UNIVERSIDADE FEDERAL DO RIO GRANDE DO SUL

INSTITUTO DE BIOCIÊNCIAS

PROGRAMA DE PÓS-GRADUAÇÃO EM BOTÂNICA

MAYRA CATALINA JIMÉNEZ PESÁNTEZ

Diversidade e distribuição de plantas vasculares esporocóricas sobre escarpas areníticas imersas na Floresta Atlântica Sul-brasileira

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Dissertação apresentada ao Programa de Pós-Graduação em Botânica da Universidade Federal do Rio Grande do Sul como parte dos requisitos para a obtenção do título de Mestre em Botânica.

Orientador: Prof. Dr. Jorge Luiz Waechter

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Sumário

Resumo

Afloramentos rochosos são feições geomórficas comuns, frequentemente reconhecidos por abrigar um elevado número de espécies endêmicas ou ameaçadas de extinção. As plantas vasculares dispersadas por esporos compreendem as pteridófitas, um grupo taxonômico típico e diverso em afloramentos rochosos Neotrópicos. Pteridófitas são atualmente formados por duas classes monofiléticas Lycopodiopsida e Polypodiopsida. Neste trabalho, avaliamos os padrões de diversidade e distribuição das pteridófitas em afloramentos rochosos inseridos da matriz da Mata Atlântica no Sul do Brasil. Vinte e quatro escarpas foram amostradas em duas matrizes florestais, sendo 12 dentro da Floresta Costeira Perene e 12 dentro da Floresta Estacional Semidecidual. Foram registradas 67 espécies de pteridófitas, muito desigualmente distribuídos entre Lycopodiopsida (5) e Polypodiopsida (62). A riqueza genérica e específica total foi levemente maior na Floresta Ombrófila (38/51) quando comparada à Floresta Estacional (30/43). Nossos resultados também mostraram que a diversidade alfa de pteridófitas não estava diretamente relacionada à área da escarpa, nem ao grau de isolamento dos afloramentos de arenito amostrados. Estes resultados divergem das previsões básicas da Teoria da Biogeografia Insular. A avaliação dos componentes da diversidade beta mostrou uma contribuição significativamente maior de substituição quando comparada ao aninhamento. A partição de variações resultou em baixos valores atribuíveis a fatores espaciais e ambientais, indicando um alto percentual relacionado a variáveis não explicadas. Nossas análises indicam que os fatores de macroescala têm pouca influência na distribuição das pteridófitas, e que de outra forma os fatores de microescala, como exposição, declividade e estrutura da vegetação circundante, são questões importantes para futuras investigações.

Palavras chave: composição florística, espécies rupestres, biogeografia insular, diversidade alfa, diversidade beta.

Abstract

Rocky outcrops are common island-like geomorphic features, often recognized for harboring a high number of endemic or endangered species. Vascular plants dispersed by spores comprise the so-known pteridophytes, a typical and diverse taxonomic group on neotropical rocky outcrops. Pteridophytes are presently formed by two monophyletic classes, the Lycopodiopsida and Polypodiopsida. In this work, we evaluated the patterns of diversity and distribution of pteridophytes on sandstone cliffs immersed in the Atlantic Forest matrix of southern Brazil. Twenty-four escarpments were sampled in two forest matrixes, namely 12 within the Evergreen Coastal Forest, and 12 within the Seasonal Semideciduous Forest. We registered 67 species of pteridophytes, very unequally distributed between Lycopodiopsida (5) and Polypodiopsida (62). The total generic and specific richness were slightly higher in the Evergreen Forest (38/51) when compared to the Seasonal Forest (30/43). Our results also showed that alpha diversity of pteridophytes was not directly related to cliff area, neither to the degree of isolation of the sampled sandstone outcrops. These results diverge from the basic predictions of the Theory of Island Biogeography. The evaluation of beta diversity components showed a significantly higher contribution of turnover when compared to nestedness. Variation partitioning resulted in low values attributable to spatial and environmental factors, and thus indicating a high percentage related to not explained variables. Our analyzes indicate that macroscale factors have little influence on the distribution of pteridophytes, and that otherwise microscale factors, as exposure, declivity, and the structure of surrounding vegetation, are important issues for future investigations.

Key words: floristic composition, rupestrial species, island biogeography, alpha diversity, beta diversity.

Spore dispersion in island habitats: the case of pteridophytes on sandstone cliffs within the south Brazilian Atlantic Forest

Introdução geral

Os afloramentos rochosos são ecossistemas de estrutura diferenciada, que em geral se destacam na paisagem, constituindo um habitat singular (Meirelles *et al*. 1999; Porembski & Barthlott 2000; Ribeiro *et al*. 2007). No Brasil, grande parte dos afloramentos rochosos, estão localizados no *hotspot* global de biodiversidade da Mata Atlântica, principalmente na região Sudeste (Porembski *et al*. 1998; Myers *et al*. 2000; Scarano 2007). Na Mata Atlântica os afloramentos aparecem geralmente como escarpas ou paredões com manchas de floresta na parte superior, e eventualmente na base ou, podem consistir apenas de rochas expostas que se elevam da vegetação florestal (Meirelles *et al*. 1999). Estudos sobre os afloramentos rochosos mostram que estes ambientes são refúgios, no sentido de limitar a ocorrência de espécies terrestres higrófilas e, por outro lado, permitir a sobrevivência de espécies xerófilas (Saraiva & Souza 2012; Fitzsimons & Michael 2016). As espécies restritas a estes ambientes, apresentam maior risco de extinção quando comparadas a espécies de outros hábitats ou tipos de vegetação da Mata Atlântica (Leão *et al*. 2014), um aspecto que demonstra a importância para a conservação.

Afloramentos rochosos são hábitats que têm em comum um conjunto de características estressantes, como uma alta exposição à radiação solar, grandes variações térmicas diárias, alta evapotranspiração e baixa retenção de água (Porembski *et al*. 1994; Porembski & Barthlott 2000). Além dessas peculiaridades ambientais, a vegetação dos afloramentos rochosos mostra padrões interessantes de distribuição e adaptação ao substrato rochoso (Meirelles *et al*. 1999). As espécies geralmente se instalam diretamente na rocha, em fendas, ou em solos muito reduzidos, que variam em função da natureza geológica, características geomorfológicas e a disponibilidade do solo (França *et al*. 1997; Abreu *et al*. 2012). Devido a estas características, os afloramentos rochosos são reconhecidos como centros mundiais de diversidade e endemismo (Barthlott *et al*. 1993; Fitzsimons *et al*. 2016).

Estudos de afloramentos rochosos no Brasil começaram a aumentar a partir de 1990 e, o crescente número de publicações em relativamente pouco tempo demonstra que esses ecossistemas estão recebendo maior atenção nos últimos anos (Silva 2016). A maior parte focalizou inventários florísticos (Jacobi *et al*. 2007; Ribeiro *et al*. 2007; de Paula *et al*. 2020); porém diversos outros enfoques podem ser reconhecidos, como padrões ecológicos centrados em grupos específicos de plantas (Melo & Waechter 2020), analises da estrutura da vegetação (Conceição 2002; Caiafa & da Silva 2005), síndromes de dispersão de espécies rupestres (Araújo *et al*. 2008), influência da matriz circundante (Ribeiro *et al*. 2007; Melo & Waechter 2018)e efeitos de fatores que determinam a composição florística (Benites *et al*. 2007; Abreu *et al*. 2012).

A vegetação de afloramentos apresenta composição florística e distribuição espacial de espécies bastante heterogênea, devido aos diversos tipos de hábitats que podem ocorrer (Porembski *et al*. 1998). Entre os grupos que se destacam nas ilhas de vegetação sobre afloramentos rochosos encontram-se as plantas vasculares dispersas por esporos, tratadas como pteridófitas. As adaptações morfológicas e fisiológicas peculiares destes grupos incluem, a capacidade de sobreviver a altas salinidades (*Acrostichum*), períodos de seca prolongados (*Selaginella*) e, eventos de fogo (*Pteridium*) (Hietz 2010). Além da capacidade de dispersão de longa distância que, continua sendo uma das principais razões da ampla distribuição e ocupação de variedade de nichos (Wolf *et al*. 2001; Rose & Dassler 2017).

Estudos florísticos e ecológicos de pteridófitas nas regiões Sudeste e Sul são vários e tem diversos focos, um dos primeiros constitui do Sehnem (1977) acerca da diversidade, ecologia e rotas de migração. Outros estudos estão focados em inventários florísticos e padrões de distribuição (Senna & Waechter 1997; Dittrich *et al*. 2005), fatores que influem na distribuição (Gasper *et al*. 2013; Nettesheim *et al*. 2014), produção de esporas e dispersão (Coelho *et al*. 2017), gradientes ambientais (Nervo *et al*. 2019).

A proposta deste trabalho foi avaliar os padrões diversidade e distribuição das plantas vasculares dispersas por esporos (pteridófitas) que crescem sobre escarpas areníticas inseridas numa zona de transição entre a Floresta Ombrófila Densa e a Floresta Sazonal Semidecidual, localizada no nordeste do Rio Grande do Sul e sudeste de Santa Catarina. Além disso, procurou-se entender os mecanismos que atuam na estruturação de comunidades com discussões baseadas em teorias ecológicas (Teoria de biogeografia de ilhas e Teoria Neutra).

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Spore dispersion in island habitats: the case of pteridophytes on sandstone cliffs within the south Brazilian Atlantic Forest

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Introduction

Rock outcrops constitute a selective barrier to the occupation and establishment of plant species (Pereira et al. 2018). The flora on rocky outcrops is mainly different from the surrounding vegetation, contrasting with the predominant landscape (matrix) and often hosts a distinct and rare biota that grows on absent or less developed soils (Porembski and Barthlott 2000; Ribeiro et al. 2007). These habitats have a set of stressful characteristics in common, such as high exposure to solar radiation, large daily thermal variations, high evapotranspiration, and low water retention (Porembski et al. 1994; Porembski and Barthlott 2000). In the Atlantic Forest of Southern Brazil, rocky outcrops are also widely distributed in different physiognomies, varying according to different lithologies and topographical features. Rocky outcrops also occur as island habitats, and thus form mosaics within the forest landscape (Oliveira-Filho and Fontes 2000; IBGE 2012).

Species diversity and distribution patterns in island or patch systems are widely discussed according to the Theory of Islands Biogeography (TIB), which basically considers that island dynamics is influenced by geographical aspects, such as size and isolation of islands, and by biological processes, such as immigration and extinction of species (MacArthur and Wilson 1967). The limitation of dispersion is also one of the main subjects of the TIB, the Neural Theory (Hubbell 2001), which considers that species are ecologically equivalent, and that they are the similarities between species, which explain the high diversity of many natural systems. Both the TIB and the Neutral Theory provide a clear explanation linking evolutionary and ecological processes that, in short, propose that individuals of all species of a given trophic level have identical probabilities in their demographic birth rates, mortality, speciation and migration (limited dispersion).

Almost simultaneously with the TIB premises of MacArthur and Wilson (1967), Whittaker (1972) also analyzes the diversity and composition of species assemblages in islands and introduces the concept of diversity. The total diversity of an area results from the combination of the diversity within each island (alpha diversity) and the degree of differentiation between the pool of species in all islands (beta diversity). The application of alpha diversity has been the most studied, but beta diversity has gradually gained more space in ecology, given its importance in the study of communities, and its application in the conservation of biodiversity (Magurran 1988). Beta diversity is the variation in species composition between sites, comprising two components: rotation, i.e., the

substitution of species from one site by different species at the other site, and nesting, i.e., nesting loss (or gain) species, which implies the elimination (or addition) of species in only one of the sites, and leads to the poorest set being a strict subset of the richest (Toumisto 2010; Carvalho et al. 2012).

Vascular plants dispersed by spores are a typical and diverse taxonomic group on neotropical rocky outcrops (Meirelles et al. 1999; de Paula et al. 2020). This ecological or functional group has been traditionally treated as pteridophytes, ferns and allied plants (Tryon and Tryon 1982), and ferns and lycophytes (Gonzatti et al. 2014). More recently again as pteridophytes (PPG 2016), divided into two monophyletic classes, the Lycopodiopsida and the Polypodiopsida. Pteridophytes exhibit a wide distribution and marked floristic variation among distinct areas around the world (Tryon and Tryon 1982; Weigand et al. 2020), as well as varied life forms, including herbaceous geophytes, climbers, hemiepiphytes, epiphytes, lithophytes, hydrophytes and arborescent tree-ferns (Page 1979).

This floristic diversity of the group is closely related to the plurality of habitats, which promotes distinct adaptation processes (Sharpe et al. 2010). In xerophytic environments some apparent adaptations to prevent water loss include both large and coriaceous leaves (*Niphidium*) and extremely reduced leaves (*Psilotum*), high trichome coverage (*Elaphoglossum, Anemia)*, cespitose habit designed to accumulate humus and water (*Asplenium, Polypodium*) and other strategies such as poikilohydric plants (*Selaginella, Pecluma)* (Page 2002; Mehltreter 2008).

The wide geographical distribution of vascular plant species with sporochorous dispersion results in part from the ability to reach long distances and overcome barriers (vicarance), mainly as a result of large spore production (Wolf et al. 2001; Moran 2008; Rose and Dassler 2017). In sporochoric dispersion, the main strategy consists of the reduced size (usually 30-50 μm) and the large number of diaspores produced, which provide propagation at greater distances, away from the mother plant (Moran 2008; Coelho et al. 2017). At the same time, extrinsic factors such as environmental heterogeneity strongly influence the increased diversity of these groups of plants (Dittrich et al. 2005). Studies in the neotropical region show that at this scale factors such as environmental humidity and topography influence the distribution and at the local scale, where soil factors become relevant (Nervo et al. 2018). The richness of these groups in the Atlantic Forest is estimated in 39 families, 145 genera, and 944 species, which

correspond to 67% of the pteridophyte species in Brazil, and approximately 17% are part of the vegetation of the rocky outcrops (BFG 2023).

Considering the great dispersion capacity of sporochoric plants, our main questions are: i) How composition and taxonomic diversity vary between the sandstone outcrops immersed in the Evergreen and the Seasonal forests? ii) How is alpha and beta diversity affected by the main premises of the Theory of Island Biogeography (TIB), i.e., the area of outcrops and the distance between these insular areas? iii) How is beta diversity, i.e., floristic variation between rocky islands influenced by spatial and environmental variables in the two major vegetation matrices?

The main expected answers to our questions above are: i) Evergreen forests are more diversified in relation to Seasonal forests, especially because of higher humidity, which influences the entire biota of rain forest formations; ii) Larger rocky outcrops comprise a higher species diversity than smaller ones, since the former provide more potential space for larger populations; iii) despite the local influence of area, floristic variation is expected to be lower within each forest formation and higher between the two forest formations.

Materials and Methods

Study area

We analyzed 24 sandstone outcrops immersed in the Atlantic Forest biome and distributed in the southern region of Brazil, approximately between latitudes 29ºS and 30ºS, comprising the lowlands between the coastline and the slopes of the Serra Geral. The study area encompasses the southeast of Santa Catarina and the northeast of Rio Grande do Sul (Table 1 & Fig. 1). The rocky outcrops were selected on the basis of three main criteria: 1) geological substrate identified as sandstone (not basalt, which also occurs in the region); 2) elevation close to the sea-level (coastal lowlands or inner depressions); 3) relatively easy physical access, allowing more accurate sampling and species identification (directly and with the aid of binoculars).

All the studied sandstone outcrops were located at low elevations, not exceeding 200 m. The landscapes around the escarpments were heterogeneous, including both relatively well-preserved near rivers, streams or lagoons, and others more or less disturbed, surrounded by pastures for livestock breeding, secondary vegetation or

roadsides (Fig. S1). Two study sites are eventually used as tourist attractions (Riozinho II), one for religious purposes (Dom Pedro de Alcântara III) and the other for climbing practices (Sapiranga I).

Table 1 List of study sites with sandstone cliffs sampled in the Atlantic Forest region of Southern Brazil. Code: E = Evergreen Forest area; S = Seasonal Forest area. Elev.: elevation above sea level near the base of the cliff; DCL: distance from the coastline. Expo: general exposition of the cliffs.

Study site	Code	Latitude S	Longitude W	Elev m	Area m²	DCL Km	Expo
DP de Alcântara I	E1	29°24'22.4"	49°51'03.8"	21	1424	6.2	SE
DP de Alcântara II	E2	29°24'24.0"	49°50'54.7"	14	1152	5.9	SO
DP de Alcântara III	E3	29°22'22.6"	49°51'43.9"	43	2917	9.1	L
DP de Alcântara IV	E4	29°24'17.9"	49°50'58.4"	32	504	6.1	SE
DP de Alcântara V	E5	29°24'22.4"	49°51'03.8"	21	2320	6.1	SE
DP de Alcântara VI	E6	29°22'44.9"	49°50'18.3"	33	2608	6.8	O
Santa Rosa do Sul	E7	29°07'32.4"	49°41'16.4"	58	5279	11.1	SE
Maquiné I	E8	29°35'07.3"	50°16'47.8"	69	1058	31.7	N
Maquiné II	E9	29°33'47.6"	50°16'28.6"	79	1321	32.2	S
Maquiné III	E10	29°33'47.6"	50°16'28.6"	76	514	32.3	L
Itati	E11	29°23'06.0"	50°10'33.9"	133	1222	34.1	L
Sombrio	E12	29°07'23.5"	49°39'9.27"	12	1185	8.6	SE
Sapiranga I	S1	29°36'50.4"	50°58'34.3"	165	340	92.8	S
Sapiranga II	S2	29°36'50.4"	50°58'34.3"	165	778	93.0	O
Rolante I	S3	29°39'24.4"	50°35´02.7"	200	654	55.6	NE
Rolante II	S4	29°34'17.9"	50°28'51.1"	84	268	50.1	O
Rolante III	S5	29°37'07.3"	50°29'34.4"	87	5425	52.7	L
Rolante IV	S6	29°37'07.3"	50°29'34.4"	87	1978	47.6	N
Riozinho I	S7	29°39'2.59"	50°26'53.6"	75	1425	43.6	NE
Riozinho II	S8	29°35'58.2"	50°28'53.7"	102	3900	48.8	NO
SA da Patrulha I	S9	29°47'21.7"	50°33'27.1"	93	1566	47.6	L
SA da Patrulha II	S10	29°46'04.7"	50°32'50.0"	62	140	47.2	O
SA da Patrulha III	S11	29°46'04.7"	50°32'50.0"	62	50	47.2	NE
SA da Patrulha IV	S12	29°47'07.3"	50°33'36.4"	46	2553	47.8	N

Municipality names partially abbreviated above: DP = Dom Pedro; SA = Santo Antonio.
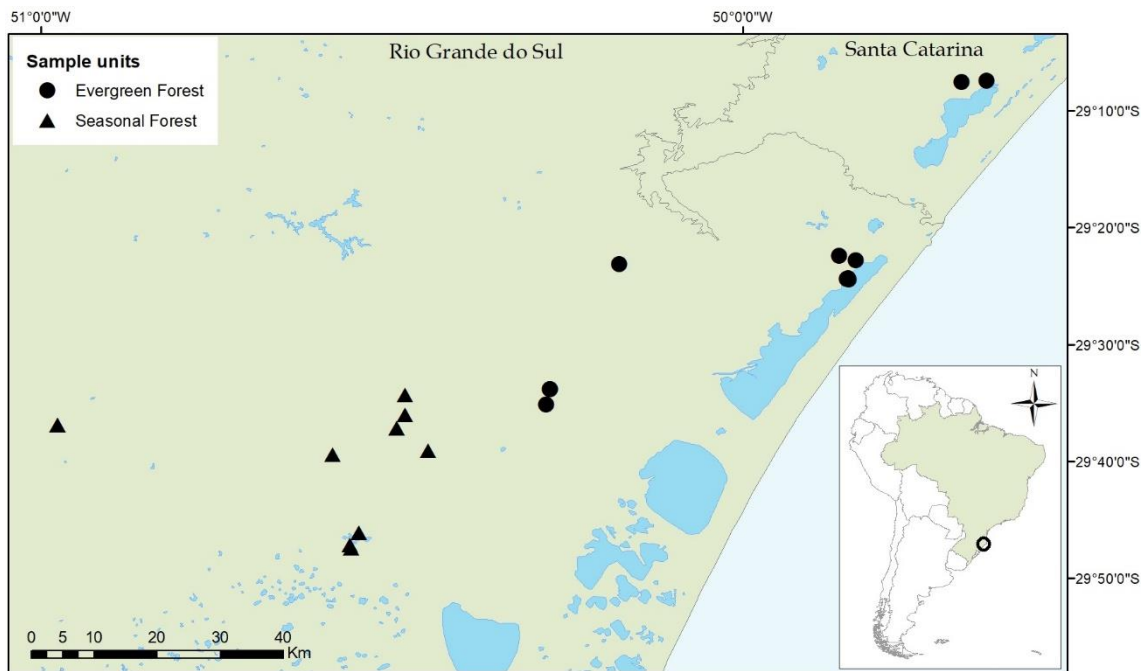
Fig. 1 Geographic location of the 24 study sites in the south Brazilian Atlantic Forest, comprising part of states of Rio Grande do Sul and Santa Catarina.

According to the Köppen-classification system, the entire study area has a humid subtropical climate (Cfa), which is typical for lower elevations of South Brazil (IBGE 2012). The Cfa climate is characterized by hot summers, the temperature of the warmest month above 22°C and relatively well distributed rainfall throughout the year. Based on data from Alvares et al. (2013), the annual temperature averages are very similar in 10 climate stations located in the study area, ranging around 18°C. The values of total annual precipitation are higher in the Seasonal Forest region (1850 mm) than in the Evergreen Forest region (1660 mm), so that seasonality in the inland areas is mainly defined by the rainfall regime, that is, by the difference between more and less rainy months.

The sandstone outcrops belong to the Botucatu Formation of the Paraná Sedimentary Basin, originated in the Triassic period and together with the Pirambóia and Serra Geral form the São Bento Group (Azevedo et al. 1981). The Botucatu Formation is composed of medium to fine sandstones of high sphericity and they are extremely fragile from the point of view of erosion resistance; currently they extend mainly in south-central Brazil (Soares et al. 2008).

All the studied outcrops studied are inserted in two distinct physiognomies of the Atlantic Forest, here designed as The Evergreen Forest (*Floresta Ombrófila*) and

Seasonal Forest (*Floresta Estacional*) as proposed by Orihuela et al. (2015). The main differences between rainforests and seasonal forests in southern Brazil can be summarized by a few aspects concerning floristic composition, species diversity, and canopy deciduousness. In the coastal rainforests, several common tree species belong to ancestral evergreen magnoliids, of the genera *Magnolia, Virola, Annona,* and *Xylopia.* In the more inland seasonal forests, several tall legume trees appear as winter-deciduous canopy trees, such those of the genera *Apuleia, Erythrina, Myrocarpus,* and *Parapiptadenia*.

Sampling method

The study was based on floristic and ecological collected by Melo and Waechter (2018; 2020) focusing the composition, abundance, and distribution of the Bromeliaceae on the same rocky outcrops. These authors also collected a general survey of spore-dispersed vascular plants, i.e., the species of pteridophytes. After the two most critical pandemic years (2020-2021), some of the previous sampled rocky outcrops were visited and resampled during 2022, aiming to check the original data on composition and abundance, and so to improve the general floristic data matrix.

The sampling resulted in 24 sampling units (sandstone cliffs), 12 in each forest formation, all of them comprising escarpments with a predominantly vertical or strongly inclined slope. The species present on the scarps were recorded through direct macroscopic observations and in some cases with the aid of high-resolution binoculars. The sampling process usually finished after a time without finding new additions to the species list. Abundance estimations data were performed according to a simplified scale of three quantities 1 = few; 2 = several; 3 = many individuals or colonies. Some species were easily recognized and identified in the field, while others were collected and later identified in the ICN Herbarium of the Federal University of Rio Grande do Sul, and in the HUCS Herbarium of the University of Caxias do Sul (acronyms based on Thiers 2023). The classification system adopted for the circumscription of families and genera was the one proposed by The Pteridophyte Phylogeny Group (PPG 2016). Abbreviations of the author names of species follow the Flora e Funga do Brasil (BFG 2023). The fertile specimens were incorporated into the ICN Herbarium.

For each sampled escarpment we compiled geographic coordinates (latitude, longitude, altitude) and spatial metrics, such as length, height, and distance from the coastline (DCL). Cliff length was simply measured with a tape, and height was estimated by a trigonometric equation, combining distance from the cliff, height of the observer, and the angle given by a clinometer. The surface area of each cliff was calculated by multiplying length by height. The total sampled area in each plant formation resulted to be very similar, with 19,713 m^2 in the Evergreen Forest and 19,277 m^2 in the Seasonal Forest. The distances between sample units were measured by the function "distm", in the package Geosphere (Hijmans 2022), in the R Development Core Team (2021), which calculates the distance matrix of a set of points, or between two sets of points considering the closest distance between two outcrops.

Data analysis

We organized data matrixes of species per study sites for the analyses of abundance, richness and similarity. The species occurrences on distinct types of substrates were based on field observations, the Flora of Brazil (BFG 2023), data base, and publications on pteridophytes from the region (Dittrich et al. 2005; Gonzatti et al. 2014, 2016; Nervo et al. 2016; Costa et al. 2020). Besides rupestrial, epipetric or lithophytic (as observed in the field), the species were also cited as terrestrial (geophytic or rooted in the soil) and epiphytic (corticolous or rooted on bark surfaces). Species *Lomaridium plumieri, Mickelia scandens* and *Vandenboschia radicans,* eventually considered as scandent-epiphytic (Tryon and Tryon 1982) or secondary hemiepiphytes (Orihuela and Waechter 2010) were recorded as terrestrial and epiphytic.

The relationship between species richness and the area of outcrops was analyzed through generalized linear models (GLM). To evaluate significance, a Pearson correlation coefficient was applied to the 5% significance level. A logarithmic transformation was applied to the data in order to improve homoscedasticity and a Shapiro-Wilk test to detect if the data follow a normal distribution. To evaluate a relationship between species richness and distance between rocky outcrops a Mantel test was used. The Mantel test was used to calculate the linear correlation between two proximity matrices (similarity or distance) calculated on the same objects (Legendre and Legendre 2002). In this case, the

correlation between a spatial distance matrix and a floristic distance matrix (Jaccard) was evaluated. The "vegan" package was used in these analyses (Venables and Ripley 2002; Oksanen et al. 2020).

A non-metric multidimensional scaling (NMDS) analysis was performed to show similarities between the outcrops from the two forest types, using the Jaccard index as a measure of dissimilarity applied to a binary matrix. To compare the floristic similarity between the two forest types, we used the Jaccard index. The Jaccard index is the proportion of species out of the total species list of two sites, which is common to both sites (Jongman et al. 1995). These analyses were performed using the "vegan" package (Oksanen et al. 2020).

Aiming to know how beta diversity varies in terms of turnover and nestedness, a partitioning analysis was applied according to the methodology proposed by Baselga and Orme (2012), which consists in calculating the dissimilarity index of Sørensen (βSOR) and divide this estimation into turnover, i.e., the Simpson dissimilarity index (βSIM) and nestedness (βSNE) i.e., the difference between βSOR and βSIM. The estimations were performed with the package "Betapart" in R (Baselga et al. 2022).

The relative contribution of spatial and environmental variables in the structuring of communities was analyzed by partitioning the variation, this analysis is based in Redundancy Analysis (RDA) and the division of variation based on adjusted R^2 (Legendre and Legendre 1998; Borcard et al. 2011). The RDA is a method that reports the contribution of each predictor matrix separately, as well as the percentage of variation that is explained by the two variables at the same time (Borcard et al. 2011). Thereafter, the variation in the community matrix was decomposed into several explanation components: purely environmental, both spatial and environmental, purely spatial, and residual or unexplained factors (Borcard et al. 2011). For this analysis, we used three matrices: a binary presence/absence matrix, the environmental variables matrix and spatial variables matrix. The significance of each component was calculated through an ANOVA like permutation test for Constrained Correspondence Analysis with 1000 permutations, using the *cca* function of the "vegan" package (Oksanen et al. 2020).

In the climate variables matrix, we initially worked with 18 variables for each site obtained at the CHELSA database (Brun et al. 2022), with a spatial resolution of 30" (~1

km). We used a PERMANOVA - Permutational Multivariate Analysis of Variance (Anderson 2001), to test the relationship between each predictive environmental variable in each study region. This analysis resulted in five significant variables: Annual range of air temperature, mean daily air temperatures of the wettest quarter, mean daily air temperatures of the coldest quarter, annual precipitation, mean daily maximum air temperature of the warmest month. After running an RDA, we verified multicollinearity by the variance inflation factor (VIF). The procedure was performed by the *vif.cca* function of the "vegan" package (Oksanen et al. 2020).

The matrix of spatial variables was built with the Moran Eigenvector Maps (MEM, Dray et al. 2006) and its original form, the PCNM - Principal Coordinates of Neighbor Matrices (Borcard and Legendre 2002). The first MEM axes indicate the broad scale of spatial variables, and the last axes the fine scale of these variables (Dray et al. 2006). This procedure generated a total of seven MEM filters. An RDA procedure was applied to the spatial dataset. Only the significant spatial filters were retained for variation partitioning (MEM1, MEM5, MEM6), corresponding to a broad scale filter (MEM1) and two finer scale filters (MEM5, MEM6).

The distance-based Moran's Eigenvector Maps were performed with the "vegan" package (Oksanen et al. 2020). The RDA analysis, variation partitioning and Moran spectral randomization was executed with the "vegan" and "ade4" packages (Dray and Dufour 2007; Oksanen et al. 2020). All analyses were performed in the statistical program R (R Development Core Team 2021).

Results

Taxonomic diversity and occurrence on alternative substrates

Our floristic inventory resulted in 67 species, belonging to 44 genera and 18 families. The class Lycopodiopsida comprised a small group with two families and five species. The class Polypodiopsida otherwise comprised a much larger group with 16 families and 62 species. Polypodiaceae and Pteridaceae were the most diversified families, with 12 and 11 species respectively, when all studied sites are pooled. The Blechnaceae and Dryopteridaceae followed with eight species each. Additionally, a set of seven families appeared with five species or less, while another set of seven species occurred with a single individual (Table 2).

Table 2 Floristic composition of pteridophytes occurring on 24 sandstone outcrops sampled in Evergreen and Seasonal Forest matrixes in south Brazil. For each species, other habits besides rupestrian or epipetric, as well as the total abundance and frequency are given. T = terrestrial; E = epiphytic; AB = sum of estimated abundances; FR = total frequency, i.e., the number of occupied rocky outcrops.

Class / Family	Species	Habits	Evergreen		Seasonal	
			AB	FR	AB	FR
Lycopodiopsida						
Lycopodiaceae	Palhinhaea cernua*	T	2	2	1	1
	Phlegmariurus reflexus	T	1	1	0	0
Selaginellaceae	Selaginella microphylla	T	4	2	1	1
	Selaginella muscosa	T	10	6	6	6
	Selaginella sellowii	T	0	0	4	2
Polypodiopsida						
Anemiaceae	Anemia phyllitidis	T	11	8	5	5
	Anemia tomentosa	T	2	2	4	4
Aspleniaceae	Asplenium claussenii	T	2	1	0	0
	Asplenium serra	T, E	1	1	0	0
Athyriaceae	Diplazium cristatum	T	0	0	2	1
Blechnaceae	Blechnum austrobrasilianum*	T	1	1	0	0
	Blechnum laevigatum	T	4	3	3	3
	Blechnum occidentale	T	0	0	2	1
	Blechnum polypodioides	T	0	0	2	1
	Lomaridium plumieri	T, E	1	1	1	1
	Neoblechnum brasiliense*	T	7	6	3	3
	Parablechnum cordatum*	T	1	1	0	0
	Telmatoblechnum serrulatum	T	2	2	0	0
Dennstaedtiaceae	Dennstaedtia globulifera*	T	0	0	1	1
	Histiopteris incisa	T	1	1	0	0
	Pteridium esculentum	T	2	2	0	0
Didymochlaenaceae	Didymochlaena truncatula*	T	1	1	1	1
Dryopteridaceae	Elaphoglossum glaziovii	T, E	2	1	0	0
	Elaphoglossum hybridum	T, E	0	0	2	2
	Elaphoglossum luridum	T, E	3	1	0	0
	Elaphoglossum pachydermum	T	1	1	0	0
	Parapolystichum effusum	T	0	0	1	1
	Mickelia scandens*	T, E	1	1	0	0
	Olfersia cervina	T, E	3	2	1	1
	Rumohra adiantiformis	T, E	18	11	14	8
Hymenophyllaceae	Didymoglossum hymenoides	E	2	1	0	0
	Hymenophyllum asplenioides	E	1	1	0	0
	Hymenophyllum caudiculatum	E	1	1	0	0
	Polyphlebium angustatum	E	2	2	0	0
	Vandenboschia radicans	T, E	1	1	0	0

Lygodiaceae	*Lygodium volubile**	T	1	1	0	0
Nephrolepidaceae	*Nephrolepis cordifolia**	T	0	0	3	1
Osmundaceae	*Osmunda spectabilis**	T	1	1	1	1
Polypodiaceae	*Campyloneurum nitidum*	T, E	16	10	9	7
	Microgramma squamulosa	E	1	1	6	4
	Microgramma vacciniifolia	E	11	8	11	8
	Niphidium rufosquamatum	E	6	4	2	2
	Pecluma pectinatiformis	T, E	4	4	0	0
	Pecluma sicca	E	0	0	2	1
	Phlebodium pseudoaureum	E	1	1	2	2
	*Pleopeltis lepidopteris**	T	8	6	11	8
	Pleopeltis minima	E	0	0	1	1
	Pleopeltis pleopeltifolia	E	1	1	7	6
	Serpocaulon catharinae	E	2	2	1	1
	Serpocaulon meniscifolium	E	7	6	2	1
Psilotaceae	*Psilotum nudum*	T, E	4	3	4	3
Pteridaceae	*Adiantum pentadactylon**	T	1	1	0	0
	Adiantum raddianum	T	16	9	9	8
	Cheilanthes juergensii	T	1	1	0	0
	Doryopteris lorentzii	T	1	1	2	2
	Doryopteris pentagona	T	1	1	0	0
	Doryopteris triphylla	T	0	0	2	2
	Pteris brasiliensis	T	1	1	0	0
	*Pteris deflexa**	T	0	0	1	1
	Pteris denticulata	T	0	0	2	2
	Pteris vittata	T	0	0	4	3
	*Vittaria lineata**	E	4	4	1	1
Tectariaceae	*Tectaria incisa**	T	1	1	0	0
Thelypteridaceae	*Amauropelta stierii**	T	0	0	1	1
	*Christella hispidula**	T	12	9	8	8
	*Pelazoneuron patens**	T	1	1	1	1
	Macrothelypteris torresiana	T	0	0	2	2

(*) species first recorded as rupicolas

All genera were recorded less than five species. *Blechnum, Elaphoglossum and Pteris* were the richest genera, with four species each. A total of 31 genera, representing more than 70% of the sporochorus flora, were represented by a single species. Among the 67 species recorded in the study, almost half (27 species, 40.30%) occurred in both forest types.

The Evergreen Forest, 51 species were recorded and 24 were restricted to this forest matrix. The number of species per rocky outcrop ranged from six to 25. In the Seasonal Forest, 43 species were recorded and 16 occurred only in this forest matrix. Most families occurred in both forest matrixes, and in general with a relatively low

number of species. At the family level, two taxa were not sampled in the Evergreen matrix, namely the Athyriaceae and Nephrolepidaceae. Otherwise, in the Seasonal matrix four families were absent, including the Aspleniaceae, Hymenophyllaceae, Lygodiaceae and Tectariaceae (see Fig. S2, S3, S4 for examples).

The comparison of different substrate occupation of rupestrial pteridophytes showed that most species also occur in geophytic or terrestrial habitats, both in the Evergreen (67.1%) and Seasonal (56.7%) forest matrixes (Fig 2). The occurrence as equally epiphytic and widespread plants. i.e., occurring on all three habitats, appeared with lower percentages (less than 25.0%), again in the two forest matrixes. Interesting, the epipetric habitat showed no exclusive or restricted species of vascular sporochores.
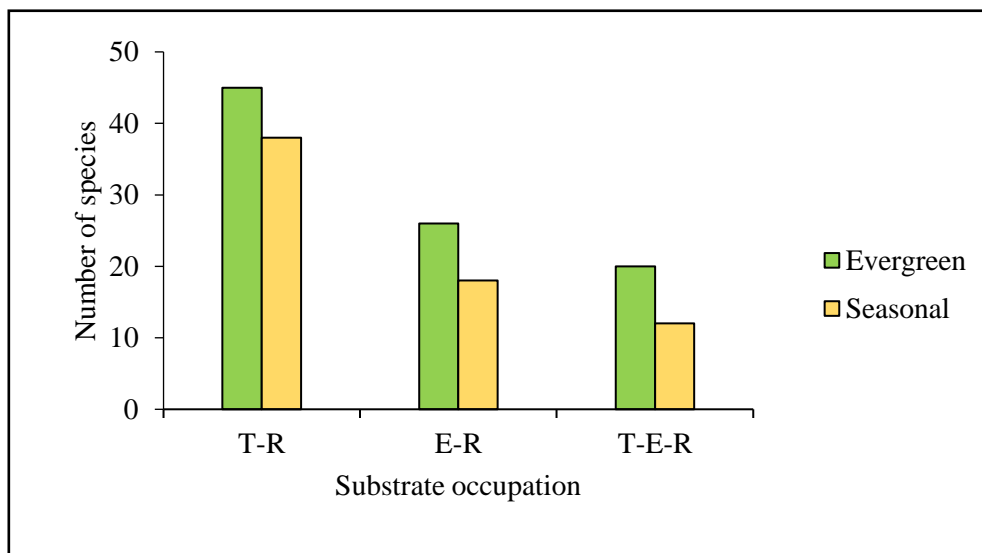

Fig. 2 Alternative substrate occupation of rupestrian sporochorus vascular plants in the two studied forest matrixes. T = terrestrial or geophytic; E = epiphytic or corticolous; R = rupestrian or epipetric.

The Theory of Island Biogeography applied to pteridophyte communities on sandstone cliffs

The results indicated no relationship between the area of rocky outcrops and the richness of pteridophyte species (p = 0.6). A Pearson correlation coefficient was 0.36 (Fig. S5). The ordination analysis (NMDS) indicated a general overlap of the studied cliffs, i.e., no clear influence of the two forest matrixes on the differentiation of epipetric pteridophyte communities (Fig. 3). The mixture of sample units also indicated a low effect

of the cliff areas, which varied greatly from one to another. Two sites from the Evergreen matrix showed a somewhat outstanding position in the ordination diagram, the upper right (E12) and the lower left (E6). These two sites correspond to the richest area, with 25 species, and one of the two northern marginal areas, respectively. In a similar way, one site of the Seasonal matrix appeared as more distantly related, the one in the lower right position (S12). This site showed the lowest species richness in the entire Seasonal area (seven species). However, on this outcrop the single occurrence of *Nephrolepis cordifolia* (Nephrolepidaceae) was registered.

The Jaccard index of similarity showed 40.3% of shared species between the two vegetation matrixes for the pteridophyte communities. According to the Mantel's test, differences in floristic composition between closest outcrops and beta diversity were not related to geographical distance. Since the test showed that geographical distance between locations was insignificant (p = 0.274).
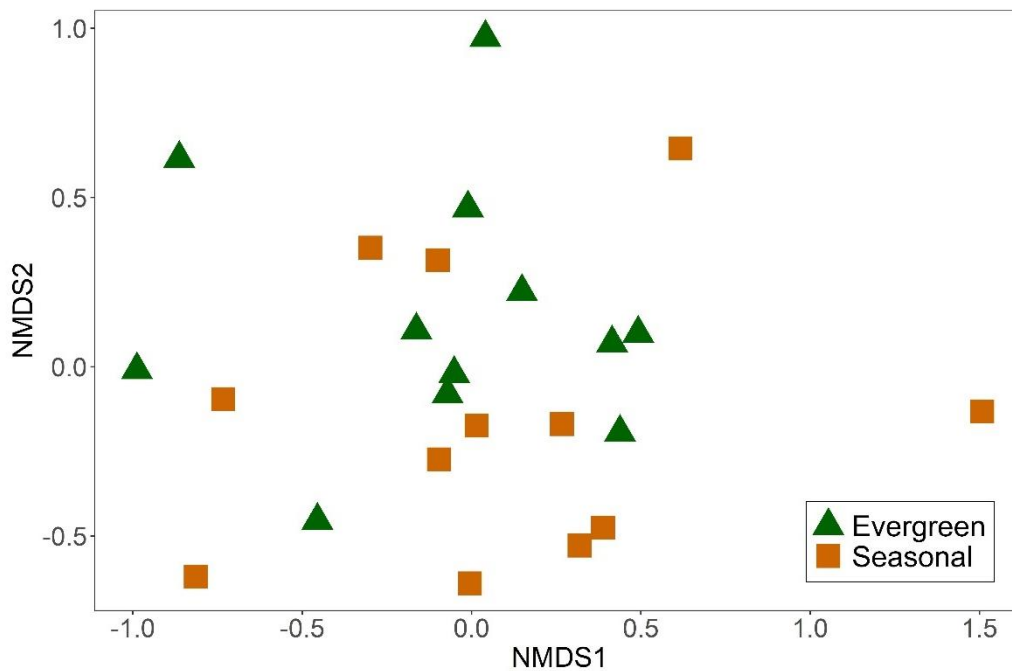

Fig. 3 Ordination diagram of 24 sandstone outcrops, 12 in each forest matrix (evergreen and seasonal). Spatial ordination of sample units derived from non-metric multidimensional scaling analysis (NMDS), using Bray-Curtis distance. Stress = 0.180.

Beta diversity and the relative influence of spatial and environmental variables

Total beta diversity (pairwise βSOR) was 0.905 for Evergreen Forest was 0.835 and 0.844 for Seasonal Forest. When evaluating the portion of each component of beta diversity, turnover (pairwise βSIM) had a significant contribution both in the Evergreen Forest (0.744), and in the Seasonal Forest (0.793), as well as in the two plant formations (0.862). The component nestedness (pairwise βSNE) showed a low contribution, the values ranged between 0.043 and 0.091 (Table 3).

Table 3 Total beta diversity, i.e., Sørensen dissimilarity (βSOR) and its two components, turnover (Simpson dissimilarity, βSIM) and nestedness (βSNE) in Evergreen Forest, Seasonal Forest and Both Forest Types.

Forest types	βSOR	βSIM	βSNE
Evergreen Forest	0.835	0.744	0.091
Seasonal Forest	0.844	0.793	0.050
Both Forests	0.905	0.862	0.043

Considering both forest-types, seasonal temperature fluctuations were the variables that most influenced the variation in the composition of vascular plants dispersed by spores. By applying a dbRDA on the spatial variables we observed that both wide-scale (MEM1) and finer-scale MEMs (MEM5 and MEM6) were significant, indicating that beta diversity is spatially structured (PCNM = 0.394).

The partitioning of variation showed that the spatially structured portion of the environmental variables explained 11,6% of the floristic patterns of pteridophyte communities. The purely spatial component explained 5.1% of the variation, while the purely environmental fraction explained 7.4% of the variation. These percentages indicated that 88.3% of the variation in beta diversity, i.e., the composition of pteridophyte communities, may be explained by other factors. Both the purely environmental and spatial variables, as well as the variables together resulted to be significant (Table 4).

Table 4 Results of the partial RDA analysis (variation partitioning) for the composition of pteridophytes growing on sandstone cliffs immersed in Atlantic Forest matrix.

Partition of variation	Adj. R^2	F	Significance
[a+b] = Enviromental	0.064	1.31	0.014
[b+c] = Spatial	0.041	1.33	0.029
[a+b+c] = Enviromental + Spatial Individual fractions	0.116	1.37	0.003
[a] = Only environmental	0.074	1.33	0.023
[b] = Environmental spatially structured	0.009	----	----
[c] = Only spatial	0.051	1.35	0.043
[d] = Residuals (Undetermined)	0.883	----	----

Discussion

Taxonomic diversity and occurrence on alternative substrates

Our study shows a relatively high diversity of vascular plants dispersed by spores growing on subtropical rocky outcrops. The species richness observed in this study corresponds approximately to 40% of the species reported on rocky outcrops in the Flora of Brazil (BFG 2023). Studies focusing these groups of plants on sandstone outcrops are scarce and very distinct in species number, varying from 29 species (Michelon and Labiak 2013) to 60 species (Schwartsburd and Labiak 2007). According to Silva (2016) on the diversity studies of rocky outcrops have increased since the 1990s, but most of them focused angiosperms and bryophytes (Meirelles et al. 1999; Silva et al. 2018) and, from the rock type point of view, on granitic-gneissic outcrops (Porembski et al. 1998; Araújo et al. 2008).

The sporochoric vascular species found on the rocky outcrops are also reported for other substrates. This ability can also be observed in several studies carried out in neotropical forests (Dittrich et al. 2005) and along elevation gradients (Paciencia 2008; Nervo et al. 2016). According to Page (1979), the truly rupestrian species of pteridophytes are found only in temperate localities or in areas of the tropics with intense dry periods. Among the different types of co-occurrences reported, species showing both terrestrial and epiphytic habit are usually the most frequent. In this study we found a 45% of co-occurrence between these two substrates in the two formations. Similar results have also been reported in others studies conducted in the Atlantic Forest (Santos and Windisch 2008; Gonzatti et al. 2014). This low general habitat specificity regarding the three substrate types can be viewed as an indication of the high adaptability of some species to

environmental variations, but also as similar habitats on different substrates, i.e., dry sandy soils similar to sandstones or humus accumulations on trees similar to terrestrial habitats.

This dominance of the terrestrial habit against the epiphytic in the rocky outcrops is due to characteristic of the environment, the epiphytic habitat is quite restrictive; the lack of relationship with the soil implies a high risk of drying and the obligatory ability to use rainwater or moisture quickly and directly (Dubuisson et al. 2009). Another aspect concerning to the substrate preference is the variation depending on the habitat where it is collected and according to the region of the species in which it is found; for example, predominantly terrestrial species may occasionally be found as accidental epiphytes such as, *Anemia phyllitidis* and *Olfersia cervina*. These species manage to settle on phorophytes according to appropriate environmental conditions, such as high relative air humidity and humus or sediment accumulations at the base of the trunks (Costa et al. 2017).

The Theory of Island Biogeography applied to pteridophyte communities on sandstone cliffs

Our study did not find a relationship between the area and the species richness. The lack of the relationship between the area and the richness of species of the pteridophyte communities in the sandstone outcrops was also recorded in a study by Paciencia and Prado (2005) on fragments of lowland woodlands and other studies with nonvascular plants dispersed by spores (Kimmerer and Driscoll 2000; Silva et al. 2018). On the other hand, some studies showed a significant dependence on total area, as Murakami et al. (2005), focusing pteridophytes in fragmented patches, Meirelles et al. (1999) including all vascular plants on rocky outcrops, and Magalhães and Lopes (2015) concerning vascular epiphytes and the relation with host-tree size.

There are two possible reasons why the diversity of pteridophytes cannot surely be predicted by the size of the rocky outcrops. First, pteridophytes mostly occur among other rupestrial plant species, especially bromeliads, cacti, orchids, and gesneriads. Second, the habitat heterogeneity, more pronounced features generate richer ecological habitats (Murakami et al. 2005).

The geographical distances between sandstone outcrops do not influence the distribution of these plants, coinciding with the results of a similar study carried out by Lautert *et al*. (2015) with the same plant groups but restricted in areas of semideciduous forest. The lack of relationship between isolation and beta diversity could be masked by the biological traits of each species (Watson et al. 2004). For example, some species are not affected by isolation because they are very mobile (Ambuel and Temple 1983), or because of the permeability of the matrices (Dondina et al. 2017). Kimmerer and Driscoll (2000) found that soil island size, isolation and microhabitat heterogeneity had no influence on the richness of nonvascular plants dispersed by spores, suggesting that the richness of this group may be the result of intrinsic traits, such as population-level processes governing dispersion and establishment.

The responses of the isolation effect and dispersal capacity in spore-dispersed vascular plants varies by community. On the one hand, there are studies stating that the spores of pteridophytes can reach great distances (Wolf et al. 2001; De Groot et al. 2012). On the other hand, despite the high dispersion capacity of these plants, most spores fall near the mother plant (Pajarón et al. 2017) and, so some spatial structure determined by dispersion limitation is expected. In addition, the responses to distance vary according to species composition, and by taxonomic groups in the same community. An interesting example constitutes the study by Melo and Waechter (2018), in a study with bromeliads in the same area of study of our research, found a positive relationship between area and richness, and a clear distinction in the composition of the two types of formations affected by distance. Thus, both dispersion as well as other properties of organisms determine differently the rates of immigration and extinction, and the colonization process, under the same conditions (Pâslaru 2014).

Although the TIB still represents an important basis for studying colonization processes, the identification of conservation areas (Matthews et al. 2014), and the application in terrestrial communities the theory is sometimes criticized because some of the required assumptions are often not evident in the study. In addition to area and isolation, the characteristics of islands that contribute to species composition and diversity include the influence of ocean currents, human transport and other factors disrupting the permeability of barriers, and so affecting the persistence of native plants (Brown and Lomolino 2000). Although dispersion has a very important role in the Neutral Theory (Hubbell 2001), the premise of this model is based on the limitation of dispersion, which

is not the case for pteridophytes. In summary, it seems necessary to evaluate the role of dispersion in light of the controversy that the process has generated (Zillio and Condit 2007).

Beta diversity and the relative influence of spatial and environmental variables

Our study revealed a high beta diversity within each and the two forest matrixes. The high degree of beta diversity for the two forest types found in our study is not surprising because the study area is a transitional area and agrees with other studies reporting that on tropical rocky outcrops high beta diversity is expected, due to their isolation (Burke 2002), and to the heterogeneity of the surrounding matrix. For example, granite outcrops dispersed within the Atlantic Forest showed to be more diverse than similar habitats in Africa, and this diversity was attributed to the rich species reserve pool in the surrounding habitat (Porembski et al. 1998).

The patterns of beta diversity showed a much higher contribution by turnover than by nestedness, which is reflected in the high number of exclusive species by each formation type. This result was expected, considering that species turnover reveals the variation in the community structure from one sampling unit to another along a spatial, temporal or environmental gradient (Anderson et al. 2011). The high proportion of species occurring at a single site and the high number of rare species reflects the complexity and heterogeneity of rock outcrops. In addition, high species turnover rates and beta diversity generally support other studies and reinforce the need to protect rocky habitats within distinct type of formations (Meirelles et al. 1999; Bergamin et al. 2017).

The substitution of species along space is in addition related to the distribution with the environmental variations in the whole study area, which comprises several climatic regimes and landscape variations, affecting the structure of forest communities in the Southern Brazilian Atlantic Forest (Bergamin et al. 2012). Beta diversity of rock-dwelling pteridophytes is affected by several factors, mainly precipitation and temperature, including both daily and year-round variations. In subtropical Brazil, the distribution of species and vegetation types is frequently related to differences in regional amounts of temperature and precipitation, causing the differentiation between evergreen and seasonal physiognomies of the Atlantic Forest (Oliveira-Filho and Fontes 2000; Bergamin et al. 2012).

Our results help understand what factors affect the distribution of pteridophyte species in rock outcrops on sandstone outcrops of both evergreen and seasonal forests. The spatially structured fraction of environment was the main determinant among the explained portions of variance. Diniz-Filho et al. (2012) argued that the spatially structured environment fraction can also be used to justify distance-decay similarity, but this distance-decay needs not necessarily be related only to neutral processes, could also be explained by differential responses of species abundance and niche processes to environmental gradients or patches (Gasper et al. 2012). On the other hand, although low in percentage, but significant the diversity of rupicolous plant communities on rocky outcrops is largely determined by fine-scale environmental factors (e.g., microhabitat) and limited dispersal. However, the studied pteridophyte species are not exclusively rupicolous and "dispersal limitation" is not to be assumed in this group of plants. Alternatively, the distribution of pteridophytes could be favored more by niche selection than by neutral processes.

In studies of tropical plant communities, much of the variation in species turnover generally remains unexplained (Tuomisto et al. 2003). This unexplained variation may be truly stochastic and unstructured, but it may also be related to variables that were not measured but, in some studies, showed a deterministic influence, such as soil factors properties (Conceição et al. 2007; Zuquim et al. 2012), slope exposition (Nettesheim et al. 2014), continentality (Meirelles et al. 1999) and, the degree of disturbance in the areas surrounding the cliffs (Fitzimons and Michael 2017).

Conclusions

Our results indicate that the species richness of pteridophyte communities on rocky outcrops may be mostly influenced by processes unrelated to area and isolation, as expected by the Theory of Island Biogeography. The forest permeability might be one important factor, although this permeability possibly varies differently for distinct taxonomic and ecological (adaptive) groups. In addition, macro-scale environmental and spatial factors are also of little importance to the pteridophyte communities of rocky outcrops. Future studies should address those fine-scale variables related to the substrate, microhabitat, microclimate, and vegetation structure (i.e., height and coverage, disturbance). The presence of rare and endangered species (e.g., *Cheilanthes juergensii*) on the outcrops shows the importance of preserving the sandstone cliffs for the maintenance of local and regional floristic diversity.

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Declarations

Conflicts of Interest The authors have no conflicts of interest or relevant financial or non-financial interests to disclose

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Considerações finais

Esta investigação representa uma importante contribuição para o conhecimento da diversidade e distribuição das plantas vasculares dispersas por esporos (pteridófitas), em escarpas rochosas inseridas em das principais fisionomias da Floresta Atlântica do Sul do Brasil, a Floresta Ombrófila Densa e a Floresta Estacional Semidecidual. Até o presente, estas plantas rupestres foram incluídas sobretudo em contextos florísticos mais amplos e, portanto, sujeitas a inventários menos precisos em termos de composição e distribuição. Nosso trabalho descreve e analisa diversos aspectos relacionados a riqueza e abundância das espécies de pteridófitas encontradas sobre 24 afloramentos rochosos areníticos da área de estudo.

Classificamos as espécies rupestres ou rupícolas de acordo com dois substratos alternativos principais, o terrestre, e o epifítico, tendo por base numerosas observações pessoais na natureza complementadas por informações disponíveis na literatura ecológica e florística. Registramos um total de 67 espécies em toda a área de estudo, com um número relativamente elevado de espécies compartilhadas (27 – 40,3%) e exclusivas na floresta ombrófila (24 – 35,8%), enquanto um número ligeiramente menor de espécies restritas na floresta sazonal (16 – 23,8%). Um contingente de 19 espécies (28,4%) foi registrado como rupícola pela primeira vez, sendo que antes contavam na literatura apenas como terrestres ou epifíticas. Considerando os três principais substratos ocupados por licófitas e monilófitas, observamos uma maior co-ocorrência com o substrato terrestre do que com o epifítico. Nenhuma das espécies amostradas pode ser considerada como rupícola exclusiva, embora no extremo sul do Brasil duas samambaias ocorram preferencialmente nesta condição: *Nephrolepis cordifolia* (Nephrolepidaceae) e *Phlebodium pseudoaureum* (Polypodiaceae).

Com base na Teoria de Biogeografia de Ilhas de MacArthur & Wilson fizemos análises para verificar se existe relação entre área e riqueza taxonômica, assim como, a influência da distância entre afloramentos na riqueza e composição das licófitas e monilófitas. Encontramos uma relação significativa entre essas variáveis, possivelmente como resultado do foco em variáveis a macro-escala.

As análises para identificar as variáveis espaciais e ambientais que estão influenciando a distribuição das espécies de pteridófitas nas escarpas rochosas, levaram a descoberta de que algumas, variáveis ambientais foram significativas, como a precipitação anual e a amplitude térmica provocada pela sazonalidade. Quanto às variáveis espaciais, tanto aquelas em escala mais ampla (regional) como as de escala mais restrita (local) pouco influenciaram a estrutura das comunidades destes grupos. Por tanto, sem uma contribuição significativa para a diferenciação comunitária.

A variação da diversidade beta através de cada componente (substituição e aninhamento) resultou em valores similares para os afloramentos inseridos nas duas matrizes florestais (ombrófila e semidecidual), porém com valores maiores para o componente substituição (*turnover*). A falta de relação significativa, tanto da área dos afloramentos como da distância entre afloramentos, assim como e a baixa contribuição das variáveis espaciais e ambientais, levou-nos a concluir que a dispersão é o fator mais importante que está impulsionando diferentes padrões de distribuição. Em outros termos,

a vegetação rupestre esporocórica parece ser mais influenciada por processos estocásticos do que determinísticos.

Nossas descobertas podem contribuir para uma melhor compreensão da interação entre espécies de habitats rochosos e outros ambientes florestais, e mesmo campestres, considerando que rochas expostas também ocorrem em áreas abertas. Por outro lado, nosso trabalho deixa em aberto outras questões para serem respondidas em trabalhos futuros, tais como: (i) Qual a influência de variáveis espaciais e ambientais em microescala, ou seja, a heterogeneidade interna de cada afloramento? (ii) Como a dispersão por esporos se relaciona com outros mecanismos (e.g. zoocoria) de ilhas rupestres? (iii) Qual o efeito de outros tipos de rocha, considerando que a diversidade geológica da Região Sul também contempla afloramentos graníticos e basálticos?

As questões levantadas por nós no artigo, assim como, aquelas mencionadas nas considerações finais logo acima, são fundamentais para o conhecimento e a conservação de ambientes rochosos como refúgios ecológicos e substratos alternativos de espécies em áreas florestais cada vez mais fragmentadas.

Supplementary material

Fig. S1 Examples of sandstone cliffs from the South Brazilian Atlantic Forest matrix: the upper three from the Evergreen Forest, while the lower three from the Seasonal Forest.

Fig. S2 Species of pteridophytes sampled on sandstone cliffs in both Evergreen and Seasonal forest types a) *Adiantum raddianum* (PTE), b) *Anemia phyllitidis* (ANE), c) *Anemia tomentosa* (ANE), d) *Campyloneurum nitidum* (POL), e) *Christella hispidula* (THE), f) *Doryopteris lorentzii* (PTE), g) *Didymochlaena truncatula* (DID), h) *Micrograma squamulosa* (POL), i) *Micrograma vacciniifolia* (POL), j) *Neoblechnum brasiliense* (BLE), k) *Olfersia cervina* (DRY), l) *Selaginella muscosa* (SEL). Family names abbreviated with three first letters.
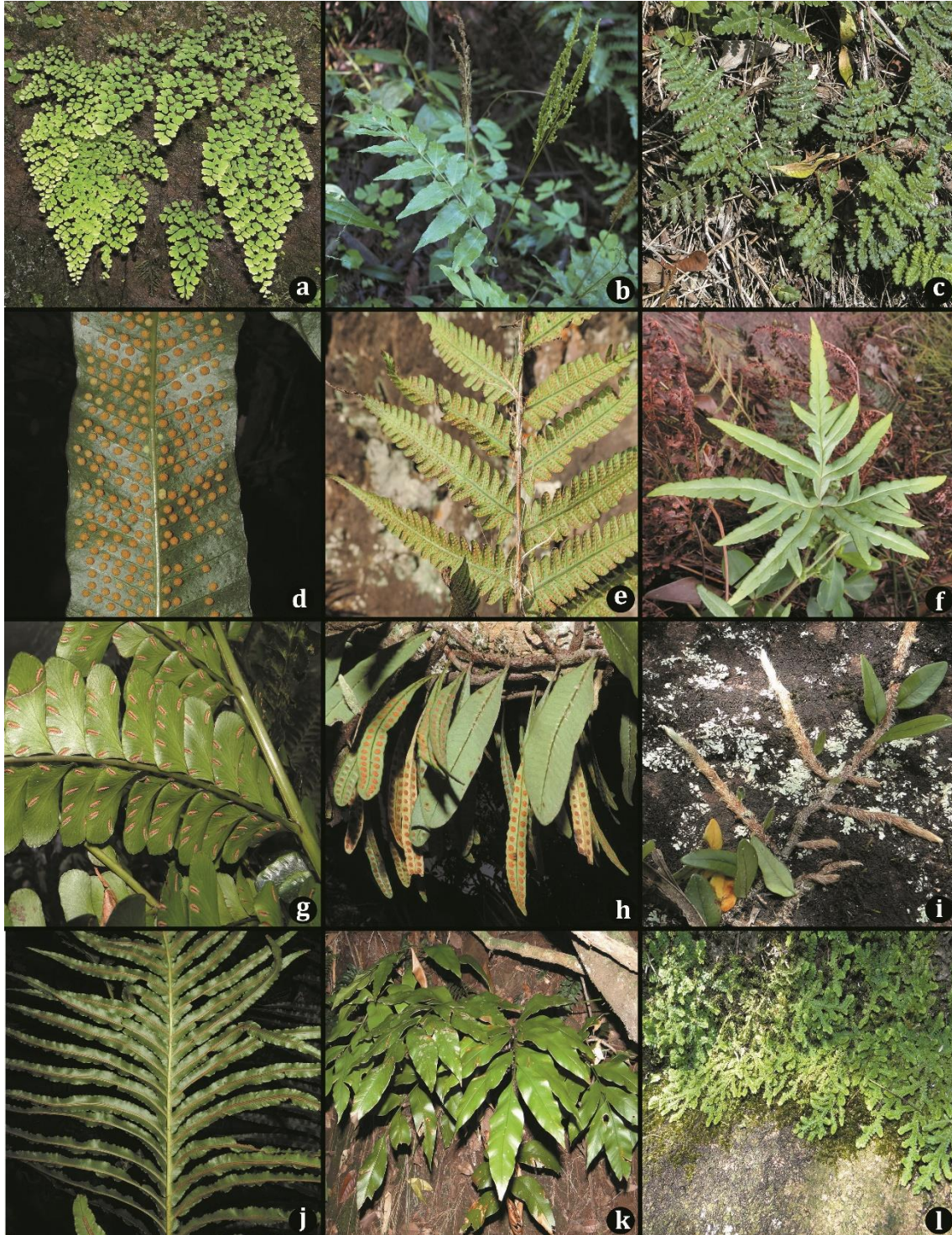
Fig. S3 Sandstone cliffs and species of pteridohytes sampled in the Evergreen Forest area of Southern of Brazil. a) *Asplenium claussenii* (ASP), b) *Blechnum austrobrasilianum* (BLE), c) *Doryopteris pentagona* (PTE), d) *Didymoglossum hymenoides* (HYM), e) *Elaphoglossum glaziovii (DRY),* f) *Elaphoglossum luridum* (DRY), g) *Hymenophyllum asplenioides* (HYM), h) *Hymenophyllum caudiculatum* (HYM), i) *Mickelia scandens* (DRY), j) *Pecluma pectinatiformis* (POL), k) *Phlegmariurus reflexus* (LYC), l) *Vandenboschia radicans* (HYM). Family names abbreviated with three first letters.
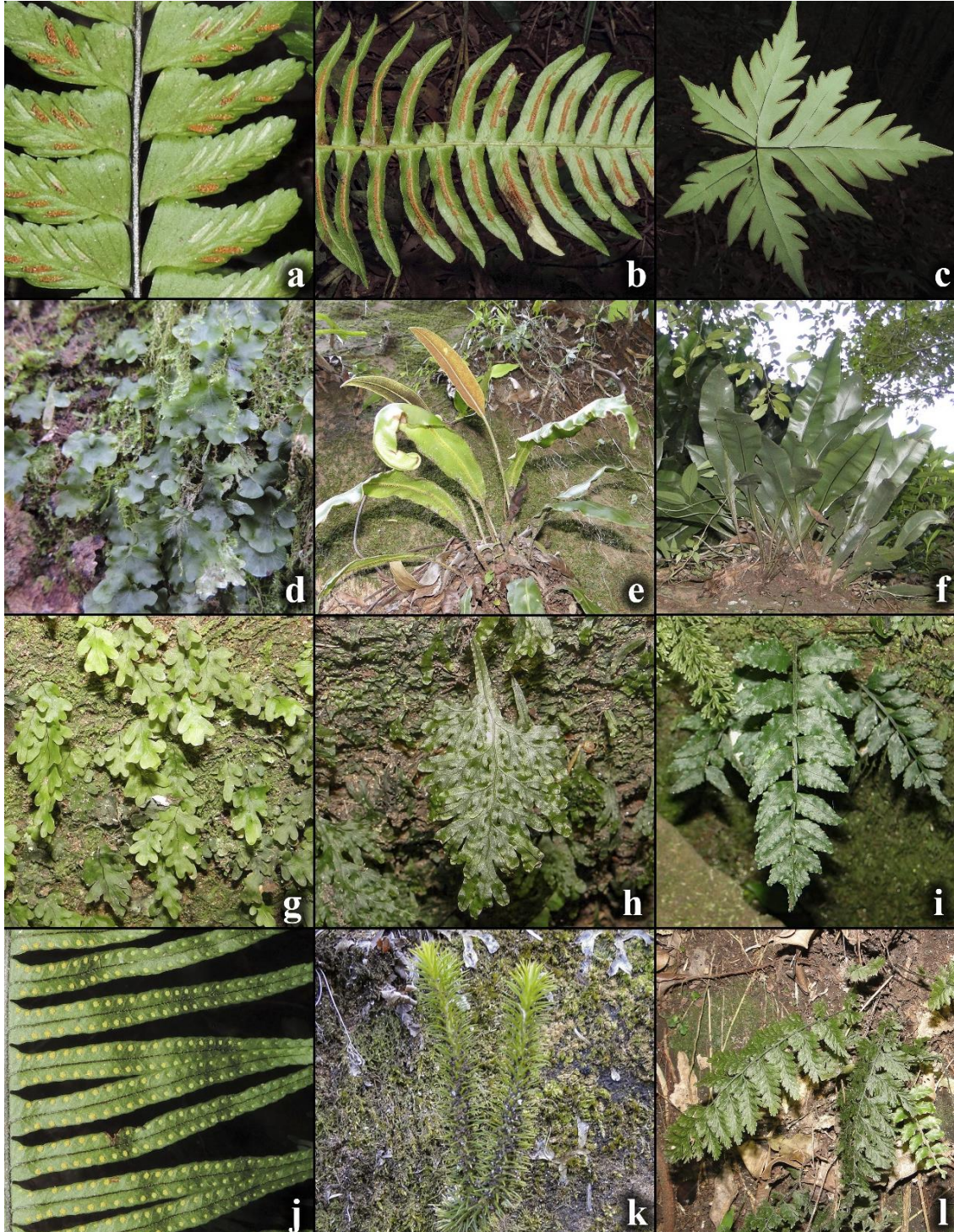
Fig. S4 Sandstone cliffs and species of pteridohytes sampled in the Seasonal Forest area of Southern of Brazil. a) *Adiantum pentadactylon* (PTE), b) *Blechnum occidentale* (BLE), c) *Blechnum polypodioides* (BLE), d) *Diplazium cristatum* (ATH), e) *Doryopteris triphylla* (PTE), f) *Macrothelypteris torresiana* (THE), g) *Nephrolepis cordifolia* (NEP), h) *Pleopeltis lepidopteris* (POL), i) *Pleopeltis minima* (POL), j) *Pteris deflexa* (PTE), k) *Pteris vittata* (PTE), l) *Selaginella sellowii* (SEL). Family names abbreviated with three first letters.

Fig. S5 Relationship between the area of the outcrop and the species richness. The figure shows that there is no relationship between the area of the scarps and the species richness. Gray shading around the line represents the 95% confidence interval.