Title. Global Distribution of Vascular Epiphyte Diversity

Authors. Nora M. Cavanaugh[1,*], Amy E. Zanne[1,2,†], William K. Cornwell[3,†]

[1]Department of Biological Sciences, George Washington University, Washington, DC, 20009, USA

[2]Department of Biology, University of Miami, Coral Gables, FL, 33146, USA

[3]School of Biological, Earth & Environmental Sciences, University of New South Wales, Sydney, 2052, Australia

[*]corresponding author: nora.m.cavanaugh@gmail.com

[†]co-senior authors

Abstract.

Epiphytes are a large and understudied part of global diversity. Classic work by Gentry and Dodson argued that Neotropical, mid-elevation forests are centers of diversity for this growth form. We assessed this hypothesis with modern global geospatial and climatic datasets. By connecting growth form and occurrence data with climatic records at the same locations, we quantified spatial and climatic distributions of epiphyte species richness. Latitude was a powerful driver of epiphyte distributions, with peaks at the equator; here, epiphytes contributed significantly to vascular plant species richness with greatest prevalence at mid elevations and in the Neotropics. Climatically, precipitation was a stronger determinant than temperature as to where epiphytic species thrive. The study provides robust support for the hypotheses that plant diversity in Neotropical, mid-elevation forests is unusually concentrated in the epiphytic growth form, and the lower proportion of epiphytic diversity elsewhere may have both physiological or biogeographic explanations. The particular features of climate change in Neotropical mid-elevation habitats, and the implications for epiphyte diversity, are worthy of urgent research.

Keywords. Diversity, Elevation, Epiphyte, GAMs, Global, Latitude

Background

Shifts in plant growth forms across the world's continents and climates have long fascinated plant biogeographers. Geographic variation in growth form is evident in the vast variety of plant structures we observe globally, with key transitions from tropical to temperate regions [1]. Biogeographic patterns in the frequency of vascular epiphytes [2], where plants grow on other plants without roots in the soil (Figure 1), is an especially striking example [3]. Despite the long history of interest, epiphytic taxa remain among the most disproportionately undersampled plant groups, perhaps due to the difficult logistics of studying them [4].

Lacking soil access, epiphytic plants rely on atmospheric moisture and organic decay for water and nutrients [5]; many have adaptations, such as thick water-storing leaves, reduced photosynthesis rates, and CAM photosynthesis [6]. Their distinct nutrient and water strategies, combined with heightened exposure to the elements in tree canopies, make them sensitive to environmental changes [7]. At regional- to global-scales, temperature and precipitation are thought to be critical drivers of epiphyte abundance and species-richness determining their latitudinal and elevational distributions [7–9]. Regionally, epiphyte richness and relative abundance are highest in wet than dry or extremely wet forests [7]. Further, frost [8] and freezing events also limit epiphytes. These strong temperature and precipitation sensitivities are thought to produce steep latitudinal and elevational gradients in epiphyte presence and diversity, with peaks in low latitude forests. Interestingly, Gentry and Dodson [7] argued that the peak for epiphyte diversity is in mid-elevation tropical forests where epiphytes may account for as much as 30% of forest foliar biomass [7], while other works suggests regionally 39% of the vascular flora [9] may be epiphytes in some places.

Insights into global distributions of epiphytes have primarily been derived from plot sampling, lists from specific countries, and informal observations. For instance, the Neotropics are thought to have a higher epiphyte diversity than the Paleotropics, a notion attributed to biogeographic history of certain epiphyte clades [7,10,11]. But quantitative comparisons of relative epiphytic contributions to plant diversity remain largely unreported. Notably, key theories on epiphyte spatial and climatic distributions, including Gentry and Dodson's [7] tropical mid-elevation peak hypothesis, await testing.

Our study capitalizes on a large growth form database [12] with ~47% of named vascular plant species [13]; this dataset also includes true negatives, i.e. species that are known to not be epiphytes. Combining this database with global occurrence and climatic data, we modeled vascular epiphyte species richness over latitudinal, elevational, temperature and precipitation gradients to illuminate global trends of vascular epiphyte medians and limits. Specifically, we asked the following two questions:

1. Where do epiphytes contribute most to plant diversity? We hypothesized that epiphytes are most prevalent in tropical regions [9] at intermediate elevations in the Neotropics [7,10,11].

2. What are the spatial and climatic limits of the epiphytic growth form?

We hypothesized that as few epiphytes can survive freezing temperatures and low moisture, epiphyte diversity will rapidly decline outside of tropical warm, wet conditions. Building on Gentry and Dodson [7], we focus on the proportion of documented diversity that is epiphytic.

Methods

Growth Form Data

A global growth form database [12] for 143,616 vascular plant species from 445 families was used to classify growth form by species, including 21,110 epiphytic species. The Taseski *et al.* [12] database classifies each of the included species into one of seven growth forms: aquatic, obligate epiphytes, hemiepiphytes, climbing, parasitic, holo-mycoheterotrophic and free-standing. Following a definition of epiphytism from Madison [10] the database excludes 1) very rare, "accidental" epiphytes, 2) hemiepiphytes, and 3) haustorial parasites. We used the authors' static consensus "species-level" dataset to exclude taxa with variable growth forms.

Spatial and Bioclimatic Data

To establish species geographic midpoints and limits, we obtained georeferenced records for vascular plants from the Global Biodiversity Information Facility (GBIF) [14], totaling 168,516,597 records. Common data quality issues were cleaned via both the GBIF filters and Coordinate Cleaner [15]. After excluding select records around biodiversity institutions, 162,494,125 locations remained.

For all remaining locations, we extracted climate and elevation data from WorldClim v2.1 [16] (1970-2000) records of bioclimatic variables. We used records of annual mean temperature (BIO1) and precipitation (BIO12) to obtain estimates of bioclimatic variables for each record.

For both geographic and climatic distributions, we tested both midpoints (i.e., range centers as medians) and limits (i.e., range edges as maximum and minimum). For limits, we defined 'maximum' as the 97.5th percentile and 'minimum' as the 2.5th percentile. Locational data from GBIF were analyzed to obtain median latitude and maximum latitude and elevation for each species. The maximum of the absolute value of latitude (maximum absolute latitude) for each species was calculated to quantify how far from the equator species were observed. We analyzed minimum climatic values for each species. The cleaned dataset comprising records from all databases included 103,077 species, each of which had a record for growth form, minimum, median and maximum absolute latitude, median and maximum elevation, and minimum and median precipitation and temperature.

Analyses

Epiphyte spatial and climatic medians and limits were analyzed using Generalized Additive Models (GAMs), in which the linear dependent variable responds to smooth functions of predictor variables. A GAM approach serves as a middle ground between linear models and complex machine learning models for more closely fit outcomes; it does not make assumptions of linearity as for linear models, while allowing for greater interpretation of the resulting model compared to prediction-focused machine learning approaches.

The GAM models were logistic, assuming a binomial distribution and log-link. For more intuitive visualization, the log-odds scales were transformed to probability. Smoothing parameters were selected using the Restricted Maximum Likelihood (REML). The number of basis functions, k, was 3 for all GAMs to avoid overfitting and model biologically reasonable smoothed relationships [17]. Smoothers were applied to all predictor variables, as environmental factors rarely have linear relationships with ecological response variables. Concurvity, a generalization of collinearity for nonlinear models, was assessed [18]). We investigated the relative importance of spatial and climatic medians and limits explaining epiphyte distributions. We present models with 1, 2, 3, and 5 predictors (mean annual precipitation, mean annual temperature, maximum absolute latitude, elevation, and continent) and compare percentage deviance explained among models. More complex climate variables were also considered but to avoid strongly covarying predictors and compare with literature predictions, we focused on these 5 variables. Models were run for both distribution midpoints and limits. We used the "mgcv" package [19] of the R program [20].

Results

Overall, of the plants around the globe for which we identified growth form, 10.6% were epiphytes.

Global Median Distribution of Epiphytes

Epiphytes contributed the most to vascular plant diversity in the Neotropics near the equator at intermediate elevations, <2000 mn; from GAM analyses with three predictors (continent, latitude and elevation) estimates, for species whose range medians were close to the equator at 2000 m elevation in the Neotropics 54.8% were epiphytes (Figure 2A; Table S1). This is higher than any other considered environment in the world. For the same elevation at the equator in the Paleotropics, the estimate was 31.2%. Away from the equator, the proportion of epiphyte species declines steeply into both northern and southern hemispheres. At the tropical limits (i.e., the tropic of cancer and capricorn) and 2000 m, the estimates were 20.1% epiphytes for the Neotropics and 8.6 % for the Paleotropics. Climatically, vascular epiphytes contributed most to plant diversity at intermediate precipitation, peaking between 3500 and 4000 mm, and intermediate temperatures, peaking just over 15°C (Figure 2B; Table S1). The single strongest predictor was latitude followed by precipitation and then continent (Neotropics versus Paleotropics) (Table S1).

Geographic and Climatic Limits to the Distribution of Epiphytes Compared to Non-Epiphytes

At cold temperatures, few species were epiphytes, while the proportion of epiphytic species increased rapidly towards warmer climates (Figure 2B). 96.7% of epiphytic species had latitudinal limits at ~30° or less; 98.4% of species had elevational limits at ~4000 m or less (Figure 2C). Of the models with only one predictor, the maximum absolute latitude explained the most deviance followed by minimum annual precipitation, minimum temperature of the coldest month and maximum elevation (Table S1). An additive minimum climatic model including minimum annual precipitation and minimum temperature of the coldest month explained 14.7% deviance, which was less than the best single spatial predictor (maximum absolute latitude at 17.7% deviance; Table S2). For both temperature and precipitation minimum values explained more deviance than maximum values (Table S1).

Discussion

Epiphytes are rule breakers. While most plants reach from the soil towards the sun, epiphytes remain detached from the ground, high in canopies, constantly exposed to the elements without moisture reserves from the soil to buffer dry periods. The rules epiphytes break and the necessary survival strategies they acquired dictate where they survive. In this global data-driven study, we find quantitative support for Gentry and Dodson's [7] hypothesis that the peak contribution of epiphytes to total plant diversity occurs in mid-elevation tropical montane cloud forests (TMCF) in the Neotropics. Gentry and Dodson [8] called this pattern a "somewhat tenuously established trend", but the data here strongly support it. They also wrote, "In the Andes, the peak in epiphyte diversity appears to be between 1,000 m and 2,000 m". Our analysis of the mid-point of species ranges (Figure 2A) suggests a peak close to the upper end of their postulated range.

As previously suggested by Taylor *et al.* [9], of the considered predictors, latitude shaped epiphyte distribution more than any other variable. Epiphytes made up almost 40% of those vascular plant species with distributions limited to the equator. Epiphyte species' distributions rapidly declined away from the equator; this pattern was true for latitudinal medians and limits.

In addition to latitude, continent was also an important predictor with much diversity higher in the Neotropics; this is consistent with plot and country list studies [7,9–11]. Based on our results, the pattern may be driven by greater availability of mid-elevation area near the equator (Table 1) leading to considerably more area at ideal epiphyte conditions in the Neotropics. Along these lines, Gentry and Dodson [8] speculated that higher meso- and micro-site diversity within the Andes compared to the Paleotropic mountains may have led to especially high beta diversity in the Neotropics. This difference in areas of high elevation habitat close to the equator may have generated epiphyte diversity and/or maintained it through historical climate changes [7].

In models of proportion of epiphytes with median precipitation and temperature, temperature had a hump-shaped relationship with a peak around 20°C. For precipitation, these models predicted a monotonic increase. Interestingly, few epiphytes were present at high temperatures even when the rainfall is very high both in the Neo- and Paleotropics, perhaps due to episodic high vapor pressure deficit. Also, few epiphytes occurred below freezing temperatures, although minimum temperature did not explain as much deviance as minimum annual precipitation.

Our results here for distributions of epiphytes and tropical montane cloud forests (TMCFs) appear to share closely aligned climatic boundaries, with understanding of climatic limits for both being vital with changing climates. The definition of TMCF varies throughout the literature, but consistently they may be recognized by cloud cover [21], which suppresses vapour pressure deficit. Most TMCFs are found within a narrow band of elevation (~2000m and 3500m), although several exist lower [21]. Our results suggested overlapping temperature preferences for epiphytes and TMCFs; a quantitative analysis of epiphyte ranges could be a powerful and objective way to approach conservation of this complex and diverse ecosystem.

Conclusions

An understanding of epiphyte distribution and ecology has long been a challenge as they live their lives well above our heads, beyond our notice. However, given large epiphyte contributions to species diversity in particular regions, an understanding of where epiphytes exist and what shapes their distribution is critical. Depending on how they are impacted by climate change, we run a risk of losing these taxa before we understand their climatic distribution of epiphytes [22].

Acknowledgements. The authors thank the Zanne lab for comments on earlier drafts.

Funding. This work was supported by George Washington University, Department of Biological Sciences Harlan undergraduate research program (NMC).

References.

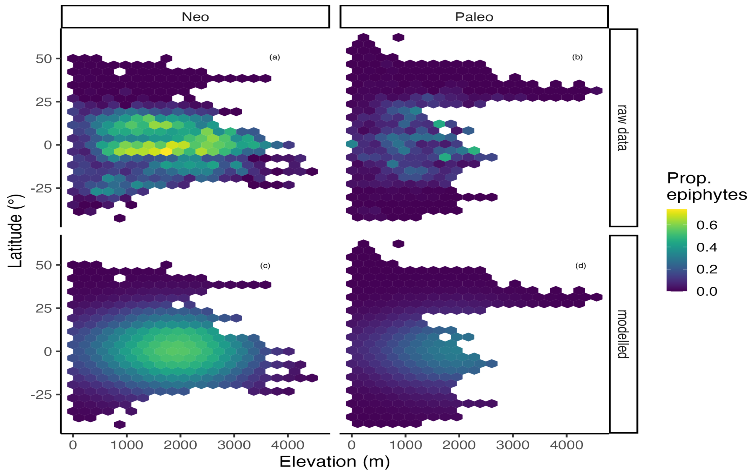
1. Zanne AE *et al.* 2014 Three keys to the radiation of angiosperms into freezing environments. *Nature* **506**, 89–92.
2. Benzing DH. 1987 Vascular epiphytism: taxonomic participation and adaptive diversity. *Ann. Mo. Bot. Gard.* , 183–204.
3. Schimper AFW. 1888 *Die epiphytische vegetation Amerikas*. Fischer.
4. Cornwell WK *et al.* 2014 Functional distinctiveness of major plant lineages. *J. Ecol.* **102**, 345–356.
5. Jansky SH, Roble J, Spooner DM. 2016 *Solanum clarum* and *S. morelliforme* as novel model species for studies of epiphytism. *Front. Plant Sci.* **7**, 231.
6. Hietz P *et al.* 2022 Putting vascular epiphytes on the traits map. *J. Ecol.* **110**, 340–358.
7. Gentry AH, Dodson C. 1987 Diversity and biogeography of neotropical vascular epiphytes. *Ann. Mo. Bot. Gard.* **74**, 205–233.
8. Zotz G. 2005 Vascular epiphytes in the temperate zones–a review. *Plant Ecol.* **176**, 173–183.
9. Taylor A, Zotz G, Weigelt P, Cai L, Karger DN, König C, Kreft H. 2022 Vascular epiphytes contribute disproportionately to global centres of plant diversity. *Glob. Ecol. Biogeogr.* **31**, 62–74.
10. Madison M. 1977 Vascular epiphytes: their systematic occurrence and salient features. *Selbyana* **2**, 1–13.
11. Couvreur TL. 2015 Odd man out: why are there fewer plant species in African rain forests? *Plant Syst. Evol.* **301**, 1299–1313.
12. Taseski GM, Beloe CJ, Gallagher RV, Chan JY, Dalrymple RL, Cornwell WK. 2019 A global growth-form database for 143,616 vascular plant species. *Ecology.* e02614
13. Christenhusz MJ, Byng JW. 2016 The number of known plants species in the world and its annual increase. *Phytotaxa* **261**, 201–217.
14. GBIF.org (16 June 2022) GBIF Occurrence Download https://doi.org/10.15468/dl.qzwbba
15. Zizka A *et al.* 2019 CoordinateCleaner: Standardized cleaning of occurrence records from biological collection databases. *Methods Ecol. Evol.* **10**, 744–751.
16. Fick SE, Hijmans RJ. 2017 WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *Int. J. Climatol.* **37**, 4302–4315.
17. Duursma RA, Falster DS. 2016 Leaf mass per area, not total leaf area, drives differences in above-ground biomass distribution among woody plant functional types. *New Phytol.* **212**, 368–376.
18. Wood S.N., N. Pya and B. Saefken (2016) Smoothing parameter and model selection for general smooth models (with discussion). *J. of the Amer. Stat Assoc* **111**,1548-1575.
19. Ross N. In press. GAMs in R: A Free, Interactive Course using mgcv.
20. R Core Team. 2022 R: A language and environment for statistical computing.
21. Aldrich M, Billington C, Edwards M, Laidlaw R. 1997 Tropical montane cloud forests: an urgent priority for conservation. *WCMC Biodivers. Bull.* **2**, 1–14.
22. Ramírez-Barahona S, Cuervo-Robayo ÁP, Feeley K, Ortiz-Rodríguez A, Vásquez-Aguilar A, Ornelas JF, Rodríquez-Correa H. 2021 Climate change and deforestation drive the displacement and contraction of tropical montane cloud forests.

Table 1. Area of land (km^2) in different elevation bands from 0-5000 m above sea level in the Neotropics versus Paleotropics (with the tropics defined as between tropic of cancer and tropic of capricorn). Data from WorldClim v2.1. Note that the high elevation Himalaya and Tibetan Plateau in Paleo landmasses fall outside of the tropics by this definition.

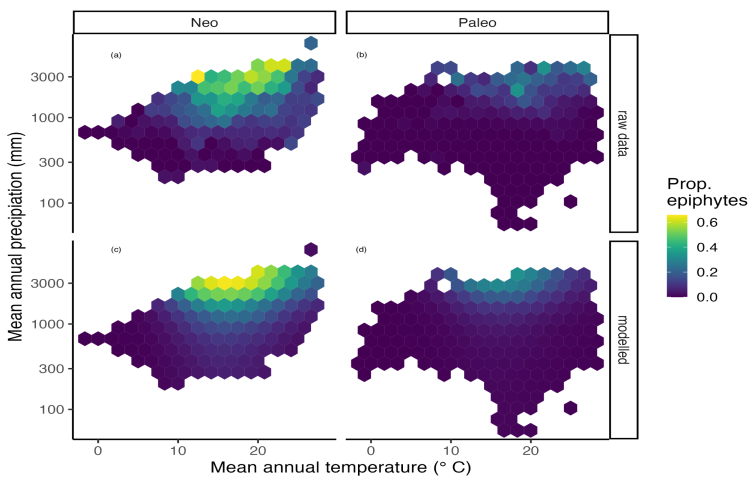
Elevational bands (m)	Neotropics	Paleotropics
0-1000	13,185,033	29,006,359
1000-2000	902,479	5,472,605
2000-3000	462,335	358,880
3000-4000	393,835	31,096
4000-5000	297,012	979

Figure 1. Epiphytic bromeliad (*Tillandsia caloura)* overlooking cloud forest on the Sierra Nevada de Santa Marta, Colombia (Photo: Riley Fortier, Identification: Julian Andres Aguirre Santoro https://www.inaturalist.org/observations/187959544).

A.



B.



C.

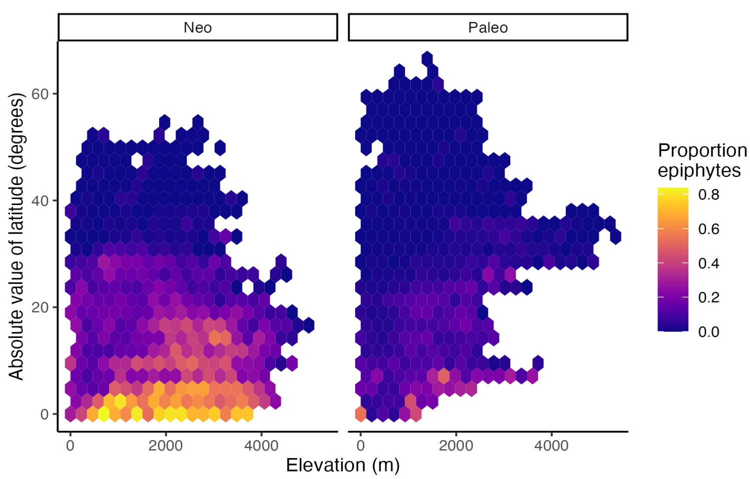


Figure 2. Proportion of epiphytes for all species median distributions with respect to A. elevation, latitude, and continent. The large amount of very high elevation area (Table 1) from

25-35 N latitude in the Paleotropics is principally the Himalayas and Tibetan Plateau. In the Neotropics, the large high elevation areas are principally the Andes. B. MAP (log scale), MAT, and continent. Panels (left) are raw data and (right) are modeled distribution with 3-predictor GAMs. C. Proportion of epiphytes for all species with limit distributions with respect to elevation, the absolute value of latitude, and continent. Panels are modeled distribution with 3-predictor GAMs. Bins with fewer than 20 species were excluded from the visualization.

Supplementary Materials.

Table S1. The single predictor models for proportion of epiphytes. Maximum is the 97.5% quantile of observations, minimum is the 2.5% quantile of observations representing a statistical estimate of the species range limit either spatially or climatically. Continent, which is a binary variable, is not a smoothed term. Precipitation is the mean annual precipitation and temperature is the mean annual temperature from Worldclim.

Quantile and Model	EDF	Deviance explained (%)
Median		
Latitude	2	16
Elevation	1.999	5.38
Precipitation	1.999	11.7
Temperature	1.999	3.22
Continent		9.1
Maximum		
Abs. Value Latitude	1.996	17.7
Elevation	1.998	1.88
Precipitation	2	8.1
Temperature	2	1.9
Minimum		
Precipitation	1.999	12.5
Temperature	1.997	7.76

Table S2. Multi-predictor models for proportion of epiphytes. Maximum is the 97.5% quantile of observations, minimum is the 2.5% quantile of observations representing a statistical estimate of the species range limit either spatially or climatically. Precipitation is the mean annual precipitation, and temperature is the mean annual temperature from Worldclim.

Quantile and Model	EDF	Deviance explained (%)
Median spatial and climatic		
Overall		24.5
Latitude	1.999	
Elevation	1.762	
Precipitation	1.997	
Temperature	1.998	
Maximum spatial, minimum climatic		
Overall		22.9
Latitude	1.976	
Elevation	1.997	
Precipitation	1.996	
Temperature	1.984	
Median spatial		
Overall		21
Latitude	2.000	
Elevation	1.999	
Median climatic		
Overall		15.8
Precipitation	1.999	
Temperature	1.999	
Maximum spatial		
Overall		20.4

Latitude	1.995	
Elevation	1.999	
Minimum climatic		
Overall		14.7
Precipitation	1.999	
Temperature	1.999	