.nz/resources/maps-satellites/lenz](http://landcareresearch.co.nz/resources/maps-satellites/lenz); Leathwick 2002) and Land Information New Zealand (LINZ) databases ([linz.govt.nz](http://linz.govt.nz)). I discuss the differences between the three *Astelia* spp. in their relationships with the abiotic variables and interpret the outcomes of the SDM.

Chapter three presents the results of ground-based surveys of the three *Astelia* spp. at three forest sites across the greater Auckland and Waikato region, as well as drone surveys of individual trees in the Hunua Ranges (south east of Auckland). First, I used data from ground-based surveys of each species at each site to build zero-inflated
models to determine which abiotic variables were correlated with *Astelia* spp. abundances among and within sites. Second, I used the data collected with the drone to build log-linear models to determine which abiotic variables were correlated with *Astelia* spp. abundance on individual host trees. A discussion of the results from each of these two surveys follows and the ecological significance of strongly correlated abiotic features in relation to drivers of *Astelia* spp. distributions described.

Chapter four presents results from surveys that were carried out concurrently with those presented in Chapter three, but with the intention of evaluating the SGH and the role of facilitation by *Astelia* spp. in epiphyte communities. In this case, the focus was on the relationship between *Astelia* spp. and other vascular epiphytes, and how these relationships changed along gradients, among and within forests, as well as along vertical and radial strata in individual host trees. To analyse differences in association status both among and within forests a Principle Co-ordinates Analysis (PCoA) was conducted and analysed graphically. The effect of abiotic factors on individual host tree-epiphyte distributions, heat maps depicting the changes in co-association of *Astelia* spp. with other vascular epiphytes along abiotic gradients. A discussion on the changes in species specific association status is presented.

Chapter five presents a synthesis of the results of my research discussing the interaction between the abiotic correlates that were deemed important in chapters two and three, and how these might be related to the changes in biotic interaction described in Chapter four. I conclude by relating my findings to past research in an effort to elucidate some of the abiotic and biotic drivers associated with epiphyte communities and suggest some avenues for future research. Additionally, I offer some preliminary observations on the use of drones in epiphyte research and discuss their future applications.
Chapter 2 - Regional scale distributions of native nest epiphytes

2.1 Introduction

A key aspect of ecology is understanding the environmental and geographic controls on species distributions (Lehmann et al. 2002). As the rate and degree to which natural habitats are altered by human activity increases, ecologists are being asked to not only understand why organisms have the distributions they do, but also to predict how these distributions will change in the future (Lehmann et al. 2002; Van der Putten et al. 2010; Guisan et al. 2013; Wisz et al. 2013). Understanding how and why species occur where they do can inform conservation and restoration management of sites that will potentially become less habitable for some extant species (Kumar & Stohlgren 2009; Guisan et al. 2013).

The assembly of terrestrial plant communities are relatively well understood conceptually, with evidence from a number of biomes at a range of scales (Weiher et al. 1998; Cornwell & Ackerly 2009; Pavoine et al. 2011; Kardol et al. 2013). However, little research has considered the regional scale abiotic controls of vascular epiphyte distributions, resulting in a lack of understanding of the coarsest abiotic filters influencing the assembly of epiphyte communities. The coarsest abiotic filters acting on epiphytic species are those influencing their regional distributions in the landscape. To my knowledge, only two studies have sought to identify the abiotic correlates of regional distribution of vascular epiphytes. Lehmann et al. (2002) found that the presence of some epiphytic ferns in New Zealand was correlated with gradients of temperature and light. However, Lehmann et al.’s (2002) study was focussed on ferns in general and did not make links to epiphyte community assembly. A study conducted a
neotropical system in the Andean mountains of Columbia found that increased water availability was negatively correlated with mortality in vascular epiphyte communities at the regional scale (Zuleta et al. 2016). However, it was unclear to what degree water availability affected mortality, whether the effects were species specific, or how this influenced community assembly. The lack of understanding of the coarse abiotic filters acting on epiphyte communities is a gap in our knowledge that is becoming increasingly apparent as restoration projects aim to re-establish epiphyte communities in secondary forests.

Understanding how abiotic filters influence the coexistence and co-occurrence of species in plant communities can provide insights into the ways in which plants interact with each other. New Zealand, in particular, has particularly nested assemblages of epiphytes, suggesting that the communities form sequentially (Burns 2007; Taylor et al. 2016). The nesting of these assemblages has been partly attributed to the high proportion of New Zealand’s epiphytes that are obligate compared to those in northern temperate latitudes (Burns 2010) and partly to the presence of epiphytic Astelia spp., which may facilitate other vascular epiphytes through habitat formation (Taylor et al. 2016). If epiphytic Astelia spp. are facilitating other vascular epiphytes, characterising their fundamental niche would inform management as to which species to plant where in order to leverage the natural pathways for community assembly these organisms provide.

Species distribution models (SDMs) allow for the estimation of the relationship between particular species presences (and/or absences) and environmental or spatial correlations of sites (Franklin 2010). These models are implemented for a broad range of purposes in ecology, biogeography and conservation (Elith & Leathwick 2009). The
aims of this study were to develop SDMs of epiphytic Astelia spp. to (i) identify the climatic variables correlated with the presence of the three epiphytic Astelia spp. endemic to New Zealand, and so identify some of the abiotic filters influencing their distributions at the regional scale, and (ii) determine if there is any apparent niche differentiation between these three Astelia species at the regional scale.

2.2 Methods

2.2.1 Study Area
Initially, the study area encompassed all of mainland NZ and its offshore islands. Spatial layers were then masked using a layer denoting the presence of indigenous forest in New Zealand, sourced from the Land Information New Zealand database (LINZ, https://data.linz.govt.nz/layer/50174-nz-native-polygons-topo-1250k), to limit the area modelled to the potential extant habitat for epiphytes. The masking of non-forest areas was done to avoid any biases created by the inclusion of sites that were not suitable for epiphytes due to lack of suitable habitat for hosts.

2.2.2 Modelling
Distribution data are often gathered that describe where a species is, or has been, present, but without explicit inclusion of where it is absent. This lack of data explicitly denoting the absence of the species presents a problem for many classical modelling techniques (Elith et al. 2011). The Maximum Entropy (MaxEnt) algorithm is one approach capable of predicting the likelihood of a species occurring given presence-only data and some predictor variables (Phillips et al. 2006; Elith et al. 2011). The MaxEnt algorithm estimates the target distribution associated with each of the predictor variables by iteratively searching for the distribution that is closest to uniform (i.e. the maximum entropy distribution) (Phillips et al. 2006; Elith et al. 2011). The distribution for each predictor variable is constrained to have its expected value equivalent to the
empirical average of the predictor but allows for each predictor to have a different distribution. The modelling of species occurrences was carried out using the Maxent software (version 3.4.1, Phillips et al. 2017) through the R package ‘dismo’ (version 1.1-4, Hijmans et al. 2017).

2.2.3 Astelia spp. presence data
A subset of 7652 unique 20 m × 20 m Reconnaissance (REECE) plots (Hurst & Allen 2007) were provided by the National Vegetation Survey (NVS) database (Wiser, Bellingham, & Burrows, 2001). These 7652 plots included all confirmed presences in the NVS database of the three epiphytic Astelia spp. across New Zealand. Of the 7652 unique plots, the number of records for A. solandri, A. hastata and A. microsperma were 5991 (73.1% of plots), 2519 (32.9%) and 751 (9.8%), respectively.

2.2.4 Environmental data
Data describing potential covariates of these nest epiphytes occurrences were obtained from the Land Environments of New Zealand (LENZ) climate layers (Leathwick 2002). The original resolution of these raster layers was 25m × 25m. These layers were then aggregated into 100 m × 100 m resolution due to uncertainty in the initial estimates of NVS plot locations, which could have led to misleading results. All layer conversions were carried out in QGIS (version 2.18.15 with GRASS 7.2.2) using the raster calculator. Variables were initially selected for their biological relevance (Table 2.1) and then a subset based on the results of a Pearson Correlation Coefficient (r) to test for multicollinearity. Cross-correlations between predictor variables were assessed after masking with the native forest layer, and one of those variables in each pair that displayed a correlation > |0.6| was excluded (Graham 2003; Dormann et al. 2008). A correlation matrix was produced using the s20x package (version 3.1-27 - Balemi et al.
Each case of (multi)collinearity was assessed individually, with variables chosen either based on them having lowest correlations with other variables or selecting those deemed a priori to have the greatest ecological relevance. Ecological relevance was based on which of the variables were most likely to relate to physiological thresholds (i.e. minimum temperature linked to cell death). Additional information on the basis for variable choice is provided in the Appendix 1 (Fig. A-1.1).

The geographic coordinate information for both the presence data and the environmental covariates were stored in New Zealand Transverse Mercator (NZTM) 2000 coordinate system. The environmental data were downloaded directly in this coordinate system as ASCII grid files, while the Astelia spp. presence data were transformed to this format using the ‘proj4’ package in R (version 1.0-8, Urbanek 2008).
<table>
<thead>
<tr>
<th>Covariate</th>
<th>Abbreviation</th>
<th>Unit</th>
<th>Range</th>
<th>Mean ± S.D.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Annual water deficit</td>
<td>WaterDeficit</td>
<td>millimeters (mm)</td>
<td>0–391</td>
<td>36.2 ± 56.9</td>
</tr>
<tr>
<td>Mean annual solar radiation</td>
<td>SolarRadiation</td>
<td>MJ/m²/day</td>
<td>115–155</td>
<td>138.8 ± 9.3</td>
</tr>
<tr>
<td>Winter solar radiation</td>
<td>WinterRadiation</td>
<td>MJ/m²/day</td>
<td>27–71</td>
<td>46.0 ± 9.3</td>
</tr>
<tr>
<td>Mean annual temperature</td>
<td>MeanTemp</td>
<td>degrees Celcius (°)</td>
<td>−6.8–16.2</td>
<td>10.1 ± 2.9</td>
</tr>
<tr>
<td>Minimum temperature of coldest month</td>
<td>MinTemp</td>
<td>degrees Celcius (°)</td>
<td>−9.6–10.2</td>
<td>7.6 ± 3.0</td>
</tr>
<tr>
<td>Monthly water balance ratio</td>
<td>MWBR</td>
<td>millimeters (mm)</td>
<td>6.0–487.3</td>
<td>47.3 ± 41.5</td>
</tr>
<tr>
<td>October vapour pressure deficit</td>
<td>VapourPressure</td>
<td>kPa</td>
<td>0–66</td>
<td>32.7 ± 11.5</td>
</tr>
<tr>
<td>Slope of terrain</td>
<td>Slope</td>
<td>degrees (°)</td>
<td>0–76</td>
<td>13.5 ± 12.0</td>
</tr>
</tbody>
</table>

Table 2.1 – Summary of environmental variables selected as potential covariates in the SDMs developed for three epiphyte *Astelia* spp.
2.2.5 Model evaluation

To evaluate the performance of the SDMs some data were excluded from the predictive model development and subsequently used to test the predictive model's performance. The portion of data that is included in modelling in this way is known as the ‘training set’, while the excluded set is called the ‘test set’. Resampling by cross-validation extends this idea by dividing the data into \( k \) partitions (folds) where one of the \( k \) partitions is used as a test set while the other \( k - 1 \) portions are used as training sets. This process is repeated until all \( k \) partitions have been used as a test set and the results of all iterations are then averaged (James et al. 2013). For each of the SDMs I performed five-fold cross-validation to estimate the predictive error of each covariate across its range, as well as to determine the variability in the pathway that the MaxEnt algorithm followed to reach its optimal solution.

The MaxEnt software produced five metrics to assess the overall predictive performance of the model (see descriptions in Fielding & Bell 1997): sensitivity (the true positive rate), specificity (true negative rate), true skill statistic (TSS), and the area under the (AUC) receiver-operator curve (ROC). Between these two metrics a model's prediction error can be accurately estimated, and its limits better understood. An extension of these are the TSS and AUC of the ROC. TSS is defined as sensitivity + specificity – 1 and characterises the relative capabilities of the model to accurately predict any given point (Allouche et al. 2006). The AUC is calculated by plotting the sensitivity and specificity values against one another (ROC plot) and then determining the AUC created by these values (Bradley 1997). AUC values range between 0.0 and 1.0, with 0.5 meaning the model is no better than a coin flip and 1.0 meaning the model perfectly predicts points, with no overlap between the presence and absence group distributions (Bradley 1997; Fielding & Bell 1997). However, AUC is not sufficient on its own as a metric of model performance, as species with narrow ranges relative to the area encompassed by the environmental variables tend to show higher AUC values, which are effectively data artefacts (Fielding & Bell 1997; Phillips et al. 2004).
The MaxEnt software provides several metrics for determining the contribution of each variable: AUC, Regularised Training Gain (RTG) and test gain (Phillips et al. 2017). For the purpose of estimating variable importance, AUC performs in much the same way as it does for assessing overall model importance. Given the large spatial extent over which I estimated distribution relative to the range of each of the three species, I did not use the AUC to assess variable importance. RTG measures the effective gain in predictive performance of the training model at each iteration of the MaxEnt algorithm with respect to the variable in question. As our study encompassed the entire region of interest and was aimed at determining regional correlates with epiphytic Astelia spp. presence, the change in RTG between when the variable was left out, used as the sole predictor, and included in a full model provided an accurate estimate of each variable’s importance. To quantify the importance of each variable was assessed on the basis of its response to random permutation. Each predictor variable had its values randomly permuted across the landscape for a given presence observation in the training dataset, with the model subsequently being re-evaluated. The change in AUC is then recalculated and normalised to a percentage to determine the importance of the given predictor (Phillips et al. 2017). Moreover, these permutational estimates were the average of the five cross-validated runs of the modelling procedure. As I accounted for collinearity prior to model implementation the estimated contribution of the individual variables should be reasonably independent of that of the other predictors (Graham 2003; Dormann et al. 2008).

The five-fold cross-validation provided a further indication of the uncertainty in the association of species presence with each predictor variable (Hijmans 2012). All response curves were plotted on a complementary log-log (clog-log) scale following the guidelines of Elith et al. (2011) and Phillips et al. (2017). The response curve graphs also show the variability in the cross-validated replicates across the ranges of the predictor variables. The predictions of a SDM across all abiotic gradients can be visualised and projected onto a region with known predictor values. As my study aimed to determine the distribution of epiphytic Astelia spp., the
predictions from the SDM were projected back onto a New Zealand using the predictor data. These predictions were visualised as heat maps for each Astelia spp. distribution. These were produced using the average predictions of the five cross-validated replicate of each species MaxEnt model and were displayed on the clog-log scale to represent the species probability of occurrence following the guidelines of Phillips et al. (2017).

2.3 Results

2.3.1 Multi-collinearity

Preliminary checks for multi-collinearity between the environmental predictor variables revealed that half of them were highly correlated with some other predictor variable(s). Correlations were calculated and visualised in a matric of plots (Appendix – Fig. A-1.1). The upper triangle showed pairwise scatter plots, while the lower triangle displayed pairwise correlation values. Four variables were excluded due to multi-collinearity: MWBR, VapourPressure, MeanTemp and WinterRadiation. In particular, VapourPressure was excluded due to having high correlations with SolarRadiation. VapourPressure was excluded instead of SolarRadiation as it had stronger correlations with the other remaining three variables than SolarRadiation did, suggesting it explained less independent variation.

2.3.2 Presence of Astelia spp. in native forests of New Zealand

The majority of the remaining native forest in New Zealand is restricted to the west coast of the South Island, although there are also large sections throughout the northern end of the South Island (Fig. 2.1). The majority of the native forest in the North Island is around the central plateau and along the coasts around the middle of the Island. Effectively, the majority of the extant native forest exists around the axial ranges of each island. All three epiphytic Astelia spp. were predominantly observed in the North Island, with a few sightings in the upper north-west coast of the South Island. There is a conspicuous lack of observations for both A. microsperma and A. solandri along the west coast of the upper half of the North Island. However, given the dataset is sourced from the NVS following the REECE protocol there is little chance of their
being any observation biases amongst species or locations. The remaining environmental space of the abiotic predictor variables after masking by the native forest raster was well sampled with all three species showing distinct patterns in this space (Appendix 1; Fig. A-1.2).

**Figure 2.1** – The extent of native forest in New Zealand as estimated by LENZ, overlain with the presence data from the NVS database of each of the three epiphytic *Astelia* spp. modelled.
2.3.3 Model evaluation
All three SDMs performed relatively well (Table 2.2), with all showing high sensitivities indicating that these models accurately predict species presences. However, all three SDMs were less accurate in predicting true absences. The SDM for *A. solandri* was the least accurate model of the three having the lowest values in each metric, although even this model had satisfactory performance.

Table 2.2 – Metrics showing the average performance of the SDMs across the five cross-validated replicates for each *Astelia* spp. In the cases of sensitivity, specificity and TSS the metrics are scaled 0 - 1 with higher values indicating better performance. AUC ranges between 0.0 – 1.0, with 0.5 indicating the model performs no better than a coin flip.

<table>
<thead>
<tr>
<th>Species</th>
<th>Sensitivity</th>
<th>Specificity</th>
<th>True Skill Statistic</th>
<th>AUC</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>A. hastata</em></td>
<td>0.937</td>
<td>0.718</td>
<td>0.655</td>
<td>0.878</td>
</tr>
<tr>
<td><em>A. microsperma</em></td>
<td>0.876</td>
<td>0.754</td>
<td>0.630</td>
<td>0.813</td>
</tr>
<tr>
<td><em>A. solandri</em></td>
<td>0.812</td>
<td>0.696</td>
<td>0.508</td>
<td>0.794</td>
</tr>
</tbody>
</table>

2.3.4 Variable Importance
Based on permutational importance, mean minimum temperature of the coldest month (minTemp) and mean solar radiation (solarRadiation) were the most important predictors of the distribution for all three species (Table 2.3). Mean annual water deficit (annual water deficit) was consistently the least important.
Table 2.3– Permutational importance and percent contribution of each environmental predictor included in the SDM for each epiphytic *Astelia* spp.

<table>
<thead>
<tr>
<th>Covariate</th>
<th><em>A. hastata</em></th>
<th><em>A. microsperma</em></th>
<th><em>A. solandri</em></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Permutation importance (%)</td>
<td>Permutation importance (%)</td>
<td>Permutation importance (%)</td>
</tr>
<tr>
<td>SolarRadiation</td>
<td>30.4</td>
<td>55.2</td>
<td>55.6</td>
</tr>
<tr>
<td>MinTemp</td>
<td>68.7</td>
<td>39.4</td>
<td>42.5</td>
</tr>
<tr>
<td>Slope</td>
<td>0.8</td>
<td>2.6</td>
<td>1.4</td>
</tr>
<tr>
<td>WaterDeficit</td>
<td>0.2</td>
<td>2.8</td>
<td>0.5</td>
</tr>
</tbody>
</table>
For *A. hastata* minimum temperature and solar radiation accounted for most of the variation in this species distribution (Fig. 2.2). Minimum temperature alone accounted for almost as much RTG by itself as did all the variables combined (≈ 0.33 vs. ≈ 0.37, Fig. 2.2). Slope and annual water deficit were not useful predictors of *A. hastata* distribution.

**Figure 2.2** – Jackknife cross-validation evaluation of the relative importance of the environmental variables used to predict the distribution of *A. hastata*

Solar radiation was the single most useful predictor of the distribution of *A. microsperma*, followed closely by minimum temperature (Fig. 2.3). Slope accounted for some of the variation when it was the only term included, but only increased the regularized training gain a little when the other variables were included. Annual water deficit was not a useful predictor of the distribution of *A. microsperma*.

**Figure 2.3** - Jackknife cross-validation for evaluation of the relative importance of the environmental variables used to predict the distributions of *A. microsperma*.
Solar radiation and minimum temperature were again the two most important terms in the model for *A. solandri*, with the inclusion of both being required to attain high RTG, compared to the full model (Fig. 2.4). Slope explained a small amount of variation not captured by either solar radiation or minimum temperature. However, annual water deficit contributed nothing either in isolation or when the other variables where included.

**Figure 2.4** - Jackknife cross-validation for evaluation of the relative importance of the environmental variables used to predict the distributions of *A. solandri*

### 2.3.5 Marginal response curves

Marginal response curves show the change in probability of occurrence for each of the epiphytic *Astelia* spp. across the range of values for a given predictor, while holding all other predictors constant at their mean. The majority of the variation in probability of occurrence was observed in solar radiation and minimum temperature (Fig. 2.5). Each of the species showed a distinct difference in the shape of their marginal response curves for these two predictors, although they had similar response curves for both slope and annual water deficit. However, all three species have a higher probability of occurrence at locations with low annual water deficit and slope values.

Each of the epiphytic *Astelia* show some degree of differentiation along the solar radiation and minimum temperature gradients, with the curves clearly separating, particularly at the ends of the gradients (Fig. 2.6).
Figure 2.5 – Predicted marginal response curves for the three epiphytic Astelia spp. along four abiotic gradients. The blue ribbons around the lines represent ± 1 standard deviation as estimated from the five-fold cross-validated replicates run for each sub-plot indicate the percent contribution of that variable.
2.3.6 Mean annual solar radiation

*A. solandri* has the widest range of tolerance to solar radiation values of the three *Astelia* species considered (Fig. 2.6). In particular, *A. solandri*'s probability of occurrence is highest where both *A. hastata* and *A. microsperma* probabilities approach zero at relatively low solar radiation values. Conversely, at high solar radiation values, *A. solandri* probabilities decline as the probability of *A. hastata* occurring exceeds 0.45. *A. microsperma* peaks along this gradient at the same point as *A. hastata* shows its first peak. Beyond this peak, *A. microsperma* declines and is predicted to have a low probability of occurrence at high solar radiation values. In contrast, *A. hastata* probability shows a small dip before climbing monotonically as solar radiation values increase. *A. hastata* is the most likely species to occur in environments that experience high solar radiation values, relative to the range observed in New Zealand.

2.3.7 Mean minimum temperature of the coldest month

In contrast to the patterns observed in solar radiation, *A. microsperma* appears to be the species most tolerant of low and high minimum temperatures (Fig. 2.6). Both *A. hastata* and *A. solandri* follow similar trends to one another, although *A. solandri* has the lowest likelihood of occurrence at the maximum observed minimum temperatures. However, *A. solandri* has the slowest approach to zero probability of occurrence of the three species at sub-zero temperatures, suggesting that it may be more cold tolerant.
Figure 2.6 – The probability of occurrence predicted by the MaxEnt model plotted against solar radiation (MJ/m²/day) and minimum temperature (°C) with the three epiphytic Astelia spp. overlaid. The ribbon around each line represents ± one standard deviation around the estimate, as calculated from the five-fold cross-validated replicates of each MaxEnt model.
2.3.8 Predicted distributions of epiphytic Astelia spp.
The predictions of a SDM across all abiotic gradients can be visualised and projected onto a region with known predictor values to assess spatial trends in the distribution of a species that go beyond the environmental data used to form the predictions (Fig. 2.7). *A. hastata* has the highest probability of occurrence in the northern North Island, while *A. microsperma* is predicted to be more common around the centre of the North Island and particularly on the central plateau (Fig. 2.7). In contrast, *A. solandri* is relatively common in the northern North Island but is predicted to be most common around the coastlines of New Zealand. Moreover, *A. solandri* has a relatively high probability of occurrence much further south than the other two species.
Figure 2.7 – The predicted distributions of (A) A. hastata; (B) A. microsperma and; (C) A. solandri, as calculated from the MaxEnt models. Warm colours indicate a high probability of occurrence, with darker colours representing the reverse. The probability is represented on a clog-log scale.
Each of the SDMs were originally constrained to areas of extant native forest in New Zealand, to avoid any bias that might be created by areas where there are no suitable phorophytes. The heat maps have been projected across New Zealand, regardless of the locations of forests in the contemporary landscape. As such, some deforested areas may show high probability of occurrences due to those habitats having a suitable climatic envelope for the epiphytic Astelia spp.

2.4 Discussion

2.4.1 Model evaluation
The high sensitivity of the models suggests that they can accurately predict where the species will occur along the abiotic gradients assessed. The models' specificity values were lower than their respective sensitivities; however, they were able to predict at least 70% of true absences. In all cases, the overall AUC and TSS scores indicate that the models perform much better than one of random class allocation (Table 2.3). It is possible that the importance of the climatic variables as predictors is the result of the country-wide scale at which they vary rather than direct relevance to the species distributions (Franklin 1995; Iverson & Prasad 1998; Leathwick 2002; Lehmann et al. 2002). However, the predictor variables were chosen based on biological relevance, such as links to physiological limits, meaning that the correlations and their predictive importance is supported by the ecological model underlying the SDMs.

2.4.2 Abiotic gradients
Abiotic gradients are often the first and coarsest filters acting upon a species regional scale distributions (Levin 1992; Poff 1997), assuming its presence in the greater meta-community (HilleRisLambers et al. 2012). These abiotic variables commonly impose some limits on a species fundamental niche and niche differentiation across these abiotic gradients can be discerned between functionally similar species. Moreover, identifying the features that give rise to regional-scale patterns in species distributions and how they influence them is critical to
defining that species habitat (Gaston et al. 1998; Estrada et al. 2016) and understanding how these habitats will change in the future (Davis & Shaw 2001; Reich et al. 2015).

In the case of the three epiphytic Astelia spp. considered here, solar radiation and minimum temperature were consistently the two most important predictors of their regional scale distribution. These two predictors accounted for almost all the variation in epiphytic Astelia spp. distributions explained by the model. Both solar radiation and temperature covariates have been identified as predictors of the spatial distribution of flora in New Zealand. Leathwick et al. (1998) found that both light and temperature were strong correlates of alpha tree diversity. Similarly, Lehmann et al. (2002) reported strong correlations (> 0.7) between the species richness of ferns and both temperature and light. In both studies the authors found that the diversity of the flora in question was positively associated with solar radiation. The authors suggested that these relationships were the result of plants seeking habitats with the highest potential productivity, as they did not believe that the habitats considered were moisture limited. However, both of these studies considered species that had access to soil moisture stores, except for a few epiphytic fern species in the case of Lehmann et al. (2002).

All three Astelia spp. curves peak at different points on the solar radiation gradient, with A. solandri being the most likely to occur in low solar radiation input environments, and A. hastata the most likely to occur in high solar input environments. While A. hastata appears to associate with the highest productivity environments (i.e., highest solar radiation), the fact that A. microsperma and A. solandri peak before the maximum suggests that they are either being excluded competitively, or conditions are beyond their fundamental niche. Given the strong positive correlation (0.67; Fig. A-1.2) of mean annual solar radiation with mean October vapour pressure deficit (a measure of moisture of water availability in the air), it may be that A. microsperma and A. solandri are limited in environments at the upper range of radiation values by moisture availability. While annual water deficit was included in the model as a measure of
water availability, it did not contribute much to predictions of the distributions of any of the *Astelia* spp. (Table 2.3). It may be that this lack of importance arises from water deficit not adequately capturing water availability for epiphytes. Most epiphytes do not have access to soil moisture reserves and depend primarily on water stored in the air. Moreover, sun epiphytes, in particular, commonly have a number of morphological and physiological features that aid them in collecting, storing and retaining water (Oliver 1930; Wardle et al. 2003; Kirby 2016). The probability of *A. hastata* occurrence tended to increase in high light environments, suggesting that it may be more drought tolerant, possibly due to the reservoirs at the base of its leaves, which are much more pronounced than in the other two epiphytic *Astelia* spp. (Moore & Edgar 1970). My results concur with the observations of Dawson & Sneddon (1969) who noted that *A. hastata* and *A. microsperma* tended to occur in the upper tiers of trees, while *A. solandri* was more commonly found in the more shaded sections. Water availability has been identified as a limiting resource for the bird’s nest fern (*Asplenium nidus*) from north-eastern Australia, albeit over a much smaller spatial extent. (Taylor & Burns 2016) found that the radial distributions of a number of other epiphytes in New Zealand were negatively correlated with light, and as such positively correlated with moisture availability.

*A. microsperma* was the species most likely to occur at high minimum temperatures, but it also showed a distinct plateau in occurrence between approximately 0 and 5 °C, where the other two species probability of occurrence rapidly declined (Fig. 2.6). This plateau could be due to it being forced to occupy fewer ideal sites, such as at high elevation, areas due to competitive exclusion from areas dominated by *A. hastata*. *A. solandri* maintained a small probability of occurrence at sub-zero temperatures, where the other two were not predicted to occur; this species may be more frost-tolerant than the other two (Kirby 2016). However, more experimental assessments would be needed to determine if there are differences between the epiphytic *Astelia* spp., perhaps following similar methodology to (Sakai & Wardle 1978; Warrington & Stanley 1987). *A. hastata* had the narrowest distribution of the three species,
with its predicted absence at sub-zero temperatures possibly being due to the reservoirs that aid it in dry environments. It may be the water which accumulates here could freeze at low temperatures and may cause frost damage to the plants, whereas the other two species form smaller deposits and are less exposed to the air due to their morphology (Chapter One). The difference in each of the three Astelia spp. responses to the two environmental gradients suggests that these species are associated with slightly different climatic envelopes and/or that some species may be being competitively excluded from their preferred habitat.

2.5 Conclusions

As all three distributions models performed well in terms of sensitivity, specificity, TSS and AUC, I am confident in their predictions. Moreover, the model performance demonstrates that SDMs built with the MaxEnt algorithm can be effective tools for determining abiotic correlates of the regional scale distributions of plants for which presence-only data exist.

The presence of all three epiphytic Astelia spp. was strongly correlated with mean annual solar radiation and mean minimum temperature of the coldest month. The high correlation of solar radiation with vapour pressure deficit suggests that solar radiation may be both directly and indirectly affecting the distribution of each of the three species by accounting for both light and atmospheric water availability. Annual soil water deficit did not predict the distribution of any of the three species studied, although this may be due to their lack of access to soil moisture stores. Minimum temperature could be directly influencing the occurrence of species, particularly at low minima as each of these species may be reaching a physiological threshold. These results suggest a link between epiphytic occurrence and gradients of light, temperature and/or vapour pressure deficit at the regional scale. Moreover, the separation of the three epiphytic Astelia spp. along these two gradients lends some support, albeit purely correlative, to the hypothesis that the three species exhibit some degree of niche differentiation at the regional scale. Therefore, the species niche differentiation may be due to differing degrees of
specialisation, with *A. hastata* specialising in water-limited conditions, *A. microsperma* being tolerant of low temperatures and *A. solandri* being more of a generalist. Overall, these models provide suggests that communities assemble through abiotic filters. However, these results raise the question as to whether the epiphytic *Astelia* spp. are being driven by their need for relatively warm and sunny microsites or if these variables are solely of importance at the macro-scale.
Chapter Three - A multi-scale approach to abiotic and biotic drivers of epiphytic *Astelia* spp. distributions.

3.1 Introduction

The assembly of ecological communities is influenced by a range of abiotic and biotic drivers, which interact to determine the species present and how abundant each species is (HilleRisLambers *et al.* 2012; Kraft *et al.* 2015). However, the relative influence of these drivers is dependent on the scale at which a community is defined or an individual organism's distribution assessed (Levin 1992; Chave 2013). At regional scales, abiotic and biotic filters can influence whether organisms are part of the greater meta-community, acting as the coarsest filter for which species are prospective members, with smaller scales reflecting the results of successive filters which species must pass through to join more local communities (Levin 1992). Identifying which drivers are important and how these interact with one another at different scales broadens our understanding of coexistence theory, allowing us to better understand how these communities might respond to change and how to restore them (Laughlin & Laughlin 2013; Laughlin *et al.* 2018).

Several abiotic and biotic drivers influencing the assembly of epiphyte communities have been identified in the past. A common abiotic gradient associated with epiphyte distributions and abundance is light availability and the inversely related atmospheric water availability, which is important at regional (Zuleta *et al.* 2016), local (McCune 1993; Zuleta *et al.* 2016; Toivonen *et al.* 2017) and individual host scales (Krömer *et al.* 2007; Fritz 2009; Parra *et al.* 2009; Taylor & Burns 2016; Acebey *et al.* 2017). Less research has considered the biotic drivers that influence epiphyte community development, particularly for vascular epiphytes. Host species identity influences epiphyte communities; this effect attributed to the physical characteristics of the phorophyte (Callaway *et al.* 2002; Wyse & Burns 2011; Taylor & Burns 2015). It has also been well documented that epiphyte communities typically undergo succession, suggesting
that the epiphyte species are interacting and altering local abiotic conditions, as well as the phorophyte surface conditions changing though time (Woods 2017).

New Zealand epiphyte communities are hierarchical in form (Burns 2007) in that many epiphytes are dependent on the presence of another species in order to gain membership. Several studies have suggested that epiphytic *Astelia* spp. (‘nest epiphytes’) may be facilitating other vascular epiphyte species through habitat formation (Dawson 1988; Burns 2007; Taylor & Burns 2015; Kirby 2016), which could be leading to the highly nested (hierarchically) distributions seen in New Zealand (Taylor *et al.* 2016). If epiphytic *Astelia* spp. are facilitating other epiphytes, then understanding what influences epiphytic *Astelia* spp. presence and abundance is crucial for the effective restoration of epiphyte communities. However, to date no quantitative research has been carried out on what determines the distributions of epiphytic *Astelia* spp., even though restoration of epiphyte communities has been identified as a goal of restoration management (Oishi & Doei 2015; Reid *et al.* 2016).

In Chapter two I found evidence that mean annual solar radiation and mean minimum temperature of the coldest month are correlated with *Astelia* spp. distributions at the regional scale. However, it is unclear if this relationship holds at finer grains, such as among and within forest stands or on individual phorophytes. By collecting observational data at three forest sites across the abiotic gradients identified as important in Chapter two, as well as data on epiphyte distributions relative to the structure of individual trees I will determine: (i) whether the presence and/or abundance of *Astelia* spp. changes across the environmental gradients identified by the SDM, and if these changes are species-specific or there is niche differentiation among *Astelia* spp.; (ii) The primary correlates between presence and abundance of *Astelia* spp. within and among forest stands; (iii) the relationship between *Astelia* spp. distributions and the vertical or radial position that they occupy on a host; and whether these species favour a
particular position on the host tree (i.e. the trunk, the branch or the crook formed between the two).

3.2 Methods

3.2.1 Selection and characteristics of study sites

Three study sites (Fig. 3.1) were selected based on gradients in annual solar radiation and mean minimum temperature of the coldest month (Table 3.1), as well as site logistics and perceived similarity in terms of both forest composition (all ecosystems were classed as WF9 – as determined from the framework developed by (Singers & Rogers 2014), and disturbance history. There are, however, some distinct differences between the three study sites that could not be controlled for. For instance, the Taumata Covenant block is on Great Barrier Island, which does not have a brushtailed possum (*Trichosurus vulpecula*) population, a known herbivore of native plants, while both Pirongia and Hunua do. However, the latter two sites do conduct extensive pest management regimes to maintain low density possum populations.
Figure 3.1 – Approximate location of the three study sites used for determining correlates of Astelia spp. abundance within and among forest blocks: Taumata Covenant Forest Block (red triangle); Hunua Ranges (Massey Track) (yellow triangle); Mount Pirongia (Mahaukura Track) (blue triangle). Image credit: PatternUniverse.com (Outline of NZ); Google Earth (Satellite photo).

Table 3.1 – Summary of the environmental variables deemed important by the SDMs at the three selected field sites. Values were taken from the LENZ rasters used in Chapter 2 at the approximate centre point of the field sites.

<table>
<thead>
<tr>
<th>Site</th>
<th>Mean annual solar radiation (MJ/m²/day)</th>
<th>Mean minimum temperature (°C)</th>
<th>Mean vapour pressure deficit (kPa)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Taumata</td>
<td>154</td>
<td>7.1</td>
<td>41</td>
</tr>
<tr>
<td>Hunua</td>
<td>149</td>
<td>4.6</td>
<td>31</td>
</tr>
<tr>
<td>Pirongia</td>
<td>144</td>
<td>3.4</td>
<td>25</td>
</tr>
</tbody>
</table>

Note: Mean minimum temperature is an average of the daily minimum temperatures of the coldest month (July), and vapour pressure deficit (VPD) is calculated as the mean daily VPD for the month of October.
3.2.2 Surveys

Forest surveys

At each site, I identified an area that was deemed both accessible and roughly consistent with the other sites in terms of the dominant tree species, tree size distribution, and topographic features, then randomised the placement of transect lines within this area. I selected the starting point for each transect non-randomly by choosing a point that had at least one tree hosting an *Astelia* spp. While not truly random, the purpose of my survey was to assess *Astelia* spp. distributions, which are relatively uncommon throughout the forest. I biased the start point to ensure some *Astelia* spp. were included. Then at random, I chose the direction of each transect from a selection of bearings that would lead into a section of forest that had approximately similar canopy species composition for at least 100 metres (m).

Each transect extended 100 m in a straight line, with Point-Centred Quarter (PCQ) observations (Cottam & Curtis 1956; Mitchell 2015) carried out at 20 m intervals, starting at zero. Each PCQ sample was a minimum of 20 m apart to avoid remeasurement of the same host trees. In each quarter I selected the nearest tree within 15 m of the point, with a diameter at breast height (DBH; at 1.3 m high) > 15 centimetres (cm) and the nearest tree fern (*Cyathea* or *Dicksonia* spp.) or *Rhopalostylis sapida* (palm) within 15 m and greater than 1.5 m in height (measured to apical bud). The size cut-off for trees with true secondary growth was chosen based on the findings of Taylor & Burns (2015) who noted that epiphyte communities did not typically begin to accumulate on host trees with a DBH of less than 5.6 cm, but that this minimum could range up to 43.4 cm depending on the species of phorophyte. As a compromise between surveying an adequate number of trees and aiming to include all trees which acted as hosts, a 15 cm cut-off was chosen. If there were no trees of this minimum size within 15 m, I noted an absence for that quarter. I carried out six transects each comprising six PCQ at each site, which resulted in the survey of 864 hosts (3 sites × 36 points × 4 quarters × 2 hosts).
At each PCQ I also recorded the aspect, slope and topographic index (Perry et al. 2010). Topographic index was used to classify whether the sampled point was located at the bottom of a gully (1) or at the top of a ridge (5), with intervening values spaced evenly between these extremes (i.e. 3 is the approximate mid-slope between gully and ridge). For each host tree, I recorded the species identity, DBH and height. Moreover, I noted the percentages of the surface area of each tree covered by non-vascular epiphytes and non-epiphytic climbers. These quantities were estimated by myself and another surveyor independently and then the two estimates averaged.

Each tree was surveyed from the ground with binoculars and the number of clumps (colonies comprised of several individual plants) of adult and juvenile Astelia spp. were counted. Here, I defined an adult Astelia spp. as one estimated to be greater than 30 cm in width and height (see Fig. 3.2 and Fig. 3.3 for examples of juvenile and mature Astelia spp.). I used this cut-off as smaller individuals appear to have much smaller accumulations of canopy soil and moisture stores, which are likely to be the primary way in which the Astelia spp. facilitate other organisms. In addition, due to the Astelia spp. growth form, it can be difficult to precisely estimate the number of individuals comprising a clump. For this reason, I specified three discrete clump sizes: Those consisting of one adult individual (Fig. 3.3); two to three adult individuals (Fig. 3.4), and; more than four adult individuals (Fig. 3.5). Due to the morphological similarities between A. hastata and A. microsperma, whenever I was uncertain as to an individual's identity I recorded it as the more common of the two species: A. hastata.
Figure 3.2 – Juvenile Astelia spp. Photo Credit: author’s own.

Figure 3.3 – An individual A. hastata plant – Photo credit: Kuanjin Lee.
**Figure 3.4** – A medium clump (2-3 individuals) of *Astelia* spp. Photo credit: Edin Whitehead.

**Figure 3.5** – A large clump (4+ individuals) of *A. hastata* growing near the top of a *D. cupressinum* tree in the Hunua ranges. Photo Credit: author's own.
Drone surveys

Surveys of individual host trees were carried out using an Unmanned Aerial Vehicle (UAV), or drone, to observe the radial and vertical distributions of *Astelia* spp. on their hosts. These surveys were executed using a DJI Mavic Pro drone on individual large (DBH > 45 cm) *D. cupressinum* trees in the Hunua Ranges. The DBH threshold was selected on the basis of (Taylor & Burns 2015)'s results which estimated that this was the size at which *D. cupressinum* began to accumulate epiphytes. I limited my observations to *D. cupressinum* trees in the Hunua Ranges due to time restrictions. Only *A. hastata* and *A. solandri* were observed occurring in these Ranges. I chose *D. cupressinum* as the host species for surveys for three reasons: (i) they can host rich epiphyte communities (Dickinson *et al.* 1993; Hofstede *et al.* 2001; Taylor & Burns 2015), (ii) they commonly emerge above the primary canopy of the forest meaning they have greater vertical stratification in terms of exposure to abiotic factors than non-emergent trees (Clark & Clark 1992), and (iii) they are relatively accessible for surveys via drones. Accessibility for drones is due to the branch architecture of *D. cupressinum* and relatively sparse foliage they have (Norton & Kelly 1988; Dörken & Parsons 2016), which allows for relatively unobstructed views along branches and the primary trunk providing consistent surveys of the tree. All *D. cupressinum* individuals >45 cm DBH encountered along the Cossey Dam track (-37.064632, 175.091472) in the Hunua Ranges were surveyed.

To standardise the survey effort on each tree, survey time was limited to a single battery charge on the drone which amounted to approximately 25 minutes of flight time. Each tree was surveyed systematically by taking 4K video footage vertically along the tree's primary axis at each of the four cardinal axes (N, S, E, W). Additionally, all trees had multiple photos taken with a 12-megapixel camera mounted on the drone to attain high-quality static images for identification of epiphytes.
Meta-data on the DBH of each tree, and the aspect, slope and topographical index of its terrain location were collected (but were not used further in my analysis). Data from the drone were analysed post-collection using the default photo and video viewer in Windows 10 (version 1.22). Data describing the vertical, radial and structural position (i.e., whether the individual occurred on the branch, trunk or in the crook between the two; see Fig. 3.6) of all Astelia spp. present on each host were recorded. The bearing of the drone’s initial approach to the tree was used to establish the cardinal direction being viewed when I analysed the footage.

![Diagram of tree strata and orientations](image-url)

**Figure 3.6** – (A) Division of vertical strata on tree (adapted from Johansson 1974), (B) the three structural positions epiphytes could occupy, and; (C) Division of radial strata based on the cardinal directions showing the sides of the tree surveyed. Image credit: tree Silhouette – [www.thephantom.org](http://www.thephantom.org); tree ring - [www.123rf.com](http://www.123rf.com).

### 3.2.4 Statistical methods

**Forest scale distributions**

To determine how Astelia spp. abundance and environmental correlates of abundance differed among sites the data collected from the ground surveys of the three forest sites were used. In this context no true (statistical) replicates were available, as I was looking at regional-scale differences among forests for which no true replicates exist, as is unavoidable in landscape
level ecological analyses (Hargrove & Pickering 1992; Oksanen 2001). For the questions regarding the distribution and abundance of Astelia spp. within forest sites or on individual trees, each tree could be treated as a replicate.

To determine the environmental correlates of local-scale epiphytic Astelia spp. distributions within and among forests, the count of each Astelia spp. per host was transformed to create an index reflecting the number of individuals on each host. To create a pseudo-count for each Astelia spp. the three size categories for Astelia clump sizes were multiplied by one, three and six, respectively, and then summed across the host tree. These scalars were estimated to be the approximate medians of the number of individuals in each of these clump categories.

Model selection began with predictor variables being screened for multi-collinearity based on the results of a Pearson Correlation Coefficient (r) matrix and one of each pair of variables with correlations > |0.6| were excluded based on ecological relevance and the degree of multicollinearity each variable exhibited. Three model types were considered following the methodology of (Linder & Lawler 2012). Generalised linear models (GLMs), zero-inflated (ZI) and hurdle models were all assessed, with the latter two being included due to the high number of zero counts present in the data. Proportionately large zero counts in the response variable present problems for the underlying assumptions of generalised linear models (GLMs; Zuur et al. 2007). The hurdle and ZI models both separately model the zero counts in the response with a Binomial family, essentially creating a model for whether an individual will be present based on the predictor variables. The positive count data (> 0), and some of the zero-count data in the case of ZI models, are then regressed against the environmental predictor data to determine if any of the variables correlate with the species abundance. GLMs, Hurdle models and ZI models were each constructed with either Poisson or Negative Binomial families, along with the predictor variables remaining post-screening (Table 3.2). For each of the hurdle and ZI models both the Binomial and count portions of the regression could use a
separate suite of predictor variables. To determine which model/error combination was most suitable, Akaike Information Criterion second order estimate (AICc) scores were compared (Burnham & Anderson 2003) and tests for differences in log-likelihood conducted using a log-likelihood ratio test where AICc scores were similar (Zuur et al. 2007). The distribution of each Astelia spp. was modelled separately at each site. Modelling was carried out on a site-by-site basis due to the limited degrees of freedom available for estimating parameters in the count portion of the hurdle and ZI models. The same limits imposed by the degrees of freedom precluded the use of higher-order variable interactions, so only additive models were assessed.

Classical regression techniques implicitly assume that zero counts and non-zero counts come from the same distribution (Zuur et al. 2007); ZI and hurdle models both allow for multiple distributions to be used for regression of the predictions against differing sections of the response data (Cragg 1971; Mullahy 1986; Lambert 1992). In both cases, the probability of an event occurring is estimated first, and then given that an event has occurred the abundance of that is then estimated. Essentially, in my case, a hurdle model is a sequential process whereby the epiphyte either ‘decides’ to occur, and if it does occur must do so at a count greater or equal to one. In contrast, my ZI models allow the ‘decision’ to occur at a count of zero (i.e. remain absent), after the possibility of occurrence has been determined.
Table 3.2 – Summary of the types of models assessed, with their associated error families, the response variables and the predictor variables used in modelling.

<table>
<thead>
<tr>
<th>Models</th>
<th>Abbreviations</th>
</tr>
</thead>
<tbody>
<tr>
<td>Generalised Linear Models</td>
<td>GLM</td>
</tr>
<tr>
<td>Hurdle Models</td>
<td>Hurdle</td>
</tr>
<tr>
<td>Zero-Inflated Models</td>
<td>ZI</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Error Family</th>
</tr>
</thead>
<tbody>
<tr>
<td>Poisson</td>
</tr>
<tr>
<td>Negative Binomial</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Response Variables</th>
</tr>
</thead>
<tbody>
<tr>
<td>Estimated count of <em>A. solandri</em></td>
</tr>
<tr>
<td>Estimated count of <em>A. hastata</em></td>
</tr>
<tr>
<td>Estimated count of <em>A. microsperma</em></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Predictor Variables</th>
</tr>
</thead>
<tbody>
<tr>
<td>Slope</td>
</tr>
<tr>
<td>Aspect</td>
</tr>
<tr>
<td>Topographic Index</td>
</tr>
<tr>
<td>Non-Vascular plant coverage</td>
</tr>
<tr>
<td>Vascular climber coverage</td>
</tr>
<tr>
<td>Host Species</td>
</tr>
<tr>
<td>Host DBH</td>
</tr>
<tr>
<td>Host Height</td>
</tr>
</tbody>
</table>

**Variable selection**

I used model selection to narrow the six candidate models for each site × species combination down to one on which I carried out variable selection. Due to the exploratory nature of my study, a large number of variables were collected to identify possible environmental correlates. As even small correlations between predictor variables can alter the resulting significance of other predictors, each of the full models needed to be reduced to only the terms significant at the $\alpha = 0.05$ level. To reduce the variables systematically each candidate model was assessed via the `dredge` function in the MuMln package (version 1.40.4; Barton 2009) to identify a list of possible models whose AICc scores could not be differentiated, based on delta values less than four (Burnham & Anderson 2003). All terms from these models were incorporated into a single
model, and then reduced using backwards elimination until only terms significant at the $\alpha = 0.05$ level were included.

**Host-scale distributions**

The abundance and distribution of each *Astelia* spp. on *D. cupressinum* were analysed using log-linear models with a Poisson error, with the predictors based on the positional data recorded (Fig. 3.6). Models were reduced using backwards elimination via AICc scores. Moreover, the distributions of each species were visualised using rose graphs.

All analyses were conducted in Rx64 (Version 3.5.1; Team, 2013) using the RStudio interface (Version 1.1.447; Team 2015). All data manipulations were conducted with either the base R package, or the tidyverse package (Version 0.8.1; Wickham 2017). Zero-Inflated and hurdle models were constructed with the pscl package (Version 1.5.2; Jackman et al., 2007), while GLMs were built using the stats package (Version 3.6.0; Team & Worldwide 2002). Variable selection was performed partly with the MuMln package (Version 1.42.1; Barton 2009). All plots were produced using ggplot2 (version 3.0.0; Wickham 2010).

### 3.3 Results

#### 3.3.1 Forest scale results

Of the 864 quarters surveyed across all PCQs, 13 had no hosts within 15 metres. Ten of these were the absence of a tree fern (*Cyathea* or *Dicksonia* spp.) or *R. sapida* within this distance range, and the remaining three represented the absence of any branching tree species. As these 13 represent a small proportion (0.015) of the total number of quadrats the density corrections recommended by Warde & Petranka (1981) will not affect the overall analysis of these results.

The observations taken at Taumata and Hunua spanned similar abiotic conditions, although Hunua had a slightly greater range in the aspects sampled and was at a slightly higher elevation (Table 3.3). However, the observations taken at Pirongia were quite different in terms of aspect
compared to Taumata, although similar to Hunua in most regards. Ohlemüller & Wilson (2002) suggested that broadleaf/podocarp forest composition does not differ significantly over ranges of 100 m elevation at relatively low elevations like these. While my study cannot definitively exclude an elevation effect between sites it is unlikely that this difference would have led to substantial changes in the overall epiphyte communities. However, changes in elevation may affect individual species, such as A. microsperma, which is purported to occur primarily at elevations > 300 m (Kirby 2016).

Table 3.3– Summary statistics of the abiotic features at each site surveyed from the ground. Elevation and Aspect are presented as ranges, while topographic index show the minimum, median and maximum values for each site.

<table>
<thead>
<tr>
<th>Site</th>
<th>Elevation (metres a.s.l.)</th>
<th>Aspect (degrees)</th>
<th>Topographic Index (min – median – max)</th>
<th>Slope (%) (min – median – max)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hunua</td>
<td>180–250</td>
<td>136–325</td>
<td>1 – 4 – 5</td>
<td>11 – 35 – 70</td>
</tr>
<tr>
<td>Pirongia</td>
<td>200–250</td>
<td>60–170</td>
<td>2 – 3 – 5</td>
<td>3 – 14 – 49</td>
</tr>
</tbody>
</table>

Analysis of the host meta-data suggested that the vegetation composition was similar among sites, but that median canopy height and tree diameters differed (Table 3.4). All three sites were dominated by Beilschmiedia spp. with Cyathea dealbata abundant in the understorey. A post-hoc analysis of variance (ANOVA) was carried out to determine if there were statistically significant differences in mean height or diameter of branching trees across the sites. Both height and DBH were found to be statistically different between sites ($F$-value = 71.85, $p$-value $< 2.2 \times 10^{-16}$, $F$-value = 10.22, $p$-value $= 4.6 \times 10^{-5}$), with Taumata having the smallest trees by both measures, and Pirongia the largest (Table 3.4). Both tests had their respective assumptions met. These results suggest that any differences across covariates of Astelia spp. abundance may be confounded by the underlying structural differences among these forests.
Table 3.4 – Summary of dominant trees for each combination of site × tree-type, with DBH, height and basal area (means ± standard error).

Basal areas are displayed with 95% confidence limits below point estimates rather than standard errors.

<table>
<thead>
<tr>
<th>Site</th>
<th>Dominant Branching Tree spp. (%)</th>
<th>Branching Tree DBH (cm)</th>
<th>Branching Tree Height (m)</th>
<th>Basal Area Branching Trees (m²/hectare)</th>
<th>Dominant Palm/Tree fern spp. (count)</th>
<th>Palm/Tree fern DBH (cm)</th>
<th>Palm/Tree fern Height (m)</th>
<th>Basal Area Palms/Tree ferns (m²/hectare)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Taumata</td>
<td><em>Beilschmiedia tarairi</em> (0.39)</td>
<td>32.9 ± 1.90</td>
<td>10.7 ± 0.29</td>
<td>61.0</td>
<td><em>Rhopalostylis sapida</em> (0.56)</td>
<td>17.3 ± 0.4</td>
<td>4.8 ± 0.3</td>
<td>11.5</td>
</tr>
<tr>
<td></td>
<td><em>Coprosma arborea</em> (0.17)</td>
<td></td>
<td></td>
<td></td>
<td><em>Cyathea dealbata</em> (0.44)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Vitex lucens</em> (0.10)</td>
<td></td>
<td></td>
<td></td>
<td>NA</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hunua</td>
<td><em>Beilschmiedia tarairi</em> (0.56)</td>
<td>38.6 ± 1.26</td>
<td>14.1 ± 0.24</td>
<td>39.5</td>
<td><em>Rhopalostylis sapida</em> (0.57)</td>
<td>14.4 ± 0.26</td>
<td>5.8 ± 0.2</td>
<td>3.1</td>
</tr>
<tr>
<td></td>
<td><em>Dysoxylum spectabile</em> (0.20)</td>
<td></td>
<td></td>
<td></td>
<td><em>Cyathea dealbata</em> (0.43)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Knightia excelsa</em> (0.10)</td>
<td></td>
<td></td>
<td></td>
<td>NA</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pirongia</td>
<td><em>Beilschmiedia tawa</em> (0.41)</td>
<td>44.9 ± 2.25</td>
<td>16.9 ± 0.51</td>
<td>59.3</td>
<td><em>Cyathea dealbata</em> (0.72)</td>
<td>17.1 ± 0.59</td>
<td>4.9 ± 0.2</td>
<td>14.7</td>
</tr>
<tr>
<td></td>
<td><em>Knightia excelsa</em> (0.13)</td>
<td></td>
<td></td>
<td></td>
<td><em>Dicksonia squarrosa</em> (0.28)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Elaeocarpus dentatus</em> (0.12)</td>
<td></td>
<td></td>
<td></td>
<td><em>Rhopalostylis sapida</em> (&gt;0.01)</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Note: The NA’s recorded for non-tree spp. were due to the face that only two species of plant in this category were observed in these locations.
A strong host effect was observed across the aggregated tree data (Table 3.5), although this was not assessed statistically. Species that *Astelia* spp. occupied most commonly included *D. cupressinum, Laurelia novae-zelandiae, Metrosideros excelsa*, and *Vitex lucens*. Species that supported *Astelia* spp. rarely included *Hedycara arborea, Melicytus ramiflorus, Litsaea calicaris*, and *Dacrycarpus dacrydioides*. However, differences between tree species in their ability to host *Astelia* spp. may be an artefact resulting from the intrinsic difference in the tree sizes of these species. It is unclear if there are any differences in preference for particular host species of different *Astelia* spp. as these data were aggregated over sites.

Tree ferns (*Cyathea* and *Dicksonia* spp.) and palms (*R. sapida*) were rare hosts with only a small proportion of individuals (≤ 0.05) hosting any *Astelia* spp. (Table 3.5). *C. arborea* also appeared to be a non-preferred host, even though a relatively high number of individuals were surveyed (Table 3.5). Several other species of phorophyte were also relatively uncommon in terms of occurrence in the landscape, so their host quality for *Astelia* spp. could not be effectively assessed (Appendix 2; Table A-2.1).

Phorophyte species that were uncommon (n < 5) or were not commonly hosts to *Astelia* spp. (proportion ≤ 0.05) were excluded from the subsequent modelling. These were excluded to remove false zeros and limit the dispersion in these data, as they likely represented poor hosts, although this may be partly an effect of tree size. Excluding these host trees from the analysis removed 477 of the original 851 observations and eliminated 16 of the 29 host species observed. The partially randomised selection of trees precluded the collection of balanced sample sizes across all host species. Furthermore, the wide range of host species sampled and the small proportion of trees that acted as hosts prevented any form of robust analysis of a host species effect, although this has been described in previous studies (Callaway *et al.* 2002; Parra *et al.* 2009; Wyse & Burns 2011; Jueriado *et al.* 2012; Taylor & Burns 2015; Li *et al.* 2017).
Table 3.5 – Counts of each host species surveyed that hosted at least one Astelia spp., the number and the proportion along with the estimated count for each Astelia spp. Data accumulated over all three sites. See full table in Appendix. Host DBH presented as mean ± SE.

<table>
<thead>
<tr>
<th>Host Species</th>
<th>Host spp. count</th>
<th>Hosts with Astelia spp.</th>
<th>Proportion with Astelia spp.</th>
<th>Host DBH (cm)</th>
<th>A. hastata count</th>
<th>A. microsperma count</th>
<th>A. solandri count</th>
</tr>
</thead>
<tbody>
<tr>
<td>Beilschmiedia tarairi</td>
<td>136</td>
<td>52</td>
<td>0.38</td>
<td>36.7 ± 1.3</td>
<td>358</td>
<td>0</td>
<td>7</td>
</tr>
<tr>
<td>Beilschmiedia tawa</td>
<td>73</td>
<td>39</td>
<td>0.53</td>
<td>56.1 ± 3.5</td>
<td>146</td>
<td>354</td>
<td>33</td>
</tr>
<tr>
<td>Knightia excelsa</td>
<td>37</td>
<td>15</td>
<td>0.41</td>
<td>34.2 ± 1.9</td>
<td>83</td>
<td>14</td>
<td>1</td>
</tr>
<tr>
<td>Dysoxylum spectabile</td>
<td>42</td>
<td>11</td>
<td>0.26</td>
<td>29.0 ± 2.2</td>
<td>54</td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td>Vitex lucens</td>
<td>15</td>
<td>9</td>
<td>0.60</td>
<td>61.5 ± 7.3</td>
<td>32</td>
<td>0</td>
<td>14</td>
</tr>
<tr>
<td>Elaeocarpus dentatus</td>
<td>17</td>
<td>7</td>
<td>0.41</td>
<td>50.8 ± 3.9</td>
<td>0</td>
<td>62</td>
<td>0</td>
</tr>
<tr>
<td>Laurelia novae-zelandiae</td>
<td>5</td>
<td>3</td>
<td>0.60</td>
<td>62.5 ± 25.3</td>
<td>2</td>
<td>42</td>
<td>0</td>
</tr>
<tr>
<td>Metrosideros robusta</td>
<td>5</td>
<td>3</td>
<td>0.60</td>
<td>103.7 ± 31.5</td>
<td>33</td>
<td>0</td>
<td>9</td>
</tr>
<tr>
<td>Dacrydium cupressinum</td>
<td>4</td>
<td>3</td>
<td>0.75</td>
<td>70.9 ± 17.2</td>
<td>28</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Dacrycatus dacrydioides</td>
<td>11</td>
<td>2</td>
<td>0.18</td>
<td>38.1 ± 4.1</td>
<td>12</td>
<td>0</td>
<td>4</td>
</tr>
<tr>
<td>Hedycarya arborea</td>
<td>9</td>
<td>1</td>
<td>0.11</td>
<td>25.9 ± 3.0</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Litsea calicaris</td>
<td>7</td>
<td>1</td>
<td>0.14</td>
<td>46.4 ± 19.3</td>
<td>0</td>
<td>2</td>
<td>3</td>
</tr>
<tr>
<td>Melicytus ramiflorus</td>
<td>8</td>
<td>1</td>
<td>0.12</td>
<td>22.9 ± 4.2</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Coprosma arborea</td>
<td>33</td>
<td>1</td>
<td>0.03</td>
<td>22.4 ± 0.9</td>
<td>8</td>
<td>0</td>
<td>7</td>
</tr>
<tr>
<td>Cyathea dealbata</td>
<td>223</td>
<td>9</td>
<td>0.04</td>
<td>16.5 ± 0.4</td>
<td>0</td>
<td>8</td>
<td>4</td>
</tr>
<tr>
<td>Rhopalostylis sapida</td>
<td>160</td>
<td>5</td>
<td>0.03</td>
<td>17.3 ± 0.3</td>
<td>9</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Dicksonia squarrosa</td>
<td>39</td>
<td>2</td>
<td>0.05</td>
<td>10.7 ± 0.4</td>
<td>2</td>
<td>11</td>
<td>0</td>
</tr>
<tr>
<td>Totals</td>
<td>455</td>
<td>166</td>
<td>778</td>
<td>507</td>
<td>85</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Note: Those below the double line are host species which were excluded from subsequent analyses
The number of clumps observed in each species × size class combination differed among and within the study sites (Fig. 3.7). *A. hastata* presented a reverse J-curve at Taumata, suggesting that the population may be self-replacing (Virillo *et al.* 2011). In contrast, *A. hastata* peaked in the 2-3 clump size-class at Hunua, suggesting that the population may be regenerating or there was a previous period of relatively high establishment or low mortality. *A. microsperma* had a reverse J-curve at Pirongia; the only site at which this species was observed, again indicating the species may be self-replacing. *A. solandri* occurred in relatively small numbers at all sites and rarely occurred in large clumps, most commonly occurring individually, although one clump consisting of four or more individuals was observed at Pirongia.

![Graph](image)

**Figure 3.7** – The number of each clump size seen at each site, coloured by *Astelia* spp. The dotted line indicates a count of zero. Note: the same number of trees were sampled at each site, so the sampling intensity was constant.

The log-linear model of abundance in *A. hastata* across the forest sites showed that all forest sites were significantly different, with Hunua having the highest count of individuals and Taumata a close second (Table 3.6). In contrast, *A. solandri* was more abundant at Taumata and
Hunua than at Pirongia. *A. microsperma* was only observed at Pirongia where it was extremely abundant (Fig. 3.7).

**Table 3.6** – Log-linear models of abundance of *A. hastata* and *A. solandri* among the three forest sites.

<table>
<thead>
<tr>
<th>Species</th>
<th>Coefficients</th>
<th>Estimates</th>
<th>Standard Error</th>
<th>z-values</th>
<th>p-values</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>A. hastata</em></td>
<td>Intercept</td>
<td>4.52</td>
<td>0.06</td>
<td>75.12</td>
<td>&lt; 2.2 × e⁻¹⁶</td>
</tr>
<tr>
<td></td>
<td>Hunua</td>
<td>0.57</td>
<td>0.08</td>
<td>7.57</td>
<td>3.82 × e⁻¹⁴</td>
</tr>
<tr>
<td></td>
<td>Pirongia</td>
<td>-1.51</td>
<td>0.14</td>
<td>-10.67</td>
<td>&lt; 2.2 × e⁻¹⁶</td>
</tr>
<tr>
<td></td>
<td>Intercept</td>
<td>3.04</td>
<td>0.13</td>
<td>24.17</td>
<td>&lt; 2.2 × e⁻¹⁶</td>
</tr>
<tr>
<td><em>A. solandri</em></td>
<td>Hunua</td>
<td>-0.25</td>
<td>0.19</td>
<td>-1.32</td>
<td>0.19</td>
</tr>
<tr>
<td></td>
<td>Pirongia</td>
<td>-1.01</td>
<td>0.24</td>
<td>-4.14</td>
<td>3.5 × e⁻⁵</td>
</tr>
</tbody>
</table>

Note: The intercept codes for the estimated abundance at Taumata, while all other coefficients show the respective sites’ difference relative to estimated abundance at Taumata.

The model assessment for *A. hastata* showed that the ZINB model had the lowest AICc score for the Taumata site (Table A-2.2) and that the log-likelihood was significantly higher than the model with the next lowest AICc score according to a post-hoc likelihood ratio test ($X^2 = 10.6$, $p$-value = 2.2 × e⁻¹⁶). The ZINB models at Hunua and Pirongia had support given the data compared to the Hurdle NB models at these sites. As mentioned previously the ZI models are likely more correct from an ecological standpoint, as they allow the possibility that even if conditions are ideal for *Astelia* spp. to establish and survive, lack of dispersal or chance acting alone can lead to absences. As such, ZI models were chosen over hurdle models when all else was equal. The ZINB *A. hastata* models at all three sites could not be distinguished from their hurdle model counterparts and as such the ZINB were chosen for variable selection. Similarly, the ZINB model for *A. microsperma* at Pirongia could not be distinguished from the hurdle NB model, so the ZINB model was used during variable selection for this species (Table A-2.3). For each of the site models of *A. solandri* distributions the Poisson family tended to have lower AICc scores than the negative binominal counterpart (Table A-2.4). Hurdle and ZI models with
Poisson errors could not be differentiated in terms of AICc or log-likelihood, so ZIP models were chosen in each case following Ockham’s razor.

After variable selection, all seven models included HostDBH as a significant covariate of Astelia spp. presence or absence (Table 3.7). In the model for *A. hastata* at Pirongia, HostHgt was also a significant covariate. The estimates for both parameters were negative for all models meaning that for each unit increase, *Astelia* spp. were more likely to be present (Figures 3.8 – 3.9). Host DBH was the only variable deemed important for the distribution of *A. microsperma*, which may partly be the result of the species being observed at only one site and therefore detected in a narrower range of conditions than the other two species.

An exploration of the abiotic features at each site showed that there was an unbalanced design with regards to the east – west gradient across the three sites, due to idiosyncrasies associated with each site and the availability of sampling locations. In particular, the sampling sites accessible at Pirongia were either true north, true east or somewhere in between the two (Table 3.3). As such, the significance of the effect of easting at the Pirongia site (Table A-2.5) is likely the result of unbalanced sampling rather than a true effect and will not be discussed further.

**Table 3.7** - Output from each of the seven ZI models after variable selection. Log-odd estimates, standard error of the mean, z-values and p-values are shown for all significant variables for each possible species × site combination.

<table>
<thead>
<tr>
<th>Site</th>
<th>Species</th>
<th>Model</th>
<th>Parameter</th>
<th>Estimate</th>
<th>S.E.</th>
<th>z-value</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Taumata</td>
<td><em>A. hastata</em></td>
<td>zero</td>
<td>HostDBH</td>
<td>-0.09</td>
<td>0.03</td>
<td>-2.89</td>
<td>0.004</td>
</tr>
<tr>
<td>Taumata</td>
<td><em>A. hastata</em></td>
<td>count</td>
<td>HostDBH</td>
<td>0.02</td>
<td>0.01</td>
<td>3.67</td>
<td>0.000</td>
</tr>
<tr>
<td>Taumata</td>
<td><em>A. hastata</em></td>
<td>count</td>
<td>Northing</td>
<td>-0.85</td>
<td>0.31</td>
<td>-2.71</td>
<td>0.007</td>
</tr>
<tr>
<td>Hunua</td>
<td><em>A. hastata</em></td>
<td>zero</td>
<td>HostDBH</td>
<td>-0.08</td>
<td>0.02</td>
<td>-4.16</td>
<td>0.000</td>
</tr>
<tr>
<td>Hunua</td>
<td><em>A. hastata</em></td>
<td>count</td>
<td>(Intercept)</td>
<td>-0.70</td>
<td>0.75</td>
<td>-0.94</td>
<td>0.347</td>
</tr>
<tr>
<td>Hunua</td>
<td><em>A. hastata</em></td>
<td>count</td>
<td>HostDBH</td>
<td>0.02</td>
<td>0.01</td>
<td>3.70</td>
<td>0.000</td>
</tr>
<tr>
<td>Hunua</td>
<td><em>A. hastata</em></td>
<td>count</td>
<td>TopoIndex2</td>
<td>1.47</td>
<td>0.91</td>
<td>1.60</td>
<td>0.109</td>
</tr>
<tr>
<td>Hunua</td>
<td><em>A. hastata</em></td>
<td>count</td>
<td>TopoIndex3</td>
<td>1.39</td>
<td>0.76</td>
<td>1.82</td>
<td>0.069</td>
</tr>
<tr>
<td>Hunua</td>
<td><em>A. hastata</em></td>
<td>count</td>
<td>TopoIndex4</td>
<td>1.57</td>
<td>0.73</td>
<td>2.14</td>
<td>0.032</td>
</tr>
<tr>
<td>Location</td>
<td>Species</td>
<td>Count</td>
<td>Covariate</td>
<td>TopoIndex5</td>
<td>HostDBH</td>
<td>HostHgt</td>
<td>Northing</td>
</tr>
<tr>
<td>----------</td>
<td>---------</td>
<td>-------</td>
<td>-----------</td>
<td>------------</td>
<td>---------</td>
<td>---------</td>
<td>----------</td>
</tr>
<tr>
<td>Hunua</td>
<td>A. hastata</td>
<td>count</td>
<td>TopoIndex5</td>
<td>2.05</td>
<td>0.74</td>
<td>2.78</td>
<td>0.005</td>
</tr>
<tr>
<td>Pirongia</td>
<td>A. hastata</td>
<td>zero</td>
<td>HostDBH</td>
<td>-0.03</td>
<td>0.01</td>
<td>-2.29</td>
<td>0.022</td>
</tr>
<tr>
<td>Pirongia</td>
<td>A. hastata</td>
<td>zero</td>
<td>HostHgt</td>
<td>-0.24</td>
<td>0.08</td>
<td>-3.09</td>
<td>0.002</td>
</tr>
<tr>
<td>Pirongia</td>
<td>A. hastata</td>
<td>count</td>
<td>HostDBH</td>
<td>0.01</td>
<td>0.00</td>
<td>2.38</td>
<td>0.017</td>
</tr>
<tr>
<td>Pirongia</td>
<td>A. hastata</td>
<td>count</td>
<td>Northing</td>
<td>1.28</td>
<td>0.31</td>
<td>4.10</td>
<td>0.000</td>
</tr>
<tr>
<td>Pirongia</td>
<td>A. microsperma</td>
<td>zero</td>
<td>HostDBH</td>
<td>-0.10</td>
<td>0.03</td>
<td>-3.79</td>
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</tr>
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<td>count</td>
<td>HostDBH</td>
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<td>0.01</td>
<td>2.52</td>
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</tr>
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<td>zero</td>
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</tr>
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</tr>
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</tr>
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<td>HostDBH</td>
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<td>0.03</td>
<td>-2.00</td>
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</tr>
<tr>
<td>Hunua</td>
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<td>count</td>
<td>Slope</td>
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<td>0.01</td>
<td>3.00</td>
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</tr>
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<td>count</td>
<td>HostDBH</td>
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</tr>
<tr>
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<td>HostDBH</td>
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<td>count</td>
<td>Northing</td>
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<td>2.71</td>
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</table>

Note: The intercept term in the zero portion of each of the ZINB models describes the log-odds ratio of the respective species being absent when all other parameters are held at zero or their baseline. Intercepts for the count portion of the model were displayed only when there was a factor, for which the intercept acted as a baseline (i.e. TopoIndex1). Finally, certain terms which were deemed biased (i.e. easting in Pirongia) were excluded from this table, although the full table can be found in the Appendix 2 (Table A-2.5).

No parameter plot was produced for A. microsperma as it was only recorded at one site, and the model determined only host DBH was significant. What is clear from these models is that all three species tended to increase in abundance with increasing host DBH (Table 3.7, Figs. 3.8, 3.9). Moreover, all three species abundances have relatively strong relationships with covariates that are related to both light and moisture availability, although the direction of association is dependent on the combination of site × species. For instance, a more northerly aspect, steeper slope or being closer to a ridge than a gully are all associated with higher levels of light and lower levels of humidity, on average, due to breaks in the canopy and greater
exposure to sunlight (Oliver 1930). The humidity is likely to be even lower in sections of forest which are near a ridge and/or have steep slopes as the canopy is more likely to be broken allowing the passage of wind through the understory (Oliver 1930; Shuttleworth 1985).

**Figure 3.8** – Log parameter estimates from the count portion of the three ZINB models of *A. hastata*. The error bars are ± one standard error. Parameters below zero are negatively correlated with *A. hastata* abundance, while those above zero are positively correlated with abundance.
Figure 3.9 – Log parameter estimates from the count portion of the three ZIP models for *A. solandri*. The error bars are ± the associated standard error. Parameters below zero are negatively correlated with *A. solandri* abundance, while those above zero are positively correlated with abundance.

### 3.3.2 Individual host tree scale results

A total of 156 *A. hastata* and 38 *A. solandri* plants were observed across the 15 *D. cupressinum* host trees, showing that *A. hastata* was the more common of the two species. The log-linear model of *A. hastata* distributions on individual hosts showed that there was a strong positive correlation with northerly aspects relative to other aspects (Fig. 3.10). Moreover, there was an increasing abundance of *Astelia* at higher vertical strata, with the emergent tier having the highest abundance (Fig. 3.10). Finally, the crook and branch of the tree were not found to differ from each other in abundance, but the trunk had significantly lower abundances of *A. hastata* (Fig. 3.11). No interaction between any of the terms was found as indicated by the parallel lines in Fig. 3.10 and 3.11, meaning that the effects of these factors were strictly additive.
The assumptions of this model were met as there was no evidence that the abundance data of *A. hastata* on individual host trees departed from a Poisson distribution ($\chi^2$: 7.75, 5; *p*-value = 0.17). A full table of output for the log-linear model can be found in Appendix 2 (Table A-2.6).

**Figure 3.10** - Summary of the log-linear model for *A. hastata*, showing the relationship between the radial and vertical strata, with associated least significant differences (LSD) bar showing differences significant at an $\alpha = 0.05$ level after False Discovery Rate (FDR) error correction.
Figure 3.11 - Summary of the log-linear model for *A. hastata*, showing the relationship between the radial strata and position, with associated least significant differences (LSD) bar showing differences significant at an $\alpha = 0.05$ level after False Discovery Rate (FDR) error correction.

There were no significant differences in the abundance of *A. solandri* in terms of the radial strata, vertical strata, or position on the branch (Figs. 3.12, 3.13; Table A-2.7). However, there were differences in terms of the vertical strata which the species occupied; similar abundances of *A. solandri* were observed in the canopy and emergent tiers and significantly lower abundances in the understory (Fig. 3.12). The assumptions of the log-linear model for *A. solandri* were not met and as such the model should be interpreted with caution. For a full summary of the assumptions see Appendix 2.
Figure 3.12 - Summary of the log-linear model for *A. solandri*, showing the relationship between the radial and vertical strata, with associated LSD bar showing differences significant at an $\alpha = 0.05$ level after False Discovery Rate (FDR) error correction.
Figure 3.13 - Summary of the log-linear model for *A. solandri*, showing the relationship between the radial strata and position, with associated LSD bar showing differences significant at an $\alpha = 0.05$ level after False Discovery Rate (FDR) error correction.

A comparison of the abundance of each species across the radial and vertical strata suggested that *A. hastata* is more likely to occur in higher light conditions, as it is all but absent in the understory tier and becomes increasingly abundant higher up the host surface (Fig. 3.14). Moreover, the species is most abundant on the northern face of the tree. In contrast, *A. solandri* tends to occur more on the southerly side of the host and the canopy tier over the emergent tier (Fig. 3.14). Interestingly, its abundance on the northerly face of the host appears to be
primarily in the canopy tier. Both species only occurred in the understory in relatively small proportion.
Figure 3.14 – Rose diagram displaying the proportion of *A. hastata* (red) and *A. solandri* (blue) on each cardinal face of the host grouped by vertical strata. Proportions were calculated from the total number observed of the respective species.
3.4 Discussion

3.4.1 Distributions between and within forest sites

Changes in *Astelia* spp. abundances across the three forest sites were observed and were largely species-specific. These differences in abundances between sites were consistent with the probability of occurrences as predicted by the SDMs (Chapter 2). The SDMs predicted that the niche spaces of each of these species were at least partly dependent on the abiotic conditions at the site, particularly the solar radiation and minimum temperature (Table 3.1). The changes in abundance along these gradients suggests that the niche differentiation of epiphytic *Astelia* spp. occurs not only across New Zealand, but even along a relatively small gradient in the North Island. While high probabilities of occurrence are not necessarily an indicator of habitat quality, *A. hastata*’s relative prominence at each site was in line with the high probability of occurrence predicted by the SDM. Similarly, *A. solandri* had low predicted likelihoods of occurrence and was only present in relatively small abundances at each site. The absences of *A. microsperma* at Taumata and Hunua were not consistent with the predictions of the SDM, however, which predicted relatively high probabilities of occurrence, suggesting that something else was excluding this species. The abundance of *A. microsperma* at Pirongia supports the claims of (Kirby 2016), who purported that they typically occur at elevations around 300 m or higher.

The high abundance of *A. hastata* relative to the other two *Astelia* spp. at both Taumata and Hunua could be due to *A. hastata* being able to tolerate higher VPDs. Most epiphytes are thought to meet their moisture requirements by accessing humidity, as they lack access to the stores of moisture present in the soil (Benzing 2008). However, all three epiphytic *Astelia* spp. form phytotelma at the base of their leaves enabling them to store water in the leaf axil, which is accessed via roots that grow between the leaves (Moore &
Edgar 1970; Killick et al. 2014; Kirby 2016). In particular, *A. hastata* typically has larger phytotelma than are present in the other two epiphytic *Astelia* spp. as a result of greater width and erectness of the leaves, allowing this species to store more water, although this has yet to be precisely quantified (Moore & Edgar 1970; Killick et al. 2014; Kirby 2016). The presence of larger phytotelma may make *A. hastata* more tolerant of water-limited conditions, like at Taumata and Hunua, as compared to *A. microsperma* and *A. solandri*.

Similar differences in abundance among the three species were observed within the forests in individual parameters correlated with light. The presence of *A. hastata* was positively correlated with host height at Pirongia (Fig. 3.8), which may be the result of the relatively low solar inputs there (Table 3.1) negatively impacting on *A. hastata* establishment/persistence on smaller sub-canopy trees relative to other sites. In addition, *A. hastata* abundances were positively correlated with other variables associated with increased light levels (i.e. northerly aspects and steep slopes), at both Pirongia and Hunua. However, at Taumata, *A. hastata* abundance was negatively correlated with northing, perhaps suggesting that the light on northerly aspects was in excess of requirements and/or that solar radiation was so high on these aspects as to reduce water availability, so negatively impacting on the species establishment/persistence there. Similarly, *A. solandri* abundance was negatively correlated with host height at Taumata (Fig. 3.9). The propensity of *A. solandri* to establish and persist on smaller hosts may be indicative of an inability to tolerate water-limited conditions, as Taumata had a larger VPD (Table 3.1), or potentially being competitively excluded. The common trend among the *Astelia* spp. within forests was a tendency to occur in higher light conditions, with the above-mentioned exceptions. These results are consistent with the observations of (Oliver 1930) who suggested that
the epiphytic *Astelia* spp. he observed were sun epiphytes, a characterization also supported by (Dawson & Sneddon 1969). The observed correlations are likely the result of the ability of all three epiphytic *Astelia* spp. to store water in their phytotelma as well as their propensity for trapping litter and forming canopy soil. Access to these moisture stores may allow them to occur in conditions where water-limits might otherwise exclude other vascular epiphytes.

Across all three *Astelia* spp. there appears to be a consistent requirement for a tree of a certain size for colonisation, and this size threshold is host specific as shown by Taylor et al. (2015). Abundance increases with the host’s DBH at all three sites (Table 3.7). A correlation between host tree DBH and either vascular epiphyte species richness and/or abundance has been noted numerous times in New Zealand (Knightbridge & Ogden 1998; Taylor & Burns 2015) and in forests overseas (Flores-Palacios & García-Franco 2006; Benzing 2008). This correlation may be the cumulative result of several factors simultaneously changing with an increased DBH, such as time for colonisation, increased structure/water-holding capacity of thicker bark, pH, roughness, or habitat heterogeneity associated with increased height or branch architecture (Bergey et al. 1995; Zotz et al. 1999; Belinchón et al. 2009; Jueriado et al. 2012; Woods 2017). There were also some host preferences among *Astelia* spp., although it is unclear how much of this is due to differences in the diameters that each phorophyte species commonly attains (Table 3.5).

**Niche differentiation on host trees**

Niche differentiation between *A. hastata* and *A. solandri* is much clearer at the scale of host trees than across entire forests, with these two species appearing to differ in their tolerance of water-limits. *A. hastata* tended to occur in higher vertical tiers and the
northern face of their hosts, while A. solandri was common in the canopy and more southerly positions (Fig. 3.14). A. solandri may be favouring these positions as they experience a relatively higher humidity (Dickinson et al. 1993; Sanger & Kirkpatrick 2017b) or it could be due to competitive exclusion by A. hastata for niche space.

The vertical separation of these two species supports Dawson & Sneddon’s (1969) observation that A. hastata typically occupied higher vertical strata than A. solandri. Vertical stratification of epiphyte species has been previously documented in tank epiphytes (Graham & Andrade 2004), other vascular epiphytes (Krömer et al. 2007; Parra et al. 2009) and non-vascular epiphytes (McCune 1993; Fritz 2009; Acebey et al. 2017). The vertical stratification of epiphytes has been attributed to changes in microclimatic gradients, particularly increased light availability and the associated increase in VPD in the higher tiers of the tree (Denmead & Bradley 1985; Graham & Andrade 2004; Krömer et al. 2007; Parra et al. 2009). Similarly, vascular epiphyte distributions may be influenced by cardinal direction (Taylor & Burns 2016), as well as other non-vascular epiphytes (Giordani 2006; Jueriado et al. 2012; Ódor et al. 2013; Farias et al. 2017). The northern face (or southern face in the Northern Hemisphere) of phorophytes is more exposed and associated with higher light, lower humidity and a more variable microclimate compared to the inverse cardinal direction (McCutchan & Fox 1986). The differences in the abundance of A. hastata and A. solandri across the vertical and radial strata of D. cupressinum are likely the result of niche separation of these two species along gradients of water-stress. This niche differentiation may be based on morphological and physiological differences influencing their tolerance of moisture-limits, as previously noted. However it is unclear as to whether these differences are due to A. solandri being competitively displaced from sites favoured by A. hastata, not
being able to establish/persist in these conditions, or some combination of the two (Van Horne 1983).

The lack of either species in the understory tier may be the result of a lack of suitable structural position on which to establish and/or the relatively lower light levels that would be associated with this vertical tier. The strong correlation of *A. hastata* with branches and the crook where the branch grows out of the tree suggest that the species requires horizontal surfaces for establishment and/or persistence. During my surveys I regularly encountered fallen *Astelia* clumps that had been dislodged from the canopy, which may have fallen from lower quality establishment sites that could not support their weight. However, the lack of interaction between tree position and either radial or vertical strata suggests that they are being driven by a need for secure establishment sites rather than differences in water availability that might be associated with these structural positions. *A. solandri* abundance did not differ between the three structural positions, although this may be due to the relatively low counts observed of this species. Alternatively, the lack of a preference for particular positions on the host could be indicative of a further degree of niche differentiation between these two species.

### 3.5 Conclusion

The niches of epiphytic *Astelia* spp. appears to differ at the regional scale, as evidenced by changes in abundances across the three forest sites. At the dry end of the regional gradient (Taumata), both *A. hastata* and *A. solandri* were found to have some negative correlations with variables aligned with light and VPD, suggesting that these species may be at the upper end of their tolerance for water-stress there. At both other sites, both species were always positively correlated with variables aligned with light and VPD, suggesting that they could tolerate the limits on water-availability. The absence of
A. microsperma at all sites but Pirongia was unexpected given the predictions of the SDM but was congruous with other authors’ observations in terms of their preference for higher elevations. The abundances of all three species increased with the DBH of the host, which is consistent with past studies. At the scale of individual hosts, niche differentiation between A. hastata and A. solandri was observed, with A. hastata favouring conditions associated with higher light and VPDs. I hypothesize that the differences in abundance are the result of A. hastata having morphological features that increase its tolerance of water stress, relative to A. solandri, although further work is needed to confirm this.
Chapter Four - Vascular epiphyte associations with *Astelia* spp.

4.1 Introduction

The abiotic and biotic filters influencing community assembly often interact with one another, determining which group of species will ultimately co-exist (HilleRisLambers *et al.* 2012). A species tolerance or intolerance of abiotic conditions can be mediated by competitive and facilitative interactions (HilleRisLambers *et al.* 2012; Kraft *et al.* 2015; Bulleri *et al.* 2016), and understanding this dynamic is at the core of coexistence theory. However, the net direction of interaction (i.e. competitive or facilitative) among a set of organisms also depends on the scale at which it is studied (Levin 1992; Chave 2013). Moreover, the importance of different interactions can also vary across abiotic gradients associated with stress, as articulated in the Stress-Gradient Hypothesis (SGH) (Bertness & Callaway 1994; Pugnaire & Luque 2001; Stachowicz 2001; Kawai & Tokeshi 2007; Armas *et al.* 2011). The SGH predicts that with increasing environmental stress, organisms are more likely to interact in a facilitative rather than competitive manner (Pugnaire & Luque 2001; Stachowicz 2001), although the direction of the net interaction between organisms at extremely high stress levels is not entirely resolved (Malkinson & Tielbörger 2010). Evidence for the SGH has been reported many times across different scales, environmental conditions, communities and species, although not all studies describe the same relationship between stressors and net interaction, particularly when multiple stressors vary simultaneously (Maestre *et al.* 2006; Kawai & Tokeshi 2007b; Maestre *et al.* 2009; Malkinson & Tielbörger 2010; He *et al.* 2013; Liancourt *et al.* 2017).
In the case of epiphyte communities, water and light availability are two common stressors and their availability is typically negatively correlated (Adibah & Ainuddin 2011). The extremes of this water-light gradient exert high levels of stress on plants, as plants need to be either highly shade or drought tolerant to survive in them (Adibah & Ainuddin 2011). Such stress gradients can span relatively large distances (i.e. regionally) (Krömer et al. 2007; Fritz 2009; de la Rosa-Manzano et al. 2017; Sanger & Kirkpatrick 2017b) or occur at the scale of individual host trees with aspect-related changes in micro-climate (Graham & Andrade 2004; Krömer et al. 2007; Taylor & Burns 2016; Sanger & Kirkpatrick 2017b, a). Some of these stressors may shift in their importance as epiphyte communities undergo succession and/or sequential colonisation (Johansson 1974; Connell & Slatyer 1977; Dickinson et al. 1993; Taylor & Burns 2015; Woods 2017). Woods (2017) showed that phorophytes accumulate epiphytes through time, with pioneering species being displaced to the crown sections of the tree where environmental conditions are more akin to those experienced in early successional communities. However, only a few studies have considered the role of facilitation in the assembly of epiphyte communities (Turner & Foster 2006; Freiberg & Turton 2007; Jian et al. 2013) or how habitat heterogeneity affects plant-plant interactions. None to my knowledge have considered the role of the SGH in these interactions.

The highly nested nature of New Zealand’s vascular epiphyte assemblages (Burns 2007; Taylor et al. 2016) is indicative of some form of facilitation, and this has been attributed to the habitat formation of nest epiphytes (Astelia spp.) (Dawson & Sneddon 1969; Burns 2007; Taylor & Burns 2015). However, the vascular epiphyte species that nest epiphytes are facilitating, the mechanisms of any such facilitation, and under what conditions the net interaction is commensal/mutualistic are unclear. To broaden
understanding of epiphytic interactions in New Zealand assemblages, I observed species-specific associations of vascular epiphytes with *Astelia* spp. at three environmentally distinct forest sites to determine if there are regional-scale differences in these associations. Moreover, I recorded the spatial distribution of vascular epiphytes on individual phorophytes via a UAV to determine if: (i) these associations stay constant between scales; (ii) if there are any changes in association status among vertical strata up the host tree, and; (iii) if there are any changes in these associations radially around the host tree.

**4.2 Methods**

**4.2.1 Ground-based surveys**

Survey sites were selected based on the environmental gradients identified as important (by the SDM; Chapter 2) for *Astelia* spp., as these are likely either correlated with variables that influence epiphyte occurrence or directly impact on epiphyte establishment and survival (i.e. light, water availability and minimum temperature). The data for this chapter were also the result of the surveys described in Chapter 3. In addition to the meta-data collected on each host tree (described in Section 3.2.2), the occurrences of all vascular plant species growing epiphytically on each host sampled during the PCQ survey were recorded. The time spent surveying each host for vascular epiphytes was standardised following the methodology of (Burns & Dawson 2005), where the time taken to fully survey the tree was recorded, and then an additional one-third of that total time was spent again searching the host for epiphytes after the last was believed to be observed. If any more epiphytes were found, then one-third of total time was recalculated, and the survey restarted. In addition to the presence of vascular epiphytes, any associations of epiphytes with adult *Astelia* spp., defined as physical contact of any living part of the two organisms, was recorded. Only associations with
adult *Astelia* spp. were recorded as juveniles do not typically have large phytotelma or accumulated much soil, which is a putative mechanism for the facilitation of other vascular epiphytes by *Astelia* spp. In Chapter 3, tree ferns (*Cyathea* spp. and *Dicksonia* spp.) and *R. sapida* were found to be relatively poor hosts of *Astelia* spp. and so were excluded from these analyses.

### 4.2.2 Drone surveys

The same drone surveys carried out on 15 mature *D. cupressinum* individuals in the Hunua Ranges that were described in Chapter 3 were also used to collect the data presented in this chapter. In addition to the counts of *Astelia* spp. described in Chapter 3, the occurrences and locations within vertical and radial strata (Fig. 3.6) of all vascular epiphytes were also recorded. Any physical contacts between the vascular epiphytes and adult *Astelia* spp. were noted.

### 4.2.3 Statistical analyses

#### Forest scale statistics

The surveys along transects at each of the three forest sites resulted in a host × species matrix, with each row representing the particular epiphyte community on a given host, along with corresponding meta-data on the host tree. To determine how these epiphyte communities differed both between the different forest sites and within each site, the epiphyte host × species matrix was ordinated using Principle Co-ordinate Analysis (PCoA), after calculating dissimilarities using the Bray-Curtis dissimilarity coefficient (Bray & Curtis 1957). Correlations between the position on the PCoA axes and the meta-data collected on the host tree and the trees topographical context were overlaid if the variable had a correlation significant at the $\alpha = 0.05$ level. The ordinations were then assessed to determine if there were any trends in the association of vascular epiphytes with *Astelia* spp. along environmental gradients. To determine if the epiphyte
communities differed between any of the three forest sites a Permutational Multivariate Analysis of Variance (PERMANOVA) with 999 permutations was carried out (Anderson 2001). To check if the PERMANOVA assumption of multivariate homogeneity of group dispersions was met a multivariate analogue of a Levene’s test was carried out.

Associations on a pairwise basis between Astelia spp. and other vascular species among the forest sites were visualised by calculating the correlations for each species at each site and Astelia spp. and plotting these as a heat map.

Host tree scale statistics

Similar heat maps as produced for correlations among forest sites were produced for the correlations of each species with Astelia spp. on individual trees based on either the vertical strata occupied, or the radial position on the tree.

All analyses were conducted in R-X64 (Version 3.5.1; Team 2013), through the RStudio interface (Version 1.1.447; Team 2015). All multivariate analyses were conducted using the vegan package (Version 2.5.1; Oksanen et al. 2007) with ordination plots produced using base R. Heat maps were produced using ggplot2 (Version 2.2.1; Wickham 2010).

4.3 Results

4.3.1 Site level associations

There were statistically significant differences in epiphyte communities between the three forest sites (Fig. 4.1a, PERMANOVA: $F_{2,304} = 35.9, P = 0.001$). The assumption of homogenous dispersion from the group median centroids was approximately met.

The PCoA showed that there was much commonality between the epiphyte communities at different sites in the trends that they followed. Of the 143 branching trees surveyed at each site, roughly the same number of hosts at each site had at least
one epiphyte present (Fig. 4.1). The PCoA captured 61% of the variation in epiphyte communities with the first two axes. The primary variation between epiphyte communities was strongly correlated with the DBH and the height of the host (Fig. 4.1). The abundance of all three *Astelia* spp. increased along the horizontal axis (i.e. axis 1). The second axis of variation in the epiphyte communities was strongly correlated with slope and aspect of the host tree location. The epiphyte communities sampled on Mount Pirongia occurred on more easterly aspects and gentler slopes than those sampled at either the Taumata forest block or in the Hunua Ranges, so this axis could simply represent a site effect. Epiphyte communities at Taumata also typically occurred on smaller trees than at the other sites, although this may be due to the trees at this site having smaller trees on average (Table 3.4).

Positive associations between *G. lucida* with *Astelia* spp. were more prevalent at Taumata and Hunua than at Pirongia, suggesting that *G. lucida* may be more dependent on *Astelia* spp. where there is a greater VPD (Table 3.1; Fig. 4.2). Moreover, positive associations were more prevalent in forests in relatively water-limited conditions (i.e. north facing, high slope environments) and decreased as the environments became less water-limited (Fig. 4.3). The same trend was observed in *A. polyodon*, which showed a strong positive association with *Astelia* spp. at Taumata and less positive associations at Hunua and Pirongia, although observed abundance remained relatively constant (Figs. 4.2, 4.3). In contrast, the early pioneer fern *Pyrrosia eleagnifolia* had strong negative associations with *Astelia* spp. at all three sites, suggesting that this species either has different habitat requirements or competes for space. The latter seems more likely as *A. hastata* has similar habitat requirements to *P. eleagnifolia*. Both species tended to occur in the highest light and most water-limited positions (Chapter 3). A number of species tended to have intermediate or slightly negative associations with *Astelia* spp. (i.e. *M.*
*pustulatum, A. flaccidum*, etc.), although it was unclear what was driving these associations (Figs. 4.2, 4.3). Moreover, the fraction of all vascular epiphytes having a positive association with *Astelia* spp. became more positive among the sites as abiotic stress increased (Fig. 4.3).
Figure 4.1 – (a) Biplot of the ordination space created by the PCoA on the Bray-Curtis dissimilarity matrix of epiphyte communities on individual host trees, overlaid with a projection of environmental variables with significant ($P < 0.05$) correlations with the PCoA axes. The direction of the arrow indicates the sign (+/-) of the correlation, and the length indicates the strength of the correlation. Symbol indicates the presence/absence of *Astelia* spp.; (b) Bubble plot of the similarity relationships of epiphyte communities present on individual hosts with the colour indicating the *Astelia* spp. present on the host and the bubble size indicating the log count of the species. Grey points are hosts with epiphyte communities that did not have any *Astelia* spp. present.
Figure 4.2 – A series of PCoA ordinations of epiphyte communities on host trees highlighting the occurrence of individual species. Each plot indicates which trees played host to a given epiphyte species, with the symbol indicating whether the species was also observed associating with an Astelia spp., and the colour indicating which forest site the point originated from.
Figure 4.3 – Heat map of the correlations each species showed with *Astelia* spp. by site. A correlation of 1 indicates the species was always observed to be associating with an *Astelia* spp. at a given site, while -1 means the two species were never observed associating. The size of the bubble corresponded to the number of observations, scaled by 0.1, of a particular species and the number inside the bubble representing the correlation score to two significant figures. Note: When a species was only observed once at a site, the correlation score is not shown.
4.3.2 Host level correlations

No differences in correlation between Astelia spp. and other vascular epiphytes were observed among the cardinal directions of the host trees surface (Fig. 4.4). There were, however, differences in the number of individuals observed on a north/south orientation compared to an east/west gradient, as indicated by changes in the size of the bubbles (Fig. 4.4). What is also clear is that some species, such as Phlegmariurus varius, Griselinia lucida and Asplenium polyodon, tend to associate with Astelia spp., while other species, like Microsorum pustulatum, Dendrobium cunninghamii and A. flaccidum do not show strong correlations with Astelia spp. regardless of orientation (Fig. 4.4). Finally, P. eleagnifolia was the only species to consistently show negative correlations with Astelia spp. at this scale (Fig. 4.4).

Across all the species the number of epiphyte individuals observed increased up the vertical strata (Fig. 4.5). Interestingly, some species also changed in their correlation with Astelia spp. along these vertical gradients (Fig. 4.5). For instance, A. polyodon not only increased in abundance (number of observations) with increasing vertical stratum, but also became more strongly associated with Astelia spp. in higher tiers (Fig. 4.5). A similar, albeit weaker, trend was observed in A. flaccidum, M. pustulatum and P. eleagnifolia (Fig. 4.5). Anomalously, E. mucronata was strongly correlated with Astelia spp. in the understory but showed a negative correlation in the canopy and the emergent tiers (Fig. 4.5). However, with increasing vertical strata, interactions tended to become more positive, on average, across all species observed.

Vascular epiphyte species associations with Astelia spp. were species-specific and were relatively consistent in terms of both direction and species involved at all three scales that this study was conducted at (Figs. 4.2 – 4.5). The associations of vascular epiphytes
with epiphytic *Astelia* spp. were prevalent in later successional species (i.e. *G. lucida* and *Pittosporum cornifolium*); while pioneering species (i.e. *P. eleagnifolia, D. cunninghamii, Earina* spp.) tended to show negative associations (Dickinson et al. 1993; Taylor & Burns 2015; Kirby 2016). While facilitation or competition could not be directly inferred, it is unlikely that these species are simply showing preference for the same habitat, as association was defined as direct growth from an *Astelia* spp. clump. Moreover, the trends in association status occurred non-randomly with respect to a gradient of light/water-availability at all three scales, suggesting that *Astelia* spp. are providing access to moisture stores. For instance, *G. lucida* and *A. polyodon* showed the strongest correlations at the driest, hottest site (Table 3.1; Fig. 4.3), in communities on northerly aspects or on steep slopes (Fig. 4.2), and in the emergent tier of the canopy (Fig. 4.5). The species that were strongly negatively associated with the *Astelia* spp. were pioneer species of epiphyte communities (i.e. *P. eleagnifolia*). The consistency of most species correlations in terms of direction suggests that certain vascular epiphyte species are common associates of *Astelia* spp., others are relatively independent (i.e. *M. pustulatum*), and a few, like *P. eleagnifolia*, may be being displaced by *Astelia* spp.; longitudinal studies are needed to confirm this hypothesis.

A small degree of inconsistency between scales was observed in a few instances, but much of this can be attributed to biases in data collection. For example, *Metrosideros robusta* had negative correlations with *Astelia* spp. at all sites (Fig. 4.2), while at the scale of individual trees it showed strong positive correlations (Figs. 4.4, 4.5). Moreover, all associating *M. robusta* were those observed at the dry end of the gradient in the forests. Similarly, the change in *A. polyodon* associations between sites was likely a result of the differences in hosts being surveyed at different sites (Chapter 3). *A. polyodon* had a weak negative association with *Astelia* spp. at the forest scale, but strong
positive correlations in all strata at the host-tree scale. Moreover, *A. polyodon*’s association status at the host tree scale was prevalent on northerly orientations and in the emergent tier, with much weaker associations lower on the tree and on the southern aspect. *A. polyodon* is a facultative epiphyte, occasionally found growing on the forest floor (Lehmann et al. 2002; Burns & Dawson 2005; Kirby 2016). The distribution of *A. polyodon* on host trees showed a clear correlation with higher light and lower humidity environments and an increasing association with *Astelia* spp. along these gradients. However, some of these associations were different from those observed at the forest scale at Hunua. In both cases, such differences were likely the result of biases in terms of the tree species being surveyed. All the trees surveyed for the host scale analysis were large emergent *D. cupressinum* (DBH > 45 cm), while trees surveyed for the forest scale study were much smaller on average, with only a few emerging above the canopy (Table 3.4). It may be that *A. polyodon* was typically observed closer to the forest floor, or in the lower vertical strata of the host tree, and thus less commonly associated with *Astelia* spp. My host-tree observations showed a steadily increasing abundance of *A. polyodon* from lower to higher vertical strata (Fig. 4.5). *E. mucronata* also showed a shift in associations between and even within scales, although there was little pattern to these changes and, as such, it is unclear what might be driving these changes.
Figure 4.4 – Heat map of the correlation each species showed with Astelia spp. by the cardinal orientation of the host substrate. A value of 1 indicates that the species was always seen associating with an Astelia spp. for a given direction and a value of -1 indicates that it was never seen occurring with an Astelia spp. The size of the bubble corresponds to the number of individuals observed. Note: Correlations scores were not shown for single species occurrence once on a given orientation.
Figure 4.5 – Heat map of the correlations each species showed with *Astelia* spp. by the vertical tier on the host tree that the species occupied. A correlation of 1 indicates that the species was always seen associating with an *Astelia* spp. in each stratum, while -1 indicates the two were never seen associating. The size of the bubble corresponds to the number of observations of a given species in the respective vertical strata. Note: When a species was only observed once in a vertical stratum, the correlation score is not shown.
4.4 Discussion

At both the regional and host scales species-specific associations among vascular epiphytes and *Astelia* spp. were observed, with some showing strong positive associations with *Astelia* spp., others never occurring with *Astelia* spp., and some being less consistent. Moreover, these associations varied for each species depending upon the forest site or vertical strata occupied in the tree, although no difference could be discerned across radial strata. The positive associations between vascular epiphytes and *Astelia* spp. may be due to either shared habitat preferences between species, the *Astelia* spp. lifeform facilitating the presence of the vascular epiphytes, or a combination of the two.

The lack of a difference in species associations with *Astelia* spp. among the radial strata may have arisen because the effect of radial position was: 1) too small to detect in this study design, or did not exist, and 2) the effect of radial strata was less than that of vertical strata, over which the radial correlations were aggregated. The relatively small sample size of this study (*n* = 15 trees), and the relatively small number of observations from each unique combination of vertical and radial strata meant that there was little statistical power to detect changes in association status. For the host tree analysis, the cardinal direction observations were aggregated over the vertical tiers, with the opposite occurring when analysing the data for the vertical tiers. These aggregations were necessary as splitting samples across both vertical and radial strata led to too few observations for some combinations of these factors. It is possible that there is some interaction between these two gradients, as both are likely correlated with changes in abiotic and biotic factors, which could influence epiphyte establishment and persistence.
As identified in Chapters 2 and 3, Astelia spp. distributions vary along gradients of light and water. These gradients are key stressors altering epiphyte distributions (Hofstede et al. 2001; Affeld 2008; Adibah & Ainuddin 2011; Taylor & Burns 2016; Sanger & Kirkpatrick 2017b). However, I found that Astelia spp.-epiphyte association strength, and even direction, can change along these gradients, with the associations becoming more positive in forests experiencing greater vapour pressure deficit (VPD), or in higher vertical strata of trees, which may also have increased VPD levels (Dickinson et al. 1993; Hofstede et al. 2001; Graham & Andrade 2004; Sanger & Kirkpatrick 2017b). The monodirectional change of associations at two scales along the opposing gradients of water and light availability suggests that Astelia spp. are facilitating some vascular epiphyte species by increasing the availability of water in otherwise water-limited conditions.

The amelioration of water stress has been documented in bird’s nest epiphytes (Freiberg & Turton 2007) and bromeliad tank epiphytes (Jian et al. 2013). Astelia spp. are likely facilitating access to water through the water stored in their phytotelma in their leaf axils (Oliver 1930), moisture stored in the canopy soil/humus which they trap and form (Oliver 1930; Dawson & Sneddon 1969b), alterations to the microclimate (Turner & Foster 2006), or a combination of the three.

Across all scales assessed, positive associations tended to become more prevalent in water-limited environments, supporting the SGH. In addition, species-specific associations also tended to increase in strength with increasing abiotic stress, and with the same patterns being observed at each scale. A. polyodon and G. lucida associations with Astelia spp. increased with increasing regional VPD between forest sites (Table 3.1, Fig. 4.3), with the same trend being seen in A. polyodon and A. flaccidum on individual hosts as VPD increased near the top of the tree (Fig. 4.5). Moreover, at the forest scale
trends of increasing association in *A. polyodon* and *G. lucida* vary with abiotic variables negatively correlated with water availability (i.e. northing, slope and topographic index; Fig. 4.2).

At the tree scale three of the four species that had strong positive associations were shrub epiphytes, while the last was a facultative fern epiphyte that can grow on the ground (Dickinson *et al.* 1993; Kirby 2016). *M. robusta* and *G. lucida* (two of the shrub epiphytes), are hemi-epiphytic, sending roots to the ground to access soil moisture stores later in their life, meaning that the nature and strength of these two species interactions with *Astelia* spp. may change with ontogenetic stage, with positive associations most necessary during their initial fully epiphytic stage (Miriti 2006; Wright *et al.* 2014). *P. cornifolium* is also thought to depend on *Astelia* spp. for moisture and/or nutrients, although this may be less likely to vary with ontogeny as it is a holo-epiphyte (Clarkson *et al.* 2012). The three shrub epiphytes are particularly interesting, as these species are all thought to colonise trees later in the succession of epiphytic communities. My results suggest that this association may be due to these shrub epiphytes requiring the presence of *Astelia* spp. for their establishment and persistence, likely due to the access to moisture stores that associating with *Astelia* spp. provides.

This hypothesis is further supported by considering the species that showed the strongest negative correlations, all of which are typically regarded as pioneering species of epiphyte communities and have a number of adaptations to tolerate water stress (i.e. *P. eleagnifolia*, *D. cunninghamii* and *Earina* spp.; Dickinson *et al.* 1993; Hofstede *et al.* 2001; Kirby 2016). In particular, the strong negative correlations between epiphytic *Astelia* spp. and *P. eleagnifolia*, suggest competitive displacement, possibly due to *Astelia* spp. shading out *P. eleagnifolia*, which forms creeping mats of small leathery fronds
Moreover, *P. eleagnifolia* likely has similar establishment requirements to those of epiphytic *Astelia* spp. (Chapter 3); both appearing to establish on bare bark surfaces as pioneer epiphytes (Dickinson *et al.* 1993; Hofstede *et al.* 2001; Kirby 2016). As conditions in the crown and emergent sections of the tree are more akin to those experienced by ‘pioneer’ species (Woods 2017), it may be that later successional vascular epiphytes are being facilitated by *Astelia* spp. in these micro-habitats.

While I could not directly assess whether the interactions observed were facilitative or competitive in this study, these results provide a basis for explicitly assessing both the mechanisms and the degree to which epiphytic *Astelia* spp. may facilitate other vascular epiphytes.

### 4.5 Conclusion

Species-specific associations with epiphytic *Astelia* spp. were observed at the regional scale, with correlations becoming more positive in water-limited environments, in line with the predictions of the SGH. Similarly, positive associations became more prevalent within-forest along environmental gradients associated with increasing water-limitations and greater availability of light, with the same pattern holding ascending vertical tiers of the host trees. Moreover, the intensity of individual associations also tended to increase with water-limitations at all three scales. The species-specific associations observed at the regional and forest scales held at the scale of individual phorophytes, with positive associations tending to become increasingly positive along with water-limitations and light availability. The consistency with which associations change at each of these scales suggests that these species are associating with epiphytic *Astelia* spp. for access to water, which they provide through the formation of canopy soil.
and their phytotelmata. Species which exhibited strong negative associations with *Astelia* spp. were those that are considered to be the pioneers of epiphyte communities and drought-tolerant in their own rights. The species that were most likely to associate with epiphytic *Astelia* spp. were those that tended to arrive later in epiphyte community succession and less drought-tolerant. These results suggest that *Astelia* spp. are an integral component of epiphytic community assembly in New Zealand by supporting late-successional epiphyte species, such as shrub epiphytes, through niche-expansion.
Chapter Five

Synthesis

5.1 The distribution of epiphytic Astelia spp. and their role as habitat formers

How communities assemble is a question at the core of contemporary ecology. Given species have successfully dispersed to a site, they are thought to assemble through abiotic and biotic filters; these filters may also interact with one another and their recognition in any context is thought to be somewhat dependent on the scale of observation (Poff 1997; HilleRisLambers et al. 2012). The stress gradient hypothesis (SGH) in particular predicts that with increasing abiotic stress, the net biotic interactions will shift to more positive (facilitative) interactions (Bertness & Callaway 1994). Understanding how abiotic and biotic factors influence community assembly allows us to understand how we might restore degraded systems, or how they will respond to change.

My thesis aimed to determine the overall niche space of three epiphytic Astelia spp., how they partition this space, and then examine their role in facilitating the assembly of epiphyte communities in New Zealand. To these ends, I analysed the distribution of epiphytic Astelia spp. and their associations with other vascular epiphytes at regional, local and host tree scales. The results of my research show that there is some consistency across the three scales in terms of the abiotic drivers influencing epiphytic Astelia spp. distributions. Light (and VPD) and minimum temperature are key correlates at the regional scale, with analogues of light/VPD correlating with Astelia spp. distributions at local and host scales. Moreover, at both the regional and the host scale there is some niche differentiation between Astelia spp. along the gradients identified as
important for these species. Association of epiphytic *Astelia* spp. with other vascular epiphytes tended to be consistent across all three scales but were species-specific. In addition, the association of *Astelia* spp. with other vascular epiphyte species tended to be dependent on environmental features that were associated with light and water availability, with species becoming increasingly associated in drier conditions (Fig. 5.1). These results support the SGH and suggest that *Astelia* spp. are likely facilitating other vascular epiphytes through the provision of water when it is limited.
Figure 5.1 – The conceptual framework through which *Astelia* spp. were studied. Coloured dots represent observed vascular epiphyte species, while white/black dots represent unobserved species which were present in the regional meta-community. Stress was mainly manifested as quantum in the site’s light and annual VPD which covary. Dashed/dotted line denotes a species facilitation by *Astelia* spp., while solid lines are species capable of tolerating abiotic/biotic conditions. The dotted lines are unknown filters at the host scale. White ovals are the community present at a given scale post-filtering. While the diagram implies that organisms pass through filters linearly there are interactions between the filters leading to communities assembling in a non-linear way. Adapted from (Poff 1997; HilleRisLambers et al. 2012).
The coarsest filters acting on epiphytic *Astelia* spp. distributions at the regional scale were mean annual solar radiation (light/temperature/water availability) and mean minimum temperature of the coldest month (temperature) (Chapter two). Light availability likely explained part of these species distributions due to direct physiological limits in terms of light requirements for photosynthesis (Yordanov et al. 2000). Solar radiation, however, may also be indirectly influencing distributions through a strong positive correlation with VPD (Fig. A-1.1), which is a useful predictor of water availability (or lack of) for epiphytes (Sanger & Kirkpatrick 2017b). Thus, the reduced probability of *A. microsperma* and *A. solandri* occurring in high solar radiation environments may be the result of an intolerance to the water-limitations associated with these habitats rather than light per se. In contrast, minimum temperature gradients in the landscape describes the southern limits of species distributions, potentially through the respective abilities of the different *Astelia* spp. to tolerate frost (Warrington & Stanley 1987; Yordanov et al. 2000). In addition, the upper end of the minimum temperature spectrum is also related to increased evapotranspiration rates, which influence water availability in the form of humidity for plants (Irmak et al. 2003). Moreover, there is support for the claim that *A. microsperma* tends to occur at higher elevations (> 300 m a.s.l.; Kirby 2016), with this species appearing to be the most tolerant of low, but > 0 °C, temperatures, but in moister environments.

Along both the light and temperature gradients there is niche differentiation among the epiphytic *Astelia* spp., with *A. hastata* tending to occur in high light (and thus high VPD), environments, *A. microsperma* in high light and low, but above zero, temperatures, and *A. solandri* at lower light levels (and thus lower VPD) and low temperatures. The niche differentiation suggested by the SDMs were further confirmed by the differences in abundances of the three *Astelia* spp. among the forest sites surveyed. However, there
was no discernible differences between the niche space of the three species within a given forest site, potentially due to several parameters co-varying on each host. Within the forests, epiphytic *Astelia* spp. tended to accumulate on larger hosts, typically greater than c. 50 cm DBH, supporting the claim they tend to appear in the mid-late succession of forest communities. At the forest stand scale, epiphytic *Astelia* spp. tended to occur in higher light positions within the forests, except at Taumata where the high ambient light levels likely presented some limits on water-availability that were beyond the species tolerances.

At the host scale there was clear niche differentiation, with *A. hastata* occupying exposed high light positions, favouring the north face and emergent tier of the tree, while *A. solandri* tended to occupy relatively sheltered positions on the south face. The separation of these species suggests that *A. hastata* is more competitive and/or more tolerant of water-limited environments than *A. solandri*. The absence of *A. microsperma* from two of the sites precluded any assessment of niche separation between this species and the other two at the forest stand or host scales, but the SDMs suggest that *A. microsperma* would fall somewhere between the others in terms of tolerance of water-limitations.

The consistency with which the light-water gradient is associated with the distribution of epiphytic *Astelia* spp. is congruous with other research on the distributions of epiphytes (Hofstede *et al.* 2001; Freiberg & Turton 2007; Adibah & Ainuddin 2011; Li *et al.* 2017; Sanger & Kirkpatrick 2017b), and observations of *Astelia* spp. in New Zealand (Oliver 1930; Dawson & Sneddon 1969). Moreover, these abiotic filters can influence the epiphyte metacommunity at multiple scales, from the regional to the phorophyte (Levin 1992; Poff 1997; Leibold *et al.* 2004; Burns 2007; HilleRisLambers *et al.* 2012;
Kraft et al. 2015). These results suggest that the trade-off between drought- and shade-tolerance determines vascular epiphytes' niche space and therefore their distributions across multiple scales. However, the absence of A. solandri and A. microsperma from particular habitats may not be due entirely to an intolerance of abiotic conditions but may also be the result of other epiphytic Astelia spp. modifying their realised niche space through competitive exclusion.

The consistency with which light and water availability correlate with epiphyte distributions is also evident in associations between vascular epiphytes and epiphytic Astelia spp. (Chapter Four). While associations between vascular epiphytes and Astelia spp. were species-specific, they were relatively consistent in direction (positive/negative) across the three scales at which distributions were analysed. Moreover, the prevalence of positive interactions among vascular epiphytes and Astelia spp. increased along with abiotic stress (water-limitations), supporting the SGH. As water availability decreases either regionally, within a forest stand or across the vertical strata of trees the associations between vascular epiphytes and Astelia spp. also became more strongly positive. The phytotelmata that Astelia spp. form at their leaf axils (Oliver 1930; Killick et al. 2014), along with the humus and soil these species accumulate (Oliver 1930; Wardle et al. 2003), allow more consistent access to water during dry periods (Oliver 1930; Wardle et al. 2003; Killick et al. 2014). Moreover, nest epiphytes can stabilise nearby microclimates by releasing moisture during dry spells, effectively ameliorating conditions for adjacent flora and fauna (Turner & Foster 2006). The strength and consistency of some of the associations I observed suggest that the highly nested assemblages of New Zealand epiphyte communities may be the result of epiphytic Astelia spp. acting as a habitat former and facilitating subsequent
colonisations through the provision of water (Burns & Dawson 2005; Taylor & Burns 2015).

Community interactions are also an important consideration with changing climates, as communities adapt to changing abiotic pressures (Gilman et al. 2010). The positive associations of several vascular epiphytes with Astelia spp. has increasing relevance given temperatures in New Zealand, particularly on the east coast, are expected to rise under climate change (Royal Society of New Zealand 2017). Rising temperatures are likely to lead to increasing VPD, which suggests that there may also be a growing dependency on Astelia spp., particularly for species which are already uncommon in the wild (e.g., P. cornifolium; De Lange et al. 2013). Identifying the conditions under which each Astelia spp. naturally occurs, along with the vascular epiphytes associated with them and when, is an important step in ensuring that these communities will continue to persist.

In short, my results suggest that the assembly of vascular epiphyte communities is influenced by the relative drought- and shade-tolerances of the potential community members. By creating conditions that later-successional species require to establish and persist, epiphytic Astelia spp. are an integral component of epiphyte community assembly. It seems probable that the mechanism by which epiphytic Astelia spp. influence the niche space of other vascular epiphytes is by providing access to water and/or microclimatic stability. The degree of apparent facilitation by epiphytic Astelia spp. increases with water-stress as predicted by the SGH. Moreover, these results provide evidence of abiotic filters acting in epiphyte community assembly, which are then being bypassed through biotic interactions allowing species to exist where they otherwise would or could not.
5.2 Implications for conservation and restoration

To restore the ecological integrity of an ecosystem requires full species occupancy (Huston & Huston 1994; Lee et al. 2005). In restoration, epiphyte communities are often referred to as interstitial organisms, as they live on structural species (trees) and require them for their existence (Huston & Huston 1994; Lee et al. 2005). Moreover, epiphytes often act as habitat formers in their own right hosting a range of other organisms as described in Chapter 1. Thus, the reinstatement of epiphyte communities is integral to restoring forest ecosystems, as they not only occupy an important niche space but can also create niches, allowing for greater species occupancy (Huston & Huston 1994; Oishi & Doei 2015; Reid et al. 2016; Wallace et al. 2017). To restore epiphyte communities requires an understanding of how these communities’ form. As has been evidenced by my study, there are interactions between the abiotic and biotic elements associated with epiphytic communities, and there appears to be an ordered succession of species in these communities. Nest epiphytes appear to facilitate several other species of vascular epiphytes, although this is conditional on a site’s abiotic conditions (Chapter Four). The natural positive interactions that Astelia spp. likely have with other vascular epiphytes could, therefore, be leveraged to accelerate the restoration of epiphyte communities, especially in water-limited areas; identifying the niche space of epiphytic Astelia spp. underpins this approach.

My study identified several abiotic correlates of nest epiphytes (epiphytic Astelia spp.) at a number of scales. The SDMs (Chapter Two) predict which epiphytic Astelia spp. are the most likely inhabitants of a given region in New Zealand, which can guide restoration activities. A. hastata is a likely candidate for almost anywhere in the upper North Island, or the north-west coast of the South Island. Moreover, it appears to be the species most suited to hot, sunny sites with large annual VPDs. A. microsperma has a
similar range but would likely be an ideal candidate for higher altitude sites, such as
Nothofagaceae-dominated forests around the Central Plateau. In contrast, *A. solandri*
appears to be more of a generalist and may perform well in most forests around New
Zealand, although more research is needed to confirm this. *A. solandri* is probably the
best candidate for forest sites in the far south of New Zealand where mean minimum
temperatures can be sub-zero and annual solar radiation inputs are lower than in the
north.

At the regional scale and within forests there was some niche differentiation between
the three species. Within forest blocks, all three species tended to occur on relatively
large trees that were exposed to sunnier conditions (i.e. northerly aspects, steep slopes
or closer to the ridge). The requirement of large trees for natural establishment
suggests that candidate sites for epiphyte restoration need to be on relatively mature
trees, and that *Astelia* spp. are ideally planted in sunnier locations within the forest.
However, at Taumata, the driest site, both *A. hastata* and *A. solandri* occurred only in
less exposed positions. The aversion to exposed positions suggests that at sites with a
mean annual solar radiation of approximately 154 MJ/m$^2$/day, *Astelia* spp. may perform
better in more sheltered sections of the forest.

Based on the distribution of *A. hastata* and *A. solandri* on individual phorophytes, there
was a degree of niche differentiation, suggesting that the placement of these species on
hosts must be species-specific. However, phorophyte-level species distributions were
only examined on *D. cupressinum* in the Hunua ranges, and as such, more research is
required to determine if these trends hold for other host species and/or other forest
sites. In the Hunua ranges, *A. hastata* appears to favour the northerly face of trees and
occurs in the greatest abundance in the emergent tier. Although I have no data on
phorophytes that do not emerge above the canopy, it is likely that any *A. hastata* would favour the upper portions of the tree with the most exposed gaps, due to the increased availability of light in these positions. Moreover, any plantings of *A. hastata* may have the greatest chance of establishment or survival if planted on horizontal surfaces, such as branches or the crook formed between branches and the trunk. In contrast, *A. solandri* appears to favour more sheltered positions beneath the canopy and on the southern aspect of the tree. It may also be a good planting candidate for trees that do not emerge above the canopy due to its apparent shade-tolerance. While no difference was detected between structural positions for *A. solandri*, this could be the result of the relatively low counts of individuals which I collected. As such, I would suggest that *A. solandri* also be planted on horizontal surfaces of the host. No data were collected on *A. microsperma* at the phorophyte level. However, this species likely follows similar patterns to *A. hastata*, or, based on its apparent intermediate environmental tolerances as displayed in the regional scale drivers (Chapter 2), is possibly intermediate in preference/tolerance to those of *A. hastata* and *A. solandri*. None of the three epiphytic *Astelia* spp. commonly occurred on either tree ferns (*Cyathea* spp. and *Dicksonia* spp.) or *R. sapida*, suggesting that these are poor hosts, potentially due to their relatively small size and/or lack of horizontal surfaces (i.e. branches). Similarly, few of the many *Coprosma arborea* surveyed were hosts.

As associations with nest epiphytes appear to be dependent on site and the species under consideration, the choice of planting associated with nest epiphytes will be context-specific. *Griselinia lucida, Pittosporum cornifolium* and *Phlegmariurus varius* were strongly positively associated with *Astelia* spp. across all three sites surveyed, suggesting that they are good candidates for companion plantings from at least Pirongia northward. *Asplenium polyodon* also appears to be a common associate, but potentially
only from Hunua northwards, although there are some discrepancies between the site- and tree-scale studies. It may be that at sites such as Hunua, *A. polyodon* would best be planted with nest epiphytes when they occupy more exposed positions, such as in the canopy or emergent tiers. At the other end of the biotic interaction spectrum, nest epiphytes appear to competitively interact with some species, particularly *Pyrrosia eleagnifolia* and *Earina* spp. *P. eleagnifolia* is thought to be a pioneer species (Burns & Dawson, 2005) and as such may be facilitating the establishment and persistence of *Astelia* spp. to its own detriment. If particular individual *P. eleagnifolia* are to be preserved it may be best to avoid any plantings of nest epiphytes near them, as the nest epiphytes may be creating conditions of intolerable shade for this relatively small prostrate fern. Although the relationship between epiphytic *Astelia* spp. and *Earina* spp. is somewhat opaque, *E. mucronata* did associate with *Astelia* spp. at Taumata, albeit with a sample size of one, and had negative associations at the other two sites. Thus, these two species could potentially be planted together at sites similar to Taumata, where the VPD is high, although more study is needed to confirm this. However, it may be best to avoid planting these two genera together at sites that are not as water-limited.

5.3 The use of drones (UAVs)

While there is a growing body of research on the use of UAVs for research on forest canopies, these studies largely use two-dimensional data images looking down on the canopy (Al-Kaff *et al.* 2018; Berie & Burud 2018; Manfreda *et al.* 2018). My use of drones was novel in that it encompassed a sub-canopy survey of vascular plant life and, to my knowledge, is the first use of UAVs for scientific epiphyte surveys. The recent drop in the price of small drones with high-quality cameras, forward-facing obstacle
avoidance and the ability to maintain position to an error of less than a centimetre has meant that they are becoming increasingly accessible to consumers on a small budget (Koh & Wich 2012). Moreover, UAVs have the nimbleness, stability and size required to survey the canopy of a tree. The quality of the images and video captured by the DJI Mavic Pro used in this study were of sufficient quality that species identification of the vascular epiphytes was possible in all but one case. Moreover, by capturing these data in this format, it can be analysed later at the laboratory, and incorporated in future research. While my use of the drone was limited to one species of host tree in one forest, future studies could compare the utility and accuracy of drones as a survey tool versus surveys conducted by climbing trees or ground-based observation methods.

Although not a main aim of my study, the collection of both ground-based binocular observations and those collected via a drone provided some insight into the relative limits of each of these techniques. Unfortunately, direct comparisons of accuracy and precision of these two techniques cannot be inferred from my study, as the trees surveyed with each technique were not the same. Nevertheless some general conclusions were possible.

Ground-based observation via binoculars is relatively rapid and is particularly useful for sampling a large number of trees; however, this approach can be somewhat inaccurate, particularly where there is a dense canopy, and/or the trees are tall. Burns and Zotz (2005) found that 10% of vascular epiphytes were missed on average with binocular surveys, with no species bias, but this figure did not include any Hymenophyllum spp., which are often small, cryptic and sometimes require a microscope for identification to species-level. Moreover, Burns and Zotz’s (2005) study excluded trees where there was no clear line-of-sight to the canopy. However, recent work by Taylor et al. (2015) found
that emergent host tree species (e.g., *Dacrydium cupressinum*), and therefore often at least partially obscured from the ground, tended to accumulate the richest epiphyte communities. As indicated by the results from my drone survey, many epiphytes occur above the canopy, in the emergent tier, and coupled with Taylor *et al.* (2016) findings that emergent species have the richest epiphyte communities, this suggests that many vascular epiphytes may be missed by ground-level surveys.

Climbing the tree may produce a more accurate and precise sample of the epiphytes present than either ground-based binocular surveys or those conducted with a drone, as direct samples can be taken, and a hand lens used to identify species. However, climbing can lead to incomplete surveys as access is generally confined to the central axis of the tree (main trunk). Moreover, climbing trees in excess of 15 meters tall presents health and safety risks to those involved. To mitigate these as much as possible, this climbing technique requires that there are at least two trained individuals on the ground while another climbs the tree to ensure that they can get the climber down on their own in case of an emergency. Requiring three trained individuals, as well as rigging setup, involves considerable costs in terms of time and money. Nevertheless, the data collected via climbing would likely result in more accurate and precise observations of what is present on the host tree and does not preclude the use of footage for the sake of records to additional analyses, such as those carried out as part of the New Zealand Tree Project (Harrison & Kirby 2015).

Drones are not a panacea for the problems of canopy survey. In many countries some form of certification is required to operate them and no-fly zones are imposed, although New Zealand is currently only subject to the latter. In addition, drones are limited to locations with launch sites clear of any obstruction, and, at a minimum, require there to
be empty space around trees to fly; in northern NZ forests empty space is often limited by understory species, juvenile trees and *Ripogonum scandens*, a native climbing liana. Trees with dense foliage can also block the view to the host’s branches and trunks, potentially creating observation biases across different species, or, at the least, leaving surveys incomplete. Finally, drones have limited flight times, with a DJI Mavic Pro having approximately 27 minutes flight time per battery ($130 NZD per battery in 2018). For my study, this meant a limit of three trees surveyed per trip, which included a minimum of three hours travel time. While car chargers are available they are slow to fully charge batteries. Compared to ground-based surveys, drones likely provide a more complete view of epiphyte communities, but compared to climbing a tree, it is difficult to say if they offer as full a survey, although they do come at a considerably lower cost in terms of time and risk to those involved.

### 5.4 Future research

Future studies could use laboratory and field experimental trials to explicitly test whether there are differences in the drought/shade/frost tolerance of the three epiphytic *Astelia* spp. Controlled experiments are required to confirm the niche differentiation of these epiphytes inferred from my results. Laboratory experiments could also confirm the role of water and light as abiotic drivers of vascular epiphytes. Ideally, any laboratory study would use light/VPD levels similar to those experienced by natural populations by placing sensors in these communities in the field and using these data to define the treatments. Using a crossed experimental design with the two (or more) factors could help to determine the effect of each treatment by measuring survival, growth and seed production of individuals. Experimental longitudinal field trials could be carried out by planting individuals under known conditions and
assessing individual performance in the same manner as described for laboratory trials. Field trials such as these could also manipulate the distribution of epiphytic *Astelia* spp. structurally, radially and vertically on host trees to determine how these impact on each species performance. Moreover, field experiments could also determine the best manner, in terms of establishment success and survival, to plant *Astelia* spp., which is effectively unknown.

Laboratory and field experimental trials could also be used to not only confirm the associations described here, but to determine the primary mechanisms by which epiphytic *Astelia* facilitate other vascular epiphytes. Laboratory trials could plant nest epiphytes along with associates under a variety of controlled water/light conditions to determine the threshold at which associating with nest epiphytes provides a net benefit. Again, performance could be measured by differences in survival, biomass and/or seed production/viability (where applicable). Field manipulation experiments could assess whether the effects observed in laboratories can be generalised to natural systems by manipulating the distribution of epiphytic *Astelia* spp. relative to other vascular epiphytes. Field manipulation experiments would enable an assessment of the role of nutrient availability in facilitation by, for example, examining the exchange of nitrogen isotopes (Hunter & Aarssen 1988).

The highly clumped nature of nest epiphyte distributions also raises a number of interesting questions about the pollination and dispersal of these organisms. *Astelia* spp. are dioecious (Birch 2015), meaning that there are both female and male plants. A basic but unanswered question regarding the ecology of these organisms is whether both sexes are present in the clumps which they form or whether there are any biases in the ratio of the two sexes per clump. It may be that clumps with both genders proximate
may produce more viable seeds due to greater pollination rates, and thus form large(r) clumps and/or increase the abundance of species locally. Studies experimentally altering the distribution of sexes could assess whether viability of seeds is higher when both sexes are present, although this on its own is unlikely to drive the distribution of nest epiphytes.

Epiphytic *Astelia* spp. are dispersed via birds in New Zealand (Thorsen et al. 2009), which also nest among these epiphytes (Henwood et al. 2014). Moreover, some native frugivores which disperse *Astelia* spp. seeds, such as *Hemiphaga novaeseelandiae*, tend to perch in emergent trees (Beveridge 1964; McEwan 1978). The combination of zoochory and perching preferences may lead to a bias toward establishment on emergent trees, and particularly native podocarps, in terms of their accumulation of nest epiphytes, which could be further reinforced by pollination biases. Observational studies on native bird feeding and the dispersal behaviour of epiphytic *Astelia* spp. could assess whether birds are driving the accumulation of these epiphytes.

Further, there is a dearth in our knowledge of the ecology of *Astelia* spp. seed germination and seedling establishment in the epiphytic niche in New Zealand. What conditions need to occur on bark surfaces to allow *Astelia* spp. seed to germinate and traverse the vulnerable early establishment phases that the seedling would be exposed to. There is certainly fertile ground for future studies regarding these species pollination, the dispersal and germination of seeds, establishment, and the conditions necessary for their continued survival.
Appendix 1

Multicollinearity

Layers were excluded from the model if they were had collinear with another variable and were either derived from existing layers or were deemed less reliable based on their method of creation (i.e. rainfall was based on three measuring stations around New Zealand the interpolating). Mean annual solar radiation was chosen over winter solar radiation (which had strong correlations with one another) as it had stronger correlations with other variables with the exception of vapour pressure deficit (Fig. A-1.1). Vapour pressure deficit was excluded because it had strong correlations with mean annual solar radiation, and of the two had stronger correlations with other variables than mean annual solar radiation did. Following similar logic minimum temperature was chosen over mean annual temperature, in addition to the fact that minimum temperature likely has more biological relevance than mean annual temperature as it pertains to physiological thresholds. Finally, water balance ratio was excluded due to strong correlations with mean annual solar radiation and the fact that it was derived from this layer along with others leading to increased uncertainty in its estimates.
Figure A-1.1 – Pairwise matrix of correlation coefficients (lower triangle), scatter plots of each predictor variable regressed against each other variable (upper triangle), and histograms of each variables distribution (diagonal).
Figure A-1.2 – Mean minimum temperature plotted against mean annual solar radiation, overlain with the three epiphytic *Astelia* spp. The vertical and horizontal lines represent the means of each respective variable.
# Appendix 2

Table A-2.1 – Counts of each host species surveyed, the number and proportion which hosted at least one *Astelia* spp., along with the estimated count for each *Astelia* spp.

<table>
<thead>
<tr>
<th>Host Species</th>
<th>Host spp. count</th>
<th>Hosts with <em>Astelia</em> spp.</th>
<th>Proportion of hosts with <em>Astelia</em> spp.</th>
<th>Estimated count of <em>A. hastata</em></th>
<th>Estimated count of <em>A. microsperma</em></th>
<th>Estimated count of <em>A. solandri</em></th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Alectryon excelsior</em></td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>Beilschmiedia tarairi</em></td>
<td>136</td>
<td>52</td>
<td>0.38</td>
<td>358</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>Beilschmiedia tawa</em></td>
<td>73</td>
<td>39</td>
<td>0.53</td>
<td>146</td>
<td>354</td>
<td>33</td>
</tr>
<tr>
<td><em>Coprosma arboarea</em></td>
<td>33</td>
<td>1</td>
<td>0.03</td>
<td>8</td>
<td>0</td>
<td>7</td>
</tr>
<tr>
<td><em>Cordyline australis</em></td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>Cyathea dealbata</em></td>
<td>223</td>
<td>9</td>
<td>0.04</td>
<td>0</td>
<td>8</td>
<td>4</td>
</tr>
<tr>
<td><em>Dacrydium cupressinum</em></td>
<td>4</td>
<td>3</td>
<td>0.75</td>
<td>28</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td><em>Dacrydium dacrydioides</em></td>
<td>11</td>
<td>2</td>
<td>0.18</td>
<td>12</td>
<td>0</td>
<td>4</td>
</tr>
<tr>
<td><em>Dicksonia squarrosa</em></td>
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<td>2</td>
<td>0.05</td>
<td>2</td>
<td>11</td>
<td>0</td>
</tr>
<tr>
<td><em>Dysoxylum spectabile</em></td>
<td>42</td>
<td>11</td>
<td>0.26</td>
<td>54</td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td><em>Elaeocarpus dentatus</em></td>
<td>17</td>
<td>7</td>
<td>0.41</td>
<td>0</td>
<td>62</td>
<td>0</td>
</tr>
<tr>
<td><em>Hedycarya arborea</em></td>
<td>9</td>
<td>1</td>
<td>0.11</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td><em>Knightia excelsa</em></td>
<td>37</td>
<td>15</td>
<td>0.41</td>
<td>83</td>
<td>14</td>
<td>1</td>
</tr>
<tr>
<td><em>Kunzea robusta</em></td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>Laurelia novae-zelandiae</em></td>
<td>5</td>
<td>3</td>
<td>0.6</td>
<td>2</td>
<td>42</td>
<td>0</td>
</tr>
<tr>
<td><em>Litsea calicaris</em></td>
<td>7</td>
<td>1</td>
<td>0.14</td>
<td>0</td>
<td>2</td>
<td>3</td>
</tr>
<tr>
<td><em>Melicytus ramiflorus</em></td>
<td>8</td>
<td>1</td>
<td>0.12</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>Myrsine salicina</em></td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>Metrosideros robusta</em></td>
<td>5</td>
<td>3</td>
<td>0.6</td>
<td>33</td>
<td>0</td>
<td>9</td>
</tr>
<tr>
<td><em>Nestegis lanceolata</em></td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>Olearia rani</em></td>
<td>4</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>Prumnopitys ferruginea</em></td>
<td>5</td>
<td>2</td>
<td>0.4</td>
<td>11</td>
<td>12</td>
<td>0</td>
</tr>
<tr>
<td><em>Pseudopanax arborea</em></td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>Pseudopanax crassifolius</em></td>
<td>4</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>Pseudopanax lanceolata</em></td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>Rhopalostylis sapida</em></td>
<td>160</td>
<td>5</td>
<td>0.03</td>
<td>9</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>Vitex lucens</em></td>
<td>15</td>
<td>9</td>
<td>0.6</td>
<td>32</td>
<td>0</td>
<td>14</td>
</tr>
<tr>
<td><em>Weinmannia racemosa</em></td>
<td>3</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>Weinmannia silvicola</em></td>
<td>3</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><strong>Totals</strong></td>
<td>851</td>
<td>166</td>
<td>956</td>
<td>329</td>
<td>85</td>
<td><strong>85</strong></td>
</tr>
</tbody>
</table>

Note: Bolded rows are species which were included in the dataset used for modelling *Astelia* spp. distributions at each site.
Table A-2.2– Comparisons of each model and error families constructed for *A. hastata*. AICc scores for each model type × error family combination is shown.

<table>
<thead>
<tr>
<th>Site</th>
<th>Model</th>
<th>Family</th>
<th>Degrees of freedom</th>
<th>AICc score</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>GLM</td>
<td>Poisson</td>
<td>11</td>
<td>304.2</td>
</tr>
<tr>
<td></td>
<td>GLM</td>
<td>Negative Binomial</td>
<td>12</td>
<td>266.7</td>
</tr>
<tr>
<td></td>
<td>Hurdle</td>
<td>Poisson</td>
<td>22</td>
<td>251.4</td>
</tr>
<tr>
<td>Taumata</td>
<td>Hurdle</td>
<td>Negative Binomial</td>
<td>23</td>
<td>227.3</td>
</tr>
<tr>
<td></td>
<td>Zero-Inflated</td>
<td>Poisson</td>
<td>22</td>
<td>223.8</td>
</tr>
<tr>
<td></td>
<td><strong>Zero-Inflated</strong></td>
<td><strong>Negative Binomial</strong></td>
<td>23</td>
<td>217.3*</td>
</tr>
<tr>
<td></td>
<td>GLM</td>
<td>Poisson</td>
<td>12</td>
<td>833.1</td>
</tr>
<tr>
<td></td>
<td>GLM</td>
<td>Negative Binomial</td>
<td>13</td>
<td>569.5</td>
</tr>
<tr>
<td></td>
<td>Hurdle</td>
<td>Poisson</td>
<td>24</td>
<td>547.8</td>
</tr>
<tr>
<td>Hunua</td>
<td>Hurdle</td>
<td>Negative Binomial</td>
<td>25</td>
<td>530.6</td>
</tr>
<tr>
<td></td>
<td>Zero-Inflated</td>
<td>Poisson</td>
<td>24</td>
<td>549.6</td>
</tr>
<tr>
<td></td>
<td><strong>Zero-Inflated</strong></td>
<td><strong>Negative Binomial</strong></td>
<td>25</td>
<td>530.0</td>
</tr>
<tr>
<td></td>
<td>GLM</td>
<td>Poisson</td>
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<td>514.6</td>
</tr>
<tr>
<td></td>
<td>GLM</td>
<td>Negative Binomial</td>
<td>12</td>
<td>278.0</td>
</tr>
<tr>
<td></td>
<td>Hurdle</td>
<td>Poisson</td>
<td>22</td>
<td>259.9</td>
</tr>
<tr>
<td>Pirongia</td>
<td>Hurdle</td>
<td>Negative Binomial</td>
<td>23</td>
<td>255.4</td>
</tr>
<tr>
<td></td>
<td>Zero-Inflated</td>
<td>Poisson</td>
<td>22</td>
<td>260.0</td>
</tr>
<tr>
<td></td>
<td><strong>Zero-Inflated</strong></td>
<td><strong>Negative Binomial</strong></td>
<td>23</td>
<td>255.5</td>
</tr>
</tbody>
</table>

Note: Bolded models are those which were refined through variable selection.

Table A-2.3– Comparisons of each model and error families constructed for *A. microsperma*.

<table>
<thead>
<tr>
<th>Site</th>
<th>Model</th>
<th>Family</th>
<th>Degrees of freedom</th>
<th>AICc score</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>GLM</td>
<td>Poisson</td>
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<td>681.7</td>
</tr>
<tr>
<td></td>
<td>GLM</td>
<td>Negative Binomial</td>
<td>8</td>
<td>372.3</td>
</tr>
<tr>
<td></td>
<td>Hurdle</td>
<td>Poisson</td>
<td>14</td>
<td>460.1</td>
</tr>
<tr>
<td>Pirongia</td>
<td>Hurdle</td>
<td>Negative Binomial</td>
<td>15</td>
<td>368.4</td>
</tr>
<tr>
<td></td>
<td>Zero-Inflated</td>
<td>Poisson</td>
<td>14</td>
<td>459.7</td>
</tr>
<tr>
<td></td>
<td><strong>Zero-Inflated</strong></td>
<td><strong>Negative Binomial</strong></td>
<td>15</td>
<td>368.1</td>
</tr>
</tbody>
</table>

Note: Bolded models are those which were refined through variable selection.
Table A-2.4 – Comparisons of each model and error families constructed for *A. solandri*.

<table>
<thead>
<tr>
<th>Site</th>
<th>Model</th>
<th>Family</th>
<th>Degrees of freedom</th>
<th>AICc score</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>GLM</td>
<td>Poisson</td>
<td>11</td>
<td>105.8</td>
</tr>
<tr>
<td></td>
<td>GLM</td>
<td>Negative Binomial</td>
<td>12</td>
<td>124.5</td>
</tr>
<tr>
<td></td>
<td>Hurdle</td>
<td>Poisson</td>
<td>22</td>
<td>80.5</td>
</tr>
<tr>
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<td>Hurdle</td>
<td>Negative Binomial</td>
<td>23</td>
<td>82.5</td>
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<tr>
<td><strong>Zero-Inflated</strong></td>
<td><strong>Poisson</strong></td>
<td><strong>22</strong></td>
<td><strong>77.9</strong></td>
<td></td>
</tr>
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<td></td>
<td>Zero-Inflated</td>
<td>Negative Binomial</td>
<td>23</td>
<td>79.9</td>
</tr>
<tr>
<td></td>
<td>GLM</td>
<td>Poisson</td>
<td>11</td>
<td>128.0</td>
</tr>
<tr>
<td></td>
<td>GLM</td>
<td>Negative Binomial</td>
<td>12</td>
<td>112.4</td>
</tr>
<tr>
<td></td>
<td>Hurdle</td>
<td>Poisson</td>
<td>22</td>
<td>108.4</td>
</tr>
<tr>
<td>Hunua</td>
<td>Hurdle</td>
<td>Negative Binomial</td>
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<td>111.7</td>
</tr>
<tr>
<td><strong>Zero-Inflated</strong></td>
<td><strong>Poisson</strong></td>
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<td><strong>102.6</strong></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Zero-Inflated</td>
<td>Negative Binomial</td>
<td>23</td>
<td>104.6</td>
</tr>
<tr>
<td></td>
<td>GLM</td>
<td>Poisson</td>
<td>11</td>
<td>103.1</td>
</tr>
<tr>
<td></td>
<td>GLM</td>
<td>Negative Binomial</td>
<td>12</td>
<td>77.9</td>
</tr>
<tr>
<td></td>
<td>Hurdle</td>
<td>Poisson</td>
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<td>60.7</td>
</tr>
<tr>
<td>Pirongia</td>
<td>Hurdle</td>
<td>Negative Binomial</td>
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<td>62.7</td>
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<tr>
<td><strong>Zero-Inflated</strong></td>
<td><strong>Poisson</strong></td>
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<td><strong>36.7</strong></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Zero-Inflated</td>
<td>Negative Binomial</td>
<td>23</td>
<td>36.7</td>
</tr>
</tbody>
</table>

Note: Bolded models are those which were refined through variable selection.
Table A-2.5 - Output from each of the seven ZI models after variable selection. Log-odd estimates, standard error of the mean, z-values and p-values are shown for all significant variables for each possible species × site combination.

<table>
<thead>
<tr>
<th>Site</th>
<th>Species</th>
<th>Model</th>
<th>Parameter</th>
<th>Estimate</th>
<th>S.E.</th>
<th>z-value</th>
<th>p-value</th>
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<td>Taumata</td>
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<td>zero</td>
<td>(Intercept)</td>
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<td>1.00</td>
<td>4.00</td>
<td>0.000</td>
</tr>
<tr>
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<td>0.03</td>
<td>-2.89</td>
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<td>TopoIndex3</td>
<td>0.27</td>
<td>0.60</td>
<td>0.46</td>
<td>0.645</td>
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</table>
Taumata | *A. solandri* | count | TopoIndex4 | 5.30 | 2.03 | 2.61 | 0.009
---|---|---|---|---|---|---|---
Hunua | *A. solandri* | zero | (Intercept) | 4.13 | 1.47 | 2.82 | 0.005
Hunua | *A. solandri* | zero | HostDBH | -0.05 | 0.03 | -2.00 | 0.045
Hunua | *A. solandri* | count | (Intercept) | -3.36 | 1.43 | -2.35 | 0.019
Hunua | *A. solandri* | count | Slope | 0.03 | 0.01 | 3.00 | 0.003
Hunua | *A. solandri* | count | HostDBH | 0.05 | 0.02 | 2.59 | 0.009
Pirongia | *A. solandri* | zero | (Intercept) | 3.59 | 1.22 | 2.94 | 0.003
Pirongia | *A. solandri* | zero | HostDBH | -0.02 | 0.02 | -1.20 | 0.232
Pirongia | *A. solandri* | count | (Intercept) | 14.94 | 4.79 | 3.12 | 0.002
Pirongia | *A. solandri* | count | Slope | -1.00 | 0.35 | -2.85 | 0.004
Pirongia | *A. solandri* | count | Northing | 10.32 | 3.80 | 2.71 | 0.007

Note: The intercept term in the zero portion of each of the ZINB models describes the log-odds ratio of the respective species being absent when all other parameters are held at zero or their baseline. The log(θ) is the negative binomial parameter that is modelling the over-dispersion of these data.

Table A-2.6 – Results of the log-linear model built for *A. hastata*

<table>
<thead>
<tr>
<th>Term</th>
<th>Df</th>
<th>Deviance</th>
<th>Residual Df</th>
<th>Residual Deviance</th>
<th>p-value</th>
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</thead>
<tbody>
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<td>Radial Strata</td>
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<td>110.8</td>
<td>&lt; 2.2 × e⁻¹⁶</td>
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<tr>
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<td>42.2</td>
<td>20</td>
<td>68.6</td>
<td>7.0 × e⁻¹⁰</td>
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<td>18</td>
<td>52.3</td>
<td>2.9 × e⁻⁴</td>
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<td></td>
<td>25</td>
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Table A-2.7 – Results of the log-linear model built for *A. solandri*

<table>
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<th>Residual Df</th>
<th>Residual Deviance</th>
<th>p-value</th>
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</table>

There was strong evidence against the null hypothesis that the *A. solandri* data followed a Poisson distribution (χ²: 23.3, 7; p-value = 0.0015). However, a post-hoc LRT test showed that a Negative Binomial model did not significantly improve fit and so the Poisson model was retained. The violation of these assumptions is likely the result of there being no observations of *A. solandri* in particular positions (i.e. north-facing trunk and only one seen in the understory).
Cited Literature


using five woody species from the Cerrado (Brazilian savanna). *Acta Botanica Brasilica*, 25, 593–600.


