Ecology, 100(12), 2019, e02858

Functional composition of epiphyte communities in the Colombian Andes

Claudia Milena Agudelo,[1,2] Ana Maria Benavides,[2,3] Tyeen Taylor,[4] Kenneth J. Feeley,[4] and Alvaro Duque[1,5]

[1]*Departamento de Ciencias Forestales, Universidad Nacional de Colombia Sede Medellín, Cra 65 No. 59ª–110, Medellín, Colombia*
[2]*Corporación para Investigaciones Biológicas (CIB), Cra 72ª No. 78B–141, Medellín, Colombia*
[3]*Jardín Botánico Joaquín Antonio Uribe, Calle 73 No. 51D–14, Medellín, Colombia*
[4]*Department of Biology, The University of Miami, Coral Gables, Florida 33146 USA*

Citation: Agudelo, C. M., A. M. Benavides, T. Taylor, K. J. Feeley, and A. Duque. 2019. Functional composition of epiphyte communities in the Colombian Andes. Ecology 100(12): e02858. 10.1002/ecy.2858

Abstract. We identify changes in the functional composition of vascular epiphytes along a tropical elevational gradient with the aim of quantifying the role of climate in determining the assembly of epiphyte communities. We measured seven leaf functional traits (leaf area, specific leaf area, leaf dry-matter content, leaf thickness, force to punch, stomatal density, and potential conductance index) in the 163 most abundant epiphyte species recorded across 10 sites located along an elevational gradient between 60 and 2,900 m above sea level in the Colombian Andes. We grouped the epiphyte species into seven hierarchical functional groups according to their most characteristic leaf traits. Along the elevational gradient, the two main independent leaf trait dimensions that distinguished community assemblages were defined primarily by leaf area-photosynthetic (LAPS) and mass-carbon (LMCS) gradients. Mean annual temperature was the main determinant of species position along LAPS. In contrast, local changes in specific leaf area due to variation in the epiphytes' relative height of attachment was the main determinant of their position along the LMCS. Our findings indicate that epiphytic plant leaves have evolved to optimize and enhance photosynthesis through a leaf area–based strategy and carbon acquisition through investments in construction costs of leaf area per unit of biomass that aim to regulate light capture and tissue development. Given that most studies of plant functional traits neglect vascular epiphytes, our quantification of the multiple dimensions of epiphyte leaf traits greatly augments our understanding of vascular plant function and adaptation to changing environments.

Key words: functional groups; leaf economic traits; leaf spectrum; specific leaf area; stomatal conductance; tropical Andean forests; vascular epiphytes.

INTRODUCTION

Functional traits have been widely used to help elucidate fundamental evolutionary and ecological patterns associated with variation in plant form and function, such as the geographic distributions of woody and nonwoody species (Díaz et al. 2016). For woody plants, traits such as maximum height (m), specific wood density (g/cm^3), and leaf mass per area (g/cm^2) play important roles in determining the trade-off between demographic performance (e.g., reproduction, mortality, and growth) and the shade tolerance or longevity (Poorter et al. 2008, Wright et al. 2010). For nonwoody plant species, the importance of leaf functional traits and the leaf economic spectrum (LES) in differentiating evolutionary and ecological strategies is magnified (Wright et al. 2004). Broadly, the LES shows a trade-off between two contrasting strategies of plant function and adaptation to environmental restrictions (Wright et al. 2004, Shipley et al. 2006, Díaz et al. 2016): (1) rapid resource acquisition for fast growth vs. (2) high construction costs for well-defended leaves with longer life spans. Although trait relationships depend in part on the length of the environmental gradient and spatial scale (Messier et al. 2017), the LES is useful for characterizing the extent to which foliar area and mass determine photosynthetic rates and the rate of return on carbon investment in leaves (Osnas et al. 2018).

Most studies of plant traits overlook vascular epiphytes, nomadic vines, and hemiepiphytes (that is to say, nonparasitic plants that live part or all of their life span in trees [Benzing 1990]—hereafter referred to collectively as just epiphytes). The exclusion of epiphytes is troublesome, given their high diversity in some habitats. Vascular epiphytes often represent up to 50% of the total vascular species in tropical forests at local scales (Gentry and Dodson 1987, Haber et al. 2001) and represent

---

Manuscript received 19 November 2018; revised 11 July 2019; accepted 19 July 2019. Corresponding Editor: Nathan J. B. Kraft.

[5] Corresponding Author. E-mail: ajduque@unal.edu.co

about 10% of the total vascular plant diversity at subnational, national, or regional scales (Ibisch et al. 1996, Ek 1997, Schmidt et al. 2002, Idárraga and Callejas 2011, Zotz 2013*a, b*). Furthermore, vascular epiphytes may be particularly suited for elucidating constraints on plant adaptations and leaf development due to their capacity to grow in a complex three-dimensional environment where conditions such as light, water availability, and host tree structure can change dramatically over a distance of just a few meters (Krömer et al. 2007, Woods et al. 2015, Petter et al. 2016). Indeed, vertical environmental gradients within forests can have significant influences on the functional composition of epiphytes and on traits such as leaf dry-matter content (LDMC) and specific leaf area (SLA; Petter et al. 2016). For example, in a Panamanian forest, SLA of epiphytes decreased with increasing host tree height because of changes in exposure (Petter et al. 2016).

Another important distinction between epiphytes and other plants is that epiphytes have limited or no access to ground-based resources. This has forced epiphytes to develop many different strategies to acquire, process, and use resources (Benzing 2000, Zotz and Andrade 2002). For example, some epiphytes offset water deficits through the development of succulent leaves, optimize light interception in the dark understory by increasing foliar area, and/or resist exposure to direct sunlight or pests with tough leaves (Benzing 1990, Gotsch et al. 2015, Petter et al. 2016). Likewise, many epiphytes have developed mechanisms that increase water interception and uptake, such as the "narrow leaves syndrome" (Martorell and Ezcurra 2007, Reyes-García et al. 2008), specialized foliar trichomes and stomata (Benzing 1976, Pierce et al. 2001), modified water storage structures like tanks (Benzing 2000), and velamen (Zotz and Winkler 2013).

Documenting the ways that epiphytic species adapt and partition resources at local to regional scales (Zuleta et al. 2016) can shed new light on plant adaptive strategies and improve our understanding of the mechanisms maintaining the high diversity of epiphytes that epitomizes much of the tropics (Küper et al. 2004, Krömer et al. 2005). Furthermore, understanding how both microclimatic (e.g., vertical variation in light availability; Petter et al. 2016, Zuleta et al. 2016) and macroclimatic (e.g., rainfall and temperature) variables influence the distribution and functional composition of epiphytes at different spatial scales will increase our ability to predict their responses to global warming and other environmental changes (Zotz and Bader 2009, Hsu et al. 2012).

In this study, we investigated the extent to which the functional vascular epiphyte assemblages are determined by macro- and microclimatic variation (the former being largely shaped by geographic location and the latter being shaped primarily by the relative height of attachment and the vertical gradient of light and resources among forest strata). To do this, we surveyed epiphytes (including both epiphytes and hemiepiphytes) in 10 different sites spanning a large range of elevations and climates in northwest Colombia. Based on a survey of the leaf traits of the most abundant epiphyte species in each site, we categorized species into distinct functional groups and analyzed changes in the functional composition of epiphytes at regional and local scales. Through these analyses we aim to improve our understanding of the factors determining leaf functional traits and functional composition of tropical epiphytes.

MATERIALS AND METHODS

Study sites

This study utilized data and samples collected from 10 permanent 1-ha forest monitoring plots (each being 100 × 100 m). These plots are distributed across a large geographical area in the northern tropical Andes, mostly in the Antioquia province between 5°50′–8°61′ N and 74°61′–77°33′ W (Appendix S1: Fig. S1; see also Duque et al. 2015). The plot locations span from 60 to 2,900 m above sea level and the average total annual precipitation ranges from 2,221 to ca. 4,260 mm/yr (Appendix S1: Table S1). The topography and geology of this region are highly variable because of the presence of two mountain ranges that influence the patterns of drainage, rainfall, and soil fertility at local scales (Instituto Geográfico Agustín Codazzi [IGAC] 2007).

Sampling of epiphyte assemblages

In 2013, we surveyed and registered vascular epiphytes in each plot by adapting the SVERA method proposed by Wolf et al. (2009) to assess epiphyte richness and abundance. For the surveys, we haphazardly selected 35 host trees of the following six size classes within each of the 10 1-ha tree plots: 10 trees with a diameter at breast height (DBH) >30 cm and 25 trees in each of five smaller DBH classes (5–10, 10.1–15, 15.1–20, 20.1–25, and 25.1–30 cm DBH). The vascular epiphytes on each host tree were mapped by accessing the plants by climbing, using ladders and/or binoculars. In most cases, epiphytes were photographed for subsequent analyses and identification (see Zuleta et al. 2016). We defined epiphyte individuals as all independent stems or closely packed groups of conspecifics that were spatially separated and distinguishable from other stems/clumps (Sanford 1968). We counted spatially separated stems or plants suspected to belong to the same genet as different individuals. We counted epiphytes with climbing habits (e.g., some ferns, aroids, and gesneriads) as separate individuals if their rhizomes and stems were not visibly connected. We excluded epiphytes smaller than 5-cm height (which were in many cases seedlings) because of the difficulty of differentiating and identifying small plants at the top of the canopy. Although epiphytes, nomadic vines, and hemiepiphytes can be considered as different growth forms (Zotz 2013*a, b*), we grouped them together based on their dependence on support from trees to establish and grow (Engemann et al. 2016).

We measured the height above the ground (H) for the point of attachment for all the epiphyte individuals. We measured H to the nearest centimeter with the use of 15-m telescopic fiberglass poles (Hastings Measuring Sticks 3JF-108823). When the location of an epiphyte exceeded 15 m, we used a laser rangefinder hypsometer (Nikon 550). The lack of direct access to some epiphytes, and the obligate use of binoculars from the ground in some cases, may have introduced error and caused us to sometimes underestimate total epiphyte species abundance and richness, especially in the upper canopy (Flores-Palacios and García-Franco 2001, Gradstein et al. 2003). Given limitations, our results most accurately reflect patterns for understory to midcanopy epiphytes (Zuleta et al. 2016). The height of epiphyte attachment (H) was then standardized with regard to the maximum tree height at each site in order to minimize effects from changing canopy heights between sites. In each site, we measured 40% of the trees (selected at random; see Peña et al. 2018) and the tallest tallied tree height was used as the maximum tree height per site.

Functional traits

In 2013, we selected the epiphytic species that represented ~80% of individuals in each of the 10 study sites (Pakeman and Quested 2007; Appendix S1: Table S1). Through directed searches, we then located and collected a minimum of five healthy adult individuals of each of these most abundant species growing outside of the plots (fallen plants and plants on fallen host trees were avoided). We excluded Hymenophyllaceae species from trait analysis because their thin leaves led to difficulties when measuring some traits. Voucher specimens for each morphotype were compared with voucher specimens of the long-term monitoring study and deposited in the Herbarium of the University of Antioquia (HUA).

A total of five fully expanded and healthy leaves were sampled from each of the collected individuals. When it was not possible to get five leaves per individual because of a low number of leaves on the sampled plant, additional individuals were collected until we had a minimum of 25 leaves per species. In total, 4,254 leaves were sampled. The collected leaves were wrapped in damp paper towels, packed in sealed plastic bags, and immediately stored in dark refrigerators at temperatures of 2–6°C for transport to the lab while maintaining a standard degree of turgor (Wilson et al. 1999).

For the sampled leaves, we measured the following quantitative traits following the protocols described by Pérez-Harguindeguy et al. (2013): leaf area (LA: fresh leaf area, mm^2); leaf dry-matter content (LDMC: oven-dry mass/fresh mass; mg/g); specific leaf area (SLA: fresh leaf area/dry mass; mm^2/mg), which can also be calculated as the inverse of the leaf dry mass per area (LMA; SLA = 1/LMA mg/mm^2); leaf thickness (Lth; mm); force to punch (Fp: force needed to punch a hole through the leaf lamina; N/mm); stomatal density (SD; number of stomata/mm^2); and potential conductance index (PCI: guard cell length^2 $\times$ stomata density $\times$ 10^{-4}; Holland and Richardson 2009; earlier proposed by Sack et al. 2003 as stomatal pore area index). These traits are primarily associated with (1) the investment of resources (SLA, LDMC, Lth, Fp; Wright et al. 2004); (2) water and energetic regulation (LA, SLA, SD, PCI; Hetherington and Woodward 2003, Wright et al. 2004, Holland and Richardson 2009, Li et al. 2015, Blackman et al. 2016, Díaz et al. 2016); and (3) resistance to herbivores and pathogens (SLA, Lth, FP; Wright et al. 2004, Onoda et al. 2011).

According to standard protocols, we scanned each leaf lamina and determined its area using the software ImageJ (http://rsb.info.nih.gov/ij/). We measured the dry weight of the leaves using an analytical balance with a precision of 0.0001 g. To measure leaf thickness, we employed a manual micrometer (Mitutoyo, precision: 0.0001 mm). We measured the force needed to punch through leaves, taken as an index of the leaf toughness, with a Pesola® Medio-Line Pressure Set adapted to Spring Scales (300, 600, 1,000 and 2,500 g of capacity). For this measurement, each lamina was clamped between two acrylic plates and a steel rod (1.5-mm diameter) was forced to perforate the leaf perpendicularly. To measure stomatal density and size, we used a 40× zoom optical microscope (Nikon ECLIPSE E200 with OPTIKAM 4083.11 camera) to count and photograph stomata impressions in nail-polish molds taken from the undersides of the leaves (avoiding ribs, and after removing trichomes when necessary by carefully scraping the lamina with razor blades). We measured stomatal densities in three random points of 0.1886 mm^2 in the molds using ImageJ (http://rsb.info.nih.gov/ij/), and we measured guard cell length on three randomly selected stomata.

Definition of functional groups

We used the Ward's linkage method of agglomerative cluster analysis (Legendre and Legendre 2012) applying Euclidean distances on a trait by species matrix (7 traits × 163 species; see Appendix S1: Table S2) to categorize the epiphyte species into functional groups (FGs). The Ward's linkage method has the advantage of minimizing the variance within vs. between groups (Ward 1963). The trait value of each species was represented by the mean of all measurements made on all sampled leaves of all individuals collected for each species. In other words, the mean value of each species was obtained from a minimum of 25 samples taken from a minimum of five individuals per species. We compared means of each trait between FGs with a one-way analysis of variance with post hoc Bonferroni tests. We applied the Bonferroni test to identify the most characteristic trait associated with each functional group. Because of the low floristic similarity of the sampled species (that is to say, the species that represented 80% of individuals) between sites (0.52% ± 1.26%; rank =

0–5.19%), trait analysis is an appropriate method to overcome the high species clustering and uniqueness of epiphytes tallied in each site.

The epiphyte trait spectrum

For each of the 10 study plots, we used the quantitative inventories of epiphytes and species trait means to calculate the community weighted means (CWM; Lavorel et al. 2008) of each of the seven traits (SLA, LA, LDMC, Lth, Fp, SD, PCI) with weighting based on relative species abundances. We then applied a principal component analysis (PCA; Legendre and Legendre 2012) to the trait by site matrix (7 traits × 10 sites, Appendix S1: Table S3) of the CWMs (CWMs standardized to mean zero and standard deviation one), to analyze how the plant trait spectrum defines the functional community assemblages of the epiphytic species.

Functional epiphyte assemblages vs. micro- and macroclimate

Because the availability of water and light to epiphytes is largely determined by their location within the forest strata (Allen et al. 1972, Parker 1995), we used the aboveground relative height of attachment of each individual epiphyte (H) as a surrogate of microclimatic variation at the local scale (Petter et al. 2016, Zuleta et al. 2016). Relative H was calculated as the ratio between the observed epiphyte height of attachment and the maximum tree height measured in each plot.

To assess trait variation in relation to height of attachment, we built a matrix of mean relative H per FG and site (7 FGs × 10 sites; see Appendix S1: Table S4). We then performed a PCA (Legendre and Legendre 2012) on this matrix and used the two main (and independent) PC axes as surrogates of microclimate (Zuleta et al. 2016; Appendix S1: Table S6) in subsequent analyses (referred to hereafter as PCA 1 H and PCA 2 H). The mean values of relative H per FG were standardized across sites to mean zero and standard deviation one before performing the PCA. The PCAs were performed with the *rda* function of the R package *vegan* (Oksanen et al. 2018). The correlation between the CWM traits of each site and the site scores of the PCA H axes were assessed.

Because all of our study sites were located in wet, nonseasonal tropical forests, we chose the mean annual temperature (MAT, °C) and the average total annual precipitation (TAP, mm/yr) as our macroclimatic variables. The MAT and TAP of all sites were extracted from the CHELSA extrapolated climate rasters (http://chelsa-climate.org; Karger et al. 2017; Appendix S1: Table S1) at a spatial resolution of 30 arc-s (approximately 1 × 1-km resolution in the study area). The two macroclimatic variables (MAT and TAP) were not significantly correlated with each other ($r = 0.46$; P value > 0.1). Neither PCA 1 H nor PCA 2 H was significantly correlated with either MAT or TAP (P value > 0.1).

Finally, we used the Pearson correlation coefficient (r) to analyze the relationships between the first two axes of the functional trait assemblage PCA with the two macroclimatic (MAT and TAP) and the two microclimatic variables (PCA 1 H and PCA 2 H) to quantify the degree to which climate explains variation in functional composition.

Site and loading scores were both multiplied by −1 for graphical purposes. All analyses were performed in R 3.1.0 (R Development Core Team 2014).

RESULTS

Overall, 1,044 individuals belonging to 163 epiphyte species (53 genera of 17 families) were collected and measured. In total, 54.6% of the individuals were identified to the species level, 44.2% to the genus level, and 1.2% of individuals were unidentified. The most common groups of epiphytes were ferns (23.9%), orchids (22.7%), aroids (22.1%), and bromeliads (15.3%).

Epiphyte functional groups

The 163 epiphytic plant species were hierarchically grouped into seven distinct functional groups based on differences in leaf trait combinations (Table 1, Fig. 1). Functional Group 1 (FG1; mostly small ferns like *Elaphoglossum*) and FG2 (stranglers and treelets such as some species of the genera *Clusia* and *Cavendishia*) had high LDMC; the bromeliads and orchids of FG4 had tough leaves (high Fp); and FG3 were mostly succulent (high Lth and low LDMC) small orchids. FG5 consisted of some orchids, bromeliads, and aroids, which were characterized by high SLA as well as the lowest PCI. Finally, FG6 and FG7, mostly aroids, were characterized by the largest-thinnest-softest leaves (FG6; high LA) and high SLA (FG7; Table 1, Fig. 1).

Functional epiphyte assemblages: the leaf economic spectrums

The functional assemblages of epiphyte species in the plots were ordered about two independent axes of variation. The first PCA axis of leaf functional traits, which accounted for 47.1% of total trait variation, was primarily associated with a photosynthetic gradient driven by leaf area and leaf hydraulic traits (Fig. 2A). Hereafter, we refer to this component of the LES captured by PCA axis 1 of traits (PCA 1 Traits) as the “leaf area photosynthetic spectrum” (LAPS). This first PCA 1 Trait axis was associated with a gradient from high construction costs on the left (high PCI, Fp, SD and LDMC; low LA) to a strategy of fast resource acquisition on the right (low PCI, Fp, SD and LDMC; high LA). In other words, the PCA 1 Trait axis was positively correlated with LA (0.87), and negatively correlated with SD (−0.8), PCI (−0.79), and Fp (−0.88) (Appendix S1: Fig. S2, Table S5). The second PCA trait axis, which accounted

Table 1. Mean leaf trait values ± standard deviations of each functional group (FG) of vascular epiphytes recorded in 10 study plots in the Andes of northwest Colombia.

FG	Number of species per FG	Lth (mm)	Fp (N/mm)	PCI	SLA (mm^2/mg)	SD ($Stomata/mm^2$)	LDMC (mg/g)	LA (mm^{-2})
1	36	0.33 ± 0.09^{cd}	0.49 ± 0.24^{cd}	7.8 ± 3.0^{a}	9.9 ± 3.6^{c}	44.5 ± 25.3^{b}	301.9 ± 62.0^{a}	5502.2 ± 5522.4^{b}
2	28	0.55 ± 0.30^{b}	0.82 ± 0.37^{b}	7.4 ± 1.9^{a}	9.6 ± 4.2^{c}	158.7 ± 75.6^{a}	239.9 ± 75.6^{b}	7008.8 ± 9525.8^{b}
3	13	1.28 ± 0.39^{a}	1.22 ± 0.36^{a}	4.4 ± 0.9^{b}	8.9 ± 4.4^{c}	38.3 ± 16.7^{b}	120.9 ± 36.2^{d}	6278.0 ± 9164.9^{b}
4	12	0.33 ± 0.08^{bcd}	1.52 ± 0.21^{a}	4.4 ± 1.5^{b}	14.2 ± 2.8^{bc}	32.0 ± 7.0^{b}	218.5 ± 29.3^{bc}	18870.0 ± 12800.9^{b}
5	23	0.48 ± 0.18^{bc}	0.67 ± 0.25^{bc}	3.8 ± 1.2^{b}	17.4 ± 5.0^{b}	41.4 ± 33.1^{b}	146.6 ± 37.8^{cd}	5330.4 ± 5371.1^{b}
6	21	0.30 ± 0.09^{cd}	0.42 ± 0.19^{cd}	4.3 ± 1.5^{b}	13.7 ± 2.6^{bc}	54.6 ± 29.4^{b}	216.6 ± 42.5^{bc}	66350.1 ± 21211.6^{a}
7	30	0.23 ± 0.08^{d}	0.31 ± 0.19^{d}	5.7 ± 1.8^{ab}	23.3 ± 7.3^{a}	54.6 ± 25.4^{b}	214.5 ± 63.1^{bc}	16000.3 ± 15687.7^{b}

Notes: Groups with different letters in the same column were significantly different (P value < 0.05) in the corresponding functional trait based on one-way analysis of variance with post hoc Bonferroni tests. Lth, leaf thickness; Fp, force to punch; PCI, potential conductance index; SLA, specific leaf area; SD, stomata density; LDMC, leaf dry-matter content; LA, leaf area.

for 31.9% of the total trait variation, was positively associated with SLA (0.72), Fp (0.7), and SD (0.67), and thus, with the rate of carbon assimilation of leaves (Appendix S1: Fig. S2). This gradient is driven by the increased accumulation of leaf structural components, such as cellulose, which augment the capability of leaves to store mass. Hereafter, we refer to this component of the LES captured by our PCA 2 Trait axis as the "leaf mass-carbon spectrum" (LMCS). SLA was not significantly correlated with any of the other traits evaluated ($P > 0.05$), but Lth had a significant negative relationship with LA ($r = -0.68$; $P < 0.05$) as well as a positive correlation with PCI ($r = 0.69$; $P < 0.05$) (Appendix S1: Fig. S3).

The microclimatic environment of trait variation

The PCA in Fig. 2B distinguishes sites by relative FG attachment heights. The negative loadings of all FGs on the first axis (PCA 1 H), which accounted for 48.1% of total variation, indicate an axis of decreasing overall attachment heights with increasing PCA 1 H, particularly for FGs 1 and 2, which are both characterized by low LA. PCA 1 H was positively correlated with an overall increase in epiphyte LA (0.73), and a decrease in SD (−0.55) and Fp (−0.54) (Appendix S1: Fig. S4). Therefore, a general decrease in attachment heights relative to the canopy-surface height (increasing PCA 1 H) is associated with a gradient from high construction costs (high Fp and SD; low LA) on the left to fast resource acquisition on the right (low Fp and SD; high LA). The opposing loadings on PCA 2 H of FGs 3 and 5 (negative) compared to FGs 4, 6, and 7 (positive) indicate spectrums from more similar to more distinct attachment heights, accounting for 34.7% of site variation (Appendix S1: Table S6). Therefore, PCA 2 H represents a gradient from sites with more homogeneous epiphyte distributions (low PCA 2 H) to more stratified height distributions (high PCA 2 H). PCA 2 H was positively correlated with epiphyte community SLA (0.72), Fp (0.7), and SD (0.67) (Appendix S1: Fig. S4). None of the PCAs derived from the height of epiphyte attachments were significantly correlated with either MAT or TAP (P-value > 0.1).

Climatic determinants of the functional epiphyte assemblages

Both the LAPS (PCA 1 Trait) and the LMCS (PCA 2 Trait axis) were significantly correlated with MAT ($r = 0.64$ and $r = -0.63$, $P \leq 0.05$), a pattern primarily determined by site elevation (Fig. 3). The LMCS (PCA 2 Trait axis) was not significantly correlated with TAP, but was negative and significantly correlated with the PCA 2 H (−0.77**). The PCA 1 H did not show a significant correlation with either LAPS or LMCS (P-value >0.1).

Discussion

Our analyses of epiphytic leaf traits support the convergence of plant adaptive strategies along multiple trait dimensions (Díaz et al. 2016). In this study, the two leaf trait dimensions that best characterize epiphyte assemblages at a regional scale were defined primarily by the area-photosynthetic and mass-carbon components of the leaf spectrum (Osnas et al. 2018). The leaf area-photosynthetic spectrum was associated with variation from high to low stomatal density and conductance. In vascular plants, experimental studies have shown a positive correlation between stomatal conductance and photosynthetic rates (Tanaka et al. 2013, Lawson and Blatt 2014). A large leaf area in epiphytes must be developed by an increase in photosynthetic components at the expense of mass (Katabuchi et al. 2017). The leaf mass-carbon economic spectrum was defined by variation from high to low specific leaf area (and low to high leaf thickness), which is associated with a gradient of investment in structural components and rates of carbon assimilation (Wright et al. 2004, Osnas et al. 2018).

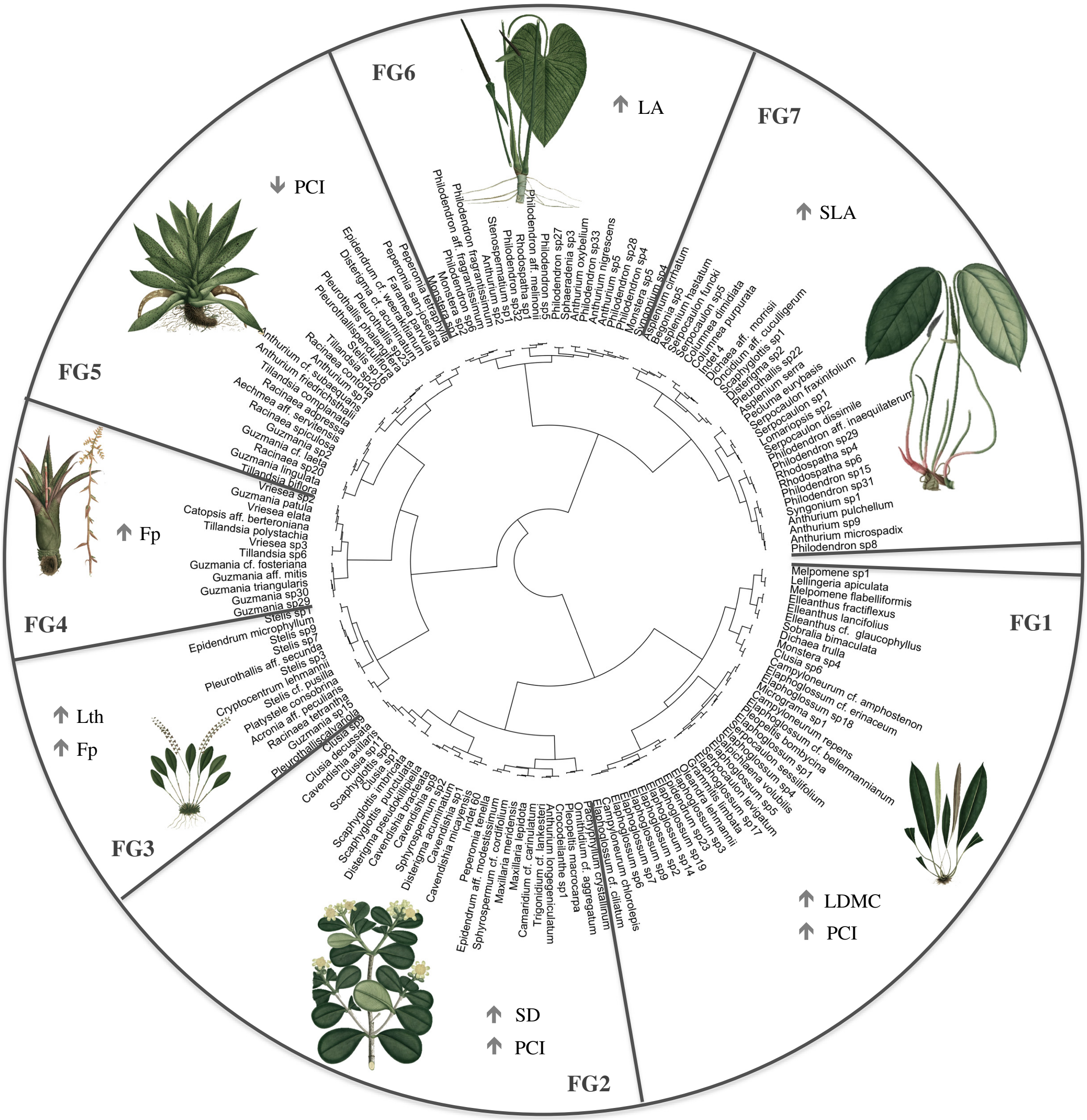

FIG. 1. Hierarchical agglomerative clustering (using Euclidean distance and Ward's linkage method) for 163 epiphyte species in 10 sites in the Andes of northwest Colombia using the following functional traits: LA: leaf area (mm^2), SLA: specific leaf area (mm^2/mg), LDMC: leaf dry-matter content (mg/g), Lth: leaf thickness (mm), Fp: force to punch (N/mm), SD: stomata density (number of stomata mm^2), PCI: potential conductance index. FG: Functional group. Plant illustrations are modified from drawings of the Royal Botanical Expedition to the New Kingdom of Granada (1783–1816) directed by José Celestino Mutis: http://www.rjb.csic.es/icones/mutis/, Royal Botanical Garden-CSIC.

However, both axes of variation can be independently interpreted as defining gradients of epiphyte assemblages from acquisitive strategies with fast growth and low construction costs to conservative strategies with slow growth and high construction cost of photosynthetic capacity (increasing leaf size) or structural components (increasing leaf mass; Díaz et al. 2004, 2016, Wright et al. 2004, Shipley et al. 2006).

The macroclimatic effects on the elevational patterns of epiphyte functional composition

Variation in the functional composition of epiphyte assemblages along the leaf area-photosynthetic spectrum was associated with changes in regional mean annual temperature between elevations. For example, communities in the hot lowlands were comprised of species with

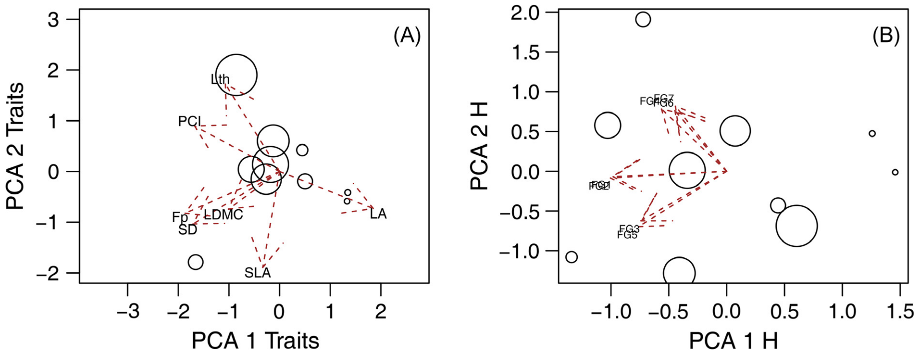

FIG. 2. (A) Principal component analysis (PCA) of the epiphyte functional composition at 10 sites in the Colombian Andes according to the community-level weighted means of trait values (CWM). The sizes of the circles are proportional to the plot elevations (meters above sea level [asl]) such that small circles represent lowland plots and large circles represent highland plots. (B) Principal component analysis of relative aboveground height of attachment of FGs of epiphyte species in 10 sites of the northwest Andes of Colombia. The size of the circles is proportional to the plot's elevation (meters asl).

larger leaves, possibly because of a higher investment by plants in metabolically active tissues that enhance photosynthetic capacity (Osnas et al. 2018). Likewise, community placement along the leaf mass-carbon economic spectrum (i.e., the second axis of trait variation, primarily defined by the specific leaf area) was also correlated with regional temperature or changes in elevation. This finding supports the existence of two independent area-photosynthetic and mass-carbon economic trait spectra in woody plant species (Osnas et al. 2018). In epiphytic species, this independent variation between area and mass can be seen as an adaptive strategy that evolved to allow the plants to adjust their functioning to large-scale environmental variation. Stomatal conductance increases, and leaf area decreases, from lower to higher elevations (hotter to colder temperatures), indicating a response to changes in potential evapotranspiration and photosynthetic rates. A paired change between plant functional turnover and elevation has been also found in other plant growth forms, such as herbs (Lawson and Blatt 2014) and trees (Poorter et al. 2009, Asner and Martin 2016, Asner et al. 2016), which emphasizes the paramount role played by temperature in structuring plant functional composition.

In our study, mean total annual precipitation (TAP mm/yr) did not have any significant effect on the mean weighted functional composition of epiphyte species along the elevational gradient. The lack of influence of TAP on epiphyte functional composition may be due to the absence of periods of water deficit (e.g., Poorter et al. 2009) that hampers the discriminate use of water by epiphyte communities in these wet forest at a regional scale In contrast, regional changes in temperature along the elevational gradient clearly differentiates epiphyte functioning in accord to variation with the properties of the functional groups. Changes in leaf area at the regional scale were primarily detected for FG1, FG2, and FG5, which have the lowest mean values for this trait. Changes in specific leaf area along the temperature gradient were strongest in FG4, FG6, and FG7, which have the highest values of SLA (Table 1). These independent responses to the same environmental factor (i.e., temperature) frame the overall epiphyte area-photosynthetic and mass-carbon economic trait spectra that drive the turnover in the epiphyte community and functional composition observed at the regional scale.

The microclimatic effect: patterns of epiphyte functional composition across forest strata

Our findings are consistent with the interpretation that the vertical distribution of microclimates within the canopy is at least as important as macroclimate in determining epiphyte community functional compositions (Petter et al. 2016, Zuleta et al. 2016). Increasing average leaf area and decreasing water conductive capacity with lower average attachment heights relative to the canopy surface (PCA 1 H, Appendix S1: Fig. S4) are consistent with a vertical gradient of light and temperature, both decreasing with distance from canopy. Community mean values of these area-photosynthetic spectrum traits correlated as strongly with PCA 1 H as they did in aggregate (PCA 1 T) with mean annual temperature (Fig. 3). Interestingly, the trends with respect to temperature were opposing. For example, leaf area increased (as a component of PCA 1 T) with mean annual temperature, but decreased with height in the canopy. In fact, for these traits, mean annual temperature might be of less direct importance than its influence on forest height, which generally increases at lower, warmer elevations, and provides deeper, darker understory environments buffered from canopy-surface conditions.

The community placement along the leaf mass-carbon economic spectrum (LMCS) was associated both with decreasing mean annual temperature (MAT) and a more homogeneous vertical distribution of epiphyte species (PCA 2 H; Fig. 3). This trait gradient shows the influence of structural and chemical components that enhance leaf mass, and thus leaf toughness (Poorter et al. 2009, Kitajima et al. 2016). The prevalence of

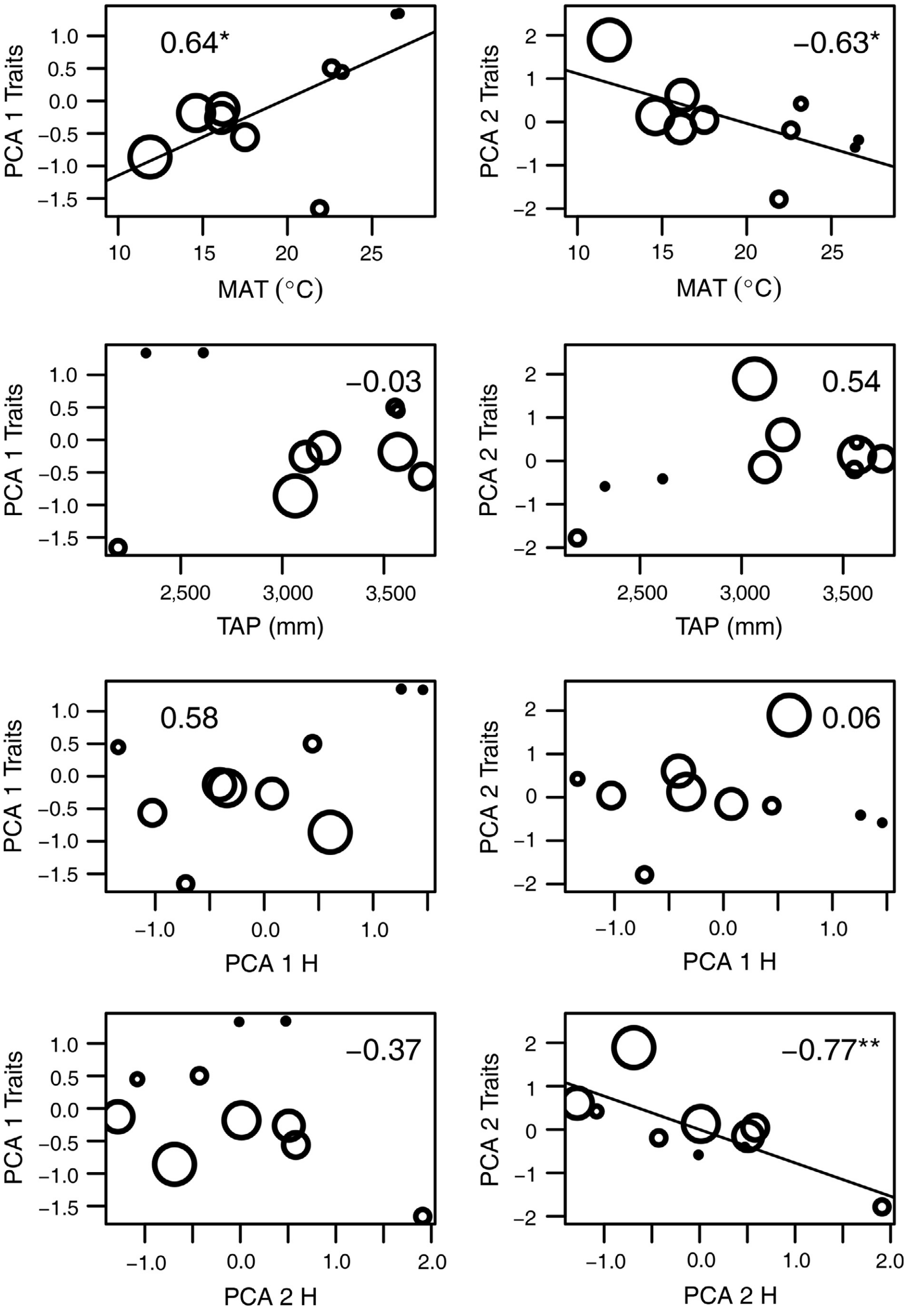

FIG. 3. The relationships between the first two axes of the PCA of the epiphyte functional composition at the study sites (Fig. 2) and proxies of both macro- and microclimatic variables. Macroclimatic variables are represented by the plots' mean annual temperatures (MAT) and mean total annual precipitations (TAP). Microclimatic variables (PCA 1 H and PCA 2 H) are the first two axes of a PCA of the epiphyte FGs' mean relative height of attachment (H) per plot. The size of the circles is proportional to the plot's elevation (meters asl) such that small circles represent lowland forest plots. The solid lines show significant correlations with $P < 0.05$. *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$; otherwise nonsignificant.

tougher leaves at sites with homogeneous height distributions indicates that these sites may be more homogeneously "canopy-like," as is expected in shorter forests at higher elevations. However, the stronger correlation of LMCS with PCA 2 H compared to MAT, and the relative independence of PCA 2 H from elevation, suggests that there are factors other than macroclimate driving the vertical distribution of forest microclimates and, consequently, epiphytes. Future studies should investigate the role of forest structural attributes, such as canopy gap fraction and vertical biomass distributions, which determine the extent to which canopy-like conditions penetrate toward the forest floor, and have been shown to structure tree biomass responses to the macroenvironment (Stark et al. 2012, Smith et al. 2019).

Concluding remarks on epiphyte functional composition

Functional response of epiphyte communities along this elevational gradient shows a high congruence between local and regional patterns, which means a similar leaf trait response to micro- and macroclimatic conditions. This conclusion is based on the fact that the PCA 1 and PCA2 derived from traits and relative epiphyte height of attachment, respectively, followed a similar trend. However, the correlation between the PCA 1 Traits and PCA 1 H (0.55) was only marginally significant (P value = 0.08), in contrast to the correlation between PCA 2 Traits and PCA 2 H (−0.77**). For the latter, the vertical distributions of light and temperature seem to determine the increase in SLA of epiphyte species from understory to canopy at a similar extent to changes in regional temperature. Strong heterogeneity in sun exposure at a given height, depending on canopy rugosities and gap distributions (Smith et al. 2019), largely controls water availability, a key factor for epiphyte survival and establishment. We hypothesize that evaporative demand increases with height because of increased sun and wind exposure (Petter et al. 2016), and influences adaptation of epiphyte species across forest strata. However, unmeasured traits, such as the development of roots and the direct contact with soils, could also facilitate the capability of leaves to survive in the darker/wetter forest understory, favoring the presence of some specific families, such as aroids. Additional studies focusing on these unmeasured traits will increase our understanding of the factors influencing patterns of trait epiphyte community assembly along tropical elevational gradients.

Despite the overall similarities in trait turnover along the elevational gradient observed between epiphytes and other growth forms, such as trees (e.g., Asner and Martin 2016), there may be structural differences in terms of the evolutionary and ecological processes that lead to the dominance of some specific traits that optimize either the area-photosynthetic or mass-carbon economic function between them. In particular, there may be a need for epiphytes to partition and adapt to the gradual changes in light and resource availability that occur between forest strata. Therefore, the functional composition of epiphyte assemblages in tropical wet forests appears to be driven by a combination of between-site mechanisms to optimize photosynthetic rates through balancing evapotranspiration rates across changes in temperature, and within-site mechanisms to optimize mass acquisition by decreasing SLA across forest strata (Petter et al. 2016). Revealing these patterns in vascular epiphytes, which have generally been excluded from studies of functional traits and community assembly, brings new insights into plant-leaf adaptation and calls for caution when trying to extrapolate patterns between different plant growth habits.

The high diversity of epiphytic forms (Fig. 1) contributes to the daunting challenge of defining general patterns and mechanisms of epiphyte distributions (Schellenberger Costa et al. 2018). Our two PCA analyses showed orthogonal axes defining community separation by elevation and the relative height of epiphyte attachment. The leaf mass-carbon spectrum axis was largely related to vertical structuring of four (FG3, FG5, FG6, FG7) out of our seven functional groups, and cannot be generalized to all other epiphyte species. It may be that hydraulic traits, such as those associated with water retention capability (e.g., tank-forming bromeliads), high potential water use (e.g., with large, thin leaves), or other unmeasured features are important for vertical structuring of other functional groups (e.g. Zotz et al. 1997). Improved theory of epiphyte distributions will likely require more detailed knowledge of the ecophysiological idiosyncrasies of each functional group, including their unique responses to substrate structure, temperature, light, and water (Woods et al. 2015, Ding et al. 2016, Müller et al. 2017, Schellenberger Costa et al. 2018).

In conclusion, the climatic trait relationships presented in this study are consistent with the general patterns reported in the literature for plant functional groups that include epiphytic forms (e.g., Engemann et al. 2016), as well as with the known patterns of taxonomic composition of epiphytes along elevational gradients (Küper et al. 2004, Krömer et al. 2005, Cardelús et al. 2006). Our findings indicate that epiphytic plant leaves have evolved to optimize and enhance photosynthesis through a leaf area–based strategy and carbon acquisition through investments in construction costs of leaf area per unit of biomass that aim to regulate light capture and tissue development (Díaz et al. 2016, Katabuchi et al. 2017). Overall, nonwoody vascular epiphyte species, which live in a complex three-dimensional environment, could serve as a model system for understanding the adaptation of plant species and their leaves to environmental variations at different scales. Ongoing studies of nonwoody vascular epiphyte species will help to inform our understanding of the functioning of plant communities and help us to predict the likely responses of species to ongoing environmental changes.

ACKNOWLEDGMENTS

This study is part of the project “Diversity and dynamics of vascular epiphytes in Colombian Andes” supported by COLCIENCIAS (contract 2115–2013). The Corporación para Investigaciones Biológicas (CIB) provided most of the logistic facilities. We especially thank Judith Carmona, who did the epiphyte survey and species identification. AD was partially funded by a The Dutch Research Council (NWO) grant from The Netherlands (Budgetnr 8011) to visit the University of Amsterdam as an invited researcher. KJF was supported though grants from the U.S. National Science Foundation (NSF, DEB-1350125) and the Swiss Agency for Development and Cooperation, and a Research Fellowship from the

Fulbright Program. TT was supported by the NSF (PRFB-1711997). Two anonymous reviewers and the handling editor (Nathan Kraft) helped to significantly improve this paper.

Literature Cited

Allen, L., E. Lemon, and L. Müller. 1972. Environment of a Costa Rican forest. Ecology 53:102–111.

Asner, G., and R. Martin. 2016. Convergent elevation trends in canopy chemical traits of tropical forests. Global Change Biology 22:2216–2227.

Asner, G. P., D. E. Knapp, C. B. Anderson, R. E. Martin, and N. Vaughn. 2016. Large-scale climatic and geophysical controls on the leaf economics spectrum. Proceedings of the National Academy of Sciences of the United States of America 113:E4043–E4051.

Benzing, D. H. 1976. Bromeliad trichomes: structure, function, and ecological significance. Selbyana 1:330–348.

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

Benzing, D. H. 2000. Bromeliaceae: profile of an adaptive radiation. Cambridge University Press, Cambridge, UK.

Blackman, C. J., M. J. Aspinwall, V. Resco de Dios, R. Smith, and D. T. Tissue. 2016. Leaf photosynthetic, economics and hydraulic traits are decoupled among genotypes of a widespread species of eucalypt grown under ambient and elevated CO_2. Functional Ecology 30:1491–1500.

Cardelús, C. L., R. K. Colwell, and J. E. Watkins. 2006. Vascular epiphyte distribution patterns: explaining the mid-elevation richness peak. Journal of Ecology 94:144–156.

Díaz, S. et al. 2004. The plant traits that drive ecosystems: Evidence from three continents. Journal of Vegetation Science 15:295–304.

Díaz, S., et al. 2016. The global spectrum of plant form and function. Nature 529:167–171.

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

Duque, A., P. R. Stevenson, and K. J. Feeley. 2015. Thermophilization of adult and juvenile tree communities in the northern tropical Andes. Proceedings of the National Academy of Sciences 112:10744–10749.

Ek, R. C. 1997. Botanical diversity in the tropical rain forest of Guyana. Trpenbos-Guyana series4. Tropenbos-Guyana Programme, George town, Guyana.

Engemann, K. et al. 2016. Patterns and drivers of plant functional group dominance across the Western Hemisphere: A macroecological re-assessment based on a massive botanical dataset. Botanical Journal of the Linnean Society 180:141–160.

Flores-Palacios, A., and J. G. García-Franco. 2001. Sampling methods for vascular epiphytes: their effectiveness in recording species richness and frequency. Selbyana 22:181–191.

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

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

Gradstein, S. R., N. M. Nadkarni, T. Krömer, I. Holz, and N. Nöske. 2003. A protocol for rapid and representative sampling of vascular and non-vascular epiphyte diversity of tropical rain forests. Selbyana 24:105–111.

Haber, W. A., N. M. Nadkarni, and N. T. Wheelwright. 2001. Number of species with different plant growth forms. Oxford University Press, New York, New York, USA.

Hetherington, A. M., and F. I. Woodward. 2003. The role of stomata in sensing and driving environmental change. Nature 424:901–908.

Holland, N., and A. D. Richardson. 2009. Stomatal length correlates with elevation of growth in four temperate species. Journal of Sustainable Forestry 28:63–73.

Hsu, R. C.-C., W. L. M. Tamis, N. Raes, G. R. de Snoo, J. H. D. Wolf, G. Oostermeijer, and S.-H. Lin. 2012. Simulating climate change impacts on forests and associated vascular epiphytes in a subtropical island of East Asia. Diversity and Distributions 18:334–347.

Ibisch, P. L., A. Boegner, J. Nieder, and W. Barthlott. 1996. How diverse are neotropical epiphytes? An analysis based on the "Catalogue of the flowering plants and gymnosperms of Peru." Ecotropica 2:13–28.

Idárraga, Á., and R. Callejas. 2011. Análisis florístico de la vegetación del Departamento de Antioquia. Page 944 *in* A. Idárraga, R. del C. Ortiz, R. Callejas, and M. Merello, editors. Flora de Antioquia: catálogo de las plantas vasculares. Vol. II. Listado de las plantas vasculares del departamento de Antioquia. Programa Expedición Antioquia-2103. Series Biodiversidad y Recursos Naturales. Universidad de Antioquia, Missouri Botanical Garden & Oficina de Planeación Departamental de la Gobernación de Antioquia, Bogotá, Colombia.

Instituto Geográfico Agustín Codazzi–IGAC. 2007. Antioquia. Características Geográficas. Instituto Geográfico Agustín Codazzi (IGAC), Bogotá, D.C., Colombia.

Karger, D. N., O. Conrad, J. Böhner, T. Kawohl, H. Kreft, R. W. Soria-auza, N. E. Zimmermann, H. P. Linder, and M. Kessler. 2017. Climatologies at high resolution for the earth's land surface areas. Scientific Data 4:170122. https://doi.org/10.1038/sdata.2017.122

Katabuchi, M., K. Kitajima, S. J. Wright, S. A. V. Bael, J. L. D. Osnas, and J. W. Lichstein. 2017. Decomposing leaf mass into photosynthetic and structural components explains 2 divergent patterns of trait variation within and among plant species. bio Rxiv. https://doi.org/10.1101/116855

Kitajima, K., S. J. Wright, and J. W. Westbrook. 2016. Leaf cellulose density as the key determinant of inter- and intra-specific variation in leaf fracture toughness in a species-rich tropical forest. Interface Focus 6:20150100.

Krömer, T., M. Kessler, and S. R. Gradstein. 2007. Vertical stratification of vascular epiphytes in submontane and montane forest of the Bolivian Andes: the importance of the understory. Plant Ecology 189:261–278.

Krömer, T., M. Kessler, G. S. Robbert, and A. Amparo. 2005. Diversity patterns of vascular epiphytes along an elevational gradient in the Andes. Journal of Biogeography 32:1799–1809.

Küper, W., H. Kreft, J. Nieder, N. Köster, and W. Barthlott. 2004. Large-scale diversity patterns of vascular epiphytes in Neotropical montane rain forests. Journal of Biogeography 31:1477–1487.

Lavorel, S., K. Grigulis, S. McIntyre, N. S. G. Williams, D. Garden, J. Dorrough, S. Berman, F. Quétier, A. Thébault, and A. Bonis. 2008. Assessing functional diversity in the field—methodology matters!. Functional Ecology 22:134–147.

Lawson, T., and M. R. Blatt. 2014. Stomatal size, speed, and responsiveness impact on photosynthesis and water use efficiency. Plant Physiology 164:1556–1570.

Legendre, P., and L. F. Legendre. 2012. Numerical ecology. Third edition. Elsevier, Amsterdam, The Netherlands..

Li, L., M. L. McCormack, C. Ma, D. Kong, Q. Zhang, X. Chen, H. Zeng, Ü. Niinemets, and D. Guo. 2015. Leaf economics and hydraulic traits are decoupled in five species-rich tropical-subtropical forests. Ecology Letters 18:899–906.

Martorell, C., and E. Ezcurra. 2007. The narrow-leaf syndrome: a functional and evolutionary approach to the form of fog-harvesting rosette plants. Oecologia 151:561–573.

Messier, J., B. J. McGill, B. J. Enquist, and M. J. Lechowicz. 2017. Trait variation and integration across scales: is the leaf economic spectrum present at local scales? Ecography 40:685–697.

Müller, L. L. B., D. C. Albach, and G. Zotz. 2017. Growth responses to elevated temperatures and the importance of ontogenetic niche shifts in Bromeliaceae. New Phytologist 217:127–139.

Oksanen, J. et al. 2018. vegan: community ecology package. Package version 2.5-3. http://CRAN.R-project.org/package=vegan

Onoda, Y., et al. 2011. Global patterns of leaf mechanical properties. Ecology Letters 14:301–312.

Osnas, J. L. D., M. Katabuchi, K. Kitajima, S. J. Wright, P. B. Reich, S. A. Van Bael, N. J. B. Kraft, M. J. Samaniego, S. W. Pacala, and J. W. Lichstein. 2018. Divergent drivers of leaf trait variation within species, among species, and among functional groups. Proceedings of the National Academy of Sciences 115:5480–5485.

Pakeman, R. J., and H. M. Quested. 2007. Sampling plant functional traits: What proportion of the species need to be measured? Applied Vegetation Science 10:91–96.

Parker, G. 1995. Structure and microclimate of forest canopies. Pages 73–106 *in* M. Lowman and N. Nadkarni, editors. Forest canopies: a review of research on a biological frontier. Academic Press, San Diego, California, USA.

Peña, M. A., K. J. Feeley, and A. Duque. 2018. Effects of endogenous and exogenous processes on aboveground biomass stocks and dynamics in Andean forests. Plant Ecology 2:1481–1492.

Pérez-Harguindeguy, N. et al. 2013. New handbook for standardised measurement of plant functional traits worldwide. Australian Journal of Botany 61:167–234.

Petter, G., K. Wagner, W. Wanek, E. J. Sánchez Delgado, G. Zotz, J. S. Cabral, and H. Kreft. 2016. Functional leaf traits of vascular epiphytes: Vertical trends within the forest, intra- and interspecific trait variability, and taxonomic signals. Functional Ecology 30:188–198.

Pierce, S., K. Maxwell, H. Griffiths, and K. Winter. 2001. Hydrophobic trichome layers and epicuticular wax powders in Bromeliaceae. American Journal of Botany 88:1371–1389.

Poorter, L. et al. 2008. Are functional traits good predictors of demographic rates? Evidence from five neotropical forests. Ecology 89:1908–1920.

Poorter, H., U. Niinemets, L. Poorter, I. J. Wright, and R. Villar. 2009. Causes and consequences of variation in leaf mass per area (LMA): a meta-analysis. New Phytologist 182:565–588.

R Development Core Team. 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. www.r-project.org

Reyes-García, C., H. Griffiths, E. Rincón, and P. Huante. 2008. Niche differentiation in tank and atmospheric epiphytic bromeliads of a seasonally dry forest. Biotropica 40:168–175.

Sack, L., P. D. Cowan, N. Jaikumar, and N. M. Holbrook. 2003. The "hydrology" of leaves: coordination of structure and function in temperate woody species. Plant, Cell and Environment 26:1343–1356.

Sanford, W. W. 1968. Distribution of epiphytic orchids in semi-deciduous tropical forest in Southern Nigeria. Journal of Ecology 56:697–705.

Schellenberger Costa, D., G. Zotz, A. Hemp, and M. Kleyer. 2018. Trait patterns of epiphytes compared to other plant life-forms along a tropical elevation gradient. Functional Ecology 32:2073–2084.

Schmidt, G., G. Zotz, and G. Rapson. 2002. Inherently slow growth in two Caribbean epiphytic species: A demographic approach. Journal of Vegetation Science 13:527–534.

Shipley, B., M. J. Lechowicz, I. Wright, and P. B. Reich. 2006. Fundamental trade-offs generating the worldwide leaf economics spectrum. Ecology 87:535–541.

Smith, M. N. et al. 2019. Seasonal and drought-related changes in leaf area profiles depend on height and light environment in an Amazon forest. New Phytologist 222:1284–1297.

Stark, S. C. et al. 2012. Amazon forest carbon dynamics predicted by profiles of canopy leaf area and light environment. Ecology Letters 15:1406–1414.

Tanaka, Y., S. S. Sugano, T. Shimada, and I. Hara-Nishimura. 2013. Enhancement of leaf photosynthetic capacity through increased stomatal density in Arabidopsis. New Phytologist 198:757–764.

Ward, J. H. 1963. Hierarchical grouping to optimize an objective function. Journal of the American Statistical Association 58:236.

Wilson, P. J., K. Thompson, and J. G. Hodgson. 1999. Specific leaf area and leaf dry matter content as alternative predictors of plant strategies. New Phytologist 143:155–162.

Wolf, J. H. D., S. R. Gradstein, and N. M. Nadkarni. 2009. A protocol for sampling vascular epiphyte richness and abundance. Journal of Tropical Ecology 25:107–121.

Woods, C. L., C. L. Cardelús, and S. J. Dewalt. 2015. Microhabitat associations of vascular epiphytes in a wet tropical forest canopy. Journal of Ecology 103:421–430.

Wright, I. J., et al. 2004. The worldwide leaf economics spectrum. Nature 428:821–827.

Wright, S. J. et al. 2010. Functional traits and the growth-mortality trade-off in tropical trees. Ecology 91:3664–3674.

Zotz, G. 2013*a*. The systematic distribution of vascular epiphytes—a critical update. Botanical Journal of the Linnean Society 171:453–481.

Zotz, G. 2013*b*. "Hemiepiphyte": A confusing term and its history. Annals of Botany 111:1015–1020.

Zotz, G., and J. L. Andrade. 2002. La ecología de las epífitas y las hemiepífitas. Pages 271–296 *in* M. R. Guariguata and G. H. Kattan, editors. Ecología y conservación de bosques neotropicales. Libro Universitario Regional, Cartago, Costa Rica.

Zotz, G., and M. Y. Bader. 2009. Epiphytic plants in a changing world-global: change effects on vascular and non-vascular epiphytes. Pages 147–170 *in* L. Ulrich, W. Beyshlag, B. Budel, and D. Francis editor. Progress in botany. Springer, Berlin, Germany.

Zotz, G., S. Patiño, and M. T. Tyree. 1997. Water relations and hydraulic architecture of woody hemiepiphytes. Journal of Experimental Botany 48:1825–1833.

Zotz, G., and U. Winkler. 2013. Aerial roots of epiphytic orchids: the velamen radicum and its role in water and nutrient uptake. Oecologia 171:733–741.

Zuleta, D., A. M. Benavides, V. Lopez-Rios, and A. J. Duque. 2016. Local and regional determinants of vascular epiphyte mortality in the Andean mountains of Colombia. Journal of Ecology 104:841–849.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/ecy.2858/suppinfo