Trade-offs between succulent and non-succulent epiphytes underlie variation in drought tolerance and avoidance

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Abstract
Epiphyte communities comprise important components of many forest ecosystems in terms of biomass and diversity, but little is known regarding trade-offs that underlie diversity and structure in these communities or the impact that microclimate has on epiphyte trait allocation. We measured 22 functional traits in vascular epiphyte communities across six sites that span a microclimatic gradient in a tropical montane cloud forest region in Costa Rica. We quantified traits that relate to carbon and nitrogen allocation, gas exchange, water storage, and drought tolerance. Functional diversity was high in all but the lowest elevation site where drought likely limits the success of certain species with particular trait combinations. For most traits, variation was explained by relationships with other traits, rather than differences in microclimate across sites. Although there were significant differences in microclimate, epiphyte abundance, and diversity, we found substantial overlap in multivariate trait space across five of the sites. We found significant correlations between functional traits, many of which related to water storage (leaf water content, leaf thickness, hydrenchymal thickness), drought tolerance (turgor loss point), and carbon allocation (specific leaf area, leaf dry matter content). This suite of trait correlations suggests that the epiphyte community has evolved functional strategies along with a drought avoidance versus drought tolerance continuum where leaf succulence emerged as a pivotal overall trait.

Keywords Functional traits · Water relations · Microclimatic gradient · Stable isotopes · Tropical montane cloud forest

Introduction

The assessment of trait variation in plant communities can identify underlying mechanisms that explain patterns of species-level diversity in both form and function within and among ecosystems (Wright et al. 2004). Measuring suites of traits that relate to carbon (C) or nutrient allocation can elucidate trade-offs in ecological strategies, including life-history traits, growth patterns, and defense strategies (Grime 1977; Coley et al. 1985; Reich et al. 1997; Wright et al. 2004). Early studies contributed to a fundamental understanding of C and nitrogen (N) allocation in plants, but investigations including traits pertaining to plant-water relations are far fewer. Despite this, the recent inclusion of water-related traits has contributed to a deeper understanding of the drivers of community structure in a wide range of water-limited ecosystems in many terrestrial plant communities (e.g., Bartlett et al. 2012; Blackman et al. 2012; Choat et al. 2012; Reich 2014).
One community type that has been largely neglected are epiphyte communities where variation in traits relating to water storage (succulence) seem common and may, therefore, underlie important ecological strategies.

One useful way to understand plant functional traits is by studying plants that live along environmental gradients, an approach that has long been used by ecologists to study how plant communities respond to variation in atmospheric and edaphic conditions (Turner 1989). Such gradients may serve as a proxy to understand how communities will be affected by the warmer and drier conditions of a changing climate (Diaz and Cabido 1997; Dunne et al. 2003).

On tropical mountains, narrow bands of microclimate occur over small ranges in elevation, leading to narrow and often abrupt ecotones occupied by plant communities with unique composition (Williams et al. 2007; Ray et al. 2006). Narrow species distributions may be due to constraints on the allocation to phenotypes and may indicate that these communities are vulnerable to changes in the environment (Hollenbeck 2019). Experimental work on epiphytes suggests that this community is vulnerable to changes in microclimate (Nadkarni and Solano 2002; Darby et al. 2016), suggesting that certain functional trait combinations are suited to small microclimatic envelopes that may select for narrow ecological niches.

Research focused on future climate projections and evidence from long-term datasets both indicate that the climate patterns on tropical mountains are likely to change substantially as sea and land surface temperatures rise and deforestation increases (Pounds et al. 1999, 2006; Still et al. 1999; Lawton et al. 2001; Helmer et al. 2019). Such changes will threaten plant communities that currently reside at high elevations in tropical montane cloud forests (TMCFs) (Pounds et al. 1999, 2006; Still et al. 1999; Lawton et al. 2001; Ray et al. 2006; Helmer et al. 2019). This is of particular concern because TMCFs are repositories for biodiversity, have a high degree of endemism and affect local and regional water and nutrient cycles (Zadroga 1981; Brown et al. 1996; Haber 2000; Bruijnzeel et al. 2010; Tognetti et al. 2010; Gotsch et al. 2016).

A substantial portion of the biodiversity in TMCFs is contained in epiphyte communities (Gentry and Dodson 1987; Haber 2000). The epiphyte community in the TMCF has exceedingly high biomass and contributes important ecosystem services by providing food and habitat resources and playing critical roles in water and nutrient cycling (Nadkarni et al. 2004; Gotsch et al. 2016). Epiphyte communities in the TMCF are ideal systems to study the correlation between variation in microclimate and variation in plant form and function because of their great abundance and species richness over small spatial gradients: within trees, within sites, and across sites. These communities also exhibit substantial functional trait and life-form diversity, which can be used to explore the broad spectrum of ecological strategies and the underlying traits each different strategy may possess.

In this study, we measured 22 functional traits of common vascular epiphytes at six forest sites across an elevational gradient in a TMCF in Costa Rica. We focused on water relations traits that are likely to be important for survival as drought increases and traits that relate to carbon and nutrient allocation. We addressed the following questions: (1) How do traits and trait combinations vary from warmer and drier to cooler and wetter microclimates? and (2) Do ecological trade-offs, such as the degree of succulence or drought tolerance underlie variation in functional traits within epiphyte communities? We hypothesized that differences in microclimate would explain at least some of the variation in traits given the large differences in atmospheric moisture across the sites and the slow growth patterns of epiphytes. Because these plants are disassociated from terrestrial soil resources, we also expected that the majority of functional trait variation would be explained by trade-offs relating to water storage and drought tolerance.

**Methods**

**Description of sites**

This study occurred in six forested sites along a microclimatic gradient in the TMCF region of Monteverde, Costa Rica (1100–1600 m asl) (Fig. 1, Table 1). The three highest elevation sites are located in the primary forest within the lower montane cloud forest which occurred above the current cloud base and within the cloud layer. The three lowest and driest sites are below the average cloud base and consist of secondary forests in the lower montane rainforest which contained remnant trees that were left standing after harvest of the surrounding forest (Sheldon and Nadkarni 2015). These sites fit the descriptions of cloud forest and rainforest outlined by Bruijnzeel et al. (2011). The dry season generally occurs from February through April in all sites, and although rainfall does occur during this period, it is less abundant (Nadkarni 1984, 1994). The dry season is more pronounced in the lower sites. The wet season generally occurs from May–November when rain falls almost daily and large rain events are frequent (Nadkarni 1984, 1994). In December and January, the area experiences high winds that drive substantial inputs of mist (Nadkarni 1984, 1994). The mean annual rainfall in the second to the highest site (CCT) is ca. 4000 mm, whereas the lowest site, University of Georgia-Costa Rica (UGA, now Council on International Educational Exchange or CIEE) receives 2600 mm (Pounds et al. 1999; A. Pounds, unpubl. data, [http://weather.uga.edu/index.php?content=gp&site=SANLUIS]. Regional climate is experiencing increasing inter-annual variation in
precipitation and an increasing number of days with little or no precipitation (Pounds et al. 1999, Pounds unpubl. data). Projected changes in land use and climate in this region include increases in cloud base heights, which may further increase such drying events (Lawton et al. 2001).

Although differences in elevation and distance between some of the sites were minimal, each site experiences a significantly different microclimate due to variation in topography and prevailing weather conditions (Gotsch et al. 2017). The sites in order from driest to wettest (i.e., highest to lowest average vapor pressure deficit (VPD), leaf wetness, and canopy soil moisture content throughout the year) are: Council on International Educational Exchange, San Luis Field station which was the University of Georgia-San Luis (UGA), Buen Amigo Farm (BA), Lower Curi Cancha Reserve (LCC), Upper Curi Cancha Reserve (UCC), Centro Científico Tropical-Monteverde Reserve (CCT) and El Valle, within the Children’s Eternal Rainforest (EV) (Gotsch et al. 2017, Table 1).

The epiphyte community in the Monteverde region is comprised of ca. 800 species of vascular plants (Haber 2000) and hundreds of non-vascular plant species (Gradstein et al. 2001). The biomass of epiphytes and accompanying canopy soils is also high (up to 33 t/ha, Nadkarni et al. 2004), and epiphytes cover almost every exposed tree surface. In drier sites, canopy epiphytes are common, with much lower diversity and abundance (Gotsch et al. 2017; Amici et al. 2019).

At each site, we identified 3–5 dominant canopy trees that were healthy, had large and spreading crowns, and were safe to climb (see Gotsch et al. 2017 for details of host tree selection). Each was located within ~50 m of each other to ensure that their epiphyte communities experienced similar microclimates. All host trees were within the largest size class in each site (diameter at breast height = 170–400 cm, 25–30 m in height) (Gotsch et al. 2017). These trees were likely the oldest in each site, ensuring that the canopy community was mature. Although some studies in lowland tropical rainforests and forests of temperate regions have found evidence of host specificity of epiphytes, in TMCFs, tree size has a larger impact on epiphyte biomass and composition (Hietz and Hietz-Seifert 1995; Callaway et al. 2002; Cardelús et al. 2006; Laube and Zotz 2006; Wagner et al. 2015). Because microclimate in the TMCF varies over very short distances, choosing a cluster of trees that had similar

Fig. 1 Map of the six study sites in the Monteverde region of Costa Rica. El Valle is the wettest site, and UGA is the driest site. Map Credit: Geiner Alvarado Huertas
Table 1  Microclimate and other descriptive information for each of the study sites

| Site      | Elev (m asl) | Species (n) | VPD (kPa)* | VWC (m³/m³) | Soil temp (°C) | LWS (gm/m²) | Air temp (°C) | RH (%) | Location                      | Lat           | Long                     | Forest type                              |
|-----------|--------------|-------------|------------|-------------|----------------|--------------|---------------|--------|-------------------------------|---------------|--------------------------|------------------------------------------|
| UGA**     | 1100         | 7           | 0.51       | 0.05        | 19.92          | 31.97        | 20.26         | 90.53  | Univ. of Ge., San Luis       | N 10° 16’ 5 8.83” W 084° 47’ 51.06”   | Secondary                             |
| BA        | 1070         | 9           | 0.46       | 0.02        | 19.01          | 39.06        | 20.27         | 91.95  | Private Farm                  | N 10° 16’ 4 5.29” W 084° 47’ 39.94”   | Primary w/timber removal               |
| LCC       | 1474         | 15          | 0.34       | 0.09        | 17.65          | 50.67        | 18.02         | 94.15  | Curi Cancha Reserve          | N 10° 18’ 2 2.51” W 084° 48’ 16.45”   | Secondary w/remnant trees             |
| UCC       | 1592         | 25          | 0.23       | 0.11        | 16.93          | 82.99        | 17.28         | 96.57  | Monteverde Reserve           | N 10° 18’ 3 5.47” W 084° 47’ 46.58”   | Primary                               |
| CCT       | 1554         | 26          | 0.15       | 0.14        | 16.65          | 184.84       | 17.09         | 98.37  | Monteverde Reserve           | N 10° 18’ 1 8.84” W 084° 47’ 39.30”   | Primary                               |
| EV        | 1635         | 17          | 0.08       | 0.24        | 15.81          | 160.91       | 16.64         | 98.60  | Children’s Eternal Rainforest | N 10° 19’ 1 8.25” W 084° 46’ 02.60”   | Primary                               |

The sites in order from driest to wettest are: University of Georgia-San Luis (UGA), Buen Amigo Farm (BA), Lower Curi Cancha Reserve (LCC), Upper Curi Cancha Reserve (UCC), Centro Científico Tropical-Monteverde Reserve (CCT) and El Valle, a site within the Children’s Eternal Rainforest (EV). Elev. refers to the elevation of the site (meters above sea level). Species refers to the number of species that were measured in each site. VPD refers to the vapor pressure deficit, VWC refers to the volumetric canopy soil water content, soil temp. refers to the temperature of the canopy soil, LWS refers to the in-crown leaf wetness, Air Temp refers to the in-canopy air temperature while RH refers to the in-crown relative humidity.

*The vapor pressure deficit (VPD) depicted is the average maximum daily VPD for 12 months between 2015 and 2016 (Gotsch et al. 2017)

**At the time of the study the UGA site was owned by the University of Georgia. The property is now owned by the Center for International Educational Exchange
size and physical attributes was more important than target-
ing specific host species.

**Epiphyte study species and functional groups**

In total, we included 48 epiphyte species across the six sites in this study (N = 7–26 species per site, Table 1). We included species along this gradient that we had identified as the most common species (by biomass) in a companion study (Amici et al. 2019). We also included additional species that were common in each site, even if their total biomass was not among the greatest on the site. Because wetter sites were more diverse, we measured more species in these sites. Although there was substantial community turnover across the sites, some species were common in more than one of the study locations. However, only *Anthurium scandens* was found in all six sites. There was insufficient mate-
rial to measure the target functional traits for rare species.

Because the selected species were abundant, we presumed they played relatively important roles in ecosystem function. Each site included representatives of the three most common growth forms: epiphytic shrubs, single-stemmed woody species, and herbaceous epiphytes (Gotsch et al. 2017; Supplemental Table 1). These species were variable in the succulence of their leaves. Many were woody species (shrubs or treelets), and often produced thickened leaves with a distinct layer of hydrenchymal cells known to serve a water storage function (Gotsch et al. 2015). Aside from thickened leaves, these species generally did not exhibit the more telltale characteristics of true “succulents” such as bulbous leaves or swollen stems. Therefore, for the pur-
poses of this paper, we use the term succulent to refer to plants whose leaves have a distinctive hydrenchymal layer regardless of whether they exhibited other traits generally associated with succulence. While CAM photosynthesis has been detected in bromeliads in tropical montane forests, CAM incidence is likely low in our focal taxa given the high humidity in this environment (Pierce et al. 2002; Silvera et al. 2010; Supplemental Table 1; Gotsch, unpubl. data). All functional traits were measured during the wet seasons (June–August, 2013–2017) to ensure consistency in leaf phenotypes (Gotsch et al. 2017). In a preliminary analysis, we did not find significant variation across the measurement years, so all trait data were pooled over measurement years.

**Microclimate**

In 2014, we installed canopy microclimate stations in one of the study trees at each of the sites. The sensors included air temperature and relative humidity (Hobo U32, Onset Computer Corporation, Bourne MA), canopy soil moisture (EC-5, Meter Group Inc., Pullman WA), wind speed and wind direction (Davis Cup anemometer, Meter Group Inc., Pullman WA), and leaf wetness (Phytos 31, Meter Group Inc., Pullman WA). Data from these sensors were recorded every 15 min to a datalogger (EM-50 METER Group Inc, Pullman WA, USA), and retrieved monthly by climbing the tree and downloading the data.

**Sample collection**

We gained access to tree crowns with single rope techniques and then used moving-rope systems to access lateral points in the crown (Anderson et al. 2015). We measured func-
tional traits on healthy and newly mature leaves. For large individuals such as epiphytic shrubs, a large branch (~1 m) was cut from each individual; often several traits could be measured from that sample. For small individuals, however, all of the available newly mature leaves on one individual were used to measure just one trait. Given the large varia-
tion in the size of the samples, the total sample size varied from 5 individuals if there were many leaves per individual to 15 individuals if there were very few leaves per sample. Since epiphytes often grow asexually through rhizomes, we collected individuals from different host tree branches and on different host trees to avoid sampling the same genets. All collected plant material was immediately placed into black plastic bags to maintain dark and moist conditions until arrival at our lab where stems were recut underwater. Plants were kept hydrated and in the dark until measured; most plants were processed within 1–2 days. Since there was some turnover of host tree species in different sites, we were unable to test for the effect of host tree species.

**Functional traits**

We measured 22 functional traits, selected to provide informa-
tion about plant allocation strategies known to correlate with photosynthesis, growth, and defense (Coley et al. 1985; Reich et al. 1997, 1999; Wright et al. 2004, 2005). A number of these traits also relate to water storage and cycling and drought tolerance (Table 2).

**Carbon and nutrient traits**

We measured specific leaf area (SLA = fresh area/dry weight, cm² g⁻¹) and leaf dry matter content (LDMC = dry weight/fresh weight, g g⁻¹), on entire leaves that had the pet-
iole removed. We also measured leaf toughness (TOUGH = g mm⁻², i.e. the force needed to pierce the surface of the leaf, following methods outlined in Gotsch et al. 2010) and wood density measured with the displacement method (WD = vol-
tume/dry weight, g cm⁻³) for woody species.

Dry and ground samples were analyzed for C and N content (% dry weight), and stable isotope ratios (δ¹³C and δ¹⁵N values, respectively) were extracted with an elemental
analyzer/continuous flow isotope ratio mass spectrometry using a CHNOS Elemental Analyzer (vario ISOTOPE cube, Elementar, Hanau, Germany) coupled with an IsoPrime 100 mass spectrometer (Isoprime Ltd, Cheadle, UK). The long-term analytical precision was 0.08 ‰ for C and 0.14 ‰ for N. For C-isotope analyses the standard used was V-PDB, and for N-isotope analyses we used N2-gas. All isotope analyses were conducted at the Center for Stable Isotope Biogeochemistry at the University of California, Berkeley, CA, USA.

Water relations traits

We measured leaf water content (LWC = (fresh weight-dry weight)/fresh weight *100%,) and leaf water storage (LWS = fresh weight/fresh area g cm⁻² converted to mm) and generated pressure–volume (PV) curves to understand water storage dynamics and the ability to withstand desiccation across the gradient. Each PV curve often took several days to complete on epiphytes; therefore, the number of species evaluated for PV curves was lower than for other traits. We measured a representative group of species in each site, including all growth forms for both succulent and non-succulent epiphytes. The two driest sites contained fewer species in general and had the lowest sample sizes for PV curves (6 species in UGA and 10 in BA); in the wettest sites (CCT, EV), we sampled 20 species or more (6–23 species per site, minimum of five individuals per species in all sites, 355 PV curves total across all sites). From the relationship between water potential and relative water content of the dehydrating sample, we estimated the following water relations traits: turgor loss point (TLP, MPa), relative water content at the turgor loss point (RWCₜlp, %), saturated water content (SWC, g), bulk elastic modulus (ε, MPa), capacitance at full turgor (Cᶠt, MPa⁻¹), capacitance at the turgor loss point (Cₜlp, MPa⁻¹), and capacitance at full turgor on a leaf-area basis (C*, mmol m⁻² MPa⁻¹), and lastly the osmotic potential at full turgor (πₒ; MPa) (Tyree and Hammel 1972; Koide et al. 2000).

We also measured the minimum leaf conductance (gₘᵢₙ, mmol m⁻² s⁻¹) and stomatal density (SD, count cm⁻²) because these variables convey information about the ability of leaves to regulate water loss (Duursma et al. 2019). Minimum leaf conductance is often referred to as cuticular conductance. However, in our study area, gₘᵢₙ is likely a combination of stomatal and cuticular conductance after the stomata close as much as possible (Duursma et al. 2019; Gotsch et al. 2018). To measure minimum leaf conductance, rehydrated leaves were removed from the stem, and the petiole was sealed with parafilm. In a well-ventilated location, leaves were weighed every 30 min for 4–6 h while air temperature and relative humidity were recorded. The gₘᵢₙ could then be estimated as the slope of the mass over time divided by the average mole fraction VPD taken over

| Abbreviation | Description | Units          |
|--------------|-------------|----------------|
| gₘᵢₙ         | Minimum leaf conductance | mmol m⁻² s⁻¹    |
| Tough        | Leaf toughness | g mm⁻²         |
| LDMC         | Leaf dry matter content | g g⁻¹     |
| SLA          | Specific leaf area | cm m⁻²        |
| WD           | Wood density   | cm m⁻²        |
| SWC          | Saturated water content | g         |
| δ¹⁵N         | Osmotic potential at full turgor | MPa   |
| TLP          | Turgor loss point | MPa          |
| RWCTLP       | Relative water content at the turgor loss point | %    |
| ε            | Bulk elastic modulus | MPa        |
| Cᶠt          | Capacitance at full turgor | MPa⁻¹    |
| Cₜlp         | Capacitance at the turgor loss point | MPa⁻¹    |
| C*           | Capacitance at full turgor on a per leaf area basis | mol m⁻² MPa⁻¹ |
| SD           | Stomatal density | stomata cm⁻²  |
| LT           | Leaf thickness  | mm             |
| Total Hydro  | Total hydrenchymal thickness (both layers added if present) | mm    |
| CUT          | Total cuticle thickness (summation of both cuticle layers) | μm    |
| LWC          | Leaf water content | %              |
| LWS          | Leaf water storage | mm          |
| C:N          | Ratio of the percent leaf carbon to nitrogen | %      |
| δ¹⁵N         | Nitrogen isotope ratio | %e    |
| δ¹³C         | Carbon isotope ratio | %e      |

Table 2 Abbreviations and units for the functional traits measured in this study
the measurement period (Scoffoni et al. 2018). This value was then normalized by the average leaf area from the beginning to the end of the experiment to consider leaf shrinkage during dehydration (Scoffoni et al. 2018). To measure stomatal density, we coated the abaxial side of fresh leaves with clear nail varnish, allowed it to dry, peeled it off, and placed it on a glass slide where the stomatal impressions were viewed at 100–200 × magnification using a compound light microscope (Motic BA210E, Richmond, British Colombia, Canada). Digital images were taken with a camera mounted to the microscope for counting with ImageJ software (v1.48, U.S. National Institutes of Health, Bethesda, Maryland, USA).

We also measured thicknesses of the leaf lamina (LT, mm), cuticle (CUT, μm), and thickness of hydrenchymal layer (Total hydro, mm) if present, on transverse sections of the fresh leaves that were sectioned with a razor blade and stained with safranin. Leaf sections were magnified at 200–400 × under a compound light microscope, photographed with a digital camera, and measured in ImageJ. All thicknesses were measured in the middle of the leaf lamina, away from major veins and the leaf margin.

Data analyses

Traits were evaluated for normality prior to statistical analyses; non-normal data were log-transformed. All traits were log-normally distributed with the exceptions of the following traits whose raw data were normally distributed: LDMC, LWC, δ13C and δ15N. We performed a two-way ANOVA for each trait separately to determine whether the effect of site and functional group (herbaceous, shrub, and single-stemmed woody epiphytes) played a significant role in trait variation. We applied a Benjamini–Hochberg procedure for multiple comparisons for each factor in the analysis to determine the threshold for significance (Q = 0.05). Intraspecific variation could not be assessed because most species were restricted in their distribution. For the two widely distributed species, Clusia sp. (5 sites) and A. scandens (6 sites), we examined intraspecific variation across the sites using one-way ANOVAs. In a separate series of two-way ANOVAs, we tested whether the presence of succulent leaves affected functional trait variation (main effects: site, succulence, and their interaction). We used an ANOVA to assess whether variation in stable isotopes was impacted by whether a site was situated within or below the cloud layer. This additional test was performed following a visual examination of the data that highlighted a grouping based on this factor. Determining the abundance of our target species in relation to the rest of this hyper-diverse community was beyond the scope of our study. Since calculating community weighted means was not possible, species means were used in all comparisons.

We conducted pairwise correlations among all traits (232 unique trait combinations in total). A Benjamini–Hochberg procedure for multiple comparisons was performed to determine the critical threshold for significance. We carried out a linear regression analysis to evaluate the effect of stomatal density on δ13C across all species and sites. We performed a Principal Components Analysis (PCA) on species averages for a representative subset of functional traits (LDMC, SD, LT, gₘᵦ TLP) to examine overlap in multivariate trait space across all six sites. Principal components loading scores for the first two axes were analyzed with ANOVAs to test for the effect of site on multivariate trait values. To visualize differences in sites based on species presence/absence data across the study sites, we performed a discriminant analysis (Supplemental Fig. 1).

Results

Trait variation across sites

Microclimatic differences across the sites did not explain the variation of most individual functional traits (Fig. 2a–f). For 7 of the 22 traits, however, the effect of site was significant in the two-way ANOVAs (SLA, d15N, d13C, LT, CUT, Mesophyll and Cₚ) (Table 3). Although epiphyte leaves generally had lower stomatal density in drier sites and higher stomatal density in wetter sites, there was substantial variation in δ13C across all species and sites. We performed a linear regression analysis to evaluate the effect of stomatal density on δ13C across all species and sites. We performed a Principal Components Analysis (PCA) on species averages for a representative subset of functional traits (LDMC, SD, LT, gₘᵦ TLP) to examine overlap in multivariate trait space across all six sites. Principal components loading scores for the first two axes were analyzed with ANOVAs to test for the effect of site on multivariate trait values. To visualize differences in sites based on species presence/absence data across the study sites, we performed a discriminant analysis (Supplemental Fig. 1).
UGA) (Fig. 3, $\delta^{13}$C: $F_{1,1}=52.73$, $P<0.0001$; and $\delta^{15}$N: $F_{1,1}=10.47$, $P=0.002$). Sites below the cloud base generally had higher $\delta^{13}$C values than sites currently within the cloud layer (e.g., $-28 \%e$ at UGA versus $-32 \%e$ at El Valle), while average $\delta^{15}$N increased from $-6.4\%e$ above the cloud base to $-1.86 \%e$ below the clouds.

**Variation across functional groups and growth forms**

Although most traits did not vary in a systematic way across sites, there were clear differences between succulent and non-succulent epiphytes. Not only were there a larger number of significant differences in traits in the comparison of
these groups, but the F-values were in many cases a degree of magnitude greater than the effect of the site in the analyses, indicating the importance of this factor in trait variation (Table 3). Plants that were more succulent generally had higher $g_{\text{min}}$, C*, and LWS but had lower LDMC, SD and TLP (Fig. 4a–f; Table 3). Traits such as SWC, LT, and LWS that relate specifically to water storage were approximately two-fold greater in epiphytes with more succulent leaves (Supplemental Table 3). Although many important traits differed between more and less succulent epiphytes, many traits did not exhibit significant differences, including SLA, TOUGH, $\sigma_v$, WC, $C_{\text{up}}$, $\delta^{13}$C, $\delta^{15}$N, and leaf C:N (Table 3, Supplemental Table 3). In an examination of trait variation across sites and functional groups, we found that epiphytic shrubs had the lowest TLP and the highest LDMC and SD, though following an adjustment for multiple comparisons, the effect of growth form was only significant for SD ($F_{2,2} = 8.98, P < 0.0001$).

| Functional trait | Statistic | Site | Leaf succulence | Site*Leaf succulence |
|------------------|-----------|-----|-----------------|----------------------|
| $g_{\text{min}}$ (mmol m$^{-2}$ s$^{-1}$) | $P$-value | 0.03 | 0.001 | 0.85 |
| F-ratio | 2.61 | 11.09 | 0.4 |
| LDMC (g g$^{-1}$) | $P$-value | 0.67 | $< 0.0001$ | 0.75 |
| F-ratio | 0.64 | 56.06 | 0.53 |
| SLA (cm m$^{-2}$) | $P$-value | $< 0.0001$ | 0.13 | 0.39 |
| F-ratio | 14.34 | 2.36 | 1.06 |
| SWC (g) | $P$-value | 0.72 | $< 0.0001$ | 0.79 |
| F-ratio | 0.58 | 27.26 | 0.48 |
| $C_{\text{n}}$ * (mol m$^{-2}$ MPa$^{-1}$) | $P$-value | 0.0003 | $< 0.0001$ | 0.02 |
| F-ratio | 5.14 | 53.26 | 3.34 |
| SD (# cm$^{-2}$) | $P$-value | 0.2 | $< 0.0001$ | 0.87 |
| F-ratio | 1.51 | 19.17 | 0.36 |
| LT (mm) | $P$-value | 0.0002 | $< 0.0001$ | 0.07 |
| F-ratio | 5.36 | 83.17 | 2.13 |
| Total Hydro (mm) | $P$-value | 0.09 | $< 0.0001$ | 0.28 |
| F-ratio | 2.01 | 69.05 | 1.29 |
| CUT (mm) | $P$-value | 0.03 | $< 0.0001$ | 0.05 |
| F-ratio | 4.46 | 19.89 | 2.27 |
| LWC (%) | $P$-value | 0.36 | $< 0.0001$ | 0.22 |
| F-ratio | 1.12 | 28.25 | 1.44 |
| LWS (mm) | $P$-value | 0.0002 | $< 0.0001$ | 0.01 |
| F-ratio | 5.68 | 120.93 | 3.68 |
| $\delta^{15}$N (‰) | $P$-value | $< 0.0001$ | 0.23 | 0.002 |
| F-ratio | 19.39 | 1.51 | 4.7 |
| $\delta^{13}$C (‰) | $P$-value | $< 0.0001$ | 0.86 | 0.57 |
| F-ratio | 10.44 | 0.03 | 0.78 |
| Mesophyll (mm) | $P$-value | 0.0027 | 0.66 | 0.089 |
| F-ratio | 3.97 | 0.1839 | 1.98 |

Traits are shown here if at least one of the effects was significant after evaluation with a Benjamini–Hochberg procedure for multiple comparisons ($Q = 0.05$). P-values indicating significant differences are underlined. Descriptions of the trait abbreviations can be found in Table 2.

SLA, TOUGH, $\sigma_v$, WC, $C_{\text{up}}$, $\delta^{13}$C, $\delta^{15}$N, and leaf C:N (Table 3, Supplemental Table 3). In an examination of trait variation across sites and functional groups, we found that epiphytic shrubs had the lowest TLP and the highest LDMC and SD, though following an adjustment for multiple comparisons, the effect of growth form was only significant for SD ($F_{2,2} = 8.98, P < 0.0001$).

Relationships between traits

Pairwise correlations including plants at all sites revealed 65 significant relationships (following an evaluation of the significance threshold with the Benjamini–Hochberg procedure) which likely reveal trade-offs in allocation in more succulent and less succulent epiphytes (Fig. 5, Supplemental Table 4). We found 12 significant correlations including LDMC and 14 significant correlations including LWC (Fig. 5, Supplemental Table 3). There were negative relationships between LDMC and $g_{\text{min}}$ ($R = -0.56, P < 0.0001$), LT ($R = -0.61, P < 0.0001$), and TLP ($R = -0.33, P = 0.0010$) and a positive relationship between LDMC and SD ($R = 0.52, P < 0.0001$, Fig. 5a, c, e, g). We also found a positive correlation between LWC and $g_{\text{min}}$ ($R = 0.49, P < 0.0001$), LT ($R = 0.5, P < 0.0001$), and TLP ($R = 0.38, P = 0.001$) and a negative correlation between LWC and SD ($R = -0.49$, Fig. 5b, d, f, h). The relationship between LDMC and LWC was also highly significant ($R = -0.92$, Fig. 5c, d).
Since more succulent epiphytes have a higher LWC, these relationships can be used to further understand ecological trade-offs in different epiphyte groups.

We examined visually the relationship between C and N isotopes above and below the cloud base since this factor seemed uniquely important in explaining the variation in these traits ($R = 0.38$, $P < 0.0001$, Fig. 6). Individuals residing in sites above the current cloud base tended to have more negative $\delta^{13}C$ and $\delta^{15}N$ values compared to individuals below the current cloud base where conditions were warmer and drier (ANOVA, effect of “cloud layer”: $\delta^{13}C: F_{1,1} = 52.73$, $P < 0.0001$; and $\delta^{15}N: F_{1,1} = 10.47$, $P = 0.002$, Figs. 3 and 6).

Fig. 4 Box and whiskers plots depicting the variation in representative functional traits (a–f) between succulent and non-succulent species across all sites. The line in the center of the box represents the median while the top and bottom of the box represent the 25th and 75th percentiles. The whiskers represent the 10th and 90th percentiles and the dots are outliers which lie above or below these values. ANOVA analyses (with Benjamini–Hochberg procedure for multiple comparisons) indicated that all comparisons were significant, as indicated with a ‘*’ in the panels, with the exception of turgor loss point (f) ($g_{\text{f}}$: $F_{1,1} = 11.09$, $P = 0.001$; $C_{\text{f}}$: $F_{1,1} = 53.26$, $P < 0.0001$; LWS: $F_{1,1} = 120.93$, $P < 0.0001$; LDMC: $F_{1,1} = 56.06$, $P < 0.0001$; SD: $F_{1,1} = 19.17$, $P < 0.0001$). Error bars represent the standard error of the mean.
Although we found few significant relationships between stable isotope values and other functional traits, an interesting and significant pattern occurred between $\delta^{13}C$ and SD (Fig. 7, $r^2 = 0.11$, $P = 0.01$). Although in general there was a large range in SD across the sites, species with the highest SD were restricted to wetter sites. The relationship between $\delta^{13}C$ and SD improved dramatically when the species within a site were averaged (Fig. 7 inset, $r^2 = 0.83$, $P = 0.01$). This figure also highlights the substantial variation in $\delta^{13}C$ values within sites. Despite this variability, the most negative $\delta^{13}C$ values were restricted to the wettest sites.

There was a high degree of overlap in multivariate trait space with no clear separation of sites; variation in both axes was similar in five of the six sites (Fig. 8). However, variation in trait space was reduced in the driest site (UGA, Fig. 8). PC1 explained 50.7% of the variation in the dataset while PC2 explained 19.2%. We found no significant difference in the loading values of traits associated with either PC1 ($F_{5,5} = 1.61$, $P = 0.16$) or PC2 ($F_{5,5} = 1.26$, $P = 0.28$) across sites.

Discussion

Of the 22 traits measured, variation in only a few of these was explained by differences in microclimate across the sites (Figs. 2, 3 and 6). In contrast, we found substantial variation driven by a continuum of trait combinations expressed by more succulent versus less succulent species (Figs. 5, 9). Such trade-offs indicate differences in ecological strategies relating to drought avoidance and drought tolerance in the epiphyte community. Below, we address the questions presented in the Introduction.
How do traits and trait combinations vary from warmer and drier to cooler and wetter microclimates?

There are clear differences in microclimate across the six study sites. In general, the higher sites have more moisture in the system exemplified by lower VPD but higher leaf wetness and canopy soil moisture (Table 1, Gotsch et al. 2017). This variation in microclimate appears to have a substantial effect on the community composition of vascular epiphytes in the Monteverde region, where epiphyte communities in cloud forest sites at higher elevations have higher species richness and epiphyte abundance compared with drier sites below the cloud base (Gotsch et al. 2017;
Thus, we expected to find significant variation across sites in at least some traits relating to water relations and the leaf economics spectrum. Although variation in most traits appeared to be driven only by trait relationships underlying drought tolerance or avoidance in this community, variation in C and N isotopes were most notably influenced by a microclimate.

δ¹³C varied predictably across the gradient—plants in drier sites (i.e., below the current cloud base) had more positive δ¹³C values (Fig. 3, Supplemental Table 2). These results are consistent with observations that stomatal conductance tends to be greater over the lifespan of leaves at wetter sites, providing RuBisCO with more opportunities to discriminate against the heavier isotope (Farquhar et al. 1989). Although the δ¹³C values are consistent with C₃ photosynthesis, the range of values (−28‰ to −32‰) is at the low end of the distribution of plants with C₃ photosynthesis and may be a result of within-crown recycling of soil-respired carbon, especially in the wetter sites (Da Silveira et al. 1989). It is possible that the high biomass of epiphytes and their associated canopy soils in wetter sites create a buffer from atmospheric CO₂, which could cause more localized C-recycling and more negative δ¹³C values. In contrast, in the drier sites, tree crowns are more open and the epiphyte abundance is much lower (Gotsch et al. 2017; Amici et al. 2019), which could facilitate greater mixing between in- and above-canopy air masses.

We also found significant differences in δ¹⁵N across sites (Fig. 3), which could be due to atmospheric sources of N being preferred over N in canopy soils. The range of δ¹⁵N values we documented was similar to those found in studies on vascular epiphytes (Hietz et al. 1999; Hietz et al. 2002; Reich et al. 2003; Cardelus and Mack 2010; Craine et al. 2015). For example, in Monteverde, epiphytes living on small branches had more negative δ¹⁵N values, whereas higher values were found for plants rooted in canopy soil (Hietz et al. 2002). Smaller individuals that receive a greater proportion of their N from atmospheric sources had more negative δ¹⁵N values compared with larger bromeliads that received a greater proportion of their N from canopy soil and had more positive δ¹⁵N values (Reich et al. 2003). The δ¹⁵N values in our three premontane rain forest sites below the current cloud base were significantly higher than sites located above the cloud base (Fig. 3). In our study, all individuals were in the interior of the canopy and had root access to canopy soil, with greater access to canopy soils in the upper sites. Nonetheless, we found that δ¹⁵N values were more negative in higher elevation sites where inputs from wet deposition, which are presumed to have lower δ¹⁵N values, were greater (Cornell et al. 1995; Heaton et al. 1997; Koopmans et al. 1997; Hietz et al. 2002). This pattern suggests that atmospheric sources of
N are preferred over N in canopy soils, even in sites where canopy soils are abundant. Alternatively, it is possible that epiphytes in wetter sites receive a large proportion of their N from canopy soils, but that the wetter canopy soil conditions promote mineralization, which lowers the δ¹⁵N. Additional measures of δ¹⁵N in canopy soils across our gradient are needed to disentangle these two patterns.

Although functional traits in several plant communities vary along environmental gradients, substantial trait variation has also been documented within communities (Wright and Westoby 1999; Wright et al. 2004, 2005; ter Steege et al. 2006; Ordoñez et al. 2009). Variation within communities can be due to niche partitioning whereby different species express unique trait combinations resulting in alternative ecological strategies (Ludlow 1989; Reich et al. 1997; Kobe 1999; Grime 2001; Diaz et al. 2004; Ackerly and Cornwell 2007; Kraft et al. 2008). Such partitioning can provide alternate solutions in response to a common limiting resource and can also promote diversity in communities. We are aware of only two studies that have examined sources of trait variation in epiphytes, and these have also found substantial variation within-site variation (Petter et al. 2015; Costa et al. 2018). In both studies, the target traits related most closely to leaf carbon and nutrient allocation rather than water relations, even though water limitation is a ubiquitous feature of the epiphytic life form. In fact, it was through the inclusion of a number of water relations traits in this study (e.g., TLP, LWS, LWC, LT, C, SD, and $g_{\text{min}}$) that a clear understanding of the continuum of trait patterns relating to succulence emerged.

**Do ecological trade-offs, such as the degree of succulence or drought tolerance underlie variation in functional traits within epiphyte communities?**

In contrast to variation across sites, we found substantial variation within sites that relate to functional groups and to an even greater degree, leaf succulence. Despite substantial variation in leaf size, shape and species-level diversity in this system, most of the traits we measured underlie trade-offs in allocation between more succulent and less succulent epiphytes (Figs. 4, 5, and 9). In general, epiphytes with more succulent leaves expressed traits conferring avoidance of rather than tolerance to low water potentials. These plants have high water storage and area-normalized hydraulic capacitance, and also have thick and tough leaves with thick cuticles. These species also tended to have higher TLPs and may be more vulnerable to cavitation than non-succulent epiphytes. The notion of tradeoffs in allocation between more vs. less succulent epiphytes is supported by a tendency for herbaceous epiphytes—many of which are succulent—to avoid water stress during extended dry periods by greatly reducing sap flow (Gotsch et al. 2017). On the other hand, epiphytic shrubs that generally do not have succulent leaves maintained higher water use during a drought and subsequently took longer to recover (Gotsch et al. 2017).

In general, succulents also had less structural carbon and a greater allocation to water storage tissue (Figs. 4 and 5). In this system, leaf toughness can be conferred either by succulence or high allocation to structural carbon. Counterintuitively, succulent plants had a greater minimal leaf conductance while simultaneously having lower stomatal density (Figs. 4 and 5). Hydrenchymal cells tend to have greater elasticity, which allows these cell layers to release water with minimal resistance to the photosynthetically active cell layers when needed (Ogburn and Edwards 2010). It is likely that succulent plants also have higher minimal conductance values since this loosely held water in hydrenchyma may be more easily lost from leaf surfaces. The lower stomatal density of succulent plants may minimize water loss from the hydrenchyma. However, in our study, the lower stomatal density of succulent epiphytes did not seem to be sufficient to reduce the $g_{\text{min}}$ of succulent plants to below that of their non-succulent counterparts. Conversely, non-succulent epiphytes exhibit traits that confer greater drought resistance. These plants had higher stomatal density and more structural carbon while leaf water storage and $g_{\text{min}}$ were lower (Figs. 4 and 5).

These trade-offs align with and extend upon results from 11 species in the same TMCF, where foliar water uptake capacity and foliar water uptake in field sap flow trials were negatively correlated with traits relating to succulence (Gotsch et al. 2015). For example, epiphytes with high foliar water uptake tended to have thinner leaves with thinner cuticles and hydrenchymal layers, and they had a lower leaf toughness and turgor loss points (Gotsch et al. 2015). Succulent leaves on the other hand specialize in storing water, but the traits that tend to maximize storage capacity (i.e., thick cuticles and hydrenchymal layers) also limit the ability to directly absorb cloud water via leaf surfaces (Gotsch et al. 2015). The current study expanded on previous work to increase the number of species, sites, and traits we measured, which has resulted in our insights that trait relationships along a continuum of leaf succulence are likely driven by trade-offs between drought avoidance and tolerance (Fig. 9).

Our analyses revealed few significant correlations between functional traits and stable isotopes (four for δ¹³C and two for δ¹⁵N), which may be an indication of the strong within-site variation for most traits since the isotopes varied significantly across sites (Figs. 3 and 6). However, we did find a significant relationship between δ¹³C and SD (Fig. 7). Our δ¹³C data suggest that stomata tended to be more closed in lower and drier
environments and that epiphytes in these sites may be limited in the range of SD they possess. In contrast, epiphyte communities at the wetter end of the gradient supported species exhibiting higher stomatal density. Species with higher stomatal density are likely able to better use cloud water via foliar water uptake (Gotsch et al. 2015; Berry et al. 2019). In the wetter sites, species also exhibited traits indicating a succulent strategy; however, species with a high stomatal density were restricted to sites with abundant precipitation and cloud cover.

Climate change projections for this region and for other TMCFs predict increases in the cloud base height, air temperature, and the number of consecutive dry days (Pounds et al. 1999, 2006; Still et al. 1999; Lawton et al. 2001; Ray et al. 2006; Helmer et al. 2019). As water limitation intensifies in this system, functional diversity will likely decrease in the lower elevation edge of the TMCF where epiphyte taxonomic and functional diversity is lowest, whereas there will likely be some continued redundancy across sites that experience a more moderate microclimate. We suggest future research on the impacts that shifts in functional diversity will have on epiphyte community processes and the resultant changes in ecosystem services in the TMCF. This is especially important given the role that epiphytes play in the storage and cycling of water and nutrients as well as the food and habitat resources the community provides.

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Availability of data and materials Data are presented as supplementary information. Additional information is available upon request.

Code availability NA.

Declarations

Conflict of interest All authors declare that they have no conflicts of interest.

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