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Ferns and Lycophytes as new challenges

Understory epiphytic pteridophytes along altitudinal gradients on opposite slopes in the Atlantic Forest

Thiago Vieira Costa[1,4], *André Felippe Nunes-Freitas*[2] & *Lana da Silva Sylvestre*[3]

Abstract

Gradual climatic changes caused by mountains' altitudinal variation promote alterations in the structure of ecological communities. Environmental changes are also expected according to the slope's position in relation to the sea. In this study, we aimed to compare epiphytic pteridophyte communities along altitudinal gradients on opposite slopes in a section of the Atlantic Forest. We sampled a total of 10 sites in the montane and upper montane zones from the eastern (facing the sea) and western (facing away from the sea) slopes. A total of 1,742 individuals from 62 epiphytic species were recorded. The slopes showed similar epiphytic abundances and richness. Species richness showed a tendency to decrease with an increase in altitude on the western slope, and abundance was higher at intermediate altitudes, with no altitudinal trend in dominance. Conversely, on the eastern slope, there was no clear altitudinal pattern in richness or abundance; however, dominance increased with an increase in altitude from 1,200 to 1,800 m. Species compositions differed among altitudinal zones and between slopes. The eastern slope had lower species richness and no clear altitudinal gradient, although it was better preserved than the western one. Thus, there are differences in the community structure of epiphytic pteridophytes from the forest understory due to altitudinal variation and slope orientation, and these findings corroborate our hypotheses.

Key words: ferns, floristic composition, lycophytes, Parque Nacional da Serra dos Órgãos, species abundance.

Resumo

As mudanças climáticas graduais causadas pela variação altitudinal nas montanhas promovem alterações na estrutura das comunidades ecológicas. Mudanças ambientais também são esperadas de acordo com a posição das vertentes em relação ao mar. Neste estudo, nós objetivamos comparar a comunidade de pteridófitas epífitas ao longo dos gradientes altitudinais em vertentes opostas em um trecho de Floresta Atlântica. Amostramos um total de 10 sítios nas faixas montana e alto-montana das vertentes oriental (voltada para o mar) e ocidental (oposta ao mar). Um total de 1,742 indivíduos, distribuídos em 62 espécies epifíticas, foram registrados. As vertentes mostraram valores similares de abundância e riqueza epifítica. A riqueza tendeu a diminuir com o aumento da altitude na vertente ocidental; a abundância foi elevada na altitude intermediária e nenhuma tendência altitudinal na dominância foi observada. Na oriental, não houve nenhum padrão altitudinal claro na riqueza ou abundância em relação à altitude, mas um aumento na dominância de 1,200 a 1,800 m. A composição de espécies diferiu entre as faixas altitudinais e entre as vertentes. A vertente oriental teve menor riqueza e nenhum gradiente altitudinal claro, embora fosse mais preservada que a ocidental. Portanto, existem diferenças na estrutura da comunidade de pteridófitas epífitas do sub-bosque florestal devido à variação altitudinal e orientação das vertentes, e esses resultados corroboram nossas hipóteses.

Palavras-chave: samambaias, composição florística, licófitas, Parque Nacional da Serra dos Órgãos, abundância de espécies.

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[1] Universidade Federal do Rio de Janeiro, Museu Nacional, Prog. Pós-graduação em Ciências Biológicas (Botânica), Rio de Janeiro, RJ, Brazil. ORCID: <https://orcid.org/0000-0002-9292-9030>.

[2] Universidade Federal Rural do Rio de Janeiro, Instituto de Florestas, Depto. Ciências Ambientais, Seropédica, RJ, Brazil. ORCID: <https://orcid.org/0000-0002-5149-9070>.

[3] Universidade Federal do Rio de Janeiro, Instituto de Biologia, Depto. Botânica, Rio de Janeiro, RJ, Brazil. ORCID: <https://orcid.org/0000-0002-0486-0898>.

[4] Author for correspondence: costatv@ufrrj.br

Introduction

The Atlantic Forest comprises a large area of South American forest along the Brazilian coast, from the northeast to the south. It is one of the five most threatened forest regions on the planet (Myers *et al.* 2000; Mittermeier *et al.* 2004), with about 13% of its original vegetation cover (Rosa *et al.* 2021) and high endemism that reinforces the need for conserving the remaining forests to prevent the extinction of many species (Viveiros de Castro 2008). It is currently distributed in forest fragments and the largest ones are located mainly along the coastal mountains (Ribeiro *et al.* 2009).

The coastal mountain ranges concentrate high levels of moisture as they form an orographic barrier to the moist easterlies from the Atlantic Ocean (Behling 2008). Consequently, those areas have high levels of rainfall resulting in a phytogeographic region with evergreen forests classified as rainforests or tropical ombrophilous forests (Ellenberg & Mueller-Dombois 1966). High rainfall patterns favor the development of many plant species, especially bryophytes and ferns. These species are particularly dependent on high humidity due to their less efficient water regulation system (Brodribb & McAdam 2011; McAdam & Brodribb 2012), and this need for moisture extends to the fertilization process of their life cycles (Page 2002). Additionally, the mountains strongly influence the distribution and diversity of neotropical ferns and lycophytes by promoting high species richness and endemism (Moran 1995), thus contributing to the formation of different plant communities. Compared to the lowlands, the mountains have greater biological diversity and are the main habitats for some of the largest fern genera (Moran 1995). One of the reasons mentioned by researchers to explain species richness in the mountains is the variety of slopes (Moran 1995). Nettesheim *et al.* (2014) showed that significant floristic variation of the ferns and lycophytes within tropical forests can be driven by slopes with different topographic orientations.

Epiphytes are nonparasitic plants that spend most or all their lives on the bodies of other plants (Benzing 1987; Moffett 2000; Zotz 2016). They are among the most conspicuous components of tropical rainforests and form a significant part of their flora; the presence and abundance of epiphytes are often used as a descriptor of ombrophilous forests (Johansson 1974; Zotz 2016). The epiphyte community is recognized as the first to decline when disturbances occur in a fragile ecosystem (Dubuisson *et al.* 2009). Orchidaceae represent approximately 68% of all vascular epiphytes, with almost 21,170 species. Bromeliaceae and Polypodiaceae are the second- and third-most common families, respectively, and they contribute significantly to the high diversity of epiphytes in these forests (Zotz 2013; Zotz *et al.* 2021). However, records from the Atlantic Forest have indicated a unique pattern, with Bromeliaceae containing more representatives than Orchidaceae (Ramos *et al.* 2019). Ferns and lycophytes represent between 36 and 72% of epiphytic diversity in many palaeotropical forests, where they may be more diverse than orchids (Benzing 1990). Zotz (2016) mentioned that vascular epiphytes are particularly prevalent among ferns.

Based on the current classification system (PPG I 2016), two of the three lycophyte families - particularly Lycopodiaceae - and 11 of the 51 fern families have epiphytic species (Smith *et al.* 2006; Rothfels *et al.* 2012). Polypodiaceae, the most derived family among the ferns, is predominantly represented by epiphytes (Schuettpelz & Pryer 2009; Sundue *et al.* 2015; Zotz *et al.* 2021). The first paper to catalog epiphytes in the Parque Nacional (PN) da Serra dos Órgãos was *Flora Organensis* (Rizzini 1954), in which 285 species of ferns and lycophytes were listed. More recently, Engelmann *et al.* (2007) listed the species found in the understory of the eastern part of the park, inventorying 116 species, 47% of which were epiphytes or hemiepiphytes. Although epiphytes are important components of diversity in rainforests, few studies about epiphytism among seedless vascular plants are conducted compared to studies of other components of flora. Furthermore, studies have indicated that ferns and lycophytes can respond to environmental variations, thus revealing some indicator species for these variations (Krömer *et al.* 2005), especially the epiphytic flora (Damasceno 2010, 2015). Indeed, epiphytic ferns have different degrees of habitat specialization according to the vegetation types at different altitudes (Acebey *et al.* 2017).

Although knowledge of ferns and lycophytes in Brazil has improved in recent years (Prado *et al.* 2015), studies that aim to understand the dynamics of tropical forests are still required due to the increasing losses in plant diversity. Endemic species are well-represented in isolated habitats such as mountainous extensions, as tropical mountains are considered biodiversity hotspots for ferns (Kessler 2010). The study of seedless vascular plants is especially important since these groups are sensitive to sudden changes in the environment, making them extremely vulnerable to extinction (Arcand & Ranker 2008). Furthermore, their ability to adapt to various types of disturbances makes seedless vascular plants valuable subjects for conservation and restoration studies (Sharpe *et al.* 2010).

In this study, we aimed to compare the structure of epiphytic communities of ferns and lycophytes from the forest understories in different altitudinal zones and on opposite slopes (relative to the sea) in a section of the Atlantic Forest in southeastern Brazil. We first hypothesized that there is a difference in the community structure of epiphytic ferns and lycophytes at different elevations of the forest understory on both slopes, as altitudinal variation causes environmental changes that affect their distribution. Second, we hypothesized that the community structure of epiphytic ferns and lycophytes differs on the opposite slopes due to their distinct environmental characteristics; plants often found in disturbed areas or urban centers are expected to be found on the drier slope, such as some *Microgramma* species.

Materials and Methods

Study area

PN da Serra dos Órgãos is a Conservation Unit of Integral Protection and is located in the Atlantic Forest of SE Brazil, in Serra do Mar, state of Rio de Janeiro. The vegetation can be classified as dense ombrophilous forests (Veloso *et al.* 1991); it consists of secondary forests in advanced stages of succession, with some primary vegetation areas (Cronemberger & Castro 2007). The park is 200.2 km^2 in area, and its topography is mountainous, ranging between 200 and 2,263 m above sea level. Its climate can be classified as mesothermal, with mild summers and no dry season. It is characterized by abundant rainfall in the winter months and temperatures that decrease with greater altitude (Cronemberger & Castro 2007). The average temperature is 11 °C (significantly lower than the average in the region), reaching lows of around 1 °C in winter or -5 °C in high parts of the mountains. Serra do Mar receives air masses from the ocean and thus has greater precipitation (Viveiros de Castro 2008). The spatial variability of precipitation in that region may be justified by its orographic heterogeneity. In general, the eastern slope has higher precipitation levels (271.4 mm in Teresópolis City in 2013) than the western slope (~219.7 mm in Petrópolis City in 2013) (Ottero *et al.* 2018). In addition, the humidity of the eastern slope is quite high, as it receives less insolation than the western slope, which faces the continent. The western slope consists of secondary forests and some fragmented forest remnants interspersed with agricultural areas and degraded pastures (Viveiros de Castro 2008). The vegetation in the area, according to the Manual of Classification of Brazilian Vegetation (Veloso *et al.* 1991), is divided into three altimetric zones based on the variation between the latitudes of 16º and 24º S: a submontane zone of altitudes between 50 and 500 m, a montane zone between 500 and 1,500 m, and an upper montane zone above this limit.

Sampling

From June 2013 to March 2014, at approximately two-month intervals, we sampled five sites (Fig. 1) between 1,200 and 2,000 m in altitude, at an interval of 200 m in altitude, on each of the eastern and western slopes of the park. Although the park ranges from 200 m to 2,263 m above sea level, the forest areas on the western slope begin at 1,200 m. As a result, we sampled the cited altitudinal gradient. At each site, we implemented four plots of 10 × 10 m per altitude (Nervo *et al.* 2016) and recorded the species richness and respective abundance of ferns and lycophytes on all phorophytes, which are considered the natural sampling units (Giongo & Waechter 2004). Epiphytes found at the basal part (0–2 m high) of the phorophyte's trunk were recorded (Tuomisto & Ruokolainen 1993; Tuomisto *et al.* 2002; Paciencia 2008; Damasceno 2010). The phorophytes' basal part was chosen, as indicated by Kelly (1985), who demonstrated that the lower trunk could serve as a critical area for fern richness in rainforests, where atmospheric humidity and bryophyte cover are apparently highest (ter Steege & Cornelissen 1989). To determine species abundance with clonal growth, the continuity of stolons or long-creeping stems was observed to identify each individual. In some cases, each isolated cluster of fronds on the same phorophyte was considered an individual of a particular species. Very young epiphytic individuals were disregarded since precise identifications could not be made (Kersten & Silva 2001).

All phorophytes containing epiphytic ferns or lycophytes were included, independently of their heights and diameters. In addition to those found on lianas, epiphytes found on dead phorophytes were also considered, provided that they were still erect. However, epiphytes occurring on phorophytes lying on the ground were disregarded, as this sampling was unsuitable for estimating the diversity of the epiphytic communities (Flores-Palacios & Garcia-Franco 2001; Gradstein *et al.* 2003).

For each epiphytic species, we collected and herborized a specimen as a testimonial (SISBIO License Nº 38664-1), according to techniques described for seedless vascular plants in Silva

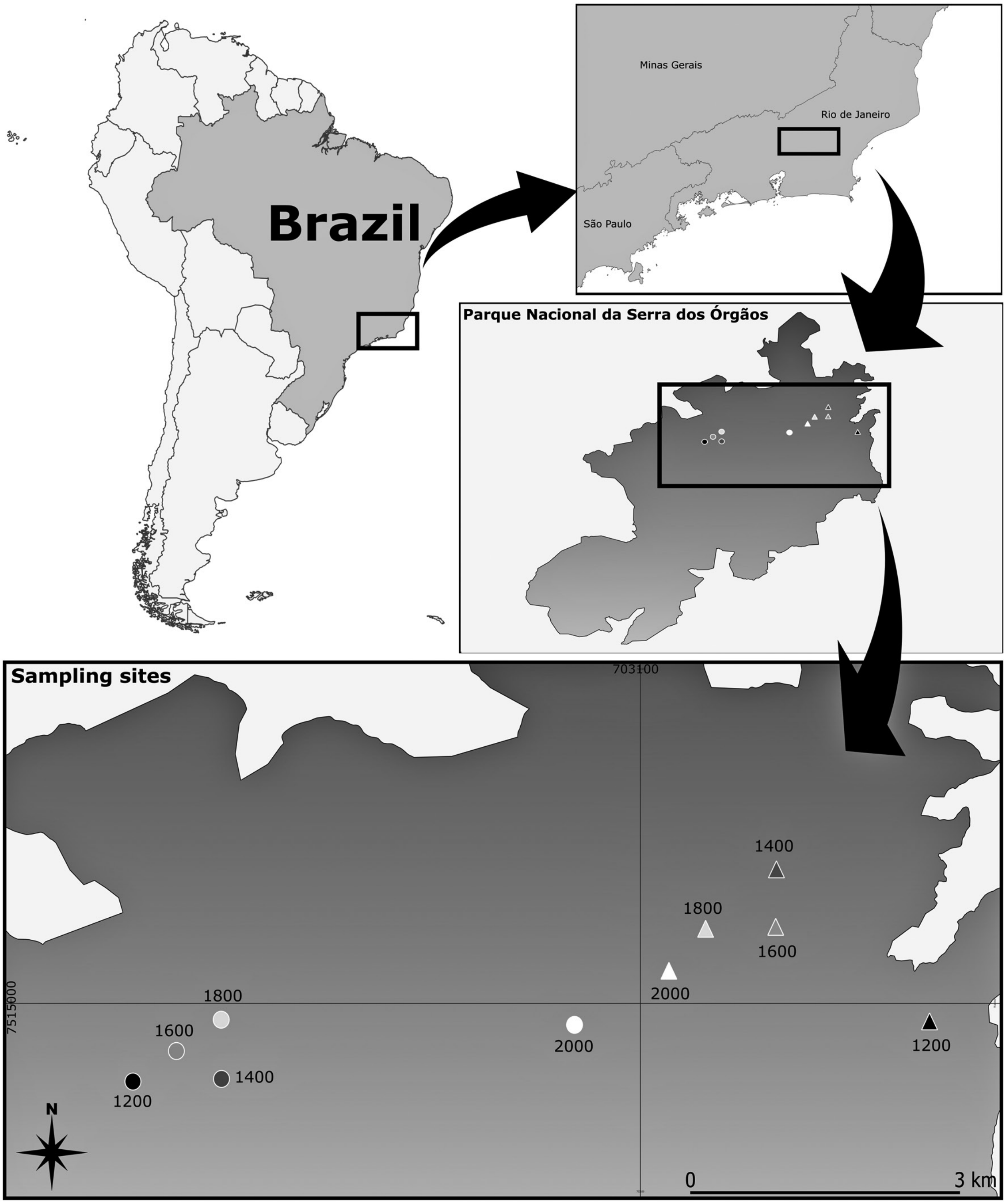

Figure 1 – Sampling sites in the Parque Nacional da Serra dos Órgãos. The eastern and western slopes are marked with triangles and circles, respectively: Cartão Postal Trail (eastern slope 1,200 m), Pedra do Sino Trail (eastern slope 1,400–2,000 m), Morro Açu Trail (western slope 1,200 m), Pico do Glória Trail (western slope 1,400 m), Morro do Cubaio Trail (western slope 1,600–1,800 m), Travessia Trail (western slope 2,000 m).

(1984). We then incorporated these samples into the collections of the Museu Nacional (R Herbarium) of the Universidade Federal do Rio de Janeiro and the Jardim Botânico do Rio de Janeiro (RB Herbarium). The families and genera were identified following the classification system of Smith *et al.* (2006) and the PPG I (2016). The taxa were identified from specific literature for each group and by comparison with specimens from herbaria.

Richness, rarefaction, and species accumulation curve analysis

From the sampling of individuals, the richness of each altitudinal zone was obtained. To compare epiphytic communities, rarefaction curves for each altitudinal zone were prepared from the first-order Chao nonparametric estimator using EstimateS software version 9.1.0 (Colwell 2013). The sufficiency of the sample was tested by making comparisons between rarefaction and species accumulation curves. To test the statistical difference between slopes' richness values, the Student's *t*-test was employed, computed with PAST software version 3.21 (Hammer *et al.* 2001), considering $P < 0.05$ for the significance level.

Abundance, dominance, ecological categories, and indicator species analysis

From individual counts, the abundance by altitudinal zone was obtained. The dominance index was defined as $D = (ni[ni\text{-}1]/N[N\text{-}1])$, where ni is the number of epiphytic individuals in the ith species and N is the total number of individuals. It was calculated using PAST software version 3.21 (Hammer *et al.* 2001). To test the statistical difference between slopes' abundance and dominance values, the Student's *t*-test was employed, considering $P < 0.05$ for the significance level, computed with the same software.

The species were arranged into ecological categories based on their relationships with the phorophytes (Benzing 1990): true epiphyte, facultative epiphyte, accidental epiphyte, or hemiepiphyte. Some climbing ferns, traditionally considered secondary hemiepiphytes, were included in our sampling since they shared the same zone as the epiphytic plants.

To identify the possible indicator species for different altitudinal gradients, the Indicator Species Analysis test (Dufrêne & Legendre 1997) was applied, developed by PC-ORD software version 4.10 (McCune & Mefford 1999). Indicator species were considered to be those with $P \leq 0.05$ and an indicator value (IV) above 25%, as suggested by Dufrêne & Legendre (1997).

Floristic composition analysis

The parameter used for the structural analysis of epiphytic ferns and lycophytes was relative specific abundance ($RA\% = (Ni/\sum Ni) \times 100$), where Ni is the number of epiphytic individuals (Vuono 2002).

A comparison of the floristic composition for both slopes and a pairwise comparison for altitudinal zones within each slope was carried out using principal coordinates analysis (Legendre & Legendre 1998) and the Bray-Curtis dissimilarity method (Bray & Curtis 1957). A significance test with 999 permutations (permutation test for homogeneity of multivariate dispersions) was applied in R software version 3.1.1 (R Core Team 2014).

Results

Richness, rarefaction, and species accumulation curves

A total of 60 ferns and two lycophyte species were found in 23 genera and seven families (Tab. S1, available on supplementary material <https://doi.org/10.6084/m9.figshare.24418327.v1>). The richness values by altitude changed between seven and 22 species. In general, the richest zones were in the montane forest (1,200 m, eastern slope; 1,400 m, western slope) and in the transition to the upper montane forest (1,600 m). The western slope was slightly richer than the eastern slope regarding absolute values, but there was no significant difference (*t*-test: $P = 0.082$). On the western slope, the richness decreased as the altitude increased between 1,400 and 1,800 m. However, on the eastern slope, the richness values did not show an altitudinal pattern (Tab. 1; Fig. 2).

The most important families in the entire data set were Polypodiaceae (22 species), Aspleniaceae and Dryopteridaceae (12 species each), and Hymenophyllaceae (nine species); together, these encompassed 88% of the total species (Fig. 3). Aspleniaceae was the only family on the eastern slope that decreased in richness as altitude increased. Most families did not show a clear altitudinal gradient in the study area.

Table 1 – Richness, abundance, and dominance values for all altitudinal zones on both slopes in the Parque Nacional da Serra dos Órgãos.

Parameters	**Eastern slope altitudes (m)**					**Western slope altitudes (m)**				
	1200	**1400**	**1600**	**1800**	**2000**	**1200**	**1400**	**1600**	**1800**	**2000**
Richness (number of species)	17	7	12	9	10	13	22	17	13	14
Abundance (number of individuals)	271	47	183	310	54	126	150	345	156	100
Dominance index	0.16	0.21	0.41	0.45	0.26	0.11	0.17	0.18	0.14	0.20

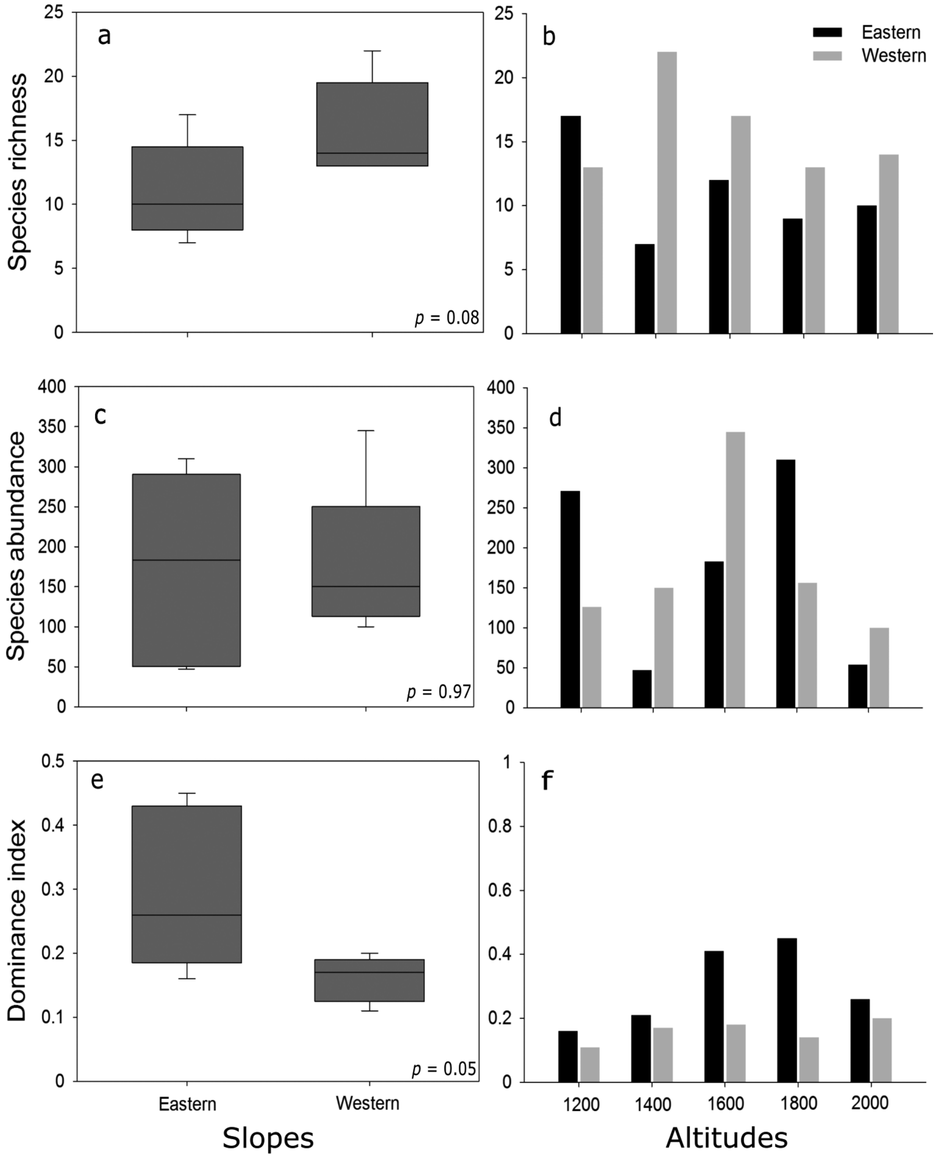

Figure 2 – a-b. Comparison of the species richness on both slopes and at all altitudes in the Parque Nacional da Serra dos Órgãos – a. box plots show global variation on both slopes; b. a clustered column chart shows variation by altitude on both slopes. c-d. Comparison of the species abundance on both slopes and at all altitudes in the PN da Serra dos Órgãos – c. box plots show global variation on both slopes; d. a clustered column chart shows variation by altitude on both slopes. e-f. Comparison of the dominance index on both slopes and at all altitudes in the PN da Serra dos Órgãos – e. box plots show global variation on both slopes; f. a clustered column chart shows variation by altitude on both slopes. The lines inside all the boxes are median values.

Three altitudinal zones on the eastern slope (1,400, 1,600, and 2,000 m) and two on the western slope (1,400 and 2,000 m) showed a clear upward pattern in their rarefaction curves without revealing a trend or starting to stabilize. On the other hand, all the species accumulation curves were totally or partially within the standard deviation bars under the rarefactions (Fig. 4).

Therefore, species richness on the western slope was slightly higher than it was on the eastern slope regarding absolute values, but without a significant difference, and trended to decrease with altitude. Polypodiaceae was the best-represented family on both slopes and had no clear altitudinal gradient. No clear pattern regarding altitude was found in the species richness of the families (except Aspleniaceae on the eastern slope). Most of the rarefaction curves showed upward patterns, with species accumulation curves within the deviation bars.

Abundance, dominance, ecological categories, and indicator species

The abundance by altitude varied between 47 and 345 individuals, with 1,400 m on the eastern slope and 1,600 m on the western slope, respectively, being responsible for these values. There was no significant difference in abundance between the slopes (*t*-test: *P* = 0.973). On the western slope, a unimodal pattern with a peak at 1,600 m was observed, whereas the eastern slope showed no altitudinal pattern. As observed for species richness, both slopes had Polypodiaceae as the most important family, with higher abundance values distributed in the *Pleopeltis*, *Campyloneurum*, *Pecluma*, and *Serpocaulon* genera, in that order.

The dominance index on the eastern slope was significantly higher than on the western slope (*t*-test: *P* = 0.047). The eastern slope showed increasing dominance up to 1,800 m, but no pattern was found on the western slope. The highest dominance values were found at 1,600 and 1,800 m on the eastern slope due to the high abundance of *Pleopeltis pleopeltidis*.

Among ecological categories, facultative epiphytism was better represented in richness and abundance in each area of both slopes (Fig. 5), with individuals distributed in almost all families. The climbing category was the least represented, with *Lomaridium acutum* and *Polybotrya speciosa* occurring only in the montane forest (1,200 and 1,400 m) on both slopes.

The indicator species, based on relative abundance and relative frequency of occurrence in several groups of sites, were six species at four altitudes (except 1,600 m) on the eastern slope and four species at three altitudes (1,400, 1,600 and 2,000 m) on the western slope (Tab. 2). The highest values were indicated for the Polypodiaceae and Hymenophyllaceae families on the eastern and western slopes, respectively.

Floristic composition

On the eastern slope, *Pleopeltis pleopeltidis* (Fig. 6) was the fern with the highest abundance (Tab. 3) and the only one that was distributed in all elevations. In some altitudinal zones, however, other species were more abundant. The most widespread ferns were *Asplenium raddianum*, *Asplenium scandicinum*, *Campyloneurum nitidum*, *Hymenophyllum polyanthos*, and *Pleopeltis macrocarpa*, each occurring in at least three zones.

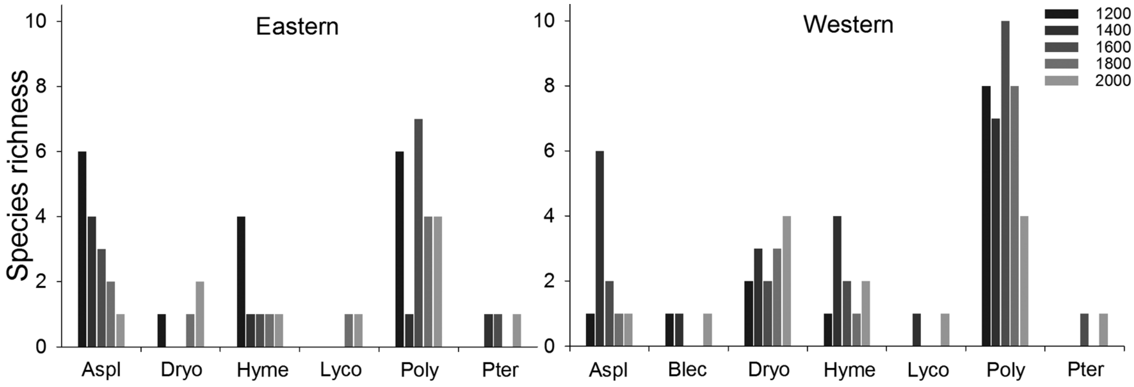

Figure 3 – Comparison of the species richness (by family) from both slopes and at all altitudes in the Parque Nacional da Serra dos Órgãos: Aspl = Aspleniaceae; Blec = Blechnaceae; Dryo = Dryopteridaceae; Hyme = Hymenophyllaceae; Lyco = Lycopodiaceae; Poly = Polypodiaceae; Pter = Pteridaceae.

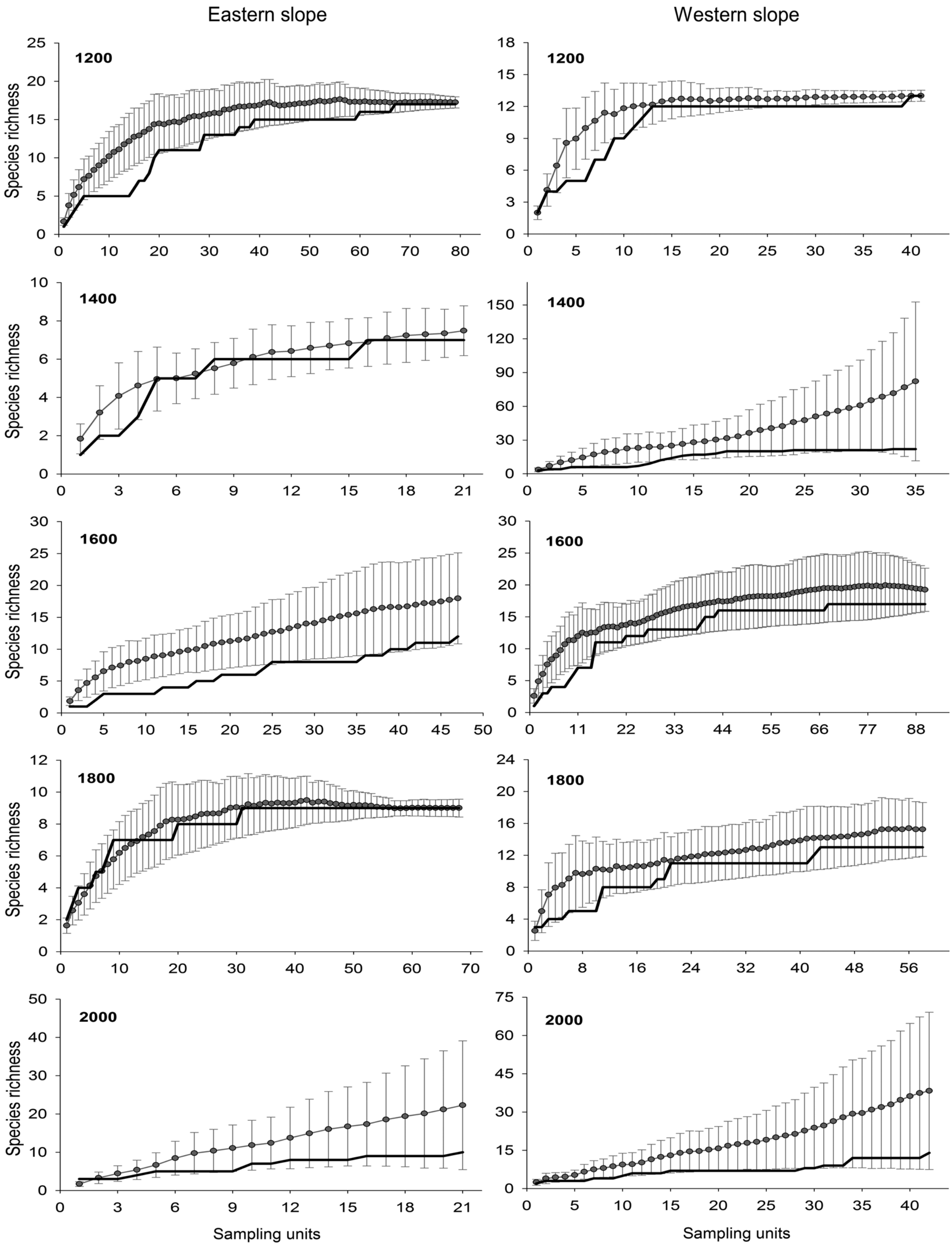

Figure 4 – Rarefaction and species-accumulation curves for epiphytic pteridophytes in the Parque Nacional da Serra dos Órgãos. Comparison between rarefaction (gray) and species accumulation curves (black) organized by altitudinal zones and slopes. The vertical bars are standard deviations.

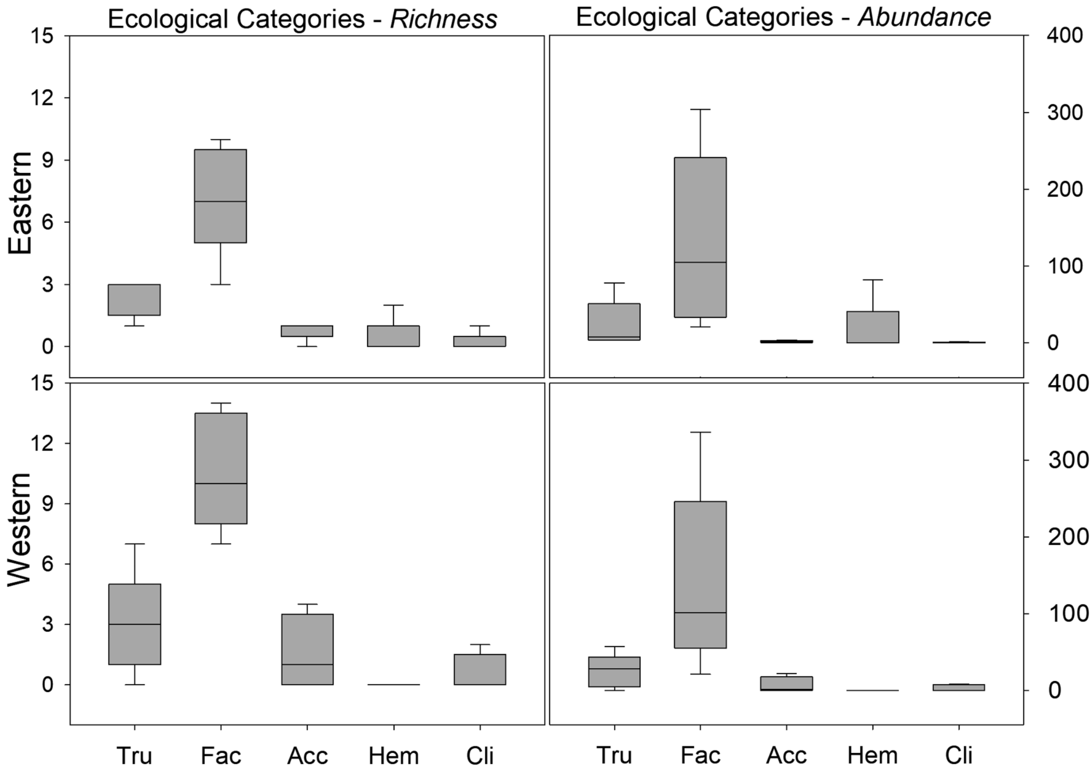

Figure 5 – Ecological categories of epiphytic pteridophytes in the Parque Nacional da Serra dos Órgãos. Box plot of the species richness and abundance variation for each ecological category on both slopes. Ecological categories: Tru = true; Fac = facultative; Acc = accidental; Hem = hemiepiphyte; Cli = climbing.

Of the 34 total species, 61% occurred only in a given altitudinal zone. They were representatives of almost all the inventoried families (Lycopodiaceae being the exception).

On the western slope, *Pleopeltis macrocarpa* (Fig. 7) was the most abundant species (Tab. 4). However, in some altitudinal zones, other species were more abundant. No species occurred at

Table 2 – Epiphytic ferns identified as indicator species in the Parque Nacional da Serra dos Órgãos, listed with their respective indicator values (IVs), organized by altitudinal zones and slopes. The significance level (*P*-value) is equal to 0.001.

Altitudes (m)	Eastern slope		Western slope	
	Species	**IV**	**Species**	**IV**
1,200	*Campyloneurum herbaceum*	51.9	no indicator species	-
	Polyphlebium angustatum	29.1		
1,400	*Asplenium oligophyllum*	49.6	*Campyloneurum nitidum*	48.9
	Asplenium scandicinum	30.6		
1,600	no indicator species	-	*Pleopeltis macrocarpa*	31.0
1,800	*Pleopeltis pleopeltidis*	42.0	no indicator species	-
2,000	*Serpocaulon catharinae*	77.0	*Hymenophyllum magellanicum*	73.8
			Elaphoglossum hirtipes	40.5

Figure 6 – a-h. Examples of epiphytic pteridophytes occurring in the Parque Nacional da Serra dos Órgãos (eastern slope) – a. *Pleopeltis pleopeltidis*; b. *Campyloneurum herbaceum*; c. *Serpocaulon catharinae*; d. *Asplenium oligophyllum*; e. *Campyloneurum nitidum*; f. *Asplenium auritum*; g. *Hymenophyllum polyanthos*; h. *Phlegmariurus biformis*. Photo credit: T.V. Costa.

Table 3 – Phytosociological parameters in decreasing order of abundance value for epiphytic pteridophytes found in the Parque Nacional da Serra dos Órgãos (eastern slope) – *Ni* = number of individuals (or abundance); *Ui* = number of sampling units where species occurred (phorophytes); RA (%) = relative abundance; AF (%) = absolute frequency; RF (%) = relative frequency.

Species	*Ni*	*Ui*	RA (%)	AF	RF (%)
Pleopeltis pleopeltidis	321	95	37.1	40.3	26.2
Campyloneurum nitidum	105	28	12.1	11.9	7.7
Campyloneurum herbaceum	71	41	8.2	17.4	11.3
Pecluma truncorum	56	10	6.5	4.2	2.8
Lellingeria brevistipes	47	2	5.4	0.8	0.6
Serpocaulon catharinae	28	20	3.2	8.5	5.5
Polyphlebium angustatum	25	23	2.9	9.7	6.3
Asplenium oligophyllum	22	17	2.5	7.2	4.7
Asplenium scandicinum	21	15	2.4	6.4	4.1
Pleopeltis macrocarpa	16	11	1.8	4.7	3.0
Asplenium auritum	16	5	1.8	2.1	1.4
Asplenium auriculatum	15	7	1.7	3.0	1.9
Pecluma pectinatiformis	12	11	1.4	4.7	3.0
Pleopeltis hirsutissima	12	10	1.4	4.2	2.8
Polyphlebium pyxidiferum	12	4	1.4	1.7	1.1
Vandenboschia radicans	11	10	1.3	4.2	2.8
Elaphoglossum sellowianum	9	4	1.0	1.7	1.1
Campyloneurum aglaolepis	8	3	0.9	1.3	0.8
Asplenium raddianum	7	6	0.8	2.5	1.7
Didymoglossum reptans	7	5	0.8	2.1	1.4
Vittaria lineata	7	4	0.8	1.7	1.1
Asplenium claussenii	5	5	0.6	2.1	1.4
Asplenium harpeodes	5	5	0.6	2.1	1.4
Hymenophyllum polyanthos	5	5	0.6	2.1	1.4
Phlegmariurus biformis	5	4	0.6	1.7	1.1
Polytaenium lineatum	5	1	0.6	0.4	0.3
Asplenium mourai	2	2	0.2	0.8	0.6
Elaphoglossum organense	2	2	0.2	0.8	0.6
Hymenophyllum hirsutum	2	2	0.2	0.8	0.6
Polybotrya speciosa	2	2	0.2	0.8	0.6
Alansmia reclinata	1	1	0.1	0.4	0.3
Elaphoglossum itatiayense	1	1	0.1	0.4	0.3
Pecluma recurvata	1	1	0.1	0.4	0.3
Pleopeltis pleopeltifolia	1	1	0.1	0.4	0.3
Total	**865**	**236**	**100**	**153.8**	**100**

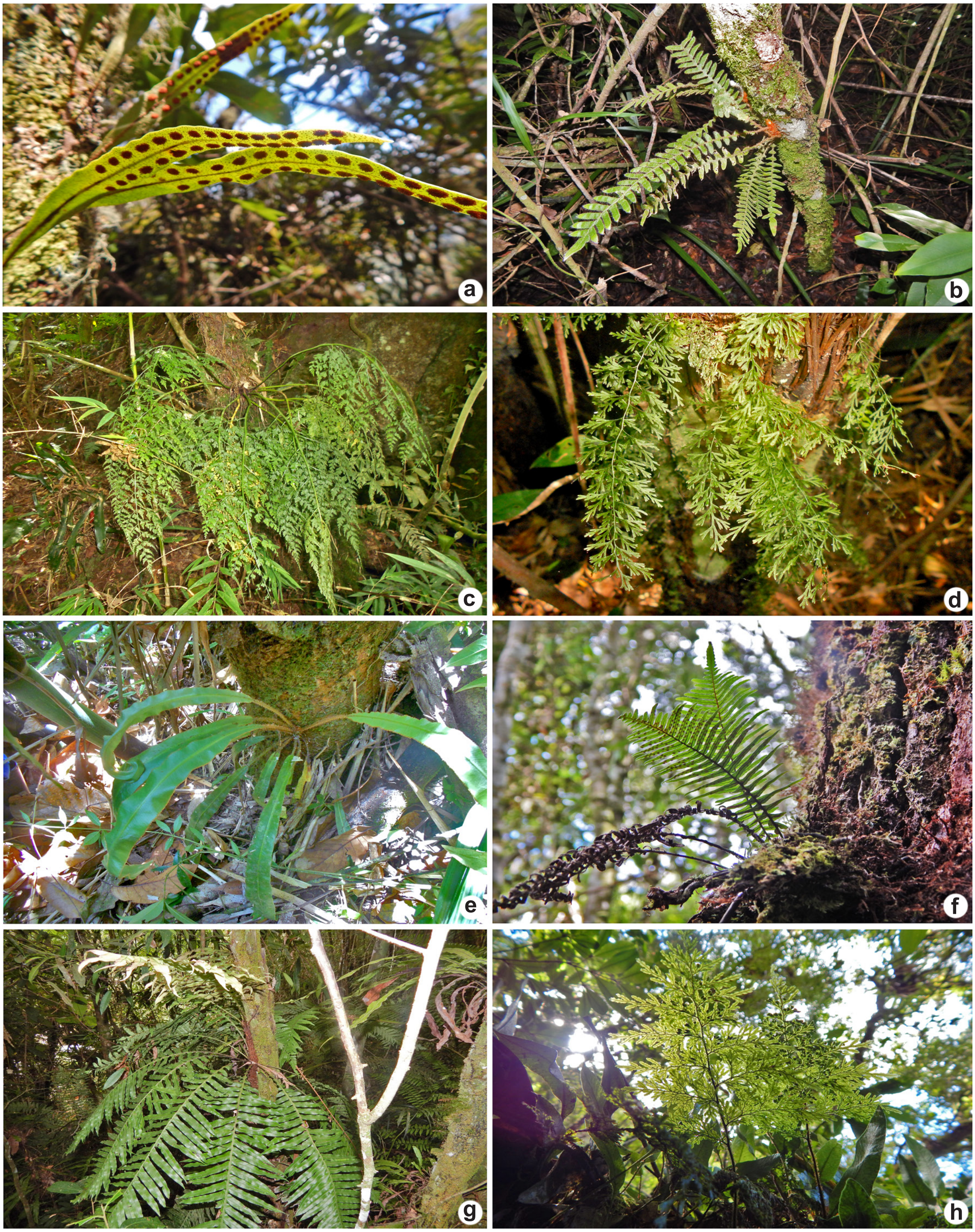

Figure 7 – a-h. Examples of epiphytic pteridophytes occurring in the Parque Nacional da Serra dos Órgãos (western slope) – a. *Pleopeltis macrocarpa*; b. *Pleopeltis hirsutissima*; c. *Asplenium scandicinum*; d. *Polyphlebium angustatum*; e. *Elaphoglossum glaziovii*; f. *Pecluma sicca*; g. *Lomaridium acutum*; h. *Hymenophyllum magellanicum*. Photo credit: T.V. Costa.

Table 4 – Phytosociological parameters in decreasing order of abundance value for epiphytic pteridophytes found in the Parque Nacional da Serra dos Órgãos (western slope) – *Ni* = number of individuals (or abundance); *Ui* = number of sampling units where species occurred (phorophytes); RA (%) = relative abundance; AF (%) = absolute frequency; RF (%) = relative frequency.

Species	***Ni***	***Ui***	**RA (%)**	**AF**	**RF (%)**
Pleopeltis macrocarpa	146	57	16.6	21.4	11.5
Pleopeltis hirsutissima	94	52	10.7	19.5	11.5
Campyloneurum nitidum	79	45	9.0	16.9	9.1
Pecluma truncorum	69	31	7.9	11.7	6.3
Serpocaulon catharinae	54	33	6.2	12.4	6.7
Pecluma pectinatiformis	37	25	4.2	9.4	5.0
Hymenophyllum magellanicum	35	31	4.0	11.7	6.3
Elaphoglossum sellowianum	35	23	4.0	8.6	4.6
Asplenium auritum	30	4	3.4	1.5	0.8
Elaphoglossum vagans	29	18	3.3	6.8	3.6
Elaphoglossum longifolium	26	13	3.0	4.9	2.6
Elaphoglossum hirtipes	19	17	2.2	6.4	3.4
Cochlidium punctatum	17	8	1.9	3.0	1.6
Leucotrichum organense	17	3	1.9	1.1	0.6
Polyphlebium angustatum	16	13	1.8	4.9	2.6
Asplenium jucundum	15	10	1.7	3.8	2.0
Lomaridium acutum	14	12	1.6	4.5	2.4
Asplenium auriculatum	13	2	1.5	0.8	0.4
Microgramma squamulosa	12	11	1.4	4.1	2.2
Elaphoglossum edwallii	11	10	1.3	3.8	2.0
Hymenophyllum polyanthos	11	8	1.3	3.0	1.6
Serpocaulon latipes	11	6	1.3	2.3	1.2
Hymenophyllum caudiculatum	8	6	0.9	2.3	1.2
Didymoglossum reptans	7	5	0.8	1.9	1.0
Vittaria graminifolia	7	4	0.8	1.5	0.8
Vittaria lineata	7	3	0.8	1.1	0.6
Asplenium harpeodes	6	6	0.7	2.3	1.2
Asplenium scandicinum	6	5	0.7	1.9	1.0
Campyloneurum austrobrasilianum	6	4	0.7	1.5	0.8
Pleopeltis pleopeltidis	5	5	0.6	1.9	1.0
Pecluma recurvata	5	4	0.6	1.5	0.8
Elaphoglossum glaziovii	5	3	0.6	1.1	0.6
Melpomene cf. *xiphopteroides*	5	1	0.6	0.4	0.2
Hymenophyllum hirsutum	3	3	0.3	1.1	0.6
Melpomene pilosissima	3	2	0.3	0.8	0.4

Species	*Ni*	*Ui*	RA (%)	AF	RF (%)
Elaphoglossum erinaceum	2	1	0.2	0.4	0.2
Asplenium incurvatum	1	1	0.1	0.4	0.2
Asplenium serra	1	1	0.1	0.4	0.2
Asplenium uniseriale	1	1	0.1	0.4	0.2
Parablechnum cordatum	1	1	0.1	0.4	0.2
Campyloneurum decurrens	1	1	0.1	0.4	0.2
Elaphoglossum beaurepairei	1	1	0.1	0.4	0.2
Hymenophyllum asplenioides	1	1	0.1	0.4	0.2
Pecluma sicca	1	1	0.1	0.4	0.2
Phlegmariurus biformis	1	1	0.1	0.4	0.2
Phlegmariurus hexastichus	1	1	0.1	0.4	0.2
Polybotrya speciosa	1	1	0.1	0.4	0.2
Polystichum auritum	1	1	0.1	0.4	0.2
Total	**877**	**266**	**100**	**186**	**100**

all elevations. The most widespread ferns were *Pecluma pectinatiformis*, *P. truncorum*, and *Pleopeltis hirsutissima*, although none existed at 2,000 m. Of the 48 total species, 58% occurred only in one altitudinal zone, and these species represented all the inventoried families.

The principal coordinates analysis indicated a significant separation of the two slopes according to floristic composition (F = 12.80; FD = 1; permutations = 999; *P* = 0.001), although there was some overlap (Fig. 8). Within each slope, differences in species composition at some altitudes were also significant (Tab. 5). On the eastern slope, the 2,000-m zone differed from the 1,200- and 1,800-m zones; the latter differed from all other zones. On the western slope, the 2,000-m zone differed from the 1,200-, 1,600-, and 1,800-m zones; the 1,400-m zone differed from the 1,200- and 1,800-m zones.

Discussion

Diversity of epiphytic ferns and lycophytes at different elevations

Our results allow us to recognize differences in the species richness and abundance of epiphytic ferns and lycophytes in a forest understory at various elevations. The floristic survey confirmed that the richest altitudes were in the montane forest. However, on the western slope, the 1,200-m elevation had a lower species richness than the other altitudes. This could indicate that this area may be subject to anthropogenic pressure, as it is widely visited by tourists (according to fieldwork observations). Furthermore, on the eastern slope, the lower richness at 1,400 m than at other altitudes indicates environmental changes since this area presented great clearings due to the felling of trees. In recent decades, composition studies in relation to altitudinal variation have shown peaks of species richness at intermediate elevations (Krömer *et al.* 2005; Cardelús *et al.* 2006; Grytnes *et al.* 2006). This well-documented pattern applies to several groups of organisms in nature (Rahbek 1995), including ferns and lycophytes (Kessler *et al.* 2001; Kluge *et al.* 2006; Watkins *et al.* 2006; Paciencia 2008). The general trend is that epiphytes are better represented in cloud forests and at intermediate elevations (Gentry & Dodson 1987; Zotz 2016). Our data align with this trend. Although the gradient is only partially sampled (on the western slope, the forest begins above 1,200 m), elevations in the montane forest (1,200–1,400 m) showed higher species richness compared to those in the upper montane forest (1,600–2,000 m). We also found higher species richness on the western slope than on the eastern slope, which can be explained by the variability of habitats on the first slope (Kluge & Kessler 2011). Despite the western slope having more extensive fragmented areas degraded by historical human occupation and being located in a dryer area, there is dense vegetation associated with watercourses, which ensures shading and mild temperatures for the understory species (according to unpublished data).

Studies have shown Polypodiaceae, Aspleniaceae, Dryopteridaceae, and Hymenophyllaceae to be the richest epiphytic pteridophyte flora in rainforests (Damasceno 2015; Nervo *et al.* 2016; Costa *et al.* 2017). Our data showed Polypodiaceae to be the main family along the altitudinal gradient on both slopes. Several studies have also identified Polypodiaceae as one of the most numerous families in the world, particularly among the neotropical epiphytic flora (Madison 1977; Gentry & Dodson 1987;

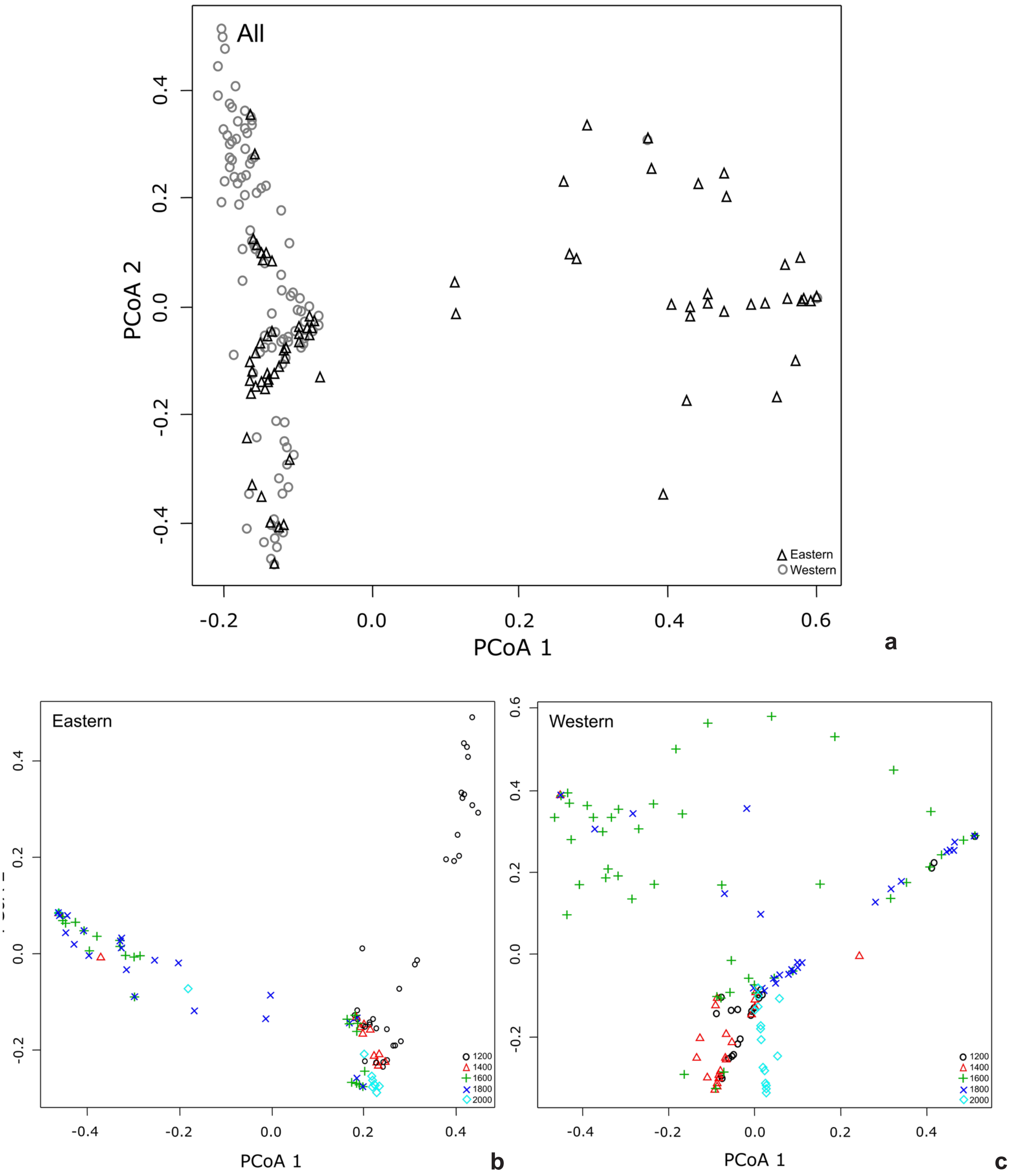

Figure 8 – a-c. Floristic composition layout of epiphytic pteridophytes on both slopes in the Parque Nacional (PN) da Serra dos Órgãos, as generated from a principal coordinates analysis – a. both slopes; b. eastern slope; c. western slope.

Table 5 – Pairwise comparison of floristic composition on each slope. Altitudinal zones on the eastern and western slopes are shown in the upper right and lower left part, respectively. Significant P-values ($P < 0.05$) are in bold.

Altitudes (m)	1,200	1,400	1,600	1,800	2,000
1,200		0.577	0.120	**0.001**	**0.023**
1,400	**0.006**		0.580	**0.001**	0.214
1,600	0.070	0.069		**0.001**	0.234
1,800	0.082	**0.032**	0.515		**0.049**
2,000	**0.002**	0.148	**0.001**	**0.002**	

Kersten & Silva 2001; Ramos *et al.* 2019). This finding has also been reported for the studied region (Engelmann *et al.* 2007) and for other regions in the Atlantic Forest, such as the Reserva Ecológica de Macaé de Cima (Fontoura *et al.* 1997), PN do Itatiaia (Damasceno 2010), and Estação Ecológica Estadual do Paraíso (Jascone 2010). In this study, there was little variation in the taxonomic diversity of families along altitudinal zones, and no clear pattern was found on either slope (except for among Aspleniaceae on the eastern slope). Gentry & Dodson (1987) reported similar findings along an altitudinal gradient for epiphytic flora in the neotropical region. Sundue *et al.* (2015) proposed that the epiphytic richness of some groups in tropical forests (particularly some Polypodiaceae, *Elaphoglossum*, and Hymenophyllaceae species containing green spores) can be linked to ecological convergence and rapid diversification.

Estimates of community richness are important in revealing the potential biodiversity of a given region. The rarefaction curves are used to estimate richness and compare communities; they are related to species accumulation curves (Magurran 2004), which may help verify the sampling effort. Upward species accumulation curves with unlikely stabilization are expected in flora-rich regions, such as tropical forests (Paciencia 2008). As expected, our data supported this statement since most altitudinal zones did not have stabilized rarefactions. The comparison between the rarefaction and accumulation curves in this study showed a satisfactory sampling effort for most altitudinal zones, as the species accumulation curves were within the estimated deviations from the rarefaction, indicating that an increased sampling effort would not result in a significant increase in new records.

Floristic composition along the altitudinal gradient and opposite slopes

Our results showed a different floristic composition for the epiphytic ferns and lycophytes on opposite slopes. The principal coordinates analysis confirmed that these differences, both between the slopes and among some altitudes, were mainly linked to environmental differences. The eastern slope receives air masses from the ocean and thus has greater precipitation than the western slope (Ottero *et al.* 2018). The humidity of this region is greater since it receives lower insolation than the western slope, which faces the continent. Our fieldwork observations allowed us to identify a higher spatial variation in the microclimatic and habitat conditions on the western slope than on the eastern one; this potentially supports greater species richness and abundance on the western slope. Acebey *et al.* (2017) also discussed the role of different microhabitats in determining the high diversity of epiphytes and cited that the degree of habitat specialization of ferns varies with changes in humidity and vegetation structure provided by the elevational gradient. In this study, the most abundant species differed, with *Pleopeltis pleopeltidis* on the eastern slope and *Pleopeltis macrocarpa* on the western slope. Both belong to the most important ecological category (facultative epiphytes) and are identified as indicator species. Furthermore, the cluster analysis indicated that the highest similarity was between 1,600 and 1,800 m in the upper montane forest. Studies comparing ferns and lycophyte flora in rainforests have revealed differences in floristic composition among different regions (Kessler *et al.* 2001) and between opposite slopes in the same region (Netteshein *et al.* 2014). Our results revealed a similar pattern. The differences in floristic composition can be explained by the higher dominance seen in the 1,600- and 1,800-m zones of the eastern slope, which caused the separation of the samples from those of the western slope. The distribution of abundances at these two altitudes was so peculiar that it not only separated the floristic composition of the opposite slopes but also grouped these two altitudes for each slope. In cluster analyses, some authors consider high floristic similarity values to be those above 30% (Borgo & Silva 2003). Overall, our data showed three clusters that had higher values than this threshold. These affinities may have resulted from environmental similarities in vegetation size, humidity, light, and ventilation, all of which exert influence on species distribution and abundance. On the western slope, montane forest zones were associated with watercourses, with taller trees protecting the understory (according to fieldwork observations). The upper montane forest zones, outside of the one at 2,000 m, had shorter and more slender phorophytes, as their constant ventilation brought moisture from rainfall and often generated cloudiness. Despite having preserved forest characteristics, the 2,000-m zone had many species that were uncommon in the overall floristic composition of the western slope. This might be the reason for the difference between this altitude and the others. The eastern slope revealed similarity only among the 1,600- and 1,800-m zones, which had similar environmental characteristics and high *Pleopeltis pleopeltidis* and *Campyloneurum nitidum* abundances. These facultative epiphytes, along with *Pleopeltis macrocarpa*, were extremely abundant, likely due to their greater ecological plasticity and competitive abilities, as these plants can grow on the trunks and large branches of trees, occasionally on fallen trunks and branches, among rocks, and even in clearings or disturbed forests at different altitudes (Tryon & Tryon 1982). Indeed, varying competitive abilities may explain regional and local abundances (Rünk *et al.* 2004). Furthermore, those species were revealed to be indicator species, as were some Aspleniaceae and Hymenophyllaceae species. The occurrence of indicator species at specific altitudes may not only suggest that these environments provide ideal conditions for the species' establishment but may also characterize unique locations, reflecting certain environmental characteristics in accordance with their presence (Damasceno 2010). Some dryer and more disturbed places on the western slope exhibit *Pleopeltis macrocarpa* predominance; this epiphytic fern has simple leaves, a characteristic that represents an adaptation to growth in dry habitats (Sundue *et al.* 2015).

In this study, we demonstrated that there are differences in the community structure of epiphytic ferns and lycophytes in the forest understory due to altitudinal variation and slope orientation, thereby confirming our hypotheses. In addition, our data are consistent with some assembly rule approaches, especially those related to the number of niches and environmental conditions (Götzenberger *et al.* 2012). Elevational gradients and slope orientation promote habitat changes and generate different ecological niches that act as environmental filters and affect species distribution. Thus, montane vegetation areas tend to be richer than other areas, and the number of species decreases as the elevation increases. In addition, a slope's orientation relative to the sea directly affects its diversity indexes due to the strong influence that orientation exerts on the distribution of humidity in the Atlantic Forest. This fact, associated with historical factors such as human occupation and deforestation (so that the soil can be used in agriculture), further accentuates the environmental differences between the slopes and culminates in differences in floristic composition within these regions.

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Data availability statement

In accordance with Open Science communication practices, the authors inform that all data are available within the manuscript.

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