

The role of host tree characteristics in epiphyte community in Northern Andean cloud forests: a case study in El Centello Nature Reserve

Rol de las características de los árboles hospederos en la comunidad de epífitas en los bosques nublados del norte de los Andes: un estudio de caso en la Reserva Natural El Centello

Maria Judith Carmona-Higuita ¹, Ana María Benavides Duque ^{2*}

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ABSTRACT

Despite their perilous status, cloud forests boast a remarkable flora, with vascular epiphytes playing a pivotal role, especially in the northern Andes. These forests are crucial for preserving biodiversity. Our study focused on the El Centello Nature Reserve, located in the western cordillera of the northern Andes, home to some of the region's last remnants of cloud forests. We explore the drivers of epiphytic species' local distribution patterns by analyzing the horizontal distribution of functional groups and the influence of host tree characteristics. Specifically, we evaluate how tree size and the spatial arrangement of host trees shape epiphyte richness, abundance, biomass, and community composition. We recorded 131 species, 25 families, and 2280 individuals over 0.25 ha using the SVERA methodology. Orchids, anthuriums, and bromeliads represent over 40 % of the abundance and are the most diverse taxa. Our findings reveal that larger and, thus, older trees harbor more diverse and abundant epiphytic and nomadic communities. Species composition was significantly related to structural variables and geographic distances of host trees. This research underscores the importance of host tree characteristics in shaping epiphyte communities and highlights the need for conservation strategies to preserve cloud forests' plant structural diversity. Understanding these distribution patterns is essential for directing conservation plans to protect this vital component of the Andean ecosystem.

Keywords: horizontal distribution, host tree effect, Orchidaceae, neotropic, suspended soil.

¹ Philipps University of Marburg, Biegenstraße 10, 35037 Marburg, Alemania maria.carmonahiguita@biologie.uni-marburg.de

² Jardín Botánico de Medellín, Cl. 73 #51d-14, Medellín, anamaria.benavides@jbotanico.org

* Corresponding author



RESUMEN

A pesar de las amenazas que enfrentan, los bosques de niebla mantienen una flora diversa en la que las epífitas vasculares cumplen un papel central, especialmente en el norte de los Andes. Estos bosques son áreas clave para la conservación de la biodiversidad. Nuestro estudio se realizó en la Reserva Natural El Centello, ubicada en la cordillera occidental del norte de los Andes, uno de los últimos remanentes de bosque nublado en la región. Analizamos los factores que determinan los patrones de distribución local de las epífitas vasculares, examinando la distribución horizontal de los grupos funcionales y la influencia de las características de los árboles hospederos. En particular, evaluamos cómo el tamaño y la disposición espacial de los árboles afectan la riqueza, abundancia, biomasa y composición de la comunidad epífita. Mediante la metodología SVERA registramos 131 especies pertenecientes a 25 familias y 2280 individuos en una parcela de 0,25 ha. Orchidaceae, Araceae y Bromeliaceae representaron más del 40 % de la abundancia y fueron los grupos más diversos. Nuestros resultados indican que los árboles más grandes —y por tanto más antiguos— sostienen comunidades epífitas y nómadas más diversas y abundantes. La composición de especies mostró una relación significativa con variables estructurales y con las distancias geográficas entre los árboles hospederos. Este estudio destaca el papel de las características del árbol hospedero en la estructura de las comunidades de epífitas y subraya la importancia de conservar la diversidad estructural de los bosques de niebla. Comprender estos patrones es fundamental para orientar estrategias de conservación en este componente del ecosistema andino.

Palabras clave: distribución horizontal, efecto del árbol hospedero, Orchidaceae, neotrópico, suelo suspendido.

INTRODUCTION

Tropical montane cloud forests (TMCFs), often referred to as montane rainforests, are unique and ecologically critical ecosystems found in mountainous regions where the atmospheric conditions allow for a consistent cover of clouds and mist (Stadtmüller 1987). These forests are renowned for their rich biodiversity and high levels of endemism. The constant moisture from cloud cover supports a diverse understory and epiphytic plant communities, providing a habitat for a wide variety of fauna (Brujinzeel *et al.* 2011).

Vascular epiphytes, which include various species of ferns, orchids, bromeliads, and other plants that grow on other plants without drawing nutrients from them, play a crucial role in TMCFs (Zotz 2016). These plants contribute significantly to the overall biodiversity and structural complexity of these ecosystems since they can represent up to 50 % of the plant diversity (Kelly *et al.* 1994) and enhance the habitat by providing additional niches and food resources for insects, birds, and mammals (Richardson *et al.* 2000, Stuntz *et al.* 2002). They also contribute to nutrient cycling and water retention within

the forest canopy (Benzing and Seemann 1978, Aguilar-Cruz *et al.* 2022). By intercepting rainfall and capturing moisture from the air, epiphytes help maintain the humid microclimate essential for many cloud forest species (Zotz *et al.* 2010, Zotz 2016). Their presence indicates a healthy, functioning ecosystem and underscores the importance of conserving these specialized plant communities within cloud forests.

Nevertheless, epiphytic communities in TMCFs face threats due to significant habitat loss due to exploitation for timber and other forest products, fragmentation, and conversion to other forms of land use – notably cattle ranching, cultivation of temperate vegetables, and coffee plantations (Brujinzeel *et al.* 2011, Toledo-Aceves *et al.* 2011, Calderón and Benavides 2021). Additionally, climate change poses another severe threat by altering precipitation patterns and increasing temperatures in TMCFs, which can disrupt the delicate microclimate essential for epiphytes (Foster 2001, Hostettler 2002).

Although cloud forest occurs at least in 60 continental countries and many tropical oceanic islands around the world (Hostettler 2002, Brujinzeel *et al.* 2011), the northern Andes region is a critical area for the preservation of cloud

forests, where the latest occur in one of the most critical “hot spot of biodiversity”, the tropical Andes hotspot (Mittermeier *et al.* 2011, Bax and Francesconi 2019). To preserve epiphytes in northern Andean cloud forests, it is necessary to underscore the factors shaping their local distribution, which are both microclimatic conditions and host tree characteristics.

To address these gaps, our study examines the drivers of local distribution patterns in vascular epiphytes within a well-preserved cloud forest of the northern Andes. We focus on how host tree characteristics—including tree size, spatial arrangement, and structural attributes—influence epiphyte richness, abundance, biomass, and community composition across different functional groups (epiphytes, hemiepiphytes, and nomadic vines). To answer this, we conducted an inventory in the El Centello Nature Reserve and analyzed horizontal distribution patterns across functional groups in relation to key host-tree attributes. Specifically, we assessed two hypotheses: (i) Larger trees, which provide greater surface area and longer periods for colonization, will support higher epiphyte richness, abundance, and biomass across functional groups. Our analysis examines the horizontal distribution patterns of the vascular epiphyte community at the functional group

level determined by the habit (epiphyte, hemiepiphyte, and nomadic vine). We hypothesize that epiphyte diversity will vary according to these habits, with true epiphytes and hemiepiphytes exhibiting higher diversity on larger, older trees compared to nomadic vines. (ii) Additionally, the spatial proximity among host trees will influence epiphyte community composition, with closer trees sharing more species due to enhanced dispersal, particularly among wind-dispersed groups. We assume that distance will affect mainly epiphytes dispersed by wind more than for fauna. Understanding these factors is crucial for elucidating epiphyte distribution patterns and informing effective conservation strategies in cloud forests.

MATERIALS AND METHODS

The study was performed in the eastern slope of the Western Cordillera of Colombia, specifically in the Medellín Botanical Garden natural reserve “El Centello” in Jardín municipality (Fig. 1). The reserve has an elevation ranging from 1800 to 2700 m and an area of 160 ha with 115 ha of preserved forest, and it is part of the natural protected area “Distrito de Manejo Integrado de los Recursos Naturales Cuchilla Jardín - Támesis”.

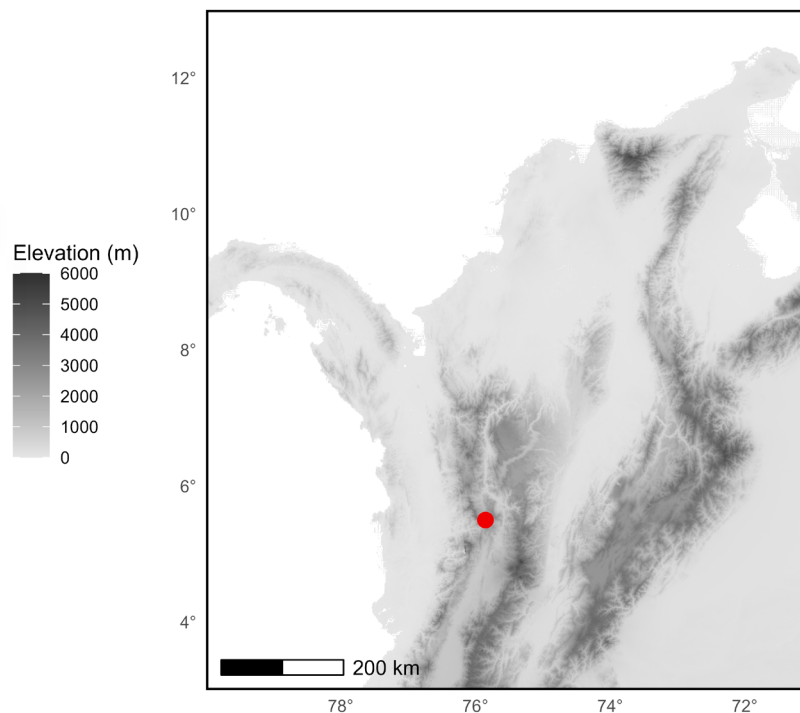


Figure 1. Location of the “El Centello” reserve in the western Cordillera of the Colombian Andes.

The sampling of epiphytes was carried out in a permanent plot of 0.25 ha, located in a TMCF (Holdridge 1967), at 5°30' North, 75°51' West. We used SVERA methodology (Sampling Vascular Epiphyte Richness and Abundance), which is designed to analyze the abundance and richness of species in an area in relation to tree size and epiphyte richness or abundance (Wolf *et al.* 2009). Thirty-five host trees were selected using the nearest random tree method in six size categories, with diameters at breast height (DBH) ranging from five to >30 cm (Wolf *et al.* 2009). Coordinates and dasometric variables (DBH, trunk height, and total height) were recorded for each host tree.

We inspected each tree from the ground using binoculars and recorded each epiphyte's morphospecies, habit, length, and size. Habit was assessed based on the life form in epiphytes, hemiepiphytes (Kress 1986, Zotz *et al.* 2021a), and nomadic vines (Zotz 2016). Plant length (L), defined as the most extended length of the main axis or rhizome, and plant size (S), defined as the greatest length from the main axis outward, were measured according to their growth form and were used to estimate biomass (Benavides *et al.* 2019). In addition, we recorded whether the plants were growing directly on bark, suspended soil or bryophytes. The species vouchers of epiphytes and host trees were deposited in the Medellín Botanical Garden herbarium (JAUM).

All analyses were performed in R software v. 4.3.3 (R. Core Team c2024) and can be accessed in the Supporting Information [Supplementary File](#). We loaded the dplyr and tidyverse libraries for data manipulation and tidying. We estimate species richness using the Chao1 estimator of the specpool function from the vegan package, and sampling completeness with the iNEXT package. Normality and homoscedasticity were tested with Shapiro.test and ncvTest in the libraries purr and car. Relationships between tree size (DBH) with richness and abundance (both biomass and individuals) were explored with linear models with the package broom. Then, we used linear regression analysis to assess the relationship between the size of trees and the richness of epiphytes while controlling for the effect of epiphyte habit with an ANOVA test. The spatial dependence of epiphyte composition was explored

by correlating the geographic distance matrix and host tree characteristic's (dasometric variables) distance matrices with a species' distance matrix using a Mantel test (Legendre and Legendre 1998) using the function mantel of the library ecodist. The Bray-Curtis similarity coefficient was used as the similarity index for the species distance matrix. Plots were made with ggplot2, and table visualization in the Supporting information were fitted with kable_styling of the kableExtra package.

RESULTS

We recorded 2279 individuals from 24 families, 62 genera, and 130 species (Supporting information). The chao index estimated 154 species but we obtained 100 % sampling completeness. All sampled host trees were colonized and hold an average of 65 epiphyte individuals per tree, ranging between ten and 175 individuals. Of the records, 41 % are monocots, 36 % are ferns, and 23 % are eudicots ([Supplementary File](#)). Orchidaceae was the richer family, followed by Araceae, Ericaceae, Polypodiaceae, Bromeliaceae, and Gesneriaceae. Orchidaceae was also the most abundant family, followed by Bromeliaceae, Dryopteridaceae, Araceae, and Hymenophyllaceae ([Table 1](#)).

Five genera (*Guzmania*, *Anthurium*, *Asplenium*, *Trichomanes*, and *Elaphoglossum*) represent more than 40 % of the abundance. *Guzmania triangularis* L.B. Sm. (Bromeliaceae) was the most abundant throughout the entire sampling, with a total of 271 individuals, accounting for more than 10 % of the total detected individuals. The species with the second highest abundance is *Trichomanes diaphanum* Kunth, which has 182 individuals, followed by *Asplenium rutaceum* (Willd.) Mett., which recorded 155 individuals. Fewer than 100 individuals represented the other epiphyte species recorded in the study; 53 species (41 % of the total richness) had five individuals or less. We recorded two endemic species: *Anthurium cupreum* Engl. and *Pleurothallis pulvinaris* Luer & R. Escobar, and two threatened species at the national level were recorded: *Masdevallia sanctae-rosae* Kraenzl. (VU) and *Masdevallia hortensis* Luer & R. Escobar (VU).

Table 1. Species richness, abundance and biomass content of the families of vascular epiphytes recorded.

Family	Individuals	Species	%Relative abundance	Biomass
Bromeliaceae	339	8	14.868	8253.093
Ericaceae	155	11	6.798	3810.833
Araceae	230	13	10.088	3447.102
Orchidaceae	363	36	15.921	2935.673
Hymenophyllaceae	198	3	8.684	2693.479
Dryopteridaceae	231	7	10.132	1698.933
Polypodiaceae	188	11	8.246	1220.234
Gesneriaceae	108	8	4.737	1163.745
Aspleniaceae	182	3	7.982	592.821
Piperaceae	57	7	2.500	220.652
Cyclanthaceae	38	1	1.667	147.880
Melastomataceae	48	4	2.105	92.854
Vittariaceae	22	1	0.965	84.281
Urticaceae	72	4	3.158	47.223
Vitaceae	1	1	0.044	46.054
Blechnaceae	6	2	0.263	43.227
Begoniaceae	10	1	0.439	39.426
Clusiaceae	13	2	0.570	29.760
Poaceae	4	1	0.175	13.922
Araliaceae	2	1	0.088	12.354
Athyriaceae	5	1	0.219	11.054
Indeterminado	1	1	0.044	6.370
Campanulaceae	3	1	0.132	5.540
Arecaceae	2	1	0.088	3.948
Rubiaceae	2	1	0.088	1.269

Host trees, on average, host 760 gr of dry epiphyte biomass, with each epiphyte weighing an average of 11 gr + 4.99. Smooth bark was present in most trees (54 %), followed by rough bark (37 %). We found more epiphytic plants in hosts with smooth texture (48 %) versus rough (34 %), ridged (12 %) and plated (6 %) as well as and they were more frequently growing on bryophytes (61 %) or suspended soil (32 %) rather than on bark directly (7 %). The average biomass per tree was 762 gr + 656, with the most contributing habits being epiphytes (E: 84 %) and nomadic vines (NO: 15 %). The contribution in dry weight of the vascular epiphytes recorded on these 35 trees amounts to approximately 27 kg, which translates to 1.7 tons per ha.

Epiphytes dominated the community, accounting for 85% of the individuals and 72 % of the species, followed

by the nomadic vine habit (11 % and 6 %) and accidental epiphytes (3.5 % and 11 %). Hemiepiphyte species have the lowest representation in the sampling. Epiphyte richness, abundance, and biomass increased significantly with the diameter of the host tree (Fig. 2A–C). Epiphyte richness showed a strong positive relationship with DBH (Fig. 2A; linear model: $F_{1,33} = 44.75$, $p < 0.001$, $R^2 = 0.58$), increasing by an average of 0.67 species per additional centimeter of DBH. Epiphyte abundance also increased significantly with tree size (Fig. 2B; $F_{1,33} = 32.08$, $p < 0.001$, $R^2 = 0.49$), corresponding to an increase of approximately 2.54 individuals per centimeter of DBH. Biomass exhibited a weaker but still significant positive relationship with DBH (Fig. 2C; $F_{1,33} = 9.02$, $p = 0.005$, $R^2 = 0.21$), increasing by an average of 0.18 g per cm of DBH. When epiphyte functional group was included in the

model, tree size and habit jointly explained a substantial proportion of the variability in epiphyte richness. The linear model was highly significant (F-statistic = 53.426, $p < 0.001$), explaining 68.7 % of the variation in richness. Tree size had a positive and significant effect (Estimate = 0.285, $p = 5.17 \times 10^{-7}$), indicating an increase of 0.285 species per tree for each additional centimeter of DBH. Additionally, both the epiphytic habit types “E” and “NO” significantly increase epiphyte richness by approximately 19.192 ($p\text{-value} < 0.001$) and 4.506 ($p\text{-value} < 0.001$) species per tree, respectively, versus no observed effect for “HE”. Overall, both tree size and specific epiphyte habits play a significant role in determining epiphyte richness.

There was no strong evidence of a significant relationship between tree characteristics and the species composition of epiphytes (Mantel test, $r = 0.0974$, $p > 0.05$). In contrast, the test between the tree’s distance and the species composition suggested a moderate positive correlation (Mantel test, $r = 0.2183$, $p < 0.05$). Distances were tested for the different habit types, obtaining that for epiphytes (E), the moderate positive correlation of species and distances is preserved and significant (Mantel test, $r = 0.1997$, $p < 0.05$). Conversely, there was no significant association between the distances of trees and hemiepiphytes (Mantel test, $r = -0.1333$, $p > 0.05$). Similarly, there was a weak

positive correlation but with a non-significant p-value of 0.120, suggesting no meaningful relationship between the spatial distribution of trees with habit type NO and the composition of epiphytic species (Mantel test, $r = 0.1114$, $p > 0.05$).

DISCUSSION

Our inventory efforts in “El Centello” reserve, located in one of the best-conserved sites in the Andes (González-Caro *et al.* 2017), revealed a rich and diverse epiphyte community, with 2279 individuals representing 130 species from 24 families and 62 genera. This is likely due to microclimatic conditions favoring colonization, establishment, and survival of the epiphyte assemblage (Gentry and Dodson 1987, Wolf 1994, Wolf and Flamenco-S 2003, Zuleta *et al.* 2016, Agudelo *et al.* 2019). The peak diversity of epiphytes is found at the elevation of the reserve, a pattern not only observed in epiphytes but also in other plant groups and even insects (Janzen *et al.* 1976, Scott 1976).

Orchidaceae emerged as the most prominent family, followed by Araceae, Ericaceae, Polypodiaceae, Bromeliaceae, and Gesneriaceae, which are reported as the richest families for the Neotropics (Gentry and Dodson 1987, Taylor *et al.* 2021). The contribution to diversity by orchids is not surprising, as

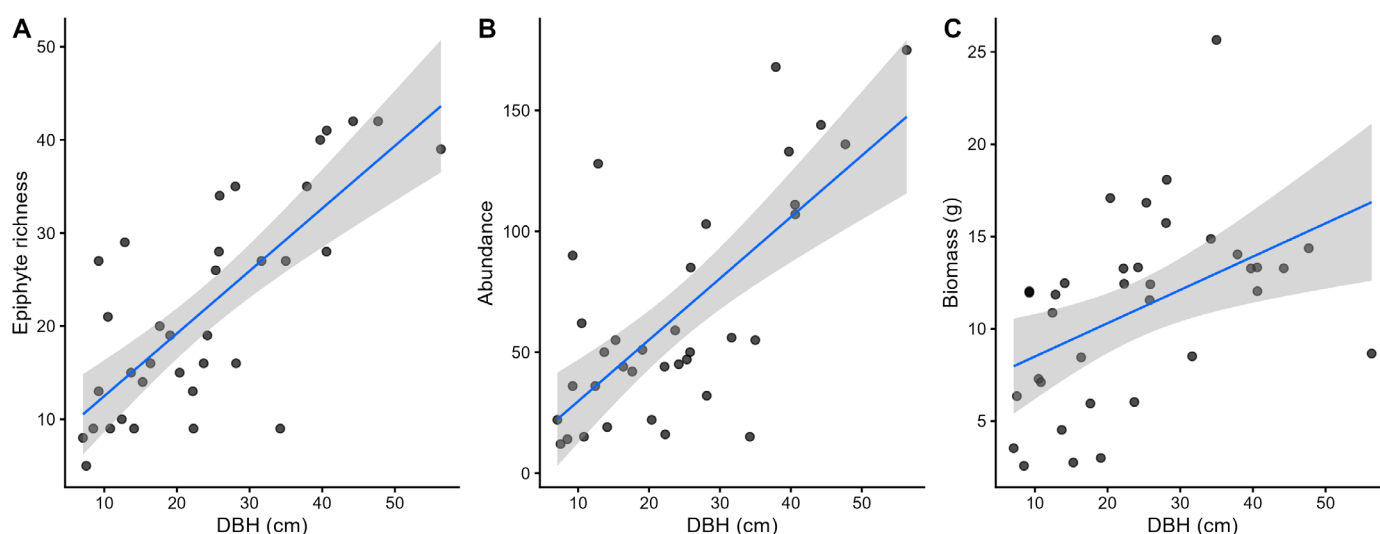


Figure 2. Linear model of epiphyte richness, abundance, and biomass with the host tree size (DBH).

they are the most diverse group of epiphytes (around 70 % of their species are epiphytic; Zotz 2016, Zotz *et al.* 2021b). In this forest, 62 % of the representativeness of eudicot families in the neotropics was recorded, highlighting the species diversity contribution of the Piperaceae, Gesneriaceae, and Ericaceae families, common in TMCs (Gentry and Dodson 1987, Sugden and Robins 1979, Taylor *et al.* 2021). The diversity (~130 species), abundance (>2000 individuals), and biomass (~1.7 tons/ha) found in the evaluated cloud forest are like those reported for other forests in the western cordillera and similar elevations (Carmona-Higuita 2014, Mendieta-Leiva *et al.* 2020).

The large number of epiphytic plants in montane forests, which can exceed hundreds of plants per tree, is overwhelming for studying processes in these communities. Therefore, when seeking an understanding of epiphyte community processes, it is useful to simplify life forms and measure abundance-related variables, such as plant size and its relationship with biomass (Nadkarni 1984, Hofstede *et al.* 1993, Freiberg and Freiberg 2000). Our results include the significant contribution to epiphytic community biomass by herbaceous plants, which, although generally small in size and weight, comprise a large number of individuals in montane forests and thus also contribute significantly to epiphyte biomass, mainly bromeliads.

Our findings provided compelling evidence supporting our initial hypotheses. The epiphytes exhibited a relationship between richness, abundance, and biomass with larger trees and certain habit types associated with higher epiphyte diversity. The linear regression analysis demonstrated a strong positive relationship between tree size and epiphyte richness, indicating that larger trees host a greater number of epiphyte species. It has been well-documented that host traits are determinants in the local distribution of epiphytes. Epiphyte species exhibit habitat selection primarily determined by branches and trunks that favor plant colonization, such as bifurcations, horizontal branches, and small branches, among others. These habitats depend, among other factors, on the age and size of the trees so that a larger tree has more available area for establishment and has been present in the forest for a longer time, increasing the probability of colonization and forming a suspended substrate on its surface (Wolf 1994, Hietz 1997, Callaway *et al.* 2002, Wagner *et al.* 2015).

However, this pattern was only observed for epiphytes and nomads. While larger trees intercept more light and water, creating diverse microclimates that support a wider range

of species (Woods *et al.* 2015), additionally this microclimate is more stable (Stanton *et al.* 2014, Wagner and Zotz 2019), which is beneficial for the growth and survival of epiphytes (moderate positive correlation) and nomadic vines (weaker positive correlation). Conversely, hemiepiphytes are less dependent on the resources available on the tree surface once they establish a root connection to the soil, which also make them less reliant on the microclimate provided by the host tree (Clemente-Arenas *et al.* 2023), resulting in a weaker relationship between their diversity and tree size. Also, larger trees often have well-defined vertical stratification, from the shaded understory to the sunlit canopy (Johansson 1974). This stratification can support different species adapted to varying light and moisture conditions, increasing overall epiphytic and nomadic diversity (Cardelus and Chazdon 2005, Wang *et al.* 2016), but hemiepiphytic presence might be more influenced by factors at the ground or canopy level rather than the vertical structure of the host tree. Moreover, the low number of hemiepiphytes found would not be comparable to the high abundance of nomadic vines and epiphytes, requiring another spatial scale and sampling units to recognize whether hemiepiphytes have an aggregate distribution pattern.

Furthermore, our results revealed interesting insights into the spatial relationships between trees and epiphyte composition. While we found no significant relationship between tree characteristics and epiphyte species composition, suggesting that other factors may be at play in shaping epiphyte communities, we observed a moderate positive correlation between tree distances and species composition. According to observations made in the field, epiphytes were more abundant in hosts with a smooth texture. Nevertheless, they grew more frequently on bryophytes and suspended soil rather than on bark directly. Most of the epiphytes on smooth bark trees were growing on bryophytes (64 %) or suspended soil (29 %), and 31 % of the total epiphytes sampled were growing on smooth bark+bryophytes followed by 21 % rough bark+bryophytes. Therefore, the substrate on which epiphytes grow can mask the effect of the host, which in these forests are mats of organic matter deposited on the surface of the trees, forming an interface between the epiphytes and the host, homogenizing possible effects that could be differentiating if they had direct contact with the bark, such as the water retention capacity of the bark (Zarate-García *et al.* 2020), exudates or resins secreted by the tree, among others (Einzmann *et al.* 2015, Tay *et al.* 2023).

The spatial proximity between trees did influence the dispersal and colonization patterns of epiphytes, particularly for certain functional types like epiphytes, which may be related to the dispersal syndrome of the diaspore through seeds with wings or feathers (pterocoric and pogonocoric, respectively). Epiphytic species are propagated mainly by tiny wind-dispersed seeds or spores (orchids and ferns), winged or plumed seeds (Tillandsioideae), so they tend to establish themselves near their parents and form an aggregated distribution (Benzing 1980, Gentry and Dodson 1987). Similarly, while there was a weak positive correlation between tree distances and epiphytic species composition for nomadic vines, the relationship was not statistically significant, suggesting that other factors may be more influential in shaping the distribution patterns of these species. Araceae, Bromelioideae, and piperoids used to have fleshy or sticky fruits dispersed by birds, bats, and other mammals, such as rodents and monkeys (Gentry and Dodson 1987), which forage in higher strata and cover more considerable distances (Snow 1981, Sorensen 1986, Horsley *et al.* 2015, Frenzke *et al.* 2015), which can contribute to their relatively wide distribution, shaping a less clustered and spatially dependent distribution. These contrasting patterns illustrate how dispersal mechanisms interact with forest structure to generate distinct spatial signatures across functional groups.

Together, these patterns illustrate how epiphyte communities respond to the combined effects of host-tree structure, substrate availability, and local spatial configuration. The interplay of these factors shapes the composition and distribution of functional groups within this montane forest, highlighting the multiple pathways through which epiphyte assemblages are structured. These findings refine our understanding of the ecological processes governing epiphyte diversity and provide a foundation for exploring how comparable mechanisms operate across different forest types and environmental contexts.

CONCLUSIONS

Our study contributes insights into the mechanisms driving epiphyte diversity in montane forests and highlights the complex interplay between tree characteristics, spatial patterns, and epiphyte community structure. Because many vascular epiphytes depend on substrates and microhabitats that form over long temporal scales, the persistence of large, mature trees becomes essential for main-

taining canopy-level biodiversity. These insights underscore the sensitivity of epiphyte communities to processes that modify forest structure —such as selective logging, fragmentation, or shifts in microclimatic regimes— and highlight the need to integrate canopy-dependent plants into conservation and forest-management planning. Incorporating epiphytes into broader assessments of ecosystem integrity will be crucial for anticipating how cloud forests respond to ongoing environmental change and for safeguarding the ecological functions they support.

AUTHOR CONTRIBUTION

AMB: Conceptualization. MJCH: Data collection and formal analysis. AMB and MJCH: Writing – original draft preparation and review & editing. All authors reviewed and approved the final version of the manuscript.

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