

# Successional forests stages influence the composition and diversity of vascular epiphytes communities from Andean Montane Forests

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## ABSTRACT

Vascular epiphytes layer is an important component of the forests; to understand their contribution to the ecosystem, it is imperative to assess the factors which affect their distribution, composition, and diversity. We studied the ecology of vascular epiphytes in Andean Mountain Forests of different successional stages, in a scenario that allowed us to determine some relationships between the composition of the epiphyte community and the tree communities, along with environmental and historic land use gradients. The research design included the sampling of 22 plots with a total of 3248 trees, including tree ferns with DBH  $\geq 10$  cm. Each tree was measured and identified to species level and was divided into three vertical strata, recording the diversity and frequency of vascular epiphytes present in each stratum. In these forests, we evaluated the variation of the composition, richness, and density of vascular epiphytes using the ADONIS analysis, evaluating the influence of two factors: the successional stage of the forest community and the tree vertical strata. We then explored which predictor variables, such as climate, spatial correlation, and host tree characteristics, explained the variation in epiphytes, using linear and variance partitioning models. In addition, we determined the preference of epiphytes for host tree species, using indicator tree species of successional stages. For each host tree species, we identified associated vascular epiphytes and their indicator species level was analyzed to determine epiphyte-host species with traits of specialist species. We found that epiphyte species richness and density were significantly higher in older forest communities. Epiphyte density was higher in the upper canopy of the hosts. The climate affected the composition of the epiphytes, while precipitation, elevation, crown height, and basal area significantly explained epiphyte richness and density. Preferential and indifferent epiphytes on indicator host species of intermediate and late succession suggest the existence of complex associations. The age of the forest succession, climatic factors, and certain characteristics of the host species have a major impact on the ecology of vascular epiphytes.

## 1. Introduction

Knowledge about the ecologic relationships among plant biotypes is fundamental to understanding the functioning of forest ecosystems. This is even more relevant in the Andean Montane Forests, which are among the most diverse ecosystems on Earth, based on their vascular plant richness (Kreft and Jetz, 2007). However, the ecology and identity of vascular epiphytes have been poorly studied, even though this group contains a large percentage of the world's plant diversity (Alvarez et al.,

2018; Mendieta-Leiva and Zotz, 2015). Vascular epiphytes represent about 10% of all tracheophyte species, Orchidaceae, Bromeliaceae, and Araceae standing out as the most diverse families (Alvarez et al., 2018; Zotz, 2013). The epiphytes contribute not only to the biological diversity in their ecosystem, but also to its structure and functioning, producing biomass, recycling nutrients, increasing the forest's water holding capacity, and providing refuge to wildlife (Nadkarni et al., 2004).

Epiphyte composition and richness depend on several biotic and abiotic factors, among which are intraspecific competition, macro and

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microclimate, and physical and chemical traits of their host (Callaway et al., 2002; Ding et al., 2016). It has been observed that the composition of vascular epiphyte communities is influenced by the composition of woody plants, which are distributed in heterogeneous environmental gradients (Ding et al., 2016). The richness and abundance of vascular epiphytes decrease by up to 50% in secondary forests when compared to the primary montane forest (Barthlott et al., 2001). This variation is related to heterogeneous environmental conditions, on which precipitation exerts a key influence (Küper et al., 2004; Zhang et al., 2015). Additionally, in fragmented landscapes, the spatial correlation affects dispersion processes and contributes to the variation in the composition of vascular epiphytes between different forest communities (Cascante-Marín et al., 2006; de la Rosa-Manzano et al., 2017).

Distribution patterns, composition, richness, and abundance of epiphytes in tropical forests also vary along gradients within their host trees. The complexity of these habitats is caused by the heterogeneous morphological characteristics of the different phorophyte species, as well as changes in the microclimate along the vertical gradient (Andersohn, 2004; Cardelús and Chazdon, 2005; Krömer et al., 2007; Pos and Slegers, 2010). Most epiphyte species are found in the highest canopy strata of host trees, due to the positive influence of light, wind, temperature, and humidity (Krömer et al., 2007). The abundance of organic material and bryophytes also favor the establishment of epiphyte communities, due to their role as water and nutrient reservoirs for their sustenance (Freiberg and Freiberg, 2000).

Tree host characteristics, such as basal area (Ding et al., 2016; Woods et al., 2015), density, and height (Arévalo and Betancur, 2006), are positively correlated with the diversity of epiphytes. However, the richness and composition of tree species do not necessarily predict the distribution of epiphytes in tropical elevational gradients (Cardelús et al., 2006). The same authors also do not report the effect of tree size on epiphyte richness, but they propose that open spaces in the phorophyte trunk and branches, free of living or dead organic matter, facilitate epiphyte colonization.

Vascular epiphytes depend on native trees as their habitat, so they are directly susceptible to deforestation, which is very common in the tropical Andes (Duque et al., 2021). In this region, there are remnants of mature and secondary forests, the latter as a result of natural regeneration in abandoned agricultural areas (Hethcoat et al., 2019; Jadán et al., 2021). Both these two scenarios constitute important habitats for vascular epiphytes (Barthlott et al., 2001; Köster et al., 2009). Here, knowledge about the attributes of epiphytes and their relationship with their environment is needed for adequate conservation of Andean forests.

In this context, we conducted the present research with the objective of understanding what factors determine the ecological parameters (diversity, distribution, and composition) of vascular epiphytes in Andean Montane Forests. For this, we proposed the following hypotheses: 1) The composition, richness, and density of epiphytes are different and greater in the forest communities of late succession and the upper canopy of the host trees. 2) The predictive climatic variables are significant when explaining the composition, richness, and density of vascular epiphytes than the characteristics of the host trees (morphology, richness, and density) or the spatial correlation (only composition) in tropical Andean forests. 3) Vascular epiphytes prefer and are specialists in trees of species that are characteristic of an advanced stage of succession.

## 2. Materials and methods

### 2.1. Study area

The study area is located in the Azuay Province, southern Ecuador, in habitats classified as High Montane Evergreen Forest. In this area, 22 sampling plots were installed. Details of their implementation and use for studies related to the structure of the forest are available in Jadán

et al. (2021) (Fig. 1). In general, the forest communities differed by age of succession and were distributed in an altitudinal range of 2900–3500 m. The average annual temperature ranges between 6 and 12 °C and the annual rainfall range between 800 and 1500 mm.

### 2.2. Sampling design

All epiphytic individuals found on trees with a diameter at breast height  $\geq 10$  cm (DBH) in each of the 22 sampling plots were counted and identified using ladders (to assess trunk and low canopies  $< 4$  m high) and tree-climbing techniques with binoculars to assess the trunk and canopies of trees  $> 4$  m high. For clonal species (they have phenotypically and genetically identical individuals) such as orchids, bromeliads, and ferns, we count and estimate their tufts or rosettes. To differentiate one tuft from another, we consider a separation of at least 5 cm and that each plant has its roots attached to the trunk or branch of the host tree. Individuals that could not be identified directly in the field were photographed or collected for later identification using taxonomic keys and comparison with specimens in the regional LOJA Herbarium, located in southern Ecuador, close to the place where the study was carried out. Characteristics of the host trees, such as total height, trunk height, and crown height, were measured using a Suunto clinometer.

The climatic and physiographic variables recorded for each site were: elevation, mean annual temperature, and annual precipitation. Climate data were obtained from the Worldclim global climate database (<https://www.worldclim.org/>) using the coordinates of the center of each plot. All diversity variables (richness and composition) and structure (diameter, basal area, density, and dominance) of tree communities derive from analyzes generated from the database of Jadán et al. (2021).

### 2.3. Data analysis

We listed the number of families, genera, and species, and determine the most diverse genera and families considering the number of taxa and their relative value.

### 2.4. 1 Composition, richness, and density of vascular epiphytes

Epiphyte's composition, richness, and density were considered as response variables, and their variation was evaluated considering two factors. The first consisted of three floristic groups (i.e. forest communities – FC) which were determined by Jadán et al. (2021). These communities are differentiated mainly according to the age of succession: FC1 is early succession, FC2 is intermediate succession, and FC3 is late succession. The age of succession was determined by combining two aspects: 1) Through a multi-temporal analysis that was carried out using photographs from 1955, 1980 and 2015 provided by the Military Geographic Institute of Ecuador (IGM); 2) Surveys of adult people from the study area. For forests  $> 70$  years, we consulted the historical records of El Cajas National Park buffer zone, to obtain an approximate age of these mature forests. The second factor was represented by the vertical strata along the host tree, such as: a) trunk (stem of the tree to the first branch), b) low crown (up to 1/3 of the total height of the crown), and c) high crown (above the low cup).

To determine the variation in the epiphyte composition, a multivariate permutational analysis of variance was applied, using distance matrices – ADONIS. This analysis compares the means of two or more biological communities to determine their similarity. The “adonis2” function in R package “Vegan” was used (Oksanen et al., 2013). An analysis of epiphytic indicator species was performed according to their frequencies and abundances per plot, using the R package “Indicspecies” (De Cáceres et al. 2012). This analysis was differentiated between the three FC of trees. To evaluate the variation in epiphyte density and richness, an analysis of variance (DGC test  $p \leq 0.05$ ) was performed considering the same factors used for the composition. We verified the assumptions of normality and homoscedasticity, and when the

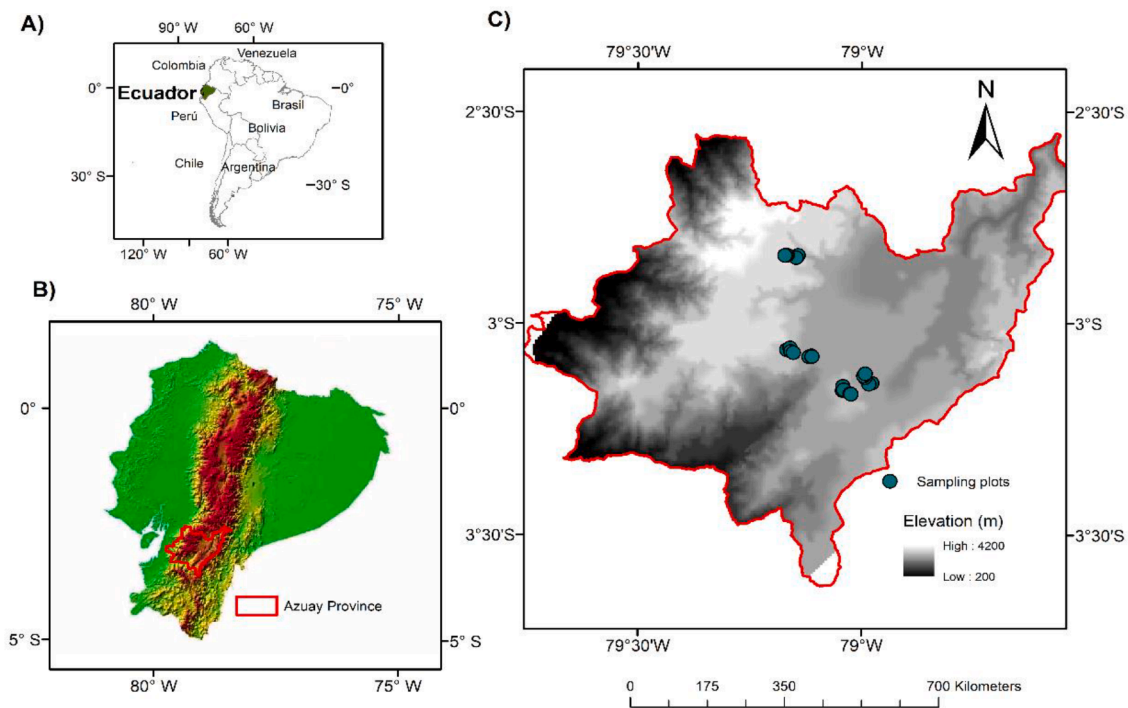


Fig. 1. Location of the study area and sampling sites in the Andean Montane Forests, from South America (A), Ecuador (B) to the province of Azuay (C).

assumptions were not met, the response variables were logarithm-transformed.

#### 2.4.1. Effect of predictor variables on the composition, richness, and density of epiphytes

The elevation (which also stands for mean annual temperature, Pearson's correlation  $R = -0.85$ ;  $p < 0.0001$ ) and mean annual precipitation were considered as climatic predictor variables (CL). The host tree traits (HT) which were used as predictor variables were basal area (that replaces age, Pearson's correlation  $R = 0.7$ ;  $p < 0.0001$ ), crown height (that replace total height, Pearson correlation = 0.96;  $p < 0.0001$ ), and richness. These variables were selected to avoid collinearity using the "find Correlation" function in the R package "Caret" (Kuhn et al., 2018). With this function, one of the variables correlated with  $r > 0.7$  was automatically eliminated. Variance partitioning test (VarPart;  $p < 0.05$ ) was used to identify which predictor variables explained most of the variation in epiphytic composition, using the "varpart" function in "Vegan" R package (Dray et al., 2012). In this analysis, we included the effect of spatial correlation (SC) as a predictor variable. This variable was calculated using geographic distance through the function "principal coordinates" in the "Vegan" R package (Oksanen et al., 2013).

Linear Models (LMs) were used and adjusted to determine which CL and HT predictors influenced the variation in the richness and density of vascular epiphytes (response variables), using the "lme" function in the R package "nlme" (Pinheiro et al., 2017). We applied the backward elimination procedure so that the correlation model retains only the significant predictor variables ( $p < 0.05$ ).

#### 2.4.2. Vascular epiphytes and their preference for host trees

First, we chose the indicator tree species that were identified in successional forest communities by Jadán et al. (2021). These species are *Hesperomeles ferruginea* (ROSACEAE) and *Myrsine dependens* (Ruiz & Pav.) Spreng. (MYRSINACEAE), for early successional communities; *Gaiadendron punctatum* (Ruiz & Pav.) G. Don. (LORANTHACEAE), *Gynoxys azuayensis* Cuatrec., *Gynoxys hallii* Hieron. (ASTERACEAE), *Hedyosmum cumbalense* H. Karst. (CHLORANTHACEAE), *Ocotea*

*infrafoveolata* van der Werff. (LAURACEAE), for intermediate succession; *Critoniopsis floribunda* (Kunth) H. Rob. (ASTERACEAE), *Hedyosmum goudotianum* Solms., *Hedyosmum racemosum* (Ruiz & Pav.) G. Don., *Hedyosmum luteyui* Todzia. (CHLORANTHACEAE), *Meriania tomentosa* (Cogn.) Wurdack. (MELASTOMATACEAE), *Nectandra membranacea* (Sw.) Griseb. (LAURACEAE), *Piper andreaeanum* C. DC. (PIPERACEAE), for late succession forests. Then, the variation in richness and abundance among indicator trees was determined with an analysis of variance with the DGC test,  $p < 0.05$ ; we used the basal area as a covariate to consider the influence of tree size. Since richness and abundance data were not normally distributed, we used Generalized Linear Models (GLMs) with a Negative Binomial distribution and a logarithmic link function with the "glm" function in the "Stats" R package (Marschner et al., 2018). This distribution was selected based on the relationship between deviation and degrees of freedom  $< 1.5$ . An indicator species analysis (Indicspecies,  $p < 0.05$ ) was performed using the "Indicspecies" R package (De Cáceres et al., 2012) to identify indicator epiphytes associated with the host species. This analysis allowed us to filter the important species in the relationship between their frequency and abundance. The significantly indicator value ( $p < 0.05$ ) for each epiphytic (range 0–0.9) was classified in the following ranges, to determine the groups of epiphytes by their preferences for host species – specialized epiphyte: 0–0.24; selective epiphyte: 0.25–0.49; preferential: 0.5–0.74; indifferent  $> 0.75$ . These categories were adapted for our analysis from de Andrade Kersten et al. (2009).

### 3. Results

A full and comprehensive description of the diversity and composition of tree communities that support epiphytes can be found in Jadán et al. (2021). Host tree species within each forest community are shown in the appendix (Table A1). The diversity of epiphytes is represented by 24 botanical families, 44 genera, and 75 species. The most diverse family is Orchidaceae with 28 species (37.3% of the total determined species), followed by Bromeliaceae with 10 species (13.3%), Piperaceae and Polypodiaceae with 7 species each (9.3%), Aspleniaceae, Asteraceae, and Urticaceae with two species each (2.7%). The rest of the 17

determined families are each represented by one species (1.3%). The most diverse genus is *Epidendrum* with 10 species, followed by *Peperomia* with 6, *Polypodium* with 5 species, *Pleurothallis* and *Tillandsia* with 4 species each, *Asplenium*, *Cyrtochilum*, *Gomphichis*, *Grammitis*, *Phenax*, *Racinaea*, and *Stelis* with two species each. The rest of the 32 genera have one species each.

### 3.1. Composition of epiphyte communities

The floristic composition of epiphytes was significantly different between the FCs ( $p = 0.001$ ) and between the vertical strata ( $p = 0.036$ ). The composition was not affected by the interaction between FC and vertical strata ( $p = 0.422$ ). FC3 recorded the greatest number of indicator species, while FC1 which recorded only one species (Table 1).

### 3.2. Richness and density of epiphytes

Epiphyte richness was significantly higher for FCs3 and FC2 compared to FC1 ( $p < 0.0001$ , Fig. 2A). The richness was not significantly different between the vertical strata ( $p = 0.0636$ ), with no effect of the interaction between FC and strata ( $p = 0.4299$ ). Density was significantly higher in FCs3 and FC 2 compared to FC1 ( $p < 0.0001$ ; Fig. 2B). Epiphyte density was higher in the upper canopy compared to the trunk and the lower canopy, which presented the lowest values ( $p = 0.0344$ ) (Fig. 2C). The density was not affected by the interaction between FC and vertical strata ( $p = 0.4665$ ).

**Table 1**  
Epiphyte indicator species from Andean Montane Forests communities.

FC – Succession state	Species	Indicator value	P
FC1 – early	<i>Vriesea tequendamae</i> (André) L.B. Sm.	0.54	0.009
	<i>Epidendrum piperinum</i> Lindl.	0.64	0.001
	<i>Munnozia senecionidis</i> Benth.	0.61	0.001
	<i>Mezobromelia capituligera</i> (Griseb.) J. R. Grant	0.8	0.002
	<i>Oncidium alticola</i> Stacy	0.75	0.002
	<i>Epidendrum cochlidium</i> Lindl.	0.61	0.003
	<i>Nephrolepis</i> sp.	0.63	0.004
	<i>Polypodium murorum</i> Hook.	0.73	0.008
	<i>Racinaea tetrantha</i> (Ruiz & Pav.) M.A. Spencer & L.B. Sm.	0.6	0.012
	<i>Pleurothallis cassidis</i> Lindl.	0.47	0.013
FC2 – intermediate	<i>Epidendrum melanotrichoides</i> Hágsater & Dodson	0.43	0.032
	<i>Asplenium auritum</i> Sw.	0.78	0.001
	<i>Asplenium sessilifolium</i> Desv.	0.73	0.001
	<i>Epidendrum excisum</i> Lindl.	0.89	0.001
	<i>Hymenophyllum fucoides</i> (Sw.) Sw.	0.75	0.001
	<i>Peperomia obtusifolia</i> (L.) A. Dietr.	0.89	0.001
	<i>Peperomia</i> sp.	0.88	0.001
	<i>Pleurothallis cordata</i> (Ruiz & Pav.) Lindl.	0.63	0.001
	<i>Polypodium sessilifolium</i> Desv.	0.7	0.001
	<i>Racinaea</i> sp.	0.82	0.001
FC3 – later	<i>Tillandsia complanata</i> Benth.	0.84	0.001
	<i>Guzmania garciaensis</i> Rauh	0.75	0.002
	<i>Tillandsia tovarensis</i> Mez	0.8	0.002
	<i>Epidendrum purum</i> Lindl.	0.72	0.003
	<i>Phenax rugosus</i> (Poir.) Wedd.	0.49	0.003
	<i>Terpsichore</i> sp.	0.52	0.003
	<i>Cyrtochilum gyriferum</i> (Rchb.f) Kraenzl.	0.67	0.005
	<i>Cyrtochilum</i> sp.	0.48	0.006
	<i>Peperomia divaricata</i> Yunck.	0.66	0.008
	<i>Vaselia</i> sp.	0.45	0.01
<i>Epidendrum philocrennum</i> Hágsater & Dodson	0.64	0.014	
<i>Pleurothallis galeata</i> Lindl.	0.51	0.032	
<i>Peperomia caespitosa</i> C. DC.	0.37	0.041	
<i>Stelis pusilla</i> Kunth	0.43	0.042	

### 3.3. Predictor variables' relationship with the variation in epiphyte composition

CL had the highest contribution in explaining the variation in the composition of epiphytes (Table 2). Climate had a greater weight on HT and the spatial correlation ( $R^2 \text{ adj} = 0.11$ ). The spatial correlation has a similar value and controls under this same magnitude the climate and the HT.

### 3.4. Predictor variables' relationship with the variation in epiphyte richness and density

Tree crown height was the most important predictor variable to explain the two response variables (Table 3). However, elevation, along with host crown height, was the most important predictor variable to explain variation in epiphyte richness. Mean annual precipitation, basal area, and crown height best explained epiphyte density.

### 3.5. Preference of epiphytes for host trees species

Individuals of *N. membranacea* (1) in late succession forests recorded the highest values in the abundance of epiphytes (Fig. 3A). The lowest values were recorded in the host species of intermediate and early succession. The highest richness values were recorded on *N. membranacea* (1) and *C. floribunda* (2) from late succession, and *H. cumbalense* (3) from intermediate (Fig. 3B). The other species had lower values in the richness of epiphytes.

We identified 14 indicator epiphytes based on their significant relationship between frequency and abundance (Table 4). According to the indicator value ( $p < 0.05$ ), indicator epiphytes were not encountered on trees from early successional forests. Neither specialized nor selective species were recorded in the study. However, 13 species belonging to the Orchidaceae, Bromeliaceae, Piperaceae, Grammitidaceae, Ochnaceae, and Urticaceae (descending order according to their number of species) were **preferential**. These species were recorded on intermediate and late-successional hosts. Only *Epidendrum purum* of later succession was **indifferent**. The values of all epiphytic are shown in the appendix (Table A2).

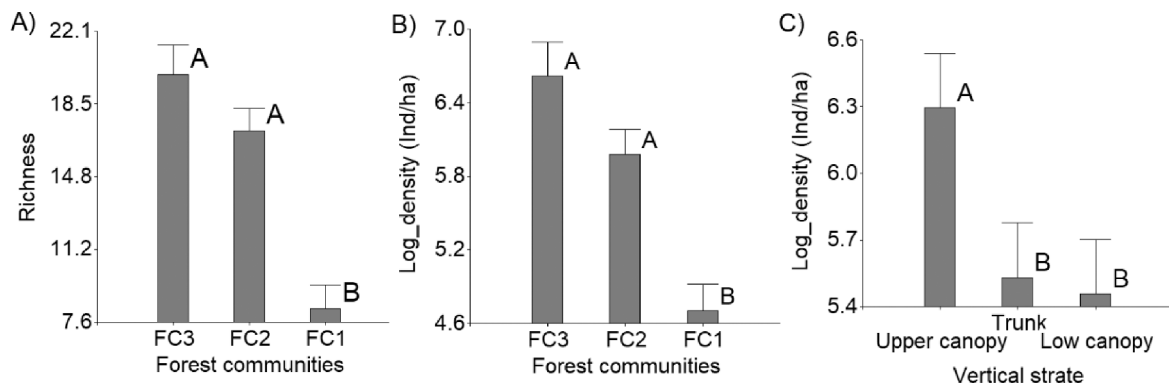
## 4. Discussion

A few decades ago, the diversity of vascular epiphytes was estimated to be over 23,000 species (Kress, 1989). In our study, we registered 75 species, which is less than the number of species reported in Andean forests in Bolivia (Krömer and Gradstein, 2003). Also, studies conducted on the eastern slopes of the Andes in southern (Bussmann, 2002) and northern Ecuador (Nieder and Barthlott, 2001) similarly found higher diversity levels. This might be caused by heterogeneity in sampling protocols or quantification, and most importantly, by differences in ecology and level of disturbance at each site. These differences induce changes in biotic and abiotic parameters in the landscape, habitat, and microhabitat where these plants develop (Mendieta-Leiva and Zotz, 2015; Werner et al., 2005). Although in our study fewer species were registered compared to other sites, the main epiphyte families in terms of their ecological relevance were Orchidaceae, Bromeliaceae, and Polypodiaceae, which showed the greatest species richness and abundance. These families have been registered in Andean primary and secondary forests, as well as in disturbed areas (Krömer and Gradstein, 2003; Werner et al., 2005).

### 4.1. Composition of epiphytes and their relationship with predictor variables

The dissimilarity in the composition of epiphytes is evidenced by the indicator species, which are different in all forest communities. Indicator species are important because of their affinity to certain floristic groups





**Fig. 2.** Mean ± standard error of the richness (A) and density (B) of epiphytes in floristic groups and density in vertical strata (C), registered in Andean Montane Forests.

**Table 2**

Variance partitioning of predictor variables ( $F$ ;  $p < 0.05$ ) on the composition of vascular epiphytes, in Andean Montane Forests.

Variables	$R^2$ adj	$F$	$p$
Climate (CL): elevation and mean annual precipitation	0.1	4.7	0.001
Host trees (HT): Basal area, crown height, and richness.	0.07	2.7	0.001
Spatial correlation (SC)	0.08	6.9	0.001
CL/HT + SC	0.11	5.4	0.001
HT/CL + SC	0.07	2.9	0.001
SC/CL + HT	0.11	10.1	0.001
All	0.27	4.9	0.001
Residuals	0.73		

**Table 3**

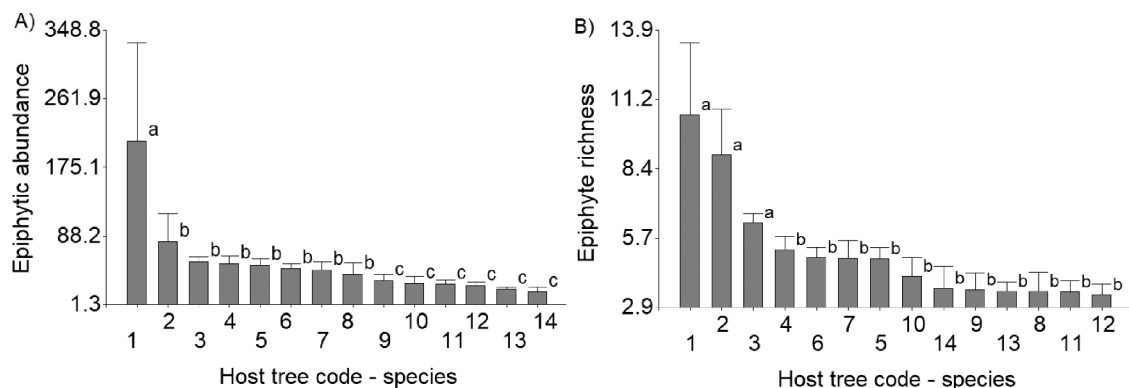
Result of LM evaluating the relationship between predictor variables and the richness and abundance of vascular epiphytes in Andean Montane Forests.

Response variables	Predictor variables	Coefficient	SE	$t$ -value	$p$
Richness	Intercept	-43.2	14.2	-3	0.0035
	Elevation (m)	0.02	0.004	3.5	0.0009
	Crown height (m)	1.7	0.5	3.7	0.0004
Log-density (Ind/ha)	Intercept	8	1.3	6.1	<0.0001
	Mean annual precipitation (mm)	-0.01	0.001	-3	0.0038
	Basal area ( $m^2/ha$ )	0.02	0.007	2.7	0.0075
	Crown height (m)	0.6	0.2	3.4	0.0009

and they suggest heterogeneity of the ecosystem or habitat (Ding et al., 2016; Siddig et al., 2016). In FC1, which has the lowest successional age, only one indicator species was recorded. However, the number of indicator species increases markedly in communities with a higher age of succession (FC2 and FC3). Our study emphasizes that good management and conservation practices are important for both the natural regeneration and the associated epiphytic plants, but also that conserving epiphytes is an essential component in all forest communities regardless of their successional age.

Our results pointed out that climatic variables mostly explained the composition of epiphytes, suggesting environmental heterogeneity, which is common in fragmented landscapes (Werner et al., 2005). Elevation (associated to mean annual temperature) and mean annual precipitation explained to a large extent the species composition, as it was seen in other tropical forests (Hietz and Hietz-Seifert, 1995). In forests with higher environmental heterogeneity, elevation is associated with other predictor variables that help explain species composition more precisely (Ding et al., 2016). These complex environmental congruences prevent us from drawing simple conclusions by saying that certain species grow in hot or cold areas. Soil variables explained the composition of host tree communities (Jadán et al., 2021), which in turn affects the presence and abundance of epiphytes. Within the functional integrity of the landscape, the edaphic elements associated with climate variables (precipitation and temperature) influence the floristic composition and structure of host trees (Boelter et al., 2014; Naik et al., 2006). This happens both in evergreen forests (Veintimilla et al., 2019) and in seasonal forests (Castellanos-Castro and Newton, 2015).

Although our results did not show variations in the composition of epiphytes between the different vertical strata, these habitats are important within forests to maintain balance and synergies in



**Fig. 3.** Mean ± standard error of the abundance and richness of epiphytic registered at indicator host species of forest communities at Andean Montane Forests. 1) *N. membranacea*, 2) *C. floribunda*, 3) *H. cumbalense*, 4) *H. goudotianum*, 5) *O. infrafoveolata*, 6) *H. racemosum*, 7) *Gaiadendron punctatum*, 8) *Meriania tomentosa* (Cogn.) Wurdack., 9) *M. dependens*, 10) *H. luteynii* 11) *H. ferruginea*, 12) *P. andreanum*, 13) *G. azuayensis*, 14) *G. hallii*.

**Table 4**

Epiphytes with their indicator value and preference category over host trees which correspond to different stages of succession, registered at Andean Montane Forests. IV: indicator value.

Indicator epiphyte species	IV	<i>p</i>	Category of preference	Host specie	Succession stage of host species
<i>Huperzia selago</i> (L.) Bernh. ex Schrank & Mart. – Lycopodiaceae	0.5	0.02	Preferential	<i>C. floribunda</i>	Later
<i>Stelis pusilla</i> Kunth – Orchidaceae	0.5	0.03	Preferential	<i>C. floribunda</i>	Later
<i>Pleurothallis galeata</i> Lindl. – Orchidaceae	0.51	0.04	Preferential	<i>C. floribunda</i>	Later
<i>Tillandsia cernua</i> L.B. Sm. – Bromeliaceae	0.51	0.04	Preferential	<i>M. tomentosa</i>	Later
<i>Grammitis lanigera</i> (Desv.) C.V. Morton – Grammitidaceae	0.51	0.03	Preferential	<i>N. membranacea</i>	Later
<i>Guzmania garciaensis</i> Rauh – Bromeliaceae	0.55	0.03	Preferential	<i>M. tomentosa</i>	Later
<i>Oncidium alticola</i> Stacy – Orchidaceae	0.56	0.02	Preferential	<i>N. membranacea</i>	Later
<i>Cyrtochilum gyriferum</i> Kraenzl. – Orchidaceae	0.59	0.01	Preferential	<i>C. floribunda</i>	Later
<i>Peperomia obtusifolia</i> Miq. – Piperaceae	0.6	0.01	Preferential	<i>N. membranacea</i>	Later
<i>Phenax rugosus</i> (Poir.) Wedd. – Urticaceae	0.66	0.01	Preferential	<i>N. membranacea</i>	Later
<i>Stelis atrocaerulea</i> Luer – Orchidaceae	0.68	0.01	Preferential	<i>C. floribunda</i>	Later
<i>Mezobromelia capituligera</i> (Griseb.) J.R. Grant – Bromeliaceae	0.69	0.01	Preferential	<i>O. infrafoveolata</i>	Intermedia
<i>Tillandsia tovarensis</i> Mez – Bromeliaceae	0.7	<0.0001	Preferential	<i>C. floribunda</i>	Later
<i>Epidendrum philocremnum</i> Hágsater & Dodson – Orchidaceae	0.71	<0.0001	Preferential	<i>C. floribunda</i>	Later
<i>Vaselia</i> sp. – Ochnaceae	0.71	0.01	Preferential	<i>N. membranacea</i>	Later
<i>Epidendrum purum</i> Lindl. – Orchidaceae	0.84	<0.0001	Indifferent	<i>N. membranacea</i>	Later

interspecific ecological relationships (Hietz, 2010). Within the vertical structure of the hosts, the composition of epiphytes was not any different. However, species richness and abundance can vary between vertical strata (Gotsch et al., 2015), emphasizing the need to further investigate the composition of the epiphytes about the morphological and structural characteristics of the host trees.

#### 4.2. Richness and density of epiphytes and their relationship with predictor variables

The richness and density of epiphytes were higher in forest communities with the highest age of succession, as we expected. Our results are consistent with those reported by Barthlott et al. (2001), who noted that the richness of epiphytes decreases by 50% between mature and secondary forests. This is probably because the composition and structure of epiphytes are positively associated with the quality of natural systems, both in structure and composition (Krömer et al., 2014). Although in our case the richness did not differ between the vertical strata (unexpected result). Studies carried out in primary forests, although the canopy has been divided into several vertical sections, have reported greater diversity and richness in the upper vertical strata (Pos and Slegers, 2010; Krömer et al., 2007). In these types of forests, the colonization of epiphytes has probably occurred at its maximum, which is directly related to time. Furthermore, Cascante-Marín et al. (2006) state that the diversity changes during forest succession according to the availability and dispersal of seeds, in addition to the physiological performance and survival of individual plants, their ability, and time to flower.

The density was higher in the upper canopy, as we expected. This result highlights the importance of this strata to provide habitat for a greater number of epiphytic individuals without differentiating communities of early and late succession. This was evidenced in the non-significant interaction between communities and vertical strata. In upper canopy is open to light and wind causing lower humidity and a more xeric habitat. Granados-Sánchez et al. (2003) state that in this habitat within the canopies, the colonization of several botanical families of vascular epiphytes is facilitated, favoring the existence of a larger number of individuals compared to the other vertical strata.

Elevation (associated with mean annual temperature) has a significant effect on the richness of epiphytes at the forest community level. The elevation is inevitably associated with environmental heterogeneity and plays an important role, both at the level of forest communities and in the vertical strata (Apaza-Quevedo et al., 2015; Petter et al., 2016). To the environmental heterogeneity, the height of the crown is articulated at a local habitat level to significantly explain the epiphytes' richness. This last variable was highly and positively correlated with the age of

succession. Based on these results, we conclude that the highest epiphyte richness occurs in mature trees that have larger crowns and are present in forest communities with greater successional age. The same pattern was observed in the richness of epiphytes in the Brazilian Amazon (Benavides et al., 2006).

Basal area (correlated with successional age), along with crown height, positively explained epiphyte density at the forest community level. This result allows us to state that there are more epiphytic individuals in larger and older trees, which coincides with other studies (Küper et al., 2004; Woods et al., 2015). On the other hand, Flores-Palacios and García-Franco (2006) observed that the density of epiphytes is not directly associated with the size of the trees, but rather with the space not saturated by biomass or vascular or non-vascular individuals available for young trees, which could be an explanatory alternative. These peculiarities should be investigated in more detail in the future.

Mean annual precipitation negatively influenced epiphyte density, which differs from other studies showing that epiphyte abundance is climatically dependent on precipitation associated with relative humidity (Ding et al., 2016; Hietz, 2010). However, given the low seasonality that characterizes our study sites, the influence of precipitation on the formation of habitats, which further conditions the density values of epiphytes, cannot be accurately predicted.

#### 4.3. Preference of vascular epiphytes for host trees

In the forest communities, the age of succession was positively related to the number of indicator species (Jadán et al., 2021). The groups of indicator species differ in their composition and structure, especially in the basal area, which determines specific and heterogeneous habitat conditions for epiphytes (Rasmussen and Rasmussen, 2018). According to our results, the general trend of older communities having the highest values of richness and abundance was markedly repeated at the level of the indicator species. This suggests that quantitative parameters of vascular epiphytes are positively associated with the quality of the habitats, in our case, trees of greater ecological importance.

According to the value of the indicator, the absence of indicator epiphytes ( $p < 0.05$ ) in the indicator trees of early succession is an expected result, which allows us to affirm that the preference of epiphytes is for older host trees, which are available as phorophytes by more time. Malizia (2003) concluded that the preference of epiphytes for hosts is partially explained by the measurable characteristics of the host tree. Similarly, the absence of specialist and selective epiphytes is possibly influenced by host vegetation attributes. Functional morphological and anatomical traits of the host vegetation would allow the future to be

clear about the conditioning attributes for the specificity of epiphytes (Wagner et al., 2021).

The high proportion of preferential and indifferent epiphytic is based on the significant relationship between measurable parameters of species. Ecologically, the epiphytes that stand out for their frequency and abundance on indicator hosts of intermediate and advanced succession are present in different aspects. On tree species, there are possible variations in their biological (endophytic by microorganisms), chemical (allelopathy), and morphological characteristics (Apaza-Quevedo et al., 2015; Salazar et al., 2020; Werner et al., 2012). The other peculiarity is the climatic incidence on which the epiphytes respond favorably to fulfill their plant functions (Apaza-Quevedo et al., 2015; Marini et al., 2011). More studies of the physiological particularities of these taxonomic groups are needed.

## 5. Conclusions

In montane forests, the composition of epiphytes differs according to the age of succession. However, in FC2, of intermediate succession, the presence of Orchids as climax species of the native forest ecosystems shows an ecologically efficient development of the habitats in their stages of succession. Therefore, the conservation of these secondary forests is important. The greater richness and abundance of epiphytes recorded in the forest communities of greater successional age suggests that the best-preserved natural forests through natural regeneration are efficient ecosystems, in terms of colonization processes and development of these vascular biotypes. The composition, richness, and density are explained by diverse predictor variables, due to the abiotic and interspecific synergic relations that exist in tropical montane forests. Based on their dependence on indicator tree host species, epiphytes from intermediate and late succession were grouped in either preferential or indifferent categories, emphasizing the complex associations which are established in montane forests of different successional stages.

## CRedit authorship contribution statement

**Jadán Oswaldo:** Funding acquisition, Investigation, Project administration, Resources, Conceptualization, Data curation, Methodology, Software, Visualization, Writing – original draft, Writing – review & editing. **Cedillo Hugo:** Investigation, Methodology. **Tapay Wilmer:** Investigation, Methodology. **Pangol Ismael:** Investigation, Methodology. **Quizphe Wilson:** Data curation. **Cabrera Omar:** Methodology, Software, Supervision, Validation, Writing – review & editing.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Data availability

Data will be made available on request.

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## Appendix A. Supplementary data

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