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**Diversidade e distribuição de Bromeliaceae em escarpas rochosas da Floresta Atlântica Sul-Brasileira**

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Tese de doutorado apresentada ao Programa de Pós-Graduação em Botânica da Universidade Federal do Rio Grande do Sul, como parte dos requisitos para obtenção do título de Doutora em Ciências: Botânica.

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## Agradecimentos

# Sumário

# Resumo

Os afloramentos rochosos são considerados ilhas terrestres por apresentarem condições ambientais e comunidades bióticas distintas do entorno. Essas formações rochosas podem apresentar grande heterogeneidade topográfica, desde horizontais ou inclinadas até verticais ou escarpadas. Os ambientes rupestres são colonizados por uma vegetação altamente especializada, exposta a condições microclimáticas e edáficas particulares, como temperaturas mais elevadas em relação ao entorno, retenção de calor e ausência de solo. Bromeliaceae é uma das famílias com maior frequência e diversidade em afloramentos rochosos neotropicais por apresentarem diversos atributos funcionais que permitem a sobrevivência em condições de estresse hídrico. Neste trabalho avaliamos os padrões de diversidade e distribuição de Bromeliaceae em escarpas rochosas inseridas em matriz de Floresta Atlântica no sul do Brasil. Foram amostradas 24 escarpas rochosas, sendo 12 associadas à Floresta Ombrófila Densa e 12 associadas à Floresta Estacional Semidecidual. No primeiro capítulo avaliamos os padrões florísticos de bromélias rupestres associadas às diferentes fisionomias florestais, analisando composição, riqueza e mecanismos de dispersão. No segundo analisamos os padrões de diversidade beta de bromélias rupestres, identificando variáveis ambientais e espaciais que podem atuar na estruturação de comunidades rupestres de florestas pluviais e sazonais. No terceiro avaliamos a vulnerabilidade ambiental das escarpas por diversos critérios, associando o grau de ameaça com a diversidade e a abundância de bromélias rupestres, evidenciando assim a importância dos afloramentos para a conservação das espécies. Amostramos 26 espécies de bromélias e nossos dados mostraram diferenças florísticas evidentes entre comunidades de bromélias rupestres associadas à Floresta Ombrófila Densa e à Floresta Estacional Semidecidual. Nossos resultados mostraram que a diversidade de bromélias não está diretamente relacionada ao grau de isolamento das escarpas amostradas. No entanto, a similaridade florística diminuiu com o aumento da distância entre as unidades amostradas, corroborando uma das previsões da Teoria da Biogeografia de Ilhas. Ao avaliar os padrões de diversidade beta, observamos uma contribuição significativamente maior de substituição (*turnover*) em relação ao aninhamento (*nestedness*). A sazonalidade térmica, a precipitação anual e a distância da linha da costa foram os fatores mais importantes que afetaram a variação na composição florística. Entretanto, mais uma vez ficou evidente que o espaço exerce uma influência importante nos padrões de distribuição das espécies estudadas. Nossos resultados demonstram que tanto os fatores ambientais determinísticos quanto os efeitos espaciais estocásticos podem atuar em conjunto para definir a estrutura das comunidades de bromélias que ocorrem sobre rochas. Durante nosso trabalho de campo registramos também diferentes tipos de impactos ambientais e de possíveis ameaças que ocorrem sobre e no entorno dos afloramentos. Neste contexto, nossos resultados mostraram que tanto a riqueza quanto a abundância das bromélias diminuem à medida que aumenta o grau de ameaça nos afloramentos rochosos, mostrando a importância da conservação desses ambientes para a manutenção da flora local e regional.

**Palavras-chave:** Afloramentos Rochosos; Floresta Ombrófila; Floresta Estacional; Bromélias.

**Abstract**

Rock outcrops are considered terrestrial islands, because they have different environmental conditions and biotic communities when compared to the surroundings. These rock formations have great topographic heterogeneity, from horizontal or inclined to vertical. The rock environments are colonized by highly specialized vegetation, exposed to particular microclimatic and edaphic conditions, such as higher temperatures in relation to the surroundings, heat retention and absence of soil. Bromeliaceae is one of the families with the highest frequency and diversity in neotropical rock outcrops, because they have several functional traits that allow survival under conditions of water stress. In this work we evaluate the diversity and distribution patterns of Bromeliaceae in rocky cliffs immersed in the original matrix of the Atlantic Forest in southern Brazil. Twenty-four rocky cliffs were sampled, 12 of which were associated with the Dense Ombrophylous Forest and 12 associated with the Semidecidual Seasonal Forest. This study presents two original articles and one short communication. In the first one we evaluated the floristic patterns of rock bromeliads associated to different forest physiognomies, analyzing composition, richness and dispersion mechanisms. In the second, we analyzed the beta diversity patterns of rupestrial bromeliads, identifying environmental and spatial variables that can act in the structuring of rainforest and seasonal forest communities. In the third chapter, we evaluated the environmental vulnerability of cliffs by several criteria, associating the degree of threat with the diversity and abundance of rock bromeliads, thus evidencing the importance of outcrops for species conservation. We sampled 26 species of bromeliads and our data showed evident floristic differences between rupestrial bromeliad communities associated to the Dense Ombrophylous Forest and the Semidecidual Seasonal Forest. Our results showed that bromeliad diversity is not directly related to the degree of isolation of the cliffs sampled. However, floristic similarity decreased with increasing distance between the sampled units, corroborating one of the predictions of the Islands Biogeography Theory. When evaluating the beta diversity patterns, we observed a significantly greater contribution of turnover than nestedness. Thermal seasonality, annual precipitation and distance from the coastline were the most important factors that affected the variation in floristic composition. However, once again, it was evident that space exerts an important influence on the patterns of distribution of the species studied. Our results demonstrate that both deterministic environmental factors and stochastic spatial effects can act together to define the structure of bromeliad communities occurring on rocks. During our field work we have recorded different types of environmental impacts and possible threats that occur on and around outcrops. In this context, our results showed that both the richness and the abundance of the bromeliads decrease as the degree of threat in the rock outcrops increases, showing the importance of the conservation of these environments for the maintenance of the local and regional flora.

**Keywords:** Rock outcrops; Evergreen Forest; Seasonal Forest; Bromeliads.

**Introdução geral**

Afloramentos rochosos são ambientes peculiares, que comumente se destacam no meio da paisagem como ilhas terrestres com características florísticas e ecológicas diferenciadas (Porembski and Barthlott 2000; Ribeiro et al. 2007; Moura et al. 2011). Esses ambientes podem apresentar tamanhos e formas topográficas distintas, formando domos em meio a paisagens planas, como nos inselbergues graníticos do sudeste do Brasil (Porembski and Barthlott 2000; Porembski 2007; de Paula et al. 2016) ou apresentando formas irregulares como nas bancadas lateríticas da região centro-oeste (Takahasi and Meirelles 2014). Muitos desses afloramentos exibem também escarpas rochosas, caracterizadas como a face exposta do afloramento e como um penhasco íngreme (Larson et al. 2000).

As escarpas rochosas raramente são incluídas em inventários florísticos ou estudos ecológicos, principalmente pelas dificuldades de acesso. Este fato torna estes ambientes negligenciados em relação a outros, e, portanto, com estrutura florística muitas vezes pouco conhecida. Apesar disso, pesquisadores tem mostrado que as escarpas rochosas também podem sustentar uma alta diversidade florística, resultante de muitos micro-habitats, formados principalmente por fissuras e saliências nas rochas (Kuntz and Larson 2006).

Considerando a diversidade geológica, climática e vegetacional, o Brasil apresenta também uma grande quantidade de ambientes rochosos distintos, que se distribuem de norte ao sul do país (Moura et al. 2011). Diversos estudos foram realizados em afloramentos rochosos, principalmente nas regiões Nordeste (Conceição et al. 2007; Neves and Conceição 2007; Gomes and Alves 2009; Costa et al. 2015) e Sudeste do país (Ribeiro et al. 2007; Jacobi and Carmo 2011; Do Carmo and Jacobi 2013; do Carmo et al. 2016; de Paula et al. 2016). Na região Sul do Brasil, as plantas rupestres foram também estudadas nas floras do estado do Rio Grande do Sul (Rambo 1967; Winkler 1982) e Santa Catarina (Reitz 1983), em vários estudos locais focados ou incluindo a composição florística de afloramentos ou de escarpas (Femandes and Baptista 1988; Waldemar 1998; Bauer and Larocca 2003; Silva Filho et al. 2013; Ferreira et al. 2014) e em estudos ecológicos focando grupos de plantas específicos (Rocha 2009; Carlucci et al. 2011; Saraiva et al. 2015).

Os afloramentos rochosos por apresentarem características xéricas, como ausência de solo, retenção de calor e baixa disponibilidade de água, possuem uma vegetação majoritariamente especializada, com características morfológicas e fisiológicas adaptadas às condições de estresse hídrico (Parmentier 2003; Oliveira e Godoy 2007). A família Bromeliaceae tem sido destacada como uma das mais frequentes e diversificadas em ambientes rochosos, sobretudo pelo papel ecológico no processo de sucessão, atuando como plantas berçários, formando ilhas que aumentam a disponibilidade de água e suporte mecânico para outras espécies, bem como no fornecimento de recursos para a fauna local (Medina et al. 2006; Rocha et al. 2014; de Paula et al. 2016). A formação de cisternas pela disposição espiralada de folhas, a presença de tricomas e a suculência das folhas, são algumas

características que conferem as bromélias a capacidade de se estabelecer nesses ambientes (Benzing 2000).

Estudos florísticos e ecológicos com a família Bromeliaceae também tem sido realizados na região sul do Brasil (Bonnet et al. 2010a; Bonnet et al. 2010b; Hoeltgebaum et al. 2013). Considerando as espécies rupestres, destacamos trabalhos ecológicos com espécies dos gêneros *Dyckia* e *Bromelia* (Waldemar and Irgang 2003; Rocha et al. 2014), além de diversas descrições de novas espécies rupestres e reófitas, especialmente as dos gêneros *Dyckia* e *Tillandsia* (Strehl 2000; Büneker et al. 2015; Büneker et al. 2015). Os ecossistemas de Mata Atlântica, especialmente as áreas de domínio das Florestas Ombrófilas na costa leste do Brasil, são conhecidos por abrigar a maior diversidade e o maior número de endemismos de bromélias (Martinelli et al. 2008).

Na Floresta Atlântica do sul do Brasil, os afloramentos rochosos também são amplamente distribuídos em diferentes fisionomias, apresentando diferentes litologias e grande heterogeneidade topográfica que formam mosaicos em meio à paisagem florestal, muitas vezes fragmentada. Três principais fisionomias formam a Floresta Atlântica Sul Brasileira: Floresta Ombrófila Densa, caracterizada pela ocorrência de temperaturas elevadas e precipitações bem distribuídas durante o ano; Floresta Estacional, caracterizada pela dupla estacionalidade climática e Floresta Ombrófila Mista, também conhecida como Mata das Araucárias, que é característica de regiões mais frias do planalto sul brasileiro (Veloso et al. 1991; Oliveira Filho e Fontes 2000; IBGE 2012).

A proposta desse trabalho foi avaliar os padrões de distribuição de bromélias rupestres que crescem sobre escarpas aréniticas inseridas em uma zona de transição entre a Floresta Ombrófila Densa e a Floresta Estacional Semidecidual, localizada no nordeste do Rio Grande do Sul e sudeste de Santa Catarina. Neste cenário, buscou-se entender os mecanismos que atuam na estruturação de comunidades, apresentando discussões fundamentadas em teorias ecológicas, além de debater a importância dessas formações para manutenção da biodiversidade de bromélias, incluindo espécies raras e endêmicas.

O trabalho está organizado em três capítulos, constituindo três artigos independentes e formatados segundo as normas específicas de cada revista. No primeiro capítulo identificamos os padrões florísticos de bromélias rupestres nas regiões de florestas Ombrófila e Estacional, analisando as diferenças na composição, riqueza e mecanismos de dispersão entre as diferentes fisionomias, e a influência da área e do isolamento sobre esses atributos. No segundo capítulo, analisamos os padrões de diversidade beta de bromélias ao longo das escarpas rochosas e identificamos os mecanismos que podem atuar na estruturação de comunidades. No terceiro capítulo avaliamos a vulnerabilidade ambiental das escarpas estudadas, para identificar o grau de ameaça por diferentes fatores de distúrbio e discutir a importância de conservação desses ambientes para a manutenção da diversidade de bromélias rupestres.

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# CHAPTER 1

**Effect of vegetation matrix on diversity and distribution of epipetric bromeliads in a transitional region between Evergreen and Seasonal Forest**

# Effect of vegetation matrix on diversity and distribution of epipetric bromeliads in a transitional region between Evergreen and Seasonal Forest

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**Abstract**

Bromeliaceae is frequently an important family in several distinct environments of the Brazilian Atlantic Forest, including rocky habitats. They are also one of the most common and diverse taxonomic groups in neotropical rocky outcrops. For the first time, diversity and distribution patterns of epipetric bromeliads immersed in forest matrix were evaluated in different forest physiognomies. We tested the precepts of the Theory of Island Biogeography to verify the isolation effect that rocky areas operate on Bromeliaceae. We hypothesize that epipetric bromeliads are represented by exclusively rupestrial species, but also by species commonly epiphytic, coming from the flora of the surrounding matrix. Furthermore, composition and diversity of Bromeliaceae are influenced by the forest type, area of the rocky surface, and the distance between these habitats. The study area comprises sandstone cliffs immersed in the fragmented Atlantic Forest on Southern Brazil. Twenty-four mostly vertical rocky outcrops were sampled, 12 in each forest physiognomy. We used diversity curves, analysis of variance, and indicator species analysis to evaluate how bromeliad communities vary among the two forest types. Generalized linear models and correlation tests were used to evaluate the relationship between species richness, cliff area, and distance. The relationship between species similarity and geographical distance of the cliffs was estimated by a Mantel test. We recorded 26 bromeliad species. The data showed floristic differentiation between bromeliad communities in Evergreen and Seasonal forests. Species richness was positively correlated to the cliff area. Our results showed that bromeliad diversity is not directly related to the degree of isolation of the cliffs. However, floristic similarity decreased with inter-cliff distance. In general, our results corroborated our hypotheses and the predictions of the Theory of Island Biogeography, reflecting additionally the possibility of environmental filters, and limitations in species dispersion.

**Keywords:** Bromeliaceae; rocky outcrops; sandstone cliffs; Rainforest; Theory of Island Biogeography

# 1. Introduction

Rock outcrops are common in many tropical forest landscapes (Ibisch et al., 1995; Pérez-García et al., 2009; Parmentier et al., 2009). Those rocky environments can be considered xeric islands with several ecological peculiarities, such as extreme environmental conditions, and high species diversity and endemism (Parmentier, 2003; Oliveira and Godoy, 2007). The flora on rocky outcrops is mostly different from the surrounding vegetation, contrasting with the predominant landscape of the matrix, differing in composition, and often harbouring a distinct and rare biota that grows on absent or less developed soils (Porembski and Barthlott, 2000; Ribeiro et al., 2007; Moura et al., 2011).

Bromeliaceae are a typical and diverse taxonomic group on neotropical rocky outcrops (Meirelles et al., 1999; Porembski, 2005, 2007; de Paula et al., 2016). This diversity is probably related to the presence of several strategies to endure water stress, such as leaf succulence, the peculiar formation of water tanks and the absorbing trichomes on leaves, all with the primary function of water caption and retention (Benzing, 2000; de Paula et al., 2016). Some studies on rocky outcrops showed that pioneer Bromeliaceae mats favour the establishment of other species through facilitation mechanisms (Ibisch et al., 1995; Porembski et al., 1998; De Paula et al., 2016). Furthermore, they represent one of the most important taxonomic groups in South American rainforests, due to a high degree of diversity and endemism, and to a high ecological importance, especially for the many interactions with other organisms (Martinelli et al., 2008).

The geographical distribution of bromeliad species is affected by several extrinsic factors, such as light and moisture availability, as well as intrinsic factors, such as growth-habit and type of dispersion (Fischer and Araújo, 1995; Benzing, 2000). A study of epiphytic bromeliads in the Brazilian Atlantic forest showed that spatial variables, such as latitude, altitude, and continentality, may largely affect species composition and geographic distribution within a single biome (Fontoura et al., 2012). The presence of distinct morphological traits possibly allows the occurrence of bromeliads in quite different environments of the neotropical region, from closed forests to open grasslands, may occur as terrestrial, epiphytic, and epipetric plants.

The composition and species richness on rocky outcrops can also be attributed to the environmental of the surrounding matrix in which these communities are immersed (Burke, 2002; Ribeiro et al., 2007). Variation in habitat heterogeneity influences the composition of species assemblages (Ricklefs, 1977), and dissimilar forest matrices present distinct environmental characteristics, including both biotic and abiotic resources that may determine the occurrence of a particular species. The Atlantic Forest shows a great physiognomic heterogeneity due to its latitudinal, continental, and elevational range (Ribeiro et al., 2009). Climate variables such as annual temperature and precipitation may vary according to the geographic zones in which particular types of forests are established (Porembski et al., 1998). Richness, endemism and species rarity in the Atlantic Forest is frequently related to habitat heterogeneity (Scarano, 2009). In general, considerable variation in floristic composition exists among forest physiognomies in this biome (Oliveira Filho and Fontes, 2000; Bergamin et al., 2012; Vieira et al., 2015), as pattern of species distribution are determined by the

environment, selecting species able to establish in particular habitat conditions (Hutchinson, 1957; Laliberté et al. 2014).

The influence of the vegetation matrix has rarely been measured when the floristic diversity in isolated systems was evaluated. Some studies that have addressed the relationships between vegetation matrix and epipetric plants have shown a high number of matrix-derived species on rocky outcrops, indicating a relationship between these environments and the surrounding vegetation (Watson, 2002; Wiser and Buxton, 2008). However, to date little is known about how the composition of epipetric plants vary in different Atlantic forest types, and what insular effect that rock outcrops inserted in a forest matrix exert on these plant communities.

Species diversity and distribution patterns on island or patches systems are also widely discussed according to the Theory of Island Biogeography (TIB), which considers two main spatial factors: island area and degree of isolation (MacArthur and Wilson, 1967). The TIB has been used to describe the patterns of species richness in oceanic islands (Keppel et al., 2010), in long-term fragmented landscapes, such as forest remnants (Liira et al., 2014; Dondina et al., 2016), and also rock outcrops (Meirelles et al., 1999; Porembski and Barthlott, 2000). Dispersal limitation is one of the principal topics of the TIB, which also emphasizes the influence of stochastic processes in colonization or establishment of species. Thus, spatial distance is a determinant factor for communities structuring (MacArthur and Wilson, 1967; Brown and Lomolino, 2000).

In this research, we evaluate the diversity and distribution patterns of bromeliads on cliffs in two distinct physiognomies of the Atlantic Forest in southern Brazil that are found in close contact, namely Evergreen and Seasonal forest (IBGE, 2012; Oliveira-Filho et al., 2014; Oriuhela et al. 2015). We defined cliff systems as vertical rock outcrops, as defined by Larson et al. (2000). Thus, we evaluate the influence of the surrounding forest matrix and the island effect on composition and richness of these communities.

Assuming a close relationship between epipetric plants and the surrounding vegetation matrix, considering that there will be species shared between these two habitats (Larson et al., 2000; Burke, 2002), and that bromeliad communities on cliffs could respond to the precepts of the Theory of Island Biogeography (MacArthur and Wilson, 1967), we hypothesized that: (i) Epipetric bromeliads will show an important participation of the mostly rupestrial subfamily Pitcairnioideae, but also by the mostly epiphytic subfamilies, as Tillandsioideae and Bromelioideae, coming from of the surrounding matrix forest; (ii) Bromeliaceae composition on cliffs is related to the forest type in which they are immersed; (iii) species richness will be directly proportional to the area of cliff; (iv) species richness and dissimilarity will be inversely proportional to the distance between cliffs.

## 2. Materials and Methods

### 2.1 Study Area

The study area comprises sandstone cliffs immersed in the Atlantic Forest in southern Brazil, approximately between latitudes 29° and 30°S. All rocky outcrops selected for this research are located in a range of 10 to 200m above the sea level, between the coastline of the Atlantic Ocean and the abrupt slopes of the Serra Geral Mountain Range, from southeastern Santa Catarina state to the northeastern Rio Grande do Sul state (Figure 1, Table 1). The landscapes around the cliffs are variable and comprised by disturbed habitats, as roadsides, pastures for livestock raising, or secondary vegetation, eventually including pioneer trees (e.g. *Cecropia*, *Trema*) or cultivated trees (e.g. *Acacia*, *Eucalyptus*). The top of the cliffs is mostly covered by low woody vegetation, possibly reflecting shallow soils susceptible to water deficit in the drier summer months. Some sandstone cliffs are unusual as bordering water bodies, as a creek or river or a coastal lake. Two of the studied outcrops presented a well-developed cave at the base (Dom Pedro de Alcântara - I and Sombrio), constituting a special habitat for animals and some plant species, mainly ferns of the genera *Blechnum (latu sensu)*, *Histiopteris and Olfersia.*
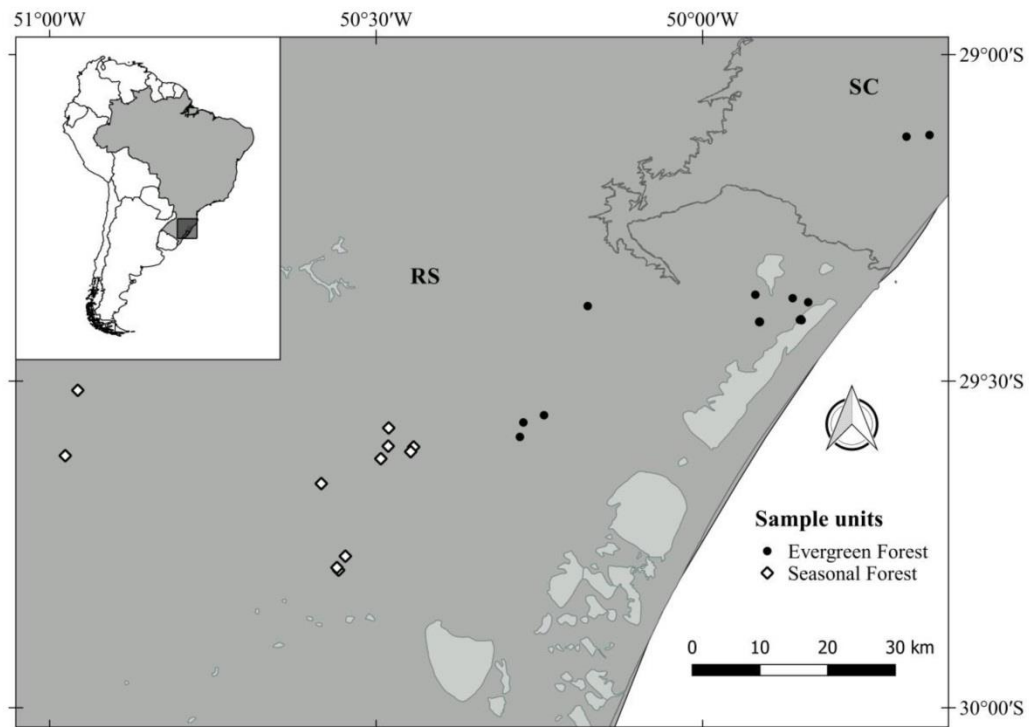


**Fig. 1** Location of the studied sites in southern Brazil. Black circles represent the cliffs immersed in Evergreen forest region and white squares those immersed in Seasonal forest region. RS = Rio Grande do Sul state; SC = Santa Catarina state.

**Table 1** List of study sites with sandstone cliffs sampled in the Atlantic Forest region of Southern Brazil (E = Evergreen forest area; S = Seasonal forest area). EAS = elevation above sea level near the base of the cliff; DCL = distance from the coastline. Expo = general exposition of the cliffs; S = number of bromeliad species observed on the escarpment surface.

| Study Site (*) | Code | Latitude S | Longitude W | EAS m | DCL km | Area m² | Expo -- | S |
|---|---|---|---|---|---|---|---|---|
| DP Alcântara - I | E1 | 29°24'22.4" | 49°51'03.8" | 21 | 6.1 | 1424 | SE | 5 |
| DP Alcântara - II | E2 | 29°24'24.0" | 49°50'54.7" | 14 | 5.9 | 1152 | SW | 11 |
| DP Alcântara - III | E3 | 29°22'22.6" | 49°51'43.9" | 43 | 9.1 | 2917 | E | 9 |
| DP Alcântara - IV | E4 | 29°24'17.9" | 49°50'58.4" | 25 | 6.1 | 504 | SE | 5 |
| DP Alcântara - V | E5 | 29°24'23.6" | 49°51'06.8" | 21 | 6.1 | 2320 | SE | 3 |
| DP Alcântara - VI | E6 | 29°22'44.9" | 49°50'18.3" | 33 | 6.8 | 2608 | W | 8 |
| Itati | E7 | 29°23'17.6" | 50°10'40.6" | 133 | 34.1 | 1222 | E | 5 |
| Maquiné - I | E8 | 29°35'07.3" | 50°16'47.8" | 69 | 31.7 | 1282 | N | 8 |
| Maquiné - II | E9 | 29°33'47.6" | 50°16'28.6" | 79 | 32.3 | 1321 | S | 3 |
| Maquiné - III | E10 | 29°33'48.2" | 50°16'33.7" | 76 | 32.3 | 514 | E | 3 |
| Santa Rosa do Sul | E11 | 29°07'32.4" | 49°41'16.4" | 58 | 11.1 | 3264 | SE | 6 |
| Sombrio | E12 | 29°07'23.5" | 49°39'9.27" | 12 | 8.6 | 1185 | SE | 1 |
| Riozinho - I | S1 | 29°39'02.5" | 50°26'53.6" | 106 | 43.6 | 1425 | NE | 3 |
| Riozinho - II | S2 | 29°35'58.2" | 50°28'53.7" | 102 | 48.8 | 3900 | NW | 3 |
| Rolante - I | S3 | 29°39'24.4" | 50°35´02.7" | 76 | 55.6 | 654 | NE | 3 |
| Rolante - II | S4 | 29°37'07.3" | 50°29'34.4" | 87 | 52.7 | 5425 | E | 3 |
| Rolante - III | S5 | 29°34'17.9" | 50°28'51.1" | 150 | 50.1 | 268 | W | 1 |
| Rolante - IV | S6 | 29°37'08.5" | 50°29'35.9" | 87 | 47.6 | 1978 | N | 3 |
| SA Patrulha - I | S7 | 29°47'21.7" | 50°33'27.1" | 93 | 47.6 | 1566 | E | 7 |
| SA Patrulha - II | S8 | 29°46'04.7" | 50°32'50.0" | 62 | 47.2 | 190 | W | 2 |
| SA Patrulha - III | S9 | 29°46'04.6" | 50°32'48.2" | 62 | 47.2 | 200 | NE | 2 |
| SA Patrulha - IV | S10 | 29°47'07.3" | 50°33'36.4" | 46 | 47.8 | 2553 | N | 2 |
| Sapiranga - I | S11 | 29°36'50.4" | 50°58'34.3" | 165 | 92.8 | 340 | S | 2 |
| Sapiranga - II | S12 | 29°36'49.5" | 50°58'36.5" | 165 | 93.0 | 778 | W | 2 |

(*) Study sites were defined as the names of municipalities; DP stands for Dom Pedro and SA for Santo Antonio; roman numbers are replicates in the same municipality.

According to the Köppen classification system, the entire study area has a humid subtropical climate (Cfa), usually characterized by hot summers and abundant rainfall throughout the year. The regional climate has a mean annual temperature around 18°C and the total annual rainfall varies between 1500mm and 1900mm (Alvares et al., 2013). The climatic differences between the Evergreen and Seasonal forests in this particular transitional zone is rather small, the main differences between those forest types are related to the seasonality of temperature and annual precipitation, as observed in meteorological station data around the study areas. (all values taken from the 10 municipalities reported as supplementary material in Alvares et al. 2013).

The geological structure in the study region comprises the Botucatu Formation of the Paraná Sedimentary Basin, corresponding mainly to Mesozoic (Bigarella and Salamuni, 1961; Kaul, 1990). The studied sandstone outcrops show a great topographic heterogeneity, from horizontal to abrupt cliffs and escarpments. Both Evergreen forest and Seasonal forest occur on the slopes of the Serra Geral Mountain Range, but on quite different expositions, the former on generally east-facing hillsides and the latter on generally south-facing hillsides.

The regional vegetation comprises the contact between two major physiognomies of the Brazilian Atlantic Forest biome (IBGE, 2012), namely the southernmost part of the Evergreen Forest (Rainforest) and the easternmost part of the Seasonal Forest, which extends westwards along the central Rio Grande do Sul state. The differentiation between these forests types is mainly based on temperature and rainfall regimes, which affect species composition or dominance, seasonality, and deciduity of trees (Veloso et al., 1991; IBGE, 2012; Oliveira-Filho et al., 2014). The most diversified families in both forests are the Myrtaceae and Lauraceae, mostly with evergreen species. One of the main compositional differences in the tree layer of Evergreen and Seasonal forests is the common occurrence of Magnoliids (*Magnolia*, *Virola, Xylopia* etc.) in the former, and of tall winter-deciduous legumes (*Apuleia*, *Erythrina*, *Myrocarpus* etc.) in the latter. The third major physiognomy of southern Atlantic forest, the Araucaria forest on the upper parts of the South Brazilian Plateau (900-1200m) was not included in this study.

## 2.2 Sampling method

Twenty-four essentially vertical sandstone rocky outcrops were selected for the study of bromeliad composition, abundance, and distribution. Each isolated escarpment with a particular exposition constituted a sample unit. We sampled 12 cliffs immersed in the region of Evergreen Forest and 12 immersed in the region of Seasonal Forest. The area of each cliff was estimated by multiplying the length and height of the rocky exposure, measured with a tape and a clinometer, respectively. The total area sampled in each forest region was almost identical, i.e., 19,713m$^2$ in the Evergreen forest and 19,277m$^2$ in the Seasonal forest. To assess the isolation degree of the sampled cliffs we considered the closest distance between two cliffs. The distances were measured by the "distm" function, in package Geosphere (Hijmans, 2016), in the R Development Core Team (2016), which calculates the distance matrix of a set of points, or between two sets of points.

All species of bromeliads growing on the escarpments were registered by means of direct observations and with the aid of high-resolution binoculars. Most species are easily detected and identified due to evident variation in rosette (leaf) form, size, and color patterns, which are well documented in regional floras (Reitz, 1983; Leme, 1984). The patterns of inflorescence ramification are also an important feature for identification, even in dry condition after flowering and fruiting. Although *Tillandsia usneoides* apparently does not grow directly on the rocks, the species was included in the sample when retained by other small plants on the cliff. Fertile specimens were collected and incorporated into the Herbarium ICN in the Federal University of Rio Grande do Sul.

Quantitative participation of bromeliads was estimated by the multiplication of two field estimations, one concerning local abundance and another concerning plant size, each

with three ordinal values. The local abundance scale comprised 1 = until five rosettes; 2 = from 6 to 15 rosettes; 3 = more than 16 rosettes. The plant size scale comprised: 1 = small, up to 20cm in diameter; 2 = medium-sized, from 20 to 40cm; and 3 = large, greater than 40cm in height and/or diameter.

We preferred the term epipetric instead of rupicolous or lithophytic, because it sounds more contrasting when comparing with epiphytic species, which is often the case. Additionally, epipetric was widely used by Winkler (1982) and Smith et al. (2006).


## 2.3 Data analysis

The bromeliads sampled in the sandstone cliffs were categorized according to the most common habit (terrestrial, epipetric or epiphytic), following descriptions of the species on study region (Winkler, 1982; Reitz, 1983; Waechter, 1998). An importance value was estimated as a mean between relative frequency (RF = number of occurrences of a species divided by the total number of cliffs in the forest type – in percentage) and relative abundance (RA = abundance of a species divided by the total abundance on cliffs in the forest type - in percentage). This estimate was used to compare dominance-diversity curves in both forest types (Whittaker, 1965; Magurran, 2004). The diversity of bromeliad communities of Evergreen and Seasonal forests was also compared by diversity profiles based on Rényi's entropy, which displays the overall patterns of alpha diversity with 95% confidence intervals after 2000 permutations (Rényi, 1961). Individual-based rarefaction curves were also used to compare the two forest types by evaluating the effect of total abundance in species richness, using 95% confidence intervals (Colwell et al., 2004).

We also used analysis of variance to examine if Bromeliaceae richness on rocky escarpments varies between Evergreen and Seasonal forests. A logarithmic transformation was applied to the data in order to improve homoscedasticity. We also evaluated the species diversity of zoochoric and anemochoric dispersion syndromes in both forests. A Mann-Whitney test was used to compare the dispersion data between the two communities. For both analyses, we adopted a p-value ≤ 0.05 as indicating a significant difference.

The similarity between areas was evaluated using Bray-Curtis quantitative coefficient and Sørensen qualitative coefficient. We performed non-metric multidimensional scaling (NMDS) to show pairwise similarities among cliffs and forest types and chose Bray-Curtis's index as a dissimilarity measure. We implemented a permutational multivariate analysis of variance (PERMANOVA), using 1000 permutations, to verified the differences in species composition between the forest types. PERMANOVA is an analysis of variance which uses distance matrices, and assumed a robust alternative for non-parametric data, describing how variation is attributed to different experimental treatments (Anderson, 2001).

An indicator species analysis was used to identify selective species in each of the two forest types (Dufrêne and Legendre, 1997). Indicator values, ranging from 0 (no association) to 1 (complete association), were calculated using the method of strength of species site-group associations with 1000 bootstrap samples (Caceres and Legendre, 2009). Significant differences were considered for P ≤ 0.05.

We used generalized linear models (GLM) to evaluate the relationship between species richness with cliff area. We also verified the residual errors and the best-fit model was

a negative binomial error family. To evaluate the relationship between species richness and distance between closest cliffs, we performed a Spearman correlation test, due to the distribution of non-normality data. Significant differences were considered as P ≤ 0.05. The correlation between species similarity and distance between cliffs was evaluated by a Mantel test, comparing the correlation between a spatial distance matrix and a floristic distance matrix (Jaccard). To assess significance, we used a Pearson correlation coefficient at the 5% significance level.

The NMDS analysis and the diversity profiles were run in the PAST statistical software (Hammer et al., 2001). All the others analyses were performed in the R statistical software, using packages Mass, Vegan, Indicspecies, Geosphere, Fitdistrplus, and Car (Venables and Ripley, 2002; Caceres and Legendre, 2009; Fox and Weisberg, 2011; Delignette-Muller and Dutang, 2015; R Development Core Team, 2016; Hijmans, 2016; Oksanen et al., 2017).

## 3. Results

We recorded 26 species of bromeliads, distributed in nine genera and three subfamilies. The most species-rich genus was *Tillandsia*, with nine species, followed by *Vriesea* and *Aechmea*, with six and four species, respectively. The remaining six genera occurred with only one or two species. Almost half of this flora (10 species - 42%), was found on rocky outcrops of both forest types. In the Evergreen forests, we found a total of 23 bromeliad species, 13 exclusive to this vegetation. In the Seasonal forest, we found 13 species, only three exclusives (Table 2).

**Table 2** List of bromeliads sampled on sandstone cliffs in the South Brazilian Atlantic Forest, with some adaptive features and quantitative estimations in Evergreen and Seasonal forest types. Most common habit: E = epiphytic, R = rupestral, T = terrestrial; Average plant size (rosettes): S = small (up to 20 cm), M = medium-sized (around 20-40 cm), L = large (from 40 to 80 cm or more); Dispersion type (D-type): A = anemochorous, Z = zoochorous. FR = frequency on cliffs (N = 12); AB = sum of abundance estimations (1 = one or few; 2 = several; 3 = many to dominant).

| Species \ Attributes | Habit | Size | D-type | Evergreen | | Seasonal | |
|---|---|---|---|---|---|---|---|
| | | | | FR | AB | FR | AB |
| *Aechmea comata* | E | M | Z | 2 | 4 | 5 | 14 |
| *Aechmea gamosepala* | E | M | Z | 9 | 36 | 0 | 0 |
| *Aechmea nudicaulis* | E | M | Z | 1 | 2 | 0 | 0 |
| *Aechmea recurvata* | E | M | Z | 0 | 0 | 1 | 2 |
| *Billbergia nutans* | E | S | Z | 0 | 0 | 5 | 6 |
| *Billbergia zebrina* | E | M | Z | 1 | 2 | 0 | 0 |
| *Bromelia antiacantha* | T | L | Z | 3 | 18 | 1 | 3 |
| *Dyckia maritima* | R | L | A | 4 | 27 | 5 | 33 |
| *Edmundoa lindenii* | E | L | Z | 2 | 9 | 0 | 0 |
| *Nidularium innocentii* | T | M | Z | 1 | 2 | 0 | 0 |
| *Tillandsia aeranthos* | E | S | A | 2 | 2 | 3 | 4 |
| *Tillandsia gardneri* | E | S | A | 2 | 2 | 1 | 1 |
| *Tillandsia geminiflora* | E | S | A | 1 | 1 | 1 | 1 |
| *Tillandsia mallemontii* | E | S | A | 1 | 1 | 0 | 0 |
| *Tillandsia polzii* | R | S | A | 2 | 5 | 5 | 14 |
| *Tillandsia recurvata* | E | S | A | 3 | 4 | 1 | 1 |
| *Tillandsia stricta* | E | S | A | 1 | 1 | 0 | 0 |
| *Tillandsia usneoides* | E | S | A | 8 | 10 | 2 | 2 |
| *Tillandsia xiphioides* | R | S | A | 2 | 4 | 0 | 0 |
| *Vriesea carinata* | E | S | A | 1 | 2 | 0 | 0 |
| *Vriesea friburgensis* | E | M | A | 0 | 0 | 2 | 6 |
| *Vriesea gigantea* | E | L | A | 8 | 33 | 1 | 6 |
| *Vriesea philippocoburgii* | E | L | A | 4 | 21 | 0 | 0 |
| *Vriesea platynema* | E | M | A | 2 | 4 | 0 | 0 |
| *Vriesea vagans* | E | M | A | 1 | 2 | 0 | 0 |
| *Wittrockia superba* | E | L | Z | 6 | 36 | 0 | 0 |
| Sum of values | | | | 67 | 228 | 33 | 93 |

The dominance-diversity curves showed striking differences between the two forest types (Figure 2), the Evergreen forest being characterized by its relatively higher richness, composed by several rare species, and the Seasonal forest distinguished by the evident dominance of a single species. This species was *Dyckia maritima,* standing out among other bromeliads on rocky outcrops due to its abundance and large size of rosettes. The most common species in the Evergreen forest region were *Aechmea gamosepala, Vriesea gigantea,* and *Wittrockia superba*, none of them standing out as evidently dominant. In Seasonal forests, besides the above mentioned dominance of *Dyckia maritima*, two other species could be regarded as co-dominant, namely *Aechmea comata* and *Tillandsia polzii*. These two species

mostly occurred in different habitat conditions, the former in protected – shaded and moister sites – and the last in exposed cliffs, eventually forming large hanging gardens.
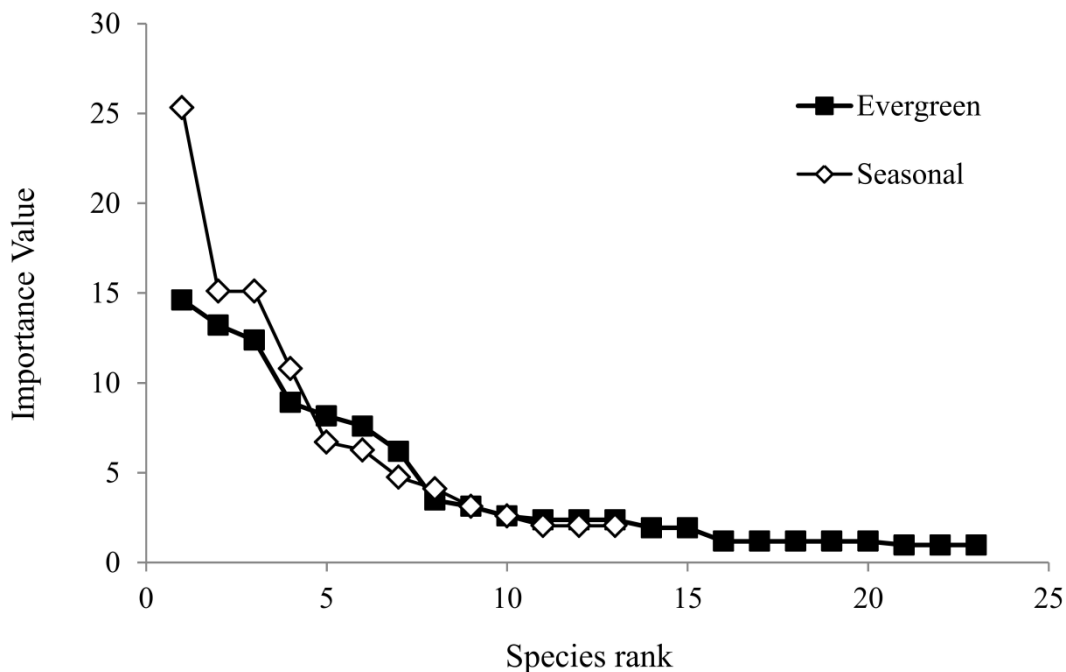


**Fig. 2** Dominance - diversity curves of rupestrial bromeliads in Evergreen and Seasonal Atlantic forests in Southern Brazil. The species are ranked in decreasing order of importance value, estimated as the mean between relative frequency and relative abundance (see Table 2 for absolute estimations).

The diversity profiles and rarefaction curves were contrasting between the two forest types, showing higher alpha species diversity on cliffs immersed surrounded by Evergreen forest (Figure 3 and 4) and species richness was significantly higher in the Evergreen forest ($F_{1,22} = 7.79$, $P = 0.01$).
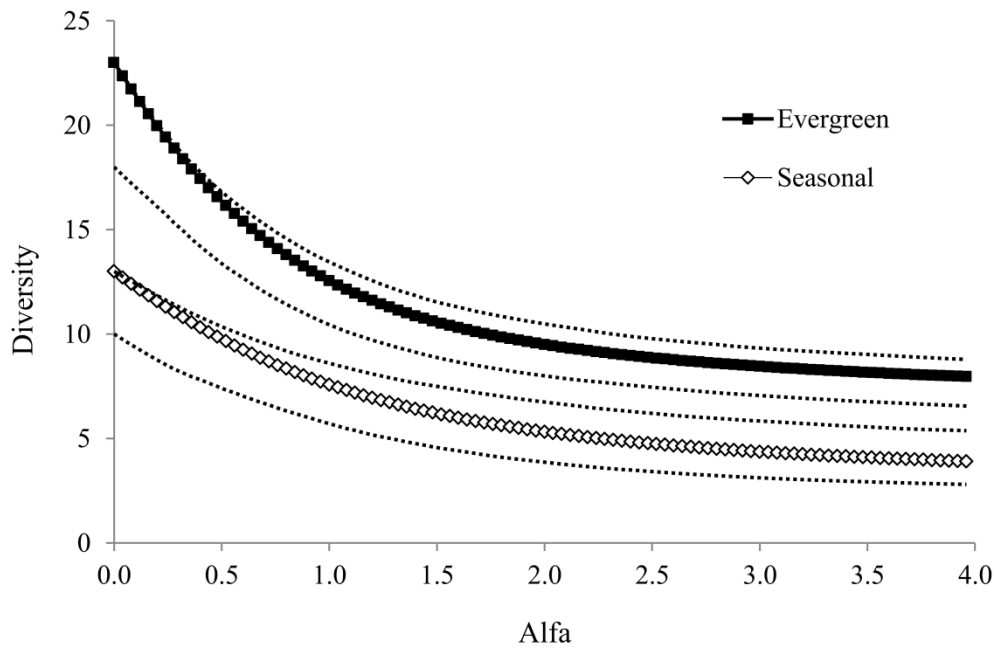
**Fig. 3** Rényi diversity profiles for epipetric bromeliads in Evergreen and Seasonal forests in southern Brazil. The dotted lines represent confidence intervals of 95% for these curves.
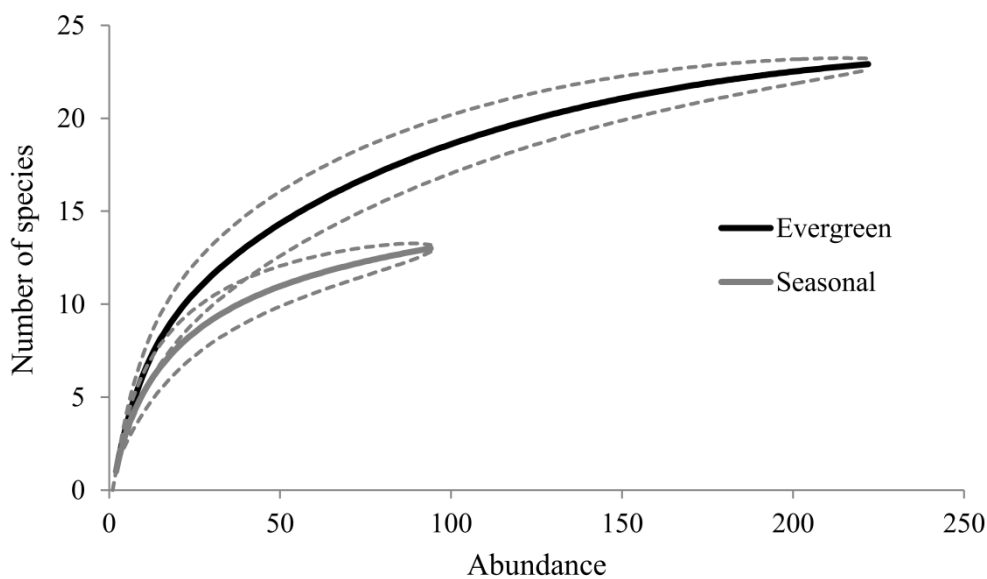


**Fig. 4** Individual-based rarefaction curves of epipetric bromeliads in two forest types of the south Brazilian Atlantic Forest. The dashed lines represent confidence intervals of 95% for both curves.

More than 60% of the recorded bromeliads were anemochorous, as a result of the regionally most diversified genera *Tillandsia* and *Vriesea*. The proportion of anemochoric and zoochoric dispersion was quite distinct between the two forest types. In Evergreen forest, the

species abundance in both syndromes was very similar (52.2% and 47.8%, respectively), contrasting with the Seasonal forest, with a higher proportion of anemochorous species (73.1% and 26.9%, respectively). Significant differences were observed in the abundance of zoochoric species in the two forest regions (W = 129.5, p-value = 0.0009) (Figure 5).
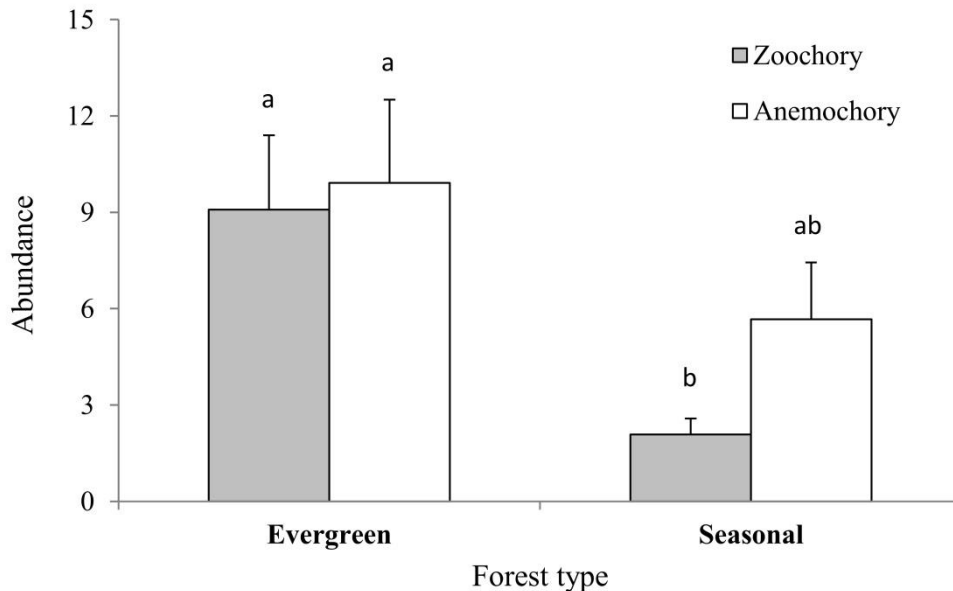


**Fig. 5** Abundance of dispersion types of epipetric bromeliads in Evergreen and Seasonal Atlantic forests regions. Different letters represent significant differences between groups.

The ordination diagram resulting from the NMDS analysis showed a clear distinction between the sample of the two vegetation types (Figure 6) and the bromeliad communities showed floristic differences between the two forest types (PERMANOVA, $F_{1,22} = 5.91$, P = 0.0009). The similarity in species composition between the two forest types was low when estimated both by the Sørensen qualitative index (0.55) and the Bray-Curtis quantitative index (0.32). The analysis of indicator species highlighted a set of six species as strong indicators for forest types (IndVal $\geq$ 0.55, P $\leq$ 0.05), four for the Evergreen forest and two for the Seasonal forest (Table 3).
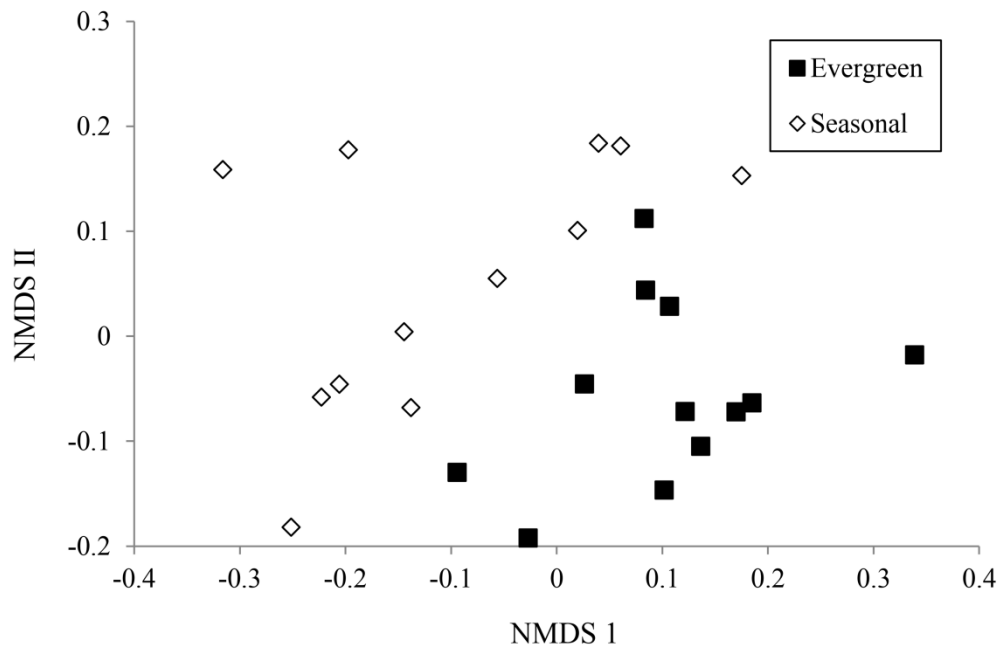
**Fig. 6** Ordination diagram of 24 sample units derived from non-metric multidimensional scaling analysis (NMDS), using Bray-Curtis distance. Black squares represent sandstone cliffs in Evergreen forest and open diamonds represent cliffs in Seasonal forest. Stress = 0.3485.

**Table 3** Indicator species of bromeliads growing on cliffs in two different forest types of Atlantic Forest in southern Brazil.

| Forest type | Indicator species | Indicator value | P-value |
|---|---|---|---|
| **Evergreen Forest** | *Aechmea gamosepala* | 0.86 | 0.005 |
| | *Vriesea gigantea* | 0.77 | 0.010 |
| | *Wittrockia superba* | 0.71 | 0.010 |
| | *Tillandsia usneoides* | 0.70 | 0.030 |
| | | | |
| **Seasonal Forest** | *Billbergia nutans* | 0.65 | 0.040 |
| | *Tillandsia polzii* | 0.58 | 0.050 |

Our results showed that species richness is positively related to cliff area ($\Theta = 10.35$, log-likelihood = -104.836, AIC = 110.84, $F_{1,22} = 4.17$, P = 0.04). The distance between the closest outcrops was not a factor correlated with species richness (S = 1830.9, P = 0.3391, rho = 0.2039). However, the graphical analysis, the values of the Mantel r statistic (0.530) and the significance of the test (P = 0.001) showed that the epipetric bromeliad community presents significant spatial dependence (Figure 7). The distance among rocky outcrops affected the floristic similarity of bromeliads since composition becomes more distinct as the rocky outcrops are further away from each other.

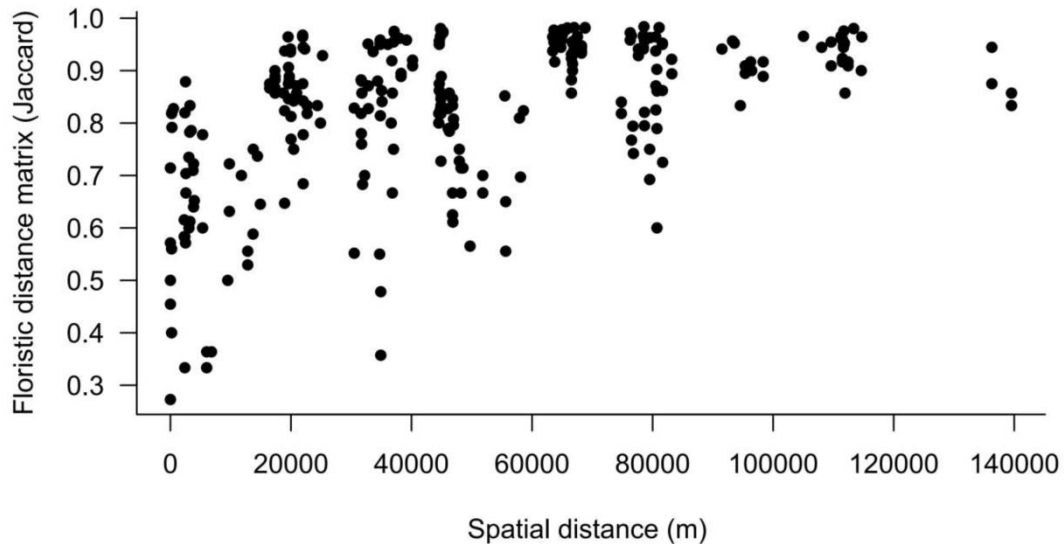**Fig. 7** Relationship between Bromeliaceae dissimilarity and spatial distance of cliffs, in a transitional zone between Evergreen and Seasonal Atlantic Forest in South Brazil.

## 4. Discussion

This research represents an ecogeographic study focusing on bromeliads on cliffs, based on compositional and quantitative data collected systematically in two distinct forest formations in the South Brazilian Atlantic Forest. In this study, we showed the effect of the vegetation matrix on diversity of epipetric assemblages. Furthermore, we analysed the island effect that rocky areas immersed in a forest matrix operate on the diversity of rupestrial Bromeliaceae.

Sandstone cliffs are important habitats since they provide ecological conditions for a unique bromeliad community, composed by the overlapping of commonly terrestrial species (*Bromelia antiacantha*), predominantly or exclusive epipetric species (*Dyckia maritima*, *Tillandsia polzii,* and *T. xiphioides*) and mostly typical epiphytic species (all other genera and species). The ability of bromeliads to establish in diverse habitats with extreme environmental conditions has already been observed and described in several studies that have highlighted the remarkable success of some species in areas characterized by the scarcity of water, as rocky outcrops and desert regions of South America (Ibisch et al., 1995; Rundel and Dillon, 1998). The adaptive capacity of bromeliads is strongly related to several morphological and physiological attributes of the species, as water accumulation in tanks and absorptive foliar trichomes, crassulacean acid metabolism (CAM), rhizomatous habit and succulence (Pittendrigh, 1948; Benzing, 2000). In French Guiana, several species on rocky outcrops were also found in other habitats (Sarthou and Jean-François, 1998), and Bromeliaceae together with Orchidaceae, besides being among the main families occurring on rocky outcrops, are also composed of many species appearing both as epipetric and epiphytic plants (Porembski and Barthlott, 2000).

All three subfamilies found in southern Brazil were sampled in our study area, with the highest generic diversity in the Bromelioideae (*Aechmea*, *Billbergia*, *Bromelia*, *Canistrum*, *Nidularium* and *Wittrockia*), and highest species diversity in the Tillandsioideae (*Tillandsia* and *Vriesea*). The relatively high number of genera in the Bromelioideae is in accordance with the center of diversity and endemism Brazilian Atlantic of this subfamily (Martinelli et al., 2008; Givnish et al., 2011). The high species diversity in the Tillandsioideae possibly reflects the large size of the genus *Tillandsia* in the neotropics and of *Vriesea* in the coastal Atlantic forest in particular (Benzing, 2000; Martinelli et al., 2008; Barfuss et al., 2016). In accordance with our findings, *Tillandsia* was also one of the most species-rich genera of Bromeliaceae on rocky outcrops studied in Venezuela, Bolivia, Chile and Peru (Ibisch et al., 1995; Rundel and Dillon, 1998; Gröger and Huber, 2007). The high species concentration in Bromelioideae and Tillandsioideae also reflects the great ability of these bromeliads to colonize both epiphytic and or epipetric environments (Zotz, 2013).

The subfamily Pitcairnioideae occurred within a single genus (*Dyckia*) and surprisingly with a single species. The subfamily is formed mostly by epipetric and terrestrial species, and *Dyckia* is one of the most diversified bromeliad genera on southern Brazil, with around 25-30 species (Krapp et al., 2014; Forzza et al., 2015). Differing to our hypothesis, exclusively rupestrial species were not well represented in our areas. One possible explication for a single *Dyckia* species is the moist forested region circumscribed in this study, acting as an unsuitable environment for highly xerophytic genera as *Dyckia*.

Floristic differences between epipetric bromeliad communities in Evergreen and Seasonal forest types corroborate our hypotheses and additionally agree with previous studies on forest tree species (Oliveira Filho and Fontes, 2000; Marques et al., 2011; Bergamin et al., 2012) and geophytic herb communities (Vieira et al., 2015) in the Atlantic forest of southern Brazil. Up to the present time, the differences among forest types were mostly evidenced by studies focusing the overstory (trees), or alternatively the understory (herbs) components of these formations. Our study demonstrated that a single family in a particular marginal habitat can also provide evidence for the distinction of forest types.

The higher plant diversity in Evergreen forest regions is often attributed to the relatively warm and moist climatic conditions, and the great variations in topography and soil heterogeneity (Bergamin et al., 2012; Vieira et al., 2015). Possibly, this higher bromeliads richness in Evergreen Forest is a consequence of a large species-pool in this region, and it supports the patterns found for epiphytes in the Atlantic Forest as a whole, where the composition of Seasonal Forest epiphyte communities may represent a subset of a more humid forest type (Leitman et al., 2015; Menini Neto et al., 2016).

As a probable consequence of the higher diversity, the number of indicator bromeliad species in the Evergreen forest was twice the number when compared to the Seasonal forest (four versus two). However, this proportion is not only the result of species richness but it is also influenced by frequency and abundance, which are both important community metrics considered in the analysis (Dufrêne and Legendre, 1997). Furthermore, the indicator species are functionally distinct in both forest types, since mostly tank-forming species occurred in the region of Evergreen forest, while atmospheric species occurred in the Seasonal forest region (*Billbergia nutans* has weakly developed tanks, resembling a *Tillandsia* in the absence of flowers). The relatively high indicator value of the widespread *Tillandsia usneoides* for

Evergreen forest is probably related to its more common occurrence as an epiphyte in the coastal humid forests. Functional plant traits also explain patterns of species distribution in fragmented landscapes (Tremlová and Münzbergová, 2007), and are usually related with environmental conditions, as the filtering effect of climate, disturbance, and biotic factors (Diaz et al., 1998).

The very distinct proportions between zoochoric dispersion in Evergreen and Seasonal forests can be related to the higher diversification of Bromelioideae in the Atlantic Rainforest. This subfamily is entirely dispersed by fleshy fruits (Benzing, 2000) and it has at least three genera restricted to Evergreen forests in the study area: *Edmundoa*, *Nidularium,* and *Wittrockia*. The absence of these genera in southern Seasonal forests is possibly due to direct climatic constraints or indirectly to the limitation of animal dispersers (Tabarelli et al., 2003; Correa et al., 2015). In both forest types, the anemochoric dispersion was greater than zoochoric. Similarly, species of the inselberg vegetation in Sudan often have numerous seeds adapted to anemochory (Porembski et al., 1994). This dispersion type is also majority found in bromeliads of neotropical rocky outcrops (De Paula et al. 2016). Both findings may result from the effect of environmental filters on the selection of reproductive traits in epipetric species.

The relationship between cliff area and the number of bromeliad species was positive. This result supports the Theory of Island Biogeography in one of its basic predictions – the increase of species diversity with increasing island area (MacArthur and Wilson, 1967). However, there are several possible reasons why bromeliad diversity cannot be surely predicted by the size of rocky outcrops, seeing that this relationship, despite being significant, was not as strong as we expected. First, bromeliads, in general, do not occur exclusively (as a single taxon), but otherwise co-occur and possibly compete with other xerophytes, especially cacti, orchids, gesneriads and many fern species. Additionally, it is not area itself that matters as a determinant for the richness of communities, but rather the fact that larger areas may contain higher heterogeneity of habitats which then can lead to the occurrence of more species with distinct habitat requirements (Pâslaru, 2014). In the case of bromeliads, it is important that the area able to colonize only small parts of the rocky cliffs, where conditions allow for germination and fixation of the plant. Finally, apart from habitat heterogeneity, other factors such as regional species pool and anthropic disturbance may affect structure and diversity of rock outcrop communities (Larson et al., 2000; Ribeiro et al., 2007).

The distance between nearest cliffs did not influence bromeliad richness. This result disagrees with the premise proposed by MacArthur and Wilson (1967), which predicts that more isolated islands tend to have fewer species. Although studies on African inselbergs have reported that the insular character of rocky outcrops is much more pronounced in the rainforest zone than in other vegetation types (Porembski et al. 1994), some South American studies have shown that the species on rocky outcrops are frequently also found in the surrounding rainforest, which means that there actually no isolation situation exists (Ibish et al. 1995; Sarthou and Jean-François, 1998).

In fragmented habitats, spill-over of matrix species may obscure the actual effects of both the area and the distance between the islands, and different integrated processes can define patterns of species composition and richness (Cook et al., 2002). In our situation, this probably occurred because most species of cliff bromeliads also occur as epiphytes, both in

closed forest remnants as on isolated trees. Thus, the forest environment stands as a permeable matrix for these species. However, the rocky outcrops possibly represent unfavourable islands for several locally common epiphytic bromeliads, which were not found in these habitats. These apparently high-selective epiphytic species include mostly species of the genus *Vriesea*, such as *V. flammea, V. incurvata, V. platzmannii, V. procera*, and *V. rodigasiana*. Otherwise, three species were never observed on trees near the rocky outcrops, and seem thus be exclusively epipetric, namely *Dyckia maritima*, *Tillandsia xiphioides*, and *Tillandsia polzii*. In the case of these species, the forest matrix can be a highly unfavourable environment, impeding establishment. This assumption, which essentially applies to the exclusively epipetric species, probably explains the high degree of bromeliad endemism in neotropical rocky outcrops (Porembski, 2007). These data are especially relevant when considering that those species restricted to rocky outcrops in the Atlantic Forest are one of the most vulnerable groups of plants facing extinction (Leão et al., 2014). In face of these remarks, rocky environments can be defined as typical patchy systems in forest matrices, even if the effects of isolation or habitat differentiation do not fully apply to bromeliads.

The dissimilarity of bromeliad flora between cliffs showed a positive correlation with the distances between them. Studies with epiphytic bromeliads of the Brazilian Atlantic Forest showed that spatial distance was highly correlated with floristic similarity (Leitman et al., 2015). Similar results were also found for inselberg plant communities in the African rainforest region, showing that floristic similarity between sites increase with the spatial distance between them (Parmentier et al., 2009). Spatial autocorrelation in island system may better explain patterns of endemism and composition, suggesting dispersal limitations among island (Keppel et al., 2010). This proposition is therefore based on neutral mechanisms and predicts that similarity in a community decreases with increasing geographic distance between sites, which can also be a result of limitations in species dispersal (MacArthur and Wilson, 1967; Hubbell, 2001). Besides, deterministic processes may also influence the establishment of these species, in the way that occurrence might be influenced by environmental gradients or habitat heterogeneity of the surrounding landscape.

## 5. Conclusions

This research represents an important contribution facing the scarce number of studies that present quantitative data and habitat tolerance of the bromeliads. Our findings may contribute to a better understanding of the interaction between rocky and forest habitat species, and support the importance of outcrops as ecological refuges of species in increasingly fragmented forest areas.

The surrounding type of forest matrix has a great influence on bromeliad composition and diversity in cliff environments. Our study showed that, in the case of bromeliads, rocky outcrops are not actually "islands" at least in the sense commonly attributed to these environments. Instead, the permeability of the forest is an important factor to be considered in the research of rocky outcrops, although this permeability can be very different among taxonomic groups.

Considering the influence of the forest matrix on the richness and composition of species, the positive relationship between bromeliad richness and cliff area, and the increasing

similarity between species composition as a consequence of spatial proximity, it can be assumed that both environmental and geographical factors represent dispersion barriers and thus influence the distribution patterns of species. Future research is needed to understand the extent to which spatial and environmental variables influence the structuring of these communities.

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**Supplementary Files**
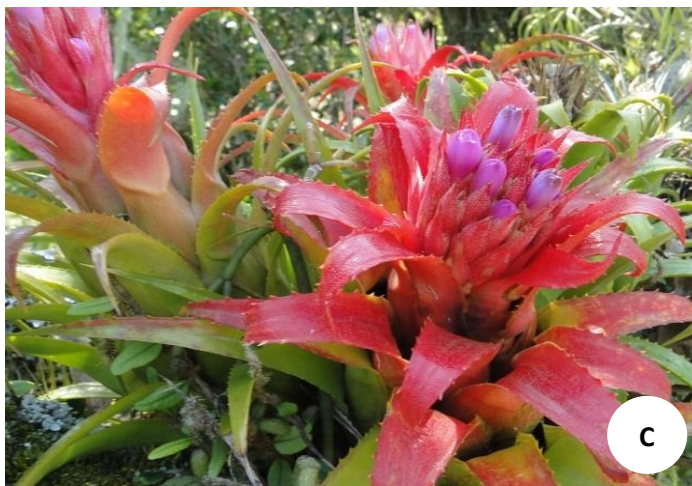
**Plate 1.** A: *Aechmea gamosepala* – flowering scape with *Heliconius ethilla* (Lepidoptera: Nymphalidae – Det. Gilson R.P. Moreira, UFRGS). B: *A. gamosepala* in rocky habitat with *Dyckia maritima* and *Tillandsia usneoides*. C: *Aechmea recurvata* flowering rosettes. D: *Aechmea recurvata* population on rocky cliff. E: *Bromelia antiacantha* with ripe berries. F: *Bromelia antiacantha* on exposed sandstone outcrop.
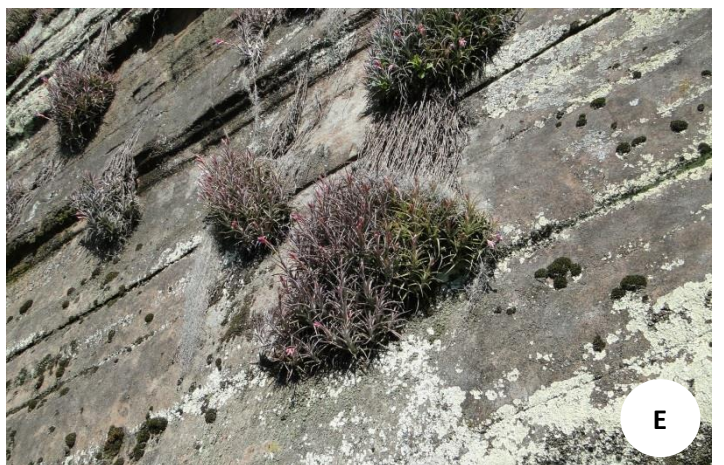
**Plate 2.** A: *Dyckia maritima* – apex of a flowering branch with *Apis mellifera* (Hymenoptera: Apidae – Det. Betina Blochtein, PUCRS). B: *D. maritima* on the top of a sandstone cliff. C: *Tillandsia recurvata* growing on cliffs among two species of cacti. D: *Tillandsia polzii* – plants in flower. E: *T. polzii* forming hanging mats with long dry stems at the base.

**Plate 3.** A: *Tillandsia xiphioides* – closer view of single flower. B: *T. xiphioides* growing in large populations on sandstone outcrops. C: *Vriesea gigantea* – a single open flower per branch, opening only at night. D: *V. gigantea* growing on a semi-shadowed sandstone cliff. E - F: *Wittrockia superba* – view of the short and dense nest-shaped inflorescence. *W. superba* growing on a rocky fragment and displaying the red-tipped leaves which are typical for the species.

# CHAPTER 2

**Beta diversity patterns of Bromeliaceae on rocky cliffs associated with the Atlantic Forest in southern Brazil**

# Beta diversity patterns of Bromeliaceae on rocky cliffs associated with the Atlantic Forest in southern Brazil

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**Abstract**

Investigating patterns of species diversity is one of the main objectives of community ecology, and in recent years there has been increasing attention in patterns of β-diversity and mechanisms related to variations in species composition. In this study, we evaluated beta diversity patterns of bromeliads growing on cliffs immersed in South Brazilian Atlantic Forest and identified the mechanisms that can act in the structuring of these communities. The study was carried out on sandstone cliffs included in contiguous but distinct forest regions: the Evergreen and the Seasonal physiognomies. Twenty-four mostly vertical Rock outcrops were sampled, 12 in each forest physiognomy. The spatial variation in species composition was evaluated by an index of beta diversity and its two components, turnover and nestedness. Multivariate analysis was performed to identify spatial and environmental factors responsible for species diversity and distribution, and partitioning of variation from the redundancy analysis was performed to distinguish niche and neutral processes. Total bromeliad richness was 26 species, 23 in Evergreen forest and 13 in Seasonal forest. Temperature seasonality, annual precipitation, and distance from the coastline were the most important factors affecting bromeliad composition and diversity. However, space exerts an important influence on the distribution patterns of the species studied. Our results demonstrate that both deterministic environmental factors and spatial effects can act together to define the structure of rock-dwelling bromeliad communities.

**Keywords:** Sandstone outcrops; bromeliad distribution; evergreen forest; seasonal forest; Niche Theory; Neutral Theory.

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**Introduction**

The Brazilian Atlantic Forest comprises a noticeably heterogeneous vegetation, including several associated ecosystems, such those occurring on rock outcrops (Scarano 2002, Leão et al. 2014). Several rock outcrops have a vertical or near-vertical exposure, commonly known as cliffs (Larson et al. 2000). The vegetation on rock outcrops, including on cliffs, differs from the surrounding forest matrix mainly due to absent or incipient soils, and microclimatic conditions resulting from high insolation and low water availability (Porembski & Barthlott 2000).

Bromeliads are one of the most interesting plant groups to evaluate theoretical concepts concerning distribution patterns of communities on cliffs. The Bromeliaceae is one of the most diverse botanical families in neotropical rock outcrops, occurring as well as terrestrial and epiphytic plants in different Atlantic Forest ecosystems, presenting great ecological importance resulting from the many interactions with other organisms (Martinelli et al. 2008, Givnish et al. 2011, Machado et al. 2016). The great ecological versatility of bromeliads is enhanced by the capacity of capturing and storing water in urns or tanks, formed by overlapping leaf-bases (sheaths), and the presence of scale-shaped trichomes, which are highly effective for water and nutrient absorption in xeric environments (Benzing 2000, Givnish et al. 2011).

The influence of the forest matrix on bromeliads of rocky outcrops has recently been described (Andrade Melo and Waechter, 2018). However, patterns of species distribution and theoretical approaches related to the effects of spatial and environmental variables in composition of these communities have not yet been addressed. Cliffs are embedded in the landscapes of the Atlantic Forest, covered by suspended natural gardens, whose floristic composition and community structure are still little known.

In South Brazil, the Atlantic Forest biome is classified into three main types: Evergreen Forest (tropical rain forest), Araucaria Forest (subtropical araucaria forest) and Seasonal Forest (tropical deciduous and semideciduous forest) (Veloso et al. 1991, IBGE 2012). The compositional differences between these forest types and the mechanisms acting in the structuring of plant communities were generally focused on distinct life-forms, such as herbs (Vieira et al. 2015), epiphytes (Menini Neto et al. 2016) and trees (Oliveira Filho & Fontes 2000, Marques et al. 2011, Bergamin et al. 2012). For the first time, in this study, we evaluated the effects of environmental and spatial variables in plant communities growing on rocky cliffs associated with the Brazilian Atlantic Forest (Ribeiro et al. 2009, Mittermeier et al. 2015).

Variations in species composition, generally known as beta diversity, comprise two major phenomena: species turnover and species nestedness (Baselga et al. 2007, Baselga 2010). Turnover and nestedness are considered two antagonistic processes, the first related to species replacement by new species (Qian et al. 2005), the last to species

loss in a community, when species found in one site represent a subset of another site (Ulrich & Gotelli 2007). Through of the beta diversity we can understand how the species distribute along a geographic space, inferring effects on the limitations of dispersion and the capacity of establishment of the species according to the environment.

The coexistence of plant species in a community can be directly or indirectly related to different factors, as the variations in environmental conditions or the intrinsic characteristic adaptations of the species (Tilman 1982, Hubbell 2001). Niche and stochastic processes are frequently used to explain patterns of species composition. The Niche-based theory predicts that the pattern of species composition is determined by environmental characteristics by selecting species capable to establish in the environment (Hutchinson 1957). The neutral theory assumes that ecological communities are stochastically structured, and so the mechanisms that generate differences between species composition are linked to the dispersal capacity of individuals or species (McGill et al. 2006).

The objective of this research was to evaluate beta diversity patterns of bromeliads growing on cliffs immersed in Atlantic Forest and to identify the mechanisms that act in the structuring of communities. In this approach two types of Atlantic Forest were considered, namely Evergreen (rain forest) and Seasonal (semideciduous forest), following Leão et al. (2014) and Orihuela et al. (2015). In this study, we investigate the following questions: (i) How do beta diversity of rock-dwelling Bromeliaceae vary in a transition zone between Evergreen and Seasonal Atlantic Forest? (ii) Which are the spatial and environmental variables affecting composition variations of bromeliads on rocky cliffs? (iii) What amount of explanation for floristic variations can be attributed to environment (deterministic), space (stochastic), and to both processes?

In face of these issues, we expected that (i) the composition of species varies according to the spatial scale and between forest types, meaning that there is a substitution of species along space. (ii) The substitution of species is influenced directly or indirectly by climatic factors, such as precipitation and temperature, besides the distance from the coastline. (iii) Beta diversity is caused mainly by spatially structured environmental variables, so that both deterministic and stochastic processes are important for epipetric or rupestrial bromeliad communities.

**Material and methods**

**Study Area**

The study area is located in the southern region of Brazil, comprising the northeast of Rio Grande do Sul and the southeast of Santa Catarina states (roughly between latitudes 29° and 30°S). All the investigated cliffs are sandstone outcrops inserted in two different types of Atlantic Forest, the Evergreen and Seasonal physiognomies. The studied rocky outcrops are located at low elevations (below 200 m)

between the coastline of the Atlantic Ocean and the abrupt slopes of the Serra Geral Mountain Range, in a heterogeneous landscape now mostly comprising some disturbed habitats, as roadsides, meadows for cattle rise, or secondary vegetation.

The entire study area has a humid subtropical climate (Cfa), according to the Köppen classification system, with hot summers and abundant rainfall throughout the year. The regional climate has a mean annual temperature around 18°C and a mean annual rainfall around 1750 mm (Alvares et al. 2013). The mean annual temperature varies between 18.4 ºC in the Evergreen forest region and 17.9 ºC in the Seasonal forest region while the rainfall in these regions may achieve an annual mean of 1660mm and 1850mm, respectively (Alvares et al. 2013).

The studied sandstone outcrops belong the Botucatu Formation of the Paraná Sedimentary Basin, originated in the Mesozoic era and presently extending mainly in south-central Brazil (Bigarella & Salamuni 1961, Kaul 1990). Sandstone outcrops present a relatively great topographic heterogeneity, with different sizes, orientations, and from almost horizontal to very abrupt slopes and escarpments. Both the Evergreen and the Seasonal forests occur mostly on the slopes of the Serra Geral Mountain Range, but differing by their predominant exposition.

The regional vegetation comprises the contact between two major physiognomies of the Brazilian Atlantic Forest biome (IBGE 2012), namely the southernmost part of the coastal Atlantic Evergreen forest (rainforest) and the easternmost part of the more inland Seasonal forest. The third major physiognomy of southern Atlantic forest, the Araucaria forest on the upper parts of the South Brazilian Plateau (900-1200m) was not included in this study.

**Sampling method**

For this study were selected 24 sample units, which consisted of cliffs isolated with a particular exposure. All cliffs sampled are composed of sandstone and have an essentially vertical slope. Of the 24 cliffs, 12 were immersed in the Evergreen Coastal Forest region and 12 were immersed in the semideciduous Seasonal Forest region.

The total cliff area sampled in each forest region was similar, 19,713m2 in Evergreen forests and 19,277m2 in Seasonal forest. Distance from the Coastline (DC) was measured with the aid of a GPS (Global Position System). Climate variables selected for analyses were Mean Annual Temperature (AT), Temperature Seasonality (TS), Annual Temperature Range (TR), Precipitation Seasonality (PS), Annual Precipitation (AP), all obtained from the WorldClim Global Climate with spatial resolution equivalent to 30" (~1 km) (Hijmans et al. 2005).

All species of bromeliads growing on the escarpments were registered by means of direct observations and with the aid of high-resolution binoculars, collected through climbing or pruning tools. The Bromeliaceae present diagnostic characteristics that facilitate the identification of species due to evident variation in rosette form, size, and

color patterns (Winkler 1982, Reitz 1983). The patterns of inflorescence ramification are also an important facilitating feature for identification, even in a dry condition, after flowering and fruiting. Fertile specimens were collected and incorporated into the ICN Herbarium in the Federal University of Rio Grande do Sul.

**Data analysis**

We measured the spatial variation in species composition using beta diversity with its two components, turnover and nestedness, according to the methodology described by Baselga (2010). For each forest type region, we calculated the Sørensen dissimilarity index (βSOR) and partitioned it into its turnover, i.e., Simpson dissimilarity index (βSIM) and nestedness (βSNE) components. Nestedness is defined as the difference between βSOR and βSIM. The estimations were performed with the package "Betapart" in R (R Development Core Team 2011, Baselga & Orme 2012). Despite being two antithetic phenomena, turnover and nestedness can occur simultaneously in communities, i.e., they are not mutually excluding (Baselga 2010).

We used PERMANOVA - Permutational Multivariate Analysis of Variance (Anderson 2001), to test the individual relationships between each of the environmental predictor matrices and the beta diversity metrics (βSOR, βSIM and βSNE), in each study region. Thus, we analyzed whether areas with more dissimilar species compositions were associated with increasing environmental distances. These relationships were examined based on the partial R2, and the significance was estimated using 999 permutations, in the R package Vegan (Oksanen et al. 2013).

The relative contributions of environmental and spatial factors in the structuring of communities were analysed by partitioning the variation from redundancy analysis (RDA) (Borcard et al. 1992, Legendre & Legendre 1998, Smith & Lundholm 2010). Initially, separate analyses were run for the set of spatial and environmental variables. In the RDA analysis, an abundance matrix of species previously submitted to Hellinger transformation was used as the response variable. The environmental predictor matrix comprises bioclimatic variables and distances from the coastline, these data were also standardized. The spatial descriptors used in the analysis were obtained by the principal coordinates of neighbour matrices method (PCNM), which transforms pairs of geographic coordinates into a truncated Euclidean distance matrix. The eigenvectors generated are the PCNMs used as spatial variables in the analyses (Griffith & Peres-Neto 2006).

To select the variables, an RDA analysis was performed. Based on the adjusted $R^2$ a forward selection was made for both predictor matrices separately. The RDA with only the selected variables served as the model for the analysis of variance partitioning (Borcard et al. 1992). The significance of the environmental and spatial models generated by the RDAs was tested with analysis of variance. Thereafter, the variation in the matrix of the community was decomposed into components of explanation: purely environmental, both spatial and environmental, purely spatial and residual or

unexplained (Borcard et al. 1992). The PCNM analysis was performed with the 'PCNM' and 'Boot' packages, the RDA and the split of the variance with the Vegan package, all in the statistical program R (R Development Core Team 2011).

**Results**

We sampled a total of 26 bromeliads, belonging to nine genera (*Aechmea, Bromelia, Billbergia, Dyckia, Edmundoa, Nidularium, Tillandsia, Vriesea, Witrockia*) and three subfamilies (Bromelioideae, Tillandsioideae and Pitcairnoideae). The number of species per cliff ranged from one to 11 in Evergreen forest and from one to seven for Seasonal forest. The total richness in each region was 23 species in Evergreen forest and 13 species in Seasonal forest, and 10 species were shared between the two environments (Table 1).

In assessing the proportion of each component of beta diversity, we observed a significantly higher contribution of turnover in relation to the nestedness, both when considering all the study area and those cliffs sampled in each forest type (Figure 1), with values ranging from 0.766 to 0.876 (pairwise βSIM). Total beta diversity (pairwise βSOR) was 0.851 for Evergreen forest, 0.900 for Seasonal forest and 0.925 for both forest types. (Table 2).

In Evergreen forest, the Annual Mean Temperature (AT) was the variable that best predicted the variation in species composition, taking into account βSIM. Beside this variable, Temperature Seasonality (TS) also explained the total beta diversity (βSOR) in this forest type. In Seasonal forest, both βSIM and βSOR were influenced by the Annual Mean Temperature (AT), Temperature Seasonality (TS) and Distance from the Coastline (DC). Considering both forest types, only the Seasonality Precipitation did not influence beta diversity of rupestrial bromeliad communities. In general, the models revealed that the strongest environmental effects were on total beta diversity (βSOR), followed by the turnover component of beta diversity (βSIM) (Table 3).

From the total set of environmental variables, considering all sampled areas, the subset of independent variables explaining better the species composition and which were retained after the selection procedure (forward selection) were: Annual Precipitation (AP), Temperature Seasonality (TS) and Distance from the Coastline (DC). On the other hand, the spatial predictors selected were those related to the largest spatial amplitude (first, second, fourth and five PCNM) (Figures 2 e 3).

The permutation tests for the redundancy analyses were significant for both environmental and spatial variables. Our results showed that the distribution of rock-dwelling Bromeliaceae is limited both by spatial distances and by environmental variables acting within these limits. The spatial and environmental variables explained 43.1% of the variation found in the structure of the bromeliad communities. The purely spatial component explained 15.6% ($P = 0.001$), while the environmental fraction alone accounted for 11.7% of the variation ($P = 0.001$). The percentage of the shared variation between environmental and spatial variables was 15.8%. However, 56.9% of the variation in beta diversity could not be explained by either of these variables (Table 3).

**Discussion**

      This research represents one first attempt to provide ecological information on the Bromeliaceae inhabiting rocky escarpments in southern Brazil. Our results showed how the composition of bromeliads growing on this substrate varies in two regional scales and how environmental and spatial factors influence the structuring of these communities.

      The total beta diversity patterns showed a much larger contribution of species turnover than species nestedness. This result was actually expected, considering that species turnover reveals the variation in community structure from one sampling unit to another along a spatial, temporal or environmental gradient (Anderson et al. 2011). The studied region comprises several climatic and landscape variations that influence the structure of the forest communities of the South Brazilian Atlantic Forest, as described by other authors (Oliveira Filho and Fontes 2000; Bergamin et al. 2012). Contrary to nestedness, spatial turnover indicates the replacement of some species by others, as a consequence of environmental arrangements or spatial and historical restrictions (Qian et al. 2005).

      Our results evidenced the influence of environmental factors on the composition of Bromeliaceae growing on cliffs, particularly the $\beta$SIM diversity component. Mean Annual Temperature (AT) was an important variable in the substitution of species in Evergreen forest, in Seasonal forest, and especially when considering the entire studied area. This is probably because coastal to inland climatic and topographic gradient affects several species even in areas with the same forest physiognomy, which is evidenced by lower temperatures, especially in winter, towards the Serra Geral Mountain Range (Alvares et al. 2013). This inland gradient possibly also explains the influence of distance from the coast line as an important environmental filter for the distribution of species in the bromeliad family, expressed by large proportions of explained variation in species turnover and total beta diversity. Corroborating this assumption, the pattern of geographical distribution of bromeliads in Rio Grande do Sul and Santa Catarina has great longitudinal influences, mainly due to the effect of the Serra Geral Highlands (South Brazilian Plateau) and the irradiation of the more tropical Atlantic Forest into the more southern Serra Geral Mountains (Winkler 1982; Reitz 1983; Waechter 2007).

      The physiological sensitivity and performance of bromeliads are directly related to temperature and their thermal tolerances (Benzing 2000), which also corroborates the importance of variables such as Annual Range and Seasonality in temperature on Beta diversity patterns of rock-dwelling bromeliads. Several supra-generic systematic groups of bromeliads are associated with different biogeographic regions or particular environmental conditions, and thus promoting the replacement of species according to environmental characteristics. Large-scale overviews in the Neotropical region have also pointed out that the diversity and distribution of genera and species of Bromeliaceae are influenced by the latitudinal gradient, mainly due to the effects of

temperature and rainfall (Benzing 2000). Moreover, the richness of the bromeliads in coastal Brazil shows strong latitudinal variations, decreasing both towards northern and southern directions from a central hotspot around Rio de Janeiro and São Paulo (Martinelli et al. 2008).

Beta diversity was not influenced by precipitation when cliffs immersed in Evergreen and Seasonal forest were evaluated independently, probably because there is no great variation in rainfall amounts and regimes within the same physiognomy. However, when considering the entire area sampled in both forests types, rainfall was an important factor conditioning the turnover component of beta diversity (βSIM) of epipetric bromeliad communities. Considering the studied region as a transition between two different forest types, differences in precipitation are less evident. Many bromeliads are adapted to environmental conditions with low water availability, being favoured by several functional attributes capable of efficiently capturing water and minimizing loss, These adaptations are also effective in moist forests, for those bromeliad species growing on intermittently dry habitats, as the upper canopy of rainforests (Benzing 2000).

In the South Brazilian Atlantic Forest, temperature, precipitation and continentality (when measured by the distance from the coast line) are the most important factors affecting bromeliad species composition on cliffs. Similar results were found with the tree component, where the differentiation between Ombrophilous (Evergreen) and Semideciduous (Seasonal) forests was strongly correlated with rainfall regime and temperature variation (Oliveira Filho and Fontes 2000). An ecological analysis of the cliff vegetation in north-east Ireland also showed that the distance from the sea was a significant factor in species composition along this gradient (Cooper 1997). Furthermore, the distance from the ocean is considered an important variable in the composition of epiphytic bromeliads in South Brazilian Atlantic Forest (Fontoura et al. 2012). The most important spatial variables (PCNM) correspond to the larger amplitudes, demonstrating that the larger the spatial scale the larger the difference in the species composition.

The detected variation in the structure of bromeliad communities is a result of spatial and environmental variables, as well as environmental variables structured along the geographic space, which actually had a major proportion in the explanation of data variation. Of course this result excludes the undetermined fraction that may be related to local environmental variations and possibly to biological interactions not measured in this study. Bromeliads are mostly pollinated by hummingbirds, but eventually also by bats, bees and butterflies (Fischer and Araujo 1995; Varassin and Sazima 2012). The dispersion mechanisms of bromeliads vary according to the subfamilies, the Tillandsioideae and Pitcairnioideae being wind-dispersed while the Bromelioideae are animal-dispersed (Givnish et al. 2011). Surprisingly the higher beta diversity in Seasonal forest outcrops coincides with a much lower alfa diversity, which probably indicates a reduction in reproductive interactions when compared to Evergreen forest.

Furthermore, these variations may be related to local environmental heterogeneity and mainly to the degree of disturbance in the areas surrounding the cliffs.

Environmental variables have a great implication in the variation of the rupestrial bromeliad communities and the effect of the geographic distance had a relatively large explanation on our data. However, the environmental spatially structured had an even major explanation. This result may be related to the low dispersion capacity of some species of bromeliads, showing that regional environmental differences also affect the floristic differences in this spatial scale (Brown and Lomolino 2000).

Previous studies have reported that both stochastic and deterministic processes, which are the essential basis for the Neutral Theory and the Niche Theory, respectively, can act at different spatial scales to define composition and diversity patterns (Ricklefs and Schluter 1995; Duarte et al. 2010; Segre et al. 2014). The Niche Theory otherwise considers environmental heterogeneity, biotic interactions and resource availability as the main causes of the gradual substitution of species in a regional scale (Hutchinson 1957; Segre et al. 2014). The Neutral Theory emphasizes the spatial variation as intrinsically related to the distance between habitats and the physical structure of the landscape, and so highlights the role of dispersion and colonization in the variation of species composition (Hubbell 2001). Actually, both neutral and niche processes can operate together to define the patterns of species diversity and distribution (Segre et al. 2014), and our results clearly corroborate this premise, indicating that the two processes are important in the structuring of rupestrial bromeliad communities and in the maintenance of local and regional biodiversity.

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Winkler S (1982) Die Bromeliaceae von Rio Grande do Sul. Doc Naturae 3:1–90.

**Tables**

**Table 1** List of bromeliads sampled on sandstone cliffs in the South Brazilian Atlantic Forest, with some quantitative estimations in Evergreen and Seasonal forest types. FR = frequency on cliffs (N = 12); AB = abundance estimations.

| Subfamilies | Species | Evergreen | | Seasonal | |
|---|---|---|---|---|---|
| | | FR | AB | FR | AB |
| Bromeliodeae | *Aechmea comata* | 2 | 4 | 5 | 14 |
| | *Aechmea gamosepala* | 9 | 36 | 0 | 0 |
| | *Aechmea nudicaulis* | 1 | 2 | 0 | 0 |
| | *Aechmea recurvata* | 0 | 0 | 1 | 2 |
| | *Billbergia nutans* | 0 | 0 | 5 | 6 |
| | *Billbergia zebrina* | 1 | 2 | 0 | 0 |
| | *Bromelia antiacantha* | 3 | 18 | 1 | 3 |
| | *Edmundoa lindenii* | 2 | 9 | 0 | 0 |
| | *Nidularium innocentii* | 1 | 2 | 0 | 0 |
| | *Wittrockia superba* | 6 | 36 | 0 | 0 |
| Pitcairnoideae | *Dyckia maritima* | 4 | 27 | 5 | 33 |
| Tillandsiodeae | *Tillandsia aeranthos* | 2 | 2 | 3 | 4 |
| | *Tillandsia gardneri* | 2 | 2 | 1 | 1 |
| | *Tillandsia geminiflora* | 1 | 1 | 1 | 1 |
| | *Tillandsia mallemontii* | 1 | 1 | 0 | 0 |
| | *Tillandsia polzii* | 2 | 5 | 5 | 14 |
| | *Tillandsia recurvata* | 3 | 4 | 1 | 1 |
| | *Tillandsia stricta* | 1 | 1 | 0 | 0 |
| | *Tillandsia usneoides* | 8 | 10 | 2 | 2 |
| | *Tillandsia xiphioides* | 2 | 4 | 0 | 0 |
| | *Vriesea carinata* | 1 | 2 | 0 | 0 |
| | *Vriesea friburgensis* | 0 | 0 | 2 | 6 |
| | *Vriesea gigantea* | 8 | 33 | 1 | 6 |
| | *Vriesea philippocoburgii* | 4 | 21 | 0 | 0 |
| | *Vriesea platynema* | 2 | 4 | 0 | 0 |
| | *Vriesea vagans* | 1 | 2 | 0 | 0 |
| Sum of values | | 67 | 228 | 33 | 93 |

**Table 2** 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 | 0.851 | 0.766 | 0.084 |
| Seasonal Forest | 0.900 | 0.847 | 0.053 |
| Both Forests | 0.925 | 0.876 | 0.049 |

**Table 3** Explained variation ($R^2$) of distance matrices representing effects of Annual Mean Temperature (AT), Temperature Seasonality (TS), Annual Temperature Range (TR), Precipitation Seasonality (PS), Annual Precipitation (AP) and Distance from the Coast Line (DC) on total beta diversity (Sørensen dissimilarity, βSOR) and its turnover (Simpson dissimilarity, βSIM) and nestedness (βSNE) components of bromeliads on cliffs immersed in Evergreen Forest, Seasonal Forest and Both Forest Types.

| | Evergreen Forest | | | Seasonal Forest | | | Both Forest Types | | |
|---|---|---|---|---|---|---|---|---|---|
| | βSOR | βSIM | βSNE | βSOR | βSIM | βSNE | βSOR | βSIM | βSNE |
| AT | 0.159 * | 0.245* | - | 0.305** | 0.384** | - | 0.103** | 0.139** | - |
| TS | 0.162* | - | - | 0.227** | 0.221** | - | 0.201** | 0.243** | - |
| TR | - | - | - | - | - | - | 0.064* | 0.077** | - |
| PS | - | - | - | - | - | - | - | - | - |
| AP | - | - | - | - | - | - | 0.074** | 0.135** | |
| DC | - | - | - | 0.150** | 0.185** | - | 0.118** | 0.074* | - |

Signif. codes:  * P-value < 0.05;  ** P-value < 0.01.

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

| Partition of variation | Adj.$R^2$ | F | P-value |
|---|---|---|---|
| [a+b] = Spatial | 0.314 | 3.635 | 0.001 |
| [b+c] = Environmental | 0.276 | 3.919 | 0.001 |
| [a+b+c] = Spatial + Environmental | 0.431 | 3.494 | 0.001 |
| **Individual fractions** | | | |
| [a] = Only spatial | 0.156 | 2.370 | 0.001 |
| [b] = Environmental spatially structured | 0.158 | | |
| [c] = Only environmental | 0.117 | 2.307 | 0.001 |
| [d] = Residuals (Undetermined) | 0.569 | | |

[a] fraction of explanation exclusive of spatial variables;[b] fraction of explanation shared between spatial and environmental variables; [c] fraction of explanation exclusive of environmental variables and [d] residuals. The Adj.$R^2$ corresponds to the coefficient of determination adjusted for the number of predictors in the model. P-values were obtained after 999 permutations.
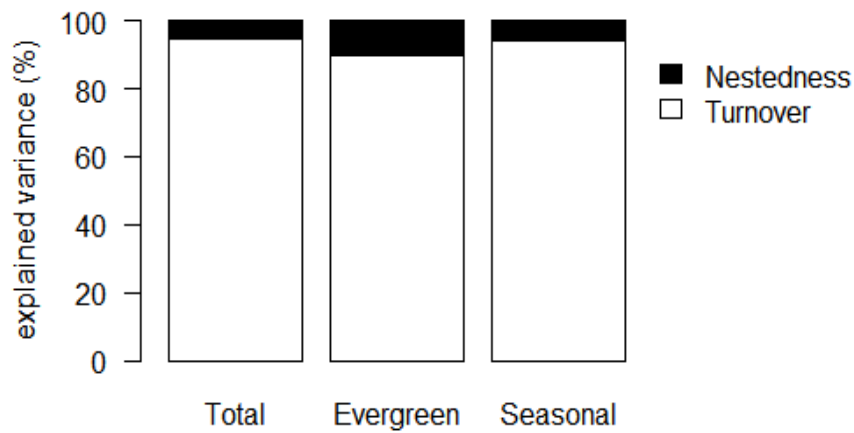
# Figures



**Fig. 1** Percentage of nestedness (black) and turnover (white) in Evergreen Forest, Seasonal Forest, and both forest types.
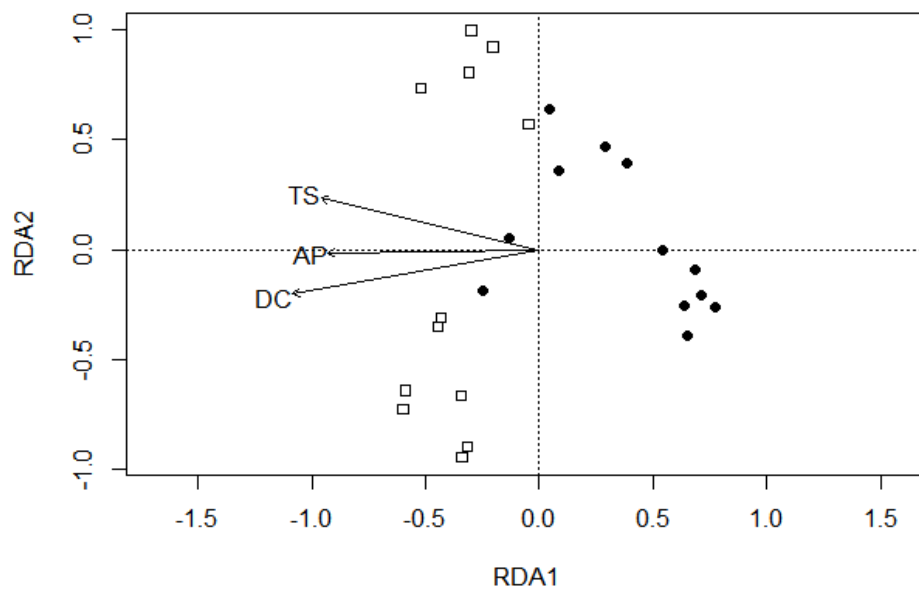


**Fig. 2** Canonical redundancy analysis diagram (RDA, axis 1 = 20%, axis 2 = 8%). Selected environmental variables (forward selection): TS - Temperature Seasonality; AP - Annual Precipitation; DC - Distance from the coastline. White squares correspond to cliffs in Seasonal forest and black circles correspond to cliffs in Evergreen forest.

**Fig. 3** Canonical redundancy analysis diagram (RDA, axis 1 = 21%, axis 2 = 9%). Selected spatial variables (forward selection): PCNM 1, PCNM 2, PCNM 4 and PCNM 5. White squares correspond to cliffs in Seasonal forest and black circles correspond to cliffs in Evergreen forest. The spatial descriptors used in the analysis were obtained by the principal coordinates of neighbour matrices method (PCNM).
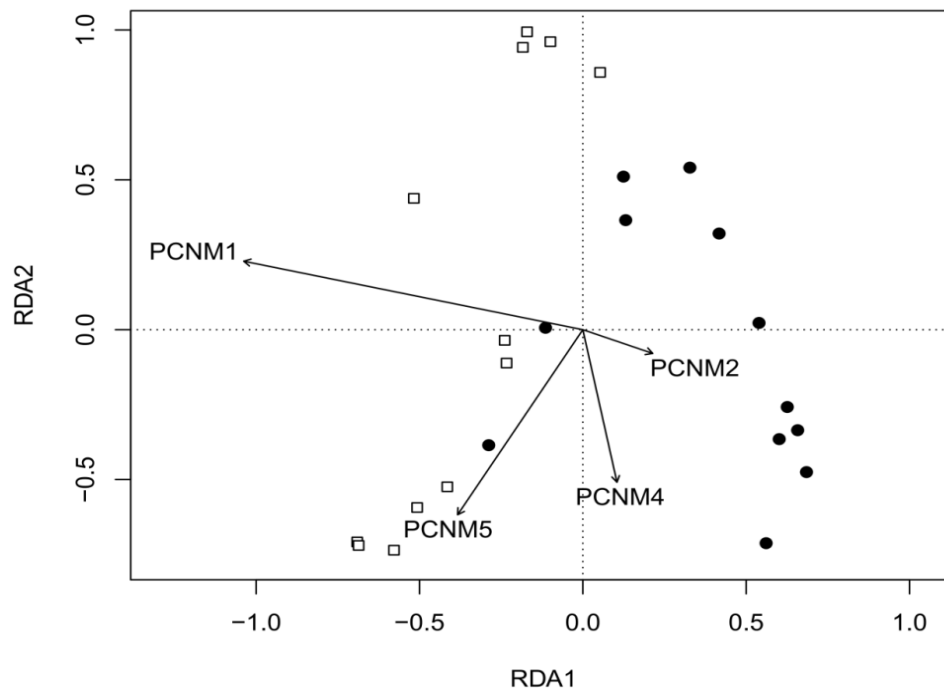
# CHAPTER 3

# Degree of disturbance affects the diversity of bromeliads on rocky outcrops

# Degree of disturbance affects the diversity of bromeliads on rocky outcrops

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## Abstract

Despite being common within forest environments, cliffs are still poorly known when their ecological function and biotic structure are taken into account. For the first time, we present an overview of the degree of human disturbance in these environments, and how these impacts can affect the biodiversity of bromeliad communities. Based on the theoretical assumption that the influence of selection on community patterns includes species' responses to the disturbance, the objective of this study was to evaluate the environmental vulnerability of cliffs immersed in the South Brazilian Atlantic Forest and the response of lithophyte bromeliads in terms of diversity and abundance. We selected and measured 24 vertical sandstone rocky outcrops, and estimated the abundance of all bromeliad species growing on the escarpments. For each cliff we generated an index for the degree of disturbance, based on scores attributed to several local human activities and landscape characteristics. We recorded 26 species of bromeliads, distributed in nine genera. Our results evidenced 18 cliffs with a medium vulnerability index, and six with a high vulnerability index. Correlation analyses showed that both richness and abundance of bromeliads significantly decreased as the degree of threat on rocky outcrops increased. These correlations and the occurrence of several rare and endangered species shows the importance of conserving sandstone cliffs for the maintenance of local and regional floristic diversity.

**Keywords:** Environmental vulnerability; cliff ecology; Atlantic Forest; epipetric plants; landscape ecology.

**1. Introduction**

Rocky outcrops are regarded as stressful environments, mainly due to the scarcity of water and nutrients, and an extremely adapted flora growing under these conditions (Porembski and Barthlott 2000). Among the most important families occurring on neotropical outcrops are the Bromeliaceae. Bromeliads occupy different microhabitats on vertical rocky outcrops (cliffs), occurring either isolated or grouped, and forming small to large vegetation islands (Andrade Melo and Waechter 2018). Studies showed that the formation of bromeliad islands on rocky outcrops can favour the establishment of other species through facilitation mechanisms, demonstrating that the participation of bromeliads in early stages of plant succession, on rocky environments, providing protection against herbivores and against high temperatures that can limit the establishment of less tolerant plants (de Paula et al. 2016; Rocha et al. 2014). Furthermore, the presence of tanks in many species promotes a unique microhabitat providing water supply, food, and shelter so that several animal species depend on these plants to survive (Leroy et al. 2013; Carmo et al. 2014).

Bromeliads are frequently well represented in several distinct environments of the Atlantic Forest, including terrestrial, epiphytic and epipetric habitats. Although epiphytic is the most common habit, the rocky outcrops are considered important spaces for Bromeliaceae, especially for endemics (Versieux and Wendt 2007; de Paula et al. 2016). This information has become even more relevant when recent research showed that among habitat types of the Brazilian Atlantic Forest, plants restricted to rocky outcrops are one the most vulnerable to extinction (Leão et al. 2014). Nevertheless, rock outcrops have faced different types of threats, most of them related to human actions, that have direct effects on local biodiversity (Fitzsimons and Michael 2017).

According the Theory of Ecological Community, different disturbance regimes may imply the input or output of species in a community; these disturbances can modify the processes of speciation and dispersion, and impact patterns of the community structure, also influencing the regional pool of species (Vellend 2010). Anthropogenic effects on natural environments and on biodiversity are not easy to measure, especially in situations with difficult access, such as cliffs. Vulnerability indicators are considered an alternative to identify the degree of threat through indices, and have been used in different situations as caves (Tanalgo et al. 2018) and rocky outcrop (Carmo 2010).

In this work, we evaluate the environmental vulnerability of sandstone cliffs immersed in Atlantic Forest, relating the degree of disturbance to the abundance and diversity of epipetric bromeliads. Our objective was to highlight the disturbances, the importance of these environments, and also to provide a tool to support decision making for environmental planning in areas where cliffs are existent. We hypothesize that cliffs present common bromeliads, which can also be found in the forest environment, but also rare and threatened species, whose occurrence is restricted to the rocky environment, in addition the degree of threat would have a significant impact on the diversity of bromeliads.

## 2. Material and Methods

The study area is located in the southern region of Brazil, in the northeast of Rio Grande do Sul and in the southeast of Santa Catarina states, between latitudes 29° and 30°S. The area has a humid subtropical climate (Cfa), according to the Köppen classification system. The regional climate has a mean annual temperature around 18°C and a mean annual rainfall around 1750 mm (Alvares et al. 2013). The geological structure in the study region comprises sandstone rocky outcrops of Mesozoic origin

(Bigarella and Salamuni 1961; Kaul 1990). The evaluated sandstone cliffs are scattered in a contact zone between two types of Atlantic Forest, defined as Evergreen and Seasonal forest (IBGE 2012).

Twenty-four vertical sandstone rocky outcrops were selected for the study. Each isolated cliff with a particular exposition constituted a sample unit. The total area sampled was 38,990m$^2$. All species of bromeliads growing on the cliff were registered. Fertile specimens were collected and deposited in the Herbarium ICN in the Federal University of Rio Grande do Sul. The quantitative participation of bromeliads was estimated by the multiplication of two three-level field estimations, one concerning local abundance (1 = up to five rosettes; 2 = from 6 to 15 rosettes; 3 = more than 15 rosettes), and another concerning average plant size (1 = small, up to 20cm; 2 = medium-sized, from 20 to 40cm; and 3 = large, greater than 40cm in diameter).

The categories of environmental impact were based on the methodology used by Carmo (2010), applied to the conservation status of rocky outcrop vegetation in southeast Brazil. The evaluation of individual cliffs was performed by the use of scoring procedures, which represent a current estimate of conservation degree, based on observations in the field and measures from geographic information systems (GIS). Environmental vulnerability indices were estimated as the sum of scores attributed to eight disturbance variables: the presence of roads and highways; agriculture; urban areas; abseiling and climbing; tourism and entertaining; forestry; original forest fragments and cliff area. Livestock activities were added to the agriculture variable. The choice of these indicator variables took into account the imminent risks to biodiversity on rocky outcrops, following the reference by several authors (Camp and Knight 1998; Cao et al. 2010; Porembski et al. 2016; Fitzsimons and Michael 2017).

We used Google Earth satellite images to identify the land use around the sampled cliffs. The areas of agriculture, forestry and forest fragments were calculated in a circular area with a radius of 500m around the referenced point of each cliff. We used a GIS (Geographic Information System) with ArcGIS$^{TM}$ software (ESRI 2014) to establish the intersect between the drawn areas and the 500m buffer, in order to calculate the area destined to each specific land use. The presence of roads and urban areas was also considered in this buffer. The area of each cliff was estimated by multiplying the length and height of the rocky exposure. The other types of disturbance were evaluated qualitatively. The resulting indicator values of environmental vulnerability and their scoring are shown in table 1.

The total index of environmental vulnerability was used as a quantitative variable to evaluate the relationship between species richness and abundance of rock-dwelling bromeliads. A logarithmic transformation was applied in order to improve homoscedasticity. We used linear regression models to test these relationships and the Shapiro-Wilk test to evaluate normality of the data Significant differences were considered as P ≤ 0.05. The analyses were conducted in the software R (Development Core Team 2011).

## 3. Results

We recorded 26 species of bromeliads, belonging to nine genera and three subfamilies (Table - supplementary file). The floristic list comprises several common and widespread species, but also contains two endangered species (*Dyckia maritima* and *Wittrockia superba*) and one critically endangered (*Tillandsia xiphioides*). Four species are evaluated as near threatened (*Tillandsia mallemontii*, *Vriesea carinata*, *V. gigantea* and *V. platynema*) and another set of four species are labelled as data deficient

(*Aechmea nudicaulis*, *Edmundoa lindenii*, *Nidularium innocentii*, *Tillandsia polzii*) (IUCN 2013; Rio Grande do Sul 2014).

During our field work we noticed that cliffs are submitted to different types of environmental impacts, presenting disturbances and heterogeneous landscapes, when compared to cliffs in more conserved areas (Plates – supplementary file).  The total vulnerability index of cliffs varied between 1 and 21. For practical purposes this range can be divided into four levels: low (1 - 4), medium (5 - 10), high (11 - 16), very high (above 17). The resulting values of vulnerability indicated that 18 cliffs were classified with medium vulnerability index and six with high vulnerability index. The regression analyses showed that both richness and abundance of bromeliads are negatively and significantly related to the degree of threat estimated for the rocky outcrops ($R^2$=0.406, F=15.03, P=0.0008 and $R^2$=0.436, F=16.99, P=0.0004, respectively) (Figures 1 and 2).

## 4. Discussion

Among the species listed in this study, three are included in some category of endangered of extinction and four are classified as near threatened. These conservation categories mostly derive from the relatively small extension of Evergreen rainforest in northeast Rio Grande do Sul, which strongly limits the geographic distribution of tropical plant species within this state (Winkler 1982). Another reason for assessing bromeliads as endangered species is the scarce number of studies concerning population sizes, sampling of ornamentals, and geographic distribution. In this way, our study represents an important contribution to improve information about these species.

Rocky outcrops can be regarded as important plant refuges, especially because many of them are presently located in a highly degraded landscape, which replaced the original forest matrix. Furthermore, researches have shown that cliffs also provide an

important refuge for several stress-tolerant species (Larson et al. 1989). Rocky outcrops may not be a very favourable habitat for some bromeliad species (e.g. epiphytes), but in face of the present situation of deforestation and human occupation they stand as an important alternative habitat for plant survival and seed dispersal. Most of the sampled cliffs are in a medium degree of threat. This situation is perhaps not entirely bad, but it is worrying in view of the increasing threats to natural environments and loss of biodiversity on rocky habitats (Fonty et al. 2009; Leão et al. 2014).

The loss of habitats on cliffs can be also caused by the fragmentation and reduction of surrounding forest remnants. The protection of the surrounding forest matrixes is essential because many bromeliads found on rocky outcrops are also commonly epiphytic in forests, suggesting a close relationship between habitats or life-forms, which in turn improves the possibilities of biological interactions, such as pollination and dispersal processes (Andrade Melo and Waechter 2018). The loss of forest habitats happens mainly by replacement of natural remnants by areas of pasture, forestry, agriculture and urbanization (Tabarelli et al. 2004; Wassenaar et al. 2007; Ribeiro et al. 2011). This substitution affects directly and indirectly local and regional diversity, especially where grazing and cultivated areas are still expanding, as studied region (Feix et al. 2016).

Besides to the loss or reduction of habitats, the change in local landscape structure increasing the surrounding environmental degradation of rock outcrops. Researchers have shown, for example, that the road construction near of cliffs should include biodiversity protection and careful control during the construction process, because the effect of a road on the environment is complex and includes disturbances long after the construction is finished (Cao et al. 2010). Local change in landscape structure is also motived for disorders tourism and sport practices. In Brazil, it is

common for rock-carved caves to serve as sanctuaries and attract religious visitors. On cliffs, practice of climbing and abseiling is also very common, but some researchers have shown that the number of plants decreases with increased climbing use, whose intensity has an impact on species richness and abundance of vascular plants and lichens (Camp and Knight 1998; Clark and Hessl 2015).

The bromeliad richness and abundance decrease as a result of the increase in cliff environmental vulnerability index of the cliff, considering that direct and indirect disturbances produce effects at the landscape, habitat and microhabitat levels that possibly prevent the propagation or establishment of these species. The several types of disturbance observed on cliffs affect bromeliad diversity and may compromise various ecological interactions for which Bromeliaceae are important, such as facilitation in along the succession process (Medina et al. 2006; Lopez et al. 2009; Rocha et al. 2014; de Paula et al. 2016). However, threats in general can impact not only bromeliads but also the entire biotic community that grows on cliffs. Cliff environments can sustain a high floristic diversity, possibly resulting from many distinct microhabitats, such as flat surfaces, small terraces, and more or less deep crevices (Kuntz and Larson 2006).

Cliffs are viewed as important landscape elements, especially for maintaining biodiversity and providing key ecosystem services (Jacobi et al. 2007; de Paula et al. 2016; Porembski et al. 2016). In the Atlantic forest region of southern Brazil, these habitats contribute substantially to regional plant diversity, particularly for the specialized flora, like Bromeliaceae, Cactaceae, and Gesneriaceae. Thus, we emphasize the importance of these environments and their biological diversity in face of increasing endangerment situations, leaving cliffs in great need to be considered in conservation policies.

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# Tables

**Table 1 -** Variables used to measure the environmental vulnerability of cliffs immersed in Southern Brazilian Atlantic Forest, with distinct scores describing the increasing degree of disturbance at each site.

| Code | Disturbance | Score | Definition |
|------|-------------|-------|------------|
| V1 | Roads and highways (*) | 0 | absent |
|  |  | 1 | secondary roads |
|  |  | 2 | highways |
| V2 | Agriculture (*) | 1 | area up to 0,1 km² |
|  |  | 2 | area between 0,1 e 0,4 km² |
|  |  | 3 | area more than 0,4 km² |
| V3 | Residential areas (*) | 0 | absent |
|  |  | 1 | rural area |
|  |  | 2 | urban area |
| V4 | Climbing and abseiling | 0 | absent |
|  |  | 1 | infrequently |
|  |  | 2 | frequently |
| V5 | Tourism & entertaining | 0 | absent |
|  |  | 1 | present (without infrastructure) |
|  |  | 2 | presente (with infrastructure) |
| V6 | Forestry (*) | 1 | area up to 0,1 km² |
|  |  | 2 | area between 0,1 e 0,4 km² |
|  |  | 3 | area more than 0,4 km² |
| V7 | Cliff area | 3 | area up to 0,1 km² |
|  |  | 2 | area between 0,1 e 0,4 km² |
|  |  | 1 | area more than 0,4 km² |
| V8 | Forest remnants (*) | 3 | area up to 0,1 km² |
|  |  | 2 | area between 0,1 e 0,4 km² |
|  |  | 1 | area more than 0,4 km² |

(*) evaluated in a 500 m radium around the cliff.
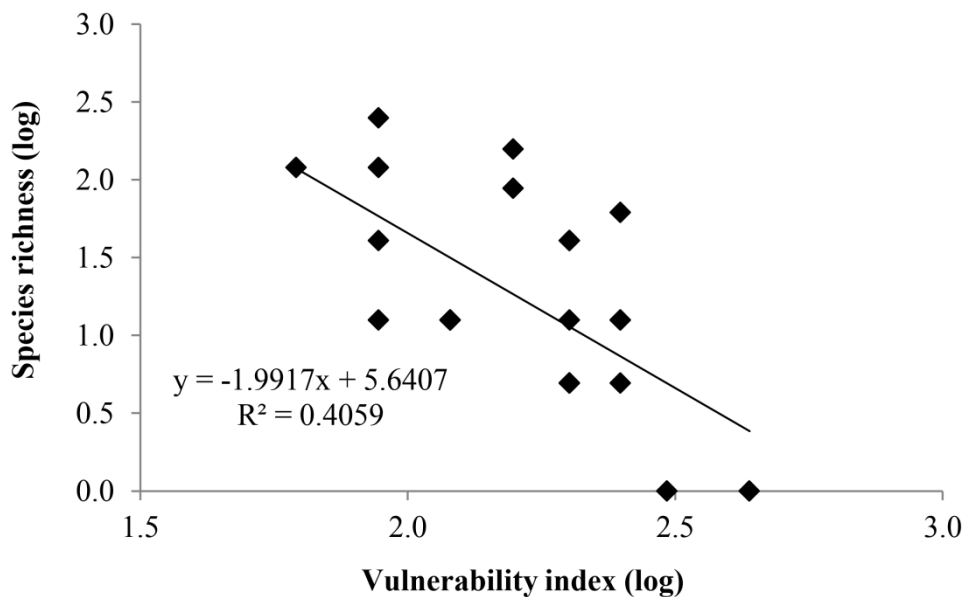
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**Figure 1.** Relationship between the lithophyte bromeliads richness and the environmental vulnerability index of sandstone cliffs with the South Brazilian Atlantic Forest.
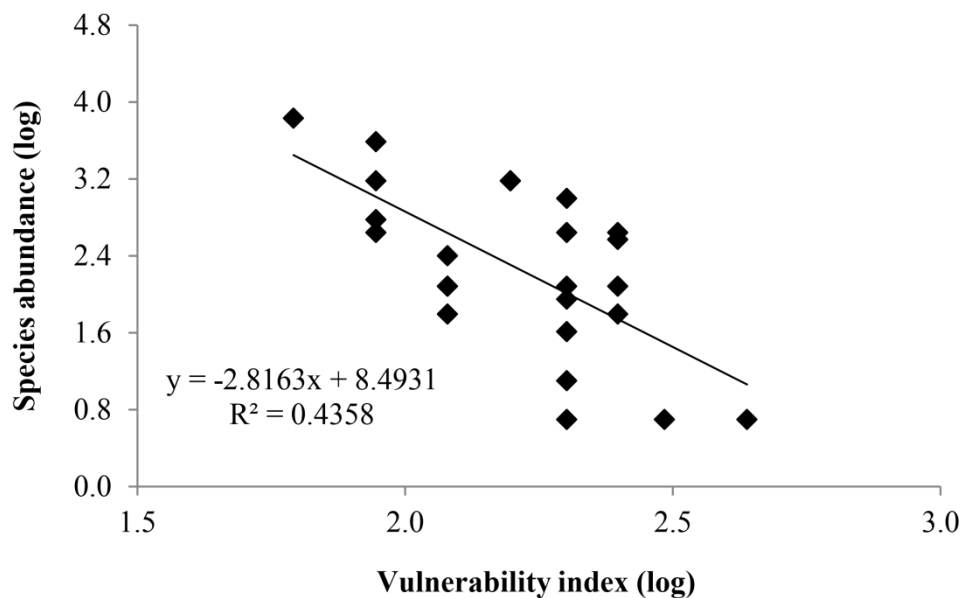


**Figure 2.** Relationship between the lithophyte bromeliads abundance and the environmental vulnerability index of sandstone cliffs associated with the South Brazilian Atlantic Forest.

**Plates**





Plate 1. Types of human activities on sandstone cliffs: Above: Several bromeliad species growing beside an almost vertical concrete staircase conducting to a sanctuary in Dom Pedro de Alcântara (Evergreen Forest). Below: Hanging ropes for climbing purposes on Pedra da Jacobina in Sapiranga (Seasonal Forest) (image courtesy of Jacqueline Dias). See Table 1 for more information.

Plate 2. Types of human activities on sandstone cliffs. Above: Large colonies of *Tillandsia polzii* growing on an exposed cliff surrounded by pastures and topped by remaining seasonal forest in Riozinho (Evergreen Forest). Below: A natural cave eroded by past higher sea level and now used for religious practice, as evidenced by statues and candles in Sombrio (Evergreen Forest).

Plate 3. Sandstone cliffs, both located in Santo Antônio da Patrulha, Rio Grande do Sul, with a well conserved forest vegetation matrix.

**Considerações Finais**

Nossa pesquisa representa o primeiro estudo florístico e ecológico com Bromeliaceae em escarpas rochosas inseridas em duas das três maiores fisionomias da Floresta Atlântica do Sul do Brasil, a Floresta Ombrófila e a Floresta Semidecidual. Composição florística e dados quantitativos das espécies foram coletados na área de contato entre esses dois tipos de floresta, e assim avaliamos a influência da matriz florestal na riqueza e composição de bromélias rupestres, contribuindo para o conhecimento da flora em afloramentos rochosos do sul do Brasil.

À luz da Teoria da Biogeografia de Ilhas, testamos algumas premissas importantes, e verificamos como a área e a distância entre as ilhas rupestres influenciam a riqueza e a composição de espécies. Além disso, nossa pesquisa buscou entender quais mecanismos são determinantes na estruturação de comunidade de bromélias que crescem sobre esses afloramentos. Ainda que haja um microclima diferenciado em relação à matriz do entorno, os padrões de diversidade e distribuição de bromélias rupestres são influenciados por fatores ambientais espacialmente estruturados. Desse modo, os resultados obtidos fornecem evidências que corroboram tanto à importância de fatores determinísticos, quanto à importância de fatores estocásticos, para a composição de espécies nos ambientes estudados.

Os afloramentos rochosos são habitats essenciais para estabelecimento de bromélias exclusivamente rupestres, mas também são importantes para bromélias de hábito facultativo, ou seja, que também ocorrem como epifíticas e/ou terrestres. Esses ambientes contribuem para diversidade regional de plantas e são muitas vezes considerados refúgios de espécies, especialmente porque muitos deles estão atualmente localizados em uma paisagem altamente degradada. Diferentes ameaças ambientais foram observadas nas escarpas estudadas, incluindo a redução de hábitat para espécies, a modificação da paisagem local e a prática de atividades humanas desordenadas. Esses distúrbios apresentaram um significativo impacto na diversidade de bromélias, e por isso nossa pesquisa enfatiza a importância de proteção tanto dos ambientes rochosos quanto das matrizes florestais do entorno, com intuito de reduzir esses impactos e conservar a biota local e regional.

Estudos com enfoque na diversidade funcional trariam hipóteses interessantes, tendo em vista as condições ambientais restritivas, em termos de estresse hídrico e mineral dos afloramentos rochosos. Assim, analisar as relações florísticas e funcionais entre Bromeliaceae de ambientes rupestres e da matriz florestal do entorno poderia fornecer respostas mais específicas sobre padrões de distribuição das espécies. Análises complementares poderão incluir amostragens realizadas em diferentes tipos de rocha, já que na região sul existe uma diversidade geológica que contempla afloramentos areníticos, basálticos e graníticos. Além disso, outras famílias e formas biológicas podem ser foco de estudos em escarpas rochosas, que poderiam ser somados aos resultados obtidos nessa pesquisa.