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RESEARCH ARTICLE

Disentangling the roles of chance, abiotic factors and biotic interactions among epiphytic bryophyte communities in a tropical rainforest (Yunnan, China)

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ABSTRACT

- Epiphytes offer an appealing framework to disentangle the contributions of chance, biotic and abiotic drivers of species distributions. In the context of the stress-gradient theory, we test the hypotheses that (i) deterministic (*i.e.*, non-random) factors play an increasing role in communities from young to old trees, (ii) negative biotic interactions increase on older trees and towards the tree base, and (iii) positive interactions show the reverse pattern.
- Bryophyte species distributions and abiotic conditions were recorded on a 1.1 ha tropical rainforest canopy crane site. We analysed co-occurrence patterns in a niche modelling framework to disentangle the roles of chance, abiotic factors and putative biotic interactions among species pairs.
- 76% of species pairs resulted from chance. Abiotic factors explained 78% of non-randomly associated species pairs, and co-occurrences prevailed over non-coincidences in the remaining species pairs. Positive and negative interactions mostly involved species pairs from the same *versus* different communities (mosses *versus* liverworts) and life forms, respectively. There was an increase in randomly associated pairs from large to small trees. No increase in negative interactions from young to old trees or from the canopy to the base was observed.
- Our results suggest that epiphytic bryophyte community composition is primarily driven by environmental filtering, whose importance increases with niche complexity and diversity. Biotic interactions play a secondary role, with a very marginal contribution of competitive exclusion. Biotic interactions vary among communities (mosses *versus* liverworts) and life forms, facilitation prevailing among species from the same community and life form, and competition among species from different communities and life forms.

INTRODUCTION

Trees are striking examples of habitat islands, characterized by substantial spatiotemporal variations in their characteristics as hosts, such as the area available for colonization and habitat conditions in terms of branching architecture, bark texture and chemistry, from the base to the canopy, and from young to old trees (Taylor & Burns 2015). In this context, epiphytes offer an appealing framework to disentangle the contributions of chance, biotic and abiotic drivers of species distributions, because specific hypotheses regarding the contributions of these factors to variations in species co-occurrence patterns depending on their position on the tree and tree age can be formulated (Spicer & Woods 2022).

During early colonization stages, species are expected to progressively accumulate, with high levels of stochasticity associated with dispersal chance (Taylor & Burns 2015). Reproductive traits determine the order of appearance of species, driving the segregation of primary and late successional species assemblages, as evidenced in epiphyllous communities (Sierra *et al.* 2019). In line with the idea that, during community succession, niche-based processes (niche preference and biotic interactions) progressively prevail over neutral processes associated with stochastic dispersal events. As Mežaka *et al.* (2022) hypothesized in epiphyllous communities, the contribution of random factors to community composition can be expected to decrease on ageing trees. Following an optimal stage of ontogenetic development of the host tree, during which both primary

and late successional species can be found, competition is expected to play an increasing role, as suggested by the decrease in species richness following an optimum reported in epiphytic lichens (Ellis & Ellis 2013).

The importance of biotic interactions in epiphytic community composition is also expected to vary vertically on the same tree because of variations in light intensity, relative humidity, wind exposure, temperature, and nutrient availability. The stress gradient hypothesis, primarily developed in terrestrial ecosystems (Bertness & Callaway 1994; Qi et al. 2018), has most recently been applied to epiphytic communities (Mežaka et al. 2022; Spicer & Woods 2022) and provides a framework for predicting when and where interactions among epiphytes may be important. For epiphytes, the outer canopy is a high stress environment characterized by high exposure to UV radiation and large daily temperature and relative humidity fluctuations, wherein facilitation is expected to prevail (Soliveres et al. 2015). For instance, the likelihood of vascular epiphyte colonization increases with the extent of bryophyte cover thanks to the high water-holding capacities, and hence, the humid microhabitats provided by the latter (Acevedo et al. 2020). The relevance of facilitation by bryophytes for vascular epiphytes is such that bryophyte cover contributed more to models of vascular epiphyte richness than host tree size, which has been identified as the major predictor of epiphyte richness (Zotz & Vollrath 2003; Zotz & Schultz 2008; Francisco et al. 2021). As light exposure and daily variations in temperature and relative humidity decrease towards the tree base, interactions are expected to become more competitive (see Spicer & Woods 2022 for review), especially among epiphytes from different communities, as reported in moss, liverwort, and epiphyllous lichen communities (Mežaka et al. 2022).

Here, we focused on epiphytic bryophyte communities, which are a key component in tropical forest ecosystems for water and nutrient cycles, enhancing seed anchorage and germination, and providing shelter for diverse and abundant fauna (Holz & Gradstein 2005, and references therein), and wherein biotic interactions are thought to play an important role. As a comparison, facilitation and competition were, respectively, the focus of 22% and 35% of the non-vascular epiphyte literature, but only 8% and 5% of the vascular epiphyte literature (Spicer & Woods 2022).

Bryophyte species may compete with each other by producing allelopathic substances that prevent the growth of protonema (Whitehead et al. 2018), or by having a life form and growth strategy promoting the development of dense colonies that quickly invade available space. For example, fast spreading, thick mats of colonies formed by dendroid growth forms, such as *Isothecium* in temperate rainforests, whose creeping primary shoots rapidly spread over the surface and where erect secondary shoots overarch underlying species, potentially entering into competition for light with the latter, are considered as typical examples of effective competitors (Peck & Frelich 2008; Woods et al. 2019). The role of competition among bryophyte communities has, however, remained an area of controversy (Frego & Carleton 1995; McAlister 1995; Økland & Økland 1996; Rydin 1997; Bates 1998; Økland 2000; Bergamini et al. 2001; Mälson & Rydin 2009; Udd et al. 2016). In Grime's (1977) description of competitive, ruderal and stress-tolerant strategies in plants, for instance, bryophytes are not included in the competitors (Grime et al. 1990). Bryophytes are

traditionally viewed as pioneer organisms that are efficiently wind-dispersed through small spores. This would, at first sight, suggest that they disperse to newly available suitable habitats instead of competing locally for persistence. In such groups with high dispersal capacities, the notion that trees represent habitat islands has been challenged (Cook et al. 2004; Belinchón et al. 2009). Several lines of evidence suggest, however, that epiphytic bryophytes experience severe dispersal limitation, making them suitable models in an island habitat context. In fact, epiphytic mosses are typically characterized by reduction of the peristome (Hedenäs 2012), whose teeth movements enhance spore dispersal. Peristome reduction is correlated with hygrochasy, i.e., the release of spores under wet conditions, which decreases their chances of long-distance dispersal, and might be seen as a safe-site strategy, forcing spores to land in appropriate, nearby patches where their survival is favoured (Medina et al. 2014). Aggregated distribution patterns are frequently reported in epiphytic bryophytes (e.g., Snäll et al. 2003, 2004; Löbel et al. 2006, Wagner et al. 2015), and strong spatial genetic structures at fine spatial scales were consistently reported in the (few) epiphytic bryophyte species investigated so far (Snäll et al. 2004; Vanderpoorten et al. 2019; Ledent et al.).

Here, we take advantage of a canopy crane in a tropical rainforest to test the following hypotheses: (i) the proportion of randomly associated species pairs decreases on old trees due to the increasing role of deterministic (i.e., non-random) factors (H1); (ii) non-coincident species distribution patterns, potentially associated with negative biotic interactions, play an increasing role as trees age (H2) and from the canopy to the tree base (H3); (iii) species co-occurrences, potentially associated with positive interactions, show the reverse pattern. We further hypothesize that competition prevails among, rather than within, moss and liverwort communities (Mežaka et al. 2022) (H4a). Within moss and liverwort communities, we expect competition to prevail among species of different life forms because of the higher competitive ability of certain life forms over others. We also expect facilitation to prevail among species sharing the same life form to maximize shoot density within colonies, and hence, water retention thorugh capillarity (H4b).

MATERIAL AND METHODS

Study area and data collection

This study took place in a 1.44 ha square plot in a lowland (643–700 m a.s.l.) seasonal rain forest (101°34′59.1″ E, 21°37′2.6″ N) in Xishuangbanna National Natural Reserve (Yunnan, SW China). This site was chosen because of the availability of comprehensive, fine-scale information on environmental conditions and epiphyte species distributions (Shen et al. 2018, 2022a,b), which could be collected thanks to an 81-m-tall canopy crane (TCT7015-10E, Zoomlion Heavy Industry, Changsha, China), whose 60-m-long arm provides access to the canopy within a 1.1-ha circle.

Sampling protocols and environmental data collection were described in Shen et al. (2022a,b) and are briefly summarized below. Bryophyte species composition was determined for 408 plots of 1600 cm^2 on 42 *Parashorea chinensis* host trees using a stratified sampling across three height zones: lower trunk (from

tree base to the middle height of the trunk), upper trunk (from the middle height of the trunk to the lowest third of the canopy), and canopy top (from to the middle third of the canopy to the upper third of the canopy). Since tree age was not available for each individual tree investigated, we used diameter at breast height (DBH) as a proxy for tree age based on very accurate allometric equations ($r^2 = 0.99$) linking the age of individual *P. chinensis* with their DBH in Xishuangbanna (Tang *et al.* 2008). Three DBH classes were considered: small (DBH ≤20 cm, n = 16), medium (≥20 & < 40 cm, n = 15), and large (≥40 cm, n = 11), corresponding to trees <60 years, 60–100 years, and >100 years, respectively.

Forty-six environmental variables were recorded or derived (Table 1), including microclimate (relative humidity and temperature; HYS15 air temperature and relative Moisture Sensors, Unism) and light (intensity and photosynthetically active radiation; LI-190R Quantum Sensor, LI-COR Biosciences) recorded at 1-h intervals from 12 trees (one in the lower trunk, two in the upper trunk, and two in the canopy) from July 2017 to December 2019 and predicted in an x-y-z space (Shen *et al.* 2022a) using Random Forest (Liaw & Wiener 2002).

Community modelling

We disentangled the contribution of chance, abiotic environmental drivers, and biotic interactions to explain species associations using a community modelling framework in three steps (Fig. 1, based on a slightly modified version of D'Amen *et al.* 2018). This approach first involves the identification of species pairs that can be explained by abiotic environmental conditions (species co-occurring due to shared niche preferences – *i.e.*, environmental filtering – or avoiding each other – *i.e.*, limiting similarity – because of niche divergence) through species distribution modelling (see below). Focusing on species pairs whose co-occurrence or non-coincident patterns cannot be explained in terms of abiotic environmental conditions, the second step involves the identification of non-randomly associated species pairs (*i.e.*, species that tend to co-occur or exclude each other more than expected by chance). The third step involves an analysis of species distribution ranges to identify, among non-coinciding distributions, which of these concern species with non-overlapping ranges. Allopatric ranges were interpreted by D'Amen *et al.* (2018) in terms of dispersal limitations, but at the very fine spatial scale investigated here, non-overlapping distributions in the x-y-z space, rather characterize differences in habitat conditions that would not have been considered. Finally, non-randomly associated species pairs with overlapping ranges, which cannot be explained in terms of abiotic environmental conditions, are interpreted in terms of facilitation (co-occurrences) or competition (non-coincidences).

During the first step, which involves environmentally constrained null models to determine whether two species tend to co-occur or to be spatially segregated more than expected given their niche preferences, the strength of association between each pair of species is measured by the C-score index (Stone & Roberts 1990). The C-score index is based on the number of records for the first species, for the second species, and for the number of plots where both species co-occur and are rescaled between 0 and 1. A value of 0 means that the species pair is maximally aggregated, and 1 is where a species pair is maximally segregated. Observed C-scores are then compared to a

Table 1. Abiotic environmental variables used to describe the niche of epiphytic bryophyte species at the Xishuangbanna canopy crane facility (Yunnan, SW China).

environmental variable	definition
DBH	Diameter at breast height (m) at 1.3 m above ground
Z	Vertical height from tree base to sampling location
W	Degree of regularity of the spatial distribution of the four trees nearest to the focal tree based on the classification of the angles between these four neighbours (Zhang *et al.* 2018)
U	Dominance index (relationship between size of the focal tree and its four nearest neighbours, describing whether a focal tree is larger or smaller than its neighbours) (Zhang *et al.* 2018)
meanDist	Average distance (m) between the focal tree and its four nearest-neighbour trees
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 (°) 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)
Bio1RH	Annual mean relative humidity
Bio2RH	Average monthly relative humidity ranges
Bio3RH	(Bio2RH/Bio7RH) (×100)
Bio4RH	Relative humidity seasonality (standard deviation ×100)
Bio5RH	Maximum relative humidity (%)
Bio6RH	Minimum relative humidity (%)
Bio7RH	Relative humidity annual range (%, Bio5RH − Bio6RH)
Bio8RH	Mean relative humidity of wet season
Bio9RH	Mean relative humidity of dry season
Bio1T	Annual mean temperature
Bio2T	Average monthly temperature ranges
Bio3T	Isothermality (Bio2T/Bio7T) (×100)
Bio4T	Temperature seasonality (standard deviation)
Bio5T	Maximum temperature (°C)
Bio6T	Minimum temperature (°C)
Bio7T	Temperature annual range (°C, Bio5T − Bio6T)
Bio8T	Mean temperature of wet season
Bio9T	Mean temperature of dry season
Bio1PAR	Annual mean photosynthetic active radiation
Bio2PAR	Average monthly photosynthetic active radiation ranges
Bio3PAR	(Bio2RAR/Bio7RAR) (×100)
Bio4PAR	Photosynthetic active radiation seasonality (standard deviation)
Bio5PAR	Maximum photosynthetic active radiation ($\mu mol \cdot m^{-2} \cdot s^{-1}$)
Bio6PAR	Minimum photosynthetic active radiation ($\mu mol \cdot m^{-2} \cdot s^{-1}$)
Bio7PAR	Photosynthetic active radiation annual range (W/m^2; Bio5RAR − Bio6RAR)
Bio8PAR	Mean photosynthetic active radiation of wet season
Bio9PAR	Mean photosynthetic active radiation of dry season
Bio1Light	Annual mean light intensity
Bio2Light	Average monthly light intensity ranges
Bio3Light	(Bio2Light/Bio7Light) (×100)
Bio4Light	Light intensity seasonality (standard deviation)
Bio5Light	Maximum light intensity (W·m^{-2})

Table 1. (Continued)

environmental variable	definition
Bio6Light	Minimum light intensity (W·m^{-2})
Bio7Light	Light intensity annual range (W·m^{-2}; Bio5Light − Bio6Light)
Bio8Light	Mean light intensity of wet season
Bio9Light	Mean light intensity of dry season

distribution of C-scores from a set of 10,000 null communities. The null communities were simulated by shuffling species occurrences among plots, according to their habitat suitability values resulting from SDMs (see below), as if niche preferences were the only driver of species distributions, regardless of biotic interactions. To control for false positives, a Bayesian approach, assuming independence of probabilities, was employed. This approach consists of comparing the C-score of each species pair with those resulting from the same species pair in the null matrices (Gotelli & Ulrich 2010).

The second step involves removing randomly associated species pairs. A total of 10,000 null communities were generated by reshuffling species among plots while preserving species

occurrence frequencies. Observed C-scores were then compared to C-scores expected by chance, as described above.

The third step involves determining whether two species have overlapping or non-coincident ranges. For this, we compared the minimum convex hulls encompassing all of their occurrence points in an x-y space (ICUN 1994). If these ranges overlapped, we then determined whether their vertical range (z-axis, which includes height of the plots on the tree and the elevation) overlapped. If the ranges in the x-y space and along the z-axis both overlapped, a multivariate ANOVA (MANOVA) of coordinates in the x-y space depending on the factor species was implemented. A significant MANOVA test was interpreted as partial overlap, while a non-significant difference of species coordinates in the x-y space was interpreted as complete overlap.

The above analyses were performed at the level of the entire dataset to test H1; of lower trunks, upper trunks and canopy tops, respectively, to test H2; and of small, medium and large trees, respectively, to test H3.

To determine whether the observed association patterns were associated with life-forms (H4), we assigned all species to one of the following functional groups, as defined by Mägdefrau (1982) (Table S1): smooth mat (shoots creeping over the substrate with rhizoids adhering to substratum, with flat branches); rough mat (idem, with many erect lateral
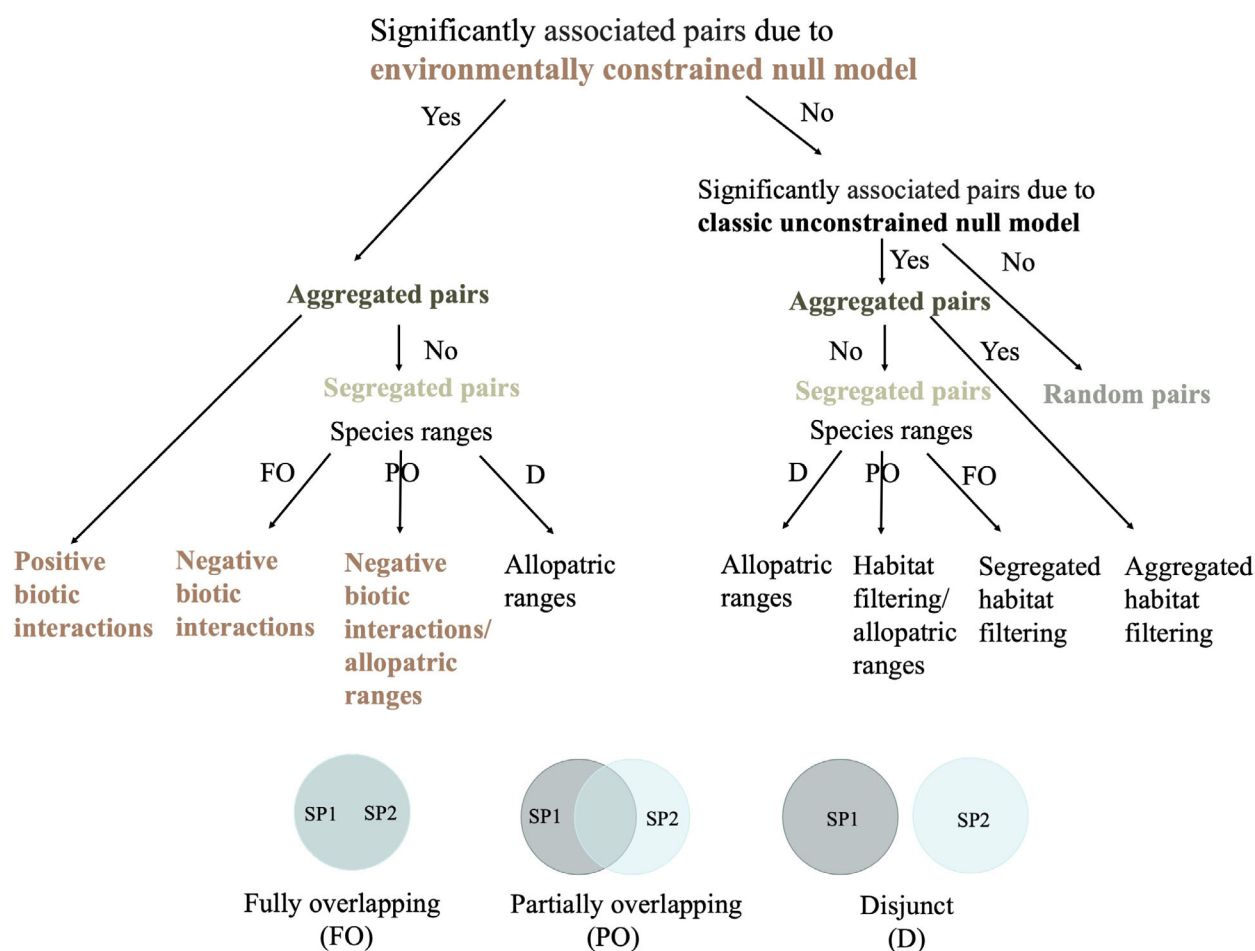

Fig. 1. Decision tree to disentangle community drivers (adapted from D'Amen et al. 2018) using a combination of environmentally constrained null models and classic unconstrained null models.

branches); fan (creeping on vertical substrate, with branches in one plane and leaves usually flat); dendroid (main shoots creeping, secondary shoots erect); pendant (hanging shoots); weft (shoots growing erect and horizontally, with multiple branching stems distributed throughout the main stem); turf (stems erect, parallel and close together, often covering extensive areas). As suggested by Lett *et al.* (2022), we further considered more broadly defined functional groups resulting from the collation of individual groups. In particular, since the Lett *et al.* classification includes leafy liverworts as a group, we added a 13th category, mosses, in the analyses to determine whether specific traits of moss and liverwort could help interpret the observed species association patterns.

Species distribution models

From an initial number of 102 species, we retained 40 with at least ten occurrences, which was defined as the lowest limit for model evaluation based on AUC from presence–absence data (Jiménez-Valverde 2020). To decrease the number of predictors and avoid multicollinearity, the variation among these predictors was reduced using Principal Components Analysis. The first two axes, which explained 73% of the total variance, were used as predictors.

To take model uncertainty into account, we used an ensemble modelling approach (Araújo & New 2007). We generated SDMs with the R package biomod2 (Thuiller *et al.* 2021) using five algorithms: Generalized Linear Models (GLM), Generalized Additive Models (GAM), Gradient Boosting Machine (GBM), Random Forest (RF), and Maximum Entropy (MaxEnt) using the default parameters in biomod2 (Thuiller *et al.* 2021).

Models were evaluated using the area under the ROC curve (AUC), the maximum value of the true skill statistic (MaxTSS)

and the Boyce Index (Hirzel *et al.* 2006; Guisan *et al.* 2017). For model evaluation, 20 replicates were run, each comprising 70% of the data to calibrate the models (training set) and 30% to evaluate them (test set). Given the small size of each individual test set, we refrained from computing AUC, MaxTSS and the Boyce Index from each individual test set, and then averaging them across replicates, as in Breiner *et al.* (2015, 2018). Instead, following Collart *et al.* (2021), we pooled the suitability values from the 20 test sets. As the same presence point is likely to be sampled in multiple replicates of the test set, the suitability values for each presence point were averaged across replicates.

This generated a series of suitability values independent from the data used to calibrate the models, but with a much larger size than the individual test sets, roughly equal to the initial occurrence dataset (as some occurrence points may not have been sampled in any of the 20 replicates). This recomposed evaluation dataset allowed direct computing of the Boyce index, and by combining it with the absence points, the AUC and maxTSS, using ecospat ersion 3.4 (Broennimann *et al.* 2022). We finally generated ensemble models, wherein each individual model contributed proportionally to its Somer's D (Somer's D = 2AUC − 1) value.

RESULTS

Ensemble species distribution models exhibited AUC, SomersD, Boyce, and MaxTSS values ranging between 0.78 ± 0.08, 0.56 ± 0.17, 0.74 ± 0.16 and 0.51 ± 0.15 across species, respectively (Table S2).

Globally, the observed C-scores of 76% of species pairs were not significantly different than random C-scores (Fig. 2). Among the 24% of remaining non-random pairs, 78% could be explained by abiotic environmental
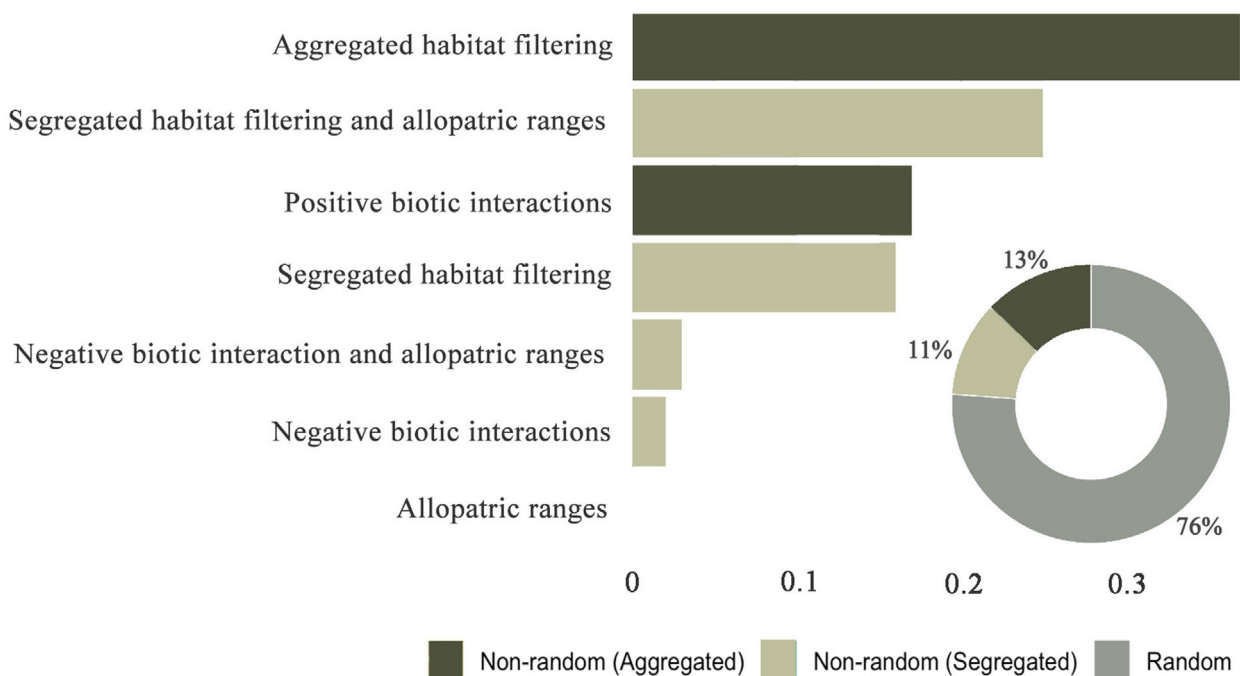

Fig. 2. Proportion of randomly and non-randomly associated species pairs among epiphytic bryophytes in a tropical rainforest (Yunnan, China) and contribution (%) of the factors accounting for non-random species associations.
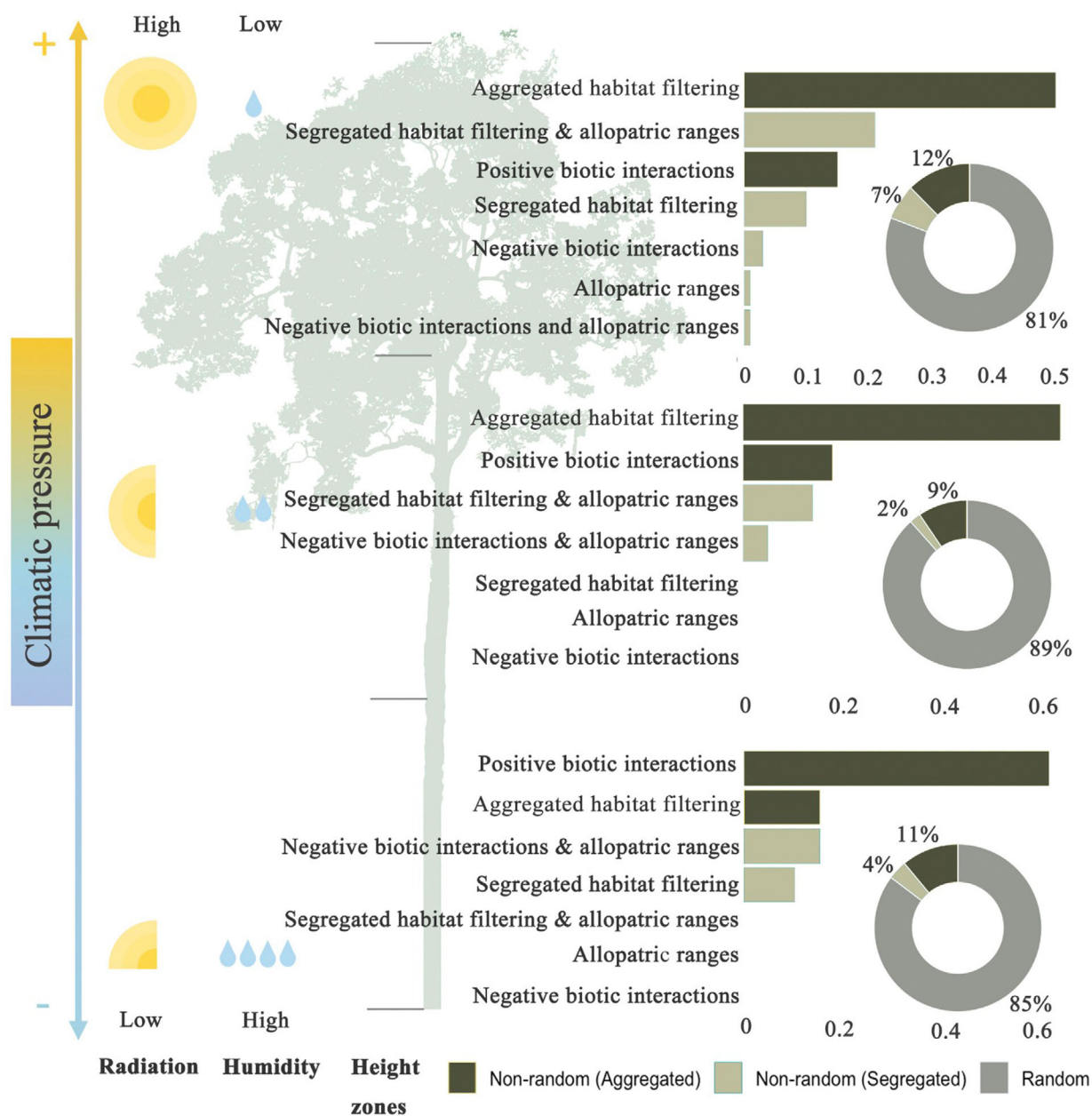
Fig. 3. Proportion of randomly and non-randomly associated species pairs among epiphytic bryophyte communities of the lower trunk, the upper trunk, and the canopy in a tropical rainforest (Yunnan, China) and contribution (%) of the factors accounting for non-random species associations.

conditions, 17% by positive interactions, and 2% by negative interactions. Abiotic factor was the most important factor among communities from the canopy and the upper trunk, but not from the tree base, wherein positive interactions prevailed (Fig. 3). The proportion of randomly associated species pairs increased from large (77%) to small (88%) trees (Fig. 4). Among non-randomly associated species pairs, positive biotic interactions were almost as important (36%) as abiotic environmental conditions on small trees but explained only 21% and 7% of non-randomly associated species pairs on medium and large trees, respectively (Fig. 4).

The taxonomic identity of the species involved in either positive or negative biotic interactions on small, medium, and large-sized trees and at the lower trunk, upper trunk and in the canopy are listed in Tables S3 and S4, respectively. Species from the same (moss–moss pairs or liverwort–liverwort pairs) and from different communities (mosses *versus* liverworts) tended to be involved in positive and negative interactions, respectively (Fig. 5a). Species sharing the same life form tended to be involved in positive associations, whereas species of different life forms tended to be involved in negative associations, with the exception of the lower trunk, where the reverse pattern prevailed (Fig. 5b).
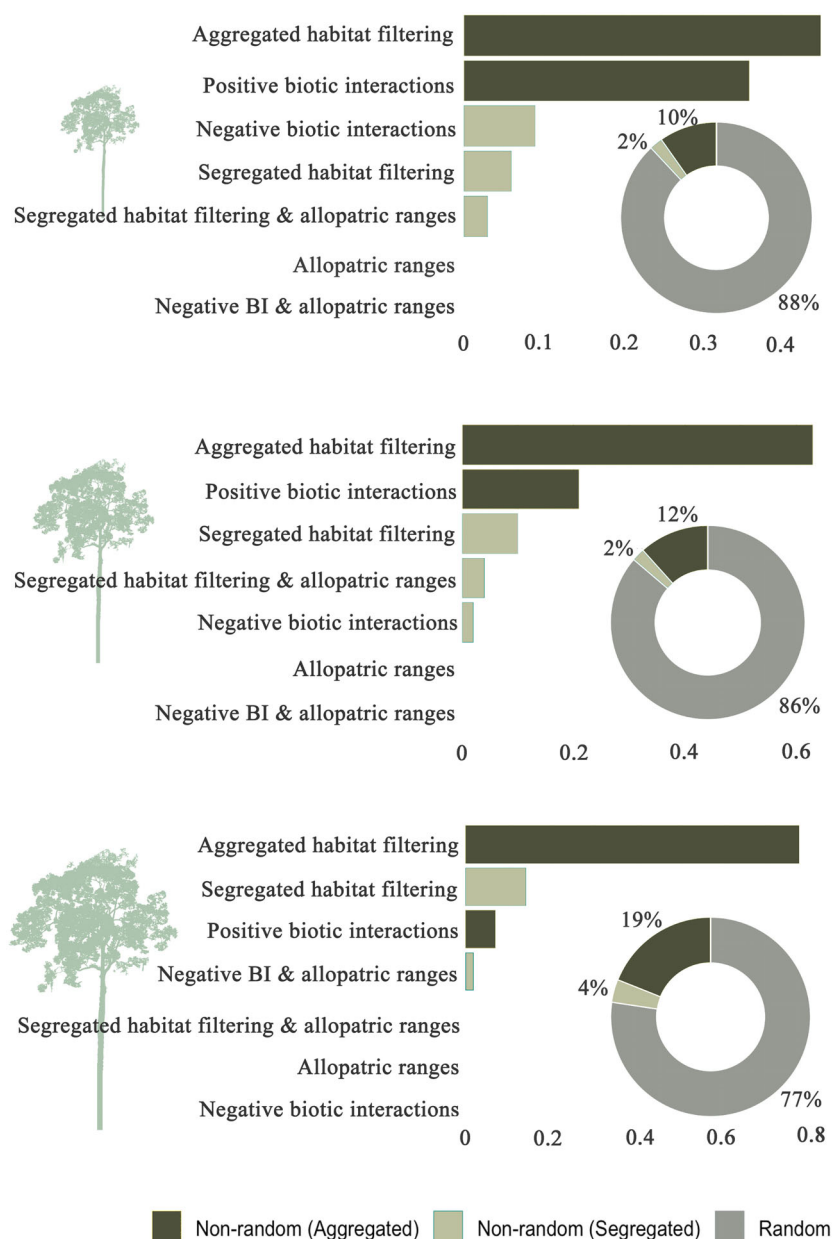
Fig. 4. Proportion of randomly and non-randomly associated species pairs among epiphytic bryophyte communities on small, medium-sized and large trees in a tropical rainforest (Yunnan, China) and contribution (%) of the factors accounting for non-random species associations.

DISCUSSION

A large majority (76%) of species pairs formed by epiphytic bryophytes was not significantly higher than expected by chance, in line with previous assessments on the role of chance in plant communities (D'Amen *et al.* 2018; Scherrer *et al.* 2019). Among non-randomly associated species pairs, abiotic environmental conditions explained more than 78% of the remaining variation. Biotic interactions, although widely accepted as an important driver of plant species distributions (Grant *et al.* 2014; Gavini *et al.* 2019), especially at the fine spatial scale investigated here (Götzenberger *et al.* 2012; Mod *et al.* 2020; Rossignaud *et al.* 2022, and references therein), contributed less than 20% of the observed co-occurrences. This is

in line with the general perception that assembly mechanisms in bryophyte communities, especially epiphytic ones (Mota de Oliveira *et al.* 2009; Mota de Oliveira & ter Steege 2015), are primarily driven by niche preferences at this scale, with biotic interactions playing a secondary role (Slack 1990). The contribution of biotic interactions may even be overestimated here. We implemented a method (D'Amen *et al.* 2018) which assumes that non-randomly associated species pairs that cannot be explained in terms of abiotic environmental conditions or dispersal limitations result from biotic interactions. Although we attempted to describe species niches from a wide range of abiotic environmental conditions, it cannot be excluded that residual associations arise from missing environmental factors (Blanchet *et al.* 2020), such as bark texture and
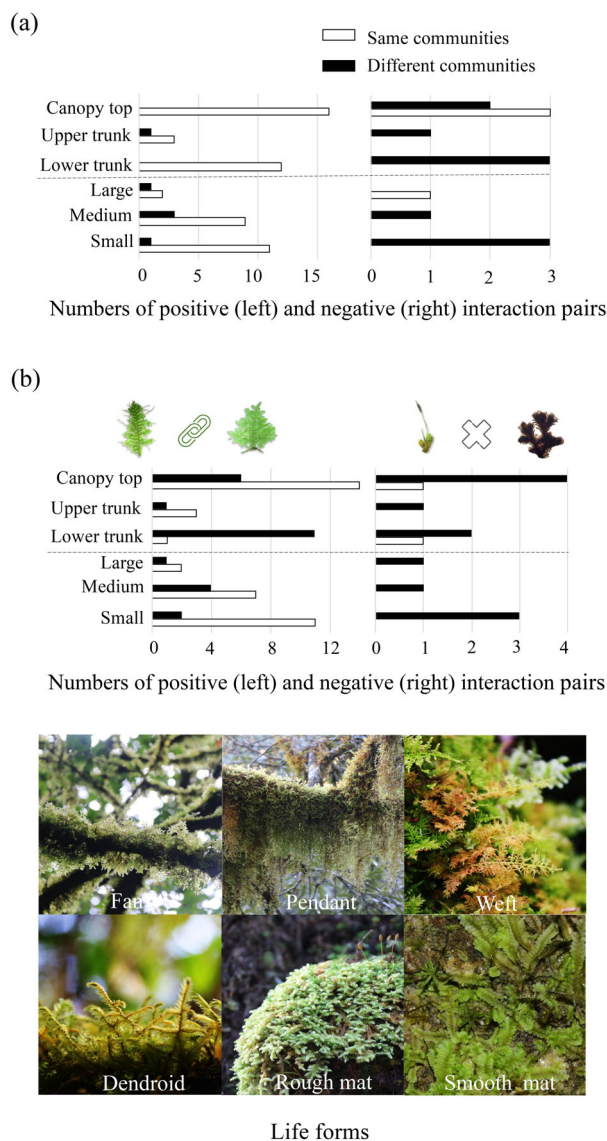
Fig. 5. (a) Numbers of positive and negative interactions among epiphytic bryophyte species in a tropical rainforest (Yunnan, China) involving pairs of species from the same (moss–moss pairs or liverwort–liverwort pairs) *versus* different communities (mosses *versus* liverworts). (b) Numbers of positive and negative interactions among epiphytic bryophyte species involving pairs of species from the same *versus* different life forms.

chemistry, branch diameter, or percentage cover of canopy humus (Woods *et al.* 2015).

Among the non-random species pairs that could not be explained by ecological preferences, co-occurrences prevailed over non-coincidences, involving 17% and 2% of non-randomly associated species pairs, respectively. A similar prevalence of co-occurrences over non-coincidences was previously reported among boral forest bryophyte communities (Økland 1994). The clustering of epiphyte species on the same tree may reflect a succession of species sharing similar ecological and/or dispersal traits. Early colonizers are characterized by higher rates of expression of traits involved in sexual and asexual reproduction (Sierra *et al.* 2019). As trees develop, characteristics such as bark texture and chemistry change, leading to a

turnover of specialized communities that segregate on the tree as a function of its characteristics as a host. Furthermore, early colonizers initiate the process of soil formation, subsequently allowing late-succession species that depend on canopy soil to establish themselves (Victoriano-Romero *et al.* 2020), leading to 'facilitation cascades' (Zotz 2016). Together, these processes could account for the observed non-random species co-occurrences. We observed, however, similar proportions of co-occurring species pairs among communities growing at the same level of the tree and on trees within the same DBH class, thus sharing similar characteristics associated with their age. The fact, that observed co-occurrences cannot be explained by community succession, suggests that actual facilitation occurs, as proposed for plants in harsh environments (D'Amen *et al.* 2018; Scherrer *et al.* 2019). Epiphytes rely on rainfall for water, and species occurring in the canopy are exposed to extremely harsh conditions in terms of light and wind exposure, temperature range, and periods of drought. One strategy to mitigate the impact of such harsh conditions is to grow in dense colonies to enhance facilitation, explaining why vascular epiphyte distributions are typically aggregated and density-dependent and their communities are nested (see Spicer & Woods 2022 for review). This is especially true for bryophytes due to their poikilohydric nature. Moderately dense stands are dehydrated less rapidly than loose stands or isolated shoots because a dense packing of shoots may reduce water loss by effectively reducing the diameter of capillary spaces among close neighbours. Bryophytes growing in dense communities are therefore able to remain physiologically active for a larger part of the growing season, resulting in higher biomass (Bates 1998). Hence, shoot size, biomass production, and species diversity are often positively related to shoot density (Økland & Økland 1996; Økland 2000; Bergamini *et al.* 2001).

In agreement with our first hypothesis (H1), we observed a decrease in randomly associated species pairs from small to large trees, supporting the idea that deterministic processes play an increasingly important role in explaining species composition as habitat complexity and diversity increase (Måren *et al.* 2018). In contrast, in epiphyllous communities, Mežaka *et al.* (2022) found similar random and aggregated species distribution patterns across young and old leaves. These differences may be explained by the fact that epiphylls occupy a very temporary substrate that, as opposed to an entire tree, offers similar habitat conditions through time. Although early colonizers were shown to exhibit higher probabilities of sexual and specialized asexual expression than late colonizers (Sierra *et al.* 2019), all epiphylls must exhibit high dispersal capacities, and changes in species composition on leaves with time reflect a random process of progressive accumulation of species due to increased chances of colonization with time, rather than species turnover (Mežaka *et al.* 2019). In epiphytic bryophyte communities, in contrast, species turnover contributes substantially more to changes in species composition over time than nestedness, illustrating the suite of specialized communities that succeed on a tree through time in response to the increasing number of niches as the tree develops (Patiño *et al.* 2018).

In turn, the marginal contribution of negative interactions reported here supports the notion that competitive exclusion is a rare process in bryophyte communities (Steel *et al.* 2004; Mälson & Rydin 2009; Udd *et al.* 2016). The weak role of

competition on old trees reported here challenges the idea that competition would be important enough to have a negative impact on the accumulation of species richness on trees following an optimum on middle-aged trees, when both pioneers and competitors co-exist (Ellis & Ellis 2013). Observations of co-occurrence patterns may, however, fail to fully capture negative interactions as they already represent the outcome of their effect (Poggiato *et al.* 2021). To avoid competition, species may, in fact, disperse or shift niche (Stroud *et al.* 2019, and references therein). Although its importance would require further research, niche displacement has, however, very rarely been reported in bryophytes (Wiklund & Rydin 2004).

In contrast to our second and third hypotheses (H2 and H3), no increase in competition from young to old trees or from the canopy to the base was observed. To the reverse, positive interactions potentially associated with facilitation prevailed at the tree base. These results were unexpected because, in line with a number of studies supporting the application of the stress-gradient theory in plant communities (Casalini & Bisigato 2018; Kjær *et al.* 2018; Muscarella *et al.* 2018; but see Maestre *et al.* 2006; Qi *et al.* 2018), positive and negative interactions are thought to prevail in communities exposed to harsh and mild environmental conditions, respectively. Although microclimatic conditions substantially vary in terms of daily variations in light exposure, temperature and relative humidity along a tree (Shen *et al.* 2022a), at first sight generating strong stress gradients from the base to the canopy, the stress-gradient hypothesis is not always supported, even along apparently strong stress gradients (Maestre *et al.* 2006; Qi *et al.* 2018). For instance, Scherrer *et al.* (2019) similarly failed to identify changes in biotic interaction patterns among plant communities along an elevation gradient, and no support for the stress-gradient hypothesis was reported among epiphyllous bryophyte communities from gap and closed forest sites (Mežaka *et al.* 2022). In line with Mežaka *et al.* (2022), we tentatively suggest that different stress factors may operate and affect species co-occurrence patterns. For example, while canopies are typically regarded as high-stress habitats exposed to severe drought, temperature and light conditions, tree bases are characterized by extreme shade conditions, acting as a major stress factor (Körner 2003). The similarly low levels of competition observed on trees from all DBH classes suggests that competition on old trees is counter-balanced by the increasing diversity of microhabitats.

In agreement with our hypothesis H4a, co-occurrences involved species pairs from the same community (moss–moss pairs or liverwort–liverwort pairs), whereas non-coincidences involved pairs from different communities (moss–liverwort pairs). Negative interactions leading to spatial segregation were similarly reported in epiphyll communities composed of various communities, but play a minor role among species from the same community (Mežaka *et al.* 2022). This suggests that specific traits of moss and liverwort, or potentially, lineage-specific allelopathic substances, shape their biotic interactions, promoting facilitation among species from the same community and competition among species from different life forms.

Following our hypothesis H4b, negative interactions primarily occurred among species from different life forms. Some life forms are indeed prone to exclude others by competition. In particular, dendroids typically form dense colonies of erect secondary shoots expanding outwards from their primary, creeping shoots that behave as 'runners'. They thus combine the two extreme strategies developed by competitive clonal species, *i.e.*, the 'guerilla' strategy, wherein shoots infiltrate surrounding vegetation, maximizing interspecific contact, and allowing for a rapid spread and the 'phalanx' strategy, involving tightly packed advancing fronts of shoots (Doust 1981). The dendroid life form has therefore been interpreted as the result of selection for high-competitive ability (Bates 1998). Here, we observed that dendroids (*Pinnatella ambigua*), but also fans (*Caduciella mariei*, *Circulifolium microdendron*, and *Plagiochila* spp.), were recurrently involved in competitive interactions. In fact, fans, like dendroids, possess primary shoots creeping along the substrate and erect secondary shoots, the only difference being that fans exhibit strongly complanate leaves.

In turn, the higher proportion of species from the same life form than of species of different life forms in positive associations suggests that facilitation involves species sharing similar architectures. Experimental investigations indeed revealed that the strongest mutually beneficial association occurred between structurally similar species (Michel *et al.* 2012), maximizing a dense packaging of shoots, necessary for maintaining a maximum amount of water among shoots by capillarity and, hence, longer periods of physiological activity.

A different pattern was, however, observed in the lower trunk, wherein co-occurrence patterns involved species of different life forms. We hypothesize that, while communities in the canopy are exposed to severe drought stress, leading to the observed clustering of species sharing the same life form to enhance water retention, communities from the tree base do not or to a much lower extent suffer from water limitation. In those conditions, wherein dense communities are not necessarily adaptive, combinations of species of different life forms may result in a better partitioning of available space and resources.

The findings presented here provide a first quantitative assessment of the contributions of environmental filtering and biotic interactions to epiphytic bryophyte species composition. The main benefit of the current approach over experimental investigations is that it allows for analyses at the level of the entire community. The interpretation of co-occurrence patterns in terms of biotic interactions has, however, been challenged, notably because undetected environmental factors could be erroneously attributed to competition or facilitation (Blanchet *et al.* 2020; Zurell *et al.* 2020; Poggiato *et al.* 2021). In particular, while our experimental setting allowed us to generate a 3D micro-climatic model, suitable to describe vertical and horizontal variations on trees at fine spatial scales, the microclimate that organisms actually experience depends on their size (Pincebourde & Woods 2020). On the surface of rugose trunks, up to 10 °C temperature differences have been reported between the bottom and edge of ridges (Nicolai 1986). Tall bryophyte species themselves may affect the climate conditions experienced by smaller species. Further characterizing the climate conditions actually experienced by epiphytic bryophytes would involve the shift from micro- to nano-climates, which would allow us to better characterize the niches of epiphytic bryophytes and, hence, improve our assessment of their biotic interactions based on the community modelling implemented here. Although this does not undermine our preliminary conclusion that competitive interactions may play a minimal role in the investigated epiphytic bryophyte communities, we propose that the species pairs interpreted here as

positive or negative interactions could be targeted for subsequent experiments on the variation in their fitness when grown in pure stands or mixed colonies.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

F. Collart, T. Shen, and A. Vanderpoorten conceived the project. T. Shen, L. Song, W.-Z. Ma, J. Wang, and L. Mouton collected the data. F. Collart and T. Shen performed the analyses. R. T. Corlett and A. Guisan provided suggestions on the manuscript. T. Shen and A. Vanderpoorten wrote the manuscript, with the assistance of all co-authors.

DATA AVAILABILITY STATEMENT

The dataset analysed in the current study is available in the Figshare repository, with the identifiers (1) https://figshare.com/s/c282472053224783bbf1; (2) https://doi.org/10.6084/m9.figshare.17057624 (Shen *et al.* 2022a).

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Life-forms of the dominant epiphytic bryophyte species recorded on *Parashorea chinensis* at the Xishuangbanna canopy crane site (Yunnan, China).

Table S2. Evaluations of the species distribution models (ensemble and individual algorithms: GAM, BBM and GLM) for dominant epiphytic bryophyte species recorded on *Parashorea chinensis* at the Xishuangbanna canopy crane site (Yunnan, China).

Table S3. Epiphytic bryophyte species pairs involved in positive and negative biotic interactions on small, medium-sized and large specimens of *Parashorea chinensis* at the Xishuangbanna canopy crane site (Yunnan, China).

Table S4. Epiphytic bryophyte species pairs involved in positive and negative biotic interactions on the lower trunk, upper trunk and canopy of *Parashorea chinensis* in a tropical rainforest (Yunnan, China).

REFERENCES

Økland R.H. (1994) Patterns of bryophyte associations at different scales in a Norwegian boreal spruce forest. *Journal of Vegetation Science*, **5**, 127–138. https://doi.org/10.2307/3235646

Økland R.H. (2000) Population biology of the clonal moss *Hylocomium splendens* in Norwegian boreal spruce forests. 5. Vertical dynamics of individual shoot segments. *Oikos*, **88**, 449–469. https://doi.org/10.1034/j.1600-0706.2000.880301.x

Økland R.H., Økland T. (1996) Population biology of the clonal moss *Hylocomium splendens* in Norwegian boreal spruce forests. II. Effects of density. *Journal of Ecology*, **84**, 63–69. https://doi.org/10.2307/2261700

Acevedo M.A., Beaudrot L., Meléndez-Ackerman E.J., Tremblay R.L. (2020) Local extinction risk under climate change in a neotropical asymmetrically dispersed epiphyte. *Journal of Ecology*, **108**, 1553–1564. https://doi.org/10.1111/1365-2745.13361

Araújo M.B., New M. (2007) Ensemble forecasting of species distributions. *Trends in Ecology and Evolution*, **22**, 42–47. https://doi.org/10.1016/j.tree.2006.09.010

Bates J.W. (1998) Is "life-form" a useful concept in bryophyte ecology? *Oikos*, **82**, 223–237. https://doi.org/10.2307/3546962

Belinchón R., Martínez I., Otálora M.A., Aragón G., Dimas J., Escudero A. (2009) Fragment quality and matrix affect epiphytic performance in a Mediterranean forest landscape. *American Journal of Botany*, **96**, 1974–1982. https://doi.org/10.3732/ajb.0900040

Bergamini A., Pauli D., Peintinger M., Schmid B. (2001) Relationships between productivity, number of shoots and number of species in bryophytes and vascular plants. *Journal of Ecology*, **89**, 920–929. https://doi.org/10.1111/j.1365-2745.2001.00613.x

Bertness M.D., Callaway R. (1994) Positive interactions in communities. *Trends in Ecology & Evolution*, **9**, 191–193. https://doi.org/10.1016/0169-5347(94)90088-4

Blanchet F.G., Cazelles K., Gravel D. (2020) Co-occurrence is not evidence of ecological interactions. *Ecology Letters*, **23**, 1050–1063. https://doi.org/10.1111/ele.13525

Breiner F.T., Guisan A.B.A., Nobis M.P. (2015) Overcoming limitations of modelling rare species by using ensembles of small models. *Methods in Ecology and Evolution*, **6**, 1210–1218. https://doi.org/10.1111/2041-210X.12403

Breiner F.T., Nobis M.P., Bergamini A., Guisan A. (2018) Optimizing ensembles of small models for predicting the distribution of species with few occurrences. *Methods in Ecology and Evolution*, **9**, 802–808. https://doi.org/10.1111/2041-210X.12957

Broennimann O., Di Cola V., Guisan A. (2022) ecospat: spatial ecology miscellaneous methods. R package version 3.2.1 Available from https://cran.r-project.org/web/packages/ecospat/ecospat.pdf

Casalini A.I., Bisigato A.J. (2018) Stress-gradient hypothesis and plant distribution along ecotonal gradients. *Austral Ecology*, **43**, 807–816. https://doi.org/10.1111/aec.12623

Collart F., Hedenäs L., Brönnimann O., Guisan A., Vanderpoorten A. (2021) Intraspecific differentiation: implications for niche and distribution modelling. *Journal of Biogeography*, **48**, 415–426. https://doi.org/10.1111/jbi.14009

Cook W.M., Anderson R.M., Schweiger E.W. (2004) Is the matrix really inhospitable? Vole runway distribution in an experimentally fragmented landscape. *Oikos*, **104**, 5–14. https://doi.org/10.1111/j.0030-1299.2004.12761.x

D'Amen M., Mod H.K., Gotelli N.J., Guisan A. (2018) Disentangling biotic interactions, environmental filters, and dispersal limitation as drivers of species co-occurrence. *Ecography*, **41**, 1233–1244. https://doi.org/10.1111/ecog.03148

Doust L.L. (1981) Population dynamics and local specialization in a clonal perennial (*Ranunculus repens*). I. The dynamics of ramets in contrasting habitats. *Journal of Ecology*, **69**, 743–755. https://doi.org/10.2307/2259633

Ellis C.J., Ellis S.C. (2013) Signatures of autogenic epiphyte succession for an aspen chronosequence.

Journal of Vegetation Science, **24**, 688–701. https://doi.org/10.1111/j.1654-1103.2012.01492.x

Francisco T.M., Couto D.R., Garbin M.L., Misaki F., Ruiz-Miranda C.R. (2021) Role of spatial and environmental factors in structuring vascular epiphyte communities in two neotropical ecosystems. *Perspectives in Plant Ecology, Evolution and Systematics*, **51**, 125621. https://doi.org/10.1016/j.ppees.2021.125621

Frego K.A., Carleton T.J. (1995) Microsite tolerance of four bryophytes in a mature black spruce stand: reciprocal transplants. *The Bryologist*, **98**, 452–458. https://doi.org/10.2307/3243584

Götzenberger L., de Bello F., Bråthen K.A., Davison J., Dubuis A., Guisan A., Lepš J., Lindborg R., Moora M., Pärtel M., Pellissier L., Pottier J., Vittoz P., Zobel K., Zobel M. (2012) Ecological assembly rules in plant communities – approaches, patterns and prospects. *Biological Reviews*, **87**, 111–127. https://doi.org/10.1111/j.1469-185X.2011.00187.x

García-Girón J., Heino J., García-Criado F., Fernández-Aláez C., Alahuhta J. (2020) Biotic interactions hold the key to understanding metacommunity organization. *Ecography*, **43**, 1180–1190. https://doi.org/10.1111/ecog.05032

Gavini S.S., Ezcurra C., Aizen M.A. (2019) Plant–plant interactions promote alpine diversification. *Evolutionary Ecology*, **33**, 195–209. https://doi.org/10.1007/s10682-019-09972-5

Gotelli N.J., Ulrich W. (2010) The empirical Bayes approach as a tool to identify non-random species associations. *Oecologia*, **162**, 463–477. https://doi.org/10.1007/s00442-009-1474-y

Grant K., Kreyling J., Heilmeier H., Beierkuhnlein C., Jentsch A. (2014) Extreme weather events and plant–plant interactions: shifts between competition and facilitation among grassland species in the face of drought and heavy rainfall. *Ecological Research*, **29**, 991–1001. https://doi.org/10.1007/s11284-014-1187-5

Grime J.P. (1977) Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *American Naturalist*, **111**, 1169–1194 https://www.jstor.org/stable/2460262

Grime J.P., Rincon E.R., Wickerson B.E. (1990) Bryophytes and plant strategy theory. *Botanical Journal of the Linnean society*, **104**, 175–186. https://doi.org/10.1111/j.1095-8339.1990.tb02217.x

Guisan A., Thuiller W., Zimmermann N.E. (2017) *Habitat suitability and distribution models: with applications in R*. Cambridge University Press. https://doi.org/10.1017/9781139028271

Hedenäs L. (2012) Morphological and anatomical features associated with epiphytism among the pleurocarpous mosses—one basis for further research on adaptations and their evolution. *Journal of Bryology*, **34**, 79–100. https://doi.org/10.1179/1743282011Y.0000000049

Hirzel A.H., Le Lay G., Helfer V., Randin C., Guisan A. (2006) Evaluating the ability of habitat suitability models to predict species presences. *Ecological Modelling*, **199**, 142–152.

Holz I., Gradstein R.S. (2005) Cryptogamic epiphytes in primary and recovering upper montane oak forests of Costa Rica – species richness, community composition and ecology. *Plant Ecology*, **178**, 89–109. https://doi.org/10.1007/s11258-004-2496-5

IUCN (1994) 1994 IUCN Red List categories and Criteria version 2.3. Prepared by International Union for the Conservation of Nature, Species Survival Commission, Gland, Switzerland Available from

https://web.archive.org/web/20140722073142/http://www.iucnredlist.org/technical-documents/categories-and-criteria/1994-categories-criteria

Jiménez-Valverde A. (2020) Sample size for the evaluation of presence–absence models. *Ecological Indicators*, **114**, 106289. https://doi.org/10.1016/j.ecolind.2020.106289

Körner C. (2003) Limitation and stress – always or never? *Journal of Vegetation Science*, **14**, 141–143. https://doi.org/10.1658/1100-9233(2003)014[0141:LASAON]2.0.CO;2

Kjær U., Olsen S.L., Klanderud K. (2018) Shift from facilitative to neutral interactions by the cushion plant *Silene acaulis* along a primary succession gradient. *Journal of Vegetation Science*, **29**, 42–51. https://doi.org/10.1111/jvs.12584

Löbel S., Snäll T., Rydin H. (2006) Species richness patterns and metapopulation processes–evidence from epiphyte communities in boreo-nemoral forests. *Ecography*, **29**, 169–182. https://doi.org/10.1111/j.2006.0906-7590.04348.x

Ledent A., Gauthier J., Pereira M., Overson R., Laenen B., Mardulyn P., Gradstein S.R., De Haan M., Ballings P., Van der Beeten I., Zartman C.E. (2020) What do tropical cryptogams reveal? Strong genetic structure in Amazonian bryophytes. *New Phytologist*, **228**, 640–650.

Lett S., Jónsdóttir I.S., Becker-Scarpitta A., Christiansen C.T., During H., Ekelund F., Henry G.H.R., Lang S.I., Michelsen A., Rousk K., Alatalo J.M., Betway K.R., Rui S.B., Callaghan T., Carbognani M., Cooper E.J., Cornelissen J.H.C., Dorrepaal E., Egelkraut D., Elumeeva T.G., Haugum S.V., Hollister R.D., Jägerbrand A.K., Keuper F., Klanderud K., Lévesque E., Liu X., May J., Michel P., Mörsdorf M., Petraglia A., Rixen C., Robroek B.J.M., Rzepczynska A.M., Soudzilovskaia N.A., Tolvanen A., Vandvik V., Volkov I., Volkova I., Zuijlen K. (2022) Can bryophyte groups increase functional resolution in tundra ecosystems? *Arctic Science*, **8**, 609–637. https://doi.org/10.1139/as-2020-0057

Liaw A., Wiener M. (2002) Classification and regression by RandomForest. *R News*, **2**, 18–22 Available from https://cogns.northwestern.edu/cbmg/LiawAndWiener2002.pdf

Mägdefrau K. (1982) Life-forms of bryophytes. In: Smith A.J.E. (Ed), *Bryophyte ecology*. Chapman and Hall, London, UK, pp 45–58. https://doi.org/10.1007/978-94-009-5891-3_2

Mälson K., Rydin H. (2009) Competitive hierarchy, but no competitive exclusions in experiments with rich fen bryophytes. *Journal of Bryology*, **31**, 41–45. https://doi.org/10.1179/174328209X404916

Måren I.E., Kapfer J., Aarrestad P.A., Grytnes J.-A., Vandvik V. (2018) Changing contributions of stochastic and deterministic processes in community assembly over a successional gradient. *Ecology*, **99**, 148–157. https://doi.org/10.1002/ecy.2052

Maestre F.T., Valladares F., Reynolds J.F. (2006) The stress-gradient hypothesis does not fit all relationships between plant–plant interactions and abiotic stress: further insights from arid environments. *Journal of Ecology*, **94**, 17–22. https://doi.org/10.1111/j.1365-2745.2005.01089.x

McAlister S. (1995) Species interactions and substrate-specificity among log-inhabiting bryophyte species. *Ecology*, **76**, 2184–2195. https://doi.org/10.2307/1941692

Mežaka A., Bader M.Y., Salazar A.N., Mendieta-Leiva G. (2019) Epiphyll specialization for leaf and forest

successional stages in a tropical lowland rainforest. *Journal of Vegetation Science*, **31**, 118–128. https://doi.org/10.1111/jvs.12830

Mežaka A., Salazar A.N., Mendieta-Leiva G., Bader M.Y. (2022) Life on a leaf: the development of spatial structure in epiphyll communities. *Journal of Ecology*, **110**, 619–630. https://doi.org/10.1111/1365-2745.13824

Medina N.G., Estébanez B. (2014) Does spore ultra-structure mirror different dispersal strategies in mosses? A study of seven Iberian Orthotrichum species. *PLoS One*, **9**, e112867. https://doi.org/10.1371/journal.pone.0112867

Michel P., Lee W.G., During H.J., Cornelissen J.H.C. (2012) Species traits and their non-additive interactions control the water economy of bryophyte cushions. *Journal of Ecology*, **100**, 222–231. https://doi.org/10.1111/j.1365-2745.2011.01898.x

Mod H.K., Chevalier M., Luoto M., Guisan A. (2020) Scale dependence of ecological assembly rules: insights from empirical datasets and joint species distribution modelling. *Journal of Ecology*, **108**, 1967–1977. https://doi.org/10.1111/1365-2745.13434

Mota de Oliveira S., ter Steege H. (2015) Bryophyte communities in the Amazon forest are regulated by height on the host tree and site elevation. *Journal of Ecology*, **103**, 441–450. https://doi.org/10.1111/1365-2745.12359

Mota de Oliveira S., ter Steege H., Cornelissen J.H., Gradstein S.R. (2009) Niche assembly of epiphytic bryophyte communities in the Guianas: a regional approach. *Journal of Biogeography*, **36**, 20762084. https://doi.org/10.1111/j.1365-2699.2009.02144.x

Muscarella R., Messier J., Condit R., Hubbell S.P., Svenning J.-C. (2018) Effects of biotic interactions on tropical tree performance depend on abiotic conditions. *Ecology*, **99**, 2740–2750. https://doi.org/10.1002/ecy.2537

Nicolai V. (1986) The bark of trees: thermal properties, microclimate and fauna. *Oecologia*, **69**, 148–160. https://doi.org/10.1007/BF00399052

Patiño J., Gómez-Rodríguez C., Pupo-Correia A., Sequeira M., Vanderpoorten A. (2018) Trees as habitat islands: temporal variation of alpha and beta diversity in epiphytic laurel forest bryophyte communities. *Journal of Biogeography*, **45**, 1727–1738. https://doi.org/10.1111/jbi.13359

Peck J.E., Frelich L.E. (2008) Moss harvest truncates the successional development of epiphytic bryophytes in the Pacific Northwest. *Ecological Applications*, **18**, 146–158. https://doi.org/10.1890/07-0145.1

Pincebourde S., Woods H.A. (2020) There is plenty of room at the bottom: microclimates drive insect vulnerability to climate change. *Current Opinion in Insect Science*, **41**, 63–70. https://doi.org/10.1016/j.cois.2020.07.001

Poggiato G., Munkemuller T., Bystrova D., Arbel J., Clark J.S., Thuiller W. (2021) On the interpretations of joint modeling in community ecology. *Trends in Ecology and Evolution*, **36**, 391–401. https://doi.org/10.1016/j.tree.2021.01.002

Qi M., Sun T., Xue S.F., Yang W., Shao D.D., Martínez-López J. (2018) Competitive ability, stress tolerance and plant interactions along stress gradients. *Ecology*, **99**, 848–857. https://doi.org/10.1002/ecy.2147

Rossignaud L., Kimberley M.O., Kelly D., Fei S., Brockerhoff E.G. (2022) Effects of competition and habitat heterogeneity on native–exotic plant richness relationships across spatial scales. *Diversity and*

Distributions, **28**, 1093–1104. https://doi.org/10.1111/ddi.13516

Rydin H. (1997) Competition among bryophytes. *Advances in Bryology*, **6**, 135–168.

Scherrer D., Mod H., Pottier J., Dubuis A., Pellissier L., Vittoz P., Götzenberger L., Zobel M., Guisan A. (2019) Disentangling the processes driving plant assemblages in mountain grasslands across spatial scales and environmental gradients. *Journal of Ecology*, **107**, 265–278. https://doi.org/10.1111/1365-2745.13037

Shen T., Corlett R.T., Collart F., Kasprzyk T., Guo X.L., Patiño J., Su Y., Hardy O.J., Ma W.Z., Wang J., Wei Y.M., Mouton L., Li Y., Song L., Vanderpoorten A. (2022a) Microclimatic variation in tropical canopies: a glimpse into the processes of community assembly in epiphytic bryophyte communities. *Journal of Ecology*, **110**, 3023–3038. https://doi.org/10.1111/1365-2745.14011

Shen T., Corlett R.T., Song L., Ma W.Z., Guo X.L., Song Y., Wu Y. (2018) Vertical gradient in bryophyte diversity and species composition in tropical and subtropical forests in Yunnan, SW China. *Journal of Vegetation Science*, **29**, 1075–1087. https://doi.org/10.1111/jvs.12692

Shen T., Song L., Collart F., Guisan A., Su Y., Hu H.-X., Wu Y., Dong J.-L., Vanderpoorten A. (2022b) What makes a good phorophyte? Predicting occupancy, species richness and abundance of vascular epiphytes in a lowland seasonal tropical forest. *Frontiers in Forests and Global Change*, **5**, 1007473. https://doi.org/10.3389/ffgc.2022.1007473

Sierra A.M., Toledo J.J., Salazar A.N., Zartman C.E. (2019) Reproductive traits as predictors of assembly chronosequence patterns in epiphyllous bryophyte metacommunities. *Journal of Ecology*, **107**, 875–886. https://doi.org/10.1111/1365-2745.13058

Slack N.G. (1990) Bryophytes and ecological niche theory. *Botanical Journal of the Linnean Society*, **104**, 187–213. https://doi.org/10.1111/j.1095-8339.1990.tb02218.x

Snäll T., Hagström A., Rudolphi J., Rydin H. (2004) Distribution pattern of the epiphyte Neckera pennata on three spatial scales–importance of past landscape structure, connectivity and local conditions. *Ecography*, **27**, 757–766. https://doi.org/10.1111/j.0906-7590.2004.04026.x

Snäll T., Ribeiro P.J., Jr., Rydin H. (2003) Spatial occurrence and colonisations in patch-tracking metapopulations: local conditions versus dispersal. *Oikos*, **103**, 566–578. https://doi.org/10.1034/j.1600-0706.2003.12551.x

Soliveres S., Smit C., Maestre F.T. (2015) Moving forward on facilitation research: response to changing environments and effects on the diversity, functioning and evolution of plant communities. *Biological Reviews*, **90**, 297–313. https://doi.org/10.1111/brv.12110

Spicer M.E., Woods C.L. (2022) A case for studying biotic interactions in epiphyte ecology and evolution. *Perspectives in Plant Ecology, Evolution and Systematics*, **54**, 125658. https://doi.org/10.1016/j.ppees.2021.125658

Steel J.B., Wilson J.B., Anderson B.J., Lodge R.H.E., Tangney R.S. (2004) Are bryophyte communities different from higher-plant communities? Abundance relations. *Oikos*, **104**, 479–486. https://doi.org/10.1111/j.0030-1299.2004.12840.x

Stone L., Roberts A. (1990) The checkerboard score and species distributions. *Oecologia*, **85**, 74–79. https://doi.org/10.1007/BF00317345

Stroud J.T., Giery S.T., Outerbridge M., Feeley K.J. (2019) Ecological character displacement alters the outcome of priority effects during community assembly. *Ecology*, **100**, e02727. https://doi.org/10.1002/ecy.2727

Tang J.W., Shi J.P., Zhang G.M., Bai K.J. (2008) Density, structure and biomass of *Parashorea chinensis* populations in different patches in Xishuangbanna, SW China. *Chinese Journal of Plant Ecology*, **32**, 40. https://doi.org/10.3773/j.issn.1005-264x.2008.01.005

Taylor A., Burns K. (2015) Epiphyte community development throughout tree ontogeny: an Island ontogeny framework. *Journal of Vegetation Science*, **26**, 902–910. https://doi.org/10.1111/jvs.12289

Thuiller W., Georges D., Gueguen M., Engler R., Breiner F. (2021) biomod2: ensemble platform for species distribution modeling. R package version 3.5.1 Available from https://CRAN.R-project.org/package=biomod2

Udd D., Sundberg S., Rydin H. (2016) Multi-species competition experiments with peatland bryophytes. *Journal of Vegetation Science*, **27**, 165–175. https://doi.org/10.1111/jvs.12322

Vanderpoorten A., Patiño J., Désamoré A., Laenen B., Górski P., Papp B., Holá E., Korpelainen H., Hardy O. (2019) To what extent are bryophytes efficient dispersers? *Journal of Ecology*, **107**, 2149–2154.

Victoriano-Romero E., García-Franco J.G., Mehltreter K., Valencia-Díaz S., Toledo-Hernández V.H., Flores-Palacios A. (2020) Epiphyte associations and canopy soil volume: nutrient capital and factors influencing soil retention in the canopy. *Plant Biology*, **22**, 541–552. https://doi.org/10.1111/plb.13080

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. https://doi.org/10.1093/aobpla/plu092

Whitehead J., Wittemann M., Cronberg N. (2018) Allelopathy in bryophytes – a review. *Lindbergia*, **41**, 01097. https://doi.org/10.25227/linbg.01097

Wiklund K., Rydin H. (2004) Modelled growth rate and effect of microclimate, competition, and precipitation. *Bryologist*, **107**, 293–301. https://doi.org/10.1639/0007-2745(2004)107[0293:CEONPM]2.0.CO;2

Woods C.L., Cardelús C.L., De Walt S.J. (2015) Microhabitat associations of vascular epiphytes in a tropical wet forest canopy. *Journal of Ecology*, **103**, 421–430. https://doi.org/10.1111/1365-2745.12357

Woods C.L., Nevins L.M., Didier E.J. (2019) Structural heterogeneity of trees influences epiphyte distributions in a northern temperate rainforest. *Journal of Vegetation Science*, **30**, 1134–1142. https://doi.org/10.1111/jvs.12797

Zhang L., Hui G., Hu Y., Zhao Z. (2018) Spatial structural characteristics of forests dominated by *Pinus tabulaeformis* Carr. *PLoS One*, **13**, e0194710. https://doi.org/10.1371/journal.pone.0194710

Zotz G., Schultz S. (2008) The vascular epiphytes of a lowland forest in Panama – species composition and spatial structure. *Plant Ecology*, **195**, 131–141. https://doi.org/10.1007/s11258-007-9310-0

Zotz G., Vollrath B. (2003) The epiphyte vegetation of the palm *Socratea exorrhiza* – correlations with tree size, tree age and bryophyte cover. *Journal Tropical Ecology*, **19**, 81–90. https://doi.org/10.1017/S0266467403003092

Zotz G. (2016) *Plants on plants – the biology of vascular epiphytes*. Switzerland: Springer International Publishing. https://doi.org/10.1007/978-3-319-39237-0

Zurell D., Zimmermann N.E., Gross H., Baltensweiler A., Sattler T., Wuest R.O. (2020) Testing species assemblage predictions from stacked and joint species distribution models. *Journal of Biogeography*, **47**, 101–113. https://doi.org/10.1111/jbi.13608