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Factors Influencing the Distribution and Structure of Tropical Vascular Epiphyte Communities at Multiple Scales

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FACTORS INFLUENCING THE DISTRIBUTION AND STRUCTURE OF TROPICAL VASCULAR EPIPHYTE COMMUNITIES AT MULTIPLE SCALES

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by
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Accepted by:
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Abstract

Understanding the factors that determine species distributions is a central question in ecology. Niche-based theories stress the importance of environmental heterogeneity in influencing species distributions while neutral-based theories emphasize the effects of dispersal limitation. The relative importance of these factors in influencing species distributions may depend on spatial scale – deterministic factors may be more important at small spatial scales where fine-scale habitat factors become more relevant and stochastic factors may be more important at larger spatial scales where dispersal limitation becomes more relevant. I examined the influence of deterministic and stochastic factors on the distribution and structure of vascular epiphyte communities in lowland tropical forests at multiple scales. Vascular epiphytes, non-parasitic plants that often inhabit tropical tree canopies, contribute up to 35% of the local floral diversity and up to 25% of the floral biomass in tropical forests. Yet our understanding of how habitat selection or random colonization events related to dispersal influence the distribution and floristic composition of epiphytes lags far behind that of terrestrial-based plant communities. I surveyed epiphytes among different-aged forests, different-sized trees, and within emergent tree crowns and examined whether habitat characteristics influenced epiphyte community structure. Among different-aged forests, forest structure and age influenced epiphyte species composition as density and species richness increased with forest age, and many epiphyte species were confined to microhabitats unique to old-growth forests. Among different-sized trees, epiphyte species exhibited significant associations to particular tree sizes and microhabitats. Emergent canopy trees had steep environmental and resource gradients that created a high diversity of microhabitats to which many epiphyte species were specialized. Environmental filtering played a role in epiphyte species distributions as species found in the same microhabitat showed convergence in ecological strategy. Among closely related species within a functional group, there was evidence of trait divergence, supporting the hypothesis of niche differentiation. At large spatial scales, habitat structure and dispersal influenced epiphyte community structure among forest stands. At smaller spatial scales, habitat specialization and differences in plant ecological strategies along environmental gradients suggest niche-based processes in driving local patterns of epiphyte diversity.

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Finally, I'd like to acknowledge the movie Medicine Man, a 1992 American film about an eccentric biochemist played by Sean Connery who finds the cure for cancer in an epiphytic bromeliad. After seeing this movie at the age of 15, it completely changed the course of my life and ignited an obsession with the tropical canopy epiphyte community that continues today.

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Chapter 1

Introduction

Species-rich plant communities, such as those found in wet tropical forests, challenge many theories on the maintenance of diversity because all plants require the same set of resources (Silvertown 2004). Neutral theory posits that species are competitively equivalent, niche differences are irrelevant, and species diversity is governed by the stochastic balance between immigration and extinction on a local scale, and between speciation and extinction on a regional scale (Hubbell 2001). Therefore, all species have the same probability of colonizing empty sites, and dispersal limitation, whereby individuals fail to occupy all possible empty sites because their seeds can't get there, is an important factor structuring ecological communities (Hubbell 2001, Etienne and Alonso 2005). Alternatively, niche theory posits that species are in competition for limiting resources, and, therefore, differ in some way that reduces competition (Gause 1934, Hutchinson 1959, MacArthur and Levins 1967, Tokeshi 1999). The segregation of plant species along environmental niche axes, including gradients of light, soil moisture, and rooting depth, along with differences in ecological strategies and trade-offs are mechanisms by which niche theory explains species diversity (Silvertown 2004 and references therein). Determining the importance of neutral- and niche-based processes in structuring species rich communities remains a central challenge of community ecology. Differences in plant ecological strategies and evidence of habitat specialization would support niche-based processes in driving patterns of species diversity, whereby random patterns in species turnover along environmental gradients and functional equivalence would support neutral-based processes.

The distributions of plant species may be influenced by niche factors such as variations in habitat structures, substrate characteristics, resource gradients, and environmental conditions, or neutral factors such as dispersal limitation. For species-rich tropical forests, the distribution of many plant species has been linked to heterogeneity in topography or hydrology (Lieberman and Lieberman 1985, Denslow 1987, Clark et al. 1998, Webb and Peart 2000, Harms et al. 2001, Valencia et al. 2004, Fine et al. 2005, DeWalt et al. 2006, Schnitzer et al. 2008, Dalling et al. 2012), soil resource gradients (Newbery and Proctor 1984, Potts et al. 2002, Phillips et al. 2003, Baldeck et al. 2012), or gradients in light through the presence of gaps (Schnitzer and Carson 2001, Schnitzer et al. 2008). Species distributions with no relationship to topography, edaphic resources, or light are assumed to be driven by dispersal limitation (Hubbell and Foster 1986, Dalling et al. 2002, Valencia et al. 2004) or density-dependent mechanisms such as disease from soil microbes (Connell 1971, Clark and Clark 1984, Bagchi et al. 2010, Mangan et al. 2010, Schnitzer et al. 2011). The relative importance of these factors in influencing species distributions seems to depend on spatial scale such that deterministic factors, such as habitat associations, play a larger role at small spatial scales where fine-scale habitat factors become more relevant, and stochastic factors, such as dispersal limitation, play a larger role at larger spatial scales where dispersal limitation becomes more relevant (Potts et al. 2002).

Neutral theory was developed to explain coexistence in diverse tropical forests, where it seemed implausible that each species could occupy a distinct niche (Hubbell 2001). However, recent research into tree species coexistence and diversity has unveiled that tropical tree species found in different topographic habitats differ in their ecological strategies (Kraft et al. 2008). For example, functional strategies of trees are related to gradients in light availability such that plants with high light requirements have higher growth rates, higher specific leaf area (SLA), higher leaf nitrogen (N), and higher mortality rates than those with lower light requirements, representing a trade-off between growth and survival (Poorter and Bongers 2006, Poorter et al. 2008). The diversity of strategies employed by plants in a particular environment is related to their ecological function along gradients of environmental conditions and resource availability.

Although it is unlikely that niche differences in plant ecological strategies along environmental axes is the only mechanism of coexistence in any large community, it now seems to play a greater role than was previously appreciated (Kraft et al. 2008, McGill et al. 2008, Violle and Jiang 2009). Habitat partitioning among terrestrial plants with different traits has been found along gradients of forest age, temperature, light, soil humidity, and disturbance in a variety of ecosystems (Solbrig 1994 and references therein, Kobe 1999, Meinzer et al. 1999, Montgomery and Chazdon 2002). Environments with steep gradients in resource availability and environmental conditions often contain plants with a greater diversity of traits arising from a greater number of microhabitats. By relating the function of a plant to the environment, we can better predict and understand the distribution and coexistence of species (Grime 2001, Westoby and Wright 2006, Swenson and Weiser 2010), as well as plant performance and trade-offs (Garnier et al. 2001, Poorter and Bongers 2006, Poorter et al. 2008).

The goal of my dissertation is to understand what factors influence the distribution and community structure of a set of tropical plant species and determine whether the importance of these factors changes with scale. Here, I examine the influence of habitat structure, environmental conditions, resources, and geographic space on patterns in the distribution of tropical vascular epiphyte communities at multiple scales: among forests, among trees, and within a single tree canopy. I also examine habitat partitioning and ecological strategies of vascular epiphytes along environmental and resource gradients within tree crowns. These studies increase our understanding of how diversity is maintained in a hyperdiverse group of plants.

The current understanding of epiphyte assemblages is based primarily on descriptive patterns and not causality (Bartels and Chen 2012). The mechanisms underlying epiphyte diversity are not well understood because a clear synthesis linking observation to theory is lacking. Furthermore, the scale of a study may be an important consideration in predictions of the patterns in epiphyte species assemblages. Therefore, multi-scale approaches that link pattern to theory are needed in order to disentangle the mechanisms of epiphyte diversity (Bartels and Chen 2012).

VASCULAR EPIPHYTES

Vascular epiphytes are plants that live non-parasitically on other plants, often high in the canopy of tropical forests. They are a distinctive and integral component of tropical forests contributing between 25-35% of the floral diversity (Gentry and Dodson 1987, Nieder et al. 2001) and up to 35% of the foliar biomass (Nadkarni 1984). Epiphytes increase the spatial and structural complexity of the canopy and create habitats for a diversity of canopy fauna including many species of birds and insects (Nadkarni and Matelson 1989, Ellwood et al. 2002, Ellwood and Foster 2004). Epiphytes have intrigued biologists ever since Schimper's (1888) extensive monograph on Neotropical epiphytes. Interest in epiphytes has continued as researchers try to understand how epiphytes survive and maintain their precarious existence detached from the forest floor. For example, their sole source of nutrients and water is through atmospheric deposition or from canopy soil that accumulates from decomposed plant material (Benzing 2004, Nadkarni 2004). Therefore, unlike forest floor-rooted plants, epiphytes must contend with inconsistent supplies of water and nutrients as well as the increased abiotic stresses from UV-radiation, wind, and high temperatures (Benzing 1987, 1990, Cardelús and Chazdon 2005).

Vascular epiphyte species have evolved an array of functional adaptations to maximize water and nutrient uptake and storage capacity that are unique among plants. For example, epiphytic tank bromeliads have a rosette form from overlapping leaves that impounds water and collects detritus, microorganisms, and nutrients (Fig. 1.1A). The absorptive trichomes that line the lower third of the tank are the sole water and nutrient uptake mechanism as the plants' roots are used for anchoring to their host tree (Benzing 2000). Atmospheric bromeliads have absorptive trichomes covering their leaf surface that take up atmospheric sources of water and nutrients (Fig. 1.1B; Benzing et al. 1976). Because atmospheric bromeliads are completely independent of canopy soil for sources of nutrients and water, they are often found growing on bare bark or inorganic surfaces such as electrical wires (Benzing et al. 1978). Aroids (Fig. 1.1C) and orchids (Fig. 1.1F) have a unique spongy structure of dead cells around their roots called velamen radiculum, that, when dry, hardens and protects their roots from water loss and, when wet, is able to take up atmospheric sources of water and nutrients (Zotz and Winkler in press, Benzing 1990). Many species, including soil ferns (Fig. 1.1D), root in canopy soil and exploit the nutrients and water stored in soil (Nadkarni 2004). Ferns found on bare bark (Fig. 1.1E) are able to exploit microhabitats with low water availability as they grow along a rhizome and are able to drop their leaves under severe drought (Benzing 1990). Given that water and nutrients are so limiting, strategies to capture and store the intermittent water and

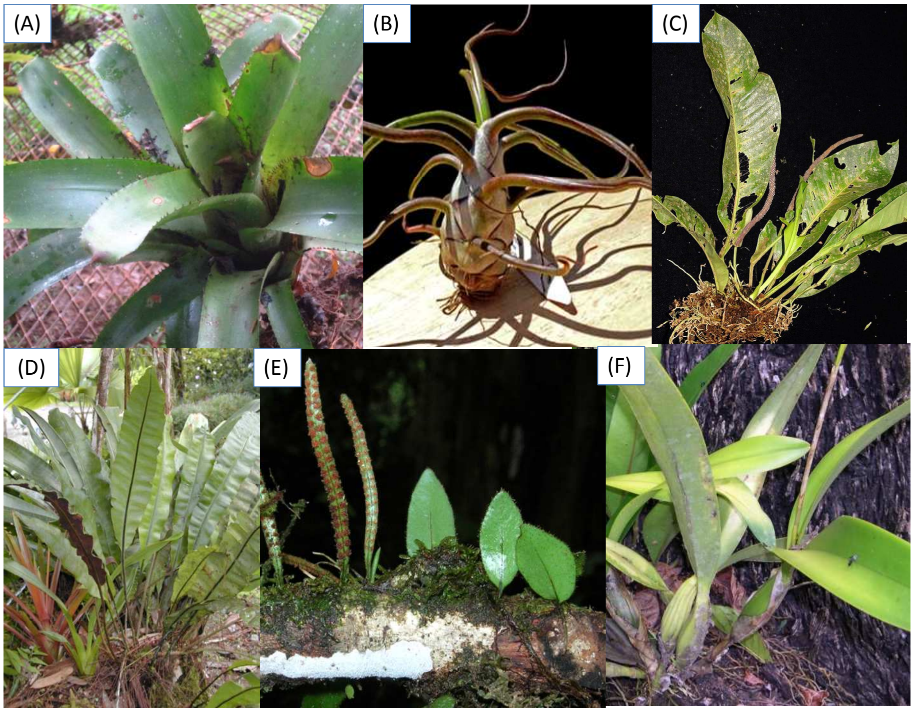

Figure 1.1 Functional group classifications of the most common vascular epiphytes surveyed on *Virola koschnyi* trees at La Selva Biological Research Station, Costa Rica. (A) tank bromeliads; (B) atmospheric bromeliads; (C) aroids; (D) ferns in canopy soil; (E) ferns on bare bark; and (F) orchids.

nutrient supply are thought to be the selective force behind such marked divergence in functional morphologies (Watkins Jr. and Cardelús 2012).

Epiphyte distributions are influenced by stand characteristics, such as stand age and tree species composition, as well as by dispersal limitation. Generally, species composition differs and epiphyte richness and density are lower in young secondary forests relative to old-growth forests (Barthlott et al. 2001, Krömer and Gradstein 2003, Benavides et al. 2006, Cascante-Marin et al. 2006, Woods and DeWalt 2012). The lower density, species richness, and differences in species composition among different-aged forests could be due to dispersal or recruitment limitation. For example, younger forests often lack the unique conditions found in old-growth trees such as canopy soil and shady sites, which may limit the ability of some epiphyte species to successfully colonize secondary forests (Barthlott et al. 2001, Woods and DeWalt 2012). Alternatively, epiphyte species may not be able to colonize younger forests because they are limited by dispersal (Cascante-Marin et al. 2008, 2009). Thus, forest stand age, structure, and tree species composition can have profound impacts on epiphyte richness, abundance, and species composition.

Host tree identity can be an important driver of epiphyte community structure. Epiphytes usually establish on tree bark and branches and in trapped soil or organic matter in crevices on bark surface or branches. Thus, epiphyte establishment can be influenced by tree size, age, and bark texture (Callaway et al. 2002, Cardelús 2007, Zotz and Schultz 2008). One species of host tree can contain a diverse community of epiphytes that is often different from other host tree species' (Laube and Zotz 2006, Cardelús

2007). Host-specific differences in epiphyte assemblages suggest that epiphyte diversity may be related to variation in microhabitats within individual host trees (Cardelús and Chazdon 2005, Cardelús 2007).

Within tree canopies, vascular epiphyte distributions have been hypothesized to be influenced by gradients in light, water availability, drought stress, and substrate characteristics (Johansson 1974, ter Steege and Cornelissen 1989, Zimmerman and Olmsted 1992, Nieder et al. 2000, Zotz and Vollrath 2003, Kelly et al. 2004, Reyes-Garcia et al. 2008). The vertical distribution of different epiphyte species from the lower to the upper canopy within a single tree suggests that different epiphyte species are adapted to different habitats that exist within host trees (Johansson 1974, Hietz and Briones 1998, Zotz 2007). The rainforest canopy is structurally complex with a diversity of habitats created by gradients in light, canopy soil, resource sources (*e.g.*, canopy soil and atmospheric deposition), and environmental conditions (Parker 1995, Nadkarni 2004). Therefore, a host tree with high heterogeneity in habitat structures, environmental conditions, and resources could theoretically support a high diversity of epiphytes that show various kinds of adaptations to specific microhabitats.

DISSERTATION STRUCTURE

I chose to study vascular epiphyte communities at three different scales in order to understand first, what factors influence the distribution and community structure of vascular epiphytes and, second, how those factors may change with spatial scale. I use the vascular epiphyte community at small scales (*i.e.*, within large tree crowns) as a model system to test theories on the maintenance of species diversity.

In Chapter 2, I test the alternate hypotheses that niche-based (*i.e.*, forest structure) and neutral-based processes (*i.e.*, forest age) affect epiphyte communities by comparing epiphyte community structure between secondary and old-growth forests in central Panama. I surveyed the entire vascular epiphyte community in replicate secondary forest stands of 35, 55, 85, and 115 y post land-abandonment as well as in two old-growth forests. Previously, studies on epiphytes in secondary forests were limited to forests younger than 50 yr and, therefore, this study was the first to examine epiphyte communities in older secondary forests.

In Chapter 3, I examine how the diversity of habitats within tree crowns change with tree size, and how those changes explain differences in epiphyte community structure among different-sized trees. I studied the epiphyte community and measured environmental conditions, structural features, and resources within different-sized trees (2.5–103.3 cm dbh) of one host tree species, *Virola koschnyi* (Myristicaceae). I chose to conduct my research in *V. koschnyi* trees because their branches extend from the main trunk at a 90° angle, which would potentially result in steep environmental gradients along the branches from the bole to the outer canopy (Fig. 1.2). Furthermore, *V. koschnyi* have few trunk epiphytes, which enabled me to examine the distribution of epiphytes and habitats solely within tree crowns. Finally, emergent *V. koschnyi* trees are relatively more abundant and accessible than other emergent trees at La Selva Biological Research Station, where I conducted this research. I examined the degree to which epiphyte species exhibit significant associations to particular microhabitats within tree crowns. I tested the

Figure 1.2. *Virola koschnyi* (Myristicaceae) tree at La Selva Biological Research Station, Costa Rica.

habitat heterogeneity hypothesis that a greater diversity of habitats in large trees would result in a greater diversity of epiphyte species and functional groups.

In Chapter 4, I test niche-based coexistence theory of vascular epiphytes within large tree crowns using trait-environment relationships. I examined the distribution of leaf traits of epiphyte species along environmental gradients to determine if vascular epiphyte species are differentiated along measured environmental axes. I test the hypotheses that environmental filters will result in convergence in strategy by co-occurring species (*i.e.*, in the same microhabitat within a single tree crown) and that niche differentiation among co-occurring species will result in a divergence in strategy. This is the first study to examine differences in functional leaf traits among multiple epiphyte species and link them to environmental gradients.

Chapter 5 provides a general conclusion, the importance of the research, and future directions for research. This dissertation provides a greater understanding of the maintenance of diversity in species-rich plant communities, such as the tropical vascular epiphyte community. Particularly, this dissertation highlights the importance of microhabitat selection on the structure and diversity of a hyperdiverse plant community.

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Chapter 2

The Conservation Value of Secondary Forests for Vascular Epiphytes in Central Panama

INTRODUCTION

Tropical forest canopies support a high diversity of plants and animals (Ellwood and Foster 2004, Kelly et al. 2004). The vascular epiphytic plants that inhabit the tropical canopy are a conspicuous and integral component of tropical rainforests. Not only do epiphytes contribute up to a third of the vascular species in tropical forests (Gentry and Dodson 1987), they can also play an important role in nutrient and water cycling (Nadkarni 1986, Clark et al. 2005, Holwerda et al. 2010) and in providing habitat and food for an array of arboreal animals (Davis and Sutton 1998, Ellwood et al. 2002, Ellwood and Foster 2004). Thus, how quickly epiphyte communities recover after stand-destroying disturbances has important implications for conservation of tropical forest diversity and ecosystem functioning.

There has been a contentious debate about the conservation value of secondary tropical forests (Christensen and Peet 1984, Brown and Lugo 1990, Turner et al. 1997, Johnson et al. 2000, Guariguata and Ostertag 2001, Chazdon 2003, Barlow et al. 2007, Dent and Wright 2009). Secondary forests developing on lands that were not intensively used and are close to seed sources tend to have high conservation value for trees and lianas because they rapidly attain many aspects of the forest structure and species richness of old-growth forests, but species composition may take centuries to converge on old-growth forest (Brown and Lugo 1990, DeWalt et al. 2000, Guariguata and Ostertag 2001, Chazdon et al. 2007, Dent and Wright 2009). Thus, if conservation value is determined solely by the number of species and forest biomass of trees and lianas, then secondary forests that were not intensively used and are close to seed sources can reach species richness and biomass values comparable to old-growth forest within a few decades (Saldarriaga et al. 1988, DeWalt et al. 2000, Guariguata and Ostertag 2001). However, some plants and animals may be highly specialized to old-growth forest because of the resources and conditions found only in that habitat (reviewed in DeWalt et al. 2003). For example, many cavity-nesting animals require standing dead trees that are less abundant in secondary forests (DeWalt et al. 2003, Chazdon et al. 2009), and some rare shade-tolerant species are absent from secondary forests (Thomlinson et al. 1996, Guariguata and Ostertag 2001, Liebsch et al. 2008, Chazdon et al. 2009). Secondary forests may take centuries to recover the conservation value of old-growth forests for these more specialized taxa (Christensen and Peet 1984, Turner et al. 1997, Barlow et al. 2007).

In particular, secondary forests may take much longer to attain high conservation value for epiphytes than for plants of other habits. Epiphytes are dispersal limited and may take 8 to 12 yr to colonize regenerating trees in secondary forests (Nadkarni 2000, Cascante-Marin et al. 2009). In addition, individual epiphytes grow very slowly and can take more than 10 yr to reach reproductive maturity (Gerold and Zotz 2002, Hietz et al. 2002, Laube and Zotz 2003). Finally, many epiphytes appear to be old-growth specialists (Barthlott et al. 2001, Acebey et al. 2003, Krömer and Gradstein 2003, Köster et al.

2009). In montane forests of Venezuela and Costa Rica, for example, orchids and ferns were much less common in secondary forests than in old-growth forests (Barthlott et al. 2001, Nadkarni 2004). Epiphytes may be old-growth specialists if they only establish on large trees, on host tree species present only in old-growth forests, or in conditions found only in older forests such as the presence of canopy soil or particular microclimatic conditions including shade and high relative humidity (Barthlott et al. 2001, Callaway et al. 2002, Acebey et al. 2003, Krömer and Gradstein 2003, Laube and Zotz 2006, Cardelús 2007, Zotz and Schultz 2008, Werner 2011). The conservation value of secondary forests for epiphytes thus depends to a large part on the degree to which secondary forest epiphyte communities contain species found in old-growth forests. If the species composition of a young secondary forest is a subset of old-growth forest and the similarity to old-growth increases with secondary forest age, then it is likely that community composition of secondary forests will eventually approach that of old-growth forests.

To date, studies on epiphytes in secondary forests have been limited to forests younger than 50 yr (Barthlott et al. 2001, Krömer and Gradstein 2003, Nadkarni 2004, Benavides et al. 2006, Cascante-Marin et al. 2006). In those studies, epiphyte communities in secondary forests had substantially different species composition as well as lower epiphyte densities and species richness compared to old-growth forests (Barthlott et al. 2001, Krömer and Gradstein 2003, Benavides et al. 2006, Cascante-Marin et al. 2006). It is therefore not known when, if ever, epiphyte community structure (density, species richness, and composition) in secondary forests approaches that of old-growth forests.

In this study, we employed a chronosequence approach (secondary forest stands of different ages since land abandonment) in central Panama, focusing on older secondary forest stands ranging in age from 35 to 115 yr, to examine whether there is convergence on old-growth forests over time in secondary forests in terms of epiphyte community structure. All stands were in close proximity to old-growth forest and were located on relatively fertile soils. We studied the density, species richness, and composition of holoepiphytes (*i.e.*, plants sustained entirely by nutrients and water received non-parasitically from within the canopy in which they reside) as well as hemiepiphytes (*i.e.*, plants that spend only part of their life cycle with a terrestrial connection, Benzing 1990, Moffett 2000). We included primary hemiepiphytes, which start in the canopy and eventually send roots to the ground, and secondary hemiepiphytes, which start in the ground and eventually lose their terrestrial connection (Benzing 1990, Moffett 2000). For those species whose classification as either a vine or a hemiepiphyte is still unresolved (e.g., *Monstera*, Andrade and Mayo 1998, López-Portillo et al. 2000), we included them as a hemiepiphyte. We surveyed trees, lianas, and downed coarse woody debris. For epiphytes occurring on trees, we also examined relationships between epiphyte occurrence and host-tree size.

METHODS

Study site and plant survey

Secondary and old-growth forest stands were located within the Barro Colorado Nature Monument (BCNM) of central Panama, which includes Barro Colorado Island (BCI, 9°9′N; 79°51′W) as well as several adjacent mainland peninsulas (Fig. 2.1). Forests in the BCNM receive approximately 2600 mm of annual rainfall, predominantly during the wet season from May through December. The vegetation is classified as tropical moist forest and ranges in altitude from 120 m to 160 m asl (Holdridge and Budowski 1956, Leigh Jr. et al. 2004).

We surveyed vascular epiphytes in 10 forest stands that included two in each of four ages of secondary forest and two stands in old-growth. When our epiphyte survey was conducted in 2009, the secondary forests were approximately 35, 55, 85, and 115 yr old. The two old-growth stands provided a reference level of epiphyte species richness, density, and species composition. This chronosequence was established in 1994 by J. S. Denslow, during which time trees ≥ 5 cm diameter at breast height (dbh) were measured in contiguous 10 m x 10 m quadrats within transects of 160 m x 10 m in each stand (Denslow 2000, Denslow and Guzman 2000). In 1994, two transects, totaling 0.32 ha, were established in nine stands, but only one transect was established in one of the 35-yr-old stands, which was deemed too small for an additional transect. Stand ages were estimated by reference to early publications of the establishment of BCI (Kenoyer 1929, Standley 1933, Enders 1935, Chapman 1938), digitized aerial photographs taken in the late 1920s and between 1955 and 1983, and land-use history in the BCNM

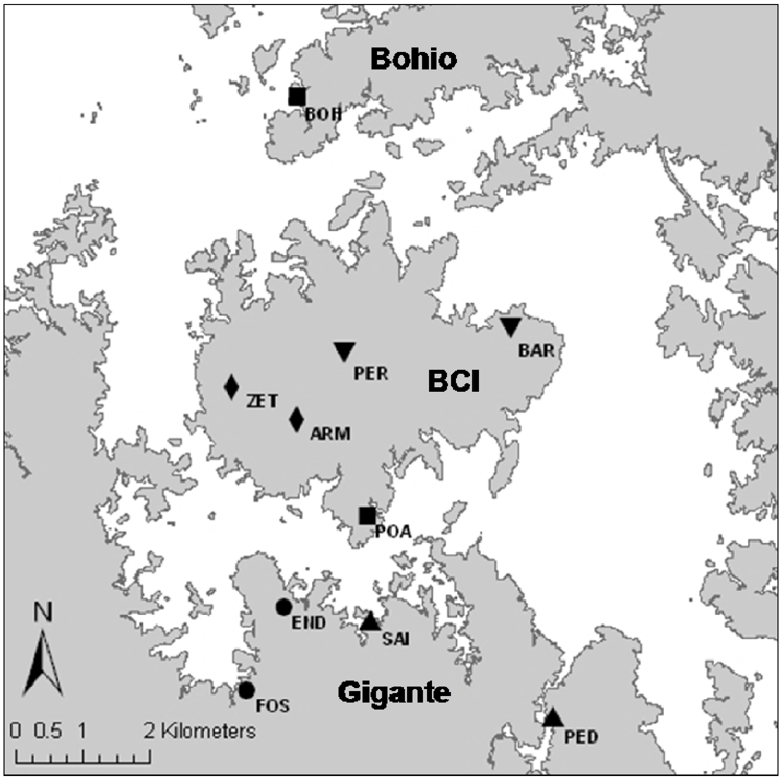

Figure 2.1. Map of the locations of studied secondary forest and old-growth stands on the Bohio and Gigante peninsulas and Barro Colorado Island (BCI) in the Barro Colorado Nature Monument in central Panama. Symbols refer to the approximate age of the stand (upward-facing triangles = 35 yr, circles = 55 yr, squares = 85 yr, downward-facing triangles = 115 yr, diamonds = old-growth). Site codes are denoted with three letters (SAI = Saino, PED = Pedro Gomez, END = Enders, FOS = Fosters, POA = Poachers, BOH = Bohio, BAR = Barbour, PER = Pearson, ARM = Armour, ZET = Zetek).

(Denslow and Guzman 2000, DeWalt et al. 2000). In 2002, trees ≥ 5 cm dbh were permanently tagged and remeasured. More detailed descriptions of the chronosequence design and census methods are provided in Denslow and Guzman (2000) and DeWalt *et al.* (2000).

Within each stand, we counted and identified all holo- and hemiepiphytes that occurred on trees ≥ 1 cm dbh (living or dead), lianas, or downed coarse woody debris (DCWD). For epiphytes occurring on living trees ≥ 5 cm dbh, we noted the tag number of the tree to later determine the dbh from the 2002 dataset. Epiphytes occurring in crowns were identified with the help of binoculars or by climbing the trees using modified rope climbing techniques (Perry 1978) when binoculars were insufficient for proper identification. Given the low density of epiphytes in forests along the chronosequence (a maximum of 25 individuals/ tree) and the fact that ground-based surveys have been found to capture > 90 percent of epiphyte occurrences (Burns 2007), ground-based epiphyte surveys were conducted for all trees ≤ 60 cm dbh and most (63%) of trees > 60 cm dbh, as the canopies of these trees were easily visible from the ground. A total of 10 trees > 60 cm dbh were climbed as these canopies were difficult to view from the ground. Species names of flowering plants followed the Flora of Panama Checklist and Index (D'Arcy 1987). Other sources were used for the identification of seedless vascular plants (Croat 1978, Lellinger 1989).

Statistical analysis

One sub-plot in Enders, a 55-yr-old secondary forest, had a 10 m x 20 m gap in which 150 individuals of one hemiepiphytic aroid, *Philodendron rigidifolium*, were found. There were no similar gaps in other stands, and such high densities of *P. rigidifolium* were not found elsewhere. This sub-plot was found to be an outlier of all sub-plots in Enders according to a Grubb's test ($Z = 3.28$, $P < 0.05$) and was therefore removed from the analysis.

To compare epiphyte species richness among forest ages, we conducted sample-based Mao Tau rarefaction analysis using EstimateS software v. 8.2 (Colwell 2009). We used the 10 m x 10 m sub-plots within each stand as samples. The expected species accumulation curves were rescaled by individuals to compare the stands in terms of species richness (Gotelli and Colwell 2001). We compared the rarefied species richness among stands for 60 individuals, which is the maximum number of individuals found in 55-yr-old forests.

All statistical analyses were conducted using R version 2.11.0 (R Development Core Team 2009). We examined the relationships between epiphyte density, species richness, and rarefied species richness (E_{60}) and secondary forest age using simple linear regression. Because their ages are unknown, old-growth stands were omitted from regression analyses but are estimated to be > 500 yr old (Piperno 1990). Stand age was $\log_{10}$ transformed for all analyses. We tested whether holoepiphytes and hemiepiphytes differed in their relationship to stand age using analysis of covariance (ANCOVA) with stand age as the covariate and epiphyte type as the categorical predictor variable. To determine at what age, if ever, epiphyte density, species richness, and rarefied species richness in secondary forests were similar to old-growth forests, we conducted analysis of variance (ANOVA) using *a priori* orthogonal linear contrasts that compared each secondary forest age to old-growth forests. ANOVA was also used to compare if the percentage, density, and basal area of trees colonized by epiphytes and the maximum dbh of trees in each stand differed between secondary forest and old-growth. We used the latter measure because the same total tree basal area could be achieved in two stands but be divided into a few large trees or many small trees. Maximum tree dbh values from the census in 2002 were used for this analysis. Although the values from 2002 may under-estimate the maximum dbh of each stand, these differences would be small given the slow change in dbh of large trees (Lieberman et al. 1985, Clark et al. 2003).

We tested whether holoepiphytes and hemiepiphytes were more common on larger trees using logistic regression. Diameters of trees ≥ 5 cm from the census in 2002 were used for this analysis.

We examined whether similarity in epiphyte species composition of secondary forests converged on old-growth forests with time by conducting linear regression of community similarity on approximate forest age. We calculated similarity with two metrics: the Sørensen similarity index using species incidence (presence/absence) and the Morisita-Horn similarity index, which uses species relative abundance. Of the traditional abundance-based similarity indices, the Morisita-Horn index is the most robust to uneven and insufficient sampling (Chao et al. 2006). It examines the probability of two randomly chosen individuals being of the same, shared species (Chao et al. 2006). We applied the jackknife method to the Morisita-Horn index to remove biases associated with under-sampling and henceforth refer to the index as Jackknife Morisita-Horn. For each secondary forest age, we averaged the pairwise similarity indices between each secondary forest stand and each of the two old-growth stands (i.e. four comparisons per forest age).

Finally, we tested whether epiphyte communities in secondary forests were statistically nested subsets of old-growth forests using the NODF (Nestedness metric based on Overlap and Decreasing Fill) index for incidence data and the WNODF (Weighted NODF) index for abundance data using the NODF-Program (Almeida-Neto and Ulrich 2010). Only the 21 species represented by at least two individuals across the chronosequence were included in this analysis.

RESULTS

In a total of 3.02 ha (eight stands of 0.32 ha, one stand of 0.30 ha, and one stand of 0.16 ha), we found 1099 individual epiphytes in 27 species and 7 families (Table 2.1). Three Araceae species (aroids) were identified only to morphospecies. Fifteen epiphyte species were classified as holoepiphytes, and 12 species were classified as hemiepiphytes (Table 2.1; Appendix B). All of the hemiepiphytes were classified as secondary hemiepiphytes. No primary hemiepiphytes were found in the survey. Across the chronosequence, Araceae was the most diverse and abundant epiphyte family, representing 64 percent of all individuals and 39 percent of all species; Orchidaceae and Polypodiaceae were less abundant and speciose; Bromeliaceae and Cactaceae were found only in old-growth stands (Table 2.1).

Over 90 percent of epiphytes were found on living trees, but only 11 percent of trees ≥ 5 cm dbh as measured in 2002 hosted at least one epiphyte. For these host trees, the mean epiphyte load was 3.9 epiphytes/tree. The probability that a tree would host an epiphyte increased significantly with dbh for holoepiphytes ($Z = 11.63$, $P < 0.0001$) and hemiepiphytes ($Z = 10.82$, $P < 0.0001$; Fig. 2.2). Small trees had a higher probability of hosting a hemiepiphyte than a holoepiphyte, but both epiphyte types had equal probabilities of being on large trees (*i.e.*, > 100 cm dbh; Fig. 2.2).

At the stand level, density ($R^2 = 0.03$, $P = 0.68$) and basal area ($R^2 = 0.3$, $P = 0.16$) of trees that hosted epiphytes did not increase with forest age. However, the

Table 2.1. Number of individuals and number of species for all epiphytes (All), holoepiphytes (Holo), and hemiepiphytes (Hemi) found in the seven most abundant plant families along a forest chronosequence in the Barro Colorado Nature Monument in central Panama. [a] old-growth only.

	Number of individuals			Number of species		
Family	All	Holo	Hemi	All	Holo	Hemi
Araceae	712	13	699	14	3	11
Orchidaceae	188	188	0	4	4	0
Polypodiaceae	184	136	48	3	2	1
Bromeliaceae[a]	5	5	0	3	3	0
Aspleniaceae	4	4	0	1	1	0
Cactaceae[a]	3	3	0	1	1	0
Gesneriaceae	3	3	0	1	1	0
Total	1099	352	747	27	15	12

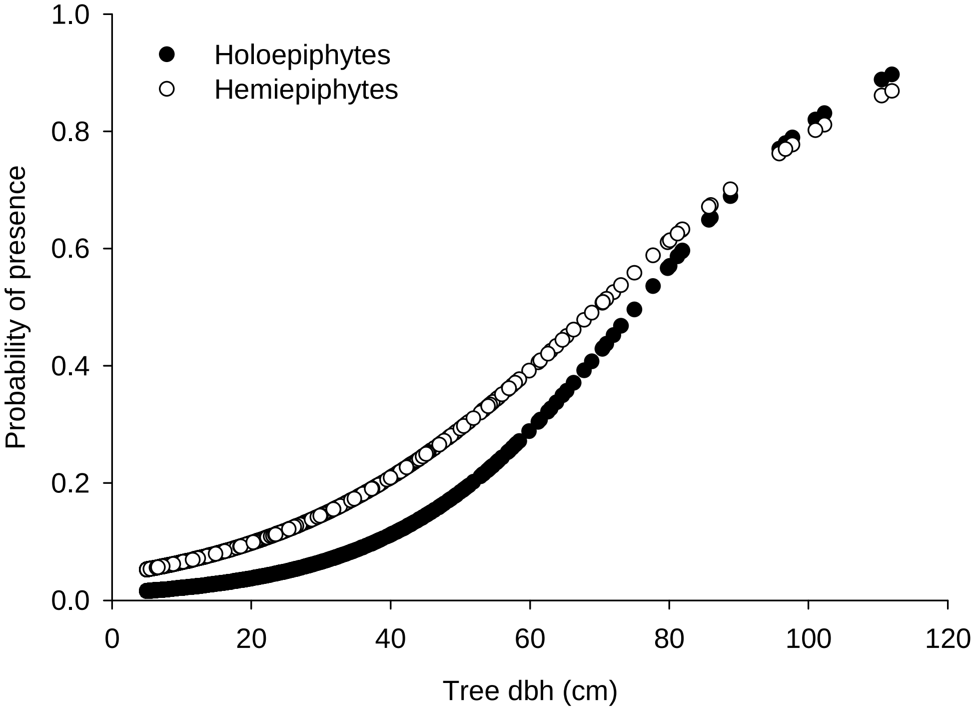

Figure 2.2. Logistic regression curves showing the relationship between tree dbh and predicted probability that a holoepiphyte ($e^{-4.4 + 0.06(dbh)}/(1 + e^{-4.4 + 0.06(dbh)})$) or a hemiepiphyte ($e^{-3.12 + 0.04*dbh}/(1 + e^{-3.12 + 0.04*dbh})$) occurred on the tree along a forest chronosequence in central Panama.

maximum tree dbh of trees that hosted epiphytes increased with forest age ($R^2 = 0.74$, $P = 0.006$), with the highest maximum dbh found in 85-yr-old forests (Fig. 2.3). The percentage of trees colonized by epiphytes also increased with forest age ($R^2 = 0.86$, $P < 0.001$) and was maximal in old-growth forests (Fig. 2.3).

Density and Species Richness

Density of all epiphytes ($R^2 = 0.80$, $P = 0.003$), holoepiphytes ($R^2 = 0.62$, $P = 0.02$), and hemiepiphytes ($R^2 = 0.85$, $P = 0.001$) increased significantly with forest age (Fig. 2.4A). The youngest stands in the chronosequence were virtually devoid of epiphytes; in fact, no epiphytes were found in one 35-yr-old stand (Saino) and only 11 individual holoepiphytes of two species were found in the other (Pedro Gomez). The density of hemiepiphytes across stands was significantly higher than holoepiphytes ($F_{1,12} = 5.8$, $P = 0.03$), but there was no difference between holo- and hemiepiphytes in their responses to forest age (*i.e.*, no significant interaction of age and epiphyte type; $F_{1,12} = 1.9$, $P = 0.20$). Old-growth forests had significantly greater densities than all other forest ages for all epiphytes, holo and hemiepiphytes (Table 2.2). Epiphyte densities in 35-yr-old forests were less than 1 percent of that in old-growth, whereas epiphyte densities in 115-yr-old forests were 49 percent of that in old-growth forests.

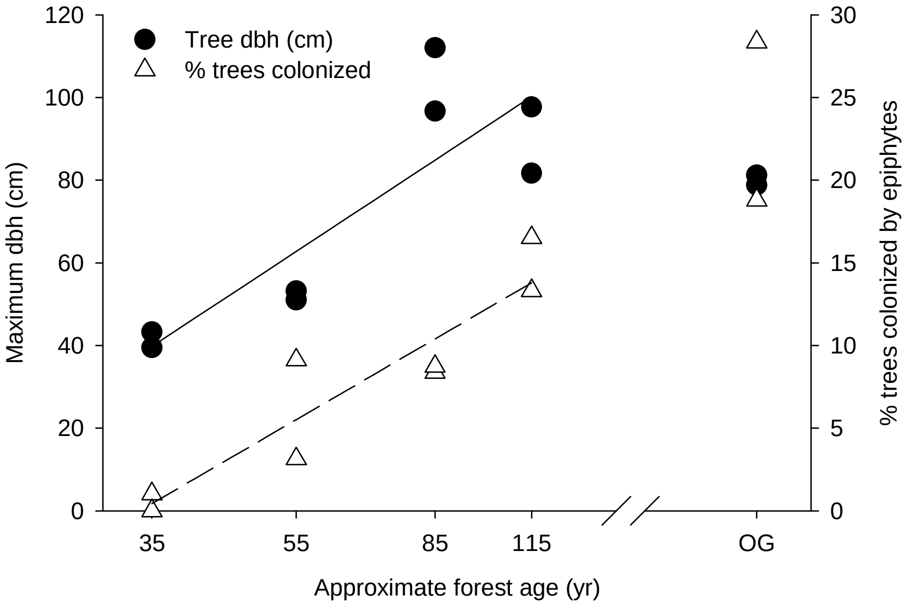

Figure 2.3. Relationship between maximum tree dbh (solid line) and percent of trees colonized by epiphytes (dashed line) with approximate forest age along a forest chronosequence in central Panama.

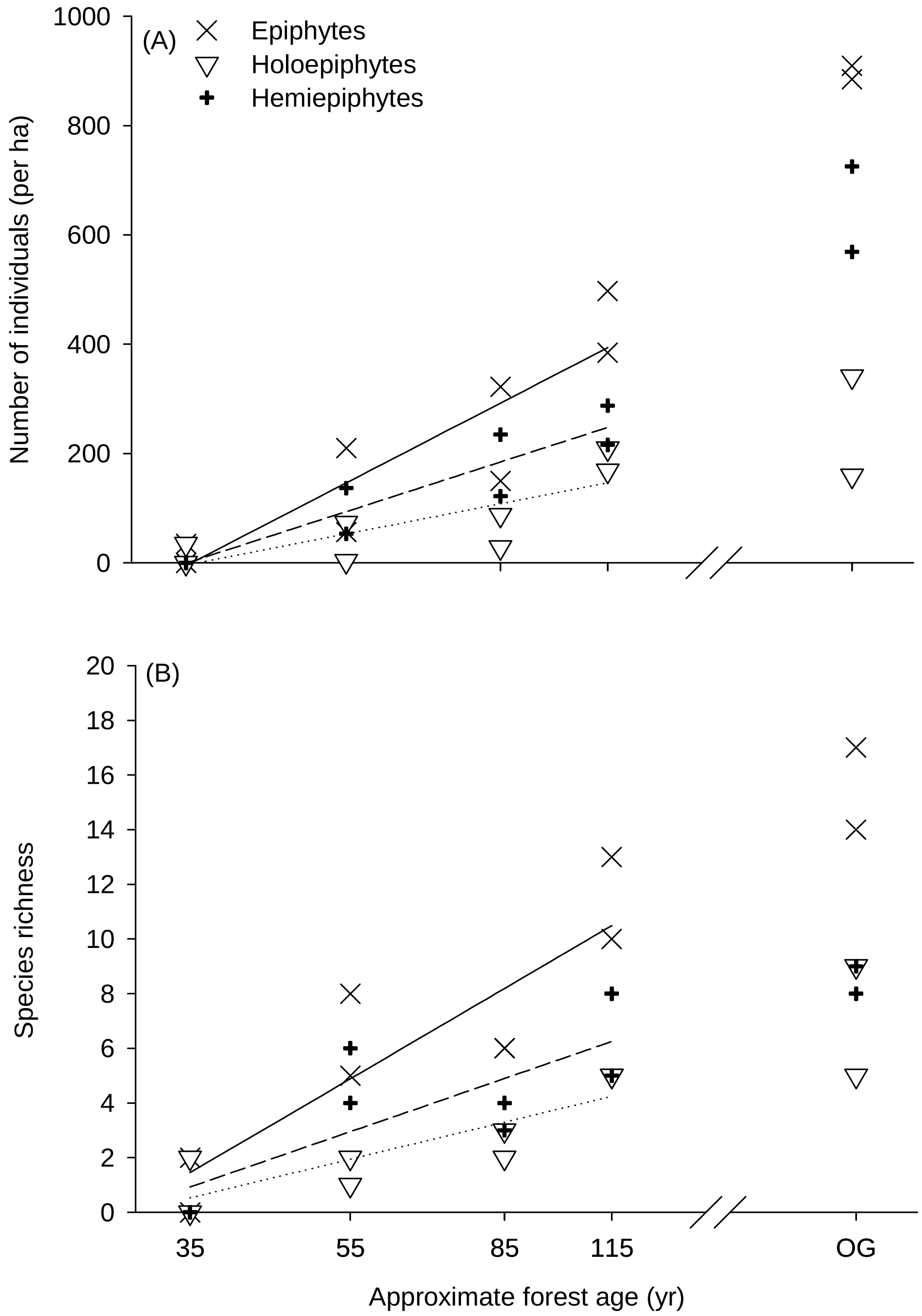

Figure 2.4. Relationship between density (A) and species richness (B) of epiphytes (solid line), holoepiphytes (dashed line), and hemiepiphytes (dotted line) and approximate forest age along a forest chronosequence in central Panama.

Table 2.2. Density (mean per ha ± SE) and species richness (mean raw counts ± SE) of all epiphytes (All), holoepiphytes (Holo), and hemiepiphytes (Hemi), and species richness rarefied to 60 individuals (maximum number of epiphytes in 55-yr-old forests) for all epiphytes found in different-aged secondary and old-growth forests (OG) along a chronosequence in the Barro Colorado Nature Monument in central Panama. The area sampled for each forest stand was 0.32 ha except for one 35-yr-old stand of 0.16 ha and one 55-yr-old stand of 0.30 ha. Values with different letters are significantly different from OG forests according to linear orthogonal contrasts ($P < 0.05$). $^*P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$.

	Density			Species richness			Rarefied species richness (E_{60})
Age	All	Holo	Hemi	All	Holo	Hemi	All
35	17.0 ± 24.0^a	17.0 ± 24.3	0 ± 0^a	1.0 ± 1.4^a	1.0 ± 1.4^a	0 ± 0^a	2.0 ± 2.4^a
55	133.0 ± 108.9^a	38.0 ± 49.6	95.0 ± 59.3^a	6.5 ± 2.1^a	1.5 ± 0.7^a	5.0 ± 1.4^a	8.0 ± 0.3^b
85	236.0 ± 121.6^a	58.0 ± 42.0	178.0 ± 79.2^a	6.0 ± 0^a	2.5 ± 0.7^a	3.5 ± 0.7^a	6.0 ± 0.5^b
115	440.5 ± 79.9^a	189.0 ± 28.7	252.0 ± 50.9^a	11.5 ± 1.2^b	5.0 ± 0^b	6.5 ± 2.1^b	9.0 ± 0.8^b
OG	896.5 ± 17.7^b	250.0 ± 128.2	647.0 ± 110.3^b	15.5 ± 2.1^b	7.0 ± 2.8^b	8.5 ± 0.7^b	9.0 ± 1.4^b
$F_{4,5}$	35.2***	4.8	25.2**	19.9**	5.8*	13.8**	9.9*

Species richness of all epiphytes ($R^2 = 0.77$, $P = 0.004$), holoepiphytes ($R^2 = 0.72$, $P = 0.008$), and hemiepiphytes ($R^2 = 0.60$, $P = 0.02$) increased significantly with forest age (Fig. 2.4B), with no overall difference between holoepiphyte and hemiepiphyte species richness ($F_{1,12} = 2.6$, $P = 0.13$) or their response to forest age ($F_{1,12} = 0.32$, $P = 0.58$). Species richness rarefied to 60 individuals increased significantly with forest age ($R^2 = 0.59$, $P = 0.03$). Compared to old-growth stands, epiphyte species richness in 35-yr-old secondary stands was only 6 percent of the old-growth value, whereas it was 74 percent in 115-yr-old secondary forests. Old-growth and 115-yr-old stands were equivalent in species richness of all epiphytes, holoepiphytes, and hemiepiphytes, as well as rarefied species richness for all epiphytes (Table 2.2).

Community composition

Similarity of secondary forests to old-growth forests in terms of species composition increased with forest age (Fig. 2.5; Jackknife Morisita-Horn index, $R^2 = 0.91$, $P = 0.04$; Sørensen index, $R^2 = 0.89$, $P = 0.05$). However, the slope for the incidence-based measure of similarity (Sørensen) was higher than the abundance-based measure (Jackknife Morisita-Horn), indicating faster convergence in the presence of species found in old-growth forests than in relative species abundance.

Epiphyte communities in secondary forests were nested subsets of the species found in older secondary forests and in old-growth forests, both in terms of the species present and their relative abundance (Fig. 2.6; NODF: $z = -4.09$, $P < 0.001$; WNODF: $z = -4.35$, $P < 0.001$). Of all the species found along the chronosequence, old-growth forests

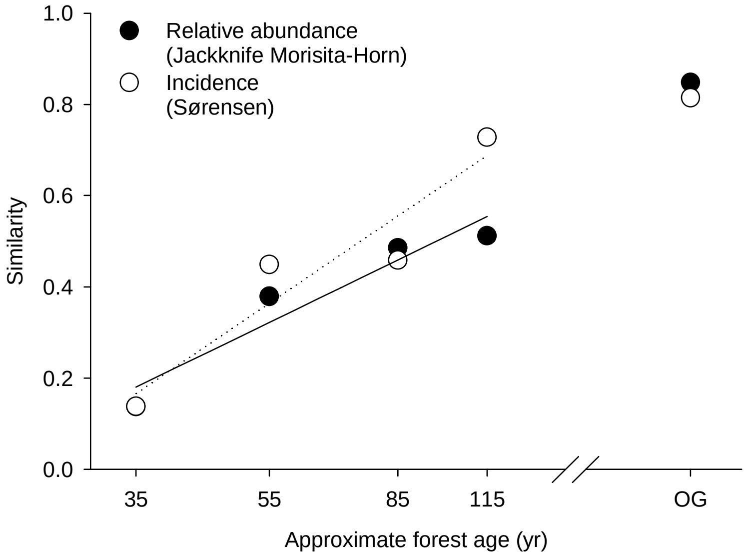

Figure 2.5. Linear regression of similarity in epiphyte species composition between secondary forest stands and old-growth forest stands and approximate forest age using a Jackknife Morisita-Horn similarity matrix on relative abundance and a Sørensen similarity matrix on incidence for epiphytes found along a forest chronosequence in central Panama. Pairwise distances between each secondary forest stand and each of the two old-growth stands were averaged for each secondary forest age. For clarity, the average similarity between each secondary forest age and old-growth stands is shown.

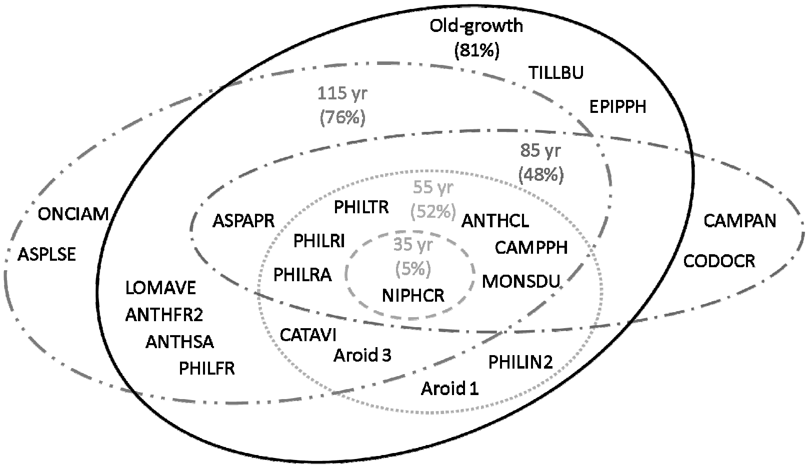

Figure 2.6. Nested diagram of species composition for epiphyte species in each forest age along a secondary forest chronosequence and old-growth forests in central Panama generated using NODF (Nestedness Overlap based on Decreasing Fill) index for incidence data. Species are denoted by codes defined in Appendix B. Below each forest age is the percentage of species found along the chronosequence that were present in stands of that forest age.

contained 81%, with only four species (each with fewer than seven individuals) being absent from old-growth stands.

DISCUSSION

Based on this chronosequence of secondary forests between 35 and 115 yr old, it appears that epiphyte community structure in secondary forests in central Panama becomes more similar to old-growth forest over time, and that 115 yr is sufficient for some community properties to attain levels found in old-growth forest. In our study, 115-yr-old secondary forests and old-growth forests were equivalent in the density, basal area, and percent of trees colonized by epiphytes, as well as the species richness of epiphytes. Species richness increased with forest age and was 74 percent that of old-growth forests by 115 yr. Similarity in community composition to old-growth forest also increased with forest age and reached approximately 75 percent similarity in terms of species presence in 115-yr-old forests. This increase in similarity to old-growth forest with time and the high degree of nestedness among forest stands suggest that, given sufficient time, epiphyte community composition in secondary forests would recover to old-growth forest composition. For epiphyte density, however, more time is needed to recover to old-growth levels. Secondary forests had substantially lower epiphyte densities than in old-growth forests, with 115-yr-old forest having only 49 percent of the density of old-growth forest epiphytes.

Epiphyte succession in central Panamanian lowland forest appears to occur more slowly than in upper Amazonian and Costa Rican premontane forests, where epiphyte densities were almost 50 percent of old-growth levels by 30 to 40 yr after land abandonment (Benavides et al. 2006, Cascante-Marin et al. 2006). In contrast, 55-yr-old secondary forests in our study site had only 14 percent of the density of old-growth forest epiphytes. Similarly, the density of epiphytes in old-growth forests in central Panama is lower than in other tropical forests with the number of epiphytes per ha averaging approximately 800 compared to 1550 in upper Amazonia (Benavides et al. 2006) and 2100 in premontane Costa Rican forests (Cascante-Marin et al. 2006). The low density of epiphytes in our study site compared to these aseasonal tropical wet forests may be due to drought stress resulting from the 4-mo-long dry season and the lower annual rainfall in central Panama (2600 mm) compared to upper Amazonia (3200 mm, Benavides et al. 2006) and premontane forests in Costa Rica (3282 mm, Cascante-Marin et al. 2006). A low density of epiphytes would equate to fewer reproductive adults and fewer propagules, which may explain the slow colonization of secondary forests in central Panamanian lowland forest.

In contrast to density, the recovery of epiphyte species richness in central Panamanian forests appears quite rapid with 55-yr-old forests containing 65 percent of the number of epiphyte species found in old-growth forests. The rapid recovery of epiphyte species in our secondary forests is similar to other lowland and premontane forests where almost 70 percent of old-growth epiphyte species richness was found in 30 to 40-yr-old secondary forests (Benavides et al. 2006, Cascante-Marin et al. 2006). In our study, secondary forest plots are in close proximity to old-growth forest (DeWalt et al. 2003), which may explain the rapid recovery of species richness to old-growth levels (Chazdon 2003, Chazdon et al. 2009).

Similar levels of species richness between secondary and old-growth forests may not indicate high conservation value for secondary forests if there are large differences in species composition. In premontane forests in Costa Rica, for example, the number of species per ha between 35 to 40-yr-old forests and old-growth forests was similar, but the identity of the dominant species changed dramatically between forest types (Cascante-Marin et al. 2006). Thus, the recovery of similarity of epiphyte species composition to old-growth forests may be a much better indicator of the value of secondary forests for this life form.

In central Panama, similarity in species composition of secondary forests to old-growth levels increased with forest age and recovered quite rapidly with 55-yr-old forests having an average similarity to old-growth forests of 45 percent. The increasing similarity in species composition of secondary forests to old-growth forests with forest age may be due to the increasing heterogeneity in canopy structure, light, and microclimate that accompanies forest succession. The structural heterogeneity found in older forests results in a combination of drought-resistant epiphyte species common to hotter and drier secondary forests along with shade-tolerant epiphytes that specialize in moist and shady habitats of older forests (Barthlott et al. 2001, Acebey et al. 2003, Krömer and Gradstein 2003). In central Panama, epiphyte communities in young secondary forests were nested subsets of the epiphyte communities in older secondary forests and old-growth forests. The majority of epiphyte species that could inhabit drier sites in secondary forests in our study were also found within old-growth forests, and several species that had more specific microclimatic and structural requirements were only found in old-growth forests. For example, *Niphidium crassifolium* was found in all forest ages and can inhabit drought-prone microhabitats in tropical canopies on BCI (Andrade and Nobel 1997). In contrast, species that were only found in old-growth forests, such as *Vriesea gladioliflora* and *Guzmania lingulata*, require shady sites with high humidity (Merwin et al. 2003) that are likely not available in secondary forests (Barthlott et al. 2001, Krömer and Gradstein 2003).

Compared to other plant groups studied along the BCNM chronosequence, epiphyte communities need more time to approach old-growth forest species richness and density as they depend on the establishment of the forest before colonizing. Within 20 yr after land abandonment, secondary forests quickly attain old-growth levels of density and diversity for lianas and trees (Denslow and Guzman 2000, DeWalt et al. 2000, 2003). Epiphytes would thus require a minimum lag-time of approximately 20 yr before colonizing secondary forests in central Panama. Because epiphytes are inherently slow-growing, dispersal-limited plants that take a long time to establish on bare branches (Nadkarni 2000, Gerold and Zotz 2002, Cascante-Marin et al. 2009), the lag-time for successful establishment after forest development may be even greater than 20 yr. We found support for this hypothesis as 35-yr-old forests had only 6 percent of the species richness of old-growth forests, while 55-yr-old forests had 42 percent of old-growth epiphyte species richness. Epiphyte establishment in young secondary forests in the BCNM may be further inhibited by the 4-mo-long dry season as epiphyte species richness in younger secondary forests has been found to be much higher in more aseasonal forests such as in premontane Costa Rican forests (22% of old-growth species richness in 12-yr-old forests, Cascante-Marin *et al.* 2006) and in upper Amazonian forests (36% of old-growth species richness in 16-yr-old forests, Benavides *et al.* 2006).

As in other studies, we found the probability of occurrence of all epiphytes to increase with tree dbh (Zimmerman and Olmsted 1992, Zotz and Vollrath 2003, Zotz and Schultz 2008), potentially because small trees have less substrate on which epiphytes may establish, provide lower quality substrate (e.g., lower water-holding capacity, Hyvärinen et al. 1992, Callaway et al. 2002), or represent less time for colonization (Zotz and Schultz 2008). Along the BCNM chronosequence, the highest number of large trees, and hence the greatest area of substrate on which epiphytes may establish, occurred in stands that were approximately 85 yr old (Denslow 2000). Despite the greater amount of substrate in 85-yr-old forests, epiphyte density was highest in old-growth forests, suggesting that epiphyte colonization is not limited by tree size but by time for colonization or a lack of suitable substrate in secondary forest trees. The high similarity in forest structure and epiphyte species composition between 115-yr-old secondary forests and old-growth forests, however, suggests that the majority of old-growth epiphyte specialists are also colonizing 115-yr-old secondary forests. Given that epiphytes are often dispersal-limited (Cascante-Marin et al. 2009), less time for colonization better explains the low epiphyte densities in secondary forests.

In forests that were > 55 yr, the density of hemiepiphytes was greater than that of holoepiphytes across the chronosequence and composed, on average, 70 percent of the total epiphyte density. Hemiepiphytes were, however, absent in 35-yr-old forests, which may be due to hemi-epiphytic vegetative fragments or seeds not surviving forest conversion (Benavides et al. 2006). The higher density of hemiepiphytes compared to holoepiphytes in mid- to old-secondary forests (*i.e.*, > 55 yr) and old-growth forests could result from low host-tree specificity. Secondary hemiepiphytes generally are less host-specific than holoepiphytes and will ascend the closest tree, regardless of tree species identity or size (Atwell et al. 1999, Nieder et al. 2000). Holoepiphytes, on the other hand, are more commonly found on a particular subset of tree species that are generally large in crown volume (Zimmerman and Olmsted 1992, Nieder et al. 2000, Laube and Zotz 2006, Hirata et al. 2009, Burns and Zotz 2010). The size of trees climbed by hemiepiphytes in our study was generally smaller than holoepiphytes, which supports the idea that colonization of trees by hemiepiphytes is less dependent on the size of the tree.

CONCLUSION

Although other studies on epiphytes in secondary forests have been limited to sites less than 50-yr-old, our study was able to examine epiphytes in older secondary forests to examine if epiphyte community structure ever approached old-growth levels. We found convergence in the number and identity of species with secondary forest age with 115 yr being sufficient time to recover old-growth species richness and composition. Epiphyte densities did not recover to old-growth levels, however, which may be due to a low probability of colonization of young host trees caused by epiphyte dispersal limitation. Given another 100 yr, epiphyte densities in secondary forests in central Panama might approach old-growth levels, but we conclude that, in the short-term, secondary moist forests are unlikely to compensate biologically for the loss of biological diversity and ecosystem functioning that high epiphyte densities provide. In tropical moist forests, old-growth forests are invaluable for the conservation of epiphytes, and secondary forests need more than 115 yr to recover all aspects of old-growth forest community structure.

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Chapter 3

Diversity Begets Diversity in a Wet Tropical Forest Canopy: The Importance of Habitat Associations

INTRODUCTION

The promotion of species diversity by habitat heterogeneity is a central paradigm in ecology (Hutchinson 1959, MacArthur and MacArthur 1961, Ricklefs 1977, Huston 1979, Tilman 1986, Rosenzweig 1995). Habitats that are structurally complex with a diversity of resources provide more niches for species with specific habitat and resource requirements to coexist (Hutchinson 1959, MacArthur and MacArthur 1961, Tilman 1986, Chesson 2000, Chase and Leibold 2003, Tews et al. 2004). Greater habitat heterogeneity is associated with greater species diversity in many taxa and environments including fish in coral reefs (Gratwicke and Speight 2005, Messmer et al. 2011), mammals in terrestrial environments (Kerr and Packer 1997, Tews et al. 2004), birds (Kissling et al. 2008), insects (Siemann 1998, Kerr et al. 2001), nematodes in intertidal habitats (Gingold et al. 2010), and tropical trees (Newbery and Proctor 1984, Clark et al. 1998, Harms et al. 2001, Potts et al. 2002, Phillips et al. 2003, Valencia et al. 2004, Fine et al. 2005, John et al. 2007). In many of these studies, habitat heterogeneity promotes species diversity and coexistence through habitat specialization (*i.e.*, different species are best suited to different habitats, Clark et al. 1998, Kerr et al. 2001, Harms et al. 2001, Messmer et al. 2011). Thus, habitat heterogeneity as a determinant of species diversity should be particularly important where environmental, structural, and resource gradients are steep and where species exhibit strong habitat associations.

For plant communities in tropical systems, variation in species composition and diversity have been linked to heterogeneity in edaphic characteristics. Tropical tree and liana species distributions often are associated with topographical features of the landscape or differences in soil hydrology, with many woody plants exhibiting significant habitat associations (Clark et al. 1998, Webb and Peart 2000, Harms et al. 2001, Valencia et al. 2004, Fine et al. 2005, DeWalt et al. 2006, Dalling et al. 2012). Greater heterogeneity in edaphic characteristics would, thus, support a greater number of species. Other studies have observed variation in species composition along soil-resource gradients (Newbery and Proctor 1984, Clark et al. 1998, Harms et al. 2001, Potts et al. 2002, Phillips et al. 2003, Valencia et al. 2004, Fine et al. 2005, John et al. 2007) or light gradients through the presence of gaps (Schnitzer and Carson 2001, Schnitzer et al. 2008), which suggests habitat specialization based on differences in soil or light resources. Species distributions with no relationship to topography, edaphic resources, or light are assumed to be driven by dispersal limitation (Hubbell and Foster 1986, Dalling et al. 2002, Valencia et al. 2004) or distance- or density-dependent mechanisms such as disease from soil microbes (Connell 1971, Clark and Clark 1984, Bagchi et al. 2010, Mangan et al. 2010, Schnitzer et al. 2011).

One system in which habitat heterogeneity may be a driver of species diversity is in the tropical rainforest canopy. The rainforest canopy is structurally complex, with a diversity of habitats created by different-sized trees that have different gradients in light, canopy soil, resource sources (*e.g.*, canopy soil and atmospheric deposition), and environmental conditions (Parker 1995, Nadkarni 2004). The rainforest canopy is also host to a large proportion of the tropical diversity in wet tropical forests (Gentry and Dodson 1987, Ellwood and Foster 2004) including up to 35% of the vascular flora (Nieder et al. 2001), a richness that often exceeds that of the forest floor. Steep environmental, structural, and resource gradients exist within large tree crowns both vertically (lower to upper canopy) and horizontally (bole to outer canopy) and may influence the distribution of epiphytic vascular plants, which are non-parasitic arboreal plants, and promote their coexistence if different habitats favor different sets of species. These gradients are not as steep in smaller trees, which may reduce the number of habitats in small trees. Small trees are also younger than large trees, which introduces a temporal element that may influence epiphyte distributions and diversity among different-sized trees. Habitat diversity in tropical canopies includes diversity in environmental conditions (*i.e.*, relative humidity, vapor pressure deficit), structure (*i.e.*, branch size, tree size), and resources (*i.e.*, atmospheric deposition, canopy soil, and gradients in light). The vertical distribution of different epiphyte species from the lower to the upper canopy suggests that different epiphyte species are adapted to different habitats that exist within host trees (Johansson 1974, Hietz and Briones 1998, Zotz 2007). Although many studies have suggested that epiphyte distributions are related to the distribution of different habitats, none have directly tested whether habitat characteristics influence epiphyte distributions. Thus, a mechanistic understanding of epiphyte diversity is lacking (Bartels and Chen 2012).

We studied the vascular epiphyte community and measured environmental conditions, structural features, and resources for epiphytes within different-sized trees (2.5–103.3 cm dbh) of one host tree species, *Virola koschnyi*, to examine whether the diversity of habitats within tree crowns explains differences in epiphyte community structure among different-sized trees. Figure 3.1 shows our hypothesized gradients in habitat features among different-sized tree canopies and within the canopies of the largest trees. We expect habitat heterogeneity to be highest in large trees where environmental and resource gradients are steepest and lowest in small trees where gradients are not as steep. Therefore, habitat differences between the inner (*i.e.*, closest to the bole) and outer crown should be largest in large trees. We asked whether the diversity, abundance, and composition of vascular epiphyte communities were related to environmental conditions,

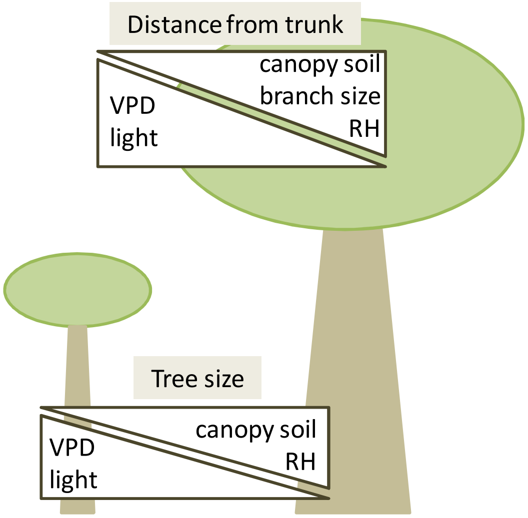

Figure 3.1. Hypothesized gradients in habitats among tree size classes and among the canopy zones within the largest trees. Habitat measurements include environmental conditions [vapor pressure deficit (VPD), relative humidity (RH)], structural features (branch size, tree dbh), and resources (canopy soil, light).

structural characteristics, or resources among different-sized tree crowns. We examined whether epiphyte species exhibit strong habitat associations among different-sized tree crowns and determined which habitat features (environmental conditions, structural characteristics, or resources) best explained variation in epiphyte community structure and composition. As trees increase in size, the diversity of habitats should also increase because environmental and resource gradients should get steeper. We, therefore, predicted that species found within small trees would be a nested subset of the species found within large-tree canopies. Species composition of smaller trees should come to resemble that of larger trees as they increase in size and add new habitats and their associated species to their canopies. We further expected low overlap in communities where habitats differ, such as between the inner canopies of small and large trees and among different habitats within large-tree crowns. From these results, we aim to assess whether habitat heterogeneity influences the diversity of vascular epiphytes.

MATERIALS AND METHODS

Study Area

This study was conducted at La Selva Biological Research Station (84°00'12" W, 10°25'52" N, 40 m a.s.l.) in northeastern Costa Rica. The 1600 ha of the La Selva forest are characterized as tropical wet forest (Holdridge 1967) and receive approximately 4000 mm of annual precipitation, predominantly during the wet season, May–January, with an average monthly precipitation of 382 mm. The drier season, February–April receives an average monthly precipitation of 172 mm. Average monthly temperature is 25.8°C ± 0.2 and varies little throughout the year (McDade et al. 1994).

Sampling

To examine how epiphyte species richness, abundance, and species composition changed with tree size, we surveyed vascular epiphytes within the canopies of 61 individual *Virola koschnyi* trees (Myristicaceae) ranging in diameter at breast height (dbh) from 2.5–103.3 cm. We did not include non-vascular epiphytes in our survey. *Virola koschnyi* trees have branches that extend out at a 90° angle from the trunk and do not have any vascular epiphytes along the trunk (except for some hemiepiphytes, which were not included in this study). We, therefore, only examined the influence of horizontal habitat diversity on epiphyte community structure and did not examine vertical gradients from the base of the trunk to the tree crown. We chose one species of tree to control for variation in host characteristics that might influence environmental gradients and epiphyte establishment and growth (Callaway et al. 2002, Cardelús 2007). We grouped trees into size classes based on dbh resulting in 5–25 trees in each size class: 15 cm = 2.5–15 cm dbh; 30 cm = 15.1–30 cm dbh; 70 cm = 30.1–70 cm dbh; and > 70 cm dbh.

Within trees, vascular epiphytes were surveyed on each branch every 1 m from the bole to the branch tips. Ground-based epiphyte surveys were conducted for most trees ≤ 70 cm dbh as the canopies of these trees were easily visible from the ground, and ground-based surveys have been shown to capture > 90% of epiphyte occurrences (Burns 2007). For the ground-based surveys, meter increments along each branch were estimated. We climbed all trees > 70 cm dbh and some trees ≤ 70 cm dbh whose canopies were not easily visible with binoculars using modified rope climbing techniques (Perry 1978). The first 3–4 m along each branch were measured using a measuring tape, and the remaining meter increments were estimated. Epiphyte surveys in the outer branches of trees > 70 cm dbh were conducted using binoculars while in the canopy. Small individuals with leaves < 5 cm that were not identified to genus or species were included in the surveys by family and were included in the abundance analyses, but they were not included in the species richness or species composition analyses. Within the canopies of the largest trees (*i.e.*, > 70 cm dbh), we designated three canopy zones based on distance from the trunk: inner canopy (0–2 m), mid canopy (2–5 m), and outer canopy (> 5 m). Our canopy zone delineations were similar to Johansson (1974).

We classified each epiphyte species into *a priori* functional groups based on taxonomy: aroids, bromeliads, cactuses, ferns, and orchids (Fig. 1.1). We further divided bromeliads based on nutrient uptake mechanisms into tank bromeliads (impounding) and atmospheric bromeliads (nonimpounding) as per Benzing et al. (1978), and we divided ferns based on rooting medium into soil ferns (always root in humus) and bark ferns (independent of rooting medium) as per *Scheme V* in Benzing (1990).

To determine the diversity of habitats within tree canopies, we measured several variables that we hypothesized might be related to epiphyte species distributions: temperature (T), relative humidity (RH), vapor pressure deficit (VPD), structural features of the habitats including branch size or tree size, the amount or presence of canopy soil, and the amount of light. Environmental variables were measured in the inner canopies of 3–5 individuals in each tree size class and in the mid and outer canopies of trees in the largest tree size class. Environmental variables could not be measured in the mid and outer canopies of smaller tree size classes due to logistical constraints. We recorded T and RH every 6 min for at least 8 wk during the wet season (July–September) in 2011 using LogTag dataloggers (MicroDAQ, Contoocook, New Hampshire U.S.A.). We calculated VPD, the difference between the amount of moisture in the air and the amount of moisture it can have when fully saturated, from T, RH, and the saturation vapor pressure (SVP) using the following equations (Murray 1967):

$$\mathrm{SVP\ (Pascals)} = 610.7 * 10^{\frac{7.5\mathrm{T}}{237.3+\mathrm{T}}} \tag{1}$$

$$\mathrm{VPD\ (Pascals)} = \frac{(100 - \mathrm{RH})}{100} * \mathrm{SVP} \tag{3}$$

Habitats with high VPD values have a greater atmospheric demand for water and the greater the potential to pull water from inside plants. Therefore, habitats with high VPD may only contain plants that can withstand a large transpirational demand (Rawson et al. 1977, Fletcher et al. 2007). Because structural aspects of trees, such as branch diameters, increase with tree size (Groot and Schneider 2011), we assessed canopy habitat structural differences among tree size classes using dbh. Within the largest trees, we examined whether habitat structure differed among canopy zones by measuring branch diameters in the inner and mid canopy with a dbh tape and estimating them for the outer canopy. We examined the amount of light reaching the entire crowns of 5–20 *V. koschnyi* tree from each size class using the Crown Illumination Index (CII), which is an ordinal scale used to qualitatively assess the amount of exposure of each tree crown. CII is quantitatively related to the proportion of visible sky, and the proportion of indirect, direct, and total radiation reaching a point compared to an open site that ranges from a value of 1, which is a canopy with no direct light reaching the entire crown and an average canopy openness above the crown of 4%, to a value of 5, which is a completely exposed crown and an average canopy openness above the crown of 37% (Clark and Clark 1992, Keeling and Phillips 2007). We used the CII to examine whether different-sized trees were in the understory or emergent above the canopy – lower values would indicate a tree in the understory. Within the inner canopy of the five largest trees, we measured the percent of canopy cover using a densiometer (Forestry Suppliers Inc., Jackson, Mississippi, USA) as an indirect measure of the amount of light reaching the inner canopy. We estimated the percent canopy cover in the mid and outer canopies by measuring the percent of canopy cover in smaller trees in open areas at the Arboleda at La Selva that had similar cover as the mid and outer canopies of large trees. We subtracted the percent canopy cover from 100 to estimate the percent of canopy openness in each canopy zone. Our percent canopy openness values were similar to what was measured by Johansson (1974) for the inner, mid, and outer canopy. We compared the percent canopy openness in each canopy zone to the CII to estimate the amount of shading in each canopy zone by the tree canopy. Within the largest tree canopies, we measured canopy soil cover in the inner and mid canopies of each branch in each tree by placing a grid for a total area of 1-m^2 over the branch and visually estimating percent cover. The outer canopy had no soil and so was given a percent soil cover of zero.

Statistical Analysis: Tree Size

We used negative binomial regression to examine tree size as a predictor of epiphyte species richness and abundance. We used ANOVA to examine differences in species richness and abundance of epiphytes among the four tree-size classes and canopy zones with post-hoc comparisons using a Tukey's HSD test.

To examine similarities in epiphyte species composition among the four tree size classes, we used non-metric multidimensional scaling (NMS) using a Bray-Curtis dissimilarity metric. We chose NMS because it maximizes the correlation between differences in species composition among individual trees and distances in the ordination, and yields solutions with a low dimensionality that permits a better visual examination of the data than other ordination techniques that have hidden axes of variation. Only 45 of the 61 trees were included in the NMS analysis because trees with fewer than two epiphyte individuals were excluded from the analyses (*i.e.*, 13 trees in the 15 cm dbh size class and 3 trees in the 30 cm dbh size class were excluded). Only epiphyte species found in at least two trees were included in the analyses, which resulted in the inclusion of 68 epiphyte species. We used the metaMDS function in the vegan package in R for NMS analyses (Oksanen et al. 2010).

We tested whether epiphyte species composition differs among tree size classes by conducting a permutational analysis of variance (PERMANOVA) from the adonis procedure in the vegan package, which tests the response of a variable (tree size) to a factor (species composition) on the basis of a distance measure (Bray-Curtis) using a permutation procedure whereby an *F*-statistic is generated under a null model and compared to the *F*-statistic of the model (Oksanen et al. 2010). We chose PERMANOVA analyses because it partitions the multivariate variation according to individual factors in an ANOVA design. We examined differences in epiphyte species composition among tree size classes using pair-wise contrasts. We added ellipses representing the covariance matrix centered on the mean of each tree size class using the veganCovEllipse function in the vegan package to denote differences in variation in species composition among tree sizes – larger ellipses denote greater variance in species composition among trees within the same size class.

To examine if epiphyte communities in smaller tree size classes were nested within the largest trees, a nestedness analysis was conducted using the Nestedness metric based on Overlap and Decreasing Fill (NODF) index based on presence-absence data (Almeida-Neto and Ulrich 2010). Only species with at least two individuals were included in this analysis (n = 60).

To examine differences in habitats within the canopies of different tree size classes, we conducted ANOVAs on T, RH, VPD, and CII that we measured or calculated for each tree followed by Tukey's HSD tests. We choose to examine the range of T, RH, and VPD between the hottest and coolest days (as recorded by the La Selva meteorological station) during the 8 wk period that we measured environmental conditions *in situ* because the goal was to examine the limitations on epiphyte distributions, which would occur through the extremes in environmental conditions.

To examine if epiphyte species composition among tree size classes was related to geographic location or habitats, we used Mantel tests and canonical correspondence analysis (CCA). We ran a Mantel test on a Euclidean distance matrix of geographic space with a Jaccard dissimilarity matrix of community composition to examine if epiphyte species composition was related to geographic location, which would indicate that dispersal is an important factor influencing epiphyte distributions among different-sized trees. We examined the influence of habitats on epiphyte community structure using CCA with the cca function in the vegan package (Oksanen et al. 2010). Because CCA constrains the ordination by the environmental variables chosen, we used CCA to test the *a priori* hypothesis that epiphyte composition is related to the changes in measured habitat features (*i.e.*, environmental conditions, habitat structures, and resources) that accompany changes in tree size. Because we were interested in the extreme environmental conditions that would limit epiphyte distributions, we used the difference in T, RH, and VPD between the hottest and coolest day, as explained above, in our CCA analysis. We ran permutation tests to examine if the CCA was significantly different from random. Variation inflation tests (vif) showed high multi-collinearity between the differences in RH, T, and VPD between the hottest and coolest day, and therefore T and RH were not included in the CCA analysis. We examined which factors explained a significant amount of variation in species compositional differences among tree size classes using stepwise forward-selection procedures. We used the ordistep function in the vegan package for this analysis (Oksanen et al. 2010). Monte Carlo permutation tests (1000 permutations) determined which factors explained a significant amount of variation in species compositional data.

Statistical Analysis: Canopy Zones within the Largest Tree Size Class

We used ANOVA followed by Tukey HSD tests to examine differences in species richness and abundance among canopy zones in the largest trees. To examine if similarity in epiphyte species composition is greater among tree canopies with more similar habitat and resource conditions, another NMS was conducted with the largest tree canopies separated into canopy zones. We tested whether epiphyte species composition differed among canopy zones by conducting a PERMANOVA from the adonis procedure in the vegan package followed by pair-wise contrasts between canopy zones (Oksanen et al. 2010). Again, we added ellipses representing the confidence region defined by a covariance matrix centered on the mean of each canopy zone using the veganCovEllipse function in the vegan package to denote differences in the variation in species composition among canopy zones.

We examined differences in habitats among canopy zones using ANOVA followed by Tukey's HSD test. Measures of habitat features included environmental conditions (*i.e.*, VPD and RH), structure (*i.e.*, branch diameter), % canopy soil cover, and % canopy openness.

We examined the influence of habitat heterogeneity within large tree canopies on epiphyte species composition using CCA. We tested the *a priori* hypothesis that epiphyte composition is related to the differences in measured habitat features among canopy zones within large trees (*i.e.*, branch diameter, VPD, % canopy soil cover, and % canopy openness). Again, we used the difference in VPD between the hottest and coolest day in our CCA analysis. Percent canopy soil cover had high multicollinearity with branch diameter and % canopy openness according to a vif test. Therefore, % canopy soil cover was not included in the CCA. We ran permutation and stepwise forward-selection procedures with Monte Carlo permutation tests as above.

Statistical Analysis: Habitat Associations

We examined habitat associations of epiphytes to tree size classes and canopy zones within the largest tree size class using conservative randomization tests for single-species associations (DeWalt et al. 2006). The randomization tests used in this study are conservative because other analyses, such as goodness-of-fit χ^2 tests, do not take into account the clumped nature of plants and non-independence of individuals and, therefore, may overestimate the association of a plant species to a particular habitat. We tested habitat associations for epiphyte species represented by at least 10 individuals (n = 33). The randomization tests compared the observed relative density of each species to the expected relative density generated by 1000 iterations of shuffling the 6 habitats, which were the tree-size categories and canopy zones within large trees (*i.e.* 15 cm, 30 cm, 70 cm, > 70 cm inner, > 70 cm mid, and > 70 cm outer). The observed relative density of a species in a particular habitat was calculated for each tree-size category or canopy zone by calculating the average density across individual trees or canopy zones. The relative density in a particular tree or canopy zone was calculated as the proportion of epiphytes comprised by that species in a particular tree or crown position. If its observed relative density was greater than 97.5% of the expected relative density (two-tailed test with α = 0.05), a species was positively statistically associated with that habitat; if its observed relative density was less than 97.5% of the expected density, a species was negatively statistically associated with that habitat.

RESULTS

We found 6250 epiphyte individuals in 118 species spanning 51 genera and 15 families within 61 *Virola koschnyi* trees. Within this one tree species, we found 31% of all epiphyte species at La Selva (McDade et al. 1994). We observed a maximum of 65 species in one single tree. Most individuals surveyed were members of the Bromeliaceae (64%) with 5 genera and 20 species, and the Orchidaceae (7%) with 24 genera and 37 species (Table 3.1).

Tree size

As expected, tree size was a significant predictor of epiphyte species richness and abundance, with the number of species and individuals increasing with tree dbh (Fig. 3.2) and tree-size class (Table 3.2). Species composition was also influenced by tree size. Similarity in species composition among the smaller tree-size classes was significantly lower than similarity among the largest tree-size classes (PERMANOVA, $F_{5,54} = 7.2$, $P = 0.001$) as is shown in the NMS − the largest trees form a tighter cluster than the other tree size classes (Fig. 3.3A).

Habitats differed among different-sized trees. The amount of light reaching the tree crown significantly differed among tree size classes as the 15 cm and 30 cm tree size classes had significantly lower CII values than the larger tree size classes. Environmental conditions among tree size classes showed a peaked distribution for T and VPD and the opposite pattern for RH such that values were similar between the smallest (15 cm size class) and largest (>70 cm size class) trees and were either highest (T and VPD) or lowest (RH) in the medium-sized trees (70 cm size class). On the hottest day, T and VPD did not

Table 3.1. The number of epiphyte families, unique epiphyte families, epiphyte genera, unique epiphyte genera, functional groups, unique functional groups, and the number of individuals of each epiphyte family in total and within each *Virola koschnyi* tree diameter size class at La Selva Biological Research Station (see Table 2 for size class delineations). The numbers in brackets beside each family represent the number of genera followed by the number of species in each family.

	Tree size class				
Family (genera, species)	15 cm	30 cm	70 cm	> 70	Total
# Families	4	6	9	15	15
# Unique Families	0	0	0	6	
# Genera	5	11	27	50	51
# Unique Genera	0	0	0	23	
# Functional Groups	3	5	7	7	7
# Unique Functional Groups	0	0	2	2	
Bromeliaceae (5, 20)	29	147	723	3084	3983
Orchidaceae (24, 37)	0	2	129	352	483
Polypodiaceae (5, 8)	27	28	122	293	470
Elaphoglossaceae (1, 5)*	0	0	5	435	440
Piperaceae (1, 3)	17	138	71	42	268
Araceae (3, 17)*	0	3	14	230	247
Vittariaceae (2, 3)*	3	0	5	130	138
Cactaceae (2, 6)*	0	1	8	80	89
Cyclanthaceae (2, 2)*	0	0	0	77	77
Clusiaceae (1, 1)	0	0	1	20	21
Lomariopsidaceae (1, 1)	0	0	0	15	15
Gesneriaceae (1, 1)*	0	0	0	14	14
Melastomataceae (1, 1)	0	0	0	3	3
Aspleniaceae (1, 1)	0	0	0	1	1
Hymenophyllaceae (1, 1)	0	0	0	1	1

*found predominantly in canopy soil

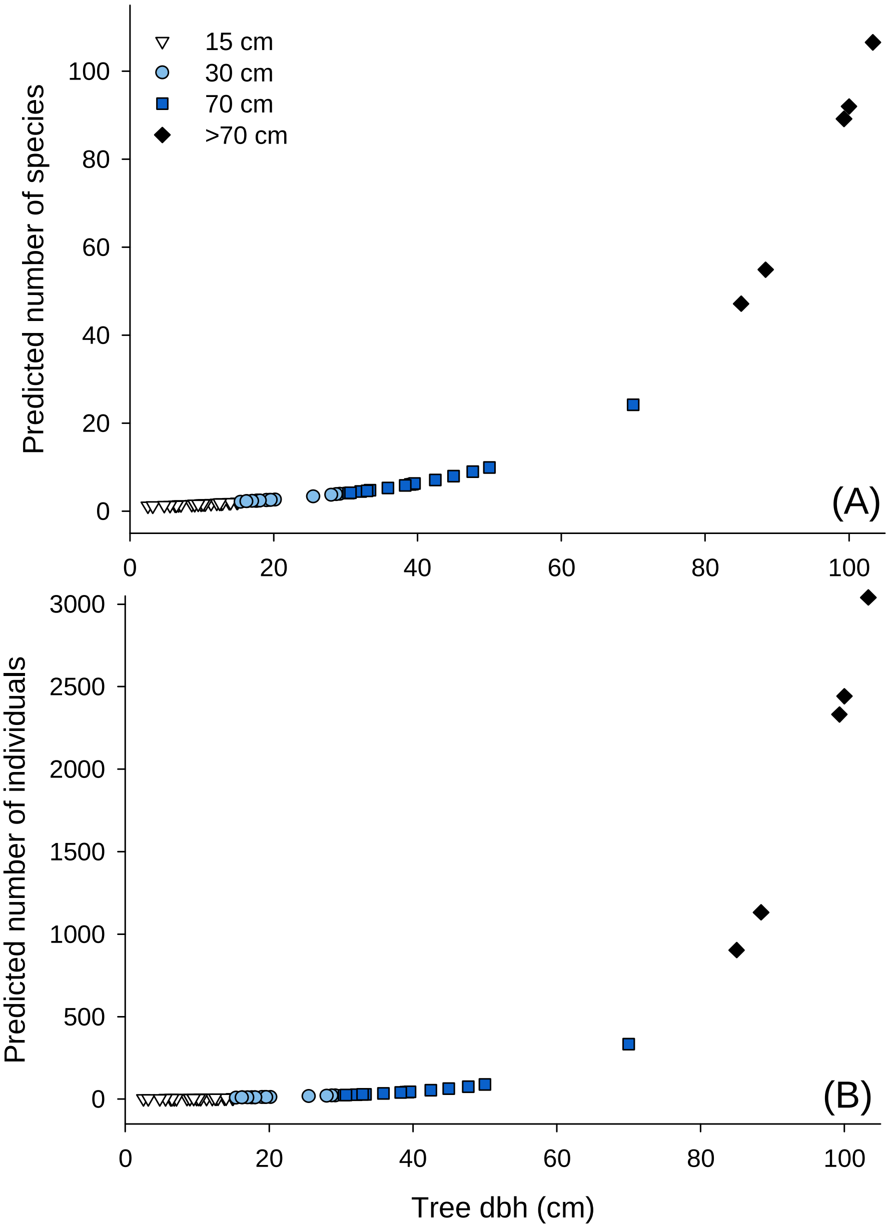

Figure 3.2. Negative binomial regression model examining tree diameter (dbh) as a predictor of (A) epiphyte species richness and (B) epiphyte abundance for 61 *Virola koschnyi* trees separated into four size classes from lowland wet rain forest in Costa Rica. Trees were classified into size classes based on diameter. Regression equation for (A): log(species richness) = dbh*0.05 + 0.07; dispersion = 3.18 ± 1.15; 2 x log-likelihood = -282.4; dbh predictor value = 1.04 (95% CI = 1.04–1.06). Regression equation for (B): log(abundance) = dbh*0.06 + 1.17; dispersion = 0.61 ± 0.12; 2 x log-likelihood = -482.2; dbh predictor value = 1.05 (95% CI = 1.05–1.09).

Table 3.2. Mean vascular epiphyte species richness and abundance (± 1 SE) among 5–25 replicate *Virola koschnyi* trees in each size class (15 cm = 0–15 cm dbh; 30 cm = 15.1–30 cm dbh; 70 cm = 30.1–70 cm dbh; > 70 cm = > 70 cm dbh) and among canopy zones (inner = 0–2 m; mid = 2–5 m; outer = > 5 m) within the 5 trees in the largest size class at La Selva Biological Research Station. The results of an ANOVA for species richness and abundance are included. Values with different letters are significantly different according to a Tukey's HSD test ($P< 0.05$). *$P< 0.05$; **$P< 0.0001$.

Size Class	Species richness	Abundance
15 cm	1.1 ± 0.3 a	3.0 ± 0.8 a
30 cm	3.0 ± 0.5 b	20.0 ± 7.9 a
70 cm	9.5 ± 2.0 c	72.0 ± 19.9 b
> 70 cm inner	28.6 ± 2.1 d	190.2 ± 34.1 c
> 70 cm mid	36.0 ± 2.8 d	419.6 ± 28.1 d
> 70 cm outer	± 2.0 d	345.6 ± 92.8 cd
> 70 cm	52.0 ± 3.7	955.4 ± 117.0
$F_{5,65}$	65.1**	60.3**
Canopy zone	Species richness	Abundance
Inner	28.6 ± 2.1 ab	190.2 ± 34.1 a
Mid	36.0 ± 2.8 a	419.6 ± 28.1 b
Outer	26.8 ± 2.0 b	345.6 ± 92.8 ab
$F_{2,12}$	4.3*	3.9*

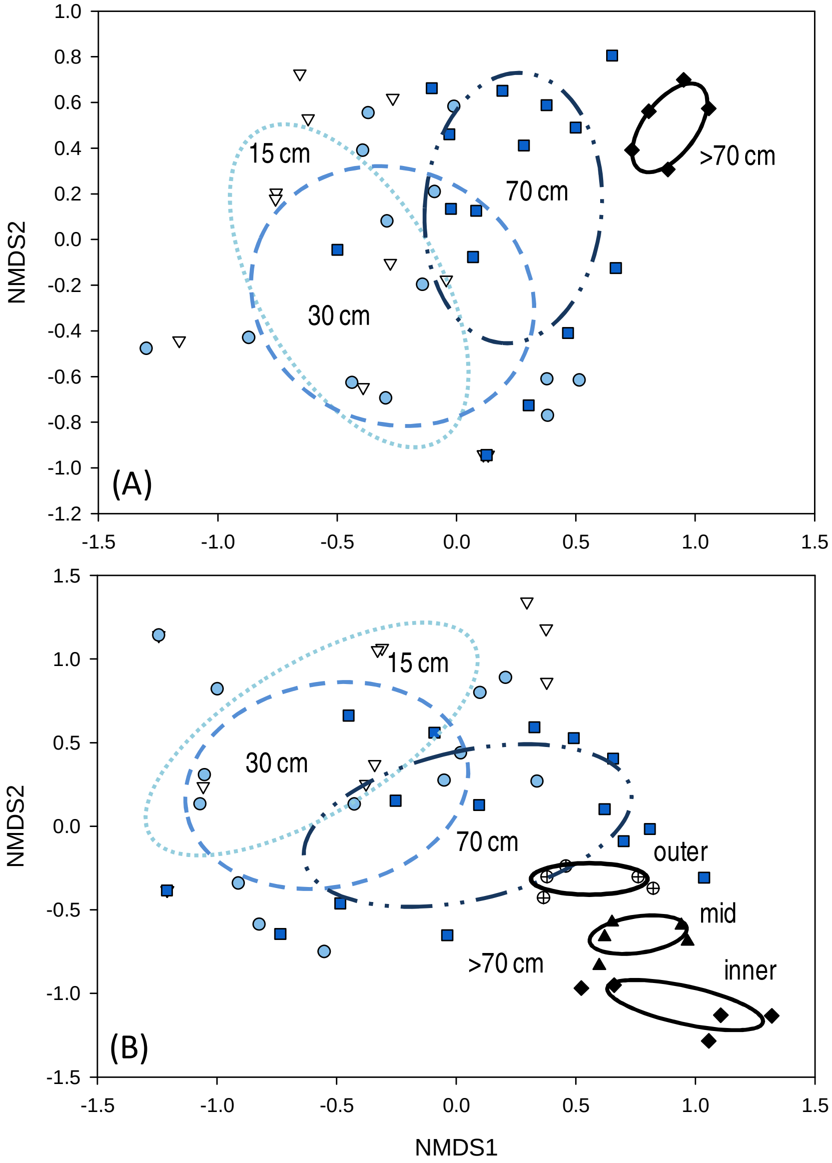

Figure 3.3.Non-metric multidimensional scaling (NMS) ordination of epiphyte community composition within the canopies of 5–25 *Virola koschnyi* trees from each of four size classes from lowland wet rain forest in Costa Rica using a Bray-Curtis distance matrix on relative abundance for all trees (A) and with the largest trees separated into canopy zones (B). Two-dimensional stress = 18.02 for (A), and two-dimensional stress = 15.77 for (B). Trees were classified into diameter classes as in Figure 2. For (B), trees > 70 cm dbh were separated into canopy zones: diamonds = inner canopy (0–2 m from the trunk); upward facing triangles = mid canopy (2–5 m from the trunk); circle with a cross = outer canopy (> 5 m from the trunk). The ellipses show the covariance matrix centered on the mean of each tree size class or zone: dotted = 15 cm dbh; dashed = 30 cm dbh; dotted and dashed = 70 cm dbh; solid = > 70 cm dbh.

differ among tree size classes, but RH in the 15 cm trees was significantly lower than in the 70 cm trees (Table 3.3). On the coolest day, the 15 cm trees had significantly lower T and VPD and significantly higher RH than 70 cm trees (Table 3.3). The minimum tree size class in which canopy soil was detected was in the 70 cm dbh size class.

Epiphyte community composition differed among different-sized trees. Similarity in species composition to the largest tree size classes increased with tree size (Fig. 3.4), and the species composition of small trees was significantly nested within the species composition of the largest trees (NODF: Z = -2.79, *P* = 0.0026). Nestedness in species composition was driven by the species and functional groups found in the outer canopy of the largest trees such as bark ferns and species in the Piperaceae because they were also found in smaller trees (Fig. 3.5). The NMS including canopy zones of the largest trees supports the nestedness analysis as the epiphyte community in the outer canopy zone of large trees is compositionally more similar to smaller trees than the inner canopy of large trees is to smaller trees (Fig. 3.3B). The few epiphytes that were found on small trees were bark ferns or tank bromeliads (Fig. 3.5). With increasing tree size, more functional groups were found. The largest trees hosted all seven functional groups. The inner canopy fern community changed from dominance by bark ferns on small trees to dominance by soil ferns in large trees. Tank bromeliads composed a quarter to a half of all epiphytes on trees greater than 15 cm dbh (Fig. 3.5; Table 3.1).

Table 3.3. Mean temperature (Temp, °C), relative humidity (RH, %), and vapor pressure deficit (VPD, kPa) in the inner canopy for 3–4 *Virola koschnyi* trees in each diameter size class, and microclimate data along with branch diameter (cm), % canopy soil cover, and % canopy openness in the inner, mid, and outer canopy of trees > 70 cm dbh at La Selva Biological Research Station in Costa Rica on the hottest day and coolest day during the 8 weeks dataloggers were deployed. The hottest and coolest days were determined from the the La Selva meterological data. One datalogger in the 50 cm size class stopped working before the coolest day was recorded. See Table 1 for tree size class and canopy zone delineations. The canopy illumination index (CII) is included for 5–20 *V. koschnyi* trees in each diameter size class. The degrees of freedom (df) and *F* values from ANOVAs are shown. Values with different letters are significantly different according to a Tukey's HSD test. **P* < 0.05, ***P* < 0.0001.

	Hottest day			Coolest day					
Size class	Temp	RH	VPD	Temp	RH	VPD	# trees	CII	# trees (CII)
15 cm	31.8 ± 0.5	61.2 ± 3.3^{a}	1.8 ± 0.2	26.0 ± 0.2^{a}	94.9 ± 0.5^{a}	0.2 ± 0.1^{a}	4	2.1 ± 0.3^{a}	12
30 cm	33.1 ± 0.1	59.3 ± 1.2^{ab}	2.1 ± 0.1	26.9 ± 0.3^{ab}	86.7 ± 4.2^{ab}	0.5 ± 0.2^{ab}	3	2.3 ± 0.3^{a}	12
70 cm	35.2 ± 1.8	47.7 ± 4.3^{b}	3.0 ± 0.5	27.4 ± 0.4^{b}	83.9 ± 1.8^{b}	0.6 ± 0.1^{b}	3	3.5 ± 0.2^{b}	20
>70 cm	33.0 ± 0.4	56.1 ± 1.6^{ab}	2.2 ± 0.1	26.6 ± 0.1^{ab}	90.8 ± 0.9^{ab}	0.3 ± 0.1^{ab}	3	3.8 ± 0.2^{b}	5
df	3,9	3,9	3,9	3,8	3,8	3,8		3,41	
F	2.6	3.9*	3.5	5.5	4.6*	4.7*		11.77*	
Canopy zone	Temp	RH	VPD	Temp	RH	VPD	Branch diameter	% canopy soil cover	% canopy openness
Inner	32.9 ± 0.4	55.1 ± 2.0^{a}	2.2 ± 0.1^{a}	26.6 ± 0.1	90.8 ± 0.9	0.3 ± 0.1	27.3 ± 0.9^{a}	85.0 ± 4.5^{a}	19.6 ± 1.9^{a}
Mid	33.2 ± 0.2	53.3 ± 0.3^{ab}	2.3 ± 0.1^{ab}	26.4 ± 0.1	90.7 ± 0.6	0.3 ± 0.1	15.6 ± 0.7^{b}	35.0 ± 3.5^{b}	36.6 ± 0.7^{b}
Outer	33.8 ± 0.1	33.8 ± 0.1^{b}	2.6 ± 0.1^{b}	26.2 ± 0.1	90.7 ± 1.6	0.3 ± 0.1	6.2 ± 0.6^{c}	0.0 ± 0^{c}	54.6 ± 1.1^{c}
df	2,6	2,6	2,6	2,6	2,6	2,6	2,12	2,12	2,12
F	2.4	5.9*	4.9*	0.006	0.001	3.8	214.3**	168.5**	170.8**

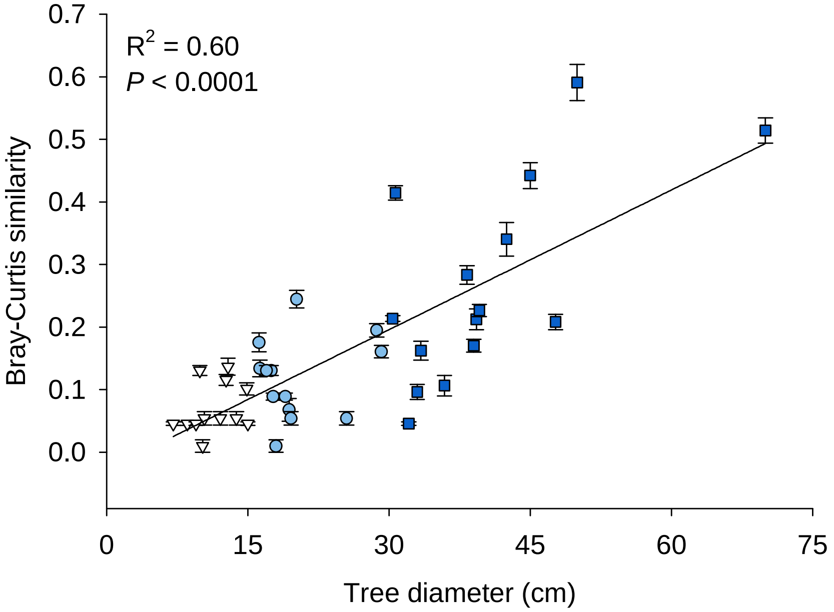

Figure 3.4. Relationship between tree diameter and Bray-Curtis similarity in species composition of each individual *Virola koschnyi* tree ≤ 70 cm dbh to trees > 70 cm dbh at La Selva Biological Research Station. Symbols represent mean ± 1 S. E. of similarity in epiphyte composition between each tree ≤ 70 cm dbh and the five trees > 70 cm dbh.

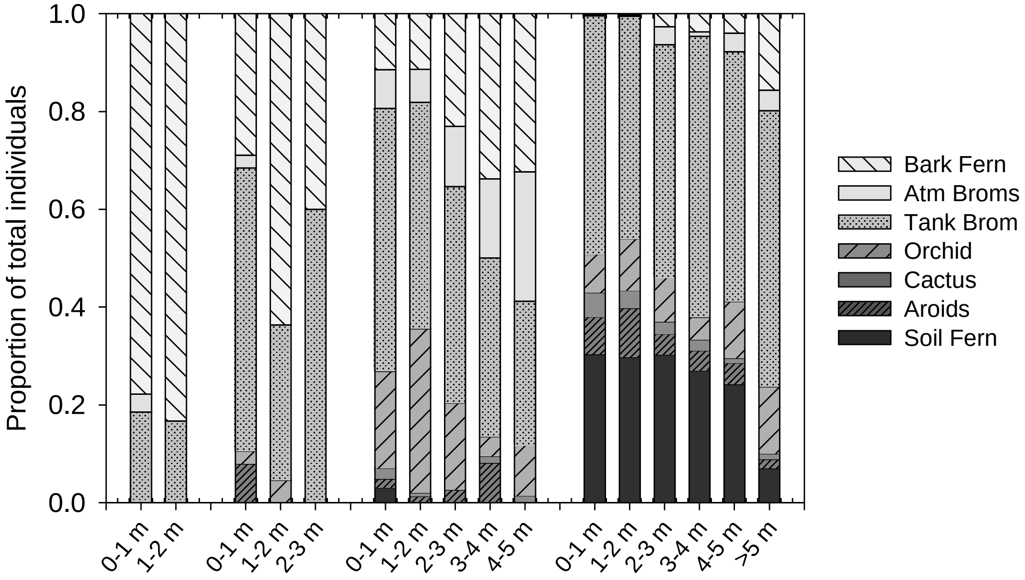

Figure 3.5. Proportion of individuals found at different distances from the tree trunk of different size classes of *Virola koschnyi* trees that were composed by each functional group.

Epiphyte species composition was related to differences in habitat, environmental conditions, and resources among tree size classes. The CCA showed that measured habitat features explained 57% of the variation in species composition among tree size classes. The overall relationship between species and environmental variables was significantly different from random according to a Monte Carlo test (*P* = 0.001).
The first CCA axis was related to tree size, and the second CCA axis was related to the difference in VPD between the hottest and coolest days. The largest variation in species composition was found in the 70 cm dbh size class and the smallest variation in was found in the >70 cm dbh size class as indicated by the largest and smallest convex hull around the individual trees in the 70 cm and >70 cm size class, respectively (Fig. 3.6A). The greatest difference in VPD between the hottest and coolest day was found in the 70 cm dbh size class (Fig. 3.6A). All other tree size classes had similar VPD ranges between the hottest and coolest day. Two of the three habitat variables were significantly related to species composition: VPD difference (*F* = 6.9, *P* = 0.01) and dbh (*F* = 4.8, *P* = 0.04; Fig. 3.6A). CII was not significantly related to epiphyte species composition (*F* = 0.7, *P* = 0.90). The geographic location of the *V. koschnyi* trees at La Selva was not related to epiphyte species composition (Mantel test, geographic location, r = -0.006, *P* = 0.50).

Canopy Zones within the Largest Tree Size Class

Epiphyte community structure differed among canopy zones within the canopies of the largest trees. Species richness and abundance were highest in the mid canopy (Table 3.2). The inner canopy of the largest trees had species and functional groups that were not found in large numbers in any other tree size class or canopy zone (*i.e.*, aroids,

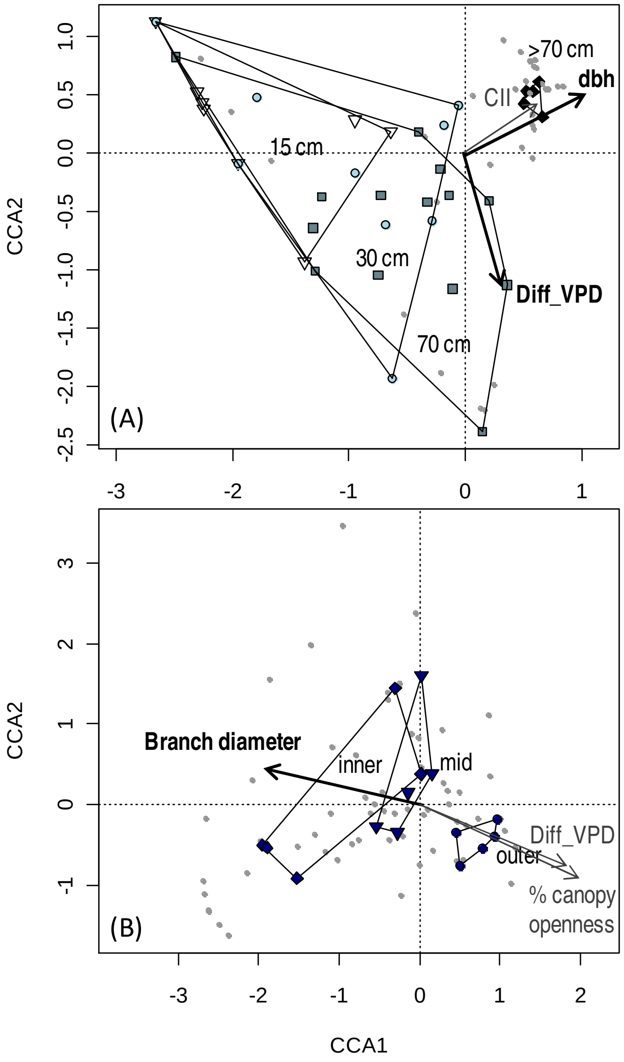

Figure 3.6. Canonical correspondence analysis (CCA) ordination of epiphyte community composition within the canopies of 5–25 *Virola koschnyi* trees from each of four size classes from lowland wet rain forest in Costa Rica for all trees (A) and with the largest trees separated into canopy zones (B). Tree size classes are defined in Figure 3.2, and canopy zones are defined in Figure 3.3. Arrows represent multiple regressions of each environmental variable with species composition. Environmental variables that explain a significant proportion of variation in species composition are shown as arrows in black, and non-significant environmental variables are shown as arrows in grey. Diff_VPD is the difference in VPD between the hottest and coolest day during the study period according to the La Selva meterological data. Tree classes and zones are denoted by the same shapes as in Figure 3.2 and Figure 3.3, respectively. Lines represent the minimum convex hulls for each tree size and canopy zone, which is the minimum space that contains each tree in each size class or canopy zone. Species are shown as small grey dots.

cactuses, and soil ferns), all of which were never found without canopy soil around their roots (Fig. 3.5; Table 3.1). Inner-canopy species composition was significantly different from outer-canopy species composition (PERMANOVA $F_{1,14} = 2.9$, $P = 0.03$). This result is shown visually in the NMS ordination, which shows the inner canopy cluster to be separate from the outer canopy cluster (Fig. 3.3B).

Habitat structure and resources differed among canopy zones. Inner canopies had significantly larger branches, a greater percent canopy soil cover, and lower % canopy openness than mid or outer canopy zones (Table 3.3). On the hottest day, RH was significantly higher and VPD was significantly lower in the inner canopy than in the outer canopy but they were not significantly different on the coolest day (Table 3.3).

Epiphyte species composition among canopy zones within the largest trees was associated with the measured habitat characteristics. Habitat factors explained 55% of the variation in epiphyte species composition among canopy zones according to the CCA. The first CCA axis was negatively related with branch diameter and positively related with % canopy openness and VPD difference (Fig. 3.6B). Branch diameter was the only habitat characteristic that was significantly associated with species composition (P = 0.05).

Habitat Associations

Twenty-five of the 33 species (76%) exhibited a significant association to one of the six habitats, defined by tree size and canopy zone (Table 3.4). Eighteen species (55%) showed positive associations to habitats, 14 species (42%) showed negative associations, and seven species (21%) exhibited positive associations to some habitats and negative

Table 3.4. Results from the randomization tests showing significant positive (+) or negative (-) habitat associations of abundant epiphyte species from different functional groups to different tree size classes or canopy zones within the largest tree size class of *Virola koschnyi* trees at La Selva Biological Research Station in Costa Rica. Tree size classes and canopy zones are as in Table 3.2. Abundances of each species are included in parentheses beside species' names.

Functional group/Family	Species	> 70 cm			70 cm	30 cm	15 cm
		inner	mid	outer			
Aroids	*Anthurium ramonense* (32)	+				-	
	Anthurium upalaense (75)				-		-
	Philodendron wendlandii (15)	+	+				
	Stenospermation angustifolium (79)		+				
Atmospheric bromeliads	*Tillandsia bulbosa* (73)			+	-	-	
	Tillandsia festucoides (90)						
Bark ferns	*Microgramma lycopodioides* (118)						
	Microgramma percussa (56)						
	Microgramma reptans (227)	-	-				+
Cactuses	*Rhipsalis baccifera* (37)					-	-
	Epiphyllum hookeri (28)						
Cyclanthaceae	*Chorigyne pendula* (63)		+				
	Sphaeradenia acutitepala (12)	+					
Gesneriaceae	*Codonanthe* sp. (14)			+			
Orchids	*Nidema boothii* (224)			+			
	Elleanthus cynarocephalus (14)		+				
	Prosthechea sp. (69)						
	Pleurothallis sp. (16)	+					
Piperaceae	*Peperomia rotundifolia* (172)					+	+
Soil ferns	*Elaphoglossum herminieri* (212)	+			-	-	-
	Elaphoglossum latifolium (220)	+	+		-	-	
	Phlebodium pseudoaureum (42)	+					
	Vittaria lineata (120)	+	+				-
Tank bromeliads	*Aechmea nudicaulis* (392)					-	-
	Guzmania lingulata (382)						
	Guzmania monostachya (386)						-
	Guzmania sp. (35)						
	Tillandsia anceps (320)				-	-	
	Tillandsia monadelpha (175)	+				-	-
	Tillandsia venusta (12)						
	Vriesea vittata (17)			+			
	Werauhia gladioliflora (168)						-
	Werauhia kupperiana (123)					-	-

associations to other habitats (Table 3.4). Species within functional groups showed significant habitat associations related to the distribution of habitats within the canopies of the largest tree size class. For example, of the eight species of soil ferns and aroids, seven showed a positive association to the inner or mid canopy of large trees, where canopy soil was available. Six of the 10 tank bromeliad species showed negative associations to small tree size classes, and two species showed a positive habitat association to the largest tree size class. Only one bark fern species and a species in the Piperaceae showed positive associations with small trees (Table 3.4).

DISCUSSION

Habitat heterogeneity coupled with species-specific habitat associations appear to contribute substantially to epiphyte community structure in *Virola koschnyi* trees in the lowland wet tropical forests of La Selva. In our study, the diversity of habitats for epiphytes increased within tree canopies as they increased in size. Small trees had uniform branch sizes, no canopy soil, and low light reaching their crowns because they were in the understory. With greater tree size, a greater diversity of microhabitats was present, leading to inner canopies with canopy soil, low VPD, and low light and outer canopies with no canopy soil, high VPD, and high light. Epiphyte species composition was related to habitats – habitats with similar structure and resources, such as in the outer canopy of large trees and the canopy of small-trees, had similar species composition. Habitats with different structure and resources, such as in the inner and outer canopy zones of large trees, had different species composition. With 76% of species showing significant associations to particular habitats, the high diversity of habitats in large tree crowns is important for epiphyte diversity and community structure.

To our knowledge, our study is the first to link epiphyte distributions to measured T, RH, VPD, habitat structure, and resources *in situ* in tree canopies. Although gradients in light, water availability, drought stress, and substrate features have been hypothesized to explain epiphyte distributions within tropical tree canopies (Johansson 1974, ter Steege and Cornelissen 1989, Zimmerman and Olmsted 1992, Nieder et al. 2000, Zotz and Vollrath 2003, Kelly et al. 2004, Reyes-Garcia et al. 2008), few studies have measured these resources and habitat characteristics *in situ*. Light was measured in several tropical canopies (Johansson 1974, ter Steege and Cornelissen 1989, Reyes-Garcia et al. 2008), but only one study has measured T, VPD, and RH, and they were measured only in the inner canopy (Cardelús and Chazdon 2005). Among different-sized trees, we found that epiphyte composition was significantly associated with tree size and range in VPD (Fig. 3.6A). Inner canopy VPD was lowest in the smallest trees and largest trees and highest in the medium-sized trees (70 cm dbh size class), which is likely due to the amount of exposure to light each tree size experiences. The change in exposure of the canopy with tree size is evident in the increasing CII values with tree size. The small tree crowns are shaded by the canopy above them, and the medium-sized trees are more exposed. Although the largest trees have the most exposure, inner canopy light availability was low, which is shown by the low % canopy openness in the inner canopy of large trees (20%; Table 3.3) despite the CII value of large trees (*i.e.*, 4) being equivalent to an average of 37% of visible sky (Keeling and Phillips 2007). The high exposure and extreme fluctuations in VPD in the inner canopy of medium-sized trees (70 cm dbh) may limit the colonization by species that require more stable and more protected conditions, such as those found in the inner canopy of the largest trees (> 70 cm dbh). Indeed, some soil fern species that were positively associated with the inner canopy of the largest trees were negatively associated with the inner canopies of medium-sized trees.

Within the canopies of the largest trees, epiphyte composition was significantly associated with habitat differences among canopy zones. The inner canopy had canopy soil and was buffered from extreme fluctuations in environmental conditions, while the outer canopy lacked canopy soil and had the largest range in VPD between the hottest and coolest days. The outer canopy appears to be the least buffered of the habitats, and these more extreme conditions appear to limit the establishment of many epiphyte species, leading to the observed significant associations with the inner canopy and no associations with the outer canopy.

Determining the relative influence of different factors of habitats in driving community structure can be difficult as habitat factors are often confounded. For example, the relative importance of resource and habitat heterogeneity in influencing patterns in rodent community structure in a desert habitat was difficult to determine using vegetative characteristics because plants provide both habitat structure and seed resources for rodents (Stevens and Tello 2011). In a study examining the influence of coral diversity on fish diversity, coral species provided food resources as well as habitat for fish; therefore the relative influence of habitat structural and resource heterogeneity on fish community structure was difficult to assess (Messmer et al. 2011). In tropical forests, determining the relative influence of habitat and resource heterogeneity on tropical tree distributions is difficult because the spatial heterogeneity of soil chemistry and topography can be related (Barthold et al. 2008, Yavitt et al. 2009). Although we found support that local epiphyte diversity in tropical tree canopies is explained more by structural features of the habitat (*i.e.*, branch diameter), differences in habitat structure, such as branch diameter, may also relate to differences in resources (canopy soil is only found on the largest branches). For example, branch diameter and % canopy openness showed high collinearity with % canopy soil cover suggesting that either all of these factors are important in creating microhabitats or that different epiphyte species are influenced by different factors. The relative importance of habitat structural features and resources in structuring epiphyte communities has yet to be evaluated and would require experimental studies with reciprocal transplants among habitats.

Within large tree crowns, the measured habitat factors may combine to create a gradient in some other unmeasured factor, such as drought stress as has been proposed previously (Johansson 1974, Hietz and Briones 1998, Zotz and Vollrath 2003, Kelly et al. 2004, Reyes-Garcia et al. 2012). The inner canopy of the largest trees in our study had canopy soil, which buffers plants from experiencing drought conditions (Frieberg 1996), and a lower VPD, while the outer canopy had bare bark, which has a lower water holding capacity than soil and a higher VPD. Species that had significant associations to the inner canopy of trees, such as many soil ferns, are less adapted to drought than those found in the outer canopy, such as bark ferns and atmospheric bromeliads (Benzing et al. 1978, Benzing 1990, Watkins Jr et al. 2007). Differences in strategies to avoid or tolerate drought may explain epiphyte distributions within large tree crowns.

In tropical forests, substrate characteristics influence the composition and structure of plant communities (Newbery and Proctor 1984, Lescure and Boulet 1985, Lieberman and Lieberman 1985, Clark et al. 1995, 1998). For example, many plant species have significant associations to particular substrate structures or resources (Ledo et al. in press., Clark et al. 1998, Harms et al. 2001, Phillips et al. 2003, Cannon and Leighton 2004, DeWalt et al. 2006). Despite the conservative nature of our analysis that took into account the non-independence of individuals in each habitat, our study shows one of the highest percentage of plant species with a significant association to a particular habitat (our study, 76%, Clark et al. 1998, 66%, Ledo et al. in press, 36%, Harms et al. 2001, 51%, Cannon and Leighton 2004, 67%, DeWalt et al. 2006, 71%, Phillips et al. 2003, 76%). Substrate characteristics are also important for structuring tropical trees in the Amazon (Phillips et al. 2003) and lianas in Borneo (DeWalt et al. 2006) where a similar percentage of plant species showed significant habitat associations as the current study. The high degree of habitat specialization within our study and in others (Phillips et al. 2003, DeWalt et al. 2006) is likely due to large differences among habitat types. For example, nutrient composition was significantly different among soil types in the Amazon (Phillips et al. 2003), and there were large differences in the nutrient content and water retention capacity among soil types in Borneo (DeWalt et al. 2006). The steep structural, environmental, and resource gradients within *V. koschnyi* trees created a diversity of habitats that differed significantly in many characteristics. Therefore, habitat specialization and the distinctness of different habitats seem to play a similar role in the maintenance of epiphyte diversity in tropical wet forest canopies as in other tropical plant communities.

Although some tropical plant species appear to have specialized to particular habitats, the lack of a relationship of many tropical plant species to habitats suggests that habitat partitioning explains only a portion of the floral diversity in tropical rain forests (Harms et al. 2001, Valencia et al. 2004). Additional effects of species distributions may be dispersal limitation (Hubbell and Foster 1986, Valencia et al. 2004), other un-measured habitat factor, density- or frequency-dependent mortality imposed by natural enemies (Janzen 1970, Connell 1971, Clark and Clark 1984, Mangan et al. 2010), or a wide tolerance to varying habitats (*i.e.*, are generalists, Valencia et al. 2004). In our study, tank bromeliads showed little distributional relationship to habitat gradients within tree canopies. Although several tank bromeliad species showed significant negative associations with small trees, only a couple of species showed any significant association to a particular canopy zone within the largest trees. The lack of relationship with measured gradients and their wide distribution suggest that tank bromeliads may be generalists that may not be limited by dispersal, may have a wide tolerance for habitat types, or may be limited by other factors that we didn't measure. Tank bromeliads form tanks from overlapping leaves that impound water from which they uptake water and nutrients through leaf trichomes and use their roots solely for anchorage to their host tree (Benzing 1990, 2000). The wide distribution of tank bromeliads may result from their ability to access and store water and nutrients from a variety of sources. Many tank bromeliad species are also facultative CAM, which they will use when water in their tanks is low or gone (Benzing, 2000). These traits reduce the likelihood that they are tied to particular substrate characteristics, like other epiphyte taxa are (Zotz and Thomas 1999, Benzing 2000, Reyes-Garcia et al. 2008).

Accounting for the factors controlling patterns of local species diversity, distribution, and abundance is a major challenge in ecology (Ricklefs 1977, Huston 1979, Hubbell 2001). We found support for the hypothesis that habitat heterogeneity is an important driver of vascular epiphyte community structure and distributions. In particular, our results highlight the importance of habitat structures and environmental extremes in promoting and maintaining local epiphyte diversity in tropical tree canopies. In addition to better understanding the processes producing positive relationships between habitat and species diversity, our results also show that distinct and large differences among habitats is important in establishing this relationship.

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Chapter 4

Leaf Traits Explain Niche Partitioning in a Tropical Wet Forest Canopy

INTRODUCTION

A fundamental challenge of community ecology is to understand how numerous species coexist in diverse communities. Neutral theory assumes that species are adapted to common field conditions and coexist by chance (Hubbell 2001), while niche theory predicts that species are functionally different and coexist because they are specialized for different niches (Hutchinson 1959, MacArthur and MacArthur 1961, Silvertown 2004). Among the major niche axes for the evolution and differentiation of terrestrial plants are gradients in environmental conditions and resources (Tilman 1986). The association of plant species to particular environmental conditions or resources may explain the non-random spatial distributions of woody plants in tropical forests along gradients in topography, soil resources, and light (Newbery and Proctor 1984, Clark et al. 1998a, Webb and Peart 2000, Schnitzer and Carson 2001, Harms et al. 2001, Potts et al. 2002, Phillips et al. 2003, Valencia et al. 2004, Fine et al. 2005, DeWalt et al. 2006, John et al. 2007, Schnitzer et al. 2008, Dalling et al. 2012). Plant-habitat associations can result from adaptations to environmental conditions at a particular site. These adaptations often impose trade-offs in performance, such that an adaptation or trait that results in high performance in one habitat can result in low performance in another. These trade-offs reduce competition among species because each species is competitive in only a subset of habitats. Plant-habitat associations may, therefore, explain niche partitioning in environments with a high diversity of microhabitats.

Differences in ecological strategies among coexisting plant species could explain niche partitioning if species are differentiated in the traits that determine their response to major biotic or abiotic pressures (Tilman 1988, Kraft et al. 2008). One axis of evolutionary specialization across ecosystems and biomes is that of rapid acquisition of resources at one end of the spectrum and conservative use of resources at the other. Plant species across the globe exhibit this fundamental tradeoff in leaf investment where, at one end, plants put investment into leaf structure resulting in leaves that are long-lived and tolerant of environmental stresses and, at the other end, plants put investment into metabolism resulting in leaves that are highly productive but unprotected and short-lived (Westoby et al. 2002, Wright et al. 2004). Strategy differentiation, as measured by plant functional traits, appears to contribute to coexistence among tree species in Amazonian forests, one of the most diverse tropical forests in the world (Kraft et al. 2008). Leaf trait values of trees are correlated with soil fertility in Australian temperate forests (Gallagher and Leishman 2012), light gradients in highly diverse moist tropical forests of French Guiana (Laurans et al. 2012), and soil water gradients in tropical forests in Panama (Engelbrecht et al. 2007). Functional traits, therefore, reflect differences in ecological strategies and trade-offs amongst co-occurring plant species and may contribute to niche partitioning by species-rich communities if those traits are segregated along environmental and resource axes.

The tropical rainforest canopy is a structurally complex environment with steep environmental and resource gradients that create a diversity of microhabitats within tree crowns. The ability of a large number of vascular epiphyte species to inhabit a single tree crown (65 epiphyte species; Woods et al. in prep) may reflect differentiation along the steep environmental and resource niche axes. Epiphytes appear to partition the canopy habitat based on variation in habitat structure such as branch size, availability of resources such as canopy soil, and microclimate gradients of vapor pressure deficit (VPD) and light (Woods et al. in prep, Johansson 1974, ter Steege and Cornelissen 1989, Zimmerman and Olmsted 1992, Nieder et al. 2000, Zotz and Vollrath 2003, Kelly et al. 2004, Reyes-Garcia et al. 2008). Woods et al. (in prep) found significant associations of many vascular epiphyte species to particular microhabitats within large tree crowns in lowland wet forest in Costa Rica. Some vascular epiphyte species were significantly associated with the inner canopy of large trees (*i.e.*, close to the bole), where thick branches are covered in canopy soil, and light and VPD are low. Other epiphyte species were significantly associated with the outer canopy (*i.e.*, far from the bole in the outer branches), where thin branches lack canopy soil, and light and VPD are high. Many species, some closely related, were associated with the same habitat. The co-occurrence of epiphyte species in similar habitats may be explained by differences in ecological strategies.

In this study, I test whether there is niche partitioning in the hyperdiverse vascular epiphyte community of wet tropical rainforest canopies using functional leaf traits. I examine two niche-based hypotheses: (1) barriers to establishment or survival imposed by the abiotic environment (*i.e.*, environmental filters; Cornwell et al. 2006, Engelbrecht et al. 2007) will result in a convergence in strategy by co-occurring species in similar habitats as evidenced by similar functional leaf traits; and (2) niche differentiation amongst closely related and co-occurring species will result in divergence in strategy as evidenced by differences in functional leaf traits. I will examine the distribution of traits along environmental gradients to determine if vascular epiphyte species are differentiated along measured environmental and resource axes. Other factors, such as density-dependence mediated by natural enemies, may also explain niche differentiation among vascular epiphytes, but, presently, information on the interactions of epiphytic plants with different trophic levels is sparse. Furthermore, epiphytes evolved under severe nutrient- and water-limitation: the only nutrient sources are canopy soil, precipitation and throughfall, all of which tend to be low compared to nutrient sources for terrestrial plants in forest floor soils (Clark et al. 1998b, Cardelús et al. 2009). The low supply of water and nutrients and the distribution and specialization of epiphyte species to particular habitats within tree crowns suggest that niche differentiation could be along gradients in nutrient and water availability.

MATERIALS AND METHODS

Study area

This study was conducted at La Selva Biological Research Station (84°00'12" W, 10°25'52" N, 40 m a.s.l.) in northeastern Costa Rica. La Selva is characterized as tropical wet forest (Holdridge 1967) and receives approximately 4000 mm of annual precipitation, predominantly during the wet season, May–January, with an average monthly precipitation of 382 mm. The dry season, February–April receives an average monthly precipitation of 172 mm. Average monthly temperature is 25.8°C ± 0.2 and varies little throughout the year (McDade et al. 1994).

Sampling

I selected the 10 most abundant and widespread vascular epiphyte species from four families found on *Virola koschnyi* trees as determined by a previous survey (Woods et al. in prep). I restricted my study to the most common species to obtain a good representation of the vascular epiphyte community. I chose species that spanned four functional groups and environmental gradients from the bole to the outer canopy (Table 4.1). I selected leaf traits that would reflect plant responses to the environment (Table 4.2; Cornelissen et al. 2003).

I selected two fully expanded leaves without evidence of damage from 6-10 adult individuals of each species found in *V. koschnyi* trees. Tree canopies were accessed using modified rope climbing techniques (Perry 1978). Leaves were stored in humidified plastic bags and brought back to the laboratory within 1-4 h of collection. Leaves were placed in tubes filled with deionized water and hydrated at 7°C for at least 12 h to reduce microbial growth on leaf surfaces. After this period, leaves were blotted and weighed on precision balances (0.1 mg) to obtain maximum fresh weight (MFW). One set of leaves was left to dry on the laboratory bench in order to determine the rate of epidermal water loss (EWL) over a 72 h period. For each leaf, the fresh weight (FW) was measured every 2-4 h for 72 h (Lorenzo et al. 2010). After 72 h, leaves were oven-dried to constant

Table 4.1. List of the 10 most abundant and cosmopolitan vascular epiphyte species, along with their species code, functional group, location within the canopies of *Virola koschnyi* trees at La Selva Biological Research Station, Costa Rica, and number of individuals sampled for each species (#). Tank = tank bromeliad. All individuals sampled of each species were the same size. Canopy location was determined from Woods et al. (in prep).

Family	Species	Species code	Functional group	Canopy location	#
Elaphoglossaceae	*Elaphoglossum herminieri*	ElaHer	Soil fern	Inner	10
Elaphoglossaceae	*Elaphoglossum latifolium*	ElaLat	Soil fern	Inner	7
Araceae	*Anthurium upalaense*	AntUpa	Aroid	Inner	9
Araceae	*Anthurium ramonense*	AntRam	Aroid	Inner	6
Bromeliaceae	*Aechmea nudicaulis*	AecNud	Tank	Inner	10
Bromeliaceae	*Tillandsia anceps*	TilAnc	Tank	Inner	10
Bromeliaceae	*Tillandsia monadelpha*	TilMon	Tank	Outer	9
Bromeliaceae	*Guzmania lingulata*	GuzLin	Tank	Mid	10
Bromeliaceae	*Guzmania monastachya*	GuzMon	Tank	Mid	6
Polypodiaceae	*Microgramma reptans*	MicRep	Bark fern	Outer	10

weight (3-5 days) at 60°C to obtain dry weight (DW). Relative water content was calculated every time FW was measured (every 2-4 h) as:

$$\mathrm{RWC}\ (\%) = \frac{(\mathrm{MFW} - \mathrm{DW})}{\mathrm{FW} - \mathrm{DW}}\ \mathrm{x}\ 100 \qquad (1)$$

The EWL was determined by the change in relative water content (RWC) during the 72 h period. The second set of leaves was used to determine other leaf traits (Table 4.2).

Each leaf area (LA) was obtained using a LI-3100 leaf area meter (Li-Cor, Lincoln, Nebraska, U.S.A.). Leaf thickness (LT) was measured as the average of three areas of the leaf lamina using a digital micrometer. Leaf resistance to fracture (LRF) was measured using a leaf penetrometer in the same locations that LT was measured.

Table 4.2. Description of leaf traits measured on 10 most common vascular epiphyte species found in *Virola koschnyi* trees at La Selva Biological Research Station, Costa Rica.

Functional leaf trait	Formula	Units	Relation to plant performance
Specific leaf area (SLA)	$\frac{\mathrm{LA}}{\mathrm{DW}}$	$\mathrm{mm}^2\ \mathrm{mg}^{-1}$	Correlates positively with growth rate and negatively with leaf life span[1]
Leaf dry matter content (LDMC)	$\frac{\mathrm{DW}}{\mathrm{MFW}}$	$\mathrm{mg}\ \mathrm{g}^{-1}$	Correlates negatively with SLA and growth rate, and positively with leaf life span[1]
Succulence	$\frac{\mathrm{MFW}-\mathrm{DW}}{\mathrm{LA}}$	$\mathrm{g}\ \mathrm{m}^{-2}$	Correlates with amount of water storage in plant tissue[2,3]
Leaf thickness (LT)	average from 3 measures	mm	Correlates with leaf life span, and with high light and low moisture environments[4]
Leaf resistance to fracture (LRF)	force / penetrometer circumference	$\mathrm{N}\ \mathrm{mm}^{-1}$	Indicates carbon investment in structural protection; correlates positively with leaf life span[1]
Leaf toughness	$\frac{\mathrm{LRF}}{\mathrm{LT}}$	$\mathrm{N}\ \mathrm{mm}^{-2}$	Correlates positively with leaf life span[5]
Rate of epidermal water loss (EWL)	$\frac{\Delta\%\mathrm{RWC}}{\mathrm{h}}$	$\%\mathrm{RWC}\ \mathrm{h}^{-1}$	Relates to cuticle thickness and is low in low water environments[3]

[1]Cornelissen et al. 2003, [2]Mantovani 1999, [3]Lorenzo et al. 2010, [4]Witkowski and Lamont 1991, [5]Wright and Cannon 2001

For soil ferns and aroids, I also sampled roots from the same individuals from which I sampled leaves and examined the EWL of root tissue following the same protocol as above.

Environmental variables

When each leaf was collected from each individual, I measured environmental variables that I hypothesized would be related to leaf traits including air temperature (T), relative humidity (RH), vapor pressure deficit (VPD), substrate temperature (ST; canopy soil or bare bark), and percent canopy openness (CO). RH (%) and T (°C) were measured 10 cm above the center of the plant for 2 min using LogTag dataloggers (MicroDAQ, Contoocook, New Hampshire, USA). I calculated VPD, the difference between the amount of moisture in the air and the amount of moisture the air can have when fully saturated, from T, RH, and the saturation vapor pressure (SVP) using the following equations (Murray 1967):

$$\text{SVP (Pascals)} = 610.7 * 10^{\frac{7.5\text{T}}{237.3+\text{T}}} \tag{2}$$

$$\text{VPD (Pascals)} = \frac{(100 - \text{RH})}{100} * \text{SVP} \tag{3}$$

Substrate temperature was measured using a digital infrared temperature gun with laser sight. Percent canopy openness was estimated using a densiometer (Forestry Supplies Inc., Jackson, Mississippi, USA).

Statistical analyses

To determine whether epiphyte species and functional groups separate along environmental gradients based on their functional leaf traits, I used a principal components analysis (PCA) on a correlation matrix of 10 species x 12 trait values. I chose a PCA because the axes are orthogonal and enabled me to correlate the PCA axes 1 and 2 with the eigenvector scores of the eight traits as well as the environmental variables. I used the metaMDS function in the vegan package in R for the PCA (R Development Core Team 2009, Oksanen et al. 2010). I also compared the range of scores of epiphyte functional groups and species along PCA axis 1 and 2 to examine niche overlap.

To examine if epiphyte species and functional groups differ in their leaf traits, I ran an ANOVA on each leaf trait followed by Tukey HSD tests. To examine if soil ferns and aroids differed in the EWL of roots, I ran a t-test.

RESULTS

Vascular epiphyte species and functional groups showed specialization to particular habitats based on their functional leaf traits with different species and functional groups converging on a similar strategy when in a similar habitat. Epiphyte species and functional groups with similar leaf traits were found in habitats with similar environmental conditions as shown in the PCA (Fig. 4.1). Accounting for 39.9% of the variation, the first PCA axis reflected the gradient from high to low leaf construction costs and was strongly related to environmental conditions (Table 4.3). Species and functional groups found in cooler sites with high RH, low VPD, and low light, such as aroids and soil ferns, had high energy investment into the structural aspect of their leaves, which was demonstrated by a high LDMC, thick leaves, and a high degree of succulence (lower end of first PCA axis). Species and functional groups found in hotter, drier, and more open sites, such as most tank bromeliad species and bark ferns, did not invest much in the structural component of their leaves as they had a low LDMC and a high SLA (higher end of first PCA axis). The second PCA axis accounted for 23.0% of the variation and appeared to be related to a gradient in leaf strength. Species found in hotter, open sites had weaker leaves as evidenced by their low LRF and LTo values and high EWL, while species found in cooler, shadier sites had tougher leaves (*i.e.*, high LRF and LTo).

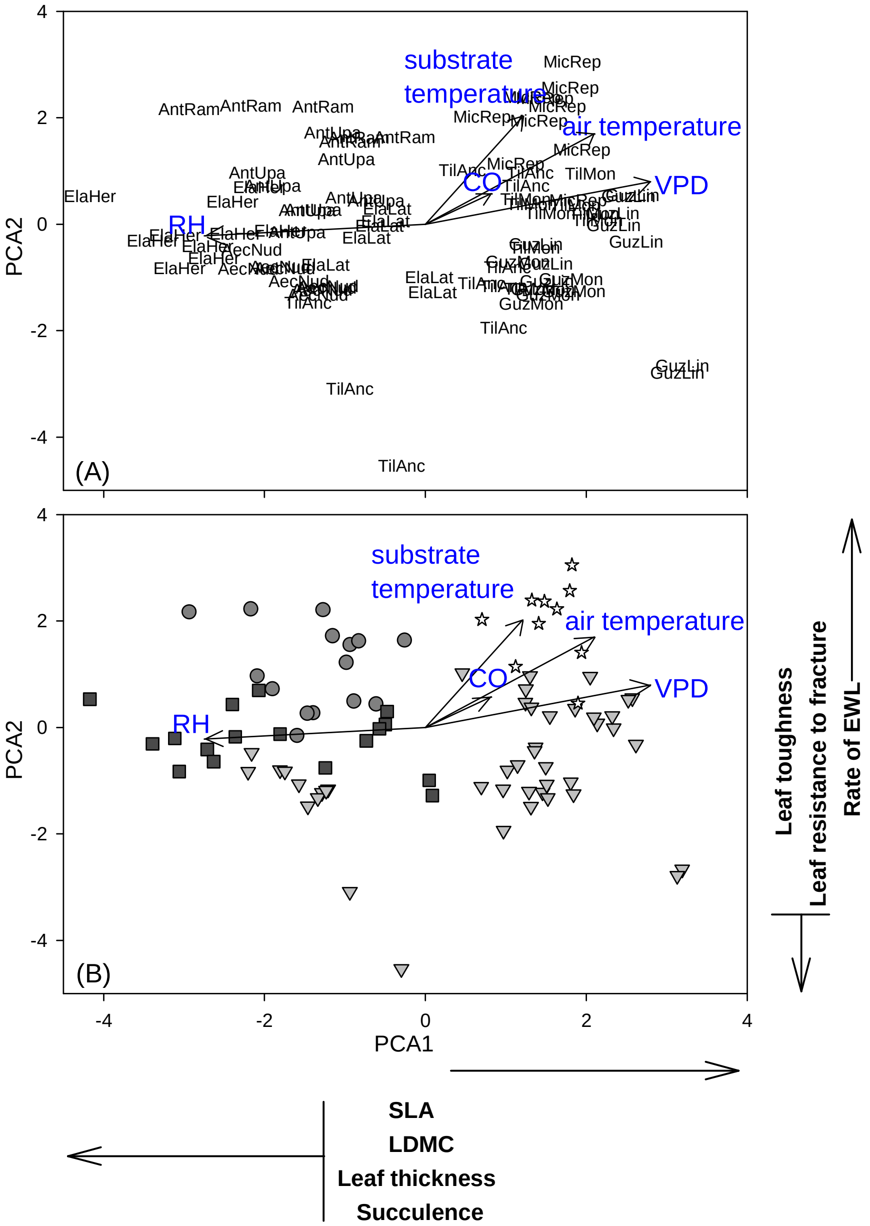

Figure 4.1. PCA ordination of the 10 most common vascular epiphytic plant species in *Virola koschnyi* trees at La Selva Biological Station, Costa Rica on the basis of 8 leaf traits. Measured environmental variables are shown as arrows that represent correlations of environmental variables with the axes. For (A), species codes are as in Table 4.1. For (B), symbol colors and shapes denote different epiphyte functional groups: dark grey squares = soil ferns; grey circles = aroids; light grey triangles = tank bromeliads; stars = bark ferns. Labels show traits with the highest eigenvector scores on PCA axes 1 and 2 for both (A) and (B), with the label with the highest score presented nearest to the axis. Eigenvector scores of all traits along PCA axes 1 and 2 are in Table 4.3.

Table 4.3.Eigenvector scores of plant traits with two main PCA axes, obtained from a matrix of 8 traits x 10 most common vascular epiphyte species in *Virola koschnyi* trees at La Selva Biological Research Station, Costa Rica. Values are ranked in order of absolute magnitude along PCA 1. Eigenvector scores > 0.500 are in bold. Values in parentheses indicate variance accounted for by each axis.

Functional leaf trait	PCA 1 (39.9%)	PCA 2 (23.0%)
Specific leaf area	**0.930**	0.107
Leaf dry matter content	**-0.706**	-0.254
Leaf thickness	**-0.624**	-0.049
Succulence	**-0.587**	0.298
Leaf toughness	0.303	**-0.845**
Leaf resistance to fracture	-0.285	**-0.792**
Rate of epidermal water loss	-0.248	**0.577**

Patterns of habitat specialization were evident in the distribution of epiphyte functional groups and species along the PCA axes. Soil ferns and aroids were specialized to shady sites with high RH and low VPD, while most tank bromeliads and bark ferns were specialized to more open sites that were hotter and drier (Fig. 4.2A). Species showed a more narrow specialization to particular habitats than functional groups with differences among species within each functional group (Fig. 4.2C & 4.2D). When species showed overlap along one axis, they often showed less overlap along the other axis.

Closely related species found in the same microhabitat had different strategies as evidenced by their different trait values. Among two soil ferns that inhabit the inner canopy, *Elaphoglossum herminieri* had a significantly lower SLA and higher succulence than *E. latifolium*. *Elaphoglossum herminieri* was more restricted to the darker inner canopy than *E. latifolium*, which is evident in the little niche overlap along PCA axis 1

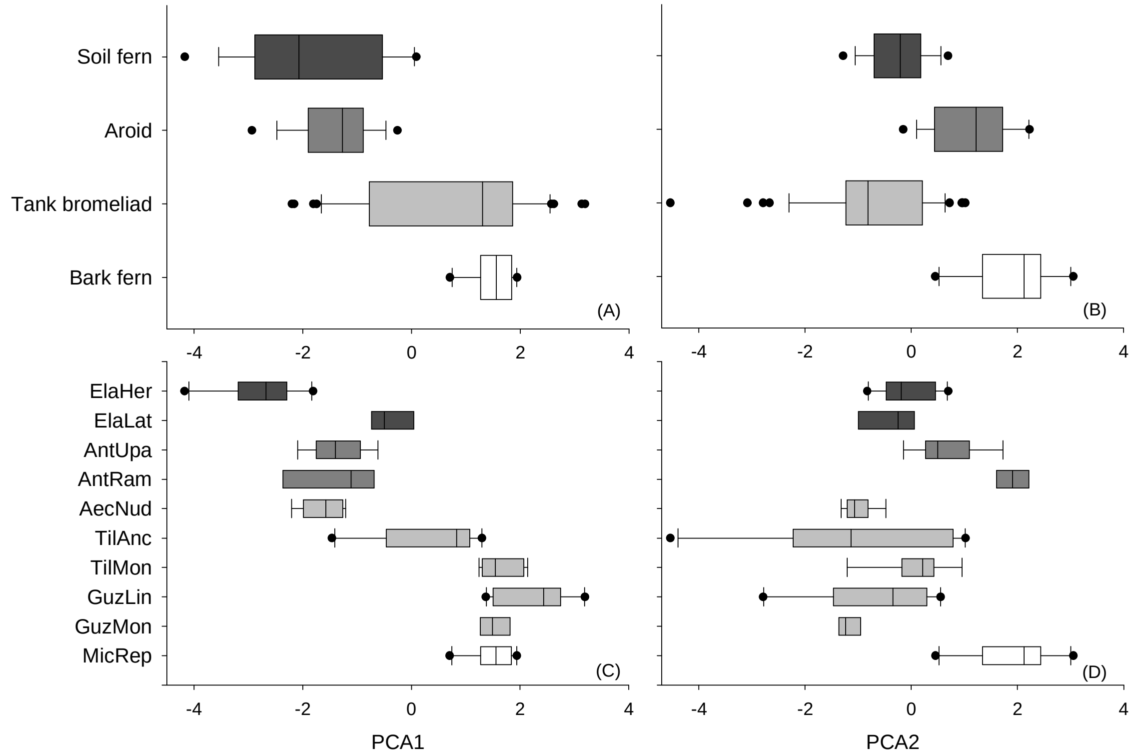

Figure 4.2. Box plots showing the distribution of epiphyte functional groups along PCA axes 1 (A) and 2 (B), and epiphyte species along PCA axes 1 (C) and 2 (D). Values correspond to scores of functional groups and species of the PCA. The line in each box represents the median trait value, the error bars represent the 10th and 90th percentiles for each trait value, and the dots represent the outlying trait values for each species and functional group. For species or functional groups that have no error bars or dots, the box represents the 10th and 90th percentile. Box shades are as in Figure 4.1, and species codes are as in Table 4.1.

(Fig. 4.2C). Although *Anthurium ramonense* and *A. upalaense* had high distributional overlap along PCA axis 1, they were differentiated along PCA axis 2. *Anthurium ramonense* had lower investment in leaf structure than *A. upalaense* (*i.e.*, lower LDMC) but had a higher degree of succulence and inhabited slightly hotter microhabitats (Fig. 4.1A). *Tillandsia* species showed distinct distributions within the canopy with *T. anceps* found more in the inner canopy and *T. monadelpha* found more in the outer canopy (Fig.

4.2C). Leaf traits between these species, with the exception of leaf succulence, were significantly different, showing divergent strategies along an environmental niche axis (Table 4.4). The two species of *Guzmania* showed high overlap along both PCA axes, as well as no significant differences in their leaf traits (Table 4.4).

Soil ferns and aroids put the most structural investment into their leaves as they had significantly lower values of SLA and significantly higher values of LDMC and succulence than tank bromeliads and bark ferns (Table 4.4). The EWL of soil fern roots (-32.7 ± 1.42) was significantly greater than that of aroid roots (-12.5 ± 1.02; t = 11.6, df = 28, $P < 0.0001$).

DISCUSSION

Functional leaf traits explained niche partitioning by vascular epiphytes in tropical tree canopies. Species found in the same microhabitat showed convergence in leaf traits, supporting the hypothesis that environmental filtering plays a role in epiphyte species distributions. There were no significant differences in leaf traits among aroids and soil ferns, which were both confined to microhabitats with high RH, low light, and low VPD. Similarly, most tank bromeliads and bark ferns showed similar leaf traits and were found predominantly in microhabitats with high light, low RH, and high VPD. Closely related species within a functional group differed significantly in at least one leaf trait suggesting that there was evidence of trait divergence, supporting the hypothesis of niche differentiation. The two soil fern species, for example, had different strategies within the same microhabitat, which was reflected in significant differences in SLA, and the two aroid species showed significant differences in leaf succulence. Thus, different ecological

Table 4.4. Means (± S.E.) of functional leaf traits that were correlated with the first PCA axis of epiphyte species and functional groups from *Virola koschnyi* trees at La Selva Biological Research Station, Costa Rica. Leaf thickness was not included here as it varied little among species, and differences among functional groups were pulled by one species, *Aechmea nudicaulis*. For LDMC, three data points were removed as outliers in the ANOVA for functional groups as deemed by a Cook's D test ($P < 0.05$) making the degrees of freedom 3,79 for that test. Species codes are as in Table 4.1. Values with different letters are significantly different according to a Tukey's HSD test ($P < 0.05$). *$P < 0.0001$.

Species	Functional Group	SLA (mm^2 mg^{-1})	LDMC (mg g^{-1})	Succulence (g mm^{-2})
ElaHer	Soil fern	4.4 ± 0.27^{a}	325 ± 12.2^{a}	489 ± 34.1^{ad}
ElaLat	Soil fern	7.4 ± 0.37^{bce}	327 ± 12.5^{a}	287 ± 23.4^{cde}
AntUpa	Aroid	6.4 ± 0.30^{b}	224 ± 6.8^{bd}	563 ± 37.8^{a}
AntRam	Aroid	7.0 ± 0.91^{bc}	180 ± 14.6^{bcd}	690 ± 36.8^{b}
AecNud	Bromeliad	8.6 ± 0.16^{ce}	171 ± 5.8^{bcd}	571 ± 22.9^{ab}
TilAnc	Bromeliad	10.3 ± 1.04^{e}	225 ± 27.5^{d}	379 ± 18.4^{e}
TilMon	Bromeliad	17.1 ± 0.82^{d}	127 ± 3.8^{e}	411 ± 14.4^{de}
GuzLin	Bromeliad	21.1 ± 1.32^{d}	119 ± 10.8^{e}	378 ± 22.4^{cde}
GuzMon	Bromeliad	15.8 ± 0.31^{d}	146 ± 2.6^{ce}	371 ± 4.6^{de}
MicRep	Bark fern	17.4 ± 0.68^{d}	139 ± 4.6^{ce}	362 ± 9.4^{e}
$F_{9,76}$		62.2*	32.1*	21.3*
Functional group				
Soil fern		5.6 ± 0.42^{a}	325 ± 8.6^{a}	406 ± 33.0^{a}
Aroid		6.6 ± 0.40^{a}	206 ± 8.9^{b}	614 ± 31.0^{b}
Tank		14.5 ± 0.83^{b}	159 ± 9.0^{c}	427 ± 14.3^{a}
Bark fern		17.4 ± 0.68^{b}	139 ± 4.6^{c}	362 ± 9.4^{a}
$F_{3,82}$		46.5*	77.5*	16.7*

strategies along an environmental niche axis suggest that the steep environmental and resource gradients within tree crowns leads to niche differentiation by vascular epiphytes.

The partitioning of the tropical canopy by vascular epiphytes seems to entail a niche axis of resource conservation at one end and resource acquisition at the other. Canopy soil is high in nitrogen but low in phosphorus (Cardelús et al. 2009). As a result, the concentration of N and P in leaves of species dependent on canopy soil, such as soil ferns and aroids, is often higher than species not dependent on canopy soil, such as tank bromeliads (Cardelús and Mack 2010). Although soil ferns and aroids have greater leaf nutrient concentrations than bromeliads (Cardelús and Mack 2010), they may be more limited by water availability and light than bromeliads in the outer canopy (Zotz and Hietz 2001), which may explain their resource conservation strategy. Habitats with limited resources favor slow-growing plants, which in turn favors long-lived leaves that put a large investment in antiherbivore defenses (Coley et al. 1985). The large investment in leaf tissue in soil ferns and aroids, as evidenced by their low SLA and high LDMC, may be due to a combination of water- and nutrient-limitation, a long leaf life-span, and, as a result, a large investment in herbivore and pathogen defense (Coley et al. 1985, Wright and Cannon 2001, Westoby et al. 2002). Tank bromeliads have essentially a constant source of water and nutrients in their tanks, the ability to switch into CAM photosynthesis under drought (Benzing 1990), and are not limited by the availability of canopy soil. Thus, tank bromeliads are not limited to shady microhabitats where canopy soil is available, such as soil ferns and aroids are, and can inhabit more open sites on bare bark. Although they invest little in their leaf tissue in terms of dry matter, tank bromeliads had the toughest leaves with the highest LRF values, which is likely to maintain their tank structures. Bark ferns are drought deciduous, which may explain the small structural investment in their leaf tissue (Benzing 1990).

The trade-off between rapid acquisition of resources and conservation of resources within well-protected tissues has been found to exist in many taxa across environmental conditions and biomes. For example, in an analysis of 640 plant taxa spanning three continents, the same functional leaf traits measured in this study were predictors of resource capture and utilization (Díaz et al. 2004). For tropical trees in moist forests, wood density explained >80% of the variation in species positions along a growth-mortality trade-off axis in central Panama (Wright et al. 2010), and leaf traits explained the growth-mortality trade-off for 54 species in Bolivia (Poorter and Bongers 2006). This study is the first to demonstrate the same trade-off of resource conservation and resource acquisition in vascular epiphytes.

According to classic niche theory, despite a convergence in traits, species and functional groups found in the same microhabitat either partition the microhabitat further or access basic plant resources in different ways (Hutchinson 1959, MacArthur and Levins 1967). For inner canopy ferns, the majority of their nutrients and water comes from canopy soil, as evidenced by their nutrient concentrations being similar to that of their host tree and canopy soil (Cardelús et al. 2009, Cardelús and Mack 2010). Furthermore, because of the extremely high EWL rate of their roots, soil fern roots likely need canopy soil around them to maintain water in their roots. Aroids access nutrients and water from canopy soil as evidenced by their roots penetrating soil mats, but they also have velamen radiculum over the aerial roots which, when wet, becomes absorbent and is able to uptake atmospheric sources of nutrients and water (Benzing 1990). Because aroids partly depend on atmospheric sources of water and nutrients, they may be more water-limited than soil ferns, which could explain why aroid leaf succulence values were significantly higher than that of soil ferns. The subtle differences in how soil ferns and aroids access nutrients and water may help explain their ability to occupy a similar habitat in the inner canopy, and examining the sources of nutrients and water for soil ferns and aroids should be the focus of future studies.

Trait differences may provide the niche axis by which many sympatric congeners coexist. The two *Tillandsia* species had significant differences in their trait values as well as little overlap in their distributions. *Tillandsia anceps* put more investment in leaf structure than *T. monadelpha* as evidenced by a lower SLA and higher LDMC, and was found more often in shadier sites with lower VPD. The two soil fern species were both found in the inner canopy, but *Elaphoglossum herminieri* had a lower SLA than *E. latifolium*. These trait differences may help explain the 3-dimensional partitioning of the inner canopy by the *Elaphoglossum* species because *E. herminieri* hangs below the branch where horizontal light levels are higher and *E. latifolium* rests on top of the branch. *Elaphoglossum herminieri* has a blue iridescence in its leaves that acts as a sunscreen against UV-radiation under these higher light levels (E. Watkins and M. Britton, unpublished data). The two aroid species differed only in leaf succulence: *Anthurium ramonense* had significantly higher leaf succulence than *A. upalaense*, which may explain its ability to inhabit sites that are slightly brighter and hotter. The two *Guzmania* species, however, showed no significant differences in trait values and overlapped in habitat distribution, which suggests that there is competition between these species, resources are not limiting, or their coexistence is maintained by other factors, such as disturbance. To better understand how the *Guzmania* species co-occur, future research could examine their growth rates and responses to disturbance.

Using a functional trait approach, I found evidence for niche-based habitat specialization and strategy differentiation among vascular epiphytes. The structural complexity of the tropical canopy seems to be the main driver of vascular epiphyte diversity. The steep gradients of light, canopy soil, branch size, and environmental conditions within large tree crowns create a diversity of habitats on which different epiphyte species can specialize. Interestingly, in similar habitats, distantly related species show trait convergence (*i.e.*, a fern and an angiosperm), while closely related species in a similar habitat show trait divergence (*i.e.*, between fern species). Functional differences among vascular epiphyte species contributes to niche separation along environmental and resource gradients.

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Chapter 5

Conclusions, Applications, and Future Directions

CONCLUSIONS

The goal of this dissertation was to understand the factors that influence community structure and maintenance of diversity in a species-rich plant community. Because some of the most species-rich plant communities are found in the tropics, I focused on examining what influences the diversity of tropical vascular epiphytes. In tropical forests, many hypotheses have been proposed to explain how diversity is maintained. Current theories can be divided into those that posit that species are functionally different and diversity is maintained by the partitioning of resources or habitats (Hutchinson 1959, MacArthur and Levins 1967, Chase and Leibold 2003), and those that assume that all species are functionally equivalent and diversity is maintained by stochastic factors such as dispersal limitation (Hubbell 2001). Niche-based factors, such as habitat specialization, may influence diversity and species distributions at small spatial scales, while neutral-based factors, such as dispersal, may have a greater influence on diversity and community structure at larger spatial scales (Potts et al. 2002). I, therefore, examined what factors influence vascular epiphyte communities at multiple scales.

At the scale of the forest stand, I tested the alternate hypotheses that forest structure and forest age affect epiphyte communities by comparing epiphyte communities between secondary and old-growth forests in central Panama. I examined community structure of vascular epiphytes in older secondary forests between 35-115 yr after land abandonment and nearby old-growth forests. Even though the recovery of epiphyte species richness was rapid, with 55-yr-old forests containing 65 percent of old-growth epiphyte species richness, differences in forest structure between secondary and primary forests such as the presence of large, old-growth trees appeared to influence epiphyte community composition. As in other studies, young forests contained the most drought-tolerant epiphyte species while the structural heterogeneity found in older forests resulted in a combination of drought tolerant epiphyte species common to hotter and drier secondary forests along with shade-tolerant epiphytes that specialized in moist and shady habitats of older forests (Barthlott *et al.* 2001, Acebey *et al.* 2003, Krömer & Gradstein 2003). There was a high degree of nestedness among forest ages such that young secondary forests were significantly nested within older secondary forests and old-growth forests. Furthermore, similarity in epiphyte species composition of secondary forests to old-growth forests increased with forest age suggesting that different habitats upon which different epiphyte species are specialized accumulate in forests as forests age. Thus, forest structure seems to play a large role in explaining differences in epiphyte community structure among forest stands. However, forest age (potentially a proxy for dispersal) explained the low number of individuals in young forests and the linear increase in epiphyte abundance with forest age. These results suggest that deterministic factors influence epiphyte community structure at the small scale of the forest stand while stochastic factors may play a larger role in influencing epiphyte community structure at a larger scale among forest stands.

I further examined the importance of habitat heterogeneity in promoting species diversity by examining whether epiphyte species exhibit significant associations to particular microhabitats. Habitats that are structurally complex with a diversity of resources provide more niches for species with specific habitat and resource requirements (Hutchinson 1959, MacArthur and MacArthur 1961, Tilman 1986, Chesson 2000, Chase and Leibold 2003, Tews et al. 2004). Species that exhibit no associations to particular habitats are assumed to be driven by dispersal limitation (Hubbell and Foster 1986, Hubbell 2001). I measured habitat diversity and epiphyte community structure in different-sized *Virola koschnyi* trees in Costa Rica. Habitat heterogeneity coupled with species-specific habitat associations appeared to contribute substantially to differences in epiphyte community structure among tree size classes. The diversity of habitats for epiphytes increased within tree canopies as they increased in size. Small trees had uniform branch sizes, no canopy soil, and low light reaching the crown. With greater tree size, a greater diversity of microhabitats was present, leading to inner canopies with canopy soil, low vapor pressure deficit (VPD), and low light and outer canopies with no canopy soil, high VPD, and high light. Among the different-sized *V. koschnyi* trees, 76% of epiphyte species exhibited a significant association to a particular tree size or location within tree crowns (*i.e.*, inner or outer). Therefore, habitat heterogeneity, and not dispersal, appears more important in driving diversity and community structure in vascular epiphyte communities among different-sized trees.

I used a trait-based approach to explore the mechanisms underlying epiphyte species distributions along natural environmental gradients found within large tree crowns. According to theory, functional traits reflect differences in ecological strategies and trade-offs among co-occurring plant species and may explain niche differentiation of species-rich communities if those traits are segregated along environmental and resource axes (Tilman 1988, Kraft et al. 2008). Niche theory posits that habitat filtering will select for similar traits among co-occurring species that share similar habitat conditions, whereas competitive exclusion limits the ecological similarity of co-occurring species leading to trait differentiation (Andersen et al. 2012). Epiphyte species found in the same microhabitat showed convergence in leaf traits, supporting the hypothesis that environmental filtering plays a role in epiphyte community structure. Among closely related species within a functional group, there was evidence of trait divergence, supporting the hypothesis of niche differentiation. Different ecological strategies along an environmental niche axis, therefore, explain niche partitioning of tree crowns by vascular epiphytes.

In summary, niche factors appear to be more important in explaining epiphyte diversity and species distributions than neutral factors at small scales while dispersal limitation seems to play a role in structuring species-rich vascular epiphyte communities at larger scales. Epiphyte species are functionally different and exhibited significant associations to particular microhabitats within tree canopies. Therefore, the large contribution to floral diversity by vascular epiphytes in tropical forests can be attributed to the structural complexity of the tropical canopy. The steep gradients in environmental conditions, resources, and structures within large tree crowns create a large diversity of microhabitats into which epiphyte species appear to have evolved specializations and unique adaptations.

APPLICATIONS

Loss of old-growth forests through deforestation and an increase in secondary forests following land abandonment in tropical areas is a growing trend. Within tropical regions, secondary, logged, or disturbed forests now cover more area than mature forests (FAO 2005). This trend has resulted in a greater focus on whether secondary forests can recover the biodiversity and ecosystem functioning losses that accompany the deforestation of old-growth forests. For trees and lianas, secondary forests developing on lands that were not intensively used and are close to seed sources rapidly attain many aspects of the forest structure and species richness of old-growth forests (Brown and Lugo 1990, DeWalt et al. 2000, Guariguata and Ostertag 2001, Chazdon et al. 2007, Dent and Wright 2009). However, the recovery of tree species composition to old-growth levels could take centuries and may not ever fully recover (Corlett 1992, Finegan 1996). The lack of some old-growth tree species in secondary forests could limit the colonization of secondary forests by species that are highly specialized to old-growth forest trees (DeWalt et al. 2003).

My research, along with other studies, has found that many epiphyte species appear to be specialized to particular microhabitats that may be found only in older forests such as those with canopy soil, low VPD, and low light (Woods et al. in prep., Barthlott et al. 2001, Acebey et al. 2003, Krömer and Gradstein 2003, Köster et al. 2009). The inner canopy of *Virola koschnyi* trees at La Selva, for example, developed into a rare and important microhabitat for a large number of species that was buffered from extremes in environmental conditions. Given current climate change predictions for Latin America of less overall rainfall and a larger number of days without rain (Magrin et al. 2007), the buffered inner canopy microhabitat in large trees could be even more important for these epiphyte species. Therefore, the lack of these trees in secondary forests suggests that, secondary forests need to be protected and given sufficient time to recover old-growth tree species composition so that the species that depend on old-growth trees, such as many epiphyte species and the canopy fauna that depend on them (Nadkarni and Matelson 1989, Barthlott et al. 2001, Ellwood et al. 2002) are able to recover. Furthermore, old-growth forests with large old-growth trees that host a large number of epiphyte species should be foci for conservation efforts as source pools for the recovering secondary forests.

FUTURE DIRECTIONS

There are numerous directions for future research on what factors drive the maintenance of diversity in species-rich communities and, in particular, vascular epiphytes. I have already begun to move in several of these. My work suggested that many old-growth epiphyte species were lacking in secondary forests due to a lack of particular microhabitats. To test whether epiphytes are indeed limited by the presence of particular structures such as old-growth tree bark or canopy soil and not simply dispersal, I have installed plastic branches that contain loofa as a proxy for rough bark and canopy soil in secondary forests in Costa Rica. Recruitment of old-growth epiphyte species in these branches would suggest that substrate characteristics unique to old-growth tree species' are more important for epiphyte recruitment than microclimate. A lack of recruitment could suggest dispersal limitation. A seed addition experiment where seeds of old-growth epiphyte species are added to these plastic branches would definitively determine what limits the colonization of secondary forests by old-growth epiphyte species.

A similar line of reasoning and experiments could work for examining what limits the colonization of young trees or particular canopy zones in large trees by many vascular epiphyte species. To this end, I installed small, plastic branches with canopy soil in both the inner and outer branches of large *Virola koschnyi* trees in Costa Rica in order to examine if inner canopy species that rely on canopy soil would be able to disperse to and grow in the more exposed, hot environment in the outer canopy. My study lasted only a few weeks as monkeys and wind destroyed the plastic branches. However, a repeat of this study with an added seed addition treatment would help determine whether inner canopy species are confined to the inner canopy solely because of the presence of canopy soil.

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Appendices

APPENDIX A

Permission for use of Published Material

Permission is granted for you to use the material requested [Woods, C. L. and DeWalt, S. J. (2013), The Conservation Value of Secondary Forests for Vascular Epiphytes in Central Panama. Biotropica, 45: 119–127. doi: 10.1111/j.1744-7429.2012.00883.x] for your thesis/dissertation subject to the usual acknowledgements and on the understanding that you will reapply for permission if you wish to distribute or publish your thesis/dissertation commercially.

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APPENDIX B

Number of holoepiphytes (Holo) and hemiepiphytes (Hemi) for each epiphyte species of each family in two replicate stands of each forest age along a chronosequence in the Barro Colorado Nature Monument, Panama. The total area for each forest age was 0.64 ha (two stands each of 0.32 ha), except for 35-yr-old forests, which were 0.48 ha (one 0.32-ha plot and one 0.16-ha plot) and 55-yr-old forests, which were 0.62 ha (one 0.32-ha plot and one 0.30-ha plot). Counts include individuals found on trees (living and dead), lianas, and downed coarse woody debris.

				Approximate forest age (yr)					
Family	Epiphyte species	Species code[a]	Type	35	55	85	115	OG	Total
Araceae	*Anthurium clavigerum* Poepp.	ANTHCL	Hemi	0	3	5	21	26	55
	Anthurium friedrichsthalii Schott	ANTHFR2	Holo	0	0	0	2	8	10
	Anthurium littorale Engl.	ANTHLI	Holo	0	0	0	0	1	1
	Anthurium salvinii Hemsl.	ANTHSA	Holo	0	0	0	1	1	2
	Monstera dubia (Kunth) Engl. & K. Krause	MONSDU	Hemi	0	3	31	16	25	75
	Monstera pinnatipartita Schott	MONSPI	Hemi	0	1	0	0	0	1
	Philodendron fragrantissimum (Hook.) G. Don	PHILFR	Hemi	0	0	0	9	30	39
	Philodendron inaequilaterum Liebm.	PHILIN2	Hemi	0	13	0	0	43	56
	Philodendron radiatum Schott	PHILRA	Hemi	0	11	16	20	2	49
	Philodendron rigidifolium K. Krause	PHILRI	Hemi	0	20	51	27	227	325
	Philodendron tripartitum (Jacq.) Schott	PHILTR	Hemi	0	2	10	36	39	87
	Unidentified Aroid 1	Aroid 1	Hemi	0	4	0	0	2	6
	Unidentified Aroid 2	Aroid 2	Hemi	0	0	1	0	0	1
	Unidentified Aroid 3	Aroid 3	Hemi	0	1	0	1	3	5
Aspleniaceae	*Asplenium serratum* L.	ASPLSE	Holo	0	0	0	4	0	4
Bromeliaceae	*Guzmania lingulata* (L.) Mez	GUZMLI	Holo	0	0	0	0	1	1
	Tillandsia bulbosa Hook.	TILLBU	Holo	0	0	0	0	3	3
	Vriesea gladioliflora (H. Wendl.) Antoine	VRIEGL	Holo	0	0	0	0	1	1

				Approximate forest age (yr)					
Family	Epiphyte species	Species code[a]	Type	35	55	85	115	OG	Total
Cactaceae	*Epiphyllum phyllanthus* (L.) Haw.	EPIPPH	Holo	0	0	0	0	3	3
Gesneriaceae	*Codonanthe crassifolia* (Focke) Morton	CODOCR	Holo	0	0	3	0	0	3
Orchidaceae	*Aspasia principissa*Rchb. f.	ASPAPR	Holo	0	0	23	69	86	178
	Catasetum viridiflavum Hook.	CATAVI	Holo	0	2	0	1	0	3
	Oncidium ampliatum Lindl.	ONCIAM	Holo	0	0	0	6	0	6
	Oncidium stipitatum Lindl. ex Benth.	ONCIST	Holo	1	0	0	0	0	1
Polypodiaceae	*Campyloneurum angustifolium* (Sw.) Fée	CAMPAN	Holo	0	0	5	0	0	5
	Campyloneurum phyllitidis (L.) C. Presl	CAMPPH	Holo	0	1	5	19	8	33
	Lomariopsis vestita E. Fourn.	LOMAVE	Hemi	0	0	0	31	17	48
	Niphidium crassifolium (L.) Lellinger	NIPHCR	Holo	10	20	1	19	48	98
Number of Hemiepiphytes				0	58	114	161	414	747
Number of Holoepiphytes				11	23	37	122	160	353
Grand Total				11	81	151	282	574	1099

[a] The species codes correspond to those in Figure 2.6