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Epiphytic ferns in swamp forest remnants of the coastal plain of southern Brazil: latitudinal effects on the plant community

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ABSTRACT

Community structure and spatial distribution of epiphytic ferns in swamp forest remnants along the coastal plain of the state of Rio Grande do Sul were analyzed. A total of 440 trees were sampled in fifty-seven 10 x 10 m plots. Each phorophyte was divided into five ecological zones (strata), where all species of epiphytic ferns were recorded. A total of 34 species representing 18 genera in six families were recorded. Polypodiaceae was the most represented family with 17 species, and *Microgramma vacciniifolia* had the highest epiphytic importance value. Characteristic holoepiphyte was the predominant ecological category, representing 70 % of the species. Ordination analysis showed a gradual change in floristic composition between ecological zones with richness differing significantly between strata. We observed that with increasing latitude there was a decrease in mean temperature and total rainfall, but an increase in frosts. These climatic and phytogeography changes result in a reduction in species richness and a change in the structure of epiphytic fern communities in a north-to-south direction. The importance of swamp forest remnants of the coastal plain to the diversity of epiphytic ferns is discussed.

Keywords: community structure, conservation, environmental factors, epiphytism, spatial distribution

Introduction

Vascular epiphytes represent 9 % of the world's vascular flora and comprise approximately 27,600 species (Zotz 2013). Their abundance and species diversity vary according to environmental factors along latitudinal, altitudinal and continental gradients (Gentry & Dodson 1987). Spatial distribution of vascular epiphytes varies in two directions: horizontally, among forest formations and phorophytes, and vertically, throughout each tree (Steege & Cornelissen 1989). Vertical distribution is mainly influenced by significant differences in air temperature, relative humidity, and the amount and quality of light from the ground to the canopy, providing a range of niches that are exploited by different species (Steege & Cornelissen 1989; Hietz & Briones 1998; Werneck & Espírito-Santo 2002).

In Brazil, there have several studies of the floristic composition, community structure and spatial distribution of vascular epiphytes (Waechter 1986; Kersten & Silva 2001; 2002; Gonçalves & Waechter 2003; Giongo & Waechter 2004; Alves *et al.* 2008; Dettke *et al.* 2008; Kersten *et al.* 2009; Menini Neto *et al.* 2009; Bataghin *et al.* 2010; Mania & Monteiro 2010; Blum *et al.* 2011; Caglioni *et al.* 2012; Oliveira *et al.* 2013; Leitman *et al.* 2014; 2015; Barbosa *et al.* 2015; Padilha *et al.* 2015; Couto *et al.* 2016; Dislich & Mantovani 2016; Freitas *et al.* 2016; Furtado & Menini Neto

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2016). Among the seven works that focused on epiphytism of seedless vascular plants (ferns and lycophytes), four were carried out exclusively with tree ferns (Schmitt *et al.* 2005; Fraga *et al.* 2008; Schmitt & Windisch 2010; Schneider & Schmitt 2011) while the other studies included all types of phorophytes (Labiak & Prado 1998; Barros *et al.* 2014; Quevedo *et al.* 2014).

As discussed by Tryon & Tryon (1982) ferns are widely distributed throughout the world. In general, this broad distribution is due to their spores, which are small, lightweight (only a few heterosporous genera) and can be dispersed by wind over long distances. Thus, the establishment of individuals depends more on environmental conditions than on dispersal capacity (Tryon 1972; 1986; Barrington 1993).

Ferns occupy environments from sea level to high altitudes, including alpine and subdesertic areas, but their greatest species richness is found in mountainous tropical rain forests (Holttum 1938; Page 1979; Tryon & Tryon 1982). Moran (1995) relates this high diversity in mountainous regions to the high environmental heterogeneity of these environments, such as the presence of different types of rocks, soils, slopes, light intensities and microclimates. Sota (1971) points out that the climatic conditions conferred by moderate altitudes, like mild temperatures, strong thermal oscillation between day and night, cloudiness and rainfall, are crucial factors for the development of epiphytism.

There are approximately 12,240 fern species (Moran 2008) of which ca. 20 % are epiphytic (Zotz 2013). In Brazil, the greatest diversity of this group occurs in the Atlantic Forest and its associated ecosystems (Freitas *et. al* 2016), which is considered one of the priority areas for biodiversity conservation (Myers *et al.* 2000; Mittermeier *et al.* 2005). This biodiversity hotspot is currently reduced to about 12% of its original coverage (Ribeiro *et al.* 2009), with many of the remaining remnants being secondary forest (Mynssen & Windisch 2004).

In the state of Rio Grande do Sul, ca. 330 species of ferns are recognized, 100 of which are epiphytes (Prado & Sylvestre 2015). In the northeast region of the state, the narrow coastal plain between the slopes of the Southern Brazilian Plateau (to the west) and the Atlantic Ocean (to the east) forms a gateway for tropical species whose distribution extends along the Atlantic coast, forming a contingent of species in a north-south direction. Rambo (1950) named this geographic region within Rio Grande do Sul as "Porta de Torres" ("Torres Gateway"), which is associated with the Serra Geral mountain formation (south) which is continuous with the Serra do Mar formation (south and southeast).

Though many fern species occur in Rio Grande do Sul, through Torres Gateway there is a strong latitudinal gradient of diversity along the north – south regions of the coastal plain of Rio Grande do Sul (see Gonzatti *et al.* 2016) because of climatic differences along this region (Waechter 1998a). In addition, the paleogeographical evolution of the region of the coastal plain also contributed to the latitudinal gradient of fern diversity (Lorscheitter 2003). These latitudinal effects diversity and distribution of species are also related to various botanical groups in the study area, such as orchids (Waechter 1998a), vascular epiphytes (JL Waechter unpubl. res.) and vegetation in general (Rambo 1950; Waechter 1990; A Scherer unpubl. res.). Factors like low temperatures, scarce rainfall, increase number of days with frost and changes in phytogeographic influences were identified by these authors as determinant elements in the reduction of diversity in the direction of the extreme south.

The swamp forests of state of Rio Grande do Sul provide a refuge for populations of a diversity of ferns species at the limits of their distribution, a fact that should be considered in conservation strategies aimed at the preservation of the genetic diversity of these species (Windisch 2002). Considering the presence of this latitudinal gradient of diversity of ferns on the coastal plain of the state of Rio Grande do Sul, the present study aims to investigate variation in species richness, composition and structure of epiphytic fern communities in swamp forests throughout the study area.

Materials and methods

Study site

The coastal plain of the state of Rio Grande do Sul occupies 33,000 km² of the state (from 29°17 to 33°41'S and from 49°43' to 53°31'W; Fig. 1) and extends for over 620 km from the municipality of Torres to the municipality of Chuí (Rambo 1956). It represents the most recently formed geomorphological unit in the state, having been formed by sediments of a depositional system that originated from marine transgressions and regressions during Quaternary period (Tomazelli & Villwock 2000).

Soils vary between well-drained sandy soils at low elevations (dystrophic quartz sands and red-yellow podzolic soils) and poorly-drained sandy, clay or peat soils in the lowlands. Poorly-drained soils are more diversified, comprising organic, alluvial, eutrophic humic glei, planosols and hydromorphic quartz sands (Waechter 1985).

The climate in the region is *Cfa*, humid mesothermal (Nimer 1977). According to the INMET database (National Institute for Meteorology), in the northern portion of the study area the mean temperature in the coldest month varies between 16 and 18 °C and in the warmest month between 22 and 24 °C. In the southern portion, mean temperatures in the coldest month vary between 12 and 15 °C and in the warmest month between 22 and 24 °C. The total annual rainfall is approximately 1,600 mm in the north and 1,250 mm in the south (Fig. 2). Frosts may occur in winter from a single day in the north, to more than 15 days in the south (Moreno 1961; Nimer 1977).

Variation in soil structure, climatic factors and

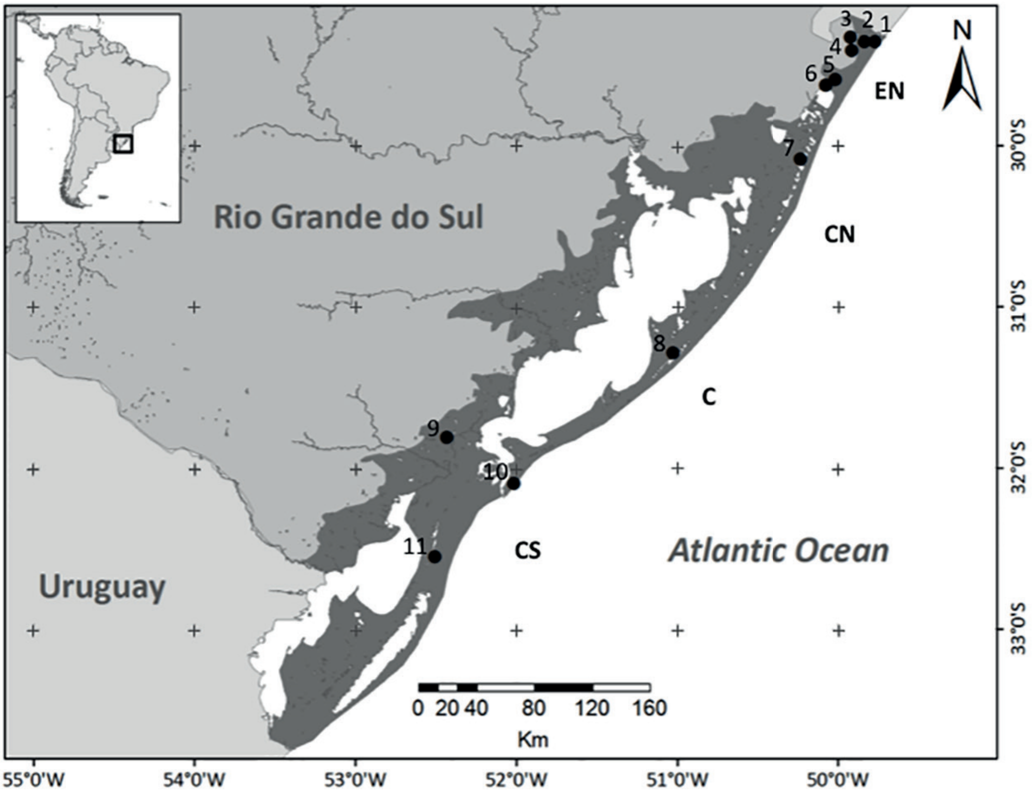

Figure 1. Study area, coastal plain of State of Rio Grande do Sul (dark grey), and sampled locations (dots). 1: Torres; 2: Dom Pedro de Alcântara; 3-4: Morrinhos do Sul; 5-6: Terra de Areia; 7: Cidreira; 8: Tavares; 9: Pelotas; 10-11: Rio Grande.

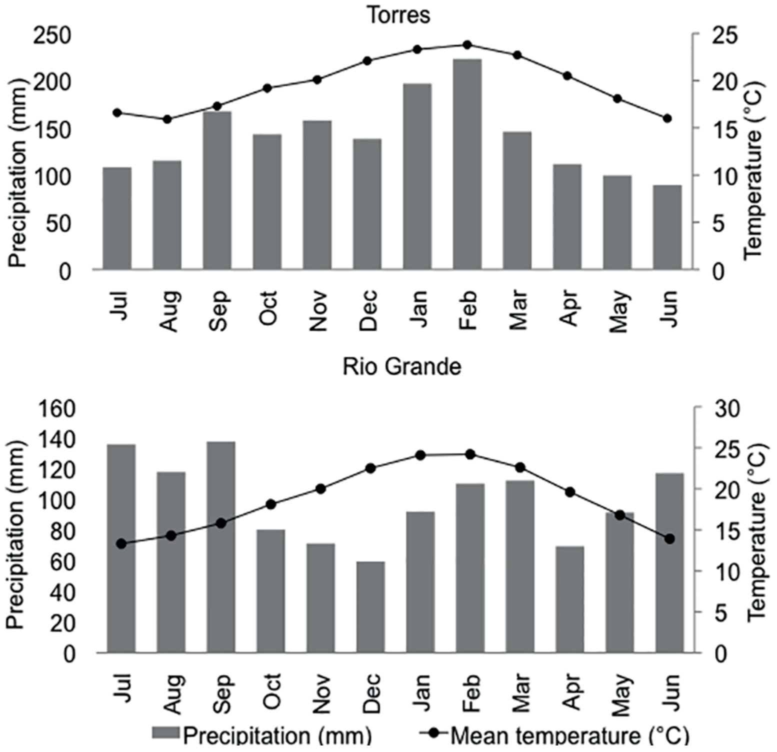

Figure 2. Climate diagrams of northern (Torres, above) and southern (Rio Grande, below) study area, coastal plain of State of Rio Grande do Sul. Values are mensal average of climatic variables in period of 2004-2014 (INMET).

successional stage in the coastal plain results in a vegetation mosaic including: sandy forests, swamps, rain and riparian forests, dunes, fields, palm formations ("butiazais", genus *Butia* (Becc.) Becc.), wetlands and a large number of lagoons (Waechter 1985). According to the Brazilian Geographical Institute - IBGE (2004), the region is classified as a Pioneer Formation Area with fluvial-lacustrine-marine influence.

Among the forest types of the coastal plain, swamp forests were chosen for sampling because they extend throughout the extent of the study area and provide optimal conditions for epiphyte occurrence. In the north, typical tree species include *Alchornea triplinervia* (Spreng.) Müll. Arg., *Handroanthus umbellatus* (Sond.) Mattos, *Myrcia multiflora* (Lam.) DC., *Myrcia brasiliensis* Kiaersk, *Ocotea pulchela* (Nees & Mart.) Mez and the palms *Euterpe edulis* Mart., *Syagrus romanzoffiana* (Cham.) Glassman, *Geonoma schottiana* Mart. and *Bactris setosa* Mart. In the south, the dominant trees are *Erythrina crista-galli* L. and *Ficus cestrifolia* Schott. For more information see Waechter (1985).

Sampling

Data were collected between July 2013 and July 2014, during 12 field expeditions. To analyze the structure and distribution of epiphytic ferns, the study area was divided into five latitudinal bands (Waechter 1998a): extreme-north (EN): 29º17'- 29º59'S; central-north (CN): 30º0'- 30º59'S; central (C): 31º0'- 31º59'S, central-south (CS): 32º0'- 32º59'S and extreme-south (33°0' – 33°45'S), however, only the first four were sampled.

Eleven remnants of swamp forest in nine localities were studied (Fig. 1). In each remnant, multiple 10x10 m^2 sample plots were established, with the number ranging from four in smaller fragments to ten in larger fragments, for a total of 57 plots (5,700 m^2).

All living trees with epiphytic ferns and with 2.5 cm of diameter of breast height (DBH) within each plot were considered (adapted Kersten & Waechter 2011a). We chose to sample only trees with epiphytic ferns because we wanted to assess variation in this community along the latitudinal gradient. When possible, phorophytes were identified and measured for height. In addition, each phorophyte was divided into five ecological zones according to Braun-Blanquet (1932): lower trunk (LT); median trunk (MT); crown base (CB), inner crown (IC) and outer crown (OC).

In each zone, the presence or absence of species of epiphytic ferns were recorded with the help of binoculars or by climbing the phorophyte itself. Voucher specimens were prepared following the methods described by Windisch (1992). Taxa were identified using the literature and by comparisons with herbarium specimens identified by specialists. Vouchers were deposited in the Herbarium of the Biosciences Institute at the Federal University of Rio Grande do Sul (ICN), and duplicates sent to other regional herbaria. Acronyms of herbaria follow Thiers (2016). Species author´s names are based on the Species List of Brazil Flora edited by Prado & Sylvestre (2015). The classification system adopted follows Smith *et al*. (2008).

Epiphyte-phorophyte relationships were classified according Benzing (1990): characteristic holoepiphytes (CHA) - exclusively found in an epiphytic environment; facultative holoepiphytes (FAC) - observed both in epiphytic and terrestrial environments; accidental holoepiphytes (ACC) - preferably terrestrial; and secondary hemiepiphytes (HEM) - starting on the ground and after settling on a tree, losing contact with the soil due to the degeneration of basal parts.

Data for environmental variables were acquired from INMET and the Agrometeorological Monitoring System (Agritempo) database. Annual averages of the last 10 years precipitation (Precip) and temperature – minimum (Tmin), mean (Tmed) and maximum – were obtained for Torres (extreme-north), Porto Alegre (central-north), Pelotas (central) and Rio Grande (central-south). Frost records were obtained from the literature (Mota *et al*. 1970; Nimer 1977).

Data Analysis

Sampling sufficiency was tested using a collector curve (Mueller-Dombois & Ellenberg 1974). Phytosociological parameters used to evaluate epiphytic community structure were: absolute frequency (AFi) and relative frequency (RFi) of each species on trees (Waechter 1998b); and absolute frequency (AFe) and relative frequency (RFe) of each species in ecological zones (Kersten & Silva 2001). Epiphytic importance value (IVe) was based on the average of the relative frequencies (IVe = (RFi + RFe)/2).

Differences in species richness among ecological zones were tested with analysis of variance (One-way ANOVA) using SYSTAT 12.0 software (Systat Software Inc 2007). Spearman's correlation between species richness of epiphytes and height and DHB of phorophytes was also tested. The floristic composition of ecological zones was evaluated by ordination analysis with non-metric multidimensional scaling (NMDS), based on a dissimilarity matrix using the coefficient of Bray-Curtis, where each ecological zone was considered a sample unit (lines), and variables were described by presence/absence of species (columns). Species with less than eight records were excluded from the analysis in order to reduce the inaccuracy of the data, but were discussed separately. Sample units that are more similar in species composition are positioned closer to each other in the graph (Melo & Hepp 2008). NMDS calculates distortion (stress) between the ordination produced in graphical representation of axes and the dissimilarity matrix, to evaluate NMDS reliability. Stress values ranges from 0 to 1, with the best adjustment results having a stress value closer to 0 (Clarke & Warwick 2001).

The NMDS ordination was also used to assess relationships between sample plot composition and climatic variables. For this purpose, a matrix of dissimilarity between plots was produced, describing the presence and absence of species, and using the distance measure of Bray-Curtis. The generated matrix was correlated with environmental variables and the significance of the relationship was tested by 1000 permutations. The R Program was used to perform NMDS and test the relationship between community composition and climatic variables, using MDS and envfit functions, respectively, of the Vegan package (Oksanen *et al*. 2011).

Results

A total of 1,583 epiphytes were found in 440 phorophytes, representing 34 species, 18 genera and 6 families (Tab. 1). Polypodiaceae was the richest family with 17 species, followed by Hymenophyllaceae with six, Dryopteridaceae with five and Aspleniaceae with four species. Blechnaceae and Pteridaceae only had one species each. *Pecluma* was the richest genus (five spp.), followed by *Pleopeltis* (four spp.) and *Asplenium* (four spp.).

Regarding epiphyte-phorophyte relationships, 23 species (68 %) were classified as characteristic holoepiphytes; seven (17 %) as accidental holoepiphytes; three (9 %) as secondary hemiepiphytes and two (6 %) as facultative holoepiphytes (Tab. 1). Their distribution along the study area was very heterogenic, and only characteristic and facultative holoepiphytes occurred in all latitudinal bands. Among the hemiepiphyte species, only *Polybotrya cylindrica* occurred as far south as 30°S, whereas all the other hemiepiphyte species were only found in the extreme north. Accidental holoepiphytes also showed a reduction of occurrence along the latitudinal gradient, going from five in extreme north to none on cental-south (Tab. 2).

The 440 phorophytes analyzed included, among others, the following: *Alchornea triplinervia* (Euphorbiaceae), *Cedrela fissilis*, *Guarea macrophylla* (Meliaceae), *Caussapoa microcarpa*, *Ficus cestrifolia* (Moraceae), and *Erythrina cristagalli* (Fabaceae); palms such as *Euterpe edulis* and *Syagrus romanzoffiana* (Arecaceae); and tree fens such as *Alsophila setosa* and *Cyathea atrovirens* (Cyatheaceae). Other phorophytes, such as *Ficus cestrifolia* and *Syagrus romanzoffiana,* occurred in all latitudinal bands analyzed. Species such as *Achornea triplinervia, Guarea macrophylla, Euterpe edulis* and *Alsophila setosa* were restricted to the extreme north of sampled area.

Average DBH of the phorophytes was 21.9 cm (SD ± 14.8), ranging from 3 to 102 cm. Average tree height was 8.8 m (SD ± 2.78), ranging from 2 to 16 m. The average number of species per plot was five (SD ± 2.6), varying from 2 to 11, and average number of species per tree was 4.2 (SD ± 2.1) ranging from one to nine. The number of phorophytes was eight trees per sample plot (SD ± 1.45), varying from seven to 11. The collector curve stabilized at 33 plots (254 phorophytes), indicating that the sampling was sufficient to represent the floristic composition of the study area (Fig. 3).

The highest DBH values recorded for phorophytes were for *Ficus cestrifolia* (102 cm) and *Erythrina cristagalli* (92 cm), whereas the greatest heights recorded were for *Ficus cestrifolia* (16 m) and *Syagrus romanzoffiana* (14 m).

Trees of DBH between 5 and 20 cm possessed the most epiphytes. Species in the study area with more restricted occurrences on phorophytes included *Asplenium mucronatum*, *Pecluma truncorum* and all Hymenophyllaceae species (except *Didymoglossum hymenoides*), which were recorded only on trees of DBH less than 20 cm. However, the results of the analysis of the correlation between epiphyte richness and porophyte DBH ($r^2 = 0.37$, $P < 0.001$) and height ($r^2 = 0.39$, $P < 0.001$) were low and not demonstrating a strong relationship among the analyzed variables.

The 15 individual tree ferns found in the sample plots possessed nine epiphytic species: *Asplenium mucronatum*, *Asplenium serra*, *Blechnum acutum*, *Campyloneurum nitidum*, *Pecluma chnoophora*, *Pecluma pectinatiformis*, *Pecluma truncorum*, *Polybotrya cylindrica* and *Trichomanes polypodioides*. Three of these species (*Asplenium mucronatum*, *Pecluma truncorum* and *Trichomanes polypodioides*) occur only on these types of phorophytes, specifically on the caudex of *Alsophila setosa*. This phorophyte was only recorded in the extreme north of the study area, sometimes possessing epiphytes and sometimes not. *Cyathea atrovirens* was observed throughout the entire sampled latitudinal gradient, but was only recorded with epiphytes in EN (Tab. 3).

Latitudinal influence on floristic composition was observed (NMDS, *stress*= 0.14; K=3; Fig. 4). For example, *Niphidium rufosquamatum* was found throughout the study area, but becoming more frequent in the southern plots. Despite the high frequency of *Elaphoglossum luridum* and *Serpocaulon catharinae,* they were recorded only in the northern portions of the study area. Species of Hymenophyllaceae were recorded only in the northern portions, where they occupied few phorophytes (except *Didymoglossum hymenoides*). Fifteen species were associated with plots at lower latitudes, occurring only in the extreme north of the study area (Tabs. 1, 2). At the other extreme, *Asplenium gastonis*, *Niphidium rufosquamatum* and *Vittaria lineata* were correlated with higher latitudes (Tabs. 1, 2). Overall, there was a north-to-south decrease in species richness in the study area.

The highest species richness was observed in the extreme-north (32), followed by central-north (17), central (10) and central-south (7) (Tab. 3). Among the 34 species recorded, 16 (50 %) were restricted to forest fragments in the north of the study area and only seven (20 %) occurred throughout the region. These changes in floristic composition were associated with the incidence of frost ($r^2 = 0.61$; $P < 0.01$), rainfall ($r^2 = 0.49$; $P < 0.001$), lower temperatures ($r^2 = 0.60$; $P < 0.001$) and mean temperatures

Table 1. List of families and species recorded in swamp Forest patches of coastal plain of Rio Grande do Sul. Species name abbreviations; number of records in ecological zones; presence or absence on latitudinal bands and ecological category of species are also showed. Voucher in ICN herbarium.

Family/Species	Abbrev	Ecological zones					Latitudinal bands				Ecological category	ICN number
		LT	MT	BC	IC	OC	EN	CN	C	CS		
Aspleniaceae (4)												
Asplenium gastonis Fée	*Ag*	1	12	2	7	0	1	1	1	1	CHA	1788331
Asplenium martianum C.Chr.	*Ama*	2	0	0	0	0	1	0	0	0	ACC	176747
Asplenium mucronatum C.Presl	*Am*	0	4	0	0	0	1	0	0	0	CHA	178335
Asplenium serra Langsd. & Fisch.	*As*	2	16	0	0	0	1	0	0	0	ACC	161391
Blechnaceae (1)												
Blechnum acutum (Desv.) Mett.	*Ba*	0	2	0	0	0	1	0	0	0	HEM	161381
Dryopteridaceae (5)												
Elaphoglossum luridum (Fée) Christ	*El*	5	35	4	4	0	1	0	0	0	CHA	178330
Elaphoglossum vagans (Mett.) Hieron.	*Ev*	0	1	0	0	0	1	0	0	0	CHA	178328
Olfersia cervina (L.) Kunze	*Oc*	0	1	0	0	0	1	0	0	0	ACC	173684
Polybotrya cylindrica Kaulf.	*Pc*	4	70	1	10	0	1	0	1	0	ACC	176730
Rumohra adiantiformis (G.Forst.) Ching	*Ra*	1	5	1	1	0	1	1	1	1	FAC	166405
Hymenophyllaceae (6)												
Didymoglossum hymenoides (Hedw.) Desv.	*Dh*	3	6	2	1	0	1	1	0	0	CHA	184461
Didymoglossum reptans (Sw.) C.Presl	*Dr*	3	0	0	0	0	1	0	0	0	CHA	178345
Hymenophyllum polyanthos (Sw.) Sw.	*Hp*	0	2	0	0	0	1	0	0	0	CHA	184462
Polyphlebium angustatum (Carmich.) Ebihara & Dubuisson	*Pan*	2	2	0	0	0	1	0	0	0	CHA	161400
Trichomanes polypodioides Raddi	*Tp*	1	3	0	0	0	1	0	0	0	CHA	178353
Vandenboschia radicans (Sw.) Copel.	*Vr*	0	1	0	0	0	1	0	0	0	HEM	184454
Polypodiaceae (17)												
Campyloneurum acrocarpon Fée	*Ca*	8	7	0	0	0	1	0	0	0	CHA	178310
Campyloneurum austrobrasilianum (Alston) de la Sota	*Cau*	0	0	1	0	0	0	1	0	0	CHA	178313
Campyloneurum nitidum (Kaulf.) C.Presl	*Cn*	5	23	7	13	0	1	1	1	0	FAC	178305
Microgramma squamulosa (Kaulf.) de la Sota	*Ms*	0	4	4	31	13	1	1	1	1	CHA	178360
Microgramma vacciniifolia (Langsd. & Fisch.) Copel.	*Mv*	12	194	206	286	187	1	1	1	1	CHA	178363
Niphidium rufosquamatum Lellinger	*Nr*	0	23	19	19	0	1	1	1	1	CHA	184449
Pecluma chnoophora (Kunze) Salino & Costa Assis	*Pch*	8	0	0	0	0	1	0	0	0	ACC	184461
Pecluma paradiseae (Langsd. & Fisch.) M.G.Price	*Ppa*	4	1	0	0	0	1	1	1	0	ACC	134575
Pecluma pectinatiformis (Lindm.) M.G.Price	*Ppe*	0	5	0	0	0	1	1	0	0	CHA	184466
Pecluma sicca (Lindm.) M.G.Price	*Ps*	0	4	0	1	0	1	0	0	0	CHA	184456
Pecluma truncorum (Lindm.) M.G.Price	*Pt*	0	2	1	0	0	1	0	0	0	CHA	184452
Pleopeltis hirsutissima (Raddi) de la Sota	*Ph*	0	1	6	16	2	1	1	0	0	CHA	178390
Pleopeltis macrocarpa (Bory ex Willd.) Kaulf.	*Pma*	0	1	2	0	0	0	1	0	0	CHA	178372
Pleopeltis minima (Bory) J. Prado & R.Y. Hirai	*Pmi*	0	0	0	2	0	1	1	0	0	CHA	176217
Pleopeltis pleopeltifolia (Raddi) Alston	*Pp*	0	41	11	54	15	1	1	1	1	CHA	178376
Serpocaulon catharinae (Langsd. & Fisch.) A.R.Sm.	*Sc*	2	35	6	30	4	1	1	0	0	CHA	178383
Serpocaulon latipes (Langsd. & Fisch.) A.R.Sm.	*Sl*	12	1	0	0	0	1	1	0	0	ACC	178379
Pteridaceae (1)												
Vittaria lineata (L.) Sm.	*Vt*	3	20	8	6	0	1	1	1	1	CHA	184468
Total		72	486	271	468	221	32	17	10	7		

($r^2 = 0.59$; $P < 0.58$). Localities in lower latitudes exhibited greater rainfall, higher temperatures and lower incidence of frost, whereas the opposite was recorded for all variables in higher latitudes (Fig. 4).

The three most common species with the greatest IVe belong to Polypodiaceae (*Microgramma vacciniifolia*, *Pleopeltis pleopeltifolia*) and Dryopteridaceae (*Polybotrya cylindrica*). *Microgramma vacciniifolia* corresponded to 50 % of IVe (47) and occurred in 80 % of the phorophytes and 41% of the sampled ecological zones. All other species had lower IVe (Tab. 2). With the exception of *Microgramma vaccinifolia,* which had higher IVe in all latitudinal bands, other species had different IVe along the gradient, indicating different community composition among the latitudinal bands (Tab. 2).

As to the vertical distribution of epiphytes on phorophytes, *Microgramma vacciniifolia*, *Serpocaulon*

Table 2. Ferns epiphytes recorded in phytosociological survey in swamp forest patches of coastal plain of Rio Grande do Sul. Species are organized and sequenced according to decreasing epiphytic importance value (IVe) by latitudinal bands. Ni: total number of trees where species occurred; Ne: total number of ecological zones where species occurred; AFi: absolute frequency in trees; RFi: relative frequency in trees; AFe: absolute frequency in ecological zones; RFe: relative frequency in ecological zone. H': Shannon diversity index.

Species/Latitudinal bands	Ni	Ne	AFi	RFi	AFe	RFe	IVe	H'
Extreme-north (EN)								
Microgramma vacciniifolia (Langsd. & Fisch.) Copel.	185	458	75.8	35.6	37.5	53.3	44.4	0.36
Serpocaulon catharinae (Langsd. & Fisch.) A.R.Sm.	46	62	18.9	8.8	5.1	7.2	8.03	0.21
Polybotrya cylindrica Kaulf.	49	52	20.1	9.4	4.3	6.1	7.73	0.22
Elaphoglossum luridum (Fée) Christ	44	48	18.0	8.5	3.9	5.6	7.02	0.20
Pleopeltis pleopeltifolia (Raddi) Alston	41	47	16.8	7.9	3.9	5.5	6.67	0.20
Microgramma squamulosa (Kaulf.) de la Sota	21	42	8.6	4.0	3.4	4.9	4.46	0.13
Campyloneurum nitidum (Kaulf.) C.Presl	26	29	10.7	5.0	2.4	3.4	4.18	0.15
Asplenium serra Langsd. & Fisch.	19	19	7.8	3.7	1.6	2.2	2.93	0.12
Campyloneurum acrocarpon Fée	14	14	5.7	2.7	1.1	1.6	2.16	0.09
Pleopeltis hirsutissima (Raddi) de la Sota	10	10	4.1	1.9	0.8	1.2	1.54	0.07
Vittaria lineata (L.) Sm.	9	11	3.7	1.7	0.9	1.3	1.50	0.07
Pecluma chnoophora (Kunze) Salino & Costa Assis	8	8	3.3	1.5	0.7	0.9	1.23	0.06
Pecluma sicca (Lindm.) M.G.Price	5	6	2.0	1.0	0.5	0.7	0.83	0.04
Didymoglossum hymenoides (Hedw.) Desv.	4	7	1.6	0.8	0.6	0.8	0.79	0.03
Asplenium mucronatum C.Presl	4	5	1.6	0.8	0.4	0.6	0.67	0.03
Rumohra adiantiformis (G.Forst.) Ching	4	5	1.6	0.8	0.4	0.6	0.67	0.03
Pecluma pectinatiformis (Lindm.) M.G.Price	3	4	1.2	0.6	0.3	0.5	0.52	0.03
Trichomanes polypodioides Raddi	3	4	1.2	0.6	0.3	0.5	0.52	0.03
Asplenium gastonis Fée	3	3	1.2	0.6	0.24	0.3	0.46	0.03
Didymoglossum reptans (Sw.) C.Presl	3	3	1.2	0.6	0.2	0.3	0.46	0.03
Niphidium rufosquamatum Lellinger	3	3	1.2	0.6	0.2	0.3	0.46	0.03
Polyphlebium angustatum (Carmich.) Ebihara & Dubuisson	2	4	0.8	0.4	0.3	0.5	0.42	0.02
Pecluma truncorum (Lindm.) M.G.Price	2	3	0.8	0.4	0.2	0.3	0.36	0.02
Asplenium martianum C.Chr.	2	2	0.8	0.4	0.2	0.2	0.30	0.02
Blechnum acutum (Desv.) Mett.	2	2	0.8	0.4	0.2	0.2	0.30	0.02
Hymenophyllum polyanthos (Sw.) Sw.	2	2	0.8	0.4	0.2	0.2	0.30	0.02
Elaphoglossum vagans (Mett.) Hieron.	1	1	0.4	0.2	0.1	0.1	0.15	0.01
Olfersia cervina (L.) Kunze	1	1	0.4	0.2	0.1	0.1	0.15	0.01
Pecluma paradiseae (Langsd. & Fisch.) M.G.Price	1	1	0.4	0.2	0.1	0.1	0.15	0.01
Pleopeltis minima (Bory) J. Prado & R.Y. Hirai	1	1	0.4	0.2	0.1	0.1	0.15	0.01
Serpocaulon latipes (Langsd. & Fisch.) A.R.Sm.	1	1	0.4	0.2	0.1	0.1	0.15	0.01
Vandenboschia radicans (Sw.) Copel.	1	1	0.4	0.2	0.1	0.1	0.15	0.01
Total	520	859	213.1	100	70.4	100	100	2.4
Central-north (CN)								
Microgramma vacciniifolia (Langsd. & Fisch.) Copel.	42	91	89.4	29.0	38.7	39.9	34.4	0.35
Pleopeltis pleopeltifolia (Raddi) Alston	27	44	57.4	18.6	18.7	19.3	18.9	0.31
Serpocaulon catharinae (Langsd. & Fisch.) A.R.Sm.	15	15	31.9	10.3	6.4	6.6	8.46	0.23
Campyloneurum nitidum (Kaulf.) C.Presl	13	17	27.7	9.0	7.2	7.5	8.21	0.21
Pleopeltis hirsutissima (Raddi) de la Sota	12	15	25.5	8.3	6.4	6.6	7.42	0.20
Serpocaulon latipes (Langsd. & Fisch.) A.R.Sm.	11	12	23.4	7.6	5.1	5.3	6.42	0.19
Niphidium rufosquamatum Lellinger	9	11	19.1	6.2	4.7	4.8	5.51	0.17
Vittaria lineata (L.) Sm.	6	10	12.8	4.1	4.3	4.4	4.26	0.13
Didymoglossum hymenoides (Hedw.) Desv.	3	5	6.4	2.1	2.1	2.2	2.13	0.08
Microgramma squamulosa (Kaulf.) de la Sota	1	2	2.1	0.7	0.9	0.9	0.78	0.03
Campyloneurum acrocarpon Fée	1	1	2.1	0.7	0.4	0.4	0.56	0.03
Campyloneurum austrobrasilianum (Alston) de la Sota	1	1	2.1	0.7	0.4	0.4	0.56	0.03
Pecluma paradiseae (Langsd. & Fisch.) M.G.Price	1	1	2.1	0.7	0.4	0.4	0.56	0.03
Pecluma pectinatiformis (Lindm.) M.G.Price	1	1	2.1	0.7	0.4	0.4	0.56	0.03
Pleopeltis minima (Bory) J. Prado & R.Y. Hirai	1	1	2.1	0.7	0.4	0.4	0.56	0.03
Rumohra adiantiformis (G.Forst.) Ching	1	1	2.1	0.7	0.4	0.4	0.56	0.03
Total	145	228	308.5	100	97	100	100	2.1

Table 2. Cont.

Species/Latitudinal bands	Ni	Ne	AFi	RFi	AFe	RFe	IVe	H'
Central (C)								
Microgramma vacciniifolia (Langsd. & Fisch.) Copel.	64	153	78.0	56.1	34.8	70.8	63.4	0.32
Polybotrya cylindrica Kaulf.	28	32	34.1	24.6	7.3	14.8	19.6	0.34
Pleopeltis pleopeltifolia (Raddi) Alston	6	8	7.3	5.3	1.8	3.7	4.48	0.15
Asplenium gastonis Fée	5	7	6.1	4.4	1.59	3.2	3.81	0.13
Niphidium rufosquamatum Lellinger	5	7	6.1	4.4	1.6	3.2	3.81	0.13
Pecluma paradiseae (Langsd. & Fisch.) M.G.Price	3	4	3.7	2.6	0.9	1.9	2.24	0.09
Microgramma squamulosa (Kaulf.) de la Sota	1	3	1.2	0.9	0.7	1.4	1.13	0.04
Campyloneurum nitidum (Kaulf.) C.Presl	1	1	1.2	0.9	0.2	0.5	0.67	0.04
Vittaria lineata (L.) Sm.	1	1	1.2	0.9	0.2	0.5	0.67	0.04
Total	114	216	139	100	49.1	100	100	1.3
Central-south (CS)								
Microgramma vacciniifolia (Langsd. & Fisch.) Copel.	65	183	97.0	48.5	54.6	65.4	56.9	0.35
Niphidium rufosquamatum Lellinger	28	40	41.8	20.9	11.9	14.3	17.5	0.32
Pleopeltis pleopeltifolia (Raddi) Alston	16	22	23.9	11.9	6.6	7.9	9.89	0.25
Vittaria lineata (L.) Sm.	11	15	16.4	8.2	4.5	5.4	6.78	0.20
Asplenium gastonis Fée	8	12	11.9	6.0	3.58	4.3	5.12	0.16
Microgramma squamulosa (Kaulf.) de la Sota	3	5	4.5	2.2	1.5	1.8	2.01	0.08
Rumohra adiantiformis (G.Forst.) Ching	2	2	3.0	1.5	0.6	0.7	1.10	0.06
Campyloneurum nitidum (Kaulf.) C.Presl	1	1	1.5	0.7	0.3	0.4	0.55	0.03
Total	134	280	200	100	83.6	100	100	1.4

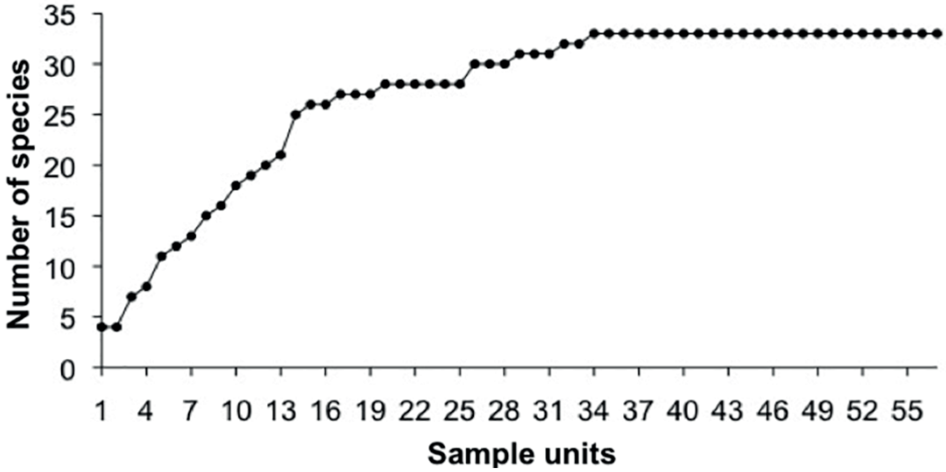

Figure 3. Cumulative curve of ferns epiphytes in swamp forests patches of coastal plain of State of Rio Grande do Sul.

catharinae and *Vittaria lineata* were recorded in all ecological zones. *Campyloneurum nitidum*, *Didymoglossum hymenoides*, *Pleopeltis pleopeltifolia*, *Pleopletis hirsutissima*, *Polybotrya cylindrica* and *Ruhmora adiantiformis* occupied at least four zones. Of the species considered rare in the study area (17 species with less than eight occurrences and that were not included in the NMDS analysis), *Didymoglossum reptans* and *Asplenium martianum* were restricted to the lower trunk (12 occurrences). *Blechnum acutum*, *Hymenophyllum polyanthos*, *Pecluma truncorum*, *Elaphoglossum vagans* and *Vandenboschia radicans* were restricted to the median trunk (29 occurrences). *Campyloneurum austrobrasilianum* and *Pleopeltis minima* were restricted to the crown base and inner crown, respectively. Others species, such as as *Pleopeltis macrocarpa*, *P. pleopeltifolia*, *Pecluma sicca*, *P. pectinatiformis*, *Polyphlebium angustatum* and *Trichomanes polypodioides*, were recorded in more than one ecological zone (Tab. 1). Species with hemiepiphyte life forms, with the exception of *Polybotrya cylindrica*, were restricted to the lower trunk, as well as most accidental species.

There was slight variation in floristic composition from the lower trunk to the crown (NMDS, *stress*=0.035; K=3; Fig. 5). Crown base and inner and outer crown shared many species, while the lower trunk exhibited more differences; median trunk was intermediate in variation of species composition. Ferns occurred more on the lower and median trunk (18 and 29 species, respectively) while only five species inhabited outer crown (F= 129.42, P<0.001). The number

Table 3. Variation of environment variables and community structure along the four latitudinal bands. Tmin: average of minimum temperature; Precip: average of total precipitation; number of frost days - Values are annual means of last ten years (2004-2014). Average of phorophytes sampled; number of tree ferns found; average height of phorophytes; average of DBH; epiphytic richness.

Latitudinal bands	Tmin (°C)	Precip (mm)	Frost (days)	N° Phorophytes (average)	Tree ferns (Total)	Phorophytes height (average)	Phorophytes diameter (average)	Epiphytes richness
Extreme-north	15.2 (Torres)	1.600	1-3	8.1	15	9.0	20.6	32
Central-north	15 (Porto Alegre)	1.420	1-3	7.8	0	9.9	21.4	17
Central	13.7 (Pelotas)	1.260	6-7	8.3	0	9	20.9	10
Central-south	14 (Rio Grande)	1.200	6-7	6.7	0	6.9	28.4	7

of occurrences varied among ecological zones (Tab. 1), with median trunk having the highest number of occurrences (486), followed by inner crown (468), base of crown (271), outer crown (221) and lower trunk (72).

Discussion

The richness of epiphytic ferns on angiosperms and tree ferns of the present study (34 spp.) was similar to the 31 species found by Schmitt & Windisch (2010) on 160 individuals of *Alsophila setosa* in different forest types in Rio Grande do Sul. In a forest with *Araucaria* in Rio Grande do Sul, Schmitt *et al.* (2005) sampled 40 tree ferns of *Dicksonia sellowiana* Hook. and found 11 species of epiphytic ferns, while Fraga *et al.* (2008) found 20 fern species on 164 individuals.

The most represented fern families in this study are the world's most species rich in the epiphytic environment (Madison 1977; Kress 1986; Zotz 2016). Polypodiaceae is considered one of the richest families among Neotropical vascular epiphytic flora, along with Orchidaceae and Bromeliaceae (Gentry & Dodson 1987). The dominance of Polypodiaceae has also been recorded in numerous other studies of fern epiphytes in the Neotropical Region (Sota 1971; Labiak & Prado 1998; Moran *et al.* 2003; Schmitt et *al.* 2005; Schmitt & Windisch 2010; Schneider & Schmitt 2011; Barros *et al.* 2014; Quevedo *et al.* 2014). Zotz (2016) estimated that there are approximately 2,900 fern epiphytes, of which 50 % belong to Polypodiaceae (broad sense).

Having characteristic holoepiphytes as the most common epiphyte-phorophyte relationship, as found in the present study, is a pattern commonly reported in studies of fern epiphytes (Labiak & Prado 1998; Schmitt *et al.* 2005; Fraga *et al.* 2008; Schmitt & Windisch 2010; Barros *et al.* 2014) as well as for vascular epiphytes in general (Kersten & Silva 2001; 2002; Borgo & Silva 2003; Gonçalves & Waechter 2003; Rogalski & Zanin 2003; Alves *et al.* 2008; Dettke *et al.* 2008; Bataghin *et al.* 2010; Blum *et al.* 2011; Caglioni *et al.* 2012; Staudt *et al.* 2012; Oliveira *et al.* 2013; Barbosa *et al.* 2015, Furtado & Menini Neto 2016). This pattern

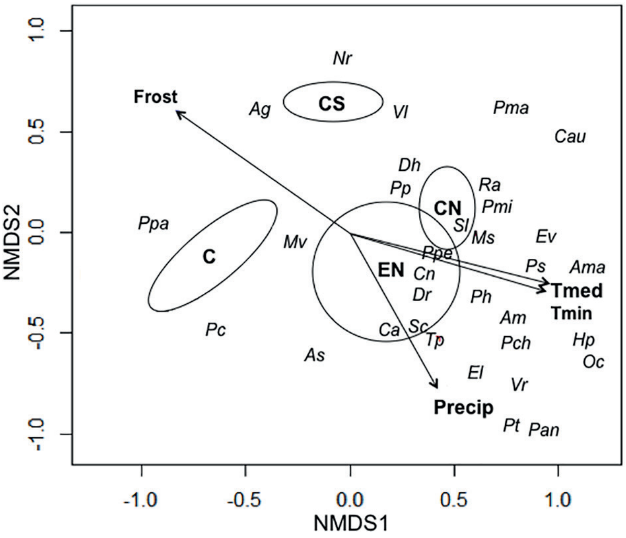

Figure 4. Non-metric multidimensional (NMDS) scaling of 57 sample plots (ellipse) described by presence/ausence of ferns species and relationship variables (vectors) in coastal plain of State of Rio Grande do Sul. Species names and environmental variables abbreviations are in Table 1 and 3, respectively

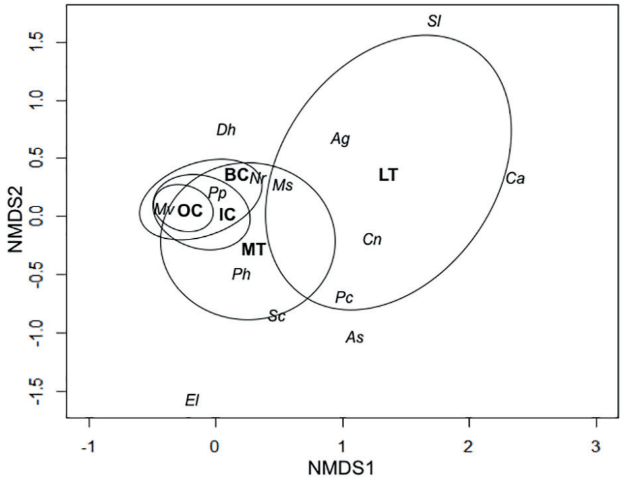

Figure 5. Non-metric multidimensional scaling (NMDS) of ecological zones (ellipse) described by presence/ausence of fern species in coastal plain of State of Rio Grande do Sul.

suggests that most species of epiphytic synusiae possess a set of morphological and physiological adaptations to occupying this environment (Benzing 1990). However, the occurrence of accidental holoepiphytes was also notable in the study area where typically terrestrial species (*Asplenium serra*, *Asplenium martianum*, *Pecluma chnoophora*, *Pecluma paradisae*, *Serpocaulon latipes* and *Olfersia cervina*) were observed on the base of the trunk of certain trees. Water saturation of soil in the swamp forests can restrict the occurrence of many species of terricolous plants (Citadini-Zanette 1984; Záchia & Waechter 2011), consequently an accumulated thick humus layer on the basal portion of tree trunks can serve as a better substrate for the establishment and development of these plants. Such conditions also favor a greater occurrence of hemiephiphytic species, as observed in the extreme north of the study area. These species are restricted to these environments due to their need for high humidity and closed canopies with less light incidence (Orihuela & Waechter 2010; Orihuela *et al.* 2013). The distribution of species such as *Blechnum acutum, Polybotrya cylindrica,* and *Vandenboschia radicans,* did not extend to the center south of the study area and Uruguay (Zuloaga *et al.* 2008), possibly due to the rarefaction of tropical climatic conditions that occurs around the 30ºS parallel.

The trunks of arborescent ferns provide optimal conditions of humidity and porosity for the establishment and development of epiphytic species (*e.g.* Cortez 2001; Mehltreter *et al.* 2005). Both humidity and porosity may explain the high species richness of epiphytes in studies that considered only tree ferns. Moreover, epiphyte-phorophyte specificity is common (Cortez 2001; Windisch 2002; Schmitt *et al.* 2005). The concentrated distribution of arborescent ferns in the extreme north of the coastal region, and their gradual reduction to south (Gonzatti *et al.* 2016), along with epiphyte-phorophyte specificity, can explain why the distribution of many epiphytic species is limited to the south of study area. In this context, the epiphyte species are limited, not only by local microclimatic conditions, but also by the lack of specific phorophytes, that become more sparse or absent toward the south, which is also influenced by climatic changes.

The inclusion of all types of trees with fern epiphytes in the present study increased the chances of recording rare and more restricted species, as they were found on trees with smaller diameters. This result demonstrates the importance of the criteria used in quantitative studies with fern epiphytes, as the richness of a region may be underestimated if only larger diameter trees are considered. Zotz (2007) indicated that epiphyte sampling of only large trees may lead to a biased representation of the community. Mehltreter *et al.* (2005) also reinforced the importance of sampling phorophytes with smaller diameters with their study in rain forests in Veracruz, Mexico, where they found high species diversity in trunks with DBH around 10 to 20 cm in angiosperms and 20 to 30 cm in tree ferns. These authors also emphasized that trees with larger diameters possessed greater floristic richness and abundance of vascular epiphytes, which differs from our results were we did not find a direct relationship between the structure of the arboreal component (DBH and height) and the abundance and richness of epiphytic ferns. These data further reinforce the influence of climatic and phytogeographic factors on the community structure of epiphytic ferns along the coastal plain.

Part of the variation in species composition among the different ecological zones can be attributed to changes in microclimate throughout the phorophytes (Johansson 1974; Steege & Cornelissen 1989; Dickinson *et al.* 1993; Freiberg 1997; Nieder *et al.* 1999; 2001; Werneck & Espírito-Santo 2002; Kersten & Waechter 2011b). Werneck & Espírito-Santo (2002) emphasize that the vertical zonation is only observed in forests with a closed canopy. Moisture tends to decrease from the ground up to the crown, while temperature and light intensity tend to increase (Benzing 1990; Parker 1995). Thus, species susceptible to desiccation are limited by long periods of solar radiation, and thus are found predominantly in more humid and shaded areas of forests (Dubuisson *et al.* 2009). On the other hand, several species can tolerate extreme conditions because of morphological and physiological adaptations (Benzing 1990; Ranal 1991; 1993; 1995a; b).

Ecological zones closer to the ground (lower and median trunk) had higher species richness, with some species occurring predominantly in these areas. In general, ferns prefer more humid environments due to their less efficient system for conveying / holding water, and lower photosynthetic rates than those of angiosperms (Page 2002).

Among the species observed only in the lower vertical zone, those of Hymenophyllaceae stand out, but they are restricted to more humid and shady locations, as was also found by Zotz & Büeche (2000), Schmitt *et al.* (2005) and Parra *et al.* (2009). As mentioned by several authors, including Dubuisson *et al.* (2003), the hygrophilous nature of species of Hymenophyllaceae is due to the absence of a cuticle and the presence of only one layer of cells in the leaf blade. Since there are no specialized structures controlling water loss, these species completely depend on environmental humidity for their hydric balance. Moreover, species of Hymenophyllaceae produce spores with chloroplasts that have short viability (2-3 days), and which can germinate even before release (Nayar & Kaur 1971), thus represent a limiting factor for long-distance dispersal. Dubuisson *et al.* (2009) pointed out that small size and the form of colonial growth strategies are important to the success of epiphytism in Hymenophyllaceae. Susceptibility to environmental changes and greater dependence on the substrate by species of Hymenophyllaceae indicate that the presence of such species in our study area may be correlated with the conservation status of the forest patches.

The upper ecological zones were occupied by species with greater vertical amplitude and frequency. In the outer crown, only Polypodiaceae were recorded. *Microgramma vacciniifolia* was the most common species of the canopy, while *Microgramma squamulosa*, *Niphidium rufosquamatum, Pleopeltis hirsutissima* and *P. pleopeltifolia* were most frequent in the inner crown. According Tryon (1964), approximately 10 % of fern epiphytes grow in tropical xeric environments, and several species have morphological characteristics and mechanisms that allow them to tolerate water stress, such as reduced leaf surface area and leathery textured leaf blades.

Studying the establishment of epiphytic ferns in semideciduous forest, Ranal (1995a; b) found that *Microgramma squamulosa, Pleopeltis hirsutissima* and *Pleopeltis pleopeltifolia* are common on substrates with less water holding capacity, but too occurring in wetter substrates. The presence of scales on leaves and on rhizomes and curling of fronds in response to water deficit (poikilohydry) were emphasized by Ranal (1995a; b). The creeping habit and scaly rhizomes of *Microgramma squamulosa* promote water and debris retention (Ranal 1995a), while other species of the genus perform leaf abscission in the dry season, leaving only the scaly stem (Ranal 1991).

The finding of a decrease in the number of families and species of epiphytic ferns with increasing of latitude in the present study corroborates the observation by Waechter (unpubl. res.) for vascular epiphytes of the coastal plain of the state of Rio Grande do Sul. This author also points out that this decrease is even more pronounced around the 30th parallel, due to climate differentiation which coincides with the biogeographic boundary between the Atlantic Forest and the Pampa provinces. While in the extreme-north of the study area average temperatures remain constant throughout the year, in the southern part there is a decreasing trend in the colder months as well as an increase in the number of days with frost (Tab. 3). With regard to rainfall, while the extreme-north experiences a water surplus in the warmer months, the south experiences periods of drought (Mota *et al.* 1970).

Changes in the dominant species of canopy trees also occur along the latitudinal gradient. The climatic discontinuity along coastal plain associated with changes in biome influence, generate distinctly different tree compositions in the north and south extreme of the coastal plain. In the extreme north of the study area, the influence of the Atlantic Forest is very strong and gives rise to a forest with a dense canopy, tall trees and high arboreal diversity. In contrast, the south is influenced by Deciduous Forests from southwestern Rio Grande do Sul, with a predominance of short and deciduous forests with low diversity (Waechter 1985; Waechter & Jarenkow 1998; Záchia & Waechter 2011; A Scherer unpubl. res.) (Tab. 3). These authors also point out that in the southern coastal plan the process of "insularization" occurs, which is when the forest becomes less dense and naturally more fragmented. In the southern portion of the study area *Erythrina cristagalli* and *Ficus cestrifolia* comprised the majority of phorophytes found (68 %). These species partially or completely lose their leaves in the winter months, thereby producing a seasonal character to these forests (Waechter & Jarenkow 1998). Forest insularization increases edge effects and the exposure of epiphytic flora to sun. The opening of the canopy, associated with low temperatures, greater exposure to winds and incidences of frost in the south may limit the occurrence of tropical species.

All these factors (cited above) combined can explain the differences among the epiphyte communities along the coastal plain. Our data show (Fig. 4) a clear differentiation of epiphytic communities in north-south direction, influenced mainly by increased frost frequency. Species with higher frequencies in C (central), such as *Pecluma paradiseae* and *Polybotrya cylindrica* have their southern limit of distribution in this portion of the coastal plain. On the other hand, species *Asplenium gastonis*, *Niphidium rufosquamatum* and *Vittaria lineata*, which are widely distributed in extreme southern Brazil and Uruguay (Zuloaga *et al*. 2008; Prado & Sylvestre 2015), have higher frequencies in the southernmost portion of the study area (CS – central south). This suggests that there may be substitution of epiphytic species along the latitudinal gradient, and not only in species composition, as presented in tab. 1 and 2, but also in the pattern of frequencies along the latitudinal gradient. These changes may be a result of some species being better adapted to certain climatic and phytogeographical changes along the north-south gradient, plus the lack of competition from other more selective species restricted to EN and CN regions (extreme north and central north).

Thus, Rio Grande do Sul possesses a refuge for populations of a diversity of species at the extreme limit of their distribution; a fact that should be considered in conservation strategies aiming to preserve the genetic diversity of these species (Windisch 2002). The results of the present study indicate high species richness in swamp forests of the coastal plain of the state of Rio Grande do Sul, especially considering the recent geological history of the formation. Vertical zonation of epiphytic ferns on phorophytes, and the recognition of many species that are sensitive to environmental variation, are important considerations for future conservation strategies for ferns in the forest patches of Rio Grande do Sul coastal plain. According to our results, the latitudinal gradient of species richness and composition is mainly due to the influence of different climatic conditions and phytogeographic changes throughout the study area. Thus, the decrease in species richness toward higher latitudes is related to an increase in the number of days of frost, as well as to decreases in temperature and precipitation.

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