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Articles

Vascular epiphytes diversity and phytogeographical patterns in southern Brazilian cloud forests

Padrões fitogeográficos e de diversidade de epífitas vasculares em florestas altomontanas do sul do Brasil

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ABSTRACT

Aiming to analyze vascular epiphytes biogeographic, endemism, and beta diversity in southern Brazilian cloud forest, all published papers up to February - 2023 on the theme and four surveyed sites were analyzed. We built a dataset about the species' presence/absence in the study locations. The floristic relationship was assessed by non-metric multidimensional scaling (NMDS) using Jaccard as a measurement parameter and testing group differences by using the Analysis of similarities (ANOSIN) and Mantel test. Correlations among floristic diversity and WorldClim variables and phytogeographical parameters were evaluated. The diversity analysis was carried out by Sorensen's total dissimilarity and Simpson's dissimilarity. The cloud forest was divided into two distinct groups - Atlantic Forest in Paraná, and Atlantic Forest in Santa Catarina, while subtropical mixed forests were disconnected. A strong correlation between diversity and precipitation, and precipitation seasonality was found. The diversity-β analysis indicated that substitution is the main factor for total diversity. Brazilian cloud forests have a characteristic flora, each mountain has, however, a distinct community with unique species which justifies the preservation of those forests in different mountains and regions.

Keywords: Dissimilarity floristic; Beta diversity; Non-tree flora; Atlantic Forest; Serra do Mar Mountain Rage

RESUMO

Visando verificar a suscetibilidade das comunidades a alterações ambientais analisamos a distribuição biogeográfica e a diversidade beta (diversidade-β) de epífitas vasculares de Florestas Altomontanas do Sul e Sudeste do Brasil. Foram analisados levantamentos publicados até fevereiro de 2023, além de quatro levantamentos realizados pelos autores. A relação florística entre os estudos foi avaliada pela Análise de Escalonamento Multidimensional Não Métrico (NMDS), baseada na distância de Jaccard, a diferença entre os grupos foi avaliada por meio de uma Análise de Similaridades (ANOSIN). Foram testadas as correlações da riqueza com variáveis climáticas do WorldClim. Foi também analisada a correlação entre a similaridade de Jaccard e a Distância Geográfica (Mantel) entre a riqueza das *áreas* com parâmetros fitogeográficos. Para a análise de diversidade, foram utilizadas a dissimilaridade de Sorensen, a dissimilaridade total e a dissimilaridade de Simpson. As florestas se reuniram em dois grupos: Ombrófilas Densas do Paraná e Ombrófilas Densas de Santa Catarina; as Ombrófilas Mistas apareceram disjuntas. Foi registrada forte correlação da riqueza com a precipitação e sazonalidade. A análise de diversidade-β indicou que a substituição *é* o principal fator para a diversidade total. As florestas altomontanas possuem flora característica e diferenciada em relação *às* florestas montanas. Apesar disso, foram observadas comunidades distintas e espécies exclusivas em cada montanha, o que reforça a importância da preservação de localidades em diferentes serras e regiões.

Palavras-chave: Dissimilaridade florística; Diversidade beta; Flora não-arbórea; Floresta Atlântica; Serra do Mar

1 INTRODUCTION

Differences in species compositional turnover among sites (β-diversity) occurring along gradients are often used to infer variation in the processes structuring communities, and understanding the species distribution mechanisms at different spatial scales is a central theme in community ecology (Kraft *et al*., 2011). In natural ecosystems, species diversity is influenced both directly and indirectly by a set of abiotic and biotic variables. These factors have distinct effects on species distribution and abundance. Distinguishing their relative importance improves our understanding of species distribution mechanisms and helps promote biodiversity conservation in natural ecosystems (Ding *et al*., 2016).

Epiphytes are more abundant in tropical regions, especially in montane ecosystems, where they can exceed the richness of all the other lifeforms combined (Kersten, 2010) and play a crucial role in ecosystem hydrology (Hargis *et al*., 2019). Their diversity patterns are strongly related to water availability (Zotz, 2016), with substantial diversity observed in areas with higher rainfall and shorter drought periods (Krömer *et al*., 2005). Despite that, the processes that shape the epiphyte's disposition have not been studied how they should have, especially compared to terrestrial plants).

Although mountain ecosystems are key features of the Earth's surface and its forests host a substantial proportion of the world's species diversity, the connection between the distribution of biodiversity and the montane ecosystems remains poorly understood. Temperature and precipitation vary according to altitude, influencing the entire plant community composition and structure (Antonelli *et al*., 2018).

The tropical montane cloud forest (or simply cloud forest, because all Brazilian cloud forests are montane) occurs at high altitudes of around 1.000 m above sea level and upwards and is largely associated with the highlands of the Serra do Mar mountains and with the Aparados da Serra Geral (Falkenberg; Voltolini, 1995; Higuchi *et al*., 2013) but also observed on other mountain ranges (Furtado; Menini-Neto, 2015; Furtado; Menini Neto, 2018).

The theoretical frameworks to understand diversity patterns are linked to three distinct levels: *α*, the locality diversity; *β*, the variation among localities; and *γ*, the variation between ecosystems. Differences in species compositional turnover among sites (*β*-diversity) occurring along gradients are often used to infer variation in the processes structuring communities (Kraft *et al*., 2011). Species composition differences among areas can reveal two distinct phenomena: turnover and nestedness. Both events result from antagonistic processes: species replacement in areas or their simple disappearance. Replacement occurs when one area is colonized with species not observed in others, without necessarily a richness reduction. Nestedness, nonetheless, occurs when less diverse areas are home to only species subgroups from richer areas, corresponding to simple species loss along a gradient (Baselga; Andrés, 2010).

From this perspective, this study sought to analyze how phytogeographic and beta diversity patterns influence the vascular epiphyte communities in cloud Forests in southern and southeastern Brazil regions.

2 MATERIALS AND METHODS

Four surveys were carried out in mountains localized in the Serra do Mar (mountain range), Paraná state, Brazil: (I) Morro[I] do Anhangava, located in the Serra da Baitaca (in a state-protected area), in Quatro Barras county; (II) Pico[II] Capivari Grande, located in the Serra do Mar (protected area), between Campina Grande do Sul and Antonina counties; (III) Pico Caratuva, located in the Pico Paraná (in a state-protected area), between Campina Grande, do Sul and Antonina counties; (IV) Morro dos Perdidos, located in the Guaratuba (protected area), Guaratuba county. Except for Pico Caratuva, the other areas are formed by the fragments of montane forest (interspersed with high-elevation grasslands) that have already suffered some anthropogenic interference in the recent past.

Fertile specimens were prepared and deposited in the herbarium HUCP, with duplicate samples sent to herbarium MBM and/or UPCB (acronyms according to THIERS, 2023). Species names, authors, synonyms, and IUCN threat level categories according to the National Center for Flora Conservation (CNCFLora) were verified in Flora E Funga Do Brasil (2024) with Flora pack (Carvalho, 2020) in the R environment.

For phytogeographic comparisons, all known studies on vascular epiphytes in the south and southeast of Brazil, in which the authors explicitly surveyed cloud forests (Table 1), were considered. For comparative purposes, two studies, the geographically closest to the cloud forest considered, one in Paraná state (Bianchi; Michelon; Kersten, 2012) and one in Santa Catarina state (Bonnet *et al*., 2013) were included. The locations were plotted on a map (Figure 1). The vegetation formations were determined by using the Atlantic Forest Law shapefile with Google Earth Pro and Qgis software.

Based on our surveys and the published ones we built a checklist indicating species' presence and absence. Species not identified to species level and those classified as accidental epiphytes were excluded.

[I] A proper name, which is possible to translate as mountains or hills.

[II] Pico is also a proper name, which can be translated as mount.

Table 1 – From north to south of Brazil: considered areas for studies on the diversity and phytogeography of vascular epiphytes

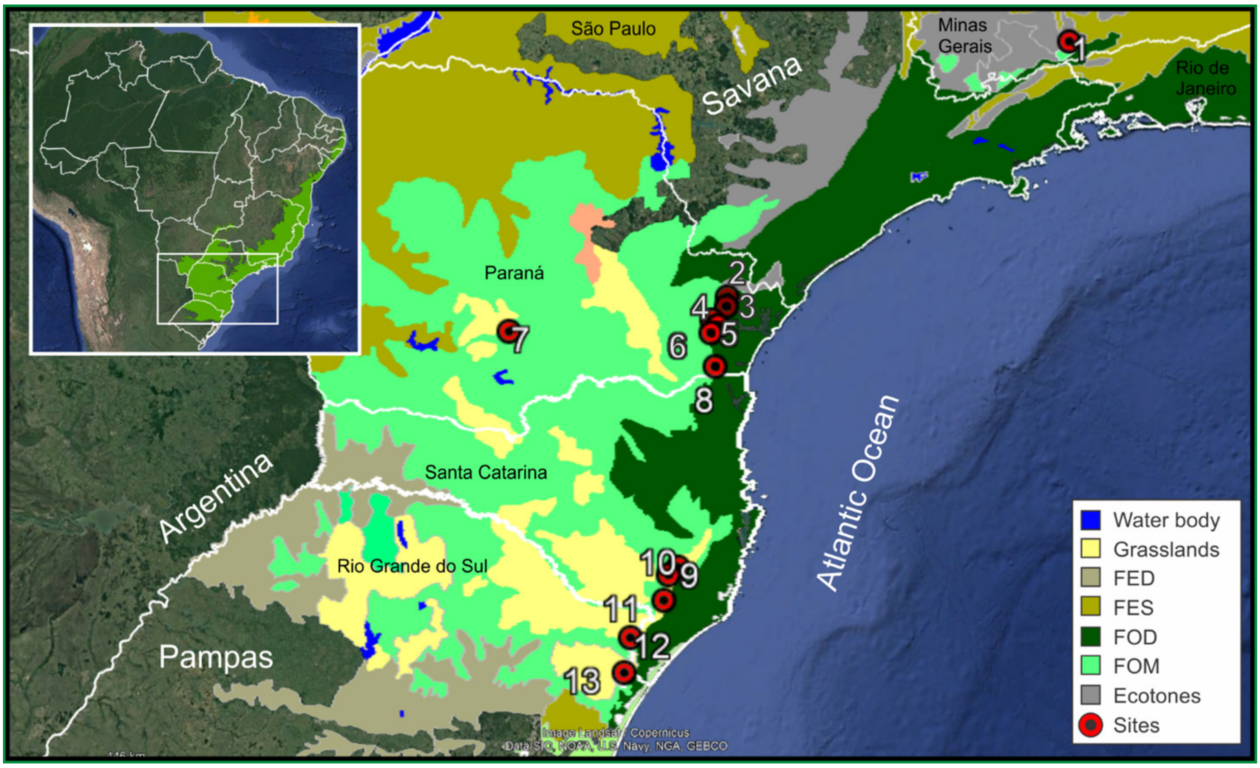
	Local	State	Veg.	Lat.	Long.	Alt.	Dist.	Reference
1	PESP	MG	FOM	22,14	44,73	1750	130	Furtado; Menini-Neto (2015)
2	Capivari	PR	FOD	25,14	48,82	1664	73	Este Estudo
3	Caratuva	PR	FOD	25,24	48,84	1750	60	Este Estudo
4	Anhangava	PR	FOD	25,38	49,00	1440	63	Este Estudo
5	Marumbi	PR	FOD	25,45	48,93	1100	54	Petean (2003)
6	Mananciais	PR	Ecotono	25,50	48,98	1000	55	Bianchi; Michelon; Kersten (2012)
7	São Jerônimo	PR	FOM	25,52	51,42	1200	298	Kersten; Kuniyoshi; Roderjan (2009)
8	Perdidos	PR	FOD	25,88	48,95	1439	36	Este Estudo
9	Corvo Branco	SC	FOD	28,05	49,37	1400	70	Falkenberg (2003)
10	Morro da Igreja	SC	FOD	28,13	49,48	1820	79	Falkenberg (2003)
11	Rio do Rastro	SC	FOD	28,40	49,55	1400	57	Falkenberg (2003)
12	Rocinha	SC	FOD	28,78	49,95	1200	55	Falkenberg (2003)
13	Faxinal	SC	FOD	29,18	50,02	958	34	Bonnet; Caglioni; Schmitt *et al*. (2013)

Source: Authors (2024)

In where: UF: federation unit, Veg: FED: Decidual Forest, FES: Semidecidual Forest, FOD: Tropical Rain Forest, FOM: Subtropical Rain Forest, Lat: Latitude (decimal degrees), Long.: longitude (decimal degrees), Alt.: Mountain Altitude (in meters), Dist. Ocean distance (in kilometers), and Reference.

The floristic relationship was assessed by a Nonmetric multidimensional scaling (NMDS) based on a Jaccard similarity as a distance measure, including the latitude climatic data, continentality (distance from the sea), and altitude considered as environmental variables. The following WorldClim bioclimatic variables were used: BIO1 (Annual Mean Temperature), BIO6 (minimum temperature of Coldest Month), BIO12 (Annual Precipitation), BIO13 (Precipitation of Wettest Month), BIO14 (Precipitation of Driest Month), BIO15 (Precipitation Seasonality), BIO16 (Precipitation of Wettest Quarter) and BIO17 (Precipitation of Driest Quarter), with a resolution of 30 seconds (0.93 x 0.93 km at the equator).

Figure 1 – Plots considered for the cloud forest vascular epiphyte community analysis within the South and Southeast Brazilian Atlantic Forest



Source: Authors (2024)

In where: FED: Decidual Forest, FES: Semidecidual Forest, FOD: Tropical Rain Forest, FOM: Subtropical Rain Forest, 1- Parque Estadual da Serra do Papagaio, 2 – Capivari, 3 – Caratuva, 4 – Anhangava, 5 – Marumbi, 6 – Mananciais, 7 – São Jerônimo, 8 – Perdidos, 9 – Corvo Branco, 10 – Morro da Igreja, 11 – Rio do Rastro, 12 – Rocinha, 13 – Faxinal.

The difference between groups was assessed an ANOSIN test. The correlation between Jaccard's similarity and geographic distance, and between the richness of the areas and the phytogeographic parameters latitude, altitude continentality, and climatic variables was also analyzed by multiple regressions. These analyses were carried out using the PCORD 6 and Past 4.03 software.

To analyze the cloud forest diversity patterns and check the dissimilarity between the environments is due to species replacement or nestedness, three NMDS analyses were carried out: Sørensen dissimilarity (*β-sor*), which assesses the total dissimilarity; Simpson index of dissimilarity (*β-sim*), which assesses species replacement (turnover);

and nesting distance (nestedness – *β-nes*), which assesses if the less rich communities are subsets of the richer ones. These analyses were conducted in the R environment, with the betapart (Baselga; Orme, 2012) and vegan (Oksanen *et al*., 2016) pack; the Mantel test was carried out to verify if the similarity between the areas was correlated with geographical distance. In this last analysis, only cloud forests were considered.

3 RESULTS AND DISCUSSIONS

In the four inventoried sites we found 102 species of vascular epiphytes in 16 families and 52 genera (Table 2). Of those, 55 species (54%) seven families, and 23 genera were ferns and 47 species (46%), 11 families, and 29 genera were Angiosperms. The most species-rich families were Polypodiaceae (23 species), Orchidaceae (19 species), and Hymenophyllaceae (14 species). The genera with the highest number of species were *Hymenophyllum* (11 species), *Peperomia* (eight species), and *Campyloneurum* (six species). 21 species were classified as "Least Concern" (LC), one as "Near Threatened" (NT), one as "Vulnerable" (VU), and two as "Endangered" (EN) though most of the species are still Not Evaluated (NE). Despite that, each site had at least one species classified on one of the three most restrictive categories (NT, VU, EN). The Caratuva and Capivari mountains had two species in these categories each. No exotic species were found. The areas with the most species were Caratuva (73 species), Capivari-Grande (46 species), Perdidos (42 species), and Anhangava (35 species).

Considering all the cloud forest areas in southern and southeastern Brazil, 210 species were recorded, belonging to 20 families and 76 genera. 72 species of Ferns (34% of all) and 138 species of angiosperms (66%). Regarding the IUCN Red List Categories, 49 (23%) species were classified as "Least Concern" (LC), two (1%) as "Near Threatened" (NT), four (2%) as "Vulnerable" (VU), eight (4%) as "Endangered" (EN)). The vast majority (70%) although are still Not Evaluated (NE). Only the Anhangava, Rio do Rastro, and Rocinha mountains had no species listed in the three most restrictive categories (NT, VU, EN). The state park called Serra do Papagaio had five species each in these categories. No exotic species were found. The families with the highest richness were Orchidaceae (72 species), Bromeliaceae (31 species), and Polypodiaceae (31 species), as recurrent for vascular epiphytes surveys in Brazil (Kersten, 2010). In addition to these three major families, it is possible to highlight the presence of Piperaceae (15 species), Hymenophyllaceae (14 species), and Aspleniaceae (eight species), which are not usually among the major epiphyte families. Hymenophyllaceae can be considered a common cloud forest element.

Table 2 – Vascular epiphytes on Cloud forest at Caratuva, Anhangava, Capivari-Grande, and Perdidos, in Paraná state, Brazil, indicating IUCN Red List Categories

TÁXON	IUCN	Ct	Ah	Cp	Pd
Araceae					
Anthurium scandens (Aubl.) Engl.				x	
Philodendron meridionale Buturi & Sakur.		x			
Aspleniaceae					
Asplenium gastonis Fée.		x			
Asplenium harpeodes Kunze		x			
Asplenium incurvatum Fée.		x		x	
Asplenium martianum F. Chr.		x			
Asplenium scandicinum Kaulf.					x
Begoniaceae					
Begonia fruticosa A. Dc.	LC	x			
Blechnaceae					
Blechnum acutum (Desv.) Mett.		x			
Bromeliaceae					
Aechmea gamosepala Wittm.	LC	x			
Aechmea organensis Wawra					x
Aechmea ornata Baker		x	x	x	
Nidularium innocentii Lem.	LC	x			
Nidularium procerum Lindm.		x			
Tillandsia geminiflora Brongn.	LC				x
Vriesea altodaserrae L.B.Sm.					x
Vriesea platynema Gaudich.	LC	x	x	x	x
Cactaceae					
Lepismium houlletianum (Lem.) Barthlott		x	x		
Rhipsalis floccosa Salm-dyck ex Pfeiff.		x			
Rhipsalis teres (Vell.) Steud.				x	
Schlumbergera rosea (Lagerh.) Calvente & Zappi		x		x	x

To be continued ...

Table 2 – Continuation

TÁXON	IUCN	Ct	Ah	Cp	Pd
Cunoniaceae					
Weinmannia humilis Engl.		x			
Dryopteridaceae					
Elaphoglossum alpestre (Gardner) T. Moore		x			
Elaphoglossum glaziovii (Fée) Brade		x			x
Elaphoglossum squamipes (Hook.) T.Moore			x		x
Elaphoglossum vagans (Mett.) Hieron.		x	x	x	x
Rumohra adiantiformis (Sw.) J. Sm.		x			x
Gesneriaceae					
Nematanthus australis Chautems		x		x	
Sinningia cooperi (Paxton) Wiehler	LC	x	x		
Sinningia douglasii (Lindl.) Chautems	LC	x	x	x	x
Griseliniaceae					
Griselinia ruscifolia (Clos) Taub.	NT	x	x	x	x
Hymenophyllaceae					
Crepidomanes pyxidiferum (L.) Dubuisson & Ebihara		x			
Didymoglossum reptans (Sw.) C. Presl		x			
Hymenophyllum asplenioides (Sw.) Sw.		x	x		
Hymenophyllum caudiculatum Mart.		x	x	x	
Hymenophyllum fragile (Hedw.) C.V. Morton	LC	x			
Hymenophyllum fucoides (Sw.) Sw.		x		x	
Hymenophyllum hirsutum (L.) Sw.			x	x	x
Hymenophyllum magellanicum Willd. Ex Kunze	LC	x	x	x	x
Hymenophyllum peltatum (Poir.) Desv.		x			x
Hymenophyllum polyanthos Sw.		x	x	x	x
Hymenophyllum pulchellum Schltdl. & Cham.	LC			x	
Hymenophyllum rufum Fée		x			
Hymenophyllum vestitum (C. Presl) Bosch		x	x		
Trichomanes polypodioides L.				x	x
Lycopodiaceae					
Phlegmariurus acerosus (Sw.) B.øllg.		x	x	x	x
Phlegmariurus fontinaloides (Spring) B.øllg.	LC			x	
Phlegmariurus heterocarpon (Fée) B.øllg.		x		x	x
Phlegmariurus quadrifariatus (Bory) B.øllg.	LC	x		x	x
Phlegmariurus taxifolius (Sw.) Á. Löve & d. Löve	EN	x		x	
Melastomataceae					
Leandra carrassana (Dc.) Cogn.		x			
Onagraceae					
Fuchsia regia (vell.) Munz	LC	x	x	x	x

To be continued ...

Table 2 – Continuation

TÁXON	IUCN	Ct	Ah	Cp	Pd
Orchidaceae					
Acianthera luteola (Lindl.) Pridgeon & M.W.Chase				x	
Acianthera octophrys (Rchb. F.) Pridgeon & M.W. Chase		x			
Acianthera saundersiana (Rchb. F.) Pridgeon & M.W. Chase		x		x	
Acianthera serpentula (Barb.Rodr.) F.Barros					x
Anathallis linearifolia (Cogn.) Pridgeon & M.W.Chase				x	
Bifrenaria harrisoniae (Hook.) Rchb.f.	LC				x
Bulbophyllum granulosum Barb. Rodr.		x			
Bulbophyllum regnellii Rchb.f.					x
Cattleya coccinea Lindl.	LC	x	x	x	x
Gomesa concolor (Hook.) M.W.Chase & N.H.Williams	LC	x			
Gomesa gomezoides (Barb.Rodr.) Pabst	LC	x	x	x	x
Grandiphyllum divaricatum (Lindl.) Docha Neto	VU			x	x
Maxillaria neowiedii Rchb.f.		x			x
Maxillaria picta Hook.		x			x
Octomeria diaphana Lindl.	LC	x		x	x
Octomeria warmingii Rchb.f.	LC				x
Pabstiella trifida (Lindl.) Luer					x
Prescottia stachyodes (Sw.) Lindl.		x			
Stelis argentata Lindl.				x	
Piperaceae					
Peperomia castelosensis Yunck.				x	
Peperomia catharinae Miq.				x	
Peperomia hispidula (Sw.) A. Dietr.		x			
Peperomia quadrifolia (L.) Kunth	LC			x	x
Peperomia rizzinii Yunck.	LC		x		
Peperomia subretusa Yunck.		x			
Peperomia tetraphylla Yunck.		x			
Peperomia trineuroides Miq.		x			
Polypodiaceae					
Alansmia reclinata (Brack) Moguel & m. Kessler		x	x	x	
Campyloneurum crispum Fée		x	x		
Campyloneurum aglaolepis (Alston) de La Sota		x			
Campyloneurum fallax Fée		x	x	x	
Campyloneurum aphanophlebium (Kunze) T.Moore			x	x	x
Campyloneurum nitidum (Kaulf.) C.Presl			x		x
Ceradenia albidula (Baker) L.E. Bishop		x	x		
Cochlidium punctatum (Raddi) L.E. Bishop		x	x	x	x
Grammitis fluminensis Fée	EN	x			
Lellingeria apiculata (Kunze ex Klotzsch) A.R.Sm. & R.C.Moran			x		

To be continued ...

Table 2 – Conclusion

TÁXON	IUCN	Ct	Ah	Cp	Pd
Polypodiaceae					
Lellingeria depressa (C.Chr.) A.R.Sm. & R.C.Moran					x
Leucotrichum organense (Gardner) Labiak		x	x	x	x
Leucotrichum schenckii (Hieron.) Labiak				x	
Melpomene pilosissima (Desv.) A.R. Sm. & R.C. Moran		x			
Microgramma squamulosa (Kaulf.) De la Sota		x	x	x	x
Moranopteris achilleifolia (Kaulf.) R.Y. Hirai & J. Prado		x	x	x	x
Moranopteris gradata (Baker) R.Y. Hirai & J. Prado		x	x		x
Pecluma pectinatiformis (Lindm.) M.G. Price		x	x		
Pecluma recurvata (Kaulf.) M.G. Price		x		x	
Pleopeltis hirsutissima (Raddi) Alston		x	x		x
Pleopeltis pleopeltidis (Fée) De la Sota		x		x	
Serpocaulon catharinae (Langsd. & Fisch.) A.R. Sm.		x	x		x
Pteridaceae					
Polytaenium lineatum (Sw.) Kaulf.		x			
Vittaria lineata (L.) Sm.		x		x	

Source: Authors (2024)

In where: Mountains (Ct = Caratuva, Ah = Anhangava, Cp = Capivari, Pd = Perdidos). IUCN Red List Categories (LC: least concern, NT: near threatened, VU: vulnerable, EN: endangered).

The most specie-rich area (Marumbi) presented richness similar to epiphytes in lower altitude Araucaria Forest (Subtropical Rain Forest) on Paraná (Bizarro; Blum, 2022) and much higher than the tree components in cloud forests (Koehler; Galvão; Longhi Jonas, 2002). This site is at the lowest altitude (1,100 m) of all analyzed areas, and is located at the base of a larger group of mountains (altitudes close to 1,800 m). it is possible to hypothesize that this local relief condition reduces the vegetation's exposure to a harsher climate, allowing less wind and fog presence for long periods - reducing water withdrawal from the system and allowing a higher species number development (Table 3).

Besides Marumbi State Park (PR), Serra do Papagaio State Park (MG) (Furtado; Menini Neto, 2016) and Caratuva (PR) (this study) areas stand out in terms of richness. Minas Gerais state area, regardless of being localized at 1,600-1,700 m, is different from the aforementioned areas due to its three tree strata, the canopy being 30 m high. This pattern is different from the other areas, compared to those presented here and those already published, which have forests with only one tree stratum, sometimes 10 meters in height or less. Caratuva is in a well-preserved Paraná state region, in a protected area, and shows no signs been affected by deforestation or wildfires in the areas sampled. All the other areas showed similar richness, and no correlation was recorded with latitude, altitude, or continentality.

Table 3 – Floristic characteristics of the cloud forest sites considered in this study

N	Local	Spp	Gen	Fam	Ang	Pte	Orc	Bro	Pol	Hym
1	PESP	72	38	13	48	24	27	9	13	1
2	Capivari	46	31	14	20	26	8	3	10	7
3	Caratuva	71	42	17	28	43	9	5	17	11
4	Anhangava	35	24	11	11	24	81	2	15	6
5	Marumbi	85	49	21	56	29	32	12	15	3
7	São Jerônimo	51	29	10	38	13	21	9	9	0
8	Perdidos	42	30	11	19	23	11	4	10	5
9	Corvo Branco	39	26	14	13	26	4	4	12	4
10	Morro da Igreja	26	19	14	12	14	2	2	4	3
11	Rio do Rastro	37	25	13	15	22	3	4	12	3
12	Rocinha	31	24	13	14	17	4	3	8	3

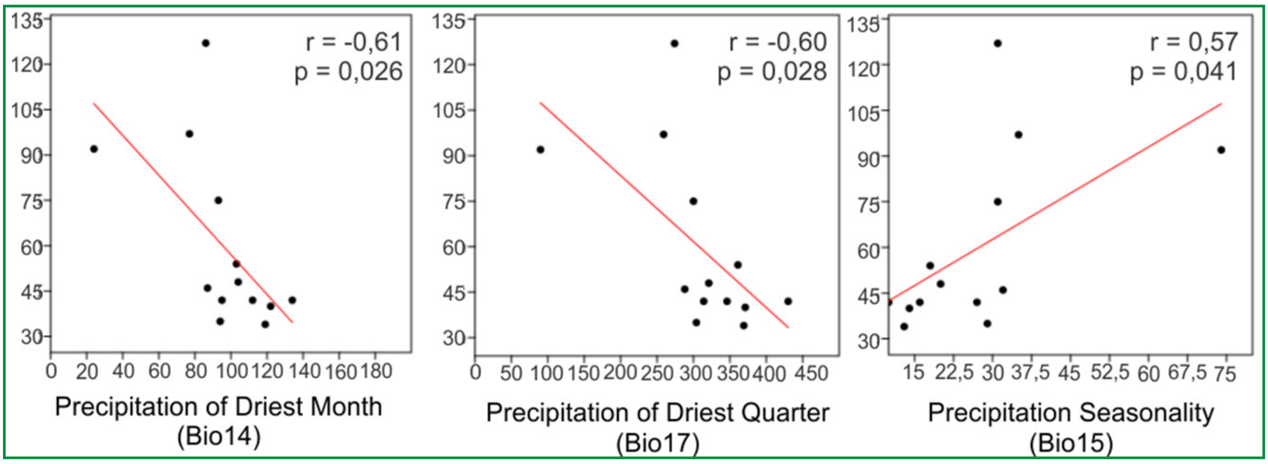
Source: Authors (2024)

In where: Spp: species richness, Gen: genera richness, Fam: family richness, Ang: angiosperms richness, Pte: fern richness, Orc: Orchidaceae richness, Bro: Bromeliaceae richness, Pol: Polypodiaceae richness, Hym: Hymenophyllaceae richness.

The tropical cloud forests of Paraná harbor 134 epiphyte species, Santa Catarina areas 53, and the subtropical ombrophilous cloud forests 103 species. One of the most frequently documented patterns in ecology corresponds to species richness decreasing along latitude and elevation increasing (Kraft *et al*., 2011). A pattern has already been recorded for epiphytes in the Andes (Krömer *et al*., 2005) and for epiphytic orchids in southern Brazil (Waechter, 1996), being a direct response to climatic factors. Species richness is higher in Paraná than in Santa Catarina state, and a higher species number in Paraná is mainly due to two areas: Marumbi and Caratuva. However, even excluding these areas, the average richness remained higher in Paraná.

In this study, species richness was significantly correlated with the climatic variables Bio14 (Precipitation of Driest Month), Bio15 (Precipitation Seasonality/ Coefficient of Variation), and Bio17 (Precipitation of Driest Quarter) (Figure 2). The negative correlation recorded with precipitation in the dry season was expected, as epiphytes respond quickly to drought (Kersten, 2010). For instance, the Atlantic Forest, and its predominantly humid climate, has four times more epiphytes than the entire Amazon rainforest (Ramos *et al*., 2019; Quaresma *et al*., 2022), which has a predominantly seasonal climate. Cerrado (Brazilian savanna), which has a similar richness to the Amazon, has only 3.5% of its flora is epiphytes, while the Amazon has more than 10% and the Atlantic Forest around 15% (Flora E Funga Do Brasil, 2024).

Figure 2 – Relation among climatic variables and vascular epiphytes floristic diversity on the considered forests, showing only the significant ones (p<0,05), best fit for all: linear regression

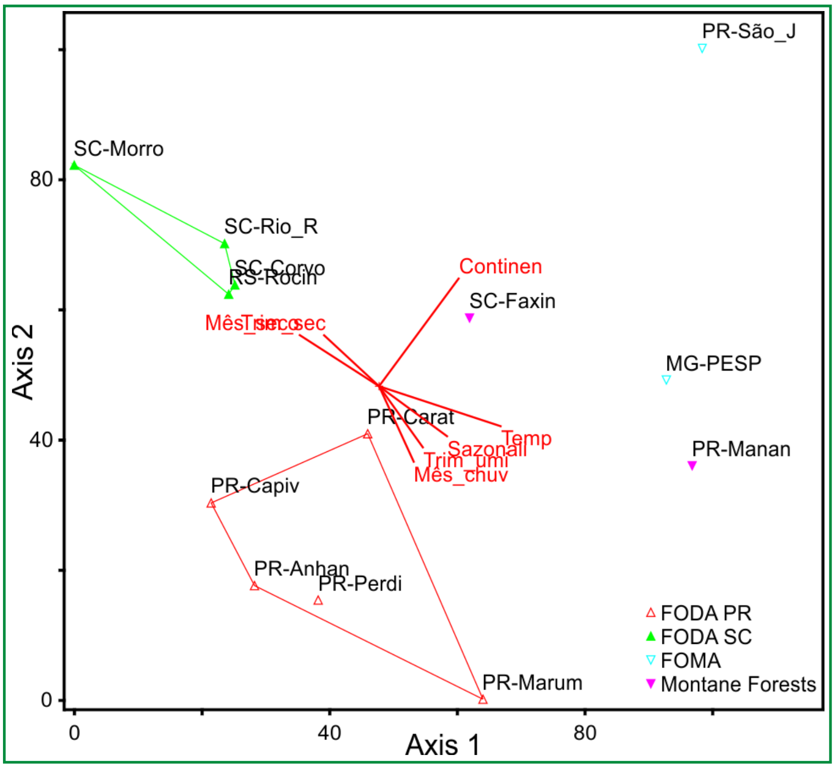


Source: Authors (2024)

The positive correlation between richness and seasonality may seem antagonistic, leading one to believe that a dry period is favorable for epiphytes, the opposite of what was observed in the other correlations. However, the fact is that the areas considered do not have a water deficit, and the climate is always humid (Wrege *et al*., 2012). As a result, a higher variation in precipitation (Bio15) indicates a long summer-winter (O'donnel; Ignizio, 2012), which corresponds, in this case, to winters without rainfall deficit and, therefore, humid summers. The opposite, a lower variation in precipitation, leads to summers and winters with similarities in terms of rainfall, a phenomenon observed in the pampas (flat grassland biome in the southern temperate zone), for example. A homogeneous precipitation distribution usually leads to a water deficit in summer. At higher temperatures, evapotranspiration is higher, relative humidity is lower, and plant water need is higher (Thornthwaite, 1948). Thus, adequate precipitation distribution for epiphytic flora includes more rain in a warmer period and less water demand in a time with lower temperatures.

The NMDS analysis (Figure 3) indicated that the tropical rain cloud forests localized in Paraná and Santa Catarina states formed two distinct groups, while the subtropical ones did not establish a cohesive group. The groups were statistically different in their floristic composition (ANOSIN: R = 0.675, p < 0.01). The isolation of the cloud forests indicates that the communities have their specific floras and are not just subgroups of the lower forests' level.

Figure 3 – NMDS analysis showing species similarity among vascular epiphyte communities (Jaccard index) in Brazil. Acronyms were formed by the locality name's first eight characters as shown in table one



Source: Authors (2024)

In where: FODA –Cloud Tropical Rain Forest, FOMA – Cloud Subtropical Rain Forest.

Two groups were created for analysis purposes due to the differences between the floras (Waechter, 1996) and as well as to the scarcity of surveys in intermediate areas. Perhaps more surveys in these areas would lead to a more gradual and subtle change between the regions.

Considering each area individually, the highest Jaccard numbers were registered in the Rio do Rastro, Serra da Igreja, Corvo Branco, and Morro da Rocinha areas (Falkenberg, 2003). Rocinha and Rio do Rastro were the only places higher than 0.4, reaching 0.75. Furthermore, numbers between 0.3 and 0.4 were registered in the areas in this study (Caratuva, Capivari, Anhangava, and Perdidos). The area with the lowest overall Jaccard index was São Jerônimo (PR), which was also lower than the Minas Gerais (PESP) area (Table 3).

Table 3 – Species similarity (Jaccard index) among vascular epiphyte communities studied sites

	PESP	**Capivari**	**Caratuva**	**Anhangava**	**Marumbi**	**Mananciais**	**São Jerônimo**	**Perdidos**	**Corvo Branco**	**Morro da Igreja**	**Rio do Rastro**	**Rocinha**
Capivari	0,14											
Caratuva	0,22	0,38										
Anhangava	0,16	0,34	0,35									
Marumbi	0,16	0,24	0,27	0,24								
Mananciais	0,20	0,19	0,26	0,15	0,23							
São Jerônimo	0,20	0,09	0,13	0,10	0,11	0,18						
Perdidos	0,16	0,34	0,26	0,36	0,30	0,17	0,09					
Corvo Branco	0,16	0,29	0,34	0,26	0,15	0,12	0,13	0,22				
Morro da Igreja	0,12	0,21	0,19	0,15	0,10	0,07	0,10	0,15	0,45			
Rio do Rastro	0,16	0,29	0,25	0,23	0,15	0,13	0,15	0,21	0,58	0,55		
Rocinha	0,17	0,30	0,27	0,26	0,14	0,12	0,17	0,23	0,59	0,59	0,75	
Faxinal	0,16	0,17	0,28	0,18	0,18	0,20	0,16	0,15	0,22	0,15	0,16	0,21

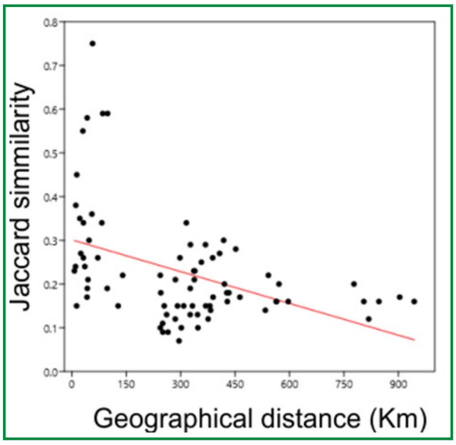
Source: Authors (2024)

These cloud forests are currently threatened by anthropogenic activities, surrounding vegetation removal, wildfires, attractive species extraction, and invasion by invasive exotic species (Martinelli, 2007). Their existence may also be threatened by climate change (Wrege *et al*., 2017), leading to a possible replacement by montane forests (Foster, 2001).

As susceptibility to climate change is associated with the ecological niche (Molina-Venegas; Fischer; Hemp, 2020), any environmental change can lead to specific niche losses; regarding the epiphytes, this is related to both climate and phorophytes they are present in (Kersten, 2010). From an environmental protection perspective, the most appropriate action for this group of plants would be to create more conservation units distributed along the considered gradient.

There was a low negative correlation (r2: 0.19; p<0.0001, Figure 4) between geographical distance and floristic similarity. Although a spatial correlation between different areas has already been documented for epiphytes (Alves; Menini-Neto, 2014), and geographical distance as part of the similarity, the opposite, a low relationship between similarity and geographical distance has also been registered (Küper *et al*., 2004; Menini-Neto; Forzza; Zappi, 2009). According to that study, pattern absence was explained by the altitude difference in the areas. In this research, something different has been observed, altitudinal differences were not the determining factor, and areas close to each other had different communities. This points out that the cloud forest environment, at least for vascular epiphytes, appears to be more varied than in the lower mountain range levels, possibly due to the fewer connections among the areas.

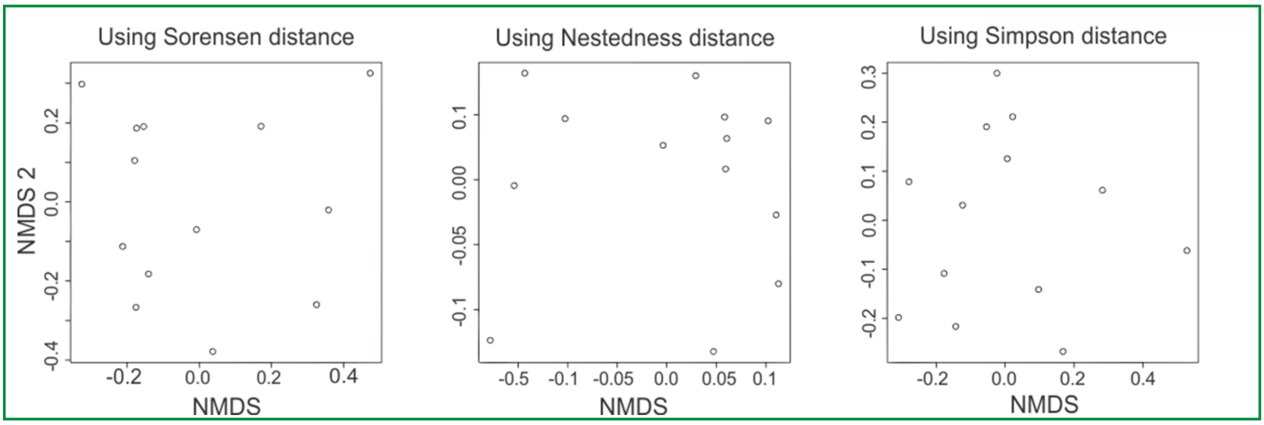
Figure 4 – Relation between geographical distance and Jaccard's similarity. Each point represents a pair of sites. Best fit: linear regression, p<0,0001, r2 = 0,19



Source: Authors (2024)

In the analysis of diversity -*β* (Figure 5), the three graphs were different compared to each other. Nonetheless, the contribution of the substitution (Simpson = 0.77) to the total distance (Sorensen = 0.83) was far more significant than nestedness (0.069). Moreover, the localities, even the southern ones, presented different species in their communities, and the formation of sub-communities was not only the richness decrease.

Figure 5 – *β*-similarity analysis among cloud forests vascular epiphyte communities at southern Brazilian Atlantic forest



Source: Authors (2024)

A clear tendency towards substitution can be seen in the species distribution. Out of the considered species, none were present in all the localities, 54% in only one place, 18% in two, and only 9% in more than 50% of them. Even when analyzed separately, the cloud forest communities in Santa Catarina (Simpson = 0.56; Nestedness = 0.068, Sorensen = 0.62) and Paraná (Simpson = 0.55; Nestedness = 0.13, Sorensen = 0.68) did not present high nestedness values.

Similar patterns regarding the composition of communities (Waechter, 1996) and in the epiphytes diversity in cloud forests have been observed by researchers. Registers of higher substitution rates in cloud forest than in their submontane counterparts (Küper *et al*., 2004), or even the absence of a neatness or substitution pattern, have also been found (Burns, 2008).

Cloud forests have characteristic vascular epiphyte communities that differ from those localized in the lower levels. In Paraná state, they are more like each other than those in the neighboring state. As well, the Santa Catarina forests are more similar to each other than to those in Paraná. Although they share species, each mountain has a distinct community with exclusive species, indicating that the high-montane environment is more varied than the lower levels, possibly due to the fewer connections between areas. In the light of conservation, these results justify the preservation of different areas of montane cloud Forests in mountains and regions of southern Brazil and suggest that global warming could lead to the loss of these ecosystems.

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