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EDITED BY

Glenda Mendieta Leiva,
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REVIEWED BY

Philipp Porada,
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Academy of Sciences of the Czech
Republic (ASCR), Czechia
Klaus Mehlreter,
Instituto de Ecología (INECOL), Mexico

*CORRESPONDENCE

Liang Song
songliang@xtbg.ac.cn
Alain Vanderpoorten
a.vanderpoorten@uliege.be

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What makes a good phorophyte? Predicting occupancy, species richness and abundance of vascular epiphytes in a lowland seasonal tropical forest

Ting Shen^{1,2,3,4}, Liang Song^{1,5*}, Flavien Collart³,
Antoine Guisan^{3,6}, Yang Su⁷, Hai-Xia Hu^{1,8}, Yi Wu¹,
Jin-Long Dong^{1,8,9} and Alain Vanderpoorten^{2*}

¹CAS Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Mengla, Yunnan, China, ²Institute of Botany, University of Liège, Liège, Belgium, ³Department of Ecology and Evolution, University of Lausanne, Lausanne, Switzerland, ⁴Center for Integrative Conservation, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Mengla, Yunnan, China, ⁵Ailaoshan Station for Subtropical Forest Ecosystem Studies, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Jingdong, China, ⁶Institute of Earth Surface Dynamics, University of Lausanne, Lausanne, Switzerland, ⁷UMR ECOSYS, INRAE AgroParisTech, Université Paris-Saclay, Thiverval-Grignon, France, ⁸University of Chinese Academy of Sciences, Beijing, China, ⁹National Forest Ecosystem Research Station at Xishuangbanna, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Mengla, Yunnan, China

Epiphytes typically exhibit clustered distribution patterns, but predicting the spatial variation of their distribution at fine scales has long been a challenge. Taking advantage of a canopy crane giving access to 1.1 ha of lowland seasonal rainforest in Yunnan (China), we assess here which factors promote the probability that a given tree hosts epiphytes, and the variation of species richness and abundance of epiphytic spermatophytes and ferns among trees. Variation in epiphyte species richness as a function of host tree size, characteristics of its surrounding environment, topography and microclimatic conditions, were analyzed by Random Forest. Epiphytic spermatophytes and ferns occupied 2.3 and 10.8% of the available host trees, respectively. Significant models predicting which trees are more likely to host epiphytes than others were obtained, indicating that host tree characteristics and their local environment play a significant role in determining which host tree is most likely to be colonized. These models, as well as models for species richness and abundance, however, exhibited a moderate to low accuracy (r^2 0.28 and 0.24 and of 0.12 and 0.14 for spermatophyte and fern richness and abundance, respectively). The best predictor of the presence of epiphytes on a tree, of its epiphytic species richness and abundance, was its DBH. In ferns, however, two peaks of species richness were observed, representing shade-loving ferns on small trees and sun-loving ferns on large trees. Microclimatic conditions and light intensity were the second best factor accounting for variation in species

richness and abundance among trees. The contribution of liana infestation, host tree identity, and characteristics of neighboring trees were marginal. Our inclusion of a large number of host-tree characteristics and their local environment did not allow for an apparent improvement of model accuracy over studies with a more limited number of predictors, pointing to the role of chance upon tree colonization. Our results confirm the utmost importance of large trees with emergent canopies for the conservation of the epiphytic flora, but also indicate that epiphytic diversity assessments in tropical forests must also include small understorey trees, which should be further considered for conservation. The importance of the micro-climatic conditions that prevail at the level of each individual host tree further points to the necessity of maintaining a buffer zone around large host trees targeted for conservation.

KEYWORDS

vascular epiphytes, colonization, richness, abundance, microclimate, conservation, forest canopy

Introduction

Forest canopy harbors 40–50% of the global terrestrial biodiversity, of which nearly 10% is restricted to this specific environment (Ozanne et al., 2003; Basset et al., 2012). The so-called “last biological frontier” (Lowman and Nadkarni, 1995; Stork et al., 1997; Lowman and Rinker, 2004) has been considered as one of the most diverse, but little-known habitats in the biosphere (Lowman and Schowalter, 2012). If forest canopy science has indeed been an active discipline since the nineteenth century, its progress has been slow, partly due to the limited accessibility of canopies. Since 1990, the development of a canopy crane network, presently operating at 22 locations around the globe, has substantially boosted research on the biodiversity and functioning of forest canopies (Nakamura et al., 2017).

Among the wide array of organisms occurring in canopies, epiphytes represent approximately 10% of vascular plant diversity (Zotz et al., 2021). At the interface between atmosphere and forest canopy, they are exposed to harsh conditions of temperature and humidity, are physiologically dependent on rainfall for water and nutrient supply, and are, hence, extremely sensitive to climatic conditions (Nadkarni, 2010).

Vascular epiphytes comprise about 28,000 species, of which 68% are orchids and 10% are ferns. They typically occur on different parts of their host tree, with orchids prevailing in the outer canopy, whereas hygrophilous ferns dominate in the lower strata (Zotz, 2016). These patterns reflect the sharp gradients in light, micro-climatic conditions, and physical properties of the substrate, such as bark texture and physico-chemistry, branch orientation and diameter, which prevail from the base to the uppermost canopy (ter Steege and Cornelissen, 1989). These conditions further vary along horizontal gradients due to

both extrinsic and intrinsic factors. Intrinsic factors include the successive ontogenetic stages of development of the host tree, during which variation in tree architecture, bark characteristics, canopy soil chemistry, microclimate conditions and host tree size occur (Taylor and Burns, 2015), but also among tree species with different branching architecture, bark texture and physico-chemistry (Hidasi-Neto et al., 2019). Therefore, host specificity has been reported in many instances (Sáyago et al., 2013; Zhao et al., 2015; Hayward et al., 2017; Wang et al., 2017; Adhikari et al., 2021). Determining the degree of host specificity is important in a conservation context because specialist species are generally more vulnerable to habitat alterations and climate change than generalist species, and host specialists, in particular, are threatened by coextinction with their hosts (Wagner et al., 2015). Host specificity is, however, complex to demonstrate and, if applicable, control for, especially in tropical rainforests, which typically host hundreds of tree species. Furthermore, host tree identity cannot be analyzed independently from all other factors that jointly shape epiphyte distributions (Wagner et al., 2015).

Extrinsic factors include the direct environment of the host tree, which may further contribute to account for epiphytic distribution patterns. Such factors include local light and micro-climatic conditions at the focal tree, which may be influenced by tree height and size (Baker et al., 2014), tree density (Von Arx et al., 2013), tree species (Kovács et al., 2017), the distance to neighbor trees, and topography (Bramer et al., 2018). If the impact of climatic variation on epiphytes has been evidenced at regional scales through analyses of elevational diversity patterns (Nadyeina et al., 2014; Reina-Rodríguez et al., 2016; Eaton et al., 2018; Flores-Tolentino et al., 2020), and at local scales through analyses of the vertical stratification of epiphytic species distributions within trees (Krömer et al., 2007; Woods et al., 2015; Murakami et al., 2022), relatively

little is known about the importance of fine-scale variation in climatic conditions between individual host trees on the distribution of epiphytes (Toivonen et al., 2017). As a matter of fact, predicting whether a given tree is likely to host epiphytes, and the factors promoting epiphytic species richness remains challenging. In many instances, even large, old trees lack any epiphytes. Johansson (1974), Zotz et al. (1999) and Zotz and Vollrath (2003) reported epiphytic occupancy rates of about 50% in tropical forests, raising the question of the factors driving host tree selection by epiphytes. While epiphytes typically exhibit non-random, clustered distribution patterns (Nieder et al., 2000; Seto et al., 2020; but see Hirata et al., 2008), models attempting at predicting which trees are more likely to be colonized than others, and how epiphytes species richness varies, typically exhibit low predicting power, which has been interpreted in terms of the role of chance during epiphytic dispersal and tree colonization (Zotz and Vollrath, 2003; Zotz and Schultz, 2008).

Here, we took advantage of a tropical canopy crane facility to conduct a comprehensive census of vascular epiphytes and record detailed information on both the intrinsic factors of each individual tree and extrinsic factors describing their environment. In particular, the prime importance of microclimates actually experienced by organisms has been increasingly acknowledged (De Frenne et al., 2021), but it is only recently that microclimatic conditions have been monitored, modeled and used to explain the spatial variation of epiphyte distributions (Murakami et al., 2022; Shen et al., 2022). In this framework, we address the following questions: (1) if epiphytes are not randomly distributed among trees, to what extent can we, using a comprehensive description of the characteristics of individual trees and their local environment, predict which trees are likely to host epiphytes and which trees are not, and how epiphytic species richness and abundance vary among individual trees? What are the variables involved? (2) How do these patterns vary between epiphytic ferns and epiphytic spermatophytes? (3) Which management strategies can be accordingly proposed to promote the conservation of vascular epiphytes?

Material and methods

Study site and sampling design

This study took place in a pristine lowland seasonal rainforest within the core area of Mengla subdistrict (101°35'E, 21°37'N), Xishuangbanna National Natural Reserve in Yunnan, SW China. Mean monthly relative humidity and mean monthly temperature recorded by 12 dataloggers at 2 m during 2017–2019 were 95.3% (minimum of 90.3% in June and maximum of 98.3% in July) and 20.8°C (minimum of 15.8°C in January and maximum of 25.2°C in June), respectively. This site offers

the unique opportunity to explore epiphyte diversity along entire trees, up to 70 m, thanks to a canopy crane. The crane provides access to 1.1 ha, wherein 8,477 healthy individuals of 297 tree species were reported by the Xishuangbanna Station for Tropical Rainforest Ecosystem Studies (XTRES) in 2019. The emergent tree layer (30–70 m high) is dominated by *Parashorea chinensis*, which reaches 45–70 m, and a layer of 30–45 m high trees, such as *Canarium album*, *Pometia tomentosa*, *Sloanea tomentosa*, *Semecarpus reticulata* and *Nephelium chryseum*. The canopy layer (18–30 m high) is mainly comprised of *Barringtonia fuscicarpa*, *Diospyros hasseltii*, *Drypetes hoensis*, and *Pseuduvaria indochinensis*. The understorey layer (6–18 m) high is composed of *Cleidion brevipetiolatum*, *Dichapetalum gelonioides*, *Diospyros xishuangbannaensis*, *Garcinia cowa*, and *Pittosporopsis kerrii*.

We focused on 1,334 individual trees (excluding tree ferns) belonging to 47 species with a diameter at breast height (DBH) greater than 5 cm. Each individual (or selected leaves or flowers in the case of rare species) of vascular epiphyte was collected and identified in the herbarium of Restoration Ecology Group, CAS Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden.

The vertical location of epiphytes was measured using a tape from the gondola of the canopy crane. An occupancy rate was computed as the number of trees occupied by at least one individual fern or one individual spermatophyte, respectively, divided by the total number of trees (1,334). We also partitioned this occupancy rate by DBH class, using three DBH classes as defined by Bradford and Murphy (2019): small (DBH < 30 cm), medium-sized (DBH ≥ 30 and < 70 cm), and large (DBH ≥ 70 cm).

Environmental variables

Thirty-eight variables, including 6 intrinsic tree variables and 32 extrinsic variables describing the local environment of each tree, were recorded (Table 1). Intrinsic factors included size (DBH, height (Z), and tree layer (1) emergent (30–70 m high), (2) canopy (18–30 m high), (3) understorey (6–18 m high), canopy width (W1: largest length of canopy crown; W2: canopy length perpendicular to W1), and canopy crown area ($\pi/4 \cdot W1 \cdot W2$), taxonomic identity, and relative abundance of individual host-tree species (Supplementary Table 2). Extrinsic factors included 32 variables describing the environment of each host tree. The mangling index (M) defines the probability that the focal tree belongs to the same species as its four nearest neighbors. The dominance index (U) defines the relationship between the DBH of the focal tree and its four nearest neighbors, describing whether a focal tree is larger or smaller than its neighbors (Zhang et al., 2018). The average distance between the focal tree and its four nearest-neighbor trees (meanDist) was computed to characterize geographic isolation. These variables

TABLE 1 Environmental variables used to predict the probability of occurrence, species richness and abundance of epiphytic spermatophytes and ferns on individual trees in a 1.1 ha tropical rainforest (Yunnan, SW China).

Environmental variables	Definition
DBH	Diameter at breast height (m) at 1.3 m above ground
Z	Tree height (m)
Canopy area	Canopy crown area (m ²), measured as $\pi/4 \cdot W1 \cdot W2$. W1: largest length of canopy crown. W2: canopy length perpendicular to W1
Proportion	Proportion of each tree species among all tree individuals
Tree layer	Categorical variable describing whether an individual tree is an emergent (30–70 m high), canopy (18–30 m high) or understorey (6–18 m high) tree
Tree species	Taxonomic identity of host tree species
M	Mangling index (probability that the focal tree belongs to the same species as its four nearest neighbors)
U	Dominance index (relationship between the size of the focal tree and its four nearest neighbors, describing whether a focal tree is larger or smaller than its neighbors)
meanDist	Average distance (m) between the focal tree and its four nearest-neighbor trees
X	x-coordinate (m)
Y	y-coordinate (m)
Illumination index	1: no direct light, 2: < 10% of lateral light, 3: 10–90% of overhead light, 4: \geq 90% overhead light, 5: crown completely exposed
Liana infestation	Categorical index (0–5) describing whether a tree is liana-free to fully invaded
Elevation	Elevation (m)
TPI	Topographic position index (relative topographic position of a focal tree as the difference between its elevation and the mean elevation of all other trees)
Slope	Slope ($^{\circ}$) of the ground at the level of each focal tree
Eastwest	East/west orientation of the ground at the level of each focal tree; value from -1 (West) to 1 (East)
Northsouth	North/south orientation of the ground at the level of each focal tree; value from -1 (South) to 1 (North)
MeanT	Annual average temperature
MeanRH	Annual average relative humidity
MeanL	Annual average light intensity
MeanPAR	Annual average photosynthetic active radiation
MaxT	Annual maximum of temperature
MaxRH	Annual maximum of relative humidity
MaxL	Annual maximum of light intensity
MaxPAR	Annual maximum of photosynthetic active radiation
MinT	Annual minimum of temperature
MinRH	Annual minimum of relative humidity
MinL	Annual minimum of light intensity
MinPAR	Annual minimum of photosynthetic active radiation
RangeT	Annual temperature range
RangeRH	Annual range of relative humidity
RangeL	Annual range of light intensity
RangePAR	Annual range of photosynthetic active radiation
SDT	Standard deviation of annual temperature
SDRH	Standard deviation of annual relative humidity
SDL	Standard deviation of annual light intensity
SDPAR	Standard deviation of annual photosynthetic active radiation

were computed using the nnIndex and fsasN4 functions from the forestSAS package (Chai, 2021). The crown illumination index was divided into 5 scales (1: no direct light, 2: < 10% of lateral light, 3: 10–90% of overhead light, 4: \geq 90% overhead light, 5: crown completely exposed, Dawkins and Field, 1978). Liana infestation was evaluated using Rutishauser et al. (2011)

index (0–5). The X-Y coordinates of each tree were obtained from the XTRES. A topographic map (Elevation) was produced with the raster package (Hijmans, 2021) from measurements made by the autopilot vehicle (LiAIR VUX-1350, Beijing, China) equipped with VUX-1UAV Laser (RIEGL Laser Measurement Systems GmbH, Horn, Austria) at 10 m intervals. This 10

m resolution topographic map was employed to derive the topographic position index (TPI, characterizing the relative topographic position of each focal tree as the difference between its elevation and the mean elevation of all other trees (Gallant and Wilson, 2000), the slope (in degrees), and the orientation (Eastwest and Northsouth, in radiant) by SAGA-GIS v7.9.1. Light intensity ('L', W/m^2), air temperature ('T', °C), relative humidity ('RH', %) and photosynthetic active radiation ('PAR', $\mu mol \cdot m^{-2} \cdot s^{-1}$) were recorded at 1-hr intervals from 12 trees at five height zones (tree base, middle trunk, inner canopy, middle canopy and outer canopy) from July 2017 to December 2019. To predict the spatial variation of light and microclimatic conditions from the data collected by 54 dataloggers, we modeled hourly variation in T, L, RH and PAR in an X-Y-Z space (thus including tree height and elevation) using Random Forest (Shen et al., 2022) as implemented by the randomForest package (Liaw and Wiener, 2002) in R v4.0.4 (R Core Team, 2021). The microclimatic conditions that prevail on each tree substantially vary from the base to the canopy. Between 2 and 62 m above ground, day (8 a.m.–7 p.m.) relative humidity ranged between 53.6 and 99.9% and day temperature between 12.0 and 31.7°C (Shen et al., 2022), challenging the description of the global microclimatic conditions that prevail at each host tree. Each epiphytic fern and spermatophyte community was, however, restricted to a specific height zone on a tree (Figure 1B). To best characterize the microclimatic conditions that prevail at the level of each community, we determined the “centroid” point, i.e., the average height, at which epiphytic spermatophytes and ferns, respectively, were recorded. The climatic conditions prevailing at the “centroid” of each of the 1,344 trees were summarized using several statistics, including the annual average (meanT, meanRH, meanPAR, meanL), maximum (maxT, maxRH, maxPAR, maxL), minimum (minT, minRH, minPAR, minL), range (difference of maximum and minimum rangeT, rangeRH, rangePAR, rangeL), and standard deviation (SDT, SDRH, SDPAR, SDL).

Statistical analyses

All statistical analyses were conducted in R v 4.0.4 (R Core Team, 2021). To test the null hypothesis that epiphytes are randomly distributed among trees, we randomized 1,000 times the distribution of epiphyte individuals across the 1,334 host trees and computed 1,000 random occupancy rates. Based on this, we determined whether the observed occupancy rate significantly differed from values expected by chance, i.e., whether the observed occupancy rate was lower than 95% of the 1,000 random occupancy rates. To control for DBH, we assigned each individual tree to one of three DBH classes and repeated the above procedure for each DBH class.

To determine whether a given tree is likely to be occupied by epiphytes, how many epiphytic species it is likely to

host and at which abundance, we applied classification and regression Random Forest, respectively, using the randomForest package (Liaw and Wiener, 2002). Predictors included the 9 intrinsic and 32 extrinsic factors listed above, respectively. We computed Pearson's correlation coefficients (r) among each pair of predictors (Supplementary Figure 1). To avoid multicollinearity issues, one predictor in a pair correlated at r higher than $|0.7|$ was kept (Dormann et al., 2013). We took advantage of the ability of Random Forest to handle large numbers of predictors (Speiser et al., 2019). As our goal was to find which factors affect variation in species richness for interpretation purposes rather than to develop a prediction model, we kept all variables (except the correlated ones to avoid multicollinearity) in the model, and ranked them by importance, i.e., their contribution to the model. The contribution of the retained predictors to the model was measured by the mean decrease in accuracy for classification and the mean decrease in node impurity for regression models, respectively (Liaw and Wiener, 2002). These metrics characterize the difference in accuracy between full models and models, wherein individual variables are successively removed. High, positive values characterize variables that substantially contribute to the model, whereas negative values characterize variables that do not contribute to the model.

To evaluate the models, we applied 100 repeated split-sampling cross-validation, where 70% of the data are used to calibrate the models and the remaining 30% to compute the different evaluation metrics from the “train” function of the caret package (Kuhn, 2021). We set the number of trees to 1,000. We computed the average, across the 100 cross-validation replicates, of the following statistics to evaluate model accuracy: sensitivity (true positive rate, ranging between 0 and 1), specificity (true negative rate, ranging between 0 and 1) and two statistics derived from sensitivity and specificity (Area Under the ROC Curve, AUC and True Skill Statistic, TSS), for classification-type models and RMSE (Root Mean Square Error), MAE (Mean Absolute Error) and R^2 for regression-type models. AUC ranges between 0 and 1, with a value of 0.5 characterizing a model with no discriminatory power and values of 0.7–0.8 characterizing acceptable models. TSS ranges between -1 and 1, with a negative value characterizing a model with no discriminatory power and values > 0.6 characterizing useful models (Guisan et al., 2017). The best value of the mtry (number of variables available for splitting at each tree node) parameter was selected, during the cross-validation procedure, via the AUC and RMSE, for classification and regression-type models, respectively.

Results

Fifty-six species of vascular epiphytes were recorded on trees with a DBH > 5 cm, including 44 spermatophytes (36 orchids,

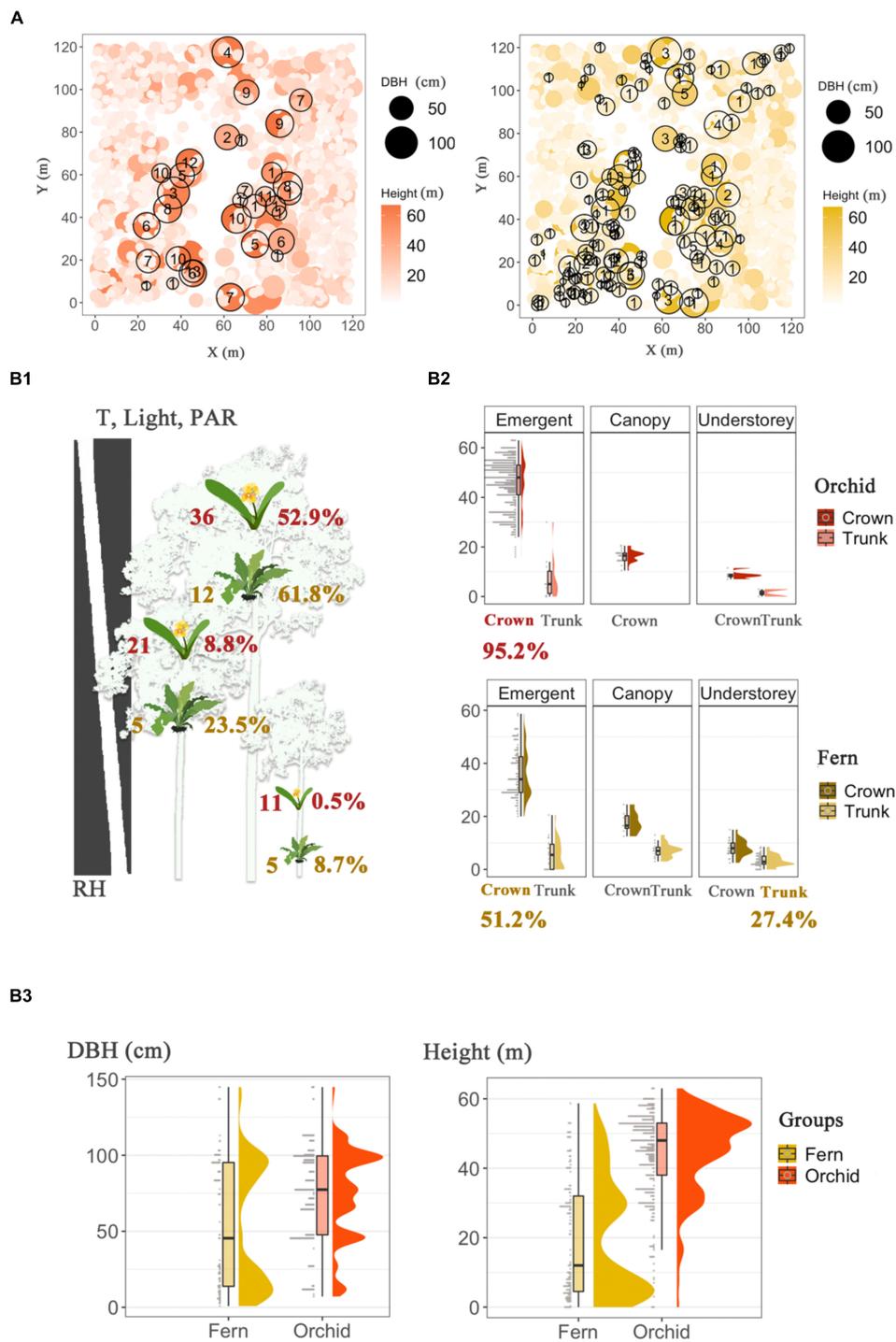


FIGURE 1

Horizontal and vertical distribution of epiphytic spermatophyte and fern richness and abundance on individual trees in a 1.1 ha tropical canopy crane facility, Yunnan, SW China. **(A)** Horizontal distribution of epiphyte spermatophytes (left) and fern (right) richness on individual trees in a x-y space (120 m*120 m) depending on DBH and tree height. **(B1)** Vertical distribution of epiphyte richness and the ratio of epiphytic individuals on canopies or trunks to the total number of epiphytic individuals controlling for tree size. **(B2)** Box plots [showing the 1st and 3rd quartiles (upper and lower bounds), 2nd quartile (center), 1.5* interquartile range (whiskers) and minima-maxima beyond the whiskers] of the number of individuals controlling for tree layers and tree structures. **(B3)** Histogram of species abundance of two groups depending on DBH and height, respectively. Gray triangles represent relative humidity (RH), temperature (T), light intensity (Light) and photosynthetically active radiation (PAR) along a tree.

3 *Hoya*, 1 *Dischidia*, and 4 *Aeschynanthus*) and 12 fern species (Supplementary Table 1, see also <https://doi.org/10.6084/m9.figshare.21186049.v3> for comprehensive information on individual trees). The most predominant spermatophytes were orchid species (*Oberonia jenkinsian*, *Phalaenopsis marriottiana* var. *parishii*, *Pinalia amica*, *Cleisostoma fuerstenbergianum*, and *Luisia morsei*). *Asplenium nidus* and *Microsorium punctatum* were the most frequent epiphytic ferns. Eleven species are listed in the IUCN red list of threatened species, including the fern *Goniophlebium subauriculatum* (CR) and 10 orchid species [*Coelogyne suaveolens* (EN), *Cymbidium dayanum* (VU), *Dendrobium aphyllum* (VU), *D. densiflorum* (VU), *D. devonianum* (EN), *D. exile* (VU), *D. fimbriatum* (VU), *Oberonia rufilabris* (EN), *Pelatantheria rivesii* (VU), *Sarcoglyphis smithiana* (VU)]. Epiphytes were not randomly distributed across host trees, but were instead significantly clustered on specific tree individuals. In fact, the observed occupancy rates of 2.3 and 10.8% in epiphytic spermatophytes and ferns, respectively, were substantially and significantly lower than the occupancy rate expected if epiphyte individuals would randomly colonize any available tree (Table 2). This pattern prevailed for small, medium and large trees, except for ferns on small trees (Table 2). This clustered pattern can be visualized by the distribution of epiphytic spermatophytes and ferns in a two/three-dimensional space (Figure 1A and Supplementary Figure 2). Both epiphytic spermatophytes and ferns exhibited a higher abundance along a central ridge and a higher richness on large and tall trees (Figures 1A,B). Globally, the average fern and spermatophyte species richness per occupied tree was 1.32 ± 0.87 and 5.77 ± 3.79 , respectively. Species richness was higher on large trees, with an average of 2.67 ± 1.43 and 6.56 ± 2.94 fern and spermatophyte species, respectively, than on small trees, with an average of 1.04 ± 0.23 and 2 ± 2.45 fern and spermatophyte species, respectively. In ferns, however, the distribution of species richness depending on DBH exhibited a bimodal response. The two peaks of species richness represent shade-loving ferns on small trees and sun-loving ferns on large trees (Figure 1B). *Davallia trichomanoides*,

Drynaria roosii, *Nephrolepis cordifolia*, *Drynaria coronans*, *Pyrrosia nummulariifolia*, and *Goniophlebium subauriculatum* were strictly restricted to large trees.

Among occupied host trees, 95.2% of epiphytic spermatophyte individuals and 51.2% of epiphytic fern individuals were restricted to the canopy crown of emergent trees. Among them, 10 red-listed species were completely constrained to the emergent canopy crown. 27.4% of epiphytic fern individuals occurred on the trunk of understory trees (Figure 1B2).

Based on the correlation matrix among variables (Supplementary Figure 1), DBH, canopy area, tree species, proportion, M, U, meanDist, elevation, slope, Eastwest, Northsouth, illumination index, maxT, minRH, maxPAR, minPAR, maxL, minL, liana infestation, tree layers and the taxonomic identity of tree species were retained as predictors of species richness.

The Random Forest models predicting whether a given tree is likely to host epiphytes exhibited a higher accuracy for epiphytic spermatophytes than for epiphytic ferns due to a lower model specificity in the latter (Table 3). The models describing variation in epiphytic spermatophyte and fern species richness and abundance exhibited a cross-validated r-square of 0.28 and 0.24, and of 0.12 and 0.14, respectively. For all models, features of tree size, (DBH and canopy area) were the most important variables followed, with an almost similar contribution, by microclimatic conditions (maxT, minRH, maxPAR, maxL) (Figures 2, 3). The contribution of liana infestation, host tree identity, and characteristics of neighboring trees (M, U) were marginal.

Discussion

Vascular epiphytes were not randomly distributed but tended to cluster on specific host trees. Significant models predicting whether a tree is likely to be colonized in a landscape dominated by non-colonized ones were obtained, indicating

TABLE 2 Spatial patterns of epiphytic spermatophytes and ferns in a 1.1 ha tropical rainforest (Yunnan, SW China).

Groups	Host tree size	Host tree individuals	Epiphyte richness	Epiphyte abundance	Epiphytic occupancy rate	Randomized occupancy rate (mean \pm SD)
Spermatophytes	All	1,334	40	801	2.30%	12.2 \pm 0.22%
	Small (< 30 cm)	1,232	11	39	0.50%	0.96 \pm 0.02%
	Medium (\geq 30 and < 70 cm)	68	21	223	8.80%	48.40 \pm 3.23%
	Large (\geq 70 cm)	34	33	539	52.90%	97.89 \pm 0.02%
Ferns	All	1,334	12	362	10.80%	13.64 \pm 0.19%
	Small (< 30 cm)	1,232	5	170	8.70%	0.90 \pm 0.06%
	Medium (\geq 30 and < 70 cm)	68	5	39	23.50%	30.50 \pm 1.83%
	Large (\geq 70 cm)	34	12	153	61.80%	84.81 \pm 4.66%

For each group, the observed occupancy rate is compared with a randomized occupancy rate, wherein individual epiphytes are reshuffled across all individual trees. All *p*-values (proportion of randomized occupancy rates that are higher than the observed occupancy rate across 100 replicates) are < 0.001.

TABLE 3 AUC, TSS, sensitivity and specificity of Random Forest models predicting the probability that a tree is colonized by epiphytic spermatophytes and ferns in a lowland tropical rain forest (Xishuangbanna, Yunnan, SW China).

Group	AUC	TSS	Sensitivity	Specificity
Spermatophyte	0.94 ± 0.04	0.78 ± 0.10	0.82 ± 0.10	0.96 ± 0.03
Fern	0.79 ± 0.03	0.48 ± 0.05	0.72 ± 0.07	0.76 ± 0.07

Values are average ± SD across 100-fold cross-validation replicates.

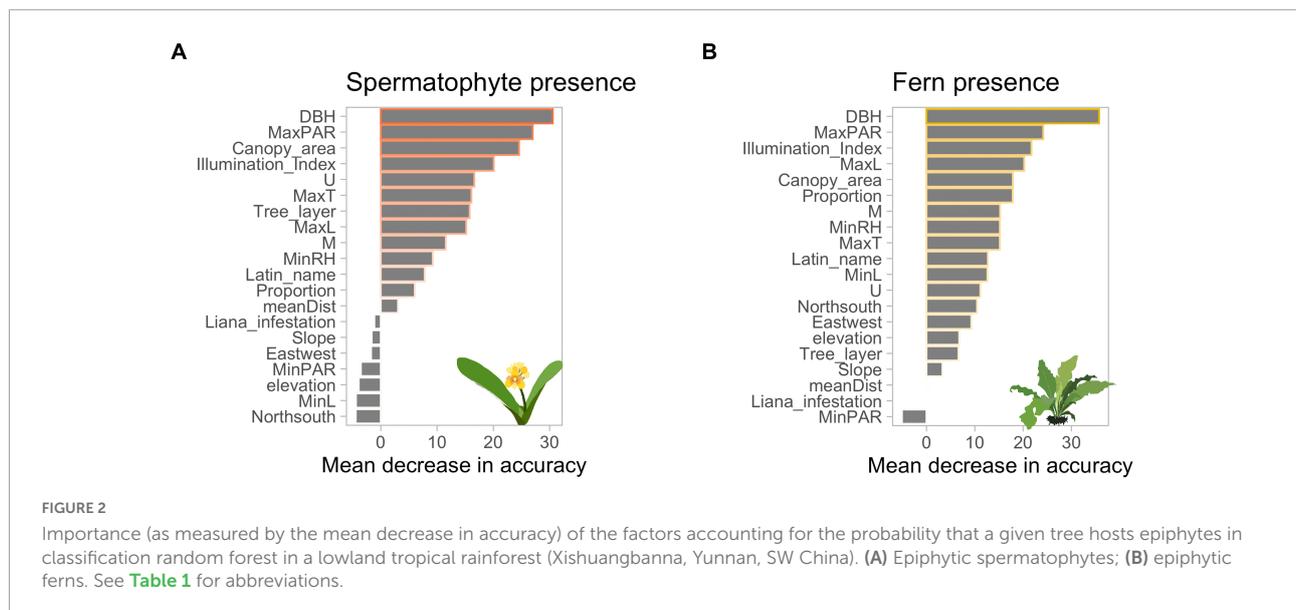
that, at the local scale, host tree colonization is not random as host tree characteristics and their specific environment play a significant role in determining which host tree is most likely to be colonized (Zotz and Schultz, 2008). Bypassing the random effect associated with dispersal and establishment, Callaway et al. (2002) showed that transplanted epiphytes grow faster on trees hosting massive loads of epiphytes than on trees with no or few epiphytes, evidencing that the former exhibit key properties that are responsible for their suitability as hosts. Our models exhibited, however, a moderate (AUC of 0.93, TSS of 0.78) to low (AUC of 0.79, TSS of 0.48) accuracy for spermatophytes and ferns, respectively. These values are in the range of similar studies aiming at modeling epiphytic species distributions (mean AUC in epiphytic lichens of 0.79 ± 0.08 (Dymytrova et al., 2016), AUC range of 0.67–0.96 in epiphytic orchids in Colombia (Reina-Rodríguez et al., 2016), AUC of 0.97 in the epiphytic orchid *Laelia speciosa* in Mexico (Flores-Tolentino et al., 2020), median AUC of 0.50–0.90 in epiphytic lichens in temperate forests (Eaton et al., 2018). Similarly, the models describing variation in epiphytic fern and spermatophytes richness exhibited r-squares of 0.28 and 0.24, respectively, in the range to slightly lower than similar reports for epiphytic ferns and spermatophytes (e.g., $r^2 = 0.44$ and 0.32 for orchid and fern species richness; Adhikari et al., 2017). This suggests that our inclusion of a large number of host-tree characteristics, including host tree identity, features of tree size, light and microclimatic conditions, characteristics of the neighbor trees, and liana abundance, did not allow for an apparent improvement of model accuracy over studies with a more limited number of predictors. Additional variables characterizing microhabitat conditions, such as bark texture and chemistry, branch diameter, or percentage cover of canopy humus (Woods et al., 2015), would possibly increase model accuracy. Although not necessarily contributing more than other variables such as DBH, tree age, and hence, growth rate, is another important variable to consider as DBH is an imperfect proxy for tree age, so that trees of similar DBH may exhibit very different areas and age (Wagner and Zotz, 2019). The relatively low explanatory power of the models reported here and in previous studies suggests, however, that the distribution of epiphytes among trees is largely stochastic.

Epiphytes need to track patches of suitable trees in a dynamic landscape for persistence (Snäll et al., 2005) and are,

at first sight, expected to display high dispersal capacities. This is especially true in ferns and orchids, whose dust-like seeds are the smallest among spermatophytes, and hence, display a large potential for long-distance dispersal (Einmann and Zotz, 2017). Accordingly, the composition of epiphyte communities is better explained by host-tree characteristics than by the distance among trees (Mota de Oliveira and ter Steege, 2015; Mendieta-Leiva et al., 2022), suggesting that niche-based mechanisms prevail over dispersal limitations. Mounting evidence points, however, to substantial limitations in the capacities of epiphytes to successfully disperse and colonize new trees. Epiphytes distribution patterns are spatially aggregated (Zotz and Schultz, 2008; Zhang et al., 2010), in line with the dependence of epiphyte occupancy rates on tree density, and hence, connectivity among trees (Francisco et al., 2021), and accessibility (distance to major population sources). In dry forests, these factors were shown to be the most important for explaining the distribution of epiphytic orchids (Reina-Rodríguez et al., 2016).

Colonization may further be hampered upon establishment. Spicer et al. (2022) in fact reported that, if substrates with a high rugosity initially host more epiphytes than smooth substrates, seedling mortality was eventually very high, regardless of substrate texture, due to severe climatic conditions, and seed or seedling removal by rain or animals, especially ants (Vergara-Torres et al., 2018). Furthermore, the establishment of some “late-successional” epiphytes depends upon the accumulation of sufficient canopy soil (Victoriano-Romero et al., 2020). First colonizers (bryophytes and lichens) initiate the process of soil formation, subsequently allowing late-succession vascular epiphytes to establish, thereby participating in the clustering of epiphytes on specific host trees. Altogether, these results suggest that colonization of new trees is compromised during the establishment phase, contributing to the role of chance upon tree colonization, and accounting for the comparatively low proportion of the variation in epiphytic species richness among trees explained by environmental variables. This was particularly the case in the present study, where occupancy rates of 2.3 and 10.8% in orchids and ferns, respectively, pale by comparison with other studies in tropical rainforests (48%, Zotz and Vollrath, 2003; 30%, Zotz and Schultz, 2008; 56–100%, Zhao et al., 2015), which may be explained by the length of the dry season (May–October) in the study area.

If chance associated with dispersal limitations plays such an important role in epiphytic distributions, models with higher accuracy would be expected in good than in poor dispersers. In contrast, despite higher occupancy rates in ferns than in spermatophytes, our models displayed a lower accuracy in the former due to a lower specificity, pointing to suitable, but unoccupied trees. Although zoochory might play a more important role in fern dispersal than previously thought (Boch et al., 2013, 2016), fern spores are typically dispersed by wind. Fern spores are smaller than orchid seeds and exhibit



a lower settling velocity (0.06 m/s) than orchid seeds (0.09–0.4), enhancing long-distance wind dispersal (Zotz et al., 2016). Analyses of population genetic structure in tropical epiphytic ferns further revealed that most of the genetic diversity was distributed within populations and failed to evidence any significant clustering, pointing to strong migration rates among populations (Winkler et al., 2011). Analyses of epiphytic tropical bryophytes, which produce smaller spores than those of ferns, revealed, however, spatial genetic structures comparable to those documented for spermatoytes, whose diaspores are orders of magnitude larger (Ledent et al., 2020). In fact, anemochorous plants in dense tropical rainforests typically exhibit tighter clusters than animal-dispersed species because of the barriers imposed by the dense forest canopy on wind speed (Seidler and Plotkin, 2006).

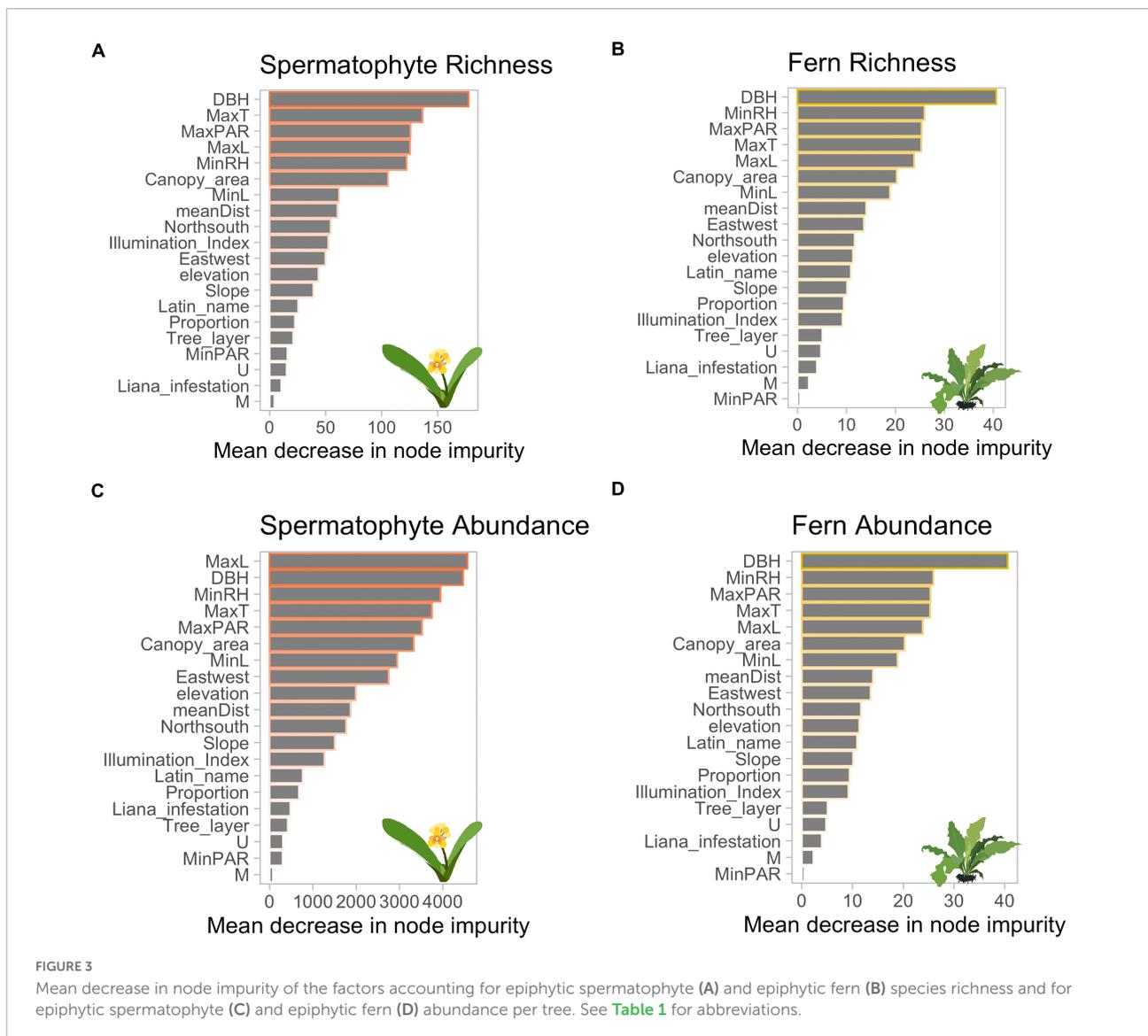
Globally, epiphytic spermatoyte and fern species richness was described by the same predictors. The best predictors of the presence of epiphytes on a tree, but also its epiphytic species richness and abundance, included features of tree size, mostly DBH and, to a lesser extent, canopy area. Tree size has indeed been invariably identified as the main driver of epiphytic species richness and abundance (Zotz and Vollrath, 2003; Zotz and Schultz, 2008; Francisco et al., 2021). Tree size is a complex factor that integrates several ecological processes relevant to epiphyte community assembly (Zhao et al., 2015). It is linked to the exposure time of the host to epiphyte seed rain, but also the greater available space for epiphytes and the increased number of microhabitats available on the tree (Paillet et al., 2019).

Microclimatic conditions were precisely the second factor after DBH most accounting for variation in species richness and abundance among trees. In fact, epiphytes are constantly exposed to light, water and nutrient stress, whose intensity increases from the base to the canopy, leading to a succession

of communities with increasing levels of stress tolerance (Dias-Pereira et al., 2022, and references therein). Microclimate is thus a major determinant of the local distribution of vascular epiphytes, as can be deduced from the vertical stratification of species recurrently reported (ter Steege and Cornelissen, 1989; Krömer et al., 2007; Zotz and Schultz, 2008; Dias-Pereira et al., 2022). Our results suggest that microclimatic variations among trees, caused by a series of factors including topography, tree height and the relative position of each tree as compared to its neighbors, must hence be taken into account in analyses of epiphytic species distributions. Although our analyses did not include an index of canopy openness *per se*, they included information on the neighboring environment of focal trees (M, U...), which did not prevail over microclimatic and light variables in our models, questioning the use of easy-to-measure variables such as canopy openness, as suggested by Toivonen et al. (2017) in such analyses.

The importance of light and PAR in the models accounts for the high light demand of epiphytic orchids to photosynthesize and reproduce (Tremblay, 2008), but also for a substantial proportion of the fern community, which was restricted to the inner canopy. The inclusion of the illumination index, which was negatively correlated with the dominance index (U), likely explains why the latter, and other potentially important variables describing the surrounding environment of each host tree (Fardhani et al., 2021), did not or marginally contribute to the present models.

Other factors, such as host tree identity, played a marginal role in the models. While host trees may differ in their branching architecture, bark texture and pH (Zotz and Schultz, 2008; Francisco et al., 2021), the impact of host tree specificity on epiphytes has been challenged based on the fact that upper canopy branches, where the bulk of orchids occur, may



accumulate bryophytes, lichens and dead organic material (Zotz and Vollrath, 2003), potentially homogenizing habitat structure among host tree species. Furthermore, host tree identity may impact species composition, but not necessarily species richness, as in temperate forests at least, the range of microhabitats across host-tree taxa is very similar (Paillet et al., 2019).

Our results have several implications in terms of conservation. In fact, if the total species richness (56 species) is not higher, and even somewhat lower than that reported in other areas (21–48 species in 1ha mountain Asian tropical forest plots, Zhao et al., 2015; 66–85 species in 2 ha Neotropical cloud forest and inselberg, Francisco et al., 2021, 37–188 species in ca 1 ha plots of Neotropical rainforest, Zotz and Vollrath, 2003; Zotz and Schultz, 2008, and references therein), the proportion of almost 19.6% of threatened species of high conservation relevance is remarkable. Remarkably,

51.2% of epiphytic fern individuals and 95.2% of epiphytic spermatophyte individuals were only limited to the canopy crown of large trees. Given the substantial contribution of DBH to explain variation in species richness, we confirm the utmost importance of large trees with emergent canopies for the conservation of the epiphytic flora (Shen et al., 2018; Adhikari et al., 2021; Francisco et al., 2021). In ferns, six species were strictly associated with large trees. 81.3% of tropical dominant fern, *Asplenium nidus*, which can offer a cool and moist microhabitat for arboreal fauna, prefers growing on small trees. Species richness of liverworts was also maximum on small trees (Shen et al., 2022). Altogether, these observations support the idea that epiphytic diversity assessments in tropical forests must also include small understorey trees (Sporn et al., 2010), which should be further considered for conservation.

The low occupancy rates reported here further suggest that, for optimal epiphyte conservation, a much higher proportion of large trees than the ones that are actually occupied would need to be kept outside of protected areas to maintain the colonization dynamics of new host trees. This is especially true for trees located in ridges, which experience suitable micro-climatic conditions for the epiphytic flora. Given the importance of the micro-climatic conditions that prevail at the level of each individual host tree, however, the impact of the harvesting of trees in the vicinity of conserved individuals raises the question of the maintenance of suitable conditions at the level of isolated trees. In fact, occupancy rates vary depending on the density of available trees due to increased connectivity among them (Francisco et al., 2021), but also likely due to differences in micro-climatic conditions, further pointing to the necessity to maintain a buffer zone around large host trees targeted for conservation.

Data availability statement

The original contributions presented in this study are included in the article/**Supplementary material**, further inquiries can be directed to the corresponding authors.

Author contributions

LS, AV, and TS conceived and designed the research. LS, YW, and J-LD conducted field work. TS and FC performed the analyses. FC, AG, and YS provided suggestions on data analysis. TS, AV, and LS wrote the manuscript with the assistance of all co-authors. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/ffgc.2022.1007473/full#supplementary-material>

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