BIOTA COLOMBIANA
ISSN impreso 0124-5376
ISSN digital 2539-200X
DOI 10.21068/c001

Artículo

Functional and taxonomic spatial structure of vascular epiphytes in a neotropical montane cloud forest

Estructura espacial funcional y taxonómica de epífitas vasculares en un bosque nublado montano neotropical

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Recibido: marzo 20, 2025
Aceptado: julio 2, 2025

https://doi.org/10.21068/2539200X.1306

Abstract

The distribution of vascular epiphytes on host trees has been linked to deterministic factors associated with host characteristics and microclimatic variation. To evaluate the taxonomic and functional spatial structure of vascular epiphytes in a lower montane cloud forest of the Colombian Andes, epiphytes were sampled following the SVERA protocol, and their position was recorded using Johansson's zonation scheme. Taxonomic structure was assessed through patterns of species composition, richness, and diversity across host zones, while functional structure was evaluated using trait composition and functional indices: functional richness (FRic), functional evenness (FEve), and functional divergence (FDiv). Epiphytes showed higher abundance below the first branching zones (Z1 and Z2), which also exhibited the highest functional richness, encompassing most of the functional space on host trees. In contrast, specialized nutrient uptake strategies and CAM metabolism were more frequent in upper zones, suggesting environmental filtering along the host gradient. These results demonstrate clear taxonomic and functional spatial structuring of vascular epiphyte assemblages in this lower montane cloud forest.

Keywords: Andean biodiversity, canopy stratification, microclimatic gradients, trait-based ecology, community assembly processes.

Resumen

La distribución de las epífitas vasculares en los árboles hospederos se ha relacionado con factores determinísticos asociados a las características del hospedero y a la variación microclimática. Para evaluar la estructura espacial taxonómica y funcional de las epífitas vasculares en un bosque nublado montano bajo de los Andes colombianos, las epífitas vasculares se muestrearon siguiendo el protocolo SVERA y su posición se registró usando el esquema de zonación de Johansson. La estructura espacial taxonómica se evaluó mediante patrones de composición, riqueza y diversidad de especies a lo largo de las zonas del hospedero, mientras que la estructura funcional se analizó a partir de la composición de rasgos e índices funcionales: riqueza funcional (FRic), equidad funcional (FEve) y divergencia funcional (FDiv). Las epífitas mostraron mayor abundancia por debajo de la primera ramificación (Z1 y Z2), zonas que también presentaron la mayor riqueza funcional, lo que abarcó la mayor parte del espacio funcional disponible en los hospederos. En contraste, las estrategias especializadas de toma de nutrientes y el metabolismo CAM fueron más frecuentes en las zonas superiores, lo que sugiere la presencia de filtros ambientales a lo largo del gradiente del hospedero. Estos resultados demuestran una clara estructuración espacial taxonómica y funcional de los ensamblajes de epífitas vasculares en este bosque nublado montano bajo.

Palabras clave: biodiversidad andina, estratificación del dosel, gradientes microclimáticos, ecología basada en rasgos, procesos de ensamblaje de comunidades.

Introduction

Vascular epiphytes are a diverse group of plants that rely on other plants for physical support. According to their life-history strategies, these plants can be grouped into three main types: true epiphytes, hemiepiphytes, and nomadic vines. True epiphytes germinate on a host and maintain all roots attached to it throughout their life cycle. Hemiepiphytes also germinate on a host but establish a connection with the soil through feeder roots at some stages of their development. In contrast, nomadic vines germinate in the soil and may lose older portions of the stem as they ascend their host (Zotz, 2013).

At fine spatial scales, epiphyte distribution can be characterized by examining how species are arranged within individual hosts, commonly referred to as spatial structure. Traditionally, this structure has been studied by dividing the host into vertical zones, such as Johansson's zonation scheme (Zotz, 2007). Several taxonomic studies have reported a positive relationship between species richness and host height, likely reflecting greater habitat availability and higher microclimatic heterogeneity in large trees (Woods et al., 2015; Francisco et al., 2021). Additionally, host characteristics such as stem diameter, bark rugosity, and tree age have been associated with variation in epiphyte assemblages (Wagner et al., 2015).

Although a universal pattern of vascular epiphyte spatial structure has not yet been identified (Wagner et al., 2015; Zotz, 2016), some general tendencies have been observed. For instance, the upper, more exposed zones of host plants are often dominated by orchids and bromeliads, whereas lower trunk zones tend to be dominated by ferns (Zotz & Büche, 2000; Zotz, 2016). Such distribution patterns have been attributed to adaptive responses to microclimatic gradients along the host (Hietz & Hietz-Seifert, 1995; Hietz & Briones, 1998; Nieder et al., 2000; Krömer et al., 2007). Typically, upper zones experience higher temperatures, greater wind exposure, and light availability, whereas lower zones show higher humidity and greater nutrient availability (Cardelús & Chazdon, 2005; Werner, 2011; de la Rosa-Manzano et al., 2014; Vinod et al., 2023).

Strong evidence for spatial structuring in epiphyte assemblages has emerged from studies examining the relationship between host position and functional traits, particularly foliar traits (Petter et al., 2016; Guzmán-Jacob et al., 2022; Richards & Damschen, 2022). Overall, these studies indicate that species occupying upper host zones tend to exhibit traits associated with improved tolerance to water stress

(Hietz & Briones, 1998; Petter et al., 2016; Guzmán-Jacob et al., 2022; Richards & Damschen, 2022). However, the strong focus on leaf traits may obscure broader functional or physiological responses that also contribute to spatial structuring. Expanding analyses to include additional functional traits may therefore improve our understanding of how epiphyte assemblages are structured along hosts.

Theoretical frameworks explaining the mechanisms shaping epiphyte distributions are still emerging (Janzen et al., 2020). Combining taxonomic and functional approaches to describe spatial structure can provide new insights into host-level distributions. For example, Petter et al. (2016) showed that relationships between functional traits and vertical position could partly explain the distribution of certain taxa. Moreover, functional approaches offer a valuable perspective for linking epiphyte assemblages with ecosystem functioning (Garnier et al., 2016).

Using both taxonomic and functional perspectives, we conducted a preliminary assessment of the spatial structure of an epiphyte assemblage in a humid Andean forest in Colombia. From a taxonomic perspective, following approaches proposed by Hietz and Briones (1998) and Woods et al. (2015), we anticipated higher abundances in lower and middle zones, where microhabitats are more stable and resource availability is higher, and lower abundances in upper zones, where stronger environmental exposure and limited resources may restrict epiphyte establishment.

From a functional perspective, we evaluated several traits (see Table 1 for detailed descriptions and hypotheses), assuming that life form, clonality, spinescence, nutrient uptake strategies, dispersal syndromes, and photosynthetic metabolism respond to variation in host-level resource availability. In upper host zones, typically characterized by drier and more exposed conditions, we expected a higher frequency of species exhibiting traits associated with stress tolerance. These include clonal species capable of resource sharing among ramets, spiny species commonly associated with dry environments, species with specialized nutrient uptake structures, and species performing CAM (crassulacean acid metabolism), which enhances water-use efficiency. We also predicted that wind-dispersed species would be more frequent in these exposed zones. In contrast, in lower and middle host zones, where environmental conditions tend to be more humid and stable, we expected higher abundances of true epiphytes, which are typically favored by buffered microclimates and more stable substrates.

Methods and materials

Study Area

The Civil Society Nature Reserve Cerro El Inglés is located in Las Amarillas, a rural settlement of El Brillante, municipality of El Cairo, Valle del Cauca, Colombia (4°45′ N, 76°17′ W), within the Serranía de los Paraguas, part of the Tatáma-Paraguas corridor. This mountainous region lies in the central sector of the Colombian Western Cordillera, between two biodiversity hotspots: the Tropical Andes and the Chocó Biogeográfico.

The reserve corresponds to a lower montane very humid life zone and is predominantly covered by primary forest. Vegetation is characterized by a closed canopy dominated by mature trees, with an understory composed mainly of shrubs and herbs. Elevation in the reserve reaches up to 2400 m a.s.l. Mean annual temperature is approximately 17.8 °C, and mean annual precipitation reaches 2476 mm.

Sampling

Sampling was conducted in February and August 2021, corresponding to the wet and dry seasons, respectively. Vascular epiphytes were sampled following the SVERA protocol (Wolf et al., 2009), with several modifications. A total of 35 host trees were sampled, distributed among six diameter at breast height (DBH) categories: ten trees with DBH > 30 cm; five trees with DBH 5–10 cm; five with DBH 10.1–15 cm; five with DBH between 15.5–20 cm; five with DBH 20.1–25 cm; five with DBH 25.1–30 cm.

As a modification of Wolf et al. (2009), the first host tree selected had a DBH > 30 cm and was chosen for its high representativeness of epiphyte diversity. All vascular epiphytes found on this tree, including true epiphytes, hemiepiphytes, and nomadic vines, were collected and counted, avoiding additional collection of morpho-species already identified unless necessary for confirmation. This procedure was repeated until 35 hosts were sampled. To incorporate additional host variables into the analyses, tree height was measured with a clinometer and DBH was measured for each sampled individual.

For taxa forming dense aggregations in which individual plants were difficult to distinguish, the number of individuals was estimated following the concept of a "dense stad" proposed by Sanford (1968). However, this method proved unsuitable for Hymenophyllaceae, and this family was therefore excluded from abundance analyses. Species of *Elaphoglossum* were also excluded from abundance analyses due to difficulties in reliable field identification based on morphology. Seedlings were excluded from all analyses.

Table 1. Functional traits, expected hypotheses, and observed spatial patterns of vascular epiphytes along host zones.

Trait	**Justification**	**Hypothesis**	**Conclusion**
Life form	Reflects the degree to which plants depend on the host for water and nutrients. True epiphytes rely entirely on canopy resources, whereas nomadic vines and hemiepiphytes may access soil resources during part of their life cycle.	True epiphytes would be more prevalent in the lower zones, where moisture and nutrient availability are higher, while hemiepiphytes and nomadic vines would be more frequent in higher zones.	No detectable spatial pattern was observed.
Clonality	Clonal growth structures allow interconnected ramets to share resources, potentially improving water acquisition under limiting conditions (Stuefer, 1998; Liu et al., 2016).	Clonal species would be more frequent in higher zones, where water availability is lower and resource sharing may be advantageous.	No detectable spatial pattern was observed.
Spinescence	Spines may provide protection against herbivory and reduce water loss under stressful conditions (Vilela et al., 2012; Bezzalla et al., 2018).	Spiny epiphytes would be more abundant in upper zones exposed to drier conditions.	No detectable spatial pattern was observed.
Nutrient uptake strategy	Nutrient availability along hosts is spatially heterogeneous (Zotz, 2016), favoring species with specialized nutrient acquisition mechanisms in resource-limited environments.	Epiphytes with specialized nutrient uptake structures would be more abundant in upper zones.	The proportion of individuals with specialized nutrient uptake increased from Z1 to Z4.
Dispersal syndrome	Wind-dispersed (anemochorous) propagules generally disperse over shorter distances than animal-dispersed (endozoochorous) propagules (Vittoz & Engler, 2007).	Anemochorous species would be more frequent in exposed zones, whereas endozoochorous species may be more evenly distributed along the host.	Anemochory decreased with increasing DBH, whereas the endozoochory increased with DBH.
Photosynthetic metabolism	CAM metabolistm is associated with increased water-use efficiency and is common in species adapted to drier environments.	CAM species would be more prevalent in upper zones exposed to stronger water stress.	The proportion of CAM species increased from Z1 to Z3.

Sampling of taller trees required the use of tree-climbing equipment, whereas smaller trees were sampled from the ground level using an extendable tree pruner. All specimens were processed and deposited at the Herbarium of the Universidad del Valle (CUVC Luis Sigifredo Espinal-Tascón). Species identification was carried out using taxonomic keys, digitized colletions from the Herbario Nacional Colombiano (COL), the Missouri Botanical Garden (MO), and the New York Botanical Garden Herbarium (NY), as well as consultation with taxonomic specialists.

Taxonomic and functional spatial structure

Epiphyte presence on hosts was determined using the vertical categorization proposed by Johansson (1974). Five zones were established along each host. Zone 1 (Z1) corresponded to the tree base, from ground level up to 3 m; Zone 2 (Z2) extended from the upper boundary of Zone 1 to the first major branching point; Zone 3 (Z3) comprised the basal portion of the larger branches; Zone 4 (Z4) represented the middle portions of these branches; and Zone five (Z5) included the outermost portions of the larger branches (see Supplementary Material, Figure S1, for details of the stratification). The position of each individual was recorded according to its anchor point on the bark. For climbing vines, the assigned zone corresponded to the highest attachment point observed during climbing or by binocular inspection.

Several analyses were conducted to evaluate taxonomic spatial structure. First, Shannon diversity indices were calculated for each zone, and differences among zones were tested using Hutcheson's t-test implemented in the *vegan* package in R (Oksanen et al., 2022). Second, generalized linear models (GLM) were constructed to evaluate whether zone, host height, DBH, or their interactions explained epiphyte abundance. Models were fitted using Poisson and negative binomial distributions with the functions *glm* and *glmer* functions in R (Oksanen et al., 2022), including and excluding host identity as a random effect to evaluate potential variation among hosts. Model selection was based on AIC and BIC criteria.

Third, to assess differences in assemblage composition among zones using non-metric multidimensional scaling (NMDS) with Bray-Curtis distance in PAST, we first evaluated whether host size variables (height and DBH) generated distinct host groups through a Multivariate Regression Tree (MRT) analysis. This procedure allowed us to identify grouping structures potentially driven by host size and to control host-related variation before evaluating spatial patterns. NMDS analyses were subsequently performed within each MRT group. Finally, species and family fidelity to each zone was estimated using the *indicspecies* package in R (de Cáceres, 2023), which applies a combinatorial approach to identify taxa most strongly associated with particular zones.

Functional spatial structure was evaluated using a matrix of functional traits for each species combined with species abundances recorded in each zone. Most traits followed the framework proposed by Pérez-Harguindeguy et al. (2016). Information on life form, clonality, spinescence, nutrient uptake strategy, dispersal syndrome, and photosynthetic metabolism was compiled from primary and secondary sources (Table S1 and S2). When species-level information was unavailable, trait data were assigned at the genus or family level.

To evaluate spatial functional structure, functional richness (FRic), functional evenness (FEve), and functional divergence (FDiv) were estimated for each host zone using the *FD* package in R (Laliberté et al., 2024). These metrics were calculated using species abundance per zone and the functional trait matrix as inputs. FRic represents the volume of functional trait space occupied by the community, FEve reflects the regularity with which species fill that space, and FDiv indicates how species abundances are distributed within the occupied trait space. Together, these indices capture complementary aspects of functional diversity and provide insight into mechanisms linking biodiversity patterns and ecosystem functioning (Pla et al., 2012).

As in the taxonomic analyses, potential effects of host size were controlled by first identifying host groups using MRT analysis (with trait-species as fixed effects). Subsequently, Beta GLMs were fitted to examine relationships between each functional index and the explanatory variables (zone, DBH, and height), with host identity included as a random effect. Model selection was again based on AIC and BIC criteria. As an additional approach, the relationship between each function trait, expressed as proportional data, and zone, DBH, and height was evaluated using binomial and quasibinomial GLMs, also with and without host as a random effect. Best-fitting models were selected using AIC and BIC.

Because functional richness is strongly correlated with species richness, a null model approach was implemented to evaluate whether observed FRic values deviated from random expectations. One hundred random communities were simulated using a modified version of the *randomizeMatrix* function from the *picante* package in R (Kembel et al., 2010), and FRic was calculated for each simulation. Standardized effect sizes (SES = [observed value - mean simulated values] / SD of simulated values; Gotelli & McCabe, 2002), and deviations from null expectations were tested using a posterior Wilcoxon signed-rank test.

Before constructing GLMs, potential collinearity between DBH and host height was evaluated using variance inflation factors (VIFs). Values below 5 indicate no problematic collinearity between predictors.

Results

Taxonomic spatial structure

Z2 contained the highest number of individuals, whereas Z4 showed the lowest abundance (Table 2). Epiphytes in Z5 could not be directly sampled due to safety constraints; however, binocular observations indicated a low presence of epiphytes in this zone. Alternative approaches, such as drone or pole-mounted cameras, could allow future sampling of this stratum.

Species richness and Shannon diversity followed a similar pattern, with the highest values recorded in Z2 and the lowest in Z4 (Table 2). It is important to note that epiphyte abundance in Z1 and Z2 may be underestimated because the Hymenophyllaceae ferns were excluded from abundance analyses. The concentration of individuals in Z2 was also evident when the most abundant families were analyzed independently (Figure S2). In contrast, ferns were mainly concentrated near the ground (Z1) and progressively decreased in abundance towards Z4 (Figure S2).

At the family level, Z1 was dominated by Orchidaceae, Melastomataceae, Ericaceae, Pteridaceae and Araceae, and several fern groups. Orchidaceae, Ericaceae, Bromeliaceae, and Araceae mainly occupied Z2. In Z3, Orchidaceae remained dominant, followed by Ericaceae and Bromeliaceae. Finally, Z4 was primarily dominated by Orchidaceae, followed by Bromeliaceae (Figure S3).

Table 2. Total abundance, species richness, and Shannon diversity index (H') recorded in each host zone.

Zone	Abundance	Species richness	Shannon diversity
Z1	431^{ab}	100	4.10^{a}
Z2	577^{a}	140	4.45^{b}
Z3	372^{b}	88	3.95^{c}
Z4	130^{c}	50	3.62^{d}

Note. Different superscript letters indicate significant differences among zones ($p < 0.05$).

A negative binomial GLM including host identity as a random effect provided the best explanation for variation in epiphyte abundance across zones, DBH and height (Table 3). In this model, only DBH and zone showed significant effects ($p < 0.05$), with differences among zones becoming more pronounced as DBH increased (Figure 1).

MRT analysis identified two host groups significantly separated by the DBH ($p < 0.05$): hosts with DBH ≤ 21.65 cm (n = 80) and those with DBH > 21.65 cm (n = 60). Subsequent NMDS analyses showed no clear differences in species composition among zones within either DBH group (Figure 2; Figure 3). However, studies of family-level spatial distribution (Figure S4) revealed significant fidelity to Z1 for Pteridaceae, Urticaceae, Polypodiaceae, Dryopteridaceae, Piperaceae, and Gesneriaceae. In Z2 fidelity was significant only for Dryopteridaceae, Piperaceae, Gesneriaceae and Polypodiaceae. In Z3, only Polypodiaceae showed significant fidelity, while no family exhibited significant fidelity to Z4.

Functional spatial structure

True epiphytes were the dominant life form across all zones and showed no clear preference for any particular host zone. Species with C3 photosynthetic metabolism dominated across all zones, although the proportion of CAM species increased slightly in Z2 and Z3. Dispersal was mainly mediated by wind and animals, without evident zonal preferences (Figure 4).

Most individuals exhibited specialized nutrient uptake strategies, with proportions increasing from Z1 toward Z4 (Figure 4H). Spinescence was rare and restricted to a few individuals of two species occurring only in Z1 and Z2 (Figure 4I). Clonality structures were widespread across species and did not show a clear spatial pattern (Figure 4J).

Because the second MRT analysis did not generate host groups when zone, DBH, height, and trait-species matrices were included as predictors, functional analyses were conducted without host-group partitioning. For individual traits, binomial GLMs with host as a random effect provided the best-fitting models. Among the evaluated traits, only nutrient strategy uptake was significantly related to zone, whereas C3 and CAM metabolism were significantly related to both zone and DBH. Anemochory and endozoochory were associated considerably only with DBH, while no significant effects were detected for the remaining traits (Table 3). However, post-hoc multiple comparisons did not detect significant differences among zones. Nonetheless, CAM species tended to increase in proportion in Z2 and Z3 compared with Z1 (Figure 4E), and nutrient uptake strategies similarly showed increasing proportions from Z1 to Z3 (Figure 4H). Regarding functional diversity indices, FRic was best explained by a beta GLM including host as a random effect, with significant effects of both zone and DBH (Table 3). FRic increased with DBH, whereas differences among zones were not statistically significant, although a tendency toward higher values in Z2 was observed (Figure 5A). Null model analysis indicated that the observed FRic differed significantly from random expectations (SES significantly different from zero; $p < 0.05$), showing that functional richness patterns were not attributable to chance.

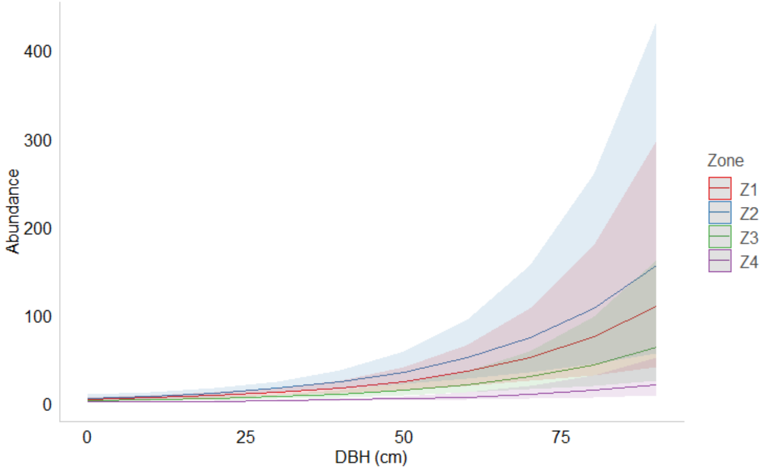
FEve was best explained by zone and host height. FEve decreased with increasing host height, while values were similar between Z3 and Z4, and between Z1 and Z2 (Figure 5B). Finally, FDiv was significantly influenced by both zone and height in a beta GLM including host as a random effect. FDiv increased with host height and tended to higher values in Z4 (Figure 5C).

Table 3. GLM models used to evaluate whether zone, height, DBH, and their interactions explained epiphyte abundance, with and without host identity included as a random effect.

Model	Distribution	Random effect	Interactions included	AIC	BIC
1	Poisson	Yes	No	1321.9	1342.5
2	Poisson	Yes	Yes	1222.9	1264.1
3	Poisson	No	No	1600.8	1618.4
4	Poisson	No	Yes	1469.9	1508.2
5	**Negative Binomial**	**Yes**	**No**	886.9	**910.5**
6	Negative Binomial	Yes	Yes	**875.3**	919.4
7	Negative Binomial	No	No	890.1	910.7
8	Negative Binomial	No	Yes	879.5	920.7

Note. Models 5 and 6 showed the lowest AIC and BIC values; therefore, the most parsimonious model was selected.

Figure 1. Partial effect plot showing the variation in epiphyte abundance across host zones as a function of DBH.



Note. Lines represent predicted abundance for each zone (Z1: red, Z2: blue, Z3: green, and Z4: purple).

Figure 2. NMDS ordination of species abundance across host zones for trees with DBH > 21.65 cm.

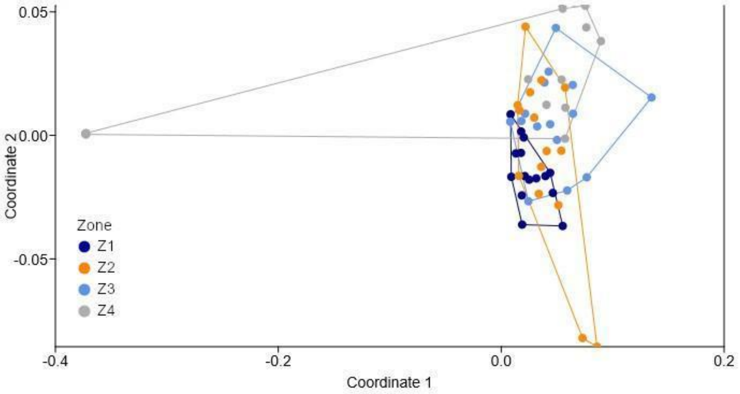


Figure 3. NMDS ordination of species abundance across host zones for trees with DBH ≤ 21.65 cm.

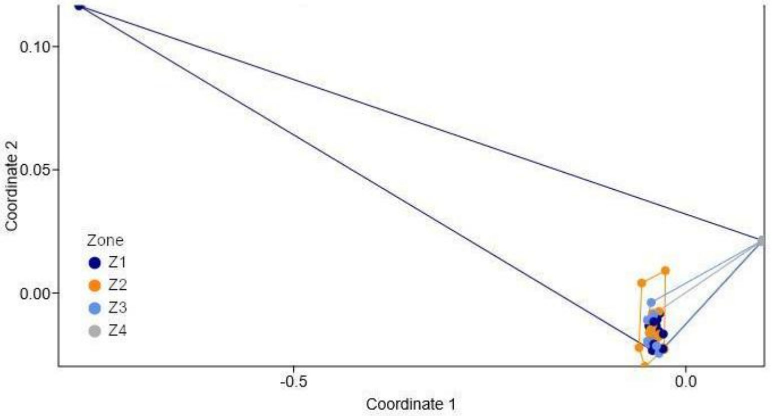
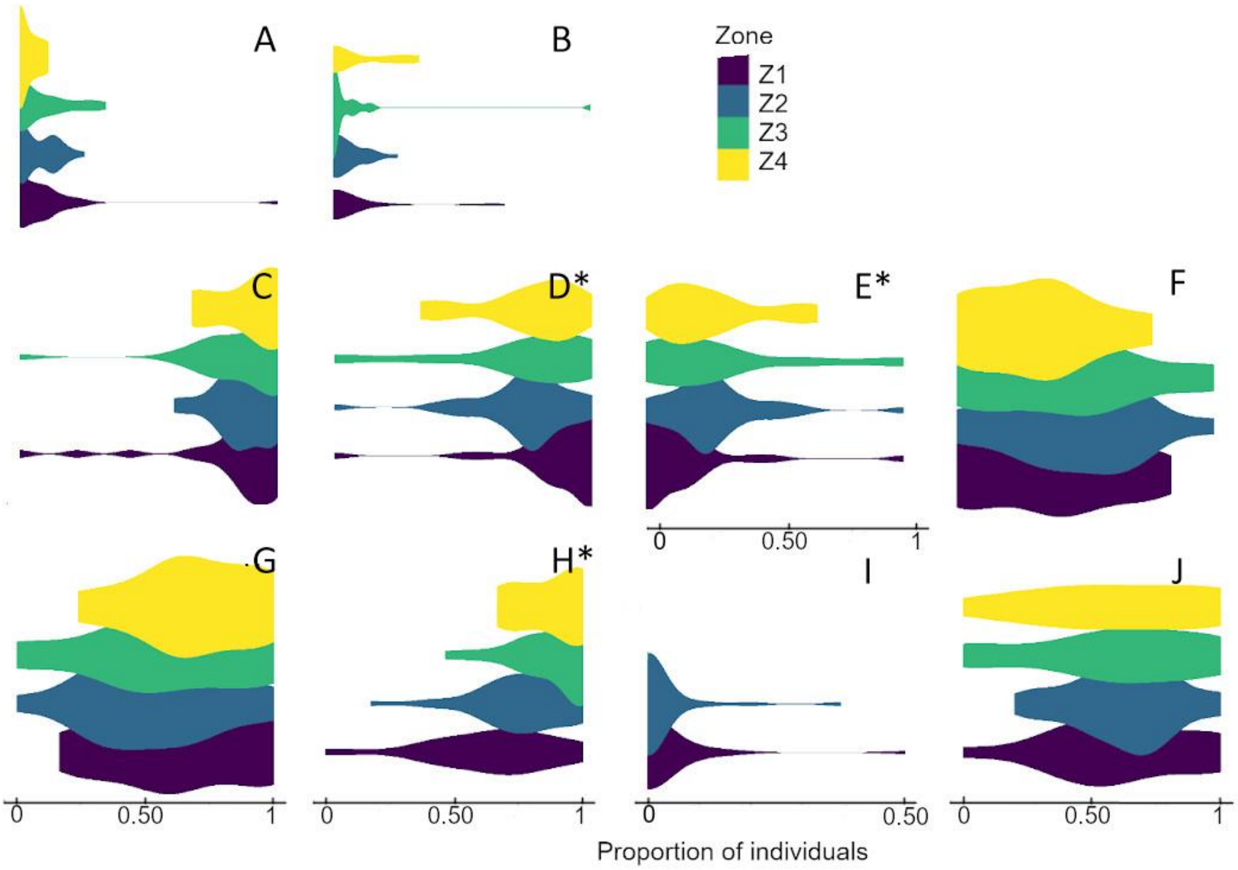
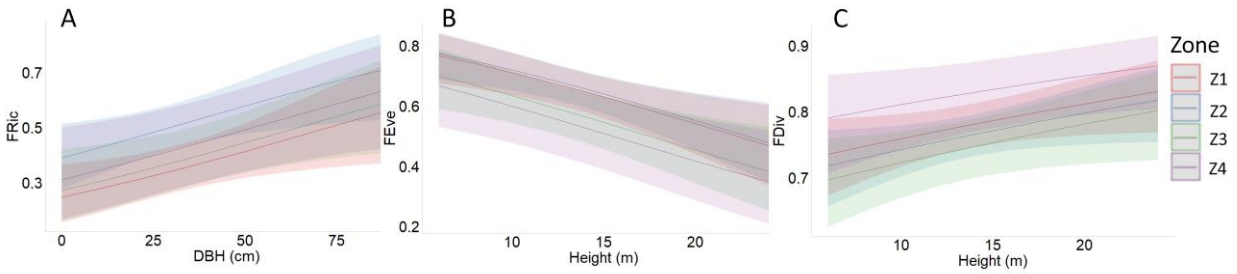


Figure 4. Proportional distribution of individuals exhibiting each functional trait across host zones.



Notes. A) Nomadic vines; B) hemiepiphytes; C) true epiphyte; D) C3 photosynthetic metabolism; E) CAM photosynthetic metabolism; F) endozoochory; G) anemochory; H) specialized nutrient uptake strategy; I) spines; J clonality structures. An asterisk (*) indicates a significant relationship between functional traits and zones ($p < 0.05$).

Figure 5. Partial effect plots showing variation in functional diversity indices across host zones.



Note. A) FRic as a function of zone and DBH; B) FEve as a function of zone and host height; C) FDiv as a function of zone and host height.

Discussion

Taxonomic spatial structure

Differences in epiphyte abundance among host zones—particularly the higher number of individuals recorded in the stem zone (Z2) and the significantly lower presence in the upper branches (Z4)—may partly be explained by variation in available surface area and substrate diameter (Wang et al., 2016). However, microenvironmental heterogeneity along the host is likely to play an important role in explaining the higher abundance observed in the stem zone (Hietz & Briones, 1998; Woods et al., 2015). Upper host zones, such as Z4, are more exposed to solar radiation and wind, creating less favorable conditions for epiphyte establishment (Hietz & Briones, 1998; Acebey & Krömer, 2001; Krömer et al., 2007; Petter et al., 2016; Guzmán-Jacob et al., 2022), whereas the trunk typically provides more buffered microclimatic conditions and more stable substrates (Acebey & Krömer, 2001; Quaresma & Jardim, 2014).

A high concentration of epiphytes in trunk zones has also been reported in coastal forests (Quaresma & Jardim, 2014) and neotropical rainforests (Acebey & Krömer, 2001). Conversely, low epiphyte presence in upper host zones has been documented in several assemblages (Hietz & Briones, 1998; Acebey & Krömer, 2001; Zotz & Schultz, 2007). The marked difference between Z3 and Z4 observed here may reflect more favorable substrate conditions at the base of large branches, where greater surface area and nutrient water accumulation can support higher epiphyte establishment (Krömer et al., 2007; Woods et al., 2015).

Our results reinforce previous findings indicating that host position influences variability in epiphyte richness, diversity, and abundance (Woods et al., 2015; Marí et al., 2016). Nevertheless, no universal spatial pattern has been demonstrated, as some studies report greater epiphyte abundance in upper zones than on trunks (Krömer et al., 2007; Wang et al., 2016). This variability highlights the importance of examining epiphyte distribution in a context-dependent manner.

In this study, DBH emerged as an essential factor influencing abundance patterns, with thicker trees hosting more individuals due to increased available substrate area. Our results also suggest that abundance dynamics among zones may be more complex in large-diameter trees, where upper zones such as Z3 and Z4 offer larger potential colonization surfaces than in smaller hosts.

The significance of host identity as a random effect further indicates that additional host traits likely influence epiphyte abundance patterns. Previous studies have emphasized the role of tree architecture, forest composition, height above ground, and bark characteristics, in shaping epiphyte distributions (Wagner et al., 2015). For instance, bark traits have been shown to influence epiphyte establishment positively (da Silva et al., 2024).

Although most abundant families peaked in Z2 (Figure S2), ferns showed a contrasting pattern, being concentrated in lower host zones and decreasing toward the canopy, consistent with previous findings (Zotz, 2007). This pattern likely reflects moisture gradients along the host (Tewari et al., 2009). Future studies could test this hypothesis by examining whether ferns occupying higher zones possess traits associated with greater drought tolerance.

Families such as Urticaceae and Pteridaceae, along with several representative species, showed strong fidelity to Z1, consistent with their higher abundance in this zone. The basal portion of hosts may provide favorable moisture and resource conditions, particularly in this ecosystem, where bryophyte accumulation was notable in Z1 and Z2. Bryophytes are known to facilitate the establishment of vascular epiphytes by retaining moisture and organic matter (Zotz & Vollrath, 2003).

Overall, our results reveal a clear spatial pattern in abundance, with most individuals occurring below the first major branching point (Z3). However, species composition did not differ significantly among zones. Previous studies have similarly found only weak or inconsistent taxonomic spatial structuring, with substantial variability among hosts (Nieder et al., 2000; Zotz, 2007; Woods et al., 2015). Given the absence of a strong, deterministic taxonomic pattern, future studies should incorporate multifactorial approaches that consider host architecture, vertical distance from the ground, physicochemical parameters, and additional abiotic and biotic drivers. Null models also help disentangle stochastic and deterministic processes shaping epiphyte spatial structure.

Functional spatial structure

This study provides an initial characterization of epiphyte assemblages, allowing identification of potential functional patterns and environmental filters. However, these patterns must be complemented by direct measurements of biotic and abiotic factors driving functional distribution. Additionally, evaluating intraspecific variability in functional traits is important, especially those traits known to exhibit substantial variability, such as metabolic type and nutrient acquisition strategy.

Three functional traits showed significant relationships with zone and/or DBH: nutrient acquisition strategy, photosynthetic metabolism, and dispersal mode. Species with specialized nutrient-acquisition strategies increased in proportion as host zones became higher. Strategies such as velamen roots in orchids, tank-forming structures in bromeliads, and ericoid mycorrhizae structures in Ericaceae may facilitate persistence in upper zones where resource availability is lower (Van Leerdam et al., 1990). However, direct measurements of nutrient availability are required, given the highly heterogeneous and temporally dynamic distribution of nutrients along hosts (Zotz, 2016).

A second pattern was an increase in CAM metabolism from Z1 to Z3, although this pattern may be underestimated due to limited sampling in Z5, where exposure is highest. This distribution likely reflects increased water stress associated with higher temperatures and greater evapotranspiration toward upper host zones (Petter et al., 2016).

A third pattern of dispersal was observed, explained solely by DBH. Anemochory decreased with increasing DBH, whereas endozoochory increased. This may suggest that wind dispersal is more effective on smaller trees, whereas larger trees may provide conditions that attract animal dispersers. Experimental approaches would be required to evaluate whether wind dispersal indeed confers an advantage in smaller hosts.

Other functional traits did not show clear distribution patterns, suggesting weak or absent environmental filtering at this scale. Alternatively, functional redundancy among species or phylogenetic conservatism could reduce detectable variation (Pillar et al., 2013). True epiphytes dominated all zones, consistent with previous records showing higher frequencies of true epiphytes relative to hemiepiphytes and nomadic vines (Nieder et al., 2000; Acebey & Krömer, 2001; Krömer et al., 2007). However, no clear spatial preferences were detected among life forms. Whether the life cycles of hemiepiphytes and nomadic vines influence their vertical distribution remains poorly understood.

Clonal growth structures occurred across all zones without detectable spatial patterns, contrasting with the commonly reported association of these structures with disturbed or resource-limited environments (Bellingham & Sparrow, 2000; Klimešová et al., 2021). This discrepancy may reflect the limited spatial scale considered here, and future studies should quantify resource gradients along hosts to evaluate potential filtering effects. The rarity of spinescence observed here is consistent with the typically low herbivory pressure reported for epiphytes (Zotz, 2016).

This study also provides the first multifunctional characterization of a vascular epiphyte assemblage in this region. FDiv increased with host height, suggesting greater segregation of abundant species in functional space on taller hosts. This pattern may indicate reduced competitive overlap, although host-related factors likely also influence this relationship, as indicated by the significant host random effect. FEve, in contrast, decreased with host height, suggesting less uniform occupation of functional space and potential underutilization of functional niches in taller trees (Mason et al., 2005). Finally, FRic increased with host diameter, indicating expansion of functional space in larger hosts. Although null models suggest this pattern is not driven solely by chance, the strong relationship between FRic and species richness warrants cautious interpretation.

Conclusions

The results of this study contribute to a better understanding of the local taxonomic and functional structure of vascular epiphyte assemblages and provide a first approach to functional diversity patterns along host trees.

We found a spatial structure characterized by higher epiphyte abundance below the first major branching point of the hosts (Z1 and Z2). This pattern may reflect the influence of microclimatic and/or biotic filters favoring epiphyte establishment in these zones. However, these deterministic factors do not generate strong filters for most families, species, or functional traits. Additional factors related to host characteristics likely influence epiphyte spatial structure in the study area.

For photosynthetic metabolism and nutrient uptake strategies, we found evidence of spatial structuring. The proportion of individuals possessing specialized nutrient uptake strategies increased from Z1 to Z4, while CAM became more frequent from Z1 to Z3. These patterns suggest the importance of stress-tolerance traits related to nutrient and water acquisition in more exposed host zones. In contrast, the remaining functional traits did not show spatial structuring and thus did not support our initial hypotheses.

Our results highlight the importance of Z2 for conservation purposes, as this zone contains both high epiphyte abundance and high functional richness. Future studies incorporating finer taxonomic resolution, primary measurements of functional traits, phylogenetics comparative approaches, and additional functional dimensions are recommended to clarify the mechanisms underlying epiphyte spatial patterns.

Acknowledgments

We thank the Serraniagua Community Environmental Organization for logistical support. We are grateful to Juan Diego Gamez, Melisa Alegría, Katherin Arango, Ricardo Cardona, and Ronald Viafara for their unwavering support during fieldwork. We also thank to Juan Sebastian Moreno, Laura Clavijo, and David Sanín for their support in the taxonomic identification of several plant groups. Finally, we acknowledge Ana Cristina Bolaños and Ana María Benavides for their important contributions to this study.

Disclosure statements

The authors declare that no funds, grants, or other support were received during the preparation of this manuscript. The authors have no relevant financial or no-financial interest to disclose.

Authors' Contributions

Leidy Laura Arias Martinez was responsible for conceptualizing, methodology, investigation, formal analysis, original draft preparation, and review and editing. Juan Camilo González contributed to investigation, review and editing. Alejandro Zuluaga contributed to methodology, investigation, review and editing.

Ethical guidelines

This study was reviewed and approved by the Central Research Ethics Committee (CCEI) of the Universidad del Valle, Colombia.

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