

# Vapor pressure deficit predicts epiphyte abundance across an elevational gradient in a tropical montane region<sup>1</sup>

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**PREMISE OF THE STUDY:** Tropical Montane Cloud Forests (TMCFs) are important ecosystems to study and preserve because of their high biodiversity and critical roles in local and regional ecosystem processes. TMCFs may be particularly affected by changes in climate because of the narrow bands of microclimate they occupy and the vulnerability of TMCF species to projected increases in cloud base heights and drought. A comprehensive understanding of the structure and function of TMCFs is lacking and difficult to attain because of variation in topography within and across TMCF sites. This causes large differences in microclimate and forest structure at both large and small scales.

**METHODS:** In this study, we estimated the abundance of the entire epiphyte community in the canopy (bryophytes, herbaceous vascular plants, woody epiphytes, and canopy dead organic matter) in six sites. In each of the sites we installed a complete canopy weather station to link epiphyte abundance to a number of microclimatic parameters.

**KEY RESULTS:** We found significant differences in epiphyte abundance across the sites; epiphyte abundance increased with elevation and leaf wetness, but decreased as vapor pressure deficit (VPD) increased. Epiphyte abundance had the strongest relationship with VPD; there were differences in VPD that could not be explained by elevation alone.

**CONCLUSIONS:** By measuring this proxy of canopy VPD, TMCF researchers will better understand differences in microclimate and plant community composition across TMCF sites. Incorporating such information in comparative studies will allow for more meaningful comparisons across TMCFs and will further conservation and management efforts in this ecosystem.

**KEY WORDS** microclimate; Monteverde; Costa Rica; elevation gradient; vascular epiphytes; hemi-epiphytes; bryophytes

Tropical Montane Cloud Forests (TMCFs) are ecosystems with exceedingly high biodiversity and endemism, and play key roles in local and regional hydrology (Zadroga, 1981; Brown et al., 1996; Bruijnzeel et al., 2010a, b). One of the defining features of this rain-forest ecosystem is that there is frequently direct contact between low-lying clouds and vegetation (i.e., fog; Bruijnzeel et al., 2011a). These ecosystems exist in steep montane regions where narrow bands of microclimate change significantly over short distances; small changes in temperature or cloud base heights can alter microclimatic conditions and threaten existing communities (Nadkarni

and Solano, 2002; Williams et al., 2003, 2007; Ray et al., 2006; Zotz and Bader, 2009). Recently, the frequency of cloud cover and precipitation have been changing in some TMCFs, and projected changes in climate include increases in cloud base heights and drought; such changes will likely have large effects on community structure and function in the TMCF (Pounds et al., 1999; Still et al., 1999; Lawton et al., 2001; Ray et al., 2006; Gotsch et al., 2016a, b).

Because of the difficulty of terrain and remoteness, TMCFs have been understudied relative to their lowland counterparts (Bruijnzeel et al., 2011b). In the last 20 yr however, there has been an increase in research in TMCF's, with recent syntheses (Oliveira et al., 2014; Dalling et al., 2015; Fahey et al., 2016; Crausbay and Martin, 2016; Gotsch et al., 2016a, b; Hu and Riveros-Iregui, 2016). However, it is still difficult to compare results across sites because of differences in nomenclature, sampling protocols, and analyses in different TMCF regions (Hamilton et al., 1995; Ashton, 2003; Bach, 2004; Bubb et al., 2004; Martin et al., 2007; Mulligan, 2011; Bruijnzeel et al., 2011b).

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Because microclimate changes over short distances in the TMCF, it is also difficult to compare results of research efforts across TMCF sites unless the microclimate in each study area has been determined. Within the TMCF zone, Bruijnzeel et al. (2010a) defined three distinct forest types in this ecosystem: lower montane cloud forest, upper montane cloud forest, and elfin cloud forest, which differ both in microclimate and forest composition. In addition to such broad-scale differences within a region, there are also local topographic features that can cause waterlogged or exposed forests that have distinct microclimates from surrounding areas (Santiago et al., 2000). While such differences generally correlate at small scales with elevation, at large scales, such comparisons are difficult because TMCFs occur at different elevations in coastal and inland sites, and because slope and exposure play such a large role on microclimate in the TMCF (Holwerda et al., 2006; 2010a; Giambelluca et al., 2010, 2011; Bruijnzeel et al., 2011a, b). Comparing sites by microclimate may be ideal, but can be cost prohibitive or impractical across many locations.

Microclimate influences the distribution of TMCF vegetation. Because of this, one way to estimate the microclimate of a site is to determine the presence of particular plant groups that are associated with particular microclimates. One of the most distinguishing features of the plant community in the TMCF is the abundance and diversity of epiphytes. Epiphytes—nonparasitic plants that live on other plants—are common in the TMCF and include bryophytes and other types of herbaceous plants as well as larger-statured shrubs, treelets, and woody hemiepiphytes. This canopy community plays a valuable role in the functioning of the TMCF ecosystem via water and nutrient cycling and storage, as well as in providing habitat and food resources for wildlife (Gotsch et al., 2016b). Epiphytes tend to respond strongly to atmospheric conditions, such as relative humidity and air temperature, because these plants are dissociated from ground-based resources (Cardelus and Chazdon, 2005; Gehrig-Downie et al., 2012; Karger et al., 2012; dos Santos et al., 2014; Batke et al., 2015). While the aforementioned studies indicate a strong link between microclimate and epiphyte abundance, these studies mostly focused on one functional group of plants. In most cases, vertical gradients of temperature or relative humidity were investigated within a single site. Epiphyte communities in the TMCF can be very diverse and contain a number of plant functional groups (Haber, 2000). It is unknown the degree to which studies on one group of plants (i.e., bryophytes) accurately represent the relationship between the entire epiphyte community and microclimate. In a recent study in the lowland tropical rainforest of Costa Rica, Woods et al. (2015) examined the canopy community in different microhabitats of emergent trees, and found a significant effect of vapor pressure deficit on epiphyte community composition. While the aforementioned research has helped to elucidate the affect of microclimate on canopy epiphyte composition, studies in one site may not represent relationships between epiphyte abundance and microclimate at larger spatial scales.

In June 2015, at a meeting of CloudNet (<http://cloudnet.agsci.colostate.edu/>)—an international research coordination network focused on increasing collaboration among cloud forest researchers—a number of limitations in our current understanding of cloud forest ecosystems were identified. At the top of this list was that our understanding was limited by a lack of cross-site studies, as well as incompatibility in methods in different sites. One difficulty in comparing data across regions is the lack of a comprehensive method to distinguish between cloud-affected forests in different ecotones. Furthermore,

elevation alone is an insufficient metric to use to determine if TMCF sites in different regions are similar (Santiago et al., 2000).

The goal of this study was to determine the relationship between the abundance of the entire community of canopy epiphytes and different measures of canopy microclimate along an elevation gradient. We installed and maintained canopy weather stations at six sites in the montane region of Central Costa Rica, and conducted ground- and canopy-based surveys to determine the abundance of the canopy epiphyte community. Our research addressed the following questions:

- (1) How does canopy microclimate vary across the gradient?
- (2) What is the relationship between canopy microclimate and elevation across the sites?
- (3) What is the relationship between canopy microclimate and canopy epiphyte and soil abundance across an elevation gradient?
- (4) How well can a ground-based protocol to estimate canopy epiphyte and soil abundance align with a canopy-based assessment?

## METHODS

**Study Sites**—This research took place in the TMCF of Monteverde, Costa Rica (CCT), as well as in four nearby cloud forest and premontane rain forest sites in Costa Rica (Table 1, Fig. 1). The epiphyte community in the Monteverde region is composed of approximately 800 vascular plant species and hundreds more bryophyte species (Haber, 2000). In the wettest sites, there also is a layer of canopy organic matter (30 cm or more thick) that is comprised largely of decomposing bryophytes, roots and leaves of vascular epiphytes as well as deposits brought in as dust and in clouds (Nadkarni et al., 2004). These sites overlap with locations used in a previous study to determine the diversity of species (epiphytes included) in this tropical montane region (Haber, 2000). Our sites span an elevation of 1100–1635 m above sea level (m a.s.l.) and represent a range in microclimate that is representative of this and other TMCF ecosystems (Gotsch et al., 2014a, b; Jarvis and Mulligan, 2011). Sites were selected in 2014 as part of a long-term study on the ecophysiology of epiphytes. Sites were identified at different elevations in continuous forest to provide an opportunity to study epiphyte communities that experience distinct microclimates. In addition, when possible, sites within a similar elevation that appeared to host distinct epiphyte communities were also identified to allow for comparisons of microclimate at smaller scales (Table 1).

Along this gradient in microclimate there are only long-term weather stations in two sites, one in the Monteverde Reserve (elevation 1530 m a.s.l.) and another at the University of Georgia field station (UGA, 1080 m a.s.l.) in San Luis, Costa Rica. Average annual precipitation in the Monteverde Cloud Forest Reserve (MCFR) is estimated at 4000 mm, while at UGA the average annual precipitation over the last 4 yr is 2300 mm (A. Pounds, unpublished data). The wettest site was presumed to be the El Valle Refuge within the Children's Eternal Rainforest. While there is no weather station at this site, its location on the Atlantic side of the continental divide at 1635 m ensures high annual rainfall and consistent cloud cover. This site was also the only one of the six to have a nearly continuous cover of bryophytes on all surfaces of the forest (trunks, branches, exposed soil embankments, etc.) providing additional evidence of the moisture present there.

The weather in all sites is seasonal but droughts are more severe in the lower elevation sites due to a greater number of days without

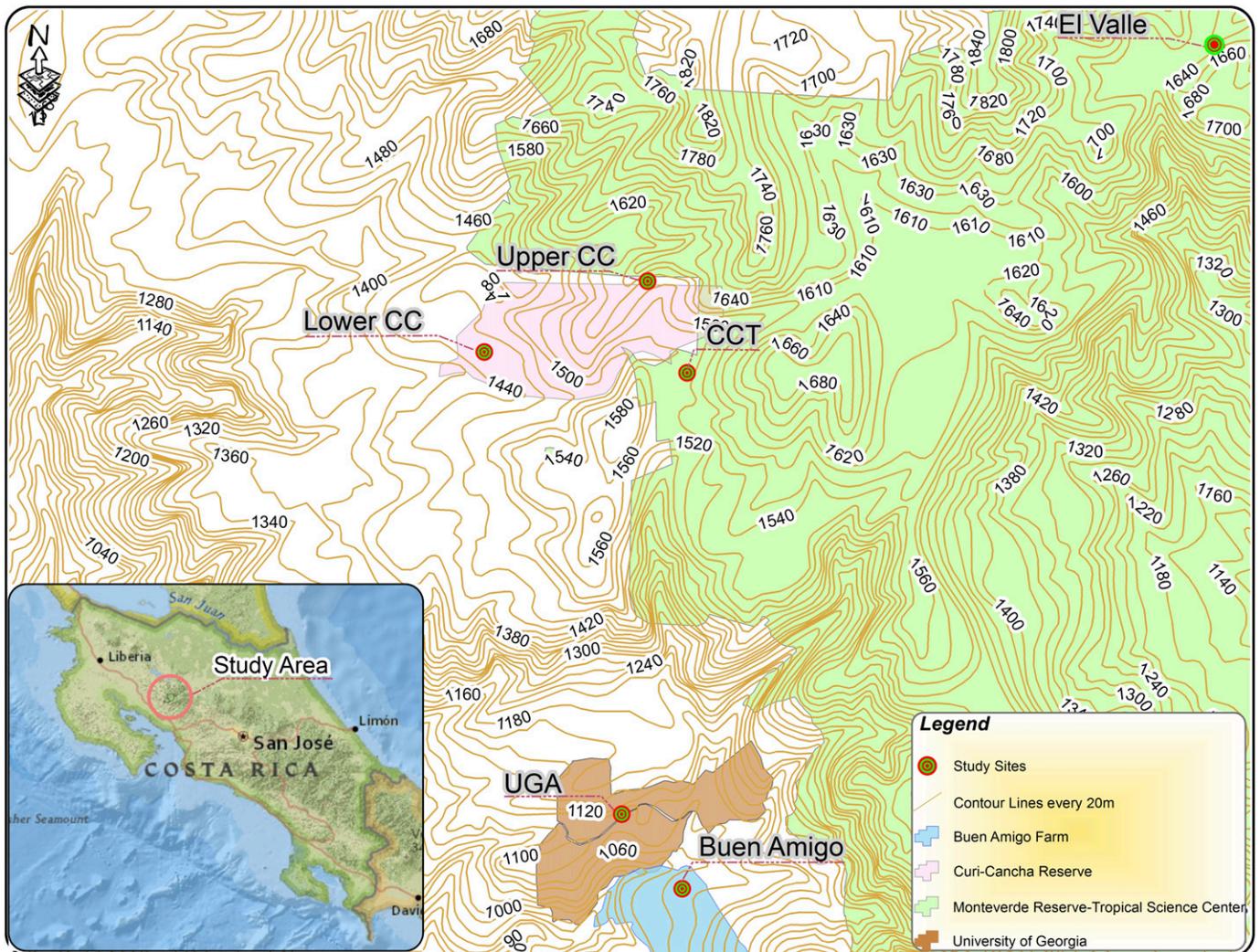
**TABLE 1.** Location information and forest type for each of the six sites.

Site Name	Location	Latitude	Longitude	Elevation	Forest Type
UGA	University of Georgia, San Luis	N10°16'58.83"	W084°47'51.06"	1100 m	Secondary
Buen Amigo	Private Farm, San Luis	N10°16'45.29"	W084°47'39.94"	1070 m	Primary w/ timber removal
Lower CC	Curi Cancha Reserve, Monteverde	N10°18'22.51"	W084°48'16.45"	1474 m	Secondary w/ remnant trees
Upper CC	Curi Cancha Reserve, Monteverde	N10°18'35.47"	W084°47'46.58"	1592 m	Primary
CCT	Monteverde Reserve	N10°18'18.84"	W084°47'39.30"	1554 m	Primary
El Valle	The Children's Eternal Rainforest	N10°19'18.25"	W084°46'02.60"	1635 m	Primary

rainfall and warmer temperatures. The dry season generally occurs from February-April (Nadkarni, 1994). During this time, there are periods of rain and mist but less than at other times of the year. From May-November it is generally wet with almost daily inputs of rain (Nadkarni, 1985, 1994). During this time the cloud water inputs to the ecosystem are also greatest (Goldsmith et al., 2011). In December and January, the area tends to receive high winds and mist (Nadkarni, 1994; Nadkarni et al., 2004). The average temperature in the Monteverde Cloud Forest Reserve is 22°C and in general, daily fluctuations surpass monthly averages (Nadkarni, 1994). Climate in the region has experienced increased interannual variation in

precipitation as well as an increase in the number of days with little or no mist (Pounds et al., 1999). Projected changes in climate include increases in cloud base heights, which may further increase such drying events (Lawton et al., 2001).

The three highest elevation sites are located in primary forest. The canopy in all the sites is between 25-35 m tall (S. Gotsch, unpublished data). Emergent trees reach up to 35 m in height and in general there is a poorly developed herbaceous layer (Nadkarni and Matelson, 1991). The three driest sites are in secondary forests that contain primary forest remnant trees. The canopy height is similar in all six sites; our study in the lower three sites takes place in remnant trees.


**FIGURE 1** Map of the six sites in this study. El Valle is the wettest forested site; UGA is the driest of the six sites.

Data collection took place on the ground near the trunk and in the crown of three trees in each of the six sites. In all sites, three canopy (but not emergent) trees were chosen that were in close proximity (within 50 m) to one another and had similar crown exposure and topography. In addition, we chose trees with large spreading and healthy canopies, which would ensure that they would be relatively safe to climb. The DBH of all host trees was within in largest size class in each site (DBH 170–400 cm, Nadkarni et al., 1995). These trees are likely the oldest in each area and therefore have had the most time to develop a robust community of canopy epiphytes. Since the microclimate in the TMCV varies over short distances, choosing a cluster of trees that had similar size and physical attributes was more important than targeting specific host species. While studies in lowland tropical rainforests and forests of the Southeastern and Northwestern United States have found host specificity of epiphytes, the effect of tree size has been found to have a larger impact on epiphyte biomass and composition in TMCVs (Hietz and Hietz-Seifert, 1995; Callaway et al., 2002; Cardelús et al., 2006; Laube and Zott, 2006; Wagner et al., 2015). Host tree species were in the following genera: *Ficus* (Moraceae), *Sapium* (Sapindaceae) and *Ocotea* (Lauraceae). In all sites the host trees consisted of at least one strangler fig (*Ficus* sp.) and one *Sapium* sp. tree. These genera are among the most common in all sites (Nadkarni et al., 1995).

**Microclimate Measurements**—Microclimate stations were installed in the mid canopy near the center of one of the study trees in each of the six sites between June and July of 2014. The heights of the weather station ranged from 24–26 m. Rather than choose a specific height for the weather station, we chose the same point in the canopy (inner midcrown) to standardize our measurements by the host tree crown architecture. Data were collected continuously every 15 min and were downloaded monthly when possible. Sensors were changed and repaired from May–August of 2014 and 2015 when the field team was present on site. The station was placed in the center of the site to minimize the distance to the other trees ( $\leq 50$  m). Each station contained one data logger that measured air temperature ( $^{\circ}\text{C}$ ) and relative humidity (%), HOBO U23 Pro v2 External U23-002, Onset Corporation, Cape Cod, Massachusetts, USA) and a data logger (Em50), which collected data from a soil moisture probe ( $\text{mm}^3/\text{mm}^3$ , EC-5) and a leaf wetness sensor ( $\text{g}/\text{m}^2$ ). All devices were purchased from Decagon Devices, Pullman, Washington, USA. Soil probes were placed on a 45-degree angle in the middle of the canopy organic soil layer (a depth of 10–15 cm).

Temperature and relative humidity were used to calculate the vapor pressure deficit using the following equation:

$$VPD = \left( 1 - \left( \frac{RH}{100} \right) \right) * SVP \quad \text{Eq. 1}$$

Where SVP is the saturated vapor pressure, which is calculated using the following equation (Monteith and Unsworth, 2008):

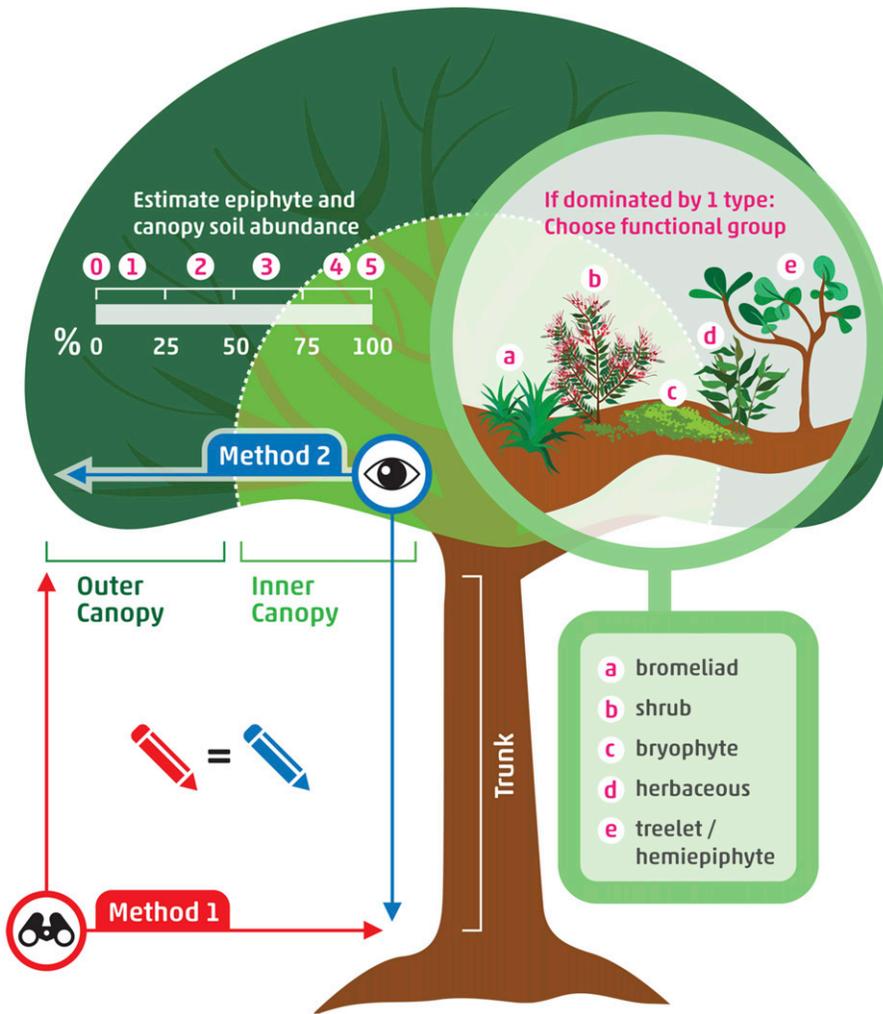
$$SVP = 0.61078 e^{\left( \frac{17.27T}{T + 237.3} \right)} \quad \text{Eq. 2}$$

Because we did not have a continuous presence at the sites, mechanical, electrical, and weather problems caused gaps in the data sets.

Nonetheless, there are windows of multiple months of error-free data (representing 2–3 mo periods in the wet and dry seasons) at all the sites. These windows are representative of the wet and dry periods that are frequently experienced at these sites. While soil sensors were calibrated prior to deployment, canopy soils are very dynamic and we found that frequent calibration was needed in this system to maintain accurate baseline values. This was not possible in the current study. While baseline values can shift without calibration, the range of values would remain consistent across the sites (Starr and Paltineanu, 2002). We calculated the percentage of the maximum volumetric water content (% max VWC) in each site between a very wet period in the wet season, and the driest period at the end of the dry season of 2015. We expect the range of VWC to be maximized between these two time points.

All data that resulted from failed sensors were removed from the data set. Following the aforementioned culling of the data set, a master data sheet was created for all microclimate variables (VPD, % max VWC, and leaf wetness), which only contained windows of data when all sensors were working at all sites. For all sensors, there was representation from both the wet and dry seasons in 2014 and 2015, and the data set from 2016 contained 85% of all possible days.

**Epiphyte Abundance Estimates**—In each site, three trained observers recorded a categorical variable corresponding to a range in epiphyte abundance (of the entire community) in the inner and outer tree crown and trunk first from the ground using binoculars, and then from the crown using single-rope techniques (Anderson et al., 2015). Our goal was to evaluate the percentage of the host tree that was covered by epiphytes. Three dominant focal trees within 50 m of each long-term microclimate station were observed at each site. First, the tree was visually separated into trunk, inner crown, and outer crown (Fig. 2). In addition to estimating the abundance of epiphytes, we estimated the percentage cover of canopy humus. We noted the cover of darker brown and black components of the epiphyte mat, and also compared the underside diameter of the branch with the upper side, where epiphyte cover is greater. That gave us a sense of the width of the mat and therefore the presence of humus. This was a difficult assessment from the ground, but was more easily completed when the observers climbed into the crown. The epiphyte abundance and percentage humus cover were estimated by each observer throughout the entire crown using the following class ranking: 0 = 0%, 1 = 1–24%, 2 = 25–49%, 3 = 50–74%, 4 = 75–99%, and 5 = 100%. This broad class system was employed because our primary research questions related to large-scale differences in epiphyte abundance across sites that would be easier to detect with a visual estimate than smaller-scale patterns within trees. The inner crown was defined as the point where branches begin off the trunk to the middle point along the branch surface. The outer canopy was defined from the halfway point along the branch to the outer-most branch tips (Fig. 2). Observers also noted if the crown community assembly was well mixed or if there was a particular functional group that was dominant. If a dominant epiphyte functional group was observed, that group was noted (Fig. 2). The functional groups of epiphytes were examined for this study were bromeliad, shrubs, bryophytes, herbaceous, and treelet/hemipiphyte (Nadkarni et al., 2004). These groups were chosen after a close inspection from the ground of these and other functional groups. While a more detailed direct measure can identify numerous additional taxa/functional groups, these were the groups we felt we could confidently identify using binoculars. The herbaceous category



**FIGURE 2** Method employed for the estimation of canopy humus and epiphyte abundance used in this study. The tree was visually separated into trunk, inner crown, and outer crown (brown, light green, and dark green respectively). The canopy epiphyte and humus abundance were estimated using the scale shown in the upper left portion of the figure (0 = 0%, 1 = 1–24%, 2 = 25–49%, 3 = 50–74%, 4 = 75–99% and 5 = 100%). Estimates were made from the ground using binoculars and from the crown using single-rope climbing techniques. We also made note of whether the epiphyte community was well mixed or if it was dominated by one functional group. If there was a dominant functional group, the plant type was identified and noted (right side of image). *Image credit:* Floortje van Osch

excluded bromeliads. Because bromeliads are a dominant functional group at the dry site (primarily tank bromeliads), they are clearly visible from the ground and therefore we felt, deserved their own category. Other common categories of taxa within the herbaceous group (e.g., orchids, ferns) are often much smaller in stature and were difficult to distinguish from the ground; they were therefore grouped with other herbaceous species. Only woody plants were included in the treelet/hemiepiphyte category. These plants ranged from 0.5–2.0 m in height. All observers noted the categorical variable that represented the abundance category in each of the three trees at the six sites. These categories were then converted to the midpoint for the range of that category (i.e., 1 = 1–24% was scored as 12.5%). Following conversion, averages across observers were calculated for all estimates; these values are displayed in the figures.

**Data analyses**—A mixed-model ANOVA was performed for the hourly average VPD and % max VWC where the effects of site and forest type were tested (Q1). The site (fixed effect) is largely associated with elevation although some sites had similar elevations. The forest type (primary vs. secondary) was included as a random variable. Following this analysis, pairwise comparisons were made for all sites using posthoc multiple means comparisons. A mixed-model ANOVA was also performed to determine the effect of site on the different abundance estimates. For each estimate, the effects tested were site (fixed), tree (random), and observer (random). A mixed-model ANOVA was also performed to determine whether significant differences occurred between ground- and crown-based estimates of epiphyte abundance (fixed effect, Q4) and whether estimates varied significantly across observers (random effect). It was not possible to combine the aforementioned analyses in a single analysis because of the lack of statistical power in our data set. In addition, we performed a two-way ANOVA on epiphyte abundance and canopy humus percentage cover where the effects tested were the site and the location within crown (inner vs. outer crown), as well as the interaction between these two effects.

Linear and nonlinear regressions were performed to examine relationships between elevation and all microclimate variables, as well as epiphyte abundance in all trees (Q2 and 3). In addition, we examined relationships between microclimate and epiphyte abundance (Q1).

We also conducted an Akaike information criterion analysis (AIC) to directly compare the regression analyses that examined the effects of VPD and elevation on epiphyte abundance. The VPD was included in this analysis because the regression equations between VPD and epiphyte abundance yielded the greatest  $r^2$  values, while elevation was included because this variable is often used as an explanatory variable for microclimate and plant community composition. The goal of the AIC was to determine which of two competing models explained more of the variability in epiphyte abundance (Akaike, 1974; Burnham and Anderson, 2002). This analysis was based on the average values per site. The VPD and elevation were coded as continuous variables, while epiphyte estimates were coded as categorical variables. Data for all analyses were either normally distributed or log-transformed to achieve normality. All analyses were performed using R statistical software V 3.3.1 (R Core Team, 2013).

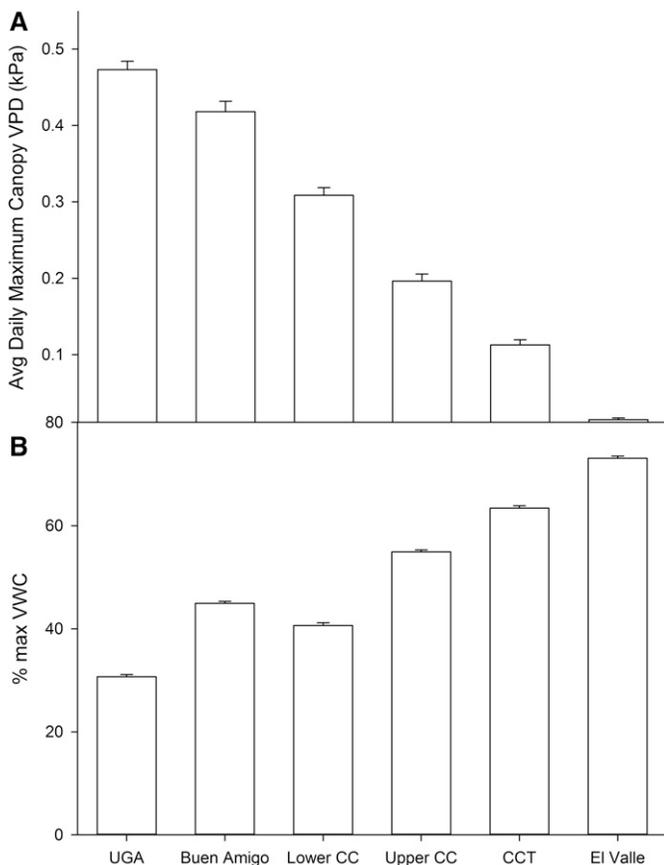
## RESULTS

**Patterns of microclimate across the gradient**—Air temperature and relative humidity, expressed as the calculated average daily

maximum VPD, showed a clear step-wise decrease from the lowest to highest site (Fig. 3A). The maximum and mean VPD exhibited an identical relationship. In El Valle, the site at the highest elevation, the average daily maximum VPD was 0.08 kPa, while at UGA, the average daily maximum VPD was 0.51 kPa. The daily maximum VPD was significantly different across sites ( $F_{5,4505} = 174.6$ ,  $P < 0.0001$ ). The sites ordered from driest to wettest were: UGA, Buen Amigo, LCC, UCC, CCT and El Valle (Fig. 3A). While elevation is associated with these microclimatic differences, UCC and CCT, as well as UGA and Buen Amigo, were at similar elevations (Table 1).

The percentage of the maximum soil volumetric water content (% max VWC) also varied significantly across sites ( $F_{5,14628} = 1261.09$ ,  $P < 0.0001$ , Fig. 3B). The lower sites exhibited lower % max VWC indicating more drying in sites where VPD is higher. These sites also had lower percentage cover of canopy humus, which would also promote drying. The sites that experience the greatest VPD (UGA, Buen Amigo, Lower CC) had the % max VWC below 50%, while the % max VWC in the three wettest sites (Upper CC, CCT and El Valle) ranged from 55–73% (Fig. 3B).

**Epiphyte Abundance**—For each of the five abundance or percentage cover parameters (inner and outer epiphyte abundance, inner



**FIGURE 3** (A) The average daily maximum vapor pressure deficit (VPD) for 11 mo in 2014 and 2015 in six sites along a gradient in elevation and microclimate. An ANOVA and posthoc comparisons indicate that all sites are significantly different from one another. (B) The percentage of the maximum volumetric water content of canopy humus (% max VWC) across the six sites.

and outer percentage cover canopy humus, and trunk epiphyte abundance), the site had a significant effect on epiphyte abundance and canopy humus cover ( $F_{5,12.5} = 80.6$  for outer humus,  $F_{5,9.55} = 197.2$  for outer epiphytes,  $F_{5,11.9} = 83.7$  for inner humus,  $F_{5,10.7} = 78.1$  for inner epiphytes,  $F_{5,12.1} = 17.0$  for trunk epiphytes, all  $P < 0.001$ , Fig. 4). In the wettest sites (El Valle and CCT), epiphyte and canopy humus abundance in the inner and outer crown were similar and values were generally  $\geq 80\%$ . There was a significant effect of the crown location (inner vs. outer) on abundance estimates, which was consistent across sites for both epiphytes (site:  $F_{5,72} = 138.09$ ,  $P < 0.0001$ ; location:  $F_{1,72} = 5.04$ ,  $P = 0.027$ ; site\*location:  $F_{5,72} = 1.1$ ,  $P = 0.36$ ) and canopy humus (site:  $F_{5,72} = 131.6$ ,  $P < 0.0001$ ; location:  $F_{1,72} = 9.2$ ,  $P = 0.003$ ; site\*location:  $F_{5,72} = 0.5$ ,  $P = 0.77$ ). At the two low elevation sites (BA and UGA), epiphyte and canopy humus cover was similar and generally between 10–25%. While the site had a significant effect on all abundance parameters (see statistics above), visual examination, and pairwise  $t$  tests suggest that epiphyte abundance estimates in the outer crown were clearest in distinguishing between the drier sites (Figs. 4A, B, Appendix S1, while epiphyte abundance estimates in the inner crown provided clearer differences among the three wettest sites, but not the driest sites (Fig. 4D, Appendix S1).

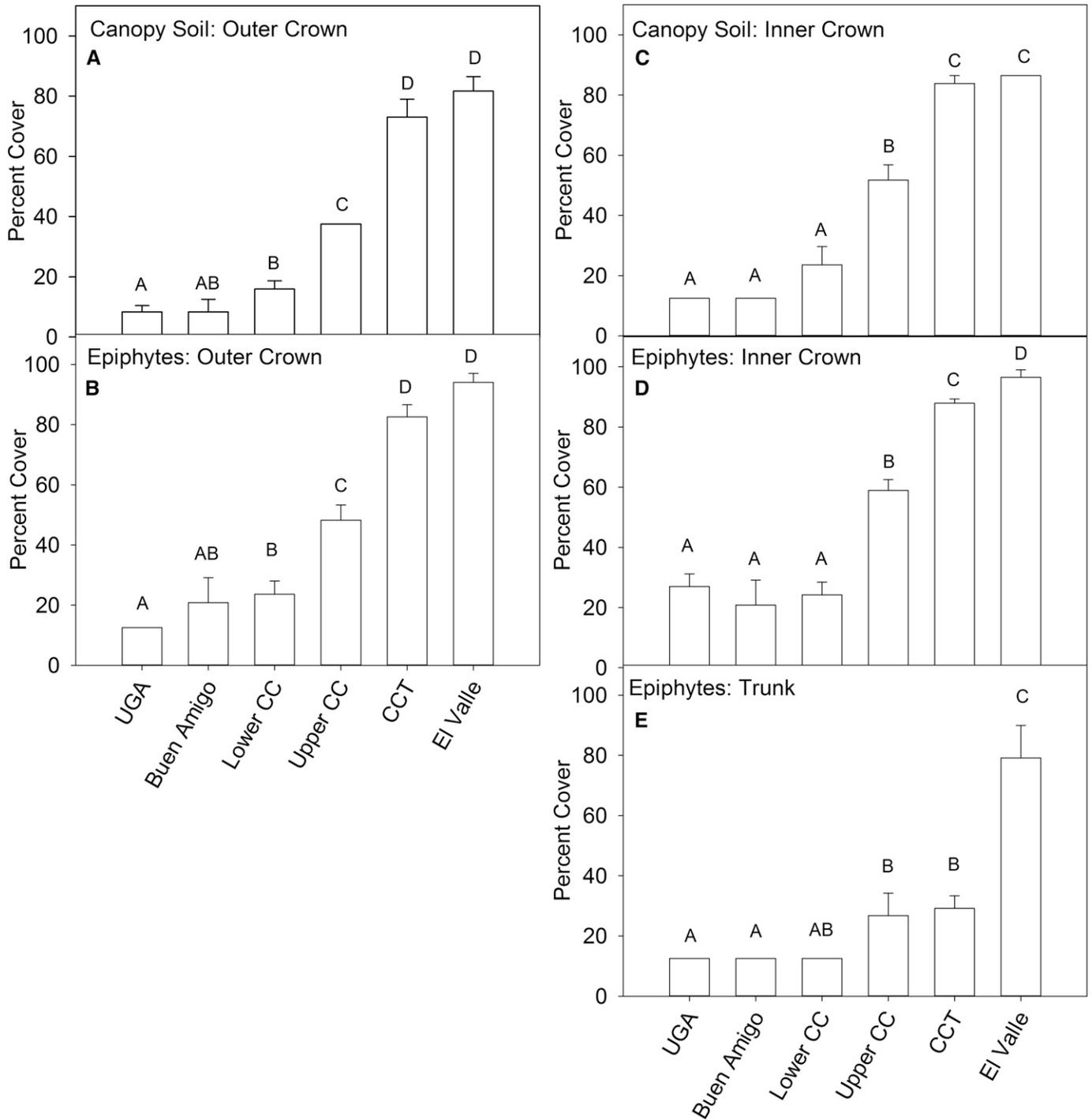
We found that the effect of functional group was marginally significant ( $F_{4,36} = 2.3$ ,  $P = 0.06$ ) overall, but that this result did not vary consistently with microclimate. We found that both the wettest and the driest sites tended to have one dominant functional group present in the canopy (El Valle: bryophytes, UGA: shrubs), whereas the four intermediate sites had a canopy community that was more well mixed.

#### Relationships between microclimate and epiphyte abundance—

We found significant relationships between elevation and canopy VPD, leaf wetness, and % max VWC (Fig. 5, for all pairs:  $df = 5$ ,  $P \leq 0.05$ ). As elevation increased, there was a linear decrease in VPD (Fig. 5A,  $r^2 = 0.86$ ). In contrast, there was a nonlinear increase in leaf wetness as elevation increased, but this relationship was not as strong (Fig. 5B,  $r^2 = 0.39$ ). The % max VWC exhibited a linear increase as elevation increased (Fig. 5C,  $r^2 = 0.59$ ).

We also found significant nonlinear relationships between elevation and different estimates of epiphyte abundance (Fig. 6). As elevation increased, the epiphyte abundance in the inner crown (Fig. 6A) and outer crown (Fig. 6B), as well as canopy humus cover in the inner (Fig. 6C) and outer crown (Fig. 6D), increased. All of these relationships were significant ( $P \leq 0.05$ ),  $r^2$  values ranged from 0.63–0.72.

We also examined relationships between microclimate and epiphyte abundance. We found strong ( $r^2 \geq 0.83$ ) and significant ( $P \leq 0.05$ ) relationships between all canopy estimates and microclimate (Figs. 7A–H). The strongest predictive relationships were found between epiphyte abundance and VPD (Figs. 7A–D). These relationships were stronger than those found between elevation and epiphyte abundance (Fig. 6). The AIC analysis also indicated that epiphyte abundance explained more of the variability in VPD than elevation (AIC =  $-13.13$ , elevation vs. AIC =  $-19.36$ , epiphyte abundance). We also found a significant positive relationship between the % max VWC across sites and epiphyte abundance (Fig. 7). We found that there were no significant relationships between trunk epiphyte abundance and microclimate, therefore these relationships were not included in Fig. 7. Regression equations and parameters can be found in Appendix S2.

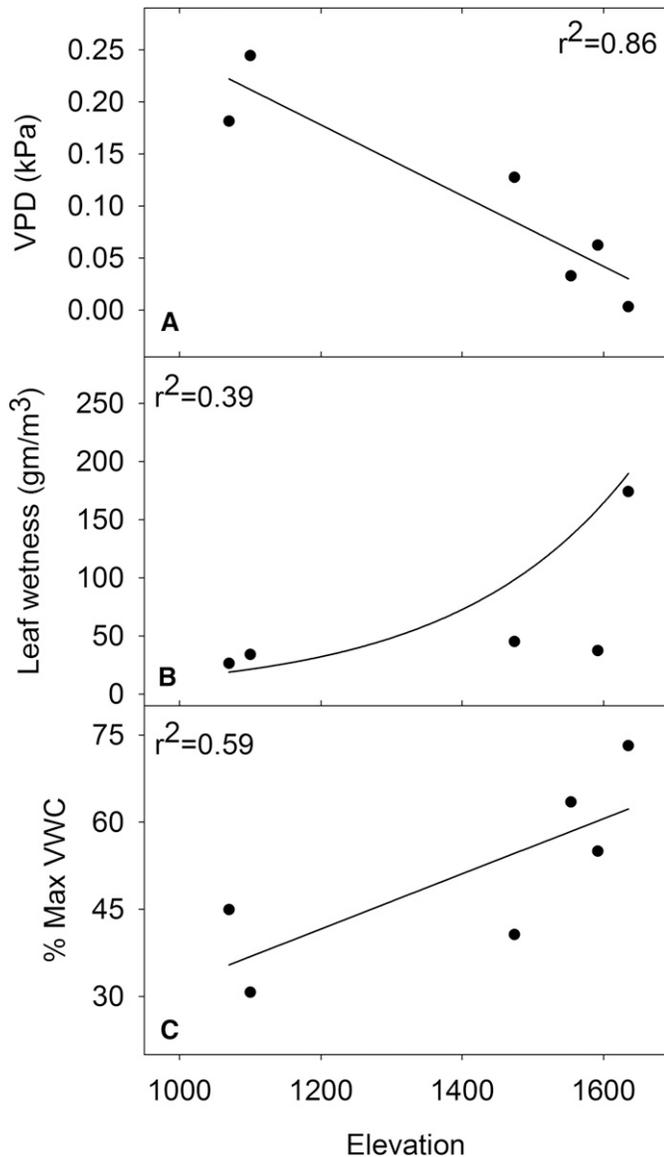


**FIGURE 4** Outer crown percentage cover of canopy humus (A) and epiphytes (B) in the six sites. Inner crown percentage cover of canopy soil (C) and epiphytes (D), as well as the percentage cover of epiphytes on the trunk (E) of six trees in the six sites. The letters above the bars indicate significant site differences, determined by pairwise *t* tests (for all comparisons:  $P < 0.05$  and  $df = 1$ ). See Appendix S2 for the output of all comparisons.

**DISCUSSION**

This is the first study that we are aware of that links canopy microclimate along a gradient in elevation with the abundance of the entire community of canopy epiphytes. While elevation at the large

scale has clear effects on microclimate, our results indicate that canopy VPD was the best predictor of epiphyte abundance. The VPD has been shown to be an important driver of evapotranspiration at the stand level in a number of ecosystems (Bucci et al., 2004; Dawson et al., 2007; Eller et al., 2015; Gotsch et al., 2014a, b; Motzer



**FIGURE 5** The relationship between elevation and vapor pressure deficit (A), leaf wetness (B), and the percentage of the maximum volumetric water content (% max VWC) for the 18 trees in six sites (C). Fewer than 18 dots are seen because of complete overlap of values in some trees. In panels (A) and (C), the relationships were determined with linear regression analyses, while a nonlinear regression was the relationship that had the best fit between leaf wetness and elevation (B). All relationships were significant at  $P < 0.01$ .

et al., 2005). Estimates of epiphyte abundance can be used as a proxy for canopy VPD, which can be used to compare the microclimate of TMCF sites and facilitate comparative research.

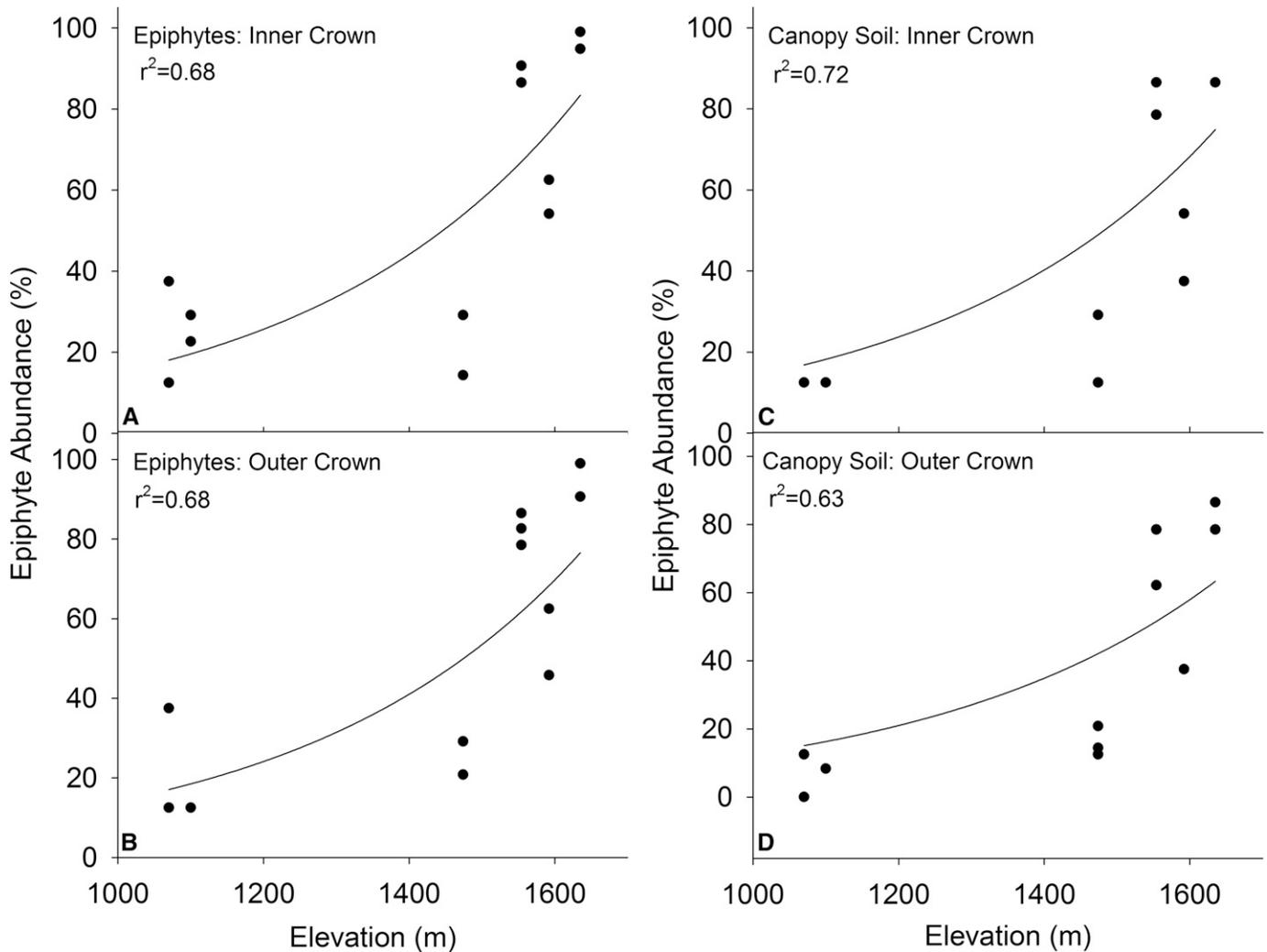
While this work took place in one TMCF region, the range in microclimate and epiphyte abundance in this study is representative of TMCFs elsewhere, and it is likely that the relationships found here will be applicable to other TMCFs. In contrast to the relationship between total abundance and VPD, we expect that the relationship between microclimate and community composition of epiphytes will vary greatly across TMCFs. In addition to microclimate, the composition of the epiphyte community will be affected

by the site location (mainland vs. island), and if it is on an island, the size of the land mass and the distance from the mainland. While epiphyte community composition is likely to vary greatly across TMCFs, the relationship between total community abundance and microclimate is more likely to remain constant given the reliance of this community on consistent amounts of atmospheric moisture.

**Variation in microclimate across the gradient**—The six sites included in this study exhibited clear differences in leaf wetness, % max VWC, and VPD (Figs. 3, 5). While variation across the gradient indicates a near 5-fold increase in VPD from the highest to the lowest site, these values are low relative to the daily maximum VPDs found in lowland tropical forest, which can often exceed 2.0 kPa (Dolman et al., 1991; Meinzer et al., 1993; Meinzer et al., 1997; Rosado et al., 2012). In this study, the maximum recorded VPD was 1.2 kPa. Interestingly, despite relatively low VPDs across these six sites, we found significant and predictable differences in epiphyte abundance.

While the driest sites were at the lowest elevations and the wettest sites were at the highest elevations, there were also significant differences within a small range of elevation (Fig. 3). For example, the UGA and Buen Amigo sites differed by only 30 m in elevation and yet the latter site had a significantly lower average daily maximum VPD. These two sites are on opposite sides of the San Luis River and their degrees of exposure differ. The UGA site may receive direct sunlight for a greater portion of the day than trees in the Buen Amigo site (Gotsch, personal observation). In addition, Upper CC and CCT sites were also at a similar elevation, but the Upper CC site was consistently drier than the CCT site (Figs. 4A, B). The Upper CC is in a more exposed area, while CCT is in a small topographic depression (Fig. 1, Gotsch, personal observation). These topographic differences have been found to affect microclimate and tree transpiration in a TMCF in Hawai'i and are likely a cause of the differences in microclimate in this study (Santiago et al., 2000). Despite similarities in the elevation of some sites, VPD was significantly different across all sites (Fig. 3A). Given the limited number of sites that could be implemented with microclimate stations, we were unable to include the effects of slope and exposure in this study. We suggest future research to elucidate the effects of topography on epiphyte abundance.

**Relationship between epiphyte abundance and microclimate**—Epiphyte abundance varied greatly across the sites (Fig. 4). Trees in the wettest sites were largely covered with epiphytes on the inner and outer crown, as well as on the trunk, while in the driest sites, the average epiphyte abundance throughout the host crown was generally under 25%. Both mean VPD and the % max VWC were correlated with canopy soil and epiphyte abundance; however, the strongest relationship was between epiphyte abundance and VPD (Fig. 7). In previous studies, we found that epiphyte sap flow (i.e., a measure of water movement in plant stems that is related to transpiration and water uptake) is very responsive to even small changes in VPD, which would in turn affect water balance and overall plant success (Darby et al., 2016; Gotsch et al., 2015). Epiphyte abundance generally increased as VPD decreased (Figs. 7A, B), although the pattern was not consistent for all estimates. The estimate for trunk epiphyte abundance was the least effective in distinguishing site location. Because our categorical values 1–4 encompassed a large range, it is possible that there was a significant (but smaller) effect of site on trunk epiphyte abundance that was missed by our coarse-scale sampling scheme.



**FIGURE 6** The relationship between elevation and epiphyte abundance for each of the abundance parameters: epiphyte abundance in the inner canopy (A) and outer canopy (B), and the canopy humus abundance in the inner canopy (C) and outer canopy (D) for the 18 study trees in six sites. Fewer than 18 dots are seen because of the complete overlap of values in some trees. All relationships were fit using a nonlinear regression analysis. All relationships were significant at  $P < 0.01$ .

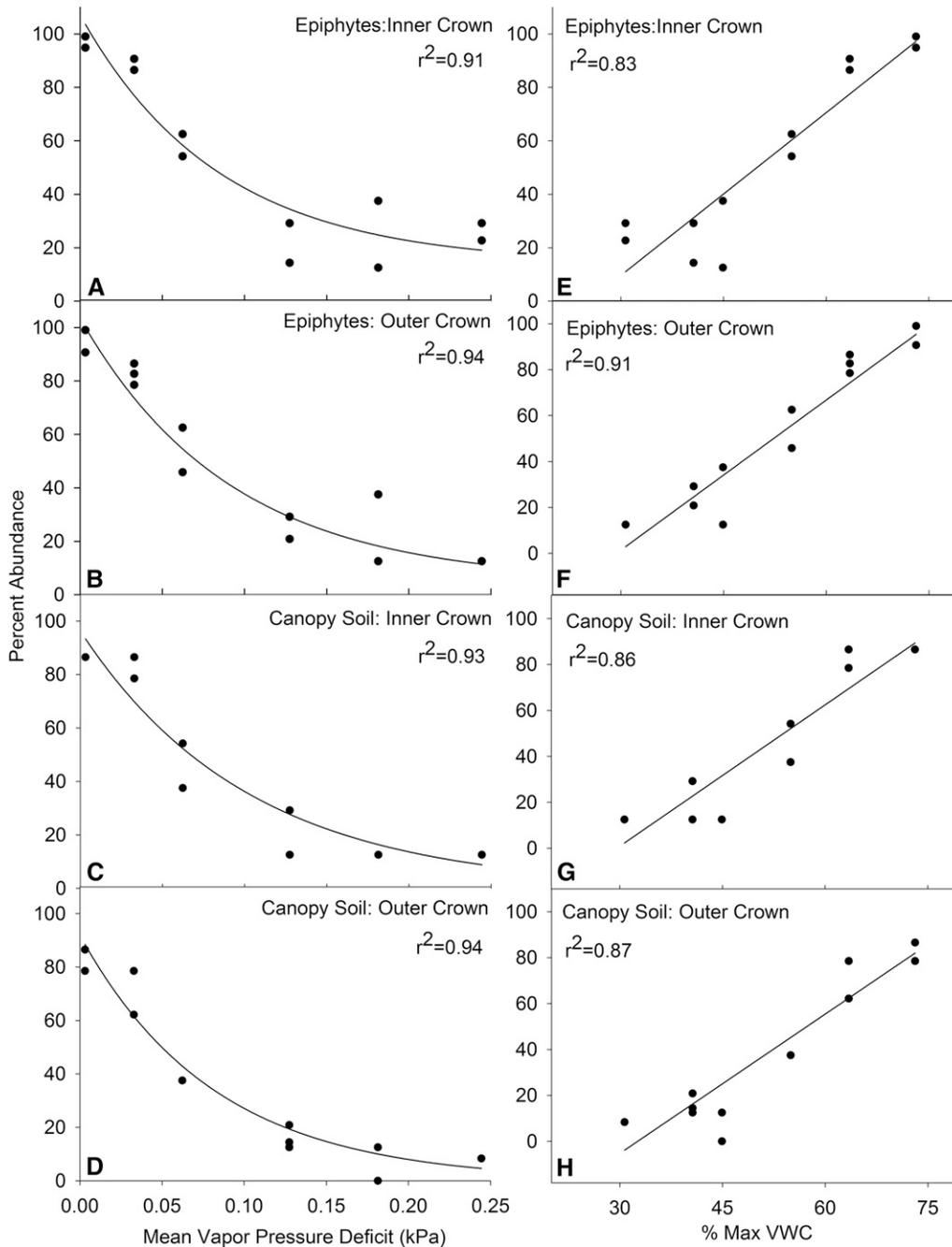
These results are consistent with previous work from a lowland rainforest in Costa Rica where VPD had a significant effect on the species composition of canopy epiphytes (Woods et al., 2015). In studies focusing on bryophytes or liverworts, either the relative humidity or temperature had a significant effect on abundance (Karger et al., 2012; dos Santos et al., 2014; Batke et al., 2015), but these effects were not as strong as those in this study and reported here. The VPD is likely a better predictor because it takes into account both temperature and relative humidity, which will also vary as elevation changes.

Vapor pressure deficit is an important microclimatic driver of plant diversity, performance, and abundance in the TMCF (Bruijnzeel et al., 2011a; Gotsch et al., 2016a). This microclimatic driver will be affected by projected changes in cloud base heights, air temperature, and precipitation patterns, which will in turn affect the distribution of the TMCF in the future (Still et al., 1999; Pounds et al., 1999; Ray et al., 2006; Bruijnzeel et al., 2011b). Because epiphytes have few if any roots, such shifts in VPD will disproportionately affect this community. Shifts in epiphyte composition

may lead to large changes in ecosystem function including water and nutrient interception and storage, as well as habitat for birds, mammals, and insects (Gotsch et al., 2016b). Our ability to quickly and reliably estimate VPD with an epiphyte census indicates that such a sampling protocol can be used in remote TMCF sites, or on research teams with limited funds to adequately characterize microclimate or compare sites in different regions based on epiphyte abundance.

## CONCLUSIONS

In this study, we found a strong predictive relationship between epiphyte abundance and canopy VPD, which is an important driver of stand-level evapotranspiration and productivity in the TMCF. Predicted changes in precipitation patterns or cloud base heights, which are projected for many TMCFs, may have large effects on canopy VPD and lead to changes in plant productivity and community composition in this ecosystem. While the TMCF is thought



**FIGURE 7** Nonlinear regressions between vapor pressure deficit and epiphyte abundance in the inner crown (A), epiphyte abundance in the outer crown (B), canopy humus abundance in the inner crown (C), and canopy humus abundance in the outer crown (D). Linear regressions between the percentage of the maximum volumetric water content (% max VWC) and epiphyte abundance in the inner crown (E), epiphyte abundance in the outer crown (F), canopy humus abundance in the inner crown (G) and canopy humus abundance in the outer crown (H). All relationships were significant at  $P < 0.01$ .

to be vulnerable to projected changes in climate in general, epiphyte communities may be particularly vulnerable because of their reliance on atmospheric moisture. By using epiphyte abundance as a proxy for VPD, canopy microclimate can be assessed quickly across many sites to determine variability in canopy microclimate within and across TMCF ecosystems. Finally, because of variation in topography in the TMCF, it is often difficult to compare research across different TMCF sites. Estimating canopy VPD using epiphyte abundance provides a simple and cost-effective technique to determine

the microclimatic similarity of different sites. Such research efforts are necessary to interpret differences in productivity and community dynamics in different TMCFs and aid in management and conservation efforts of this important ecosystem.

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## LITERATURE CITED

- Akaike, H. 1974. A new look at the statistical model identification. *IEEE Transactions on Automatic Control* 19: 716–723.
- Anderson, D. L., W. Koomjian, B. French, S. R. Altenhoff, and J. Luce. 2015. Review of rope-based access methods for the forest canopy: safe and unsafe practices in published information sources and a summary of current methods. *Methods in Ecology and Evolution* 6: 865–872.
- Ashton, P. S. 2003. Floristic zonation of tree communities on wet tropical mountains revisited. *Perspectives in Plant Ecology, Evolution and Systematics* 6: 87–104.
- Bach, K. 2004. Vegetationskundliche Untersuchungen zur Höhenzonierung tropischer Bergregenwälder in den Anden Boliviens. Ph.D. dissertation, University of Göttingen Göttingen, Germany.
- Batke, S. P., B. R. Murphy, N. Hill, and D. L. Kelly. 2015. Can air humidity and temperature regimes within cloud forest canopies be predicted from bryophyte and lichen cover? *Ecological Indicators* 56: 1–5.
- Brown, M. B., I. de la Roca, A. Vallejo, G. Ford, J. Casey, B. Aguilar, and R. Haacker. 1996. A Valuation Analysis of the Role of Cloud Forests in Watershed Protection. Sierra de las Minas Biosphere Reserve, Guatemala and Cusuco N.P. Honduras, RARE Center for Tropical Conservation: Philadelphia, USA.
- Brujinzeel, L. A., M. Kappelle, M. Mulligan, and F. N. Scatena. 2010a. Tropical montane cloud forests: state of knowledge and sustainability perspectives in a changing world. *In* L.A.
- Brujinzeel, L. A., M. Mulligan, and F. N. Scatena. 2011a. Hydrometeorology of tropical montane cloud forests: emerging patterns. *Hydrological Processes* 25: 465–498.
- Brujinzeel, L. A., F. N. Scatena, and L. S. Hamilton (eds). 2010b. *Tropical Montane Cloud Forests: Science for Conservation and Management*. Cambridge University Press: Cambridge, United Kingdom.
- Brujinzeel, L. A., F. N. Scatena, L. S. Hamilton (eds.). 2011b. *Tropical Montane Cloud Forests. Science for Conservation and Management*. Cambridge University Press: Cambridge, United Kingdom; 691–740.
- Bubb, P., I. May, L. Miles, and J. Sayer. 2004. Cloud Forest Agenda, UNEP World Conservation Monitoring Centre: Cambridge, UK (available at: <http://sea.unepwcmc.org/forest/cloudforest/index.cfm>). [Accessed in October 2015].
- Bucci, S. J., F. G. Scholz, G. Goldstein, F. C. Meinzer, J. A. Hinojosa, W. A. Hoffmann, and A. C. Franco. 2004. Processes preventing nocturnal equilibration between leaf and soil water potential in tropical savanna woody species. *Tree Physiology* 24: 1119–1127.
- Burnham, K. P., and D. R. Anderson. 2002. *Model Selection and Multimodel Inference A Practical Information-Theoretic Approach*. 2<sup>nd</sup> ed. Springer Verlag, New York, New York.
- Callaway, R. M., K. O. Reinhart, G. W. Moore, D. J. Moore, and S. C. Pennings. 2002. Epiphyte host preferences and host traits: mechanisms for species-specific interactions. *Oecologia* 132: 221–230.
- Cardelús, C. L., and R. L. Chazdon. 2005. Inner-crown microenvironments of two emergent tree species in a lowland wet forest. *Biotropica* 37: 238–244.
- Cardelús, C. L., R. C. Colwell, and J. E. Watkins Jr. 2006. Vascular epiphyte distribution patterns: explaining the mid-elevation richness peak. *Journal of Ecology* 94: 144–156.
- Crausbay, S. D., and P. H. Martin. 2016. Natural disturbance, vegetation patterns and ecological dynamics in tropical montane forests. *Journal of Tropical Ecology* 32: 384–403.
- Dalling, J. W., K. Heineman, G. González, and R. Ostertag. 2015. Geographic, environmental and biotic sources of variation in the nutrient relations of tropical montane forests. *Journal of Tropical Ecology* 32: 368–383.
- Darby, A., D. Draguljic, A. Glunk, and S. G. Gotsch. 2016. Habitat moisture drives transpiration and foliar water uptake in a tropical montane cloud forest canopy. *Oecologia* 182: 357–371.
- Dawson, T. E., S. S. O. Burgess, K. P. Tu, R. S. Ra, L. S. Santiago, J. B. Fisher, K. A. Simonin, and A. R. Ambrose. 2007. Nighttime transpiration in woody plants from contrasting ecosystems. *Tree Physiology* 27: 561–575.
- Dolman, A. J., J. H. C. Gash, J. Roberts, and W. J. Shuttleworth. 1991. Stomatal and surface conductance of tropical rainforest. *Agricultural and Forest Meteorology* 54: 303–318.
- dos Santos, N. D., D. P. da Costa, L. S. Kinoshita, and G. J. Shepherd. 2014. Windborne: Can liverworts be used as indicators of altitudinal gradient in the Brazilian Atlantic Forest? *Ecological Indicators* 36: 431–440.
- Eller, C. B., S. O. Burgess, and R. S. Oliveira. 2015. Environmental controls in water use patterns of a tropical cloud forest tree species, *Drimys brasiliensis* (Winteraceae). *Tree Physiology* 35: 387–399.
- Fahey, T. J., R. E. Sherman, and E. V. J. Tanner. 2016. Tropical montane cloud forest: environmental drivers of vegetation structure and ecosystem function. *Journal of Tropical Ecology* 32: 355–367.
- Gehrig-Downie, C., J. Marquardt, A. Obregon, J. Bendix, and S. R. Gradstein. 2012. Diversity and vertical distribution of filmy ferns as a tool for identifying the novel forest type “Tropical Lowland Cloud Forest”. *Ecotropica (Bonn)* 18: 35–44.
- Giambelluca, T. W., J. K. DeLay, M. A. Nullet, M. A. Scholl, and S. B. Gingerich. 2010. Interpreting canopy water balance and fog screen observations: Separating cloud water from wind-blown rainfall at two contrasting forest sites in Hawai‘i. *In* Brujinzeel, L.A., F. N. Scatena, L. S. Hamilton, [eds.], *Tropical Montane Cloud Forests. Science for Conservation and Management*. Cambridge University Press: Cambridge, UK; 342–351.
- Giambelluca, T. W., J. K. DeLay, M. A. Nullet, M. A. Scholl, and S. B. Gingerich. 2011. Canopy water balance of windward and leeward Hawaiian cloud forests on Haleakala, Maui, Hawai‘i. *Hydrological Processes* 25: 438–447.
- Gotsch, S. G., H. Asbjornsen, and G. R. Goldsmith. 2016a. Plant carbon and water fluxes in tropical montane cloud forests. *Journal of Tropical Ecology* 32: 404–420.
- Gotsch, S. G., H. Asbjornsen, A. E. Weintraub, F. Holwerda, G. R. Goldsmith, and T. E. Dawson. 2014a. Foggy days and dry nights determine crown-level water balance in a seasonal tropical montane cloud forest. *Plant, Cell & Environment* 37: 261–272.
- Gotsch, S. G., S. D. Crausbay, T. W. Giambelluca, A. E. Weintraub, R. Longman, A. Asbjornsen, S. C. Hotchkiss, and T. E. Dawson. 2014b. Water relations and micro-climate around the upper limit of cloud forest in Maui, Hawai‘i. *Tree Physiology* 34: 766–777.
- Gotsch, S. G., N. Nadkarni, and A. Amici. 2016b. The functional roles of epiphytes and arboreal soils in tropical montane cloud forests. *Journal of Tropical Ecology* 32: 455–468.
- Gotsch, S. G., N. Nadkarni, A. Darby, A. Glunk, M. Dix, K. Davidson, and T. Dawson. 2015. Life in the Treetops: Ecophysiological Strategies of Canopy Epiphytes in a Tropical Montane Cloud Forest. *Ecological Monographs* 85: 393–412.
- Haber, W. A. 2000. Appendix 2. Number of species with different growth forms. *In* Nadkarni, N. M. and N. T. Wheelwright, [eds.], *Monteverde: ecology and conservation of tropical cloud forest*. Oxford University Press, New York, USA. 519–522.
- Hamilton, L. S., J. O. Juvik, and F. N. Scatena. [eds.], 1995. *Tropical Montane Cloud Forests, Ecological Studies* 110. Springer Verlag: New York.
- Hietz, P., and U. Hietz-Seifert. 1995. Composition and ecology of vascular epiphyte communities along an altitudinal gradient in Central Veracruz, Mexico. *Journal of Vegetation Science* 6: 487–498.

- Holwerda, F., L. A. Bruijnzeel, A. L. Oord, and F. N. Scatena. 2010a. Fog interception in a Puerto Rican elfin cloud forest: a wet-canopy water budget approach. In L. A. Bruijnzeel, F. N. Scatena, L. S. Hamilton, [eds.], *Tropical Montane Cloud Forests. Science for Conservation and Management*. Cambridge University Press: Cambridge, UK; 282–292.
- Holwerda, F., R. Burkard, W. Eugster, F. N. Scatena, A. G. C. A. Meesters, and L. A. Bruijnzeel. 2006. Estimating fog deposition at a Puerto Rican elfin cloud forest site: comparison of the water-budget and eddy covariance methods. *Hydrological Processes* 20: 2669–2692.
- Hu, J., and D. A. Riveros-Iregui. 2016. Life in the clouds: are tropical montane cloud forests responding to changes in climate? *Oecologia* 180: 1061–1073.
- Jarvis, A., and M. Mulligan. 2011. The climate of cloud forests. In Bruijnzeel, L. A., F. N. Scatena, L. S. Hamilton (eds). *Tropical Montane Cloud Forests. Science for Conservation and Management*, Cambridge University Press: Cambridge, UK; 691–740.
- Karger, D. N., J. Kluge, S. Abrahamczyk, L. Salazar, J. Homeier, M. Lehnert, V. B. Amoroso, and M. Kessler. 2012. Bryophyte cover on trees as proxy for air humidity in the tropics. *Ecological Indicators* 20: 277–281.
- Laube, S., and G. Zotz. 2006. Neither host-specific nor random: vascular epiphytes on three tree species in a Panamanian lowland forest. *Annals of Botany* 97: 1103–1114.
- Lawton, R. O., U. S. Nair, R. A. Pielke, and R. M. Sr. Welch. 2001. Climatic impact of tropical lowland deforestation on nearby montane cloud forests. *Science* 294: 584–587.
- Martin, P. H., R. E. Sherman, and T. J. Fahey. 2007. Tropical montane forest ecotones: Climate gradients, natural disturbance, and vegetation zonation in the Cordillera Central, Dominican Republic. *Journal of Biogeography* 34: 1792–1806.
- Meinzer, F. C., J. L. Andrade, G. Goldstein, N. M. Holbrook, J. Cavelier, and P. Jackson. 1997. Control of transpiration from the upper canopy of a tropical forest: The role of stomatal, boundary layer and hydraulic architecture components. *Plant, Cell & Environment* 20: 1242–1252.
- Meinzer, F. C., G. Goldstein, N. M. Holbrook, P. Jackson, and J. Cavelier. 1993. Stomatal and environmental control of transpiration in a lowland tropical forest tree. *Plant, Cell & Environment* 16: 429–436.
- Monteith, J. L., and M. H. Unsworth. 2008. *Principles of Environmental Physics*. Third Ed. AP, Amsterdam.
- Motzer, T., N. Munz, M. Kupperts, D. Schmitt, and D. Anhof. 2005. Stomatal conductance, transpiration and sap flow of tropical montane rain forest trees in the southern Ecuadorian Andes. *Tree Physiology* 25: 1283–1293.
- Nadkarni, N. M. 1994. Factors affecting the initiation and growth of above-ground adventitious roots in a tropical cloud forest tree: an experimental approach. *Oecologia* 100: 94–97.
- Nadkarni, N. M., and T. J. Matelson. 1991. Dynamics of fine litterfall within the canopy of a tropical cloud forest, Monteverde. *Ecology* 72: 2071–2082.
- Nadkarni, N. M., T. Matelson, and W. Haber. 1995. Structural characteristics and floristic composition of a neotropical cloud forest, Monteverde, Costa Rica. *Journal of Tropical Ecology* 11: 481–495.
- Nadkarni, N. M., D. A. Schaefer, T. J. Matelson, and R. Solano. 2004. Biomass and nutrient pools of canopy and terrestrial components in a primary and a secondary montane cloud forest, Costa Rica. *Forest Ecology and Management* 198: 223–236.
- Nadkarni, N. M., and R. Solano. 2002. Potential effects of climate change on canopy communities in a tropical cloud forest: an experimental approach. *Oecologia* 131: 580–586.
- Oliveira, R. S., C. B. Eller, P. R. L. Bittencourt, and M. Mulligan. 2014. The hydroclimatic and ecophysiological basis of cloud forest distributions under current and projected climates. *Annals of Botany* 113: 909–920.
- Pounds, J. A., M. P. L. Fogden, and J. H. Campbell. 1999. Biological response to climate change on a tropical mountain. *Nature* 398: 611–615.
- R Core Team. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org/>.
- Ray, D. K., U. S. Nair, L. O. Lawton, R. M. Welch, and R. A. Pielke Sr. 2006. Impact of land use on Costa Rican tropical montane cloud forests: sensitivity of orographic cloud formation to deforestation in the plains. *Journal of Geophysical Research* 111 (D2): D02108.
- Rosado, B. H. P., R. S. Oliveira, C. A. Joly, M. P. M. Aïdar, and S. S. O. Burgess. 2012. Diversity in nighttime transpiration behavior of woody species of the Atlantic Rainforest, Brazil. *Agricultural and Forest Meteorology* 158–159: 13–20.
- Santiago, L. S., G. Goldstein, F. C. Meinzer, J. Fownes, and D. Mueller-Dombois. 2000. Transpiration and forest structure in relation to soil waterlogging in a Hawaiian montane cloud forest. *Tree Physiology* 20: 673–681.
- Starr, J. L., and I. C. Paltineanu. 2002. Methods for Measurement of Soil Water Content: Capacitance Devices. p. 463–474. In Dane, J. H., and G. C. Topp, [eds.], *Methods of Soil Analysis: Part 4 Physical Methods*. Soil Science Society of America, Inc., Soil Science Society of America, Inc.
- Still, C. J., P. N. Foster, and S. H. Schneider. 1999. Simulating the effects of climate change on tropical montane cloud forests. *Nature* 789: 608–610.
- Wagner, K., G. Mendieta-Lieva, and G. Zotz. 2015. Host specificity in vascular epiphytes: a review of methodology, empirical evidence and potential mechanisms. *Annals of Botany* 7: plu092.
- Williams, S., E. Bolitho, and S. Fox. 2003. Climate change in Australian tropical rainforests: an impending environmental catastrophe. *Proceedings. Biological Sciences* 270: 1887–1892.
- Williams, J. W., S. T. Jackson, and J. E. Kutzbach. 2007. Projected distributions of novel and disappearing climates by 2100 AD. *Proceedings of the National Academy of Sciences, USA* 104: 5738–5742.
- Woods, C. L., C. L. Cardelus, and S. L. DeWalt. 2015. Microhabitat associations of vascular epiphytes in a wet tropical forest canopy. *Journal of Ecology* 103: 421–430.
- Zadroga, F. 1981. The hydrological importance of a montane cloud forest area of Costa Rica. In Lal, R., and E. W. Russell, [eds.], *Tropical Agricultural Hydrology*. John Wiley and Sons: New York, New York; 59–73.
- Zotz, G., and M. Y. Bader. 2009. Epiphytic plants in a changing world—Global change effects on vascular and non-vascular epiphytes. *Progress in Botany* 70: 147–170.