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Edge effect on vascular epiphytes in a subtropical Atlantic Forest fragment

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ABSTRACT

The Atlantic Forest is a hotspot for epiphyte richness; however, it is experiencing one of the highest rates of degradation, exposing epiphytes to edge effects. This study aimed to evaluate the floristic composition and richness of vascular epiphytes and their relationship with phorophyte features and microenvironmental variables at the edge and in the interior of a subtropical Atlantic Forest fragment in Brazil. Twenty-five trees were analyzed, respectively, at the edge and in the interior of the fragment, totaling fifty individuals. The height and diameter of phorophytes, temperature, relative air humidity, photosynthetically active radiation, and canopy opening were measured. A total of 41 epiphytic species were recorded, 40 occurring in the interior and 23 at the edge. Orchidaceae, Bromeliaceae, and Polypodiaceae were the richest families, representing 75% of all species. The average number of species per tree in the interior was twice that for the edge. *Pleopeltis pleopeltifolia*, *Microgramma squamulosa*, *M. vacciniifolia*, and *Rhipsalis teres* concentrated great biomass in both environments, with twice as much in the interior. Epiphyte richness and biomass were lower on thinner trees with more open canopies at the edge. Our results indicate that the forest interior is more beneficial for epiphytes, which are sensitive to the edge effect. The contrast between the epiphytic communities of the edge and the interior reveals the need to increase the richness and abundance of native trees and prevent cattle grazing, the planting of exotic species, and more human settlements in the habitat matrix.

Keywords: Biodiversity, epiphytic community, fragmentation, matrix quality, subtropical forest.

Introduction

Fragmentation occurs when continuous forests are divided into isolated patches surrounded by different matrices (Metzger, 2001), which often fails to provide adequate habitats for native species (Liu & Slik, 2014). Accelerated human population growth and agricultural expansion are considered the most common causes of edge formation of anthropogenic origin, which increases pressure on remaining fragments (Saito et al., 2016). The composition of the adjacent matrix is a decisive factor in the dynamics of forest fragments (Kupfer, Malanson & Franklin, 2006; Aragón et al., 2015; Ceballos, 2020). However, even when surrounded by monocultures, remaining forests must be effectively preserved, since they provide important services to society, especially when located in densely populated areas (Soares-Filho et al., 2014).

Increased edge effects alter the functioning of forest ecosystems by changing the distribution of local species (Haddad et al., 2015; Silva, Mehltreter & Schmitt, 2018), reducing diversity (Razafindratsima et al., 2017), and increasing the richness of pioneer species by replacing the vegetation present before the disturbance (Laurance et al., 2000). These factors expose communities to an increased risk of homogenization (Tabarelli, Lopes & Peres, 2008). In addition, there has been little research into the long-term effects of the formation of artificial edges such as possible modifications to the phylogenetic or functional components of biodiversity and their connections with the ecosystem (Magnago et al., 2017).

Peripheral microclimatic conditions differ from those in the interior of remaining forests, mainly due to decreased humidity and increased luminosity, temperature, and wind incidence (Murcia, 1995; Silva, Mehltreter & Schmitt, 2018). The use of surrounding land affects the intensity of microclimatic stresses at forest edges, with a direct connection between the type of use and the response of forest remnants to edge effects (Laurance et al., 2007; Müller et al., 2020). Understanding these responses is fundamental to the implementation of effective forest management actions according to distinct situations and edge effect patterns (Hardt et al., 2013).

Epiphytes are considered excellent indicators of environmental quality because they require favorable abiotic conditions for their occurrence on phorophytes and, thus, are susceptible to changes in both anthropogenic and natural variables (Becker et al., 2017). These plants are sensitive to microclimatic conditions since they are located at the interface between vegetation and the atmosphere (Zotz & Bader, 2009). On the other hand, this condition causes epiphytic biomass to influence the canopy microclimate (Freiberg & Freiberg, 2000), and affect the phenomorphology of epiphytes (Freiberg, 1996). The organic matter accumulated by epiphytes is also efficient at collecting and retaining rainwater, which plays an important role in the water cycle of the ecosystem (Pócs, 1980; Freiberg & Freiberg, 2000). In addition, epiphytes serve as a food source and provide habitat resources for many species of invertebrates, birds, and mammals (Gotsch, Nadkarni & Amici, 2016). Modifications or loss of this component in the plant community can generate changes to water and nutrient cycles, as well as to the general ecology of the forest ecosystem (Gotsch, Dawson & Draguljić, 2018).

Despite the importance of vascular epiphytes for biodiversity, ecological studies about the group are scarce compared with other vegetal life forms. Studies involving orchid reintroduction and herbivory (Endres Júnior et al., 2018), and bromeliad dispersal limitation (Cascante-Marín et al., 2009), have shown that the analysis of biotic and abiotic variables is fundamental to understanding the edge effect and knowing how species respond to habitat fragmentation (Ries et al., 2017).

The Atlantic Forest is one of the regions in the world with the highest number of epiphytic plants (Freitas et al., 2016), harboring about 3,000 species (Kersten, 2010). The remaining vegetation cover of the Atlantic Forest in Brazil is between 11 and 16% (Ribeiro et al., 2009). There is increasing evidence of biotic homogenization, disfigurement, and secondarization of the Atlantic Forest at multiple spatial scales as consequences of habitat loss and fragmentation (Joly et al., 2014), and reintroduction programs will be necessary for these new forest habitats (Rezende et al., 2018).

Given this scenario of habitat fragmentation, there remains a knowledge gap regarding the alteration of the spatial distribution of epiphytes at the forest edge, compared to the interior, and its relationship with biotic and abiotic variables, as a cascade effect of landscape modification. Through the analysis of the edge effect and the epiphytic community in a subtropical Atlantic Forest remnant inserted in an urban environment, this study aimed to answer the following questions: (1) Is there a reduction in richness and simplification of the epiphytic community at the edge of the forest fragment, when compared to its interior? (2) Is epiphytic richness related to the height and diameter of phorophytes, air humidity, temperature, photosynthetically active radiation, and canopy opening of the two environments? (3) Does the edge effect influence the distribution of vascular epiphytes resulting in the prevalence of more generalist species at the forest edge?

This study contributes to evidence responses of the plant community to microclimatic variation caused by the edge effect in the Atlantic Forest, which is third on the global list of priority areas for the conservation of vascular plants (Myers et al., 2000). Our assumptions were: (a) there is a reduction in the richness and simplification of the epiphytic community at the edge of the forest fragment when compared to its interior; (b) epiphytic richness is related to phorophyte height and diameter, air humidity, temperature, photosynthetically active radiation and canopy opening in both environments; (c) the edge effect influences the distribution of vascular epiphytes, resulting in the prevalence of more generalist species at the edge of the forest. Understanding the consequences that creating forest edges has on the diversity and functioning of forest ecosystems is indispensable for the management and conservation of resources.

Material and Methods

Study area

The study was conducted in a 60-hectare Atlantic Forest fragment in the urban area of the municipality of Campo Bom (29°40'23.37"S and 51°01'56.65"W, 45 m asl), in the state of Rio Grande do Sul (RS), southern Brazil, over two years (2016-2017). The area is inserted in the

Semideciduous Lowland Forest, a formation of the Atlantic Forest (IBGE, 1992), in the lower part of the Sinos River basin (Figure 1). There is anthropogenic interference at the northern boundary of the fragment, where households have existed for at least ten years. The matrix to the east and south is characterized by cattle grazing, fields, and plantations of exotic species (*Acacia decurrens* Willd., *Eucalyptus* sp., *Pinus elliottii* L.) for obtaining wood, while adjacent to the west border there is a solid waste processing center.

Based on the Köppen climate classification (Peel, Finlayson & McMahon, 2007), the climate of the region is Cfa - subtropical humid type without a dry period. According to data obtained from a Mobile Climatological Station installed in the area bordering the study, during 2016 the average annual temperature in Campo Bom, from January to December was 20.12ºC, with the highest average temperature monthly being recorded in February (26.4°C) and the lowest in June (11.4°C). The accumulated rainfall in 12 months was 1,426.2 mm, with the monthly minimum recorded in June (6.2 mm).

Tree selection

For the selection of trees on the edge (up to 10 m from the border), the perimeter of the fragment (approximately 3,000 m) was considered, where a tree was systematically marked every 100 m, totaling 25 trees (Figure 1).

Each tree at the edge was partnered with a tree 100 m away in the interior of the fragment, totaling a sampling of 50 trees (Figure 1). The inclusion criterion was diameter breast height (DBH) equal to or greater than 10 cm. Trees without epiphytes were also considered. All trees were identified and measured for height.

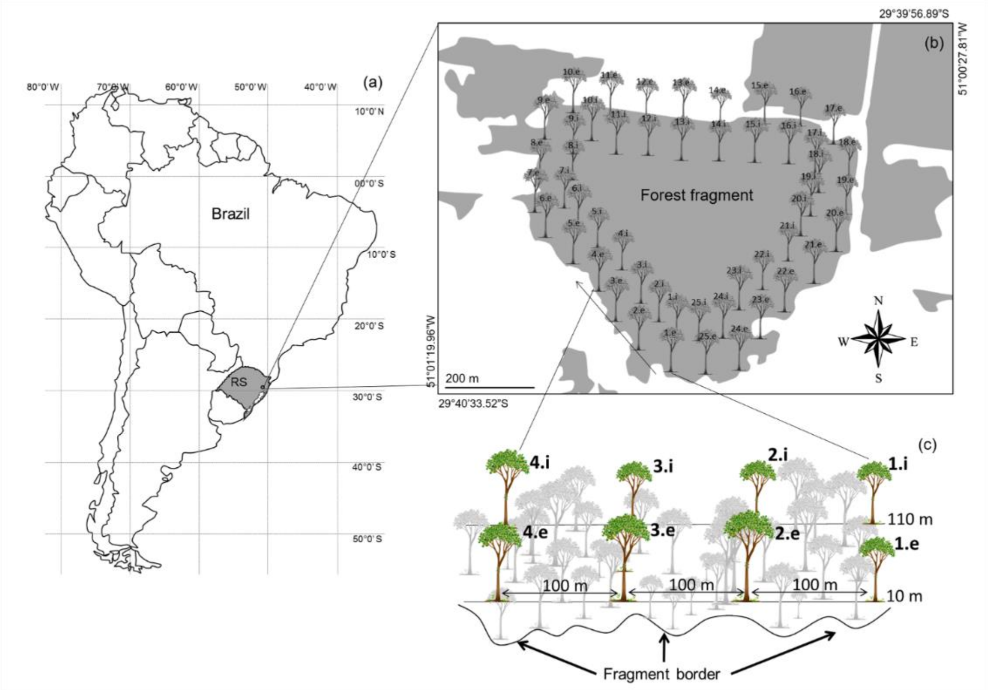

Figure 1. (a) South America, Brazil, and Rio Grande do Sul State (RS); (b) study area in the municipality of Campo Bom with schematic representation showing the systematic methodology of tree selection; and (c) schematic representation showing the tree sampling at the edge and in the interior of the fragment. Font: Lippert et al. (2022).

Floristic inventory

Epiphytic species were surveyed during monthly expeditions throughout the course of a year (2016) and considered the presence/absence of all vascular epiphytes of the selected trees at the edge and in the interior. Epiphytes were identified by recording and collecting via the tree-climbing method of Perry (1978) and remote observation with binoculars. Epiphytes were classified into four different ecological categories according to their relationship with phorophytes. True holoepiphytes are organisms that normally originate and then grow on other plants without coming into contact with the ground; facultative holoepiphytes are those that can grow as either epiphyte or terrestrially in the same community, and accidental holoepiphytes are those that are occasionally found as epiphytic; hemiepiphytes, on the other hand, are those that establish contact with the soil during some stage of their life cycle (Benzing, 1990).

Taxonomic identifications were concluded by consulting bibliographical references, making comparisons with herborized material, and analysis by specialists. Scientific names were verified according to Flora do Brasil (2022). Angiosperms and ferns were classified into families according to the APG IV system (APG IV, 2016) and the PPG I system (PPG I, 2016), respectively. The collected material was herborized and placed in the Herbarium Anchieta (PACA) of the Instituto Anchietano de Pesquisas (a research institute of the University of Vale do Rio dos Sinos), located in São Leopoldo (RS, Brazil).

Epiphyte richness and biomass

Each tree had its height categorized into four zones, adapted from the methodology proposed by Ceballos (2020), in which the occurrence of epiphytes was recorded: Zone 1 - basal part of the stem up to 2 m; Zone 2 - stem from 2 m up to the first ramification; Zone 3 - inner canopy (the main point of ramification and basal part of large branches); and Zone 4 - outer canopy (the upper part of large branches). Five scores were used to estimate the biomass of each tree species (1, 3, 5, 7, and 10), as proposed by Kersten & Waechter (2011), such that the larger individual size and/or the greater the number of individuals, the higher the score. The sum of scores determined the biomass estimate of the respective species in the community.

Microenvironmental variables

Data of temperature and relative air humidity were obtained in winter (July) and summer (January) at five points, respectively, and simultaneously, at the edge and in the interior every two hours for 10 consecutive hours (8 a.m. to 6 p.m.). A portable digital thermo-hygro-anemometer luximeter (Instruterm - Thal-300, model 0211) coupled to a 0.75-m tall tripod (VF WT-3111) supported on the ground was used to measure temperature (in °C) and relative air humidity (in %). Similarly, photosynthetically active radiation was measured for a period of one minute using an LI-COR Line Quantum Sensor (LI-190) light sensor set on a stand 1 m above the ground (Bernardi & Budke, 2010) and coupled to an LI-COR DataLogger (LI-1400).

Differences in the degree of canopy opening between the edge and the interior were analyzed using hemispherical photos taken at five equidistant points distributed around each tree. Photos were taken with a Sony H5 camera coupled to a Raynox digital fisheye lens (model DCR-CF 85 Pro). The camera was leveled at 0.75 m above the soil and positioned facing north as described by Garcia et al. (2007). The images were analyzed in ImageJ 1.48 software (Schneider, Rasband & Eliceiri, 2012).

Statistical analysis

The quality of species richness sampling at the edge and in the interior was analyzed by constructing rarefaction curves from the presence/absence data of the species found in both environments using EstimateS 8.2 software with 95% probability confidence intervals (Colwell, 2005). This software was also used to estimate richness using the nonparametric estimator Jackknife 1.

Non-metric multidimensional scaling analysis (NMDS) was performed with data from the species biomass for each tree, which allows the best spatial representation of the samples according to their similarities, associating them with a reliability value (perturbation value or "stress"). These data were used with a Bray-Curtis similarity matrix. A similarity analysis (ANOSIM), using presence/absence data with 999 permutations was performed to determine if there were significant differences among the floristic compositions of the groups of epiphytes ordered by NMDS.

A similarity percentage analysis (SIMPER) was used to identify the species that contributed the most to the similarity of phorophytes at the edge and in the interior of the studied area, as well as to dissimilarity among them in the different groups ordered by the NMDS. The NMDS, ANOSIM, and SIMPER analyses were carried out in PRIMER-E software (Clarke & Gorley, 2002), version 5.2.9.

Means of total richness, stem (Z1 + Z2) richness, canopy (Z3 + Z4) richness, total biomass, stem biomass (Z1 + Z2), canopy biomass (Z1 + Z2), tree height, tree diameter, degree of canopy opening, photosynthetically active radiation, relative air humidity and temperature at the edge and in the interior were tested for normality using the Shapiro-Wilk test. As none of the data met the assumption of normality, means for edge and interior were compared by the Mann-Whitney test. Spearman’s correlation test was carried out with both epiphyte richness and biomass as references, to assess the correlations of these two epiphyte variables with the remaining monitored variables. The analyses were carried out at the 5% probability level using IBM SPSS Statistics 25.

A principal component analysis (PCA) was performed to evaluate the relationship between the biotic variables of the epiphytes, the parameters of the phorophytes, and the microclimatic variables at the edge and in the interior of the forest, and to find groups of variables with similar behaviors. Sample adequacy was verified using the Kaiser-Meyer-Olkin test (KMO) and Bartlett’s test of sphericity. Extraction was based on eigenvalues greater than 1. Varimax rotation was applied to simplify the interpretation of the principal components. Only variables with communalities greater than 0.5 were used (Singh et al., 2005). All the analyses were carried out at the 5% probability level using IBM SPSS Statistics 25.

Results

Richness and composition of epiphytes

A total of 41 species of vascular epiphytes were identified, belonging to 28 genera and 10 families. The forest interior had greater tree species richness (40) than the edge (23) (Table 1).

Table 1. Families and species of vascular epiphytes recorded at the edge and in the interior of a subtropical Atlantic Forest fragment (Brazil). Ecological categories: true holoepiphytes, TRU; facultative holoepiphytes, FAC; hemiepiphytes, HEM; accidental holoepiphytes, ACI. Font: Lippert et al. (2022).

Family/Species	Ecological category	Edge	Interior
ASPLENIACEAE			
Asplenium gastonis Fée	TRU	-	X
BLECHNACEAE			
Lomaridium acutum (Desv.) Gasper & V.A.O. Dittrich	HEM	-	X
BROMELIACEAE			
Aechmea recurvata (Klotzsch) L.B.Sm.	TRU	-	X
Tillandsia aeranthos (Loisel.) L.B.Sm.	TRU	X	X
Tillandsia geminiflora Brongn.	TRU	X	X
Tillandsia recurvata (L.) L.	TRU	X	X
Tillandsia gardneri Lindl.	TRU	X	X
Tillandsia stricta Sol.	TRU	X	X
Vriesea gigantea Gaudich.	TRU	X	X
Vriesea rodigasiana E.Morren	TRU	X	-
Vriesea psittacina (Hook.) Lindl.	TRU	X	X
CACTACEAE			
Lepismium cruciforme (Vell.) Miq.	TRU	X	X
Rhipsalis teres (Vell.) Steud.	TRU	X	X
DRYOPTERIDACEAE			
Polybotrya cylindrica Kaulf.	HEM	-	X
Rumohra adiantiformis (G. Forst.) Ching	FAC	-	X
ORCHIDACEAE			
Acianthera glumacea (Lindl.) Pridgeon & M.W.Chase	TRU	X	X
Acianthera luteola (Lindl.) Pridgeon & M.W.Chase	TRU	-	X
Acianthera saundersiana (Rchb.f.) Pridgeon & M.W.Chase	TRU	-	X
Campylocentrum aromaticum Barb.Rodr.	TRU	X	X
Epidendrum strobiliferum Rchb.f.	TRU	X	X
Gomesa cornigera (Lindl.) M.W.Chase & N.H.Williams	TRU	-	X
Gomesa flexuosa (Lodd.) M.W.Chase & N.H.Williams	TRU	-	X
Gomesa uniflora (Booth ex Lindl.) M.W.Chase & N.H.Williams	TRU	-	X
Isochilus linearis (Jacq.) R.Br.	TRU	-	X
Octomeria crassifolia Lindl.	TRU	-	X
Platyrhiza quadricolor Barb.Rodr.	TRU	X	X
Polystachya concreta (Jacq.) Garay & Sweet	TRU	X	X
Prosthechea vespa (Vell.) W.E.Higgins	TRU	X	X
Stelis sp.	TRU	-	X
Trichocentrum pumilum (Lindl.) M.W.Chase & N.H.Williams	TRU	-	X
PIPERACEAE			
Peperomia delicatula Henschen	TRU	X	X
Peperomia trineura Miq.	FAC	-	X
PTERIDACEAE			
Vittaria lineata (L.) Sm.	TRU	-	X
POLYPODIACEAE			
Campyloneurum nitidum (Kaulf.) C. Presl	TRU	X	X
Microgramma squamulosa (Kaulf.) de la Sota	TRU	X	X
Microgramma vacciniifolia (Langsd. & Fisch.) Copel.	TRU	X	X
Pecluma sicca (Lindm.) M.G. Price	TRU	X	X
Pleopeltis hirsutissima (Raddi) de la Sota	TRU	X	X
Pleopeltis pleopeltifolia (Raddi) Alston	TRU	X	X
Serpocaulon catharinae (Langsd. & Fisch.) A.R. Sm.	FAC	-	X
THELYPTERIDACEAE			

Thelypteris sp.	ACI	-	X
TOTAL		23	40

The richest families were Orchidaceae (36.6% of all recorded species), Bromeliaceae (21.9%), and Polypodiaceae (17.1%). Aspleniaceae, Blechnaceae, Piperaceae, Pteridaceae, and Thelypteridaceae were the families with the lowest richness, being represented by only one species each. The richest genera were *Tillandsia* (17%), *Acianthera* (10%), and *Vriesea* (10%).

The species were classified into four different ecological categories, of which the true holoepiphytes had the greatest richness (35 species). Only true holoepiphytes were registered at the forest edge, while in the interior there were three facultative holoepiphytes, two hemiepiphytes, and one accidental holoepiphyte.

Based on epiphytic species biomass, SIMPER found a low percentage of epiphyte similarity within both the edge and interior of the forest (Table 2) and that the dissimilarity between the two environments was high (Table 3). The species that contributed the most to the similarity of the edge were also those responsible for similarity in the interior. These same species (*Microgramma vacciniifolia*, *M. squamulosa*, *Rhipsalis teres*, and *Pleopeltis pleopeltifolia*) contributed the most to the high heterogeneity between the edge and the interior (77.98%).

Table 2. Similarity of vascular epiphytes (SIMPER analysis) among all trees within the edge and the interior and the relative contribution of the first four species. Font: Lippert et al. (2022).

Species	**Mean similarity (%)**	
	Edge 21.19	**Interior 25.41**
	Contribution (%)	
Microgramma vacciniifolia	25.79	26.12
Rhipsalis teres	23.85	24.67
Pleopeltis pleopeltifolia	29.95	12.52
Microgramma squamulosa	12.79	12.22

Table 3. Dissimilarity of vascular epiphytes (SIMPER analysis) between the edge and the interior of the fragment. Font: Lippert et al. (2022).

Dissimilarity (%)	**77.98**
Species	**Contribution (%)**
Microgramma vacciniifolia	14.4
Rhipsalis teres	13.4
Microgramma squamulosa	8.6
Pleopeltis pleopeltifolia	8.3
Vriesea gigantea	6.3
Pecluma sicca	5.1
Lepismium cruciforme	4.9
Aechmea recurvata	3.9
Peperomia trineura	3.6
Tillandsia aeranthos	3.6
Tillandsia geminiflora	2.8
Gomesa flexuosa	2.6
Polystachya concreta	2.3
Pleopeltis hirsutissima	2.1
Vriesea psittacina	2.0
Tillandsia recurvata	1.7
Acianthera luteola	1.5
Epidendrum strobiliferum	1.5
Acianthera saundersiana	1.2
Campylocentrum aromaticum	1.1

Trees from the forest interior had greater total epiphyte richness. Four trees from the forest edge and one from the interior did not possess epiphytes. The rarefaction curves for the edge and the interior did not reach an asymptote, and the richness estimator indicated that richness would tend to increase to 32 and 53 species, respectively (Figure 2).

Epiphytic species had higher total biomass in the interior, except for five species that had higher values at the edge and four that had equivalent biomass (Figure 3). The species with the highest biomass were the same for both sites, with *Vriesea gigantea* and *Rhipsalis teres* reaching the highest score (10) and being among the four highest biomass sums. Most of the exclusive species had low biomass, although two of them found in the interior (*Aechmea recurvata* and *Peperomia trineura*) were among the ten species with higher biomass in both environments.

Edge effect on phorophyte structure

Analysis of the NMDS, which ordered the 50 trees by the occurrence of epiphytes, revealed that trees from the edge and the interior of the forest did not form distinct groupings (there was some distance between trees, but not enough to completely distinguish between edge and interior), which evidences partial differences in the epiphytic composition between environments (Figure 4). The reliability value (stress = 0.17) indicated that the ordering is suitable for interpretation. These results were confirmed by ANOSIM (R = 0.126; P = 0.01).

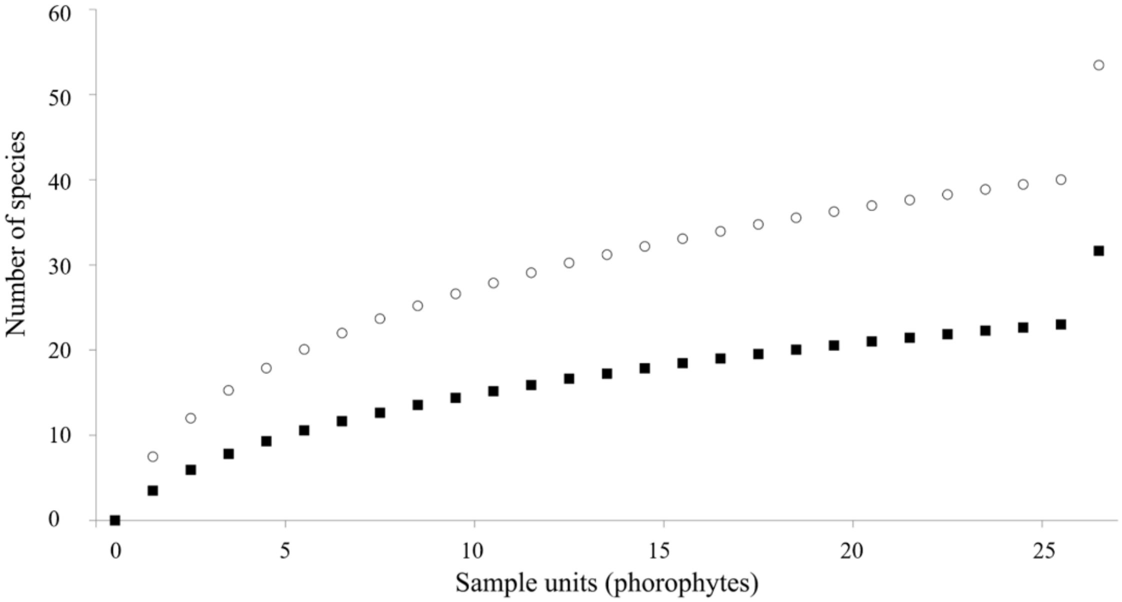

Figure 2. Rarefaction curves for epiphytic ferns sampled at the edge (■) and interior (○) of a subtropical Atlantic Forest fragment (Brazil) with their respective Jackknife1 richness estimations (edge = ■; interior = ○). Font: Lippert et al. (2022).

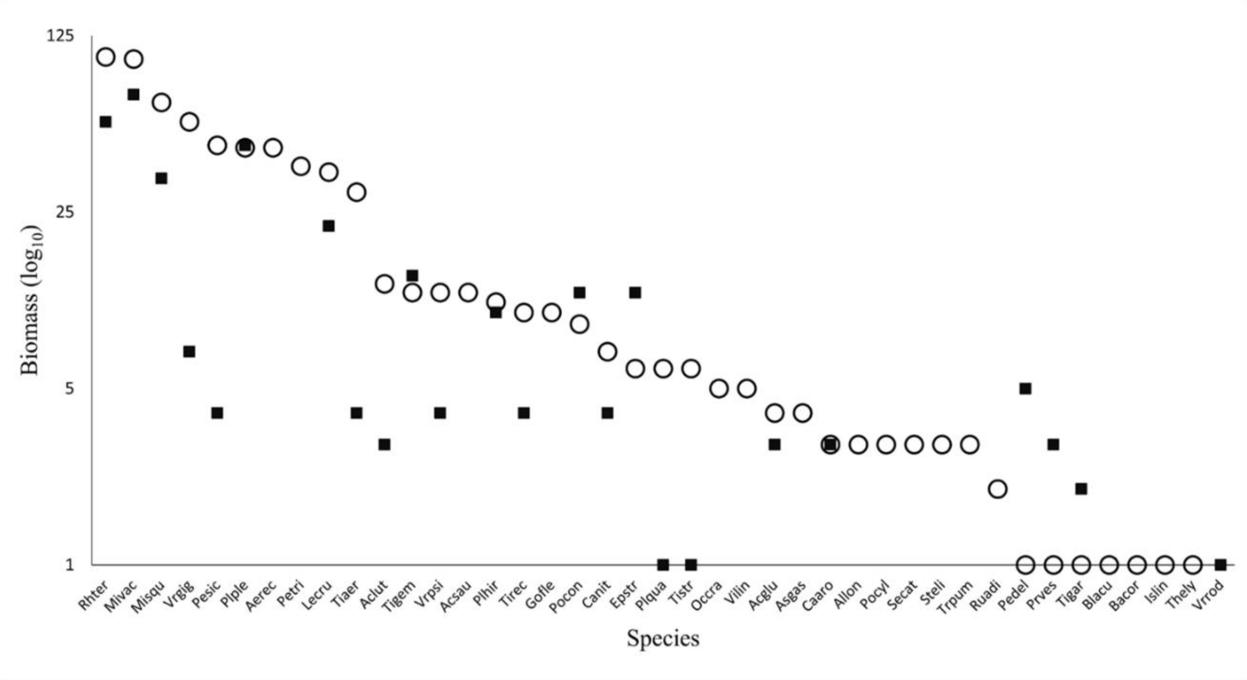

Figure 3. Sum of biomass for the vascular epiphyte species at the edge (■) and in the interior (○) of a fragment of subtropical Atlantic Forest (Brazil). *Rhipsalis teres*: Rhter, *Microgramma vacciniifolia*: Mivac, *Microgramma squamulosa*: Misqu, *Vriesea gigantea*: Vrgig, *Pecluma sicca*: Pesic, *Pleopeltis pleopeltifolia*: Plple, *Aechmea recurvata*: Aerec, *Peperomia trineura*: Petri, *Lepismium cruciforme*: Lecru, *Tillandsia aeranthos*: Tiaer, *Acianthera luteola*: Aclut, *Tillandsia geminiflora*: Tigem, *Vriesea psittacina*: Vrpsi, *Acianthera saundersiana*: Acsau, *Pleopeltis hirsutissima*: Plhir, *Tillandsia recurvata*: Tirec, *Gomesa flexuosa*: Gofle, Polystachya concreta: Pocon, Campyloneurum nitidum: Canit, Epidendrum strobiliferum: Epstr, *Platyrhiza quadricolor*: Plqua, *Tillandsia stricta*: Tistr, *Octomeria crassifolia*: Occra, *Vittaria lineata*: Vilin, *Acianthera glumacea*: Acglu, *Asplenium gastonis*: Asgas, *Campylocentrum aromaticum*: Caaro, *Alatiglossum longipes*: Allon, *Polybotrya cylindrica*: Pocyl, *Serpocaulon catharinae*: Secat, *Stelis* sp: Steli, *Trichocentrum pumilum*: Trpum, *Rumohra adiantiformis*: Ruadi, *Peperomia delicatula*: Pedel, *Prosthechea vespa*: Prves, *Tillandsia gardneri*: Tigar, *Lomaridium acutum*: Blacu, *Baptistonia cornigera*: Bacor, *Isochilus linearis*: Islin, *Thelypteris* sp.: Thely, Vriesea rodigasiana: Vrrod. Font: Lippert et al. (2022).

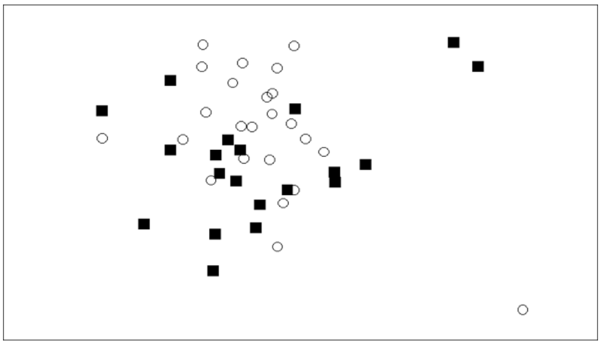

Figure 4. Graphical representation of the ordering resulting from non-metric multidimensional scaling analysis (NMDS) based on the biomass of vascular species from the edge (■) and interior (○) of a subtropical Atlantic Forest fragment (Brazil). Stress = 0.17. Font: Lippert et al. (2022).

Mean values for epiphyte richness for stem and canopy were significantly higher in the interior than at the edge. These values were not only higher but doubled in the interior, which was also true for canopy biomass (Table 4). The size of arboreal individuals between edge and interior did not differ significantly in DBH.

Table 4. Vegetation and abiotic variables for the edge and interior of a subtropical Atlantic Forest fragment (Brazil). Font: Lippert et al. (2022).

	Edge			Interior				
Variable	**Min.**	**Mean. ± SD**	**Max.**	**Min.**	**Mean ± SD**	**Max.**	**U**	**P**
TR (sp tree^{-1})	0.0	3.4 ± 2.4	9.0	0.0	7.4 ± 3.8	13.0	122.5	**0.000**
SR (sp tree^{-1})	0.0	2.4 ± 2.1	9.0	0.0	4.8 ± 2.5	9.0	148.0	**0.001**
CR (sp tree^{-1})	0.0	2.3 ± 1.9	8.0	0.0	5.0 ± 3.9	12.0	193.5	0.020
TBS (sp tree^{-1})	0.0	13.3 ±13.9	57.0	0.0	29.9 ± 20.2	71.0	158.0	**0.003**
SBS (sp tree^{-1})	0.0	6.1 ± 8.2	37.0	0.0	10.9 ± 7.8	25.0	183.0	**0.012**
CBS (sp tree^{-1})	0.0	7.1 ± 8.9	42.0	0.0	18.4 ± 17.0	49.0	195.5	0.023
TH (m)	6.0	8.7 ± 3.1	17.0	6.0	12.6 ± 3.8	18.0	161.5	**0.003**
DBH (cm)	10.0	21.6 ± 9.9	48.0	11.0	32.4 ± 12.2	72.0	268.0	0.393
DCO (%)	11.0	21.7 ± 9.7	48.1	7.4	15.8 ± 4.3	25.9	162.0	**0.004**
PAR (µmol m^{-2} s^{-1})	0.6	13.0 ± 18.9	86.9	0.3	11.6 ±12.3	63.2	1,560.0	0.107
RAH (%)	57.6	66.9 ± 9.5	85.9	62.2	71.8 ± 7.7	88.7	1,025.5	**0.004**
T (°C)	15.1	22.6 ± 4.2	30.0	13.5	22.2 ± 4.2	30.3	1,396.5	0.632

Minimum values, Min.; mean values ± standard deviation, Mean ± SD; maximum values, Max.; total richness, TR; stem richness, SR (Z1+Z2); canopy richness, CR (Z3+Z4); total biomass score, TBS; stem biomass score (Z1+Z2), SBS; canopy biomass score (Z3+Z4), CBS; tree height: TH; diameter at breast height, DBH; degree of canopy opening: DCO; photosynthetically active radiation, PAR; relative air humidity, RAH; temperature, T; Mann-Whitney test, U; 5% significance level, P.

The canopy formed was significantly more open at the edge and taller in the forest interior (Table 4). Photosynthetically active radiation and temperature did not differ significantly between edge and interior, but air humidity was greater in the forest interior. Maximum humidity of 71.8% was recorded in the interior, while the relative humidity of the edge was on average 5% lower.

The total richness and total biomass were strongly related to phorophyte trunk diameter and degree of canopy opening at the edge of the forest fragment, which was not observed in the interior. This finding was due to the positive relationship between stem richness and stem biomass with phorophyte diameter, as well as the negative relationship found between canopy richness and canopy biomass and the degree of canopy opening (Table 5). In the interior, total biomass and canopy biomass were positively correlated with tree height, whereas canopy richness correlated positively with phorophyte trunk diameter. No relationship was observed for epiphyte richness and biomass with photosynthetically active radiation, atmospheric humidity, and temperature, in both environments.

Table 5. Spearman’s correlation coefficient matrix, with epiphyte richness and biomass as reference variables, for the edge and the interior of a subtropical Atlantic Forest fragment (Brazil). Font: Lippert et al. (2022).

Variable		**TH**	**DBH**	**DCO**	**PAR**	**RAH**	**T**
TR (sp tree^{-1})	Edge	0.145	**0.650****	**-0.437***	0.299	-0.068	-0.028
	Interior	0.319	0.247	0.012	-0.346	0.038	0.066
SR (sp tree^{-1})	Edge	0.064	**0.717****	-0.217	0.278	-0.048	-0.071

	Interior	0.209	0.176	-0.025	-0.203	0.044	-0.071
CR (sp $tree^{-1}$)	Edge	0.075	0.377	**-0.659****	0.176	0.013	0.093
	Interior	0.289	**0.433***	-0.022	-0.330	-0.004	0.098
TBS (sp $tree^{-1}$)	Edge	0.048	**0.588****	**-0.476****	0.234	-0.010	-0.060
	Interior	**0.420***	0.347	0.119	-0.372	0.120	0.069
SBS (sp $tree^{-1}$)	Edge	-0.082	**0.686****	-0.269	0.206	-0.084	-0.095
	Interior	0.208	0.172	0.125	-0.330	0.167	-0.184
CBS (sp $tree^{-1}$)	Edge	0.144	0.326	**-0.561****	0.116	0.070	-0.058
	Interior	**0.426***	0.373	0.060	-0.236	0.001	0.130

Total richness, TR; stem richness, SR (Z1+Z2); canopy richness, CR (Z3+Z4); total biomass score, TBS; stem biomass score, SBS (Z1+Z2); canopy biomass score, CBS (Z3+Z4); tree height: TH (m); diameter at breast height: DBH (cm); degree of canopy opening: DCO (%); photosynthetically active radiation, PAR (μmol m-2 s^{-1}); relative air humidity, RAH (%); temperature, T (°C). *Correlation is significant at the 0.05 level. **Correlation is significant at the 0.01 level.

The results of the KMO test were 0.612 and 0.570 for edge and interior, respectively, which indicate sample adequacy for the PCA. The significance of Bartlett's test of sphericity <0.001 for both data sets indicated that they are factorable. No variable had a commonality below 0.6. The PCA resulted in four principal components for each environment, which explained 79,26, and 83.95% of the variance in the data for the edge and the interior, respectively. The rotated component matrix is shown in Table 6.

Table 6. Component matrix after varimax rotation with Kaiser normalization. Font: Lippert et al. (2022).

Variable	Edge				Interior			
	PC1	PC2	PC3	PC4	PC1	PC2	PC3	PC4
TR (sp $tree^{-1}$)	0.911	0.311	0.016	0.060	0.686	0.609	-0.284	0.153
TBS (sp $tree^{-1}$)	0.790	0.524	-0.050	0.159	0.732	0.574	-0.213	0.236
TH (m)	0.507	-0.149	0.604	0.064	0.765	-0.171	0.078	0.061
DBH (cm)	0.596	-0.434	0.256	-0.175	0.670	-0.229	0.015	-0.532
DCO (%)	-0.586	0.180	0.591	0.175	0.219	-0.530	0.038	0.774
PAR (μmol m^{-2} s^{-1})	0.021	-0.024	-0.580	0.645	-0.656	0.097	-0.393	0.246
RAH	-0.299	0.832	0.272	0.114	0.131	0.256	0.898	0.183
T (°C)	-0.019	0.370	-0.335	-0.775	-0.546	0.746	0.187	0.000
Variance (%)	31.25	18.05	16.30	13.66	35.41	21.17	14.12	13.24

Total richness, TR; total biomass score, TBS; tree height, TH; diameter at breast height, DBH; degree of canopy opening, DCO; photosynthetically active radiation, PAR (μmol m^{-2} s^{-1}); relative air humidity, RAH (%); temperature, T (°C). Bold values represent the dominant parameters for each principal component.

The first principal component (PC1) explained 31.25 and 35.41% of the total variance for the edge and the interior, respectively. This component presented positive loadings for total richness, total biomass, and phorophyte diameter, for both the edge and the interior. The second component (PC2) explained 18.05 and 21.17% of the total variance for the edge and the interior, respectively. Only relative air humidity (edge) and temperature (interior) had high positive loadings for this component. The third component (PC3) explained 16.30 and 14.12% of the total variance, respectively, for the edge and interior. For the edge, this component presented a high positive loading for tree height and degree of canopy opening. For the interior, this component presented a high positive loading for relative humidity. The fourth component (PC4) explained 13.66 and 13.24% of the total variance for the edge and interior, respectively. Photosynthetically active radiation (positive) and relative air humidity (negative) had high loadings in this component for the edge. For the interior, this component had a high positive loading for a degree of canopy opening.

Discussion

The total richness of the epiphytic community of the studied fragment demonstrates its importance for the conservation of subtropical forest plant biodiversity. The number of species was approximately twice that inventoried in other fragments of similar size in the same river basin

(Barbosa et al., 2015; Rocha-Uriartt et al., 2015), and in an area of transition between seasonal semideciduous forest and Araucaria-forest in the state of Rio Grande do Sul (Bernardi & Budke, 2010), which recorded around 20 species.

The found predominance of true holoepiphytes, corresponding to 85% of all vascular epiphytic species inventoried, is a common trend in studies on epiphytes (Bernardi & Budke, 2010; Barbosa et al., 2015; Rocha-Uriartt et al., 2015; Graeff et al., 2015; Rocha-Uriartt et al., 2021). True holoepiphytes possess more specialized and diversified adaptations (see Rocha et al., 2013; Rocha et al., 2014) that favor a generalized distribution in different forest formations (Staudt et al., 2012), including the studied environments.

Considering total floristic inventory, Orchidaceae, Bromeliaceae, and Polypodiaceae were the richest families, together representing 75.6% of all species. The pronounced richness of Orchidaceae was mainly due to exclusive species recorded in the interior of the fragment (60% of the species of the family), evidencing a preference for this site. Orchids establish complex obligatory relationships with pollinators (Hutchings et al., 2018) and mycorrhizal fungi (McCormick & Jacquemyn, 2014). Changes in forest environments that lead to the disappearance of these organisms reduce or even locally extinguish orchids due to disruption of their reproductive behavior, which threatens the maintenance of their populations (Fay, 2018; Gale et al., 2018).

The high richness of Bromeliaceae, and the presence of the majority of bromeliad species in both environments (except *A. recurvata* e *V. rodigasiana*), is related to their plasticity in different habitats, as verified by studies of epiphytes in the South Region of Brazil (Bernardi & Budke, 2010; Staudt et al., 2012; Graeff et al., 2015; Costa et al., 2020). The only species recorded as exclusive for the edge belongs to Bromeliaceae, which may be associated with adaptations to dry periods or environments and high luminosity (Barthlott et al., 2001), such as the rhizomatous growth habit and the presence of phytotelma and foliar trichomes (Benzing, 2000). Phytotelma - water tanks formed by the overlapping of the foliar sheaths - maintain adequate water status for the photosynthetic tissues of the apex when environmental conditions are unfavorable (Freschi et al., 2010). In addition, they provide shelter and food resources for other forms of life (Benzing, 2000). Foliar trichomes provide protection against solar radiation, prevent excessive transpiration, and even aid in the absorption of water and nutrients accumulated in phytotelma (Benzing, 2000).

The higher richness of vascular epiphytes in the interior compared to the edge corroborates the record of an increasing edge-interior species richness gradient of seedless terrestrial vascular plants in the same fragment (Nervo, 2012). Bianchi & Kersten (2014) also observed that richness in a community of vascular epiphytes in a fragment of Atlantic Forest in the state of Paraná (southern Brazil) doubled towards the forest interior. The factors indicated as being related to epiphyte composition and richness in the two environments of the forest fragment of the present study are attributes of host trees. In the interior, where trees are taller, greater biomass of epiphytes was recorded in the canopies of larger phorophytes. Smaller trees growing in the shade of larger trees tended to harbor fewer epiphytes, even in their canopy. Height is associated with other intrinsic factors of phorophytes, such as humidity retention, age, architecture, and morphology (Benzing, 1990), and large trees offer more microhabitats for epiphytes than small trees so their richness is related to tree size (Woods, Cardelús & DeWalt, 2015).

Phorophyte diameter was positively related to epiphyte richness and biomass in both environments. Trees from forest edges generally have smaller diameters, which is characteristic of the beginning of succession, and the greater the distance into the forest from the edge, the more that diameter increases (Nascimento & Laurance, 2006). Nevertheless, this trend was not evidenced among the trees sampled in the present study, which did not differ significantly between edge and interior, as currently, the fragment is not suffering substantial anthropogenic pressure.

Even if some microenvironmental variables differ punctually between the edge and interior of the same fragment, as occurred with relative humidity in the present study, temperature and photosynthetically active radiation seem to play a less determining role in distinguishing the conformation of epiphytic communities between microenvironments, as already suggested by Endres Júnior et al. (2015, 2018) for the same forest fragment. The temperature did not present significant differences between interior and edge in the present study, corroborating Nervo (2012) and Endres Júnior et al. (2018) for the same forest fragment, and Silva et al. (2017) for a fragment of mixed ombrophilous forest in the state of Rio Grande do Sul (Brazil). The equivalence of photosynthetically active radiation between the two environments may be associated with several natural trees falling in the forest interior, which opened clearings, and the intrinsic characteristic of seasonal semideciduous forest with a portion of tree species losing their leaves, thus increasing the incidence of sunlight.

Fragmentation and the invasion of forests by matrices of different characteristics and qualities are among the main factors responsible for biodiversity reduction, which has particular effects on epiphytes because of their exclusive dependence on trees (Ceballos, 2020). The loss of diversity of vascular epiphytes, which largely have important ecological roles, such as Orchidaceae and Bromeliaceae, the richest families in the studied fragment, consequently also threatens species that interact directly with these plants (Endres Júnior et al., 2018).

Pleopeltis pleopeltifolia, *Microgramma squamulosa*, *M. vacciniifolia*, and *Rhipsalis teres* concentrated great biomass. The success of these four species is associated with adaptations of plants of Polypodiaceae to withstand water deficits (Rocha et al., 2013). *Microgramma squamulosa* presents special adaptations for epiphytic life, such as the presence of sclerified tissue, hypoderm, and an increased number of stomata in sterile leaves (Rocha et al., 2013). Although species of Cactaceae are found mainly in arid and semi-arid environments, they also have adapted to epiphytic life in humid tropical and subtropical forests (Bauer & Waechter, 2006), as is the case for *Rhipsalis teres*.

In the studied fragment, *P. pleopeltifolia*, *M. squamulosa*, *M. vacciniifolia*, and *R. teres* were generalist species adapted to persist in more adverse environments, such as the edge. The process of forest fragmentation favored the development of these species to the detriment of the establishment of other more sensitive ones. However, forest interior specialists are more negatively influenced by fragmentation and sensitive to changes in the matrix, which would imply decreased fitness and the disappearance of many species susceptible to biotic and abiotic changes. The species belonging to the five families with the lowest biomass (Aspleniaceae, Blechnaceae, Dryopteridaceae, Pteridaceae, and Thelypteridaceae) occurred only in the forest interior, where they are protected, indicating that many species are sensitive to edge environments (Pereira et al., 2010; Silva & Schmitt, 2015).

Conclusion

Our data support the idea that there is a reduction in the richness and a simplification of the epiphytic community at the edge of the forest fragment, when compared to its interior.

The epiphytic richness was related to the diameter of the phorophytes at the edge and in the interior, and with the canopy opening at the edge. The biomass showed a relationship with tree diameter and with canopy opening at the edge, and tree height, in the interior.

The edge effect influenced the distribution of vascular epiphytes, to the point that generalist species occupied the forest interior. The species responsible for the floristic similarity and higher biomass on the edge were the same which caused the similarity in the interior, associated with the reduction of biomass of specialist species. Besides forest restoration, improving the quality of the surrounding matrix can serve as a strategy to buffer the negative edge. Minimizing the contrast between matrix and forest, such as increasing tree cover in the matrix, implementing agroforestry systems, and preventing human settlements, may protect the intrinsic value and ecosystem services of the vascular epiphyte community and support the conservation of biodiversity.

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References

APG IV. 2016. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. Botanical Journal of the Linnean Society, 181, 1-20. https://doi.org/10.1111/boj.12385

Aragón, G.; Abuja, L.; Belinchón. R.; Martínez, I. 2015. Edge type determines the intensity of forest edge effect on epiphytic communities. European Journal of Forest Research, 134, 443-451. https://doi.org/10.1007/s10342-015-0863-5

Barbosa, M. D.; Becker, D. F. P.; Cunha, S.; Droste, A.; Schmitt, J. L. 2015. Vascular epiphytes of the Atlantic Forest in the Sinos River basin, state of Rio Grande do Sul, Brazil: richness, floristic composition and community structure. Brazilian Journal of

Biology, 75, 25-35. https://doi.org/10.1590/1519-6984.0913

Barthlott, W.; Schmit-Neuerburg, V.; Nieder, J.; Engwald, S. 2001. Diversity and abundance of vascular epiphytes: a comparison of secondary vegetation and primary montane rain forest in the Venezuelan Andes. Plant Ecology, 152, 145-156. https://doi.org/10.1023/A:1011483901452

Bauer, D.; Waechter, J. L. 2006. Sinopse taxonômica de Cactaceae epifíticas no Rio Grande do Sul, Brasil. Acta Botanica Brasilica, 20, 225-239. https://doi.org/10.1590/S0102-33062006000100021

Becker, D. F. P.; Linden, R.; Schmitt, J. L. 2017. Richness, coverage and concentration of heavy metals in vascular epiphytes along an urbanization gradient. Science of the Total Environment, 584-585, 48-54. https://doi.org/10.1016/j.scitotenv.2017.01.092

Benzing, D. H. 1990. Vascular Epiphytes. Cambridge University Press, Cambridge. 354p. http://dx.doi.org/10.1017/CBO9780511525438

Benzing, D. H. 2000. Bromeliaceae: profile of an adaptive radiation. Cambridge University Press, Cambridge. 690p. http://dx.doi.org/10.1017/CBO9780511565175

Bernardi, S.; Budke, J. C. 2010. Estrutura da sinúsia epifítica e efeito de borda em uma área de transição entre Floresta Estacional Semidecídua e Floresta Ombrófila Mista. Floresta, 40, 81-92.

Bianchi, J. S.; Kersten, R. A. 2014. Edge effect on vascular epiphytes in a subtropical Atlantic Forest. Acta Botanica Brasilica, 28, 120-126. https://doi.org/10.1590/S0102-33062014000100012

Cascante-Marín, A.; Meijenfeldt, N.; Leeuw, H. M. H.; Wolf, J. H. D.; Oostermeijer, J. G. B.; Nijs, J. C. M. 2009. Dispersal limitation in epiphytic bromeliad communities in a Costa Rica fragmented montane landscape. Journal of Tropical Ecology, 25, 63-73. https://doi.org/10.1017/S0266467408005622

Ceballos, S. J. 2020. Vascular epiphyte communities in secondary and mature forests of a subtropical montane area. Acta Oecologica, 105, 103571. https://doi.org/10.1016/j.actao.2020.103571

Clarke, K. R.; Gorley, R. N. 2002. Primer v5.2.9. 2002 User manual/tutorial, PRIMER-E91 Plymouth, United Kingdom. 91p.

Colwell, R. K. 2005. Estimates: Statistical estimation of species richness and shared species from samples. Version 8.2. User's Guide and application. http://purl.oclc.org/estimates.

Costa, G. M.; Graeff, V.; Marcon, C.; Mottin, I. G.; Schmitt, J. L.; Droste, A. 2020. Genotoxicidade do ar atmosférico e epífitos vasculares em uma Unidade de Conservação de uma Região Metropolitana no sul do Brasil. Revista Brasileira de Geografia Física, 13, 2515-2530. https://doi.org/10.26848/rbgf.v13.6.p2515-2530

Endres Júnior, D.; Sasamori, M. H.; Schmitt, J. L.; Droste, A. 2018. Survival and development of reintroduced *Cattleya intermedia* plants related to abiotic factors and herbivory at the edge and in the interior of a forest fragment in South Brazil. Acta Botanica Brasilica, 32, 555-566. http://dx.doi.org/10.1590/0102-33062018abb0009

Endres Júnior, D.; Sasamori, M. H.; Silveira, T.; Schmitt, J. L.; Droste, A. 2015. Reintrodução de *Cattleya intermedia* Graham (Orchidaceae) em borda e interior de um fragmento de Floresta Estacional Semidecidual no sul do Brasil. Revista Brasileira de Biociências, 13, 33-40.

Fay, M. 2018. Orchid conservation: how can we meet the challenges in the twenty-first century? Botanical Studies, 59, 1-6. https://doi.org/10.1186/s40529-018-0232-z

Flora do Brasil. Jardim Botânico do Rio de Janeiro. Available at: http://floradobrasil.jbrj.gov.br/. Access at: 17 February 2022.

Freiberg, M. 1996. Phenotype expression of epiphytic Gesneriaceae under different microclimatic conditions in Costa Rica. Ecotropica, 2, 49-57.

Freiberg, M.; Freiberg, E. 2000. Epiphyte diversity and biomass in the canopy of lowland and montane forests in Ecuador. Journal of Tropical Biology, 16, 673-688. https://doi.org/10.1017/S0266467400001644

Freitas, L.; Salino, A.; Menini Neto, L.; Almeida, T. E.; Mortara, S. R.; Stehmann, J. R.; Amorim, A. M.; Guimarães, E. F.; Coelho, M. N.; Zanin, A.; Forzza, R. C. 2016. A comprehensive checklist of vascular epiphytes of the Atlantic Forest reveals outstanding endemic rates. PhytoKeys, 58, 65-79. https://doi.org/10.3897/phytokeys.58.5643

Freschi, L.; Takahashi, C. A.; Cambui, C. A.; Semprebom, T. R.; Cruz, A. B.; Mioto, P. T. 2010. Specific leaf areas of the tank bromeliad *Guzmania monostachia* perform distinct functions in response to water shortage. Journal of Plant Physiology, 167, 526-33. https://doi.org/10.1016/j.jplph.2009.10.011

Gale, S. W.; Fischer, G. A.; Cribb, P. J.; Fay, M. F. 2018. Orchid conservation: bridging the gap between science and practice. Botanical Journal of the Linnean Society, 186, 425-434. https://doi.org/10.1093/botlinnean/boy003

Garcia, L. C.; Rezende, M. Q.; Pimenta, M. A.; Machado, R. M.; Lemos Filho, J. P. 2007. Heterogeneidade do dossel e quantidade de luz no recrutamento do sub-bosque de uma mata ciliar no Alto São Francisco, Minas Gerais: análise através de fotos hemisféricas. Revista Brasileira de Biociências, 5, 99-101.

Gotsch, S. G.; Dawson, T. E.; Draguljić, D. 2018. Variation in the resilience of cloud forest vascular epiphytes to severe drought. New Phytologist, 219, 900-913. https://doi.org/10.1111/nph.14866

Gotsch, S. G.; Nadkarni, N.; Amici, A. 2016. The functional roles of epiphytes and arboreal soils in tropical montane cloud forests. Journal of Tropical Ecology, 32, 455-468. https://doi.org/10.1017/S026646741600033X

Graeff, V.; Parode, M. F.; Paz, M. L.; Silva, V. R. S. P.; Marchioretto, M. S.; Schmitt, J. L. 2015. Composição, estrutura comunitária, distribuição vertical e horizontal da sinúsia epifítica em fragmento de restinga, no Rio Grande do Sul, Brasil. Pesquisas, Botânica, 68, 239-255.

Haddad, N. M.; Brudvig, L. A.; Clobert, J.; Davies, K. F.; Gonzalez, A.; Holt, R. D.; Lovejoy, T. E.; Sexton, J. O.; Austin, M. P.; Collins, C. D.; Cook, W. M.; Damschen, E. I.; Ewers, R. M.; Foster, B. L.; Jenkins, C. N.; King, A. J.; Laurance, W. F.; Levey, D. J.; Margules, C. R.; Melbourne, B. A.; Nicholls, A. O.; Orrock, J. L.; Song, D.-X.; Townshend, J. R. 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. Science Advances, 1, e1500052. https://doi.org/10.1126/sciadv.1500052

Hardt, E.; Pereira-Silva, E. F. L.; Santos, R. F.; Tamashiro, J. Y.; Ragazzi, S.; Lins, D. B. 2013. The influence of natural and anthropogenic landscapes on edge effects. Landscape and Urban Planning, 120, 59-69. http://dx.doi.org/10.1016%2Fj.landurbplan.2013.08.014

Hutchings, M. J.; Robbirt, K. M.; Roberts, D. L.; Davy, A. J. 2018. Vulnerability of a specialized pollination mechanism to climate change revealed by a 356-year analysis. Botanical Journal of the Linnean Society, 186, 498-509. https://doi.org/10.1093/botlinnean/box086

Instituto Brasileiro de Geografia e Estatística (IBGE), 1992. Manual Técnico da Vegetação Brasileira. Available at: http://www.biodiversidade.rs.gov.br/portal/index.php?acao=secoes_portal&id=26&submenu=14. Access at: 10 February 2022.

Joly, C. A.; Metzger, J. P.; Tabarelli, M. 2014. Experiences from the Brazilian Atlantic Forest: ecological findings and conservation initiatives. New Phytologist, 204, 459-473. https://dx.doi.org/10.1111/nph.12989

Kersten, R. A. 2010. Epífitas vasculares - histórico, participação taxonômica e aspectos relevantes, com ênfase na Mata Atlântica. Hoehnea, 37, 9-38. https://doi.org/10.1590/S2236-89062010000100001

Kersten, R. A.; Waechter, J. L. 2011. Métodos quantitativos no estudo de comunidades epifíticas. In: Felfili-Fagg, J. M.; Eisenlohr, P. V.; Melo, M. M. R. F.; Andrade, L. A.; Meira Neto, J. A. A. (eds.). Fitossociologia no Brasil: métodos e estudos de caso, 1, pp. 231-254. Editora UFV, Viçosa.

Kupfer, J. A.; Malanson, G. P.; Franklin, S. B. 2006. Not seeing the ocean for the islands: the mediating influence of matrix-based processes on forest fragmentation effects. Global Ecology and Biogeography, 15, 8-20. https://doi.org/10.1111/j.1466-822X.2006.00204.x

Laurance, W. F.; Nascimento, H. E.; Laurance, S. G.; Andrade, A.; Ewers, R. M.; Harms, K. E.; Luizão, R. C.; Ribeiro, J. E. 2007. Habitat fragmentation, variable edge effects, and the landscape-divergence hypothesis. PLoS One, 2, e1017. https://doi.org/10.1371/journal.pone.0001017

Laurance, W. F.; Delamonica, P.; Laurance, S. G.; Vasconcelos, H. L.; Lovejoy, T. E. 2000. Conservation: rainforest fragmentation kills big trees. Nature, 404, 836. https://doi.org/10.1038/35009032

Liu, J.; Slik, J. W. F. 2014. Forest fragment spatial distribution matters for tropical tree conservation. Biological Conservation, 171, 99-106. https://doi.org/10.1016/j.biocon.2014.01.004

Magnago, L. F. S.; Magrach, A.; Barlow, J.; Schaefer, C. E. G. R.; Laurance, W. F.; Martins, S. V.; Edwards, D. P. 2017. Do fragment size and edge effects predict carbon stocks in trees and lianas in tropical forests? Functional Ecology, 31, 542-552. https://doi.org/10.1111/1365-2435.12752

McCormick, M. K.; Jacquemyn, H. 2014. What constrains the distribution of orchid populations? New Phytologist, 202, 392-400. https://doi.org/10.1111/nph.12639

Metzger, J. P. 2001. O que é ecologia de paisagens? Biota Neotropica, 1, 1-9.

Müller, A.; Correa, M. Z.; Führ, C. S.; Padoin, T. O. H.; Quevedo, D. M.; Schmitt, J. L. 2020. The effects of natural and artificial edges on phenology: a case study of *Ctenitis submarginalis*. Austral Ecology, 46, 387-397. https://doi.org/10.1111/aec.12994

Murcia, C. 1995. Edge effects in fragmented forests: implications for conservation. Trends in Ecology and Evolution, 10, 58-62. https://doi.org/10.1016/S0169-5347(00)88977-6

Myers, N.; Mittermeier, R. A.; Mittermeier, C. G.; Fonseca, G. A. B.; Kent, J. 2000. Biodiversity hotspots for conservation priorities. Nature, 403, 853-858. https://doi.org/10.1038/35002501

Nascimento, H. E. M.; Laurance, W. F. 2006. Efeitos de área e de borda sobre a estrutura florestal em fragmentos de floresta de terra-firme após 13-17 anos de isolamento. Acta Amazonica, 36, 183-192. http://dx.doi.org/10.1590/S0044-59672006000200008

Nervo, M. H. 2012. Diagnóstico da composição florística e do efeito de borda sobre a comunidade de samambais e licófitas em remanescente de Floresta Atlântica da Bacia do Rio dos Sinos, RS, Brasil. Dissertação de Mestrado, Universidade Feevale. Novo Hamburgo, Rio Grande do Sul, Brasil. 77p.

Peel, M. C.; Finlayson, B. L.; McMahon, T. A. 2007. Updated world map of the Köppen-Geiger climate classification. Hydrology and Earth System Sciences, 11, 1633-1644. http://dx.doi.org/10.5194/hess-11-1633-

Pereira, I. M.; Berg, E. V. D.; Pinto, L. V. A.; Higuchi, P.; Carvalho, D. A. 2010. Avaliação e proposta de conectividade dos fragmentos remanescentes no Campus da Universidade federal de Lavras, Minas Gerais. Cerne, 16, 305-321.

Perry, D. R. 1978. A method of access into the crowns of emergent and canopy trees. Biotropica, 10, 155-157. https://doi.org/10.2307/2388019

Pócs, T. 1980. The epiphytic biomass and its effect on the water balance of two rain forest types in the Uluguru Mountains (Tanzania, East Africa). Acta Biologica Academiae Scientiarum Hungaricae, 26, 143-167.

PPG I. 2016. The Pteridophyte Phylogeny Group. A community-derived classification for extant lycophytes and ferns. Journal of Systematics and Evolution, 54, 563-603. https://doi.org/10.1111/jse.12229

Razafindratsima, O. H.; Brown, K. A.; Carvalho, F.; Johnson, S. E.; Wright, P. C.; Dunham, A. E. 2017. Edge effects on components of diversity and above-ground biomass in a tropical rainforest. Journal of Applied Ecology, 38, 42-49. https://doi.org/10.1111/1365-2664.12985

Rezende, C. L.; Scarano, F. R.; Assad, E. D.; Joly, C. A.; Metzger, J. P.; Strassburg, B. B. N.; Tabarelli, M.; Fonseca, G. A.; Mittermeier, R. A. 2018. From hotspot to hopespot: An opportunity for the Brazilian Atlantic Forest. Perspectives in Ecology and Conservation, 16, 208-214, 2018. https://doi.org/10.1016/j.pecon.2018.10.002

Ribeiro, M. C.; Metzger, J. P.; Martensem, A. C.; Ponzoni, F. J.; Hirota, M. M. 2009. The Brazilian Atlantic Forest: How much is left, and how is the remaining forest distributed? Implications for conservation. Biological Conservation, 142, 1141-1153. https://doi.org/10.1016/j.biocon.2009.02.021

Ries, L.; Murphy, S. M.; Wimp, G. M.; Fletcher, R. J. J. 2017. Closing persistent gaps in knowledge about edge ecology. Current Landscape Ecology Reports, 2:30-41. https://doi.org/10.1007/s40823-017-0022-4

Rocha, L. D.; Costa, G. M.; Gehlen, G.; Droste A.; Schmitt, J. L. 2014. Morphometric differences of *Microgramma squamulosa* (Kaulf.) de la Sota (Polypodiaceae) leaves in environments with distinct atmospheric air quality. Anais da Academia Brasileira de Ciências, 86, 1137-1146. https://doi.org/10.1590/0001-3765201420130094

Rocha, L. D.; Droste, A.; Gehlen, G.; Schmitt, J. L. 2013. Leaf dimorphism of *Microgramma squamulosa* (Polypodiaceae): a qualitative and quantitative analysis focusing on adaptations to epiphytism. Revista de Biologia Tropical, 61, 291-299.

Rocha-Uriartt, L.; Becker, D. F. P.; Junges, F.; Costa, N. A. T.; Souza, M. A.; Pavão, J. M. S. J.; Schmitt, J. L. 2021.Vascular epiphytism on the Sinos River riparian forest: phytosociological and conservation analysis. Revista Brasileira de Geografia Física, 14, 3497-3509.

Rocha-Uriartt, L. D.; Cassanego, M. B. B.; Becker, D. F. P.; Droste, A.; Schmitt, J. L. 2015. Diagnóstico ambiental de mata ciliar: uma análise integrada de parâmetros botânicos, meteorológicos e da genotoxicidade do ar atmosférico. Revista Brasileira de Ciências Ambientais, 35, 102-115.

Saito, N. S.; Moreira, M. A.; Santos, A. R.; Eugenio, F. C.; Figueiredo, A. C. 2016. Geotecnologia e ecologia da paisagem no monitoramento da fragmentação florestal. Floresta e Ambiente, 23, 201-210. https://doi.org/10.1590/2179-8087.119814

Schneider, C. A.; Rasband, W. S.; Eliceiri, K. W. 2012. NIH Image to ImageJ: 25 years of image analysis. Nature Methods, 9, 671-675. https://doi.org/10.1038/nmeth.2089

Silva, V. L.; Mallmann, I. T.; Cunha, S.; Schmitt, J. L. 2017. Impacto do efeito de borda sobre a comunidade de samambaias epifíticas em floresta com Araucária. Revista Brasileira de Ciências Ambientais, 45, 19-32.

Silva, V. L.; Mehltreter, K.; Schmitt, J. L. 2018. Ferns as potential ecological indicators of edge effects in two types of Mexican forests. Ecological Indicators, 93, 669-676. https://doi.org/10.1016/j.ecolind.2018.05.029

Silva, V. L.; Schmitt, J. L. 2015. The effects of fragmentation on Araucaria Forest: analysis of the fern and lycophyte communities at sites subject to different edge conditions. Acta Botanica Brasilica, 29, 223-230. https://doi.org/10.1590/0102-3062014abb3760

Singh, K. P.; Malik, A.; Sinha, S. 2005. Water quality assessment and apportionment of pollution sources of Gomti river (India) using multivariate statistical techniques - a case study. Analytica Chimica Acta, 538, 355-374. https://doi.org/10.1016/j.aca.2005.02.006

Soares-Filho, B.; Rajao, R.; Macedo, M.; Carneiro, A.; Costa, W.; Coe, M.; Rodrigues, H.; Alencar, A. 2014. Cracking Brazil's Forest Code. Science, 344, 363-364. https://doi.org/10.1126/science.1246663

Staudt, M. G.; Lippert, A. P. U.; Becker, D. F. P.; Cunha, S.; Marchioretto, M. S.; Schmitt, J. L. 2012. Composição florística de epífitos vasculares do Parque Natural Municipal Tupancy, Arroio do Sal, RS-Brasil. Pesquisas, Botânica, 63, 177-188.

Tabarelli, M.; Lopes, A. V.; Peres, C. A. 2008. Edge-effects drive tropical forest fragments towards and early-successional system. Biotropica, 40, 657-661. https://doi.org/10.1111/j.1744-7429.2008.00454.x

Woods, C. L.; Cardelús, C. L.; DeWalt, S. J. 2015. Microhabitat associations of vascular epiphytes in a wet tropical forest canopy. Journal of Ecology, 103, 421-430. https://doi.org/10.1111/1365-2745.12357

Zotz, G.; Bader, M. Y. 2009. Epiphytic plants in a changing world-global: change effects on vascular and non-vascular epiphytes. Progress in Botany, 70, 147-170. https://doi.org/10.1007/978-3-540-68421-3_7