Botanical Conservation in Coffee Farms:

An Ecological and Social Evaluation of Shade Trees as Vascular Epiphyte Habitat

By

Jeannine H. Richards

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The dissertation is approved by the following members of the Final Oral Committee:
Ellen I. Damschen, Professor, Integrative Biology
Thomas J. Givnish, Professor, Botany
Katherine A. McCulloh, Associate Professor, Botany
Paul Robbins, Dean, Nelson Institute for Environmental Studies
Alberto Vargas, Associate Director, Latin American, Iberian, and Caribbean Studies

For the plants and people who have shared their stories with me.

I hope I have done you justice in the retelling.

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Acknowledgements

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Abstract

As forests become increasingly fragmented and degraded, land-sharing practices that allow human uses and biodiversity to coexist become even more important. In this dissertation, I evaluate the potential for shade-grown coffee farms to offer habitat for epiphytes—plants that grow in trees without connection to the ground—while simultaneously benefitting farmers. My work combines methods from community and functional ecology with those from people-environment geography. I integrate these data to paint a comprehensive picture of the potential for shade coffee farms to fulfill the needs of both plants and people.

In the chapters that follow, I use data from 31 shade coffee farms and 2 protected forests to consider the ecology of epiphytes in shade coffee, including community assembly and environmental filtering, and the interests of farmers in managing trees within their farms. I first investigate how epiphytes initially colonize shade trees, looking at a chronosequence of tree age across 87 plots to follow epiphyte accumulation over time. Epiphytes take several years to initially colonize trees, but colonization accelerates over time. Key taxonomic groups accumulate in shade trees at different rates and environmental filtering and dispersal limitation appear to drive community assembly. Because epiphyte communities take considerable time to establish, newly planted trees in coffee farms require consistent land tenure and long-term management to become valuable habitat for diverse epiphyte communities.

Stand age and complexity interact with farm macroclimate to determine epiphyte species composition in shade coffee farms. I use structural equation modelling to assess the relative strength of these factors in structuring epiphyte communities. While stand structure and climate both have strong effects on epiphyte richness, the effect of climate is mostly mediated through bryophyte cover. Since bryophytes are highly susceptible to desiccation and vulnerable to climate change, vascular epiphyte species that strongly associate with them may also be at risk.

Abiotic conditions in shade coffee farms are warmer and drier than in forests, so differences in functional traits between epiphytes in the two habitat types may foreshadow functional shifts under climate change scenarios. Distributional data from two coffee farms and adjacent protected forest and functional trait data for 37 common species suggest that epiphytes in coffee farms may be responding to multiple layers of abiotic factors including microclimate within the tree, microclimate within the farm, and macroclimate across the landscape. Moreover, while some epiphyte groups seem to follow similar trait spectra as ground-rooted taxa, those rules may not hold true for all epiphytes.

To put these ecological findings into context, I conducted 33 semi-structured interviews with owners and managers of shade coffee farms. While coffee producers value trees for the many ecosystem services they provide, they know very little about epiphytes. Economic situation, access to technical knowledge, and producers’ personal values all influence tree management, and thus epiphyte habitat, on farms. Because farmers saw many benefits from trees and few detrimental effects of epiphytes, there is great potential for conservation interventions to add and maintain trees in coffee farms, providing suitable substitute habitat for many epiphyte species.

Introduction

We are in the midst of a biodiversity crisis. Species extinctions already far exceed background rates and new species become endangered every year (Ceballos et al. 2015; Brummitt et al. 2015). Land use change and deforestation reduce the available habitat, while human-induced climate change simultaneously alters the suitability of that habitat for many species (Laurance et al. 2014; Haddad et al. 2015; Peters et al. 2019). Faced with this reality, traditional conservation approaches, such as parks and protected areas, can only go so far in supporting wildlife (DeFries et al. 2005; Symes et al. 2016). Supplementing land preservation with strategies that integrate human needs and conservation goals will be critical to the future of biodiversity (Fischer et al. 2011; Tscharntke et al. 2012). One solution lies in embracing what has long been considered an enemy of conservation: agriculture. Agroforestry, agriculture that includes trees, holds particular promise because it can concurrently improve human lives and livelihoods, provide key ecosystem services, and offer substitute habitat for many native plants and animals (Bhagwat et al. 2008; Jose 2009; Tscharntke et al. 2011; De Beenhouwer et al. 2013). Particularly where much of the original vegetation cover has been altered or lost, agroecosystems can buffer protected areas, serve as corridors and stepping-stones that enhance landscape connectivity, and wholly support the food and habitat needs of some wild species (Perfecto et al. 2009).

In this dissertation, I investigate the potential for shade-grown coffee farms to provide substitute habitat for epiphytes—air plants, like orchids and bromeliads, that inhabit the trees of tropical forests. My work takes place in the social-ecological landscape of northern Nicaragua, a patchwork of many small farms, a few large plantations, and scattered remnants of forest, where the primary crop is coffee. Most people who live here are farmers, dependent on meeting their subsistence and livelihood needs from agriculture. The region is part of the Mesoamerica biodiversity hotspot (Myers et al. 2000) and represents the southernmost extent of the Central American Montane Forest ecoregion, island-like montane forests that house many endemic and endangered species (World Wildlife Fund 2019).

Coffee is one of the top globally traded commodities and coffee cultivation coincides spatially with some of the most biodiverse and threatened ecosystems on the planet (Myers et al. 2000; Donald 2004). However, coffee can be grown in a variety of ways from full sun monoculture to diversified shade cultivation that includes dozens of tree species (Moguel & Toledo 1999). Shade coffee has been widely recognized for its multifunctional benefits to farmers and wildlife (Bhagwat et al. 2008; Tscharntke et al. 2011; Jha et al. 2014; Perfecto & Vandermeer 2015). Trees within coffee farms provide farmers with subsistence provisioning (Beer 1987; Albertin & Nair 2004; Rice 2008) while also improving soil fertility, conserving water, and reducing erosion (Jose 2009; Tscharntke et al. 2011). Species that depend on trees for habitat, including epiphytes, benefit from the forest-like structure of shade coffee farms (Cruz-Angón & Greenberg 2005; Hietz 2005; Philpott et al. 2008).

Epiphytes are a highly diverse group of plants, especially in the montane tropics (Cardelús et al. 2006). The epiphytic habit was an important evolutionary development that sparked radiations in several key vascular plant groups, including the families Orchidaceae (Givnish et al. 2015) and Bromeliaceae (Givnish et al. 2015), the genus *Peperomia* (Frenzke et al. 2016)*,* and several lineages of ferns (Dubuisson et al. 2009; Watkins & Cardelús 2012). Epiphytes can represent up to half of the vascular plant diversity in some tropical forests (Nieder et al. 2001). They provide food and habitat for many animal species, including birds, insects, and amphibians, and can be considered ecological keystones of the forest (Nadkarni & Matelson 1989; Nadkarni 1994;

Yanoviak et al. 2004; McCracken & Forstner 2014). They also serve important roles in water and nutrient cycling (Stanton et al. 2014; Van Stan & Pypker 2015). Many epiphytes, however, are rare and have small geographic ranges, putting them at high risk of extinction. Moreover, because epiphytes depend on trees, they are vulnerable to habitat loss from deforestation and may be more sensitive to climate changes than ground-rooted plants (Zotz & Bader 2009).

Where forests are highly fragmented, many epiphytes inhabit open-grown trees in pastures, roadsides, and agroforestry systems (Hietz 2005; Köster et al. 2009; Einzmann & Zotz 2016, 2017). Bark characteristics, branching structure, leaf phenology, size, and age all influence the habitat suitability of a tree for epiphytes (Merwin et al. 2003; Zotz & Vollrath 2003; Einzmann et al. 2015; Woods et al. 2015; Chaves et al. 2016). Epiphyte species accumulate in trees over time (Taylor & Burns 2016; Einzmann & Zotz 2017; Spruch et al. 2019). Larger, older trees have more surface area on which propagules can land, more microhabitats that can accommodate the abiotic requirements of more species, and have had more opportunities over time for rare dispersal events to occur (Zotz & Vollrath 2003; Flores-Palacios & García-Franco 2006; Woods et al. 2015). Tree size and age in shade coffee farms varies greatly. In some farms, shade coffee was developed by clearing the understory of forest and planting coffee shrubs, resulting in many large, old shade trees with rich epiphyte floras. In other instances, farmers plant coffee and shade trees on land formerly in pasture or annual crops. Where stands were planted recently, the trees are quite small with few epiphytes, but how quickly newly planted trees accumulate epiphytes is not well understood.

Climate also affects epiphyte species composition and abundance. In general, wetter climates host more species (Gentry & Dodson 1987; Gotsch et al. 2017) and there is an altitudinal gradient of diversity that peaks at mid-elevations (Cardelús et al. 2006). Water is typically the most limiting factor for epiphytes (Zotz & Hietz 2001; Laube & Zotz 2003), and species' distributions both within trees and across the landscape may be delineated by their water stress tolerance (Zotz 2007; Poltz & Zotz 2011; Petter et al. 2016). Climate change alters both the means and extremes of temperature and moisture availability, so epiphytes that are particularly sensitive to abiotic conditions may be at risk of declines or extinction. Montane species may be more susceptible to climate change than their lowland counterparts (Zotz & Bader 2009). In coffee farms, conditions are already warmer, drier, sunnier, and windier than epiphytes would typically experience inside closed-canopy forests in the same locations, so the effects of climate changes may be exacerbated.

To withstand the extreme conditions of the aerial environment, many epiphytes have developed specialized physiological and morphological adaptations to tolerate water shortages and high light exposure. Traits such as succulent leaves, CAM photosynthesis, tank or basket morphology, absorptive and reflective trichomes, drought deciduousness, and poikilohydry, all relatively rare among ground-rooted taxa, are common among epiphytes and aid in water and nutrient capture, water storage, drought avoidance, and photoprotection (Zotz 2016). Epiphytes are typically slow-growing, and reflect a more conservative strategy of resource use, including low rates of photosynthesis, low leaf nutrient concentrations, and long-lived, well-defended leaves (Stuntz & Zotz 2001; Zotz & Hietz 2001; Zotz 2016). Since coffee farms have more stressful conditions as compared to forests, epiphytes found there should have a greater prevalence of traits that confer resilience to drought- and light-induced stress.

Trees on coffee farms provide myriad benefits to producers, including provisioning of firewood and timber for household use, soil and water conservation, and improvements in soil fertility without additions of chemical fertilizers (Beer 1987; Tscharntke et al. 2011). However, unlike in forests, epiphytes in coffee farms need to survive a suite of management practices imposed by farmers, including tree pruning and thinning, herbicide use, and sometimes even epiphyte removal (Toledo-Aceves et al. 2013). These practices vary from farm to farm, and may particularly differ with farm size, wealth, and education (Guadarrama-Zugasti 2008). Understanding the drivers of decision-making on farms and linking those decisions to habitat suitability for epiphytes is necessary to complete the picture for this social-ecological system (Robbins et al. 2015).

In the chapters that follow, I evaluate the suitability of shade coffee farms as substitute habitat for epiphytes from ecological and social perspectives (Fig. 1). In my first chapter, I use shade coffee established at different times as a chronosequence to trace how epiphyte species accumulate in shade trees over time. My second chapter explores the relative importance of climate, tree age, and tree diversity in structuring epiphyte communities in coffee farms. In my third chapter, I use functional traits to look at species adaptations that aid or inhibit epiphyte success in the higher stress environment of coffee farms. Finally, in my fourth chapter, I use interviews with producers to determine the opportunities and limitations for conservation of epiphytes within shade coffee farms.

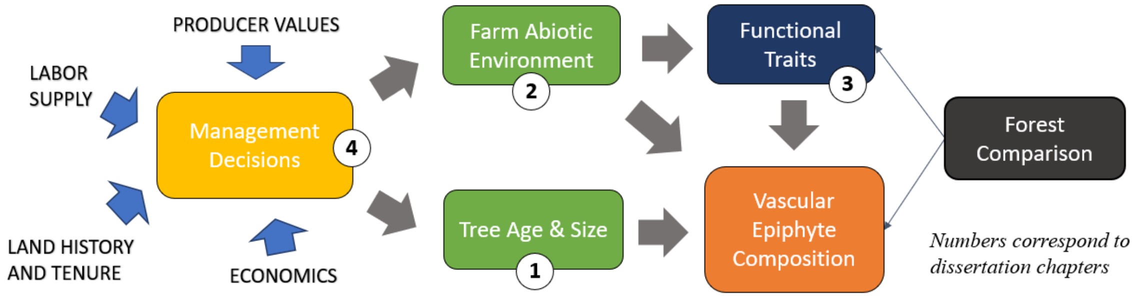

Fig. 1. Conceptual framework for my research on how tropical epiphytes in shade coffee farms are affected by ecological and social factors. Each of my dissertation chapters (circled numbers) addresses a different relationship among these factors.

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Chapter 1: Tree longevity drives conservation value of shade coffee farms for vascular epiphytes

Jeannine H. Richards[1*], Ingrid M. Torrez Luna[2], Donald M. Waller[3]

[1] Nelson Institute for Environmental Studies, University of Wisconsin-Madison

[2] Centro Agronómico Tropical de Investigación y Enseñanza (CATIE), Nicaragua

[3] Department of Botany, University of Wisconsin-Madison

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ABSTRACT

Forest loss and fragmentation threaten the high diversity of tropical forests. Tropical epiphytes are a key component of plant diversity and significant for ecosystem functioning, but they are vulnerable to these forces. We explored the potential of shade trees in agroforestry systems to sustain and restore epiphyte communities where forest cover has been lost. We investigated how quickly epiphytes colonize trees of increasing size and age within coffee agroecosystems using surveys of 748 trees occurring in 87 stands in northern Nicaragua. Species richness increased with stand age, reflecting effects of area, time, and niche differentiation within larger trees. Young trees near mature trees were almost five times more likely to support epiphytes as those surrounded by other young trees, suggesting that propagule sources may be severely limited in young, even-aged stands. We identified three stages of epiphyte colonization: an initial stage lacking epiphytes; a colonization stage where epiphyte abundance increases slowly, and a stage of accelerated accumulation once trees become large enough to contain distinct microhabitats. Atmospheric bromeliads and several fern species arrived first in young trees, suggesting their traits facilitate dispersal, colonization, and persistence under the often extreme environmental conditions present in young coffee farms. Both environmental filtering and dispersal limitation appear to drive community assembly in agroforests. Because epiphytes colonize gradually, consistent land tenure and long-term management are required for newly planted trees in shade coffee farms to develop to the size and structural complexity necessary to support diverse epiphyte communities.

Keywords: agroforestry, colonization dynamics, dispersal limitation, environmental filtering, niche partitioning, vertical stratification

INTRODUCTION

Epiphytes, air plants that are structurally dependent on trees, play a keystone role in tropical forests. They provide food and habitat for many birds, invertebrates, and amphibians (Cruz-Angón and Greenberg, 2005; Nadkarni et al., 2004) and intercept precipitation and fog, changing the quantity and biochemistry of water reaching the forest floor (Stanton et al., 2014; Van Stan and Pypker, 2015). Worldwide, a tenth of all vascular plant species are epiphytes and they may account for up to 50% of vascular plant diversity in some tropical forests (Gentry and Dodson, 1987). Yet, compared with terrestrial and temperate plants, they have not been well studied (Cornwell et al., 2019; Zotz and Bader, 2011).

Epiphytes are highly sensitive to abiotic conditions, making them powerful indicators of climate and land use changes (Köster et al., 2013; Larrea and Werner, 2010; Laube and Zotz, 2003). Agricultural expansion threatens tropical forests, and forest-dwelling species, including epiphytes, are rapidly being lost (Laurance et al., 2014). Despite widespread deforestation and habitat alteration, some epiphytes may be preadapted to survive in urban and agricultural systems that include trees because of their arboreal habit. They are ubiquitous in the humid tropics, even in lone trees and heavily modified landscapes (Einzmann and Zotz, 2017a; Larrea and Werner, 2010; Poltz and Zotz, 2011). Agroforestry—the practice of raising crops or livestock under the protection of shade trees—is already widespread in tropical countries and may hold promise for epiphyte conservation. Agroforests have received considerable attention for their conservation value as a land sharing strategy (Bhagwat et al., 2008; Tscharntke et al., 2011) and may be able to serve a restoration role, acting as substitute habitat in deforested areas.

Coffee grown underneath shade trees (shade coffee) has become a model system for exploring ecological relationships in agroforestry (De Beenhouwer et al., 2013; Jha et al., 2014; Perfecto et al., 1996; Philpott et al., 2008). In the humid tropics, vascular epiphyte diversity peaks in mid-elevation cloud forests (Cardelús et al., 2006; Hietz and Hietz-Seifert, 1995), overlapping with prime coffee-growing regions. Previous studies reveal similar epiphyte abundance and species richness per tree between shade coffee farms and nearby forests (Hietz, 2005; Moorhead et al., 2010). As the effects of climate change intensify, shade cultivation can help coffee farmers maintain productivity, and adding trees to the landscape may provide a win-win opportunity for conservation of epiphytes as well. Tree cover helps attenuate the effects of changing climate and may become increasingly attractive to farmers

(Lasco et al., 2014; Rahn et al., 2018; Vignola et al., 2015). Shade lowers leaf temperatures on coffee plants, reducing heat stress (Siles et al., 2010). Shade trees also intercept heavy rains, reducing harm to coffee shrubs and soil erosion (Tscharntke et al., 2011). Shade cultivation of coffee is a valuable land restoration technique that benefits birds and other taxa (Cruz-Angón and Greenberg, 2005; De Beenhouwer et al., 2013; Philpott et al., 2008). We predict that adding shade trees to coffee and other tropical crops should also benefit epiphytes.

Epiphytes can disperse long distances and successfully establish in trees in open landscapes (Einzmann and Zotz, 2017a, 2017b). Following island biogeography theory (MacArthur and Wilson, 1963), we expect epiphyte colonization to increase with tree size and decrease with distance from propagule source populations. Increases in epiphyte abundance and richness with tree diameter have been well documented (Flores-Palacios and García-Franco, 2006; Hietz and Hietz-Seifert, 1995; Zotz and Vollrath, 2002). Two recent conceptual models use island biogeography as a basis for predicting patterns of epiphyte community assembly. Spruch et al. (2019) proposed that initially rapid epiphyte colonization lasts for approximately the first 30 years of a host tree's life, during which time species richness accumulates quickly and total abundance increases slowly. A second phase of community development then occurs, characterized by slow increases in richness and a linear increase in abundance that never levels off. Taylor and Burns (2015) similarly suggested that epiphyte colonization in new trees follows a model of island ontogeny with an initial period of no epiphytes followed by colonization and linear accrual over the life of the tree.

We test how well these conceptual models predict epiphyte colonization in shade coffee farms to understand how farms at various stages of development support epiphytes. Although the ability of agroecosystems to support biodiversity is well-documented for many taxa (Bhagwat et al. 2008; Perfecto and Vandermeer 2008; DeBeenhouwer et al. 2013), few studies have explored epiphyte ecology in shade coffee (but see Heitz 2005; Moorhead et al. 2010; Toledo Aceves et al. 2012, 2013; DeBeenhouwer et al. 2015). To date, no research exists examining how epiphytes colonize newly planted shade trees or how colonization dynamics change as trees age. This knowledge is critical for evaluating whether shade trees in coffee plantations can effectively serve to conserve epiphyte communities.

We studied 31 shade coffee farms across a range of stand ages to assess how epiphytes colonize shade trees over time. We ask:

(1) How long does initial epiphyte colonization take on newly planted coffee shade trees and how quickly do epiphyte communities diversify?

(2) Do species and epiphyte groups differ in their colonization dynamics?

(3) Does vertical partitioning of epiphyte groups within shade trees change as trees grow?

We used tree size and stand age to simulate a chronosequence across the farms we studied. We predicted that colonization would follow patterns from island biogeography according to the models proposed by Spruch et al. (2019) and Taylor and Burns (2016) and expected that colonization would begin slowly and then accelerate, with a few common, drought-tolerant species colonizing first, followed by less common and more diverse later-successional species. We also predicted that different tree zones would follow different successional trajectories, and particularly that the inner crown would show the greatest change in epiphyte communities over time as microhabitats diversify with tree size.

METHODS

Study Sites

In April and May of 2018, we visited 31 farms growing shade coffee in the north-central highlands of Nicaragua (Fig. 1). These ranged in size from a few to several hundred hectares at 1000 to 1300m elevation. Twenty-nine farms were part of a previous bird conservation project conducted by the American Bird Conservancy (ABC) and had many received trees and technical assistance from ABC between 2015-2017. Two additional farms were included because of prior connections with the researchers.

Survey Methods

On each farm we established two to five 20x20m plots (total N = 87) in areas that represented the range of production management practices on the farm. The number of plots was determined by farm size and the variety of management practices and stand ages present. On most farms, land use history and current management varied among fields. We sought to capture this variation by locating at least one plot per stand type within each farm. Thus, plots are not statistically representative of the epiphyte habitat on the farm, nor do they represent the proportional distribution of habitat quality in the region, but instead characterize the range of variation in epiphyte habitat quality within shade coffee farms, from newly-established, low-diversity shade trees only a few years old to remnant forest trees 50+ years old. Frequently, we found conditions at both ends of the spectrum within a single farm. Because most farms in the region are dominated by relatively young shade trees, we preferentially selected plots with older planted or ancestral shade trees when available to achieve similar coverage across age classes.

We surveyed plots at a nested series of scales. Within each plot, we recorded all vascular epiphytes present on trees by morphospecies. We assigned species identifications later where possible following the *Flora de Nicaragua* (Stevens et al., 2001). For each tree, we recorded diameter at breast height (dbh) and measured tree height using a laser range finder. Following Johansson's (1974) tree zonation (see Fig. 7), we counted the numbers of orchids, bromeliads, ferns, and other epiphytes in each zone from the ground using binoculars. For species with clonal growth, we defined an "individual" as the amount of vegetative growth equivalent to the average size of known genetically unique individuals elsewhere. Since many of the trees sampled were small, we adjusted the zone framework as follows: if the trunk below the first branch was less than 2m tall, zone 2 was excluded; if the branches were less than 2m long, zone 4 was excluded; and on trees whose branch tips had been recently pruned, zone 5 (and occasionally zone 4) were excluded. The truncated sampling had little effect on our data analysis because it was only applied to small trees that had few, if any, epiphytes present.

Analysis

All analyses were conducted in R version 3.6.0. We averaged variables measured at each lower level within our nested data structure to include in the next higher level (e.g., dbh of individual trees became mean tree diameter at the plot level). We divided plots into four age categories based on information from the farmer (Table 1). Where the farmer did not indicate stand provenance, a category was assigned based on size of largest trees, tree species richness, and presence of forest species. We omitted two plots classified as "young plantings" from plot-level analyses because they contained a single remnant tree that drove epiphyte response variables for the plot.

Epiphyte colonization and community assembly

With plot-level data, we examined compositional dissimilarity among age categories, using nonmetric multidimensional scaling (NMDS) and tested for differences in centroids on a Bray-Curtis distance matrix using PERMANOVA, also checking differences in dispersion. We compared ecological distance to geographic distance between the sites using a Pearson correlation test. We used species accumulation curves and rank abundance curves to compare patterns of species accumulation, evenness, and turnover by age category. These analyses all used the 'vegan' package in R (Oksanen et al., 2019).

We applied a generalized linear mixed model (GLMM) to compare the sizes of trees (diameter and height) with and without epiphytes, assuming a binomial distribution for residuals. Tree size variables were log transformed to meet assumptions of homogenous variances. We included farm and plot as nested random effects plot to account for spatial non-independence.

To explore how tree diameter affected epiphyte abundance, we fit linear, quadratic, and piecewise regression models to log-transformed total abundance per tree. Piecewise regression detects thresholds where the slope of a relationship changes, fitting separate linear regressions on either side of the breakpoint. We used the R package 'segmented' (Muggeo, 2019) to construct piecewise models with one and two breakpoints and compared these to linear and quadratic models using likelihood ratio tests. We duplicated this process for each epiphyte group (bromeliads, ferns, orchids, and other epiphytes) to check whether groups differed in their relationships with tree diameter.

To test for dispersal limitation, we examined young trees (dbh <15cm) divided into two groups: those located in young and mid-aged plantings (surrounded by other young trees) and those in mature and remnant stands (co-occurring with large, established trees). We tested for differences in presence and abundance of epiphytes between the two groups. To test for differences in epiphyte presence, we used a GLMM with binomial distribution. To test how epiphyte abundance differs in each group, we used a GLMM with a negative binomial distribution using the 'glmmTMB' package (Magnusson et al., 2019) including a zero inflation parameter to account for large numbers of zeros in the data (Zuur et al. 2009). We included tree diameter as a covariate. Both models included farm as a random effect.

Colonization differences among species

To test whether individual epiphyte species showed habitat associations with plot age categories, we applied a randomization test to the plot-level data following the methods of DeWalt et al. (2006). We included only common species (occurring in 12+ plots) and omitted morphospecies that could not be identified to species. We ran 1000 randomizations of the species-site matrix using the independent swap algorithm within the *randomizeMatrix* function of the 'picante' package in R (Kembel et al., 2019). Independent swap maintains species occurrence frequency and plot species richness while shuffling individual occurrences (Gotelli, 2000). We derived upper and lower limits of a 95% confidence interval from the permutation runs for each species. Observed occurrences falling above the interval are positively associated those falling below the interval are negatively associated.

Vertical partitioning

Using MANOVA, we tested for differences in epiphyte abundance within taxonomic groups and tree zone to assess vertical partitioning. We used ANOVA with Tukey post-hoc tests to test for differences among zones within each taxonomic group. To examine how vertical partitioning changed within groups over time, we constructed GLMMs for each group with negative binomial distribution and a zero inflation parameter using the ‘glmmTMB’ package (Magnusson et al., 2019). Two trees above 120cm diameter were omitted to preserve the continuity of the data. We included an interaction term between zone and tree diameter to investigate how vertical stratification changed with tree size. All models included nested random effects of farm, plot, and tree. We compared the model for each group with and without the interaction term using likelihood ratio tests to quantify the significance of the interaction.

RESULTS

Across 87 plots on 31 farms, we measured a total of 748 trees and counted 10,358 individual vascular epiphytes, including 2,426 bromeliads, 3,837 ferns, 2,569 orchids, and 1,526 other epiphytes. We recorded 131 distinct epiphyte morphospecies and 81 tree taxa. Epiphyte abundance ranged from zero to 478 individuals per tree.

Epiphyte colonization and community assembly

Plots of increasing age steadily accumulate more epiphyte species (Table 1). We also observed differences in composition among age categories (PERMANOVA, p=0.001; Fig. 2). Dispersion within these groups did not differ (p=0.73). The ecological (Bray-Curtis) distance between stands increased with geographic distance but the correlation was low (Pearson r = 0.11, p<0.001), indicating most of the compositional differences among plots reflect factors beyond geographical turnover.

In young plantings, epiphyte species accumulation rapidly plateaus (Fig. 3A). In contrast, forest remnant plots support many more species with high turnover among plots, suggesting that each contains only a small component of the regional species pool and community assembly is actively occurring. Rank abundance curves reveal that a few common species dominate younger sites, while more uncommon and rare species occupy remnant and mature sites, resulting in greater evenness across species (Fig. 3B). Species in young and mid-age stands were ubiquitous in older stands whereas mature and remnant stands hosted many unique species (Fig. 4).

Trees supporting epiphytes were larger in diameter (GLMM, $z=10.24$, $p<0.001$) and taller (GLMM, $z=6.51$, $p<0.001$) than trees lacking epiphytes. Increases in epiphyte abundance with tree size was best described by a piecewise model with two breakpoints, indicating distinct thresholds as trees transition to higher rates of epiphyte accumulation ($R^2=0.39$; Fig. 5). Similar transitions occurred in all epiphyte groups. The first breakpoint may be interpreted as the average minimum tree size for successful colonization (~12 cm), while the second reflects the size above which trees are no longer found lacking epiphytes (~40 cm). These breakpoints occurred at similar tree sizes across epiphyte groups, but bromeliads tended to colonize smaller trees whereas “other” epiphytes tended to arrive last (Fig. 5).

Trees below 15cm in diameter found in mature plantings or remnant stands usually supported epiphytes (probability = 0.72), but those of the same size found in young or mid-age plantings only rarely did (probability = 0.15; GLMM, $z = 2.83$, $p = 0.005$). Moreover, trees in older stands support 3.7 times as many epiphytes per tree as those in younger stands (controlling for differences in diameter, GLMM $z = 4.15$, $p < 0.001$; Fig. 6A) and accumulated epiphytes beginning at smaller diameters (Fig. 6B). These results strongly suggest that dispersal limits epiphyte community assembly within newly planted shade trees.

Colonization differences among species

A few species showed significant positive or negative habitat associations with a particular age category (Table 2). Several atmospheric bromeliad species preferentially inhabited mid-age stands and showed repulsion toward remnant stands. However, *Tillandsia* spp. are difficult to distinguish as juveniles, meaning that additional positive associations may have been obscured by taxonomic uncertainty. One aroid and one tank bromeliad occurred preferentially in mature plantings.

Vertical partitioning

Epiphyte groups displayed considerable vertical partitioning within trees (Fig. 7; MANOVA approx. $F=22.06$, $p<0.001$; taxonomic group $F=14.93$, $p<0.001$; zone $F=28.97$; $p<0.001$). Bromeliad abundance increased by zone going up the tree, with almost four times as many individuals in the outer crown as in trunk zones (ANOVA $F=10.31$, $p<0.001$). Orchids showed a similar pattern, with zone 4 having five times the abundance of zone 1 (ANOVA $F=9.94$, $p<0.001$). Ferns did not vary in abundance across zones, while “other” epiphytes (mainly *Peperomia* and several species of Araceae, Ericaceae, and Gesneriaceae) were more commonly located on the trunk, but only showed weak statistical difference among zones (ANOVA $F=3.29$, $p=0.01$).

The rates at which epiphyte groups accumulated differed across tree zones as tree size increased (Fig. 8). There was a significant interaction between diameter and zone for all groups (LR tests; bromeliads: $\chi^2=64.75$, $p<0.001$; ferns: $\chi^2=52.29$, $p<0.001$; orchids:

χ^2=52.63, p<0.001; other: χ^2=24.94, p<0.001), indicating that epiphyte groups accumulated at different rates in the different tree zone. In general, epiphytes accumulated most rapidly in the inner crown, particularly orchids. Epiphytes colonized trunk zones early in tree ontogeny but over time individuals accumulated more slowly there.

DISCUSSION

Epiphyte colonization and community assembly

Models of epiphyte colonization based on island biogeography appear to apply to shade trees within the coffee farms we studied. Epiphytes accumulate nonlinearly as shade trees grow. After an initial period devoid of epiphytes, small trees become large enough to support epiphyte colonization. Epiphytes then accumulate slowly with tree size, colonizing mainly on trunks early in ontogeny. Accumulation accelerates when trees become large enough to always support epiphytes. Trees needed to grow for 5+ years before epiphytes colonize, corresponding to Taylor and Burns' (2015) initial phase of tree ontogeny. The accelerating increase in accumulation later in tree development we observed follows Spruch et al.'s (2019) model. Richness increased steadily across our age categories, as documented previously (Hietz, 2005). We further observed evidence of strong dispersal limitation for epiphytes colonizing small trees. Having nearby propagule sources appears to be a critical factor in facilitating epiphyte colonization.

Epiphytes grow slowly, and epiphyte communities assembled slowly on shade trees in our study. We found that vascular epiphytes require a decade or more for multi-species assemblages to develop and only a few early colonizing species, mainly atmospheric bromeliads and ferns, arrived in five-year-old trees. Previous studies found similar patterns. Nadkarni (2000) saw no vascular epiphytes on branches stripped of plant cover until 10 years later. Epiphyte communities on coffee shade trees 8-9 years after complete removal contained just 35% of the epiphyte biomass found on control trees, with bromeliads and ferns also being the earliest colonizers (Toledo-Aceves et al., 2012, 2015).

Colonization differences among species

Young trees in coffee farms are subject to high insolation and wind exposure across all parts of the tree. These extreme conditions present challenges for colonizing epiphyte propagules and likely limit success. Species that tolerate drought and sun exposure, particularly at early life stages, should be most successful. The epiphytes we found on the youngest trees included juvenile atmospheric bromeliads (mostly unidentifiable to species), juveniles of several ferns in Polypodiaceae (*Polypodium lindenianum*, *Niphidium crassifolium*, and *Phlebodium pseudoaureum*), and one orchid (*Prosthechea ochracea*). All are adapted to survive in extreme environments, with trichomes that increase reflectance and trap atmospheric water (Watkins et al., 2006), CAM photosynthesis (Crayn et al., 2015), or water storage strategies (Reyes-García et al., 2012). Most early successional species did not disappear as trees aged, probably because larger, older trees support a variety of microhabitats. For example, the fern *Polypodium lindenianum* was the most commonly encountered species in young plantings but continued to be present in larger trees, as did most common species. These species likely shift to zones of greater exposure in older trees as they are outcompeted by later colonizing species in the more humid, shaded microhabitats developing in the inner canopy.

Extreme conditions attenuate as trees grow, allow more species to colonize successfully. We identified species and characteristics typical of succeeding stages as trees age. Although no species showed positive associations with young plantings, the atmospheric bromeliad *Catopsis nutans* and the highly lepidote fern *Pleopeltis furfuracea* were associated with mid-age plantings. These species are covered in trichomes, adapting them to high light intensities and desiccation pressure. Habitat associations that epiphytes show to particular zones of a tree (Woods et al., 2015) may obscure relationships to the tree age classes that we used. Because many of the species restricted to older stands were rare, we lacked power to test their associations. We suspect that these may be later successional species that colonize only after suitable microhabitats have developed.

Vertical partitioning

As shade trees mature, epiphytes become more abundant in the branches as the crown develops. Although some upper limit on epiphyte accumulation within trees is expected (Flores-Palacios and García-Franco, 2006), neither theoretical (Spruch et al., 2019) nor empirical (Einzmann and Zotz, 2017a) studies have substantiated this prediction. Instead, epiphyte communities appear never to saturate. The mechanisms that might account for increases in epiphyte abundance and diversity with tree size are difficult to disentangle from observational studies. These mechanisms include: a) increasing surface area on larger trees; b) higher probabilities that propagules arrive over longer time spans; and c) greater differentiation of microhabitats within larger older trees. We cannot separate the effects of size and time in our data but Zotz and Vollrath (2003) sampled equal-sized sections of bark on small and large trees and found that epiphyte density and size increased with tree age but richness did not, suggesting that abundance is related to age while richness is related to area. Our results also support the idea that microhabitat diversification plays a role in the accumulation of species and individuals as trees grow. Although epiphyte accumulation slowed on tree trunks as trees got larger, it accelerated in the inner crown as the microclimate became shadier and more humid. Many rare species occurred only on larger trees. A positive feedback wherein a larger population of epiphytes produces more propagules may additionally accelerate increases in abundance. Because the area of the substrate increases as a power of tree diameter, large trees can accommodate quadratic increases in epiphyte community size (Flores-Palacios and García-Franco, 2006).

CONCLUSIONS

To enhance conservation of epiphytes and the species dependent on them within shade coffee farms, we make several suggestions. First and foremost, shade trees should be managed to reach the larger sizes necessary to support the densest and most diverse epiphyte communities. This requires stable and sustained farm management and farm longevity. Because epiphyte communities establish slowly, policies and economic incentives that support stable land tenure and reduce the turnover of coffee to other cropping systems favor establishment of more complex and diverse epiphyte communities. Second, encouraging farmers to protect large, established trees or patches of forest whenever possible would ensure epiphyte propagule sources close to newly planted trees, speeding community assembly. The fact that a few large trees support more epiphytes than hundreds of young trees means that they have disproportionately high ecological value for epiphytes and wildlife alike and may serve as “stepping stones” across the landscape. Finally, although forest remnant trees held the highest diversity of epiphytes, clearing primary forests understories to plant coffee degrades forest habitat. When new shade coffee farms are established, they should utilize already cleared land whenever possible and retain any existing large trees. Planting complex agroforestry systems in areas previously used for pasture or annual crops constitutes an improved land use and should be encouraged as ecological restoration whose value will only increase with time.

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TABLES AND FIGURES

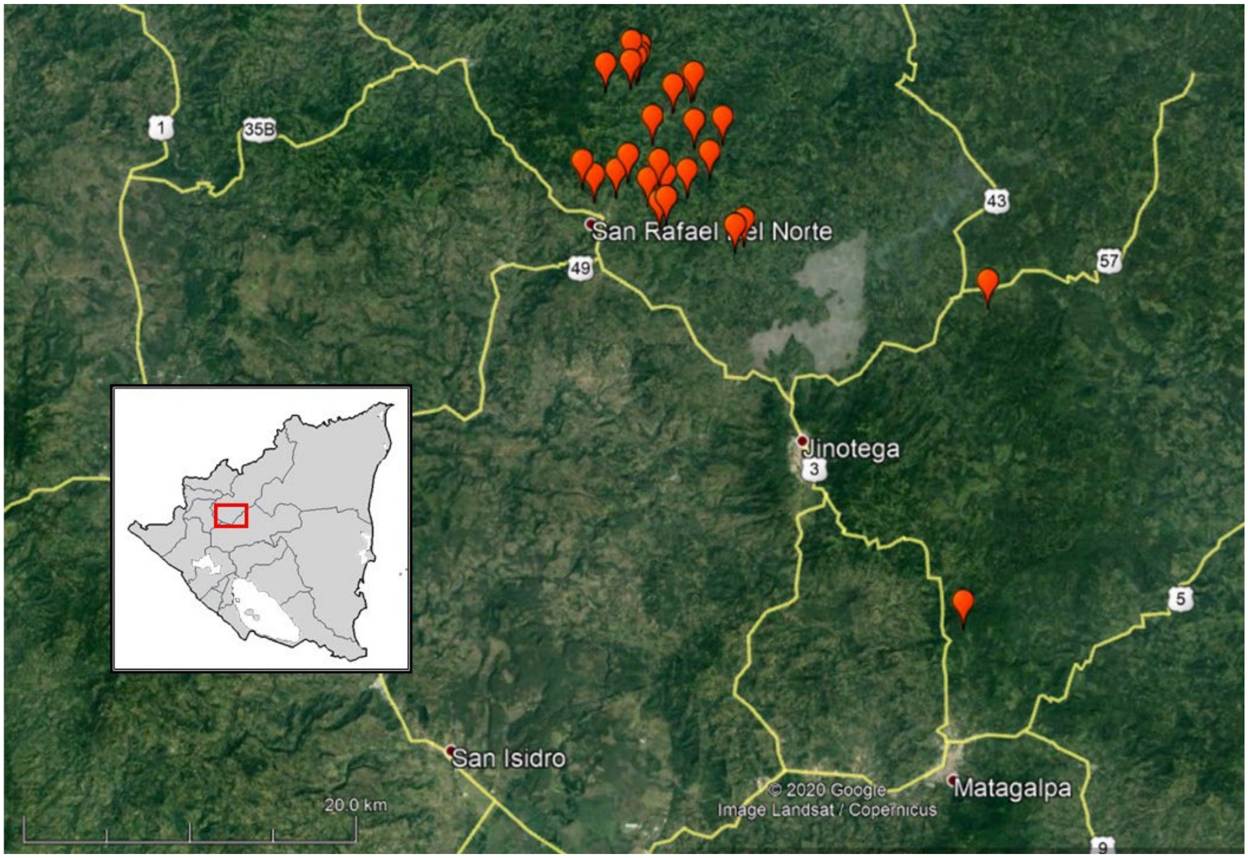

Fig. 1. Research took place at 31 farms in northcentral Nicaragua within the province of Jinotega.

Table 1. Mean stand characteristics by age category ± standard error. Letter superscripts indicate significant difference based on ANOVA with Tukey post-hoc tests. Tree relative richness is calculated as the number of trees per plot divided by the tree species richness of the plot.

	Young planting	**Mid-age planting**	**Mature planting**	**Forest remnant**
# Plots	12	20	36	17
Tree age	<5 years	5-10 years	>10 years	>10 years
Tree age evenness	Even-age	Even-age	Uneven age	Uneven age
Tree origin	Planted	Planted	Planted, self-seeded	Forest remnant, self-seeded, planted
Tree species	Common shade species, mostly leguminous	Common shade species, sometimes with fruit and timber trees	Common shade species plus fruit trees and timber trees	Forest tree species, common shade species and fruit trees added
Mean trees per plot	9.5 ± 3.5^{ab}	10.6 ± 5.2^{a}	6.9 ± 3.8^{b}	9.3 ± 4.9^{ab}
Mean tree relative richness	0.27 ± 0.11^{a}	0.42 ± 0.21^{a}	0.59 ± 0.24^{b}	0.65 ± 0.25^{b}
Total tree basal area (m^2)	1.36 ± 0.82^{a}	6.40 ± 3.46^{b}	7.81 ± 4.94^{b}	13.0 ± 8.46^{c}
Mean tree diameter (cm)	9.8 ± 2.6^{a}	19.4 ± 4.8^{b}	26.1 ± 8.1^{c}	29.0 ± 14.3^{c}
Mean tree height (m)	4.6 ± 1.1^{a}	8.3 ± 3.0^{b}	9.3 ± 3.4^{bc}	10.6 ± 2.7^{c}
Mean epiphyte species richness	0.6 ± 1.4^{a}	5.5 ± 5.2^{a}	12.3 ± 8.7^{b}	20.2 ± 9.5^{c}

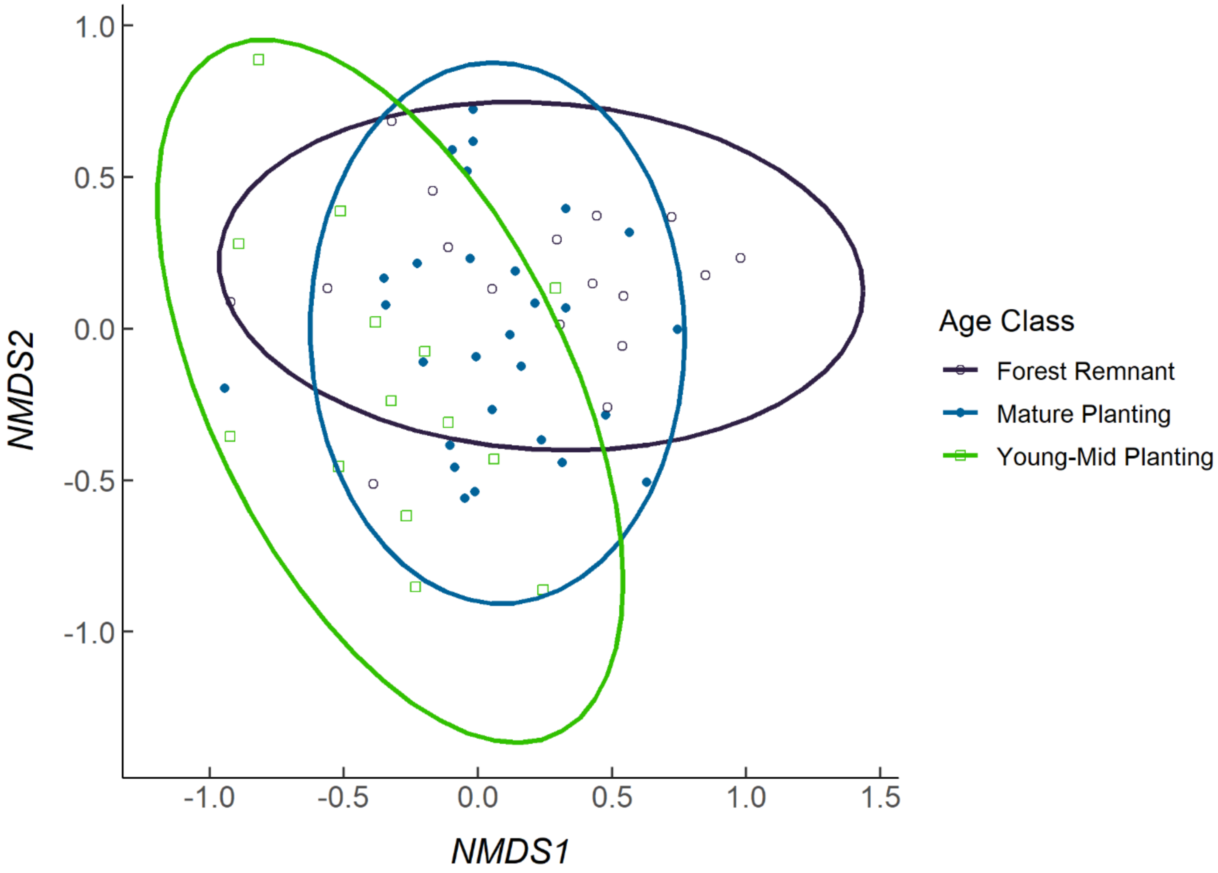

Fig. 2. NMDS with ellipses showing 95% confidence intervals shows compositional separation, although no differences in dispersion, between plot age classes. Increasing values along both axes align with increases in average tree size, moss cover, and species richness.

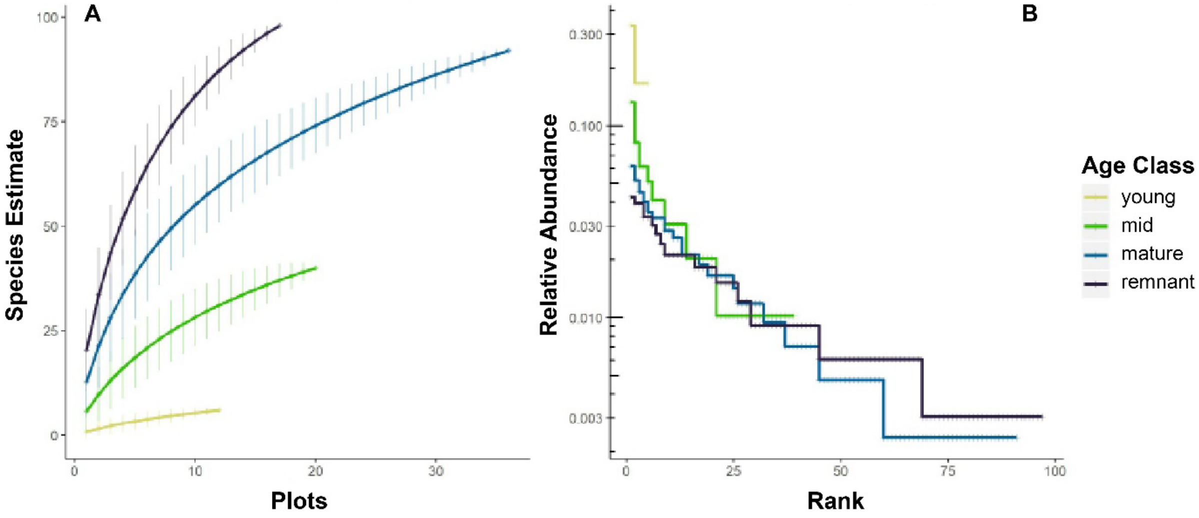

Fig. 3. A) Species accumulation curves for epiphytes growing on shade trees in four age classes. Young plantings saturate quickly, whereas forest remnant stands did not reach saturation after 17 plots. B) Rank abundance curves for epiphytes show more rare species and lower relative abundances in common species in mature and forest remnant plots. In contrast, young shade trees support mostly a few common species.

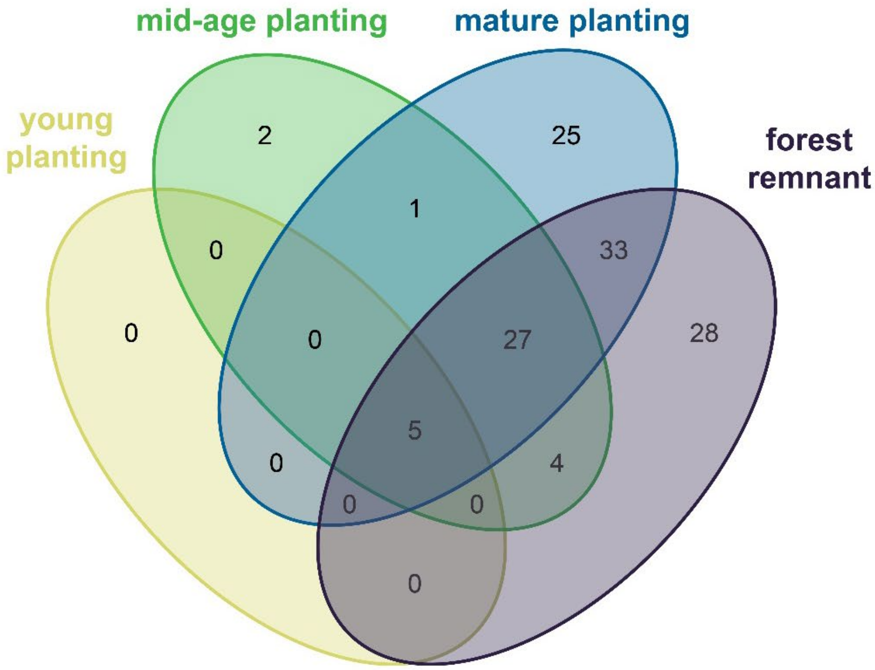

Fig. 4. Venn diagram showing the number of species that overlap among plot age categories. Only five species were found in young plantings and these also occurred in all other habitat types. Mid-age plantings overlapped considerably with mature and remnant stands, but older, larger trees supported many distinctive species, including many rare species.

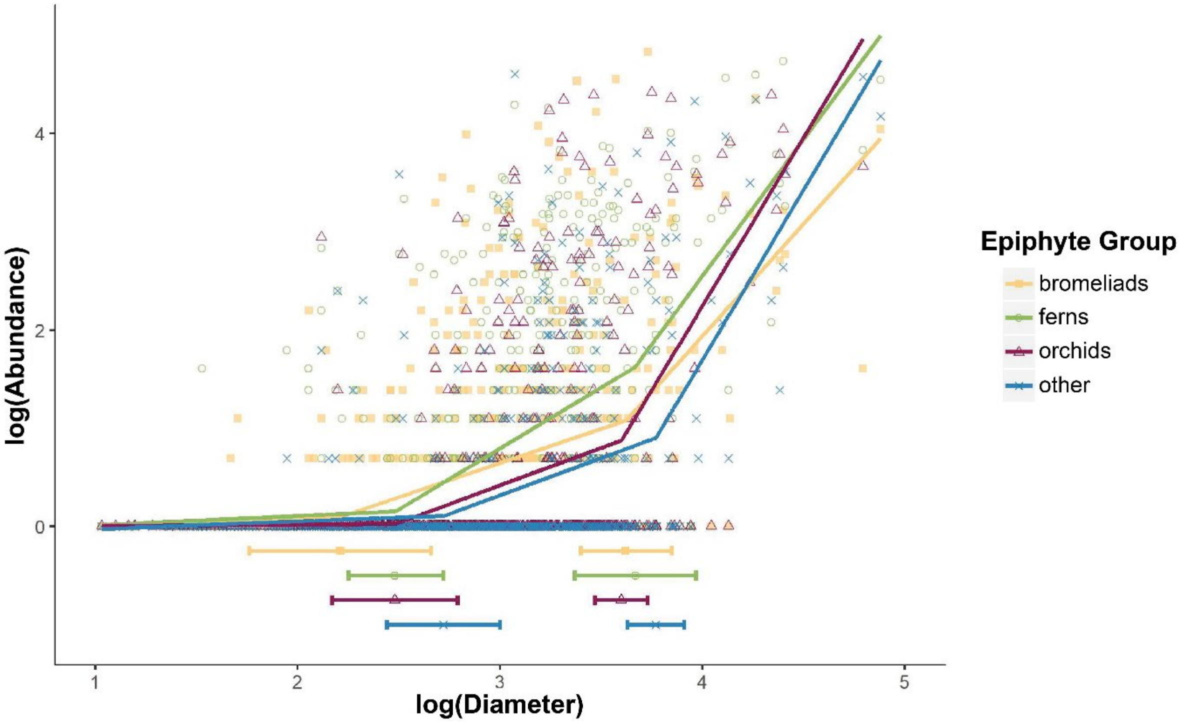

Fig. 5. Abundance of the four epiphyte groups as a function of shade tree size (log diameter). Piecewise models with two breakpoints best represent the data in all epiphyte groups. Bromeliads appear first in small trees (at ~9cm dbh or log diameter of 2.21±0.45). Ferns and orchids colonize trees above 12cm dbh (ferns: log diameter = 2.48±0.24; orchids: 2.48±0.31). Other epiphytes colonize trees above 15cm dbh (log diameter = 2.72±0.28). The second breakpoint fell at similar tree sizes for all groups (bromeliads: log diameter 3.62±0.23; ferns: 3.67±0.3; orchids: 3.60±0.13; other: 3.77±0.14).

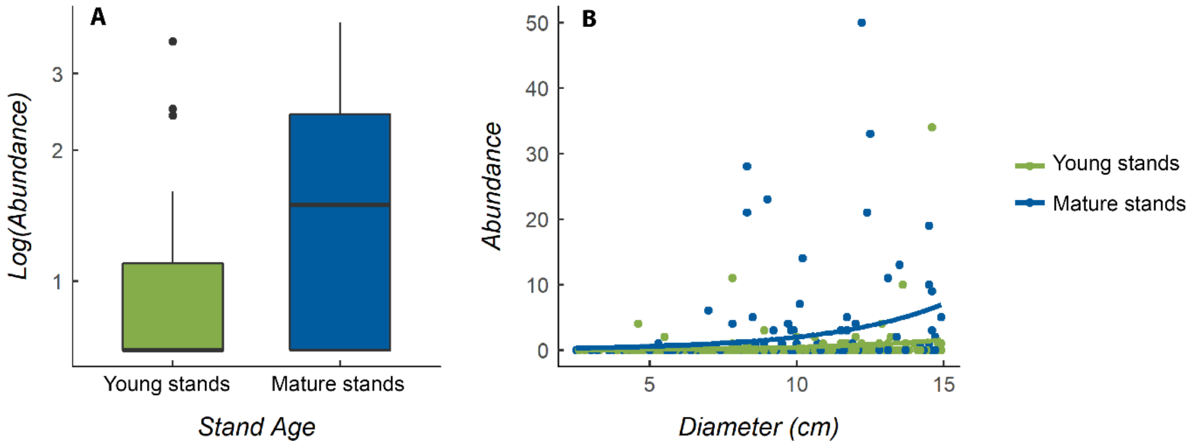

Fig. 6. A) Small trees (<15cm dbh) in stands with older trees (mature planting or forest remnant) had on average 3.7 times more epiphytes than small trees in young or mid-age plantings. B) Small trees with larger trees nearby also began accumulating epiphytes at smaller diameters and accumulated faster than trees of the same size in young, even-age plots.

Table 2. Habitat associations of common epiphyte species with stand age categories.

Species	**Remnant**	**Mature**	**Mid**	**Young**
Anthurium scandens		+		
Guzmania monostachia		+		
Tillandsia butzii				
Tillandsia fasciculata				
Tillandsia tricolor				
Catopsis nutans	-		+	
Tillandsia schiedeana				
Polypodium plebium				
Phlebodium pseudoaureum				
Campyloneurum angustifolium				
Polypodium lindenianum				
Polypodium furfuraceum			+	
Niphidium crassifolium				
Pleopeltis macrocarpa				
Prosthechea ochracea				
Prosthechea fragrans				
Epidendrum ramosum				
Isochilus linearis				
Jacquiniella teretifolia				
Epidendrum chlorocorymbos				
Peperomia quadrifolia				
Peperomia deppeana				

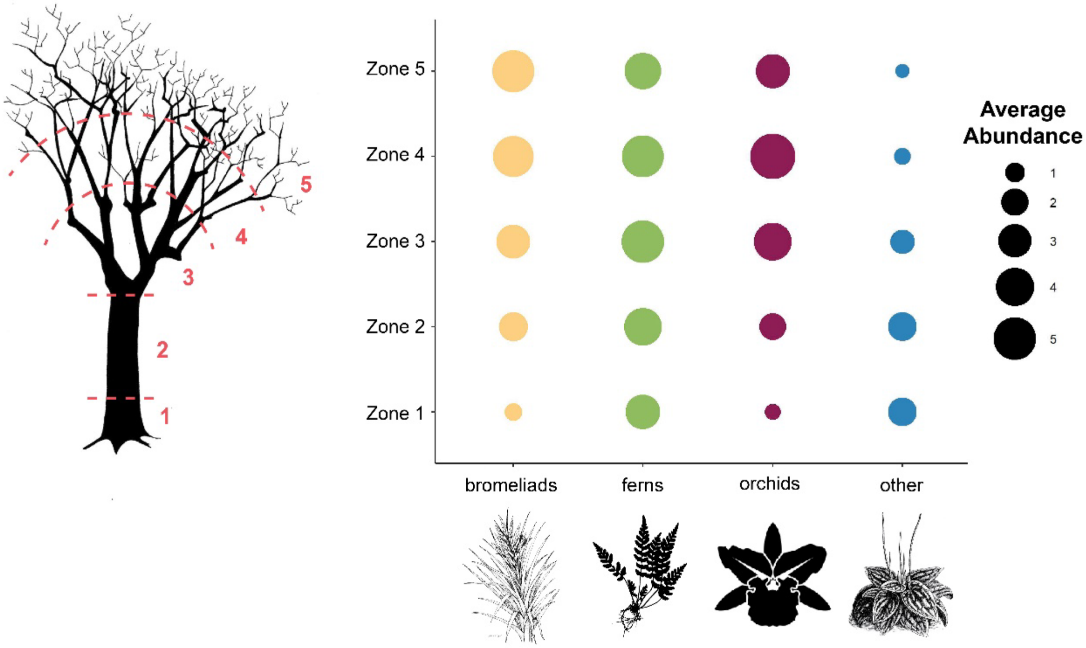

Fig. 7. Heat plot showing vertical distributions by epiphyte group by average abundance per zone. Bromeliad abundance increases continually up the tree. Ferns show no change in abundance by zone. Other epiphytes decline in abundance in higher zones. Orchids are most abundant in the inner canopy.

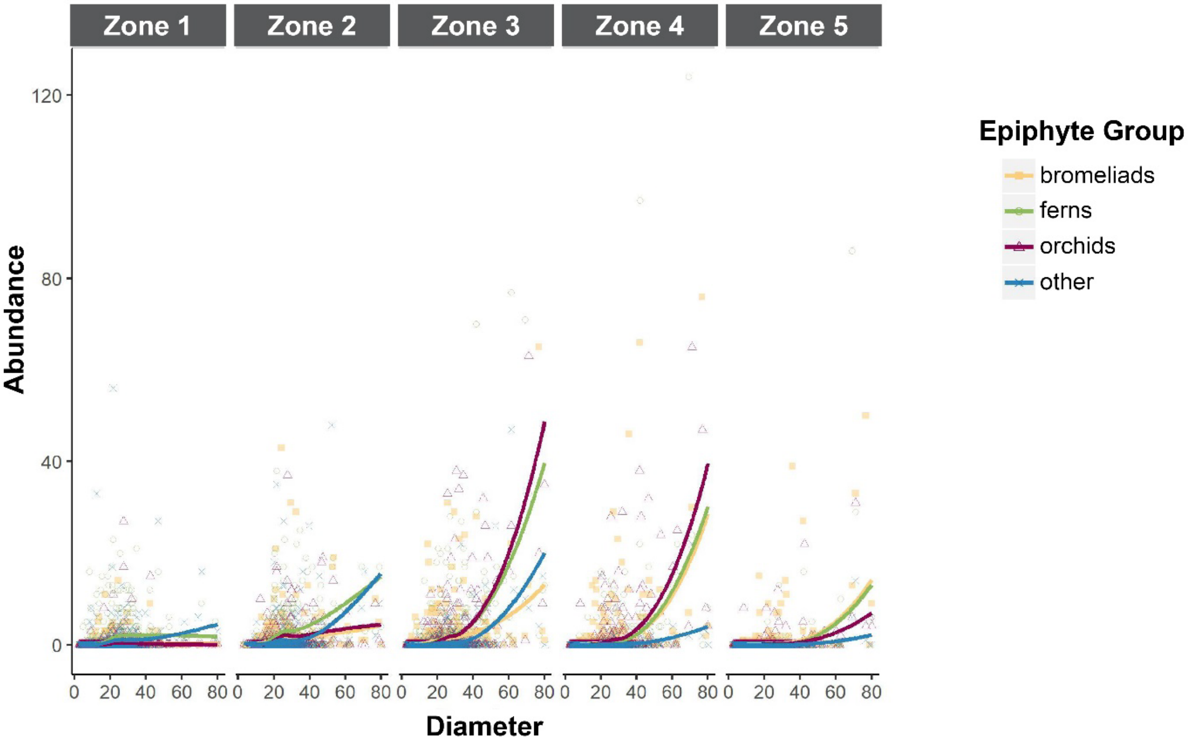

Fig. 8. Groups vary in their response to diameter across zones. In the inner crown (zones 3 and 4) epiphytes (especially orchids and ferns) accumulate most rapidly as trees grow larger. The trunk (zones 1 and 2) accumulates epiphytes earlier in tree ontogeny, but accumulation then slows or even declines as trees age, particularly for orchids and bromeliads.

Chapter 2: Climate impacts on bryophytes threaten cascading losses in tropical montane epiphyte communities

Jeannine H. Richards[1]

[1] Nelson Institute for Environmental Studies, University of Wisconsin-Madison

Richards, JH. Assessing the strength of climate and land use influences on montane epiphyte communities. *In revision.*

ABSTRACT

Epiphytes, air plants that are structurally dependent on trees, are a keystone group in tropical forests, supporting the food and habitat needs of animals and influencing water and nutrient cycles. They reach peak diversity in humid montane forests. Climate predictions for Central American mountains include increased temperatures, altered precipitation seasonality, and increased cloud base heights, all of which may challenge epiphytes. While remaining montane forests are highly fragmented, many tropical agricultural systems include trees that host epiphytes, allowing epiphyte communities to persist even in landscapes with lower forest connectivity. I tested the relative effects of climate, land use, tree characteristics, and biotic interactions on vascular epiphyte diversity using data from 31 shade coffee farms and two protected forests in northern Nicaragua. Structural equations models revealed that tree size, tree diversity, and climate all affect epiphyte richness, but climate is almost entirely mediated by bryophyte cover. Bryophytes showed strong sensitivity to multiple climate variables, especially vapor pressure deficit and insolation. A randomization test for vascular epiphyte substrate preferences showed positive associations with bryophyte mats for many ferns and orchids. The tight relationships between bryophytes and climate and between bryophytes and vascular epiphytes indicate that relatively small climate changes could result in rapid, cascading losses of montane epiphyte communities. Currently, shade coffee farms can support high bryophyte cover and diverse vascular epiphyte assemblages when larger, older trees are present. As the climate changes, impacts will likely occur first in agroforestry systems and later in closed-canopy forest. Agroforests currently serve as valuable reservoirs for epiphyte biodiversity and may be important as indicators into the future.

Keywords: agroforestry, climate change, cloud immersion, solar radiation, structural equation models, tropical montane forest, vapor pressure deficit

INTRODUCTION

Global biodiversity loss is one of the greatest crises of our time. Worldwide, an estimated 20% of plants face extinction (Brummitt et al. 2015). Pressures from landscape alteration and global climate change reduce available habitat while simultaneously changing its suitability for species (Lawton et al. 2001; Thomas et al. 2004). The global climate is warming rapidly, with up to 1.5°C increase predicted by 2040 (IPCC 2018). Climate change brings not only increased temperatures, but also changes the seasonality and extremes of precipitation and temperature (Imbach et al. 2018). Vapor pressure deficit (VPD) has already increased worldwide, with negative effects on plant growth in most regions (Yuan et al. 2019). Species with narrow abiotic tolerance, narrow distributions, or small populations will be most at risk, compounded when multiple factors interact (Thomas et al. 2004; Lozada et al. 2008;

Brummitt et al. 2015). At the same time, human agricultural expansion and development continue to fragment and degrade tropical forests worldwide (Alroy 2017).

While these threats are global, some biomes experience them more acutely than others. Polar and temperate regions will see the greatest magnitude and variance of climate effects, but ecological impacts are equally determined by species' responses and their ability to find new suitable habitat. Tropical montane forests are biodiversity hotspots uniquely threatened by both climate change and deforestation (Myers et al. 2000; Kessler & Kluge 2008; Soh et al. 2019). These ecosystems, characterized by cooler temperatures, high humidity, and periodic or persistent cloud immersion, host specialized species found nowhere else that are adapted for life in high moisture environments. Tropical species experience a narrower range of abiotic conditions than species at higher latitudes, and many have lower tolerance for deviations from their normal conditions (Mau et al. 2018). As the climate warms, cloud bases will rise, and the duration of cloud immersion will decrease (Helmer et al. 2019). Forest fragmentation further increases ambient temperatures and decreases humidity (Lawton et al. 2001; Jucker et al. 2018). Given the combined impacts of climate change and habitat fragmentation, tropical montane communities may be at extreme risk.

Epiphytes play a keystone role in tropical forests by increasing structural complexity, offering key resources to animals, and altering water and nutrient cycling (Nadkarni 1994). They may represent more than half of plant diversity and up to 30% of leaf biomass in some forests (Gentry & Dodson 1987). Montane forests have a particularly rich epiphyte flora high in endemism (Cardelús et al. 2006; Kessler & Kluge 2008). Many vascular epiphytes provide foraging substrates, fruit, and nectar resources for birds and mammals (Nadkarni & Matelson 1989; Cruz-Angón & Greenberg 2005; Godoy-Güinao et al. 2018). Arthropods inhabit canopy soil mats formed by epiphytes (Yanoviak et al. 2004; Díaz et al. 2012) and canopy amphibians utilize pools of water captured by tank bromeliads for refuge and breeding sites (McCracken & Forstner 2014). Epiphytes also play important roles in water and nutrient cycling, altering precipitation interception and incorporating atmospheric nutrients into terrestrial systems (Stanton et al. 2014; Van Stan & Pypker 2015). Reductions in epiphyte abundance and diversity could have cascading effects on tropical biodiversity.

Forest fragmentation presents an obvious loss of habitat for epiphytes structurally dependent on trees (Turner et al. 1994). In montane forests, experimental evidence suggests that declining humidity and the loss of cloud immersion will strongly impact epiphytes, particularly drought-sensitive taxa (Nadkarni & Solano 2002; Song et al. 2012; Rapp & Silman 2014). Determining which locations and species are most at risk is essential to conserving tropical biodiversity into the future. However, the scale of climate predictions (on the order of km) does not match the scale at which species experience these changes (on the order of m). Multiple drivers of epiphyte diversity and composition intersect at multiples scales, yet most epiphyte studies to date have examined these drivers singly at one spatial scale. In order to predict how epiphytes will respond under future climate and land use scenarios, understanding feedbacks and interactions among these drivers across multiple spatial scales is essential.

I propose a conceptual model of drivers and interactions at the landscape, local, and within-tree scales to understand the factors governing vascular epiphyte community composition (Fig. 1). To test this model, I use data gathered in preserved forests paired with data from shade coffee farms under an array of management practices to represent a spectrum of land use change. In my study area of northern Nicaragua, the landscape mosaic contains small forest fragments and farms, with coffee as the predominant crop. The coffee management spectrum I used encapsulates most of the variation in tree size, density, and diversity found across the landscape (i.e., the range of habitat available to epiphytes). I assess these data across multiple spatial scales, asking:

(1) Within trees, does non-vascular epiphyte cover determine abundance and community composition of vascular epiphytes?

(2) At the stand scale, do epiphyte abundance and composition differ between sites based on climate and land use differences?

(3) What are the relative influences of tree size and diversity, non-vascular epiphyte cover, and climate in predicting species richness of epiphytes?

Vascular epiphyte richness should increase with decreasing land use intensity and under more humid, cooler climate conditions, with changes in species composition expected. Bryophyte cover, species richness, and functional type have been closely linked to humidity (Karger et al. 2012; Batke et al. 2015) and I anticipated a positive relationship between vascular and non-vascular epiphytes related to common abiotic requirements and a possible facilitative role in primary succession (Nadkarni 2000; Pardow et al. 2012). Epiphyte richness should show a positive relationship with tree size (Flores-Palacios & García-Franco 2006; Spruch et al. 2019), which varied considerably across study sites. Forests and coffee farms differed based on tree density and tree diversity, both of which should inform epiphyte community composition via microhabitat conditions, propagule dispersal ability, and differing host preferences among epiphytes (Merwin et al. 2003; Cascante-Marín et al. 2009; Jucker et al. 2018). Within trees, regional and stand characteristics combine to form distinct microclimates throughout the tree, with gradients in light, temperature, and humidity that favor certain species and functional types (Woods et al. 2015; Sanger & Kirkpatrick 2017).

METHODS

Study Sites

Data were collected from coffee farms in northern Nicaragua in 2016-2018. The humid montane forests of this region contain tremendous epiphyte diversity, particularly orchids, bromeliads, peperomias, and ferns, but historical forest cover has been highly fragmented. Predicted climate changes for this region by 2050 include temperature increases from 1.6-2.0ºC, decreased wet season precipitation, and longer dry spells (Imbach et al. 2018). My work was mainly conducted at two farms, Selva Negra and El Jaguar. Selva Negra is a 125-year-old coffee farm north of Matagalpa, Nicaragua, that employs a shade cultivation system with many species of native and exotic trees. A 120-hectare preserve of primary and secondary forest is adjacent to the coffee farm. The farm faces south mid-slope on a large mountain with a warmer, drier, and largely deforested valley below. Cloud immersion tends to be persistent on the mountain peak, but cloud bases rarely reach the elevation of the farm (pers. obs.). El Jaguar, north of Jinotega, Nicaragua, contains 30 hectares of shade coffee interspersed among 100 hectares of preserved forest. The farm is on one of the higher peaks in the area but surrounded by mainly similar elevations. Cloud immersion through the morning hours or longer is frequent during the wet season (pers. obs.). Although both farms are located at similar elevations and have similar annual temperature and rainfall, El Jaguar experiences more frequent cloud immersion due to differences in mass elevation effects

(Helmer et al. 2019). Selva Negra also has greater seasonality of temperature and precipitation and greater incoming solar radiation (Table 1). In addition to these two farms, I collected data at 29 other farms in the same region during 2018.

Data Sets

Trunk data: In August 2016, I sampled the trunks of 42 trees divided among coffee farm and preserved forest at El Jaguar and Selva Negra. Trees were randomly selected in the coffee farms and along trails in the forest and included following an assessment of safety for climbing. I used single rope (SRT) climbing techniques to access 1m segments of trunk at 1m, 5m, and 10m above the ground. Within each segment, I recorded a visual estimate of bryophyte and lichen cover. For each vascular epiphyte individual found within the segment, I recorded morphospecies identity, growing substrate, and size class. I measured tree diameter and estimated tree height.

Whole tree data: In August 2017, I surveyed epiphytes in 9 trees in coffee farm and 8 trees randomly selected in preserved forest at the two farms. Following Johansson's (1974) tree zonation, I subsampled each zone as follows:

Zone 1 (lower trunk): 1m segment of trunk located between 1-2m above ground
Zone 2 (upper trunk): 1m segment of trunk 1-2m below lowest branch
Zone 3 (inner crown): inner one-third of a branch
Zone 4 (mid-crown): middle one-third of same branch (including all bifurcations)
Zone 5 (outer crown): outer one-third of same branch (including all bifurcations)

On each tree, zones 3-5 were recorded for two separate branches. Tree measurements and data within zones followed the trunk dataset methods above.

Plot-level data: In April and May of 2018, I re-visited Selva Negra and El Jaguar plus an additional 29 farms growing shade coffee in the region. Farms ranged in size from a few to several hundred hectares and were located between 1000-1300m elevation. On each farm I placed two to five 20x20m plots (n=87) to capture the range of production management within the farm. The number of plots was determined by farm size and diversity of management practices. In each plot, I recorded epiphyte species composition, diameter and height of all trees, bryophyte and lichen cover within each tree zone, and abundances of orchids, ferns, bromeliads, and other epiphytes per tree zone. All adult vascular epiphytes were identified to morphospecies in the field. Species identifications based on collections and photographs followed the *Flora de Nicaragua* (Stevens et al. 2001).

Climate data: For each plot in the plot-level dataset, I used GPS coordinates to extract 19 bioclimate variables from WorldClim (Fick & Hijmans 2017). Monthly averages for solar radiation, average temperature, maximum and minimum temperatures, and vapor pressure for each plot were also acquired from WorldClim. Average VPD for each month was derived from average temperature and vapor pressure for each month following equations in Yuan et al. (2019). Variables were summarized into the yearly maximums, minimums, and means.

Analyses

Facilitative relationships between vascular and non-vascular epiphytes

To address my first question, I tested whether bryophyte or lichen cover predicted epiphyte richness within tree zones using linear mixed-effect models with the whole tree dataset in the R package 'lme4' (Bates et al. 2019). I constructed separate models for each zone and included tree diameter (trunk zones) or branch base diameter (crown zones) as a covariate to account for size differences. I included site (coffee farm or forest at Selva Negra or El Jaguar) as a random effect in all models and added tree as a nested random effect within site in crown zones to account for duplicate plots. Bryophyte cover, diameter measures, and richness were log-transformed to meet model assumptions.

To test whether vascular epiphyte species show preference for growing substrates mediated by non-vascular epiphytes, I used a randomization test on the combined trunk and whole tree datasets. I included only species with 20 or more adult or juvenile individuals. I shuffled the substrate associated with each individual 1000 times to create null distributions for substrate occurrence for each species. I tested whether observed species occurrences on bark, bryophyte, or lichen fell above or below the 95% confidence interval for the null distribution, indicating a positive or negative association with the substrate. Several other substrate types were included in randomizations but omitted from statistical tests because of their infrequency. I then tested whether relative abundance of a species at each site predicted a positive or negative association for each substrate type using generalized linear models with binomial distribution.

Stand-level differences in climate and land use

To address my second question, I tested whether differences in climate between the two farms and land use within farms (coffee farm vs. forest) resulted in differences in epiphyte composition, abundance, and richness. I used nonmetric multidimensional scaling (NMDS) with the whole tree dataset and tested for differences in centroids on a Bray-Curtis distance matrix using permutational multivariate analysis of variance (PERMANOVA), also checking for differences in dispersion. Post-hoc differences in dispersion were compared using Tukey’s test. To further characterize site differences, I calculated total richness for all vascular epiphytes, bromeliads, orchids, and ferns in forest and coffee farm at each site. I used ANOVA models with Tukey post hoc tests to test for differences in average tree diameter, height, and per-tree lichen and bryophyte cover at each location. To examine community saturation and compositional turnover between trees, I constructed species accumulation curves for each location. Analyses were performed in the R package ‘vegan’ (Oksanen et al. 2019).

Interactions among multiple drivers

My third question sought to better understand the relative strengths of known drivers of vascular epiphyte richness, which I tested by developing a structural equation model (SEM) using the R package ‘lavaan’ (Rosseel et al. 2019). SEM allows testing of complex networks of relationships and causal hypotheses (Grace 2006). Using the relationships hypothesized in my conceptual model (Fig. 1), I developed a SEM to test the relative effects of climate variables, tree size, and tree diversity on vascular epiphyte richness and bryophyte cover. I included a facilitative path between bryophytes and vascular epiphytes.

To determine the climate variables with the greatest effects on bryophytes and vascular epiphytes, I constructed single linear regressions for each group with each of the 31 climate variables. I eliminated indicators based on low univariate R^2 values and removed highly correlated variables. I constructed linear mixed models with the remaining variables and used stepwise selection to choose the best model for each group using the ‘lme4’ R package (Bates et al. 2019). Farm was included as a random effect. Conditional R^2 values were derived using the ‘MuMIn’ R package (Bartoń 2019).

I constructed two versions of the SEM, testing: (1) total epiphyte richness, and (2) richness of bromeliads, ferns, and orchids individually. I used latent variables based on one or more indicators as the exogenous and endogenous variables in the model using data from 87 plots at 31 farms in the plot-level dataset. Latent variables allow representation of concepts in models that may be imperfectly captured by actual measurements and allow several correlated measurements to be compiled to better characterize the concept (Grace 2006). I included four exogenous latent variables for aridity, insolation, tree size, and tree diversity based on measured indicators as follows: aridity was indicated by precipitation seasonality, maximum monthly low temperature, and maximum monthly VPD; insolation was indicated by incoming solar radiation; tree height and dbh indicated tree size; and Simpson's diversity index was used as a measure of tree diversity. Indicators were selected for each latent variable using separate confirmatory factor analyses (Grace 2006). Endogenous latent variables included vascular epiphyte richness and bryophyte cover, each indicated by the observed values. Tree density, although represented in the conceptual model, was excluded from the SEM. In coffee farms, trees are uniformly spaced and pruned to maintain canopy cover at 30-40% (pers. comm. with farmers), so density variation was low and confounded with tree size. I compared models using fit statistics and eliminated paths based on modification indices to construct the most parsimonious model. All analyses were performed in R version 3.6.0.

RESULTS

Facilitative relationships between vascular and non-vascular epiphytes

I found evidence for strong facilitative relationships between bryophytes and vascular epiphytes. Bryophyte cover strongly predicted vascular epiphyte richness in all tree zones even after accounting for diameter and site differences (LMM; zone 1: t=4.41, p<0.001; zone 2: t=3.38, p=0.001; zone 3: t=3.31, p=0.002; zone 4: t=3.90; p<0.001; zone 5: t=4.36, p<0.001). Diameter was weakly significant in some but not all zones, indicating bryophyte cover may be more important for predicting vascular epiphyte richness than tree size. There was no significant effect of lichen cover on richness in any zone (full output for both models in Table S1).

Many vascular epiphyte species demonstrated substrate affinities (Table 2). Orchids and ferns largely showed positive associations with bryophytes and negative associations with lichen. Atmospheric bromeliads and several orchids exhibited the opposite. The relative abundance of species positively associated with bryophytes was significantly lower in the Selva Negra coffee farm (GLM, z=-2.95, p=0.003) and marginally higher in the El Jaguar coffee farm (z=2.29, p=0.02) and forest (z=1.88, p=0.06). Species negatively associated with bryophytes represented a greater proportion of the community at Selva Negra (coffee farm: z=3.04, p=0.002; forest: z=1.81, p=0.07). Likewise, species negatively associated with lichen occurred more frequently at El Jaguar (coffee farm: z=3.10, p=0.002; forest: z=2.47 p=0.01). Associations with bark were not over- or underrepresented at any site.

Stand-level differences in climate and land use

Differences in epiphyte composition between the two farms (characterized by climate) were greater than between land use types at either farm. Site species composition separated clearly in multidimensional space (Fig. 2; PERMANOVA: F=31.74, p=0.001). However, the El Jaguar coffee farm had greater dispersion than the other sites, indicating greater compositional dissimilarity between trees (PERMDISP: F=3.41, p=0.03). Significant environmental loadings indicated that the two farms separated primarily based on tree diameter and the non-vascular epiphyte communities present. Despite having smaller trees, both the coffee farm and forest at El Jaguar had higher total species richness than either land type at Selva Negra (Table 1), but per-tree species richness did not differ, suggesting greater turnover between trees at El Jaguar (Fig. 3). At both farms, coffee shade trees supported nearly as many epiphyte species as forest trees. There were strong taxonomic differences in species composition, with orchids representing more than a third of all species at El Jaguar, while Selva Negra had double the bromeliad species of El Jaguar. Ferns tended to be more speciose in the forests at each site (Table 1). The two sites differed strongly in the non-vascular epiphyte types, with El Jaguar showing tree bark mainly covered in bryophytes (ANOVA, F=15.24, p>0.001), while Selva Negra trees hosted mainly lichens (ANOVA, F=15.4, p>0.001).

Interactions among multiple drivers

Vascular epiphyte richness appears to be jointly controlled by tree size and diversity and by climate mediated through bryophyte cover. In both SEMs, the strongest paths were a negative relationship between both climate latent variables and bryophyte cover and a positive relationship between bryophyte cover and vascular epiphyte richness (Figs. 4 and 5). Path coefficients may be interpreted as the percent change per standard deviation of the response resulting from a one-standard-deviation increase in the indicator, holding other variables constant. The final richness model explained 59% of total vascular epiphyte richness and 62% of bryophyte cover variation (Fig. 4). Bryophyte cover showed no relationship with tree diversity and only a weak relationship with tree size, indicating that climate is most important. Vascular epiphytes had a strong relationship with tree size and a somewhat weaker relationship with tree diversity. The direct paths between climate variables and vascular epiphyte richness were weak or insignificant. The final taxonomic group model explained 36% of variation for bromeliads, 60% for ferns, 55% for orchids, and 62% for bryophyte cover (Fig. 5). Bromeliads were the only group to show a positive relationship with aridity. All groups showed positive direct relationships with insolation but little total effect. Bryophyte cover had the strongest direct effect on all groups, although, surprisingly, it was weakest for orchids. Tree size was an important predictor for all groups, and tree diversity predicted the richness of ferns and orchids, but not bromeliads.

In the linear models, average bryophyte cover was best explained by maximum VPD and mean incoming solar radiation with farm as a random effect. The full model accounted for 76% of the total variation in bryophyte cover and the fixed effects alone accounted for 58% (VPD: $t=-5.30$, $p<0.001$; srad: $t=-3.75$, $p<0.001$). The best model for vascular epiphyte richness included only maximum VPD and the farm random effect with a weakly significant response ($t=-2.37$, $p=0.02$, R^2 for fixed effects=0.09).

DISCUSSION

Facilitation between bryophytes and vascular epiphytes

My results indicate a strong and directional relationship between bryophyte cover and vascular epiphyte richness, with particularly facilitative effects on some species. Previous work has suggested that greater bryophyte cover may identify areas of high vascular epiphyte richness (Pardow et al. 2012). My work confirms this hypothesis and adds that the association may be causal rather than correlative. In other words, bryophytes may not only cohabitate with a high diversity of vascular epiphytes because of shared abiotic requirements, but rather bryophytes may support and enhance the vascular epiphyte community. Indeed, of the over 4,000 vascular epiphytes I observed, 75% were rooted in bryophyte mats, which is disproportionate to the 43% mean bryophyte cover on the same trees. Twenty-one species, mainly orchids and ferns, showed strong positive associations with bryophytes, as compared with 7 each for lichens and bare bark (Table 2).

Bryophytes showed a pronounced response to most climate variables I tested, particularly VPD, solar radiation, precipitation seasonality, and higher nighttime temperatures. They are poikilohydric and can withstand long periods of desiccation but recover more slowly with longer and more intense dry periods (Proctor et al. 2007). More frequent or longer dry periods and higher temperatures may put bryophytes into a negative carbon balance by limiting opportunities for rehydration (and thus photosynthesis) and increasing respiration costs (Proctor et al. 2007; Karger et al. 2012). The negative effects of insolation may be related to more rapid drying each morning, limiting photosynthetic potential (Proctor et al. 2007). Insolation was the most divergent climate variable between El Jaguar and Selva Negra (Table 1), indicating it may be a leading cause of compositional differences between sites.

Vascular epiphyte response to climate change and land use

Previous studies of vascular epiphyte responses to climate change have not considered facilitative relationships with bryophytes because transplant experiments included entire epiphyte mats (Nadkarni & Solano 2002; Rapp & Silman 2014). Song et al. (2012) documented a rapid and negative response of non-vascular epiphytes with transplant to warmer and less humid conditions but did not consider indirect effects on vascular epiphytes. The exact mechanisms of facilitation between bryophytes and vascular epiphytes remain undefined. In addition to moisture retention, several studies have indicated a primary succession role, suggesting that vascular epiphytes arrive in communities only after non-vascular epiphytes have established (Nadkarni 2000; Toledo-Aceves et al. 2012). Bryophytes have been linked with fern gametophyte survival and reproduction in epiphytic taxa (Watkins et al. 2007). Non-vascular epiphytes aid germination success in bromeliads and orchids (Cascante-Marín et al. 2008; Scheffknecht et al. 2010), and bryophytes may play an inhibitory role to terrestrial tree seedlings germinating in canopy soil that would potentially compete with vascular epiphytes (Nadkarni & Solano 2002). However, many open questions remain about the mechanisms behind facilitation, and more accurate predictions for the fate of epiphyte communities under climate change scenarios will only be possible with such knowledge.

My results suggest that warmer, drier, and less cloudy conditions in tropical montane forests under climate change scenarios may result in a shift from bryophyte-fern-orchid-dominated communities to more drought-tolerant lichen-bromeliad-dominated epiphyte assemblages. In places where the remaining humid forests are on peaks, as they are in the study region of Nicaragua, many of the most drought-sensitive species may eventually be lost entirely. Given the high sensitivity of bryophytes to the relatively small increments of VPD, temperature, and insolation here and in previous studies (Song et al. 2012), these shifts could occur under even modest climate changes. Forest fragmentation and tree loss will only exacerbate the speed and magnitude of these changes. Agroforestry systems and trees in open landscapes are important reservoirs for epiphyte diversity currently (Hietz 2005; Solís-

Montero et al. 2019), but they will likely experience epiphyte losses soonest and may therefore serve as valuable indicators. The differences between the two main sites, El Jaguar and Selva Negra, already offer a preview of the drastic shifts in montane epiphyte communities that we may expect as climate change continues and cloud bases rise.

Conservation implications

The strength of the abiotic and biotic relationships documented here suggest an acute threat for montane forest epiphytes in the coming decades. Epiphytes have tight ecological relationships with many forest canopy species, and their decline could have grave consequences for the birds, invertebrates, and other animals dependent on them for food and habitat resources (Nadkarni & Matelson 1989; Yanoviak et al. 2004; Cruz-Angón & Greenberg 2005; McCracken & Forstner 2014). Preserving remaining forests, particularly at the highest elevations, offers the most promise for conserving vulnerable epiphyte species, but as these forests begin to lose regular cloud immersion, they may also be at risk. Central American and Caribbean epiphytes may be particularly vulnerable because maximum elevations are lower than in many other tropical mountain ranges and cloud immersion may be completely lost (Helmer et al. 2019).

Many open questions remain and experimental work on the interactions between vascular and non-vascular epiphytes is needed to clarify these predictions and the mechanisms behind them. Long-term observation of permanent epiphyte plots would help to characterize change as it occurs, and agroforestry systems like those I studied may provide an important early warning system for cascading losses in epiphyte communities. Epiphyte decline or the dramatic shifts in community composition would have serious consequences for montane forests generally, including for many animal species, and may impinge on their ability to adapt to ongoing climate and land use changes. Since we still lack fundamental knowledge about the many ecological roles epiphytes play, the full extent of the impacts cannot yet be predicted.

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TABLES AND FIGURES

Table 1. Comparisons between El Jaguar and Selva Negra forest and coffee farm sites. Letter superscripts denote significant differences among locations based on ANOVA with Tukey post-hoc tests. Species richness for bromeliads, orchids, and ferns gives the total number of species of that group with the percent of total species represented by the group in parentheses. Climate variables show annual mean values with minimum and maximum monthly averages in parentheses.

	El Jaguar Coffee Farm	***El Jaguar Forest***	***Selva Negra Coffee Farm***	***Selva Negra Forest***
Total epiphyte abundance	1156	1023	1258	1200
Total species richness	83	87	55	64
Bromeliad richness	14 (16.7%)	8 (9.2%)	18 (32.7%)	17 (26.6%)
Orchid richness	33 (39.8%)	31 (35.6%)	13 (23.6%)	15 (23.4%)
Fern richness	12 (14.5%)	19 (21.8%)	10 (18.1%)	14 (21.8%)
Mean tree dbh (cm)	52.26 ± 7.81^{a}	54.07 ± 30.32^{a}	73.29 ± 21.78^{a}	63.03 ± 20.03^{a}
Mean tree height (m)	21.64 ± 3.79^{a}	20.93 ± 3.55^{a}	18.28 ± 3.28^{a}	27.94 ± 5.36^{b}
Average bryophyte cover (%)	53.90 ± 22.03^{a}	59.58 ± 19.83^{a}	25.35 ± 19.17^{b}	40.05 ± 18.46^{b}
Average lichen cover (%)	22.95 ± 20.61^{b}	9.35 ± 9.69^{a}	41.03 ± 17.60^{c}	27.80 ± 16.19^{bc}
Elevation (m)	1284	1283	1253	1300
Mean annual temperature (°c)	19.1 (11.8-26.0)	19.1 (11.9-26.0)	19.2 (12.3-26.0)	17.4 (10.6-24.1)
Total annual precipitation (mm)	1661 (22-260)	1663 (22-261)	1666 (21-268)	1979 (31-314)
Mean incoming solar radiation (kj m^{-2} day^{-1})	19576 (15872-23070)	19676 (16122-23149)	20187 (17307-23498)	19977 (16915-23197)
Mean vapor pressure deficit (kpa)	.451 (.327-.660)	.448 (.323-.658)	.436 (.311-.652)	.418 (.311-.624)

Table 2. Substrate associations for common species based on comparison a randomized distribution. Associations were considered to be positive or negative if observed values fell more than 2 standard deviations above or below the mean of the null distribution. P-values are indicated as *p≤0.05, **p≤0.01, ***p≤0.001.

Taxon	***Family***	***Bark***	***Lichen***	***Bryophyte***
Anthurium scandens ssp. *pusillum*	Araceae		negative *	positive **
Anthurium scandens ssp. *scandens*	Araceae		negative ***	positive **
Asplenium auriculatum	Aspleniaceae	positive ***		
Asplenium praemorsum	Aspleniaceae			
Catopsis nitida	Bromeliaceae			
Catopsis cf. paniculata	Bromeliaceae	positive ***		negative **
Guzmania monostachia	Bromeliaceae			
Guzmania nicaraguensis	Bromeliaceae		negative **	
Pitcairnia heterophylla	Bromeliaceae		negative *	positive **
Tillandsia butzii	Bromeliaceae	positive ***	positive ***	negative ***
Tillandsia fasciculata	Bromeliaceae	positive ***	positive ***	negative ***
Tillandsia festucoides	Bromeliaceae			
Tillandsia schiedeana	Bromeliaceae	positive ***	positive ***	negative ***
Tillandsia tricolor	Bromeliaceae	positive ***	positive ***	negative ***
Elaphoglossum cf. furfuraceum	Dryopteridaceae		negative ***	positive ***
Elaphoglossum cf. lonchophyllum	Dryopteridaceae		negative *	
Elaphoglossum peltatum	Dryopteridaceae	negative **	negative ***	positive ***
Sphyrospermum buxifolium	Ericaceae	negative **	negative ***	positive ***
Hymenophyllum polyanthos	Hymenophyllaceae			positive **
Epidendrum paranthicum	Orchidaceae		negative **	positive ***

Epidendrum ramosum	Orchidaceae		negative *	positive ***
Isochilus linearis	Orchidaceae	negative *	positive ***	
Jacquiniella teretifolia	Orchidaceae	negative **	positive ***	negative ***
Maxillaria cf. acervata	Orchidaceae			positive **
Maxillaria cf. cucullata	Orchidaceae			positive **
Maxillaria variabilis	Orchidaceae		negative *	positive **
Pleurothallis cf. matudana	Orchidaceae			positive **
Pleurothallis cf. platystylis	Orchidaceae			positive **
Prosthechea fragrans	Orchidaceae		negative *	
Prosthechea ochracea	Orchidaceae			
Scaphyglottis micrantha	Orchidaceae		positive ***	negative ***
Stelis parvula	Orchidaceae		negative ***	positive ***
Stelis cf. purpurescens	Orchidaceae		negative ***	positive ***
Peperomia cf. angustata	Piperaceae		negative **	
Peperomia deppeana	Piperaceae			negative **
Peperomia distachyos	Piperaceae			positive *
Peperomia obtusifolia	Piperaceae		negative ***	
Peperomia tetraphylla	Piperaceae		negative *	positive ***
Campyloneurum angustifolium	Polypodiaceae		negative **	
Melpomene anfractuosa	Polypodiaceae			positive **
Niphidium crassifolium	Polypodiaceae		negative *	positive **
Phlebodium pseudoaureum	Polypodiaceae		negative **	
Pleopeltis angusta	Polypodiaceae			
Pleopeltis macrocarpa	Polypodiaceae		negative **	negative ***
Pleopeltis polypodioides	Polypodiaceae			
Polypodium furfuraceum	Polypodiaceae	positive ***		negative *

Polypodium lindenianum	Polypodiaceae	negative **	
Polypodium plebium	Polypodiaceae	negative ***	positive **
Serpocaulon ptilorhizon	Polypodiaceae	negative ***	negative ***

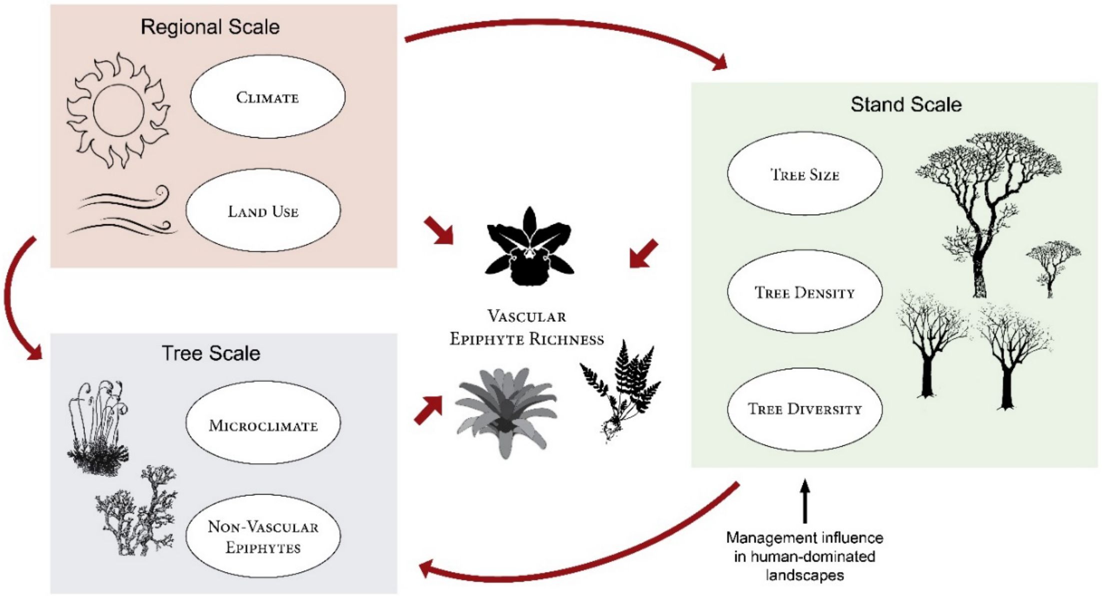

Fig. 1. Conceptual model proposing the effects of climate and land use change on epiphytes at different spatial scales. At the regional scale, climate and land use change interact and directly inform epiphyte community composition through averages and extremes of abiotic conditions and limitations to dispersal, pollination, and gene flow. Regional drivers influence tree characteristics at the stand level, including size, density, and diversity in natural systems and, to a lesser extent, in human-managed systems. Tree size increases epiphyte richness via species-area relationships, increased opportunity for propagule arrival over time, and diversification of microclimates within the tree. Tree density affects dispersal ability and microclimate. Tree diversity is expected to increase epiphyte diversity because of varying host preference of epiphytes and the different microhabitats offered by different hosts. Regional and stand characteristics combine with gradients in light, temperature, and humidity within each tree to form distinct microclimates that determine vascular and non-vascular epiphyte abundance and species composition. Finally, interactions with non-vascular epiphytes facilitate vascular epiphyte establishment and diversity.

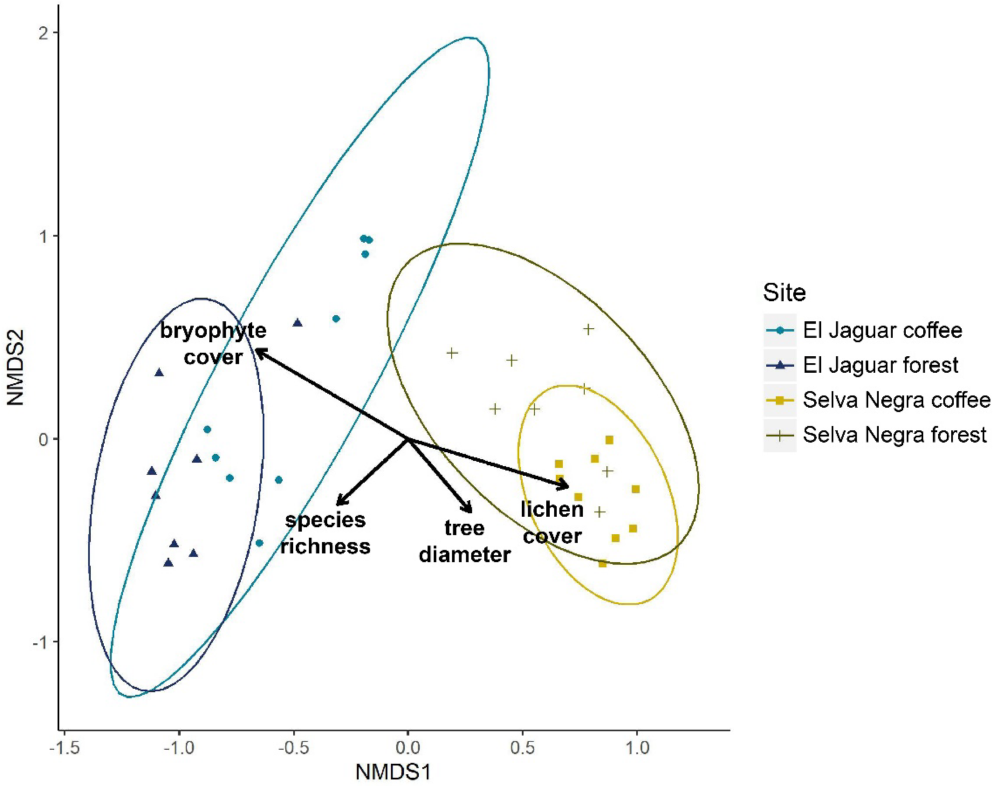

Fig. 2. Non-metric multidimensional scaling ordination of trees at each farm and land use type combination. Environmental loadings shown were all significant (lichen cover: R2=0.54, p<0.001; bryophyte cover: R2=0.63, p<0.001; tree diameter: R2=0.20, p=0.03; species richness: R2=0.20, p=0.05).

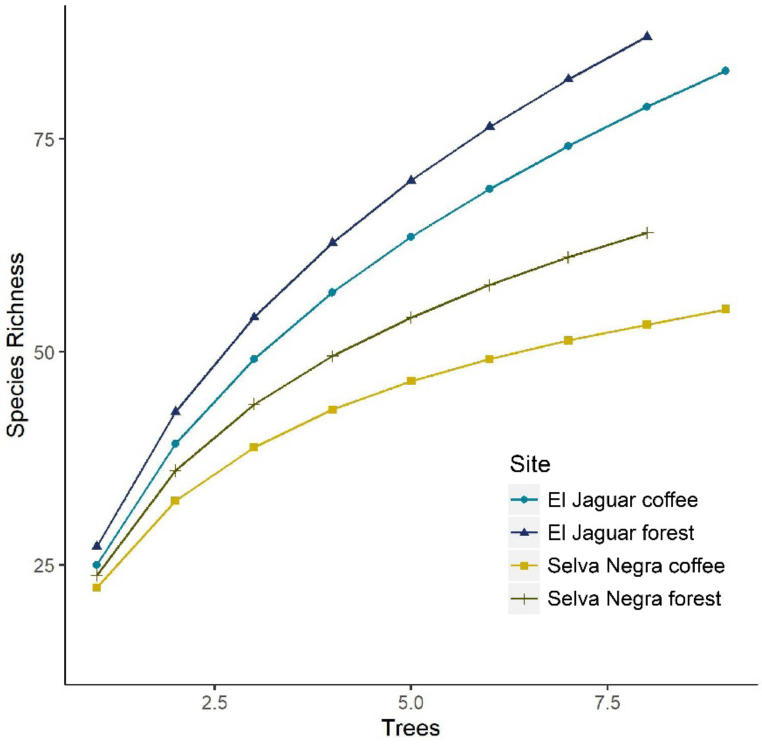

Fig. 3. Species accumulation curves showing differences between sites. In both cases, forests had higher species richness but overall rates of accumulation in coffee farms were similar. Selva Negra was less speciose than El Jaguar in both land use types and began to reach saturation in my sample size, whereas El Jaguar did not.

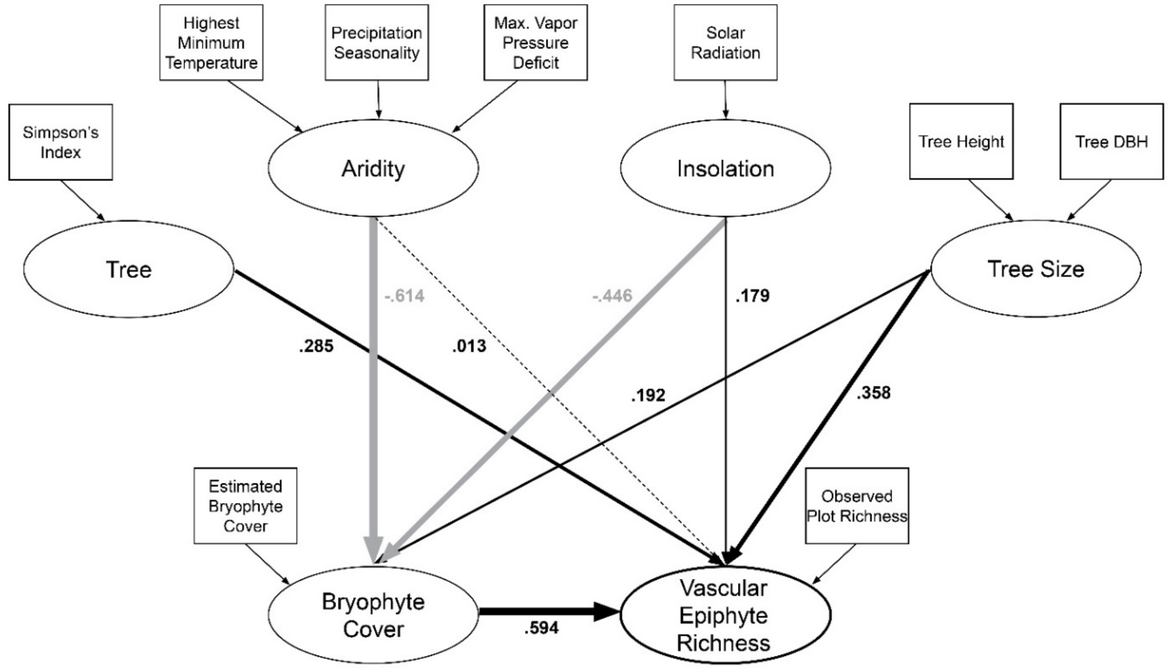

Fig. 4. SEM for relationships driving total vascular epiphyte richness. Black arrows indicate positive relationships and gray arrows indicate negative relationships. Dashed lines indication non-significant paths. Path coefficients show the magnitude of each effect. The total path coefficient for the compound effect of aridity on vascular epiphyte richness, mediated by bryophyte cover, is -.296 and the total effect of insolation on vascular epiphytes is -.086.

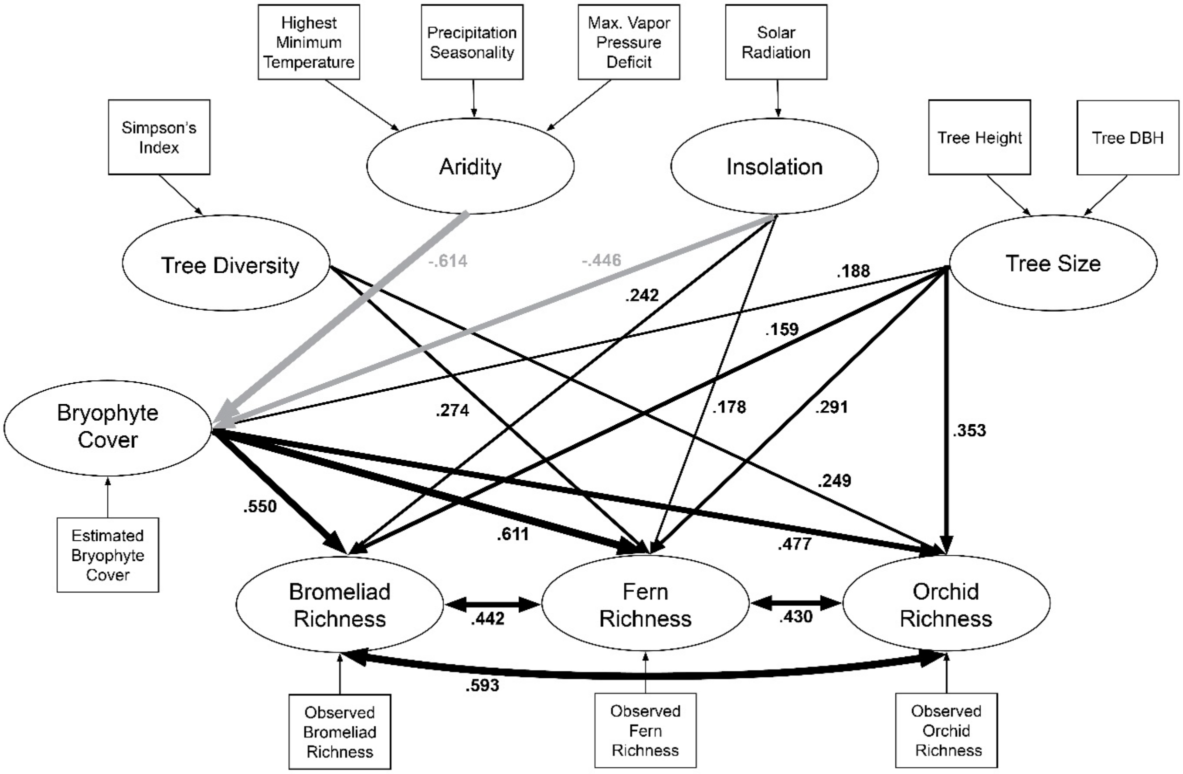

Fig. 5. SEM for relationships driving vascular epiphyte richness within major taxonomic groups. Black arrows indicate positive relationships and gray arrows indicate negative relationships. Non-significant paths are excluded for simplicity (direct effect of aridity on bromeliad richness = .244, on ferns = -.064, and on orchids = -.137; direct effect of insolation on orchids = .121; direct effect of tree diversity on bryophyte cover = .077 and on bromeliads = .125). Double-headed arrows depict correlations between response variables. Path coefficients show the magnitude of each effect. Total effects of aridity were 0.180 for bromeliads (including a non-significant direct effect of .244), -.439 for ferns, and -.430 for orchids. Total effects of insolation were .003 for bromeliads, -.094 for ferns, and -.092 for orchids.

Table S1. Model output for mixed effects models testing the response of species richness in each tree zone to bryophyte or lichen cover. Zone diameter (trunk diameter in trunk zones and basal branch diameter in branch zones) was included as a covariate to account for tree size differences. Location (El Jaguar coffee farm, El Jaguar forest, Selva Negra coffee farm, Selva Negra forest) was included as a random effect. Values are presented as T value$_{df}$, p value.

Model	***Cover***	***Zone Diameter***	***Location***
Bryophyte Zone 1	$4.41_{24.42}$, <0.001***	$2.81_{22.91}$, 0.01**	6.64, 0.01**
Bryophyte Zone 2	$3.38_{50.9}$, <0.001***	$0.87_{50.28}$, 0.39	1.16, 0.28
Bryophyte Zone 3	$3.31_{61.39}$, <0.001***	$2.4_{63.26}$, 0.02*	4.48, 0.03*
Bryophyte Zone 4	$3.9_{41.43}$, <0.001***	$1.99_{34.45}$, 0.05*	2.17, 0.14
Bryophyte Zone 5	$4.36_{56.75}$, <0.001***	$2.25_{62.94}$, 0.03*	8.55, <0.001***
Lichen Zone 1	$-1.0_{23.12}$, 0.33	$1.42_{23.61}$, 0.17	1.36, 0.24
Lichen Zone 2	$-0.84_{37.78}$, 0.4	$0.1_{50.33}$, 0.92	1.15, 0.28
Lichen Zone 3	$-0.73_{70.7}$, 0.47	$1.9_{70.99}$, 0.06*	6.61, 0.01**
Lichen Zone 4	$-0.7_{45.72}$, 0.49	$2.28_{60.36}$, 0.03*	3.95, 0.05*
Lichen Zone 5	$1.46_{60.01}$, 0.15	$1.88_{51.36}$, 0.07*	2.83, 0.09

Chapter 3: Leaf economics in a three-dimensional environment: Testing leaf trait responses in epiphytes to land use, climate, and tree position

Jeannine H. Richards[1], Ellen I. Damschen[2]

[1] Nelson Institute for Environmental Studies, University of Wisconsin-Madison

[2] Department of Integrative Biology, University of Wisconsin-Madison

ABSTRACT

The study of functional traits offers predictive power for community ecology. Particularly in cases where individual species are difficult to study, known properties of trait spectra and trait-environment relationships can provide crucial generalizable information for forecasting how species will respond to climate and land use changes and can allow comparisons between sites. Vascular epiphytes are expected to be sensitive to environmental change, but little is known about the ecology of most species. Functional traits may be an apt tool; however, baseline information is currently lacking and many basic functional trait assumptions remain untested in epiphytes. Here, we use functional traits gathered on 37 species of vascular epiphytes in remnant forests and shade coffee farms at two sites in northern Nicaragua. We compare trait-trait relationships with those of ground-rooted plants; test trait-environment relationships between sites, land use types, and zones of the tree; assess shifts in intraspecific variation that may aid plant adaptation to land use change; and compare functional and taxonomic metrics of diversity between the two sites. We find that epiphyte leaf traits fall in the mid-range of the Leaf Economics Spectrum, but with lower N per increment SLA than average. Bromeliads alone deviate from expected trait-trait relationships, suggesting overall differences in economic strategy. Trait-environment relationships varied most strongly along vertical gradients within trees, but some traits also responded to land use and climate differences. Finally, functional and taxonomic diversity metrics told different stories, suggesting that analyses should include both measures for a more complete picture. Overall, we find evidence that trait-trait patterns based on ground-rooted taxa may apply to many but not all epiphytes. Because epiphytes inhabit a three-dimensional environment, more work is still needed to distinguish trait responses among multiple, interacting environmental gradients.

Keywords: abiotic conditions, environmental filtering, functional diversity, functional traits, intraspecific variation, leaf economics spectrum, trait-environment relationships

INTRODUCTION

Rapid climate and land use changes threaten plants globally. Yet, in many cases we lack adequate predictive tools to assess which species and communities are most at risk (Brummitt et al. 2015). In tropical forests, epiphytes have been proposed as indicators of change because they are expected to be highly responsive to changes in the abiotic environment, particularly stresses imposed by insolation and water shortages (Zotz & Hietz 2001; Zotz & Bader 2009). Epiphytes inhabit trees in both intact forest ecosystems as well as disturbed areas such as roadsides, farms, and urban areas (Köster et al. 2009; Einzmann & Zotz 2017). In all of these contexts, they provide food and habitat for many animal species and contribute to high levels of biodiversity (Cruz-Angón & Greenberg 2005; Méndez-

Castro & Rao 2014). Epiphytes, therefore, may play an especially important role for achieving conservation goals across taxa in social-ecological landscapes, such as agroforests.

Utilizing epiphytes as global change indicators is challenging, however. Their environmental tolerances are not well characterized, preventing mechanistic understanding and the ability to predict extinctions (Zotz & Hietz 2001). This dearth of knowledge largely exists because of the challenges with sampling epiphytes in tree canopies and difficulty in identifying species when reproductive material is absent (Zotz & Bader 2011). Most epiphytes belong to hyperdiverse families containing many rare species with narrow ranges (Gentry & Dodson 1987; Zotz 2013). These factors have all impeded progress on developing predictive ecological frameworks for epiphytes. Furthermore, the assumption that epiphytes follow the same patterns and respond to the same constraints as terrestrial plants remains largely untested (Zotz 2016).

Functional traits offer promise as a predictive tool for community ecology (McGill et al. 2006; Violle et al. 2007). By capturing characteristics of organisms thought to correspond to fitness, functional traits can explain and predict plant distributions along gradients (Fonseca et al. 2000; Wright et al. 2005; Miller et al. 2019), habitat differentiation and coexistence (Cavender-Bares et al. 2004; Kraft et al. 2015), and responses to land use changes, succession, and climate change (Lavorel & Garnier 2002; Garnier et al. 2004; Soudzilovskaia et al. 2013; Kimberley et al. 2014; Šímová et al. 2018). Such trait-based approaches have been used predominantly for terrestrial plant communities. Given the importance of epiphytes for biodiversity and ecosystem functioning, however, adopting a trait-based approach may offer a short cut to predicting shifts in epiphyte composition and identifying species most at risk from climate and land use change. A strong framework for the functional ecology of epiphytes could obviate the need for detailed knowledge of the ecologies of individual species that are rare and difficult to sample.

Trait-based ecology requires understanding the extent and influence of different types of trait variation. First, traits themselves can be correlated, forming multivariate trait spectra where key ecological processes are represented by orthogonal axes of correlated traits (Díaz et al. 2016). For example, in terrestrial plants, the well-documented leaf economics spectrum (LES; Wright et al., 2004) places leaf traits along a continuum ranging from “slow” to “fast” strategies. “Slow” plants have thick, well-defended, long-lived leaves with low nutrient concentrations and slow rates of photosynthesis. “Fast” plants exhibit thin, short-lived leaves with less structural material, high nutrient concentrations, and few defensive chemicals to achieve high maximum photosynthetic rates. Traits and trait spectra relate morphology to function across a wide range of species and environments (Wright et al. 2005; Reich et al. 2007; Violle et al. 2014). For example, specific leaf area (SLA) alone has been shown to strongly predict harder-to-measure traits that have more direct effects on ecosystem function, like photosynthetic capacity (Reich et al. 2007). Second, intraspecific trait variation can be substantial and influence species responses to current and future abiotic conditions (Violle et al. 2012). Greater intraspecific variability may allow species to adapt to future environmental conditions.

Utilizing trait-based approaches for epiphytes, therefore, requires assessing the sources of variation and whether they are impacted by environmental conditions. Doing so first entails determining the degree to which traits are correlated and whether trait spectra mirror those documented in ground-rooted plants. Due to a lack of data, global trait analyses have largely omitted epiphytes (Wright et al. 2004; Cornwell et al. 2014; Díaz et al. 2016), so the degree to which they align with the trait relationships described in terrestrial plants is still not well understood. Epiphytes inhabit high disturbance, high stress environments and they combine small propagule size, large numbers of propagules, and abiotic dispersal with slow growth, evergreen leaves, and specialized biotic pollination. These inconsistencies and their many adaptations to prevent desiccation (e.g., succulence, CAM photosynthesis, and poikilohydry) suggest that the variance and correlation among traits may be very different for epiphytes compared to terrestrial plants. In addition, epiphytes can occupy a range of abiotic conditions within a single tree. How epiphyte trait-trait relationships, intraspecific variability, and trait values vary along environmental gradients and across management contexts are key basic ecological questions and have critical applied relevance for determining which epiphytes will be able to adapt *in situ* to climate and land use changes.

While taxonomic turnover in response to macroclimate and microclimate gradients has been well characterized in epiphytes (Hietz & Hietz-Seifert 1995; Cardelús et al. 2006; Zotz 2007; Woods et al. 2015), only a handful of studies have focused on functional trait responses to the same environmental gradients. Community weighted means for most leaf traits show strong patterns within trees corresponding to increasing light and greater water stress higher in the canopy (Petter et al. 2016; Agudelo et al. 2019). However, trait shifts along elevational gradients are less consistent, with epiphyte traits responding less to abiotic changes than ground-rooted plants in the same locations (Cardelús & Mack 2010; Schellenberger Costa et al. 2018; Agudelo et al. 2019). The only study to consider epiphyte traits across land use types found that, as expected, leaves were thicker, denser, and had lower SLA under more intense land use (Susan-Tepetlan et al. 2015), but the authors did not account for the relative abundance of species, making results difficult to interpret. Climate, land use, and vertical distribution should all affect trait values to varying degrees, but these three drivers need to be addressed simultaneously to disentangle their relative influences. Furthermore, while Agudelo et al. (2019) documented that LES traits separated onto two orthogonal axes among epiphytes, explicitly placing epiphytes in reference to ground-rooted taxa along the LES still has not been done.

Functional traits can also be informative in assessing biodiversity. Functional diversity metrics combine trait means with species abundance data to calculate the diversity, evenness, divergence, and dispersion of trait values in a community (Villéger et al. 2008; Laliberté & Legendre 2010). These measures combined with traditional taxonomic measures of diversity bring multiple dimensions to community biodiversity analysis. Like their taxonomic counterparts, functional metrics can be used to compare species assemblages for both alpha (within) and beta (between) components. Adding functional diversity measures to biodiversity analysis may help to relate the composition of an assemblage to ecosystem functioning, niche partitioning, or overall resilience (Mouillot et al. 2013; Apaza-Quevedo et al. 2015). Few studies have measured functional diversity in tropical ecosystems (Moreno et al. 2018) and these metrics have never been calculated for vascular epiphyte assemblages. Given the potential contributions of epiphytes to overall biodiversity and ecosystem functioning, determining taxonomic and functional diversity for epiphytes in tropical ecosystems is a key basic knowledge gap with significant applied relevance. For example, based on taxonomic metrics, agroforestry appears to serve as valuable substitute habitat for epiphytes in places where forests are fragmented or degraded, but abiotic conditions differ considerably from closed-canopy forest (Hietz 2005; Böhnert et al. 2016). Assessing functional diversity as well may explain compositional changes and provides critical information for managing forests and agroforests into the future.

In this study, we investigate the functional response of epiphytes to abiotic differences between forests and agroforests. We use shade coffee farms and adjacent preserved forests to investigate how epiphyte traits and functional diversity metrics shift from closed-canopy conditions to the widely spaced trees in agroforestry systems. Using epiphyte species composition measured in trees in both land use types at two climatically different sites and functional traits for 37 common epiphyte species, we ask:

(1) Do epiphyte traits follow the expected relationships proposed by the Leaf Economics Spectrum across all major taxonomic groups?

(2) Do trait averages predict species abundances across the environmental differences a) between preserved forest and coffee farm, b) between sites with different climates, and c) following vertical gradients within trees?

(3) Does intraspecific variation show directional shifts in trait values between forest and shade coffee?

(4) Do epiphyte functional and taxonomic diversity metrics change in tandem or do they show divergent patterns?

If leaf traits in epiphytes follow the same patterns as have been documented in ground-rooted plants, we predict that epiphytes in shade coffee farms, where they experience higher sun exposure, temperatures, wind, and lower humidity than in closed-canopy forest, will have smaller, thicker leaves with lower specific leaf area, lower leaf nitrogen, higher total leaf carbon and a higher ratio of carbon to nitrogen (Wright et al. 2004, 2005; Šímová et al. 2018). Epiphytes in coffee farms may also be shorter, reflecting higher stress and slower growth (Zotz & Hietz 2001), have enriched values for $\delta^{13}C$, indicating greater stomatal limitation and a higher proportion of CAM species (Silvera et al. 2010; Crayn et al. 2015), and have depleted $\delta^{15}N$ values, indicating greater nitrogen inputs from rain (Hietz et al. 2002). These patterns should be similar from the drier site to the more humid site and from the outer canopy to the base of the tree, as well as for intraspecific trends between coffee farm and forest. Major taxonomic groups, including ferns, bromeliads, and orchids, will likely exhibit greater trait similarity within groups than among groups as a result of their shared evolutionary history. Finally, we expect that functional diversity will follow similar trends to taxonomic diversity, with a reduced subset of traits and species found in coffee farms as compared to forests.

METHODS

Study locations

Our research took place at two large coffee plantations in the Central Highlands of north-central Nicaragua. Selva Negra is a 125-year-old coffee farm north of Matagalpa, Nicaragua with an adjacent 120-hectare nature reserve protected by the owners. El Jaguar is a 40-year-old shade coffee farm outside of Jinotega, Nicaragua, containing 30 hectares of coffee interspersed among 100 hectares of preserved forest. Both farms are certified for shade coffee production by the Rainforest Alliance, indicating the high ecological sustainability of their practices. Climatically, Selva Negra has higher incoming solar radiation, less cloud immersion, and greater seasonality in temperature and precipitation than El Jaguar (for a full description of the climate differences between the two sites, see Chapter 2).

Epiphyte surveys

We surveyed epiphytes from large trees in each of our study locations. Previous studies demonstrate that surveying six to eight large trees is sufficient to characterize epiphyte species richness and rank abundance for a site (Zotz & Bader 2011). For this reason, we surveyed 9 large trees in coffee farm and 8 in forest at El Jaguar and Selva Negra (Fig. 1) in August of 2017. Trees were randomly selected and included only after being assessed for climbing safety. We divided each tree into zones following the Johansson zonation scheme (Fig. 1; Johansson, 1974). Within the trunk zones, we surveyed two one-meter tall sections of trunk, one at 1-2m above the ground (zone 1) and one at 1-2m below the first branch (zone 2). We randomly selected two branches in the crown and visually divided them into thirds longitudinally along the branch including all ramifications (zone 3-5 from inner to outer crown). We used single rope climbing technique (SRT) to access the inner canopy, then used binoculars to survey branches. Species identifications were made to morphospecies in the field and then further identified wherever possible based on photographs and collections following the *Flora de Nicaragua* (Stevens et al. 2001).

Functional trait measurements

We measured nine elemental and morphological traits associate with photosynthesis, water use, and nutrient uptake on 37 common species found at our study sites. Traits were collected on two leaves per plant for at least five plants of each species (Cornelissen et al. 2003). Several species where fewer individuals were sampled (3-4 individuals; 3 species) were also included in models to improve coverage (Table 1). Plant height (cm), and leaf thickness (mm) in the field and photographs of fresh leaves were taken to calculate leaf area (cm^2) using ImageJ (version 1.52h, National Institutes of Health). Leaves were then packed in silica and transported to Wisconsin, USA, where they were oven dried at 50°C for 72 hours. Dried leaves were weighed on a Mettler Toledo microbalance to derive specific leaf area (SLA, cm^2 mg^{-1}). One leaf from 2-4 randomly selected individuals per species was ground in a Wiley Mill and tins were packed with 3-6 mg of material for elemental analysis of leaf N content, leaf C content, $\delta^{13}C$ and $\delta^{15}N$. In cases where a single leaf did not provide enough material for analysis, two leaves from the same plant were combined and, in several cases, we needed to combine leaves from multiple plants of the same species. Samples were shipped to the Idaho State University Stable Isotope Lab where analyses were performed using a 2010 ThermoFisher Delta V Plus continuous flow isotope ratio mass spectrometer coupled with ConFlo IV/EA, TC/EA, and GasBench II. From these measures, we additionally derived C:N ratio.

Finally, to consider the effects of intraspecific variation, we used a subset of 4 species representing different taxonomic groups (*Stelis parvula* [Orchidaceae], *Anthurium scandens* ssp. *pusillum* [Araceae], *Elaphoglossum peltatum* [Dryopteridaceae], and *Sphyrospermum buxifolium* [Ericaceae]) where we had collected leaves from at least 4 individuals in each coffee farm and forest at the El Jaguar farm. For these species, one leaf from every individual sampled was processed for elemental analysis.

Analysis

Trait spectra among epiphyte groups

To look at how species and taxonomic groups separate based on the combined effect of all measured traits, we used Principal Components Analysis (PCA). We tested for differences in the centroid and dispersion of each group using PERMANOVA with the R package ‘vegan’. For each trait, we used separate ANOVA tests to evaluate differences in trait means among groups.

To place epiphytes along the leaf economics spectrum (LES), we compared the relationship between SLA and N_{mass} in the trait data we collected on montane epiphytes with the global dataset from GLOPNET used by Wright et al. (2004). We tested for a difference in the slope of the relationship between the two datasets using standard major axis regression (SMA) with the R package ‘smatr’ (Warton et al. 2012). Within the epiphyte trait data, we also used SMA to test whether trait covariation between SLA, N_{mass}, C:N ratio, and leaf thickness (all traits that should relate to the LES) was significant and whether the slope of the relationship differed among orchids, bromeliads, ferns, and the other epiphytes in our data.

Trait responses to environmental conditions

To test whether traits affected the abundance of species between El Jaguar and Selva Negra (“site”), between forest and shade coffee (“type”), and within zones of the tree (“zone”), we constructed generalized linear mixed models for each trait to predict species abundance. We included models that treated the first three axes from the PCA analysis above as traits. Models elaborated on the MLM2 for testing trait-environment interactions, which reduces the Type I error rate over community weighted means (Miller et al. 2019). We used the R package ‘glmmTMB’ to construct models and included a negative binomial distribution and a zero-inflation term to address zero inflation in the count data (Magnusson et al. 2019). To test trait-environment interactions with our three environmental variables, we started with a four-way interaction among site, type, zone, and the trait value as the fixed effect and used the function *Anova* from the R package ‘car’ for backward model selection

(Fox et al. 2020). Zone was treated as a numerical rather than a categorical predictor given that the expected response would be linear in nature. We allowed the slope of the response to zone, type, and site to vary by species and included a nested random intercept to account for the sampling design of measuring zones within trees.

Intraspecific variation

Using four species collected in the coffee farm and forest at El Jaguar, we tested whether intraspecific variation shows a directional shift in trait values across land cover types. We used linear mixed models to test whether trait values responded to type allowing the response intercept to vary by species for each trait. We also considered intraspecific variation as a component of total variation in the full trait dataset by decomposing the variance in trait values for each trait among families, genera, species, and within species. We used the function *varcomp* in the R package 'ape' (Paradis et al. 2019).

Taxonomic and functional diversity

To test for differences in taxonomic diversity between sites and between forest and coffee farm epiphytes at each site, we used the 'vegan' package in R to calculate species richness, Shannon diversity index, and Pielou's evenness. We extrapolated species richness per site using Chao coverage-based rarefaction to assess sample coverage using the 'iNEXT' package in R (Hsieh & Chao 2020). We compared all diversity metrics among locations using ANOVA with Tukey post-hoc tests. For metrics of taxonomic beta diversity, we used the 'betapart' R package to calculate total beta diversity for each location and partition it into turnover and nestedness components (Baselga et al. 2018).

To compare functional diversity with taxonomic diversity, we used trait means combined with species abundances to calculate functional richness, evenness, divergence, and dispersion using the 'FD' package in R (Laliberté & Legendre 2010). Functional divergence and dispersion do not have direct analogs with taxonomic metrics. High divergence values indicate an abundant species with traits quite different from the trait mean. Dispersion measures the distance of each species from the trait centroid of all species at a site, weighted by abundance.

RESULTS

Trait spectra among epiphyte groups

Epiphyte groups separated in multidimensional trait space, with significant difference in the centroids of bromeliads, ferns, orchids, and other epiphytes (Fig. 2; PERMANOVA: f=3.87; p=0.002), but no significant difference in dispersion, indicating that centroid differences are not artificially inflated due to differences in spread. Bromeliads had less negative $\delta^{13}C$ than all other groups (ANOVA, f=13.73, $p<0.001$) and a higher C:N ratio than ferns and other epiphytes (ANOVA, f=4.92, p=0.006). Orchids had higher %C than ferns and other epiphytes (ANOVA, f=5.75, p=0.002) and on average slightly smaller leaves than ferns (ANOVA, f=3.42, p=0.03).

Compared to SLA and N_{mass} data from GLOPNET (Wright et al., 2004), epiphytes in our study fell within the midrange of values from the LES, indicating that, contrary to expectations, epiphytes are not operating at the extreme slow end of the LES. The slopes of the relationship were marginally different between the two datasets (Fig. 3; SMA, p=.04). However, when both datasets were combined, all but five of our epiphyte species had negative residuals, indicating that they had less leaf nitrogen at a given SLA than would be predicted on average. Three species of tank bromeliads showed the greatest divergences from the predicted values, with very low nitrogen, a characteristic trait of bromeliads overall in our data.

Together, all the epiphytes we measured showed significant relationships for all combinations of SLA, leaf thickness, C:N ratio, and N_{mass} (SMA, $p<0.001$ for all trait combinations). Within epiphyte groups (Fig. 4; orchids, bromeliads, ferns, and other epiphytes), all groups followed these patterns except bromeliads, which only showed significant slopes between C:N ratio and N_{mass} (slope=-1.21; $p<0.001$) and between SLA and leaf thickness (slope=-0.93, $p<0.001$).

Trait responses to environmental conditions

Models showed trait influences on abundance across all three environmental differences we tested, but different traits responded to different environmental variables. The four-way interaction between site, type, zone and trait was never significant. Reduced models include an interaction for trait with each environmental parameter and interactions among environmental variables (Table 2). There were strong interactions for $\delta^{13}C$ with land use type and with site (type x trait: z=-4.59, $p<0.001$; site x trait: z=3.37, $p<0.001$), patterns that disappeared when the three CAM bromeliads in the dataset were removed. SLA also increased in forests as compared with coffee farms (type x trait: z=2.15, p=0.03). The %C in leaves and the proportion of C:N both responded to zone, increasing higher in the tree irrespective of site or type (%C zone x trait: z=2.39, p=0.02; C:N zone x trait: z=2.70; p=0.007). Similarly, $\delta^{15}N$ showed a negative interaction with zone (zone x trait: z=-2.17, p=0.03), with more depleted $\delta^{15}N$ values in the higher branches of the tree. Leaf area and plant height were the only traits with significant three-way interactions between trait, site, and zone, indicating that the trait relationship to zone changed between the sites (leaf area: z=2.54, p=0.01; plant height: z=2.35, p=0.02). Surprisingly, leaf thickness and N_{mass} showed no response to any environmental gradients.

Incorporating the combined effect of all traits together via PC axes showed that traits varied by land use type and tree zone along PC1 (type x trait: z=-2.58, p=0.01; zone x trait: z=2.51; p=0.01). PC2 showed significant three-way interaction with site and zone, following the same pattern as leaf area and plant height showed individually (zone x site x trait: z=2.37, p=0.02). PC3, which was correlated with $\delta^{13}C$ and $\delta^{15}N$, showed weakly significant trait interactions for zone and type (type x trait: z=-2.17, p=0.03; zone x trait: z=2.00; p=0.05) Aside from the effects of $\delta^{13}C$ on abundance in response to environmental variables all traits showed mainly weak patterns, although the directionality of trait responses generally followed our predictions.

Intraspecific variation

Intraspecific variation also followed predicted trends (Fig. 5). Although we had low power to detect statistical differences due to the small number of samples, we did find, counter to our expectations, that leaf area was larger in individuals collected in the coffee farm (t=-2.49, p=0.02). Leaf thickness and SLA also showed some evidence of difference between the two land use types (leaf thickness: t=-1.73, p=0.09; SLA: t=1.71, p=0.10).

Partitioning variance among taxonomic levels revealed that intraspecific variation was greater for elemental traits than for morphological traits (Fig. 6). Percent carbon showed the highest intraspecific variance; however, this may be due to the fact that total variation among all species in the dataset was relatively small for that trait. Intraspecific variation exceeded variation between congeners in all traits except leaf area, plant height, and leaf thickness, which were remarkably consistent within species. These results indicate that the assumption of greater variation among than within species is better supported for morphological traits than for elemental traits. Across all traits, intraspecific variation accounted for 29.7% of total variation.

Taxonomic and functional diversity

On a per-tree basis, there were no differences in taxonomic alpha diversity measures between coffee farm and forest at the two farms (Table 3; ANOVA; species richness: f=0.97, p=0.41; Shannon diversity: f=1.73; p=0.18; Pielou's evenness: f=1.30, p=0.29). However, based on extrapolated species richness estimates the El Jaguar farm contained greater total richness and more similarity in richness between forest and coffee farm epiphyte assemblages (Fig. 7). Surprisingly, the forest at El Jaguar had the lowest overall beta diversity of the four locations, but the highest proportion of beta diversity attributable to turnover, whereas both coffee farm and forest at Selva Negra had higher nested proportions (Fig. 8).

Functional richness showed the opposite pattern from taxonomic richness between the two farms with the forest at Selva Negra containing significantly higher functional richness than either land use type at El Jaguar (ANOVA, f=5.02, p=0.006). Functional richness measures the convex hull volume of all trait values of all species in the community. Functional evenness tended to be higher in the coffee farms at the two sites, although the difference was not significant. Higher evenness indicates that abundance of different trait values is similar across the total range of values. Functional divergence was highest in the forest at El Jaguar and lowest in the forest at Selva Negra (ANOVA, f=3.95, p=0.02). Finally, functional dispersion showed the greatest difference among sites, with both forest and coffee at Selva Negra being higher than either land use type at El Jaguar (ANOVA, f=7.07, p<0.001). Dispersion is strongly correlated with functional richness (t=4.52, p<0.001), but also incorporates the abundance of species.

DISCUSSION

Trait spectra among epiphyte groups

Although slow rates of growth and photosynthesis are common among epiphytes (Stuntz & Zotz 2001; Zotz & Hietz 2001), we placed epiphyte values for SLA and N_{mass} on the LES for the first time and showed that their traits are less extreme than might be expected when compared to plants from arid environments. Epiphyte diversity and abundance decline steeply with precipitation (Gentry & Dodson 1987), so even the highest stress locations in humid montane forests (e.g., outer branches of the canopy) may experience less extreme water limitation than ground-rooted plants in warm arid regions. Indeed, $\delta^{13}C$ values for many of the C3 epiphytes in our study were highly negative, particularly for individuals collected in forests, indicating that, despite their adaptations to withstand drought, epiphytes in the montane tropics may not be severely water limited most of the time. In some cases, montane epiphytes may even have depleted $\delta^{13}C$ values compared with host trees (Cardelús & Mack 2010).

In comparison to the GLOPNET dataset, our epiphytes showed lower leaf N for a given SLA than the average across the dataset (Fig. 3). This mirrors a previous finding by Zotz and Hietz (2001), indicating it may be a broader trend among epiphytes. The pattern could be produced in several ways, including N limitation; the prevalence of succulent water storage tissue or aerenchyma in epiphyte leaves; or differences in how N is utilized in epiphytes compared with terrestrial plants (Zotz & Hietz 2001). Within epiphytes, bromeliads have been shown to have higher photosynthetic capacity per unit N than other groups (Stuntz & Zotz 2001), suggesting that differences in N utilization may be an important factor (Cardelús & Mack 2010; Petter et al. 2016).

While ferns, orchids, and most other groups of epiphytes showed patterns that were consistent with the LES, bromeliads differed in slope or showed no relationship for the majority of the trait-trait relationships we tested (Fig. 4). Nitrogen content was low across all bromeliad species, but tank bromeliads also manifested relatively high SLA values, possibly related to their more continuous access to water, and the result was no correlation between the two traits in bromeliads. Moreover, bromeliads tended to have less negative $\delta^{13}C$ values than other groups even after removing the CAM species, indicating greater stomatal limitation, a pattern also documented previously (Cardelús & Mack 2010). These differences between bromeliads and the rest of the epiphytes are potentially problematic because bromeliads have been more studied than other groups and their differences may skew our understanding of epiphytes generally (Zotz & Hietz 2001). More investigation is needed to understand how bromeliad trait-trait relationships relate to those of other epiphytes, but it appears they diverge more strongly from patterns observed in ground-rooted plants than other epiphyte groups. These trait differences could have important implications for bromeliad environmental tolerances and help to explain the dominance of Bromeliaceae at more arid sites (Gentry & Dodson, 1987; also see Chapter 2). For the rest of the epiphytes, the similarities we found to trait-trait relationships in terrestrial plants suggest that more standard trait assumptions may apply relatively well.

Trait responses to environmental conditions

Large compositional differences existed between our two sites that we believe to be related to climate (Chapter 2); however, these were not reflected in trait differences. Out of all our trait models, the site-by-trait interaction term was significant only for $\delta^{13}C$, reflecting considerably greater presence of CAM individuals at Selva Negra than at El Jaguar. The proportion of epiphytes utilizing CAM should increase in drier sites and with greater sun exposure, as we found (Silvera et al. 2010; Crayn et al. 2015). Between land use types, species with enriched $\delta^{13}C$ and lower SLA increased in abundance in coffee farms, indicating greater water use efficiency, more prevalence of CAM, and a slower leaf economics strategy outside of the forest. Across zones of the tree, higher %C and C:N ratio in higher tree zones indicates longer-lived and better defended leaves, consistent with the slower end of the LES. Epiphytes also showed more depleted $\delta^{15}N$ values in higher zones, suggesting that outer tree branches are dominated by atmospheric epiphyte forms that derive nutrients mainly from rainfall (Hietz et al. 2002).

We found little trait response to site despite considerable differences in species composition, suggesting that traits are less related to macroclimate than to microclimate conditions within sites (Petter et al. 2016; Schellenberger Costa et al. 2018; Agudelo et al. 2019). Comparing trait change along an elevational gradient and with attachment height within trees, Agudelo et al. (2019) documented orthogonal axes of trait variation aligned with the two gradients. We found a similar relationship where traits varied either within zones of a tree or between sites and land use types, but not both. However, we found different traits aligned with tree zones vs. landscape variables than did Agudelo et al. (2019), suggesting more work on this front is still required.

Intraspecific variation

We documented higher ratios of intraspecific variability among leaf elemental traits than among morphological traits. We attribute this partially to having multiple measurements per individual for morphological traits, but it follows previous findings for epiphytes in multiple environments (Petter et al. 2016; Schellenberger Costa et al. 2018). The lowest proportion of intraspecific variation occurred for plant height, leaf thickness, and leaf area, indicating that these traits are strongly conserved within species. We saw similar mean intraspecific variation across all traits to previous studies for both epiphytes and terrestrial plants (Petter et al. 2016; Anderegg et al. 2018), with nearly 30% of total variation occurring within species (Fig. 6). Trait plasticity within species may allow them to persist even in locations where environmental filters would eliminate mean trait values (Violle et al. 2012).

In our reduced dataset of four species from the El Jaguar coffee farm and forest, leaf area was the only trait that showed a significant intraspecific change across land use types, with larger leaves unexpectedly occurring in the higher stress environment of the coffee farm. This differed from previous work comparing intraspecific trait values between forest and coffee farm epiphytes (Susan-Tepetlan et al. 2015), and the leaves in our study still tended to be thicker with lower SLA than their forest counterparts. Unfortunately, we were unable to test intraspecific differences related to tree zone with our data. Petter et al. (2016) documented that intraspecific variation strongly correlated with the vertical range of species, and we suspect that the same pattern would apply at our study sites given the wide vertical distributions of many species. Intraspecific variation should be important in helping epiphytes to adapt to abiotic conditions associated with land use and climate changes, and could even attenuate the responses predicted based on trait means alone (Violle et al. 2012). We might even expect trait plasticity to be more important for epiphytes than for ground-rooted plants because of the large abiotic variance they experience over small distances. Much more work is still needed to relate intraspecific variation to environmental tolerances and distributions in epiphytes, and even in terrestrial plants this question has not been fully resolved (Violle et al. 2012; Anderegg et al. 2018).

Taxonomic and functional diversity

Functional diversity metrics surprisingly showed different and contradictory patterns to taxonomic measures, particularly evident in comparing species richness to functional richness. Where species richness did not vary on a per-tree basis between sites or land use types, functional richness was considerably higher at Selva Negra, the farm with greater insolation and less cloud immersion, than at El Jaguar. This pattern was driven by greater functional divergence at Selva Negra, which we attribute to stronger gradients within trees such that the most exposed locations within trees experience greater stress than the same tree positions at the cloudier site. However, previous work on tropical terrestrial plants has also documented higher functional richness at higher stress sites (Apaza-Quevedo et al. 2015), so it is possible that more stressful environments select for a few successful divergent strategies, whereas less stressful environments allow for a range of intermediate strategies. In the case of Selva Negra, two of the most abundant species fell at either end of the spectrum of orchid variation within our dataset (Fig. 2). *Jacquiniella teretifolia* has small, succulent, terete leaves with low N content, while *Isochilus linearis* has small, thin leaves with high N content and no water storage organs. Both plants are of similar stature and largely cooccur, suggesting that these two divergent strategies both succeed under similar abiotic conditions.

However, the functional diversity metrics we calculated here may not fully capture the functional diversity of the systems we studied. We only measured traits for the most common species and some rare species may also be functionally rare in these communities. Species that occur in forest understories were underrepresented in our sampling because their relative abundances were low, but they were largely missing from coffee farms. Despite these caveats, functional diversity metrics provided complementary information to our taxonomic metrics, demonstrating the importance of assessing the multiple dimensions of biodiversity within epiphyte communities (Moreno et al. 2018).

CONCLUSIONS

Epiphytes follow many of the patterns we would expect based on terrestrial plant traits. However, our work reiterates that care must be taken when generalizing, even among epiphyte groups. We documented considerable differences in trait values and trait-trait relationships between bromeliads and the rest of the epiphytes. These differences may contribute to the extreme drought tolerance in some bromeliads that allow them to colonize even dry forests where most other epiphytes are rarely found. In coffee farms, we documented only weak relationships between drought tolerance traits and species abundance, and the two land use types were indistinguishable based on most of the traits we studied. Coffee farm assemblages also showed only slightly reduced taxonomic and functional diversity as compared with forests, reinforcing the value of agroforests as epiphyte habitat. Intraspecific variation may contribute to species adaptation to these land use differences as well as to climate change. Most of the species we sampled occurred in both coffee farms and forests, although the ratio varied, and some occurred at the two climatically different sites, suggesting broad environmental tolerances across most common species. Epiphytes occupy multiple environmental gradients simultaneously, which may confound their value as indicators of global change. However, they may also provide a unique opportunity to disentangle the convoluted influences of light, moisture availability, and temperature on leaf traits by considering multiple gradients together. Indeed, we found that, when environmental gradients were considered simultaneously, the traits we measured responded differently to each variable. As more data become available, meta-analyses of epiphyte traits will be able to shed more light on these trait-environment relationships and document trait spectra for epiphytes, improving the predictive value. Future research should also strive to move beyond leaf traits and explore other axes of variation for epiphytes, including reproductive and root traits, to paint a more complete picture of epiphyte functional ecology.

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TABLES AND FIGURES

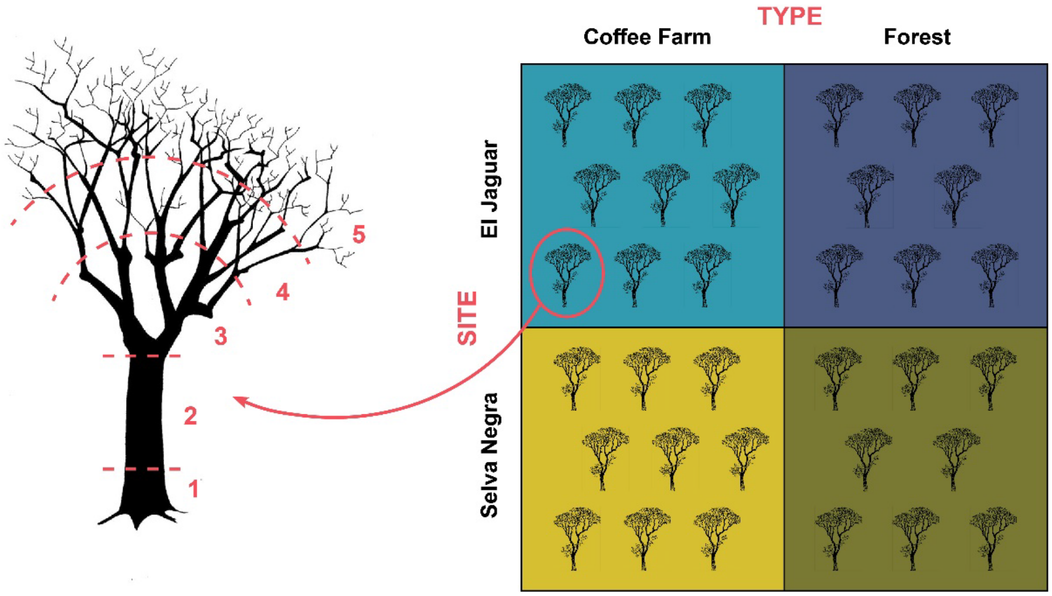

Figure 1. Study design. At each of the two farms, El Jaguar and Selva Negra, we surveyed nine trees in the coffee farm and eight trees in the forest. Sites differed climatically with Selva Negra having higher insolation and less cloud immersion than El Jaguar. Each tree was divided into zone following the Johansson zonation scheme (Johansson 1974).

Table 1. Trait means and standard deviations for all species measured. Only species with 3 or more individuals (n) were included in analyses, but all species we measured are included here. Leaf morphological traits were based on two leaves per plant, plant height included one measurement per plant, and chemical traits were based on a random subset of individuals collected.

Taxon	Family	Plant height	Leaf area	Leaf thickness	SLA	%N	%C	C:N ratio	$\delta^{13}C$	$\delta^{15}N$	n
Anthurium scandens ssp. *pusillum*	Araceae	15.8 ± 7.22	3.16 ± 1.44	0.38 ± 0.05	19.88 ± 4.95	1.79 ± 0.29	41.2 ± 4.71	23.46 ± 4.25	-28.94 ± 1.28	-6.29 ± 2.1	8
Anthurium scandens ssp. *scandens*	Araceae	33.54 ± 20.85	20.03 ± 8.3	0.48 ± 0.07	11.14 ± 2.13	1.47 ± 0.13	44.13 ± 5.81	30.16 ± 4.29	-27.91 ± 1.96	-1.98 ± 1.78	7
Liabum bourgeaui	Asteraceae	108.7 ± 31.19	76.19 ± 22.13	0.3 ± 0.03	15.84 ± 2.72	2.4 ± 0.17	50.26 ± 4.13	21.05 ± 2.69	-27.14 ± 0.88	6.16 ± 0.96	5
Catopsis nitida	Bromeliaceae	31.08 ± 4.97	140.01 ± 50.13	0.32 ± 0.06	16.48 ± 2.59	0.88 ± 0.14	52.23 ± 6.53	66.18 ± 7.04	-25.41 ± 1.24	-4.54 ± 1.29	5
Guzmania monostachia	Bromeliaceae	29.56 ± 3.42	59.99 ± 16.06	0.56 ± 0.05	18.03 ± 0.64	1.03 ± 0.2	49.06 ± 4.45	49.01 ± 9.46	-23.63 ± 1.05	-3.58 ± 2.16	5
Guzmania nicaraguensis	Bromeliaceae	34.53 ± 12.26	95.45 ± 13.88	0.47 ± 0.1	25.06 ± 1.85	1.41 ± 0.29	48.78 ± 7.88	36.18 ± 11.05	-29.93 ± 0.79	-4.16 ± 2.96	6
Tillandsia butzii	Bromeliaceae	31.15 ± 7.02	11.42 ± 3.61	1.18 ± 0.31	5.48 ± 2.05	1.01 ± 0.2	51.75 ± 4.43	53.18 ± 13.26	-13.57 ± 0.81	-11.96 ± 0.09	4
Tillandsia fasciculata	Bromeliaceae	44.25 ± 2.52	47.53 ± 10.56	1.33 ± 0.27	7.13 ± 2.01	0.92 ± 0.13	49.12 ± 4.54	54.12 ± 8.35	-16.71 ± 8.1	-3.38 ± 1.29	4
Tillandsia schiedeana	Bromeliaceae	32.73 ± 5.54	3.87 ± 1.56	1.25 ± 0.12	7.21 ± 1.42	1.12 ± 0.06	49.02 ± 4.81	52.22 ± 15.18	-13.52 ± 0.55	-10.41 ± 0.84	4
Elaphoglossum furfuraceum	Dryopteridaceae	22.2 ± 5.51	34.55 ± 8.16	0.46 ± 0.12	10.22 ± 3.77	1.25 ± 0.14	46.98 ± 4.1	37.91 ± 5.74	-29.32 ± 1.31	-5 ± 2.83	6
Elaphoglossum lonchophyllum	Dryopteridaceae	41.28 ± 3.91	112.18 ± 33.94	0.27 ± 0.03	11.53 ± 2.15	1.56 ± 0.1	46.23 ± 3.61	29.7 ± 2.53	-31.63 ± 1.53	-3.27 ± 1.14	5
Elaphoglossum peltatum	Dryopteridaceae	4.57 ± 1.24	3.83 ± 1.83	0.35 ± 0.05	19.09 ± 4.13	1.76 ± 0.3	43.51 ± 4.43	25.23 ± 3.52	-29.96 ± 1.26	-5.71 ± 1.64	12
Cavendishia bracteata	Ericaceae	73.12 ± 26.38	67.21 ± 18	0.55 ± 0.11	10.59 ± 1.88	1.33 ± 0.45	51.88 ± 4.6	41.83 ± 11.4	-30.8 ± 0.62	-6.85 ± 2.11	5
Sphyrospermum buxifolium	Ericaceae	21.98 ± 8.59	1.94 ± 0.41	1.62 ± 0.5	11.49 ± 3.36	1.11 ± 0.36	48.59 ± 2.52	46.66 ± 14.03	-31.57 ± 1.42	-6.76 ± 2.27	11

Taxon	Family	Plant height	Leaf area	Leaf thickness	SLA	%N	%C	C:N ratio	$\delta^{13}C$	$\delta^{15}N$	n
Columnea rubricaulis	Gesneriaceae	56.48 ± 18.33	6.97 ± 1.83	0.61 ± 0.1	19.88 ± 6.92	1.56 ± 0.15	42.64 ± 4.35	27.5 ± 3.88	-29.71 ± 2.29	-2.78 ± 0.81	6
Elleanthus poiformis	Orchidaceae	15.44 ± 4.06	0.31 ± 0.08	0.37 ± 0.02	8.99 ± 3.32	1.56 ± 0.18	49.66 ± 1.36	32.11 ± 4.65	-30.3 ± 0.83	-3.78 ± 1.29	5
Epidendrum chlorocorymbos	Orchidaceae	34 ± 0	10.76 ± 1.06	1.06 ± 0.04	11.66 ± 0.37	1.4 ± NA	42.25 ± NA	30.18 ± NA	-23.73 ± NA	-0.29 ± NA	1
Epidendrum laucheanum	Orchidaceae	25 ± 10.39	7.5 ± 1.04	0.92 ± 0.11	8.38 ± 0.38	0.92 ± NA	50.75 ± NA	55.16 ± NA	-24.76 ± NA	-4.89 ± NA	2
Epidendrum paranthicum	Orchidaceae	10.46 ± 3.98	0.34 ± 0.06	1.03 ± 0.17	15.36 ± 8.43	1.38 ± NA	48.94 ± NA	35.46 ± NA	-29.09 ± NA	-3.35 ± NA	7
Epidendrum ramosum	Orchidaceae	30.08 ± 10.53	6.74 ± 1.73	0.79 ± 0.18	13.94 ± 3.76	1.36 ± 0.05	48.46 ± 3.09	35.64 ± 2.07	-27.72 ± 1.23	-2.33 ± 2.76	7
Isochilus linearis	Orchidaceae	25.02 ± 7.48	0.89 ± 0.29	0.18 ± 0.02	16.13 ± 3.33	2.54 ± 0.37	55.94 ± 6.82	22.31 ± 3.55	-28.84 ± 0.92	-1.94 ± 1.03	5
Jacquiniella teretifolia	Orchidaceae	25.04 ± 5.34	0.84 ± 0.15	2.38 ± 0.21	4.72 ± 0.88	0.87 ± 0.11	49.14 ± 5.03	57.27 ± 9.82	-26.32 ± 2.28	-3.07 ± 1.36	7
Maxillaria variabilis	Orchidaceae	15.79 ± 4.34	8.67 ± 3.2	0.44 ± 0.12	9.65 ± 2.29	1.68 ± 0.49	56.92 ± 8.9	36.24 ± 12.69	-28.91 ± 1.47	-4.37 ± 2.66	7
Pleurothallis matudiana	Orchidaceae	16.45 ± 2.25	13.43 ± 3.83	2.04 ± 0.35	7.28 ± 0.96	1.08 ± 0.22	57.58 ± 0.11	54.17 ± 10.85	-28.06 ± 0.25	-4.13 ± 2.26	2
Pleurothallis platystylis	Orchidaceae	18.25 ± 3.71	17.73 ± 4.66	3.11 ± 0.59	4.3 ± 1.41	1.02 ± 0.13	44.4 ± 3.56	44.85 ± 1.97	-25.83 ± 1.46	-1.36 ± 4.03	4
Prosthechea fragrans	Orchidaceae	28.6 ± 9.13	39.29 ± 13	0.95 ± 0.09	8.42 ± 0.98	1.29 ± 0.16	53.2 ± 7.34	41.7 ± 7.03	-28.66 ± 0.78	-0.44 ± 0.42	7
Prosthechea ochracea	Orchidaceae	21.86 ± 6.1	10.63 ± 3.11	0.36 ± 0.04	14.42 ± 2.07	1.71 ± 0.24	51.16 ± 4.16	30.47 ± 5.24	-28.7 ± 1.82	-1.3 ± 3.01	7
Scaphyglottis micrantha	Orchidaceae	12.2 ± 0.91	3.99 ± 1.14	0.24 ± 0.05	17.19 ± 3	1.72 ± 0.4	57.37 ± 9.57	33.6 ± 2.17	-29.81 ± 1.35	-0.64 ± 0.52	3
Stelis parvula	Orchidaceae	11.79 ± 3.35	6.42 ± 1.65	1.24 ± 0.18	12.35 ± 3.15	1.17 ± 0.16	47.26 ± 4.23	41.15 ± 6.51	-29.74 ± 1.82	-6.33 ± 1.56	8
Stelis purpurescens	Orchidaceae	19.8 ± 1.77	10.83 ± 3.03	1.17 ± 0.26	8.72 ± 1.76	1.04 ± 0.29	48.93 ± 4.45	49.83 ± 13.43	-27.71 ± 1.87	-5.05 ± 1.31	5
Peperomia angustata	Piperaceae	10.65 ± 2.69	6.38 ± 3.31	1.23 ± 0.4	17.54 ± 4.31	1.59 ± 0.52	42.14 ± 4.9	28.37 ± 8.12	-29.04 ± 0.94	-0.6 ± 4.5	6

Taxon	Family	Plant height	Leaf area	Leaf thickness	SLA	%N	%C	C:N ratio	$\delta^{13}C$	$\delta^{15}N$	n
Peperomia deppeana	Piperaceae	2.18 ± 0.5	0.24 ± 0.07	1.1 ± 0.23	14.26 ± 5.99	1.05 ± NA	40.91 ± NA	38.96 ± NA	-28.87 ± NA	-3.18 ± NA	5
Peperomia obtusifolia	Piperaceae	17.35 ± 4.77	15.52 ± 5	1.06 ± 0.27	13.63 ± 2.96	1.32 ± 0.4	43.4 ± 6.08	35.46 ± 14.16	-29.41 ± 1.9	-1.45 ± 0.83	11
Peperomia quadrifolia	Piperaceae	8.3 ± 0	0.55 ± 0.06	0.69 ± 0.1	18.45 ± 1.97	NA	NA	NA	NA	NA	1
Peperomia tetraphylla	Piperaceae	10.13 ± 0.99	0.67 ± 0.12	2.3 ± 0.16	16.27 ± 6.42	1.1 ± 0.11	44.1 ± 0.91	40.43 ± 3.48	-29.93 ± 1.61	-2.19 ± 1.48	3
Campyloneurum angustifolium	Polypodiaceae	26.57 ± 8.44	16.83 ± 3.54	0.74 ± 0.17	7.76 ± 4.78	1.72 ± 0.54	45.97 ± 0.55	28.15 ± 9.12	-26.62 ± 0.97	-0.76 ± 3.62	7
Niphidium crassifolium	Polypodiaceae	63.12 ± 11	279.71 ± 85.24	0.62 ± 0.07	5.29 ± 0.89	0.74 ± 0.06	47.77 ± 5.27	64.8 ± 5.08	-25.55 ± 1.53	-0.93 ± 1.57	6
Phlebodium pseudoaureum	Polypodiaceae	63.4 ± 0	NA	0.34 ± 0.04	NA	1.46 ± NA	45.3 ± NA	31.03 ± NA	-25.44 ± NA	2.09 ± NA	1
Pleopeltis macrocarpa	Polypodiaceae	14.31 ± 2.34	14.64 ± 5.13	0.62 ± 0.16	8.81 ± 2.45	1.08 ± 0.32	44.53 ± 4.08	43.99 ± 11.88	-30.12 ± 1.88	-2.39 ± 1.46	7
Polypodium lindenianum	Polypodiaceae	30.17 ± 4.95	NA	0.5 ± 0.07	NA	2.24 ± 0.42	50.91 ± 5.18	23.51 ± 5.66	-27.15 ± 1.15	-4.6 ± 5.4	6
Polypodium plebium	Polypodiaceae	16.31 ± 3.23	42.06 ± 16.65	0.49 ± 0.06	15.98 ± 5.78	1.52 ± 0.57	50.54 ± 6.44	37.94 ± 17.17	-29.27 ± 1.05	-4.79 ± 2.11	9
Serpocaulon ptilorhizon	Polypodiaceae	24.04 ± 6.58	60.81 ± 19.35	0.36 ± 0.06	33.6 ± 10.78	2.04 ± 0.62	45.14 ± 1.2	23.61 ± 6.12	-30.46 ± 2.04	-4.53 ± 1.3	7
Hillia panamensis	Rubiaceae	83.43 ± 29.85	1.28 ± 0.26	0.66 ± 0.27	15.9 ± 2.3	2.16 ± 0.66	50.7 ± 3.94	25.7 ± 9.29	-30.16 ± 0.84	-3.19 ± 2.74	6

Table 2. Model output for trait GLMMs. Not all models included all terms; terms that were omitted from the best model are indicated as *NA*. Significant P values at the <0.05 level are bolded. For each term we include the model estimate (Est.), the standard error (SE), the Z value (Z), and the estimated P value (P). Models included random effects allowing site, type, and zone to vary by species and a random intercept term to account for the nested design of zones within trees. PC axes integrating all traits were also modeled.

Trait		**Intercept**	**Trait Main Effect**	**Site Main Effect**	**Type Main Effect**	**Zone Main Effect**	**Trait x Site**	**Trait x Type**	**Trait x Zone**	**Site x Type**	**Site x Zone**	**Type x Zone**	**Site x Zone x Trait**
δ^{13}C	*Est.*	-20.989	-0.307	13.947	-9.001	0.898	0.527	-0.283	0.035	2.063	-0.289	0.202	*NA*
	SE	2.787	0.097	4.378	1.826	0.499	0.156	0.061	0.017	0.444	0.137	0.118	
	Z	-3.944	-3.170	3.185	-4.929	1.798	3.379	-4.615	1.993	4.643	-2.111	1.711	
	P	**<0.001**	**0.002**	**0.001**	**<0.001**	0.072	**<0.001**	**<0.001**	**0.046**	**<0.001**	**0.035**	0.087	
% Carbon	*Est.*	8.824	-0.236	-15.135	5.313	-1.927	0.300	-0.135	0.039	2.032	-0.278	0.198	*NA*
	SE	4.340	0.090	8.392	3.485	0.786	0.173	0.072	0.016	0.446	0.137	0.118	
	Z	2.033	-2.613	-1.803	1.524	-2.450	1.735	-1.872	2.381	4.555	-2.032	1.679	
	P	**0.042**	**0.009**	0.071	0.127	**0.014**	0.083	0.061	**0.017**	**<0.001**	**0.042**	0.093	
C:N Ratio	*Est.*	0.366	-0.076	-4.216	0.727	-0.660	0.093	-0.049	0.016	2.041	-0.285	0.199	*NA*
	SE	1.328	0.032	2.569	1.131	0.243	0.062	0.026	0.006	0.446	0.137	0.118	
	Z	0.276	-2.342	-1.641	0.643	-2.718	1.483	-1.913	2.701	4.579	-2.074	1.686	
	P	0.783	**0.019**	0.101	0.520	**0.006**	0.138	0.056	**0.007**	**<0.001**	**0.038**	0.091	
Leaf Area	*Est.*	-3.266	0.008	-0.068	-0.549	0.135	-0.018	0.006	-0.003	1.895	-0.434	*NA*	0.005
	SE	0.681	0.008	1.098	0.452	0.121	0.015	0.006	0.001	0.460	0.161		0.002
	Z	-4.796	1.032	-0.062	-1.216	1.121	-1.144	1.110	-1.984	4.120	-2.699		2.541
	P	**<0.001**	0.302	0.950	0.224	0.262	0.253	0.267	**0.047**	**<0.001**	**0.007**		**0.011**
Leaf Thickness	*Est.*	-2.108	-0.534	-0.943	-0.761	-0.163	0.332	-0.479	0.123	2.019	-0.279	0.200	*NA*
	SE	0.767	0.625	1.351	0.718	0.147	1.172	0.485	0.116	0.446	0.137	0.118	
	Z	-2.750	-0.854	-0.698	-1.060	-1.106	0.283	-0.987	1.068	4.526	-2.033	1.694	
	P	**0.006**	0.393	0.485	0.289	0.269	0.777	0.324	0.285	**<0.001**	**0.042**	0.090	
δ^{15}N	*Est.*	-2.097	0.116	0.541	-0.896	-0.274	0.309	0.076	-0.057	2.050	-0.288	0.199	*NA*
	SE	0.837	0.161	1.396	0.751	0.150	0.289	0.123	0.027	0.447	0.137	0.118	
	Z	-2.505	0.716	0.388	-1.194	-1.822	1.069	0.622	-2.139	4.588	-2.099	1.697	
	P	**0.012**	0.474	0.698	0.233	0.069	0.285	0.534	**0.032**	**<0.001**	**0.036**	0.090	

Trait		Intercept	Trait Main Effect	Site Main Effect	Type Main Effect	Zone Main Effect	Trait x Site	Trait x Type	Trait x Zone	Site x Type	Site x Zone	Type x Zone	Site x Zone x Trait
N_{mass}	*Est.*	-4.153	1.142	0.612	-2.238	0.306	-0.902	0.756	-0.258	2.034	-0.281	0.199	*NA*
	SE	1.467	0.952	2.693	1.210	0.266	1.792	0.740	0.170	0.446	0.137	0.118	
	Z	-2.831	1.199	0.227	-1.850	1.153	-0.503	1.021	-1.514	4.561	-2.049	1.689	
	P	**0.005**	0.230	0.820	0.064	0.249	0.615	0.307	0.130	**<0.001**	**0.041**	0.091	
Plant Height	*Est.*	-2.418	-0.010	1.301	-1.317	0.220	-0.085	0.032	-0.008	2.007	-0.630	*NA*	0.016
	SE	0.838	0.023	1.539	0.619	0.161	0.048	0.018	0.004	0.444	0.211		0.007
	Z	-2.886	-0.415	0.845	-2.129	1.366	-1.752	1.820	-1.715	4.520	-2.982		2.354
	P	**0.004**	0.678	0.398	**0.033**	0.172	0.080	0.069	0.086	**<0.001**	**0.003**		**0.019**
SLA	*Est.*	-3.978	0.097	1.650	-2.426	0.115	-0.179	0.105	-0.013	1.961	-0.273	0.187	*NA*
	SE	1.063	0.064	1.882	0.903	0.201	0.123	0.049	0.012	0.462	0.143	0.121	
	Z	-3.742	1.509	0.877	-2.687	0.573	-1.447	2.140	-1.905	4.242	-1.904	1.538	
	P	**<0.001**	0.131	0.380	**0.007**	0.567	0.148	**0.032**	0.273	**<0.001**	0.057	0.124	
PC1	*Est.*	-2.873	-0.509	-0.790	-0.366	0.006	0.653	-0.414	0.093	1.914	-0.245	*NA*	*NA*
	SE	0.563	0.217	0.934	0.402	0.102	0.417	0.161	0.038	0.461	0.142		
	Z	-5.100	-2.345	-0.846	-0.912	0.060	1.566	-2.571	2.424	4.158	-1.729		
	P	**<0.001**	**0.019**	0.397	0.362	0.952	0.117	**0.010**	**0.015**	**<0.001**	0.084		
PC2	*Est.*	-2.926	0.028	-0.766	-0.361	0.009	-0.607	0.234	-0.107	1.926	-0.251	*NA*	0.196
	SE	0.596	0.346	0.954	0.418	0.105	0.649	0.237	0.069	0.460	0.142		0.083
	Z	-4.907	0.082	-0.803	-0.863	0.086	-0.935	0.988	-1.557	4.182	-1.767		2.367
	P	**<0.001**	0.934	0.422	0.388	0.932	0.350	0.323	0.120	**<0.001**	0.077		**0.018**
PC3	*Est.*	-2.917	-0.568	-0.741	-0.362	0.006	0.479	-0.556	0.118	1.922	-0.247	*NA*	*NA*
	SE	0.582	0.366	0.950	0.408	0.104	0.666	0.258	0.062	0.460	0.141		
	Z	-5.010	-1.55	-0.78-	-0.887	0.061	0.720	-2.152	1.913	4.175	-1.749		
	P	**<0.001**	0.121	0.436	0.375	0.951	0.472	**0.031**	0.056	**<0.001**	0.080		

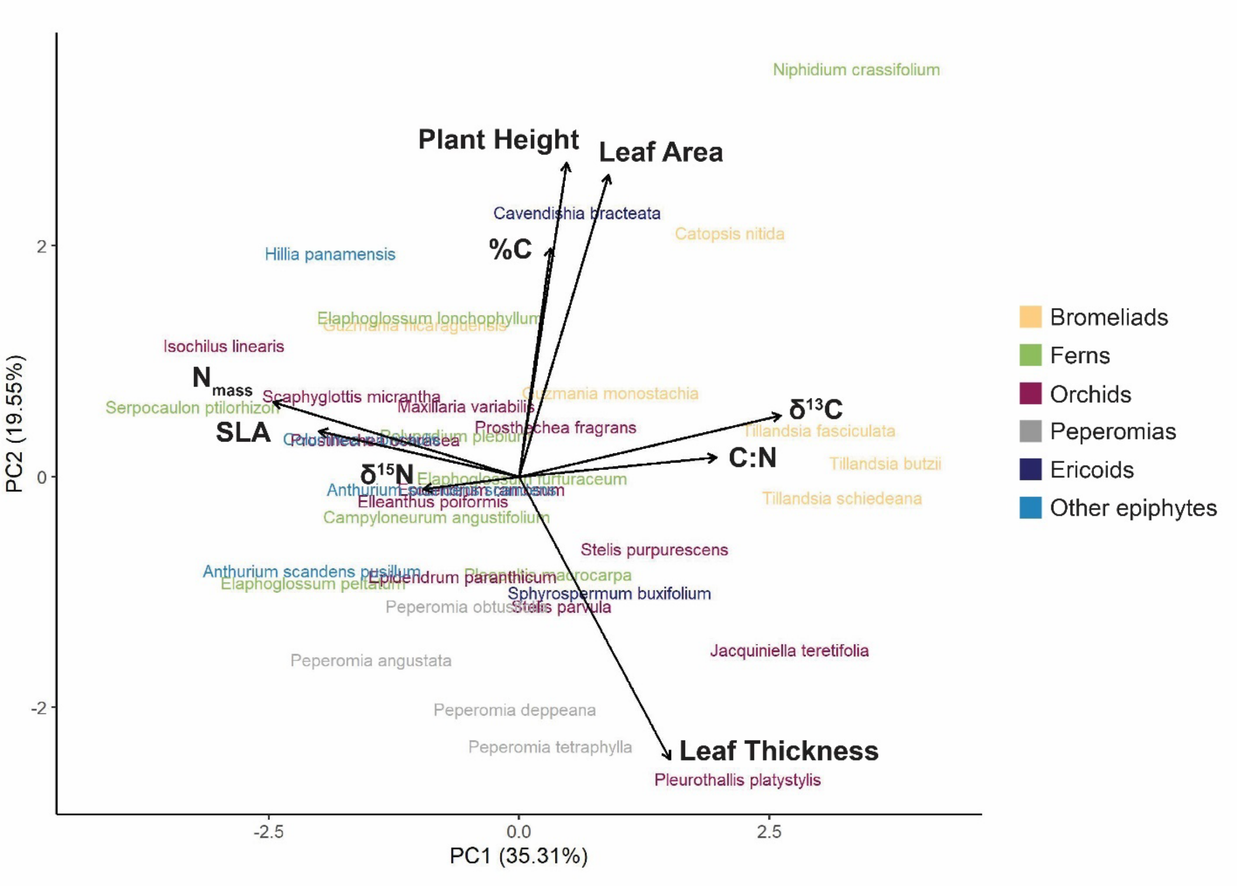

Figure 2. Principal Components Analysis shows separation among major epiphyte taxonomic groups along two primary axes of variation representing 54.86% of total trait variation. PC1 corresponds to the LES, with lower values representing the faster end of the spectrum containing ferns, some orchids, and epiphytes in other taxonomic groups. The slower, more resource conservative end of the spectrum includes atmospheric bromeliads and a few drought tolerant species of ferns and orchids. PC2 corresponds to a size-succulence axis, with large-statured, large-leaved plants with thin leaves at the highest values, and small-statured, succulent-leaved plants, mainly peperomias and orchids, at the other extreme.

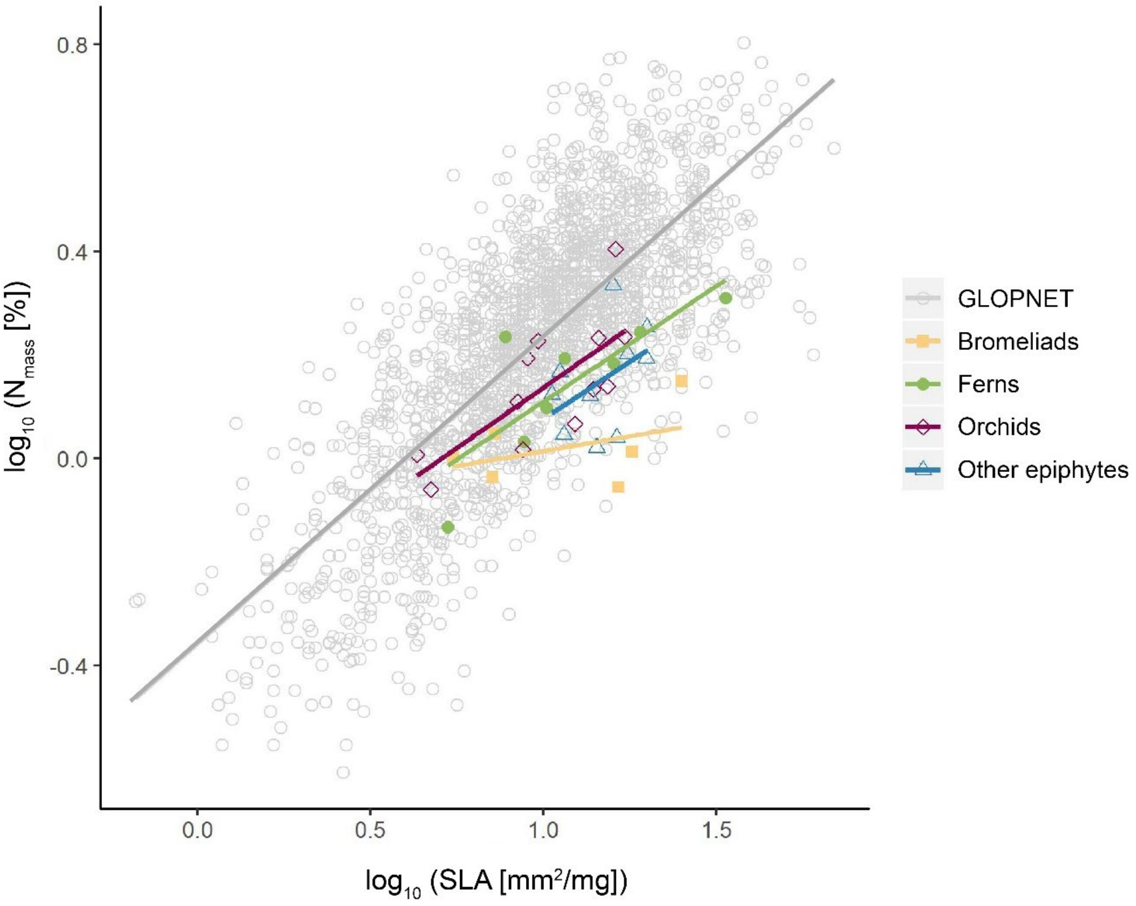

Figure 3. Epiphyte data from this study overlaid against global plant trait data from GLOPNET as published in Wright et al. (2004) showing the relationship between SLA and N_{mass}, one of the key trait-trait relationships of the leaf economics spectrum. Overall, epiphytes fall in the middle range of the LES and show a similar but less steep relationship between SLA and N_{mass}, particularly in bromeliads. Most epiphyte species also had less N_{mass} per SLA than would be predicted by the LES, perhaps indicating resource limitations.

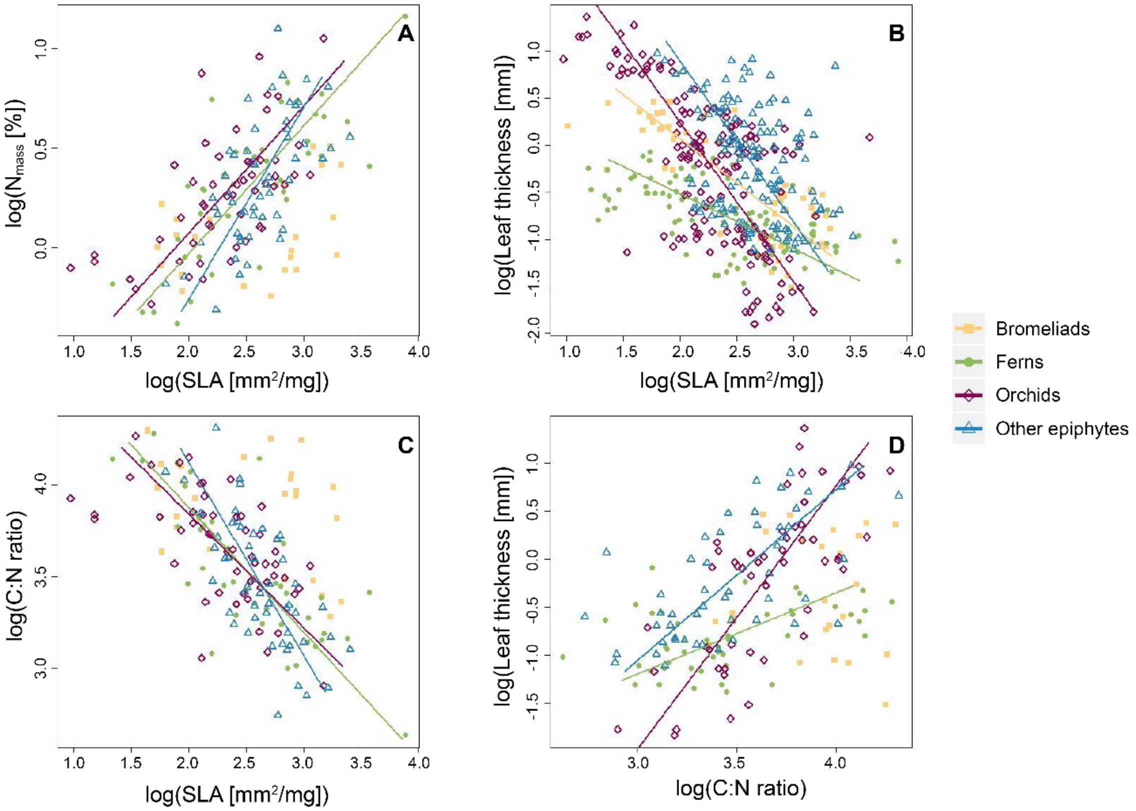

Figure 4. Standard major axis regressions comparing the slope of trait-trait relationships between bromeliads (yellow squares), ferns (green circles), orchids (purple diamonds), and other epiphytes (blue triangles. (A) The slope for N_{mass} and SLA was significantly positive for all groups except bromeliads; (B) Leaf thickness and SLA had a significant relationship for all groups, but the slope of the relationship differed for ferns and bromeliads from orchids and other epiphytes; (C) The slope for C:N ratio and SLA was significantly negative for all groups except bromeliads; (D) All groups had positive slopes for leaf thickness and C:N ratio except bromeliads, but the slopes differed. C:N ratio and N_{mass} were strongly negatively correlated so the remaining trait combinations we tested are omitted because they are inverses of those here.

Table 3. Taxonomic and functional diversity metrics for trees in coffee farm and forest at Selva Negra and El Jaguar. Superscript letters denote significant differences based on ANOVA with Tukey post-hoc tests.

Location	Taxonomic Richness	Shannon's D	Pielou's Eveness	Functional Richness	Functional Eveness	Functional Divergence	Functional Dispersion
El Jaguar Coffee	17.4 (± 8.0)	2.24 (± 0.45)	0.82 (± 0.07)	$5.52e^{-4}$ $(\pm 4.19e^{-4})^{a}$	0.68 (± 0.11)	0.74 $(\pm 0.14)^{ab}$	0.11 $(\pm 0.02)^{a}$
El Jaguar Forest	23.5 (±6.0)	2.63 (± 0.25)	0.84 (± 0.03)	$5.37e^{-4}$ $(\pm 2.65e^{-4})^{a}$	0.60 (± 0.10)	0.87 $(\pm 0.06)^{b}$	0.12 $(\pm 0.01)^{ab}$
Selva Negra Coffee	19.1 (± 7.2)	2.42 (± 0.27)	0.84 (± 0.04)	$11.64e^{-4}$ $(\pm 7.72e^{-4})^{ab}$	0.67 (± 0.07)	0.75 $(\pm 0.10)^{ab}$	0.15 $(\pm 0.03)^{c}$
Selva Negra Forest	20.8 (± 8.8)	2.36 (± 0.43)	0.80 (± 0.06)	$19.17e_{-4}$ $(\pm 14.21e^{-4})^{b}$	0.61 (± 0.06)	0.70 $(\pm 0.09)^{a}$	0.14 $(\pm 0.02)^{bc}$

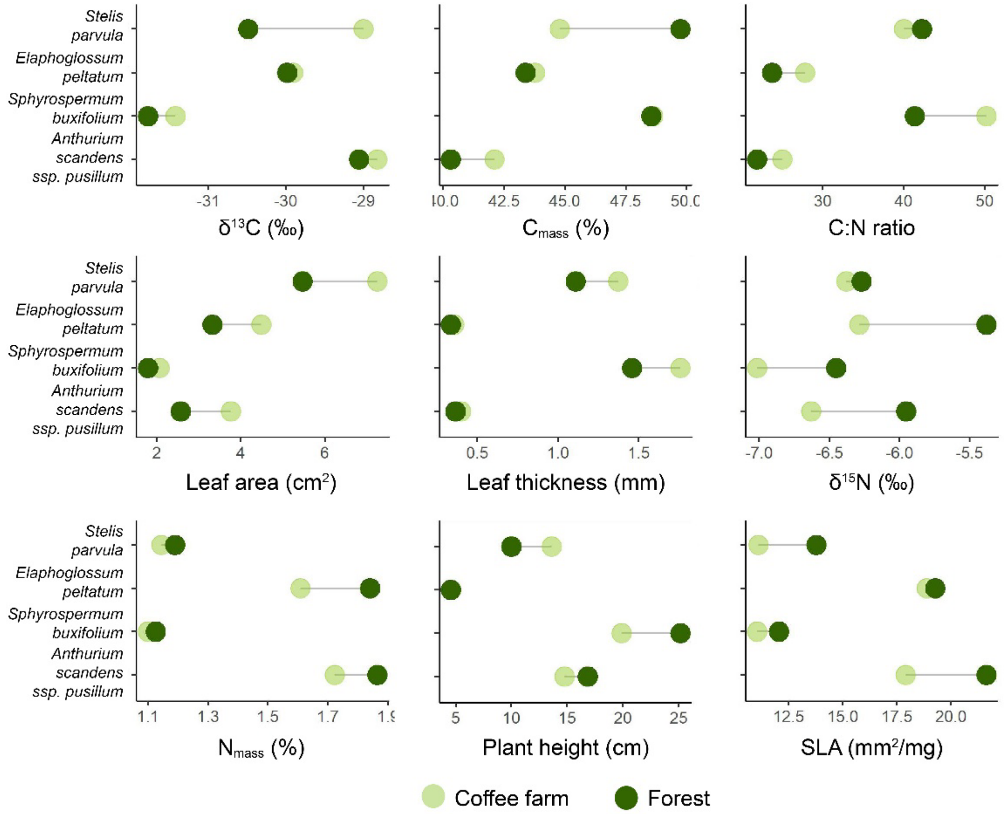

Figure 5. Shifts in trait averages by species for traits collected from individuals in coffee farms (light green) vs. in forest at the El Jaguar farm. Only leaf area shows a statistically significant change, but other traits are mainly consistent in direct across species although variable in degree.

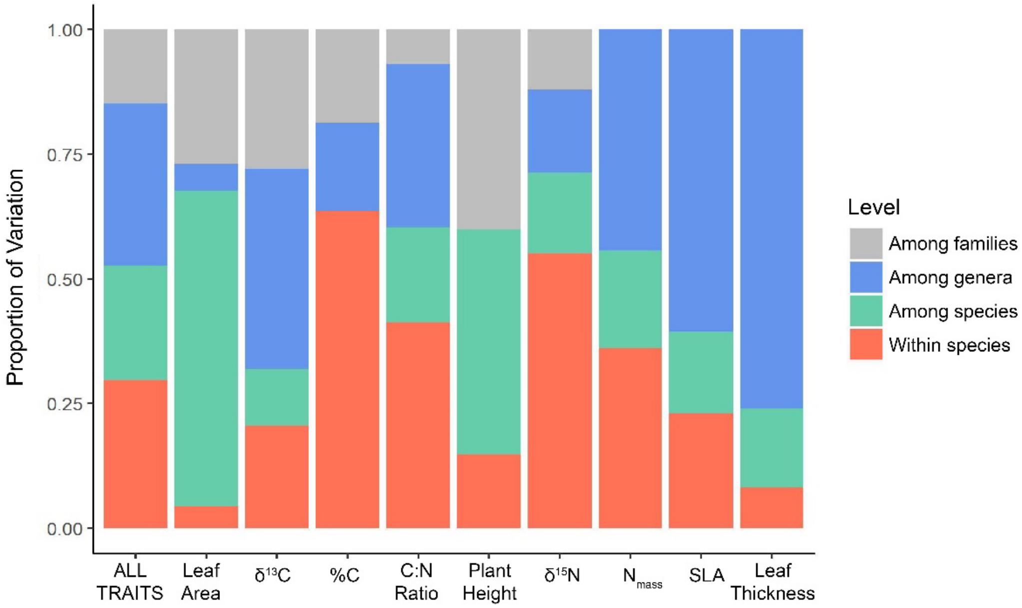

Figure 6. Variance partitioning for each trait shows that much of the variation measured occurred within species or among closely related species.

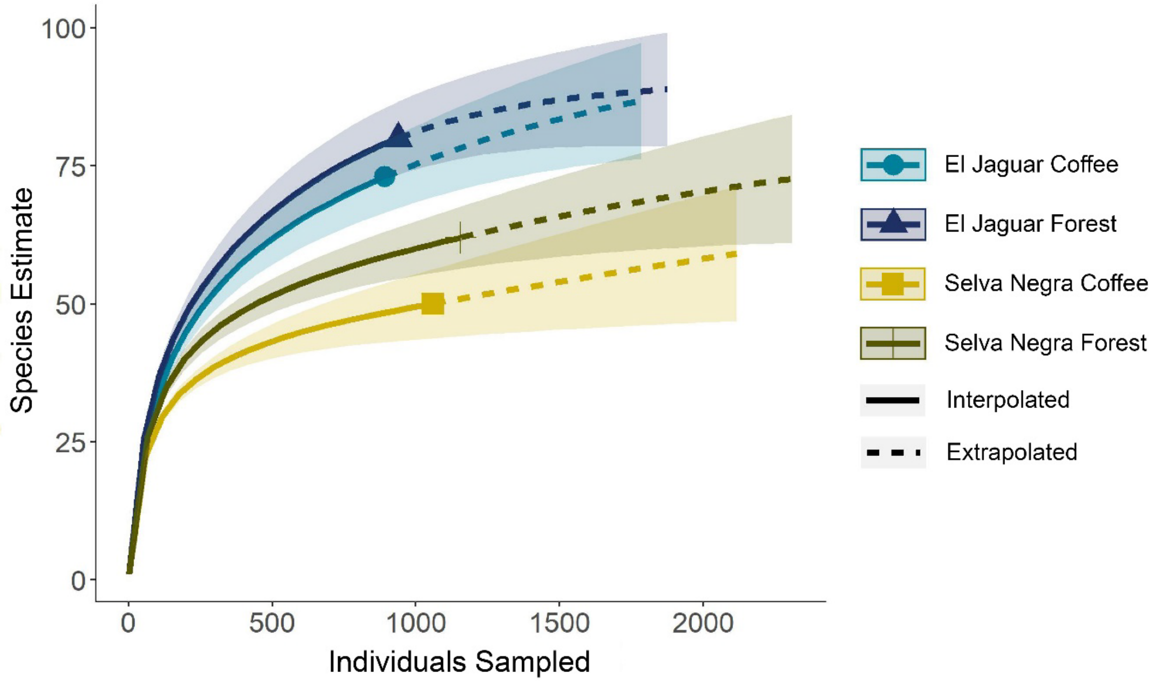

Figure 7. Species richness estimate based on extrapolation from Chao rarefaction comparing coffee farm and forest at the El Jaguar and Selva Negra sites.

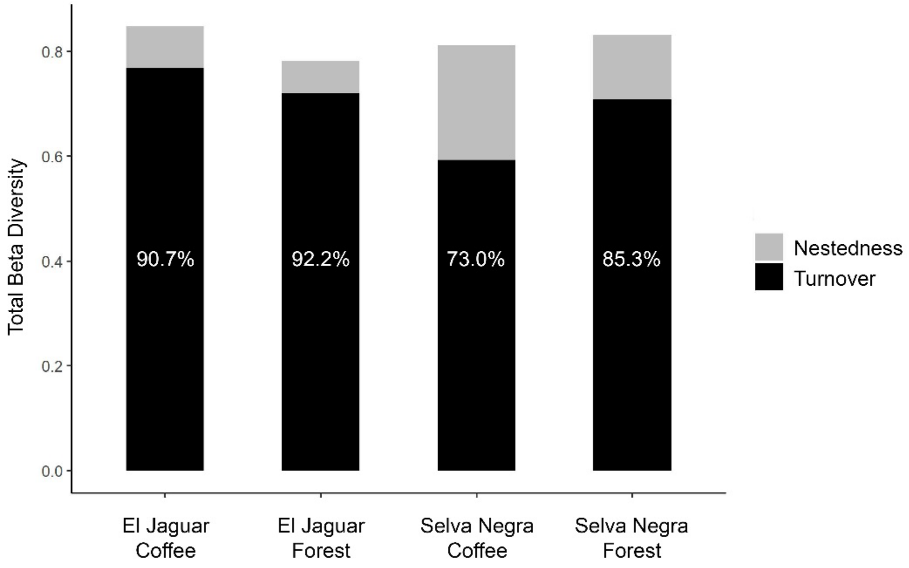

Fig. 8. Nestedness and turnover components of total beta diversity at each site.

Chapter 4: "A very noble crop": Financial stability, access to knowledge, and personal values support conservation in shade-grown coffee farms

Jeannine H. Richards[1], Ingrid M. Torrez Luna[2], Alberto Vargas[3]

[1] Nelson Institute for Environmental Studies, University of Wisconsin-Madison

[2] Centro Agronómico Tropical de Investigación y Enseñanza (CATIE), Nicaragua

[3] Latin American, Caribbean, and Iberian Studies, University of Wisconsin-Madison

ABSTRACT

Shade-grown coffee is an important reservoir for tropical biodiversity, but the quality of habitat for many species hinges on the decisions made by farmers. Here, we use epiphytes, air plants that grow on trees, to investigate the link between coffee producers' decisions and outcomes for biodiversity. We interviewed 33 producers in northern Nicaragua and used mixed-methods techniques to evaluate how producers view the trees and epiphytes on their farms. We assessed the relative strengths of personal values, technical knowledge, labor supply, and financial stability in influencing decision-making. Based on farm size, financial stability, and access to technical knowledge, we classified farms into typologies to understand how behavioral influences change with economic and social variables. Most producers had strong positive attitudes toward trees on their farms, recognizing a variety of important ecosystem services. Smallholders were more likely to connect trees with provisioning services, while producers on larger farms and with greater access to knowledge emphasized regulating services. Respondents across typologies stressed the restorative importance of shade coffee farming in repairing soil, water, and nutrient cycles on land damaged by other types of agriculture. They had fewer associations with epiphytes but connected them primarily with aesthetic values. Some producers remove epiphytes, particularly bryophytes, from coffee bushes and shade trees, but it was not the norm among our study participants. Based on the values for nature expressed by participants, shade coffee farming is conducive to conservation for epiphytes and other taxa. The conservation significance of this social-ecological system can be maintained and expanded through economic and capacity-building conservation interventions, especially when those can be connected to values already held by farmers. Such interventions can help improve livelihoods for coffee producers and sustain benefits to biodiversity at the same time.

Keywords: biodiversity conservation, bryophytes, ecosystem services, epiphytes, environmental attitudes, environmental values, farmer typology, social-ecological systems

INTRODUCTION

Shade-grown coffee has attracted considerable attention as a social-ecological system and a land-sharing practice (De Beenhouwer et al. 2013; Perfecto & Vandermeer 2015). It can support high levels of biodiversity, provide ecosystem services, and improve the livelihoods of producers (Westphal 2008; Tscharntke et al. 2011; Jha et al. 2014). Shade coffee is an umbrella term for any coffee cultivation system that adds trees, and it encompasses a wide spectrum of practices from “technified” plantations—intensively managed farms with one or a few shade tree species—to “rustic coffee,” which is planted in the understory of thinned forest trees (Toledo & Moguel 2012).

The biodiversity benefits of adding shade to coffee systems extend across diverse taxonomic groups, including birds (Cruz-Angón & Greenberg 2005; Karanth et al. 2016), invertebrates (Mas & Dietsch 2004), trees (Häger et al. 2015; Haggar et al. 2015), and epiphytes (Hietz 2005; Goodall et al. 2015). Epiphytes, our focus in this study, are non-parasitic air plants, including orchids, bromeliads, and ferns, that grow without connection to the soil, depending on trees and shrubs for structural support. Epiphytes are highly diverse, representing up to half of all plant species in tropical forests (Gentry & Dodson 1987), and they also readily inhabit open-grown trees in pastures, urban area, and agroforestry systems, including coffee farms (Hietz 2005; Köster et al. 2009; Einzmann & Zotz 2016). Producer attitudes toward epiphytes are largely unknown, but may be neutral or antagonistic based on epiphyte removal as a common practice in some countries (Toledo-Aceves et al. 2013; Solís-Montero et al. 2019). However, aesthetic appreciation of epiphytes, especially orchids, has also been noted among farmers (Méndez et al. 2010).

Coffee supports the livelihoods of millions of smallholder farmers worldwide, but much coffee production also occurs on large plantations (Bacon 2008). Peasants and plantations coexist spatially, resulting in a landscape mosaic of wealth inequality, and these farms differ in their economic situations, relative exposure to risk, and attitudes toward production (Guadarrama-Zugasti 2008; van der Ploeg 2008; Toledo & Moguel 2012). Large plantations have financial reserves to last through the year and are better positioned to take advantage of certifications, direct market relationships, and technological innovations to gain access to higher coffee prices. Large farms are production-oriented with an entrepreneurial focus on responding to markets; peasant farming, on the other hand is internally focused on sustaining the livelihoods of the family (van der Ploeg 2008; Westphal 2008). Because coffee is harvested once annually, smallholders growing coffee as their primary or only revenue source face many months without income, inducing a hunger season and accumulation of debt (Bacon et al. 2014, 2017). Smallholder livelihoods risk becoming increasingly marginal as global coffee prices decline, coffee disease threats intensify, and climate warming pushes coffee plants toward their thermal limits (Bunn et al. 2015; Bacon et al. 2017).

Adding trees to coffee farms offers numerous ecosystem services that help producers. Trees alter farm microclimate and nutrient cycling, providing key regulating services (Tscharntke et al. 2011; De Beenhouwer et al. 2013). Shade lowers coffee leaf temperatures, limits plant water demand, and reduces soil evapotranspiration (Beer 1987; Siles et al. 2010; Tscharntke et al. 2011). Leguminous trees fix nitrogen, increasing coffee productivity, and leaf litter from trees can increase soil organic matter and add nutrients (Beer 1987; van Oijen et al. 2010). Shade cover may decrease annual yields, especially at higher shade density (Soto-Pinto et al. 2000; Siles et al. 2010). Even so, the improved soil nutrition and water retention, decreased erosion, and increased resilience to climate change provide a net benefits to farmers (Siles et al. 2010; Tscharntke et al. 2011). Agroforestry also offers provisioning services to farmers, including timber, firewood, and fruit for subsistence use (Westphal 2008; Rice 2008; Méndez et al. 2010; Wagner et al. 2019). These benefits are particularly important for smallholders and can help offset financial shortfalls. Finally, trees add cultural services to farms, including aesthetic values and opportunities for ecotourism (Méndez et al. 2010; Toledo & Moguel 2012).

Given the considerable importance of shade coffee ecologically, socially, and economically, surprisingly little work has examined producer motivations for beginning or maintaining shade coffee production. Several studies have considered producers' uses for trees and perceptions of ecosystem services (Beer 1987; Albertin & Nair 2004; Rice 2008; Garen et al. 2009; Cerdán et al. 2012; Wagner et al. 2019), but few have attempted to connect producers' values and economic motivations with tree management. Further, while the ecological literature has linked management intensity and even specific management practices to biodiversity indicators, the relative importance of those practices to producers has mainly been overlooked (Toledo & Moguel 2012; Robbins et al. 2015). Understanding producers' values and motivations is critical to designing conservation interventions and improving producer livelihoods (Heberlein 2012; Jones et al. 2016). Based on previous work, we expect that producers' decisions will be influenced by a combination of their financial stability, access to labor supply, technical knowledge, and values for nature and biodiversity (Guadarrama-Zugasti 2008; Westphal 2008; Méndez et al. 2010; Robbins et al. 2015). We expect the relative strength of these influences to vary by farm size, which is presumably associated with wealth and social capital (Bacon 2008). Here, we compare small vs. large farms, asking:

(1) How do *small and large farms differ* in terms of financial stability, labor supply, and access to technical knowledge?

(2) What *benefits and services* do producers perceive from trees and epiphytes?

(3) What are the relative roles *financial stability, labor supply, access to knowledge, and personal values* in motivating producers' decisions regarding shade trees and epiphytes?

METHODS

Producer Interviews

In April-May 2018, we conducted 33 semi-structured interviews with producers on 31 coffee farms employing shade cultivation in northern Nicaragua. Farms ranged in size from 1.4 to 490 ha. We classified farms as “large” if they exceeded 13 hectares in size, following Bacon’s (2008) farm size divisions for previous work in the same region of Nicaragua but combining his “medium” (13-30 ha.) and “large” (>30 ha) classifications due to the similarities in economic measures he documented. Farms greater than 13 ha. make up only about 5% of Nicaraguan coffee farms (Bacon 2008), but represented half of our sample to allow for comparisons based on size (large: n = 16, small: n = 15).

Twenty-nine of the farms in our study had been given trees as part of a previous project led by the American Bird Conservancy (ABC). The researchers had prior connections to the remainder, which were included to increase the number of large farms. Because producers had self-selected for the ABC project, we expected they would exhibit positive values for nature, biodiversity, and trees at a higher rate than the general population of coffee farmers in our study region. However, our research questions necessitated talking with producers who already had committed themselves to shade coffee.

Interviews ranged in length from 15 minutes to 2 hours. Each interview was recorded and later transcribed. All interviews were conducted in Spanish, except for one conducted in English. We used standardized closed- and open-ended questions in each interview (Appendix 1), but additional follow-up questions differed. In one case, father and son on one farm were both interviewed; in another, the owner and farm manager on one farm were both interviewed. Some farms adjoined each other, and several had familial connections between them. Interview topics included basic farm information, management practices, financial situation, uses and benefits of trees, perceptions of climate change, and attitudes toward epiphytes. In addition to the formal interview, most producers accompanied us during field measurements and informal conversations often occurred. Notes from these conversations and impressions of the farm were recorded at the end of each day and used to inform analysis.

Ecological Measurements

On each farm we established two to five 400m^2 plots. In each plot, we measured diameter at breast height (dbh), height, and species identity (common name provided by the farmer) of all trees, counted epiphytes in 4 taxonomic groups (orchids, ferns, bromeliads, and other) on each tree, and recorded all epiphyte species within the plot. These plots document the spectrum of management practices across all farms in the study and their effect on epiphytes and are not intended to statistically represent the farms on which they were measured. The ecological results of these measurements were presented in depth in two previous papers (Chapters 1 and 2).

Analyses

We used mixed quantitative and qualitative methods to analyze interview data. To address the effects of farm size on producer economic and social characteristics, we evaluated effect of farm size based on our original categorization of small vs. large farms, but also treated farm size as a continuous variable. We used linear regression to examine relationships among farm size and other key variables, including land area in coffee, farm age, number of permanent workers, coffee planting density, and months of financial insecurity. Farm size, farm age, and number of permanent workers were log transformed to meet model assumptions. We created binomial variables (1 = yes, 0 = no) for other farm income, off-farm income, loans for subsistence, loans for farm investment and cooperative membership. Agrochemical intensity, income from coffee, access to markets, and technical assistance were each assigned to an ordinal scale based on interview responses as follows: Agrochemical intensity (1 = few agrochemicals used, typically use organic alternatives, 2 = chemical fungicides and fertilizers used, herbicide used sparingly, 3 = fungicide, herbicide, and fertilizer all used regularly, insecticide used only after other methods have failed or not used at all, 4 = no restraints indicated on chemical use); access to markets (1 = sells in local market, 2 = sells to cooperative, 3 = sells to export company, 4 = direct market relationships abroad); technical assistance (1 = credit assessor from bank or cooperative sometimes offers technical suggestions to improve production; 2 = agronomic technician provided by a cooperative for members; 3 = family member or friend with agronomic knowledge advises farm management; 4 = farm manager or owner is an agronomist). These were treated as ordinal rather than categorical to capture directionality of responses.

To better understand how financial stability, labor supply, and access to knowledge contributed to decision-making, we used the quantitative variables derived from the interviews to develop farm typologies based on multiple factors using hierarchical cluster analysis (Guadarrama-Zugasti 2008). We performed agglomerative clustering using the *hclust* function in R with the Ward algorithm designed to find compact, round clusters based on a distance matrix. We used Gower’s distance from the R package ‘FD’ (Laliberté et al. 2014) to calculate the distance matrix because it allows for missing values and inclusion of binomial and categorical variables. We calculated distance based on farm size, land area in coffee, farm age, number of permanent workers, coffee planting density, agrochemical use intensity, household income from coffee, other farm income, off-farm income, loans for subsistence, loans for farm investment, months of financial insecurity, cooperative membership, access to markets, and technical assistance.

To evaluate the ecosystem services farmers perceive and their motivators for management decisions, we manually coded qualitative interview transcripts using structural coding (Saldaña 2009), where we first grouped interviews into by topics related to our research questions: financial situation, social connections and knowledge base, management practices, uses and benefits of trees, attitudes toward epiphytes, and perceptions of climate change. Within the responses related to benefits and services from trees and epiphytes, we grouped unique responses and uses and tallied the number of respondents who mentioned each one. For each response, we grouped all relevant text from transcripts and used descriptive coding to discover the reasoning associated with each response. Responses related to financial situation, labor, access to knowledge, and personal values were treated similarly. We synthesized codes to identify themes in the responses explaining how each factor influenced producers' decisions (Saldaña 2009). Quotes included in this paper were translated from the original Spanish by the authors (Appendix 2).

RESULTS AND DISCUSSION

Farm size and typologies

Farms averaged 56.7 ha in size. The median, 14 ha, better characterizes most of the farms we visited and aligns well with our division of small vs. large farms (13 ha). Small and large farms differed in percent of land in coffee cultivation, coffee planting density, months of financial insecurity, use of loans, market access, and technical assistance (Table 1). Treating farm size as a continuous variable, the amount of land in coffee production decreased with farm size ($t = -4.07$; $p < 0.001$). As farm size increased, so did the number of permanent workers ($t = 6.75$, $p < 0.001$), level of technical assistance ($t = 3.49$; $p = 0.002$), and access to markets ($t = 4.83$, $p < 0.001$). Farm size also negatively predicted the months of financial insecurity producers experienced ($t = -3.09$, $p = 0.005$) and coffee planting density ($t = -2.44$, $p = 0.02$). Agrochemical use showed no relationship with farm size, but we did find a negative relationship between agrochemical intensity and access to technical assistance ($t = -472$, $p < 0.001$). Size was not correlated with farm age, indicating that land is not necessarily accumulated over time.

While there were clear patterns based on farm size, we found that dividing farms based on size alone failed to capture many important differences among the farms. The hierarchical cluster analysis better characterized producer groups and clustering into six typologies provided the most internal consistency (Fig. 1). We describe each typology based on interview responses (Table 2). These typologies reveal a few key differences among respondents obscured by looking at farm size alone. For example, while most small farms depended heavily on credit, we encountered several smallholders who were extremely debt-averse (Independent Small Producers) and took credit as only a last resort, expressing fear of losing their farms. Large farms generally had better access to technical knowledge, but we also encountered very large farms with lower technical expertise despite considerable economic resources (Large-scale Typical). Finally, producers who also raised cattle (Coffee & Cattle) and several producers in the Coffee Reliant group had enough land base to qualify as “large farms” according to our classification scheme, but they were more similar to smallholders in many other respects (Fig. 1).

Benefits and services from trees and epiphytes

Producers cited 16 benefits and services associated with trees and two disadvantages (Table 3). They discussed trees in reference to coffee production (88% of respondents) and ecosystem services, particularly provisioning services (88%) and regulating services (81%). Despite living in a region with some of the highest epiphyte diversity in the world, many producers had never given epiphytes much thought. Producers named considerably fewer benefits and services provided by epiphytes and their responses focused on cultural services, including aesthetic appreciation (36%), attracting wildlife (36%), and the recreational and touristic value of cultivating epiphytes (18%).

Producers differentiated among trees species and epiphyte groups in their responses. They assigned different uses to various tree species (Table 4) and sometimes planted trees that they believed were not favorable for coffee shade because they relied on them for other purposes. This is a common phenomenon among coffee producers and the abundance of each species overall should reflect the degree of benefit farmers associate with it (Albertin & Nair 2004). Similarly, producers differentiated groups of epiphytes, with orchids being the most highly regarded for their aesthetic and recreational value and bryophytes being most connected with negative impacts on coffee (Méndez et al. 2010; Solís-Montero et al. 2019).

Effects of trees and epiphytes on coffee production

Producers felt that shade improved coffee plant health (70%) and enhanced coffee flavor and cup quality (36%). However, they also believed that too much shade could be just as damaging to the coffee as too little, citing decreased production (27%) and increased fungal disease (42%) as the main problems. Producers observed that plants in full sun showed more signs of stress with yellowed leaves or leaf loss during the dry season and smaller, drier fruits. They reported that while coffee grown in sun has higher yields initially, production decreases after 2-3 years, requiring plants to be cut back and allowed to regenerate (as opposed to 3-5 years under shade cultivation). Economic losses in production under shade cultivation can be compensated by a higher price point for the improved quality of the coffee (Siles et al. 2010), a point recognized especially by Naturalistic Entrepreneurs. With slower growth under shade, producers explained, better flavors develop because the fruit matures more slowly and has more mucilage, and the bean is larger and "more beautiful":

> *If the bean takes longer to mature, it picks up more nutrients and it has a better taste in the cup, while if it is exposed to the sun, it is stressed more and throws all its energy to the bean, which matures faster and, in the case of the quality of the cup, I think it's not good. [Naturalistic Entrepreneur]*

Because coffee plants in full sun grow faster and yield more, they also require more nutrient inputs, increasing fertilizer costs for farmers. Conversely, when not enough sunlight reaches the coffee, plants may look healthy but do not flower. All producers we interviewed told us that they preferred growing coffee under shade rather than in full sun, but they qualified that it needed to be "regulated shade." As one producer explained,

> *The thing is you have to manage them [trees], you can't just plant them in the coffee and let them do whatever they will… so you do some management so that they both can live there, because we need the trees and we also need the coffee. [Off-Farm Income]*

Too much shade also increases the humidity around the coffee plants and reduces the sun reaching the leaves, which producers explained causes higher incidence of American leaf spot (*Mycena citricolor*). However, American leaf spot was only problematic at higher elevations. In warmer zones, producers struggled more with coffee leaf rust (*Hemileia vastatrix*), which they did not associate with too much shade cover, indicating a belief that the appropriate amount of shade cover should differ by elevation.

Climate predictions suggest that coffee production is becoming less favorable in many regions where it is currently grown (Bunn et al. 2015). Many producers had observed climate changes, reporting hotter weather with a shorter cold season, more rain with stronger storms, and altered seasonality. These affected coffee production by provoking flowering and fruiting earlier than normal and changing the suitability of some coffee varieties for certain elevations. Producers also cited higher incidence of disease from climate change, both for American leaf spot, because of increased rain, and for coffee leaf rust, due to elevated temperatures. Nearly half (48%) of respondents identified shade trees as important in helping their farms withstand climate change by keeping the coffee cooler, reducing sun damage, and maintaining soil moisture. As one producer reports,

> *The trees in coffee plantations help us to maintain a more homogeneous temperature within the plantation ... I am a coffee crop consultant and I go to many coffee plantations ... and we always see that it cushions the changes better, the climatic variability, when we have a number of trees in the coffee. That is undeniable. [Naturalistic Entrepreneur]*

Several producers connected epiphytes, particularly bryophytes, negatively with coffee production and none associated epiphytes positively with coffee. Epiphyte removal from coffee shrubs and shade trees is a common management practice in other countries (Toledo-Aceves et al. 2013; Solís-Montero et al. 2019), but among our study participants it was not the norm. Several producers listed removing moss as part of their annual cycle of management activities believing that it damages coffee plants:

> *"When there is moss that takes root all over, it squeezes the producing plant too much and weakens the stem, and then it weakens the foliage, in the case of coffee. And then the humidity it produces, that produces fungus and it begins to do damage, that's why everything must be controlled" [Coffee & Cattle].*

Bryophytes have been shown to decrease coffee yield (Solís-Montero et al. 2019), although the mechanism has not been investigated. A few producers also assumed that epiphytes damage shade trees. One Naturalistic Entrepreneur appreciated all epiphytes except Spanish moss (*Tillandsia usneoides*), which she believed killed trees, and she had instructed workers to remove it on her farm, although she allowed all other epiphytes to remain. In total, four producers (12%) admitted that they occasionally remove epiphytes from shade trees, although this practice seemed largely capricious and motivated by a lack of knowledge. As one producer told us, "Because we don't know the importance they [epiphytes] have, sometimes we see them on the trunks and what we do is chop them off" [Coffee Reliant].

Provisioning Services

Producers discussed firewood, timber, and fruit as provisioning services provided by trees on their farms. The importance of these three services is recognized by smallholders across many tropical regions (Albertin & Nair 2004; Rice 2008; Garen et al. 2009; Valencia et al. 2015; Lamond et al. 2019), and can provide up to half the economic value gained as cash income from coffee production (Rice 2008). The Naturalistic Entrepreneurs were the only group that did not universally discuss provisioning services, suggesting that inclusion of trees in their farms is based on other benefits and values. The large farms in other typologies expressed the importance of provisioning services to their farms. Epiphytes were not typically associated with provisioning, although several believed they could have medicinal properties. A Coffee & Cattle producer also told us that he removed epiphytes from his trees and fed them to his cattle in the dry season when forage was scarce.

Cooking over wood fires is still the norm in the study region except in wealthier households. The importance of firewood was mentioned by 82% of producers, including all respondents in the Coffee Reliant, Coffee & Cattle, Off-Farm Income, and Large-Scale Typical groups. Producers gathered firewood primarily from pruning shade trees, but also used dead trees or the wood from pruned coffee shrubs. They cited the convenience of having a supply of firewood closer to the house, taking pressure off the nearby forest, and not having the expense of buying firewood as benefits. *Guabas* (*Inga* spp.) were strongly preferred trees for firewood and were the most common shade trees in our study (Table 4).

Producers also harvested wood for construction and fenceposts from their farms, although with less frequency than firewood. They preferred different trees for timber, including walnut (*Juglans olanchana*), Spanish cedar (*Cedrela odorata*), and various types of avocado (Lauraceae spp.). Unlike in other regions (Rice 2008), no producers in our study discussed selling the timber they culled from coffee plantation; rather timber use was limited to one or a few trees only when the family needed to build or repair a structure or construct furniture on the farm.

Surprisingly, only five producers (15%) mentioned fruit production as a benefit, although this has been frequently reported in other studies (Albertin & Nair 2004; Garen et al. 2009; Valencia et al. 2015; Lamond et al. 2019). Three producers (10%) reported selling bananas as an occasional source of farm income. However, in our tree surveys (Table 4), we observed bananas or plantains (*Musa* spp.) on 74% of farms, as well as avocado (*Persea americana*;

35%), citrus (*Citrus* spp.; 29%), mombin (*Spondias purpurea*; 16%), guava (*Psidium guajava*; 13%), mango (*Mangifera indica*; 13%), nance (*Byrsonima crassifolia*; 6%), soursop (*Annona muricata*; 3%), and mamey sapote (*Pouteria sapota*; 3%).

Regulating Services

Trees provide documented regulating services on farms, including sequestering carbon, retaining soil moisture and improving soil fertility (Tscharntke et al. 2011). Nitrogen inputs from leguminous trees can also offset fertilizer costs (van Oijen et al. 2010). Producers recognized the importance of these services to their farms with 81% mentioning one or more regulating service. The most common services discussed were improving soil (45%), water conservation (42%), and reducing erosion (21%). They also frequently mentioned oxygen production as a benefit of both trees and epiphytes. Regulating services were less associated with epiphytes, although bromeliads were named for their water storage capabilities (24%).

A surprising theme that emerged from our interviews was the restorative function of coffee farming, connected to regulating services provided not only by the shade trees, but also by the coffee plants themselves. This idea transcended typology, although it was articulated somewhat differently among groups. Of the 87 plots we surveyed on all farms, 84% had been used for pasture or annual crops before conversion to coffee. Multiple producers described the transformation that had happened, indicating they felt coffee was not only a better land use than other types of farming, but could even undo years of damage from agriculture.

For producers with greater access to technical knowledge, particularly Naturalistic Entrepreneurs, these changes were related to soil moisture, fertility, and compaction. Their responses expressed a deep understanding of the ecological interactions occurring on their farms and how those interactions could be harnessed not only to improve coffee production, but also to enhance environmental sustainability. They esteemed nitrogen-fixing leguminous trees and leaf mulch for adding nutrients to the soil, reducing the amount of chemical inputs they needed to apply. Leaf mulch also added organic matter that they said improves soil structure, feeds beneficial microorganisms, and retains moisture. One producer compared the environmental impacts of shade coffee cultivation to pasture:

> *Okay, look, I think if we think about it calmly, coffee is a crop, a very noble crop and between having 50 manzanas of pasture and having 50 manzanas of coffee, I think we should have 50 manzanas of coffee, because we have 50 manzanas of trees. In 50 manzanas of trees there are 200,000 trees that produce an incredible amount of leaf area, that transpire, that respire, that purify, that give better life, that retain more moisture in the soil. So, day by day, we can see these places where the farm was really arid, that when we converted them to coffee plantations and we put them in shade—because I am in love with that shade—it has changed enormously, you can already see the differences in the soil. In fact, in fact, if we didn't have… I don't know… the people who think there should be trees, we'd be screwed. I'm reforesting the creeks, I'm reforesting the water sources, the rivers, making living fences. Just last year, we put 2,000 trees into a small farm like this one last year and we are doing all we can to try to make that work. [Naturalistic Entrepreneur]*

Producers who did not have the technical language to describe the ecological changes that had occurred nonetheless reflected on shade coffee as a solution to land degradation that they had inherited from previous landowners or caused themselves through other types of farming. One producer proudly showed us the soil conservation measures he had put in place and described how his land, degraded from years of annual tillage and erosion, had changed since planting shade coffee:

> *… you couldn't plant coffee here, the earth had been washed away, it had just a thin sheet of fertile soil, but as trees were planted new soil has been forming with the leaves that fall and the branches that rot adding to it. [Off-farm Income]*

They also connected shade coffee to protecting and restoring water sources on their farms. One man's eyes filled with tears as he described the springs that had been on his property historically coming back after he planted trees:

> *There was a spring before but there were no trees and I planted trees and that spring came back, it reverted and better than before! With trees, I have now experienced it with two springs that are here...when I bought that [parcel], the previous guys had vegetables there, the soil was running away, and I planted coffee and the trees that are there and those springs returned and they returned even more opulent. The trees are helpful for life and for many things, for all of humanity, it could be said. [Coffee & Cattle]*

Cultural Services

While producers mainly associated trees with provisioning and regulating services, they connected epiphytes with cultural services, and the attitudes expressed toward trees and epiphytes suggest underlying values for nature (Kellert 1996; Heberlein 2012). As Méndez et al. (2010) previously documented, there was a strong aesthetic value for epiphytes, particularly orchids, among our respondents. They named the beauty and fragrance of the flowers as key assets that improved their farms. Multiple producers had collected orchids from fallen branches and pruning of the shade trees that they cultivated near their homes to appreciate their beauty.

Producers also identified a touristic value for epiphytes. Several larger farms had or planned to establish *orquidiarios*, collections of orchids on display for visitors. One Coffee & Cattle producer who also engaged in a small amount of ecotourism mentioned that orchids are promoted by the tourist bureau and should be protected for their touristic value. Respondents involved in tourism or with higher levels of education, particularly the

Naturalistic Entrepreneurs, had greater knowledge of epiphytes and more nuanced explanations of their ecological importance:

> *See, once I read a study and it said that the places where you can find a large number and diversity of epiphytic plants was synonymous with health, environmental health, forest health. So for me, I arrive at a place and look: ahh, you see mosses, you see lichens, you see this, you see that, then it is a healthy place. So, for me they have an indicator value when you are looking at the environment in your farm, in your community. [Naturalistic Entrepreneur]*

Seeing wildlife, especially birds, on their farms was cherished by many producers, and they connected wildlife visits with both trees and epiphytes. Among epiphytes, producers had observed animals drinking from bromeliad tanks, and they associated nectar for birds and insects with bromeliads and orchids. Trees also attracted more birds and animals to farms, which producers attributed to the food value of flowers and fruits and to the additional habitat structure trees offered. One producer told the story of wildlife returning to his farm after planting shade coffee:

> *Birds of all kinds come, the trees have fruits then forest animals come, such as agoutis, pacas, birds of all kinds, because there's an environment of trees that's where the birds like to be. Before no, it was bare, it was grass, but now it's not, now there's a lot. There are birds, there are forest animals, it's really beautiful how they've come. One day we saw a jaguarundi. [Coffee Reliant]*

A few producers also felt strongly that having trees made their farms more beautiful and enjoyable to live in. As one noted simply, "A farm without water or trees to me isn't a farm" [Coffee Reliant].

Motivations for Management Decisions

Economic Decisions

Producers universally discussed the low prices of coffee as problematic for their farm. Even large, financially stable farms felt that coffee might not continue to be a viable option long-term:

> *The truth is that this [finances] is the most perhaps most critical issue that people who work with coffee have, with the prices that we have, with the financial drag of the deficit that we have had in previous years, the climate that sometimes isn't helping us, so we have had serious problems. I do not have bank financing, I try to do everything away from the banks because I have some fear of constraints, but people who work with credit today are enormously worried they are not covering their costs and they are definitely going to lose out on the exercise. [Naturalistic Entrepreneur]*

One Naturalistic Entrepreneur stated that coffee production used to support the ecotourist lodge on her farm and now income from the lodge subsidizes coffee farming. A farm manager on a Large-scale Typical farm explained that, due to low prices, his farm had been slowly taking land out of coffee production and putting it into other land uses. Many of the producers who depended mainly on coffee stated that they had switched to growing coffee for economic reasons. Several also indicated that sustained low prices could cause them to shift to a different crop, suggesting that all farms in our study were to some degree governed by markets (van der Ploeg 2008). In previous coffee price declines, coffee abandonment, including switching to other land uses and leaving farming altogether, has been prevalent among smallholders (Babin 2015). Given the predicted decreases in yield and land suitability for coffee under climate change scenarios (Bunn et al. 2015) combined with the already low prices identified by producers, it is reasonable to expect that coffee farming will become harder to maintain for farms of all sizes.

Economic status was self-perpetuating for within all typologies and informed decision-making. Among Naturalistic Entrepreneurs and Large-Scale Typical producers, greater financial resources allowed investments in farm infrastructure and additions to the land base to boost future profits (Guadarrama-Zugasti 2008). Several Naturalistic Entrepreneurs described plans to invest in processing equipment so that they could mill coffee on-site, increasing their profit margin. Conversely, Coffee Reliant producers were locked in a cycle of debt and credit that inhibited their ability to invest in changes that would not immediately benefit them financially. Farm diversification and off-farm work can enable greater financial independence and income smoothing to producers (Bacon 2008; Westphal 2008), and we saw some evidence of this among our respondents. One Off-Farm Income producer had just purchased a new parcel of land where he was planting coffee for the first time. Several Small Independent producers could avoid taking loans because a family member had year-round income from permanent work. Provisioning services from trees can also buffer coffee producers against years of low yield or crop failure and help them to remain in coffee production over time (Babin 2015). The high importance of firewood for our respondents indicates this may be the case in our study group as well.

The decision to initially add trees to farms may be inhibited by short-term economic calculations, especially for those experiencing the greatest economic hardship. When producers are unable to see the immediate economic value of adding trees, they may not be willing to make the investment of capital or labor, particularly when they would need to grow trees from seed themselves. One producer explained that many farmers do not see the immediate economic benefit of adding trees:

> *The thing is that the majority of producers, when we plant a coffee plant, we can see the dollars above it, but when we plant a tree, we don't. We only focus on that, in the coffee there is the dollar sign. [Coffee & Cattle]*

The farmers in this study had all received trees for free as part of the ABC project. Many indicated that they would like to receive more and some shared that their neighbors had inquired about how to receive trees. Once producers have a positive experience planting trees, they often wish to plant more (Albertin & Nair 2004; Garen et al. 2009), indicating that defraying the costs of tree planting may alone be incentive enough to increase tree cover on the landscape.

Although we hypothesized that labor shortages would be a major concern for coffee producers based on evidence from other coffee growing regions (Robbins et al., in review), our data did not support that. Large farms tended to hire workers year-round and small farms depended on family labor (Bacon 2008), although some larger farms in the Coffee & Cattle and Coffee Reliant groups mainly relied on labor from a large extended family. Large farms had little trouble recruiting migrant laborers from other departments of the country for the harvest season, particularly when they treated workers well. Smallholders collaborated with their neighbors and extended family during the harvest to bring in the crop on multiple farms, demonstrating reciprocity (van der Ploeg 2008). In our interviews, labor was discussed as an economic constraint (not being able to pay laborers) rather than in relation to availability, and producers sometimes limited labor-intensive activities like tree pruning when finances were tight. Some smallholders may also substitute external inputs (e.g., chemical fertilizer) when they can afford to rather than using environmentally-friendly but labor-intensive techniques such as composting organic fertilizer to avoid the drudgery of extra labor investments (van der Ploeg 2008).

Knowledge-Based Decisions

There was a great discrepancy in the knowledge base among the producers we interviewed. Beyond differences in general education, there was a sizeable knowledge gap between the producers who had personal training in agronomy and those whose only access to technical assistance comes in the form of a credit assessor from a bank or cooperative who examines their crop once a year and makes suggestions. The Naturalistic Entrepreneurs, many of whom were college-educated with degrees in agronomy or business, were distinct from the rest of the groups in this respect. Their greater access to knowledge was accompanied by greater financial resources and may be related to generational wealth. They gathered data on their farms, including soil analysis and weather station measurements, which they combined with their technical education to implement more innovative farming practices. As one said of his farm, “This is a center for me to experiment” [Naturalistic Entrepreneur]. Interviewees with greater technical knowledge offered lengthy discussions of management improvements they had made on their farms in recent years. They also had plans for new innovations that could help them adapt to climate change, including changing the timing and intensity of shade tree pruning to leave more foliage in place during the hotter summer months and planting new varieties of coffee they believed to be more heat tolerant.

In other groups, producers were less likely to try new practices, although whether this was due to higher perceived risk or to lower access to technical knowledge was unclear (Guadarrama-Zugasti 2008). Many stated that they had not made changes in recent years, that they did not plan to modify their practices in relation to climate change, and that their management mirrored that of their neighbors. Many expressed a desire for more technical assistance that could help them reach a level of sophistication in their farming that they witnessed on larger farms but currently considered unattainable. One Small Independent producer had previously taken part in an extension program to grow organic cabbage, but he had not applied any of the same practices to coffee production because he felt he needed someone with more technical knowledge to assist him. A Coffee Reliant producer had implemented past suggestions from a credit assessor with good success and wished for more recommendations he could try. Several producers indicated that they also would like to know more about epiphytes after talking with us.

Values-Based Decisions

According to the classification system proposed by (Kellert 1996) to categorize human values for nature, aesthetic, naturalistic, utilitarian, and ecologistic-scientific values for conservation were high among the producers we interviewed. These values were expressed across typologies and interacted with economic pressures and technical capabilities to influence decision-making. Naturalistic Entrepreneurs had high naturalistic and ecologistic-scientific values for biodiversity, including enjoyment of nature and appreciation for the ecological interactions occurring on their farms (Kellert 1996). Those values informed management decisions because they had the financial means for their behaviors to align with their attitudes (Heberlein 2012). Some of their environmentally-friendly practices, including vermicomposting of coffee waste, non-chemical insect control methods, and dyke systems for soil conservation, were more costly in terms of labor or capital or required specialized technical knowledge to implement and were thus out of reach for other producer groups despite shared values.

Aesthetic and utilitarian values, including appreciation for the beauty of nature and material benefit from the trees on their farms (Kellert 1996), were regularly expressed among producers in the other groups. These values informed some practices and were particularly apparent in the decision to grow shade coffee. One producer explained that his rationale for switching to growing coffee combined economics and values:

> *[We switched to coffee] because we realized that it would sell for a little more, but also that it would protect the soil. Because the soil in the cornfield was eroding, but with the coffee it was protected. [Small Independent]*

Although producers with higher levels of education or more access to technical assistance were better able to articulate ecological processes on their farms, producers across typologies expressed values for nature. These values informed management decisions when they were not overridden by economic constraints. For example, one producer explained his decision to preserve epiphytes based on aesthetic and naturalistic values:

> *For me they are very beautiful plants, they give a great enhancement to the farm. People here don't know them and they don't know what is beautiful, so they destroy them and get rid of them. Not us, we take care of them. Those plants are being lost, they are numbered on the farms that you have. They grab them and cut them, but we don't. You will see here on the farm how they are and we plant them, we cultivate them. We like it like that, because my wife is a lover of plants, we all are. [Small Independent]*

Producers attributed different ecosystem services to trees based on their values and financial stability. Those who rely on the provisioning services from trees tended to express their attitudes toward trees in terms of those that were best for firewood or timber. On the other hand, Naturalistic Entrepreneurs, expressed their tree preferences in terms of regulating and cultural services, including improving soil and water or supporting wildlife. In actuality, however, those preferences did not translate into differences in tree species richness or composition among typologies. Most farms contained predominantly *guaba* (*Inga* spp.), a multifunctional tree appreciated variously by all typologies for firewood, ease of maintenance, nitrogen fixation, and wildlife conservation. Interspersed were smaller numbers of a wide variety of mostly native species, which many producers preferred for timber, but the Naturalistic Entrepreneurs associated with supporting wildlife.

CONCLUSIONS AND RECOMMENDATIONS

Ours was the first study to systematically document the attitudes of coffee producers toward epiphytes. Despite generally favorable attitudes, we note several tensions between producers' management needs for coffee productivity and the conditions required for diverse epiphyte communities. Epiphytes are most diverse and abundant at the higher elevations of our study region (Gentry & Dodson 1987; Cardelús et al. 2006), a fact that was noted by several respondents as well. While the higher humidity there benefits epiphytes, producers in those zones manage shade trees more intensively to prevent American leaf spot. Thus, shade trees are pruned most aggressively in the areas that are most compatible with epiphyte conservation. Tree pruning damages epiphyte populations by regularly removing habitat substrate and killing individuals. The annual losses may structure the age and species composition of epiphyte populations within coffee farms, selecting against slower-growing species (Sarmento Cabral et al. 2015). Producers were most likely to remove epiphytic bryophytes, particularly from their coffee plants. However, bryophyte cover is important to the establishment of the epiphytes producers appreciated, especially orchids (Scheffknecht et al. 2010) and repeated bryophyte removal may lower overall bryophyte cover, inhibiting vascular epiphytes from establishing.

Despite these caveats, shade coffee systems still support considerable epiphyte populations and should be considered reservoirs for diversity, particularly in highly fragmented landscapes (Hietz 2005; Goodall et al. 2015; Solís-Montero et al. 2019). We suggest several intervention strategies to improve epiphyte habitat, and wildlife conservation generally, across coffee farming landscapes. Based on our findings, we believe that economic-based and knowledge-based interventions should be employed, particularly when they can be integrated within the values producers already hold for nature. As producers and scientists alike have recognized, shade coffee is a better land use than most other forms of agriculture (De Beenhouwer et al. 2013; Jha et al. 2014), so maintaining farms in shade coffee cultivation and adding trees to the farm landscape should be prioritized as key conservation outcomes.

Interventions aimed at improving livelihoods for producers can also have important conservation benefits. Foremost among these, programs providing free shade trees to coffee producers can offer important provisioning and regulating services that buffer farmers against economic hardship while also improving the habitat availability for numerous species. Both our results and previous studies (Albertin & Nair 2004; Garen et al. 2009) indicate that producers are likely to plant trees when the trees are provided at low or no cost. Additionally, programs to coordinate enrollment in certification programs via cooperatives may be effective in maintaining livelihoods for producers, particularly those on small farms, in the face of price downturns (Bacon 2008; Babin 2015). However, certifications may be most compatible with larger farms already producing higher quality coffee. Several Naturalistic Entrepreneurs in our study currently benefit from Rainforest Alliance certification, and others expressed interest in certifications as a means to attain higher prices.

We also found that lack of access to technical knowledge inhibited many producers from innovating their practices. This barrier is particularly acute in relation to climate change because farmers who cannot alter management practices to adapt to a warmer and more variable climate are unlikely to succeed with coffee farming in the future. Access to technical knowledge can also drive innovation to improve coffee quality, permitting access to markets with higher price points, as evidenced by some of the Naturalistic Entrepreneurs we interviewed. Additionally, while dissemination of knowledge about epiphytes is needed to reduce epiphyte removal, the aesthetic appreciation for epiphytes (Méndez et al. 2010) and the understanding of their importance to wildlife that we observed should facilitate behavioral change with a small amount of outreach effort.

Finally, interventions are most likely to succeed when they take into account producers' values and local knowledge (Heberlein 2012; Toledo & Moguel 2012; Cerdán et al. 2012; Jones et al. 2016). We documented strong values for nature among many of the producers we interviewed; in particular, their recognition of the restorative potential of shade coffee over other land use practices. Building technical and financial capacity in ways that acknowledge producers' values and understanding of ecological interactions can enhance farm resiliency and ensure continuity of coffee production over the long term. The ecosystem services provided to producers and the conservation benefits for wildlife will only continue to accrue.

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Table 1. Comparison of farm metrics between large and small farms. Asterisks indicate significance levels based on T-tests (* = p<0.05, ** = p<0.01, *** = p<0.001). ǂ indicates ordinal variables on a scale of 0-4, § indicates binomial variables (1 = yes, 0 = no).

	Large Farms (>13ha)	***Small Farms (<13ha)***
Farm size **	105.27 ± 132.87	4.85 ± 3.26
Land area in coffee *	30.93 ± 48.96	3.71 ± 3.19
Farm age	28.88 ± 17.32	20.23 ± 14.62
% Land in coffee **	0.44 ± 0.33	0.76 ± 0.29
Permanent workers	19.44 ± 38.93	0.93 ± 1.94
Coffee density *	176.41 ± 23.73	202.61 ± 31.37
Months of financial insecurity *	1.88 ± 2.55	4.15 ± 2.03
Herbicide intensity ǂ	2.31 ± 1.20	2.87 ± 1.06
Loans for investment § **	0.50 ± 0.52	0 ± 0
Loans for subsistence §	0.38 ± 0.50	0.64 ± 0.50
Market access ǂ *	2.44 ± 0.89	1.73 ± 0.70
Technical assistance ǂ *	2.38 ± 1.31	1.29 ± 0.83
Off-farm income §	0.50 ± 0.52	0.53 ± 0.52
Other farm income §	0.44 ± 0.51	0.13 ± 0.35

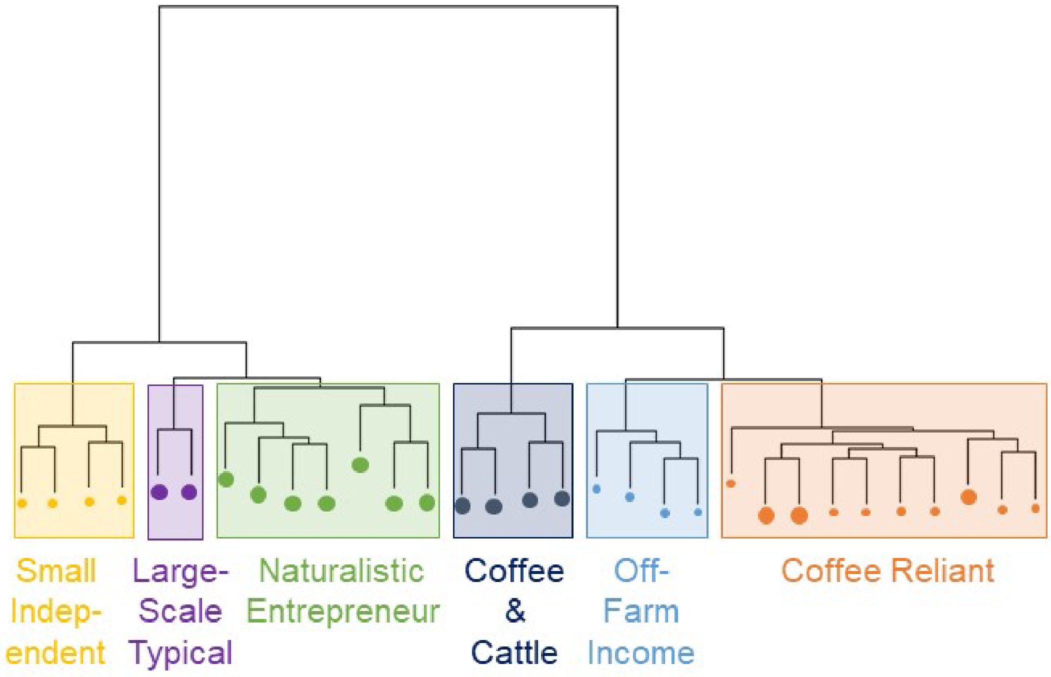

Figure 1. Hierarchical cluster analysis dendrogram showing typology divisions based on the Ward clustering algorithm. Large filled circles indicate farms larger than 13 ha. and small filled circles indicate farms smaller than 13 ha.

Table 2. Farm typologies. The number of farms in each typology (n) is listed. Farm size includes the mean in hectares with the size range in parentheses.

Typology	***n***	***Farm size (ha)***	***Description***
Coffee Reliant	10	10.3 (2.8-23.8)	Small to large farms in the same ownership for more than 10 years with all or nearly all their land base in coffee. These farms were completely dependent on coffee with no other sources of income to speak of. Most took loans to cover subsistence and farm expenses throughout the year and none mentioned loans to expand or improve their farms. They had generally low access to technical assistence and medium access to markets, with most belonging to cooperatives. They used agrochemicals with varying levels of intensity and had the highest coffee planting densities of any group.
Off-Farm Income	4	3.4 (1.8-4.9)	Small farms with most or all their land used for coffee production. This group may be distinguished from the first group by having significant off-farm income, generally in the form of at least one family member with a regular off-farm job. Most employed no permanent workers, and some took loans for subsistence and farm expenses while others did not. They had lower access to technical assistance and marketing and most used agrochemicals more intensively with high coffee planting density.
Coffee & Cattle	4	48.3 (14.0-84.0)	Large farms mostly with longer ownership. This group split their larger land base between coffee and cattle, diversifying their farm income. Some also sold additional farm products such as vegetables, maize, and beans. They did not have income from off-farm work. They tended to self-exploit, hiring few if any permanent workers and still took loans for subsistence, although some took loans to make farm investments as well. They had low access to technical assistance and marketing. Use of agrochemicals varied, but planting density was generally lower than farms with smaller land bases.
Independent Small Producers	4	3.9 (1.4-5.6)	Small farms with most of their land base in coffee. These producers may be differentiated from the previous groups by their financial independence. They avoided taking loans, preferring instead to carefully manage their resources, and were not members of cooperatives. All had some additional sources of income either on- or off-farm. Because they shunned cooperatives and farmer organizations, they had relatively low access to markets and technical assistance. They also tended to be less reliant on agrochemicals than the previous groups.

Naturalistic Entrepreneur	7	131.6 (21-490)	Large farms of varying ages with some or all their land base in coffee. These producers are less dependent on coffee for their income or have sources of wealth aside from coffee. Most had, or expressed interest in developing, agritourism or ecotourism on their farms. They employed permanent workers year-round and took loans only to make new investments in their farms, not for subsistence. They had high levels of technical expertise within the farm management and better access to markets via sales to large coffee exporting companies or direct market relationships abroad, guaranteeing them higher prices. These farms used low levels of agrochemicals, preferring less toxic alternatives whenever possible and coffee planting density was low.
Large-Scale Typical	2	255.5 (175-336)	Large farms with only a fraction of land in coffee production. These farms had additional income from farm and non-farm sources and maintained a significant number of permanent employees. This group may be distinguished from the large farms in the Naturalistic Entrepreneur category by management more similar to the smaller-scale producers in the first three groups. They also had lower access to technical assistance, lower market access, and high agrochemical use but low planting density. They took loans to make investments in the farm.

Table 3. Values for trees based on interview responses (total number, with percent of responses indicated parenthetically). Typology is if more than half of respondents in that group mentioned the value.

Value	Category	Responses	Description	Main Typologies
Improves coffee health	Coffee Production	23 (70%)	Shade improves plant longevity and decreases water stress in summer	All groups
Improves coffee flavor	Coffee Production	15 (45%)	Slower fruit development results in higher bean quality	Naturalistic Entrepreneur Large-Scale Typical Coffee & Cattle
Mitigates climate change impacts	Coffee Production	16 (48%)	Trees buffer temperature and protect from heavy rain	Naturalistic Entrepreneur Large-Scale Typical Off-Farm Income
Too much shade increases fungal disease	Coffee Production	15 (45%)	Higher humidity, less light increase American leaf spot	Coffee Reliant Off-Farm Income
Too much shade decreases production	Coffee Production	9 (27%)	Less light reduces flowering and yield	Naturalistic Entrepreneur
Protects coffee from wind damage	Coffee Production	2 (6%)	Trees attenuate winds that damage leaves and fruit	
Decreases soil nematodes	Coffee Production	1 (3%)		
Shade for workers	Coffee Production	3 (9%)	More comfortable working conditions	
Firewood	Household Provisioning	27 (82%)	Provides an important and cost-saving resource	All groups except Naturalistic Entrepreneurs
Timber	Household Provisioning	15 (45%)	Occasional culling of a tree allows for on-farm construction projects	Coffee Reliant
Fruit	Household Provisioning	5 (36%)	Fruit trees contribute to home consumption and sale	
Water conservation	Ecosystem Services	14 (42%)	Trees increase soil moisture and protect water sources	Naturalistic Entrepreneur Coffee & Cattle
Soil improvement	Ecosystem Services	15 (45%)	Trees fix nitrogen and leaf litter improves soil nutrition and structure	Naturalistic Entrepreneur
Reduce erosion	Ecosystem Services	7 (21%)	Trees reduce direct rainfall on soil and help hold soil	Off-Farm Income
Oxygen/clean air	Ecosystem Services	12 (36%)	Plants emit oxygen, trees make air cool and fresh	Off-Farm Income
Benefits to wildlife	Appreciation of Nature	12 (36%)	Birds, insects, and small mammals benefit from trees for food and habitat	Naturalistic Entrepreneur Coffee & Cattle
Aesthetics	Appreciation of Nature	4 (12%)	Trees add beauty to the farm landscape	

Table 4. Shade tree species observed in ecological surveys. We report the total number of individuals observed in 87 survey plots and the percent of interviewees who mentioned the species. When uses and positive or negative attributes were mentioned in interviews, we have included those. Origin (native or exotic) was based on records in *Flora de Nicaragua* (Stevens et al. 2001).

Common Name	***Scientific Name***	***Family***	***# in Plots***	***Interview Mentions***	***Uses***	***Positive Characteristics***	***Negative Characteristics***	***Origin***
Banano, Guineo, Plantano	*Musa spp.*	MUSACEAE	282	39%	Temporary shade, Fruit		Needs frequent replanting	Exotic
Guaba roja, Guaba colorada	*Inga oerstediana**	FABACEAE	145	88%	Shade, Firewood, Timber, Wildlife	Nitrogen fixing, grows quickly, quality of shade, good growth form, recovers well from pruning, leaves improve soil, preferred firewood		Native
Guaba negra	*Inga punctata**	FABACEAE	118	27%	Shade, Firewood	Nitrogen fixing, grows quickly, good growth form, recovers well from pruning, preferred firewood	Increases American leaf spot	Native
Nogal	*Juglans olanchana**	JUGLANDACEAE	40	61%	Shade, Timber Wildlife	Grows fast, good for construction, easy to manage		Native
Trotón	*Mosquitoxylem jamaicense*‡¶	ANACARDIACEAE	25	27%				Native
Pino	*Pinus oocarpa/ tecunumanii**	PINACEAE	24	15%	Timber		Poor shade quality ("hot")	Native
Higuera	*Ricinius comunis**	EUPHORBIACEAE	22	3%	Temporary shade			Exotic

Common Name	***Scientific Name***	***Family***	***# in Plots***	***Interview Mentions***	***Uses***	***Positive Characteristics***	***Negative Characteristics***	***Origin***
Aguacate	*Persea americana**	LAURACEAE	21	33%	Fruit, Timber, Wildlife	Good quality timber, preferred by wildlife, provides fruit		Native
Cedro rosado	*Acrocarpus fraxinifolius**	FABACEAE	20	21%	Shade, Timber	Quality of shade, good for construction, nitrogen fixing	Unattractive growth form, favored by leaf cutter ants	Exotic
Guayaba	*Psidium guajava**	MYRTACEAE	17	6%	Fruit			Exotic
Aguacate canelo	*Ocotea spp.*[¥]	LAURACEAE	16	30%	Timber, Wildlife			Native
Roble encino	*Quercus spp.*[£]	FAGACEAE	15	30%	Timber		Increases American leaf spot	Native
Espino	*Vachellia pennatula**	FABACEAE	14	9%				Native
Roble	*Quercus spp.*[£]	FAGACEAE	14	42%	Timber			Native
Cacahuillo	*Elytreria sp.*[£]	ACANTHACEAE	13	6%	Timber			Native
Lechoso	*Sapium macrocarpum*[¥£]	EUPHORBIACEAE	12	9%	Timber			Native
Cítrico	*Citrus spp.*	RUTACEAE	12	21%				Exotic
Naranja	*Citrus sinensis*[£]	RUTACEAE	11	24%	Fruit			Exotic
Mango	*Mangifera indica**¶	ANACARDIACEAE	10	3%	Fruit			Exotic
Lisaquín	*Nectandra sp.*[£]	LAURACEAE	9	12%	Timber			Native
Capulín	*Trichospermum galeottii*[§]	TILIACEAE	8	0%				Native

Common Name	Scientific Name	Family	# in Plots	Interview Mentions	Uses	Positive Characteristics	Negative Characteristics	Origin
Aguacate colorado	*Persea sp.*[£]	LAURACEAE	7	3%	Timber, Wildlife			Native
Cedro real	*Cedrela odorata*[£§]	MELIACEAE	7	6%	Timber	Highly desirable for timber	Rare, endangered	Native
Cuajiniquil	*Inga vera*[*¥]	FABACEAE	7	18%	Firewood			Native
Jocote/Jocote ciruelo	*Spondias purpurea*[§¥¶]	ANACARDIACEAE	7	3%	Fruit			Native
Búcaro	*Erythrina berteroana*[*]	FABACEAE	6	3%	Firewood	Nitrogen fixing, easy to manage		Native
Caimito	*Conostegia xalapensis*[‡]	MELASTOMATACEAE	6	12%	Firewood		Poor shade quality ("hot")	Native
Canelo	*Nectandra nitida*[*]	LAURACEAE	6	3%	Timber			Native
Guanacaste	*Enterolobium cyclocarpum*[*]	FABACEAE	6	3%				Native
Güitite	*Acnistus arborescens*[*‡§]	SOLANACEAE	6	0%				Native
Mampas	*Lippia myriocephala*[*§]	VERBENACEAE	6	6%	Firewood			Native
Tatascán, Tatascame	*Lasianthaea fruticosum*[*¶]	ASTERACEAE	6	3%	Firewood			Native
Aguasalipe, Aguacate guaslipe	*Beilschmiedia riparia*[¶]	LAURACEAE	5	21%	Timber			Native
Palanca	*Sapranthus nicaraguensis*[‡†]	ANNONACEAE	5	3%				Native
Pisquín	*Albizia carbonaria*[£]	FABACEAE	5	0%				Native
Aguacate de monte	*Persea caerulea*[§]	LAURACEAE	4	3%	Timber			Native

Common Name	***Scientific Name***	***Family***	***# in Plots***	***Interview Mentions***	***Uses***	***Positive Characteristics***	***Negative Characteristics***	***Origin***
Ciprés	*Cupressus lusitanica*¶	CUPRESSACEAE	4	12%				Native
Ficus, Chilamate	*Ficus spp.* *£	MORACEAE	4	3%	Wildlife			Native
Guaba extranjera	*Inga jinicuil*¥	FABACEAE	4	3%	Firewood			Exotic
Guarumo	*Cecropia spp.* ‡£	URTICACEAE	4	3%				Native
Limoncillo	*Trichilia havanensis* *§¶	MELIACEAE	4	0%				Native
Sarai	*Eugenia guatemalensis*¥§ *Eugenia esteliensis*¶	MYRTACEAE	4	3%				Native
Ampe			3	0%				
Guayabó	*Terminalia oblonga* *‡§	COMBRETACEAE	3	18%	Timber			Native
Madero, Madero negro	*Gliricidia sepium* *£¥	FABACEAE	3	9%			Only grows in warmer areas	Native
Nancite	*Byrsonima crassifolia* *‡¶	MALPIGHIACEAE	3	3%	Fruit			Native
Caoba	*Swietenia macrophylla* *£	MELIACEAE	2	6%	Timber	Highly desirable for timber	Rare, endangered	Native
Chaperno	*Lonchocarpus spp.* §£	FABACEAE	2	3%				Native
Coyote	*Platymiscium pinnatum*‡	FABACEAE	2	6%				Native
Huele noche			2	0%				
Limón	*Citrus limon*£	RUTACEAE	2	6%	Fruit			Exotic
Macuelizo	*Tabebuia rosea*‡§	BIGNONIACEAE	2	6%				Native

Common Name	***Scientific Name***	***Family***	***# in Plots***	***Interview Mentions***	***Uses***	***Positive Characteristics***	***Negative Characteristics***	***Origin***
Manzana			2	0%				
María	*Calophyllum brasiliense**	CLUSIACEAE	2	27%	Timber, Wildlife	Good for construction		Native
Matorral	*Eupatorium sp.*[¥]	ASTERACEAE	2	3%				Native
Muñeco	*Terminalia amazonia*[¥]	COMBRETACEAE	2	3%	Timber			Native
Posán, Aguacate Posán	*Ocotea spp.*[§¶]	LAURACEAE	2	18%	Timber			Native
San Rafael	*Cedrela sp.*[ȣ]	MELIACEAE	2	6%				
Sangregrado	*Croton draco*[§¶]	EUPHORBIACEAE	2	9%				Native
Sauce		SALICACEAE	2	6%				
Arrayán	*Eugenia sp.*[§¶]	MYRTACEAE	1	0%				Native
Azaharillo		SALICACEAE[ȣ]	1	3%				
Brasil	*Haematoxylum brasiletto**[†§]	FABACEAE	1	3%				Native
Cuajilote	*Parmentiera aculeata**[§]	BIGNONIACEAE	1	0%				Native
Cuernavaca	*Solanum wrightii**[§]	SOLANACEAE	1	0%				Exotic
Cugia			1	0%				
Eritrina, Elequeme	*Erythrina spp.*[£]	FABACEAE	1	3%	Firewood	Nitrogen fixing		Exotic
Guanábana	*Annona muricata**	ANNONACEAE	1	0%	Fruit			Native
Liquidámber	*Liquidamber stryraciflua*[¶§]	HAMMELIDACEAE	1	21%	Timber			Native
Majagua	*Heliocarpus appendiculatus*[¶§]	TILIACEAE	1	3%				Native

Common Name	***Scientific Name***	***Family***	***# in Plots***	***Interview Mentions***	***Uses***	***Positive Characteristics***	***Negative Characteristics***	***Origin***
Mana de león			1	0%				
Matapalo	*Ficus spp.*[£]	MORACEAE	1	6%				Native
Ojoche			1	0%				
Palo de hule	*Castilla elastica*[‡§]	MORACEAE	1	0%				Native
Paloma			1	0%				
Sacatinta	*Justicia sp.*[§¥]	ACANTHACEAE	1	0%				
Tostadillo	*Allophylus sp.*[‡]	SAPINDACEAE	1	0%				Native
Vara blanca			1	0%				
Zapote	*Pouteria sapota*[£]	SAPOTACEAE	1	0%	Fruit			Native
Unidentified			42					

Names were provided as common names by producers and matched with scientific names from the following sources as indicated:

* Stevens, D, CU Ulloa, A Pool, and OM Montiel. 2001. *Flora de Nicaragua.* Tropicos.
‡ Salas Estrada, JB. 1993. *Árboles de Nicaragua*. Instituto Nicaragüense de Recursos Naturales y del Ambiente.
§ Grijalva Pineda, A. 2006. *Flora Útil Etnobotánica de Nicaragua.* Ministerio del Ambiente y los Recursos Naturales.
¥ Muñoz, F. 2006. *Investigación de árboles, aves y orquídeas en zonas cafetaleras.* Cafenica.
£ Obregón, D. 2007. *Lista de árboles de la finca La Hammonia y Selva Negra*
¶ Watton, AJ. *Cloud Forest Trees at Celaque Honduras and in Nicaragua, their Climate Tolerance and Recommendations for Cloud Forests in Central America.*
ȣ Interview response

Conclusions

Over course of my research, I have found that shade coffee farms have many characteristics that support epiphytes well. In the two farms where I concentrated the majority of my work, trees inside the coffee farm hosted nearly as diverse an assemblage of epiphytes as the adjacent forest. These assemblages were also functionally diverse, supporting species with a variety of life history strategies. Many of the plants I observed had flowers and fruits, indicating that they are successfully reproducing. However, coffee farms are highly variable in age and management practices, so the habitat quality for epiphytes varies considerably among farms. Because farms are a social-ecological system, assessing them as potential habitat necessarily involves integrating human management as an additional layer of filtering through which species must pass. Below I note several key factors that dictate the strength of that filtering. Although these are specific to epiphytes in coffee farms, they may also be conceptually useful in evaluating other social-ecological systems.

1. Epiphyte diversity depends on tree size, requiring that shade coffee practices be maintained over the long term for habitat benefits to be realized. In the region of Nicaragua where I worked, many farms had recently established trees to shade their coffee. As climate change impacts become more acute, I expect to see more producers adding trees to maintain coffee production. Initially, young shade trees offer very little habitat for epiphytes. Some early colonizing species arrive on the trees within a few years, but most are slower and may need cooler, shadier microhabitats to develop and non-vascular epiphytes to colonize before they can establish. Thus, shade coffee practices need to be maintained on the farm for on the order of a decade or longer before the trees begin to accumulate a diversity of species. In the volatile world of coffee prices and changing land uses, the time needed for newly established shade coffee to reach the point of supporting self-sustaining epiphyte populations may be incompatible with the livelihoods of many smallholders whose farming decisions respond, at least partially, to short-term market fluctuations. In addition, very large trees can cast too much dense shade, which decreases coffee production, so large trees are not always preferred by farmers.

2. High humidity favors diverse epiphyte assemblages but creates problems for coffee production. Epiphytes thrive in the cooler temperature and higher humidity of cloud forests, so the coffee farms at higher elevations, some of which experience periodic cloud immersion, contained the greatest epiphyte diversity when other factors were equal. However, high humidity is less ideal for farmers. When the leaves of the coffee plants stay wet for too long, fungal diseases develop, particularly American leaf spot (*Mycena citricolor*). This disease can be devastating for producers because it spreads quickly and affects the fruit as well as the leaves. Farmers told me that, in addition to fungicides, their best defense against American leaf spot is to keep the shade in their farms very moderated. This involves heavy regular pruning of the shade trees and in some cases lower shade tree density. Therefore, while the abiotic conditions are more conducive to epiphytes at higher elevations, there may be less habitat available in the coffee farms and that habitat is disturbed more frequently.

3. Disturbance and stress both increase for epiphytes inhabiting coffee farms. In addition to the treefalls and branchfalls that all epiphytes suffer, epiphytes in coffee farms are sometimes removed by farmers due to lack of knowledge or a belief that they cause damage.

Even when epiphyte removal does not occur, trees on coffee farms are usually pruned annually. Epiphyte mortality in coffee farms is therefore higher, perhaps much higher, than in forests. Pruning removes many small branches and some large branches, and epiphytes growing on those branches will not survive. In addition, the process of pruning involves tree climbing without ropes or other equipment, which often knocks epiphytes off the trunk and larger branches. Coffee farms also have more stressful abiotic conditions than nearby forests, meaning that epiphytes essentially move to a warmer and drier climate when they disperse from forests to coffee shade trees. These two factors, disturbance and stress, are roughly inversely proportional: farmer-induced disturbance is higher where abiotic stress is lower. However, since both factors are overall greater in coffee farms, epiphyte species that are sensitive to either one may be filtered out.

4. Coffee farms are not for all epiphytes. Given the above anthropogenic filters combined with the biotic and abiotic filters of any habitat, coffee farms are suitable substitute habitat for only a subset of the regional species pool. Native climate ranges, vertical distributions, and functional traits may all be relevant in predicting which epiphytes will fare best. Species whose ranges include lower elevations are likely to succeed in the warmer, drier, and sunnier conditions of coffee farms, as are those that tend to inhabit the higher strata of the forest canopy. Twig epiphytes are well adapted to disturbance with shorter life cycles to accommodate the high rates of branch falls in forests, so they may fare better in the high disturbance environment of coffee farms. Longer lived species tend to be found in the inner canopy where natural disturbance is lower, and these species may take longer to arrive in coffee farms or may be absent. Intraspecific variation in traits may also be an important adaptive factor where extreme trait values within a species are better suited to coffee farm habitat than are the mean values. Among the major taxonomic groups, atmospheric bromeliads may be best suited to coffee farms, especially at lower elevations. Orchids and ferns that have traits to cope with low water availability can also thrive. Finally, species that inhabit the very shady and humid forest understory are likely to be absent or rare in coffee farms because those conditions are largely not replicated. While coffee farms are good substitute habitat for some species, they do not serve all epiphytes, and may provide the least value to species that are most vulnerable to climate and land use change. Shade coffee practices are offer great benefit overall for supporting biodiversity, providing ecosystem services, and improving farmers' livelihoods, but they cannot be considered a replacement for forest conservation.

Appendix 1. Interview questions and topics

Closed-ended Questions

How many *manzanas* of land do you own?

How many *manzanas* are in coffee?

What other crops/farm products do you produce?

Which crops/farm products do you sell and which are for your own use?

How many years have you owned the farm?

How many types of trees do you have on your farm (within the coffee)?

Do you use chemicals like fungicides or pesticides on coffee? For what purposes?

Are you a member of a cooperative?

Do you receive technical assistance?

How many people work on your farm?

Do you hire any laborers outside your family? How many?

Do members of your family work off farm? Who? What jobs? What parts of the year?

What portion of your household income is from coffee?

Open-ended interview topics

- Financial (in)security and debt
- Comparison with other neighboring farms
- Annual management cycle
- Process of decision-making on farm
- Perceptions of climate change and responses in farm management

- Recent management changes on the farm and why
- Uses/benefits of trees (including any disadvantages)
- Uses/benefits of epiphytes (including any disadvantages)

Appendix 2. Quotations used in original Spanish with English translations

Original: La frescura de la planta, hasta donde manejo, si un grano dura más en llegar a la maduración recoge más nutrientes, hay un mejor sabor en la taza, mientras que si está expuesto al sol se estresa más y tira todas sus energías al grano y madura mas rápido, en el caso de la calidad de la taza creo que no es bueno

Translation: *If the bean takes longer to mature, it picks up more nutrients and it has a better taste in the cup, while if it is exposed to the sun, it is stressed more and throws all its energy to the bean, which matures faster and, in the case of the quality of the cup, I think it's not good. [Naturalistic Entrepreneur]*

Original: Es que hay que darle un manejo también, no es que los va a sembrar en el café y los va a dejar que se hagan…bueno, se le hace algún manejo para que puedan vivir los dos ahí, porque los necesitamos los árboles y también necesitamos el café

Translation: *The thing is you have to manage them [trees], you can't just plant them in the coffee and let them do whatever they will… so you do some management so that they both can live there, because we need the trees and we also need the coffee. [Off-Farm Income]*

Original: Los árboles en cafetales nos sirven para mantener una temperatura más homogénea dentro de la plantación … yo soy asesor de cultivos de café y voy a muchas plantaciones de café … y siempre vemos mejor amortiguar mejor los cambios, la variabilidad climática cuando tenemos una cantidad de árboles en el café, eso es, eso es indudable.

***Translation:** The trees in coffee plantations help us to maintain a more homogeneous temperature within the plantation ... I am a coffee crop consultant and I go to many coffee plantations ... and we always see that it cushions the changes better, the climatic variability, when we have a number of trees in the coffee. That is undeniable. [Naturalistic Entrepreneur]*

Original: Cuando hay una planta de musgo que enraíza mucho, entonces a la planta productora y de tallo débil lo oprime demasiado, y entonces llama a debilitarle el follaje, en el caso del café, entonces y la humedad que produce, lo hace que le produzca hongo y comienza hacerle daño, por eso es que todo debe ser controlado.
***Translation:** When there is moss that takes root all over, it squeezes the producing plant too much and weakens the stem, and then it weakens the foliage, in the case of coffee. And then the humidity it produces, that produces fungus and it begins to do damage, that's why everything must be controlled. [Coffee & Cattle]*

Original: Pues vea, yo creo que si lo pensamos con calma, el café es un cultivo, un cultivo muy noble y entre tener 50 manzanas de pasto y tener 50 manzanas de café, yo creo que debemos tener 50 manzanas de café, porque tenemos 50 manzanas de árboles, en 50 manzanas de árboles hay 200,000 árboles que producen una cantidad increíble de lámina foliar, que transpira, que respira, que purifica, que da mejor vida, que retiene más humedad en el suelo, entonces hoy por hoy podemos ver si estos lugares que la finca tenía muy áridos, que cuando los convertimos a cafetales y les pusimos sombra porque soy amante a esa sombra, este han cambiado enormemente, ya se miran los suelos diferentes … de hecho, de hecho, si no tuviera, yo no sé la gente que piense que debe haber árboles, estamos jodidos, yo estoy reforestando las quebradas, estoy reforestando los ojos de agua, los ríos, haciendo cercas vivas, nosotros solo el año pasado pusimos 2000 árboles en una finca pequeña como esta y hacemos todo lo que podemos tratando de que eso funcione

Translation: *Okay, look, I think if we think about it calmly, coffee is a crop, a very noble crop and between having 50 manzanas of pasture and having 50 manzanas of coffee, I think we should have 50 manzanas of coffee, because we have 50 manzanas of trees. In 50 manzanas of trees there are 200,000 trees that produce an incredible amount of leaf area, that transpire, that respire, that purify, that give better life, that retain more moisture in the soil. So, day by day, we can see these places where the farm was really arid, that when we converted them to coffee plantations and we put them in shade—because I am in love with that shade—it has changed enormously, you can already see the differences in the soil. In fact, in fact, if we didn't have… I don't know… the people who think there should be trees, we'd be screwed. I'm reforesting the creeks, I'm reforesting the water sources, the rivers, making living fences. Just last year, we put 2,000 trees into a small farm like this one last year and we are doing all we can to try to make that work. [Naturalistic Entrepreneur]*

Original: …esa parte no se podía pegar café ahí, por lo que la tierra había quedado lavada de viaje, quedo una mera capita de tierra fértil, entonces a medida que se fue sembrando arboles la tierra se ha ido componiendo con la hoja que cae y la rama que se pudre todo eso ahí

Translation: *... you couldn't plant coffee here, the earth had been washed away, it had just a thin sheet of fertile soil, but as trees were planted new soil has been forming with the leaves that fall and the branches that rot adding to it. [Off-farm Income]*

Original: ahí había un ojo de agua antes y no había madera y yo le sembré madera y volvió ese ojo de agua, volvió a revertirse y mejor con la madera, ya lo tengo experimentado en dos fuentes de agua que hay ahí … cuando yo compre ahí, los muchachos anteriores tenían verduras ahí, lo habían despalado de viaje, de viaje totalmente y yo le sembré café y la siembra de madera que hay ahí volvieron esos ojos de agua y volvieron hasta más opulentos.
Translation: *There was a spring before but there were no trees and I planted trees and that spring came back, it reverted and better than before! With trees, I have now experienced it with two springs that are here ... when I bought that [parcel], the previous guys had vegetables there, the soil was running away, and I planted coffee and the trees that are there and those springs returned and they returned even more opulent. The trees are helpful for life and for many things, for all of humanity, it could be said. [Coffee & Cattle]*

Original: vea, en una ocasión leía un estudio y decía que los lugares donde puede encontrar un sin número y diversidad de plantas epifitas era sinónimo de salud, salud del ambiente, salud del bosque, entonces para mí yo llego a un lugar y miro, ahh, se miran musgos, se miran líquenes, se miran esto, se mira lo otro, entonces es un lugar sano, entonces para mi tienen el valor del indicativo adonde estas llevando el medio ambiente en tu finca, en tu comunidad
Translation: *See, once I read a study and it said that the places where you can find a large number and diversity of epiphytic plants was synonymous with health, environmental health, forest health. So for me, I arrive at a place and look: ahh, you see mosses, you see lichens,*

you see this, you see that, then it is a healthy place. So, for me they have an indicator value when you are looking at the environment in your farm, in your community. [Naturalistic Entrepreneur]

Original: ahora vienen aves de todo tipo. si, vienen aves de todo tipo, también este, como están los árboles, están las frutas entonces vienen animales del monte, como guatusas, guardiolas, aves de todo tipo, porque hay un entorno de árboles que es donde las aves les gusta estar. ya, antes no, era pelado, era zacate, ahora no, ahora hay bastante, bastante, aves, hay, hay animales de monte, bastante, bastante, bonito es, han venido, un día de estos miramos un leoncillo.

Translation: *Birds of all kinds come, the trees have fruits then forest animals come, such as agoutis, pacas, birds of all kinds, because there's an environment of trees that's where the birds like to be. Before no, it was bare, it was grass, but now it's not, now there's a lot. There are birds, there are forest animals, it's really beautiful how they've come. One day we saw a jaguarundi. [Coffee Reliant]*

Original: Una finca que no tenga agua y árboles para mí no es finca.

Translation: *A farm without water or trees to me isn't a farm [Coffee Reliant].*

Original: La verdad es que ese es el tema más tal vez más álgido que tenemos la gente que trabajamos con café, con los precios que tenemos, con el arrastre financiero deficitario que hemos tenido los años anteriores, el clima que a veces no nos está ayudando, entonces hemos tenido problemas serios, yo no tengo financiamiento bancario, todo trato de hacerlo de la manera, lejos de los bancos porque tengo cierto miedo y restricciones, pero la gente que trabaja con crédito, hoy por hoy está enormemente preocupada, no están cubriendo sus costos y definitivamente van a perder en el ejercicio

Translation: *The truth is that this [finances] is the most perhaps most critical issue that people who work with coffee have, with the prices that we have, with the financial drag of the deficit that we have had in previous years, the climate that sometimes isn't helping us, so we have had serious problems. I do not have bank financing, I try to do everything away from the banks because I have some fear of constraints, but people who work with credit today are enormously worried they are not covering their costs and they are definitely going to lose out on the exercise. [Naturalistic Entrepreneur]*

Original: Es que la mayoría de los productores, cuando nosotros sembramos un árbol de café, arriba le vemos los dólares ya, pero si sembramos un árbol no, solo nos enfocamos en eso, en el café, en el signo de córdoba o de dólar.

Translation: *The thing is that the majority of producers, when we plant a coffee plant, we can see the dollars above it, but when we plant a tree, we don't. We only focus on that, in the coffee there is the dollar sign. [Coffee & Cattle]*

Original: …porque sacamos la cuenta que daba un poquito más el café, además que se protege el suelo, porque en el caso de la huerta la estábamos erosionando, con el café se protege

Translation: *[We switched to coffee] because we realized that it would sell for a little more, but also that it would protect the soil. Because the soil in the cornfield was eroding, but with the coffee it was protected. [Small Independent]*

Original: Para mi es una planta muy bonita, te le da un gran realce a la finca, la gente aquí como no las conoce y como no sabe lo que es bonito, aquí más bien las destruye la gente, las bota, nosotros no, nosotros las cuidamos, esas plantas se van perdiendo, son contadas en las fincas que vos hayas esas plantas, las agarran, las machetean y nosotros no, ahí vas a ver aquí en la finca como están y sembramos, las cultivamos, nos gusta pues, porque mi esposa es amante de las plantas, todos lo somos

Translation: *For me they are very beautiful plants, they give a great enhancement to the farm. People here don't know them and they don't know what is beautiful, so they destroy them and get rid of them. Not us, we take care of them. Those plants are being lost, they are numbered on the farms that you have. They grab them and cut them, but we don't. You will see here on the farm how they are and we plant them, we cultivate them. We like it like that, because my wife is a lover of plants, we all are. [Small Independent]*