Vascular Epiphytic Diversity in a Neotropical Transition Zone Is Driven by Environmental and Structural Heterogeneity

Authors: de la Rosa-Manzano, Edilia, Mendieta-Leiva, Glenda, Guerra-Pérez, Antonio, Aguilar-Dorantes, Karla María, Arellano-Méndez, Leonardo Uriel, et al.

Vascular Epiphytic Diversity in a Neotropical Transition Zone Is Driven by Environmental and Structural Heterogeneity

Edilia de la Rosa-Manzano[1] ⓘ, Glenda Mendieta-Leiva[2],
Antonio Guerra-Pérez[1], Karla María Aguilar-Dorantes[3],
Leonardo Uriel Arellano-Méndez[1], and
Jorge Ariel Torres-Castillo[1]

Abstract

Vascular epiphytes contribute significantly to tropical diversity. Research on the factors that determine vascular epiphytic diversity and composition in tropical areas is flourishing. However, these factors are entirely unknown in tropical-temperate transition zones, which represent the distribution limit of several epiphytic species. We assessed the degree to which climatic and structural variables determine the diversity of vascular epiphytic assemblages (VEAs) in a transition zone in Mexico: the El Cielo Biosphere Reserve. We found 12,103 epiphytic individuals belonging to 30 species and 15 genera along a climatic gradient from 300 to 2,000 m a.s.l. Bromeliaceae and Orchidaceae were the most species-rich families. Forests along the windward slope of the Sierra Madre Oriental (semideciduous forest and tropical montane cloud forest) had higher species richness than forests along the leeward slope (pine-oak forest and submontane scrub). Species richness was largely determined by seasonality and, to a lesser degree, by forest structure, whereas abundance was mainly determined by host tree size. Variation in VEAs composition was largely explained by climatic variables, whereas forest structure was not as important. VEAs differed among forest types and slopes in terms of taxonomic and functional composition. For example, certain bromeliad indicator species reflected differences between slopes. Although within-tree epiphytic species richness (alpha diversity) was low in this transition zone relative to other habitats, species turnover among forest types (beta diversity) was high. These findings suggest that each forest type makes a unique and important contribution to epiphytic diversity in this transition zone.

Keywords

Bromeliaceae, epiphyte diversity, latitudinal gradient, Mexican transition zone and Orchidaceae

Introduction

One of the most conspicuous components of biodiversity in tropical forests is vascular epiphytes, which account for approximately 10% of vascular plants species worldwide. These plants are structurally dependent on other plants, rooting on them nonparasitically (Zotz, 2013) and are fundamentally different from soil-rooted vegetation given their strong coupling with the atmosphere, which provides them with water and nutrients (Mendieta-Leiva, Porada, & Bader, in press).

Epiphytes perform several critical ecological functions in ecosystems (Mendieta-Leiva et al., in press; Zotz & Hietz, 2001). For example, they play an

[1]Instituto de Ecología Aplicada, Universidad Autónoma de Tamaulipas, Ciudad Victoria, México
[2]Department of Geography, AG Ecological Plant Geography, Phillips University of Marburg, Germany
[3]Centro de Investigación en Biodiversidad y Conservación, Universidad Autónoma del Estado de Morelos, Cuernavaca, México

Edilia de la Rosa and Glenda Mendieta contributed equally to this work and should be regarded as co-first authors

Corresponding Author:
Edilia de la Rosa-Manzano, Instituto de Ecología Aplicada, Universidad Autónoma de Tamaulipas, Avenida División del Golfo Núm. 356, Colonia Libertad, Ciudad Victoria 87019, Tamaulipas, México.
Email: ermanzano@uat.edu.mx

important role as biodiversity amplifiers by providing resources and habitat for countless taxa (e.g., arthropods, birds, etc.; Angelini & Silliman, 2014; Méndez-Castro, Bader, Mendieta-Leiva, & Rao, 2018). Epiphytes are mostly concentrated in tropical rainforests, although they are also distributed in subtropical (Bianchi & Kersten, 2014; Hsu, Horng, & Kuo, 2002; Jian, Hu, Wang, Chiang, & Lin, 2013; Robertson & Platt, 2001) and temperate forests (Díaz, Sieving, Pena-Foxon, Larrain, & Armesto, 2010; Sillett & Bailey, 2003). Factors determining epiphytic diversity patterns have mainly been addressed in tropical rainforests at local and regional scales. The most documented local spatial pattern of epiphytes is their vertical stratification of the forest strata, which is mainly determined by humidity and light gradients (e.g., de la Rosa-Manzano, Andrade, Zotz, & Reyes-García, 2014; Petter et al., 2016) and, to a certain degree, by host species characteristics and phenology (Einzmann, Beyschlag, Hofhansl, Wanek, & Zotz, 2015; Wagner, Mendieta-Leiva, & Zotz, 2015). At a regional scale, for example, along elevational gradients, high species richness has often been positively related with water availability (i.e., precipitation), with the highest species richness often being found at middle elevations (Kessler, Kluge, Hemp, & Ohlemüller, 2011; Kreft, Köster, Küper, Nieder, & Barthlott, 2004; Krömer, Kessler, Gradstein, & Acebey, 2005).

Similarly, in the Neotropics, vascular epiphytes are a key component of forests. However, there are critical gaps in knowledge in areas outside the tropics, particularly in transition zones (e.g., the temperate-to-Mediterranean transition zone in the Andes and tropical/sub-tropical-to-temperate transition zones). Due to their strong coupling with the atmosphere and structural dependence, it is expected that epiphytes would show a high degree of specialization with respect to vegetation type. Thus, epiphytes may represent a good study system for understanding how environmental heterogeneity (e.g., forest structure and microclimatic variation; Kruckeberg & Rabinowitz, 1985) maintains diversity through habitat specialization (Harms, Condit, Hubbell, & Foster, 2001). Environmental heterogeneity is one of the most important variables that positively influences species richness (Stein, Gerstner, & Kreft, 2014). For example, the partitioning of environmental resources in structurally complex habitats results in greater species coexistence (Tews et al., 2004).

Zones of ecological transition are generally located at the boundaries of different biogeographic regions where biota from both regions co-occur (Darlington, 1975; Ferro & Morrone, 2014). The Mexican transition zone (MTZ; sensu Halffter & Morrone, 2017), where the Nearctic and Neotropical realms meet (Morrone, 2010), is characterized by a spectrum of vegetation from tropical to temperate (Beck et al., 2018; Peer, Finlayson,

& McMahon, 2007). The specific geographic area where these realms meet is the cordillera of the Sierra Madre Oriental, which is located on the western side of the MTZ. This cordillera contains short elevational gradients with sharp shifts in climate and vegetation type (Halffter, 1962; Marshall & Liebherr, 2000). It is also the northernmost limit of cloud forest, one of the most diverse vegetation types in the cordillera (Halffter, 1962; Ponce-Reyes et al., 2012). The conservation value of transition zones lies in their high levels of biodiversity (Halffter, 1962) and preservation of endemic genetic diversity (Ornelas et al., 2013). For vascular epiphytes, these zones may constitute a diversity refuge and ideal place to begin to understand which factors limit epiphytic distribution latitudinally.

In this study, we assessed vascular epiphytic diversity across vegetation types in the El Cielo Biosphere Reserve in the Sierra Madre Oriental (Morrone, 2015). We aimed to understand which factors drive vascular epiphytic diversity in this heterogeneous zone. We asked the following questions: (a) What are the most important variables determining vascular epiphytic species richness and variability in floristic composition across different forest types? (b) Are epiphytic taxa specialized to a particular forest type?, and (c) How does this specialization differ among functional groups (e.g., tank vs. atmospheric bromeliads)? We expected the following: (a) Climate would be the most important factor determining epiphytic diversity given the coupling of epiphytes with the atmosphere. (b) Forest types will show little overlap in the composition of epiphytic assemblages, and functional groups will be representative of each forest climate type. The expected differences in floristic composition and the high level of specialization of species with respect to vegetation type would indicate that each vegetation type significantly contributes to epiphytic diversity in this transition area. Moreover, some of these specialized epiphytic species may be sensitive to climatic variables and can thus be used as indicators to understand future community responses to climate change (Hsu et al., 2012).

Methods

Study Site

El Cielo Biosphere Reserve (CBR) comprises 144,000 ha in northern Mexico (Figure 1). It is located in the Sierra Madre Oriental, a cordillera with great ecological and historical complexity (Halffter, 1962). Human activities, such as deforestation and agriculture, and natural events, such as multiple treefall, caused serious disturbances in the CBR before 1984, when the CBR was declared as a protected natural area (Arriaga, 2000). Currently, low-impact agriculture is still practiced in areas adjacent to semideciduous forest (SDF), causing
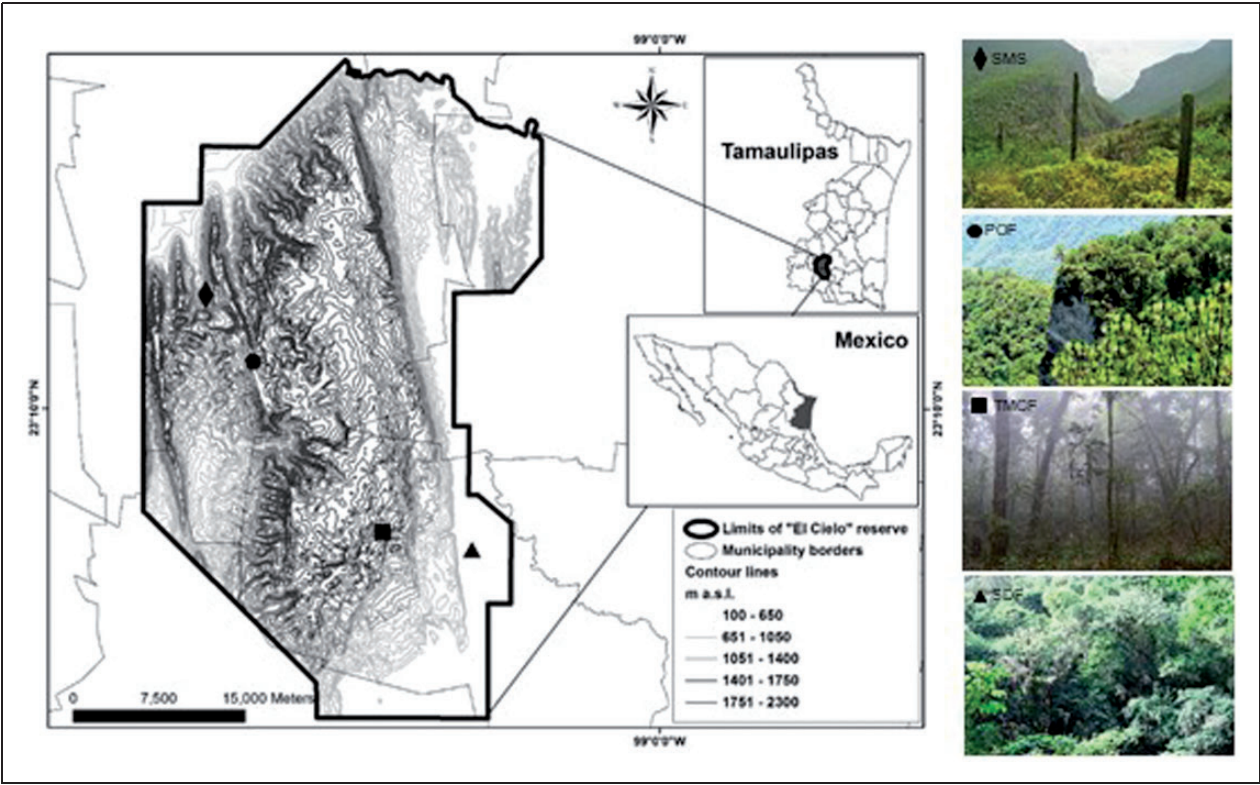
Figure 1. Distribution of different forest types in the "El Cielo" Biosphere Reserve in Tamaulipas, Mexico. The semideciduous forest (300–400 m a.s.l., triangle) and the tropical montane cloud forest (800–1600 m a.s.l., square) are distributed along the windward slope; and the pine-oak forest (1,500–2,000 m a.s.l., circle) and the submontane scrub (700–1,500 m a.s.l., diamond) are distributed along the leeward slope of the reserve.

Table 1. Summarized Data of the Vegetation Types Along the Elevational Gradient in the "El Cielo" Biosphere Reserve.

Vegetation type/elevational range (m a.s.l.)	Rainfall (mm)	Temp (°C)	Host species	Host individuals	Epiphyte species	Epiphyte abundance	Epiphyte density (ind/cm²)	Host tree surface area (m²)
SDF, 300–400	675	25	28	240	15	2839	1.42	5.57
TMCF, 800–1,600	2500	14	37	670	16	3376	0.56	19.55
SMS, 700–1,500	200	22	40	384	9	380	0.16	3.70
POF, 1,500–2,000	900	16	13	215	8	5085	2.12	14.55

Note. Rainfall corresponds to total annual precipitation (mm) and Temp is the mean annual temperature (°C). Data may differ slightly from that included in analyses since the sources are different. SDF = semideciduous forest; TMCF = tropical montane cloud forest; SMS = submontane scrub; POF = pine-oak forest.

some disturbance (Vargas-Vázquez et al., 2019). Most cloud forest in Mexico is found in the Sierra Madre Oriental, and this region, specifically the CBR (Ponce-Reyes et al., 2012; Rojas-Soto, Sosa, & Ornelas, 2012), represents the northernmost limit of cloud forest (Halffter, 1962; Ponce-Reyes et al., 2012).

In this reserve, there is a mixture of tropical and temperate species. Temperate species are dominant overall, but tropical species are dominant at lower elevations (Arriaga, 2000). Climatically, this area is considered to be temperate (warm, temperate with a hot summer climate; Beck et al., 2018; Peer et al., 2007). At a local

scale, the topography varies, resulting in a wide diversity of climates: The windward slope of the Sierra Madre Oriental is wet and influenced by marine winds, whereas the leeward slope has a dry climate (Sánchez-Santillán, Binnqüist, & Garduño, 2018) and vegetation types.

We sampled four vegetation types along a climatic gradient from 300 to 2,000 m a.s.l. (Table 1 and Figure 1; de la Rosa-Manzano et al., 2017): SDF, tropical montane cloud forest (TMCF), submontane scrub (SMS), and pine-oak forest (POF). The semideciduous forest (SDF), (300–400 m a.s.l.) is characterized by a warm, subhumid climate and is dominated by *Bursera simaruba* (L.) Sarg.,

Casimiroa greggii (S. Watson) F. Chiang, *Guazuma ulmifolia* Lam., *Lysiloma divaricatum* (Jacq.) J.F. Macbr., *Aphanthe monoica* (Hemsl.) J. F. Leroy Sharp, *Cascabela thevetia* (L.) Lippold., and *Trema micrantha* (L.) Blume, among others, with heights ranging from 8 to 15 m. The TMCF (800–1,600 m a.s.l.) is mainly characterized by a warm climate, and common tree species include *Magnolia tamaulipana* A. Vázquez, *Quercus germana* Schltdl. & Cham., *Q. sartorii* Liebm., *Podocarpus matudae* Lundell, *Acer skutchii* Rehder, *Cercis canadiensis* L., *Carpinus caroliniana* (Marshall) Fernald, *Ostrya virginiana* (Mill.) K. Koch, with heights between 18 and 25 m. These forests (SDF and TMCF) are distributed along the windward slope of the mountain range (González-Medrano, 2005).

The SMS (700–1,500 m a.s.l.) is characterized by a dry climate and species such as *Acacia berlandieri* Benth, *A. rigidula* Benth, *Acanthocereus tetragonus* (L.) Hummelinck, *Helietta parviflora* (A. Gray ex Hemsl.) Benth., *Cordia boissieri* A. D.C., *Havardia pallens* (Benth.) Briton & Rose, *Gochnatia hypoleuca* (SC.) A. Gray, and *Yucca treculeana* Carrière, among others, which reach up to 4 m in height. And, the last forest type, POF (1,500–2,000 m a.s.l.), is characterized by a dry and cool climate and dominated by *Pinus teocote* Schltdl. & Cham., *P. pseudoestrobus* Brongn., *C. caroliniana* Walter, *Carya myristiciformis* (F. Michx.) Nutt., *Carya ovata* (Mill.) K. Koch, *Q. germana* Schltdl. and Cham., *Q. affinis* Scheidw., and *Q. sartorii* Liebm., which reach up to 25 m in height (González-Medrano, 2005). These forests (SMS and POF) are distributed along the leeward slope of the mountain range (González-Medrano, 2005).

We sampled a total of 32 plots, each 400 m^2, including 5 plots in SDF, 15 in TMCF, and 6 in both SMS and POF between 2017 and 2018. The number of plots per vegetation type was determined according to the cover of each vegetation type. All plots were selected in areas with a relatively high density of epiphytes (e.g., old growth vegetation). In each plot, host trees with a diameter at breast height (DBH) of more than 1 cm were sampled; hosts other than trees were also sampled (e.g., agaves and cacti, particularly in the SMS). Host traits such as height, measured using a distance meter (D210, Leica); DBH; and species identity were also recorded. Epiphytic seedlings were not surveyed because they are difficult to identify and have high mortality rates (Winkler, Hülber, & Hietz, 2005). When epiphytic individuals were infertile, we identified them by comparing them to nearby fertile individuals of similar appearance. Epiphytic individuals were distinguished as epiphytic *stands* (*sensu* Sanford, 1968; i.e., groups of spatially aggregated stems), and vegetative clones from rhizomatous plants or clumped individuals were considered as a single individual. Sampling using binoculars

(EO-D102; Eagle optics) was carried out in the SDF and SMS and in the TMCF and POF using the single-rope climbing technique (Perry, 1978). It is possible that some species were missed in the SDF even with the use of binoculars, as the species accumulation curve did not reach the asymptote (Figure 2 and Online Appendix 2; de la Rosa-Manzano et al., 2017). Nonetheless, the use of binoculars to survey epiphytes is a common practice (Leimbeck & Balslev, 2001). Epiphytic species were divided into six functional groups considering the general ecological characteristics of their families: Bromeliaceae were divided into atmospheric and tank forms, and Orchidaceae into those with or without pseudobulbs. Cactaceae were classified as succulent, whereas Piperaceae were left as such (Table S2).

Voucher specimens of epiphytes and hosts were deposited in the Francisco González Medrano herbarium of the Applied Ecology Institute of the Autonomous University of Tamaulipas.

Data Analyses

Variables determining vascular epiphytic species richness, abundance, and composition. To assess whether differences in the number of sampled plots affected sample completeness, we calculated the proportion of the species pool found in each forest type at the plot level by means of interpolation and extrapolation analyses (Chao et al., 2014), which evaluate sample completeness based on sample coverage. We used the *iNEXT* function in the iNEXT package (Hsieh, Ma, & Chao, 2016).

To explore how the 3 structural variables (height, host DBH, and surface area), 14 climatic variables (Table 2), and elevation determined epiphytic species richness and abundance, we used linear and generalized linear models, respectively. We ran a total of four models: a structural and climatic model at the tree and plot level for each type of response variable (species richness and abundance). Then, we compared the explanatory power of the structural and climatic models according to the response variables.

At the tree level, the structural linear models included height, DBH, and surface area of host trees. Host tree surface area was calculated from the DBH and tree heights using an equation based on that described in Kershaw, Ducey, Beers, and Husch (2016). Elevation rather than forest type was included as a fixed factor to account for variation in forest structure among forest types, to economize the degrees of freedom, and to avoid multicollinearity. To achieve normality, we log-transformed the response variables (Crawley, 2005). To check whether the assumption of homoscedasticity was fulfilled (function *bptest*), we used the Breusch-Pagan test (Breusch & Pagan, 1979).
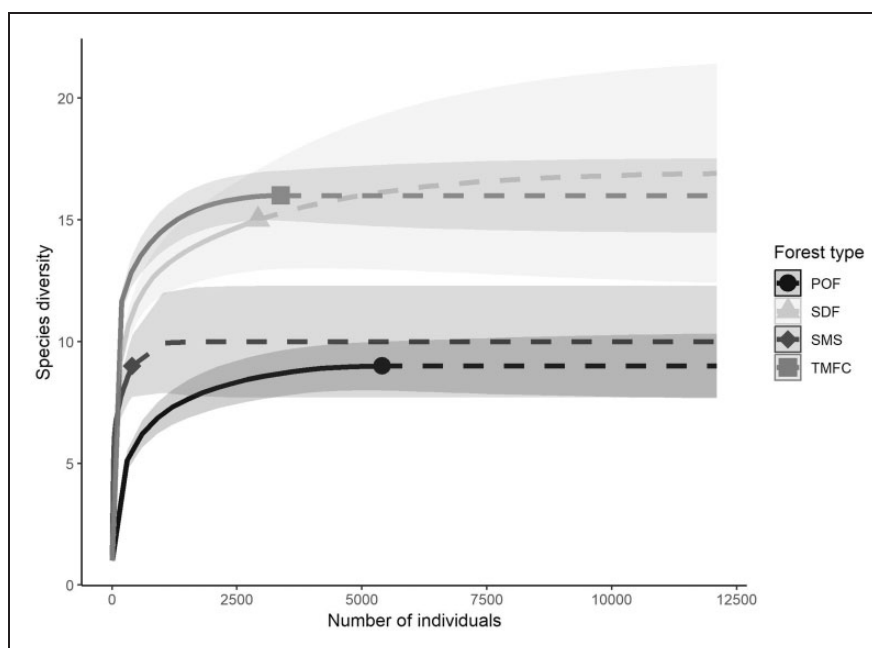
Figure 2. Inter- and extrapolation analysis (iNEXT) of epiphyte diversity according to forests type: semideciduous forest (300–400 m a.s.l.), tropical montane cloud forest (800–1,600 m a.s.l.), submontane scrub (700–1,500 m a.s.l.), and the pine-oak forest (1500–2,000 m a.s.l.; Table 1). The interpolated (observed) species richness of vascular epiphytes was obtained by merging abundance and species richness of plots per forest type. Extrapolated (expected) species richness for each forest type was based on the highest maximum number of individuals (ca. 7,500). SDF = semideciduous forest; TMCF = tropical montane cloud forest; SMS = submontane scrub; POF = pine-oak forest.

Table 2. Output of the Linear and Generalized Linear Models Assessing the Effect of Structural (DBH, Height, and Surface of Host Tree) and Climatic Variables (MTWeQ, PCQ, and APsq) on Species Richness and Abundance.

Variable	Estimate	Standard error	t	$\Pr(>|z|)$	R^2
Species richness					
Structural model					12%
DBH	0.10	0.01	7.68	<.001***	
Height	0.04	0.01	3.39	<.001***	
Climatic model					42%
MTWeQ	1.23	0.35	3.45	.001**	
PCQ	1.11	0.35	3.12	.003**	
Abundance					
Structural model					28%
DBH	0.45	0.04	11.01	<.001***	
Height	0.22	0.04	5.43	<.001***	
Elevation	0.21	0.03	6.08	<.001***	
Structural model					−0.4%
APsq	0.18	0.19	0.93	ns	

Note. Estimates, degrees of freedom, standard error, *t* value, and *p* values are shown. Estimates indicate the strength and direction of the correlation (either positive or negative). Structural variables were obtained from sampling, and climatic variables were obtained from CHELSA (see methods section, Karger et al., 2017). MTWeQ = Mean Temperature of the Wettest Quarter; PCQ = precipitation of the coldest quarter; APsq = annual precipitation quadratic term.; DBH = diameter at breast height; *ns* = not statistically significant.

At the plot level, we fitted the generalized linear models with Poisson distributions. These climatic models included climatic variables and elevation as response variables. Climatic variables were retrieved from CHELSA version 1.2, which provides climatologies at high resolution for the Earth's land surface, and a high-resolution climatic dataset (Karger et al., 2017). We retrieved a total of 19 bioclimatic variables but only

used 14; redundant variables (e.g., medium diurnal range, which is defined as the difference between the daily maximum and minimum temperature) and those with a correlation equal to or above 90% (Pearson correlation) were removed to avoid multicollinearity. The utilized climatic variables were annual mean temperature (AMT), maximum temperature of the warmest month, minimum temperature of the coldest month, mean temperature of the wettest quarter (MTWeQ), mean temperature of the driest quarter, mean temperature of the coldest quarter, mean temperature of the warmest quarter, annual precipitation (AP), precipitation of the wettest quarter, precipitation of the driest quarter, precipitation of the warmest quarter, and precipitation of the coldest quarter. We also included the quadratic terms of annual mean temperature (AMTsq) and annual precipitation (APsq) because the relationship between these variables and species richness may be nonlinear (e.g., Tang, Li, Li, & Meng, 2014). In each model, the dependent variables were standardized to assess the importance of their effects.

For the structural models, the best model was selected using backward stepwise selection based on the χ^2 test (function *drop1*). For the climatic models, the best model was selected using forward stepwise selection (function *add1*) based on the AIC values. We first ran a full model (where all explanatory variables were included) and a null model (without explanatory variables). Then, we added one variable at a time, starting with those with the smallest AIC value, to the null model. The best model was determined based on the variance inflation factor (function *vif*) calculated for each updated model (terms with values above 5 were excluded; Online Appendix 6). The significance of each variable in the final models was calculated using the analysis of variance function in the *car* package.

Specialization of epiphytic taxa to forest type. Dissimilarity of vascular epiphytic assemblages (VEAs) among forest types was evaluated by different means (all at the plot level, with the exception of a constrained correspondence analysis). We ran an ordination using nonmetric multidimensional scaling for abundance data using the Chao index (Chao, Chazdon, Colwell, & Shen, 2005). The ordinations depict distances between plots according to the metric of choice; we used the *metaMDS* function in the vegan package (Oksanen et al., 2017). Differences in species composition among forest types were evaluated with a multivariate analysis of variance (PERMANOVA) by means of the *adonis* function (999 permutations), and post hoc pairwise comparisons were carried out using a Bonferroni correction (vegan package). We calculated dissimilarity and its components, turnover, and nestedness (Baselga, 2010), within and among forest types using the *beta.multi* function in the

betapart software package (Baselga, 2012). With respect to the dissimilarity components, turnover implies that variation in species composition among sites can be the result of species replacement among sites, and nestedness implies species loss or gain from site to site (Baselga & Orme, 2012).

Complementarily, we ran an indicator species analysis to detect species indicative of each forest type using the indicspecies package (De Caceres & Jansen, 2016). Indicator values range from 0 (random distribution) to 1 (perfect association between a species and a forest type; Dufrêne & Legendre, 1997). The statistical significance of the indicator values was calculated using a permutation test (999 permutations). Finally, to understand the degree to which structural and climatic variables determined the variability of VEAs, we ran a constrained correspondence analyses (function *cca*). We used the same strategy as in the generalized linear models and modeled the variability of the VEAs using a climatic and a structural model including elevation to understand which variables varied along the axis of the climatic gradient (data were centered and scaled). All variables, climatic (12 variables) and structural (DBH, height, and surface area), were included in each full model. Thereafter, nonsignificant variables were removed and, finally, only variables with a variance inflation factor (function *vif.cca*) lower than approximately 5 were left in each model to avoid multicollinearity. In this analysis, we did not include the quadratic terms of annual mean temperature (AMTsq) and APsq because they may cause an arch effect, thus making variables appear important erroneously (Palmer, 2003). All analyses were carried out in the statistical software R version 3.3.3 (R Development Core Team, 2018).

Results

General Results

We registered a total of 12,103 epiphytic individuals belonging to 4 families, 15 genera, and 30 species. The highest species richness was found along the windward slope in the TMCF (16 species, or 33% of the total species richness on 670 trees), followed by the SDF (15 species, or 31% of the total species richness on 240 trees; Table 1 and Figure 2). Only about half this number of species, or 8 and 9 species, was found along the leeward slope in the POF and the SMS, respectively (17% on 215 trees and 19% on 384 trees, respectively; Table 1 and Figure 2). Overall, TMCF was significantly more diverse than POF and SMS. However, because the diversity profiles crossed at several points (q = 0–2), no single forest type can be considered more or less diverse than the others, that is, they had comparable diversity. The SDF was the most heterogeneous or, in other

words, had the highest number of rare species and lowest number of dominant species (Online Appendix 1). Ultimately, the species richness among forest types was comparable despite differences in sampling effort (Figure 2 and Online Appendix 2). Coverage values were very high, and extrapolated species richness indicated that only a single additional species could be found in SDF and SMS by increasing the sample size (number of individuals per plot; Figure 2 and Online Appendix 2). Finally, species richness slightly decreased with elevation, although this trend differed according to family. For example, orchid species richness showed a steep decline with elevation, while bromeliad and other species richness showed no trend (Online Appendix 3). Only the epiphytes *Tillandsia pringlei* and *Tillandsia usneoides* were shared by all vegetation types.

Interestingly, there was no correspondence between epiphytic density (ind/cm^2) and host tree species richness or between host tree abundance and surface area per forest type (Table 1). Species richness and abundance (per tree) generally increased with host tree surface area, although the relationship varied according to forest type and response variable (Online Appendix 4). Species richness steadily increased with host tree surface area, with the exception of TMCF, which showed large variability in tree size (Table 1). The relationship between abundance and host tree surface area was highly dependent on forest type, especially in the POF, where abundance largely varied (Online Appendix 4). At the plot level, the number of epiphytic species per plot was positively correlated with the number of host tree species per plot (Online Appendix 5).

Climatic and Structural Variables Determining Species Richness and Abundance

Both structural and climatic variables significantly determined species richness and abundance along the climatic gradient, but their effects varied according to response variable and scale (Online Appendix 6). For total species richness, the precipitation of the coldest quarter and MTWeQ were the most important climatic variables, having a positive effect on species richness in comparison to the structural variables (DBH and height), which also had a significant positive effect but, unlike climatic variables, only explained half of the variation in species richness (Table 2 and Online Appendix 6). For total abundance, the converse pattern was found: The structural variables largely determined abundance, and only one climatic variable had a significant negative effect, explaining a very low percentage of variability. The DBH had the strongest positive effect on abundance and was more than double the effect of height (Table 2 and Online Appendix 6). These findings suggest that climatic variables have by far the largest effect on species

richness, while structural variables mainly determine abundance.

Climatic and Structural Variables Determining Dissimilarity in VEAs Among Forests

All dissimilarity analyses showed a very clear differentiation of VEAs according to forest type in terms of both taxonomic and functional composition (plot-based comparisons; Figure 3 and Table 3) as well as a clear difference in composition between slopes (Figure 3, Table 3, and Online Appendices 8 and 9). For instance, bromeliad indicator species clearly showed differences between slopes. In the forests (POF and SMS) along the leeward slope, the atmospheric species were found to be the indicator species. In the forests (SDF and TMCF) along the windward slope, mostly tank species were indicator species, although we also found a high diversity of indicator species in the SDF (six species belonging to five functional groups; Figure 3 and Table 3).

Within-forest dissimilarity (among plots) was highest in TMCF and lowest in SDF (windward slope), whereas in the forests along the leeward slope (POF and SMS), dissimilarity was comparable (Figure 3 and Online Appendix 8). Moreover, dissimilarity between the forests on the leeward slope was lower (33%) than that of those on the windward slope (54%; Figure 3 and Online Appendix 8). Dissimilarity among the four forest types was ca. 70% and almost entirely due to species turnover. In other words, dissimilarity was due to actual differences in species composition (species turnover) and not merely to species loss from site to site (Baselga & Orme, 2012), highlighting the specificity in the epiphytic composition of each forest type (Figure 4 and Online Appendix 9).

While structural variables explained 5% of the total variability of VEAs (at the tree level; Online Appendix 7), climatic variables comparatively explained the variability by more than six fold (30.58% at the plot level; Figure 4), highlighting the differential effects of the drivers of the variability of VEAs at different scales. In the climatic model, the first axis explained over 76% of the variation and was related to AP; in contrast, the second axis explained 24% and was related to the MTWeQ (Figure 4). In the structural model, the first axis explained 68% of the variation and was related to variation in height; meanwhile, the second axis explained 32% and was related to changes in DBH. High structural variation was observed in TMCF and SDF (both along the windward slope), as observed along the second axis gradient (Online Appendix 7).
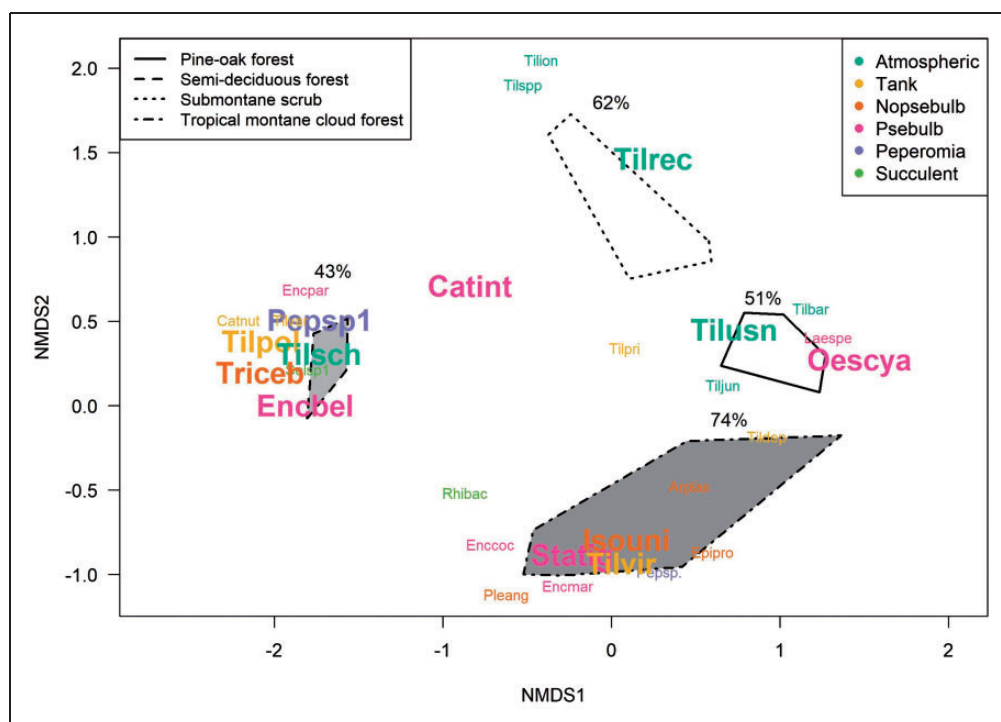
Figure 3. Nonmetric multidimensional scaling ordination showing dissimilarity of VEAs based on relative abundance (Chao index) data between forest types (at the plot level). Species shown bigger and in bold are indicator species which are categorized according to functional group (color coded, upper-right corner legend, Table 3). Polygons reflect the plot coordinates for each forest type and the border line type indicates the forest type (upper-left corner legend). Gray filled polygons indicate forest types located along the windward slope and white polygons indicate forest types located along the leeward slope. Total dissimilarity percentage among plots (within-forest type) is indicated above each forest type polygon. NMDS = nonmetric multidimensional scaling.

Discussion

Epiphytic Richness in a Transition Zone

Vascular epiphytic richness in the CBR was low (30 species in 1.28 ha) in comparison to that of tropical rainforests (e.g., Gentry & Dodson, 1987; Kreft et al., 2004). Sampling four vegetation types resulted in double the number of species compared with de la Rosa-Manzano et al. (2017), who only sampled two vegetation types. Overall, the low species richness encountered herein is comparable to that of some subtropical forests (e.g., Atlantic and broadleaf temperate forests; Barbosa, Becker, Cunha, Droste, & Schmitt, 2015; Ceballos, Chacoff, & Malizia, 2016; Díaz et al., 2010; Hsu et al., 2012; Xu & Liu, 2005) but lower than that of other subtropical forests in the southern hemisphere (e.g., Brown, 1990; Hofstede, Dickinson, & Mark, 2001). This low richness may possibly be due to the decreasing number of species per unit area toward the poles, as observed in coniferous forests (e.g., Khine, 2018). In epiphytes, the drop in the number of species seems distinctively sharp (Moran, 2008; Karger, Kluge, & Kessler, 2016; Salazar et al., 2013).

High epiphytic diversity in tropical forests is generally thought to result from the positive effect of precipitation

(Kreft et al., 2004; Wolf & Alejandro, 2003). Also, a general pattern of high richness is observed at middle elevations (Gentry & Dodson, 1987), which can be attributed to climatic conditions such as cloud formation, temperature, and precipitation (Carvajal-Hernández & Krömer, 2015; Gentry & Dodson, 1987; Hemp, 2001; Kessler, 2000; Kessler, Herzog, Fjeldsa, & Bach, 2001; Kluge, Bach, & Kessler, 2008; Kluge, Kessler, & Dunn, 2006; Stevens, 1992; Wolf, 2005). In contrast to this general trend found throughout the tropics, total species richness in the CBR decreased with elevation. However, this trend was largely due to the behavior of Orchidaceae in the transition area. Although the study site does not comprise an elevational gradient in the strict sense, the lack of a middle elevational peak in the CBR could be related with the narrow elevation range (the highest elevation reaches 2,200 m a.s.l.; González-Medrano, 2005) or the strong seasonality of the area (García-García & Zarraluqui, 2008, Salazar et al., 2013).

The overall diversity of the VEAs only differed between the TMCF, the POF, and the SMS; the TMCF was more diverse than the POF and the SMS, yet no single forest type was statistically more diverse

Table 3. Indicator Species Analysis Values.

Acronym	Epiphyte species	Family	Abundance	Functional group	SE (windward) SDF	TMFC	NW (leeward) SMS	POF
Tiljun	*Tillandsia juncea*	Bromeliaceae	3457	Atmospheric	x	x	x	x
Tilsch	***Tillandsia schiedeana***	Bromeliaceae	1906	Atmospheric	**.996*****	x	x	
Tilusn	***Tillandsia usneoides***	Bromeliaceae	1472	Atmospheric	x	x	x	**.965****
Tilrec	***Tillandsia recurvata***	Bromeliaceae	279	Atmospheric			**.996*****	0
Tilspp	*Tillandsia sp.*	Bromeliaceae	3	Atmospheric			.58.	
Tilbar	*Tillandsia bartramii*	Bromeliaceae	2	Atmospheric				.41
Tilion	*Tillandsia ionantha*	Bromeliaceae	1	Atmospheric			.41	
Tildep	*Tillandsia deppeana*	Bromeliaceae	2913	Tank		x	x	x
Tilpol	***Tillandsia polystachia***	Bromeliaceae	516	Tank	**1*****			
Tilvir	***Tillandsia viridiflora***	Bromeliaceae	102	Tank		**.775****		
Tilpri	*Tillandsia pringlei*	Bromeliaceae	86	Tank	x	x	x	x
Catnut	*Catopsis nutans*	Bromeliaceae	4	Tank	.45			
Tilvar	*Tillandsia variabilis*	Bromeliaceae	1	Tank	.45			
Rhibac	*Rhipsalis baccifera*	Cactaceae	460	Succulent	x	x		
Selspi	*Selenicereus spinulosus*	Cactaceae	10	Succulent	.45			
Isouni	***Isochilus unilateralis***	Orchidaceae	194	Nopsebulb		**.966*****		
Triceb	***Trichocentrum cebolleta***	Orchidaceae	88	Nopsebulb	**1*****			
Arplax	*Arpophyllum laxiflorum*	Orchidaceae	43	Nopsebulb		.45		
Pleang	*Pleurothallis angustifolia*	Orchidaceae	7	Nopsebulb		.52		
Epipro	*Epidendrun propinquum*	Orchidaceae	6	Nopsebulb		.37		
Statig	***Stanhopea tigrina***	Orchidaceae	158	Psebulb		**.894*****		
Prococ	*Prosthechea cochleata*	Orchidaceae	88	Psebulb	x	x		
Encbel	***Encyclia belizensis***	Orchidaceae	76	Psebulb	**.996*****	x		
Laespe	*Laelia speciosa*	Orchidaceae	25	Psebulb				.58.
Catint	***Catasetum integerrimum***	Orchidaceae	23	Psebulb	**.901*****		x	x
Oescya	***Oestlundia cyanocolumna***	Orchidaceae	11	Psebulb				**.707***
Promar	*Prosthechea mariae*	Orchidaceae	2	Psebulb		.26		
Encpar	*Encyclia parviflora*	Orchidaceae	2	Psebulb	.45			
Pepsp1	***Peperomia sp1.***	Piperaceae	137	Peperomia	**.775*****			
Pepsp.	*Peperomia sp2.*	Piperaceae	31	Peperomia		.37		

Note. Significant indicator values are bolded, and the significance level is indicated; marginally significant values are indicated with a period and the "x" indicates species present in each forest type but without indicator value. Acronyms (as used in the NMDS analysis, see Figure 3), species names, family and total abundance are indicated. Indicator values are indicated for each forest type: SDF (300–400 m a.s.l.), TMCF (800–1,600 m a.s.l.), SMS (700–1,500 m a.s.l.), and POF (1,500–2,000 m a.s.l.; Table 1). NMDS = nonmetric multidimensional scaling. SDF = semideciduous forest; TMCF = tropical montane cloud forest; SMS = submontane scrub; POF = pine-oak forest. Significance codes: 0.05; *, 0.01;**, 0.001;***.
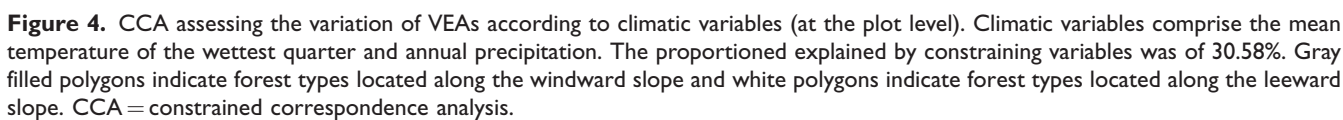
than all others, meaning that they had comparable diversity. The SDF and the TMCF along the windward slope, which corresponded with warm, subhumid, and humid climates, had higher species richness in contrast to the POF and the SMS along the leeward slope, which corresponded with temperate, subhumid, and dry climates (Sánchez-Santillán et al., 2018).

Climatic and Structural Factors as Determinants of Epiphytic Diversity

Species richness was largely determined by climatic variables in the study area, while abundance was mainly determined by forest structure. Climatic variables associated with seasonality were important determinants of species richness, while abundance was determined to a lesser degree by APsq (quadratic term). Although precipitation is known to be the main determinant of epiphytic species richness in tropical forests (Kreft et al., 2004), in this transition area, seasonality seems to be crucial for vascular epiphytic richness. The very complex topography of the CBR with two opposing slopes (windward and leeward) in conjunction with pervasive summer droughts, which are especially intense in dry areas (Sánchez-Santillán et al., 2018), and strong seasonality of precipitation (Karmalkar, Bradley, & Diaz, 2011) may explain why climatic variables related to seasonality, and not simply AP, determine vascular epiphytic richness in this transition area.

Species abundance was largely determined by structural variables, that is, DBH and height, which were also important for species richness, although to a lesser degree (Table 2). The determination of epiphytic distribution by forest structure is one of the best-known spatial patterns in vascular epiphytes (Zotz, 2007) that exists independently of forest type (e.g., Flores-Palacios & García-Franco, 2006; Hirata, Kamijo, & Saito, 2009; Laube & Zotz, 2006). This seems to be an intrinsic characteristic of vascular epiphytes

Figure 4. CCA assessing the variation of VEAs according to climatic variables (at the plot level). Climatic variables comprise the mean temperature of the wettest quarter and annual precipitation. The proportioned explained by constraining variables was of 30.58%. Gray filled polygons indicate forest types located along the windward slope and white polygons indicate forest types located along the leeward slope. CCA = constrained correspondence analysis.

given their structural dependence on a dynamic substrate, that is, host trees (Spruch, Hellwig, Zotz, & Blasius, 2019). These results suggest that, in the transition zone of the CBR, climatic seasonality at a regional scale determines species richness and at the tree level (host tree size) determines the abundance of VEAs.

The peak in orchid species richness on the windward slope (wet side) reflects the more balanced climatic conditions in contrast to the leeward slope, where extremely low temperatures occur in the POF and severe droughts in the SMS. In fact, in the latter forest type, we found a single orchid species. The TMCF on the windward slope registered the highest rainfall in the area (Table 1) and the frequent presence of fog (Hamilton et al., 1995). This fog or "horizontal precipitation" (Vogelmann, 1973) is likely to offset the short period of drought that occurs in the CBR (3–4 months; Rzedowski, 1996). Fog is known to contribute up to 20% or more of the total water input in cloud forests (Juvik & Ekern, 1978; Stadtmüller, 1987), and it may facilitate the presence of species that require wetter environments, such as orchids. On the other hand, very low temperatures at high elevations limit the distribution of orchid richness (Zotz, 2005). For instance, in the POF, only three species were registered at 1,800 m a.s.l., similar to another pine forest in Veracruz, Mexico, where only a single species of orchid

was found (Hietz & Hietz-Seifert, 1995). Meanwhile, the high orchid richness in a pine forest in Chiapas in southern Mexico (Wolf & Alejandro, 2003), located seven degrees south of the study site, highlights the strong role of temperature as the driving force of orchid richness. The high richness in this latter site may result from the beneficial effects of temperature and high humidity, which likely bypassed the negative effects of the phenolic or resinous composition of pine bark that hamper orchid establishment (Wolf & Alejandro, 2003).

On the leeward slope, atmospheric bromeliads such as *Tillandsia recurvata* and *T. usneoides* prevailed, similar to what is reported by Rzedowski (1996) for the arid regions of Mexico. In this case, mountains may prevent the passage of moist currents from the coast, thus interrupting the flux of moisture beyond the high areas and causing semi-arid regions, like SMS, where fog banks create favorable environments for epiphytes. The present findings confirm our hypothesis that climatic variables have an important effect on total epiphytic species richness and abundance.

VEAs Are Differentiated According to Forest Type

The variation in VEA composition among forests was related to gradients of structural (DBH and tree height)

and climatic variables (temperature and precipitation). The strong structural and climatic differences among forests were clearly reflected in the compositional differences of the VEAs. High dissimilarity was mostly due to turnover, especially in the forests along the leeward slope (dry and cold climate). The exception was the TMCF, where within-forest dissimilarity was very high (higher than among-forest dissimilarity), largely due to nestedness. Such nestedness patterns point out the relevance of dispersal limitations in structuring these assemblages (Baselga & Araujo, 2009), which is highly relevant considering that the TMCF harbors endemic species or those with restricted distributions. Within the small area of the CBR (144,000 ha), the four forest types shared only 2 out of 30 species, even though these species have a very wide latitudinal distribution (GBIF, 2019). These strong dissimilarities in the CBR indicate that the regional diversity is highly partitioned among forest types and trees within-forest types.

The degree of differentiation of VEAs among forest types in the CBR is surprisingly high considering that this site experienced a period of disturbances up until approximately 35 years ago (Arriaga, 2005). In a previous study, such differentiation was not evidenced in epiphytic orchid composition between pastures, regenerating forest, and old growth forest across six reserves, probably due to favorable climatic conditions (Sanchez, Armenteras, & Retana, 2016). In contrast, in another study carried out in a single site of TMCF, there were clear differences in epiphytic composition between isolated remnant trees and forests with a similar elevation that had not experienced disturbances for 50 years, although epiphytes were sampled in the same host species (Larrea & Werner, 2010). While these examples involve the comparison of disturbed sites to old growth forest, where differences in composition are expected, the contradictory results hint at the high complexity of the determinants of epiphytic diversity. Finally, in a lowland forest of the Colombian Amazonia, a similar differentiation of VEAs among landscape units was found, although this was largely explained by differences in host species composition despite structural similarity among landscape units (Benavides, Vasco, Duque, & Duivenvoorden, 2011). Although host species richness was associated with epiphytic richness in the CBR (Wagner et al., 2015), discriminating between the effect of host tree composition and structural variability is difficult and requires a more detailed analytical framework.

Notably, Bromeliaceae and Orchidaceae were specialized to forest type, supporting our prediction. In this study, bromeliad species comprised both tank and atmospheric forms. The former has broad and flat leaves that basally overlap, forming water-tight chambers that store water (Adams & Martin, 1986). The latter has very narrow leaves and abundant foliar trichomes specialized in water and nutrient absorption (Martin, McLeod, Eades, & Pitzer, 1985); these bromeliads obtain moisture and nutrient ions directly from the atmosphere (Benzing, 1990). Atmospheric bromeliads were characteristic of both forests along the leeward slope with a cold and dry climate and low precipitation. Here, drought-tolerant epiphytic species of the genus *Tillandsia* (atmospheric type) were more prevalent than in areas with high or moderate rainfall (Chilpa-Galván, Tamayo-Chim, Andrade, & Reyes-García, 2013; García-Suárez, Rico-Gray, & Serrano, 2003). In particular, *T. usneoides* was an indicator of POF and *T. recurvata* of SMS; both species show adaptations to cope with water scarcity and high temperatures (Benzing, 1990). On the other hand, tank bromeliads and both orchid groups (with and without pseudobulbs) were indicators of forests along the windward slope. In this case, the tank bromeliad *Tillandsia viridiflora* was an indicator of TMCF, which receives the highest precipitation in the CRB. It is known that tank bromeliads are usually restricted to humid forests (Pittendrigh, 1948), although in dry forests, some tank bromeliads are distributed at the top of their hosts to better access rainfall (Cach-Pérez et al., 2013; Graham & Andrade, 2004; Reyes-García, Griffiths, Rincón, & Huante, 2008).

Almost all indicator species of the orchid groups were found on the windward slope. Indicator species in the SDF have developed either large pseudobulbs (26×8 cm for *Catasetum integerrimum*; Hágsater & Salazar, 1990), deciduousness, or tilting succulent leaves (de la Rosa-Manzano, Andrade, García-Mendoza, Zotz, & Reyes-García, 2015). These adaptations can aid these orchids in storing water for long dry periods, tolerating high temperatures, avoiding water loss, and surviving in harsh environments. Functional group differentiation has been well studied in bromeliads (Benzing, 2000; Pittendrigh, 1948) but is still unclear in orchids; therefore, it is important to continue to study the inter- and intraspecific variability of orchid functional traits in heterogeneous environments.

Implications for Conservation

All studied forest types (SDF, TMCF, SMS and POF) had comparatively low epiphytic species richness. Yet, notably, their VEAs strongly differed in taxonomic and functional composition. This indicates that each forest type within the El Cielo Biosphere Reserve (CBR) uniquely contributes to the overall epiphytic richness of the reserve. Epiphytic richness in the CBR is comparable to that of subtropical forests and is mainly driven by climatic factors and, to a lesser extent, by forest structural variables. Epiphytes contribute to the local species diversity and may constitute one of the groups most threatened by the effects of climate change (Zotz &

Bader, 2009), specifically in the TMCF, due to the associated reduction in cloud occurrence and increase in temperature (Intergovernmental Panel on Climate Change, 2014; Nadkarni & Solano, 2002). The CBR comprises a great heterogeneity of habitats that maintain epiphytic diversity and may represent the northernmost distribution of some epiphytic species in the MTZ. Hence, it is extremely important to implement adequate management policies for the conservation of epiphytic diversity in this region.

ORCID iD

Edilia de la Rosa-Manzano https://orcid.org/0000-0001-5985-6266

Supplemental Material

Supplemental material for this article is available online.

References

Adams, W. W., III., & Martin, C. E. (1986). Morphological changes accompanying the transition from juvenile (atmospheric) to adult (tank) forms in the Mexican epiphyte *Tillandsia deppeana* (Bromeliaceae). *American Journal of Botany*, 73, 1207–1214.

Angelini, C., & Silliman, B. (2014). Secondary foundation species as drivers of trophic and functional diversity: Evidence from a tree—Epiphyte system. *Ecology*, 95, 185–196.

Arriaga, L. (2000). Gap-building-phase regeneration in a tropical montane cloud forest of north-eastern Mexico. *Journal of Tropical Ecology*, 16, 535–562.

Arriaga, L. (2005). Natural disturbance and regeneration of mesophilos forest. In G. Sánchez-Ramos, P. Reyes-Castillo, & R. Dirzo (Eds.), *Natural history of the El Cielo Biosphere Reserve, Tamaulipas, Mexico* (pp. 130–146). Hong Kong: Universidad Autónoma de Tamaulipas.

Barbosa, M. D., Becker, D. F. P., Cunha, S., Droste, A., & Schmitt, J. L. (2015). Vascular epiphytes of the Atlantic Forest in the Sinos River basin, state of Rio Grande do Sul, Brazil: Richness, floristic composition and community structure. *Brazilian Journal of Biology*, 75, 25–35.

Baselga, A. (2010). Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography*, 19, 134–143.

Baselga, A. (2012). The relationship between species replacement, dissimilarity derived from nestedness, and nestedness. *Global Ecology and Biogeography*, 21, 1223–1232.

Baselga, A., & Araujo, M. B. (2009). Individualistic vs community modelling of species distributions under climate change. *Ecography*, 35, 55–65.

Baselga, A., & Orme, C. D. (2012). Betapart: An R package for the study of beta diversity. *Methods in Ecology and Evolution*, 3, 808–812.

Beck, H. E., Zimmermann, N. E., McVicar, T. R., Vergopolan, N., Berg, A., & Wood, A. (2018). Present and future Koppen-Geiger climate classification maps at 1-km resolution. *Scientific Data*, 5, 180214.

Benavides, A. M., Vasco, A., Duque, A. J., & Duivenvoorden, J. F. (2011). Association of vascular epiphytes with landscape units and phorophytes in humid lowland forests of Colombian Amazonia. *Journal of Tropical Ecology*, 27, 223–237.

Benzing, D. H. (1990). *Vascular epiphytes. General biology and related biota*. Cambridge, England: Cambridge University Press.

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

Bianchi, J. S., & Kersten, R. D. (2014). Edge effect on vascular epiphytes in a subtropical Atlantic Forest. *Acta Botanica Brasilica*, 28, 120–126.

Breusch, T. S., & Pagan, A. R. (1979). A Simple test for heteroscedasticity and random coefficient variation. *Econometrica*, 47, 1287–1294.

Brown, A. D. (1990). Epiphytism in the mountain jungles of the National Park "El Rey", Argentina: Floristic composition and distribution pattern. *Revista de Biología Tropical*, 38, 155–166.

Cach-Pérez, M. J., Andrade, J. L., Chilpa-Galván, N., Tamayo-Chim, M., Orellana, R., & Reyes-García, C. (2013). Climatic and structural factors influencing epiphytic bromeliad community assemblage along a gradient of water-limited environments in the Yucatan Peninsula, Mexico. *Tropical Conservation Science*, 6, 283–302.

Carvajal-Hernández, C., & Krömer, T. (2015). Richness and distribution of ferns and lycophytes in the altitudinal gradient of the Cofre de Perote, Veracruz center, Mexico.. *Botanical Sciences*, 93, 601–614.

Ceballos, S. J., Chacoff, N. P., & Malizia, A. (2016). Interaction network of vascular epiphytes and trees in a subtropical forest. *Acta Oecologica-International Journal of Ecology*, 77, 152–159.

Chao, A., Chazdon, R. L., Colwell, R. K., & Shen, T. (2005). A new statistical approach for assessing similarity of species composition with incidence and abundance data. *Ecology Letters*, 8, 148–159.

Chao, A., Gotelli, N. J., Hsieh, T. C., Sander, E. L., Ma, K. H., Colwell, R. K., & Ellison, A. M. (2014). Rarefaction and extrapolation with Hill numbers: A framework for sampling and estimation in species diversity studies. *Ecological Monographs*, 84, 45–67.

Chilpa-Galván, N., Tamayo-Chim, M., Andrade, J. L., & Reyes-García, C. (2013). Water table depth influence the asymmetric arrangement of epiphytic bromeliads in a tropical dry forest. *Plant Ecology*, 214, 1037–1048.

Crawley, M. J. (2005). *Statistics: An introduction using R*. Chichester, England: John Wiley & Sons Ltd.

Darlington, P. (1975). *Zoogeography: The geographical distribution of animals* (p. 675). New York, NY: John Wiley & Sons Co.

De Cáceres, M. & Jansen, F. (2016). Indicspecies-package. Studying the statistical relationship between species and groups of sites (Version no. 1.7.6.). https://rdrr.io/cran/indicspecies/man/indicspecies-package.html

de la Rosa-Manzano, E., Andrade, J. L., García-Mendoza, E., Zotz, G., & Reyes-García, C. (2015). Photoprotection related to xanthophyll cycle pigments in epiphytic orchids acclimated at different light microenvironments in two tropical dry forests of the Yucatan Peninsula, Mexico. *Planta*, 242, 1425–1438.

de la Rosa-Manzano, E., Andrade, J. L., Zotz, G., & Reyes-García, C. (2014). Epiphytic orchids in tropical dry forests of Yucatan, Mexico -Species occurrence abundance and correlations with host tree characteristics and environmental conditions. *Flora*, 209, 100–109.

de la Rosa-Manzano, E., Guerra-Pérez, A., Mendieta-Leiva, G., Mora-Olivo, A., Martínez-Avalos, J. G., & Arellano-Méndez, L. U. (2017). Vascular epiphyte diversity in two forest types of "El Cielo" Biosphere Reserve, Mexico. *Botany*, 95, 599–610.

Díaz, I. A., Sieving, K. E., Pena-Foxon, M. E., Larrain, J., & Armesto, J. J. (2010). Epiphyte diversity and biomass loads of canopy emergent trees in Chilean temperate rain forests: A neglected functional component. *Forest Ecology and Management*, 259, 1490–1501.

Dufrêne, M., & Legendre, P. (1997). Species assemblages and indicator species: The need for a flexible asymmetrical approach. *Ecological Monographs*, 67, 345–366.

Einzmann, H. J. R., Beyschlag, J., Hofhansl, F., Wanek, W., & Zotz, G. (2015). Host tree phenology affects vascular epiphyte at the physiological, demographic and community level. *AoB Plants*, 7, plu073.

Ferro, I., & Morrone, J. J. (2014). Biogeographical transition zones: A search for conceptual synthesis. *Biological Journal of the Linnean Society*, 113, 1–12.

Flores-Palacios, A., & García-Franco, J. G. (2006). The relationship between tree size and epiphyte species richness: Testing four different hypotheses. *Journal of Biogeography*, 33, 323–330.

García-García, F., & Zarraluqui, V. (2008). A fog climatology for Mexico. *Die Erde*, 139, 45–60.

García-Suárez, M. D., Rico-Gray, V., & Serrano, H. (2003). Distribution and abundance of *Tillandsia* spp. (Bromeliaceae) in the Zapotitlán Valley, Puebla, México. *Plant Ecology*, 166, 207–215.

gbif.org (2019) GBIF Occurrence Download http://doi.org/10.15468/dl.ywhpmz

Gentry, A. H., & Dodson, C. H. (1987). Diversity and biogeography of neotropical vascular 470 epiphytes. *Annals of the Missouri Botanical Garden*, 74, 205–233.

González-Medrano, F. (2005). La vegetación. Diversidad florística y endemismos [Floristic diversity and endemisms]. In G. Sánchez-Ramos, G. Reyes-Castillo, & P. R. Dirzo (Eds.), *Historia natural de la Reserva de la Biósfera El Cielo, Tamaulipas, México* (pp. 88–105). Hong Kong: Universidad Autónoma de Tamaulipas.

Graham, E., & Andrade, J. L. (2004). Drought tolerance associated with vertical stratification of two co-occurring epiphytic bromeliads in a tropical dry forest. *American Journal of Botany*, 91, 699–706.

Hágsater, E., & Salazar, G. A. (1990). *Icones Orchidacearum 1: Orchids of Mexico, part 1*. México, D.F., Mexico: Herbario AMO.

Halffter, G. (1962). Preliminary explanation of the geographical distribution of the Mexican Scarabaeidae. *Acta Zoologica Mexicana*, 5, 1–17.

Halffter, G., & Morrone, J. J. (2017). An analytical review of Halffter's Mexican transition zone, and its relevance for evolutionary biogeography, ecology and biogeographical regionalization. *Zootaxa*, 4226, 1–46.

Hamilton, L. S. et al. (1995). *Tropical montane cloud forests*. New York, NY: Springer Verlag.

Harms, K. E., Condit, R., Hubbell, S. P., & Foster, R. B. (2001). Habitat associations of trees and shrubs in a 50-ha neotropical forest plot. *Journal of Ecology*, 89, 947–959.

Hemp, A. (2001). Ecology of the pteridophytes on the southern slopes of Mt. Kilimanjaro. II. Habitat selection. *Plant Biology*, 3, 493–523.

Hietz, P., & Hietz-Seifert, U. (1995). Composition and ecology of vascular epiphyte communities along an altitudinal gradient in central Veracruz, Mexico. *Journal of Vegetation Sciences*, 5, 487–498.

Hirata, A., Kamijo, T., & Saito, S. (2009). Host trait preferences and distribution of vascular epiphytes in a warm-temperate forest. *Journal of Plant Ecology*, 201, 247–254.

Hofstede, R. G., Dickinson, K. J., & Mark, A. F. (2001). Distribution, abundance and biomass of epiphyte-lianoid communities in a New Zealand lowland Nothofagus-podocarp temperate rain forest: Tropical comparisons. *Journal of Biogeography*, 28, 1033–1049.

Hsieh, T. C., Ma, K. H., & Chao, A. (2016). iNEXT: An R package for interpolation and extrapolation of species diversity (Hill numbers). *Methods in Ecology and Evolution*, 7, 1451–1456.

Hsu, C. C., Horng, F. W., & Kuo, C. M. (2002). Epiphyte biomass and nutrient capital of a moist subtropical forest in north-eastern Taiwan. *Journal of Tropical Ecology*, 18, 659–670.

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

Intergovernmental Panel on Climate Change. (2014). *Climate change: Impacts, adaptation, and vulnerability* (Fifth Assessment Report of the Intergovernmental Panel on Climate Change Cambridge). New York, NY: Cambridge University Press. doi:10.1017/CBO9781107415379

Jian, P. Y., Hu, F. S., Wang, C. P., Chiang, J. M., & Lin, T. C. (2013). Ecological facilitation between two epiphytes through drought mitigation in a subtropical rainforest. *Plos One*, *8*, e64599.

Juvik, J. O., & Ekern, P. C. (1978). *A climatology of mountain fog on Mauna Loa, Hawaii Island* (pp. 63, Hawaii Technical report No. 118). Manoa, HI: Water Resources Research Center, University of Hawaii.

Karger, D. N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R. W., . . . Immermann, N. E. et al. (2017). Climatologies at high resolution for the earth's land surface areas. *Scientific Data*, *4*, 170122.

Karger, D., Kluge, J., & Kessler, M. (2016). *Comparing species richness patterns of epiphytic and terrestrial ferns along elevational and latitudinal gradients*. In G. Zotz (Ed.), *Plants on plants—The biology of vascular epiphytes*. Cham, Switzerland: Springer.

Karmalkar, A., Bradley, R., & Díaz, H. (2011). Climate Change in Central America and Mexico: Regional Climate Model Validation and Climate Change Projections. *Climate Dynamics, 37*, 605–629.

Kershaw, J., Jr., Ducey, M. J., Beers, T. W., & Husch, B. (2016). *Forest Mensuration* (5th ed.). Hoboken, NJ: John Wiley & Sons.

Kessler, M. (2000). Elevational gradients in species richness and endemism of selected plant 498 groups in the central Bolivian Andes. *Plant Ecology*, *149*, 181–193.

Kessler, M., Herzog, S., Fjeldsa, J., & Bach, C. (2001). Species richness and endemism of plant and bird communities along two gradients of elevation, humidity and land use in the Bolivian Andes. *Diversity and Distribution*, *7*, 61–77.

Kessler, M., Kluge, J., Hemp, A., & Ohlemüller, R. (2011). A global comparative analysis of elevational species richness patterns of ferns. *Global Ecology and Biogeography*, *20*, 868–880.

Khine, P. K. (2018). Biogeographical transect studies in the high elevation mountain areas of Myanmar. (PhD. Thesis). Marburg, Germany: Philipps University.

Kluge, J., Bach, K., & Kessler, M. (2008). Elevational distribution and zonation of tropical pteridophyte assemblages in Costa Rica. *Basic and Applied Ecology*, *9*, 35–43.

Kluge, J., Kessler, M., & Dunn, R. R. (2006). What drives elevational patterns of diversity? A test of geometric constraints, climate and species pool effects for pteridophytes on an elevational gradient in Costa Rica. *Global Ecology and Biogeography*, *15*, 358–371.

Kreft, H., Köster, N., Küper, W., Nieder, J., & Barthlott, W. (2004). Diversity and biogeography of vascular epiphytes in Western Amazonia. *Yasuní. Ecuador. Journal of Biogeography*, *31*, 1463–1476.

Krömer, T., Kessler, M., Gradstein, R., & Acebey, A. (2005). Diversity patterns of vascular epiphytes along an elevational gradient in the Andes. *Journal of Biogeography*, *32*, 1799–1809.

Kruckeberg, A. R., & Rabinowitz, D. (1985). Biological aspects of endemism in higher plants. *Annual Review of Ecology and Systematics*, *16*, 447–479.

Larrea, M. L., & Werner, F. A. (2010). Response of vascular epiphyte diversity to different land-use intensities in a neotropical montane wet forest. *Forest Ecology and Management*, *260*, 1950–1955.

Laube, S., & Zotz, G. (2006). Neither host-specific nor random: Vascular epiphytes on three tree species in a Panamanian lowland forest. *Annals of Botany*, *97*, 1103–1114.

Leimbeck, R. M., & Balslev, H. (2001). Species richness and abundance of epiphytic Araceae on adjacent floodplain and upland forest in Amazonian Ecuador. *Biodiversity and Conservation*, *10*, 1579–1593.

Marshall, C. J., & Liebherr, J. K. (2000). Cladistic biogeography of the Mexican transition zone. *Journal of Biogeography*, *27*, 203–216.

Martin, C. E., McLeod, K. W., Eades, C. A., & Pitzer, A. F. (1985). Morphological and Physiological responses to irradiance in the CAM epiphyte *Tillandsia usneoides* L. (Bromeliaceae). *Botanical Gazzette*, *146*, 489–494.

Méndez-Castro, F. E., Bader, M. Y., Mendieta-Leiva, G., & Rao, D. (2018). Islands in the trees: A biogeographic exploration of epiphyte-dwelling spiders. *Journal of Biogeography*, *45*, 2262–2271.

Mendieta-Leiva, G., Porada, P., & Bader, M. Y. (in press). Chapter 11: Interactions of epiphytes with precipitation partitioning. J. Van Stan, E. Gutmann, & J. Friesen. (Eds.) *Precipitation partitioning by vegetation: A global synthesis*. Cham, Switzerland: Springer.

Moran, R. C. (2008). Diversity, biogeography, and floristics. In T. A. Ranker & C. H. Haufler 526 (Eds.), *Biology and evolution of ferns and lycophytes* (pp. 367–394). New York, NY: Cambridge University Press.

Morrone, J. J. (2010). Fundamental biogeographic patterns across the Mexican Transition Zone: An evolutionary approach. *Ecography*, *33*, 355–361.

Morrone, J. J. (2015). Biogeographical regionalisation of the Andean region. *Zootaxa*, *3936*, 207–236.

Nadkarni, N., & Solano, R. (2002). Potential effects of climate change on canopy communities in a tropical cloud forest: An experimental approach. *Oecologia*, *131*, 580–586.

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., . . . Wagner, H. (2017). Vegan: Community

ecology package (R package version 2.4-2). Retrieved from https://CRAN.R-project.org/package=vegan

Ornelas, J. F., Sosa, V., Soltis, D. E., Daza, J. M., González, C., Soltis, P. S. et al. (2013). Comparative phylogeographic analyses illustrate the complex evolutionary history of threatened cloud forests of Northern Mesoamerica. *PLoS ONE*, *8*(2), e56283.

Palmer, M. (2003). *Ordination methods for ecologists*. Retrieved from http://ordination.okstate.edu/envvar.htm

Peer, M. C., Finlayson, B. L., & McMahon, T. A. (2007). Updated world map of the Köppen-Geiger climate classification. *Hydrology and Earth System Sciences*, *11*, 1633–1644.

Perry, D. R. (1978). Factors influencing arboreal epiphytic phytosociology in Central America. *Biotropica*, *10*, 235–237.

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

Pittendrigh, C. S. (1948). The bromeliad-Anopheles-malaria complex in Trinidad. I. The bromeliad flora. *Evolution*, *2*, 58–89.

Ponce-Reyes, R., Reynoso-Rosales, V. H., Watson, J. E. M., VanDer Wal, J., Fuller, R. A., Pressey, R. L., & Possingham, H. P. (2012). Vulnerability of cloud forest reserves in Mexico to climate change. *Nature Climate Change*, *2*, 448–452.

R Development Core Team. (2018). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from https://www.r-project.org/

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

Robertson, K. M., & Platt, W. J. (2001). Effects of multiple disturbances (fire and hurricane) on epiphyte community dynamics in a subtropical forest, Florida, USA. *Biotropica*, *33*, 573–582.

Rojas-Soto, O. R., Sosa, V., & Ornelas, J. F. (2012). Forecasting cloud forest in eastern and southern Mexico: Conservation insights under future climate change scenarios. *Biodiversity and Conservation*, *21*, 2671–2690.

Rzedowski, J. (1996). Preliminary analysis of vascular flora of the montane mesophilous forests (cloud forest) of Mexico. *Acta Botánica Mexicana*, *35*, 25–44.

Salazar, L., Homeiera, J., Kessler, M., Abrahamczyk, S., Lehnertd, M., Krömer, T., & Kluge, K. (2013). Diversity patterns of ferns along elevational gradients in Andean tropical forests. *Plant Ecology & Diversity*, *8*, 13–24.

Sanchez, E. P., Armenteras, D., & Retana, J. (2016). Edge influence on diversity of orchids in andean cloud forests. *Forests*, *7*, 2–13.

Sánchez-Santillán, N., Binnqüist, C. G. S., & Garduño, L. R. (2018). Summer drought in the El Cielo Biosphere Reserve and its environment, Tamaulipas, Mexico. *Cuadernos de Geografía. Revista Colombiana*, *27*, 146–163.

Sanford, W. W. (1968). Distribution of epiphytic orchids in semideciduous tropical forest in southern Nigeria. *Journal of Ecology*, *56*, 697–705.

Sillett, S. T., & Bailey, M. G. (2003). Effects of tree crown structure on biomass of the epiphytic fern *Polypodium scouleri* (Polypodiaceae) in redwood forests. *American Journal of Botany*, *90*, 255–261.

Spruch, L., Hellwig, J., Zotz, G., & Blasius, B. (2019). Modelling community assembly on growing habitat "islands": A case study on trees and their vascular epiphyte communities. *Theoretical Ecology*. Advance online publication. doi:10.1007/s12080-019-0425-4

Stadtmüller, T. (1987). *Cloud forests in the humid tropics. A bibliographic review. The United Nations*. Tokyo, Japan: University Press.

Stein, A., Gerstner, K., & Kreft, H. (2014). Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. *Ecology Letters*, *17*, 866–880.

Stevens, G. C. (1992). The elevational gradient in altitudinal range—An extension of Rapoport's latitudinal rule to altitude. *American Naturalist*, *140*, 893–911.

Tang, L., Li, T., Li, D., & Meng, X. (2014). Elevational patterns of plant richness in the Taibai Mountain, China. *Scientific World Journal*, *2014*, 1–13.

Tews, J., Brose, U., Grimm, V., Tielborger, K., Wichmann, M. C., Schwager, M., & Jeltsch, F. (2004). Animal species diversity driven by habitat heterogeneity/diversity: The importance of keystone structures. *Journal of Biogeography*, *31*, 79–92.

Trejo-Torres, C. J., & Ackermann, J. D. (2001). Biogeography of the Antilles based on a parsimony analysis of orchid distributions. *Journal of Biogeography*, *28*, 775–794.

Vargas-Vázquez, V. A., Venegas-Barrera, C. S., Mora-Olivo, A., Martínez-Ávalos, J. G., Alanís-Rodríguez, E., & de la Rosa Manzano, E. (2019). Variation in the abundance of timber trees by edge effect in a tropical sub deciduous forest. *Botanical Sciences*, *97*, 35–49.

Vogelmann, H. W. (1973). Fog precipitation in the cloud forests of eastern Mexico. *Bioscience*, *23*, 96–100.

Wagner, K., Mendieta-Leiva, G., & Zotz, G. (2015). Host specificity in vascular epiphytes: A review of methodology, empirical evidence and potential mechanisms. *AoB Plants*, *7*, plu092.

Winkler, M., Hülber, K., & Hietz, P. (2005). Effect of canopy position on germination and seedling 580 survival of epiphytic bromeliads in a Mexican humid montane forest. *Annals of Botany*, *95*, 1039–1047.

Wolf, J. H. D. (2005). The response of epiphytes to anthropogenic disturbance of pine-oak forests in the highlands of

Chiapas, Mexico. *Forest Ecology and Management*, *212*, 376–393.

Wolf, J., & Alejandro, F. S. (2003). Patterns in species richness and distribution of vascular epiphytes in Chiapas, Mexico. *Journal of Biogeography*, *30*, 1689–1707.

Xu, H., & Liu, W. (2005). Species diversity and distribution of epiphytes in the montane moist evergreen broad-leaved forest in Ailao Mountain, Yunnan *Biodiversity Science*, *13*, 137–147.

Zotz, G., & Bader, M. (2009). Epiphytic plants in a changing world: Global change effects on vascular and non-vascular epiphytes. *Progress in Botany*, *70*, 147–170.

Zotz, G., & Hietz, P. (2001). The physiological ecology of vascular epiphytes: Current knowledge, open questions. *Journal of Experimental Botany*, *364*, 2067–2078.

Zotz, G. (2005). Vascular epiphytes in the temperate zones — a review. *Plant Ecology*, *176*, 173–183.

Zotz, G. (2007). The population structure of the vascular epiphytes in a lowland forest in Panama correlates with species abundance. *Journal of Tropical Ecology*, *23*, 337–342.

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