MICHELLE HELENA NERVO

PADRÕES DE DIVERSIDADE DE SAMAMBAIAS E LICÓFITAS EM UM GRADIENTE ALTITUDINAL NA FLORESTA ATLÂNTICA NO SUL DO BRASIL

Porto Alegre – RS

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MICHELLE HELENA NERVO

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

ORIENTAÇÃO: PROF. DR. GERHARD ERNST OVERBECK
CO-ORIENTAÇÃO: PROF. DR. PAULO GÜNTER WINDISCH

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2016

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"A mente que se abre a uma nova ideia
jamais voltará ao seu tamanho original."
Albert Einsteinr

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RESUMO

Padrões de diversidade de samambaias e licófitas em um gradiente altitudinal na Floresta Atlântica no Sul do Brasil

Michelle Helena Nervo
Gerhard Ernst Overbeck
Paulo Günter Windisch

Dados e análises de gradientes altitudinais em diversidade têm sido fundamentais para o desenvolvimento e avaliação de uma série de teorias gerais da biodiversidade. Esta proposta pretende contribuir para uma melhor compreensão dos padrões de diversidade das samambaias e licófitas ao longo de um gradiente de altitude no Sul do Brasil, abrangendo desde as formações florestais da planície, composta pela floresta de Terras Baixas, Submontana, como por formações florestais de altitude superiores, florestas Montana e Altomontana, e considerando a influência de fatores climáticos e de solo sobre as comunidades de plantas deste grupo. Assim, os objetivos deste estudo são: 1) verificar se a composição e riqueza de espécies varia ao longo do gradiente altitudinal; 2) se caso afirmativo, descrever em qual altitude podemos encontrar a maior diversidade; 3) analisar se existem diferenças ao longo do gradiente nos padrões de distribuição entre comunidade epifítica, terrícola e rupícola; 4) estabelecer quais são os fatores ambientais e de espaço que governam a distribuição das espécies de samambaias e licófitas, sua riqueza e sua cobertura na floresta brasileira ao sul do Atlântico; 5) investigar se espécies epifíticas e terrestres respondem igualmente aos condutores ambientais. Os resultados de um estudo detalhado, bem como de análises morfológicas, ecológicas, pedológicas e geográficas são: 1) a composição e riqueza de espécies variou significativamente ao longo do gradiente altitudinal; 2) riqueza e

diversidade foram maiores nas formações superiores (Montana e Altomontana); 3) comunidades ecológicas distintas (epifítica, terrícola e rupícola) diferiram quanto ao padrão de distribuição observado ao longo do gradiente; 4) os fatores ambientais (tais como: insolação solar, precipitação, velocidade do vento, umidade relativa do ar relacionados ao clima e, concentração de matéria orgânica, alumínio, pH e profundidade, relacionados ao solo) apresentam maior importância na variação da distribuição de espécies ao longo do gradiente; 5) a variação da distribuição de espécies epífitas demostrou ser mais relacionada aos condutores ambientais relacionados aos fatores climáticos enquanto que as espécies terrestres, aos fatores edáficos. Processos de nicho (teoria de nicho) são os responsáveis por modular a distribuição e a abundância das espécies de samambaias e licófitas ao longo do gradiente altitudinal da Floresta Atlântica Sul Brasileira. Adicionalmente, é descrito novo registro de *Stigmatopteris* no Estado do Rio Grande do Sul, Brasil.

Palavras-chave: distribuição, espécies epifíticas, florística, geófitas, litófitas, Neotropical, parcionamento de variância, pteridófitas, variáveis edáficas, variáveis climáticas.

ABSTRACT

Diversity patterns of ferns and lycophytes in an elevational gradient in the Atlantic Forest in southern Brazil

Michelle Helena Nervo
Gerhard Ernst Overbeck
Paulo Günter Windisch

Data and analyses of elevational gradients in diversity have been central to the development and evaluation of a range of biodiversity general theories. This proposal seeks to contribute to a better understanding of the ferns and lycophytes diversity patterns along an elevation gradient in Southern Brazil, spanning from Lowland and Submontane to Montane and Upper Montane forest formations, and considering the influence of climatic factors and soil on communities of this group plants. The objectives of this study are: 1) to verify the composition and species richness varies along the altitudinal gradient; 2) if so, describe at what altitude we find the greatest diversity; 3) to analyze if there are differences along the gradient in the distribution patterns of epiphytic community, terrestrial and rupicolous; 4) establish what are the environmental and spatial factors that govern ferns and wealth lycophyte species and its coverage in the Brazilian forest at the South of the Atlantic; 5) investigate if epiphytic and terrestrial species also respond to environmental drivers. The results of a detailed study, as well as morphological, ecological, soil and geographical study are: 1) the composition and species richness varied significantly along the altitudinal gradient; 2) richness and diversity were higher in the Montane and Upper Montane formations; 3) distinct ecological communities (epiphytic, terrestrial and rupicolous) to differ on the

distribution pattern observed along the gradient; 4) the environmental factors (such as solar insolation, precipitation, wind speed, relative humidity related to the climate, and concentration of organic matter, aluminum, pH and depth, related to soil) have greater importance in the variation species distribution along the gradient; 5) the variation of the distribution of epiphytes demonstrated to be more related to environmental drivers that are related to climatic factors, while terrestrial species are related to the soil factors. Niche processes (niche theory) are responsible for modulate distribution patterns and species abundance along elevational gradient in the Southern Brazilian Atlantic Forest. In addition, we present the new registration *Stigmatopteris* in the State of Rio Grande do Sul, Brazil.

Keywords: climatic variables, edaphic variables, environmental, epiphytes species, floristics, distribution, geophytes, lithophytes, Neotropical, pteridophytes, variance partitioning.

INTRODUÇÃO GERAL

INTRODUÇÃO GERAL

Os organismos estão sujeitos aos gradientes ambientais temporais e espaciais que podem limitar a sua distribuição de acordo com a capacidade de ajuste fisiológico (Janzen 1967, Navas 2003, Kessler 2001). O entendimento desses padrões de mudança na riqueza, na composição e na abundância das espécies ao longo desses gradientes tem sido o foco de muitos estudos de ecologia há mais de meio século (Whittaker 1965, Janzen 1967, Terborgh 1971, Qian et al. 2007).

Em escala global, diversos fatores afetam a distribuição espacial de espécies, como a altitude, visto que uma ampla gama de parâmetros varia ao longo destes gradientes, tais como precipitação pluviométrica, umidade, temperatura, interações interespecíficas, história evolutiva e grau de interferência antrópica no meio ambiente (Begon et al. 2007, Lieberman et al. 1996, Lomolino 2001, Rahbek 2005, Grytness & McCain 2007, Paciencia 2008, Kessler et al. 2011, entre outros).

A distribuição de espécies ao longo de gradientes altitudinais pode apresentar três padrões de variação na diversidade: 1) padrão unimodal-parabólico ou *hump-shaped*, distribuição em corcova, com a maior diversidade em altitudes intermediárias; 2) padrão monotônico-decrescente com a elevação da altitude, ou seja, a diversidade diminui gradativamente com o aumento da altitude; 3) padrão constante-decrescente, com a diversidade constante em baixas altitudes e decrescendo bruscamente em altas altitudes (Jansen et al. 1976, Wolda 1987, McCoy 1990, Stevens 1992, Olson 1994, Abrams 1995, Rahbek 1995, Fisher 1998, Ward 2000, Pyrcz & Wojtusiak 2002, Sanders et al. 2003, Rahbek 2005, Grytnes & McCain 2007). O primeiro padrão (unimodal-parabólico) é o mais frequentemente encontrado na distribuição da biodiversidade ao longo de gradientes altitudinais, encontrado em muitos estudos realizados com diversos grupos taxonômicos de

plantas (Kessler 2001b, Grytnes 2003) e animais (Oslon 1994, Rahbek 1997, McCain 2004, Rahbek et al. 2007).

O padrão de variação na riqueza de espécies em gradientes ambientais pode diferir entre táxons (Owen 1990), e até em um mesmo grupo taxonômico (por exemplo, samambaias ou licófitas) sob diferentes tipos de substrato (epífitas de tronco, epífitas de dossel e terrestres, Watkins et al. 2006). Estes autores, ao pesquisarem a distribuição de plantas vasculares sem sementes, epífitas e terrestres, ao longo de um gradiente altitudinal na Costa Rica, constataram que este padrão clássico de "picos" em elevações intermediárias não foi observado nas espécies nos diferentes tipos de substrato estudados, ocorrendo apenas nas epífitas, tanto de tronco, como de dossel.

Algumas hipóteses têm sido propostas para explicar a relação entre riqueza de espécies e a altitude, como a concentração de espécies em altitudes intermediárias (= efeito do domínio médio; *mid-domain effect*, Colwell & Lees 2000): maior produtividade primária, o efeito da área disponível para ocupação, limitações ambientais sobre a distribuição das populações, mudanças abruptas do hábitat (ecótonos), redução da disponibilidade de alimento e competição (ex. Randall 1982, Navarro 1991, Stevens 1992, Almeida-Neto et al. 2006). No entanto, nenhum fator único é responsável por todos os padrões de riqueza observados (Romdal & Grytnes 2007).

Para samambaias e licófitas, as explicações ecológicas fornecidas para a variação da riqueza de espécies em gradientes ambientais são baseadas na dispersão aleatória proposta pela teoria neutra (Hubbell 2001) e na heterogeneidade ambiental proposta pela teoria de nicho (Tuomisto et al. 2003). Segundo a primeira teoria, as espécies são competitivamente idênticas e, desta forma, diferenças florísticas ao longo de gradientes ambientais são criadas ao acaso, limitadas somente pela capacidade de dispersão das espécies. Assim, a similaridade decai com o aumento do logaritmo da distância geográfica.

Já na segunda teoria, atributos ambientais que existem na área de ocorrência das espécies (composição química e estrutura física do solo, microclima, etc.) proporcionam a seleção daquelas capazes de habitar as localidades dominadas por tal atributo (Tuomisto et al. 2003). Por esta forma, a similaridade decai com o aumento da distância ambiental.

De um ponto de vista biogeográfico (considerando caracteres morfológicos e fisiológicos), samambaias e licófitas se distinguem das plantas com flores por sua dispersão de esporos e suas gerações gametofíticas e esporofíticas separados. Assim, elas são

independentes de vetores de polinização e distribuição biótica (com poucas exceções, como samambaias aquáticas transportadas por aves aquáticas), eliminando dois aspectos que influenciam fortemente a biogeografia de plantas floríferas, e como resultado, apresentam uma relação biogeográfica mais influenciada pelo clima e pelo substrato (Kessler 2011). Um exemplo dessa influência são os resultados encontrados por Kessler (2000), em florestas andinas, onde observou mudanças na comunidade de criptógamas em faixas altitudinais distintas.

Estudos realizados em florestas tropicais ao longo de gradientes altitudinais (Hemp 2002, Klunge et al. 2008) mostram que as diferenças na riqueza de espécies e na composição florística nas diferentes elevações são causadas, principalmente, em função da mudança gradual de fatores climáticos. A riqueza máxima tem sido associada a uma combinação de alta umidade, alta precipitação e temperaturas moderadas em elevações intermediárias. Este padrão observado em florestas tropicais se deve ao fato de que o crescimento de samambaias e licófitas é limitado por baixas temperaturas e, especialmente, por geadas (Bhattarai et al. 2004, Klunge et al. 2006, Kessler et al. 2011).

As variações na comunidade não estão somente relacionadas aos fatores globais e regionais, como fatores climáticos, pois as mudanças na vegetação também são respostas às diferentes condições ambientais de fatores locais. Um exemplo que mostra o efeito de fatores locais são os resultados encontrados por Tuomisto & Ruokolainen (1994), ao abordarem a distribuição de samambaias, licófitas e Melastomataceae em um gradiente edáfico na Amazônia Peruana. Estes autores verificaram a influência dos diferentes substratos e da drenagem do solo sob variações da distribuição de grupos de plantas (principalmente com samambaias e licófitas). Os fatores edáficos são considerados importantes na estratificação de ambientes (Tuomisto & Poulsen 1996, Tuomisto et al. 2002), de maneira que muitas espécies – sobretudo no grupo das terrestres - são consideradas boas indicadoras de condições edáficas.

A heterogeneidade ambiental geralmente influencia a distribuição de espécies de samambaias (Parris 1985, Palmer et al. 2002). Estudos recentes (Tuomisto et al. 2014) têm confirmado que as samambaias podem ter a dispersão limitada pela ocupação exclusiva de nichos locais mais adequados. Considerando a importância relativa da dispersão aleatória e da heterogeneidade ambiental, Jones et al. (2006) na Costa Rica e Zuquim et al. (2012) na Amazônia, verificaram que as diferenças ambientais tiveram maior influência do que as distâncias geográficas na previsão da composição de samambaias e licófitas.

A investigação da importância relativa de processos estocásticos e determinísticos na estruturação das comunidades de plantas é útil para indicar quais destas perspectivas teóricas não são mutuamente exclusivas (ver também, Karst et al. 2005), como também faz parte dos esforços para compreender efeitos no ecossistema para a biodiversidade e conservação da biodiversidade (Tilman e Downing, 1994; Grytnes e Vetaas 2002). No entanto, este tipo de estudo ainda é raro na abordagem de espécies de samambaias em gradientes ambientais brasileiros (Paciencia 2008, Gasper et al. 2013).

Tryon (1972) estimou que cerca de 10% da flora de samambaias e licófitas do mundo está representada no Brasil. O mesmo autor destaca as regiões do Sudeste e Sul do Brasil como um dos três principais centros de endemismo para samambaias na América Tropical. Uma extensão considerável destas regiões é coberta pela Mata Atlântica, um dos *hotspots* mais importantes para a conservação biológica (Myers et al. 2000, Laurance 2009).

A Mata Atlântica (*sensu stricto*, Oliveira-Filho & Fontes 2005) representa um ambiente especialmente apropriado para testar hipóteses sobre os fatores que determinam padrões de distribuição de espécies ao longo de gradientes altitudinais (por ex., Bergamin et al. 2012), pois é o bioma brasileiro com a maior riqueza específica de samambaias, associadas principalmente às áreas montanhosas da Floresta Ombrófila Densa. Esta grande riqueza de espécies, associada ao fato das espécies apresentarem, de forma geral, uma baixa adaptabilidade fisiológica (Kessler et al. 2011) que torna samambaias e licófitas um grupo interessante como modelo para estudos sobre padrões de distribuição ao longo de gradientes ambientais na Floresta Atlântica. No Rio Grande do Sul, local de realização do presente estudo, não se sabe ao certo o número de espécies de samambaias e licófitas na Mata Atlântica, mas a julgar pelas estimativas de cunho mais geral, lançadas para aferir o total de samambaias e licófitas existentes na porção Sul do Brasil, acredita-se que cerca de 300 a 550 espécies componham a flora regional.

Apesar da elevada importância de conservação da Mata Atlântica, as variações florísticas de samambaias e os fatores relacionados ao longo de gradientes altitudinais ainda são pouco conhecidos, especialmente no setor sul. Estudos que abordem a importância relativa das variações espaciais e ambientais determinantes na estruturação das comunidades de samambaias e licófitas ao longo de gradiente altitudinal no Brasil na Mata Atlântica são escassos; sendo dos poucos trabalhos existentes, metade remete apenas à variação florística (Nóbrega 2013, Damasceno 2010, Condack & Sylvestre 2008), enquanto que o restante se relaciona às variáveis espaciais e ambientais (Nóbrega 2013, Paciencia 2008), dos quais as

variáveis climáticas nunca foram testadas. Acreditamos que as variáveis ambientais climáticas devam atuar fortemente na distribuição de espécies de samambaias e licófitas ao longo de gradientes altitudinais no Sul do Brasil.

A grande maioria dos trabalhos descreve ou avalia padrões de riqueza ou de diversidade (Athayde-Filho & Windisch 2006, Santos & Windisch 2008, Becker et al. 2013) considerando o grupo de samambaias e licófitas em geral, sem diferenciar entre grupos ecológicos distintos, tais como as terrícolas, rupícolas e epifíticas. Espera-se que estes grupos tenham diferido em suas respostas aos gradientes ambientais, já que as corticícolas não são diretamente influenciadas pelo solo e por suas características. Desta forma, estudos que abordam espécies terrícolas, rupícolas e epifíticas são necessários para compreender com mais clareza às respostas ao gradiente altitudinal.

A presente tese busca contribuir para um melhor conhecimento sobre os padrões de diversidade em comunidades de samambaias e licófitas ao longo de um gradiente de altitude no Sul do Brasil, considerando a influência de fatores climáticos e edáficos. Além de contribuírem para uma melhor compreensão da estrutura das comunidades vegetais na Mata Atlântica, os resultados gerados auxiliarão na conservação das espécies do grupo estudado e dos seus hábitats. Pretendemos trabalhar, pela primeira vez no Sul do Brasil, em uma escala regional, e, ainda, complementar com uma abordagem baseada na composição e abundância das espécies.

OBJETIVOS

Objetivo geral: analisar padrões de diversidade em comunidades de samambaias e licófitas ao longo de um gradiente climático na Floresta Atlântica no Sul do Brasil.

Objetivos específicos:

a) analisar a composição florística e a estrutura comunitária de samambaias e licófitas ao longo de um gradiente altitudinal na Floresta Atlântica no Rio Grande do Sul, Brasil;

b) avaliar o efeito de fatores climáticos e edáficos em comunidades de samambaias e licófitas no Rio Grande do Sul, considerando diferentes grupos ecológicos e comparando os padrões encontrados com outros grupos vegetais.

Hipotetizamos que:

(1) as diferentes formações florestais ao longo do gradiente altitudinal irão diferir quanto à composição de samambaias e licófitas, bem como quanto à riqueza, e deverão ser máxima na Floresta Ombrófila Densa Montana;

(2) grupos ecológicos distintos (por ex. terrestres, rupestres e epifíticos) responderão de forma distinta ao longo do gradiente altitudinal (ex. riqueza maior de epifíticos nas áreas com maior altitude e de terrícolas nas áreas com menor altitude);

(3) a variação na composição de espécies ao longo do gradiente altitudinal estará relacionada pelo compartilhamento de efeitos de variáveis espaciais e ambientais;

(4) na estratificação ambiental, fatores climáticos influenciam a densidade de espécies epífitos enquanto que fatores edáficos influenciam a densidade de espécies terrestres.

APRESENTAÇÃO DA TESE

Com o objetivo de organizar e estruturar diferentes abordagens, esta tese está dividida em 3 capítulos, nas quais os capítulos são apresentados em forma de artigos estruturados nos respectivos formatos dos periódicos que foram e/ou serão submetidos.

O primeiro capítulo apresenta a variação da composição de espécies e riqueza de comunidade como um todo de samambaias e licófitas sob diferentes altitudes na Mata Atlântica do Sul do Brasil, bem como a abundância e diversidade das comunidades epífitas, rupícolas e terrestres.

O segundo capítulo, realizado com base nos dados gerados pelo primeiro capítulo e, adicionado à coleta de variáveis ambientais e espaciais, aborda o efeito dos fatores espaciais e ambientais como direcionadores da composição de espécies e diversidade de samambaias e licófitas ao longo do gradiente altitudinal da Mata Atlântica no Sul do Brasil.

O terceiro capítulo, realizado com base nos dados gerados pelo primeiro capítulo, aborda o novo registro do gênero *Stigmatopteris* (Dryopteridaceae) no estado do Rio Grande do Sul, Brazil.

Por fim, no item Anexos, é apresentada a publicação de atividades adicionais produzidas durante o período da tese.

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Capítulo 1

FERN AND LYCOPHYTE COMMUNITIES AT CONTRASTING ALTITUDES IN BRAZIL'S SUBTROPICAL ATLANTIC RAIN FOREST

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Fern and lycophyte communities at contrasting altitudes in Brazil's subtropical Atlantic Rain Forest

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Abstract Ferns and lycophytes are a species-rich group in Brazil's Atlantic Rain Forest, but studies on richness and diversity patterns on a regional scope are scarce. We investigated communities at different altitudinal belts in the Atlantic Rain Forest in southern Brazil, spanning from lowland and submontane to montane and upper montane forest formations. We tested the hypotheses that each forest formation differed in its fern and lycophyte community composition and that species richness peaked in montane forests. Species composition, from the ground level to the phorophyte canopy, was studied at five sites per belt (together 120 plots of 10 × 10 m). Species were according to substrate types (epiphytic, rupicolous and terrestrial species). Analyses were conducted for the entire species set, and for the epiphytic, terrestrial and rupicolous component separately. We found a total of 139 species of ferns and lycophytes, of which Polypodiaceae was the family with the highest species number. Overall composition differed among altitudes and for the three substrate types. Richness was highest in the montane and upper montane formations. The study indicated the presence both of species with high habitat specificity and of species with broad ecological amplitude along the gradient. Altogether, our study reduces the lack of information ferns and lycophytes communities at a regional scale and confirms the high diversity of this group for biodiversity in the Brazil's Atlantic Forest.

Keywords epiphytes · floristics · geophytes · lithophytes · neotropical · pteridophytes

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Introduction

The relationship between patterns of species richness and abundance in time and space along gradients is one of the classic topics of ecological research (MacArthur 1972; Rosenzweig 1992; Pausas and Austin 2001). Work that focused on large-scale, cross-continental patterns was pioneered by botanists such as de Candolle (1874) and Copeland (1939). Subsequently, interest has focused on plant distribution along latitudinal and elevational gradients and the processes that control these patterns (Scheiner and Reybenayas 1994; Boyle 1996; Vetaas and Grytnes 2002; Colwell et al. 2004b; among others). Our better understanding of the diversity and

distribution patterns of species along altitudinal gradients contributes to advances in ecological theory and to knowledge on the potential mechanisms driving these patterns (e.g. Colwell and Hurtt 1994; Colwell and Lees 2000) and also provides an important basis for the conservation of natural resources at local and regional scales (e.g. Speziale et al. 2010).

Studies on elevation gradients have identified three main patterns of species richness: (a) a monotonic decrease in species richness as altitude increases (Gentry 1995), (b) a decline in species richness related to the decline in area with increasing altitude (Rahbek 1995, 2005), (c) a peak in diversity at intermediate elevations. There are several hypothesis for these patterns, including geometric constraints (Mid-Domain Effect; Colwell and Lees 2000). Other hypotheses include high rainfall or productivity at mid-elevations and higher habitat heterogeneity at mid elevations (Rahbek 1995; Lomolino 2001).

Variation of richness patterns of structurally complex tropical forests have especially been in the focus of research in the past decades, and these studies have considered different functional groups such as trees, vines, shrubs, and herbs (Gentry 1982, 1988; Condit et al. 1996; Kessler 2001b; Watkins et al. 2006, among others). However, few studies on elevational gradients have focused on epiphytes, and fewer still have considered both epiphytic and terrestrial species (Kessler 2001a,b; Watkins et al. 2006). Ferns and lycophytes include both life forms, which adds complexity to biogeographical studies of a fascinating group of plants that combine wind-dispersed spores and free-living gametophytes and that occupy a wide range of environments, from the equator to the circumpolar temperate regions, from semi-desert regions to the coastline (including mangroves and rocky shores of the tidal zone), both at low and at high altitudes (Page 1979; Tryon and Tryon 1982).

Ferns and lycophytes, a paraphyletic group denominated, until recently, as 'pteridophytes' in a broader sense, constitutes about 5 % of species richness of Neotropical forests (Poulsen and Nielsen 1995). For ferns and lycophytes in the neotropics, the pattern of higher richness at intermediate elevations (1,300–2,300 m a.s.l.) has been linked to a combination of high humidity and moderate temperatures (Kessler 2001a; Kluge et al. 2006), while low temperatures (especially frost) are limiting factors for species of this group (Bhattarai et al. 2004; Schmitt and Windisch 2005; Kluge et al. 2006).

In such a diverse group of plants, not all species should respond equally to environmental variation. The group contains vines, epiphytes, hemiepiphytes, rupicolous species, xerophytes, halophytes, hydrophytes (floating or rooting) or sub-arborescent species (Page 1979; Tryon 1989). In some species, it is possible to observe more than one structural types or habit, depending on the environment in which it lives (Moran 1987; Watkins et al. 2006; Windisch et al. 2008; Nervo 2012). However, biogeographical studies that consider different characteristics of the plants are still scarce despite the high importance of these traits for the interpretation of environmental filters and thus for a better understanding of the organization of communities (in general: Keddy 1992; for ferns: Karst and Lechowicz 2007).

Brazil's Atlantic Rain Forest *sensu stricto* (Oliveira-Filho and Fontes 2000) represents an especially interesting environment to study distribution patterns along altitudinal gradients (e.g. Bergamin et al. 2012). The high diversity of species in the Atlantic Rain Forest is the result of an extensive latitudinal range (3° S to 30° S) and a substantial altitudinal variation (from sea level to 1,920 m a.s.l.), over a short distance in space, creating conditions for the development and establishment of a diverse complex of plant formations. The Atlantic Forest is the Brazilian biome with the highest ferns and lycophytes species richness (Windisch 2002; Prado and Sylvestre 2013). Richness of the group is estimated to be of approximately 840 species, which correspond to 69 % of pteridophytes species in Brazil (Prado and Sylvestre 2013, continuously updated). The highest richness of ferns and lycophytes in Brazil is found in mountainous areas (800–1,400 m a.s.l.; Paciencia 2008; Damasceno 2010; Nóbrega et al. 2011; Nóbrega 2013) of the Atlantic Rain forest (631 species), and 81 % of ferns and lycophytes are endemic to the Atlantic Rain Forest (Stehmann et al. 2009). The southern part of the Atlantic Forest (located in the Brazilian states of Paraná, Santa Catarina and Rio Grande do Sul) contains about 546 species of ferns and lycophytes (Windisch 1996; Prado and Sylvestre 2013), 47 (9.5 %) of which restricted to this region (Salino and Almeida 2009).

Despite considerable advances regarding floristics of ferns and lycophytes from southern Brazil (Rosenstock 1906; Sehnem 1967a,b; Schmitt and Windisch 2005; Athayde Filho and Windisch 2006; Schmitt and Windisch 2007; Nervo et al. 2010; among many others), there is still a large gap concerning our

understanding of the relationship between altitude and the occurrence of ferns and lycophytes in forest ecosystems (Dittrich et al. 2005; Paciencia 2008). With this study, we intend to contribute to knowledge on diversity patterns of fern and lycophyte communities among four different altitudinal belts in the Atlantic Rain Forest in southern Brazil. We distinguish between different ecological groups in relation to substrate type, namely epiphytic, rupicolous and terrestrial species. We ask the following questions: (1) Do composition and species richness of ferns and lycophytes vary among altitudinal belts? (2) If so, at what altitude can we find the greatest richness of the group? (3) Which differences in distribution patterns can be observed among epiphytic, rupicolous and terrestrial species as groups?

Material and methods

Study region

The study was conducted along an altitudinal gradient in the Atlantic Rain Forest sensu stricto (ARF; Floresta Ombrófila Densa in Portuguese) in north-eastern Rio Grande do Sul (RS), Brazil. In southern Brazil (24 to 32°S), the ARF can be divided into four altitudinal zones that comprise distinct forest physiognomies (Veloso and Góes-Filho 1982; see also Teixeira et al. 1986 and Brack 2009): (1) Lowland (LO), 5–50 m altitude; (2) Submontane (SU), at the base of the Serra do Mar mountains, with an altitude between 50 and 400 m; (3) Montane (MO), covering the slopes of the Serra do Mar, at altitudes ranging from 400 to 1,000 m; and (4) Upper montane (UP), at altitudes ranging between 1,000 and 1,400 m (see Supplementary material Table 1).

Sampling design

Species composition and abundance was studied in the four forest formations that comprise this altitudinal gradient (lowland, submontane, montane and upper montane). In each altitudinal belt, we sampled ferns and lycophytes at five sites (replicates), with six plots of 10 × 10 m per site (400 m^2 per site), totalling 120 plots Our sampling effort thus exceeded the minimum value per site indicated by Kessler and Bach (1999) as necessary for studies aiming at comparing communities of ferns and lycophytes in tropical forest (400 m^2). Most study areas were situated in protected areas in reasonable good state of conservation (Table 1). The distance between sites (replicates) within an altitudinal zone was at least 1 km. Fieldwork was conducted from March 2012 to March 2015.

In each plot, cover of all fern and lycophyte species was estimated, and species were classified into one of three habits, based on the occupied substrate: epiphytic (species that grow on tree trunks or branches, i.e. corticicolous plants), rupicolous (species that grow on rocks) and terrestrial (species with rooting in the ground). Species that grew in more than one habit were included in the respective categories in each sample unit, with cover estimated separately for each category. Species cover was estimated using a modified Braun-Blanquet (1964) scale, using seven categories: 1 (species with cover smaller 1 %), 2 (2 to 5 %), 3 (6 to 10 %), 4 (11 to 25 %), 5 (26 to 50 %), 6 (51 to 75 %) and 7 (76 to 100 %). For terrestrial and rupicolous species, cover was estimated at the ground level, using four subplots (5 × 5 m) whose data was then pooled to the total plot area. For sampling of corticicolous individuals, phorophytes were used as natural sampling units. For this, we included all trees with diameter at breast height (DBH) of at least 10 cm, and recorded species presence per height interval (trunk base: the first 130 cm near the soil; medium trunk: portion between base and high trunk; high trunk: last 130 cm of the trunk before crown; internal crown: internal half of the crown; external crown: external half of the crown). We did not estimate cover values for epiphytes, due to the complex structure of trees and their over branches. The presence of the corticolous species on each phorophyte was recorded using binoculars, digital high resolution images, and when necessary, by climbing of the phorophyte. Plants were collected when necessary to confirm the identification.

Species were identified by help of literature, consultation of experts, and comparison with material of the main herbaria of the Rio Grande do Sul State (ICN, HAS and PACA, acronyms follow Thiers 2011). Families and genera were classified in accordance to Smith et al. (2006). The collected material was herborized following usual techniques for vascular plants (Windisch 1992) and incorporated into the ICN Herbarium. Citation of authorities for plant names follows Pichi-Sermolli (1996), and for names created after 1996, we follow the List of Species of the Flora of Brazil (Prado and Sylvestre 2013).

Table 1 Species richness at twenty sites in different altitudinal belts in the Atlantic Rain Forest, in northeastern Rio Grande do Sul state, Brazil. The second through fifth columns show recorded species richness at each study elevation for each substrate type and all species combined. Interpolated richness is the richness at each site under the assumption of continuous elevation ranges. Rarefaction estimates represent the expected number of species at 2,192 occurrences per site. Chao2 and Bootstrap are nonparametric estimates of total species richness, including undetected species. Percentage collected values were computed as (total species / mean of Chao2 and Bootstrap) × 100. LO – lowlands, SU – submontane, MO – montane, UP – upper montane.

Forest formation	Species richness					Rarefaction estimate	Chao2	Bootstrap	Percentage collected
	Epiphytic	Rupicolous	Terrestrial	All recorded species	Interpolated richness				
LO	38	19	41	66	66	60	74	73	90
SU	55	23	45	84	86	76	100	94	87
MO	60	19	35	87	90	76	135	100	74
UP	54	8	37	85	85	74	100	91	89
All sites pooled	93	40	81	139	139	134	141	148	96

Data analysis

All analyses were performed for the whole community and separately for the terrestrial, corticicolous (epiphytic) and rupicolous components. For the analysis of community structure of terrestrial and rupicolous species, we used the indicator value based on the combination of relative cover and relative frequency (after Mueller-Dombois and Ellenberg (1974). The importance value for epiphytic plants was calculated from the average amount of frequencies relative to phorophytes and height intervals, based on Waechter (1998) and Kersten and Waechter (2010).

For each sampling unit, we calculated the Simpson index as diversity measure. We present common and unique species in the different altitudinal zones (ARF forest types: LO, SU, MO and UM) in the form of a Venn diagram (Oliveros 2007).

We applied two distinct approaches to reduce the effects of undersampling on richness estimates. In the first approach, we compared richness, based on the rarefaction curves, at a uniform number of occurrences (Chazdon et al. 1998; Colwell et al. 2004a). In the second, we used nonparametric methods to estimate true species richness using two incidence-based estimators, Chao2 and Boostrap (Chazdon et al. 1998). In the third method, we assumed that the elevational range of each species was continuous, at the scale of our sampling. This assumption yields what we will refer to as the 'interpolated' species richness for each sampling site (Grytnes and Vetaas 2002), which includes each species actually recorded from that site, plus any additional species recorded from at least one site above and at least one site below that site. These analyses were performed in EstimateS software v. 9.1.0 (Colwell 2013).

Values of richness and cover of the three different substrate types were compared between altitudinal zones by analysis of variance (ANOVA) with permutation testing (Pillar and Orlóci 1996). Values of diversity indices were compared using the software PAST (Hammer et al. 2008). For these analyses, we used the mean value of the six sample units of each area. Differences in species composition of communities were tested with Manova and visualized by principal coordinates analysis (PCoA). For the analyses with all species, we used presence-absence data and the Sorensen index, and for the different ecological categories (epiphytic, rupicolous and terrestrial species) abundance values and Bray-Curtis distance. Analyses were performed in MULTIV (Pillar 1997) and on the R platform (The R Development Core Team 2010).

Results

General floristic composition

At the twenty study sites in the South Brazilian Atlantic Rain forest, we registered 139 species of ferns and lycophytes, representing 55 genera and 21 families, of which 34 species (25 %) are endemic to the Brazilian Atlantic Forest (Table **2** in the Electronic Supplementary

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Materia, see Prado et al. 2015). Polypodiaceae was the most representative family, with 30 species, followed by Aspleniaceae (17), Dryopteridaceae (16) and Hymenophyllaceae (15). These four families together comprised about 56 % of the sampled species. Thirteen species are included in the list of threatened species for State of Rio Grande do Sul (Assembléia Legislativa do Estado do Rio Grande do Sul 2015), two of them as 'critically endangered' (Table **S2** in the Electronic Supplementary Material). Additionally, we observed *Anemia mandioccana* Raddi outside the sampling units in one of the study areas (submontane forest), a new record for RS (Nervo et al. in prep.).

Twenty-five species (18 % of the total) were found in all forest types (Fig. **1**) and 32 species (23 %) only occurred in one forest type. Montane and upper montane forests shared 31 species, and lowland and submontane forests, 19 species (Fig. **1**). The formations at the extremes of the gradient, upper montane and lowland forest, shared only one specie. The species accumulation curve (sample-based rarefaction curve, Fig. **2**) for all sites and species combined failed to saturate, as expected for very species-rich local floras; nonetheless, 96 % of the expected species were recorded (Table **1**). Efficiency of sampling was lowest for MO, according to all indices.

Eighty-one species of ferns and lycophytes were terrestrial (see Table **1**), followed by epiphytes (93 species on 1,223 phorophytes), and rupicolous species (40). This indicates considerable overlap in terms of substrate type: only 79 species (57 %) occurred as only one of substrate type. Other 60 species (43 %) were found in two or three type of substrate, of which in two type of substrate, 45 sp. div. (32 %) and 15 sp. div. (11 %) in three types. The highest overlap was observed occurs in between epiphytic and terrestrial species (22 sp. div., 16 %) followed epiphytic and rupicolous species (20 sp. div., 14 %), and rupicolous and terrestrial species (three species, 2 %).

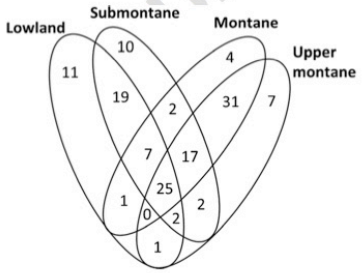


Fig. 1 Venn diagram showing proportions of shared species among the ferns and lycophytes in distinct forest formations in the Atlantic Rain Forest in northeastern Rio Grande do Sul state, Brazil.

The number of species restricted to any of the four forest formations was rather low (less than 10 % for all formations, Fig. **1** and Supplementary material Table **2**). Nontheless, multivariate analyses of the complete data set revealed that there was significant variation in species composition among all forest formations ($P < 0.05$, Table **2**). The Sørensen index calculated between areas clearly indicated the high similarity between lowland and submontane forests, and between montane and upper montane forests, with a clear decrease in floristic similarity with higher distance along the gradient (Table **3**). Areas of the upper montane forests were more similar in terms of floristic composition than areas of the other formations, as evidenced by the mean value of the Sørensen index calculated for all pairs of areas.

Richness and diversity

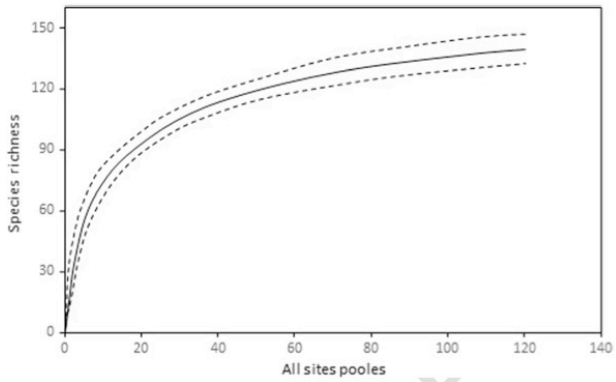
The highest total species richness was observed in the montane forest, with 87 species in all study plots, followed by upper montane forest (85), submontane forest (84) and lowland forest (66), see Fig. **3**.

Mean species richness per plot varied significantly between elevations ($P < 0.01$; Table **2**). On the plot level, total richness was very similar for montane (23 species) and upper montane forest (21) and significantly lower in the lowland forests (13) (Table **2**). Submontane forest presented intermediate values (Table **2**). Patterns were divergent for substrate types. For epiphytes, the two upper formations (MO and UP) had significantly higher values for mean species richness per plot than the two lowland forests (Fig. **3**, Table **2**). The opposite was observed for rupicolous species, with the two lowest formations presenting the highest values and montane and upper montane forest significantly lower values, even though based on a very low mean species number per plot. Terrestrial component had high average species richness in submontane, montane and upper montane forests, while values for lowland were significantly lower (Fig. **3**, Table **2**).

Community composition

The principal coordinates analysis (PCoA, Fig. **4**) using total composition indicated a clear separation between

Q6 **Fig. 2** Pooled sample-based rarefaction curve (solid line) with 95 % confidence intervals (dashed line) for all fern species recorded at twenty sites (16 to 1,001 m a.s.l.) in four different altitudinal belts in the Atlantic Rain Forest in northeastern Rio Grande do Sul state, Brazil.



lowland and submontane formations on the left side of the diagram and montane and upper montane formations on the right side, along axis 1 (explanation: 26 %). *Elaphoglossum sellowianum* and *Hymenophyllum polyanthos* (both with a correlation coefficient of 0.98 to the first axis) were associated to montane and upper montane forests, while *Didymochlaena truncatula* and *Megalastrum connexum* characterized lowland and submontane forests (Fig. 4).

Similar patterns were found analysing different components separately (based on substrate types), using abundance (rupicolous and terrestrial community) and relative frequency (epiphytic community; Fig. 4). The greater similarity of the communities of terrestrial ferns and lycophytes in Montane and Upper montane formations was evidenced by low dispersion in the ordination diagram (Fig. 4).

Community structure

Considerable differences existed between altitudinal zones regarding most important species in terms of importance value (IV; Table 4, Fig. 3). In the epiphyte communities (based on substrate types), *Microgramma vaccinifolia* was the species with the highest importance value in lowland (IV = 40.50) and submontane forests (IV = 16.99; Table 4, Fig. 3), while in upper montane and montane forest, the most important species was *Hymenophyllum polyanthos* (IV = 20.90 and 16.99, respectively). In lowland forest, this was *Microgramma vaccinifolia*, followed by *Pleopeltis pleopeltifolia* (IV = 15.5); *Mickelia guianensis* (IV = 7.63), *Campyloneurum nitidum* (IV = 4.68) and *Serpocaulon catharine* (IV = 4.26), together amounting for 72.6 % of all epiphytic species observed in lowland areas (see Table 4).

Table 2 Mean diversity and richness (± *SD*) of fern and lycophytes specie in four forest formations situated at different altitudinal belts in the Atlantic Rain Forest in northeastern Rio Grande do Sul state, Brazil. Different letters in the same line indicate statistically significant differences at 5 % probability.

Richness	Lowland	Submontane	Montane	Upper montane	*Q*	*P*
Epiphytes	6 ± 1 a	8 ± 3 a	16 ± 3 b	15 ± 3 b	353.8	0.001
Rupicolous	2 ± 1 ab	3 ± 0.6 a	1 ± 0.8 b	1 ± 0.3 b	32.9	0.010
Terrestrial	5 ± 1 a	8 ± 2 b	7 ± 1 b	7 ± 1 b	21.2	0.001
Total	13 ± 2 a	16 ± 4 ab	23 ± 3 b	21 ± 4 b	281.7	0.001
Diversity (Simpson)						
Epiphytes	0.861 ± 0.08 a	0.895 ± 0.11 b	0.935 ± 0.03 c	0.927 ± 0.05 d	105.23	0.001
Rupicolous	0.387± 0.21 a	0.538 ± 0.08 a	0.254 ± 0.18 a	0.309 ± 0.16 a	0.227	0.087
Terrestrial	0.936 ± 0.02 a	0.943 ± 0.02 b	0.900 ± 0.01 c	0.899 ± 0.01 d	137.45	0.001

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Table 3 Floristic similarity of ferns and lycophytes in four formations situated in different altitudinal belts in the Atlantic Rain Forest in northeastern Rio Grande do Sul state, Brazil, indicated by the Sørensen index. LO – lowland, SU – submontane, MO – montane, UP – upper montane, IHM – internal heterogeneity measure (= Sørensen index calculated for all pairs of areas within one formation).

	*IHM	LO	SU	MO	UP
LO	0.527	1	0.752	0.461	0.342
SU	0.612	0.752	1	0.550	0.424
MO	0.688	0.461	0.550	1	0.728
UP	0.815	0.342	0.424	0.728	1

In terrestrial communities, the arborescent fern *Dicksonia sellowiana* had the highest importance value of all species in upper montane (IV = 11.79) and montane forests (IV = 10.82; Table 4, Fig. 3). In submontane forest, the species with highest importance value was *Didymochlaena truncatula* (IV = 8.85), while in lowland forest, *Polybotrya cylindrica* (IV = 8.93).

In Upper montane forests the highest importance value (IV = 24.36) the rupicolous community was observed for *Hymenophyllum polyanthos*, while in lowland forest, *Vandenboschia radicans* (IV = 20.95). In submontane *Asplenium brasiliense* (IV = 17.41), and in montane forest, *Asplenium gastonis* (IV = 16.29).

Discussion

General floristic composition

This study is the first on communities of ferns and lycophytes in subtropical southern Brazil with a regional scope. The total number of 139 species found in the 1,2 hectares sampled in the four altitudinal belts corresponds to about 40 % of all registered ferns and lycophytes for Rio Grande do Sul state (RS) (Prado and Sylvestre 2013; Windisch 1996), indicating the high concentration of species of this group in a small region of the Atlantic Rain Forest. The importance of the region for biodiversity and conservation specifically of ferns and lycophytes also becomes obvious from the high number of threatened species (13 species, 20 % to all of threatened ferns and lycophytes species for RS), as well as from one new citation of *Anemia mandioccana* for the state. The prevalence the families Polypodiaceae, Aspleniaceae, Dryopteridaceae s.l. e

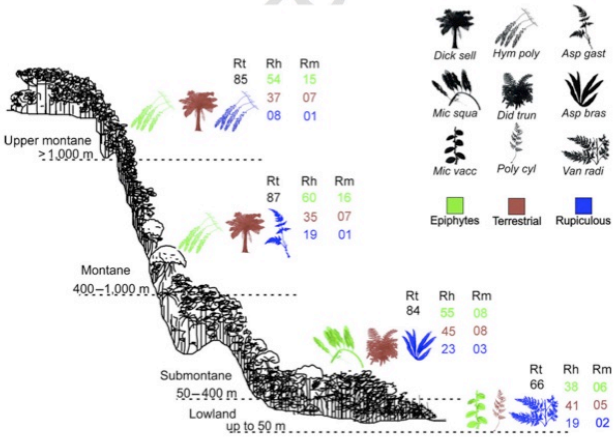

Fig. 3 Schematic profile of the altitudinal gradient in southern Atlantic Rain Forest in northeastern Rio Grande do Sul state, Brazil, with values of total and average richness of ferns and lycophytes per altitudinal belt, as found in this study. Rt – total richness; Rh – total richness of epiphytes (green), terrestrial (brown) and rupicolous (blue). Note that one species may occur in more than one group (see text); Rm – mean richness per plot for epiphytes (green), terrestrial (brown) and rupicolous (blue). For each species group, the species with highest IV is depicted. Dick sell – *Dicksonia sellowiana*, Hym poly – *Hymenophyllum polyanthos*, Asp gast – *Asplenium gastonis*, Mic squa – *Microgramma squamulosa*, Did trun – *Didymochlaena truncatula*, Asp bras – *Asplenium brasiliense*, Mic vacc – *Microgramma vaccinifolia*, Poly cyl – *Polybotria cylindrica*, Van radi – *Vandenboschia radicans*. Schematic profile modified from Brack (2009).

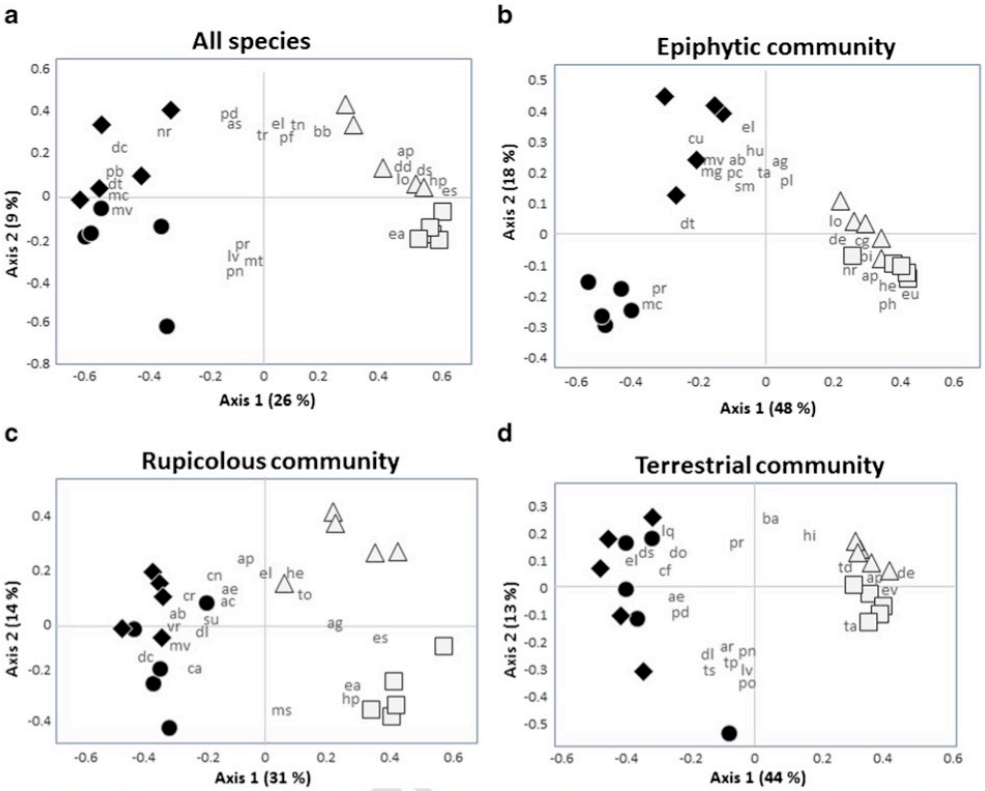

Fig. 4 PCoA of forest areas of ferns and lycophytes communities in four forest formations situated at different altitudinal belts in the Atlantic Rain Forest in northeastern Rio Grande do Sul state, Brazil: lowland (circles), submontane (rhombus), montane (triangles) and upper montane forests (squares). **a** – all species (including terrestrial, epiphytic and rupicolous species), described by presence/absence data. Explanation of axis 1 = 26 % ($P < 0.05$) and of axis 2 = 9 %; **b** – epiphytic ferns and lycophytes, described by abundance (relative frequency date), explanation of axis 1 = 48 % ($P < 0.05$) and of axis 2 = 18 %; **c** – rupicolous ferns and lycophytes, described by abundance, explanation of axis 1 = 31 % ($P < 0.05$) and of axis 2 = 14 %; **d** – terrestrial ferns and lycophytes, described by abundance, explanation of axis 1 = 44 % ($P > 0.05$) and of axis 2 = 13 %. Species with higher correlation coefficients are shown in the diagrams; ab – *Asplenium brasiliense*, ac – *Asplenium claussenii*, ae – *Asplenium sellowianianum*, ag – *Asplenium gastonis*, ap – *Aplenium pseudonitidum*, ar – *Adiantum raddianum*, as – *Asplenium scandiscinum*, ba – *Blechnum auriculatum*, bb – *Blechnum acutum*, ca – *Campyloneurum acrocarpom*, cf – *Ctenitis fasciculata*, cg – *Campyloneurum aglaolepis*, cn – *Campyloneurum nitidum*, cr – *Campyloneurum rigidum*, cu – *Campyloneurum austrobrasilianum*, dc – *Diplazium cristatum*, dd – *Dennstaedtia dissecta*, de – *Deparia petersenii*, dl – *Diplazium plantaginifolium*, do – *Diplazium rostratum*, ds – *Dicksonia sellowiana*, dt – *Didymochaena truncatula*, ea – *Elaphoglossum auricomum*, el – *Eupodium kaulfussii*, es – *Elaphoglossum sellowianum*, eu – *Elaphoglossum luridum*, ev – *Elaphoglossum vagans*, he – *Hymenophyllum peltatum*, hi – *Histiopteris incisa*, hp – *Hymenophyllum polyanthos*, hu – *Hymenophyllum pulchellum*, lo – *Leucotrichum organense*, lq – *Lindsaea quadrangularis*, lv – *Lygodium volubile*, mc – *Megalastrum connexum*, mg – *Mickelia guianensis*, ms – *Microgramma squamulosa*, mt – *Macrothelypteris torresiana*, mv – *Microgramma vaccinifolia*, nr – *Niphidium rufosquamatum*, pb – *Pteris brasiliense*, pc – *Polybotrya cylindrica*, pd – *Pteris deflexa*, pf – *Pleopeltis pleopeltifolia*, ph – *Pleopeltis hirsutissima*, pi – *Pecluma sicca*, pl – *Polytaenium lineatum*, pn – *Psilotum nudum*, po – *Pecluma* sp., pr – *Pecluma robusta*, sm – *Serpocaulon meniscifolium*, su – *Selaginella muscosa*, ta – *Thelyptheris amambayensis*, td – *Thelypteris dentata*, tn – *Trichomanes anadromum*, to – *Trichomanes polypodioides*, tp – *Tectaria pilosa*, tr – *Thelyptheris rivularoides*, ts – *Thelypteris conspersa*, vr – *Vandenboschia radicans*.

Q7 **Table 4** Species with highest Importance Values (IV) in four formations situated at different altitudinal belts in the Atlantic Rain Forest in northeastern Rio Grande do Sul state, Brazil, separately for epiphytic, terrestrial and rupicolous categories. The total corresponds to the sum of the IVs of the five most important species, for each formation.

Community	#	LOWLANDS	IV	SUBMONTANE	IV	MONTANE	IV	UPPER MONTANE	IV
Epiphytes	**1º**	*Microgramma vaccinifolia*	40.50	*Microgramma vacciniifolia*	16.99	*Hymenophyllum polyanthos*	16.17	*Hymenophyllum polyanthos*	20.90
	2º	*Pleopeltis pleopeltifolia*	15.57	*Microgramma squamulosa*	13.52	*Microgramma squamulosa*	11.23	*Pleopeltis pleopeltidis*	17.75
	3º	*Mickelia guianensis*	7.63	*Campyloneurum nitidium*	10.04	*Pleopeltis pleopeltidis*	10.28	*Elaphoglossum sellowianum*	12.02
	4º	*Campyloneurum nitidium*	4.68	*Pleopeltis pleopeltifolia*	8.22	*Pleopeltis hirsutissima*	7.90	*Pleopeltis hirsutissima*	7.43
	5º	*Serpocaulon catharinae*	4.26	*Mickelia guianensis*	6.08	*Elaphoglossum sellowianum*	7.23	*Pecluma paradiseae*	5.59
		Total	**72.64**	**Total**	**54.85**	**Total**	**52.81**	**Total**	**63.69**
Terrestrial	**1º**	*Polybotrya cylindrica*	8.93	*Didymochlaena trunculata*	8.85	*Dicksonia sellowiana*	10.82	*Dicksonia sellowiana*	11.81
	2º	*Diplazium cristatum*	6.35	*Alsophila setosa*	7.89	*Lastreopsis amplissima*	9.50	*Asplenium pseudonitidum*	7.61
	3º	*Mickelia guianensis*	6.21	*Megalastrum connexum*	6.02	*Dennstaedtia dissecta*	7.07	*Elaphoglossum sellowianum*	5.96
	4º	*Megalastrum connexum*	6.07	*Diplazium cristatum*	4.67	*Blechnum acutum*	6.14	*Pleopeltis pleopeltidis*	5.60
	5º	*Tectaria incisa*	5.86	*Mickelia guianensis*	4.24	*Asplenium pseudonitidum*	5.29	*Pecluma paradiseae*	5.51
		Total	**66.86**	**Total**	**63.34**	**Total**	**77.62**	**Total**	**72.77**
Rupicolous	**1º**	*Vandenboschia radicans*	20.95	*Asplenium brasiliense*	17.41	*Asplenium gastonis*	16.29	*Hymenophyllum polyanthos*	24.36
	2º	*Diplazium cristatum*	8.57	*Vandenboschia radicans*	15.43	*Elaphoglossum sellowianum*	11.63	*Microgramma squamulosa*	16.24
	3º	*Micrograma vacciniifolia*	8.2	*Campyloneurum rigidum*	12.07	*Didymoglossum hymenoides*	9.31	*Elaphoglossum auricomum*	16.90
	4º	*Mickelia guianensis*	7.54	*Diplazium cristatum*	6.58	*Vandenboschia radicans*	8.12	*Asplenium gastonis*	12.18
	5º	*Campyloneurum rigidum*	6.09	*Mickelia guianensis*	5.98	*Asplenium pseudonitidum*	6.98	*Elaphoglossum sellowianum*	12.04
		Total	**51.35**	**Total**	**57.47**	**Total**	**52.33**	**Total**	**81.72**

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Hymenophyllaceae, in terms of species number and abundance corroborates with other studies from Atlantic Forest and tropical forests in general, (e.g. Watkins et al. 2006; Paciencia 2008; Damasceno 2010; Nóbrega et al. 2011; Nóbrega 2013). The total species accumulation (sample-based rarefaction) curve failed to saturate, suggesting that the actual species number should be even higher (Fig. 2). Nonetheless, our species richness indicators showed expected overall richness values rather close to the observed value, i.e. posing no limitations to interpretation of our data. The richness values found by us are similar to those found along other altitudinal gradients in tropical parts of Brazil, e.g. in the studies by Paciencia (2008: 166 species in 30 plots of 600 m^2 along a gradient of 1,500 m, in the Atlantic Forest in Paraná state), Nobrega (2013: 90 species in 49 plots along a gradient of 1,000 m in the Atlantic Forest in São Paulo state) and Damasceno (2010: 115 ferns in 180 plots of 25 m^2 each along a gradient from 1,000 to 1,800 m a.s.l).

Some species presented a restricted distribution along the gradient, e.g. were only observed in montane forest (4 species, Fig. 1), while the majority of species showed a greater ecological amplitude, with wide distribution and occurring in more than one type of forest (18 % were found in all forest types). The common presence in all formations of *Adiantum raddianum*, *Blechnum acutum*, *Blechnum brasiliense*, *Microgramma vaccinifolia* and *Selaginella muscosa* conforms the wide distribution of these species, both in the continent and in RS (Nervo et al. 2010), and demonstrates high adaptability of these species to a variety of environments. In contrast, the presence of locally abundant species in only one formation, such as *Lindsaea quadrangularis* (observed exclusively in lowland formations), *Blechnum lehmannii* (submontane), *Histiopteris incisa* and *Tryonia myriophylla* (upper montane), could be indicative of their specificity to the specific climatic conditions at the respective altitudinal range.

Richness and diversity

The composition and richness of fern and lycophyte communities differed among the altitudinal belts of the Atlantic Rain Forest, with similar total richness values for submontane montane and upper montane forest, but considerably higher values for montane and upper montane forest at the plot level (Table 1, Table 2, Fig. 3). Overall, the montane and upper montane forests showed quite similar patterns: higher richness of epiphytic species in comparison to the two lower formations (even though differences to the submontane forest were not always significant). The environmental characteristics of higher altitudes, such as lower temperatures (in our case, an absolute difference of about 10°C to between lowland and upper montane), associated to low rates of decomposition, nitrogen accumulation in the soil and the frequent presence of fog through stationary clouds have been shown to be main factors that affect the occurrence and distribution patterns of species of ferns and lycophytes (Kessler 2001a; Bhattarai and Vetaas 2003; Kluge et al. 2006; Paciencia 2008; Vieira et al. 2011).

Distinct ecological groups (epiphytic species vs terrestrial and rupicolous species) showed distinct patterns in terms of species richness across altitudes. Epiphytic species responding slightly clearer to the altitudinal differences than terrestrial species (Table 2 and Fig. 4), as evidenced by the significant differences in epiphytic richness of the two higher forest formations when compared to the two lower formations. For terrestrial species, submontane forests presented the highest diversity and species richness, and lowland forest differed significantly from all other formations. For rupicolous species, the opposite result was observed, a monotonic decrease in species richness with elevation increase, with greater diversity and species richness in Submontane forest (Table 2, Fig. 4). Total species richness all substrate types combined maintained a relatively steady richness after an initial increase significative at lower elevations (Table 3, Fig. 4).

Community composition

The PCoA calculated for the total data set and for specific groups showed the same general pattern of a clear distinction of communities into the two lower and two higher forest types, with considerable overlap within each of these groups, i.e. between Lowland and Submontane Forests and between Montane and Upper montane areas. This distinction is also supported by the values of the Sørensen index, even though we do recognize that the high similarity between the two upper formations may have some influence from the fact that the montane sites were all situated in the upper range of the formation, due to lack of available study sites at the lower part of the distribution of this range. Within community variation increased with altitude, indicating

stronger environmental filtering in the higher altitudinal belts.

Adequate conditions for the development of epiphytic plants in mountain regions has been documented in the literature (Benzing 1990; Moran 2008). The overlap of substrate types (epiphytic, rupicolous and terrestrial) for pteridophytes in Neotropical forests has been reported by several authors, but in these studies, species with more than one type of substrate (or habit) hardly exceed 20–30 % of the total species number (Kornás 1977; Dittrich et al. 2005; Watkins et al. 2006; Paciencia 2008). Among the different types of overlap reported, species that show both a terrestrial and epiphytic habit usually they are the most frequent, but their percentage of the total community does not exceed 12 % (Kornás 1977; Dittrich et al. 2005; Watkins et al. 2006; Paciencia 2008). Interestingly, in our study, we found 45 % of species that colonize more than one type of substrate and 18 % of overlap specifically between terrestrial and epiphytes species. This low habitat specificity regarding substrate type can be considered indicative for the rather high adaptability of some species to environmental variations, in particular along an altitudinal gradient. Another factor that may have contributed to our results is that some species (10 %) occur quite close to the base of phorophytes, especially at very humid sites where humus may accumulate. These species belong to genera or families, which are usually not cited to occur in this habit or condition.

Final considerations

Following Rahbek (1995, 2005), species richness and altitude show complex relationships that vary according to the taxonomic group and the gradient considered. In our study, even though we recorded clear difference of composition and richness of fern and lycophyte communities, and considerably lower richness in the lowland forest, the variation of overall richness did not follow any pattern already established for altitudinal gradients, such as a mid-altitudinal peak or a decline in richness with altitude. Possibly, this is because conditions at the higher end of our gradient are not severe enough to cause a decline in species number. Data of communities with different substrate types, especially epiphytic and rupicolous species, showed opposing tendencies: while epiphytes tended to occupy the highest formations gradient (montane and upper montane forest), rupicolous species tended to occupy the lower portions (submontane forest). This indicates that environmental filters that change along the gradient act differently on different ecological groups, which should be explored further, e.g. by including functional traits of species.

The high floristic richness of ferns and lycophytes observed in the study areas shows the importance of remaining Atlantic rain forest patches for this plant group in Rio Grande do Sul. In this study, we described patterns of composition, species richness and diversity of ferns and lycophytes along an altitudinal gradient. Further studies should address the relative importance of different spatial and environmental variables, thus increasing our understanding of the drivers of community assembly of the species group in question.

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Fern and lycophyte communities at contrasting altitudes in Brazil's subtropical Atlantic Rain Forest

Folia Geobotanica

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Supplementary Material Table 1 Characteristics of the different study sites in Atlantic Rain Forest in northeastern Rio Grande do Sul state, Brazil, in four forest formations: Lowland (LO), Submontane (SU), Montane (MO), Upper montane (UP). Information on soil type from IBGE (2002); information on climatic conditions from Alvares et al. (2013).

Forest formation	Municipality	No. area	Coordinates	Mean Altitude (m)	Soil type*	Climate type (Koeppen-Geiger) **	Mean annual precipitation (mm) **	Mean annual temperature (Celsius)**
LO	Dom Pedro de Alcântara	1	29º19'29.47"S 49º50'29.47"O	26	Red Alfisol	Cfa	1600–1900	18–20
LO	Mampituba	2	29º13'41.55"S 49º54'46.74"O	29	Haplic Gleysoil	Cfa	1600–1900	18–20
LO	Morrinhos do Sul	3	29º19'08.17"S 49º55'27.55"O	20	Haplic Cambissol	Cfa	1600–1900	18–20
LO	Morrinhos do Sul	4	29º17'18.42"S 49º53'50.91"O	42	Haplic Cambissol	Cfa	1600–1900	18–20
LO	Torres	5	29º17'25.43"S 49º55'00.78"O	16	Cambissol Haplic	Cfa	1600–1900	18–20
SU	Morrinhos do Sul	6	29º26'21.24"S 49º58'33.96"O	398	Red Alfisol	Cfa	1600–1900	18–20
SU	Morrinhos do Sul	7	29º25'46.10"S 49º59'11.72"O	384	Red Alfisol	Cfa	1600–1900	18–20
SU	Morrinhos do Sul	8	29º22'57.59"S	435	Red Alfisol	Cfa	1600–1900	18–20

			49º59'57.56"O					
SU	Terra de Areia	9	29º20'54.14"S	397	Red Alfisol	Cfa	1600–1900	18–20
			49º58'24.55"O					
SU	Terra de Areia	10	29º16'58.17"S	487	Red Alfisol	Cfa	1600–1900	18–20
			49º56'59.70"O					
MO	Cambará do Sul	11	29º09'44.10"S	961	Humic Cambisol	Cfb	1900–2200	12–14
			50º06'02.56"O					
MO	Cambará do Sul	12	29º10'32.80"S	964	Humic Cambissol	Cfb	1900–2200	12–14
			50º05'56.30"O					
MO	Cambará do Sul	13	29º11'05.74"S	969	Humic Cambissol	Cfb	1900–2200	12–14
			50º05'51.26"O					
MO	Cambará do Sul	14	29º09'44.88"S	967	Humic Cambissol	Cfb	1900–2200	12–14
			50º04'20.52"O					
MO	Cambará do Sul	15	29º10'34.64"S	988	Humic Cambissol	Cfb	1900–2200	12–14
			50º04'21.73"O					
UP	Cambará do Sul	16	29º04'10.88"S	1045	Humic Cambissol	Cfb	1900–2200	12–14
			49º57'40.73"O					
UP	Cambará do Sul	17	29º04'22.47"S	1051	Humic Cambissol	Cfb	1900–2200	12–14
			49º59'38.77"O					
UP	Cambará do Sul	18	29º02'17.27"S	1101	Humic Cambissol	Cfb	1900–2200	12–14
			49º58'22.65"O					
UP	Cambará do Sul	19	29º01'30.13"S	1071	Humic Cambissol	Cfb	1900–2200	12–14
			49º56'58.03"O					
UP	Cambará do Sul	20	29º02'00.43"S	1089	Humic Cambissol	Cfb	1900–2200	12–14
			49º58'54.85"O					

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Supplementary Material Table 2 Fern and lycophyte species occurring in four different altitudinal belts in the Atlantic Rain Forest in northeastern Rio Grande do Sul state, Brazil. Threat categories (TC): en = endangered; vu = vulnerable. Substrate types (ST): e = epiphytic; r = rupicolous; t = terrestrial; LO: Lowland; SU: Submontane; MO: Montane; UP: Upper montane.

FAMILY/Species	TC	ST	LO	SU	MO	UP
ANEMIACEAE						
Anemia phyllitidis (L.) Sw.		e/t	X	X		
ASPLENIACEAE						
Asplenium brasiliense Sw.		e/r/t	X	X		
Asplenium claussenii Hieron.		e/r/t		X	X	X
Asplenium gastonis Fée		e/r		X	X	X
Asplenium harpeodes Kunze		e/t		X	X	X
Asplenium inaequilaterale Willd.		e/t	X	X		
Asplenium incurvatum Fée		e			X	X
Asplenium kunzeanum Klotzsch ex Rosenst.		e/r/t	X	X	X	
Asplenium mucronatum C.Presl	vu	e	X	X		X
Asplenium pseudonitidum Raddi		e/r/t		X	X	X
Asplenium scandicinum Kaulf.		e		X	X	X
Asplenium sellowianum (Hieron.) Hieron.		e/r/t		X	X	X
Asplenium serra Langsd. & Fisch.		t	X			
Asplenium sp1		t	X	X		
Asplenium sp2		t			X	
Asplenium sp3		t		X		
Asplenium uniseriale Raddi		t	X	X		
Hymenasplenium triquetrum (N.Murak. & R.C.Moran) L.Regalado & Prada		t	X			
ATHYRIACEAE						
Athyrium dombeyi Desv.	en	t			X	X
Deparia petersenii (Kunze) M.Kato		e/t		X	X	X
Diplazium cristatum (Desr.) Alston		e/r/t	X	X	X	
Diplazium plantaginifolium (L.) Urb.		e/r/t	X	X		
Diplazium rostratum Fée		t		X		
BLECHNACEAE						
Blechnum acutum (Desv.) Mett.		e/t	X	X	X	X
Blechnum auriculatum Cav.		t		X	X	X
Blechnum brasiliense Desv.		e/t	X	X	X	X
Blechnum cordatum (Desv.) Hieron.		t				X
Blechnum lehmannii Hieron.		t		X		

Blechnum occidentale L.		t		X		X
Blechnum schomburgkii (Klotzsch) C.Chr.		t			X	X
Blechnum serrulatum Rich.		t			X	X
Blechnum spannagelii Rosenst.		t				X
CYATHEACEAE						
Alsophila setosa Kaulf.		t	X	X	X	X
Cyathea atrovirens (Langsd. & Fisch) Domin.		t	X	X	X	X
Cyathea corcovadensis (Raddi) Domin.	vu	t	X			
Cyathea delgadii Sternb.		t			X	X
Cyathea phalerata Mart.		t			X	X
DENNSTAEDTIACEAE						
Dennstaedtia dissecta T.Moore		e/t		X	X	X
Dennstaedtia globulifera (Poir.) Hieron.		t		X		
Dennstaedtia obtusifolia (Willd.) T.Moore		t		X		
Histiopteris incisa (Thunb.) J.Sm.		t				X
DICKSONIACEAE						
Dicksonia sellowiana Hook.	vu	e/t	X	X	X	X
DRYOPTERIDACEAE						
Ctenitis falciculata (Raddi) Ching		t	X	X		
Ctenitis submarginalis (Langsd. & Fisch.) Ching		t	X	X		
Didymochlaena truncatula (Sw.) J.Sm.		e/t	X	X		
Elaphoglossum auricomum (Kunze) T.Moore		r/t			X	X
Elaphoglossum edwallii Rosenst.		t			X	X
Elaphoglossum langsdorffii (Hook. & Grev.) T.Moore		r	X			
Elaphoglossum luridum (Fée) Christ		e/r/t	X	X	X	
Elaphoglossum macrophyllum (Mett. ex Kuhn) Christ	en	e/t	X			X
Elaphoglossum sellowianum (Klotzsch. ex Kuhn) T.Moore		e/r			X	X
Elaphoglossum vagans (Mett.) Hieron.		e/r/t			X	X
Lastreopsis amplissima (C.Presl) Tindale		e/t	X	X	X	X
Mickelia guianensis (Aubl.) R.C.Moran *et al.*		e/r/t	X	X		
Megalastrum connexum (Kaulf.) A.R.Sm. & R.C.Moran		e/t	X	X		
Polybotrya cylindrica Kaulf.		e/t	X	X	X	X
Polystichum montevidense (Spreng.) Rosenst.		e/t			X	X
Rumohra adiantiformis (G.Forst.) Ching		e/r/t	X	X	X	X
HYMENOPHYLLACEAE						
Didymoglossum hymenoides (Hedw.) Desv.		e/r	X	X	X	X
Didymoglossum reptans (Sw.) C.Presl		e/r		X		
Hymenophyllum asplenioides (Sw.) Sw.		e			X	X
Hymenophyllum caudiculatum Mart.		e/r	X	X	X	
Hymenophyllum magellanicum Willd. ex Kunze	vu	e		X		
Hymenophyllum peltatum (Poir.) Lam.	vu	e/r			X	X
Hymenophyllum polyanthos (Sw.) Sw.		e/r	X	X	X	X
Hymenophyllum pulchellum Schltdl. & Cham.		e			X	X
Hymenophyllum rufum Fée		e			X	X
Hymenophyllum vestitum (C.Presl) V.D.Bosch		e		X		X
Polyphlebium angustatum (Carmich.) Ebihara & Dubuisson		e		X	X	X

Trichomanes anadromum Rosenst.		e		X	X	X
Trichomanes polypodioides Raddi		e/r	X		X	
Vandenboschia radicans (Sw.) Copel.		e/r	X	X	X	X
Vandenboschia rupestris (Raddi) Ebihara & K.Iwats.		r		X		
LINDSAEACEAE						
Lindsaea botrychioides A.St.-Hil.		e/t			X	X
Lindsaea quadrangularis Raddi		t	X			
LOMARIOPSIDACEAE						
Lomariopsis marginata (Schrad.) Kuhn		e	X			
LYCOPODIACEAE						
Phlegmariurus acerosus (Sw.) B.Øllg.		e			X	X
Phlegmariurus flexibilis (Fée) B.Øllg.		e			X	X
Phlegmariurus heterocarpon (Fée) B.Øllg.		e			X	X
Phlegmariurus hexastichus (B.Øllg. & P.G.Windisch) B.Øllg.		e			X	X
Phlegmariurus loefgrenianus (Silveira) B.Øllg.		e			X	X
Phlegmariurus mandiocanus (Raddi) B.Øllg.		e	X	X	X	X
Phlegmariurus quadrifariatus (Bory) B.Øllg.		e			X	X
LYGODIACEAE						
Lygodium volubile Sw.	vu	t	X			
MARATTIACEAE						
Eupodium kaulfussii (J.Sm.) J.Sm.		e/r/t		X	X	
OPHIOGLOSSACEAE						
Botrypus virginianus (L.) Michx.	vu	t			X	
POLYPODIACEAE						
Campyloneurum acrocarpon Fée		e/r	X	X		
Campyloneurum aglaolepis (Alston) de la Sota		e			X	X
Campyloneurum austrobrasilianum (Alston) de la Sota		e		X	X	X
Campyloneurum nitidum (Kaulf.) C.Presl.		e/r	X	X	X	X
Campyloneurum rigidum Sm.		e/r	X	X		
Campyloneurum sp		e		X	X	
Ceradenia albidula (Baker) L.E.Bishop	en	e/r			X	X
Cochlidium punctatum (Raddi) L.E.Bishop		e			X	X
Leucotrichum organense (Gardner) Labiak		e			X	X
Leucotrichum schenckii (Hieron.) Labiak		e			X	X
Microgramma vacciniifolia (Langsd. & Fisch.) Copel		e/r	X	X	X	
Microgramma squamulosa (Kaulf.) de la Sota		e/r	X	X	X	X
Niphidium rufosquamatum Lellinger		e/r	X	X	X	X
Pecluma cf. *recurvata* (Kaulf.) M.G.Price		e			X	X
Pecluma chnoophora (Kunze) Salino & Costa Assis		e	X			
Pecluma paradiseae (Langsd. & Fisch.) M.G.Price		e/t		X	X	X
Pecluma pectinatiformis (Lindm.) M.G.Price		e	X	X	X	X
Pecluma robusta (Fée) M.Kessler & A.R.Sm.		r/t	X			
Pecluma sicca (Lindm.) M.G.Price		e/r	X	X	X	X
Pecluma sp		t			X	
Pleopeltis hirsutissima (Raddi) de la Sota		e	X	X	X	X

Pleopeltis macrocarpa (Bory ex Willd.) Kaulf.		e		X	X	X
Pleopeltis pleopeltidis (Fée) de la Sota		e		X	X	X
Pleopeltis pleopeltifolia (Raddi) Alston		e/r	X	X	X	X
Pleopeltis polypodioides (L.) Andrews & Windham		e		X	X	X
Serpocaulon catharinae (Langsd. & Fisch.) A.R.Smith		e/r	X	X	X	X
Serpocaulon laetum (C.Presl) Schwartsb. & A.R.Sm.		e	X	X	X	X
Serpocaulon latipes (Langsd. & Fisch.) A.R.Sm.		e				X
Serpocaulon menisciifolium (Langsd. & Fisch.) A.R.Sm.		e	X	X	X	
Zygophlebia longipilosa (C.Chr.) L.E.Bishop		e			X	X
PSILOTACEAE						
Psilotum nudum (L.) P.Beauv.		t	X			
PTERIDACEAE						
Adiantopsis regularis Kunze		t				X
Adiantum pentadactylon Langsd. & Fisch.		e/t	X	X		
Adiantum raddianum C.Presl		e/r/t	X	X	X	X
Doryopteris pentagona Pic.Serm.		e/t	X	X		
Pityrogramma chaerophylla (Desv.) Domin		t			X	
Polytaenium lineatum (Sw.) J.Sm.	en	r/t		X		
Pteris altissima Poir.		t	X	X		
Pteris brasiliensis Sw.		t	X	X		
Pteris deflexa Link		e/r/t		X	X	X
Pteris sp		e		X		
Tryonia myriophylla (Sw.) Schuettp., J.Prado & A.T.Cochran		t				X
Vittaria lineata (L.) Sm.		e/r	X	X	X	X
SELAGINELLACEAE						
Selaginella muscosa Spring		e/r/t	X	X	X	X
TECTARIACEAE						
Tectaria incisa Cav.		e/t	X	X		
Tectaria pilosa (Fée) R.C.Moran		t	X	X		
THELYPTERIDACEAE						
Macrothelypteris torresiana (Gaudich.) Ching		t	X			
Thelypteris amambayensis Ponce		e/t			X	X
Thelypteris conspersa (Schrad.) A.R.Sm.		t	X	X		X
Thelypteris dentata (Forssk.) E.P.St.John		e/t			X	X
Thelypteris hispidula (Decne.) C.F.Reed		e/t	X	X	X	X
Thelypteris opposita (Vahl) Ching		t				X
Thelypteris rivularioides (Fée) Abbiatti		t	X	X	X	

Capítulo 2

SPACE AND ABIOTIC FACTORS ARE DRIVERS OF FERNS AND LYCOPHYTES DIVERSITY PATTERNS ALONG AN ELEVATIONAL GRADIENT IN SOUTHERN BRAZIL

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Journal Vegetation Science (a submeter)

Space and abiotic factors are drivers of ferns and lycophytes diversity patterns along an elevational gradient in Southern Brazil

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Abstract

Questions: What are the drivers that govern fern and lycophyte community composition in the South Brazilian Atlantic Forest? Does explanatory power of the models increase when we consider substrate-based life-forms separately? Do terrestrial and epiphytic species respond equally to the environmental drivers?

Location: Four distinct altitudinal zones of the Atlantic Rain Forest *sensu stricto* in Northeastern Rio Grande do Sul, Brazil.

Method: We used variation partitioning procedures to ascertain the relative influence of climatic, edaphic and spatial processes on variation in species composition at different spatial scales, considering the entire community and subsets with only epiphytic species and terrestrial species.

Results: Our results suggest that environmental variables were the most responsible for shaping the fern and lycophyte community composition at the broad scale, while edaphic filters showed higher importance at the terrestrial community and climatic filters for epiphytic species. Clearly, considering epiphytic and terrestrial species separately increased the explanatory power of the models.

Conclusions: We observed the shared evidence of neutral and niche-based processes in community structure. However, our results indicate that the niche processes are primarily responsible for modulating patterns of species distribution and abundance along the elevational gradient in the Southern Brazilian Atlantic Forest.

Keywords Pteridophytes; Environmental; Climatic Variables; Edaphic Variables; Atlantic Forest; Species Distribution; Variance Partitioning.

Introduction

The relative importance of stochastic and deterministic processes in structuring rain forest plant communities has long been a subject of debate (e.g. Fedorov 1966; Ashton 1969; Hubbell & Foster 1986), with the corresponding extreme views of community structuring now often being termed dispersal assembly (Hubbell 2001) and niche assembly (Hutchinson 1957, Chesson 2000). Under dispersal assembly, the species are considered functionally identical. This means that floristic differences are created by chance, limited only by the dispersion capacity of the species over different sites. Thus, similarity decays with increasing geographical distance. For niche assembly, in contrast, environmental variation (such as physical and chemical soil features, microclimate, etc.) acts as selective force of those species able to reach the sites characterized by specific conditions. This means that the similarity decays with increasing environmental distances. Both processes exist in nature: in a study with ferns and lycophytes species composition in the Amazonian Rain Forest, Tuomisto et al. (2002; 2003 b) demonstrated the importance of geographical distance, i.e. neutral processes, for community assembly. In contrast, Guo et al. (2003) study demonstrated the importance of suitable habitat availability, i.e. nicho process, for community assembly of ferns and lycophytes in Japan. Other studies show how both processes can act simultaneously (Tuomisto et al. 2003 b; Jones et al. 2011).

Along elevational gradients in tropical mountain systems, diversity and richness species have been shown to be maximized at situation with high humidity and moderate temperatures, often leading to highest values at intermediate elevations (Bhattarai et al. 2004; Kessler 2001a; Kluge et al. 2006). At the local scale, soil factors are additionally important to stratify the environment (Resende & Rao 1983, Tuomisto et al. 2003 a, Jones et al. 2008). An example is the study by Tuomisto & Ruokolainen (1994) that demonstrates that the distribution of ferns, lycophytes and Melastomataceae in a soil gradient in the Peruvian Amazon is driven by different substrates and soil drainage. Hence, at least may terrestrial species are considered to be good indicators of soil conditions.

Plants with similar life-forms are expected to exhibit similar responses to environmental variations and have similar effects on the dominant ecosystem processes

(Walker 1992; Noble & Gitay 1996; Pausas & Austin 2001). Where constrasting life-forms cooccur, patterns of species richness along an environmental gradient might be easier to interpret when we consider not only total species richness, but also richness of life-forms separately. This is because the relative importance of specific environmental factors may differ between different life forms (Cardelús et al. 2006). One ecologically meaningful way to group ferns and lycophytes is a classification into substrate types. Substrate types (hereafter we use the term "life-forms") can vary in abundance and diversity along environmental gradients, such as with altitude (Watkins et al. 2006). This phenomenon has been known for at least forty years for ferns, when Tryon (1964) proposed a plant community classification based on the proportion of different life forms of these plants. Since then, several studies have considered the relationship between altitude and the occurrence of different forms of ferns and lycophytes life in forest systems (Lieberman et al. 2001; Hemp 2001; Kessler 2001; Wang et al. 2002; Watkins 2006), but few studies are available in Brazil (Paciencia 2008; Nervo et al. *in press*).

For our study site in the Atlantic Forest in Southern Brazil, the elevational gradient effects on species composition, richness and diversity has been demonstrated for ferns and lycophytes (Nervo et al. *in press*). Total species richness and diversity of different species groups (substrate types: terrestrial, rupicolous and epiphytic species) presented different patterns in distinct elevational zones. However, the drivers behind these patterns - specifically the role of geographical distances and of environmental effects in structuring communities – still have not been investigated in South Brazilian forests. The only existing study (Paciencia 2008) confirms the mid-domain effect (MDE): authors argure that, at macro-scales, the gradient in richness spatial patterns is geometrically constrained (ref. for Mid-Domain effect), with addtionall effects of a number of environmental factors. However, these authors did not distinguish between life-forms.

In the present paper, we analyse the relationship between distribution patterns of ferns and lycophytes and environmental variables along an altitudinal gradient, in the Atlantic Rain Forest in Southern Brazil, based on the following questions:

1. Relative importance of environment and space for community composition. What are the environmental and spacial drivers that govern ferns and lycophytes species composition at the Southern Brazilian Atlantic Forest? To answer this question we discriminated environmental variables into climatic

and edaphic factors. Spatial factors were considered at the broad and fine scale. Due to the general high dispersal capacity of ferns and lycophytes, we expected a higher influence of environmental factors in comparison to the spatial component.

2. Differences between groups of epiphytic and terrestrial species. Do terrestrial and epiphytic species respond equally to the environmental drivers? We hypothesized that for epiphytic species, climatic variables would be of higher importance than soil factors in determining community composition variation along the gradient.

Material and Methods

Study region— The study region comprises an elevational gradient in the Atlantic Rain Forest *sensu stricto* (ARF; Floresta Ombrófila Densa in Portuguese) in the Northeastern part of the Rio Grande do Sul State, at the Southern limit of the Brazilian Atlantic Forest, a biodiversity hotspot (Mittermeier et al. 2004). The vegetation of the ARF at this latitude is commonly classified into four main forest types (Veloso & Góes-Filho 1982; see also Teixeira et al. 1986 and Brack 2009): 1) Lowland (LO), 5–50 m altitude; 2) Submontane (SU), at the base of the Serra do Mar mountains, with an altitude between 50–400 m; 3) Montane (MO), covering the slopes of the Serra do Mar, at altitudes ranging from 400–1,000 m; and 4) Upper montane (UP), at altitudes ranging between 1,000–1,400 m. Soils are highly variable, from sandy textured to very clayey textured soils (EMBRAPA 2004), with the predominance of Cambisols, Gleysols and Nitisols (IBGE 2002; EMBRAPA 2006). Climate in the region corresponds to Cfa (temperate humid with hot summers and temperature of the hottest month > 22 ºC) and Cfb (warm summers with hottest month temperature < 22 ºC) (Peel et al., 2007). Cfa predominates at lower elevations, while Cfb occurs at higher altitudes in the highlands and in the Northwestern part of the state. Mean annual temperature is 13–19 ºC and ranges from 18–22 ºC in summer to 11–15 ºC in winter, where frosts are common and snowfall may occur in the highest areas (Nimer 1989). The precipitation is evenly distributed throughout the year, ranging from 1300 mm to 2000 mm.

Study design— Five study sites (replicates) were sampled for each altitudinal belt (LO, SU, MO and UM), totalling 20 study sites. At each site, we allocated six sample plots measuring 10 × 10 m, (with a minimum distance of 30 m between plots), parallel to the forest edge (with a minimum distance of 100 to 250 m from the border),

totalling 600 m^2 each site. The distance between sites (replicates) within an altitudinal zone was at least of 1 km. Most of the study areas were situated in protected areas in a good state of conservation. Fieldwork was conducted from March 2012 to March 2015.

Vegetation data—— Fern and lycophyte communities are described in detail in Nervo et al. (*in press*), also considering abundance of epiphytic and terrestrial species. The complete species composition per site composed the response matrix Y, which was Hellinger transformed (Y_{all}) (Legendre & Gallagher 2001) for all subsequent analyses. In addition to using the full Yall matrix, we built matrices with the average cover of epiphytic and terrestrial species (Y_{epi} and Y_{ter}), considered as different ecological groups (life forms / substrate types). These matrices, Y_{epi} and Y_{ter}, also were Hellinger transformed.

Environmental variables— We compiled 27 environmental variables that described climate and soil features (Table 1). Climate data were obtained from the network of INMET weather stations between the period 1960-1990 (Inmet 2015), where 14 variables were extracted (Table 1). Soil variables (13 variables) where obtained by chemical and of soil samples analysis. For this, we collected soil samples in different depths (in intervals of 0–10 cm, 10–20 cm, 20–30 cm and 30–50 cm). From these measurements we obtained the weighted mean of the experimental values in order to get the value of the mean for chemical analysis to layer 0–50 cm, following methods described in EMBRAPA (1997). The evaluation of the soil drainage effect along elevational gradient was defined to the authors by help of the analyses of the soil depth, declivity and stoniness (IBGE 2007). Soil depth was measured with the aid of a Dutch Auger. Soil declivity was taken in the field with the help of a clinometer (degrees lecture) and stoniness was estimated in field.

Spatial variables— We recorded the geographical coordinates for the centroid of each site. Moran's Eigenvector Maps (MEM; Borcard et al. 2011) were used to generate the spatial variables. In summary, the MEM method compares geographical co-ordinates pair-to-pair using Euclidean distance. This Euclidean distance matrix was truncated at the smallest distance that keeps all points connected in a single network. Then, a principal coordinate analysis (PCoA) was performed, and the eigenvectors associated with positive eigenvalues were retained as spatial variables. Spatial axes obtained through the MEM method are well known for their capability to capture spatial trends at different range of scales (Borcard & Legendre 2002; Dray et al. 2006). This way, the first axes resultants from MEM (MEM 1–7 axes) represent a broad scale

spatial variance (matrix $X_{MEMbroad}$), while the last eigenvectors (MEM 8–14 axes) capture spatial variance at the fine scale ($X_{MEMfine}$).

Selection of explanatory variables— We ran forward selection procedures (Blanchet et al. 2008) on explanatory variables (environmental and spatial axes). The forward selection searches for explanatory variables is the one that better explains the variation in the species composition matrix (in our case Y_{all}) and variation in the species abundance matrix (in our case Y_{epi} and Y_{ter}, previously mentioned). By 'better' we can understand that the variable explains the greatest portion of the variance in the response data (higher R^2) and is also significant at a given significance level (tested by permutation).

The forward proceeding selection adds explanatory variables in the model considering two stopping criteria, alpha (given significance level) and R^2. For all proceedings we adopted the criteria alpha = 0.1, while the adopted R^2 varied according to the R^2 of the global model (i.e., model with all explanatory variables). R^2 thresholds used for each response matrix were: Y_{all} = 0.53, Y_{epi} = 0.52 and Y_{ter} = 0.50. Forward selection is stopped when no additional variable added to the model has a *P* value smaller than or equal to alpha, or if it brings the R^2 of the current model over the value of the R^2 of the global model.

The selected environmental variables were used to compose the final explanatory matrices X_{Soil} and X_{Clim}, which together composed the complete environmental matrix (X_{Env}). The spatial variables selected here through forward selection (X_{MEM}) were separated into the three first MEMs (1, 2, 3) representing the spatial variation in broad scale ($X_{MEMbroad}$). No vector that captured the spatial variation on a fine scale was selected ($X_{MEMfine}$). Significant differences of soil and climatic variables along the elevational gradient, described by NMDS, were evaluated by ANOSIM (Claire & Warwick 1994), which is based on a R statistics, variable from 0 to 1 (Appendix 1).

Analytical procedures— We used variation partitioning procedures (Legendre & Legendre 2012) to verify the influence of explanatory variables (climate, soil or spatial distance) on response variables (species composition of sites). Specific subsets of explanatory and response variables were applied to answer each of our initial questions (see end of Introduction).

Three analyses were conducted on each of the three species matrices (Y_{all}, Y_{epi} and Y_{ter}): first to discern between the influence of environment (X_{Env}) and space

(X_{MEM}); second to specify the influence of discriminated environmental variables (X_{Clim} and X_{Soil}); and last to specify the influence of broad-scale ($X_{MEMbroad}$) and fine-scale ($X_{MEMfine}$) spatial variables. Canonical correspondence analysis (CCA - ter Braak 1986) was used to illustrate the influence of environmental variables in the structure of ferns and lycophytes communities (all species, epiphytic community and terrestrial community) along the altitudinal gradient in the Southern Brazilian Atlantic Forest. The NMDS, ANOSIM, CCA, MEM analysis and Variation partitioning analyses were performed in R plataform (R Core Team 2013), using the 'vegan' package (Oksanen et al. 2012) and the 'packfor' package (Blanchet et al. 2008) was used to perform the forward selection.

Results

Two spatial and eight environmental variables (four climatic and four edaphic) were selected as predictor of the community composition of all species along the entire elevational gradient (Table 2). The selected spatial vectors 1 and 3 (Mem 1, 3) composed the matrix of broad-scale space (i.e., full gradient spatial variance), and no vector was selected that captured the spatial variation on a fine scale.

Most of the explained variation in the overall species composition matrix, i.e., including terrestrial species and epiphytes (Y_{all}), was related to the shared effect of environment and space (Fig. 1A). The percentage of variation explained by environmental factors alone was higher than that explained by space alone. The total environmental fraction, when discriminated between climate (X_{Clim}) and soil (X_{Soil}), showed that the biggest part of the species variation was related to the shared effect of climate and soil (Fig. 1B).

Precipitation, solar insolation and wind speed were variables that significantly increased along the elevational gradient (Appendix 2). Relative humidity showed similar values along the elevation gradient (see details of climatic variables in Appendix 2). Regarding edaphic variables, Aluminum content, soil depth and percentage of organic matter in soil increased along the elevational gradient, while pH decreased (see details in Appendix 2).

The CCA for the composition of all species explained 65% (axes 1 and 2) of the total data variation (Fig. 2). Axis 1 explained 48% of the total variation data and was positively related to high concentrations of aluminium and organic matter, high rainfall, high humidity of the air, deep soils , high wind intensity and high insolation, associated

to Montane and Upper Montane forests. In contrast, pH was negatively associated to this axis, with high values associated to Lowland and Submontane formations.

Different explanatory variables were selected through forward selection for Y_{Epi} and Y_{Ter} (Table 3). Most axes had already been seen in the selection for the full species matrix (see Table 2), but variation in soil calcium content and variation of minimum temperature of the coldest quarter along the gradient were exclusively related to the Epiphytic matrix, while the spatial variable MEM 2, cation exchange capacity and variation in soil potassium content were exclusively related to the Terrestrial matrix (Table 3).

The major part of variation in either epiphytic and terrestrial species abundance was once again explained by the shared effect of environment and space (32% and 36%; respectively Fig. 1C and E), followed by the pure environmental effect, explaining 17% and 13%. Considering the environmental variables, when discriminating between climate (X_{Clim}) and soil (X_{Soil}), we found that the biggest part of the variation was related to the shared effect of climate and soil (Fig. 1D and F)., followed by the pure climatic effect in the case of epiphytic species, explaining 11% and by the pure edaphic effects in the case of terrestrial species, explaining 8%.

The abundance of epiphytes species explained 65% (axes 1 and 2) of the total data variation in the CCA (Fig. 3). Axis 1 explained 50% of the total variation data and was positively related to high concentrations of aluminum and humidity air, solar insolation and high wind intensity concentrations, which were associated with the Montane and Upper Montane forest. In contrast, high values of minimum temperature, high concentrations of calcium and soil acidity (pH) were negatively related to axis 1 and associated with to Lowland and Submontane forest formations.

For terrestrial species, the canonical correspondence analysis (CCA) explained 88% (axes 1 and 2) of the total data variation (Fig. 4). Axis 1 was positively related to high concentrations of aluminum, cation exchange capacity and humidity air, solar insolation and wind intensity concentrations, which were associated to Montane and Upper montane forest. High potassium concentrations and soil acidity was associated to Lowlands and Submontane formations.

Discussion

Species diversity can be used as an indicator of ecological gradients and the environmental quality of an ecosystem (Alard et al. 1994; Alard & Poudevigne 2000),

and in another study (Nervo et al. *in press*) we showed that terrestrial and epiphytic species showed distinct patterns of community variation among elevation zones. Epiphytes species showed peaks of richness in Montane forest, whereas the terrestrial ferns showed more variable numbers with a less pronounced peak in the Submontane forest. With the presented study, we are now able to understand which factors are driving the variation in composition. Both spacial and environmental (climatic and edaphic) variables were predictors of fern and lycophytes community composition along our elevational gradient in the Southern Brazilian Atlantic Rain Forest and environmental variation was clearly structured in space (Table 2). Interestingly, the percentage of explanation of the variance partitioning procedure almost doubled when we considered ephiphytes and terrestrials separatelyz underlines the need to consider both groups separately in ecological studies, as they apparently react in distinct ways to environmental variables Lumping the groups together masks this and decreases overall explanation and in particular the percentage explained by environmental features, possibly leading to falls interpretations.

Climatic variables, such as precipitation and, consequently, humidity, have been indicated by several authors as the most relevant predictors of species composition of fern communities (Greer et al. 1997; Kessler et al. 2001; Aldasoro et al. 2004; Kessler et al. 2011; Salazar et al. 2013), and the same was shown in our study, both for terrestrial and epiphytic species. Air humidity on average was close to saturation at all elevations, which is not surprising for the mountain ecosystems in Atlantic Rain Forest with no marked 'dry' season (Köppen 1931). Nonetheless, we found significant differences between altitudes that proved to be important in shaping community composition (Appendix 2). The greatest diversity of epiphytes along elevational gradient is commonly attributed to climatic conditions such as relative humidity (Gentry & Dodson 1987; Benzing 1990), and this was also true in our study (see Nervo et al. *in press*, for details on composition): we observe the greatest diversity of epiphyte species in the altitude formations (Montane and Upper montane forest, Appendix 2), and humidity was shown to be an important drivers of the variance of epiphytic community abundance, together with other climatic variables (Fig.1 and 3). However, our models also selected edaphic factors as drivers of epiphytic species community variation. While edaphic factors are known to influence the diversity and distribution of ferns (i.e., Young & Leon 1989; Pousen & Baslev 1991; Zuquim et al. 2007), the relation

obviously should be indirect and might require stuying changes in phorophytes and their relation to the environmental factors.

With regard to edaphic variables, the variance in species composition of the entire community was related to different levels of soil Aluminum, soil depth, percentage of organic matter and pH. Paciencia (2008) found similar results for soil pH. In our study, the highest Aluminium values and the most acid soils (pH <4) and highest Aluminum concentrations occurred in the higher altitude formations (montane and upper-montane forest, Appendix 2, Fig. 1). Most of the environmental variables selected in the model with all species where also selected using only epiphytic or only terrestrial species. But some environmental variables showed exclusivity for only one of these components, such as concentrations of potassium and cation exchange capacity, both relevant for community variation of terrestrial species, but not for epiphytes. Terrestrial ferns occur on soils that span a large gradient in terms of nutrient availability (i.e., fertility), with many species exhibiting clear affinities to soil of a particular fertility (i.e., Tuomisto & Poulsen, 1996). In our study, at a local scale, the richness of terrestrial ferns appears to be greatest on sites with high fertility (in Lowland and Submontane forest, where potassium concentrations and cation exchange capacity of soils are higher (see also Tuomisto et al. 2002).

The predominance of niche processes has previously been pointed out for the assembly of fern and lycophyte communities (Hemp 2002; Klunge et al. 2008; Kessler 2000; among others). However, most studies using this approach have been conducted in tropical forest vegetation and few studies have measured the relative influence of environment and space on the forest assembly in subtropical environments (see also Paciencia 2008). In our study we found substantial evidence for the role of both environmental and spatial effects on species richness along the distribution of the elevation gradient. While pure environmental aspects contributed much more to explanation, they were, to a large proportion, structured in space. Spatial factors themselves explained very little, supporting the importance of niche-based processes in species assembly. Given the importance of niche-based processes and the improvement of the models by dividing the species into to basic functional groups based on substrate type, we suggest that future ecological studies on ferns and lycophytes should go further

towards functional approaches, i.e. by incorporating larger sets of traits, in order to better understand the relation of plants with their environment.

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LEGENDS

Figure 1. Relative contribution of environmental (X_{Env}), space ($X_{MEMbroad}$), climate (X_{Clim}) and soil (X_{Soil}) to the variation in elevational gradient in ferns and lycophytes composition and abundance. A-B: all species (Y_{all}); C-D: epiphytic (Y_{epi}); E÷D: Terrestrial species (Y_{ter}). ***P < 0.001; **P < 0.01; *P < 0.05.

Figure 2. Canonical correspondence analysis, showing the relationship between environmental variables (climate and soil) with the ferns and lycophytes composition along the altitudinal gradient of the Atlantic Forest in Southern Brazil under different forest formations. The environmental variables on the axis 1 explains 48% (CCA1) of the variation. LO: Lowland, SU: submontane, MO: montane and UP: upper montane. Al: aluminum, Depth: depth soil, Hum: relative humidity of air, Insol: solar insolation, O.M.: soil organic matter, ph: soil acidity, Prec: precipitation, Wind: wind speed.

Figure 3. Canonical correspondence analysis, showing the relationship between environmental variables (climate and soil) with the terrestrial abundance of ferns and lycophytes along the altitudinal gradient of the Atlantic Forest in Southern Brazil under different forest formations. The environmental variables on the axis 1 explains 64% (CCA1) of the variation. LO: Lowland, SU: submontane, MO: montane, UP: upper montane, Al: aluminum, CEC: cation exchange capacity, Hum: relative humidity of air, Insol: solar insolation, K: potassium, ph: soil acidity, Wind: wind speed.

Figure 4. Canonical correspondence analysis, showing the relationship between environmental variables (climate and soil) with the terrestrial abundance of ferns and lycophytes along the altitudinal gradient of the Atlantic Forest in Southern Brazil under different forest formations. The environmental variables on the axis 1 explains 54% (CCA1) of the variation. LO: Lowland, SU: submontane, MO: montane, UP: upper montane, Al: aluminum, Ca: calcium, Hum: relative humidity of air, Insol: solar insolation, ph: soil acidity, Tmin: minimum temperature, Wind: wind speed.

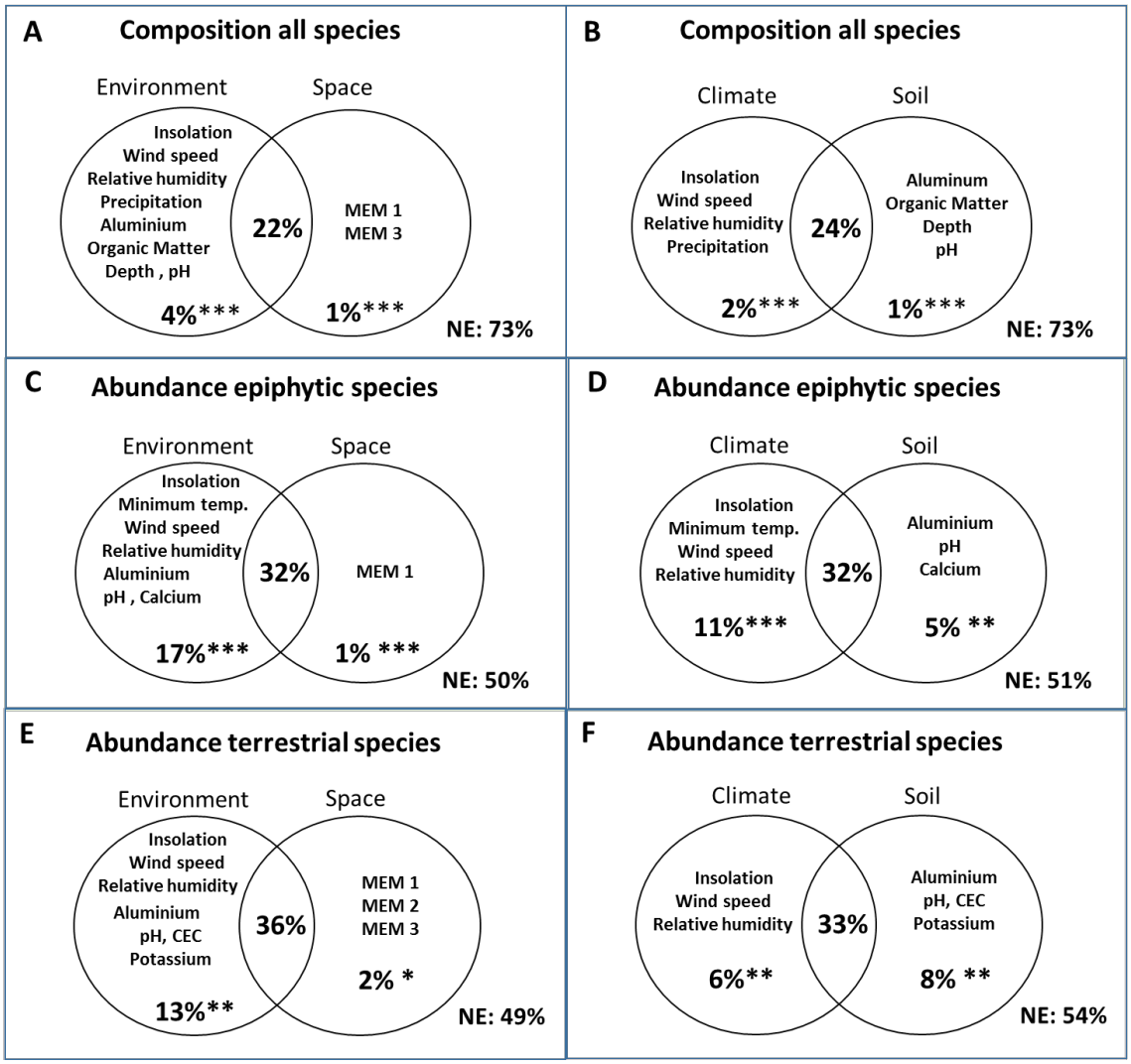
A
Composition all species
Environment
Space
Insolation
Wind speed
Relative humidity
Precipitation
Aluminium
Organic Matter
Depth , pH
22%
MEM 1
MEM 3
4%***
1%***
NE: 73%
B
Composition all species
Climate
Soil
Insolation
Wind speed
Relative humidity
Precipitation
24%
Aluminum
Organic Matter
Depth
pH
2%***
1%***
NE: 73%
C
Abundance epiphytic species
Environment
Space
Insolation
Minimum temp.
Wind speed
Relative humidity
Aluminium
pH , Calcium
32%
MEM 1
17%***
1% ***
NE: 50%
D
Abundance epiphytic species
Climate
Soil
Insolation
Minimum temp.
Wind speed
Relative humidity
32%
Aluminium
pH
Calcium
11%***
5% **
NE: 51%
E
Abundance terrestrial species
Environment
Space
Insolation
Wind speed
Relative humidity
Aluminium
pH, CEC
Potassium
36%
MEM 1
MEM 2
MEM 3
2% *
13%**
NE: 49%
F
Abundance terrestrial species
Climate
Soil
Insolation
Wind speed
Relative humidity
33%
Aluminium
pH, CEC
Potassium
6%**
8% **
NE: 54%

Figure 1

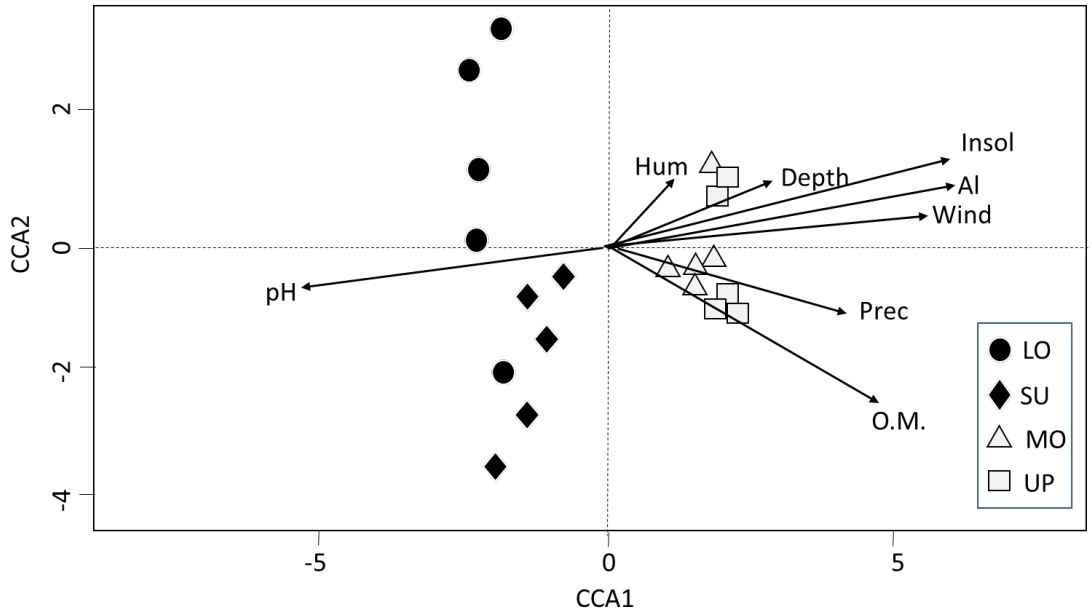
CCA2
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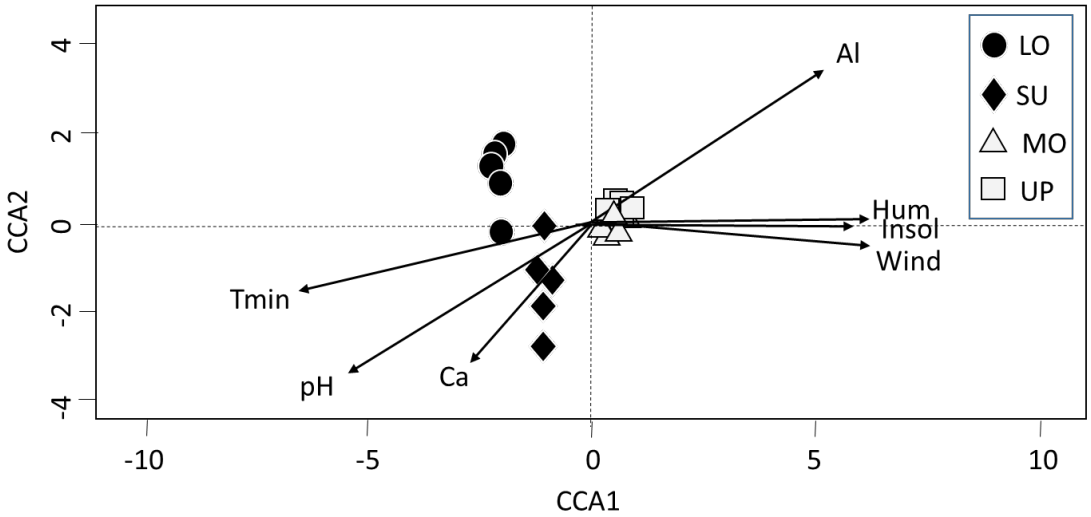
Figure 2


LO
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0
5
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Figure 3

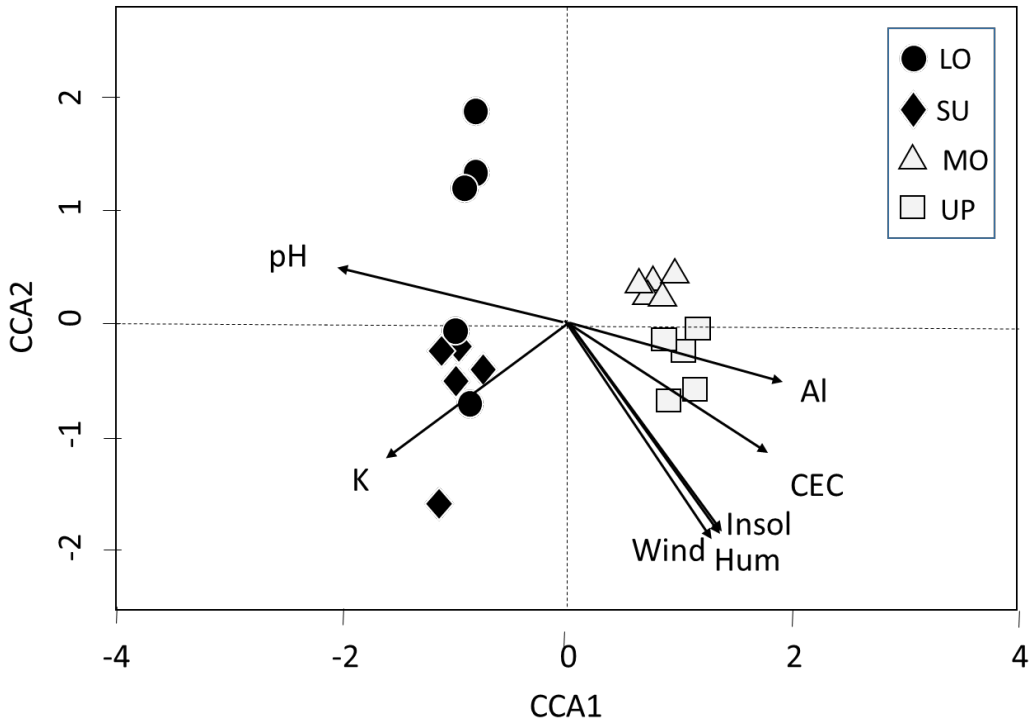


Figure 4

Table 1. Environmental variables (climatic and edaphic) evaluated as possible predictors of plant community composition in forest types in elevational gradient of the Atlantic Forest in Southern Brazil. For edaphic variables, the method for analysis is indicated.

Climatic variables	**Edaphic variables**
Insolation (hours)	Soil chemistry
Evapotranspiration	Organic matter (%): wet digestion
Mean of the coldest quarter (mm)	pH: in water
Mean of the hottest quarter (mm)	P (mg/dm^{-3}): Mehlich I method
Precipitation (mm)	K (mg/dm^{-3}): same as P
Relative humidity	Ca ($cmol_c/dm^{-3}$): same as Na
Mean of the coldest quarter (%)	Mg ($cmol_c/dm^{-3}$): same as Na
Mean of the hottest quarter (%)	Al ($cmol_c/dm^{-3}$): same as Na
Temperature	Cation exchange capacity (CEC) ($cmol_c/dm^{-3}$):
Mean of the coldest quarter (°C)	extracted with ammonium acetate
Mean of the hottest quarter (°C)	Base saturation (%): amount of bases in CEC
Maximum of the coldest quarter (°C)	Al saturation (%): amount of Al in the CEC
Maximum of the hottest quarter (°C)	Drainage soil
Minimum of the coldest quarter (°C)	Depth (meters): used a dutch auger in field
Minimum of the hottest quarter (°C)	Declivity (degrees): used a clinometer in field
Wind intensity	Stoniness (%): were estimated in field
Mean of the coldest quarter ($s\ m^{-1}$)	
Mean of the hottest quarter ($s\ m^{-1}$)	

Table 2. Environmental and spatial variables selected with forward selection as predictors of community composition for all species in elevational gradient of the Atlantic Forest in Southern Brazil.

Selected variables	**Adjusted R^2**
Solar insolation	0.22 ***
Wind intensity of the coldest quarter	0.24 **
Relative humidity of the coldest quarter	0.26 **
Precipitation	0.22 *
Alumminium	0.22 ***
Organic matter	0.23 **
pH	0.25 **
Depth soil	0.04 *
MEM 1 (broad scale)	0.22 **
MEM 3 (broad scale)	0.23 *

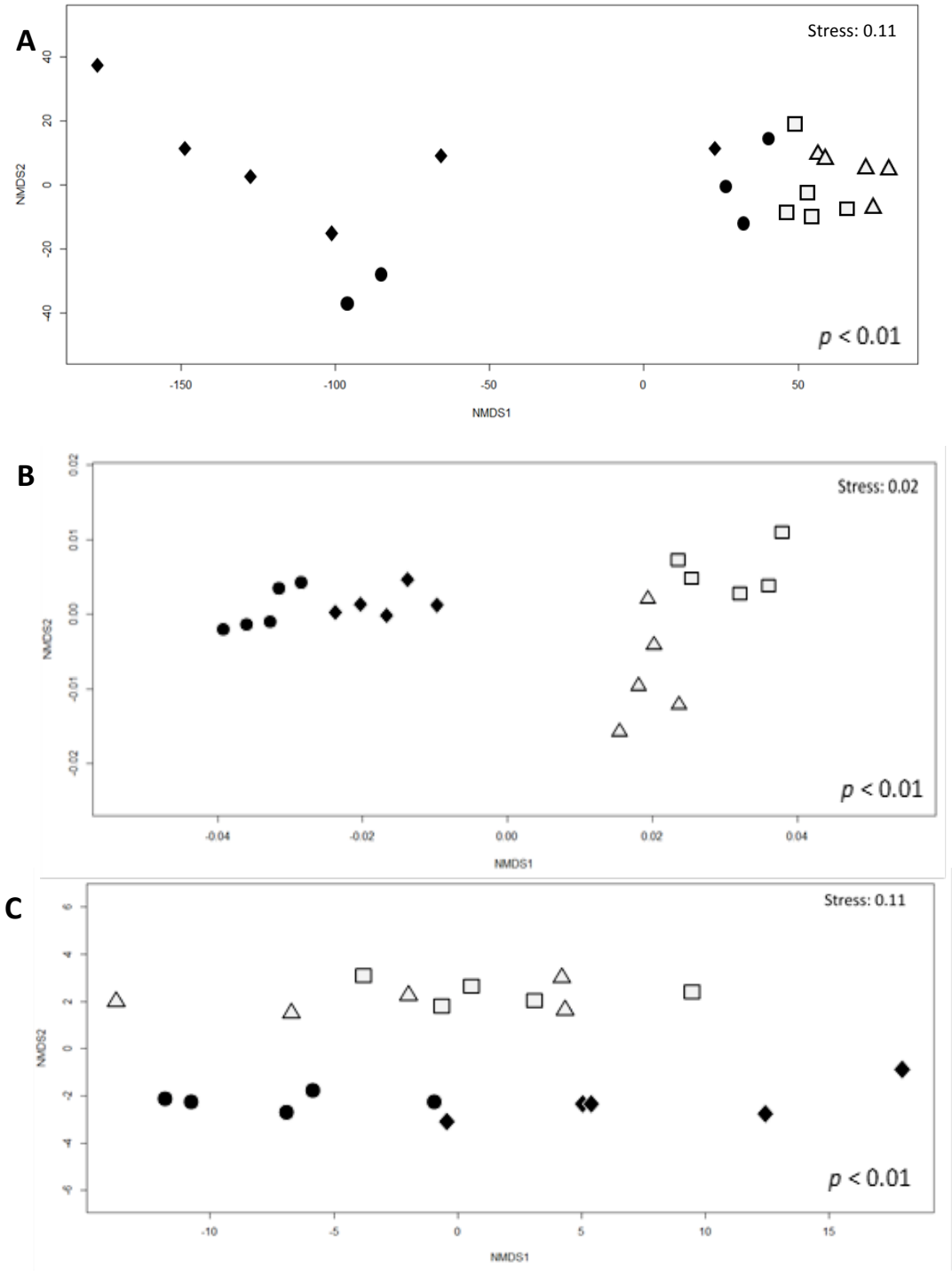
Axes of RDA were selected after 999 permutations, with the following criteria: R2 > 0.5, and not exceeding alpha = 0.1

***P < 0.001; **P < 0.01; *P < 0.05.

Table 3. Environmental and spatial variables selected with forward selection as predictors of epiphytic and terrestrial species abundance in elevational gradient of the Atlantic Forest in Southern Brazil.

Epiphytic community		**Terrestrial community**	
Selected variables	**Adjusted R^2**	**Selected variables**	**Adjusted R^2**
Solar insolation	0.38***	Solar insolation	0.22***
Minimum temperature	0.41**	Wind intensity of the coldest quarter	0.24**
Wind intensity of the coldest quarter	0.43*	Relative humidity of the coldest quarter	0.26*
Relative humidity of the coldest quarter	0.45*	Alumminium	0.31***
Alumminium	0.36***	pH	0.33*
pH	0.38*	CEC	0.34**
Calcium	0.41**	K	0.37**
MEM 1 (broad scale)	0.37***	MEM 1 (broad scale)	0.22***
		MEM 2 (broad scale)	0.23*
		MEM 3 (broad scale)	0.25*

Axes of RDA were selected after 999 permutations, with the folling criteria: R2 > 0.5, and not exceeding alpha = 0.1. ***P < 0.001; **P < 0.01; *P < 0.05.



Appendix 1. NMDS ordination analysis. A: Ordination of study sites based on fern and lycophyte community composition. B: Ordination of study sites based on the physicochemical characteristics of the soil. C: Ordination of study sites based on climatic characteristics (average values of climate variables in each forest formation).

Appendix 2. Species richness and environmental variables analysed, and their mean and range in forest formations along an elevational gradient in the Atlantic Forest in southern Brazil.

Category	Variable	Lowland Mean(range)	Submontane Mean(range)	Montane Mean(range)	Upper-montane Mean(range)	Q	*P*
Richness	All species	13±2 a	16±4 ab	23±3 b	21±4 b	281.7	*0.001*
	Epiphytic species	6±1 a	8±3 a	16±3 b	15±3 b	353.8	*0.001*
	Terrestrial species	5±1 a	8±2 b	7±1 b	7±1 b	21.2	*0.001*
Diversity	Epiphytic species	0.861 ± 0.08 a	0.895 ± 0.11 b	0.935 ± 0.03 c	0.927 ± 0.05 c	105.23	*0.001*
	Terrestrial species	0.936 ± 0.02 a	0.943 ± 0.02 b	0.900 ± 0.01 c	0.899 ± 0.01 d	137.45	*0.001*
Soils	Al (mg_c/dm^3)	0.8 (±0.8) a	0.8 (±0.6) a	4.9 (±2.7) b	8.2 (±0.9) b	242.6	*0.001*
	Ca (mg_c/dm^3)	4.8 (±3.1) a	6.7 (±2.1) a	2.2 (±0.2) b	0.5 (±0.8) b	167.1	*0.004*
	CEC (mg_c/dm^3)	14 (±2.2) a	18 (±3.7) a	24 (±4.5) b	40 (±5.8) c	2482	*0.001*
	K (mg/dm^3)	148 (±57) a	201 (±88) b	95 (±49) c	80 (±12) d	861.6	*0.003*
	Organic mater (%)	4.1 (±1.4) a	5.4 (±1.8) ab	6.6 (±1.6) bc	9.2 (±0.6) c	80.3	*0.001*
	pH (in KCL)	5.2 (±0.5) a	5.0 (±0.3) a	3.9 (±0.1) b	3.8 (±0.1) b	7.93	*0.001*
	Soil depth (cm)	53 (±23)	63 (±19)	77 (±68-86)	76 (±64-93)	1671	0.21
Climatic	Insolation (hours)	1969 (±18) a	1997 (±5) b	2182 (±11) c	2242 (±29) d	27339	*0.001*
	Min. Temperature of the hottest quarter (°C)	19.3 (±0.2) a	17.6 (±0.3) b	16.2 (±0.2) c	15.1 (±0.3) d	49.38	*0.001*
	Precipitation (mm)	1402 (±10) a	1428 (±33) a	1648 (±10) b	1719 (±38) c	14064	*0.001*
	Relative humidity of the coldest quarter (%)	80.0 (±0.2) a	80.9 (±0.2) b	81.7 (±0.2) c	82.5 (±0.2) d	17.65	*0.001*
	Wind speed of the coldest quarter ($s\ m^{-1}$)	1.5 (±0.09) a	2.0 (±0.09) a	2.7 (±0.1) b	3.0 (±0.1) c	4.37	*0.001*

Significant differences between altitudinal zones by analysis of the variance of (ANOVA) with permutation testing (by Pillar and Orlóci 1996).

Capítulo 3

FIRST RECORD OF THE GENUS STIGMATOPTERIS (DRYOPTERIDACEAE) FOR THE STATE OF RIO GRANDE DO SUL, BRAZIL

Michelle Helena Nervo, Paulo Günter Windisch e Gerhard Ernst Overbeck

Acta Botanica Brazilica – Short Communication (a submeter)

Short Communication

First record of the genus *Stigmatopteris* (Dryopteridaceae) for the State of Rio Grande do Sul, Brazil

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Abstract: *Stigmatopteris heterocarpa* (Feé) Rosenst. is reported for the first time in the State of Rio Grande do Sul, thus extending the distribution range into the southernmost part of the Brazilian Atlantic Forest. We provide information on taxonomy and distribution of the species and comment on implications for conservation.

Key words: Atlantic Forest, ferns, distribution, conservation, *Stigmatopteris heterocarpa*.

Stigmatopteris C.Chr. (Dryopteridaceae) *sensu* Smith et al. (2006; 2008) includes a total of 23 neotropical species (Moran & Labiak 2016) that occur primarily in montane regions, from the Antilles and Southern Mexico to Southern Brazil (Moran 1991; Prado *et al*. 2015). The genus comprises medium to large-sized terrestrial ferns, and is characterized by

several synapomorphies such as 1–pinnate-pinnatifid laminae, visible punctate glands in the mesophyll, the presence of hydathodes, uniseriate cilia on scale margins and indusial loss (Moran & Labiak 2016).

The Andes are the diversity center for *Stigmatopteris*, with 11 species, two of which are endemic (Moran 1991). Southeastern Brazil appears to be a secondary center of diversity for the genus, containing six endemic species: *Stigmatopteris brevinervis* (Fée) R.C.Moran, *S. caudata* (Raddi) C.Chr., *S. heterocarpa* (Fée) Rosenst., *S. prionites* (Kunze) C.Chr., *S. tyucana* (Raddi) C.Chr. and *S. ulei* (Christ.) Sehnem. All these six species grow on shaded ground in moist forests, preferentially in mountainous areas from 200–2.000 m a.s.l. (Sehnem 1979). These species form a subclade within one of the two main clades recently identified through phylogenetic analysis of the monophyletic genus *Stigmatopteris* (Moran & Labiak 2016). Although widespread in Brazil, there are no records of the genus for the Central-Western Region and for the southernmost State of Rio Grande do Sul.

During a recent study of the fern flora in Atlantic Forest remnants in Southern Brazil (Nervo et al. *in press*), a new record of *S. heterocarpa* (Fée) Rosenst. was registered in the municipality of Morrinhos do Sul, State of Rio Grande do Sul. A voucher-specimen was deposited in the Herbarium of the Botany Department of the Federal University of Rio Grande do Sul (ICN).

This species has been cited under different combinations and synonyms, for Brazil, as follows:

***Stigmatopteris heterocarpa* (Fée) Rosenst.**, Repert. Spec. Nov. Regni Veg. 21: 347. 1925. *Phegopteris heterocarpa* Fée, Crypt. Vasc. Brésil 1: 100, t. 30, fig. 2. 1869. Type: Brazil, Rio

de Janeiro, Rio de Janeiro, *A.F.M. Glaziou 2401* (holotype, P00630797! [photo]; isotype, K! [photo], P! [photo], S! [photo]).

Polypodium carrii Baker, Fl. Bras. 1(2): 597. 1870. *Dryopteris carrii* (Baker) C.Chr., Index Filic. 257. 1905. *Stigmatopteris carrii* (Baker) C.Chr., Bot. Tidsskr. 29: 298. 1909. Type: Brazil, Rio de Janeiro, Rio de Janeiro, *Carr s.n.* (holotype, K not seen).

Stigmatopteris heterocarpa var. *basilaris* Rosenst., Repert. Spec. Nov. Regni Veg. 21: 347. 1925. Type: Brazil, São Paulo, Iguape, Morro das Pedras, *A.C Brade 8231* (holotype, S not seen; isotype, US! [photo]).

Fig. 1

Description: Christensen (1909) and Moran (1991).

Illustration: Figure 1A–D.

Notes: *Stigmatopteris heterocarpa* can be distinguished from the other *Stigmatopteris* species in South Brazil by the presence of pinnae that are entirely lobed to lobed less than ¼ of the costa. *Stigmatopteris heterocarpa* is morphologically similar to *S. tyucana*, but the pinnae of *S. tyucana* are more deeply cut and generally broader than those of *S. heterocarpa*. *Stigmatopteris caudata* presents pinnae most deeply incised, and its serrate segments are separated by broad, U-shaped sinuses (see more details in Moran 1991). *S. brevinervis* closely resembles *S. tyucana*; differing by the degree of incision at the sinuses. In *S. tyucana*, the pinnae are cut ¼–½ to the costa; in *S. brevinervis*, the pinnae are larger and occur in greater number. Moran (1991) commented that the two species are very similar and that perhaps future studies will show that they are conspecific. *S. ulei* resembles *S. brevinervis*, from which

it differs by having narrow V-shaped sinuses. In *S. brevinervis*, the sinuses are broad, and U-shaped. *S. prionites* can be distinguished from all other *Stimagtopteris* in Brazil by the combination of narrow (1.1–2.2 cm) pinnae with wide incisions reaching halfway to the costa, the lobes broader, obtuse , few (3–5) veins per lobe, and with inframedial sori.

Voucher specimen: **BRAZIL. Rio Grande do Sul:** Morrinhos do Sul, 29º22'54.98" N, 049º59'59.22" W, *M.H. Nervo 1200,* 6/I/2014 (ICN).

Distribution: *Stigmatopteris heterocarpa* is endemic to Brazil and occurs in several states of the Atlantic Forest biome, namely Alagoas, São Paulo, Rio de Janeiro, Paraná, Santa Catarina and extending into Rio Grande do Sul. It can be found from the sea level to up to 900 m a.s.l. (based on information the speciesLink system, CRIA 2014, Gasper & Salino 2015, Mazziero et al. 2015, Prado et al. 2015). The species thus is rather widely distributed in the Southern/Southeastern part of the Atlantic Forest Atlantic, with disjunct populations in the Northeastern Atlantic Forest (Fig. 2).

Habitat: Moist and shady sites in the forest interior.

Comments: The presented record for the State of Rio Grande do Sul is from the municipally of Morrinhos do Sul, 155 km farther south than the previously known southern limit of the genus and species in Santa Catarina, while Alagoas is the limit to the North. The absence of records of this species in the Atlantic Forest in the Northeast (States of Sergipe and Bahia) and Southeast (State of Espírito Santo) may be related to habitat loss or to lack of sampling.

With this new record in the South of Brazil, we increase the number of species considered as the "Atlantic Forest elements" in the State of Rio Grande do Sul and the number of fern and lycophyte species in the region to 139 (Nervo et al. in press). We observed *Stigmatopteris heterocarpa* dwelling in the Atlantic rain forest *sensu stricto,* growing close to watercourses at the altitude of approximately 480 m a.s.l., i.e., in a Submontane Forest formation (Veloso & Góes-Filho 1982; see also Brack 2009). Approximately 12 adult individuals were observed in an area of less than one hectare.

More studies are needed to evaluate the conservation state and endangerment status of this species. Considering its possible inclusion in threatened species listing for the State of Rio Grande do Sul. Forest degradation and alterations in springs and watercourses caused by human activities must be considered as the main threats for the species. This species rich locality is currently not included in a protection area, increasing the need of conservation efforts.

Additional specimens examined: **BRAZIL. Paraná**: Morretes, 24/VIII/2010, *M. Verdi et al. 5492* (FURB! [photo]); 15/II/1970, *Hatschbach 24376* (PACA!); 16/XII/1964, *Dombrowski & Saito 1245* (PACA!); Guaraqueçara, 9/VIII/1967, *Hatschbach 16912* (PACA!); Marumbi, *Saito 11* (PACA!); Porto de Cima, *P.K.H. Dusén 10244* (K! [photo]); *P.K.H. Dusén 1480* (F! [photo], K! [photo]). **Rio de Janeiro**: Rio de Janeiro, 10/VI/1976, *Carauta 2074* (PACA!); Rodeio, 1869, *Lieul s.n.* (K590514! [photo]); s.loc., 1867, *Cunnigham s.n.* (K957032! [photo]). **Santa Catarina**: Blumenau, 15/I/2007, *A. Stival-Santos & M. Verdi 65* (FURB! [photo]); 18/I/2001, *Rosane s.n.* (PACA!); 20/IX/2012, *L.A. Funez 939* (FURB! [photo]); 17/IX/2014, *F. Bittencourt & M.R. Schmitt 199* (FURB! [photo]); Corupá, Poço d'Anta, 4/II/2010, *S. Dreveck & F.E. Carneiro 1739* (FURB! [photo]); Florianópolis, Morro do Antão, 22/I/1948, *Sehnem 3086* (PACA!); 07/X/1979, *Sehnem 9466* (PACA!); 18/IV/1948,

Rohr 1006 (PACA!); Imaruí, Forquilha da Aratingaúba, Parque Estadual da Serra do Tabuleiro, 4/I/2010, *M. Verdi et al. 4045* (FURB! [photo]); *F.E. Carneiro 1739* (FURB! [photo]); Joinville, XII/1904, *Schmalz s.n.* [Rosenstock, Filices autrobrasil. exsic. no. 106] (K! [photo]); s.loc., VII/1868, *F. Mueller 34* (K! [photo]). **São Paulo**: Itapecirica, VII/1901, *Wettstein et al. s.n*. (K957035! [photo]); Juquiá, *A. Salino et al. 163114* (UEC! [photo]); São Sebastião, Parque Estadual da Serra do Mar, 19/IV/2000, *A. Salino 5307* (BHCB! [photo]); Ubatuba, 3/VI/2008, *G.A. Nóbrega 442* (UEC! [photo]).

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Legend

Figure 1. Morphological details of the *Stigmatopteris heterocarpa*. A: Habit; B–D: Pinnae detail, venation and sori. Scale bar: A–C (15 cm) and D (1 cm).

Figure 2. Distribution of *Stigmatopteris heterocarpa* in Brazil (based on records shown by speciesLink Project; CRIA 2014). The red circle represents the new record (Morrinhos do Sul–Rio Grande do Sul).

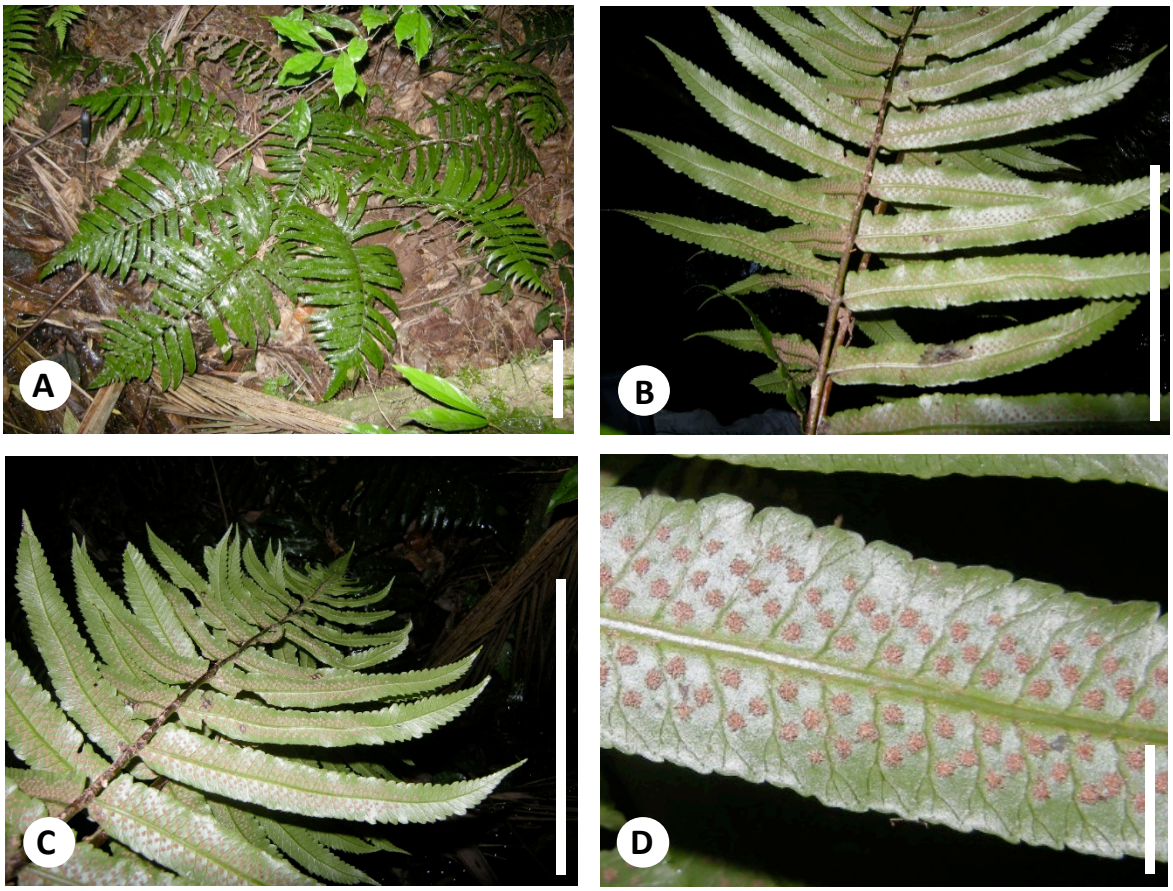

Figure 1

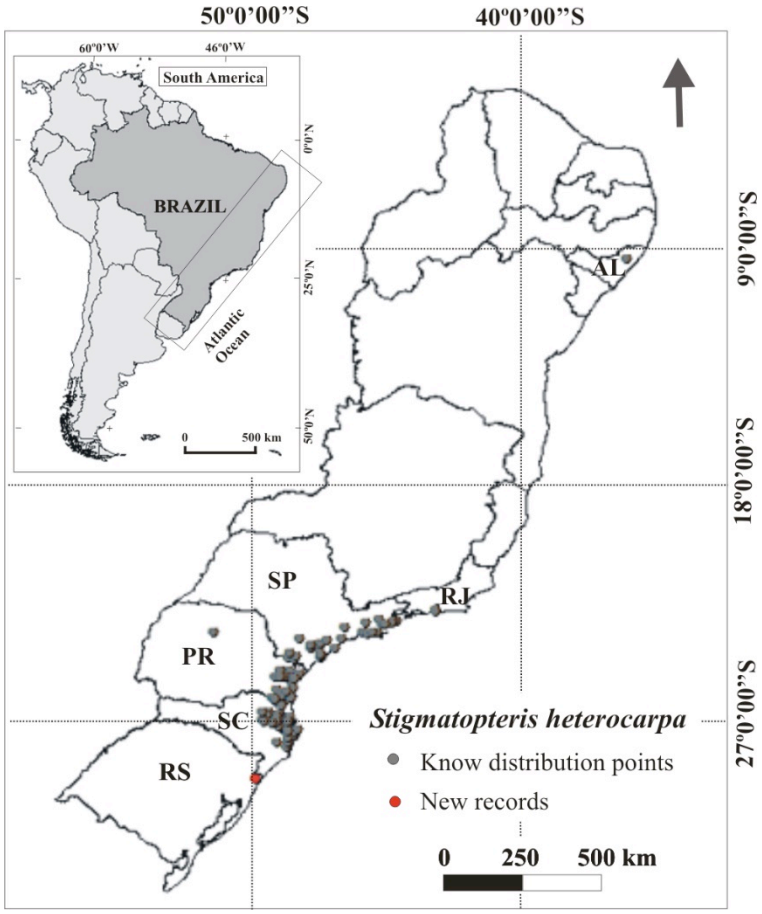
50º0'00"S
40º0'00"S
60º0'W
46º0'W
South America
BRAZIL
Atlantic Ocean
0
500 km
0º0'N
25º0'N
50º0'N
AL
SP
RJ
PR
SC
RS
9º0'00"S
18º0'00"S
27º0'00"S
Stigmatopteris heterocarpa
Know distribution points
New records
0
250
500 km

Figure 2

CONSIDERAÇÕES FINAIS

CONSIDERAÇÕES FINAIS

A riqueza média de espécies por parcela variou significativamente nas diferentes formações florestais, com maior riqueza observada na formação Floresta Montana, como o previsto. A variação da riqueza entre as altitudes não obedeceu nenhum padrão já estabelecido para o gradiente de altitude. Conforme Rahbek (1997), a riqueza de espécies e a altitude podem apresentar relações complexas que variam conforme o grupo taxonômico e o gradiente considerado. Padrões divergentes foram observados na abundância das espécies nos diferentes tipos de substrato. Maior diversidade de epífitos esteve presente em formações de maior altitude (Montana e Altomontana), enquanto que a maior diversidade de terrestres e rupícolas esteve relacionada às formações de menor altitude (Terras Baixas e Submontana).

Diante dos resultados apresentados, acreditamos que tenham sido encontradas evidências substanciais dos efeitos ambientais e espaciais da riqueza de espécies ao longo da distribuição do gradiente de elevação. Aqui, tanto a hipótese da dispersão aleatória quanto a diferenciação de nicho podem explicar a composição e a estruturação das comunidades de samambaias e licófitas ao longo do gradiente na Mata Atlântica no Sul do Brasil. É bem verdade, contudo, que a única premissa do modelo neutro (Hubbell 2001) que foi observada nos dados do presente estudo, diz respeito à variação espacial em escala ampla. Já no modelo da heterogeneidade ambiental, tanto as variações edáficas quanto as climáticas podem explicar a composição de samambaias e licófitas, sendo até mesmo estas as premissas que mais contribuem na composição de todas as espécies, bem como na abundância das espécies epífitas e terrestres. Assim, a hipótese que melhor suporta os dados presentes é a diferenciação de nichos ao longo do gradiente de altitude.

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ANEXOS

PAULO GÜNTER WINDISCH[1*], MARIA LUISA LORSCHEITTER[1] & MICHELLE HELENA NERVO[2]

Isoetes naipiana (*Isoetaceae*), a new species from southern Brazil

Abstract

Windisch P. G., Lorscheitter M. L. & Nervo M. H.: *Isoetes naipiana* (*Isoetaceae*), a new species from southern Brazil. – Willdenowia 44: 393–398. 2014. – Version of record first published online on 10 November 2014 ahead of inclusion in December 2014 issue; ISSN 1868-6397; © 2014 BGBM Berlin-Dahlem.

DOI: http://dx.doi.org/10.3372/wi.44.44309

Isoetes naipiana (*Isoetaceae*), a new species from southern Brazil, is described, illustrated and compared to similar species. So far it is known only from the original locality in the open grasslands of the upper highlands in the NE region of the State of Rio Grande do Sul (Brazil). It is characterized by megaspores with an irregular reticulum on the surface, presenting deposition of thin parallel silica strands; laevigate microspores; and arcuate microphylls with shortly alate bases, forming a compact rosette around the erect bilobate corm.

Additional key words: aquatic lycophytes, quillworts, floristics, conservation

Introduction

Worldwide the genus of *Isoetes* L. (*Isoetaceae*) is represented by c. 350 aquatic to terrestrial species, from temperate to tropical climates (Hickey & al. 2003). For South America, Fuchs-Eckert (1986) listed 75 species, while Hickey (1986) suggested 47. The diversity in Brazil is still far from being known in appropriate detail, due to poor collecting, difficulties in the preservation of samples, lack of fixed material for morphological and anatomical analysis, samples restricted to type material for many species, apparently narrow distributions, lack of easily observable characters, hybridization and polyploidy. Progress is being made due to a rising interest in the group. Prado & Sylvestre (2010) recorded 14 species (12 endemic) for Brazil, but that number was soon increased to 21 (Prado & al. 2012); most of these species occur in coastal mountain ranges in the S and SE regions. The relationships of the species occurring in Brazil still need further research.

A study of the genus for southern Brazil in the "Flora Ilustrada Catarinense" by Fuchs-Eckert (1986) included six species for the states of Paraná, Santa Catarina and Rio Grande do Sul. Lorscheitter & al. (1998, 2009) presented a detailed palynological study including distributions, habitats and short descriptions of eight species from the state of Rio Grande do Sul, two listed as "species ineditae". One of these was described as *Isoetes maxima* Hickey, Macluf & Link-Pérez (Hickey & al. 2009), and the second as *I. mourabaptistae* J. B. S. Pereira, P. G. Windisch, Lorscheitt. & Labiak (Pereira & al. 2012). Pereira (2012) presented a dissertation on *Isoetes* for southern and southeastern Brazil, with 15 species, including palynology (SEM and LM) and cytology (ploidy levels correlated with spore sizes).

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2 Programa de Pós-Graduação em Botânica, Universidade Federal do Rio Grande do Sul, 91501-970 Porto Alegre, Brazil (CAPES doctoral fellowship and FAPERGS research grant).

Extensive field work in the grassland formations in the upper highlands of the NE region of the state of Rio Grande do Sul revealed an interesting and distinctive species here described along with comments on the remaining species of the local flora.

Material and methods

Morpho-anatomical analyses — Material was collected and pressed in the traditional method for herbarium vouchers, and some samples were fixed in 70 % ethanol for morphological and anatomical analyses. Structural terms follow Lellinger (2002).

Spore analyses — The Scanning Electron Microscopy (SEM) images were generated by transferring the spores to aluminium stubs coated with an asphalt adhesive. The stubs were then coated with gold palladium and photographed with a Zeiss EVO MA-10 electron microscope. A light microscope (DIAPLAN Leitz) was used for the measurement of acetolysed microspores. Spore size descriptions include the variation and the arithmetic average of 25 measurements, the first value corresponding to the polar axis and the second to the equatorial axis. The terminology used to classify the spore surface follows that of Hickey (1986) and Tryon & Lugardon (1990).

Results and Discussion

Isoetes naipiana P. G. Windisch, Lorscheitt. & Nervo, **sp. nov.** – Fig. 1–3.
Holotype: Brazil, state of Rio Grande do Sul, municipality of Jaquirana, Tainhas river drainage, 900–950 m, submersed aquatic in rock crevices, high-altitude grasslands, 14 Jan 2014, *Windisch & Nervo 11063* (ICN; isotypes: B, ICN, RB, US).

Diagnosis — The general morphology of the plants differs markedly from the other species occurring in the region by the small size of the microphylls (up to 2.2 cm long) in mature plants, while at least twice as long in the remaining species. Furthermore, the microphylls are rigid in the living material, arched and disposed forming a flat rosette (2–3 cm in diam.), half-terete with a complanate adaxial surface (basal ⅔), distally terete and tapering to a pointed apex (Fig. 1A). The microphylls present short (3–4 mm long) abruptly ending lateral alae at the base, not extending along the margins as in *Isoetes mourabaptistae* (up to the basal ¼). In *I. weberi* Herter, these alae may extend beyond the middle of the microphyll. In *I. fuscomarginata* H. P. Fuchs, *I. ramboi* Herter, *I. sehnemii* H. P. Fuchs, *I. smithii* H. P. Fuchs, *I. spannagelii* H. P. Fuchs (from a locality in the neighbouring state of Santa Catarina, Lages municipality) and *I. weberi* the alae usually taper off gradually.

The reticulate megaspores of *Isoetes naipiana* have an equatorial diameter greater than 600 µm, which is similar to *I. fuscomarginata*, *I. mourabaptistae*, *I. ramboi* and *I. smithii* in size. It differs from those species by having thin, dense, transversely oriented and parallel silica strands forming the muri of the reticulum, this parallel disposition being more pronounced in the deeper lumina. The muri of the megaspores are a good distinctive character as they frequently cross over the trilete arms. The reticulate species occurring in Rio Grande do Sul have smaller megaspores (*I. brasiliensis* H. P. Fuchs, *I. sehnemii*), or are verrucate (*I. weberi* and *I. maxima*).

Four species of *Isoetes* from Rio Grande do Sul have megaspores with equatorial diameters greater than 600 µm, but only *I. naipiana* has smooth to slightly undulate microspores (SEM, especially the proximal face). *Isoetes mourabaptistae* has microechinate microspores. The microspores (SEM) are laevigate-granulate in *I. fuscomarginata* and *I. smithii*, and micropapillate-granulate in *I. ramboi.* The structure of the parallel silica strands forming the muri of the megaspores is quite distinctive in *I. naipiana*.

Description — *Plants* aquatic, submerged, growing in rock crevices in current. *Corm* erect, bilobed, up to 10 mm long, 3–4 mm in diam. *Roots* conspicuous, dichotomous. *Microphylls* 20–35, 1–2.2 cm long, 0.4–0.6 mm wide at middle, 0.7–1 mm wide at base above sporangium (fixed material); 0.8–1.8 cm long, 0.2–0.4 mm wide at middle, 0.4–0.8 mm wide at base above sporangium, 1.2–1.4 mm wide at sporangium (dried material), rigid in living material, arched and disposed forming a flat rosette (2–3 cm in diam.), half-terete with a complanate adaxial surface (basal ⅔), distally terete and tapering to a pointed apex. *Alae* only at base, wings membranous, hyaline, 3–4 mm long, clasping at widened base (0.6–0.9 mm wide on each side), reduced to 0.4–0.6 mm (middle), ending abruptly shortly beyond sporangium. *Ligule* deltate, c. 0.7 mm long, up to 0.6 mm wide, frequently eroded, base weakly auriculate on either side. *Velum* cover c. ½ or more with an oval opening at base. *Labium* not clearly visualized, a short projection observed in some cases. *Sporangium* roundish-elliptic, c. 1.8 mm long, c. 1.2 mm broad, covered by velum. *Microspores* (18–)20(–26) × (24–)27(–34) µm (including perispore/paraexospore), (15–)16(–18) × (21–)23(–27) µm (excluding perispore/paraexospore), reniform, monolete, laesura extending more than ¾ of microspore length; paraexospore detached from exospore, laevigate perispore (in SEM sometimes with irregular, slightly undulating surface, especially on proximal face). *Megasporangia* with 4 or 8 megaspores. *Megaspores* (500–)550(–590) × (620–)655(–690) µm, spheroidal, equatorial limb subtriangular-convex, trilete, arms equalling radius, equatorial view with largely convex proximal and distal faces and a distinct equatorial flange, curved between arms; reticulate with large irregular reticulum distributed on entire surface.

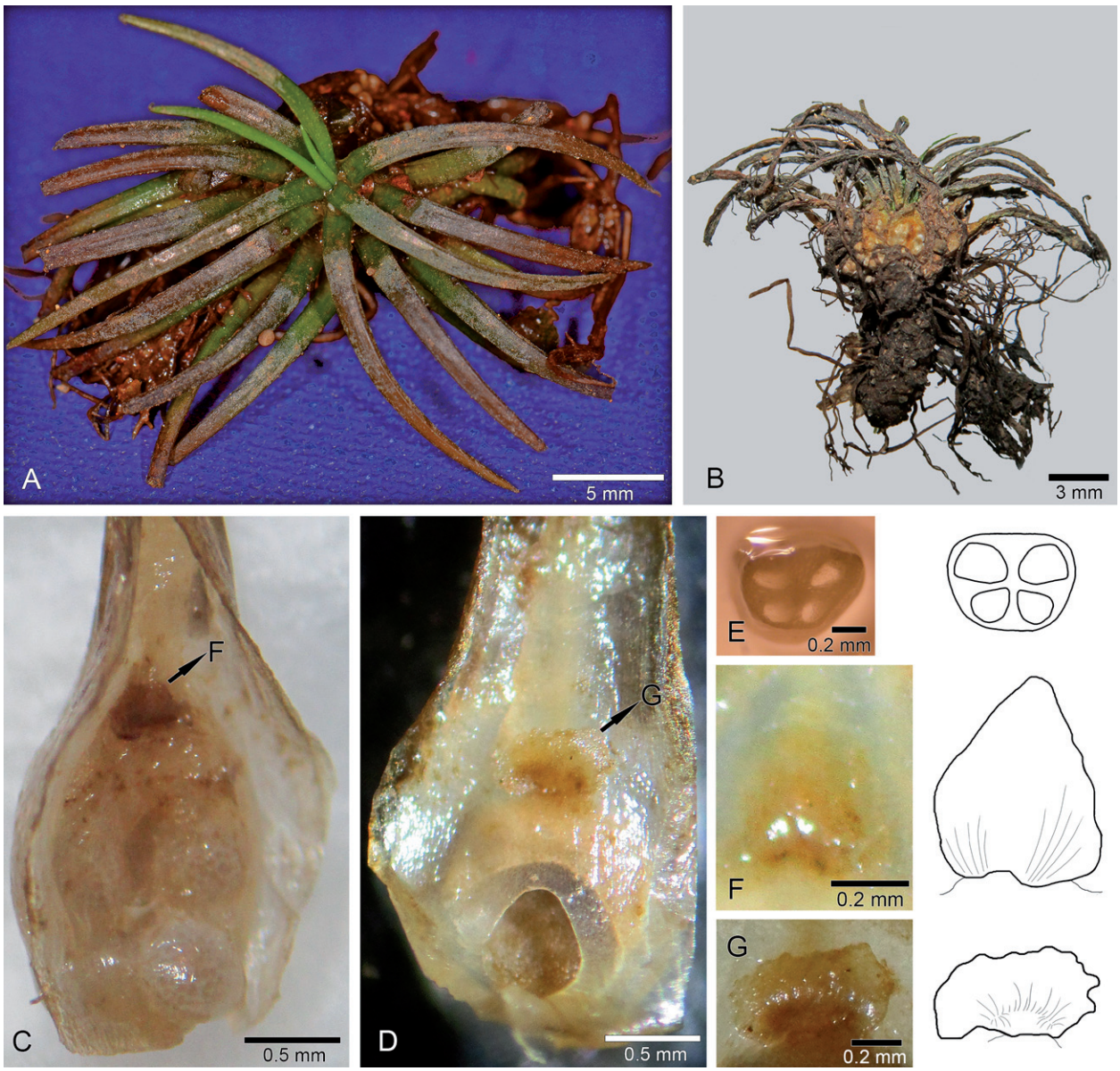

Fig. 1. *Isoetes naipiana* – A & B: habit; C: adaxial view of base of megasporophyll with megaspores; D: adaxial view of base of microphylls with velum covering more than ½ of sporangial surface; E: microsporophyll in transverse section, with accompanying illustration; F: deltate ligule, with accompanying illustration; G: deltate eroded ligule, base weakly auriculate, with accompanying illustration. – All from *Windisch & Nervo 11063*.

Distribution and ecology — *Isoetes naipiana* is currently known only from the original locality, in high-altitude grassland formations, at c. 950 m, where it grows in the rapid moving stream current, at 20 to 30 cm depth (dry season) in basaltic rock crevices.

Conservation status — The inclusion of *Isoetes naipiana* in the threatened species listings as Vulnerable VU D1+2 (IUCN 2012) is proposed here based on small population size with restricted occupancy, with two known locations in an area prone to the effects of human occupancy. The environmental changes due to the current use of the high-altitude grasslands for extensive forestry and agricultural activities require urgent action.

Etymology — The original inhabitants of the NE highlands of Rio Grande do Sul were the Kaingang, a widespread ethnic group of southern to southeastern Brazil. In their mythology, Naipi, the extremely beautiful daughter of a chief, was to be consecrated to the divinity M'boi (son of the highest divinity Tupã) who reigned in the depths of rivers in the form of a giant serpent. Just before her consecration, she escaped in a canoe with her beloved one. M'boi became furious, the canoe was destroyed in a waterfall and Naipi transformed into a rock, to be eternally battered by the running water, like this species of *Isoetes*.

Additional remarks — The size of the megaspores of *Isoetes naipiana* is quite remarkable for such diminutive

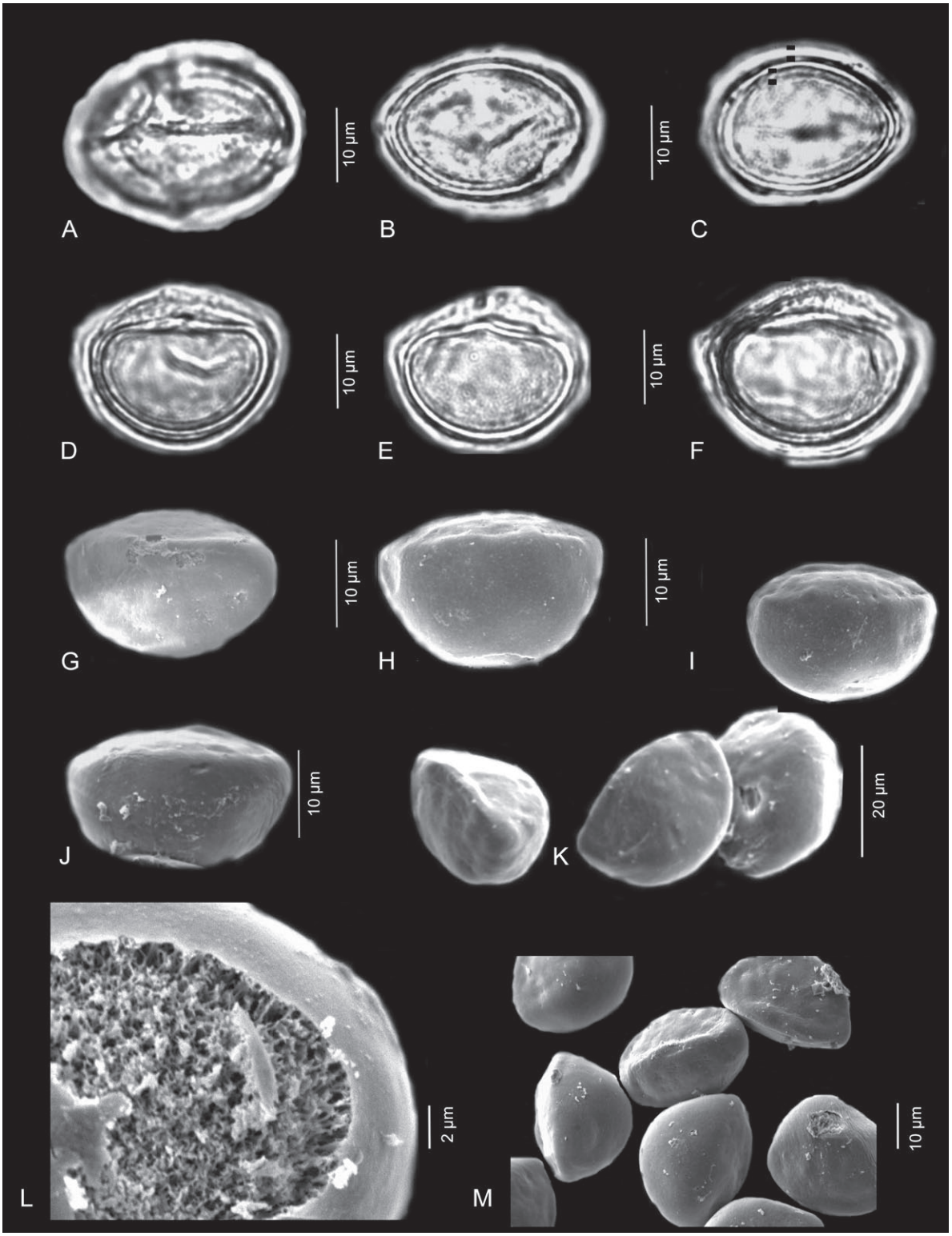

Fig. 2. *Isoetes naipiana,* microspores – A–F: LM images of paraexospore detached from exospore; A: proximal face; B & C: distal face; D–F: equatorial view; G–M: SEM images of laevigate perispore surface; G: proximal face; H–J: equatorial view; K: grains in distinct positions; L: detail of eroded surface, irregular fused strands of inner perispore/paraexospore; M: general view of microspores. – All from *Windisch & Nervo 11063*.

plants; the total length of the microphylls corresponds to 35–40 times the diameter of the megaspores. The megaspores are quite characteristic, showing an irregular reticulum, with fine, parallel fused strands, in a transverse orientation, forming the high muri with alveolar content and denser strands in the bottoms of the areolae. Gener-

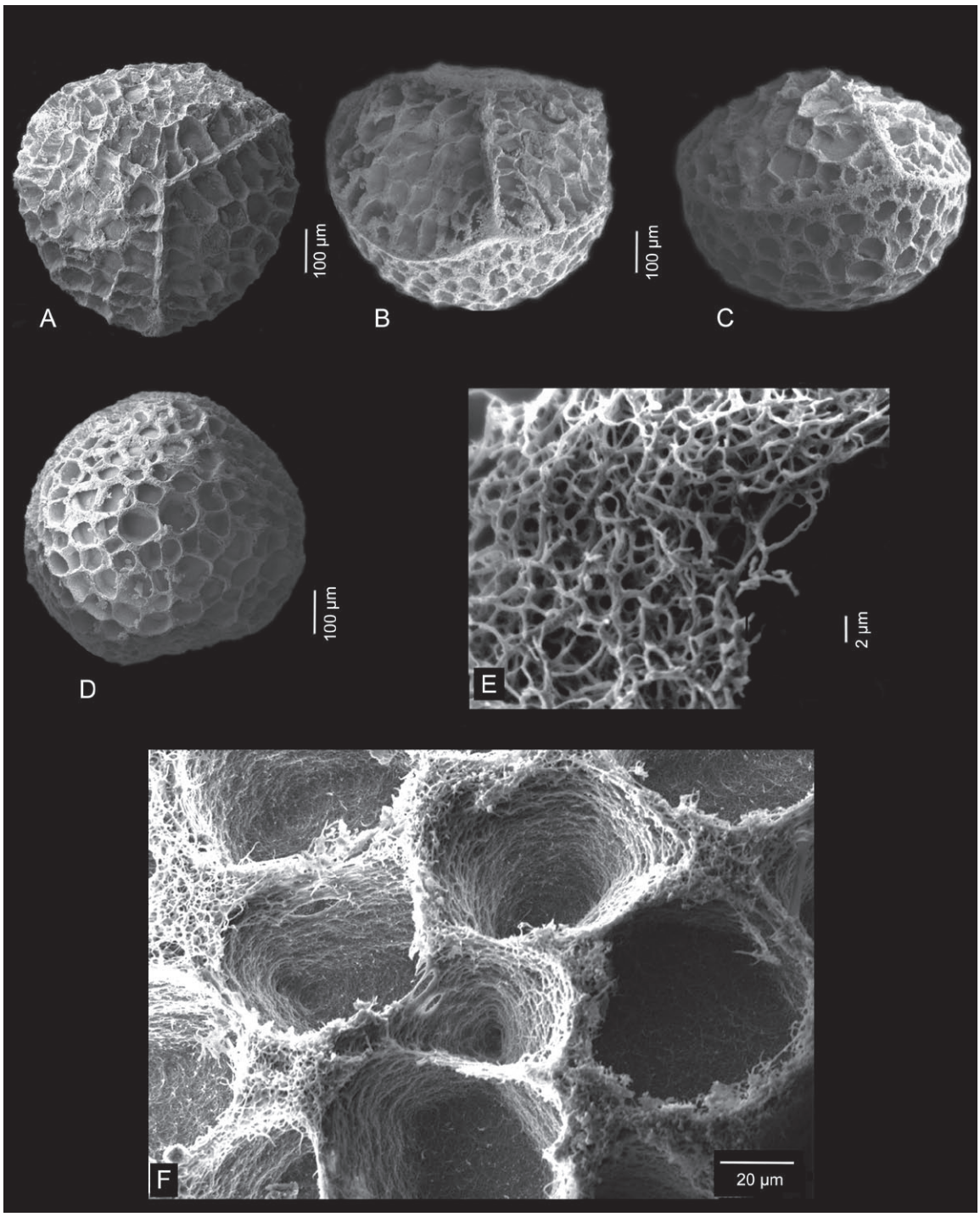

Fig 3. *Isoetes naipiana*, SEM images of megaspores – A: proximal face, longer areolae close to arms, muri crossing over trilete arms; B & C: oblique and equatorial views showing distinct equatorial flange; D: distal face; E: magnified detail of reticulum surface with alveolar strands; F: magnified view of reticulum showing fine fused strands deposited in transverse and parallel fashion forming high muri and denser disposition of strands in bottoms of areolae. – All from *Windisch & Nervo 11063*.

ally longer areolae can be observed close to the arms, the muri frequently crossing over the trilete arms.

The structure of the ligule and labium (vestigial or as a short projection) was variable, as observed by Budke & al. (2005) in a detailed study of *Isoetes tennesseensis* Luebke & Budke.

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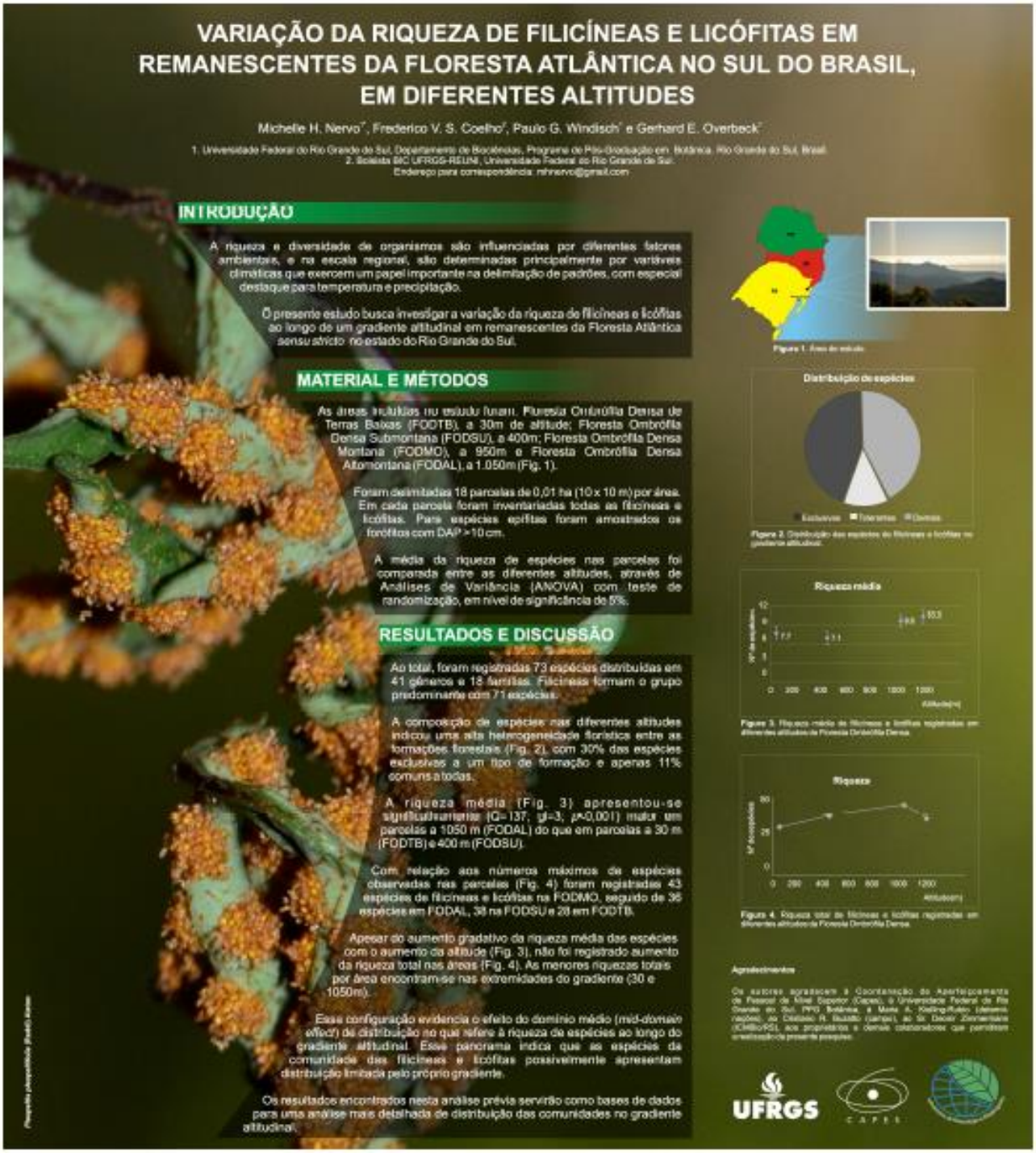

VARIAÇÃO DA RIQUEZA DE FILICÍNEAS E LICÓFITAS EM REMANESCENTES DA FLORESTA ATLÂNTICA NO SUL DO BRASIL, EM DIFERENTES ALTITUDES

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INTRODUÇÃO

A riqueza e diversidade de organismos são influenciadas por diferentes fatores ambientais, e na escala regional, são determinadas principalmente por variáveis climáticas que exercem um papel importante na delimitação de padrões, com especial destaque para temperatura e precipitação.

O presente estudo busca investigar a variação da riqueza de filicíneas e licófitas ao longo de um gradiente altitudinal em remanescentes da Floresta Atlântica *sensu stricto* no estado do Rio Grande do Sul.

MATERIAL E MÉTODOS

As áreas incluídas no estudo foram: Floresta Ombrófila Densa de Terras Baixas (FODTB), a 30m de altitude; Floresta Ombrófila Densa Submontana (FODSU), a 400m; Floresta Ombrófila Densa Montana (FODMO), a 950m e Floresta Ombrófila Densa Altomontana (FODAL), a 1.050m (Fig. 1).

Foram delimitadas 18 parcelas de 0,01 ha (10 x 10 m) por área. Em cada parcela foram inventariadas todas as filicíneas e licófitas. Para espécies epífitas foram amostrados os forófitos com DAP >10 cm.

A média da riqueza de espécies nas parcelas foi comparada entre as diferentes altitudes, através de Análises de Variância (ANOVA) com teste de randomização, em nível de significância de 5%.

RESULTADOS E DISCUSSÃO

Ao total, foram registradas 73 espécies distribuídas em 41 gêneros e 18 famílias. Filicíneas formam o grupo predominante com 71 espécies.

A composição de espécies nas diferentes altitudes indicou uma alta heterogeneidade florística entre as formações florestais (Fig. 2), com 30% das espécies exclusivas a um tipo de formação e apenas 11% comuns a todas.

A riqueza média (Fig. 3) apresentou-se significativamente ($Q=137$; $gl=3$; $p<0,001$) maior em parcelas a 1050 m (FODAL) do que em parcelas a 30 m (FODTB) e 400 m (FODSU).

Com relação aos números máximos de espécies observadas nas parcelas (Fig. 4) foram registradas 43 espécies de filicíneas e licófitas na FODMO, seguido de 36 espécies em FODAL, 38 na FODSU e 28 em FODTB.

Apesar do aumento gradativo da riqueza média das espécies com o aumento da altitude (Fig. 3), não foi registrado aumento da riqueza total nas áreas (Fig. 4). As menores riquezas totais por área encontram-se nas extremidades do gradiente (30 e 1050m).

Essa configuração evidencia o efeito do domínio médio (*mid-domain effect*) da distribuição no que refere à riqueza de espécies ao longo do gradiente altitudinal. Esse panorama indica que as espécies da comunidade das filicíneas e licófitas possivelmente apresentam distribuição limitada pelo próprio gradiente.

Os resultados encontrados nesta análise prévia servirão como bases de dados para uma análise mais detalhada da distribuição das comunidades no gradiente altitudinal.

Figura 1. Área de estudo

Figura 2. Distribuição das espécies de filicíneas e licófitas no gradiente altitudinal.

Figura 3. Riqueza média de filicíneas e licófitas registradas em diferentes altitudes da Floresta Ombrófila Densa.

Figura 4. Riqueza total de filicíneas e licófitas registradas em diferentes altitudes da Floresta Ombrófila Densa.

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UFRGS

CAPES

Nervo MN, Coelho FV, Nervo MN, Windisch PG & Overbeck G.E. 2013. Variação da riqueza de filicíneas e licófitas em remanescentes da Floresta Atlântica no sul do Brasil, em diferentes altitudes. In: 64º Congresso Nacional de Botânica, Belo Horizonte (MG), Brasil. *Resumos*, 2013.

DUAS CATEGORIAS ECOLÓGICAS DE SAMAMBAIAS SOB GRADIENTE ALTITUDINAL NA MATA ATLÂNTICA NO SUL DO BRASIL

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INTRODUÇÃO

A riqueza de organismos é influenciada por variáveis ambientais que determinam os padrões de distribuição. Desta forma espera-se que hajam diferenças nos padrões de distribuição e riqueza das famílias Dryopteridaceae (predominantemente terrícola) e Polypodiaceae (epifítica) ao longo de um gradiente de altitude na Floresta Ombrófila Densa (FOD) no Rio Grande do Sul.

METODOLOGIA

Foram delimitadas 20 áreas de estudo divididas em 4 tipos de formações florestais (Fig. 1, TB, SU, MO, AL). Em cada área 6 parcelas (10 × 10 m) foram implementadas, onde as espécies foram inventariadas. As médias de riqueza das comunidades em diferentes altitudes foram comparadas através de Análises de Variância com teste de randomização. Utilizou-se Análises de Coordenadas Principais (PCoA) para a visualização dos padrões das comunidades.

Tabela 1. Lista de espécies de samambaias que ocorrem em quatro formações da Mata Atlântica no nordeste do Rio Grande do Sul. TB: Terras Baixas; SU: Submontana; MO: Montana; AL: Altomontana.

FAMILIAS/Espécies	TB	SU	MO	AL
DRYOPTERIDACEAE				
Cteniti falciculata (Raddi) Ching	X	X		
Cteniti submarginalis (Langsd. & Fisch.) Ching	X	X		
Didymochlaena truncatula (Sw.) J.Sm.	X	X		
Elaphoglossum luridum (Fée) Christ	X	X		
Elaphoglossum sellowianum (Khtzsch.) Moore			X	X
Lastreopsis amplissima (C.Presl) Tindale	X	X	X	X
Mickelia guianensis (Aubl.) R.C. Moran	X	X	X	
Megalastrum connexum (Kaulf.) A.R.Sm. & R.C.Moran	X	X		
Polybotrya cylindrica Kaulf.	X	X	X	
Polystichum montevidense (Spreng.) Rosenst.			X	X
Rumohra adiantiformis (G.Forst.) Ching	X	X	X	X
POLYPODIACEAE				
Campyloneurum acrocarpon Fée	X	X		
Campyloneurum aglaolepis (Alston) de la Sota			X	X
Campyloneurum austrobrasilianum (Alston) de la Sota		X	X	X
Campyloneurum nitidum (Kaulf) C.Presl.	X	X	X	X
Campyloneurum rigidum J.Sw.	X	X		
Campyloneurum sp.1			X	
Ceradenia albicula (Baker) L.E.Bishop			X	X
Cochlidium punctatum (Raddi) L.E.Bishop			X	X
Lellingeria organensis (Gardner) A.R.Sm. & R.C.Moran			X	X
Lellingeria schenckii (Hieron.) A.R.Sm. & R.C.Moran			X	X
Microgramma vaccinifolia (Langsd. & Fisch.) Copel	X	X	X	
Microgramma squamulosa (Kaulf.) de la Sota	X	X	X	X
Niphidium rufosquamatum Lellinger	X	X	X	X
Pecluma cf. *recurvata* (Kaulf.) M.G.Price			X	X
Pecluma paradiseae (Langsd. & Fisch.) M.G.Price		X	X	X
Pecluma pectinatiformis (Lindm.) M.G.Price	X	X	X	X
Pecluma chnoophora (Kunze) Salino & Costa Assis	X			
Pecluma robusta (Fée) M.Kessler & A.R.Sm.	X			
Pecluma sicca (Lindm.) M.G.Price	X	X	X	X
Pleopeltis hirsutissima (Raddi) de la Sota	X	X	X	X
Pleopeltis macrocarpa (Bory ex Wild.) Kaulf.		X	X	X
Pleopeltis pleopeltidis (Fée) de la Sota	X	X	X	X
Pleopeltis pleopeltifolia (Raddi) Alston	X	X	X	X
Pleopeltis polypodioides (L.) Andrews & Windham		X	X	X
Serpocaulon catharinae (Langsd. & Fisch.) A.R.Smith	X	X	X	X
Serpocaulon lactum (C.Presl) Schwartsb. & A.R.Sm.	X	X	X	X
Serpocaulon latipes (Langsd. & L.Fisch.) A.R.Sm.				X
Serpocaulon meniscifolium (Langsd. & Fisch.) A.R.Sm.	X	X	X	
Zygophlebia longifolios (C.Chr.) L.E.Bishop			X	X

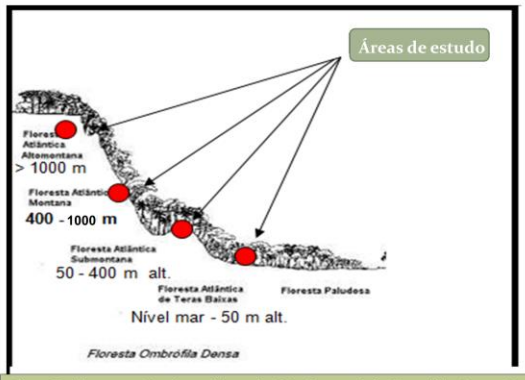

Fig. 1: Perfil esquemático do gradiente de altitude, no sul da Mata Atlântica no Rio Grande do Sul. * adaptado, Brack et al. 2009.

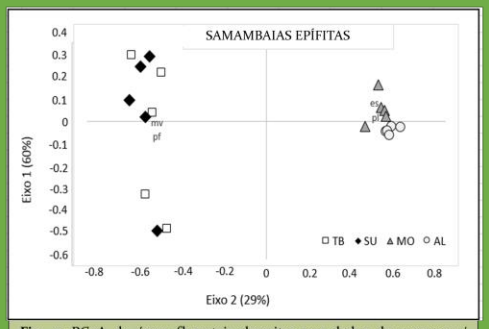

Fig. 4: PCoA de áreas florestais descritas por dados de presença / ausência das comunidades samambaias na Terras Baixas (TB - quadrados), Submontana (SU - losango), Montana (MO - triângulos) e florestas de montanha (AL - círculos). Explicação do eixo 1 = 60% e do eixo 2 = 29%. Espécie, es: *Elaphoglossum sellowianum*; mv: *Microgramma vaccinifolia*; pf: *Pleopeltis pleopeltifolia*; pl: *Pleopeltis pleopeltidis*.

RESULTADOS

Foram registradas 39 espécies (Tab. 1), sendo: 11 (Dryopteridade) e 29 (Polypodiaceae). A riqueza de espécies epifíticas (da família Polypodiaceae) aumentou significativamente com a altitude. A formação Altomontana (FODAL) apresentou o valor mais alto de riqueza média de espécies epifíticas (8 espécies) enquanto que FODTB foi o mais baixo (5). Já a categoria terrícola (Dryopteridaceae) teve distribuição similar ao longo do gradiente, com a maior riqueza média de espécies em FODSU (3 espécies). O PCoA indicou uma separação entre as formações da planície (TB e SU) e Montana (MO e AL) (Fig. 4). *Microgramma vaccinifolia* e *Pleopeltis pleopeltifolia* estão associados à planice e *Elaphoglossum sellowianum e Pleopeltis pleopeltidis* as formações Altas.

CONCLUSÃO

Os padrões de riqueza e distribuição nas famílias verificados neste estudo parecem relacionadas à hipótese da heterogeneidade ambiental ao longo do gradiente. Estudos mais aprofundados para identificar a ação dos efeitos da distribuição causada pela altitude estão sendo realizadas pelos autores.

Coelho FV, Nervo MN, Windisch PG & Overbeck G.E. 2015. Duas categorias ecológicas de samambaias sob gradiente altitudinal na Mata Atlântica no sul do Brasil. In: 66º Congresso Nacional de Botânica, Santos (SP), Brasil. *Resumos*, 2015

Estado de conservação de espécies do gênero *Isoetes* (Lycopsida, Isoetaceae) no Estado do Rio Grande do Sul.

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Introdução

Identificar as espécies que estão em risco de extinção e os fatores que as ameaçam são importantes para a adoção de estratégias conservacionistas, em programas de proteção da biodiversidade.

Neste trabalho foram analisadas espécies de *Isoetes* no Rio Grande do Sul.

Material e métodos

- Revisão principais Herbários
- Bibliografias
- Expedições em campo

Áreas espécies Tipo ↔ Áreas adjacentes

- São Francisco de Paula
- São José dos Ausentes
- Cambará do Sul

Resultados e discussão

Três espécies:

Isoetes maxima Hickey et al.

Isoetes naipiana Windisch et al.

Isoetes mourabaptistae J.B.S.Pereira *et al.*

Isoetes naipiana, I. mourabaptistae e *I. maxima* ocorrem apenas em localidades próximas às populações que originaram os tipos nomenclaturais.

Indicativo → Forte endemismo nas bacias hidrográficas

Fatores que ameaçam os habitats

A maior parte dos corpos d'água que ocorrem na região está sendo profundamente alterados pelo uso das áreas no entorno para atividades florestais e monoculturas (silvicultura de *Pinus*, culturas de batatas, brassicáceas).

Políticas públicas ➡ conservação dos corpos d'água

Sugestão de inclusão

Isoetes naipiana

Lista da Flora Gaúcha Ameaçada de Extinção & Lista da Flora Brasileira Ameaçada de Extinção

(Bbii; D2)

RED LIST — THE IUCN RED LIST OF THREATENED SPECIES

Nervo MN. & Windisch PG. 2015. Estado de conservação de espécies do gênero *Isoetes* (Lycopsida, Isoetaceae) no Estado do Rio Grande do Sul.. In: XVI Encontro Estadual de Botânicos no Rio Grande do Sul, Erechim (RS), Brasil. *Resumos*, 2015.