

# Diversity patterns of epiphytic bryophytes across spatial scales: Species-rich crowns and beta-diverse trunks

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## Abstract

Tropical forests are highly diverse at many spatial scales. In these forests, small-sized canopy organisms can form species-rich communities already within a few cm<sup>2</sup>. Understanding how species numbers increase when expanding the sampling along the tree and the forest is critical for evaluating the processes maintaining biodiversity. We therefore studied epiphytic bryophyte diversity in tree crowns and along trunks across spatial scales in a tropical lowland forest in Amazonian Ecuador, sampling bryophytes in 100-cm<sup>2</sup> quadrats on 24 trees (15–22 quadrats each) using a spatially hierarchical design, analyzing alpha and beta diversity at different spatial grains and extents. At the smallest grain, tree crowns held more bryophyte species than trunks, but at the largest grain the trunks held most species (93 vs. 77), as beta diversity was higher among trunks than among crowns. However, except for trunks at the largest extent (all 24 trees), the highest beta diversity among quadrats was always found between crowns and trunks. Species turnover strongly dominated beta diversity at all spatial scales. This and the high species richness resulted in highly unpredictable species compositions, especially in trunk communities. These patterns suggest different controls of diversity in crowns than on trunks and an important role for chance processes in shaping these communities. The high beta diversity within trees, in combination with the large effort involved in climbing trees, implies that diversity sampling of small canopy organisms is most efficient using an intensive (many plots on few trees) rather than extensive (many trees across a large area) sampling.

Abstract in Spanish is available with online material.

## KEY WORDS

beta diversity, canopy, species richness, species turnover, tropical lowland forests, vertical gradients, Yasuní national park

## 1 | INTRODUCTION

Non-vascular epiphyte communities can exhibit high species diversity at the scale of centimeters, while more and more species are

added when adding branches and trees, or when expanding to regions and continents (e.g., Draper et al., 2005; Medina et al., 2010; Mota de Oliveira & ter Steege, 2013). Processes controlling diversity can vary considerably at such widely diverging scales (Medina

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et al., 2013). Achieving multi-scale descriptions of the diversity of these communities is therefore crucial to guide tests and models of the relative importance of stochasticity, species interactions, environmental filtering, and dispersal limitations for determining the composition of their species assemblages.

For most plant communities, species richness, “*the most natural measurement of biodiversity*” (McGill et al., 2015), increases with scale in a predictable manner known as the species-area relationship (SAR; Storch, 2016). For describing how the other important measure of diversity, the dissimilarity between communities or beta diversity, varies with scale demands distinguishing between the spatial resolution (i.e., the grain: the area of each sampled unit) and the geographic extent (the area covered by all observations; Gonzalez et al., 2020). Increasing the sampled extents while maintaining a fixed grain (e.g., plot size) will result in a higher average species dissimilarity among sampling units because samples located further apart likely differ more between them than communities located closer to each other, that is, in smaller extents (Barton et al., 2013). In turn, sampling a fixed extent with increasing grain will result in a decreasing dissimilarity between sampling units, as larger sampling units contain more species and thereby likely also more shared species (Barton et al., 2013).

However, for epiphytic bryophytes, species turnover has been suggested to be lower across extents of hundreds of km than between the crown and the trunk of the very same tree in tropical lowland forests (Mota de Oliveira et al., 2009). This pattern suggests that local (environmental constraints and species interactions; McGill et al., 2015) and meta-community processes (spatial heterogeneity and dispersal limitations; McGill et al., 2015) structuring these communities at fine spatial scales are more important than long-distance environmental gradients or dispersal limitations. This is likely due to the strong environmental variation experienced by epiphytic communities along the vertical dimension of their habitat combined with easy long-distance dispersal by spores. The high turnover between crowns and trunks also suggests that processes driving diversity may differ between these tree sections. To understand these processes, an accurate description of both alpha and beta diversity within and among different vertical zones is needed, that is, with several samples per zone—a practice unfortunately uncommon in tropical bryophyte studies (Sanger & Kirkpatrick, 2017; Zotz, 2007).

In topographically diverse forests, alpha and beta diversity patterns of epiphytic bryophytes can depend strongly on local environmental conditions. For instance, tropical lowland cloud forests, where high moisture and local air drainage patterns result in frequent fog occurrence, hold richer and different epiphytic liverwort communities than lowland rain forests located on nearby slopes (Gehrig-Downie et al., 2013; Gradstein, 2006). Effects of local topography may thus be relevant while describing diversity patterns at the local and the meta-community scale (*sensu* McGill et al., 2015).

To understand how bryophyte diversity in tropical lowland forests is spatially structured, we studied vertical and horizontal patterns of alpha and beta diversity of epiphytic bryophyte communities

across varying grains and extents in the hyper-diverse forest surrounding the Yasuní Scientific Station in the Amazonian lowlands of Ecuador (Bass et al., 2010). Our research questions were as follows: How is alpha diversity distributed along vertical gradients from tree bases to canopy? How do beta diversity and its components (turnover and nestedness) vary within and between vertical zones across different spatial extents? How do vertical patterns in alpha and beta diversity compare to horizontal patterns at different spatial scales? More specifically, at which spatial extent does beta diversity become larger between trees than between trunks and crowns within a single tree?

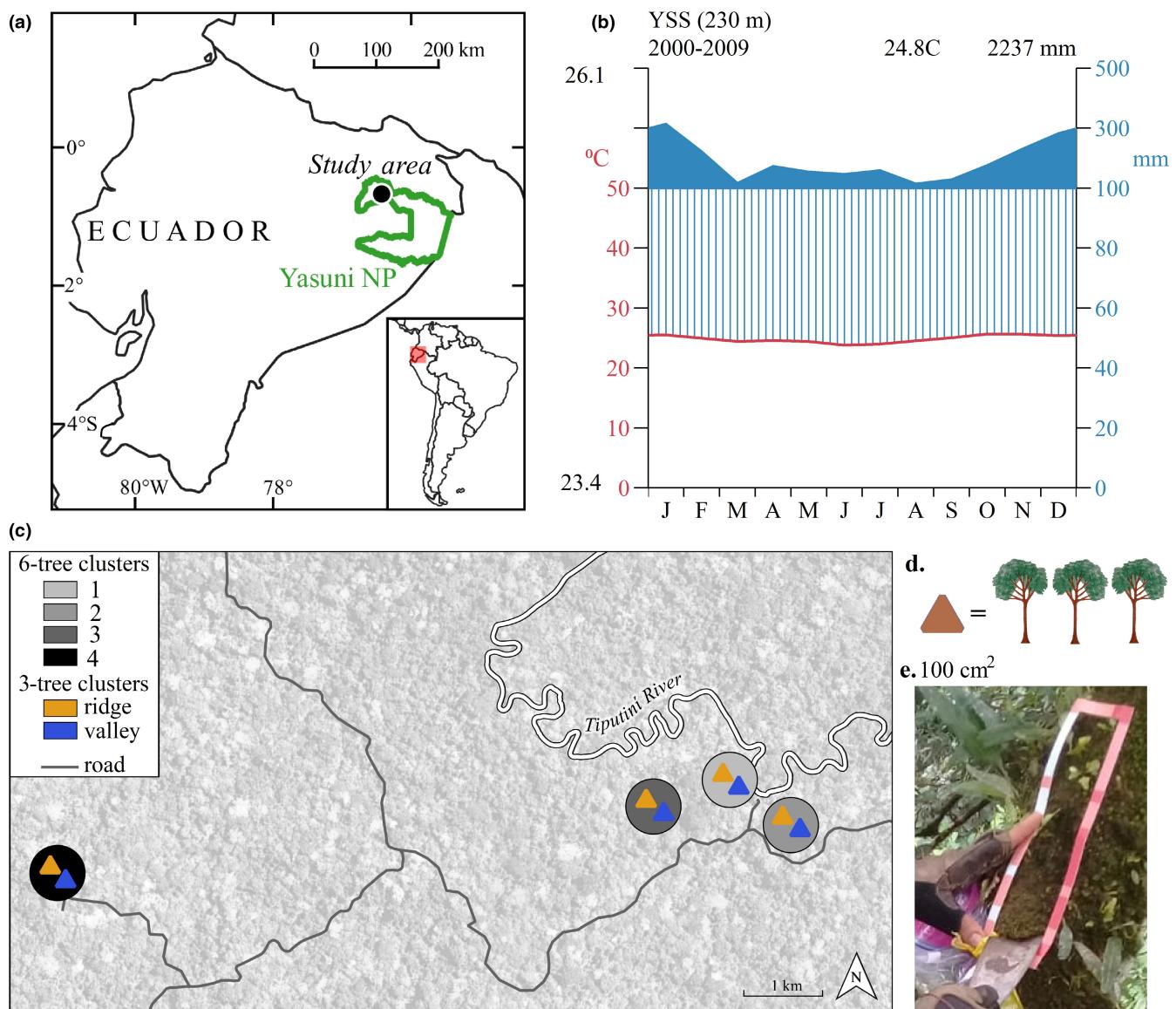
## 2 | METHODS

### 2.1 | Study area

The Yasuní Scientific Station (YSS), located in the Orellana province of Ecuador (0°40'27"S 76°23'50"W, ~230 m.a.s.l., ~90 ha) to the South of the Tiputini river (Figure 1a), is a part of the Yasuní National Park and Biosphere Reserve (190–400 m.a.s.l., 2,366,182 ha; Estación Científica Yasuní, 2015). The YSS holds highly diverse terra-firme forests with up to 150 tree species per hectare (Bass et al., 2010; Valencia et al., 1994, 2004); these forests are also rich in palm and liana species. The modestly undulating terrain (Tschoopp, 1953), where local valleys and ridges differ by less than 100 m of elevation, features poor and clayey soils originated from weathering of dominant materials of the intersection between two geological shields, Andes and Brazilian (stratified clays and sediments of the Curaray formation from the tertiary; Tschoopp, 1953). The region corresponds to the Holdridge Life Zone of tropical wet forest (Holdridge, 1947, 1964) and experiences a wet equatorial climate with imperceptible seasonality (Bailey, 2014), an annual mean temperature of ~25°C, and an average precipitation of ~2240 mm/year (Figure 1b).

### 2.2 | Study design and field data collection

We applied a hierarchical study design to survey epiphytic bryophyte communities, stratified by topography (valleys and ridges) and the distance to the Tiputini River (200, 500, 800, 6000 m). This stratification was applied because we anticipated that bryophyte diversity may increase toward local valleys and closer to the river due to higher moisture. In each of four sites, we sampled six trees: three in a local valley and three on the closest ridge (Figure 1c). Thus, the hierarchical study design encompassed five grains: the entire set of 24 trees, clusters of six trees, with a mean distance of ca. 200 m among trees within a cluster (Figure 1c); clusters of three trees, with a mean distance of ca. 90 m among trees within a cluster (Figure 1d); trees; and 100-cm<sup>2</sup> sampling quadrats. The number of sampling quadrats per tree varied between 15 and 22, depending on the height of the first canopy branch (see Section 2.2.1. Survey of bryophyte epiphyte communities); we used square sampling quadrats except when



**FIGURE 1** Study area and hierarchical study design used to understand patterns of alpha and beta diversity of epiphytic bryophytes across varying grain and extent in tropical lowland forests. Location (a) and climate (b) of the Yasuní Scientific Station (YSS); climate diagram, following Walter and Lieth (1960), based on data collected from 2000 to 2009 by a standard climate station in a forest clearing at the YSS. Spatial distribution of clusters of six trees (c) where triangles correspond to clusters of three trees (d). Epiphytic bryophytes in each tree were sampled from the ground level to the crown in 100-cm<sup>2</sup> sampling quadrats (e)

sampling thin canopy branches, where reduced diameter compelled us to use rectangular sampling quadrats (Figure 1e). We selected 24 mature canopy trees, that is, excluding emergent and subcanopy trees, that were safe for climbing. Tree DBH averaged ~60 cm, tree height averaged ~25 m, and the average crown radius averaged ~7 m. These 24 trees belonged to 18 species in 11 families (Table S1), so that tree species were mostly singletons and host preference of the epiphytes was therefore not analyzed.

### 2.2.1 | Survey of bryophyte epiphyte communities

In the selected trees, we sampled non-vascular epiphytic communities established in the middle canopy (*sensu* Johansson, 1974) and

on the tree trunk along the vertical gradient from the ground level to the first living branch of the crown, by using adapted climbing techniques (Perry, 1978). This systematic sampling at regular intervals from the tree bases to the tree crowns has been used by several authors in different South American forests (Gómez González et al., 2017; Mellado-Mansilla et al., 2017; Patiño et al., 2009; Wolf, 1994). The sampling protocol consisted of collecting the non-vascular epiphytes found in 100-cm<sup>2</sup> quadrats randomly selected from a larger set of quadrats used to estimate epiphyte cover (10 out of 20 quadrats in the medium section of crown branches and one out of four quadrats per distance from the tree base to the height of the first living canopy branch). We sampled 24 trees, with 240 sampling quadrats collected in the canopy layer (24 trees × 10 sampling quadrats), and 198 sampling quadrats collected in tree trunks

(the number of sampling quadrats collected per tree trunk varied between 5 and 12 depending on the height of the first canopy branch, which averaged 14 m). The sampling quadrat size allowed us to fix the number of sampling quadrats in the crown (10) regardless of the crown size as, even in small crown trees, there were plenty of opportunities to reach 10 locations suitable to sample.

Collected samples were air-dried and transported to the herbarium of the Pontificia Universidad Católica del Ecuador—QCA (Quito)—and to the cryptogamy collection at the Herbarium of the Muséum National d'Histoire Naturelle—PC (Paris)—for species identification. Mosses were identified using Churchill (1994), Buck (2003) and Florschütz-de Waard et al. (2011), and liverworts using Gradstein and Ilkuu-borges (2009) and a manuscript version of Gradstein (2021).

## 2.2.2 | Possible predictors of species diversity

Predictors were recorded at the tree and the quadrat level. Tree descriptors were valley/ridge position, distance from the Tiputini river (as a categorical variable identifying the 6-tree clusters), diameter at the breast height (DBH, cm), height (m) and average crown radius (m), a simple field measurement (Zhu et al., 2021) used as a proxy of crown size. The effect of tree species could not be analyzed, as most tree species were represented only once in our sample (Table S1). Quadrat descriptors were position on the trunk or in the crown and the height from the tree base (m). To estimate canopy cover, pictures were taken with a mobile phone and processed in Gap Light Analyzer (GLA Version 2.0; Frazer et al., 2008) to estimate canopy openness, as an indicator of light availability.

## 2.3 | Data processing and statistical analysis

To describe how alpha diversity distributes along vertical zones while accounting for the possible influence of additional predictors and random factors, we fit generalized linear models (GLM) predicting the number of species per quadrat, with a Poisson error distribution and “log” link function, as a function of vertical zone (crown or trunk—as these two zones provided the most parsimonious grouping of species compositions, Appendix S1 in Supporting Information), tree DBH, tree height, distance from the Tiputini river (as a categorical variable), position in the local topography, and the interaction between the last two. The random effects were tree and the interaction between tree and vertical zone. We fitted all possible models and the single best model was selected using the Akaike information criterion, corrected for small sample size (AICc). We assessed overdispersion of the model residuals by calculating the square root of the quotient between the penalized residual sum of squares and the number of observations, using the function “*dispersion\_glm*” of the R package “*blmeco*” (Korner-Nievergelt et al., 2015); a value

of 0.978 ruled out residual overdispersion in the best model. This modeling approach was performed in R, fitting models with the “*glmer*” function of the “*lme4*” package (Bates et al., 2015) and analyzing models with companion functions of the “*lmerTest*” (Kuznetsova et al., 2017), “*car*” (Fox & Weisberg, 2019), and “*MuMIn*” (Barton, 2020) R packages. To compare vertical and horizontal patterns of alpha diversity, we aggregated species richness per vertical zone and tested for differences between these zones at each spatial scale (tree, 3-tree cluster, 6-tree cluster, and the study area) with paired t-tests. Based on Mantel tests assessing the independence among trees and tree clusters (Table S2), we considered replicates at these spatial scales as independent when testing for differences between vertical zones. In addition, a Wilcoxon signed rank test was performed to test for differences between vertical zones from the raw data, that is, those gathered at the quadrat level.

The beta partitioning approach developed by Baselga (2010, 2017); Baselga and Leprieur (2015); Baselga and Orme (2012) framed our approach to respond to our questions on how beta diversity and its components vary in space. This approach discriminates turnover and nestedness as the components of beta diversity when assessing pairwise comparisons of study units. To evaluate patterns of beta diversity within trees, we calculated pairwise Sørensen dissimilarities and its components, turnover and nestedness, among sampling quadrats (species presence/absence) per tree, summarized these for the whole tree and within and between vertical zones (trunk and crown), and compared the means using either ANOVA or Kruskal-Wallis tests, depending on the distribution of the data. These analyses and corresponding visualization plots (annotated heatmaps and derived clustering classifications based on Euclidean distances) were performed and built in R (Version 4.0.2) using the packages “*betapart*” (Baselga et al., 2021), “*car*” (Fox & Weisberg, 2019), and “*ComplexHeatmap*” (Gu et al., 2016).

To study how beta diversity within and between vertical zones varies across grains and extents (cf. Barton et al., 2013), we used several analyses: (a) To assess how beta diversity varies with extent, we calculated the Sørensen dissimilarity at the extent of single trees, 3-tree clusters, 6-tree clusters, and the whole study area with sampling quadrat as a fixed spatial grain. We tested for differences in mean pairwise dissimilarities at each spatial extent within and between vertical zones (crowns and trunks) with Kruskal-Wallis tests, and for differences across spatial extents with t-tests, using as the reference the mean for the whole extent. (b) To assess how grain influences beta diversity measurements, we calculated the Sørensen dissimilarity for the whole extent of the study using different spatial grains: sampling quadrat, tree, 3-tree cluster, 6-tree cluster. We tested for differences within and between vertical zones (crowns and trunks) at each spatial grain by using Kruskal-Wallis tests, and across grains with t-tests, using as the reference the mean estimated with sampling quadrat as the spatial grain. (c) To assess how grain influences the sharing of species between vertical zones, we calculated the percentage of

species exclusive to the trunk, exclusive to the crown, and shared between the two at different grains. To this end, we aggregated the community of each vertical zone at the respective grain (e.g., per tree or group of trees) and plotted changes in the percentages of shared and exclusive species across grains in a triangular plot (Koleff et al., 2003).

We addressed the specific sub-question at what spatial extent beta diversity becomes larger between trees than between trunks and crowns within a single tree. For this, we calculated vertical beta diversity and contrasted it against horizontal beta diversity with tree as the spatial grain at different extents using 95% confidence intervals. We calculated vertical beta diversity as the mean pairwise Sørensen dissimilarity between whole trunk and whole crown within the same tree ( $n = 24$ ). Then, we calculated horizontal beta diversity for trees, tree crowns, and tree trunks (i.e., the tree as the fixed spatial grain) as the mean pairwise Sørensen dissimilarity among these units at three spatial extents: 3-tree cluster ( $n = 8$ ), 6-tree cluster ( $n = 4$ ), and the all 24 studied trees ( $n = 1$ ). To further identify the effect of spatial extent, expressed by geographical distance between trees, on beta diversity, we performed Mantel tests and identified that no correlation occurred between the community dissimilarity matrices and spatial matrices at any spatial grain (Table S2); therefore, we used trees and tree clusters as independent replicates when testing for differences between vertical zones. These analyses used the functions "mantel" ("vegan" package; Oksanen et al., 2020), "beta.pair" ("betapart" package; Baselga et al., 2021), "Ternary.Plot" ("Ternary"; Smith, 2017), and "t.test" ("stat", package; R Core Team, 2020).

## 3 | RESULTS

### 3.1 | Floristics

We recorded 2658 occurrences of 115 bryophyte species including one species new to science and five new records for Ecuador. The new species, *Lejeunea yasuniensis* Gradst. and C.Bastos (Gradstein, 2021), was collected on nine trees in total and both in trunk and in crown quadrats. Two of the new records for Ecuador occurred in trunk quadrats (*Lejeunea rionegrensis* Spruce observed on two trees, and *Xylolejeunea pellucidissima* [Spruce] Gradst. observed on a single tree) and the other three were tree crown singletons (*Acrolejeunea torulosa* (Lehm. and Lindenb.) Schiffn., *Syrrhopodon simmondsii* Steere, and *Thysananthus amazonicus* (Spruce) Steph.). In total, we recorded 72 liverwort species distributed in nine families and 34 genera, and 43 moss species distributed in 16 families and 29 genera (Appendix S2). *Cheilolejeunea rigidula* and *Ceratolejeunea cornuta* were the most frequent species, occurring in 52% and 51% of the sampling quadrats, and their botanic family, Lejeuneaceae, was the richest with 54 species. Singletons corresponded to 21% of the collected species, while a further 14% of species occurred in only two plots.

### 3.2 | Alpha diversity patterns

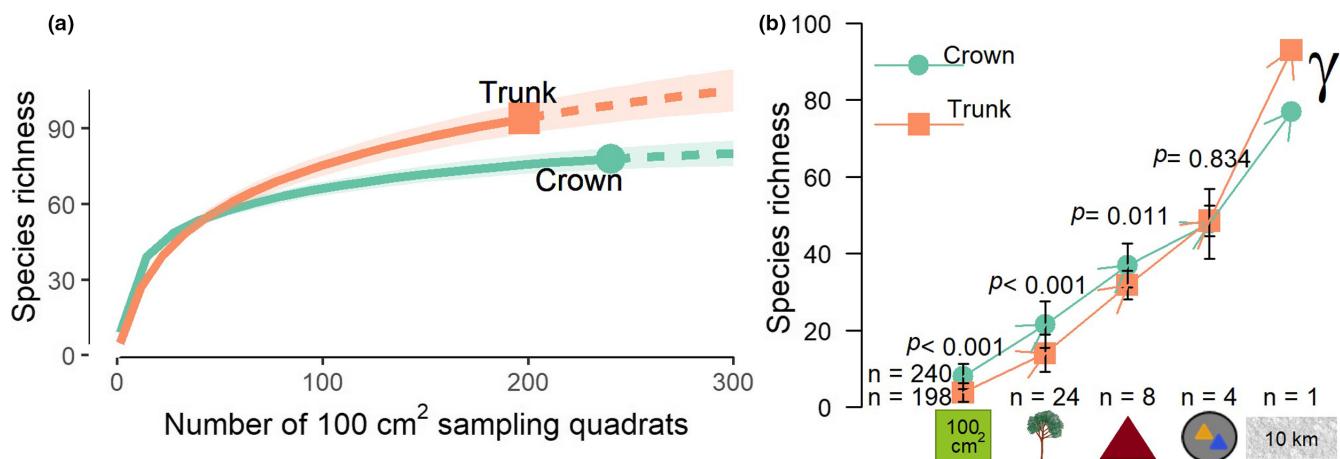
The number of species per 100-cm<sup>2</sup> quadrat in tree crowns was double that on tree trunks ( $8 \pm 3$  vs.  $4 \pm 2$  species, mean  $\pm$  SD; Kruskal-Wallis:  $x^2 = 166.85$ ,  $p < 0.01$ ). The size of the host tree modulated this alpha diversity, with species richness increasing as the average crown radius (ACR) increased and decreasing as tree height increased (Figure S1 and Table S3). Neither local topography nor distance from the main river influenced this alpha diversity metric or its vertical pattern (Tables S3 and S4). Species accumulation curves for trunks and crowns, based on rarefaction and extrapolation of species added per quadrat (Figure 2a), indicated that our sampling strategy (intensive sampling of 24 trees with a maximum distance between trees of 10 km) captured the regional pool of epiphytic bryophyte species rather well for crowns but not for trunks. These curves indicated that the species accumulation curve would require large sample sizes to ever saturate, especially on the trunks. The vertical pattern of species-rich crowns and less rich trunks was consistent at the finer spatial scales (sampling quadrat and tree) but disappeared at the scale of tree clusters (Figure 2b). Then, at the extent of the studied area, representing gamma diversity, tree trunks harbored a higher number of species (93) than tree crowns (77) (Figure 2a,b).

### 3.3 | Beta diversity patterns

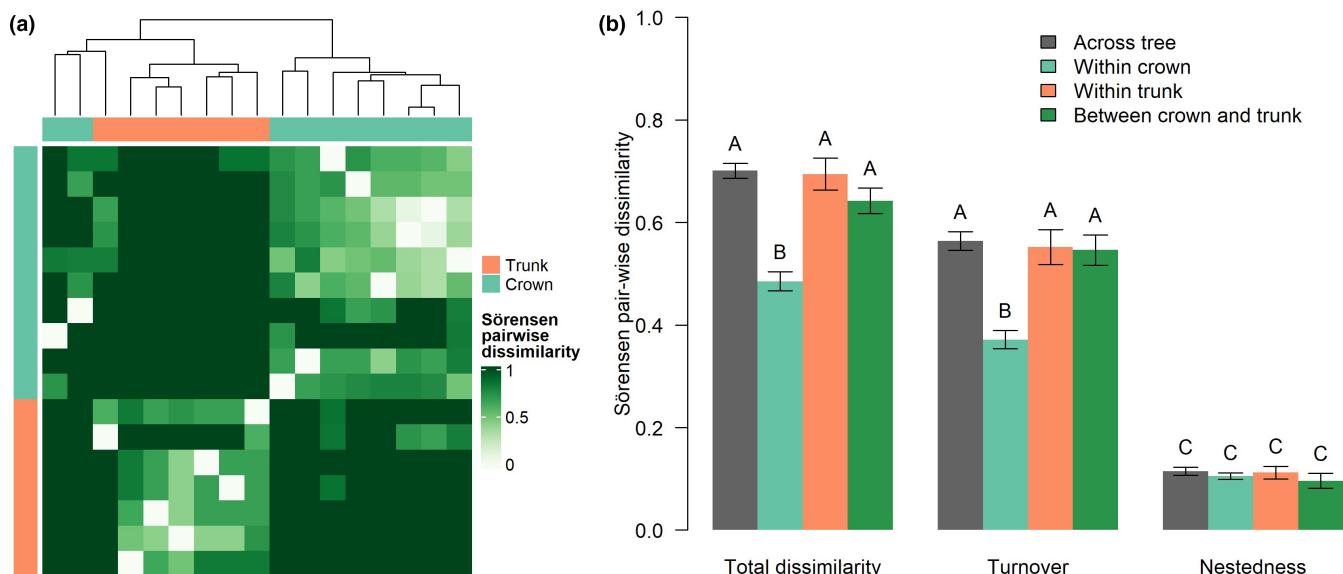
Using the 100-cm<sup>2</sup> quadrat as the spatial grain and the tree as the spatial extent, average pairwise Sørensen dissimilarity across all quadrats in a tree ( $0.70 \pm 0.02$ ) did not differ from those among trunk quadrats ( $0.69 \pm 0.03$ ) or between trunk and crown ( $0.64 \pm 0.02$ ) but was significantly higher than among crown quadrats ( $0.49 \pm 0.02$ ; Kruskal-Wallis:  $x^2 = 166.85$ ,  $p < 0.01$ ; Figure 3a). At this as well as other spatial scales, species turnover consistently dominated beta diversity (values between 0.4 and 0.8), while nestedness was very low with values around 0.1 (Figures 3b and S2).

Using the 100-cm<sup>2</sup> sampling quadrat as the spatial grain at different spatial extents (Figure 4a), pairwise Sørensen dissimilarity was lower among crown quadrats than among trunk quadrats consistently at all studied extents. Beta diversity between and within vertical zones was consistently lower at the extent of single trees than at larger extents. In addition, beta diversity within tree crowns was also lower at the extent of 3-tree clusters, compared to the whole study area (Figure 4a).

When increasing the grain at a fixed spatial extent, beta diversity between crowns and trunks and within trunk units (quadrats, trees, or tree clusters) decreased (Figure 4b). Beta diversity within crown units was consistently lower than between trunk and crown units, and lower than within trunk units, except at the largest grain (Figure 4b). Beta diversity estimates between crowns and trunks and within each vertical zone significantly differed when calculated using different grains (Figure 4b). Interestingly, the beta diversity within crowns was the lowest with 3-tree cluster as the



**FIGURE 2** Alpha diversity of epiphytic bryophytes in a tropical lowland forest in Yasuní National Park. (a) Species accumulation curve for trunks and crowns based on rarefaction (solid line segment) and extrapolation (dotted line segment) of species added per added quadrat. (b) Changes in alpha diversity (amounting to gamma diversity at the 10-km extent) with spatial scale (100-cm<sup>2</sup> quadrats, trees, groups of three trees, groups of six trees, and the whole study area with 24 trees). At the quadrat level,  $n$  for trunk communities is smaller than  $n$  for crown communities, while  $n$  is equal for both epiphytic vertical zones at broader spatial scales. Error bars indicate 1 SD and  $p$ -values indicate the significance of the test assessing for differences between crown and trunk richness at each spatial scale.  $p$ -Value at the finest spatial resolution (quadrats) based on a Wilcoxon signed rank test, while  $p$ -values at broader spatial resolutions (trees and tree clusters) are based on paired t-tests

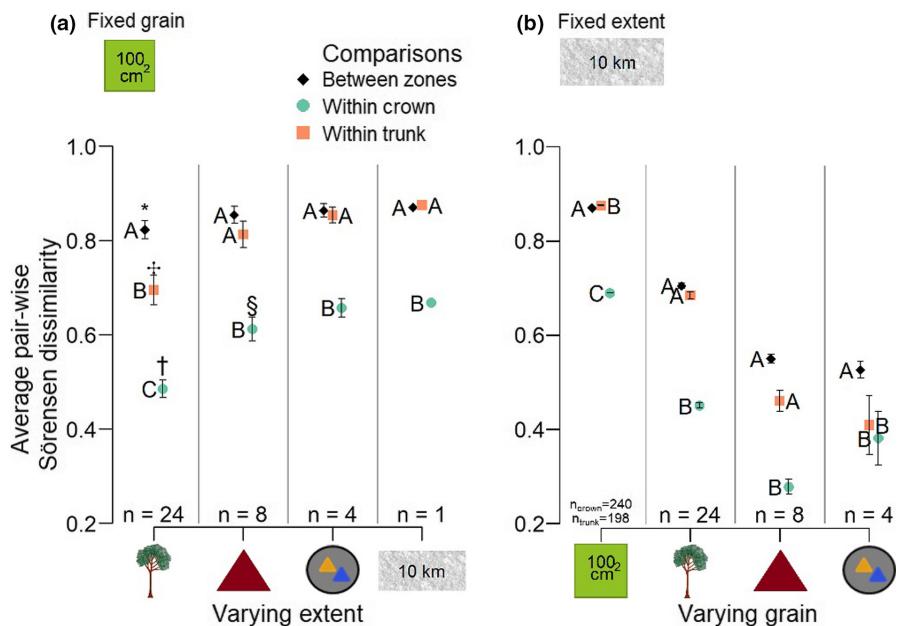


**FIGURE 3** Beta diversity patterns of epiphytic bryophytes at the grain of 100-cm<sup>2</sup> quadrats and the extent of single trees in a tropical lowland forest in Yasuní National Park, Ecuador. (a) Dissimilarity of 100-cm<sup>2</sup> quadrats ( $n = 17$ ) in an example tree (7 in Table S1). Heatmap tiles represent quadrat pairwise comparisons. Quadrat grouping (dendrogram across top) was based on Euclidean distances on a matrix of species presence/absence. Color-keyed bars indicate the seven trunk and 10 crown quadrats. (b) Comparison of beta diversity and its components within and between trunks and crowns. Shown are means and standard deviations of pairwise dissimilarities between quadrats within trees,  $n = 24$  trees). Different letters above bars indicate different means across all bars according to ANOVA tests for total dissimilarity and turnover and Kruskal-Wallis tests for Nestedness; error bars correspond to 1 SE

spatial grain (~0.3) but was higher again to ~0.4 with the broadest spatial grain (6-tree clusters). Another effect when increasing the grain, now from the tree to the whole extent of our study area, is the clear increase in the percentage of species that is shared between trunks and crowns (from 22% to 47%), while the percentage of crown-exclusive species drops strongly (from 52% to 20%)

but the number of trunk-exclusive species even increases slightly (from 26% to 34%; Figures 5 and S3).

For whole trees and for crowns, horizontal beta diversity (calculated among trees) was consistently lower than vertical beta diversity (calculated between trunk and crown within each tree), across the three broader spatial extents (Figure 6). For trunks, horizontal



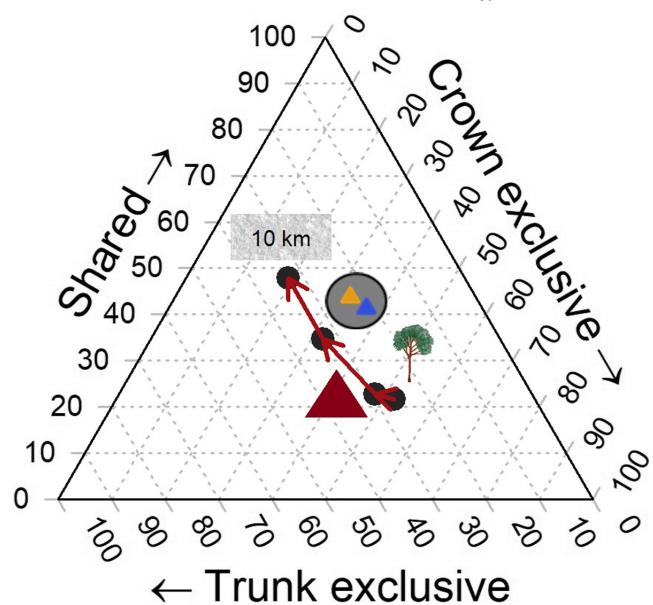
**FIGURE 4** Beta diversity patterns of epiphytic bryophytes across spatial scales in a tropical lowland forest at the Yasuní National Park, Ecuador. (a) Beta diversity among sampling quadrats (i.e., with a fixed grain) across varying spatial extents between and within vertical zones. At a given extent the number of pairwise comparisons per replicate equals trunk quadrats  $\times$  crown quadrats for comparisons between zones, while within vertical zones it equals (trunk quadrats)<sup>2</sup> and (crown quadrats)<sup>2</sup>. Error bars indicate 1 SE calculated for the number of replicates at each extent: Trees ( $n = 24$ ), 3-tree clusters ( $n = 8$ ), and 6-tree clusters ( $n = 4$ ); capital letters indicate differences within each extent, the asterisks indicate a different mean (for the same comparison, i.e., symbol type) from that calculated at the extent of the whole study area ( $p < 0.05$ ). (b) Beta diversity for the whole study area (i.e., fixed extent) calculated with varying grain between and within vertical zones. The number of pairwise comparisons varies with grain, being ( $n_{\text{crown}} \times n_{\text{trunk}}$ ), (trunk quadrats)<sup>2</sup> and (crown quadrats)<sup>2</sup> with the finest grain, while being  $n^2$  for the three broader grains (trees, 3-tree clusters, and 6-tree clusters); capital letters indicate differences among comparisons within each grain. Within comparison types, grains always differed significantly among grains ( $p < 0.05$ )

beta diversity among trees was also lower than vertical beta diversity within trees, while comparing trees within tree clusters, but no longer when comparing all trees across the study area (Figure 6).

The higher similarity of quadrats within vertical zones than between zones is of course not universal for all quadrat pairs (Figure 7a), but a clustering of quadrats based on their compositional similarity (Figure 7a, dendrogram across the top and color bars indicating potential grouping variables: tree clusters, ridge vs. valley, and crown vs. trunk) indicated that even at this small grain, the vertical zonation is a stronger determinant of species composition than spatial proximity. At higher levels of aggregation (looking at whole stems vs. whole crowns, or in clusters of three or six trees), the distinction between stems and crowns becomes more dominant (dendograms in Figure 7b–d). The landscape position (ridge or valley) and even the spatial grouping (sites, i.e., groups of six trees) do not appear to have much influence on the beta diversity, as indicated by the mixing observed in the cluster analysis (dendograms in Figures 7, S4 and S5). At the higher levels of aggregation, it becomes increasingly clear that the crowns are more similar to each other than the trunks (indicated by the lighter shading in the top right (crowns) than the bottom left (trunks) quarters in Figure 7 (white squares are to be ignored, these are the self-dissimilarities, hence always 0)).

## 4 | DISCUSSION

Crowns and trunks of the same tree differed more in species composition than crowns of different trees, even if several kilometers apart. Nearby trunks also differed less from each other than from their own crowns, but at the full extent of the study tree trunks were, on average, as dissimilar to each other as they were to their crowns. Contrary to our expectation, topography did not play a role in the similarity between quadrats or trees at any scale. Crowns and trunks were not only recognized as units based on the species composition; they also differed in diversity patterns: Crowns were more species-rich at the quadrat scale, but trunks were more species-rich at the forest scale, due to higher beta diversity on the trunks than in the crowns. The strong dispersal ability of small-sized epiphytic organisms such as bryophytes (Glime, 2017; Patiño & Vanderpoorten, 2018; Pérez et al., 2011), in particular in the more wind-exposed tree crowns, may explain the lack of horizontal structure in diversity and the higher homogenization in crowns than on trunks. The extremely high beta diversity overall, with many species occurring only once or twice in our sampled quadrats, implies that the species composition of epiphytic bryophyte communities is hardly predictable in this tropical lowland forest.

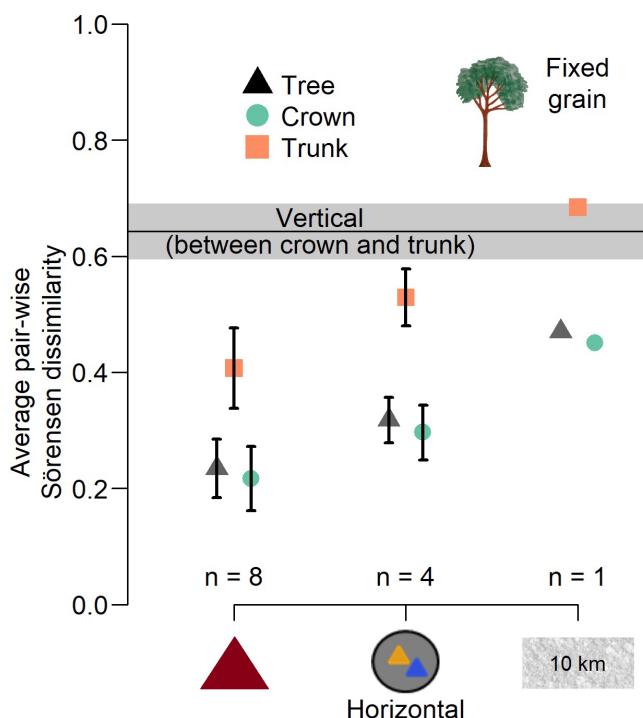


**FIGURE 5** Change (arrows) in the percentages of species that were shared between or exclusive to the crown and trunk communities at four spatial grains (black dots). Each dot represents the mean of all units at the respective grain. Detailed plots for each extent are available in Figure S3

Across scales, whether looking at the cm-scale sampling quadrats or at groups of trees several km apart, tree trunks and tree crowns in the studied forest hold different epiphytic bryophyte communities. These vertical zones differ more from each other than trees and tree crowns located up to 10-km apart. This does not mean that communities were homogeneous between trees, however. Instead, beta diversity was extremely high all over and was dominated by species turnover rather than nestedness, also within vertical zones and even within zones within trees. Given that the high complexity of forest canopies is not exclusive to tropical latitudes and that bryophytes are just one of many groups of canopy organisms, we strongly encourage comparative studies in other forest types and for other organism groups, for which our methods and the patterns found here should provide a useful reference.

#### 4.1 | Species-rich crowns and beta-diverse trunks

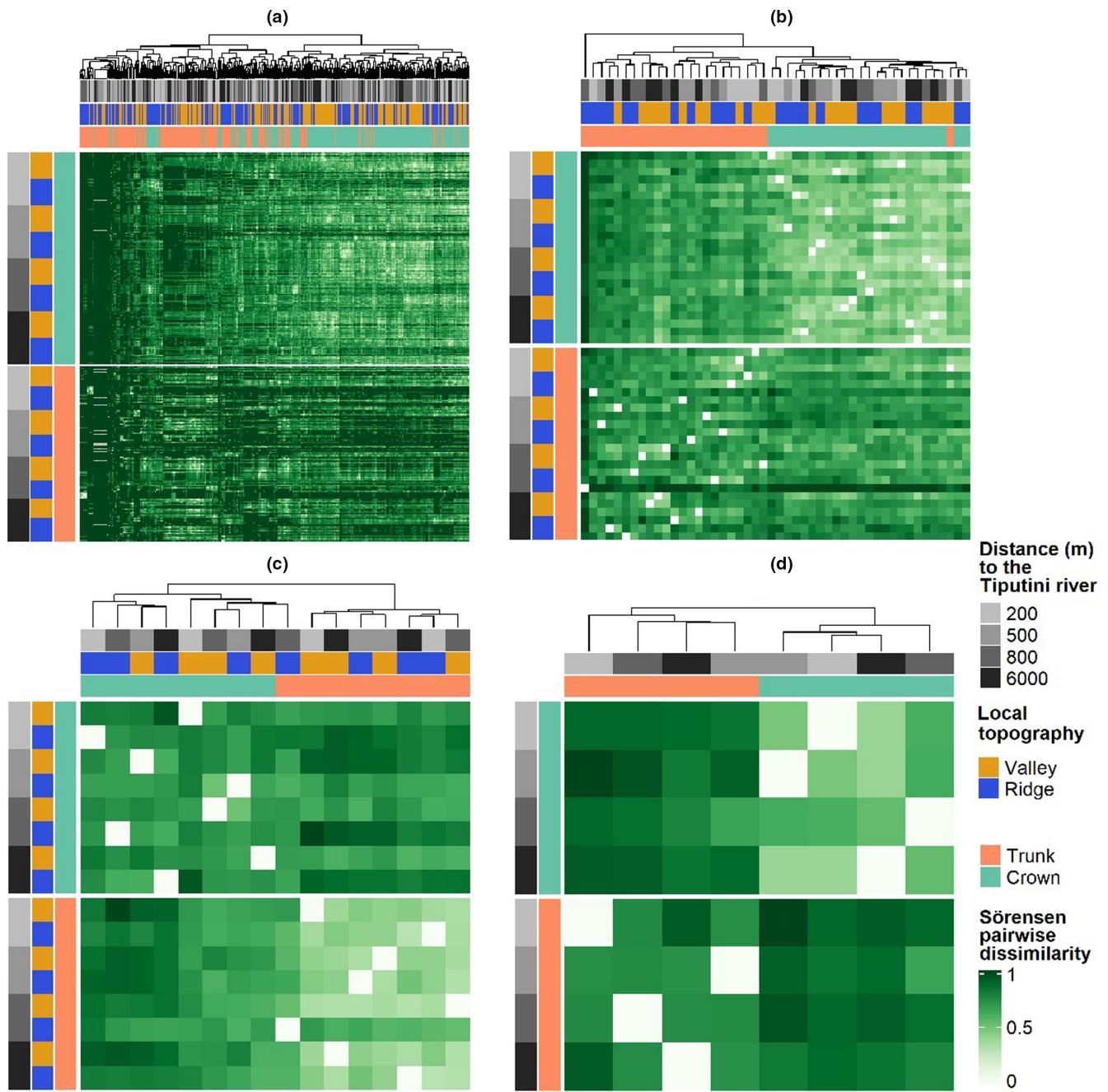
Higher species richness in sampling quadrats in crown than in trunk quadrats was also reported in other studies on diversity patterns of epiphytic bryophytes in moist tropical forests (Cornelissen & ter Steege, 1989; Gehrig-Dowrie et al., 2013; Gradstein et al., 2001; Mandl et al., 2010; Mota de Oliveira et al., 2009; Sanger & Kirkpatrick, 2017; Wolf, 1993, 1994; Zhao et al., 2015). Because light availability is often higher in the tree crowns than in the understory, higher species richness in the tree crowns may add empirical support to a positive species-energy relationship (Wright, 1983). Additionally, and probably more importantly, the tree crowns form



**FIGURE 6** Comparison between vertical and horizontal beta diversity of epiphytic bryophytes across spatial scales in a tropical lowland forest at the Yasuní National Park, Ecuador. The reference vertical beta diversity (=0.64 Sørensen dissimilarity) and its 95% confidence intervals (shaded area) were calculated at the tree grain ( $n = 24$ ), that is, comparing crown against trunk within each tree. Horizontal beta diversity was calculated among trees (i.e., with a fixed grain) in 3-tree clusters, 6-tree clusters, and in the extent of this study, that is, a maximum distance of 10 km, comparing the epiphytic community of whole trees, of trunks, and of crowns. A significant difference with vertical beta diversity exists when the error bars for horizontal beta diversity estimates (indicating 95% confidence intervals) do not overlap the confidence interval for vertical beta diversity

a more or less continuous layer and experience higher wind speeds than the lower forest layers, enhancing the already high dispersal ability of bryophyte propagules. The higher connectivity can result in a better mixing of species, allowing more different species to colonize any position, thereby increasing local species numbers while decreasing beta diversity among sampling quadrats. The filtering role of the air humidity gradient drawn from the tree bases to the tree crown (Nakamura et al., 2017) on the richness of bryophyte communities at the tree extent remains to be explicitly assessed. Including a broad range of tree sizes (treelets, subcanopy, canopy, and emergent trees) would be relevant for such assessment.

The observation that increasing the grain from quadrats to groups of trees led to a decrease of crown-exclusive but not of trunk-exclusive species also indicates that some crown species (e.g., the indicator species) can be quite widespread and can sometimes also be found on trunks. In turn, the increase in exclusive trunk-species at the larger spatial grains suggests that there may be a large



**FIGURE 7** Beta diversity of epiphytic bryophytes in the crowns and on the trunks of 24 trees in an extent of 10 km of tropical lowland forest in Yasuní National Park, Ecuador. Shown are pairwise comparisons (heatmap squares) calculated from 438 sampling quadrats (a), 24 trees (b), eight 3-tree clusters (c), and four 6-tree clusters (d). Color-keyed bars across the left and top of each graph indicate membership of the 6-tree clusters, ridge/valley positions, and vertical zones (trunk/crown). The row order is according to these categories, as shown to the left of each graph, while column order results from the cluster analysis of the units under study (dendrogram based on Euclidean distances), as shown across the top. The equivalent graphs separated per vertical zone, allowing a closer look at the patterns, can be found in the Supporting Information (Figures S4 and S5)

environmental variation at the trunk level compared to the crown level.

In our system, the high vertical beta diversity is easily explained because there are several explicit environmental gradients from the forest floor to the canopy layer, such as light, temperature, relative humidity, and vapor pressure deficit (Nakamura et al., 2017). In turn, the lack of horizontal spatial structure of bryophyte diversity in

crown communities suggests that community assemblages may experience little dispersal limitation within the canopy layer within the studied geographical extent (Mota de Oliveira & ter Steege, 2015). It also suggests that the crown environment is relatively homogeneous at large spatial scales. On the contrary, some dispersal limitation may be experienced by epiphytic communities established on trunks, which are further apart, forming a more island-like spatial

configuration, and experience less air movement than the crowns. Additionally, the forest layer below the crowns may experience a stronger influence of the topography, for example, via local moisture conditions or differences in understory vegetation. Although not captured by our explanatory variables ridge/valley or distance to the river, other causes of local environmental variability may explain why trunks were more different among them than crowns.

Although not geographically structured, the horizontal beta diversity was very high both on trunks and in the tree crowns across scales from quadrat, via tree and groups of trees to the whole forest. Horizontal beta diversity in similar forests has been attributed to the complexity of the canopy layer as a mosaic of microenvironments (Mota de Oliveira et al., 2009), while neutral processes (i.e., chance dispersal and establishment) also play a major role in these communities. The observed lack of horizontal spatial structure contrasted with the partitioning of topographic niches identified for trees in the same area (Valencia et al., 2004). This contrast reinforces the idea that, in tropical forests, diversity patterns of different plant groups, and the spatial scales at which different drivers dominate, do not necessarily coincide (Mandl et al., 2010).

Two ecological reasons likely explain the coupled observations of species-rich crowns and beta-diverse trunks: the higher connectivity among crowns than among the more island-like trunks, and the vertical gradients of light and moisture from the tree basis to the crown (e.g., Lowman & Rinker, 2004). Even if this did not result in distinct zones of consistently different communities, these environmental gradients set the stage for niche partitioning among the bryophytes within a tree. Apart from some niche partitioning, neutral processes probably explain much of the very high beta diversity in this forest; thus, we suggest that the high species turnover observed in trunk communities may result from a broad regional pool of well-dispersed colonists.

## 4.2 | Implications for sampling bryophyte diversity

The standardized methods used allow our multi-scale results to be compared to diversity patterns of epiphytic bryophyte communities in other forest types, as well as against those reported for other plant groups and even for organisms in more distant taxa. Our observation of species-rich crowns at the quadrat and tree scales as well as the higher gamma diversity on trunks than in tree crowns (Figure 2) aligns with the overall species richness pattern reported in previous studies in tropical lowland forests (Gehrig-Downie et al., 2013; Gradstein et al., 2001; Mota de Oliveira et al., 2009), but our data analysis allowed us to identify the spatial scale at which the lead in species richness shifts from crowns to trunks.

The total number of species (115) that we gathered, which included new records and a new species to science, and the total number of liverworts (72) indicate that this forest is similarly rich at the forest scale as other humid (cloud and rain) tropical lowland, and tropical forests in general (ranging between ~20 and ~90 species, see figure 3 in Gehrig-Downie et al., 2013). However, direct

comparisons among richness estimates of epiphytic bryophyte communities are hampered by the heterogeneity of applied sampling and presentation methods, in particular the discrepancy in the size and number of the sampling units (ranging from 40 to 600 cm<sup>2</sup> each, with different numbers per tree). These different grains affect not only alpha diversity estimates, but also the understanding of beta diversity patterns, which may, in the worst-case scenario, lead to erroneous regional diversity estimates. In particular for small-sized organisms like bryophytes, multi-scale analyses, including small grains and explicitly stating the grain and extent on which all reported values are based, are therefore essential. In this study, we systematically sampled 24 canopy trees with 15–22 quadrats of 100 cm<sup>2</sup> each from the ground level to the medium canopy. This sampling effort was enough to capture most of the regional species pool for tree crowns, but still insufficient to do so for tree trunks.

Increasing the sampling effort on trunks could either involve including more trees, or sampling more or larger quadrats on each tree. Beta diversity (Sørensen dissimilarity) increased from 0.7 among quadrats on the same trunk to 0.8 among quadrats in groups of three trunks, and it then stayed more or less at that level when further enlarging the extent. A similar pattern was found for the crowns, but with overall lower dissimilarity values (0.5 increasing to 0.6). This implies that sampling more than one tree is definitely necessary, but sampling 24 trees is not. Previous suggestions that eight trees are sufficient (Campos et al., 2015; Gehrig-Downie et al., 2013; Mota de Oliveira et al., 2009; Mota de Oliveira & ter Steege, 2015) are supported by this pattern, although even fewer trees would suffice in our study area, but with a higher sampling effort per tree. Seeing the high beta diversity even within trees, combined with the large effort of rigging and climbing these rainforest trees, we suggest that a more intensive sampling of each tree is a more time-efficient option than including more trees. Our sampling design does not provide empirical data to help choose between more or larger quadrats on each tree, but we expect more quadrats (i.e., a larger extent) to yield more species than larger quadrats (i.e., a larger grain), since a larger extent may cover a larger range of microhabitats and can include more moss patches where single species dominate specific trunk sections.

In summary, our analyses provide a detailed description of how alpha and beta diversity of tropical lowland epiphytic bryophyte communities vary across spatial scales. We found that the spatial grain (sampling quadrats, trees, or groups of up to six trees) strongly affects both alpha and beta diversity estimates for a given study area (extent), while the extent across which sampling units are compared additionally affects the beta diversity estimates. For alpha diversity, a grain of groups of six trees represent the approximate inflection point at which tree trunks become species-richer than tree crowns. For beta diversity, we found a higher species turnover between the trunk and crown of the same tree than among crowns and trunks of different trees across extents, except for trunks at the largest extent, that is, the whole study area, where trunks differed as much from other trunks, on average, as from their crown, while crowns were still more similar between

them. Overall, these diversity patterns suggest that the processes driving species assembly and ultimately maintaining diversity act differently on tree trunks compared with the tree crowns in this tropical lowland forest. This information is important to assess the relative importance of species interactions and environmental filtering processes across scales in forest canopies to elucidate how those processes help to maintain the remarkable diversity of epiphyte communities.

## AUTHOR CONTRIBUTIONS

Maaike Y. Bader and Monica B. Berdugo conceptualized the study; Monica B. Berdugo lead the investigation with the support of Louise Guéröt and Susana León-Yáñez in the field, and with the supervision of Maaike Y. Bader on the methodology, software, and visualization; Louise Guéröt performed the formal analysis to identify the sampled bryophyte species with the supervision and validation by S. Robbert Gradstein; Monica B. Berdugo performed the data curation and formal analysis of ecological matrices; Monica B. Berdugo and Maaike Y. Bader were equally in charge of the project administration; Maaike Y. Bader led funding acquisition with the support of Jörg Bendix and S. Robbert Gradstein; Monica B. Berdugo and Maaike Y. Bader led the writing of the original draft, which was revised and edited by all the authors.

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## CONFLICT OF INTEREST

The corresponding author confirms on behalf of all authors that there have been no involvements that might raise the question of bias in the work reported or in the conclusions, implications, or opinions stated.

## DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.gqnk98snq> (Berdugo et al., 2022).

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## REFERENCES

- Bailey, R. G. (2014). *Ecoregions* (2nd ed.). Springer. <https://doi.org/10.1007/978-1-4939-0524-9>
- Barton, K. (2020). MuMIn: Multi-Model Inference. *R Package Version 1.43.17*. <https://cran.r-project.org/package=MuMIn>
- Barton, P. S., Cunningham, S. A., Manning, A. D., Gibb, H., Lindenmayer, D. B., & Didham, R. K. (2013). The spatial scaling of beta diversity. *Global Ecology and Biogeography*, 22(6), 639–647. <https://doi.org/10.1111/geb.12031>
- Baselga, A. (2010). Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography*, 19(1), 134–143. <https://doi.org/10.1111/j.1466-8238.2009.00490.x>
- Baselga, A. (2017). Partitioning abundance-based multiple-site dissimilarity into components: Balanced variation in abundance and abundance gradients. *Methods in Ecology and Evolution*, 8(7), 799–808. <https://doi.org/10.1111/2041-210X.12693>
- Baselga, A., & Leprieur, F. (2015). Comparing methods to separate components of beta diversity. *Methods in Ecology and Evolution*, 6(9), 1069–1079. <https://doi.org/10.1111/2041-210X.12388>
- Baselga, A., & Orme, C. D. L. (2012). Betapart: An R package for the study of beta diversity. *Methods in Ecology and Evolution*, 3(5), 808–812. <https://doi.org/10.1111/j.2041-210X.2012.00224.x>
- Baselga, A., Orme, D., Villeger, S., De Bortoli, J., Leprieur, F., & Logez, M. (2021). Betapart: Partitioning beta diversity into turnover and nestedness components. *R Package Version 1.5.4*. <https://cran.r-project.org/package=betapart>
- Bass, M. S., Finer, M., Jenkins, C. N., Kreft, H., Cisneros-Heredia, D. F., McCracken, S. F., Pitman, N. C. A., English, P. H., Swing, K., Villa, G., Di Fiore, A., Voigt, C. C., & Kunz, T. H. (2010). Global conservation significance of Ecuador's Yasuní National Park. *PLoS ONE*, 5(1), e8767. <https://doi.org/10.1371/journal.pone.0008767>
- Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *ArXiv Preprint ArXiv:1406.5823*, 67(1), 1–48. <https://doi.org/10.18637/jss.v067.i01>
- Buck, W. R. (2003). *Guide to the plants of Central French Guiana, part 3. Mosses*. Memoirs of the New York Botanical Garden (Vol. 76(3), pp. 1–176).
- Berdugo, M. B., Gradstein, S. R., Guéröt, L., León-Yáñez, S., Bendix, J., & Bader, M. Y. (2022). Data from: Diversity patterns of epiphytic bryophytes across spatial scales: Species-rich crowns and beta-diverse trunks. Dryad Digital Repository. <https://doi.org/10.5061/dryad.gqnk98snq>
- Campos, L. V., Steege, H., & Uribe, J. (2015). The epiphytic bryophyte flora of the Colombian Amazon. *Caldasia*, 37(1), 47–59. <https://doi.org/10.15446/caldasia.v37n1.50980>
- Churchill, S. P. (1994). *Mosses of Amazonian Ecuador* (AAU reports 35). Department of Systematic Botany, University of Aarhus.
- Cornelissen, J. H. C., & Ter Steege, H. (1989). Distribution and ecology of epiphytic bryophytes and lichens in dry evergreen forest of Guyana. *Journal of Tropical Ecology*, 5(2), 131–150. <https://doi.org/10.1017/S0266467400003400>
- Draper, I., Mazimpaka, V., Albertos, B., Garilleti, R., & Lara, F. (2005). A survey of the epiphytic bryophyte flora of the Rif and Tazekka Mountains (northern Morocco). *Journal of Bryology*, 27(1), 23–34. <https://doi.org/10.1179/174328205X40554>
- Estación Científica Yasuní (2015). Estación Científica Yasuní. In Pontificia Universidad Católica del Ecuador (Ed.), *Estación Científica Yasuní* (Primera, p. 9). Estación Científica Yasuní.
- Floorschütz-de Waard, J., Zielman, H. R., & Bruggeman-Nannenga, M. A. (2011). *Flora of the Guianas, series C, bryophytes 2 (musci IV)* (pp. 350–369). In M. J. Jansen-Jacobs (Eds.). Royal Botanic Gardens.
- Fox, J., & Weisberg, S. (2019). *An {R} companion to applied regression* (3rd ed.). Sage. <https://CRAN.R-project.org/package=car>
- Frazer, G. W., Canham, C. D., & Lertzman, K. P. (2008). Gap light analyzer (GLA): Imaging software to extract canopy structure and gap light transmission indices from true-colour fisheye photographs. User's manual and program documentation (2.0; p. 36). Simon Fraser University. <https://www.sfu.ca/rem/forestry/downloads/gap-light-analyzer.html>

- Gehrig-Downie, C., Obregon, A., Bendix, J., & Gradstein, S. R. (2013). Diversity and vertical distribution of epiphytic liverworts in lowland rain forest and lowland cloud forest of French Guiana. *Journal of Bryology*, 35(4), 243–254. <https://doi.org/10.1179/1743282013Y.00000000070>
- Glime, J. M. (2017). Adaptive strategies. In *Bryophyte Ecology Volume 1: Physiological Ecology*. 3. Michigan Technological University. <https://digitalcommons.mtu.edu/bryophyte-ecology1/3>
- Gómez González, D. C., Quiel, C. R., Zotz, G., & Bader, M. Y. (2017). Species richness and biomass of epiphytic vegetation in a tropical montane forest in western Panama. *Tropical Conservation Science*, 10, 9–11. <https://doi.org/10.1177/1940082917698468>
- Gonzalez, A., Germain, R. M., Srivastava, D. S., Filotas, E., Dee, L. E., Gravel, D., Thompson, P. L., Isbell, F., Wang, S., Kéfi, S., Montoya, J., Zelnik, Y. R., & Loreau, M. (2020). Scaling-up biodiversity-ecosystem functioning research. *Ecology Letters*, 23(4), 757–776. <https://doi.org/10.1111/ele.13456>
- Gradstein, S. R. (2006). The lowland cloud forest of French Guiana – A liverwort hotspot. *Cryptogamie, Bryologie*, 27(1), 141–152.
- Gradstein, S. R. (2021). *The liverworts and hornworts of Colombia and Ecuador*. Springer. <https://www.springer.com/gp/book/9783030494490>
- Gradstein, S. R., & Ilkiu-borges, A. L. (2009). Guide to the plants of Central French Guiana part 4. Liverworts and hornworts. Memoirs of the New Botanical Garden (Vol. 76(4), 140 p.). New Botanical Garden.
- Gradstein, S. R., Churchill, S. P., & Salazar-Allen, N. (2001). Guide to the bryophytes of tropical America. Memoirs of the New Botanical Garden (Vol. 86, Issue December). New Botanical Garden.
- Gu, Z., Eils, R., & Schlesner, M. (2016). Complex heatmaps reveal patterns and correlations in multidimensional genomic data. *Bioinformatics*, 32(18), 2847–2849. <https://doi.org/10.1093/bioinformatics/btw313>
- Holdridge, L. R. (1947). Determination of world plant formations from simple climatic data. *Science*, 105(2727), 367–368. <https://doi.org/10.1126/science.105.2727.367>
- Holdridge, L. R. (1964). *Life zone ecology*. (Rev ed.), Tropical Science Center.
- Johansson, D. (1974). Ecology of vascular epiphytes in west African rain forests. *Acta Phytogeographica Suecica*, 59, 136.
- Koleff, P., Gaston, K. J., & Lennon, J. J. (2003). Measuring beta diversity for presence-absence data. *Journal of Animal Ecology*, 72(3), 367–382. <https://doi.org/10.1046/j.1365-2656.2003.00710.x>
- Korner-Nievergelt, F., Roth, T., von Felten, S., Guélat, J., Almasi, B., & Korner-Nievergelt, P. (2015). *Bayesian data analysis in ecology using linear models with R, BUGS and Stan*. Academic Press. <https://CRAN.R-project.org/package=blmeco>
- Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2017). lmerTest package: Tests in linear mixed effects models. *Journal of Statistical Software*, 82(13), 1–26. <https://doi.org/10.18637/jss.v082.i13>
- Lowman, M. D., & Rinker, H. B. (2004). *Forest canopies*. Elsevier.
- Mandl, N., Lehnert, M., Kessler, M., & Gradstein, S. R. (2010). A comparison of alpha and beta diversity patterns of ferns, bryophytes and macrolichens in tropical montane forests of southern Ecuador. *Biodiversity and Conservation*, 19(8), 2359–2369. <https://doi.org/10.1007/s10531-010-9839-4>
- McGill, B. J., Dornelas, M., Gotelli, N. J., & Magurran, A. E. (2015). Fifteen forms of biodiversity trend in the Anthropocene. *Trends in Ecology & Evolution*, 30(2), 104–113. <https://doi.org/10.1016/j.tree.2014.11.006>
- Medina, N. G., Albertos, B., Lara, F., Mazimpaka, V., Garilleti, R., Draper, D., & Hortal, J. (2013). Species richness of epiphytic bryophytes: Drivers across scales on the edge of the Mediterranean. *Ecography*, 37(1), 80–93. <https://doi.org/10.1111/j.1600-0587.2013.00095.x>
- Medina, R., Lara, F., Albertos, B., Draper, I., Garilleti, R., & Mazimpaka, V. (2010). Epiphytic bryophytes in harsh environments: The Juniperus thurifera forests. *Journal of Bryology*, 32(1), 23–31. <https://doi.org/10.1179/037366810X12578498135715>
- Mellado-Mansilla, D., León, C. A., Ortega-Solís, G., Godoy-Güinao, J., Moreno, R., & Díaz, I. A. (2017). Vertical patterns of epiphytic bryophyte diversity in a montane Nothofagus forest in the Chilean Andes. *New Zealand Journal of Botany*, 55(4), 514–529. <https://doi.org/10.1080/0028825X.2017.1364273>
- Mota de Oliveira, S., & ter Steege, H. (2013). Floristic overview of the epiphytic bryophytes of terra firme forests across the Amazon basin. *Acta Botanica Brasilica*, 27(2), 347–363. <https://doi.org/10.1590/S0102-33062013000200010>
- 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(2), 441–450. <https://doi.org/10.1111/1365-2745.12359>
- Mota De Oliveira, S., Ter Steege, H., Cornelissen, J. H. C., & Robbert Gradstein, S. (2009). Niche assembly of epiphytic bryophyte communities in the Guianas: A regional approach. *Journal of Biogeography*, 36(11), 2076–2084. <https://doi.org/10.1111/j.1365-2699.2009.02144.x>
- Nakamura, A., Kitching, R. L., Cao, M., Creedy, T. J., Fayle, T. M., Freiberg, M., Hewitt, C. N., Itioka, T., Koh, L. P., Ma, K., Malhi, Y., Mitchell, A., Novotny, V., Ozanne, C. M. P., Song, L., Wang, H., & Ashton, L. A. (2017). Forests and their canopies: Achievements and horizons in canopy science. *Trends in Ecology and Evolution*, 32(6), 438–451. <https://doi.org/10.1016/j.tree.2017.02.020>
- Oksanen, J., Guillaume Blanchet, F., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., Szoecs, E., & Wagner, H. (2020). vegan: Community ecology package. R Package Version 2.5-7, 1, 11. <https://cran.r-project.org/package=vegan>
- Patiño, J., & Vanderpoorten, A. (2018). Bryophyte biogeography. *Critical Reviews in Plant Sciences*, 37(2–3), 175–209. <https://doi.org/10.1080/07352689.2018.1482444>
- Patiño, J., González-Mancebo, J. M., Fernández-Palacios, J. M., Arévalo, J. R., & Bermúdez, A. (2009). Short-term effects of clear-cutting on the biomass and richness of epiphytic bryophytes in managed subtropical cloud forests. *Annals of Forest Science*, 66(6), 609. <https://doi.org/10.1051/forest/2009042>
- Pérez, B. E., Draper, I., Atauri, D. D., & Bujalance, R. M. (2011). Bryophytes: An approximation to the simplest land plants. *Memorias de La Real Sociedad Española de Historia Natural*, 2, 19–73.
- Perry, D. (1978). A method of access into the crowns of emergent and canopy trees. *Biotropica*, 10, 155–157.
- R Core Team. (2020). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. <https://www.r-project.org/>
- Sanger, J. C., & Kirkpatrick, J. B. (2017). Fine partitioning of epiphyte habitat within Johansson zones in tropical Australian rain forest trees. *Biotropica*, 49(1), 27–34. <https://doi.org/10.1111/btp.12351>
- Smith, M. R. (2017). *Ternary: An R package for creating ternary plots*. Zenodo. <https://CRAN.R-project.org/package=Ternary>
- Storch, D. (2016). The theory of the nested species-area relationship: Geometric foundations of biodiversity scaling. *Journal of Vegetation Science*, 27(5), 880–891. <https://doi.org/10.1111/jvs.12428>
- Tschopp, H. J. (1953). Oil explorations in the oriente of Ecuador, 1938–1950. *Bulleting of the American Association of Petroleum Geologists*, 37(10), 2303–2347.
- Valencia, R., Balslev, H., & Paz Y Miño C, G. (1994). High tree alpha-diversity in Amazonian Ecuador. *Biodiversity and Conservation*, 3(1), 21–28. <https://doi.org/10.1007/BF00115330>
- Valencia, R., Foster, R. B., Villa, G., Condit, R., Svenning, J. C., Hernández, C., Romoleroux, K., Losos, E., Magård, E., & Balslev, H. (2004). Tree species distributions and local habitat variation in the Amazon: Large forest plot in eastern Ecuador. *Journal of Ecology*, 92(2), 214–229. <https://doi.org/10.1111/j.0022-0477.2004.00876.x>

- Walter, H., & Lieth, H. (1960). Klimadiagramm-Weltatlas. VEB Gustav Fischer Verlag, Jena (DE) (in German).
- Wolf, J. H. D. (1993). Diversity patterns and biomass of epiphytic bryophytes and lichens along an altitudinal gradient in the northern Andes. *Annals of the Missouri Botanical Garden*, 80(4), 928–960. <https://doi.org/10.2307/2399938>
- Wolf, J. H. D. (1994). Factors controlling the distribution of vascular and non-vascular epiphytes in the northern Andes. *Vegetatio*, 112(1), 15–28. <https://doi.org/10.1007/BF00045096>
- Wright, D. H. (1983). Species-energy theory: An extension of species-area theory. *Oikos*, 41(3), 496–506. <https://doi.org/10.2307/3544109>
- Zhao, M., Geekiyanage, N., Xu, J., Khin, M. M., Nurdiana, D. R., Paudel, E., & Harrison, R. D. (2015). Structure of the epiphyte community in a tropical montane forest in SW China. *PLoS One*, 10(4), 1–19. <https://doi.org/10.1371/journal.pone.0122210>
- Zhu, Z., Kleinn, C., & Nölke, N. (2021). Assessing tree crown volume—A review. *Forestry: An International Journal of Forest Research*, 94(1), 18–35. <https://doi.org/10.1093/forestry/cpaa037>

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