

Differences in epiphyte biomass and community composition along landscape and within-crown spatial scales

Autumn A. Amici¹  | Nalini M. Nadkarni¹ | Cameron B. Williams² | Sybil G. Gotsch² 

¹School of Biological Sciences, University of Utah, Salt Lake City, UT, USA

²Department of Biology, Franklin and Marshall College, Lancaster, PA, USA

Correspondence

Autumn A. Amici, School of Biological Sciences, University of Utah, 257 South 1400 East, Salt Lake City 84112, UT, USA.
Email: autumn.amici@utah.edu

Funding information

National Science Foundation (United States), Grant/Award Number: 1556289 and 1556319; University of Utah; Franklin and Marshall College

Abstract

Vascular epiphytes contribute to the structural, compositional, and functional complexity of tropical montane cloud forests because of their high biomass, diversity, and ability to intercept and retain water and nutrients from atmospheric sources. However, human-caused climate change and forest-to-pasture conversion are rapidly altering tropical montane cloud forests. Epiphyte communities may be particularly vulnerable to these changes because of their dependence on direct atmospheric inputs and host trees for survival. In Monteverde, Costa Rica, we measured vascular epiphyte biomass, community composition, and richness at two spatial scales: (1) along an elevation gradient spanning premontane forests to montane cloud forests and (2) within trees along branches from inner to outer crown positions. We also compared epiphyte biomass and distribution at these scales between two different land-cover types, comparing trees in closed canopy forest to isolated trees in pastures. An ordination of epiphyte communities at the level of trees grouped forested sites above versus below the cloud base, and separated forest versus pasture trees. Species richness increased with increasing elevation and decreased from inner to outer branch positions. Although richness did not differ between land-cover types, there were significant differences in community composition. The variability in epiphyte community organization between the two spatial scales and between land-cover types underscores the potential complexity of epiphyte responses to climate and land-cover changes.

Abstract in Spanish is available with online material.

KEYWORDS

Costa Rica, crown position, elevation gradient, land cover, Monteverde, tropical montane cloud forest, vascular epiphytes

1 | INTRODUCTION

Vascular epiphytes reach their greatest abundance and diversity in tropical montane cloud forests (TMCFs) where thick mats of canopy soil support non-vascular and vascular plant communities (Kreft, Köster, Kuper, Nieder, & Barthlott, 2004; Nakanishi, Sungpalee, Sri-ngernyuang, &

Kanzaki, 2016; Werner, 2011). Epiphytes can comprise up to 44 tons/ha of aboveground biomass and up to 35% of the vascular plant diversity of some tropical forests (Gentry & Dodson, 1987; Hofstede, Wolf, & Benzing, 1993; Ingram, Ferrell-Ingram, & Nadkarni, 1996; Ingram & Nadkarni, 1993). The global average environmental lapse rate of 6.5°C/km (Thayyen & Dimri, 2018) applied to the rugged mountains underlying some tropical forests indicates that steep gradients in temperature and

relative humidity occur over relatively short horizontal distances. These changes in microclimate with elevation appear to be strong drivers of variation in vascular epiphyte biomass and species richness (Bussmann, 2001; Ding et al., 2016; Gehrig-Downie, Marquardt, Obregón, Bendix, & Gradstein, 2012; Gotsch, Davidson, Murray, Duarte, & Draguljić, 2017; Hietz & Hietz-Seifert, 1995; Wolf & Flamenco-S, 2003), and may explain the mid-elevation peak in vascular epiphyte species richness that has been documented in montane forests (Cardelús, Colwell, & Watkins, 2006; Hietz & Hietz-Seifert, 1995; Krömer, Kessler, Gradstein, & Acebey, 2005).

Epiphyte biomass and richness can also exhibit substantial variability within individual tree crowns. For example, epiphyte biomass was greatest on the largest diameter branches and at inner crown positions in montane forests of Ecuador, Costa Rica, and Mexico (Freiberg & Freiberg, 2000; Köhler, Tobón, Frumau, & Bruijnzeel, 2007; Nadkarni, 1984; Nadkarni, Schaefer, Matelson, & Solano, 2004). However, these within-tree patterns were not universal among taxonomic groups. Biomass of epiphytic angiosperms in Ecuador was greatest at the inner crown and on tree trunks, whereas lichens and bryophytes were more abundant on smaller diameter branches in the outer crown (Werner, Homeier, Oesker, & Boy, 2012).

Changes in land use, specifically the isolation of trees in fragmented habitats, are also likely to affect epiphyte communities. Deforestation and habitat fragmentation can isolate arboreal plant and animal populations in patches or as single trees, which may result in local extinctions and reduce biodiversity due to reductions in gene flow (Aldrich & Hamrick, 1998; Cascante-Marín, Jong, et al., 2006b; Cascante-Marín, Wolf, et al., 2006a; Kartzinel, Trapnell, & Shefferson, 2013). Isolated trees tend to experience higher light availability, air temperature, and wind speeds that could lead to higher rates of desiccation compared with trees in intact forests (Cascante-Marín et al., 2009; Larrea & Werner, 2010). Although habitat fragmentation undoubtedly affects epiphyte communities by reducing host tree availability, reports on the impacts of isolated trees on epiphyte biomass and diversity have been inconsistent. For example, remnant trees in pastures can serve as “stepping stones” for epiphyte dispersal and colonization between intact patches of forest, and forest fragments can have similar epiphyte diversity and richness to intact forests (Einzmann & Zotz, 2017; Guevara, Laborde, & Sanchez, 1998; Larrea & Werner, 2010; Nadkarni & Haber, 2009). Conversely, tree crowns in isolated pastures sometimes support unique epiphyte communities compared with trees in intact forests, presumably due to the long-term effects of an altered microclimate that increased rates of desiccation (Einzmann & Zotz, 2017; Köster, Kreft, Nieder, & Barthlott, 2013).

Climate change models suggest that TMCs will soon experience intensifying droughts and increasing temperatures that will cause a rise in the elevation of cloud formation (Hu & Riveros-Iregui, 2016; Lawton, Nair, Sr, & Welch, 2001; Pounds et al., 2006; Still, Foster, & Schneider, 1999). Because epiphytes do not have direct contact with terrestrial resources, they may be susceptible to drying atmospheric conditions such as reduced cloud water interception (Benzing, 1990, 2008; Gentry & Dodson, 1987; Zotz & Hietz, 2001). Such changes

will likely cause physiological stress in epiphyte communities that could influence patterns of biomass and diversity (Darby, Draguljić, Glunk, & Gotsch, 2016; Pounds, Fogden, & Campbell, 1999; Still et al., 1999). For example, epiphytes exposed to experimental drought and warming experienced declines in leaf thickness, stomatal conductance, and sap flow (Darby et al., 2016), and the absorption of cloud water directly through the leaf surfaces of some species suggests that cloud immersion may be important for maintaining adequate hydration (Darby et al., 2016; Gotsch et al., 2017, 2015). Understanding epiphyte patterns across multiple spatial scales can indicate at which scales taxa may be most vulnerable to changes in climate and landscape.

Although patterns of epiphyte biomass, richness, and community composition have been documented in many tropical forests, it is unclear how these communities vary at different spatial scales and land-cover types in the same region. We examined the biomass, community composition, and richness of vascular epiphytes at two spatial scales: (1) along an elevation gradient spanning premontane forests to montane cloud forests and (2) within trees along branches from inner to outer crown positions. We also compared epiphyte biomass and distribution at these scales between two different land-cover types, comparing trees in closed canopy forest to isolated trees in pastures. Specifically, we asked the following: How do elevation, land-cover type, and branch position impact epiphyte biomass, community composition, and richness?

2 | METHODS

2.1 | Study sites

The Monteverde region of Costa Rica is an ideal location for this study due to its abundant and diverse epiphyte communities occupying multiple land-cover types that are spread over a wide range of elevations. We included six forested sites along an elevation gradient from 1,131 m to 1613 m, which spanned from the cloud forest on the Atlantic side of the continental divide (El Valle Forest) to below the cloud base on the Pacific side (UGA Forest; Table 1). We did not sample between 1,200 and 1,300 m due to steep, landslide-prone slopes. Our land-cover types included closed canopy forest (primary and secondary; hereafter, “forest”) and pasture (Table 1). We selected three pasture sites based on their similarity in elevation and proximity to three of the forest sites. We were unable to find a pasture site match for all the forested sites, but the three that were included in this study were at the top, middle, and bottom of the elevation gradient and therefore encapsulated the range in microclimate throughout the gradient.

2.2 | Microclimate data

All sites occurred along an elevation gradient established in an ongoing study on the effects of microclimate on epiphyte ecophysiology (Gotsch et al., 2017). All nine sites experience seasonal dry

TABLE 1 Locations, land-cover types, mean and minimum distances among study trees, mean annual temperature, relative humidity, and vapor pressure deficit (VPD) for nine study sites across an elevation gradient including six forests and three pastures in the Monteverde region of Costa Rica. Dark borders around sites denote forest-pasture pairs of similar elevations

Site	Elevation (m)	Location	Lat, Long	Land-cover Type	Mean Dist. (m)	Min. Dist. (m)	Mean Temp. (°C)	Temp SE	Mean RH (%)	RH SE	VPD (KPA)	VPD SE
El Valle Forest ^a	1613	The Children's Eternal Rainforest	N10° 19.246', W84° 46.166'	Closed Canopy Forest-Intact/Primary	269	82	16.9	0.18	99.2	0.3	0.02	0.01
El Valle Pasture	1564	Private Farm	N10° 20.626', W84° 48.259'	Pasture	87	50	16.5	0.26	97.5	0.46	0.05	0.01
CCT Forest ^a	1563	Monteverde Reserve	N10° 18.481', W84° 47.977'	Closed Canopy Forest-Intact/Primary	179	127	16.7	0.20	98.1	0.38	0.04	0.01
Upper CC Forest ^a	1554	Curi Cancha Reserve	N10° 18.522', W84° 47.926'	Closed Canopy Forest-Intact/Primary	51	16	16.8	0.29	96.1	0.69	0.08	0.01
Lower CC Pasture	1501	Private Farm	N10° 17.691', W84° 48.027'	Pasture	57	41	17.2	0.21	97.0	0.52	0.06	0.01
Lower CC Forest ^a	1478	Curi Cancha Reserve	N10° 18.377', W84° 48.200'	Closed Canopy Forest-Secondary with remnant trees	31	23	17.6	0.18	94.2	0.64	0.12	0.01
Buen Amigo Forest ^a	1077	Private Reserve	N10° 16.648', W84° 47.573'	Closed Canopy Forest-Primary with timber removal	164	65	19.9	0.14	90.0	0.82	0.25	0.02
Buen Amigo Pasture	1060	Private Farm	N10° 16.645', W84° 47.729'	Pasture	352	112	19.9	0.19	90.0	0.68	0.24	0.02
UGA Forest ^a	1131	University of Georgia	N10° 17.004', W84° 47.932'	Closed Canopy Forest-Secondary	35	22	20.6	0.43	84.3	4.03	0.45	0.14

^aForest site selection and designations follow Gotsch et al. (2017). Elevations differ slightly from Gotsch et al. (2017) because site elevations in this study were averaged among trees sampled.

periods from about February through April, but the higher elevation sites are typically cooler and wetter compared with the lower sites where the dry periods are more severe (Gotsch et al., 2017). There are two long-term weather stations across this gradient, including the Monteverde Cloud Forest Reserve (CCT Forest) where the average annual precipitation at the upper site is 4,000 mm and at the lowest site (UGA Forest) which receives 2,300 mm (Gotsch et al., 2017). Microclimate stations were installed in forest and pasture sites, where in-canopy temperature and relative humidity (RH) were measured four times per hour using HOBO Pro v2 dataloggers

(Onset Computer Corporation, Bourne, MA). Raw data were used to calculate mean annual temperature, RH, and subsequently vapor pressure deficit (VPD) via the Tetens formula (Buck, 1981), using monthly average from 2017 to 2018 to generate standard errors.

2.3 | Tree selection and branch sampling

We sampled epiphytes in the forest sites in 2016 and in pasture sites in 2017. The trees selected in each site were common species,

appeared to be safe to climb, had similar diameters, crown architectures, and exposures (Table 2). Although epiphyte communities can vary among host tree species (e.g., Callaway, Reinhart, Moore, Moore, & Pennings, 2002), the host's physical attributes can be of overriding importance (Catling & Lefkovich, 1989; Mehltreter, Flores-Palacios, & Garcia-Franco, 2005; Woods, 2017; Zimmerman & Olmsted, 1992). In TMCFs, tree size and crown architecture are superior predictors of epiphyte richness and biomass than host species (Hietz & Hietz-Seifert, 1995; Laube & Zotz, 2006; Wagner, Mendieta-Leiva, & Zotz, 2015). For this reason, and because conspecific trees with comparable size and crown structure were difficult to find across our elevation gradient, we selected our trees based on similarity in tree size and crown structure, and not species. Mean distance among study trees at each site was measured in Google Earth using GPS coordinates for each tree and averaged ca 200 m (Table 1). The sample trees in pasture sites were isolated from the closed canopy forest, and the degree of isolation was calculated using the mean distance for the eight cardinal and subcardinal directions to nearby forest patches (Table 2).

We used stationary-rope climbing techniques to gain access to tree canopies and moving-rope systems to move laterally within crowns (Anderson, Koomjian, French, Altenhoff, & Luce, 2015; Jepson, 2000). We chose branches that supported epiphyte communities that were representative of the host tree, and which we could safely lower to the ground with minimal disturbance. Epiphyte mats, which consisted of vascular and non-vascular species and decomposing organic material, were sampled at 1-m intervals along the branch, beginning 1 m from the branch's junction with the main trunk and ending where the branch diameter narrowed to 1 cm (Nadkarni et al., 2004). One entire canopy branch (8–17 m in length) was sampled from each of the study trees. We collected epiphyte mats within the crown to the point where the branch was too small for safe access. We then cut and lowered distal portions of the outer branches to the ground to complete the epiphyte sampling. Epiphyte mat samples were a minimum of 20 cm in length, but if an individual epiphyte bisected the endpoint, the sample was extended to include the entire individual plant. This difference in epiphyte mat length among samples did not affect biomass patterns along our elevation or branch gradients (two-way ANOVA: $F_{13} = 0.45$, $p = .952$; epiphyte mat length: $F_1 = 0.76$, $p = .385$; family: $F_{18} = 2.47$, $p = .001$). To allow for relative comparisons among branches of different lengths, we aggregated epiphyte mat samples into inner, middle, and outer branch positions by dividing the total branch length into thirds (Nadkarni et al., 2004; Steege & Cornelissen, 1989; Veneklaas et al., 1990).

We transported epiphyte mats to a nearby laboratory in plastic bags. We included only live vascular plant components above the canopy soil. Canopy soil, vascular plant roots, dead organic material, and non-vascular plants were excluded. All samples were separated into morphospecies (defined by distinct morphological features), photographed, and placed into paper bags. The bags were placed into drying ovens within two to five days of collection and dried to constant weight (<2.5% change in weight). We identified 96% of the taxa to the family level and 27% of the taxa to the genus or species

level with the assistance of local taxonomic experts. All taxa that could not be identified to at least the genus level were categorized as different morphospecies.

We calculated biomass by dividing the dry mass for each species and morphospecies by the surface area of the branch location from which the sample's epiphyte mat was taken. We calculated the surface area of the supporting branch position using the formula for the surface area of a cylinder and the length of each epiphyte mat. The distal portion of the canopy branch is much like an edge habitat regardless of the branch length. Therefore, we used the relative position on the branch considering the relative distance between exposed branches and shaded crown interior no matter the absolute length of the branch (Steege & Cornelissen, 1989; Veneklaas et al., 1990). To allow for these relative comparisons among branches of different lengths, epiphyte mat samples were aggregated into "inner," "middle," and "outer" branch positions by dividing the total branch length into thirds (Nadkarni et al., 2004; Steege & Cornelissen, 1989; Veneklaas et al., 1990).

We combined all species and morphospecies at the family level for analysis, except for the ferns, which we grouped as Pteridophyta. We also categorized plants into functional groups following Gotsch et al. (2017): epiphytic shrubs, herbaceous epiphytes, single-stem woody epiphytes, and bromeliads. Bromeliads were included in both the family and functional group analyses because their tank/rosette growth form and absorptive hairs on the interior leaves may be functionally unique to this family, and their association with CAM photosynthesis allows them to often occupy drier microsites than herbaceous and other epiphyte functional groups.

2.4 | Data analysis

All analyses were conducted using R and EstimateS (Colwell, 2013; R Core Team, 2016). Shapiro-Wilk tests were used to evaluate normality of biomass and taxon richness. Biomass, which was not normally distributed, was log-transformed to achieve normality ($W = 0.98$, $p = .80$), whereas taxon richness (both number of species and rarefied richness) was normally distributed ($W = 0.95$, $p = .27$; $W = 0.98$, $p = .740$). Homoscedasticity of residuals was verified using the autoplot feature in the R package ggplot2 for each ANOVA model (Wickham, 2016). Chao2 estimates of rarefied taxon richness were calculated in EstimateS (Colwell, 2013). We present both number of species and rarefied species richness to enable comparisons with other studies that use rarefied richness across sampling sites.

We used one-way ANOVAs to examine the effects of elevation on epiphyte biomass and taxon richness and to determine the effect of position on branch on epiphyte biomass and richness. To examine the effects of elevation and land-cover type on epiphyte biomass and taxon richness, we performed two-way ANOVAs on the subset of paired pasture and forest sites. We used three-way ANOVAs to assess the interaction between elevation, land-cover type, and position on branch on epiphyte biomass and richness. To determine whether

TABLE 2 Tree species, size, and elevation data for each site. Degree of isolation from forest (calculated using the average distance for the eight cardinal and subcardinal directions to nearby forest patches) is given for each pasture tree

Site	Tree Species	DBH (cm)	Elevation (m)	Degree of isolation (m)
El Valle Forest	<i>Sapium rigidifolium</i>	109	1,607	Not isolated, forest
	<i>Sapium rigidifolium</i>	115	1,612	Not isolated, forest
	<i>Ficus crassiuscula</i>	263	1,621	Not isolated, forest
El Valle Pasture	<i>Slona ampla</i>	145	1,574	221
	<i>Sapium glandulosum</i>	77	1,559	253
	<i>Sapium rigidifolium</i>	87	1,561	208
CCT Forest	<i>Sapium rigidifolium</i>	117	1,562	Not isolated, forest
	<i>Sapium rigidifolium</i>	97	1,544	Not isolated, forest
	<i>Ficus tuerckheimii</i>	445	1,585	Not isolated, forest
Upper CC Forest	<i>Ficus tuerckheimii</i>	245	1,544	Not isolated, forest
	<i>Ficus tuerckheimii</i>	201	1,559	Not isolated, forest
	<i>Dussia macrophyllata</i>	191	1,561	Not isolated, forest
Lower CC Pasture	<i>Ocotea insularis</i>	80	1,522	87
	<i>Ocotea insularis</i>	76	1,496	113
	<i>Sapium rigidifolium</i>	81	1,487	142
Lower CC Forest	<i>Sideroxylon portoricense</i>	163	1,477	Not isolated, forest
	<i>Pouteria exfoliata</i>	176	1,479	Not isolated, forest
	<i>Sideroxylon portoricense</i>	165	1,480	Not isolated, forest
Buen Amigo Forest	<i>Pouteria fossicola</i>	172	1,076	Not isolated, forest
	<i>Mortoniendron costaricense</i>	165	1,086	Not isolated, forest
	<i>Ficus isophlebia</i>	353	1,069	Not isolated, forest
Buen Amigo Pasture	<i>Cupania glabra</i>	85	1,036	106
	<i>Pouteria reticulata</i>	164	1,053	123
	<i>Ehretia latifolia</i>	105	1,090	82
UGA Forest	<i>Ehretia latifolia</i>	184	1,123	Not isolated, forest
	<i>Sideroxylon portoricense</i>	158	1,128	Not isolated, forest
	<i>Sideroxylon portoricense</i>	125	1,144	Not isolated, forest

there was a significant association of epiphyte family and functional group biomass with elevation, land-cover type, and position on branch, we conducted nested ANOVAs and examined the patterns of each individual family and functional group using separate one-way ANOVAs. We adjusted alpha levels using Bonferroni corrections

(biomass: alpha = 0.005, richness: alpha = 0.013, individual families: alpha = 0.001, individual functional groups: alpha = 0.004).

We analyzed patterns in community composition with non-metric multidimensional scaling (NMDS) in the R package Vegan (Oksanen, 2009; Oksanen et al., 2017). The ordination plots

containing two dimensions for community composition had low stress (0.23), a non-metric fit $R^2 = 0.94$, and a linear fit $R^2 = 0.68$. We also used PERMANOVA to verify the relationships of species and morphospecies biomasses across elevation and land-cover types using the “Adonis” function (Oksanen, 2009; Oksanen et al., 2017). Environmental data were overlaid as vectors onto the ordination output using the “envfit” function to quantify correlations between microclimate variables and ordination axes. Microclimate data were overlaid as vectors onto the ordination output using the “envfit” function to quantify correlations between the ordination axes and temperature, RH, and VPD. For community composition among position on branch, there was insufficient overlap in species, so we used the composition of family-level biomass assemblies for comparisons. Variation in family-level community composition in response to position on branch was also analyzed using NMDS and PERMANOVA. The findings for each of these results are summarized in Table 3.

3 | RESULTS

3.1 | Elevation gradient

Total vascular epiphyte biomass did not vary with elevation ($F_8 = 0.76$, $p = .640$); however, the biomass of particular epiphyte families varied significantly across sites within the elevation gradient ($F_{90} = 4.67$, $p < .001$, elevation: $F_8 = 1.04$, $p = .41$). At the highest elevation forests (El Valle and CCT), the families making up the greatest percentage of the biomass were Araliaceae and Ericaceae, whereas at the middle elevations (upper CC and lower CC), Ericaceae and Orchidaceae made up the greatest proportion of biomass (Figure 1a). At the lowest elevation forested sites (Buen Amigo and UGA), Clusiaceae, Ericaceae, and Rubiaceae made up the majority of the total biomass (Figure 1a). In addition, although not statistically significant, Hymenophyllaceae were greatest in biomass at the highest elevation sites where cloud immersion is routine, decreased with elevation, and were absent at the two lowest elevation forested sites below the cloud base. The biomass of functional groups also varied significantly with elevation ($F_{27} = 7.21$, $p < .001$, elevation: $F_8 = 1.24$, $p = .29$). However, this trend was driven by variation among functional groups within sites; no single functional group varied with elevation. Among all sites, the shrub functional group made up a majority of the biomass (including Araliaceae, Clusiaceae, Ericaceae, and Rubiaceae), whereas at the middle elevation sites herbs (Orchidaceae) were an important contributor to the total vascular epiphyte biomass (Figure 1a). Rubiaceae shrubs varied significantly across the elevation gradient, reaching greatest biomass at the lowest elevation forested sites and decreasing with elevation ($F_6 = 11.57$, $p = .001$).

We found a difference in community composition for epiphytes between the three higher and three lower elevation forests (PERMANOVA: $R^2 = 0.23$, $p = .005$; envfit: $R^2 = 0.75$, $p = .001$; Figure 2, Table 4); higher elevation forests (El Valle, CCT, and upper CC) clustered together as did the lower elevation forests (lower CC, Buen Amigo, and UGA). The vectors representing temperature, relative humidity, and VPD were each significantly correlated with

NMDS axis 1 and likely structured variation in community composition along this axis. Although elevation was also significantly correlated with community composition patterns of axis 1, each of the climate variables (temperature, RH, and VPD) was more strongly correlated with differences in community composition than elevation (Table 4). An ordination that included a subset of data that contained only the individuals identified to genus or species also indicated a difference in community composition between upper and lower forests. However, in this subset analysis, the clustering of trees with respect to elevation was less distinct compared with the ordination including all species and morphospecies (PERMANOVA: $R^2 = 0.23$, $p = .005$, envfit: $R^2 = 0.47$, $p = .001$).

Taxon richness (all species and morphospecies) increased with elevation; the UGA Forest averaged just 18 taxa per branch, whereas the El Valle Forest supported an average of 52 taxa per branch (Figure 3, Table 5, ANOVA: $F_8 = 3.59$, $p = .012$). Elevation had no significant effect on rarefied taxon richness (Table 5, ANOVA: $F_8 = 1.59$, $p = .198$). There was more variation in rarefied richness across elevation, and though not statistically significant, overall the upper and middle elevation forests were greater in richness (90–120 taxa) compared with the lower elevation sites (50–60 taxa).

3.2 | Land-cover types

There was no significant difference in the total biomass per branch surface area between pairs of forest and pasture across elevation ($F_2 = 1.87$, $p = .197$; elevation: $F_2 = 0.16$, $p = .857$; land-cover type: $F_1 = 0.487$, $p = .499$). However, there were significant differences in biomass between forest and pasture sites for particular families ($F_{58} = 3.52$, $p < .001$; elevation: $F_2 = 1.89$, $p = .156$; elevation/land-cover type: $F_3 = 0.70$, $p = .554$). Bromeliaceae contributed the greatest biomass in the pasture sites, whereas in forests they were less than 10% (Figure 1b). At the lowest and middle elevation pastures, the families that made up the greatest amount of biomass were Bromeliaceae (36%) and Rubiaceae (37%; Figure 1b). Ericaceae shrubs varied between land-cover types and had greater biomass, in general, in the forested sites (Figure 1b; $F_2 = 0.37$, $p = .728$; elevation: $F_2 = 0.016$, $p = .989$; land-cover type: $F_1 = 13.24$, $p = .004$). Functional groups varied significantly with land-cover type ($F_{18} = 4.78$, $p < .001$; elevation: $F_2 = 0.65$, $p = .526$; elevation/land-cover type: $F_3 = 1.01$, $p = .395$). Shrub biomass varied between land-cover types ($F_2 = 0.71$, $p = .508$; elevation: $F_2 = 1.90$, $p = .187$; land-cover type: $F_1 = 14.91$, $p = .002$), where shrubs were greater in biomass in forested sites compared with pastures. Although the analysis of variation in shrub biomass is confounded by variation in Ericaceae between land-cover types, there were a number of other shrub taxa (including Araliaceae and Rubiaceae) that were also included in the “shrub” functional group category. Herbs were proportionally greater in the forested sites where they represented 25% of the biomass, whereas in pasture sites they composed ca. 10% of the biomass.

Community composition differed between land-cover types ($R^2 = 0.11$, $p = .005$; envfit: $R^2 = 0.36$, $p = .001$; Table 4), and pasture

TABLE 3 Summary findings for biomass, community composition, and taxon richness across the elevation gradient, between land-cover types, and across the within-branch gradient

Attribute	Elevation	Land-cover (forest/pasture comparison)	Within-branch
Biomass	Total biomass: no significant difference	Total biomass: no significant difference	Total biomass: no significant difference
	Differences in family and functional group biomass	Differences in family and functional group biomass	Differences in family and functional group biomass
Community composition	Differs with elevation	Differs between land-cover types	No significant difference
Taxon richness	Increased with elevation	No significant difference with land-cover type	Declined from inner to outer branches

trees clustered together in our ordination (Figure 2). Including only the individuals identified to genus or species was also significant in this ordination analysis, but the clustering of trees was less distinct with slightly more overlap among groups compared with the ordination that included all species and morphospecies ($R^2 = 0.07$, $p = .010$, envfit: $R^2 = 0.36$, $p = .001$). However, neither taxon richness ($F_2 = 2.47$, $p = .126$; elevation: $F_2 = 7.37$, $p = .008$; land-cover type: $F_1 = 0.03$, $p = .863$) nor rarefied richness ($F_2 = 0.68$, $p = .527$; elevation: $F_2 = 1.86$, $p = .198$; land-cover type: $F_1 = 0.32$, $p = .581$) varied between land-cover types.

3.3 | Tree branch gradient

For all nine sites, although total epiphyte biomass varied among position on branch ($F_2 = 4.12$, $p = .020$), the Bonferroni-adjusted p -value was not significant. The inner branches were always occupied by epiphytes, but none of the functional groups or families reached their highest biomass there. Families and functional groups varied significantly with position on branch (family: $F_{196} = 2.90$, $p < .001$; elevation: $F_8 = 3.19$, $p = .001$; elevation/branch position: $F_{18} = 3.13$, $p < .001$; and functional group: $F_{74} = 2.75$, $p < .001$; elevation: $F_8 = 1.74$, $p = .086$; elevation/branch position: $F_{18} = 1.69$, $p = .038$, respectively). Pteridophyta and herbs reached greatest biomass at middle branch positions.

The ordination for family-level community composition was not significant for position on branch ($R^2 = 0.03$, $p = .230$). For all sites, both taxon richness and rarefied richness were greater on the inner and middle branch positions compared with outer branch positions; however, we found no significant effect of position on branch on rarefied richness ($F_2 = 2.44$, $p = .094$), whereas taxon richness was significant ($F_2 = 20.53$, $p < .001$). Among the forested sites, inner and middle branch positions supported a greater number of taxa (5–8 taxa) compared with outer positions (1–4 taxa) (Table 5). For the pasture sites, taxon richness varied with position on branch, but this pattern was driven by significant differences at the uppermost elevation pasture (El Valle); we found no significant differences among position on branch for the middle (lower CC) or lower elevation (Buen Amigo) pastures (Table 5). An identical analysis performed on the subset of taxa identified to genus and species yielded similar results.

4 | DISCUSSION

4.1 | Elevation gradient

Epiphyte communities in forests varied between those below the cloud base (lower CC, Buen Amigo, and UGA) and those in the cloud layer (El Valle, CCT, and upper CC). In the forest sites, the three upper elevation sites supported epiphyte communities that were distinct from the three lower sites, a separation that occurred at approximately the elevation of the cloud base. We did not measure cloud immersion in this study, but previous work has documented that constant immersion of orographic clouds occurs at elevations between 1,500 and 2,500 m in TMCF regions (Welch et al., 2008). Cloud immersion increases relative humidity and water inputs from mist, and reduces transpiration and vapor pressure deficit (Hu & Riveros-Iregui, 2016; Lawton et al., 2001), which may favor taxa dependent on direct cloud contact. The importance of microclimate in driving patterns of community composition in vascular epiphytes was also previously found in this region by Gotsch et al. (2017).

Although not statistically significant, Hymenophyllaceae were greatest in biomass at the highest elevation sites where cloud immersion is routine, decreased with elevation, and were absent at the two lowest elevation forested sites below the cloud base. Members of this family are putative indicators of cloud forest habitat since they typically lack differentiated epidermises, stomata, and cuticles that would otherwise regulate water loss (Hietz & Hietz-Seifert, 1995; Kelly, 1985). This suggests that some Hymenophyllaceae could be useful indicators of cloud forest habitat. In contrast, Rubiaceae were greatest in biomass at the lowest elevation sites, which are the driest sites in our study region. Many epiphyte species within this family also possess succulent leaves that may allow them to occupy drier habitats without routine cloud immersion.

Temperature decreased and RH increased with elevation across our gradient. Such changes in microclimate with elevation have been found to be strong drivers of variation in biomass and species richness of vascular epiphytes (Bussmann, 2001; Ding et al., 2016; Gehrig-Downie et al., 2012; Gotsch et al., 2017; Hietz & Hietz-Seifert, 1995; Wolf & Flamenco-S, 2003). A mid-elevation peak in epiphyte richness (between 1,000 and 2000 m in elevation) was first observed by Gentry and Dodson (1987) and has

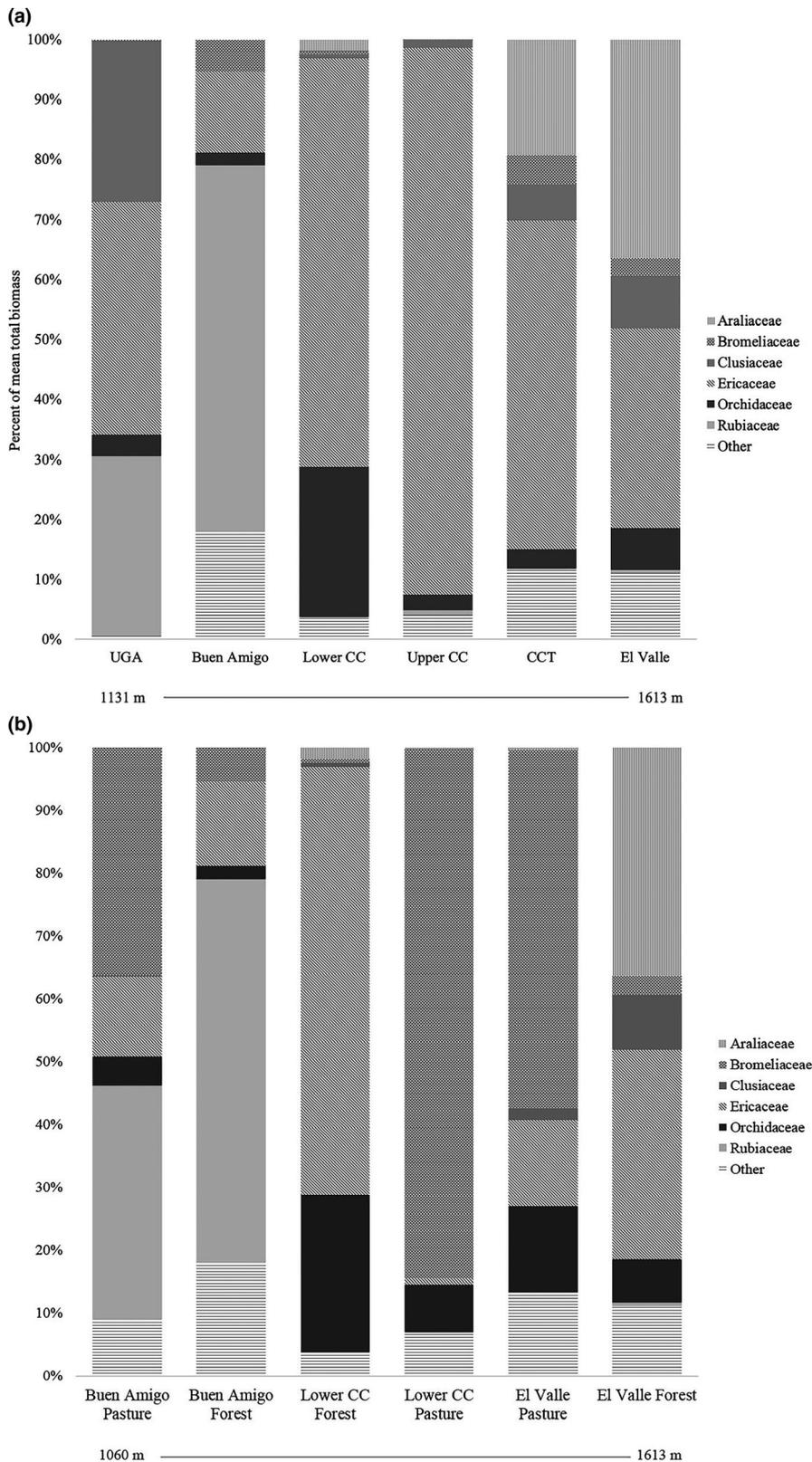


FIGURE 1 Proportion of epiphyte families contributing at least 20% of the total biomass in (A) forested sites across an elevation gradient and (B) forest versus pasture land-cover types in the Monteverde region of Costa Rica

been corroborated in studies of other tropical mountains (Acharya, Vetaas, & Birks, 2011; Bach, Kessler, & Gradstein, 2007; Cardelús et al., 2006; Hietz & Hietz-Seifert, 1995; Krömer et al., 2005; Vazquez & Givnish, 1998; Wolf & Flamenco-S, 2003). We found that taxon richness increased with elevation, and though not statistically significant, rarified richness had a slight peak at the middle

elevation sites (UCC Forest, LCC Pasture, and LCC Forest). The number of taxa was greatest at our montane forest site (El Valle), which fell within the elevation range of the mid-elevation peak in previous studies (1000–2000 m in elevation. Our study examined a narrower elevation range (600 m) than other studies that documented this mid-elevation peak. These factors likely explain the

FIGURE 2 Non-metric multidimensional scaling ordination featuring variation in epiphyte community composition among six forested and three pasture sites in the Monteverde region of Costa Rica. Input data included biomasses of taxa identified to the level of species or morphospecies. Each point represents an individual tree's epiphyte community composition, and each symbol type represents a site. Ellipses represent 95% confidence intervals for three upper elevation forested sites (above cloud base), three lower elevation forested sites (below the cloud base), and three pasture

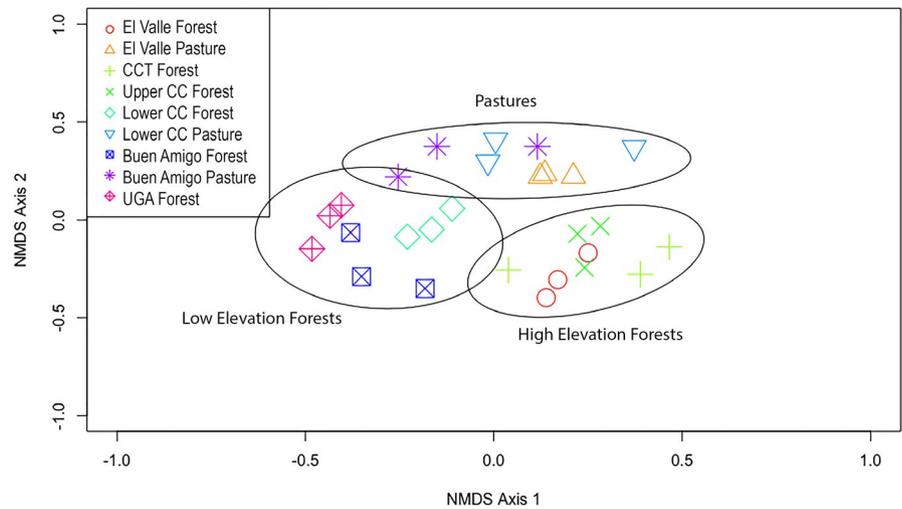


TABLE 4 NMDS ordination of variation in vascular epiphyte community composition for 27 trees at 9 sites spanning an elevation gradient from 1,060 to 1613 m and encompassing forest versus pasture land covers in the Monteverde region of Costa Rica. R^2 and p -values were derived via PERMANOVA (for factors) and envfit (for vectors)

Factors	R^2	p -value
Site (UGA, Buen Amigo, lower CC, upper CC, CCT, El Valle)	0.34	0.005
Land-cover type	0.09	0.005
Site and land-cover type	0.10	0.005
Upper elevation forests (El Valle, CCT, upper CC), lower elevation forests (lower CC, Buen Amigo, UGA), pastures	0.23	0.005
Vectors		
Elevation	0.59	0.001
Mean temperature	0.67	0.001
Mean relative humidity	0.71	0.001
Mean vapor pressure deficit	0.68	0.001
Average tree distance	0.02	0.833
Min. tree distance	0.09	0.332

lack of a unimodal peak in epiphyte taxon richness along our elevation gradient.

4.2 | Land-cover type

The increasing pressures of climate and land-cover changes are likely to shift vascular epiphyte communities toward more drought-resistant species. Pasture trees and their epiphytes likely experience drier microclimates than forests, which may be a driver for variation in epiphyte community composition between land-cover types (Köster et al., 2013; Köster, Nieder, & Barthlott, 2011). Although total biomass did not differ between land-cover types, there were significant differences in biomass of families and functional groups, and in community composition between forest and pasture trees. Some

functional groups and families may benefit from drier conditions in pasture trees. For example, Bromeliaceae and Clusiaceae were more prevalent in pasture sites compared with forested sites. Some members of these families feature Crassulacean acid metabolism (CAM) photosynthesis and water-holding leafy rosettes that are adaptations to drier microclimates (Benzing, 2000; Crayn, Winter, Schulta, & Smith, 2015).

Unlike cloud forest trees, where richness reliably declined from inner to outer branch position, taxon richness among position on branch in these isolated pasture trees had similar numbers of taxa among branch positions. One exception was the uppermost elevation pasture (El Valle), which supported more taxa on the inner and middle crown positions, compared with the outer crown. These results suggest that pasture trees in the middle and lower elevations may experience less variation in microclimate and therefore a narrower niche from inner to outer crown positions, which could constrain systematic variation in branch-level species richness. Fewer species may be able to succeed at any position on the branches in exposed pasture trees. Taxa adapted to wetter microclimates were lacking from the drier microclimates and sites, including Hymenophyllaceae. Epiphytes in isolated pasture trees are more exposed to warmer, drier, and windier conditions around the entire crown (Köster et al., 2013, 2011; van Leerdam, Zagt, & Veneklaas, 1990). While this idea is intuitive, a greater resolution of microclimatic data across branches would be needed to confirm this hypothesis.

Differences in epiphyte community composition and biomass between forest and pasture trees may have cascading effects on other species that depend on epiphyte resources. For example, the fruits and flowers of Ericaceae, a family that made up a greater proportion of biomass in forests than pastures, are important food resources for birds (Nadkarni & Matelson, 1989). Nadkarni and Matelson (1991) found that birds foraging in epiphytes commonly visited woody epiphytes, whereas herbaceous epiphytes were less commonly visited. Therefore, reductions in biomass of Ericaceae in forests and pastures could alter food resources available for wildlife (Köster et al., 2013, 2011).

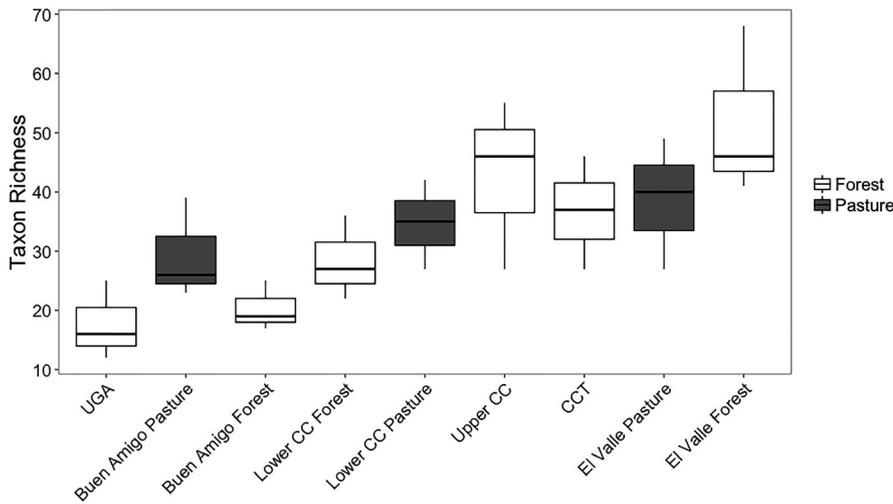


FIGURE 3 Box plot of taxon richness (number of taxa) and rarified richness (Chao 2) for all species and morphospecies among sites including six forest sites and three pastures in the Monteverde region of Costa Rica

4.3 | Tree branch gradient

We found no statistically significant differences in total branch biomass from inner to outer branch positions, though there was a trend for the inner and middle branch positions to have greater biomass than the outer branch positions. At the branch scale, we documented a decline in taxon richness from the inner to outer branch positions. Inner and middle branch positions may receive optimal amounts of light, retain more moisture, and provide more branch area for growth, therefore fostering a greater number of species compared with the warmer, drier, and more exposed outer branch positions (Cardelús & Chazdon, 2005; van Leeuwarden et al., 1990; Sanger & Kirkpatrick, 2017). The lack of difference in overall vascular epiphyte biomass with a difference in taxon richness among branch positions found in this study suggests that fewer species represent a greater proportion of the biomass in the outer branch positions and drier sites. In addition, outer branches are younger in age which provides less time for epiphyte establishment compared with the middle and inner branch positions. Heterogeneity in epiphyte species richness with position on branch may be at least partly explained by variation in substrate age, and the inner branch positions of old growth forest trees are especially important for epiphyte species that are late colonizers (Woods, 2017).

5 | CONCLUDING REMARKS

Climate change may affect spatial scales differently, and therefore, it is important to document biomass, richness, and community composition at different spatial scales and between land-cover types to understand the scales at which species may be most vulnerable. We found differences in community composition with elevation and land-cover type. Forest-to-pasture conversion at lower elevations in the tropics may encourage an increase in the elevation of cloud formation (Lawton et al., 2001), which may have more severe consequences for pasture versus forest epiphytes in TMCs (Hu & Riveros-Iregui, 2016). There may also be greater

negative effects for some species at outer branch positions and lower elevations where drier and warmer microclimates prevail, and pasture trees may be the most affected. Future research may consider sampling tree crowns more thoroughly with multiple branches in conjunction with elevation and land-cover type. Additionally, future studies should consider combining measurements of climatic variables at the sampling locations within-tree crowns, which may allow for a better understanding of community composition differences at the crown level with respect to broad-scale landscape gradients.

We compared that epiphyte community biomass, diversity, and community composition in trees at different elevations, branch positions, and land-cover characteristics. With climate change, warmer and drier conditions are projected for montane regions because of increases in cloud base heights and air temperature (Hu & Riveros-Iregui, 2016; Lawton et al., 2001; Pounds et al., 2006; Still et al., 1999). The effects of potential climate change and habitat loss through conversion of forest to pasture lands may have important impacts on epiphyte communities that depend on host trees for survival. Our results suggest that pasture trees support different communities of epiphytes, including families that have drought-tolerant species, and notably lack groups dependent on cloud water input, including Hymenophyllaceae. Understanding the impacts of land cover, particularly across a elevation gradients of cloud forest, may inform land management decisions that affect epiphyte populations that contribute to biodiversity and ecosystem function.

ACKNOWLEDGMENTS

We thank Luisa Moreno Scott and the Monteverde Institute, Yoryineth Mendez, and the Monteverde Cloud Forest Biological Reserve for logistical support. We thank Mauricio Ramirez and the Curi-Cancha Reserve, the Monteverde Reserve, the University of Georgia field station and owners of the Ortega, Guindon, Leiton, and Evans, and Buen Amigo private properties for property access to conduct this research. Noelia Solano Guindon, Todd Dawson, Stefania Mambelli, Rikke Reese Næsberg, Jessica Murray, Alexander

TABLE 5 Richness estimates across elevation, land-cover type, and branch position

Elevation	UGA Forest		Buen Amigo Pasture		Buen Amigo Forest		Lower CC Forest		Lower CC Pasture		Upper CC Forest		CCT Forest		El Valle Pasture		El Valle Forest	
	mean	se	mean	se	mean	se	mean	se	mean	se	mean	se	mean	se	mean	se	mean	se
Taxon richness	17.7	3.8	29.3	4.9	20.3	2.4	28.3	4.1	34.7	4.3	42.7	8.3	36.7	5.5	38.7	6.4	51.7	8.3
Rarified richness (Chao 2)	53.2	17	56.3	14	89.8	20.1	104.3	20.3	118.5	30.1	90.6	19.4	57.2	11	95.9	10.6	105.1	22.2
Branch position																		
Taxon richness																		
Inner	3.1	0.7	4.1	0.5	5	0.8	3.9	0.6	4.3	0.9	7.5	1.9	5.4	0.8	9.5	0.8	8.1	0.8
Middle	2.7	0.7	5	0.7	2.6	0.6	4.2	1.1	6.2	1.1	6	1.2	5	0.5	6.5	1.1	8.3	0.9
Outer	2	0.6	3.5	0.8	1.5	0.6	2.2	0.4	4	0.8	2.2	0.7	3	0.8	3.3	0.8	3.9	1
Rarified richness (Chao 2)																		
Inner	42.5	23.7	33.1	12.7	48.7	13.3	73.2	14.4	72.1	36.2	49.5	11	42	10.7	40.2	3.3	125.6	70.7
Middle	18.41	4.1	34.7	2.3	21.5	11.5	29.6	8.8	43.8	2.1	53.4	7.5	56.5	31.7	93.1	71	49.7	4.7
Outer	22	17.6	23.5	8	7.3	1.5	20.9	6.3	67.2	41.2	24.3	18.6	30.6	16.1	12.4	2.7	76.1	41.6

Darby, Andrew Glunk, Molly Lowell, Sucel Sanchez, Briana Ferguson, Laura Green, Andres Camacho, and staff at the Monteverde Cloud Forest Reserve provided help with fieldwork and data collection. Noelia Solano Guindon translated our abstract. We also thank Willow Zuchowski, Bill Haber, Mario Blanco, Emily Heyne, and Bruce Holst for help with species identification, and Helena Einzmann and Jon Seger for manuscript review. Special thanks to our arborist and climbing assistants Tyler Zuniga, Will Koomjian, Jamz Luce, Hannah Prather, and Keylor Muñoz Elizondo. Financial support is from the National Science Foundation (PI: Gotsch, IOS Award #1556289, PI: Nadkarni IOS Award #1556319), the University of Utah, and Franklin and Marshall College.

DATA AVAILABILITY STATEMENT

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.f4qrfj6s1> (Amici, Nadkarni, Williams, & Gotsch, 2019).

ORCID

Autumn A. Amici  <https://orcid.org/0000-0002-0506-2812>
 Sybil G. Gotsch  <https://orcid.org/0000-0002-8685-6576>

REFERENCES

Acharya, K. P., Vetaas, O. R., & Birks, H. J. B. (2011). Orchid species richness along Himalayan elevational gradients. *Journal of Biogeography*, 38, 1821–1833. <https://doi.org/10.1111/j.1365-2699.2011.02511.x>

Aldrich, P. R., & Hamrick, J. L. (1998). Reproductive dominance of pasture trees in a fragmented tropical forest mosaic. *Science*, 281, 103–105. <https://doi.org/10.1126/science.281.5373.103>

Amici, A. A., Nadkarni, N. M., Williams, C. B., & Gotsch, S. G. (2019). Data from: Differences in epiphyte biomass and community composition along landscape and within-crown spatial scales. Dryad Digital Repository, <https://doi.org/10.5061/dryad.f4qrfj6s1>

Anderson, D. L., Koomjian, W., French, B., Altenhoff, S. R., & Luce, J. (2015). Review of rope-based access methods for the forest canopy: Safe and unsafe practices in published information sources and a summary of current methods. *Methods in Ecology & Evolution*, 6, 865–872. <https://doi.org/10.1111/2041-210X.12393>

Bach, K., Kessler, M., & Gradstein, S. R. (2007). A simulation approach to determine statistical significance of species turnover peaks in a species-rich tropical cloud. *Diversity and Distributions*, 13, 863–870.

Benzing, D. H. (1990). *Vascular epiphytes*. Cambridge, UK: Cambridge University Press.

Benzing, D. H. (2000). *Bromeliaceae: Profile of an adaptive radiation*. Cambridge, UK: Cambridge University Press.

Benzing, D. H. (2008). *Vascular epiphytes: General biology and related biota*. Cambridge, UK: Cambridge University Press.

Buck, A. L. (1981). New equations for computing vapor pressure and enhancement factor. *Journal of Applied Meteorology*, 20, 152–1532. [https://doi.org/10.1175/1520-0450\(1981\)020<1527:NEFCVP>2.0.CO;2](https://doi.org/10.1175/1520-0450(1981)020<1527:NEFCVP>2.0.CO;2)

Bussmann, R. W. (2001). Epiphyte diversity in a tropical Andean forest- Reserva Biologica San Francisco, Zamora-Chinchipe, Ecuador. *Ecotropica*, 7, 43–59.

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

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

- Cardelús, C. L., Colwell, R. K., & Watkins, J. E. Jr (2006). Vascular epiphyte distribution patterns: Explaining the mid-elevation richness peak. *Journal of Ecology*, 94, 144–156. <https://doi.org/10.1111/j.1365-2745.2005.01052.x>
- Cascante-Marín, A., de Jong, M., Borg, E. D., Oostermeijer, J. G. B., Wolf, J. H. D., & den Nijs, J. C. M. (2006b). Reproductive strategies and colonizing ability of two sympatric epiphytic bromeliads in a tropical premontane area. *International Journal of Plant Sciences*, 167, 1187–1195. <https://doi.org/10.1086/507871>
- Cascante-Marín, A., von Meijenfeldt, N., de Leeuw, H. M. H., Wolf, J. H. D., Oostermeijer, G. B., & den Nijs, J. C. M. (2009). Dispersal limitation in epiphytic bromeliad communities in a Costa Rican fragmented montane landscape. *Journal of Tropical Ecology*, 25, 63–73. <https://doi.org/10.1017/S0266467408005622>
- Cascante-Marín, A., Wolf, J. H. D., Oostermeijer, J. G. B., den Nijs, J. C. M., Sanahuja, O., & Durán-Apuy, A. (2006a). Epiphytic bromeliad communities in secondary and mature forest in a tropical premontane area. *Basic and Applied Ecology*, 7, 520–532. <https://doi.org/10.1016/j.baec.2005.10.005>
- Catling, P. M., & Lefkovitch, L. P. (1989). Associations of vascular epiphytes in Guatemalan cloud forest. *Biotropica*, 21, 35–40.
- Colwell, R. K. (2013). EstimateS: Statistical estimation of species richness and shared species from samples. Version 9. User's Guide and application published at. <http://purl.oclc.org/estimates>
- Crayn, D. M., Winter, K., Schulta, K., & Smith, J. A. C. (2015). Photosynthetic pathways in Bromeliaceae: Phylogenetic and ecological significance of CAM and C3 based on carbon isotope ratios for 1893 species. *Botanical Journal of the Linnean Society*, 178, 169–221.
- Darby, A., Draguljić, D., Glunk, A., & Gotsch, S. G. (2016). Habitat moisture is an important driver of patterns of sap flow and water balance in tropical montane cloud forest epiphytes. *Oecologia*, 182, 357–371. <https://doi.org/10.1007/s00442-016-3659-5>
- Ding, Y., Liu, G., Zang, R., Zhang, J., Lu, X., & Huang, J. (2016). Distribution of vascular epiphytes along a tropical elevational gradient: Disentangling abiotic and biotic determinants. *Scientific Reports*, 6, 19706. <https://doi.org/10.1038/srep19706>
- Einzmann, H. J. R., & Zotz, G. (2017). "No signs of saturation": Long-term dynamics of vascular epiphyte communities in a human-modified landscape. *Biodiversity Conservation*, 26, 1393–1410. <https://doi.org/10.1007/s10531-017-1306-z>
- Freiberg, M., & Freiberg, E. (2000). Epiphyte diversity and biomass in the canopy of lowland and montane forests in Ecuador. *Journal of Tropical Ecology*, 16, 673–688. <https://doi.org/10.1017/S026646740001644>
- Gehrig-Downie, C., Marquardt, J., Obregón, A., Bendix, J., & Gradstein, S. R. (2012). Diversity and vertical distribution of filmy ferns as a tool for identifying the novel forest type "Tropical Lowland Cloud Forest". *Ecotropica*, 18, 35–44.
- Gentry, A. H., & Dodson, C. (1987). Contribution of nontrees to species richness of a tropical rain forest. *Biotropica*, 19, 149–156. <https://doi.org/10.2307/2388737>
- Gotsch, S. G., Davidson, K., Murray, J. G., Duarte, V. J., & Draguljić, D. (2017). Vapor pressure deficit predicts epiphyte abundance across an elevational gradient in a tropical montane region. *American Journal of Botany*, 104, 1790–1801. <https://doi.org/10.3732/ajb.1700247>
- Gotsch, S. G., Nadkarni, N. M., Darby, A., Glunk, A., Dix, M., Davidson, K., & Dawson, T. E. (2015). Life in the treetops: Ecophysiological strategies of canopy epiphytes in a tropical montane cloud forest. *Ecological Monographs*, 85, 393–412. <https://doi.org/10.1890/14-1076.1>
- Guevara, S., Laborde, J., & Sanchez, G. (1998). Are isolated remnant trees in pastures a fragmented canopy? *Selbyana*, 19, 34–43.
- Hietz, P., & Hietz-Seifert, U. (1995). Composition and ecology of vascular epiphyte communities along an altitudinal gradient in central Veracruz, Mexico. *Journal of Vegetation Science*, 6, 487–498. <https://doi.org/10.2307/3236347>
- Hofstede, R., Wolf, J. H. D., & Benzing, D. H. (1993). Epiphyte biomass and nutrient status of a Colombian upper montane rain forest. *Selbyana*, 15, 37–48.
- Hu, J., & Riveros-Iregui, D. A. (2016). Life in the clouds: Are tropical montane cloud forests responding to changes in climate? *Oecologia*, 180, 1061–1073. <https://doi.org/10.1007/s00442-015-3533-x>
- Ingram, S. W., Ferrell-Ingram, K., & Nadkarni, N. M. (1996). Floristic composition of vascular epiphytes in a Neotropical cloud forest, Monteverde, Costa Rica. *Selbyana*, 17, 88–103.
- Ingram, S. W., & Nadkarni, N. M. (1993). Composition and distribution of epiphytic organic matter in a Neotropical cloud forest, Costa Rica. *Biotropica*, 25, 370–383. <https://doi.org/10.2307/2388861>
- Jepson, J. (2000). *The tree climbers' companion: A reference and training manual for professional tree climbers*. Longville, MN: Beaver Tree Pub.
- Kartzinel, T. R., Trapnell, D. W., & Shefferson, R. P. (2013). Critical importance of large native trees for conservation of a rare Neotropical epiphyte. *Journal of Ecology*, 101, 1429–1438. <https://doi.org/10.1111/1365-2745.12145>
- Kelly, D. L. (1985). Epiphytes and climbers of a Jamaican rain forest: Vertical distribution, life forms and life histories. *Journal of Biogeography*, 12, 223–241.
- Köhler, L., Tobón, C., Frumau, K. F. A., & Bruijnzeel, L. A. (2007). Biomass and water storage dynamics of epiphytes in old-growth and secondary montane cloud forest stands in Costa Rica. *Plant Ecology*, 193, 171–184. <https://doi.org/10.1007/s11258-006-9256-7>
- Köster, N., Kreft, H., Nieder, J., & Barthlott, W. (2013). Range size and climatic niche correlate with the vulnerability of epiphytes to human land use in the tropics. *Journal of Biogeography*, 40, 963–976. <https://doi.org/10.1111/jbi.12050>
- Köster, N., Nieder, J., & Barthlott, W. (2011). Effect of host tree traits on epiphyte diversity in natural and anthropogenic habitats in Ecuador. *Biotropica*, 43, 685–694. <https://doi.org/10.1111/j.1744-7429.2011.00759.x>
- Kreft, H., Köster, N., Kuper, W., Nieder, J., & Barthlott, W. (2004). Diversity and biogeography of vascular epiphytes in Western Amazonia, Yasuni, Ecuador. *Journal of Biogeography*, 31, 1463–1476.
- Krömer, T., Kessler, M., Gradstein, S. R., & Acebey, A. (2005). Diversity patterns of vascular epiphytes along an elevational gradient in the Andes. *Journal of Biogeography*, 32, 1799–1809. <https://doi.org/10.1111/j.1365-2699.2005.01318.x>
- Larrea, M. L., & Werner, F. A. (2010). Response of vascular epiphyte diversity to different land-use intensities in a neotropical montane wet forest. *Forest Ecology and Management*, 260, 1950–1955. <https://doi.org/10.1016/j.foreco.2010.08.029>
- Laube, S., & Zotz, G. (2006). Neither host-specific nor random: Vascular epiphytes on three tree species in a Panamanian lowland forest. *Annals of Botany*, 97, 1103–1114. <https://doi.org/10.1093/aob/mcl067>
- Lawton, R. O., Nair, U. S., Sr, R. A. P., & Welch, R. M. (2001). Climatic impact of tropical lowland deforestation on nearby montane cloud forests. *Science*, 294, 584–588.
- Mehlreter, K., Flores-Palacios, A., & Garcia-Franco, J. G. (2005). Host preferences of low-trunk vascular epiphytes in a cloud forest of Veracruz, Mexico. *Journal of Tropical Ecology*, 21, 651–660. <https://doi.org/10.1017/S0266467405002683>
- Nadkarni, N. M. (1984). Epiphyte biomass and nutrient capital of a neotropical elfin forest. *Biotropica*, 16, 249–256. <https://doi.org/10.2307/2387932>
- Nadkarni, N. M., & Haber, W. A. (2009). Canopy seed banks as time capsules of biodiversity in pasture-remnant tree crowns. *Conservation Biology*, 23, 1117–1126. <https://doi.org/10.1111/j.1523-1739.2009.01235.x>
- Nadkarni, N. M., & Matelson, T. J. (1989). Bird use of epiphyte resources in neotropical trees. *The Condor*, 91, 891–907. <https://doi.org/10.2307/1368074>
- Nadkarni, N. M., & Matelson, T. J. (1991). Litter dynamics within the canopy of a Neotropical cloud forest, Monteverde, Costa Rica. *Ecology*, 72, 2071–2082.

- Nadkarni, N. M., Schaefer, D., Matelson, T. J., & Solano, R. (2004). Biomass and nutrient pools of canopy and terrestrial components in a primary and a secondary montane cloud forest, Costa Rica. *Forest Ecology and Management*, 198, 223–236. <https://doi.org/10.1016/j.foreco.2004.04.011>
- Nakanishi, A., Sungpalee, W., Sri-ngernyuang, K., & Kanzaki, M. (2016). Large variations in composition and spatial distribution of epiphyte biomass on large trees in a tropical montane forest of northern Thailand. *Plant Ecology*, 217, 1157–1169. <https://doi.org/10.1007/s11258-016-0640-7>
- Oksanen, J. (2009). Multivariate analysis of ecological communities in R. 1–40. Retrieved from <http://cc.oulu.fi/~jarioksa/opetus/metodi/vegantutor.pdf>
- Oksanen, J., Guillaume Blanchet, F., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., ... Wagner, H. (2017). Vegan: Community ecology package. R package version 2.4-5. Retrieved from <https://CRAN.R-project.org/package=vegan>
- Pounds, J. A., Bustamante, M. R., Coloma, L. A., Consuegra, J. A., Fogden, M. P. L., Foster, P. N., ... Young, B. E. (2006). Widespread amphibian extinctions from epidemic disease driven by global warming. *Nature*, 439, 161–167. <https://doi.org/10.1038/nature04246>
- Pounds, J. A., Fogden, M. P. L., & Campbell, J. H. (1999). Biological response to climate change on a tropical mountain. *Nature*, 398, 611–615. <https://doi.org/10.1038/19297>
- R Core Team (2016). *R: A language and environment for statistical computing*. Boston, MA: R Core Team. <https://www.R-project.org/>
- Sanger, J. C., & Kirkpatrick, J. B. (2017). Fine partitioning of epiphyte habitat within Johansson zones in tropical Australian rain forest trees. *Biotropica*, 49, 27–34. <https://doi.org/10.1111/btp.12351>
- Steege, H. T., & Cornelissen, J. H. C. (1989). Distribution and ecology of vascular epiphytes in lowland rain forest of Guyana. *Biotropica*, 21, 331–339.
- Still, C. J., Foster, P. N., & Schneider, S. H. (1999). Simulating the effects of climate change on tropical montane cloud forests. *Nature*, 398, 608–610. <https://doi.org/10.1038/19293>
- Thayyen, R. J., & Dimri, A. P. (2018). Slope environmental lapse rate (SELR) of temperature in the monsoon regime of the Western Himalaya. *Frontiers in Environmental Science*, 6, 42. <https://doi.org/10.3389/fenvs.2018.00042>
- van Leerdam, A., Zagt, R. J., & Veneklaas, E. J. (1990). The distribution of epiphyte growth-forms in the canopy of a Colombian cloud-forest. *Vegetatio*, 87, 59–71. <https://doi.org/10.1007/BF00045656>
- Vazquez, G. J. A., & Givnish, T. J. (1998). Altitudinal gradients in tropical forest composition, structure, and diversity in the Sierra de Manantlan. *Journal of Ecology*, 86, 999–1020.
- Veneklaas, E. J., Zagt, R. J., Van Leerdam, A., Van Ek, R., Broekhoven, A. J., & Van Genderen, M. (1990). Hydrological properties of the epiphyte mass of a montane tropical rain forest, Colombia. *Vegetatio*, 89, 183–192. <https://doi.org/10.1007/BF00032170>
- Wagner, K., Mendieta-Leiva, G., & Zotz, G. (2015). Host specificity in vascular epiphytes: A review of methodology, empirical evidence and potential mechanisms. *AoB Plants*, 7, plu092.
- Welch, R. M., Asefi, S., Zeng, J., Nair, U. S., Han, Q., Lawton, R. O., ... Manoharan, V. S. (2008). Biogeography of tropical montane cloud forests. Part I: Remote sensing of cloud-base heights. *Journal of Applied Meteorology and Climatology*, 47, 960–975. <https://doi.org/10.1175/2007JAMC1668.1>
- Werner, F. A. (2011). Reduced growth and survival of vascular epiphytes on isolated remnant trees in a recent tropical montane forest clear-cut. *Basic and Applied Ecology*, 12, 172–181. <https://doi.org/10.1016/j.baae.2010.11.002>
- Werner, F. A., Homeier, J., Oesker, M., & Boy, J. (2012). Epiphytic biomass of a tropical montane forest varies with topography. *Journal of Tropical Ecology*, 28, 23–31. <https://doi.org/10.1017/S0266467411000526>
- Wickham, H. (2016). *ggplot2: Elegant graphics for data analysis*. New York, NY: Springer-Verlag.
- Wolf, J. H. D., & Flamenco-S, A. (2003). Patterns in species richness and distribution of vascular epiphytes in Chiapas, Mexico. *Journal of Biogeography*, 30, 1689–1707.
- Woods, C. L. (2017). Primary ecological succession in vascular epiphytes: The species accumulation model. *Biotropica*, 49, 452–460. <https://doi.org/10.1111/btp.12443>
- Zimmerman, J. K., & Olmsted, I. C. (1992). Host tree utilization by vascular epiphytes in a seasonally inundated forest (Tintal) in Mexico. *Biotropica*, 24, 402–407. <https://doi.org/10.2307/2388610>
- Zotz, G., & Hietz, P. (2001). The physiological ecology of vascular epiphytes: Current knowledge, open questions. *Journal of Experimental Botany*, 52, 2067–2078.

How to cite this article: Amici AA, Nadkarni NM, Williams CB, Gotsch SG. Differences in epiphyte biomass and community composition along landscape and within-crown spatial scales. *Biotropica*. 2019;00:1–13. <https://doi.org/10.1111/btp.12725>