



# Importance of the vertical gradient in the variation of epiphyte community structure in the Brazilian Atlantic Forest

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## ABSTRACT

Epiphytes are strongly affected by the microclimate of the forest canopy. Therefore, understanding how microclimatic changes are related to the functional characteristics of taxa and the patterns of communities is essential. Our objective was to examine the stratification of the epiphyte community along the vertical gradient of the forests and to investigate whether the pattern of species distribution in the canopy height zones is similar among forests with different characteristics and between the families of epiphytic plants. The study was carried out in the Atlantic Forest of Ilha Grande, in southeastern Brazil, where we recorded 76 species. The highest richness and abundance were found on tree trunks. The high crown had less diversity and a characteristic set of species. The vertical stratification pattern was similar across forests with different phytophysiognomies. The main epiphytic families exhibited different patterns of diversity along the canopy. The highest richness of Araceae occurred in the trunk zones, while Polypodiaceae, Bromeliaceae, and Orchidaceae were more diverse in the trunk and inner crown, and Cactaceae were more diverse in the inner crown. Tree height zones select epiphytic taxa with distinct characteristics according to the fundamental conditions for their survival and, therefore, we suggest that the ecological niche theory is adequate to explain the assembly of epiphytic communities at a local scale.

## 1. Introduction

The architecture of treetops, branches and leaves, the presence of climbing plants and epiphytes, and other abiotic factors determine the creation and control of microclimates in forest ecosystems (Hallé et al., 1978). A vertical gradient with marked microclimatic variation is especially typical of tropical forests (Richards, 1996). It is known that towards the highest parts of the canopy moisture decreases while luminosity and temperature increase (Anhuf and Rollenbeck, 2001; Fauset et al., 2017; Hallé et al., 1978; Murakami et al., 2022; Stark et al., 2012). In addition to microclimatic variation, there is vertical stratification of other environmental conditions and resources, including humus and nutrient availability (Catling and Lefkovitch, 1989; Sillett and Van Pelt, 2007; Woods et al., 2015) and, consequently, the plant and animal communities that inhabit parts of trees (Smith, 1973; Stan et al.,

2020). According to Moffett (2000), small vertical distances in the canopy are equivalent to much larger horizontal extensions and this explains the high alpha diversity of tropical forests as ecosystems become more structurally complex.

Vascular epiphytes, non-parasitic plants that are structurally dependent on other plants, have a prominently tropical distribution (Benzing, 1990; Gentry and Dodson, 1987) and contribute about 40% of the vascular flora in neotropical forests (Taylor et al., 2021). Epiphytes are strongly influenced by the vertical gradient of a forest and the three-dimensional structure of tree crowns (Benzing, 1990) and, according to Taylor et al. (2021), the high diversity of tropical forests is precisely due to niche partition in the communities, since the many species of epiphytes present an exceptional variety of functional traits within diverse taxonomic groups. Classical studies have already shown that epiphytes do not have a random distribution along tree height zones

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(Benzing, 1990; 1995; Catling and Lefkovitch, 1989; Gentry and Dodson, 1987; Johansson, 1974; Kelly, 1985; Schimper, 1888). Recent research has detected preferential spatial patterns for specific groups of epiphytes in the canopy (Krömer et al., 2007; Martínez-Meléndez et al., 2008; Nieder et al., 2000; Wagner et al., 2013; Woods et al., 2015, 2019) and this is related to the functional characteristics of the species (Graham and Andrade, 2004; Guzmán-Jacob et al., 2022; Miranda et al., 2020; Petter et al., 2016; Rascher et al., 2012; Zotz, 2004).

Hygrophilous epiphytes dominate the lower zones of tree trunks, which include some fern families (for example, Hymenophyllaceae and Aspleniaceae) and Araceae (Zotz, 2007). Many species of this last family may have adventitious roots that connect the plant to the soil at some stage of life, making it impossible to classify them as true epiphytes (Bautista-Bello et al., 2021; Zotz, 2013; Zotz et al., 2021). The inner and middle crowns of the trees are the habitat where there is generally larger diversity, and the families Orchidaceae, Bromeliaceae, and Polypodiaceae are predominant (Woods et al., 2015). In this zone, there are plants with adaptations to drought, such as pseudobulbs, succulent leaves, or arrangement in rosettes forming tanks that accumulate water, and desiccation tolerance strategies (Hietz et al., 2022; Krömer et al., 2007). In the outer crown, diversity is lower and only heliophilous species, such as many polypodioid ferns (e.g. *Pleopeltis* and *Microgramma*), some orchids, and atmospheric bromeliads occur (Krömer et al., 2007). Small and linear leaves, smaller specific leaf area, and photosynthesis through Crassulaceae acid metabolism (CAM) are important morphophysiological adaptations for life in the high canopy (Crayn et al., 2015; Guzmán-Jacob et al., 2022; Zotz, 2004; Zotz and Hietz, 2001; Zotz and Ziegler, 1997). In addition, high crown species have very specialized trichomes with different functions, occurring mainly in bromeliads and ferns (Benzing, 2000; Benzing et al., 1976; Zotz, 2016). Learning about the specificity of epiphytes for tree height zones is important because it contributes to understanding how stratification is related to the functional characteristics of taxa and allows us to predict how microclimatic and land use changes can affect species distribution and cause changes in community patterns.

Although the number of studies on the vertical distribution of epiphytes in tropical forests in Brazil has grown in recent years, few approaches contemplate how each epiphyte family responds to the vertical gradient in different Atlantic Forest ecosystems (Bataghin et al., 2012; 2017; Bonnet and Queiroz, 2006; Fraga et al., 2008; Kersten et al., 2009; Pos and Slegers, 2010; Santana et al., 2017). Therefore, there is a lack of studies about the patterns and processes that govern the assembly of epiphyte communities, especially in southeastern Brazil, an exceptionally biodiverse area with respect to this group of plants (Furtado and Menini Neto, 2021; Leitman et al., 2015; Ramos et al., 2019). To contribute to knowledge in this area, the purpose of this research was to investigate how the vascular epiphyte community structure varies along the vertical gradient and whether the stratification pattern is similar among forests with distinct characteristics and among the main families. We tested two hypotheses. The first hypothesis is that microhabitats with higher humidity and more available substrates along the tree height zones, such as trunk and inner canopy, have larger diversity and characteristic composition, even in forests with different conditions, corroborating the ecological niche theory (Chase and Leibold, 2004; Hutchinson, 1957). The second hypothesis is that different families present different patterns of stratification and, therefore, environmental conditions and available nutritional resources along the vertical gradient of the forest operate together by selecting species, as proposed by Johansson (1974). Our null hypothesis was that there is a homogeneous distribution of all vascular epiphytes along the tree height zones. More specifically, we aimed to answer the following questions:

- (a) What is the structure of the vascular epiphyte community along the tree height zones, in terms of richness, abundance and composition?

- (b) How does the vertical stratification of epiphytes change in forests with different environmental conditions?
- (c) Which species are associated with each height zone?
- (d) How do the richness and abundance of the main taxonomic groups vary along the vertical gradient?

## 2. Material and methods

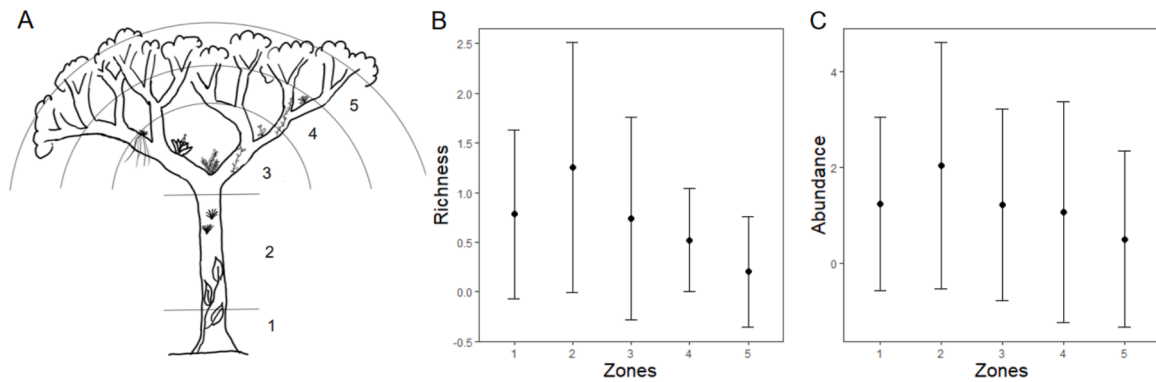
### 2.1. Study site

Ilha Grande is located in the municipality of Angra dos Reis, on the southern coast of the state of Rio de Janeiro, Brazil, and has an area of 65,258 hectares (23°09'26.77" S, 44°13'53.72" W) (Bastos and Callado, 2009) (Fig. S1). The island is home to two strict protection conservation units, Ilha Grande State Park and Praia do Sul State Biological Reserve, and is one of the largest preserved areas of Atlantic Forest in south-eastern Brazil (Alho et al., 2002). Ilha Grande is part of one of the coastal mountains of Serra do Mar, it has a mountainous relief oriented in the northeast-southwest direction and most of the territory is located below 500 m altitude (Bastos and Callado, 2009). The highest points are Pedra D'água, 1031 m, and Pico do Papagaio, 735 m. The climate is tropical, with an average annual temperature of 23.2°C and average relative humidity of 82%, without significant variations throughout the year (Bastos and Callado, 2009). Precipitation on the island is uneven due to the rugged terrain and can reach up to 4500 mm of rain in some regions (Oliveira and Neto, 2000). On average, annual rainfall is 1977 mm, with the summer months being the rainiest (above 240 mm monthly) and, despite not having a dry season, rainfall is lower in July (Bastos and Callado, 2009). The vegetation has ecosystems associated with the Atlantic Forest Domain, including rainforests in different successional stages, *restinga* and marshy forests, and mangroves (Bastos and Callado, 2009; Oliveira and Neto, 2000). Research indicates that the region has a high richness of vascular plants, especially epiphytes (Callado et al., 2009; Cruz et al., 2021; Cruz and Nunes-Freitas, 2019; Nunes-Freitas et al., 2009, 2006; Rocha et al., 2022).

Data were collected from RAPELD plots, whose acronym unites the two scales covered by the method: rapid inventories (RAP) and long-term ecological projects (PELD) (Magnusson et al., 2005). Five plots were used for sampling, all in secondary vegetation in a good state of conservation, two in *restinga* forest, one in dense lowland rainforest and two in dense submontane rainforest, following the classification of Veloso et al. (1991) and the Brazilian Institute of Geography and Statistics (IBGE, 2012) (see details about the plots in Fig. S1 and in Table S1).

### 2.2. Data collection

We established 78 subplots measuring 10 m by 10 m in the long, narrow plots of RAPELD (see plot structures in Magnusson et al., 2005). The subplots were 10 m apart. All trees with a diameter at breast height (DBH) larger than or equal to 15 cm were sampled in the subplots. All species of epiphytes were considered, including holoepiphytes and hemiepiphytes according to the classification by Benzing (1990). We opted for this simple form of categorization due to the difficulty of identifying the hemiepiphytes during fieldwork and even in the bibliography. Recent studies recommend that primary and secondary hemiepiphytes be classified as hemiepiphytes (*only*) and nomadic vines, respectively (Moffett, 2000; Sperotto et al., 2020; Zotz et al., 2021). However, the ontogeny of these species is very complex and some show large variations in the germination substrate (whether the life cycle starts on the forest soil or in the tree), therefore we cannot draw conclusions based on specific observations from the field work (Bautista-Bello et al., 2021). We used the classic method of tree division by Johansson (1974) to facilitate comparisons with other works: Z1 – trunk base to 1 meter high; Z2 – trunk (up to the first bifurcation); Z3 – inner crown; Z4 – medium crown; Z5 – outer crown (Fig. 1 - A). Protocols for



**Fig. 1.** Diversity of vascular epiphytes along height zones, according to Johansson (1974) (a), in trees in Ilha Grande, Brazilian Atlantic Forest. Mean and standard deviation of species richness (b) and abundance of individuals (c).

sampling epiphyte diversity recommend the use of single rope techniques and the census of large trees (Flores-Palacios and García-Franco, 2001; Gradstein et al., 2003). Because of the methodological difficulties in accessing the RAPELD plots and the objective of evaluating the effect of the forest structure on the epiphyte community, we chose to use the sampling of all trees with DBH larger than or equal to 45 cm in the subplots at from the ground and observation through superzoom camera. Since the forests had few emergent trees with dense canopy, the diversity was satisfactorily recorded as shown by the rarefaction curves, although this methodological bias needs to be considered. Seedlings, very young individuals, or that could not be accurately identified through visualization were not considered in the analyses. We identified the species based on specific literature, a study of herbarium material and by consulting specialists. The taxonomic classification and scientific names were checked against The International Plant Names Index.

### 2.3. Data analyses

The diversity was analyzed through species richness and abundance of individuals in order to provide additional information about the community, as recommended by Hoffmann et al. (2019). To answer questions (a) and (b), the plots were analyzed together and independently to verify if the pattern is maintained in different types of forests. To test hypothesis 1, data were compared across the five tree height zones for all epiphytes. To test hypothesis 2 and to answer the research question (d), families with the highest number of species were tested separately. The normality of the data and residuals and the homoscedasticity of the variances were verified using the Shapiro-Wilk test and Levene test, respectively, using the car package (Fox and Weisberg, 2019). Generalized linear (GLM) and Mixed GLM (GLMM) models with Poisson distribution were developed due to non-normality and homogeneity, even after data transformations with the AID, MASS and lme4 packages (Asar et al., 2017; Bates et al., 2015; Venables and Ripley, 2002). For the GLMM, the height zones were considered fixed effects and the different plots were included as a random effect, assuming the spatial dependence of the samples and assessing their individual differences (Bolker et al., 2009). An analysis of variance (ANOVA) was used to test significant differences between the models, which were then compared using the Akaike information criterion (AIC), and those with the best fit were selected with the bbmle package (Bolker and R Development Core Team, 2020). The Tukey HSD test was used to verify significant differences in richness and abundance between height zone pairs with a multcomp package (Hothorn et al., 2008).

Also to test hypothesis 1 and answer question (a), the variation in species composition was verified through a principal coordinate analysis (PCoA) and multivariate homogeneity analysis of group dispersions - variances, as well as through indices similarity with Bray-Curtis distance (1 - dissimilarity); all of these analyses were conducted with the Vegan

and BiodiversityR packages (Kindt and Coe, 2005; Oksanen et al., 2020). To answer question (c), indicator species were identified with the indicspecies package, which associated species with tree height zones based on occurrence and abundance (Cáceres and Legendre, 2009; Dufrene and Legendre, 1997). Component A corresponds to the species specificity at that location and component B is the fidelity or sensitivity of the species as an indicator of the target location (Cáceres and Legendre, 2009; Dufrene and Legendre, 1997). The statistical significance of the relationships was tested using the permutation test (Dufrene and Legendre, 1997).

Richness and abundance analyzes were previously performed with holoepiphytes and hemiepiphytes and then excluding hemiepiphytes. Since the results were very similar, we chose to present only data that considered all epiphytes together (Table S2).

All standardizations and analyzes were performed using the program R version 4.10 (R Core Team, 2020). The graphics were made with the packages ggplot2, RColorBrewer, and ggthemes (Arnold, 2021; Erich, 2014; Wickham, 2009). Each tree was considered a sampling unit and a confidence interval of 95% probability was used in all analyses.

## 3. Results

### 3.1. Vertical community patterns

We recorded 76 species of epiphytes in 271 trees (Table S3). Mean richness and abundance were larger in zone 2 and smallest in zone 5 with high data variation. There was a significant difference between the number of species and epiphyte individuals for all tree height zones, except between zones 1 and 3 for richness and 1, 3, and 4 for abundance that have intermediate mean values (Table S2 and Fig. 1). The mixed models had a better fit for both richness and abundance, assuming that there is variation in the vertical partition between the different plots (Tables S4, S5 and S6).

Regarding species composition, the eigenvalues of axes one and two of the PCoA ordination were 17.7% and 13.7%, respectively (Fig. 2). Zones 4 and 5 clustered on the right side of the ordering, while zones 1, 2, and 3 clustered on the left side. The Permutation Test for Homogeneity of Multivariate Dispersions indicated that there was a significant difference between zone 5 in relation to all others ( $F = 17.77$ ,  $p < 0.01$ ). We found the highest floristic similarities in adjacent height zones, Z3 and Z4, followed by Z2 and Z3, and Z1 and Z2, and the smallest similarities were observed in Z5 when compared to all others (Table 1).

All plots showed differences between richness and abundance by height zone when analyzed separately (Table S7). In all forest types, the highest richness and abundance were recorded in zone 2 and the lowest values were recorded in zone 5, except for plot 5 where there was no difference between the average richness in this zone compared to the others and the highest mean abundance was in zones 2 and 5 (Table 2).

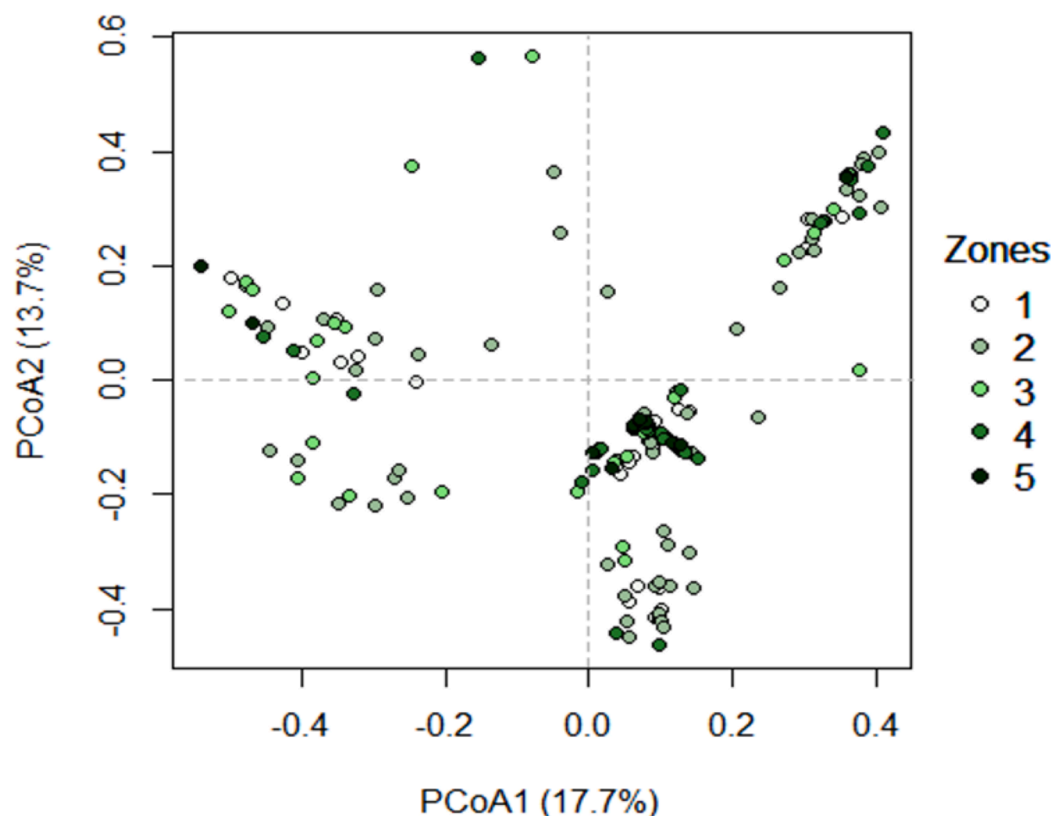


Fig. 2. Biplot of Principal Coordinate Analysis for the composition of vascular epiphytes along height zones, according to Johansson (1974), in trees in Ilha Grande, Brazilian Atlantic Forest.

Table 1

Similarity matrix based on the Bray-Curtis index for the abundance of vascular epiphytes along height zones, according to Johansson (1974), in trees in Ilha Grande, Brazilian Atlantic Forest.

	Zone 1	Zone 2	Zone 3	Zone 4
Zone 2	0.60			
Zone 3	0.41	0.64		
Zone 4	0.31	0.50	0.70	
Zone 5	0.18	0.26	0.35	0.48

### 3.2. Indicator species

The indicator species analysis showed one species associated with zone 1, one species for zone 4, three species for zone 5, two species related to the trunk (Z1 + Z2), and three species associated with the crown of trees (Z3, Z4, and Z5) (Table 3).

### 3.3. Taxon variation along the vertical gradient

The families with the highest number of species in the study area were Bromeliaceae (18), Polypodiaceae (15), Orchidaceae (13), Araceae (10), and Cactaceae (9), and there was a statistical difference in the standard stratification for each taxon (Table S3). Bromeliaceae and Orchidaceae do not differ in richness between height zones, but there was a difference in abundance, with zone 5 having the lowest averages for bromeliads and the highest averages for orchids. For Polypodiaceae, the highest diversity occurred in zones 2, 3, and 4. For Araceae, the highest means for richness occurred in zones 1 and 2, and the highest abundances occurred in zones 2 and 5. For Cactaceae, the highest diversity occurred in zones 3 and 4 (Table 4).

## 4. Discussion

### 4.1. Vertical community pattern

The results point out the heterogeneous distribution of vascular epiphyte diversity with specific taxa occurring in certain height zones of the trees, which indicates that niche theory, proposed by Hutchinson (1957), appears to apply to the assembly of these communities at a local scale, which corroborates the first hypothesis of our research. An ecological niche can be defined as a set of environmental conditions and resources that allow species to satisfy their minimum population growth requirements (Chase and Leibold, 2004). Competition between epiphytes is reduced because communities are rarely saturated, this fact allows many ecologically similar species to coexist in the same tree height zone, which increases diversity in environments (Catling and Lefkovich, 1989; Zotz, 2016).

The highest values of richness and abundance occurred in zone 2, which corresponds to the trunk of the tree (up to the first bifurcation). Our results were similar to those found by Adhikari et al. (2021) and by Acebey and Krömer (2001). The cited studies were developed in sub-tropical forests of Nepal with different types of management and higher altitudes and in the well-preserved submontane forest of Bolivia at intermediate altitude, respectively. The highest diversity in the trunk of the tree partially corroborates our hypothesis one, since we also expected high diversity in the inner canopy. Ambients with larger areas have more habitats available for colonization, as demonstrated by Richards et al. (2020) in a study on the process of colonization by epiphytes in forest fragments in Nicaragua. In addition to the larger area, the trunk may provide adequate conditions for the establishment of epiphytes, since in some large trees the trunks may have rougher bark that can accumulate organic matter (Adhikari et al., 2021; Freiberg, 1996). Additionally to larger area and time available for colonization, there is highest coverage of lichens and bryophytes on the trunk which



**Table 2**

Minimum, maximum, average and standard deviation richness and abundance of vascular epiphytes along tree height zones, according to Johansson (1974), in the Brazilian Atlantic Forest, for the RAPELD plots in Ilha Grande, RJ. Means followed by the same letter in the columns do not differ by Tukey's test ( $p < 0.05$ ).

Plots	Zones	Richness Minimum and maximum value	Average and standard deviation	Abundance Minimum and maximum value	Average and standard deviation
1	1	0–3	0.89 ± 0.82 a	0–11	1.70 ± 2.21 a
	2	0–7	1.45 ± 1.14 b	0–11	2.49 ± 2.67 b
	3	0–3	0.59 ± 0.75 a	0–6	0.93 ± 1.52 c
	4	0–2	0.30 ± 0.57 c	0–5	0.44 ± 0.98 d
	5	0–1	0.01 ± 0.12 d	0–4	0.06 ± 0.47 e
2	1	0–5	1.32 ± 1.00 a	0–11	2.25 ± 2.22 a
	2	0–5	1.91 ± 1.15 a	0–11	2.79 ± 2.00 a
	3	0–6	1.68 ± 1.27 a	0–14	2.40 ± 2.51 a
	4	0–4	1.32 ± 0.87 a	0–11	2.08 ± 1.81 a
	5	0–2	0.66 ± 0.62 b	0–5	0.96 ± 1.16 b
3	1	0–2	0.29 ± 0.51 ac	0–2	0.26 ± 0.50 a
	2	0–3	0.74 ± 0.50 b	0–9	1.55 ± 2.24 b
	3	0–4	0.62 ± 0.94 bc	0–7	1.17 ± 1.97 b
	4	0–2	0.36 ± 0.62 bc	0–15	1.29 ± 3.00 b
	5	0–1	0.02 ± 0.15 a	0–6	0.14 ± 0.93 a
4	1	0–3	0.68 ± 0.74 ab	0–6	0.95 ± 1.31 a
	2	0–6	1.09 ± 1.57 b	0–17	1.86 ± 3.4 b
	3	0–3	0.41 ± 0.82 a	0–9	1.00 ± 2.24 a
	4	0–4	0.30 ± 0.82 ac	0–12	0.59 ± 2.05 a
	5	0–1	0.02 ± 0.15 c	0–5	0.11 ± 0.75 c
5	1	0–2	0.56 ± 0.69 ab	0–4	0.65 ± 0.91 a
	2	0–6	0.85 ± 1.16 a	0–11	1.22 ± 2.07 b
	3	0–2	0.39 ± 0.38 b	0–16	0.69 ± 1.31 a
	4	0–3	0.31 ± 0.67 b	0–5	1.13 ± 3.15 ab
	5	0–5	0.30 ± 0.90 b	0–16	1.22 ± 3.57 b

increases the moisture and nutrients available to vascular epiphytes (Gehrig-Downie et al., 2011). Because of the location of the trunk in the forest understory, this provides a more humid and stable microclimate than the high canopy, as well as adequate luminosity for species that can occur there and in the inner canopy of the trees (Krömer et al., 2007).

Different methods of dividing the host tree have been used to analyze the vertical stratification of epiphytes, the most common are those by Johansson (1974); ter Steege and Cornelissen (1989), and for the Atlantic Forest, also Kersten and Silva (2002). In general, the tree is divided into trunk and crown zones. Unlike our results, where highest diversity and richness were found in the trunk, most studies show that the highest diversity of epiphytes occurs in zones located in the canopy of the trees, regardless of the tree partition method used. This is due to

**Table 3**

Significant results of multilevel pattern analysis for vascular epiphyte species indicative of clustering along the height zones, according to Johansson (1974), in trees in Ilha Grande, Brazilian Atlantic Forest, considering  $p$  values  $< 0.05$ . Component A corresponds to species specificity at that location and component B is species fidelity as an indicator.

Family	Species associated	Zones	A	B	p
Polypodiaceae	<i>Serpocaulon triseriale</i> (Sw.) A.R.Sm.	1	1.00	0.02	0.03
Orchidaceae	<i>Acianthera</i> sp.	4	1.00	0.03	<0.01
Bromeliaceae	<i>Tillandsia dura</i> Baker	5	0.63	0.09	<0.01
Piperaceae	<i>Peperomia rotundifolia</i> (L.) Kunth	5	0.59	0.09	<0.01
Orchidaceae	<i>Epidendrum filicaule</i> Lindl.	5	0.57	0.05	0.03
Bromeliaceae	<i>Billbergia amoena</i> (Lodd.) Lindl.	1 + 2	0.93	0.14	<0.01
Araceae	<i>Philodendron</i> sp.	1 + 2	1.00	0.06	<0.01
Araceae	<i>Philodendron cordatum</i>	3 + 4	0.81	0.33	<0.01
	Kunth ex Schott	+ 5			
Polypodiaceae	<i>Microgramma vacciniifolia</i> (Langsd. & Fisch.) Copel.	3 + 4	0.88	0.16	<0.01
		+ 5			
Bromeliaceae	<i>Neoregelia johannis</i> (Carrière) L.B.Sm.	3 + 4	0.92	0.05	0.03
		+ 5			

the combination of the crown architecture with the arrangement of the branches, providing places for the establishment and accumulation of humus, in addition to intermediate light (Bataghin et al., 2012; Kersten et al., 2009; Krömer et al., 2007; Nieder et al., 2000; Nieder et al., 2001; Pos and Slegers, 2010; Santana et al., 2017; Woods et al., 2015). The difference in our result, when compared to other surveys, seems to be related to the successional stages of the forests and the sampling method. The areas sampled by us represent secondary vegetation with a high density of trees and many young trees, which were also sampled. According to Richards et al. (2020), the trunk is where colonization by epiphytes begins and, therefore, only older trees will harbor many epiphytes in the crown. Our study did not only sample large trees, unlike what is suggested in the main protocols (Flores-Palacios and García-Franco, 2001; Gradstein et al., 2003). Most surveys follow these protocols and only sample larger and older trees, which may explain the higher values of diversity in the crown zones.

The species composition of the outer canopy is different from all other zones because this microhabitat has larger microclimatic variability, higher temperatures and insolation, and low air humidity compared to the lower zones (Anhuf and Rollenbeck, 2001; Fauset et al., 2017; Miranda et al., 2020; Murakami et al., 2022; Nunes-Freitas and Rocha, 2007; Stark et al., 2012). Furthermore, the smaller stable area and larger exposure to strong winds and rain explain the differentiated composition and low richness found by several authors in Z5 (Cabral et al., 2015; Nadkarni, 1984; Nieder et al., 2001; Woods et al., 2015; Zotz, 2007) and corroborated in this research. The composition of the upper canopy is subject to selection due to microclimatic variation and the restriction of moisture and nutrients, as well as substrate instability. The outer crown species have adaptations to resist drought and larger vapor pressure deficits, of which we highlight as functional traits the CAM metabolism, smaller average sizes, and smaller specific leaf area (Hietz et al., 2022; Petter et al., 2016; Zotz, 2004). Adjacent zones have larger floristic similarity because of similar environmental conditions, since the zonation scheme is an abstraction of the actual complexity of trees, and distinct but close zones can have homogeneous conditions (Zotz, 2007). The result was similar to that observed by Pos and Slegers (2010) in the Amazon rainforest, where trunk zones were more similar to each other than when compared to canopy zones.

The pattern of vertical stratification with larger diversity in the trunk and less diversity in the outer canopy was similar in all forest types in the study area, as predicted in hypothesis 1. This indicates that the variation of conditions and resources in the vertical gradient is similar in all environments analyzed. Specifically, on the microclimate, studies in the Atlantic Forest show that light slowly decreases from the upper to lower

**Table 4**

Minimum, maximum, average, and standard deviation richness and abundance of the main vascular epiphyte families along tree height zones, according to Johansson (1974), in trees in the Brazilian Atlantic Forest, for the RAPELD plots in Ilha Grande, RJ. Means followed by the same letter in the columns do not differ by Tukey's test ( $p < 0.05$ ).

Family of epiphytes	Zones	Richness Minimum and maximum value	Average and standard deviation	Abundance Minimum and maximum value	Average and standard deviation
Bromeliaceae	Z1	0–2	0.40 ± 0.52 a	0–7	0.94 ± 1.64 a
	Z2	0–3	0.48 ± 0.64 a	0–12	1.12 ± 2.08 a
	Z3	0–1	0.37 ± 0.48 a	0–8	0.76 ± 1.42 a
	Z4	0–2	0.41 ± 0.53 a	0–15	0.95 ± 2.19 a
	Z5	0–1	0.16 ± 0.37 a	0–2	0.18 ± 0.45 b
Polypodiaceae	Z1	0–3	0.25 ± 0.53 a	0–3	0.26 ± 0.54 a
	Z2	0–3	0.55 ± 0.65 b	0–6	0.74 ± 1.11 b
	Z3	0–3	0.57 ± 0.60 b	0–7	0.91 ± 1.34 bc
	Z4	0–3	0.50 ± 57 b	0–15	1.08 ± 2.12 c
	Z5	0–2	0.27 ± 0.54 ab	0–8	0.57 ± 1.56 c
Orchidaceae	Z1	0–1	0.02 ± 0.14 a	0–1	0.02 ± 0.14 a
	Z2	0–2	0.06 ± 0.26 a	0–6	0.14 ± 0.69 b
	Z3	0–1	0.04 ± 0.19 a	0–3	0.06 ± 0.35 ab
	Z4	0–1	0.06 ± 0.23 a	0–2	0.08 ± 0.33 ab
	Z5	0–1	0.09 ± 0.29 a	0–15	0.47 ± 2.32 c
Araceae	Z1	0–3	0.72 ± 0.73 ab	0–5	0.84 ± 0.97 ab
	Z2	0–3	0.73 ± 0.79 a	0–6	0.92 ± 1.11 a
	Z3	0–3	0.55 ± 0.69 b	0–4	0.82 ± 1.12 abc
	Z4	0–2	0.41 ± 0.55 bc	0–4	0.64 ± 1.00 c
	Z5	0–2	0.64 ± 0.53 c	0–4	1.09 ± 1.14 bc
Cactaceae	Z1	0–1	0.01 ± 0.11 a	0–1	0.01 ± 0.11 a
	Z2	0–1	0.04 ± 0.2 ab	0–3	0.06 ± 0.35 a
	Z3	0–2	0.11 ± 0.34 b	0–5	0.17 ± 0.61 b
	Z4	0–1	0.09 ± 0.29 ab	0–5	0.20 ± 0.75 b
	Z5	0–1	0.02 ± 0.15 ab	0–1	0.02 ± 0.15 ab

canopy zones, regardless of the successional stage (Fauset et al., 2017; Miranda et al., 2020; Nunes-Freitas and Rocha, 2007). In addition, there is a positive relation between the highest canopy zones and temperature, as well as a negative relation with relative humidity (Murakami et al., 2022). However, trees in larger stands may suffer buffering from neighboring trees and show less microclimatic variation (Murakami et al., 2022). This explains the high abundance and similar richness to other height zones in the outer canopy of the submontane forest in an advanced stage of regeneration, which may also be related to the high humidity of the forest and the larger variation in the height and composition of the trees. Due to this, the crowns of the understory trees are shaded and colonized by epiphytes with diverse functional traits and

not just those tolerant to high canopy microclimatic stress, as observed in other tropical forests (Krömer et al., 2007).

#### 4.2. Indicator species

Although there were differences in diversity and composition between height zones, few species showed high specificity and were associated with height zones of specific trees. We expected to find a larger number of indicator species due to ecological niche differentiation, however, previous studies show that really few taxa are restricted to specific height zones (Zotz, 2007). Additionally, IndVal did not indicate any indicator species for Z2 and Z3, which suggests that the compositions of these zones are subsets of the others. This is possible because these zones have intermediate environmental conditions, allowing a larger number of species, usually generalists, to occupy these strata. These generalist habitat species are more ecologically flexible and can establish themselves in various tree height zones (Krömer et al., 2007). The results differed from those found by Pos and Slegers (2010) in their study in the Amazon rainforest, in which most of the specialist species occurred at the base of the trunk, inner and middle crown.

In general, indicator species have morphological, anatomical, and behavioral adaptations that explain their classification habitats. For Z1, the indicator species was *Serpocaulon triseriale* (Sw.) A.R.Sm., which is a facultative epiphyte that can also occur in soil or on rocks. Possibly, its occurrence in this zone is because the base of the trunk is rougher and there is more humus and moisture, ensuring the necessary conditions for its establishment. However, this same species occurred exclusively as an epiphyte in lowland ombrophilous forest in Mexico in the study of Acebey et al. (2017), this difference is probably due to differences in humidity between the study areas. As for Z5, three species were classified as indicators, all with adaptations for larger microclimatic variability and lower humidity. *Epidendrum filicaule* Lindl. is a heliophilous orchid with a caespitose, graminoid, pendently curved habit, and extremely branched stems (Forster and Souza, 2013). *Tillandsia dura* Baker has linear, erect, and highly scaled leaves and has been recorded in the upper canopy in another work (Lima and Wanderley, 2007). *Peperomia rotundifolia* (L.) Kunth has prostrate growth with succulent leaves and, as opposed to our results, was recorded as dominant at the base of the trunk in a shaded environment by Bataghin et al. (2017). This may have occurred because of the shading in the high canopy of many trees, especially in the submontane forest in an advanced stage of regeneration, where the species was more abundant.

The IndVal pointed out two species as trunk epiphytes (Z1 + Z2) and three as canopy epiphytes (Z3 + Z4 + Z5), all with high specificity. *Billbergia amoena* (Lodd.) Lindl. is a facultative epiphyte that can occur as an epiphytic, terrestrial, or rupicolous plant in the understory of the study area, while *Philodendron* sp. was recorded linked to the forest floor, this indicates that it is a hemiepiphyte and may or may not break its connections with the soil and establish itself on the tree only. The canopy epiphytes noted here are heliophilic plants with adaptations to the water stress provided by life in the canopy, except *Philodendron cordatum* Kunth ex Schott. This species are a fast-growing hemiepiphyte most frequently found in restinga forests almost exclusively attached to the soil. On the other hand *Microgramma vacciniifolia* (Langsd. and Fisch.) Copel. presents a highly branched rhizome and with many adpressed scales (Almeida, 2020), and *Neoregelia johannis* (Carrière) L.B.Sm. is a bromeliad with a tank that can accumulate water and nutrients (Benzing, 1990).

#### 4.3. Taxon variation along the vertical gradient

The results corroborate hypothesis two of this research, since different families with epiphytic species showed different patterns along the vertical gradient, as we expected. Taxa have different strategies to avoid or tolerate water stress and this explains the non-random distribution in the forest canopy (Woods et al., 2015). Our results also endorse

those of Johansson (1974) and Benzing (1998), since they indicated that the diversity of epiphytes is related to the specific abiotic conditions of each microenvironment.

There was a high richness and abundance of Araceae in Z1 and Z2 due to the hemiepiphytic habit predominant in *Philodendron* and *Monstera*. A similar pattern was observed by Pos and Slegers (2010), Krömer et al. (2007) and Nieder et al. (2000), the latter two associated this fact with the direct contact with the soil that occurs in these genera. Secondary hemiepiphytes, currently classified as nomadic vines, are climbing plants that germinate in or near the ground and may lose the proximal portion of the stem during ontogeny (Moffett, 2000). For this reason, the classification and inclusion of hemiepiphytes in studies such as this one causes a lot of uncertainty, since the adventitious roots can keep them connected to the soil and they are never really epiphytes throughout their life cycle (Bautista-Bello et al., 2021; Zotz, 2013). Some researchers recommend that classification into secondary hemiepiphytes should be avoided because it confuses plants with different life cycle strategies, as these plants can supplement their water needs by the supply of adventitious roots that are connected to the soil and not exclusively dependent on the canopy (Moffett, 2000; Zotz, 2013; Zotz et al., 2021). We chose to maintain the classic classification (Benzing, 1990) since we performed the analysis with and without hemiepiphytes and there was no change in the general pattern of the community. The high abundance of Araceae in Z5 may be related to *Philodendron cordatum* Kunth ex Schott and *Monstera adansonii* Schott, since they are heliophilic species that reach high densities in the crowns of some trees in the study area, however, it is essential to consider that these species occurred mainly linked to the forest soil.

Ferns and bromeliads were dominant on the trunk and in the inner and middle crown, while orchids were more diverse in the outer crown, corroborating the results of other authors (Bonnet and Queiroz, 2006; Krömer et al., 2007; Pos and Slegers, 2010; Santana et al., 2017; Woods et al., 2015). The epiphytes that occur in the high canopy have adaptations that allow them to survive in this environment with functional traits that enable them to be more efficient in water use. We can point for example reduced specific leaf area and CAM photosynthesis (Guzmán-Jacob et al., 2022), pseudobulbs and succulent structures for water storage (as in orchids), and poikilohydria, in the case of many ferns (Hietz et al., 2022; Krömer et al., 2007). Regarding bromeliads, Miranda et al. (2020) and Bonnet and Queiroz (2006) reported that *Tillandsia* species tend to be more diverse at intermediate height zones and Nunes-Freitas and Rocha (2007) found a similar pattern for the abundance of *Canistropsis microps* (E. Morren ex Mez) Leme. For Bonnet and Queiroz (2006) there was a difference in the distribution of types of bromeliads, since atmospheric species preferentially occur in the highest canopies with larger luminosity and tank bromeliads occur in more humid and shady environments. This is supported by our research, because *Tillandsia* species were more abundant in the canopy zones, while *Canistropsis*, *Billbergia* and *Aechmea* occurred preferentially in the trunk. This information reinforces that bromeliads are heterogeneously distributed along the vertical gradient. The pattern is related to the functional characteristics of bromeliads. In the higher canopy zones, for example, there is an increase in the proportion of species with CAM metabolism because of the more intense luminosity that performs the selection of these species (Zotz and Hietz, 2001). According to Crayn et al. (2015), in the subfamily Tillandsioideae, in which all clades are epiphytes, the high dominance of CAM metabolism is related to extreme xeromorphy, since *Tillandsia* species are overwhelmingly atmospheric. In the lower zones, tank formers species occur, as they depend on the accumulation of water and humus to supply nutrients, although there are also many CAM species (Benzing et al., 1976).

Woods et al. (2015) observed that inner canopies have high humidity, humus availability, and intermediate luminosity due to self-shading, which prevents species from experiencing extremely dry conditions in the canopy. This explains the high diversity of bromeliads and ferns in these environments and not just of heliophilous species.

According to Hallé et al. (1978), tree transpiration creates a microclimate at the highest parts of the trunk and in the inner crown, and some groups of epiphytes are adapted to these regions. Cactaceae, for example despite having many xeromorphic characteristics (such as succulence and CAM photosynthesis), occurred predominantly in the inner and middle canopy. According to Benzing (1990), epiphytic cacti do not colonize areas with thin branches and direct exposure to the sun, but rather microhabitats with a higher concentration of humus. The study of Andrade and Nobel (1997) partially corroborates this because they recorded a larger abundance of epiphytic cactus in deciduous trees, with larger exposure to radiation than in evergreen trees in lowland forests in Panama. However, the species were distributed mainly in the trunk crevices, the crotches, and primary branches, which, for the authors, reinforces the importance of water interception and the accumulation of organic matter in these environments, endorsed by the fact that the species have long roots growing towards the canopy humus (Andrade and Nobel, 1997).

## 5. Conclusions

Although the relevance of variation in light and moisture levels is widely known in ecology, few studies have a more refined approach to how epiphytic taxa respond to this vertical gradient. Here we present one of the first works for the Atlantic Forest of southeastern Brazil that addresses the community as a whole, but also evaluates taxa separately, performing pattern comparison and testing hypotheses. Our conclusions can be summarized as follows: 1) the forests analyzed have highest diversity in the trunk and in the intermediate zones and the lowest values in the outer crown, where there was also a unique composition; 2) the stratification pattern is quite similar in different types of forests; 3) some species are associated with certain microhabitats, suggesting that there is high specificity for these epiphytes; and 4) the main epiphytic families exhibit different patterns of diversity along the vertical gradient, which seems is related to their adaptive strategies to deal with canopy conditions.

Although the present research does not perform microclimate measurements, our descriptive results and the two tested hypotheses contribute to understanding the microhabitat requirements of vascular epiphytes and the organization of plant communities as a whole, as well as reinforcing the need to evaluate families separately in ecological studies. Furthermore, it provides evidence of the importance of microclimatic variability for the high diversity of tropical forests. Finally, we also show that secondary forests have different patterns from what is commonly found in primary vegetation and that the analysis of trees of different sizes, and not just large ones, is important to understand the effect of forest structure on the vertical distribution of the community. Future studies should perform empirical tests involving microclimate variables of the vertical gradient relating them to patterns of epiphyte diversity in forests of different successional stages within the Atlantic Forest and other morphoclimatic domains.

## Credit author statement

Ana Carolina Rodrigues da Cruz, André Felipe Nunes-Freitas, and Lana da Silva Sylvestre conceived the conceptualization, project administration, and developed the writing (review and editing).

Ana Carolina Rodrigues da Cruz, Nadjara de Medeiros Corrêa, Mariana Moreira da Silva Murakami, and Thiago de Azevedo Amorim curated the data and investigation.

Ana Carolina Rodrigues da Cruz and Thiago de Azevedo Amorim performed the formal analysis and software.

André Felipe Nunes-Freitas and Lana da Silva Sylvestre designed the methodology, obtained the resources, and carried out the supervision and validation.

Ana Carolina Rodrigues da Cruz performed the visualization and Writing (original draft).



All authors permitted this work to be published.

## Data availability statement

The data that support the findings of this study are openly available in GitHub at: <https://github.com/AnaCruzUFRJ/Ilha-Grande-epiphyte-stratification-dataset-and-scripts.git>.

## 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.

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## Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:[10.1016/j.flora.2022.152137](https://doi.org/10.1016/j.flora.2022.152137).

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