UNIVERSIDADE ESTADUAL PAULISTA
"JÚLIO DE MESQUITA FILHO"
INSTITUTO DE BIOCIÊNCIAS – RIO CLARO

PROGRAMA DE PÓS-GRADUAÇÃO EM CIENCIAS BIOLOGICAS
(BIOLOGIA VEGETAL)

META-ANÁLISE FITOGEOGRÁFICA DAS EPÍFITAS VASCULARES NA REGIÃO NEOTROPICAL E O EFEITO DA ALTITUDE NA DIVERSIDADE E COMPOSIÇÃO: UM ESTUDO DE CASO NO SUDESTE DO BRASIL

GABRIEL MENDES MARCUSSO

Rio Claro – SP
Maio de 2021

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Orientador: Prof. Dr. Julio Antonio Lombardi
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Tese apresentada ao Instituto de Biociências do Câmpus de Rio Claro, Universidade Estadual Paulista, como parte dos requisitos para obtenção do título de Doutor em Ciências Biológicas (Biologia Vegetal).

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“O fator fundamental foi que o botânico à procura de plantas e o oficial da marinha à procura de colônias tinham uma mentalidade similar. Ambos, o cientista e o conquistador, começaram admitindo sua ignorância – ambos disseram: “Eu não sei o que existe lá”. Ambos se sentiram compelidos a sair e fazer novas descobertas. E ambos esperaram que o novo conhecimento adquirido os tornasse senhores do mundo.”

Yuval Harari em Sapiens – Uma breve história da humanidade

RESUMO GERAL

A congruência nos padrões de distribuição das espécies tem sido uma das principais ferramentas utilizadas para a classificação das entidades biogeográficas, servindo como fontes de evidência para auxiliar na compreensão nas histórias das biotas assim como gerar subsídios para conservação. As epífitas vasculares são um grupo de plantas que respondem de maneira muito eficaz às alterações ambientais, principalmente climáticas. Alguns estudos têm utilizado essa sinúsia como modelo para classificações biogeográficas, no entanto, diversas lacunas ainda restam. Nesse sentido, tivemos como objetivos explorar os padrões de distribuição das epífitas vasculares em duas escalas: uma continental (Região Neotropical) e uma regional (ao longo de um gradiente altitudinal na região serrana do Espírito Santo, Sudeste do Brasil). Para isso a tese foi dividida em cinco capítulos. No primeiro foi explorado os padrões de distribuição das epífitas vasculares na Região Neotropical com base em levantamentos exclusivos dessa sinúsia até 2017, gerando a compilação de 173 listagens oriundas de 14 países, correspondendo a 14,636 registros identificados, pertencendo a 3,849 espécies. Estes dados permitiram demonstrar alguns padrões mais amplos para localidades com poucos estudos (e.g. Amazônia), no entanto em áreas com mais publicações, como o leste do Brasil, padrões mais refinados foram encontrados, corroborando classificações biogeográficas propostas para a localidade. Ademais, fatores climáticos auxiliaram na explicação desses padrões. O segundo, terceiro e quarto capítulos compreendem os levantamentos baseados em coletas e dados de herbários das epífitas vasculares em três Unidades de Conservação do Espírito Santo, Sudeste do Brasil. Nesses estudos registrou-se uma das maiores riquezas de epífitas vasculares para o Brasil, assim como para a Região Neotropical, corroborando o destacado papel que o estado possui para a diversidade da Floresta Atlântica. Além disso, sete novos registros para o Espírito Santo foram feitos, demonstrando que a diversidade do estado ainda se encontra subestimada. Por fim, o quinto capítulo compara a diversidade das epífitas vasculares nas três áreas estudadas nos capítulos anteriores (2, 3 e 4), abordando a riqueza, composição, diversidade beta e distinção taxonômica ao longo do gradiente. Esta comparação demonstrou que a localidade situada em

altitudes intermediárias possui a maior riqueza de espécies, no entanto, a diversidade filogenética é alta em todas as altitudes. Além disso, demonstrou a importância das áreas em elevadas altitudes para a contribuição na substituição de espécies, destacando sobretudo a importância da conservação dessas áreas. Tais resultados são consequência do histórico biogeográfico da região, sobretudo as oscilações climáticas do Pleistoceno, e mantidos pela distribuição das condições climáticas atuais.

Palavras-chave: Biogeografia, Espírito Santo, gradiente, montanhas, padrão de distribuição.

ABSTRACT

The congruence in the patterns of species' distribution has been one of the main tools used for the classification of biogeographic entities, serving as sources of evidence to understanding the histories of the biotas as well as generating subsidies for conservation. Vascular epiphytes comprise a group of plants that respond very effectively to environmental changes, especially climatic. Some studies have used this synusia as a model for biogeographic classifications, however, several gaps remain. In this sense, we aimed to explore the distributional patterns of vascular epiphytes in two levels: continental (Neotropical Region, NR) and local (along an altitudinal gradient in the mountainous region of Espírito Santo, Southeast Brazil). For this, the thesis was divided into five chapters. In the first, the distributional patterns of vascular epiphytes in the NR were explored based on exclusive surveys carried out with the synusia until 2017, generating the compilation of 173 listings from 14 countries, corresponding to 14,636 identified records, belonging to 3,849 species. These data allow us to demonstrate some broader patterns for locations with few studies (e.g. Amazonia), however in areas with more publications, such as eastern Brazil, more refined patterns were found, corroborating the proposed biogeographic classifications. In addition, climatic factors helped to explain these patterns. The second, third and fourth chapters comprise surveys based on collections and data from herbariums of vascular epiphytes in three Conservation Units in Espírito Santo, Southeastern Brazil. In these studies, one of the greatest riches of vascular epiphytes was registered for Brazil, as well as for the Neotropical region, corroborating the outstanding role that the state has for the diversity of the Atlantic Forest. In addition, seven new records for Espírito Santo were made, demonstrating that the diversity of the state is underestimated. Finally, the fifth chapter compares the diversity of vascular epiphytes in the three areas studied in the previous chapters (2, 3 and 4), exploring the changes in the richness, composition, beta diversity and taxonomic distinction along the gradient. This comparison showed that the sites located at intermediate altitudes has the highest species richness, however, the phylogenetic diversity is high at all altitudes. In addition, it demonstrated the importance of areas at high altitudes for

the contribution in the replacement of species, highlighting the importance of the conservation of these areas, even with a small number of species. Such results as consequence of the biogeographical history of the region, especially the climatic fluctuations of the Pleistocene, are discussed in the text.

Keywords: Biogeography, Espírito Santo, gradient, mountains, distribution pattern.

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INTRODUÇÃO GERAL

Em todo o mundo, cerca de 28 mil espécies, ou 9% da flora vascular, são epífitas (Zotz 2013), ou seja, plantas que germinam sobre outras plantas vivas (forófitos) e as utilizam como suporte, sem parasitá-las, passando a vida sem estabelecer contato com o solo ou estabelecendo-o em parte de seu ciclo (hemiepífitas) (Benzing 1990; Zotz 2013). As famílias com maior número de representantes dessa forma de vida são: Orchidaceae, Bromeliaceae, Araceae e Polypodiaceae, concentrando grande maioria das espécies epifíticas (Küper et al. 2004; Zotz 2013). E é na Região Neotropical que a maior diversidade de espécies ocorre (Gentry and Dodson 1987; Zotz 2016).

Compreender os padrões de distribuição e diversidade dos organismos, assim como os fatores determinantes, constitui uma das principais questões da biogeografia. Para tal objetivo, estudos florísticos ou *checklists* constituem fontes de dados essenciais (e.g. Cantídio and Souza 2019). Entretanto, grande parte do conhecimento disponível sobre o tema contemplou somente a flora arbórea (Oliveira-Filho and Fontes 2000; Santos et al. 2007; Silva-Souza and Souza 2020), em detrimento de outros hábitos, como o das epífitas vasculares, mesmo com a elevada riqueza florística que estas apresentam nas regiões tropicais (Gentry and Dodson 1987; Kreft et al. 2004; Freitas et al. 2016). Além disso, pelas condições ecológicas que vive, essa sinúsia tem demonstrado responder de maneira mais direta aos fatores ambientais como temperatura e umidade (Kessler 2001; Kreft et al. 2004; Ding et al. 2016; Furtado & Menini Neto 2021), tornando-a de grande relevância para o estudo de determinados padrões (Kessler 2001).

O atual estado do conhecimento florístico, apesar de aquém do necessário, já nos permite a análise e apreciação de um bem estruturado corpo de conhecimento sobre os padrões fitogeográficos na Região Neotropical. Por outro lado, aliado à formação dessa base de conhecimentos, ampliar estudos locais são de enorme relevância, sobretudo em localidades com lacunas de conhecimento, o que permitirá tornar mais robusto e corroborar o conhecimento atual, assim como trazer novas informações. Desse modo, esse projeto tem como objetivo contribuir com o conhecimento sobre a composição e fitogeografia das epífitas vasculares em duas escalas: a nível continental (Região Neotropical) e local (na região serrana do estado do Espírito Santo, Sudeste do Brasil).

No capítulo 1 apresentamos uma síntese fitogeográfica das epífitas vasculares na Região Neotropical, buscando, especificamente: a) Investigar as relações florísticas das epífitas vasculares nas diferentes províncias fitogeográficas da Região; b) Associar os

padrões observados atualmente com os fatores climáticos, que são preponderantes para essa sinúsia. A compilação dos dados se revelou bastante útil na busca dos padrões fitogeográficos, sendo possível associá-los com alguns fatores climáticos cruciais para a distribuição das epífitas vasculares. Ademais, essa compilação serve como subsídio para demonstrar onde novos levantamentos devem ser priorizados, tendo em vista enormes lacunas que existem e a elevada diversidade e heterogeneidade da biota da Região Neotropical.

Em uma escala menor, buscamos explorar a diversidade e distribuição das epífitas vasculares em uma região mega diversa, a Floresta Atlântica, que apesar da elevada riqueza de espécies e ser considerada uma das áreas mais bem estudadas do Brasil (Marques et al. 2021), 19% das espécies de epífitas são conhecidos por apenas uma coleta e 59 % possuem menos de 10 coletas (Ramos et al. 2019), tornando-se imprescindível o aumento das buscas ativas em campo. Gerar e documentar dados e coleções de biodiversidade, assim como seu uso ou conservação correspondem às demandas da sociedade sobre taxonomia, conforme articulado na Convenção sobre Diversidade Biológica (MMA 2000). No Espírito Santo somente cerca de 7% a 10,5% da vegetação original ainda existe (SOS Mata Atlântica & INPE 2019), e desses, apenas 4% correspondem à Unidades de Conservação, sendo 77% destas de proteção integral (MMA 2019; Rosa et al. 2019). As Unidades de Conservação (UC) têm como uma das funções conservar a diversidade biológica nesses territórios delimitados, no entanto, pouco se sabe o que de fato ocorre nas UCs (e.g. Colli-Silva et al. 2016), fato que reitera a importância das contínuas coleções, tanto nessas UCs, para se documentar e conhecer o que já é protegido, quanto em outras áreas, para subsidiar a criação de novas UCs (e.g. Mello-Silva 2018; Covre et al. 2021).

Nesse sentido, nos capítulos 2, 3 e 4 analisamos a flora epifítica vascular em três Unidades de Conservação da região montanhosa do estado do Espírito Santo, onde buscamos responder basicamente a uma questão: o que as Unidades de Conservação conservam? Para isso investigamos a diversidade e composição das epífitas vasculares nessas áreas, com base em materiais depositados em herbários e, principalmente, através de coletas em campo. Apesar de o estado ser tradicionalmente reconhecido como possuidor de uma excepcional riqueza de sua flora epifítica, até pouco tempo nada se sabia sobre essa sinúsia nessa unidade federativa (Kersten 2010). Para tal, coletamos 866 amostras de epífitas vasculares em campo (238 na REBIO Duas Bocas, 395 na REBIO Augusto Ruschi e 233 na Pedra Azul). Nestes capítulos demonstramos que, de fato, a

região montanhosa desse estado corresponde a uma das localidades mais ricas em epífitas vasculares, tanto do Brasil, como da Região Neotropical. O levantamento em campo também permitiu que sete espécies de epífitas fossem registradas pela primeira vez no Espírito Santo.

Por fim, no último capítulo (5) utilizamos os dados dos capítulos 2, 3 e 4 para explorarmos a distribuição das espécies de epífitas vasculares entre as diferentes faixas altitudinais (200 a 1550 m a.s.l.). Utilizando diferentes métricas demonstramos que a riqueza e composição mudam ao longo das faixas altitudinais. Os resultados sugerem uma grande conservação de nicho, com grande contribuição de espécies das áreas mais elevadas. Além disso, apesar da variação da riqueza de espécies, uma grande diversidade de linhagens é observada em todas as faixas altitudinais. Os prováveis fatores que causaram esses padrões atuais remetem ao clima atual e ao histórico biogeográfico (e.g. oscilações climáticas do Pleistoceno) dessa cadeia de montanhas.

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Capítulo 1

Phytogeographic meta-analysis of the vascular epiphytes in the Neotropical Region

Abstract

The Neotropical Region (NR) is one of the areas with the most plant diversity globally, and its richness of vascular epiphyte (VE) species is higher than Africa and Asia combined. This richness is a consequence of the heterogeneous climate and geological history of the region, both factors also being responsible for the plant distribution patterns. Here, we aimed to explore the phytogeographic relationships of the VE in the NR using 14,636 identified records from 173 surveys exclusively of VE, carried out in 14 countries and 23 biogeographic provinces, comprising 3,849 identified species. We assessed the floristic patterns and relationships with climatic variables by multivariate analysis (cluster and ordination analyses). The clustering formed 13 main groups, partly corresponding to the biogeographic units of the NR. Our results demonstrate consistent floristic patterns confirmed through the analysis of floristic similarity, corroborating previous biogeographic classifications in well-studied areas, while broader patterns were found in poorly studied areas. We found a floristic gradient pattern, which allowed us to understand the relationships between environmental conditions and floristic patterns. Furthermore, we discuss our results under the light of the history that likely shaped the current distribution patterns and richness of the VE in the NR. The VE proved to be an important model for testing biogeographic classifications. We encourage the studies of this synusia in the several geographical gaps that remain in the NR, which undoubtedly will improve further studies and support conservationist policies.

Keywords: Amazon, Andes, Atlantic Forest, Biogeography, Central America, Flora.

Introduction

The Neotropical Region (NR) extends from Mexico to Argentina (Morrone, 2014) and presents the greatest number of plant species on Earth (Raven et al., 2020), concentrated mainly in the mountainous regions of Central America, eastern Brazil, and northwestern South America, especially in the Andes (Barthlott et al., 2005; Dick & Pennington, 2019). The geological and climatic histories of this region (Gentry, 1982; Antonelli & SanMartin, 2011; Cracraft et al., 2020), combined with the dispersal routes (Gentry, 1982; Christenhusz & Chase, 2013; Dick & Pennington, 2019), are decisive for the chorological patterns found nowadays (Gentry, 1982; Antonelli & SanMartin, 2011).

The current pattern of diversity and distribution of vascular epiphytes is mainly associated with water availability (Gentry & Dodson, 1987; Ding et al., 2016; Zotz, 2016), with the greatest diversity being found in areas with the highest precipitation values and the fewest drought months (Kreft et al., 2004; Breier, 2005; Kromer et al., 2005). However, there are exceptions in which, even with an increase in average annual precipitation, there is no increase in epiphyte richness (Wolf & Flamenco-S, 2003). At the continental scale (e.g., the Neotropical Region), the current environmental conditions alone may not justify the diversity patterns and the observed floristic relationships. In this case, historical factors (e.g., geological, dispersion, climatic fluctuations, etc.) that acted on the biota may help explain the biogeographic patterns found nowadays (Gentry, 1982; Antonelli & SanMartin, 2011; Sobral-Souza & Lima-Ribeiro, 2017; Dick & Pennington, 2019).

Biogeographic classifications have been carried out since the 19th century (e.g., Sclater, 1858; Wallace, 1876). However, the current data availability, combined with new analytical tools (Saiz et al., 2012; Ebach et al., 2015; Montaño-Arias et al., 2018) and the biogeographic nomenclature standardization (Ebach et al., 2008; Keith et al., 2020), rendered classifications much more refined, improving biogeographic knowledge and conservationist actions.

Current knowledge about the distribution patterns of VE in the NR is concentrated in specific locations, with limited coverage (Zotz, 2016), such as the Andes and the Amazon (Gentry & Dodson, 1987; Nieder et al., 1999; Kreft et al., 2004), the Andes and Central America (Küper et al., 2004; Cascante-Marín & Nivia-Ruíz, 2013), Central America (Batke et al., 2016), Peru (Ibisch et al., 1996), southern Mexico (Wolf & Flamenco-S, 2003), the southwestern Brazilian Amazon (Obermuller et al., 2014), and

the Atlantic Forest (Leitman et al., 2015; Menini Neto et al., 2016). After the classic and more comprehensive work on the diversity and distribution patterns of vascular epiphytes (VE) by Gentry and Dodson (1987), no other study considering the entire Neotropical Region has been carried out, even with the increase in local studies (Zotz, 2016). Thus, given the great expressiveness of this synusia in tropical forests (Gentry & Dodson, 1987; Zotz, 2016) and the complex phytogeographic relationships in the NR (Gentry, 1982; Burham & Graham, 1999; Antonelli & SanMartin, 2011; Fiaschi et al., 2016; Miranda et al., 2018; Dick & Pennington, 2019), it is of great relevance to carry out a phytogeographic meta-analysis such as the one performed here. Furthermore, the VE correspond to a floristic group that responds much more to climatic than edaphic conditions (Gentry & Dodson, 1987; Ding et al., 2016), serving as a model group for biogeographic classifications.

Here, with the comprehensiveness of the data, we aim to analyze the distributional patterns of the VE in the NR, searching to explore the biogeographical classification of the region (e.g. Morrone 2014; 2017). Several biogeographical hypotheses are discussed on the light of our results. We also analyzed the richness and shared species among the floristic groups. Furthermore, we investigated how the spatial patterns of species distribution should respond to differences in climatic characteristics (Whittaker, 1965; Gentry & Dodson, 1987; Zotz, 2016; Keith et al., 2020). Understanding how species distribution is related to environmental factors at a broad scale is fundamental to assess global patterns in biodiversity and variation patterns in species compositions in mega-diversity regions (Mittermeier et al., 1997; Gaston, 2001; Keith et al., 2020). At a large scale, climate factors have been linked to the variation of species distribution, with rainfall, temperature, and their interactions having been reported as the main drivers of the assembly of species compositions (Gentry & Dodson, 1987; Hawkins et al., 2003; Zotz, 2016). Thus, enabled by an extensive dataset of the occurrence of vascular epiphytes, we explored if the current climatic factors help explain the distribution pattern of VE in the NR.

Methods

Study area

The phytogeographic meta-analysis was carried out for the Neotropical Region according to Morrone (2014; 2017), which corresponds to the tropical areas of the New World, covering South America, Central America, southern Mexico, and the Antilles. The locations of the surveys were plotted on a map, and the biogeographic provinces were established according to the proposed by Morrone (2014). The areas were plotted using the Löwenberg-Neto (2014) shapefile, using the software Google Earth Pro and ArcMap 10.1. In the cases of sites situated in the border of two provinces we checked the description of the area in the sources and verified in Google Earth. Vegetation types were not considered.

Concept of vascular epiphytes

We considered the vascular epiphytes according to the classification of Benzing (1990), in characteristic holoepiphytes, primary and secondary hemiepiphytes, excluding the accidental, and facultative. Facultative epiphytes may be both holoepiphytes/hemiepiphytes or terricolous. We chose to keep the secondary hemiepiphytes (nomadic vines *sensu* Zotz, 2013a; 2016) because many studies have included them in the checklists without distinguishing between primary and secondary, becoming a not easy task to separate these categories based in database or herbarium collections (Espejo-Serna et al., 2021). It is hardly possible to know when it is a hemiepiphyte (primary) or nomadic vine, as the taxonomic groups are generally the same (e.g., Araceae and Cyclanthaceae) and, in some cases, the same species have the same habit in a single place, e.g., *Vanilla chamissonis* (Kersten & Silva, 2001). We exclude hemiparasites (e.g., Viscaceae) because they are taxonomic and ecological groups distinct from the epiphytes (Zotz, 2016). Finally, we avoid the accidental epiphytes as it is hard to know when a species is facultative or accidental. For this, the list of genera presented by Zotz (2013; 2016) was consulted.

Database compilation of the vascular epiphytes and bioclimatic variables

To construct the database, we use as a starting point the compilations made by Wolf and Flamenco-S (2003), Küper et al. (2004), Kersten (2010), Leitman et al. (2015), Dorneles (2016), and Menini Neto et al. (2016). Subsequently, searches were carried out for qualitative and/or quantitative floristic surveys exclusively of VE published by 2017 in journals and databases such as Jstor, Scielo, and Google Scholar. In addition, digitally available theses, dissertations, and books were included as well (Appendix 1 and 2). Only three of the included surveys were not found digitalized (Valdivia, 1977; Ibisch, 1996; Breier, 1999). For these searches, we used keywords such as epiphyte, epiphytic, epiphytes, and the respective names of the Neotropical countries. The literature cited was also analyzed, as well as some experts and researchers from the respective countries were consulted.

We only included surveys that exclusively considered the vascular epiphytes because generalist studies may underestimate some synusias. Among these exclusive surveys, we only included floristic and/or phytosociological studies. Surveys that included more than one location (parcel or bounded site) within a 10 km radius were considered as involving a single location (e.g., Blum et al., 2011; Bonnet et al., 2011). Ecological studies that do not have clear objectives to sample the floristic compositions were not included, neither were studies with epiphytes in urban environments (e.g., Fabricante, 2007) and large-scale checklists that considered sampled river basins, states, or countries (e.g., Schwesinger et al., 2002; Ceja-Romero et al., 2010; Obermuller et al., 2014).

We built a dataset of the presence (1) or absence (0) of the species in the study locations. Only species identified at a specific level were included in the dataset, and the *affinis* (aff.), *confer* (cf.), and hybrids were discarded, as well as subspecies, variety forms, and hybrids. To avoid taxonomic synonyms or redundancies, we used the database The Plant List (2013). When absent from this database, we used databases Flora do Brasil (Flora do Brasil, 2020) for studies in Brazil and Tropicos (http://www.tropicos.org) for other locations. All databases were verified in January 2020. Names not found or invalid names according to these databases were excluded.

To access the bioclimatic variables, we used the WorldClim (https://worldclim.org/) dataset (Fick & Hijmans, 2007), at a resolution of 30 arc-seconds (Appendix 3). Using geographic coordinates of each study area, we extracted nineteen

bioclimatic variables derived from monthly temperature and rainfall values obtained from more than 4,000 stations from 1950 to 2000. Furthermore, we included in the analysis the mean annual cloud cover extracted from Earthenv (Wilson & Jetz, 2016) (Appendix 3) since this variable has been demonstrated to be important in the VE distribution (Tobón et al., 2010; Furtado & Menini Neto, 2021).

Data analyses

To explore the biogeographic hypotheses, we evaluated the floristic relationships within sites in the Neotropical Region. Aiming to access the floristic similarity among sites, we performed Ward's hierarchical cluster analysis based on square root-transformation of Bray-Curtis distances (Singh et al., 2011; Borcard et al., 2018). We used Ward´s method since is based on a classic sum-of-squares criterion and reduces within-group dispersion at each binary fusion (Murtagh & Legendre, 2014). The major floristic epiphyte groups were defined using a level-cut of the dissimilarity index on the clustering dendrogram result. We then tested for the variations in epiphyte species composition across the floristic groups found via analyses of similarities (ANOSIM) with 999 permutations (Clarke, 1993). Finally, to summarize the species richness and floristic similarities of the sites, we calculated the total and the exclusive number of species for each floristic group and then computed the number of species shared between group pairs.

Finally, to analyses the relationships between floristic patterns and climatic variables, we first assessed the floristic variation by means of non-metric multidimensional scaling (NMDS; McCune et al. 2002), using the Simpson dissimilarity. To perform the ordination analysis, we excluded the singletons (species found at a single site) (Lepš & Šmilauer, 2003) and use the Hellinger transformation of the binary presence/absence data (Legendre & Gallagher, 2001). We then used multiple linear regressions analysis (OLS) (Quinn & Keough, 2002) to investigate relationships between floristic composition and bioclimatic variables, after removing any collinearities (variance inflation factor > 10; Borcard et al. 2018) (Appendix 4, 5 and 6). The axes of the NMDS were used in OLS models, and bioclimatic variables that were not significant ($p < 0.05$) or weakly correlated with axes ($r < 0.3$) were discarded from the models. These analyses were conducted for all sites and the main floristic groups.

All analyses were performed in software R 6.2.2 (R Core Team, 2020), using the packages ‘ape’ (Paradis & Schliep, 2019), ‘MASS’ (Venables & Ripley, 2002), ‘rich’

(Rossi, 2011) and 'vegan' (Oksanen et al., 2013). We adopted $\alpha \leq 0.05$, and permutational tests were based on 999 randomized datasets obtained from Monte Carlo permutations.

Results

We compiled data from 109 floristic studies exclusively on VE at 173 locations in the NR (Appendix 1, Fig. 1). Brazil had the largest number of studies (121 locations), followed by Colombia (8), Mexico (7), Bolivia and Ecuador (5), Panama (4), Argentina (3), Costa Rica, French Guiana, and Venezuela (2), and Guatemala, Guyana, Honduras, and Jamaica (1) (Appendix 1 and 2).

Despite the biogeographic provinces of the NR, 24 have at least one study (Fig. 1). The provinces with the largest number of surveys was the Atlantic Forest (71), followed by Parana Forest (20), *Araucaria* Forest (16), Veracruzan (9), Cerrado and Imerí (7 each), Cauca and Pampean (6 each), Yungas (5), Guajira (4), Guatuso-Talamanca and Guianan Lowlands (3 each), Madeira, Puntarenas-Chiriquí, Rondônia and Roraima (2 each), Caatinga, Chiapas Highlands, Jamaica, Mosquito, Napo, Pará, Pacific Lowlands, and Xingu-Tapajós (1 each) (Appendix 1, Fig. 1).

We registered 18,204 occurrence records, of which 14,636 were identified up to a specific level. The families, genera, and species with the highest number of records are shown in Table 1, while Table 2 presents the families and genera with the most species. The records identified up to a specific level belong to 49 families, 428 genera, and 3,849 species. Overall, 2,070 species were exclusive to a single site. Among the sites, 10 presented over 200 species identified up to a specific level (from 201 to 640), 41 from 100 to 200, and 122 less than 100 (Appendix 1).



Figure 1 Subregions, provinces, and locations of the 173 qualitative/quantitative surveys exclusively on vascular epiphytes carried out in the Neotropical Region up to 2017. Numbered are only the provinces that had any study, according to Morrone (2014). 5. Chiapas Highlands. 9. Jamaica. 13. Pacific Lowlands. 15. Veracruzan. 17. Mosquito. 18. Guatuso-Talamanca. 19. Puntarenas-Chiriquí. 21. Guajira. 26. Cauca. 30. Napo. 31. Imerí. 33. Guianan Lowlands. 34. Roraima. 35. Pará. 37. Madeira. 38. Rondônia. 39. Yungas. 40. Xingu-Tapajós. 41. Caatinga. 42. Cerrado. 44. Pampean. 45. Atlantic Forest. 46. Parana Forest. 47. *Araucaria* Forest.

Table 1 Families, genera, and species of vascular epiphytes with the highest number of records from 173 locations in the Neotropical Region.

Families	**Nº records**	**Genera**	**Nº records**	**Species**	**Nº records**
Orchidaceae	4665	*Tillandsia*	768	*Microgramma squamulosa*	92
Bromeliaceae	2331	*Peperomia*	761	*Pleopeltis hirsutissima*	92
Polypodiaceae	1839	*Vriesea*	625	*Vittaria lineata*	88
Araceae	1279	*Philodendron*	535	*Tillandsia stricta*	80
Piperaceae	774	*Epidendrum*	508	*Campyloneurum nitidum*	79
Cactaceae	582	*Anthurium*	493	*Serpocaulon catharinae*	75
Dryopteridaceae	507	*Pleopeltis*	423	*Tillandsia tenuifolia*	73
Hymenophyllaceae	492	*Asplenium*	412	*Anthurium scandens*	72
Aspleniaceae	412	*Aechmea*	368	*Peperomia tetraphylla*	72
Gesneriaceae	319	*Elaphoglossum*	355	*Tillandsia usneoides*	72
Pteridaceae	241	*Rhipsalis*	320	*Microgramma vacciniifolia*	69
Lycopodiaceae	198	*Microgramma*	298	*Pleopeltis pleopeltifolia*	68
Clusiaceae	94	*Campyloneurum*	275	*Tillandsia geminiflora*	68
Ericaceae	85	*Gomesa*	269	*Rhipsalis teres*	63
Melastomataceae	85	*Acianthera*	252	*Aechmea nudicaulis*	61
Begoniaceae	81	*Trichomanes*	246	*Peperomia glabella*	60
Blechnaceae	80	*Serpocaulon*	218	*Niphidium crassifolium*	56
Moraceae	80	*Stelis*	215	*Rhipsalis floccosa*	52
Cyclanthaceae	76	*Pecluma*	214	*Lepismium houlletianum*	50
Urticaceae	39	*Hymenophyllum*	210	*Lepismium cruciforme*	49

Table 2 Families and genera of vascular epiphytes with the largest number of species recorded in 173 locations in the Neotropical Region.

Families	**Nº species**	**Genera**	**Nº species**
Orchidaceae	1641	*Anthurium*	169
Bromeliaceae	493	*Epidendrum*	165
Araceae	368	*Tillandsia*	147
Polypodiaceae	249	*Peperomia*	143
Dryopteridaceae	154	*Philodendron*	132
Piperaceae	150	*Elaphoglossum*	122
Hymenophyllaceae	94	*Lepanthes*	93
Gesneriaceae	93	*Stelis*	93
Aspleniaceae	72	*Vriesea*	91
Cactaceae	65	*Aechmea*	76
Ericaceae	48	*Asplenium*	72
Clusiaceae	46	*Acianthera*	63
Melastomataceae	44	*Guzmania*	56
Pteridaceae	43	*Pleurothallis*	55
Lycopodiaceae	37	*Maxillaria*	49
Moraceae	27	*Hymenophyllum*	48
Cyclanthaceae	25	*Octomeria*	47
Begoniaceae	22	*Gomesa*	46
Rubiaceae	17	*Clusia*	45
Urticaceae	16	*Trichomanes*	43

Floristic patterns

Using cluster analysis, we defined 13 main groups with biogeographic meaning, although outliers occurred in some of them (Fig. 2). We found a good coefficient of cophenetic correlation (0.72) in the dendrogram, and the main floristic groups presented significant differences in their species composition, which was confirmed by the ANOSIN ($R = 0.744$, $p < 0.01$). The cluster analysis showed the segregation of three major floristic groups (Fig. 2). The first division of the branches separated (1) Amazon, Andes, Central America, and Mexico; the second division (2) clustered the coastal rainy forests in south and southeast of Brazil; and third (3) the highland rain forests and inland seasonal forests in the south, southeast, and northeast of Brazil and northern Argentina.

The first branch (1) was the more heterogeneous, including areas of the Amazon (Groups A, B, and part of C), Caribbean (C), Andes and highlands in Central America

(D), and Honduras and Mexico (E), and was congruent with the Brazilian subregion (Morrone, 2014; 2017). Group A corresponds to sites in the Amazon, including four provinces (*sensu* Morrone, 2014; 2017) besides outliers in four sites outside the Amazon. This group is represented by 10 locations and 161 species, of which 33 are exclusive to the group. Other Amazonian locations proved to be distinct (Group B), including nine sites in the Amazon basin, in four provinces, accounting 532 species with 252 exclusives. Furthermore, areas in the Guiana shield and eastern Amazon demonstrated to be related with the Caribbean region, but with a clear division of the northern areas (subgroup C1, north of Colombia, Central America, and Jamaica) and the Amazonian areas (subgroup C2, Bolivia, Brazil, Guyana, and French Guyana). This group includes 12 sites, 756 species, of which 325 exclusives.

The group D corresponded to five provinces in the Andes plus three mountains in the Central America, is characterized by sites located at high altitudes (average of 2,100 meters) and the largest numbers of total and exclusive species (respectively 1,488 and 1,142), albeit represented by only 14 locations. The Central America proved to be distinct (subgroup D1) from the Andean sites (D2), and not widespread in the cluster. Further northern, the Central America plus Mexico correspond to the Group E, fitting in Mesoamerican domain (*sensu* Morrone, 2014; Montaño-Arias et al., 2018), encompassing three provinces. This group included 11 locations and 652 species, of which 420 were exclusive.

The branch two (Fig. 2) was congruent in including coastal rainy sites in the Southern and Southeastern regions of Brazil. At low latitudes, it included areas of higher altitudes and, at higher latitudes, areas at lower altitudes. In Group F, 10 sites grouped, represented by 442 species, of which 55 exclusives to the group. This group comprises mainly coastal areas at low altitude. Group G clustered mountainous sites (average of 530 meters) in the Santa Catarina state, South Brazil, and includes 27 areas, 439 species, of which 49 exclusives.

The third branch (3) was congruent with the seasonal areas of eastern South America. Group H correspond to highlands of the Atlantic province (average of 1220 m), characterized by the cloud forests in South and Southeastern regions of Brazil. The eight sites totally 270 species, of which 27 exclusives. Group I was congruent with the *Araucaria* Forest province, represented by 15 locations in the seasonal and highlands of southern Brazil, represented by 236 species, of which 27 are exclusives. Group J included 18 sites mainly in the Parana provinces, totalizing 285 species, 36 being exclusive. Group

K, with 18 sites, corresponds to the northeastern part of the Pampa province, plus ecotonal areas between the Atlantic and Parana provinces. This group had 345 species and 34 exclusives. Group L and M corresponds to the central part of the Atlantic province, including part of the district of Bahia. The first one comprises the lowland sites, with seven localities, accounting 162 species, of which 24 are exclusives. Finally, the group M was congruent central part of the Atlantic province, mainly in mountainous relief (average of 900 m.a.s.l.), including 14 sites and the highest number of species of eastern South America, with 780 species, 292 being exclusive.

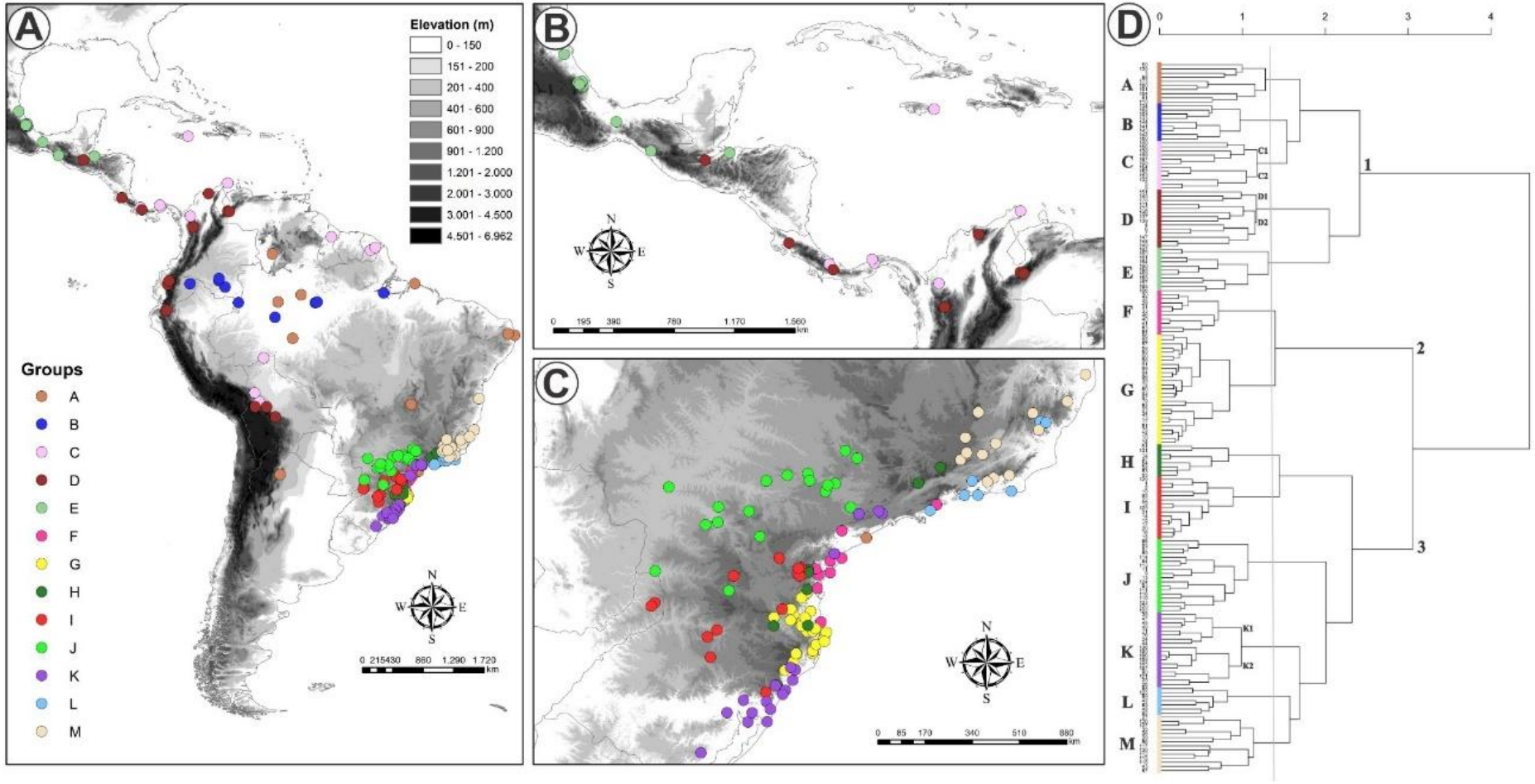


Figure 2 Sites and respective floristic groups formed in the clustering with 173 qualitative/quantitative surveys exclusively on vascular epiphytes carried out in the Neotropical Region up to 2017. A. Overall groups. B. Central America and northwestern South America detail. C. Southeastern South America detail. D. Cluster analysis.

Overall, a single group holds more than 1,000 species (Group D), and four groups (B, C, E and M) more than 500. The remaining eight groups were represented by less than 500 species (Fig. 3). The sharing of species among the groups resulted in only seven sharing equal or more than 200 species, 20 over 100 species, 20 shared from 50 to 99, and 31 less than 50 species (Fig. 3).

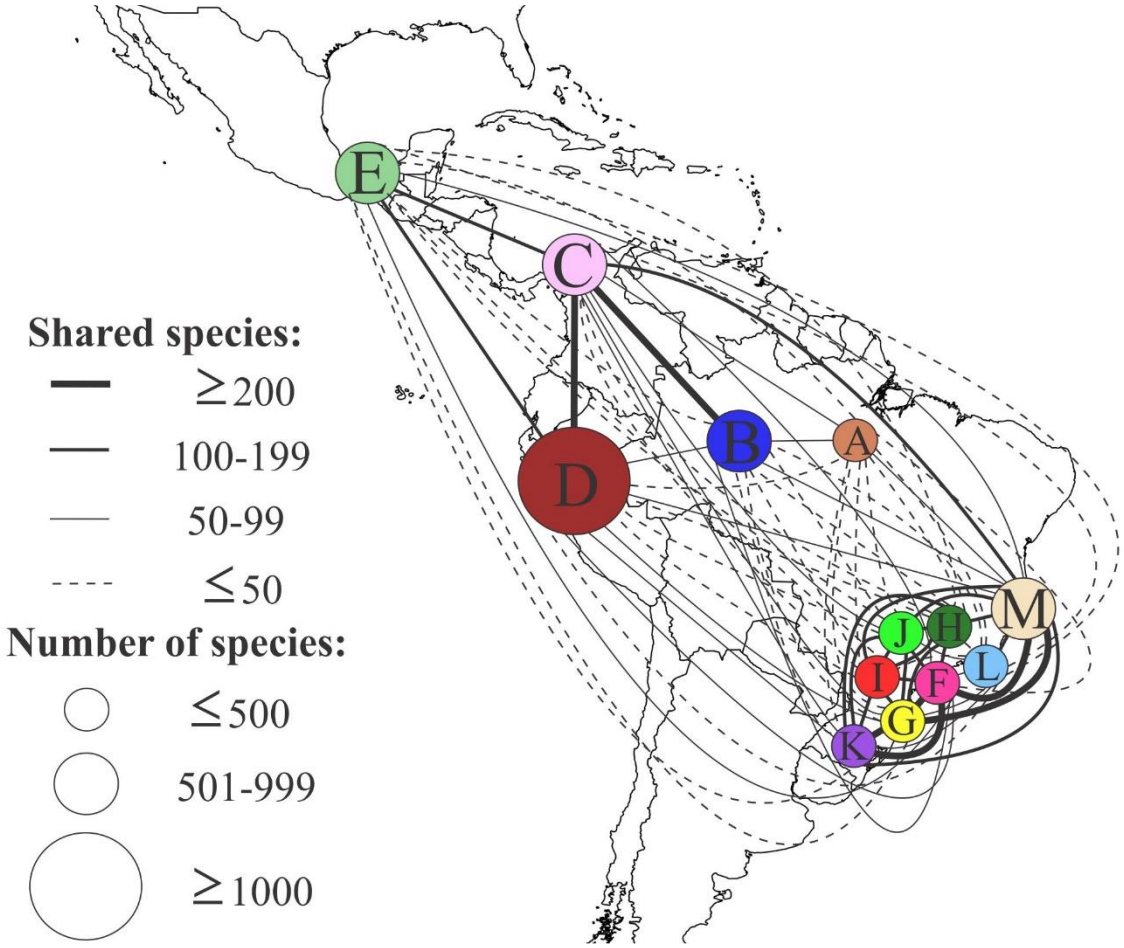


Figure 3 Richness and shared species among the vascular epiphyte groups in the Neotropical Region according to the cluster analysis (Fig. 2).

Relationships with bioclimatic variables

The distribution of the sites in the ordination by NMDS, showed a strong floristic gradient of vascular epiphytes (Fig. 4), and reinforced the floristic patterns of cluster analysis (Fig. 2). A good data fit was confirmed by the stress plot for NMDS of all sites (non-metric fit, R^2= 0.976, and a linear fit, R2 = 0.875), group 1 (non-metric fit, R^2= 0.979, and a linear fit, R2 = 0.854) and groups 2 and 3 (non-metric fit, R^2= 0.969, and a linear fit, R2 = 0.881). Also, the stress values below 0.15, for three dimensions of NMDS of all sites and the groups, suggested a good representation of the original variation by the sites on space ordination.

Considering all sites, the floristic gradient found in the ordination space by NMDS, presented strong and significant correlations with five bioclimatic variables (Table 3). The first axis mainly segregated the southeastern Brazil (plus northern Argentina) from the northern and eastern South America, Central America, Antilles, and Mexico sites. Precipitation of Warmest Quarter (BIO.18), Annual Precipitation (BIO.12), and Precipitation of Coldest Quarter (BIO.19) were positively associated with this axis (Fig. 4). The second axis of the ordination separated mainly the high-altitude sites from the lowland ones. The Cloud Cover and Mean Temperature of Wettest Quarter (BIO.8) were strongly associated with the second axis (Fig. 4).

For group 1, three bioclimatic variables were significantly correlated with the first two axes of the NMDS (Fig. 4; Table 3), where the Amazon groups (A and E) related positively with the Precipitation of Coldest Quarter (BIO.19) and segregated in the first axis from the other groups (B, C, D, and E). The first axis mainly segregated the Andean (C) and the Mexican (E) groups from the lowland sites and was strongly associated, respectively, with Cloud Cover and Precipitation Seasonality (BIO.15). Groups 2 and 3, also three variables were significantly correlated with the first two axes of the NMDS (Table 3). The first axis primarily separated the seasonal forests from pluvial forests, mostly drove by the Mean Temperature of Driest Quarter (BIO.9) associated with the hottest and seasonal forest of the central Atlantic province, and, on the other hand, the Cloud Cover with the southern mountains of Brazil. The second axis also reflected the gradient of temperature (Mean Temperature of Wettest Quarter, BIO.8), putting in different sides the lowland sites of the Atlantic province and highland ones.

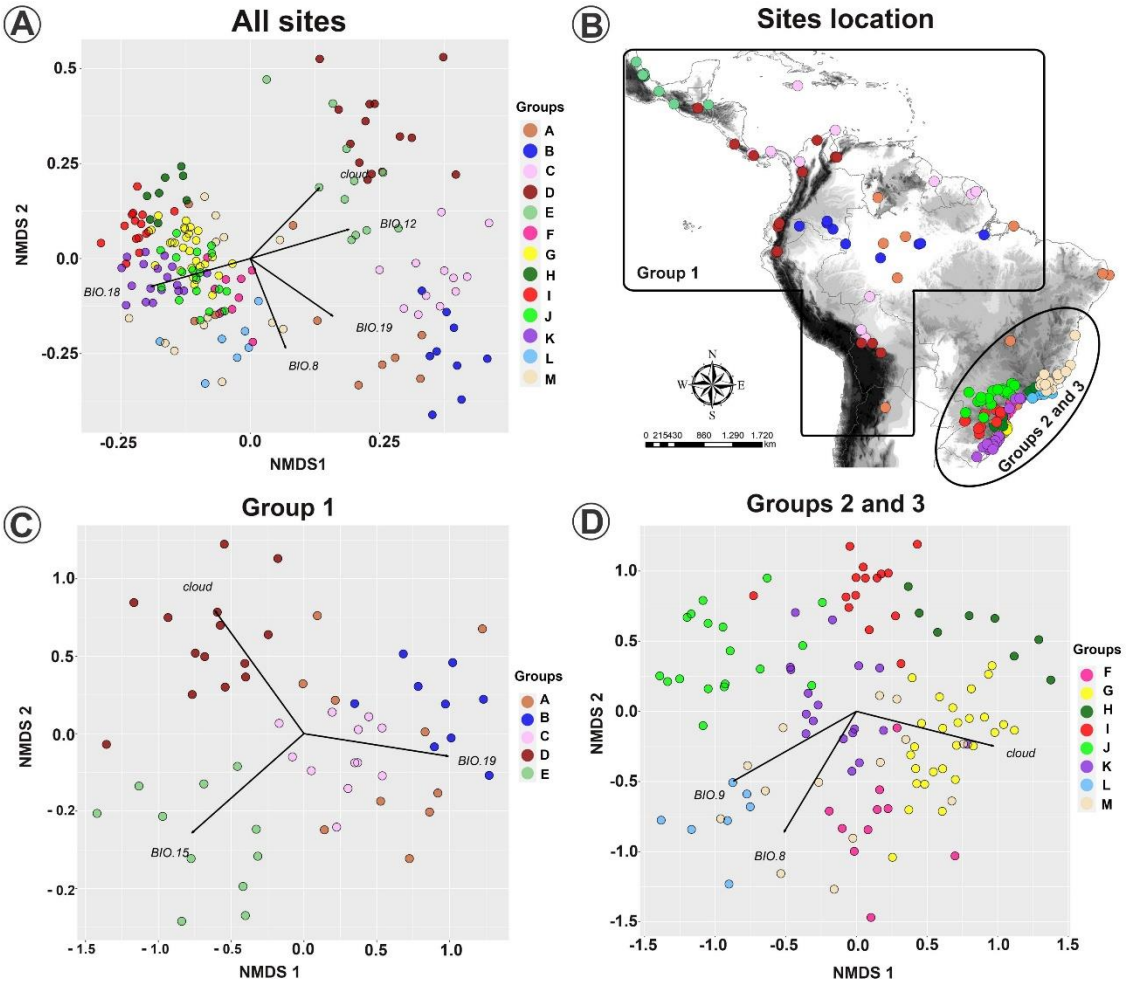


Figure 4 Relationships between species composition and bioclimatic variables for 173 qualitative/quantitative surveys exclusively on vascular epiphytes carried out in the Neotropical Region up to 2017. Sites distribution in an ordination space were assessed by NMDS. A. Analyzes conducted for all sites; B. Map showing the groups according with the cluster analyses; C. Subset considering the groups in the Amazon, Andes, Central America, and Mexico; D. Subset considering the groups of the eastern Brazil (plus northeastern Argentina). Vectors indicate the sign and strength of environmental variables that remained significantly correlated with the floristic patterns ($p \leq 0.05$) after analysis for multiple comparisons (see details in methods). BIO.8 – Mean Temperature of Wettest Quarter; BIO.9 – Mean Temperature of Driest Quarter; BIO.12 – Annual Precipitation; BIO.15 – Precipitation Seasonality; BIO.18 – Precipitation of Warmest Quarter; BIO.19 – Precipitation of Coldest Quarter; cloud – Mean Annual Cloud Cover.

Table 3 Bioclimatic variables selected in the analysis of relationships with species composition for 173 qualitative/quantitative surveys exclusively on vascular epiphytes carried out in the Neotropical Region up to 2017. The floristics patterns were assessed by NMDS. Bioclimatic variables were evaluated via adjusted coefficients of determination (R^2) and significance tests (p-value). Variance inflation factors (VIF) were obtained from correlations of the independent variables of the multiple linear regressions.

All site *Variables*	NMDS1	NMDS2	R^2	VIF	p-value
BIO.6	-0.9977	-0.0675	0.7855	1.13	0.001
BIO.8	0.33814	0.94109	0.5066	9.85	0.001
BIO.12	0.94973	-0.3131	0.1689	1.44	0.001
BIO.15	0.99436	-0.1061	0.1331	9.16	0.001
BIO.18	-0.9668	0.25545	0.0483	3.38	0.022
BIO.19	0.80822	0.58888	0.2544	6.17	0.001
Cloud	0.67763	-0.7354	0.5087	2.97	0.001
Group 1 *Variables*	NMDS1	NMDS2	R^2	VIF	p-value
BIO.12	0.4239	0.90571	0.0239	1.8	0.558
BIO.15	-0.7684	-0.64	0.2298	3.88	0.001
BIO.19	0.98938	-0.1454	0.4284	5.84	0.001
Cloud	-0.6099	0.79246	0.4296	3.13	0.001
Groups 2 and 3 *Variables*	NMDS1	NMDS2	R^2	VIF	p-value
BIO.8	-0.5121	-0.8589	0.366	9.81	0.001
BIO.9	-0.8686	-0.4956	0.5613	8.15	0.001
Cloud	0.96912	-0.2466	0.5521	3.13	0.001

Discussion

The number of floristic studies about VE in the NR compiled here are higher than previously compilations: in Brazil, the studies compiling floristic inventories of VE, including only the Atlantic Forest, listed 62 (Kersten, 2010), 57 (Leitman et al., 2015), and 86 (Menini Neto et al., 2016) sites surveyed. However, these works considered the concept of Atlantic Forest according to Fiaschi and Pirani (2009), which matches the Atlantic provinces, *Araucaria* Forest, and Parana Forest (Morrone, 2014) as a single unit. For the NR, this number was also expanded. Wolf and Flamenco-S (2003) initially listed 70, and Küper et al. (2004) estimated 120 surveys, although such compilations included general floristic studies, not just those exclusively about vascular epiphytes, thus overestimating these numbers.

The taxonomic composition at the family and genus level, in general, followed the general patterns, with a low number of taxonomic groups (ca. 19% of all families have epiphytic representants) (Zotz, 2013; 2016). As expected, Orchidaceae is the most diverse family in this synusia, accounting for 68% of all VE worldwide (Zotz, 2013; 2016). The conquest of a previously unexploited space and without competition (Zotz, 2016) may have stimulated the diversification in Orchidaceae (Gravendeel et al., 2004; Martins et al., 2018). However, in the NR, the genus *Epidendrum* stands out as the richest, while *Bulbophyllum* and *Dendrobium* are richer in the Old World (Hsu & Wolf, 2009). The Bromeliaceae family, with the richest genera being *Tillandsia*, *Vriesea*, and *Aechmea*, is a characteristic taxonomic group of the NR (Zotz, 2016). In some areas of the NR, Gesneriaceae, Ericaceae, and Melastomataceae are more important, mainly in countries with the highest mountains (Cascante-Marín & Nivia-Ruíz, 2013; Batke et al., 2017). In the Amazon, Araceae is better represented mainly by *Philodendron* (Obermuller, 2016); however, here we find *Anthurium* as the richest genus, reinforcing the richness of the genus in this synusia in NR (Reimuth & Zotz, 2020).

Floristic patterns

In general, the cluster analyses demonstrated floristic patterns with biogeographic significance (Fig. 2), corroborated by the NMDS (Fig. 4). The Chacoan subregion proved to be quite distinct from the Brazilian subregion. The split into major groups is congruent with the dry diagonal corridor, having an important vicarious role between the biotas of these two forest blocks (Fiaschi & Pirani, 2009; Zanella, 2011), although some biogeographic relationships occur between them (Amorim, 2001; Santos et al., 2007; Ledo & Colli, 2017; Maciel et al., 2017). In the Chacoan subregion, the Atlantic Forest (*sensu* Fiaschi & Pirani, 2009) proved to be quite heterogeneous, according with the altitude, latitude, and seasonality, justifying the divisions proposed by Morrone (2014; 2017). The data available for the Brazilian subregion (Amazon, Andes, Central America, and Mexico) allowed us to recognize broad floristic patterns.

Our compilation represents about one-quarter (3,849 species) of all species recorded for the NR (Gentry & Dodson, 1987; Kersten, 2010). The richness pattern of the floristic groups was congruent with the expected for the NR (Barthlott et al., 2005; Zotz, 2016). The high specificity of the niche or certain habitats may justify the high number of species that are exclusive (54% of the species) to a single location (Caiafa & Martins,

2010), thus generating high endemism rates (Menini Neto et al., 2016), although vascular epiphytes tend to have a wider distribution than terrestrial taxa due to the greater dispersion capacity (Nieder et al., 1999; Zotz, 2016). The high number of species occurring in a single location and the few occurring in many locations may also be related to the age of taxa (Willis, 1922; McLaughlin, 1992).

Brazilian subregion

The sites in the Andes, Amazon, Central America, Caribbean, and Mexico allow us to recognize major floristic groups, supporting bioregionalization proposals (Morrone 2014; 2017; Jiménez-Rivillas et al., 2018; Montaño-Arias et al., 2018). The present data allow us to show broad biogeographic pattern, with considerable species turnover. Besides, the analysis considering local sites enables us to find biogeographic units rather than political boundaries that prevent us from recognizing the patterns (e.g. Cascante-Marín & Nívia-Ruíz, 2013; Batke et al., 2017).

The sites in the Amazon (*sensu* Fiaschi & Pirani, 2009) showed congruence in the cluster, as well as has been found for the tree flora (Miranda et al., 2018; Wittmann et al., 2018). However, a refined division of the units could not be reliable with our data with epiphytic flora, perhaps the species in the flat and lowlands forests of the Amazon could represent taxa with wide range (Janzen et al., 2020). However, the Amazon seems to have a low similarity between the areas, with high species substitution along the latitudinal and longitudinal gradients (Oliveira & Nelson, 2001; Obermuller, 2016; Silva-Souza & Souza, 2020). The regionalization with several provinces for the Amazon basin (Morrone, 2014; 2017), could not be recognized here due to the low number of studies available. The increase in the number of VE surveys in the Amazon is necessary and will allow a better biogeographic classification based on this synusia or demonstrated that this is not a good model for this purpose in the Amazon.

The sites in the South and Central America (Group C) that clustered together does not supports that northern Andes act as biogeographic barrier between both sides (Gentry, 1982; Pessoa et al., 2014). Instead, it corroborated that lowland taxa may cross the Andes and spread over both sides of the mountain range (Quintana et al., 2017; Pérez-Escobar et al., 2018). In fact, immigration success may be higher in wet forests than in dry ones (Pennington & Lavin, 2016). These results support the idea of northward-moving plants extending just into the wet forests of Panama or southern Costa Rica (Burnham &

Graham, 1999; Graham, 2010; Antonelli et al., 2018b). This is the case of the Choco, which spreads into northern Ecuador up to Panamá (Morrone, 2014; 2017; Pérez-Escobar et al., 2019). Furthermore, the Caribbean and Central America shows to have a complex floristic influence, sharing elements with several sites (Luna-Vega et al., 2001; Acevedo-Rodríguez & Strong, 2008; Pérez-Escobar et al., 2019) and demonstrating that the peripheral Amazon basin (Andean foothill and Guiana shield) are composed by distinct elements of the biota (Amorim, 2001; Alvez-Valles et al., 2018).

The floristic relationships between the Andes and the Amazon, followed the orographic conditions (Gentry, 1982; Kreft et al., 2004), showing to represent two distinct biogeographic entities, where lowland forests, even in a very wide latitudinal and longitudinal spectrum, are more related to each other than with the flora occurring at higher altitudes in the Andes. The presence of Andean elements in the forests of the eastern Amazon demonstrates that many may cross this barrier (Pérez-Escobar et al., 2018), but not enough for it to be considered an extension of the Andean flora in the Amazonian lowlands (Kreft et al., 2004), supporting the *Andean-centered* and *Amazonian-centered* taxa (Gentry, 1982; Antonelli & Sanmartin, 2011).

The cloud forest in the mountains of Andes and Central America shows that altitude is a reliable predictor of the floristic groups, even they have distinctions, still shares several floristic elements among Central and South America matching it as a natural unit (Luna-Vega et al., 2001). Taxa from the uplands have a different history from the lowland lineages of Central America: they came from temperate regions until they reached South America (Gentry, 1982; Burnham & Graham, 1999; Hammel et al., 2004; Dick & Pennington, 2019). In addition, the influence of North American tree flora appears to be greater than that from South America in certain locations (Monro et al., 2017), mainly for cold-climate taxa, which migrated south through the mountains, reaching the Andes (Dick & Pennington, 2019). This partly explains the clustering of high-altitude areas of Central America, which were instead grouped with the Panama lowland sites. Supporting Bemmels et al. (2018) that Central American rain forests contain more ecological generalists than Amazon forests. Although the Jamaica site clustered with the surrounding South and Central Americas, confirming the influence of this flora in the West Indies (Acevedo-Rodríguez & Strong, 2008).

In Central America and Mexico, there was a north-south distinction in the cluster analysis, corroborating other authors who studied the vascular epiphytes in the region (Cascante-Marín & Nivia-Ruíz, 2013; Batke et al., 2017). This biogeographic break may

be due to the geological and immigrational history of the flora of southern Central America, which was more influenced by the South American taxa, whereas the north of Central American countries shows stronger Laurasian and north temperate floristic elements (Graham, 2010; Batke et al., 2017). The full contact between the floras of South and North America occurred with the complete closing of the Panama isthmus; until then, the floras of both continents remained partially connected by the Caribbean islands (Gentry, 1982; Hammel et al., 2004; Dick & Pennington, 2019; Fiaschi et al., 2016). Southern Central America suffered a great floristic influence by South America (Pérez-Escobar et al., 2019), while the north was more influenced by the North America (Laurasian) flora, which, after the closing of the isthmus, became dispersed over South America (Gentry, 1982; Burham & Graham, 1999; Graham, 2010; Willis et al., 2014; Batke et al., 2017). This is a likely explanation for the split of the Mexican and northern Central American groups (see Batke et al., 2017), which remained isolated, evolving several endemic taxa, and later becoming a mixed flora (Wendt, 1993; Burnham & Graham, 1999; Morrone, 2017).

Chacoan subregion

In the eastern South America, the subdivisions of the Atlantic Forest (*sensu* Fiaschi & Pirani, 2009) according to the latitude, longitude (Perret et al., 2006; Leitman et al., 2015; Menini Neto et al., 2016; Saiter et al., 2016b; Zwiener et al., 2019; Reginato & Michelangeli, 2020), and altitude (Scudeller et al., 2001; Bertoncello et al. 2009; Fontoura et al., 2012) were expected. The sites located in the lowest latitudes (except areas at higher altitudes) were quite different from the southern coastal portion. The distinction between the north and south of the coastal region of Brazil is probably associated with the different climatic factors (e.g., temperature, precipitation, and seasonality) (Alvares et al., 2013) and historical aspects, such as the connections between the Amazon and Atlantic Forest blocks during glaciation periods (Perret et al., 2006; Santos et al., 2017; Ledo & Colli, 2017; Maciel et al., 2017) and the stable climate during the Pleistocene in some parts of the Atlantic Forest (Cheng et al., 2013; Leite et al. 2016; Aguiar-Melo et al., 2019). The southern region of the Atlantic Province received a great floristic contribution of temperate and Andean origin, in addition to non-seasonal climate and lower temperatures that currently occur in this region (Safford, 2007; Alvares et al., 2013; Rezende et al., 2017). Our results also support the strong north-south distinction

that occurs in the Atlantic Forest because of climatic differentiation along this gradient (Prata et al.; 2018).

The subdivision (Morrone 2014; 2017) of the Atlantic Forest (*sensu* Fiaschi & Pirani, 2009) in four provinces (Atlantic, *Araucaria* Forest, Pampa, and Parana) was supported by our data. It was also possible to observe the subdivisions of the Atlantic Province into districts such as Bahia and Paulista (Morrone, 2014) along a latitudinal gradient, with the altitude exercising a strong influence within this province. The localities in the central region of the Atlantic Province matched with the district of Bahia, while the southern portion, with the Paulista (DaSilva & Pinto-da-Rocha, 2016). The northern portion (Pernambuco district) does not have enough data regarding floristic VE surveys (Gadelha Neto & Barbosa, 2012; Dias-Terceiro et al., 2014) to allow us to recognize any pattern.

About altitude in the Atlantic province, it is noteworthy that the highland sites (Group H) from southeastern Brazil clustered together with the seasonal and cold sites of the *Araucaria* Forest province, even at low altitudes, but at high latitudes (Group I) (Vieira et al., 2015; Furtado & Menini Neto, 2016). This agrees the distinction of species composition according to altitude in the Atlantic Forest (Ivanauskas et al., 2000; Scudeller et al., 2001; Fontoura et al., 2012) and supports that the cloud forest corresponds to a unique and natural vegetation type (Bertoncello et al., 2009; Furtado & Menini Neto, 2021).

The *Araucaria* Forest also supported the distinction from the Atlantic province (Trindade et al., 2020; Furtado & Menini Neto, 2021), although they are geographically close and generally included in the domain of the Atlantic Forest (Fiaschi & Pirani, 2009). Furthermore, the *Araucaria* Forest, Pampa, and Parana provinces proved to be closely related, supporting the herbaceous flora patterns (Vieira et al., 2015).

The seasonal forests of the Parana province proved to be quite different from the rain forests of the Atlantic province, corroborating the idea that this is not a subset of the ombrophilous species, more resistant to seasonality, but a distinct set (Eisenlohr & Oliveira-Filho, 2015; Vieira et al., 2015; Morrone, 2017). However, the Parana province shared many species with the forests of eastern Brazil (Fig. 3). The Pampa province comprise a grassland predominant vegetation type, but with some forest in the eastern and inland along the rivers (Oliveira-Filho et al., 2015). The forests in the northeastern Pampa grouped in the boundaries of the cold and seasonal climates in South Brazil, plus climatic equivalent sites in transitional areas between Atlantic and Paraná provinces in

São Paulo state (Ivanauskas et al., 2000; Vieira et al. 2015). This supports that this area is floristically singular and shared several species with the climatic equivalent sites at higher altitudes, but at smaller latitudes more than with the closest rain forest (Vieira et al., 2015).

In the central portion of the Atlantic province, consistent groups were formed (Groups L and M), representing part of district of Bahia (Morrone 2017). On the other hand, biogeographic breaks that usually is found in the area – e.g. Goytacazes fault, between the north of the state of Rio de Janeiro and the south of Espírito Santo and the Doce River, in northern Espírito Santo (Oliveira-Filho, 2009; Menini Neto et al., 2016) - , were not observed, reinforcing the delimitation of the Bahia district as a natural biogeographical unit. This group also supported the differentiation between the north and south of the Atlantic province, driven mainly by the seasonality and temperatures in the latitudinal gradient (Perret et al., 2006; Santos et al., 2007; Saiter et al., 2015a; 2015b; Zwiener et al., 2019). Studies with the tree flora shows a clear distinction between coastal forests (Atlantic province) and those more inland (Parana province) in this transition area of the Doce River valley (Oliveira-Filho et al., 2005; Saiter et al., 2015a). This pattern was not supported here, with the inland sites clustering with the coastal sites, instead with the southernmost seasonal forest (Group J), that are usually treated as the same biogeographical entity reaching the Bahia state, in Northeastern Brazil (Morrone 2014, 2017).

Richness and shared species

Only five groups totaled more than 500 species, the Amazon sites represents one of them, even with some marginal areas and another group (A) not included in the same (group B). Nearly 25% of the 2,003 vascular epiphyte species recorded for the Amazon (Obermuller, 2016) were included in the present work. Despite Amazon is traditionally represented with little importance for VE compared to the montane forests (e.g. Andes, Central America, and eastern Brazil) (Gentry, 1982), our results is supported also by 10 % of the Colombia Amazon flora composed of epiphytes (557 epiphytes (7 %) and 173 hemiepiphytes (2 %)) (Infante-Betancour, 2016). Furthermore, we found a high degree of exclusivity (near 50 % of the species), supporting the endemism level for the Brazilian Amazon (848 endemic species of the 1,208 occurring in the Brazilian Amazon) (Obermuller, 2016).

The forest of the Andes slopes stood out concerning species richness, with 11 sites (1229 species, excluding the three Central America sites of this group) presenting a greater number of species than, for example, nine sites in the Amazon (Group B), and richness slightly lower than the 117 surveys of the floristic groups of the Atlantic Forest (*sensu* Fiaschi & Pirani, 2009). The high richness and endemism in the Andean montane forests corroborate what is expected for that location: they are the forests with one of the greatest plant diversities on Earth, housing about half of the plant species of South America (Gentry, 1982; Myers et al., 2000; Bartlhot et al., 2005; Reimuth & Zotz, 2020). The importance of mountains for biotic evolution is quite complex; however, they may undoubtedly be considered one of the main generators of biodiversity (Gentry, 1982; Antonelli & Sanmartin, 2011; Pérez-Escobar et al., 2017; Antonelli et al., 2018; Perrigo et al., 2019). This shows the importance of environmental heterogeneity and, consequently, of the altitudinal gradient in mountainous habitats, in generating isolated places (island-like habitats) and offering different niches to occupy and evolve along the different elevations (Gentry & Dodson, 1987; Kreft & Jetz, 2007; Antonelli et al., 2018a; Perrigo et al. 2019). On the other hand, this also reinforces, at the regional scale, the latitudinal gradients in which the plants are subjected in the NR, with peaks of diversity at lower latitudes (Gentry & Dodson, 1987; Cascante-Marín & Nivia-Ruíz, 2013; Zotz, 2016).

The forests of Central America and Mexico have shown to correspond to one of the richest areas of the NR (Barthlott et al., 2005; Espejo-Serna et al., 2021), with a high number of species and endemism, although few VE surveys are available. As example are the state of Chiapas, which has about 1,200 epiphyte species occurring mainly in montane forests (Wolf & Flamenco-S, 2003), and the La Amistad National Park in Costa Rica and Panama, where 1,000 VE species have been recorded (Monro et al., 2017). These results also reinforce that the mountainous relief and the altitudinal heterogeneity are important environmental features to diversification (Pérez-Escobar et al., 2017; Antonelli et al., 2018a; Perrigo et al., 2019).

Here, we included over half of the species Atlantic Forest (1,310 species) of the about 2,300 species of VE in this region (Freitas et al., 2016). The eastern Brazil is one of the five diversity zones that present the most considerable richness and endemism on Earth (Myers et al., 2000; Barthlott et al., 2005). This domain is conditioned by several abiotic factors (Oliveira-Filho & Fontes, 2000; Zwiener et al., 2019), so some classifications treated them as separate units (Morrone, 2014; 2017). Considering only

the Atlantic province (*sensu* Morrone, 2014; 2017) subdivided into three districts, it was possible to demonstrate the high species richness of the district of Bahia (Group M): with only 14 surveys, it presented a high number of species (780 species) in comparison, for example, to the 37 surveys of Groups F and G, which match with the Paulista district (610 species). Undoubtedly, new studies in the states of Bahia, Espírito Santo, and Rio de Janeiro will increase these values even further. Besides, scattered in the high-altitude areas, an impressive species-rich group was formed (Group H), demonstrating the importance of the cloud forests to the increase of VE diversity even occupying small and scattered sites (Furtado, 2020).

The *Araucaria* Forest, Paraná Forest, and Pampa provinces showed the lowest numbers of species. These places have characteristic seasonal climate that greatly influence the VE diversity, representing an environmental constraint to colonization and diversification due to the lower temperatures and driest conditions with prolonged seasonality (Gentry & Dodson, 1987; Breier, 2005; Zotz, 2016). The decrease in species richness in subtropical environments such as the Pampa province (May, 2014) also confirms the latitudinal gradient pattern (Zotz, 2016).

Relationships with bioclimatic variables

Overall, is well stablished that the water availability (e.g. precipitation and seasonality) was the main factor explaining the floristic variance across the NR. Our results also support the influence of the annual precipitation and seasonality, mainly associated with mountainous regions, where the obstacle in the relief input a great amount of water in the vegetation by means of orographic rainfall (Gentry & Dodson, 1987; Zotz 2016). This result supports that in tropical regions the water input is the major predictor of the diversity (Hawkins et al., 2003), and that is a crucial factor also for VE distribution (Gentry & Dodson, 1987; Kreft et al., 2004; Zotz, 2016).

Noteworthy is the importance of the indirect water input by the Cloud Cover and its significance in explaining the variation of composition in all situations. Cloud forests are traditionally known as the vegetation type that holds the richest VE flora (Gentry & Dodson, 1987; Espejo-Serna et al., 2021). The combination of water input and low evapotranspiration could be the main responsible for this (Zotz, 2016), although low temperatures could constraint the diversification in such conditions (Furtado, 2020). Regarding this, the Andes, and mountains of Southern Brazil (and some high mountains

in Southeastern) are typical examples of forest associated with clouds, even under at different altitudinal ranges.

Considering a broad altitudinal and latitudinal range like occurs in NR, the temperature also exerts a strong influence in the distributional patterns of the VE (Zotz, 2016). The segregations of sites in high-altitude from the lowlands is noteworthy for all the sites, as a consequence of the changes in the temperature along altitudinal gradients (Körner, 2007; Zotz, 2016). Depicting this, is notable that in tropical sites (NMDS of Group 1) the water relative variables are the main drive, but when analyzed only the southernmost sites (southeastern South America, NMDS of Groups 2 and 3), temperature gains prominence. This fits with the great contribution of the temperature in sites in higher latitudes (Hawkins et al., 2003; Furtado & Menini Neto, 2021). By affect the crucial life stage of the VE, like the establishment, growth, and reproduction, besides water, temperature is a limiting factor at both individual to global distribution (Zotz, 2016).

In summary, the present meta-analysis carried out the most comprehensive compilation and phytogeographic analysis of vascular epiphytes in the NR to date, using a relevant portion of the vascular epiphytic flora of the Region. The results demonstrated some floristic patterns, corroborating, on the one hand, biogeographic classifications in well-studied areas such as eastern and southern Brazil, and, on the other hand, showing broad patterns in areas with few sample efforts. Furthermore, considering local surveys, instead collections in grids, demonstrated to be more informative in mountainous regions, where the composition strongly changes in small geographical distances and the latitude compensate the altitude. Overall, the climatic factors regarding humidity were responsible for most explications of the variations, however, temperature also explained the latitudinal and altitudinal changes. The VE demonstrated important floristic patterns from the biogeographic classification viewpoint, suggesting an important model group for studies on the theme. Our results also suggest the necessity of improved knowledge on the biogeographic unities, aiming to maximize the conservation actions and prospecting in future climate change scenarios. We encourage more floristic studies considering the VE in the NR, aiming for a detailed biogeographic appreciation and conservationist purposes of the biota based in this synusia.

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Capítulo 2

A first checklist of the vascular epiphytes of Duas Bocas Biological Reserve, a protected area in the Espírito Santo, Southeastern Brazil

Abstract

Vascular epiphytes comprise a characteristic habit of tropical forest, representing an important part of the plant richness and ecological functions of these forests. In Brazil, studies regarding the vascular epiphytes in the Atlantic Forest (AF) has increased in the last years, however, some states still have gaps of knowledge, like the Espírito Santo (ES), in Southeastern Brazil. In the eastern slopes of the mountainous region of the ES, there is the Duas Bocas Biological Reserve (DBBR), a protected area which comprises the main forest remnants (about 2910 hectares). Aiming to filly this gap, our goals were carried out a floristic checklist of the vascular epiphytes of the DBBR, based in field work (seven field trips) and herbarium specimens. We recorded 215 species, 91 genera, and 17 families, what fits the DBBR as one of the richest areas of the AF. The main families (Orchidaceae, Bromeliaceae, Polypodiacceae and Araceae) and genera recorded (*Aechmea, Peperomia* and *Pabstiella*) agree with the patterns founded in the AF. *Anathallis barbulata* (Lindl.) Pridgeon & M.W.Chase and *Cirrhae fuscolutea* Lindl. are recorded in ES for the first time here. Ten species are threatened at national level and 38 at state level; also 13 species recorded are classified as Data Deficient for the ES. The present study represents a first step to the knowledge of the floristic gaps in the AF of ES. However, despite the mountainous relief and difficult of access, we encourage further floristic collections in this protected area with an outstanding biological richness and with great ecosystem importance for the population.

Key words: Araceae, Atlantic Forest, Bromeliaceae, floristic, mountain, new records, Orchidaceae, seasonal forest.

Introduction

The forest which once covered the maritime mountain range of Espírito Santo state attracted the attention of the naturalists since the XIX century (e.g. Wied-Neuwied 1820; Saint-Hilaire 1833). However, today this vegetation is dramatically reduced and scattered. In Espírito Santo about 7% to 10,5% of the natural vegetation remains, with only 4% inserted in protected areas (IPEMA 2005; Rosa et al. 2019; SOS Mata Atlântica & INPE 2019). This situation is the reality in the entire Atlantic Forest, which remains only about 12% of the original vegetation (Ribeiro et al. 2009). However, it holds one of the largest biodiversity richness and endemism of the world, fitting it as a hotspot of biodiversity (Myers et al. 2000; Barthlott et al. 2005). Regarding the botanical knowledge, several forest remnants are understudied in the AF (e.g. Lima et al. 2015), mainly in the Espírito Santo, which holds one richest flora among the states of Brazil, although it's small geographical area (Werneck et al. 2011; Menini Neto et al. 2016; Rolim et al. 2016a; Dutra et al. 2015).

The vascular epiphytes are plants that lives above other plants using it just like supports (Benzing 1990; Zotz 2016). They account globally about 10% of the vascular plants, mainly in the Neotropical Region (Gentry & Dodson 1987; Kersten 2010; Zotz 2013; 2016). In the Atlantic Forest there are about 2.200 species of vascular epiphytes and the great majority are endemics (78 %) (Freitas et al. 2016). In Brazil, there are a biased effort regarding the knowledge about the vascular epiphytes in the South and Southeast Regions (Kersten 2010), however, there are several gaps even in these Regions, like the Espírito Santo state in Southeast, which have just four floristic studies (e.g. Freitas & Assis 2013; Couto et al. 2016a; 2016b; Rolim et al. 2016b).

In the eastern slopes of the Espírito Santo state, one of the biggest forest remnants is comprised by the Duas Bocas Biological Reserve (DBBR hereafter) (today the formally name is Paulo Fraga Rodrigues Biological Reserve), a state protected area (Boni et al. 2009; Rosa et al. 2019). The conservation of the vegetation in these slopes goes back to the beginning of the XX century, when the municipality of Vitória used its streams as water source for the population, which latter, in 1954, resulted in a larger river dam which was constructed to improve the water provision in the city, and is used until today supplying water for more than 50.000 peoples (Boni et al. 2009; Novelli 2010; Rosa et al. 2019). In this way, the protection of the headwaters and its vegetation, allowed that important remnant of the vegetation, which once covered great part of the slopes at

lowland and submontane ranges, became conserved. However, regarding its importance in the region, its flora is very poorly knowledge, with few botanical collections carried out in the area (e.g. Almeida & Mamede 2014; Giaretta et al. 2015). The single floristic studies carried out in the DBBR concern a floristic checklist of Arecaceae (Lima & Soares 2003). Besides, some new species were described based on collections carried out in DBBR and have restrict occurrence to the protected area or nearby (e.g. Kollmann & Peixoto 2012, Fiaschi & Pirani 2005, Camargo & Goldenberg 2011, Fraga & Saavedra, 2014, Giaretta & Fraga 2014, Carvalho-Silva et al. 2015; Bacci et al. 2016), one of them discovered during the field work of the present study (Lombardi 2021).

The gaps in knowledge of biodiversity are one of the biggest problems for conservation, so it is essential to carry out floristic studies in areas that have been little studied and with environmental heterogeneity, seeking to direct conservation efforts (Kessler 2001; Colli-Silva et al. 2016). Plant checklists provide an attractive data source based on rigorously determined plants using vouchers specimens gathered fertile and incorporated in herbaria (Clarke & Funk 2005). In this way, floristic surveys in areas that are still unknown is of great relevance for understanding the distribution patterns and processes to which biodiversity is subject (e.g. Werneck et al. 2011; Santos et al. 2014).

Here, we aim to present the first checklist of the vascular epiphytes of Duas Bocas Biological Reserve, the greatest forest fragment of the eastern slopes of the Espírito Santo mountains, in Southeaestern Brazil. We presented a list of species, ecological categories, and threatened status of the species, and compare the richness and taxonomic composition with others Atlantic Forest sites. Furthermore, we presented colour photography of 105 species.

Material and Methods

Study site

The Duas Bocas Biological Reserve (DBBR) (between 20º18′05”S and 20º19′08”S / 40º28′06”W and 40º32′28” W) covers about 2910 hectares in the eastern slopes of the mountainous coast region of the Espírito Santo State (ES), Southeastern Brazil, in Cariacica municipality (Figure 1). The conservation unit was created in 1965 to protect the vegetation and streams which supply the water provision for the municipality of Cariacica (Novelli 2010). It is situated in the Capixaba’s Mountains (*Montanhas*

Capixabas) or Castelo Mountains (*Serra do Castelo*) (Chiron & Bolsanello 2015). By occurs in the windwards slopes, the altitude in the DBBR ranges from 200 to 800 m. Consequently, the climate varies along the elevation, with the Köppen classification, ranging, in the plains from Aw to Am, and in the slopes and mountains as Cfa e Cfb (Alvares *et al.* 2013). The precipitation ranging, respectively from the low to the higher altitudes, from 1200 to 1400 mm and temperature from 20 to 24 ºC (INCAPER 2020). The dry season is from May to September, with rainfall below 100 mm per month (Alvares *et al.* 2013; INCAPER 2020). Geologically, the DBBR is situated in the slopes which comprises the mountainous region of the ES, which spreading into the interior region, mainly in central-south portion of the state (IPEMA 2005).

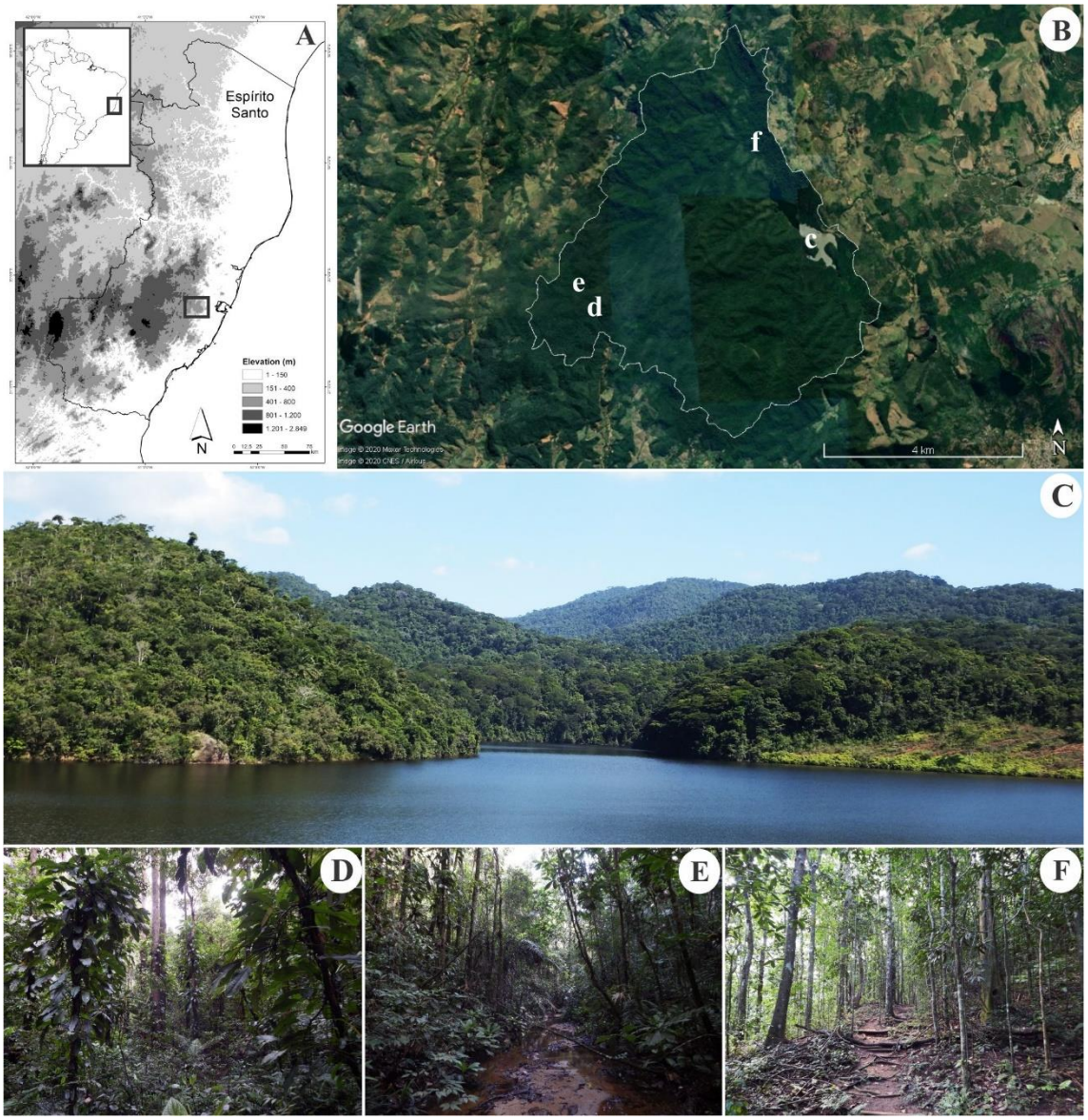


Figure 1. Geographical location of Duas Bocas Biological Reserve (DBBR), Cariacica, Espírito Santo, Southeastern Brazil. **a** Espírito Santo state, highlighting the location of

DBBR. **b** delimitation of DBBR. **c–f** Vegetation in DBBR according to the locations represented by the letters in b. (a: prepared by Henrique Lauand Ribeiro; b: adapted from Google Earth Pro; c–f: photos of Gabriel Mendes Marcusso).

The DBBR is inserted in the Atlantic Forest phytogeographical domain (Fiaschi & Pirani 2009; Thomaz 2010). The vegetation of the DBBR is usually designated as pluvial forest (Ombrophyllous Dense forest) (Magnago et al. 2007; Garbin et al. 2017; Rosa et al. 2019), which is characterized by the absence of dry season (IBGE 2012). However, the climate in the DBBR is seasonal, with a pronounced dry season (Alvares et al. 2013, INCAPER 2020), what fits it in a seasonal forest concept (IBGE 2012). Furthermore, due to the geographical location at windward slopes, with an altitudinal ranging of 600 m, the vegetation appears to be subject to a transition between a driest forest at lowlands to a moist forest in the upper belts, where orographic rains may occur (pers. obs.; Nascimento & Vale 2019). Furthermore, due to the historical of the region, the vegetation at lower altitudes of the DBBR is composed by secondary forest with intense invasion of jackfruit (*Artocarpus heterophyllus* Lam.), which occupies today the lands where in the past was used to grows coffee (*Coffea arabica* L.), banana (*Musa* spp.) and grass pasture (Boni et al. 2009).

Data collection

The floristic inventory of vascular epiphytes was carried out on seven expeditions for collection of botanical material, lasting about two days on each trip, in the months of January, May and September 2018, February, August and October 2019, and November 2020. Collections were made along the trails of *pau oco*, in the upper portion of the DBBR at about 700 m with pristine rain forest, and *represa velha*, in the low altitude portion, composed by secondary forest with jackfruit, and in the secondary forest in the road to the village of Alto Alegre, which border the ARBR. The collections were made using the trimmer on branches and fallen trees. Fertile specimens were deposited at the Herbarium Rioclarense (HRCB), and duplicates were sent to the herbaria BHCB, CESJ, RB, and UNOP (acronyms according to Index Herbariorum 2020). Sterile specimens, collected mainly fallen, were collected, and kept in a greenhouse in the Experimental Garden of

UNESP in Rio Claro for cultivation until the fertile period and subsequent process of herborization and identification. We used the SpeciesLink network (CRIA 2018) and Reflora - Virtual Herbarium (2018) to analysed specimens deposited at the herbaria BHCB, MBML, RB, SP and VIES (acronyms according to Index Herbariorum 2020) from previous collections in the DBBR, to complement the floristic inventory.

During the expeditions to the field, we observed the epiphytes' habits, and classified them in ecological categories according to their relationship with the phorophytes, following Benzing (1990): characteristic holoepiphytes, facultative holoepiphytes, primary hemiepiphytes and secondary hemiepiphytes. It was preferred to use this classification instead of that of Zotz (2013) to facilitate comparison with other studies, since most used the first one. Terrestrial species occasionally found growing in forks, hollows or cavities with accumulation of organic matter, unable to complete their biological cycle in an epiphytic state, was not considered in the study, as they are considered ephemeral epiphytes (Kersten 2010; Zotz 2016).

Taxonomic identification was made using taxonomic literature (classical works, floras, taxonomic revisions, etc.), herbarium collections of the HRCB and MBML; and consultations of specialists (taxonomists who contributed to the identification of botanical materials are cited in acknowledgements). The taxonomic classification is according to APG IV (2016) for angiosperms and PPG I (2016) for monilophytes and lycophytes. The nomenclatural determination of species and the distribution is according to BFG (2018). Conservation status at national level were obtained from Red book of Brazilian Flora (Martinelli & Moraes 2013) and at state level from Fraga et al. (2019).

Results

In the DBBR, we recorded 215 species, belonging to 91 genera and 17 families (Table 1; Figures 2-8). The richest families were Orchidaceae (85 species), Bromeliaceae (39), Polypodiaceae (21), Araceae (17) and Piperaceae (12 cada). The richest genera were *Aechmea* and *Peperomia* (12 species each), *Pabstiella* (9), *Acianthera*, *Anthurium*, *Asplenium*, *Gomesa*, *Microgramma* and *Vriesea* (7 each). According with the epiphyte's relationships with the phorophytes, the great majority of the species were characteristic holoepiphytes (177 species), followed by the facultative holoepiphytes (19), secondary hemiepiphytes (12), and primary hemiepiphytes (7).

Table 1 Vascular epiphytes species recorded in Duas Bocas Biological Reserve, Cariacica, Espírito Santo, Southeastrern Brazil. CH = characteristic holoepiphyte, FH = facultative holoepiphyte, PH = primary hemiepiphyte, SH = secondary hemiepiphyte. Voucher: ACG = A. C. Ghisolfi, APF = A. P. Fontana, AS = A. Salino, CNF = C. N. Fraga, GHM = G. H. Martins, GMM = G. M. Marcusso, GS = G. Sousa, JLMG = J. L. M. Gomes, GM = G. Martinelli, LK = L. Kollmann, MMS = M. M. Saavadera, PHL = P. H. Labiak, RCF = R. C. Forzza, TEA = T. E. Almeida. The acronyms BHCB, HRCB, MBML, RB, SP and VIES follow Index Herbariorum (2020). Threatened species were classified at national and state levels according to, respectively, Martinelli & Moraes (2013) and Fraga et al. (2019), by the following criteria: VU = vulnerable, EN = endangered, CR = critically endangered, and DD = data deficient.

Families	Species	Ecological categories	Voucher	Threatened status	
				National	State
Amaryllidaceae	*Hippeastrum aulicum* (Ker Gawl.) Herb.	CH	APF 5154 (RB)		
Araceae	*Anthurium angustifolium* Theófilo & Sakur.	CH	GMM 1580 (HRCB)		EN
Araceae	*Anthurium cleistanthum* G.Barroso	FH	GMM 1651 (HRCB)		
Araceae	*Anthurium comtum* Schott	FH	GMM 830 (HRCB)		
Araceae	*Anthurium longifolium* (Hoffmanns.) G.Don	FH	GMM 1224 (HRCB)		
Araceae	*Anthurium pentaphyllum* (Aubl.) G.Don	CH	GMM 1886 (HRCB)		
Araceae	*Anthurium scandens* (Aubl.) Engl.	CH	GMM 837 (HRCB)		
Araceae	*Anthurium solitarium* Schott	FH	GMM 1647 (HRCB)		
Araceae	*Heteropsis oblongifolia* Kunth	SH	GMM 1709 (HRCB)		
Araceae	*Monstera adansonii* Schott	PH	GMM 1518 (HRCB)		
Araceae	*Philodendron hastatum* K.Koch & Sello	SH	RCF 5378 (RB)		
Araceae	*Philodendron hatschbachii* Nadruz & Mayo	PH	GMM 1234 (HRCB)		
Araceae	*Philodendron oblongum* (Vell.) Kunth	CH	GMM 1230 (HRCB)		
Araceae	*Philodendron ornatum* Schott	PH	RCF 5006 (RB)		
Araceae	*Philodendron pedatum* (Hook.) Kunth	PH	LK 11231 (RB)		
Araceae	*Rhodospatha latifolia* Poepp.	SH	GMM 985 (HRCB)		
Araceae	*Syngonium vellozianum* Schott	SH	GMM 973 (HRCB)		
Araceae	*Thaumatophyllum stenolobum* (E.G.Gonç.) Sakur., Calazans & Mayo	PH	GMM 823 (HRCB)		

Families	Species	Ecological categories	Voucher	Threatened status	
				National	State
Aspleniaceae	*Asplenium auriculatum* Sw.	CH	GMM 1704 (HRCB)		
Aspleniaceae	*Asplenium cirrhatum* Rich. Ex Willd.	FH	GMM 839 (HRCB)		DD
Aspleniaceae	*Asplenium kunzeanum* Klotzsch ex Rosenst.	FH	GMM 1204 (HRCB)		
Aspleniaceae	*Asplenium mucronatum* C.Presl	CH	AS 14986 (BHCB)		DD
Aspleniaceae	*Asplenium oligophyllum* Kaulf.	CH	GMM 1183 (HRCB)		
Aspleniaceae	*Asplenium pteropus* Kaulf.	CH	PHL 4623 (RB)		DD
Aspleniaceae	*Asplenium serratum* L.	FH	GMM 979 (HRCB)		
Begoniaceae	*Begonia coccinea* Hook.	CH	LK 10627 (RB)	EN	EN
Begoniaceae	*Begonia convolvulacea* (Klotzsch) A.DC.	SH	GMM 1217 (HRCB)		
Begoniaceae	*Begonia fruticosa* (Klotzsch) A.DC.	SH	LK 9449 (MBML)		
Begoniaceae	*Begonia solananthera* A.DC.	SH	GMM 1530 (HRCB)		
Bromeliaceae	*Aechmea castanea* L.B.Sm.	CH	GMM 1892 (HRCB)	EN	VU
Bromeliaceae	*Aechmea coelestis* (K.Koch) E.Morren	CH	JLMG 2713 (VIES)		
Bromeliaceae	*Aechmea lamarchei* Mez	CH	GMM 1714 (HRCB)		
Bromeliaceae	*Aechmea maasii* Gouda & W.Till	FH	GM 15616 (RB)		
Bromeliaceae	*Aechmea macrochlamys* L.B.Sm.	FH	ACG 15 (VIES)	EN	VU
Bromeliaceae	*Aechmea nudicaulis* (L.) Griseb.	CH	JLMG 2722 (VIES)		
Bromeliaceae	*Aechmea patentissima* (Mart. ex Schult. & Schult.f.) Baker	FH	GM 15582 (RB)		
Bromeliaceae	*Aechmea phanerophlebia* Baker	CH	GMM 989 (HRCB)		
Bromeliaceae	*Aechmea pineliana* (Brong. ex Planch.) Baker	CH	JLMG 2514 (VIES)		
Bromeliaceae	*Aechmea racinae* L.B.Sm.	CH	GMM 1235 (HRCB)		VU
Bromeliaceae	*Aechmea ramosa* Mart. ex Schult. & Schult.f.	CH	GMM 822 (HRCB)		
Bromeliaceae	*Aechmea roberto-seidelii* E.Pereira	CH	GMM 1893 (HRCB)		EN
Bromeliaceae	*Billbergia euphemiae* E.Morren	FH	GMM 1544 (HRCB)		

Families	Species	Ecological categories	Voucher	Threatened status	
				National	State
Bromeliaceae	*Billbergia horrida* Regel	CH	GM15568 (RB)		
Bromeliaceae	*Billbergia laxiflora* L.B.Sm.	CH	GM 15619 (RB)		VU
Bromeliaceae	*Billbergia zebrina* (Herb.) Lindl.	CH	GMM 1573 (HRCB)		VU
Bromeliaceae	*Canistropsis billbergioides* (Schult. & Schult.f.) Leme	CH	GMM 1231 (HRCB)		
Bromeliaceae	*Edmundoa lindenii* (Regel) Leme	FH	APF 5211 (RB)		
Bromeliaceae	*Hohenbergia augusta* (Vell.) E.Morren	CH	GMM 1587 (HRCB)		
Bromeliaceae	*Karawata prasinata* (G. Sousa and Wanderley) J.R. Maciel and G. Sousa	CH	GS 331 (SP)		VU
Bromeliaceae	*Neoregelia farinosa* (Ule) L.B.Sm.	FH	JMLF 2718 (VIES)		VU
Bromeliaceae	*Neoregelia macrosepala* L.B.Sm.	CH	RCF 5379 (RB)		
Bromeliaceae	*Nidularium longiflorum* Ule	CH	GMM 1232 (HRCB)		
Bromeliaceae	*Nidularium procerum* Lindm.	FH	GM 15624 (RB)		
Bromeliaceae	*Quesnelia marmorata* (Lem.) R.W.Read	CH	JLMG 2731 (VIES)		DD
Bromeliaceae	*Racinaea spiculosa* (Griseb.) M.A.Spencer & L.B.Sm.	CH	GMM 1527 (HRCB)		
Bromeliaceae	*Tillandsia gardneri* Lindl.	CH	GMM 1229 (HRCB)		
Bromeliaceae	*Tillandsia geminiflora* Brongn.	CH	JLMG 2721 (VIES)		
Bromeliaceae	*Tillandsia recurvata* (L.) L.	CH	GMM 1576 (HRCB)		
Bromeliaceae	*Tillandsia stricta* Sol.	CH	GMM 990 (HRCB)		
Bromeliaceae	*Tillandsia tenuifolia* L.	CH	JLMG 2540 (VIES)		
Bromeliaceae	*Tillandsia usneoides* (L.) L.	CH	GMM 975 (HRCB)		
Bromeliaceae	*Vriesea carinata* Wawra	CH	GMM 1189 (HRCB)		
Bromeliaceae	*Vriesea drepanocarpa* (Baker) Mez	CH	JLMG 2528 (VIES)		
Bromeliaceae	*Vriesea ensiformis* (Vell.) Beer	CH	GMM 1181 (HRCB)		
Bromeliaceae	*Vriesea lubbersii* (Baker) E.Morren	CH	GMM 1233 (HRCB)		

Families	Species	Ecological categories	Voucher	Threatened status	
				National	State
Bromeliaceae	*Vriesea procera* (Mart. ex Schult. & Schult.f.) Wittm.	CH	CNF 2208 (RB)		
Bromeliaceae	*Vriesea scalaris* E.Morren	CH	RCF 5036 (RB)		
Bromeliaceae	*Vriesea simplex* (Vell.) Beer	CH	GMM 1181 (HRCB)		
Cactaceae	*Epiphyllum phyllanthus* (L.) Haw.	CH	GMM 1513 (HRCB)		
Cactaceae	*Hatiora salicornioides* (Haw.) Britton & Rose	CH	GMM 1188 (HRCB)		
Cactaceae	*Lepismium cruciforme* (Vell.) Miq.	CH	GMM 1575 (HRCB)		
Cactaceae	*Rhipsalis baccifera* (J.S.Muell.) Stearn	CH	GMM 1648 (HRCB)		
Cactaceae	*Rhipsalis elliptica* G.Lindb. ex K.Schum.	CH	GMM 821 (HRCB)		VU
Cactaceae	*Rhipsalis floccosa* Salm-Dyck ex Pfeiff.	CH	GMM 976 (HRCB)		
Cyclanthaceae	*Thoracocarpus bissectus* (Vell.) Harling	SH	GMM 1579 (HRCB)		
Dryopteridaceae	*Elaphoglossum amorimii* F.B. Matos & Mickel	CH	GMM 1715 (HRCB)		
Dryopteridaceae	*Elaphoglossum glabellum* J.Sm.	CH	AS 14975 (BHCB)		
Dryopteridaceae	*Mickelia scandens* (Raddi) R.C. Moran et al.	SH	GMM 1565 (HRCB)		
Dryopteridaceae	*Polybotrya cylindrica* Kaulf.	SH	GMM 1237 (HRCB)		
Gesneriaceae	*Codonanthe devosiana* Lem.	CH	GMM 1776 (HRCB)		VU
Gesneriaceae	*Codonanthe gracilis* (Mart.) Hanst	CH	GMM 1785 (HRCB)		
Gesneriaceae	*Nematanthus albus* Chautems	CH	GMM 1787 (HRCB)		VU
Gesneriaceae	*Nematanthus crassifolius* (Schott) Wiehler	CH	GMM 1221 (HRCB)		
Hymenophyllaceae	*Didymoglossum hymenoides* (Hedw.) Desv.	CH	PHL 5166 (RB)		
Hymenophyllaceae	*Hymenophyllum caudiculatum* Mart.	FH	GMM 1710 (HRCB)		
Hymenophyllaceae	*Hymenophyllum polyanthos* (Sw.) Sw.	FH	GMM 1703 (HRCB)		
Hymenophyllaceae	*Polyphlebium diaphanum* (Kunth) Ebihara & Dubuisson	CH	GMM 1707 (HRCB)		
Hymenophyllaceae	*Trichomanes polypodioides* L.	CH	AS 14985 (BHCB)		
Hymenophyllaceae	*Vandenboschia radicans* (Sw.) Copel.	CH	GMM 1218 (HRCB)		

Families	Species	Ecological categories	Voucher	Threatened status	
				National	State
Hymenophyllaceae	*Vandenboschia rupestris* (Raddi) Ebihara	SH	GMM 833 (HRCB)		
Lomariopsidaceae	*Lomariopsis marginata* (Schrad.) Kuhn	SH	GMM 1569 (HRCB)		
Lycopodiaceae	*Phlegmariurus flexibilis* (Fée) B.Øllg.	CH	GMM 843 (HRCB)		
Lycopodiaceae	*Phlegmariurus mandiocanus* (Raddi) B.Øllg.	CH	GMM 1196 (HRCB)		
Lycopodiaceae	*Phlegmariurus martii* (Wawra) B.Øllg.	CH	GMM 1519 (HRCB)	EN	DD
Malvaceae	*Spirotheca rivieri* (Decne.) Ulbr.	PH	GMM 1900 (HRCB)		VU
Orchidaceae	*Acianthera auriculata* (Lindl.) Pridgeon & M.W.Chase	CH	GMM 1397 (HRCB)		
Orchidaceae	*Acianthera glanduligera* (Lindl.) Luer	CH	GMM 1701 (HRCB)		
Orchidaceae	*Acianthera luteola* (Lindl.) Pridgeon & M.W.Chase	CH	GMM 1553 (HRCB)		
Orchidaceae	*Acianthera nemorosa* (Barb.Rodr.) F.Barros	CH	CNF 588 (MBML)		
Orchidaceae	*Acianthera oligantha* (Barb.Rodr.) F.Barros	CH	GMM 1391 (HRCB)		
Orchidaceae	*Acianthera pectinata* (Lindl.) Pridgeon & M.W.Chase	CH	MMS 767 (RB)		VU
Orchidaceae	*Acianthera tricarinata* (Poepp. & Endl.) Pridgeon & M.W.Chase	CH	GMM 1779 (HRCB)		
Orchidaceae	*Anathallis barbulata* (Lindl.) Pridgeon & M.W.Chase	CH	GMM 1392 (HRCB)		
Orchidaceae	*Bifrenaria aureofulva* Lindl.	CH	CNF 2335 (MBML)		EN
Orchidaceae	*Bifrenaria mellicolor* Rchb.f.	CH	GMM 1550 (HRCB)		CR
Orchidaceae	*Brasiliorchis picta* (Hook.) R.B.Singer et al.	CH	GMM 1773 (HRCB)		VU
Orchidaceae	*Campylocentrum crassirhizum* Hoehne	CH	CNF 531 (MBML)		
Orchidaceae	*Campylocentrum ornithorrhynchum* (Lindl.) Rolfe	CH	GMM 1784 (HRCB)		
Orchidaceae	*Cattleya labiata* Lindl.	CH	CNF 513 (MBML)	VU	
Orchidaceae	*Cattleya pumila* Hook.	CH	CNF 369 (MBML)	VU	CR
Orchidaceae	*Cattleya xanthina* (Lindl.) Van den Berg	CH	GMM 1749 (HRCB)	EN	EN
Orchidaceae	*Christensonella pumila* (Hook.) Szlach. et al.	CH	GMM 1780 (HRCB)		

Families	Species	Ecological categories	Voucher	Threatened status	
				National	State
Orchidaceae	*Christensonella subulata* (Lindl.) Szlach., Mytnik, Górniak & Smiszek	CH	CNF 224 (MBML)		
Orchidaceae	*Cirrhaea fuscolutea* Lindl.	CH	GMM 1396 (HRCB)	EN	
Orchidaceae	*Cirrhaea nasuta* Brade	CH	GMM 1747 (HRCB)		EN
Orchidaceae	*Dichaea brevicaulis* Cogn.	CH	GMM 1711 (HRCB)		
Orchidaceae	*Dichaea mosenii* Cogn.	CH	GMM 1381 (HRCB)	VU	
Orchidaceae	*Dichaea pendula* (Aubl.) Cogn.	CH	GMM 1187 (HRCB)		
Orchidaceae	*Elleanthus linifolius* C.Presl	CH	GMM 1922 (HRCB)		
Orchidaceae	*Encyclia patens* Hook.	CH	GMM 1777 (HRCB)		
Orchidaceae	*Epidendrum armeniacum* Lindl.	CH	GMM 1185 (HRCB)		
Orchidaceae	*Epidendrum flexuosum* G.Mey.	CH	CNF 2207 (RB)		VU
Orchidaceae	*Epidendrum geniculatum* Barb.Rodr.	CH	MMS 766 (RB)		VU
Orchidaceae	*Epidendrum proligerum* Barb.Rodr.	CH	GMM 1522 (HRCB)		
Orchidaceae	*Epidendrum rigidum* Jacq.	CH	GMM 1516 (HRCB)		
Orchidaceae	*Eurystyles actinosophila* (Barb.Rodr.) Schltr.	CH	GMM 1215 (HRCB)		
Orchidaceae	*Galeandra stangeana* Rchb.f.	CH	CNF 1865 (RB)		
Orchidaceae	*Gomesa cruciata* (Rchb.f.) M.W.Chase & N.H.Williams	CH	GMM 1778 (HRCB)		
Orchidaceae	*Gomesa flexuosa* (Lodd.) M.W.Chase & N.H.Williams	CH	CNF 252 (MBML)		
Orchidaceae	*Gomesa nitida* (Barb.Rodr.) M.W.Chase & N.H.Williams	CH	CNF 516 (MBML)		
Orchidaceae	*Gomesa pabstii* (Campacci & C.Espejo) M.W.Chase & N.H.Williams	CH	GMM 1524 (HRCB)		
Orchidaceae	*Gomesa radicans* (Rchb.f.) M.W.Chase & N.H.Williams	CH	GMM 1923 (HRCB)		
Orchidaceae	*Gomesa recurva* R.Br.	CH	GMM 1717 (HRCB)		
Orchidaceae	*Gomesa uniflora* (Booth ex Lindl.) M.W.Chase & N.H.Williams	CH	CNF 253 (MBML)		
Orchidaceae	*Heterotaxis brasiliensis* (Brieger & Illg) F.Barros	CH	GMM 1408 (HRCB)		

Families	Species	Ecological categories	Voucher	Threatened status	
				National	State
Orchidaceae	*Huntleya meleagris* Lindl.	CH	GMM 1570 (HRCB)		VU
Orchidaceae	*Jacquiniella globosa* (Jacq.) Schltr.	CH	GMM 1757 (HRCB)		VU
Orchidaceae	*Laelia gloriosa* (Rchb.f.) L.O.Williams	CH	GMM 987 (HRCB)		
Orchidaceae	*Masdevallia infracta* Lindl.	CH	GMM 1222 (HRCB)		
Orchidaceae	*Maxillaria robusta* Barb.Rodr.	CH	CNF 2 (VIES)		EN
Orchidaceae	*Miltonia candida* Lindl.	CH	CNF 985 (RB)		EN
Orchidaceae	*Miltonia clowesii* Lindl.	CH	GMM 1509 (HRCB)		
Orchidaceae	*Mormolyca rufescens* (Lindl.) M.A.Blanco	CH	GMM 1558 (HRCB)		
Orchidaceae	*Myoxanthus seidelii* (Pabst) Luer	CH	GMM 1547 (HRCB)	CR	VU
Orchidaceae	*Notylia pubescens* Lindl.	CH	GMM 1920 (HRCB)		
Orchidaceae	*Octomeria crassifolia* Lindl.	CH	GMM 1727 (HRCB)		
Orchidaceae	*Octomeria diaphana* Lindl.	CH	GMM 1364 (HRCB)		
Orchidaceae	*Octomeria juncifolia* Barb. Rodr.	CH	GMM 1774 (HRCB)		
Orchidaceae	*Octomeria linearifolia* Barb.Rodr.	CH	GMM 1748 (HRCB)		
Orchidaceae	*Octomeria praestans* Barb. Rodr.	CH	CNF 251 (MBML)		
Orchidaceae	*Octomeria tricolor* Rchb.f.	CH	GMM 1542 (HRCB)		
Orchidaceae	*Ornithocephalus myrticola* Lindl.	CH	GMM 1752 (HRCB)		
Orchidaceae	*Pabstiella biriricensis Chiron & Xim.Bols.*	CH	GMM 818 (HRCB)		DD
Orchidaceae	*Pabstiella bowmannii* (Rchb.f.) Luer	CH	APF 5186 (RB)		VU
Orchidaceae	*Pabstiella fragae* (L.Kollmann & A.P.Fontana) L.Kollmann	CH	GMM 820 (HRCB)		VU
Orchidaceae	*Pabstiella hians* (Lindl.) Luer	CH	GMM 1520 (HRCB)		
Orchidaceae	*Pabstiella imbeana* (Brade) F.Barros & C.F.Hall	CH	APF 5186 (RB)		
Orchidaceae	*Pabstiella pellifeloidis* (Barb.Rodr.) Luer	CH	GMM 1220 (HRCB)		DD
Orchidaceae	*Pabstiella punctatifolia* (Barb.Rodr.) Luer	CH	GMM 1537 (HRCB)		

Families	Species	Ecological categories	Voucher	Threatened status	
				National	State
Orchidaceae	*Pabstiella seriata* (Lindl.) Luer & Toscano	CH	GMM 1700 (HRCB)		
Orchidaceae	*Pabstiella trifida* (Lindl.) Luer	CH	GMM 1190 (HRCB)		
Orchidaceae	*Polystachya concreta* (Jacq.) Garay & Sweet	CH	GMM 1510 (HRCB)		
Orchidaceae	*Promenaea guttata* (Rchb.f.) Rchb.f.	CH	GMM 1206 (HRCB)		VU
Orchidaceae	*Prosthechea vespa* (Vell.) W.E.Higgins	CH	CNF 226 (MBML)		
Orchidaceae	*Rodriguezia pubescens* (Lindl.) Rchb.f.	CH	GMM 1880 (HRCB)		VU
Orchidaceae	*Saundersia paniculata* Brade	CH	CNF 590 (MBML)		EN
Orchidaceae	*Scaphyglottis brasiliensis* (Schltr.) Dressler	CH	GMM 1403 (HRCB)		
Orchidaceae	*Scaphyglottis modesta* (Rchb.f.) Schltr.	CH	GMM 1729 (HRCB)		
Orchidaceae	*Specklinia grobyi* (Batem. ex Lindl.) F.Barros	CH	GMM 1919 (HRCB)		
Orchidaceae	*Stanhopea lietzei* (Regel) Schltr.	CH	GMM 1394 (HRCB)		VU
Orchidaceae	*Stelis argentata* Lindl.	CH	GMM 1556 (HRCB)		
Orchidaceae	*Stelis deregularis* Barb.Rodr.	CH	GMM 1764 (HRCB)		DD
Orchidaceae	*Stelis intermedia* Poepp. & Endl.	CH	GMM 1508 (HRCB)		
Orchidaceae	*Stelis papaquerensis* Rchb.f.	CH	GMM 1557 (HRCB)		DD
Orchidaceae	*Trichocentrum pumilum* (Lindl.) M.W.Chase & N.H.Williams	CH	GMM 1718 (HRCB)		
Orchidaceae	*Trizeuxis falcata* Lindl.	CH	GMM 1728 (HRCB)		VU
Orchidaceae	*Xylobium colleyi* (Batem. ex Lindl.) Rolfe	CH	GMM 1896 (HRCB)		
Orchidaceae	*Xylobium pallidiflorum* (Hook.) G.Nicholson	CH	GMM 1770 (HRCB)		
Orchidaceae	*Xylobium undulatum* (Ruiz & Pav.) Rolfe	CH	GMM 1646 (HRCB)		
Orchidaceae	*Zygostates lunata* Lindl.	CH	GMM 1517 (HRCB)		
Piperaceae	*Peperomia alata* Ruiz & Pav.	CH	GMM 1180 (HRCB)		
Piperaceae	*Peperomia catharinae* Miq.	CH	GMM 817 (HRCB)		VU
Piperaceae	*Peperomia corcovadensis* Gardner	CH	GMM 1201 (HRCB)		

Families	Species	Ecological categories	Voucher	Threatened status	
				National	State
Piperaceae	*Peperomia glabella* (Sw.) A.Dietr.	CH	GMM 1178 (HRCB)		
Piperaceae	*Peperomia obtusifolia* (L.) A.Dietr.	CH	GMM 832 (HRCB)		
Piperaceae	*Peperomia pilicaulis* C.DC.	CH	GHM 8 (VIES)		VU
Piperaceae	*Peperomia pseudoestrellensis* C.DC.	CH	GMM 1214 (HRCB)		
Piperaceae	*Peperomia rotundifolia* (L.) Dahlst.	CH	GMM 1194 (HRCB)		
Piperaceae	*Peperomia rubricaulis* (Nees) A.Dietr.	CH	GMM 1644 (HRCB)		
Piperaceae	*Peperomia tetraphylla* (G.Forst.) Hook. & Arn.	CH	GMM 1203 (HRCB)		
Piperaceae	*Peperomia turbinata* Dahlst.	CH	GMM 966 (HRCB)		VU
Piperaceae	*Peperomia urocarpa* Fisch. & C.A.Mey.	FH	GMM 984 (HRCB)		
Polypodiaceae	*Campyloneurum crispum* Fée	FH	PHL 4898 (RB)		
Polypodiaceae	*Campyloneurum herbaceum* (Christ) Ching	PH	GMM 1564 (HRCB)		
Polypodiaceae	*Campyloneurum nitidum* (Kaulf.) C.Presl	CH	GMM 1225 (HRCB)		
Polypodiaceae	*Melpomene melanosticta* (Kunze) A.R.Sm. & R.C.Moran	CH	AS 17971 (BHCB)		
Polypodiaceae	*Microgramma crispata* (Fée) R.M.Tryon & A.F.Tryon	CH	GMM 1191 (HRCB)		DD
Polypodiaceae	*Microgramma lycopodioides* (L.) Copel.	CH	GMM 1193 (HRCB)		
Polypodiaceae	*Microgramma percussa* (Cav.) de la Sota	CH	GMM 841 (HRCB)		
Polypodiaceae	*Microgramma persicariifolia* (Schrad.) C.Presl	CH	TEA 2392 (BHCB)		DD
Polypodiaceae	*Microgramma squamulosa* (Kaulf.) de la Sota	CH	GMM 1713 (HRCB)		
Polypodiaceae	*Microgramma tecta* (Kaulf.) Alston	CH	GMM 826 (HRCB)		
Polypodiaceae	*Microgramma vacciniifolia* (Langsd. & Fisch.) Copel.	CH	GMM 977 (HRCB)		
Polypodiaceae	*Moranopteris achilleifolia* (Kaulf.) R.Y. Hirai & J. Prado	CH	AS 14976 (BHCB)		
Polypodiaceae	*Pecluma pilosa* (A.M.Evans) M.Kessler & A.R.Sm.	CH	GMM 1212 (HRCB)		DD
Polypodiaceae	*Pecluma plumula* (Willd.) M.G.Price	FH	GMM 980 (HRCB)		
Polypodiaceae	*Pecluma recurvata* (Kaulf.) M.G.Price	CH	GMM 1546 (HRCB)		

Families	Species	Ecological categories	Voucher	Threatened status	
				National	State
Polypodiaceae	*Pleopeltis astrolepis* (Liebm.) E.Fourn.	CH	GMM 1209 (HRCB)		
Polypodiaceae	*Pleopeltis furcata* (L.) A.R.Sm.	CH	GMM 836 (HRCB)		DD
Polypodiaceae	*Pleopeltis hirsutissima* (Raddi) de la Sota	CH	GMM 1176 (HRCB)		
Polypodiaceae	*Pleopeltis pleopeltifolia* (Raddi) Alston	CH	GMM 1529 (HRCB)		
Polypodiaceae	*Serpocaulon catharinae* (Langsd. & Fisch.) A.R.Sm.	CH	GMM 982 (HRCB)		
Polypodiaceae	*Serpocaulon fraxinifolium* (Jacq.) A.R.Sm.	CH	GMM 827 (HRCB)		
Pteridaceae	*Polytaenium cajenense* (Desv.) Benedict	CH	GMM 1186 (HRCB)		
Pteridaceae	*Vittaria lineata* (L.) Sm.	CH	GMM 842 (HRCB)		

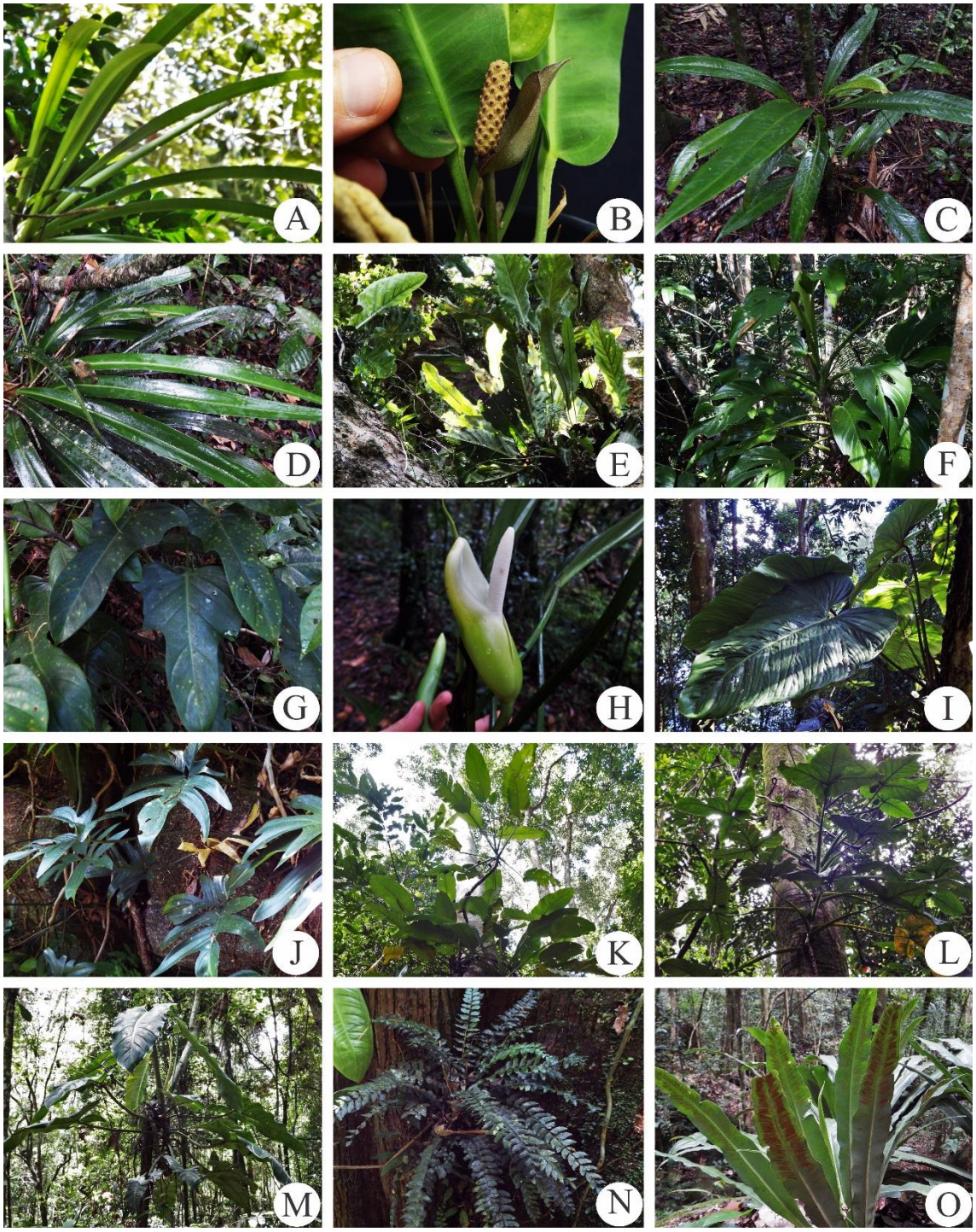


Figure 2 − Vascular epiphytes representatives of Duas Bocas Biological Reserve, Cariacica, Espírito Santo, Brazil. **a** *Hippeastrum aulicum* (Amaryllidaceae). **b-m** Araceae: **b** *Anthurium cleistanthum.* **c** *Anthurium comtum.* **d** *Anthurium longifolium*. **e** *Anthurium solitarium.* **f** *Monstera adansonii.* **g** *Philodendron hastatum*. **h** *Philodendron hatschbachii*. **i** *Philodendron ornatum.* **j** *Philodendron pedatum.* **k** *Rhodospatha latifolia.* **l** *Syngonium vellozianum.* **m** *Thaumatophyllum stenolobum.* **n-o** Aspleniaceae: **n** *Asplenium kunzeanum.* **o** *Asplenium serratum.*

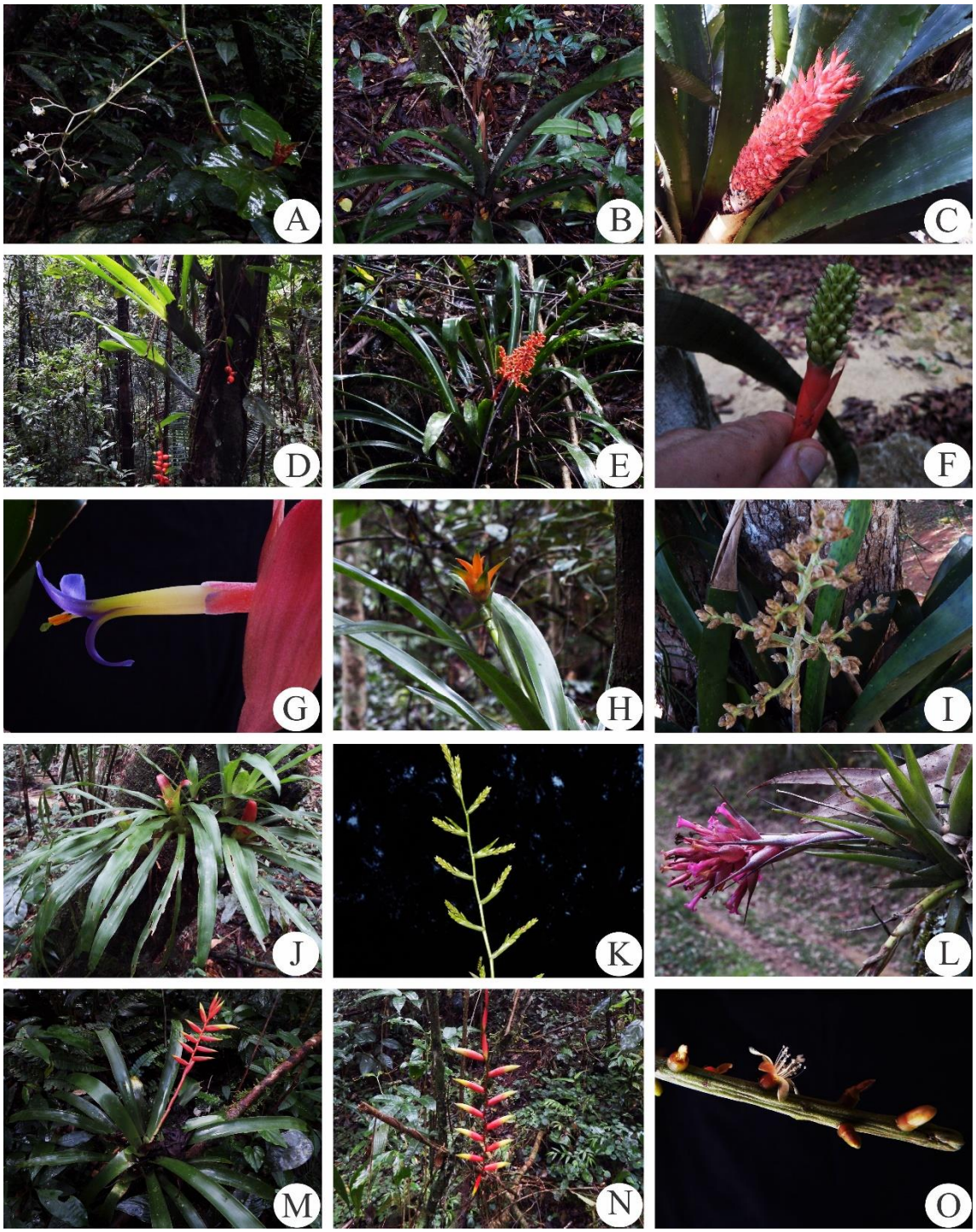


Figure 3 − Vascular epiphytes representatives of Duas Bocas Biological Reserve, Cariacica, Espírito Santo, Brazil. **a** *Begonia convolvulacea* (Begoniaceae). **b-n** Bromeliaceae: **b** *Aechmea lamarchei.* **c** *Aechmea phanerophlebia.* **d** *Aechmea racinae*. **e** *Aechmea ramosa.* **f** *Aechmea roberto-seidelii.* **g** *Billbergia euphemiae*. **h** *Canistropsis billbergioides.* **i** *Hohenbergia augusta.* **j** *Nidularium longiflorum.* **k** *Racinaea spiculosa.* **l** *Tillandsia gardneri.* **m** *Vriesea ensiformis.* **n** *Vriesea simplex.* **o** *Rhipsalis baccifera* (Cactaceae).

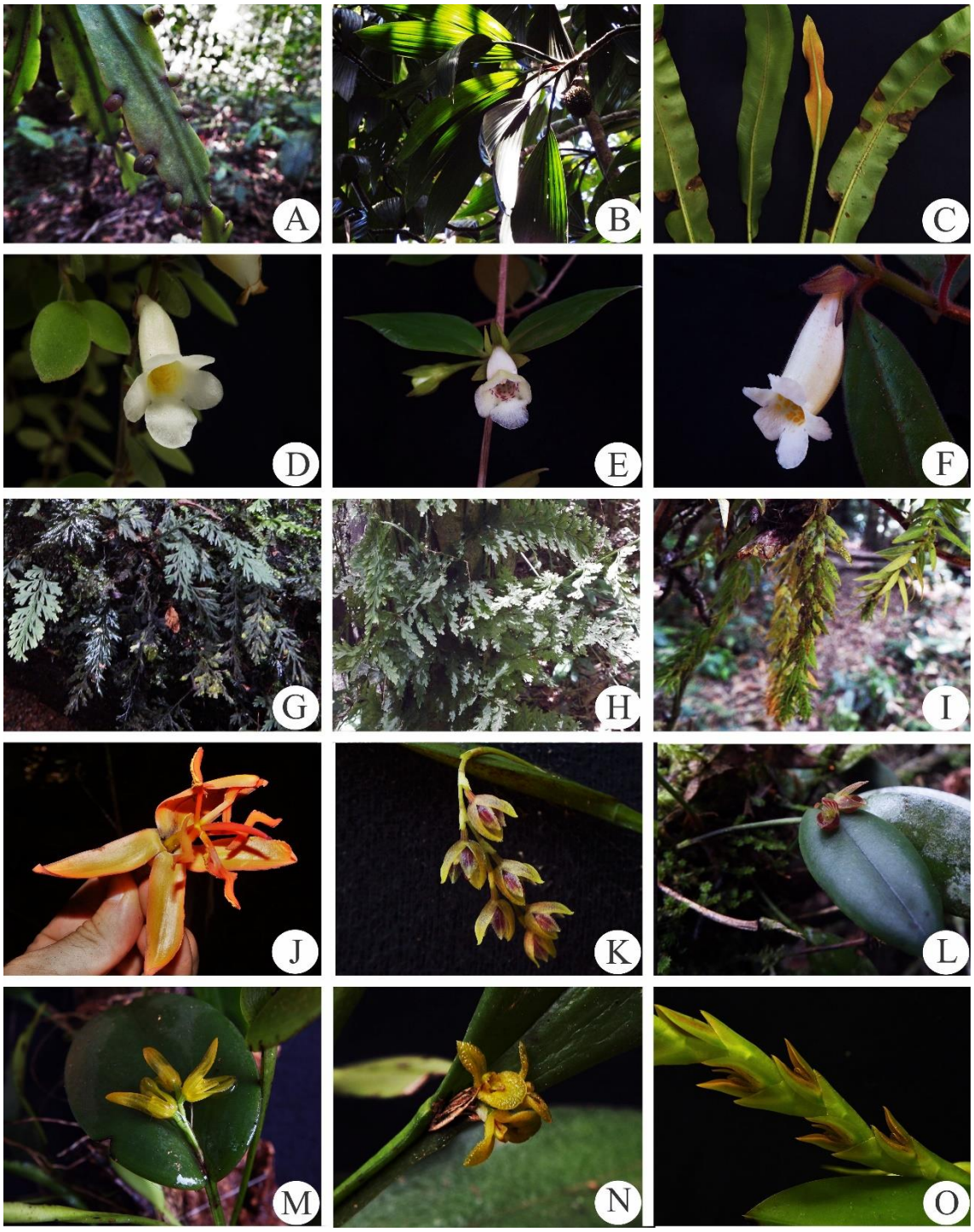


Figure 4 − Vascular epiphytes representatives of Duas Bocas Biological Reserve, Cariacica, Espírito Santo, Brazil. **a** *Rhipsalis elliptica* (Cactaceae). **b** *Thoracocarpus bissectus* (Cyclanthaceae). **c** *Elaphoglossum amorimii* (Dryopteridaceae). **d-f** Gesneriaceae: **d** *Codonanthe devosiana*. **e** *Codonanthe gracilis.* **f** *Nematanthus albus.* **g-h** Hymenophyllaceae: **g** *Hymenophyllum caudiculatum*. **h** *Vandenboschia rupestris.* **i** *Phlegmariurus flexibilis* (Lycopodiaceae). **j** *Spirotheca rivieri* (Malvaceae). **k-o** Orchidaceae: **k** *Acianthera auriculata.* **l** *Acianthera glanduligera.* **m** *Acianthera luteola.* **n** *Acianthera oligantha*. **o** *Acianthera tricarinata.*

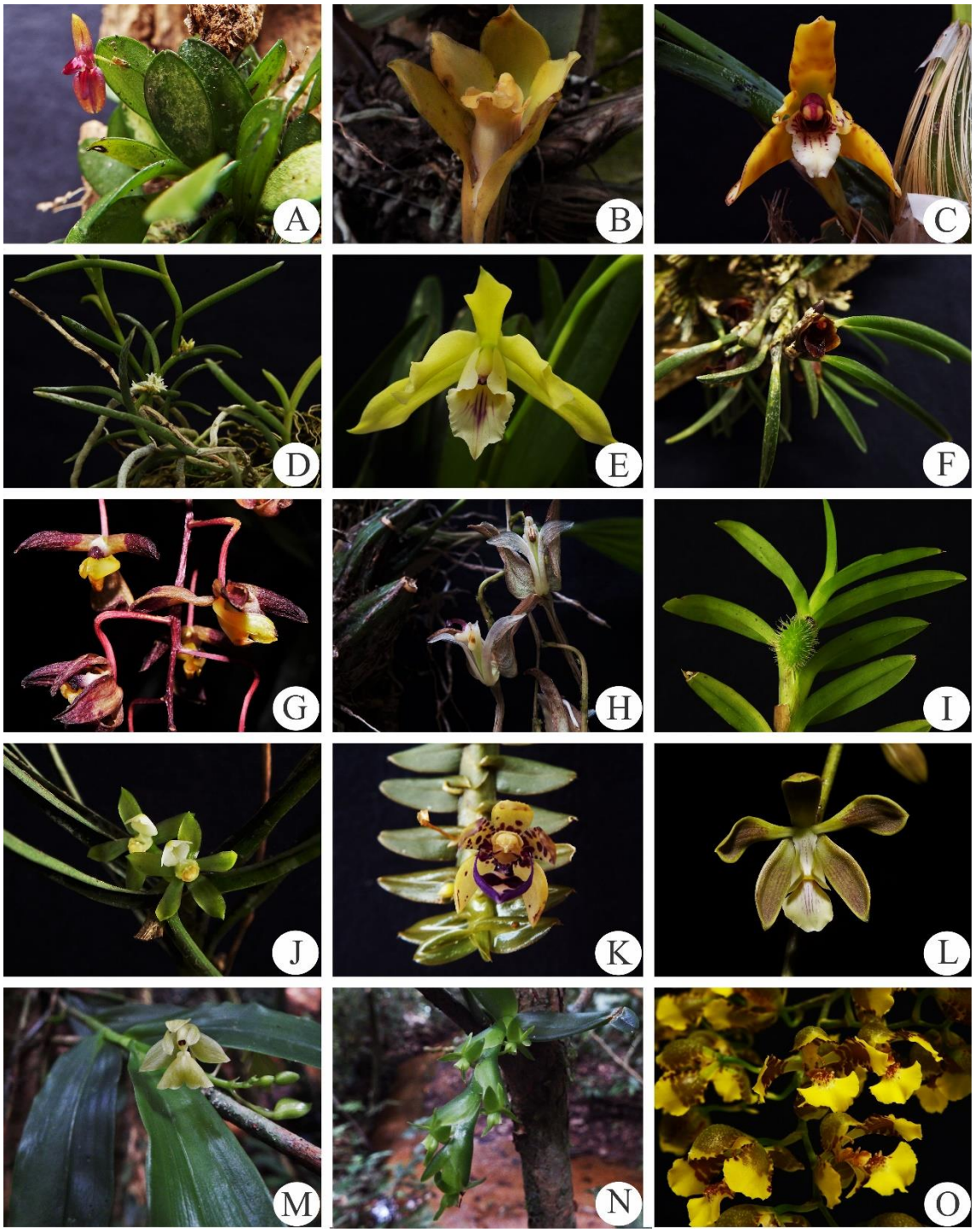


Figure 5 − Vascular epiphytes representatives of Duas Bocas Biological Reserve, Cariacica, Espírito Santo, Brazil. **a-o** Orchidaceae: **a** *Anathallis barbulata*. **b** *Bifrenaria mellicolor*. **c** *Brasiliorchis picta*. **d** *Campylocentrum ornithorrhynchum*. **e** *Cattleya xanthina*. **f** *Christensonella pumila*. **g** *Cirrhaea fuscolutea*. **h** *Cirrhaea nasuta*. **i** *Dichaea brevicaulis*. **j** *Dichaea mosenii*. **k** *Dichaea pendula*. **l** *Encyclia patens*. **m** *Epidendrum proligerum*. **n** *Epidendrum rigidum*. **o** *Gomesa cruciata*.

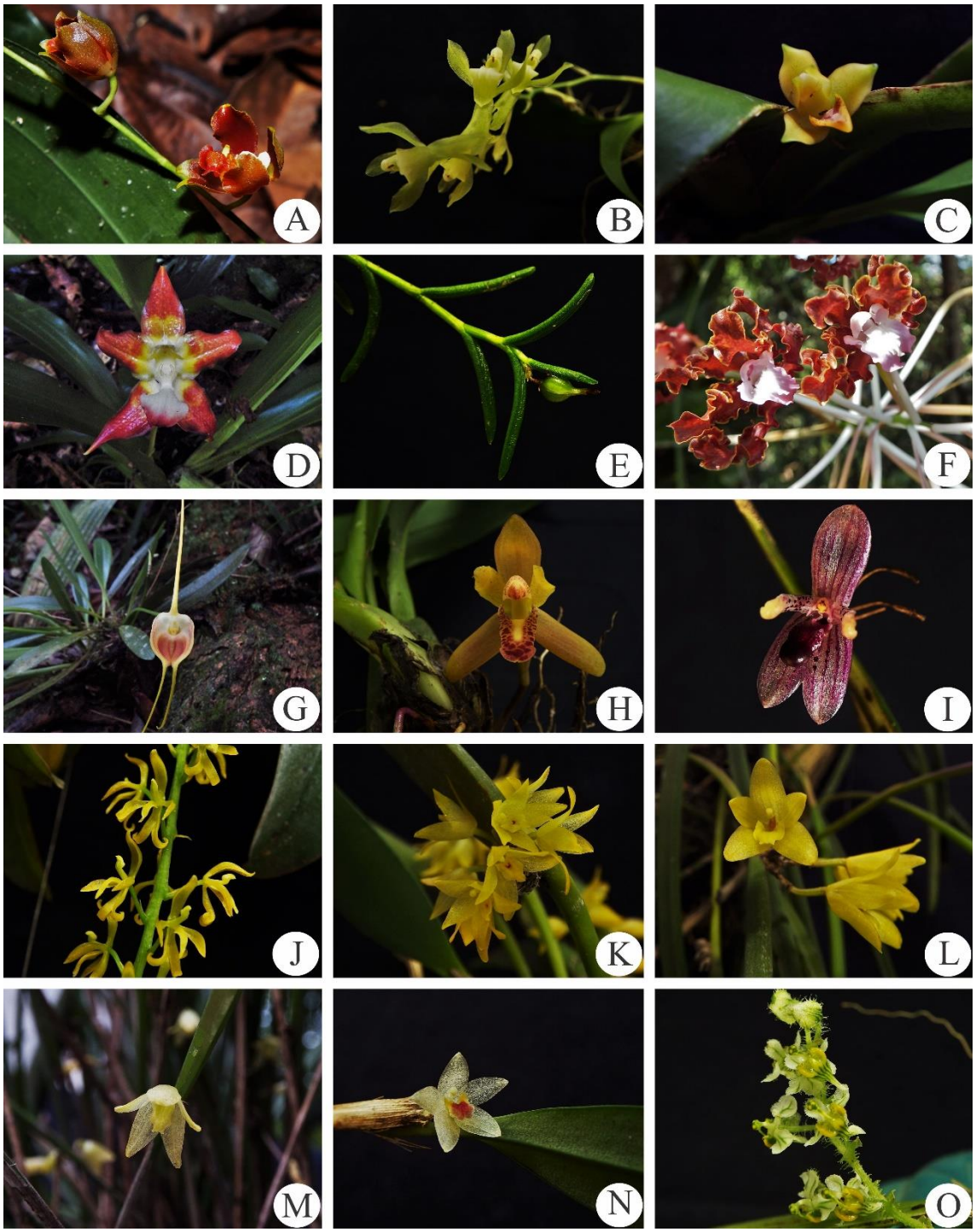


Figure 6 – Vascular epiphytes representatives of Duas Bocas Biological Reserve, Cariacica, Espírito Santo, Brazil. **a-o** Orchidaceae: **a** *Gomesa pabstii*. **b** *Gomesa recurva*. **c** *Heterotaxis brasiliensis*. **d** *Huntleya meleagris*. **e** *Jacquiniella globosa*. **f** *Laelia gloriosa*. **g** *Masdevallia infracta*. **h** *Mormolyca rufescens*. **i** *Myoxanthus seidelii*. **j** *Notylia pubescens*. **k** *Octomeria crassifolia*. **l** *Octomeria juncifolia*. **m** *Octomeria linearifolia*. **n** *Octomeria tricolor*. **o** *Ornithocephalus myrticola*.

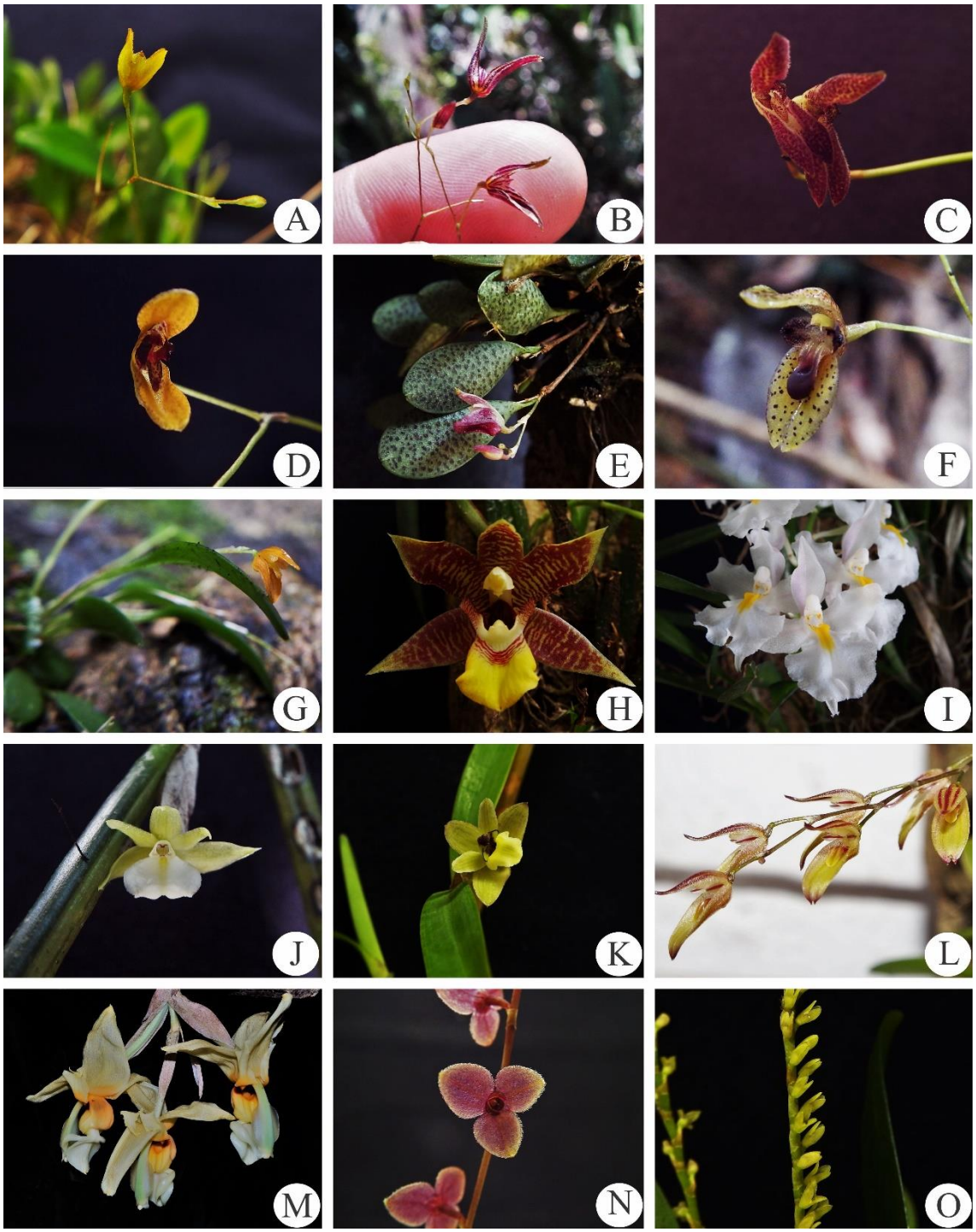


Figure 7 − Vascular epiphytes representatives of Duas Bocas Biological Reserve, Cariacica, Espírito Santo, Brazil. **a-o** Orchidaceae: **a** *Pabstiella biriricensis*. **b** *Pabstiella fragae.* **c** *Pabstiella hians.* **d** *Pabstiella pellifeloidis*. **e** *Pabstiella punctatifolia.* **f** *Pabstiella seriata.* **g** *Pabstiella trifida*. **h** *Promenaea guttata.* **i** *Rodriguezia pubescens.* **j** *Scaphyglottis brasiliensis.* **k** *Scaphyglottis modesta.* **l** *Specklinia grobyi.* **m** *Stanhopea lietzei.* **n** *Stelis argentata.* **o** *Stelis deregularis.*

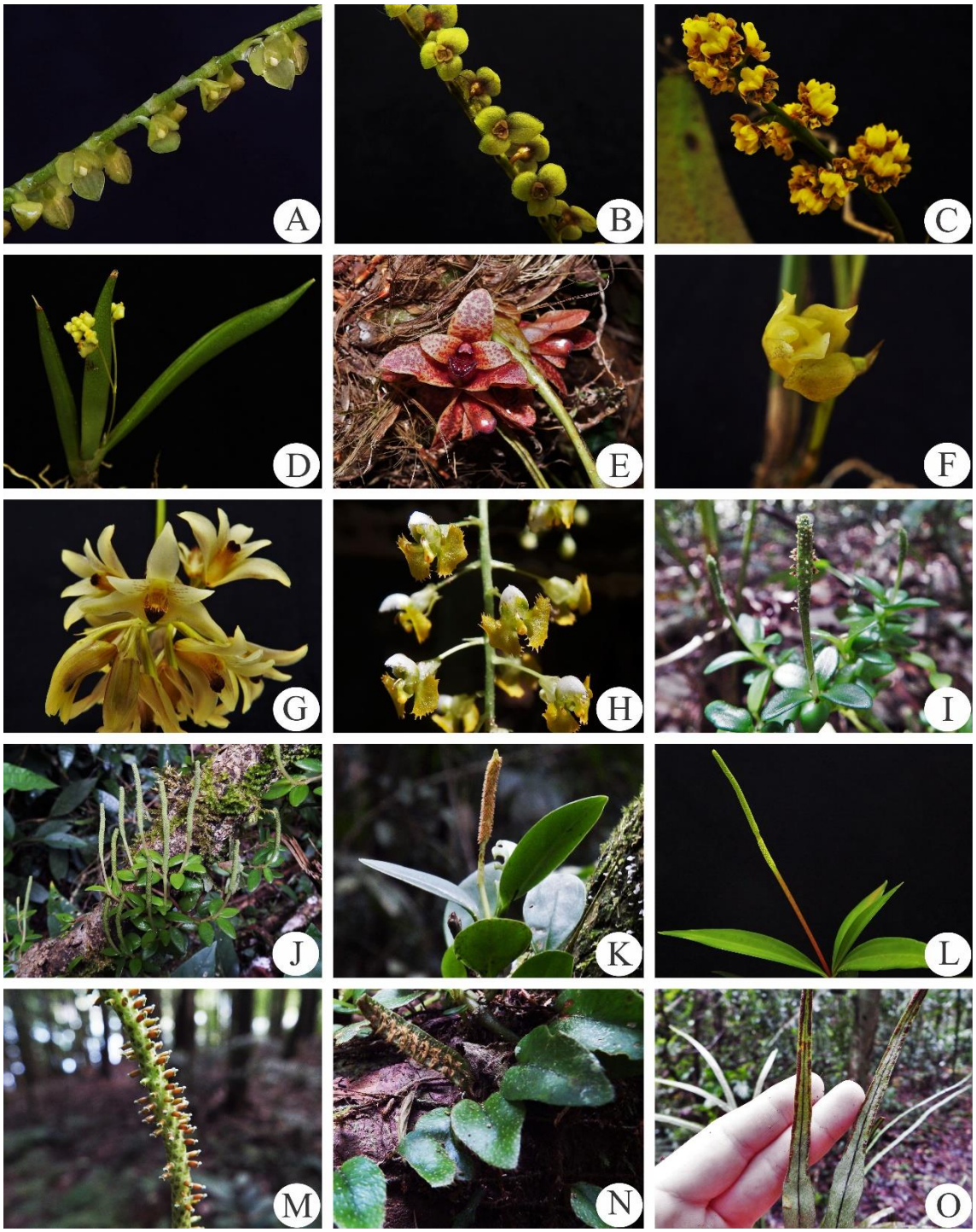


Figure 8 – Vascular epiphytes representatives of Duas Bocas Biological Reserve, Cariacica, Espírito Santo, Brazil. **a-h** Orchidaceae: **a** *Stelis intermedia*. **b** *Stelis papaquerensis*. **c** *Trichocentrum pumilum*. **d** *Trizeuxis falcata*. **e** *Xylobium colleyi*. **f** *Xylobium pallidiflorum*. **g** *Xylobium undulatum*. **h** *Zygostates lunata*. **i-m** Piperaceae: **i** *Peperomia catharinae*. **j** *Peperomia corcovadensis*. **k** *Peperomia obtusifolia*. **l** *Peperomia rubricaulis*. **m** *Peperomia turbinata*. **n-o** Polypodiaceae: **n** *Microgramma tecta*. **o** *Pleopeltis furcata*.

Discussion

The species richness recorded, in comparison with the studies carried out in Espírito Santo, fits the DBBR as one of the richest areas (Table 2). In the largest forest remnant (ca. 23,000 hectares) of the state, in the *tabuleiros* (seasonal semideciduous to evergreen forest, Saiter et al. 2017), Rolim et al. (2016b) recorded a near equall richness than we recorded in the DBBR (Table 2), in a small area and collection effort. On the other side, in southern ES, Couto et al. (2016b) surveyed the epiphytes in a seasonal semideciduous forest and recorded even smaller richness than DBBR. The epiphytic quotient in the studied area correspond to about 24% of the whole vascular flora of the DBBR (886 species, Marcusso et al. unpublished data), a number above the average for the Atlantic Forest (Kersten 2010; Freitas *et al.* 2016), as well as for the Neotropical Region (Wolf & Flamenco-S 2003).

Regarding the Atlantic Forest as a whole, the floristic surveys carried out exclusively of vascular epiphytes which recorded the highest richness, founded between 312 to 140 species (Table 2). This fact fits the DBBR as one of the richest areas in the AF. On the other hand, a small alpha diversity could be related for the DBBR, according with the surveys in the AF which sampled small areas (1 to 10 hectares) and recorded near equal richness (e.g. Schutz-Gatti 2000; Breier 2005; Petean 2009; Kersten & Waechter 2011; Caglioni 2013; 2017) (Table 2) than we recorded in the DBBR. The low alpha diversity in DBBR must be due the seasonality of the climate (Alvares et al. 2013; INCAPER 2020). In the montane region of ES, Freitas e Assis (2013) registered few species in 120 phorophytes, corroborating that a low alpha-diversity of VE occurs in the ES mountains, although a high turnover (beta-diversity) appears to occur. Further communities' surveys, in delimited sample areas, will help to improve the knowledge regarding this issue. In this way, the present floristic checklist represents a first step for further studies about the vascular epiphyte's communities in the mountainous region of ES.

Table 2 Local floristic surveys exclusively of vascular epiphytes in the Atlantic Forest, organized in descending order of species richness, comparing with the present study in the Duas Bocas Biological Reserve, Cariacica, Espírito Santo, Southeastern Brazil. (BA: Bahia, ES: Espírito Santo, MG: Minas Gerais, PR: Paraná, RJ: Rio de Janeiro, SC: Santa Catarina, SP: São Paulo; Spp: species number, Gen: genera number, Fam: families number; NI Data not informed in the source; PF Pluvial Forest, SF Seasonal Forest; Arac: Araceae, Brom: Bromeliaceae, Cact: Cactaceae, Dryo: Dryopteridaceae, Gesn: Gesneriaceae, Hyme: Hymenophyllaceae, Mora: Moraceae, Pipe: Piperaceae, Poly: Polypodiaceae). Source: 1. Fontoura et al. (1997); 2. Blum et al. (2011); 3. Leitman et al. (2014); 4. Furtado & Menini Neto (2018); 5. Present study; 6. Rolim et al. (2016b); 7. Breier (2005); 8. Schutz-Gatti (2000); 9. Caglioni (2017); 10. Breier (2005); 11. Petean (2009); 12. Caglioni (2013); 13. Kersten & Waechter (2011) (* excluded mistletoes; ** including only angiosperms).

Location	SPE	GEN	FAM	Altitude (m)	Precipitation (mm)	Temperature (C°)	Area (ha)	Vegetation type	Source	Richest families
Macaé de Cima, RJ	312	87	26	880-1720	2128	17,9	7200	PF	1*	Orch (184); Brom (40); Poly (14); Cact (7); Dryo/Gesn (6)
Serra da Prata, PR	278	109	30	300-1100	2290	NI	6,3	PF	2	Orch (103); Brom (38); Poly (28); Hyme (15); Arac/Pipe (14)
Serra das Lontras, BA	256	87	18	400-1000	1300-1600	24	11000	PF	3**	Orch (103); Brom (62); Arac (29); Pipe (15); Cact/Gesn (7)
Ibitipoca, MG	224	81	22	1000-1800	1532	18,9	300	SF-PF	4	Orch (86); Poly (27); Brom (25); Hyme (14); Aspl (11)
Duas Bocas, ES	**215**	**91**	**17**	**200-800**	**1200-1400**	**20-24**	**2910**	**SF**	**5**	**Orch (85); Brom (39); Poly (21); Arac (17); Pipe (12)**
Reserva da Vale, ES	184	82	19	30-60	1227	23,3	22000	SF	6	Orch (82); Arac (23); Brom (22); Poly (15); Mora/Pipe (10)
Cananéia, SP	178	84	33	15	2027	22,6	10,24	PF (restinga)	7*	Orch (72); Brom (33); Poly/Arac (11); Hyme (6)
Salto Morato, PR	173	73	27	60	2000	21	3,15	PF	8	Orch (56); Brom (31); Poly (12); Pipe (11); Arac (9)

Location	SPE	GEN	FAM	Altitude (m)	Precipitation (mm)	Temperature (Cº)	Area (ha)	Vegetation type	Source	Richest families
Morro do Baú, SC	168	81	23	340-810	1600-2000	21	1,5	PF	9	Orch (63); Brom (28); Poly (17); Arac/Dryo (9)
Sete Barras, SP	161	75	27	140	1591	18,1	10,24	PF	10*	Orch (42); Brom (27); Poly (14); Arac (13); Cact (11)
Antonina, PR	159	78	22	20-50	2000	21	1	PF	11	Orch (61); Brom (24); Poly (14); Arac (11); Cact (9)
Serra do Itajaí, SC	159	76	23	295-345	1399-1752	17,9-20,3	1,8	PF	12	Orch (55); Brom (24); Poly (16); Arac (9); Dryo/Hyme (8)
Piraquara, PR	140	65	24	980	1426	16,7	20	PF	13	Orch (45); Poly (23); Brom (20); Hyme (9); Cact/Dryo (6)

DBBR is a forest remnant situated in mountainous relief, with slopes, valleys, and inselbergs, without access and trails for the core areas, becoming a difficult area to access and study. Despite these facts, and the high richness recorded in a small sampled area (only three trails), additional species are expected to occur in the area, as exemplified by some species observed sterile during the study and for this they are not included in the checklist (e.g. Araceae: *Philodendron edmundoi* G.M.Barroso, *Thaumatophyllum corcovadense* (Kunth) Sakur., Calazans & Mayo; *Bifrenaria clavigera* Rchb.f., *Brasiliorchis* cf. *gracilis* (Lodd.) R.B.Singer et al., *Catasetum* sp., *Elleanthus brasiliensis* (Lindl.) Rchb.f., *Epidendrum avicula* Lindl., *Epidendrum* cf. *paranaense* Barb.Rodr., *Epidendrum vesicatum* Lindl., *Grandiphyllum* sp., *Leptotes tenuis* Rchb.f.; Rubiaceae: *Hillia* sp.).

The families recorded in the DBBR (Table 2) are in accordance with the studies carried out in the AF (Kersten 2010; Freitas et al. 2016), with few exceptions. Orchidaceae always is the richest family, followed for Bromeliaceae, which sometimes, according with the elevation, is replaced by Araceae in the low-latitude sites (Rolim et al. 2016b), and by Polypodiaceae in the high-altitude sites (Kersten & Waechter 2011; Furtado & Menini Neto 2018). Fontoura et al. (2012), also demonstrated the influence of the altitude and latitude in the distribution of Bromeliaceae, and Rocha (2011) also founded Araceae with high richness in low altitude sites in the Rio de Janeiro state. Varying the importance according with the geographical location, Piperaceae, Cactaceae, Hymenophyllaceae, and Dryopteridaceae (Table 2) also represents important families in the AF (Kersten 2010; Freitas et al. 2016), corroborated here in the present study.

In DBBR, ten species are threatened of extinction at national level, being one of them - *Myoxanthus seidelii* (Fig. 6I) - Critically Endangered (Moraes & Martinelli 2013), and 38 threatened at state level, two of then - *Bifrenaria mellicolor* and *Cattleya pumila* - Critically Endangered. Furthermore, 13 species are considered Data Deficient at state level (Fraga et al. 2019) (Table 1), highlighting the importance of floristic studies in areas with few samples, like the DBBR, to bring new data about this poor know taxa. In addition, *Anathallis barbulata* (Fig. 5A) and *Cirrhae fuscolutea* (Fig. 5G; an endangered species at national level), are here recorded in ES for the first time. More than half of the recorded species are endemic of the Atlantic Forest (120 species or near 56%), of that, 14 are endemic to ES (according to BFG 2018; Flora do Brasil 2020 under construction) supporting the high levels of endemism for the Atlantic Forest (Stehmann *et al.* 2009; Freitas *et al.* 2016).

Overall, we could improve the samples of vascular epiphytes in the DBBR, which comprises the most important forest remnant of the windward slopes of the mountains of Espírito Santo, Southeast Brazil. Here, we demonstrate that this forest patch holds a relevant richness, demonstrating the necessity of this protected area as a refuge to the species, surrounded by anthropic areas and pressed by the urban development. In this way, the DBBR could be treated as an important like-refuge to the epiphytes and consequently whole biota (Ackerman 2014).

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Capítulo 3

Augusto Ruschi Biological Reserve vascular epiphytes: a hotspot in the Atlantic Forest of Southeastern Brazil

Abstract

The Atlantic Forest is globally known as a hotspot of biodiversity, with high levels of endemism and richness. However, within the domain, different localities can show different floristic diversity. In Southeastern Brazil, the state of Espírito Santo is one of these areas. Here, we present the first comprehensive checklist of the Augusto Ruschi Biological Reserve (ARBR) vascular epiphytes, a national protected area in the mountainous region of the state. Based on field expeditions carried out between 2018 and 2020 and herbarium specimens, we reported a total of 360 species, 116 genera, and 20 families. *Epidendrum henschenii* Barb.Rodr. and *Thysanoglossa organensis* Brade are new records to the state. The richness recorded here is outstanding in the Atlantic Forest and one of the highest recorded in the Neotropical Region. The actual climatic conditions in the ARBR may help us understand this high species-richness, as well as the long-term climatic stability perhaps since the Miocene. Besides, the heterogeneity of the mountain habitats, driven mainly by erosion of the highlands since the early Cenozoic, resulted in the actual mountain's configuration of eastern Brazil, synchronously with most taxa diversification occurred in the Atlantic Forest. The present study demonstrated the importance of the protected areas for the conservation of biodiversity and the importance of floristic studies in areas still poorly known in the Atlantic Forest, mainly in mountainous regions.

Keywords: Brazil, checklist, Espírito Santo, floristic, mountains, new records

Introduction

The Atlantic Forest (AF) holds one of the highest floristic richness and endemism of the world (Myers *et al.* 2000; Barthlott *et al.* 2005). However, the high species richness of the AF is not equally distributed in the domain, with some areas presenting outstanding high floristic richness, such as the case of the southern coast of Bahia and northern Espírito Santo states (Giulietti *et al.* 2009; Werneck *et al.* 2011; Rolim *et al.* 2016a). Among the Brazilian states, Espírito Santo has one of the highest numbers of angiosperms species - almost 32% of the Brazilian native species - with one of the smallest geographic areas (occupying about 0,5 % of the Brazilian territory) (Dutra *et al.* 2015; BFG 2018).

Several studies have demonstrated the relationships of the biota diversification with stable climatic areas (Prance 1982; Perret *et al.* 2016; Carnaval & Moritz 2008), and the importance of heterogeneity, as the mountain habitats, in generating isolated places (island-like habitat) and offering different niches to occupy and evolve (Gentry & Dodson 1987a; Körner 2004; Kreft & Jetz 2007; Antonelli 2018; Perrigo *et al.* 2019). In the mountainous region of Espírito Santo, the municipality of Santa Teresa is one of the most biodiverse places of the AF, with one of the highest numbers of tree species (Saiter & Thomaz 2014; Rolim *et al.* 2019a), holding a high level of plant endemism (Werneck *et al.* 2011; Pereira *et al.* 2019), and with several new plant taxa still being discovered (*e.g.*, Campos-Rocha *et al.* 2018; Carvalho-Silva *et al.* 2019; Flores *et al.* 2019; Trad *et al.* 2020). Additionally, the municipality shows high levels of diversity for amphibians (Ferreira *et al.* 2019), birds (Simon 2000), butterflies (Brown & Freitas 2000), and small mammals (Passamani *et al.* 2000).

Worldwide, vascular epiphytes encompass about 10% of all vascular plants (Zotz 2013; 2016). In the AF, the vascular epiphytes comprise 15% of the species (Freitas *et al.* 2016). Despite this high importance of vascular epiphytes in the AF, floristic surveys focused in this synusia are still scarce in the state of Espírito Santo, with only four studies carried out in six localities (Freitas & Assis 2013; Couto *et al.* 2016a, 2016b; Rolim *et al.* 2016b). Although habit-focused efforts are important to reach better results in biodiversity research (*e.g.*, Leitman *et al.* 2014), only recently few surveys of vascular plants in Espírito Santo considered the epiphytes in the checklists (*e.g.*, Souza *et al.* 2016; Couto *et al.* 2017; Pena & Alves-Araújo 2017; Zorzanelli *et al.* 2017).

Due to this gap and the floristic diversity of the mountains of Espírito Santo, in Southeastern Brazil, we aim to present a comprehensive checklist of the floristic composition of vascular epiphytes of the Augusto Ruschi Biological Reserve, a national protected area and compare the richness with other surveys involving vascular epiphytes in the Neotropical Region. Besides, we discuss the possible biogeographical causes for the diversity observed and provided photography of living plants of 134 species.

Materials and methods

Study area – The Augusto Ruschi Biological Reserve (ARBR hereafter) (central coordinates 19°53'37"S and 40°32'46"W) (Figure 1), first called Nova Lombardia Biological Reserve, is a national protected area, created in 1982 to protect ca. 3.560 hectares mainly of pristine forest in Santa Teresa municipality, Espírito Santo (ES), Southeastern Brazil (Decree No. 87.589, 20 September 1982, Decree No. 92.753, 5 June 1986). The state is divided into two geomorphological compartments: the Barreiras formation, occurring in the narrow coastal plain of the south of the state, becoming wider in the north; and the mountainous region, occupying the interior portion of the state, with the altitude varying from sea level to 2987 m, in *Serra do Caparaó* (IPEMA 2005). The predominant climate, according to the Köppen classification, in the plain is Aw and Am and Cfa and Cfb in the mountain region (Alvares *et al.* 2013). The entire state of Espírito Santo is inserted in the Atlantic Forest domain, represented by several types of vegetation, such as Mangroves, *Restingas*, Seasonal Deciduous, Evergreen, and Semideciduous Forests, high altitude grassland, and Ombrophilous Dense Forest (Simonelli & Fraga 2007; Garbin *et al.* 2017; Saiter *et al.* 2017; 2020). In the ARBR, the seasonal forest is the main vegetation type.

The current study was carried out in the mountainous region in the south-central portion of Espírito Santo, locally known as Serra do Castelo (Chiron & Bolsanello 2015) or Montanhas Capixabas. Some authors consider these mountains as part of Serra do Mar (Scaramuzza et al. 2011), and others as Serra da Mantiqueira (Silva et al. 2018; Pereira 2019). In ES, these mountains spread by 140 km in length and 100 km wide. It is bounded in the north by the Doce River valley, in the east by the coastal plain, in the south by the Itapemirim River valley, in the southwest by Serra do Caparaó, in the northwest by the state of Minas Gerais and Serra da Chibata, and its average altitude is 700 meters, ranging

from sea level to 2050 meters (Chiron & Bolsanello 2015). In ARBR, the elevation ranges between 780 and 1150 m.

In the municipality of Santa Teresa, the annual temperature average is 20ºC, and the precipitation is 1300 mm, with seasonal drought during April and September (Alvares *et al.* 2013). The mountainous relief of Santa Teresa influences the unequal rainfall distribution in the eastern to western direction, with a high rainfall rate in the slopes at windward, characterizing an orographic rainfall with a western rain shadow (Nascimento & Vale 2019).

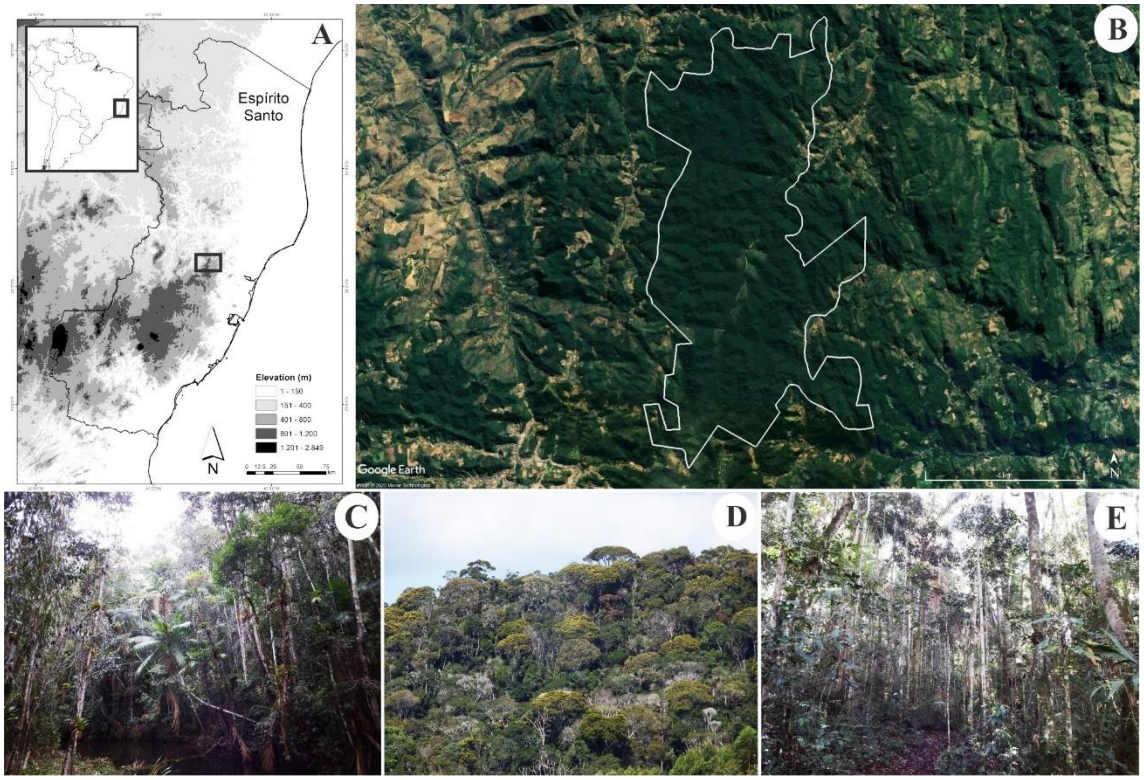


Fig. 1 Geographical location of the Augusto Ruschi Biological Reserve (ARBR), Santa Teresa, Espírito Santo, Brazil. **a** the state of Espírito Santo, highlighting the location of the ARBR. **b** delimitation of the ARBR. **c–e** ARBR vegetation. (a: prepared by Henrique Lauand Ribeiro; b: adapted from Google Earth Pro; c–e: photos of Gabriel Mendes Marcusso).

Floristic survey – The vascular epiphytes floristic inventory was carried out on six expeditions to collect botanical material. Each trip lasted about three days, in January, May, and September 2018, February, August, and October 2019, and then November 2020. Collections were made along the trails and in the roads, which crosses the ARBR. The collections were made using the trimmer on branches and fallen trees. Fertile specimens were deposited at the Herbarium Rioclarense (HRCB), and duplicates were

sent to the herbaria BHCB, CESJ, RB, and UNOP (acronyms according to Index Herbariorum 2020). Sterile specimens, collected mainly fallen, were collected, and kept in a greenhouse in the Experimental Garden of UNESP in Rio Claro for cultivation until the fertile period and subsequent herborization and identification process. We used the SpeciesLink network (CRIA 2018) and Reflora - Virtual Herbarium (2018) to analyse specimens deposited at the herbaria BHCB, HRCB, MBM, MBML, and RB (acronyms according to Index Herbariorum 2020) from previous collections in the ARBR, to complement the floristic inventory.

During the field expeditions, we observed the epiphytes' habits. According to their relationship with the phorophytes, we classified them into ecological categories, following Benzing (1990): characteristic holoepiphytes, facultative holoepiphytes, primary hemiepiphytes, and secondary hemiepiphytes. It was preferred to use this classification instead of Zotz (2013) to facilitate comparison with other studies since most of them used the first one. Terrestrial species occasionally found growing in forks, hollows, or cavities with an accumulation of organic matter, unable to complete their biological cycle in an epiphytic state, were not considered in the study, as they are considered ephemeral epiphytes (Kersten 2010; Zotz 2016).

Taxonomic identification was carried out using taxonomic literature (classical works, floras, taxonomic revisions, etc.), herbarium collections of the HRCB and MBML; and consultations with specialists (the taxonomists who contributed to the identification of botanical materials are cited in the acknowledgments). The taxonomic classification is according to APG IV (2016) for angiosperms and PPG I (2016) for monilophytes and lycophytes. The nomenclatural determination of species and the distribution is according to FLORA DO BRASIL 2020 (http://floradobrasil.jbrj.gov.br/; BFG 2018). The conservation status at the national level was obtained from Red book of Brazilian Flora (Martinelli & Moraes 2013) and at the state level from Fraga *et al.* (2019).

Results

We recorded 360 species, distributed in 116 genera and 20 families (Table 1; Figures 2-10). Ferns and lycophytes were represented by 77 species (eight families), and the other 284 were composed of angiosperms (12 families). The five richest families were Orchidaceae (156 species), Bromeliaceae (63), Araceae and Polypodiaceae (28 each), and Dryopteridaceae (22). The richest genera were *Vriesea* (27 species), *Elaphoglossum* and *Epidendrum* (16 each), *Octomeria* (13), and *Aechmea*, *Pabstiella* and *Philodendron* (12 each).

The great majority of the species were classified as characteristic holoepiphytes (301 species), followed by facultative holoepiphytes (32), secondary hemiepiphytes (20), and primary hemiepiphytes (7).

Table 1 Vascular epiphytes species recorded in the Augusto Ruschi Biological Reserve, Santa Teresa, Espírito Santo, Brazil. CH = characteristic holoepiphyte, FH = facultative holoepiphyte, PH = primary hemiepiphyte, SH = secondary hemiepiphyte. Voucher: AS = A. Salino, EL = E.Lagasa, GMFA = G.M.F. Aquije, GMM = G.M. Marcusso, HQB = H.Q. Boudet, JAL = J.A. Lombardi, JR = J. Rossini, LK = L. Kollmann, LSBC = L.S.B. Calazans, MB = M. Bolson, RRV = R.R. Vervloet and TBF = T.B. Flores. The acronyms BHCB, ESA, HRCB, MBM, MBML, and RB follow Index Herbariorum (2020). Threatened species were classified at national and state levels, respectively, according to Martinelli & Moraes (2013) and Fraga *et al.* (2019), by the following criteria: VU = vulnerable, EN = endangered, and CR = critically endangered.

Family	Species	Ecological categories	Voucher	Threatened status	
				National	State
Amaryllidaceae	*Hippeastrum aulicum* (Ker Gawl.) Herb.	CH	RRV 472 (MBML)		
Araceae	*Anthurium angustifolium* Theófilo & Sakur.	CH	GMM 1297 (HRCB)		EN
Araceae	*Anthurium comtum* Schott	CH	GMM 1244 (HRCB)		
Araceae	*Anthurium ianthinopodum* (Schott ex Engl.) Nadruz & Mayo	CH	LK 4844 (MBML)		
Araceae	*Anthurium intermedium* Kunth	FH	GMM 1290 (HRCB)		
Araceae	*Anthurium jilekii* Schott	CH	RRV 121 (MBML)		
Araceae	*Anthurium longifolium* (Hoffmanns.) G.Don	CH	GMM 1106 (HRCB)		
Araceae	*Anthurium pentaphyllum* (Aubl.) G.Don	CH	GMM 1462 (HRCB)		
Araceae	*Anthurium scandens* (Aubl.) Engl.	CH	GMM 901 (HRCB)		
Araceae	*Anthurium solitarium* Schott	FH	RRV 2224 (MBML)		
Araceae	*Heteropsis oblongifolia* Kunth	PH	GMM 1674 (HRCB)		
Araceae	*Heteropsis salicifolia* Kunth	PH	RRV 1271 (MBML)		
Araceae	*Monstera adansonii* Schott	CH	LK 4860 (MBML)		
Araceae	*Philodendron bernardopazii* E.G.Gonçalves	PH	GMM 1317 (HRCB)		
Araceae	*Philodendron cordatum* Kunth ex Schott	CH	GMM 1649 (HRCB)		
Araceae	*Philodendron edmundoi* G.M.Barroso	CH	RRV 2361 (MBML)		
Araceae	*Philodendron hastatum* K.Koch & Sello	SH	GMM 1631 (HRCB)		
Araceae	*Philodendron hatschbachii* Nadruz & Mayo	SH	GMM 1315 (HRCB)		
Araceae	*Philodendron hederaceum* (Jacq.) Schott	SH	LK 4850 (MBML)		

Family	Species	Ecological categories	Voucher	Threatened status	
				National	State
Araceae	*Philodendron oblongum* (Vell.) Kunth	SH	GMM 1112 (HRCB)		
Araceae	*Philodendron ornatum* Schott	PH	GMM 914 (HRCB)		
Araceae	*Philodendron pedatum* (Hook.) Kunth	CH	GMM 1806 (HRCB)		
Araceae	*Philodendron propinquum* Schott	PH	GMM 934 (HRCB)		
Araceae	*Philodendron rhodospermum* Calazans & Sakur.	PH	LSBC 213 (RB)		EN
Araceae	*Philodendron rudgeanum* Schott	PH	RRV 2192 (MBML)		
Araceae	*Rhodospatha latifolia* Poepp.	SH	LK 4688 (MBML)		
Araceae	*Rhodospatha oblongata* Poepp.	SH	RRV 1756 (MBML)		EN
Araceae	*Syngonium vellozianum* Schott	CH	GMM 1683 (HRCB)		
Araceae	*Thaumatophyllum corcovadense* (Kunth) Sakur., Calazans & Mayo	PH	LSBC 217 (RB)		VU
Aspleniaceae	*Asplenium auriculatum* Sw.	CH	GMM 1110 (HRCB)		
Aspleniaceae	*Asplenium harpeodes* Kunze	CH	RRV 422 (MBML)		
Aspleniaceae	*Asplenium kunzeanum* Klotzsch ex Rosenst.	CH	LK 4744 (MBML)		
Aspleniaceae	*Asplenium pteropus* Kaulf.	CH	AS 14071 (BHCB)		
Aspleniaceae	*Asplenium scandicinum* Kaulf.	CH	GMM 1682 (HRCB)		
Aspleniaceae	*Asplenium truncorum* F.B.Matos et al.	CH	RRV 559 (MBML)		EN
Begoniaceae	*Begonia convolvulacea* (Klotzsch) A.DC.	CH	GMM 1305 (HRCB)		
Begoniaceae	*Begonia fruticosa* (Klotzsch) A.DC.	CH	LK 4872 (MBML)		
Begoniaceae	*Begonia solananthera* A.DC.	SH	GMM 1461 (HRCB)		
Blechnaceae	*Lomaridium plumieri* (Desv.) C. Presl.	SH	GMM 1612 (HRCB)		
Bromeliaceae	*Aechmea araneosa* L.B.Sm.	CH	GMM 1154 (HRCB)		VU
Bromeliaceae	*Aechmea capixabae* L.B.Sm.	FH	GMM 1318 (HRCB)		EN
Bromeliaceae	*Aechmea castanea* L.B.Sm.	CH	GMM 1102 (HRCB)	EN	VU
Bromeliaceae	*Aechmea coelestis* (K.Koch) E.Morren	CH	RRV 473 (MBML)		
Bromeliaceae	*Aechmea hostilis* E.Pereira	FH	RRV 2334 (MBML)		VU

Family	Species	Ecological categories	Voucher	Threatened status	
				National	State
Bromeliaceae	*Aechmea lamarchei* Mez	CH	GMM 1291 (HRCB)		
Bromeliaceae	*Aechmea mutica* L.B.Sm.	FH	RRV 639 (MBML)	EN	EN
Bromeliaceae	*Aechmea nudicaulis* (L.) Griseb.	CH	GMM 1804 (HRCB)		
Bromeliaceae	*Aechmea perforata* L.B.Sm.	CH	RRV 852 (MBML)		EN
Bromeliaceae	*Aechmea pineliana* (Brong. ex Planch.) Baker	CH	GMM 1296 (HRCB)		
Bromeliaceae	*Aechmea ramosa* Mart. ex Schult. & Schult.f.	CH	RRV 103 (MBML)		
Bromeliaceae	*Aechmea triangularis* L.B.Sm.	CH	RRV 1073 (MBML)	EN	
Bromeliaceae	*Billbergia euphemiae* E.Morren	CH	GMM 1125 (HRCB)		
Bromeliaceae	*Billbergia lymanii* E.Pereira & Leme	CH	GMM 1670 (HRCB)		VU
Bromeliaceae	*Billbergia porteana* Brong. ex Beer	CH	LK 4898 (MBML)		VU
Bromeliaceae	*Billbergia sanderiana* E.Morren	CH	RRV 1873 (MBML)		EN
Bromeliaceae	*Billbergia vittata* Brongn. ex Morel	CH	GMM 1261 (HRCB)		VU
Bromeliaceae	*Billbergia zebrina* (Herb.) Lindl.	CH	GMM 1420 (HRCB)		VU
Bromeliaceae	*Edmundoa lindenii* (Regel) Leme	FH	LK 4824 (MBML)		
Bromeliaceae	*Neoregelia guttata* Leme	CH	GMM 1829 (HRCB)		VU
Bromeliaceae	*Neoregelia macrosepala* L.B.Sm.	CH	LK 4959 (MBML)		
Bromeliaceae	*Neoregelia pauciflora* L.B.Sm.	FH	GMM 1134 (HRCB)		
Bromeliaceae	*Nidularium cariacicaense* (W.Weber) Leme	FH	GMM 926 (HRCB)		
Bromeliaceae	*Nidularium longiflorum* Ule	FH	GMM 1140 (HRCB)		
Bromeliaceae	*Nidularium procerum* Lindm.	FH	GMM 1425 (HRCB)		
Bromeliaceae	*Portea fosteriana* L.B.Sm.	CH	GMM 1440 (HRCB)		
Bromeliaceae	*Portea petropolitana* (Wawra) Mez	CH	LK 5629 (MBML)		
Bromeliaceae	*Quesnelia quesneliana* (Brongn.) L.B.Sm.	CH	GMM 1617 (HRCB)		
Bromeliaceae	*Quesnelia strobilispica* Wawra	FH	GMM 1271 (HRCB)		
Bromeliaceae	*Racinaea aeris-incola* (Mez) M.A. Spencer & L.B. Sm	CH	GMM 907 (HRCB)		

Family	Species	Ecological categories	Voucher	Threatened status	
				National	State
Bromeliaceae	*Racinaea spiculosa* (Griseb.) M.A.Spencer & L.B.Sm.	CH	GMM 1421 (HRCB)		
Bromeliaceae	*Tillandsia geminiflora* Brongn.	CH	GMM 1260 (HRCB)		
Bromeliaceae	*Tillandsia kautskyi* E.Pereira	CH	GMM 1282 (HRCB)	VU	VU
Bromeliaceae	*Tillandsia stricta* Sol.	CH	GMM 1618 (HRCB)		
Bromeliaceae	*Tillandsia tenuifolia* L.	CH	GMM 1288 (HRCB)		
Bromeliaceae	*Tillandsia usneoides* (L.) L.	CH	GMM 906 (HRCB)		
Bromeliaceae	*Vriesea bituminosa* Wawra	CH	GMM 1417 (HRCB)		
Bromeliaceae	*Vriesea breviscapa* (E.Pereira & I.A.Penna) Leme	CH	GMM 1123 (HRCB)		VU
Bromeliaceae	*Vriesea capixabae* Leme	CH	RRV 2237 (MBML)		VU
Bromeliaceae	*Vriesea carinata* Wawra	CH	LK 5371 (MBML)		
Bromeliaceae	*Vriesea delicatula* L.B.Sm.	CH	GMM 928 (HRCB)	VU	
Bromeliaceae	*Vriesea drepanocarpa* (Baker) Mez	CH	RRV 2352 (MBML)		
Bromeliaceae	*Vriesea ensiformis* (Vell.) Beer	CH	GMM 1424 (HRCB)		
Bromeliaceae	*Vriesea erythrodactylon* E.Morren ex Mez	CH	LK 5120 (MBML)		VU
Bromeliaceae	*Vriesea gracilior* (L.B.Sm.) Leme	CH	GMM 1295 (HRCB)	VU	
Bromeliaceae	*Vriesea languida* L.B.Sm.	CH	LK 2800 (MBML)		VU
Bromeliaceae	*Vriesea longicaulis* (Baker) Mez	CH	GMM 1113 (HRCB)		
Bromeliaceae	*Vriesea longiscapa* Ule.	CH	RRV 75 (MBML)		VU
Bromeliaceae	*Vriesea menescalii* E.Pereira & Leme	CH	RRV 1464 (MBML)	EN	EN
Bromeliaceae	*Vriesea morrenii* Wawra	CH	GMM 1298 (HRCB)		EN
Bromeliaceae	*Vriesea parviflora* L.B.Sm.	CH	LK 4637 (MBML)		VU
Bromeliaceae	*Vriesea pauperrima* E.Pereira	CH	LK 5616 (MBML)		VU
Bromeliaceae	*Vriesea poenulata* (Baker) Mez	CH	GMM 1630 (HRCB)		
Bromeliaceae	*Vriesea procera* (Mart. ex Schult. & Schult.f.) Wittm.	CH	GMM 1458 (HRCB)		
Bromeliaceae	*Vriesea pulchra* Leme & L.Kollmann	CH	GMM 1686 (HRCB)		

Family	Species	Ecological categories	Voucher	Threatened status	
				National	State
Bromeliaceae	*Vriesea racinae* L.B.Sm.	CH	GMM 1455 (HRCB)	EN	VU
Bromeliaceae	*Vriesea rhodostachys* L.B.Sm.	CH	GMM 1146 (HRCB)		VU
Bromeliaceae	*Vriesea ruschii* L.B.Sm.	FH	RRV 368 (MBML)		
Bromeliaceae	*Vriesea scalaris* E.Morren	CH	RRV 120 (MBML)		
Bromeliaceae	*Vriesea seideliana* W.Weber	CH	LK 5079 (MBML)		VU
Bromeliaceae	*Vriesea simplex* (Vell.) Beer	CH	GMM 1114 (HRCB)		
Bromeliaceae	*Vriesea tijucana* E.Pereira	CH	GMM 1120 (HRCB)		EN
Bromeliaceae	*Vriesea vagans* (L.B.Sm.) L.B.Sm.	CH	GMM 1121 (HRCB)		
Cactaceae	*Hatiora salicornioides* (Haw.) Britton & Rose	CH	GMM 1675 (HRCB)		
Cactaceae	*Lepismium cruciforme* (Vell.) Miq.	CH	GMM 929 (HRCB)		
Cactaceae	*Rhipsalis clavata* F.A.C.Weber	CH	LK 5384 (MBML)		EN
Cactaceae	*Rhipsalis elliptica* G.Lindb. ex K.Schum.	CH	RRV 1847 (MBML)		EN
Cactaceae	*Rhipsalis floccosa* Salm-Dyck ex Pfeiff.	CH	GMM 930 (HRCB)		
Cactaceae	*Rhipsalis hoelleri* Barthlott & N.P.Taylor	CH	LK 4841 (MBML)		EN
Cyclanthaceae	*Thoracocarpus bissectus* (Vell.) Harling	SH	GMM 1442 (HRCB)		
Dryopteridaceae	*Elaphoglossum brevipetiolatum* F. B. Matos & Mickel	CH	GMM 1766 (HRCB)		CR
Dryopteridaceae	*Elaphoglossum burchellii* (Baker) C.Chr.	CH	GMM 1611 (HRCB)		
Dryopteridaceae	*Elaphoglossum chrysolepis* (Fée) Alston.	CH	GMM 932 (HRCB)		
Dryopteridaceae	*Elaphoglossum decoratum* (Kunze) T.Moore	FH	LK 4870a (MBML)		
Dryopteridaceae	*Elaphoglossum hymenodiastrum* (Fée) Brade	CH	AS 14035 (BHCB)		
Dryopteridaceae	*Elaphoglossum iguapense* Brade	CH	AS 14085 (BHCB)		
Dryopteridaceae	*Elaphoglossum lingua* (C.Presl) Brack.	CH	GMM 933 (HRCB)		
Dryopteridaceae	*Elaphoglossum luridum* (Fée) Christ	CH	GMM 904 (HRCB)		
Dryopteridaceae	*Elaphoglossum macahense* (Fée) Rosenst.	CH	AS 14095 (BHCB)		
Dryopteridaceae	*Elaphoglossum macrophyllum* (Mett. ex Kuhn) Christ	FH	LK 5632 (MBML)		

Family	Species	Ecological categories	Voucher	Threatened status	
				National	State
Dryopteridaceae	*Elaphoglossum mollissimum* (Fée) Hieron.	CH	AS 14065 (BHCB)		
Dryopteridaceae	*Elaphoglossum nigrescens* (Hook.) T.Moore ex Diels	FH	RRV 1176 (MBML)		
Dryopteridaceae	*Elaphoglossum paulistanum* Rosenst.	CH	AS 14075 (BHCB)		
Dryopteridaceae	*Elaphoglossum plumosum* (Fée) T.Moore	FH	GMM 1275 (HRCB)		
Dryopteridaceae	*Elaphoglossum pteropus* C.Chr.	CH	GMM 1681 (HRCB)		
Dryopteridaceae	*Elaphoglossum strictum* (Raddi) T.Moore	CH	RRV 799 (MBML)		
Dryopteridaceae	*Megalastrum grande* (C.Presl) A.R.Sm. & R.C.Moran	CH	LK 5098 (MBML)		
Dryopteridaceae	*Olfersia cervina* (L.) Kunze	CH	LK 4741 (MBML)		
Dryopteridaceae	*Polybotrya cylindrica* Kaulf.	SH	GMM 1672 (HRCB)		
Dryopteridaceae	*Polybotrya espiritosantensis* Brade	SH	GMM 939 (HRCB)		VU
Dryopteridaceae	*Polybotrya pilosa* Brade	SH	RRV 1917 (MBML)		
Dryopteridaceae	*Rumohra adiantiformis* (G.Forst.) Ching	CH	RRV 2075 (MBML)		
Gesneriaceae	*Codonanthe devosiana* Lem.	CH	GMM 1609 (HRCB)		VU
Gesneriaceae	*Codonanthe gibbosa* Rossini & Chautems	CH	GMM 1258 (HRCB)		CR
Gesneriaceae	*Columnea sanguinea* (Pers.) Hanst.	FH	RRV 1387 (MBML)		EN
Gesneriaceae	*Nematanthus albus* Chautems	CH	GMM 1786 (HRCB)		VU
Gesneriaceae	*Nematanthus crassifolius* (Schott) Wiehler	FH	GMM 1115 (HRCB)		
Gesneriaceae	*Nematanthus kautskyi* Chautems & Rossini	CH	GMM 1676 (HRCB)		EN
Gesneriaceae	*Nematanthus sericeus* (Hanst.) Chautems	CH	RRV 1141 (MBML)		VU
Gesneriaceae	*Nematanthus wiehleri* Chautems & M.Peixoto	CH	RRV 1146 (MBML)		VU
Gesneriaceae	*Sinningia cooperi* (Paxton) Wiehler	FH	LK 5670 (MBML)		EN
Hymenophyllaceae	*Didymoglossum angustifrons* Fée	CH	RRV 1928 (BHCB)		
Hymenophyllaceae	*Didymoglossum krausii* (Hook. & Grev.) C. Presl	FH	AS 14030 (BHCB)		
Hymenophyllaceae	*Didymoglossum reptans* (Sw.) C.Presl	CH	AS 14066 (BHCB)		
Hymenophyllaceae	*Hymenophyllum asplenioides* (Sw.) Sw.	CH	AS 14059 (BHCB)		

Family	Species	Ecological categories	Voucher	Threatened status	
				National	State
Hymenophyllaceae	*Hymenophyllum caudiculatum* Mart.	CH	GMM 1452 (HRCB)		
Hymenophyllaceae	*Hymenophyllum hirsutum* (L.) Sw.	CH	AS 14084 (BHCB)		
Hymenophyllaceae	*Hymenophyllum polyanthos* (Sw.) Sw.	CH	GMM 1449 (HRCB)		
Hymenophyllaceae	*Polyphlebium angustatum* (Carmich.) Ebihara & Dubuisson	CH	GMM 1306 (HRCB)		
Hymenophyllaceae	*Trichomanes arbuscula* Desv.	CH	AS 14062 (BHCB)		
Hymenophyllaceae	*Trichomanes polypodioides* L.	CH	GMM 915 (HRCB)		
Hymenophyllaceae	*Vandenboschia radicans* (Sw.) Copel.	SH	GMM 1304 (HRCB)		
Lomariopsidaceae	*Lomariopsis marginata* (Schrad.) Kuhn	SH	GMM 940 (HRCB)		
Lycopodiaceae	*Phlegmariurus acerosus* (Sw.) B.Øllg.	CH	GMM 1447 (HRCB)		
Lycopodiaceae	*Phlegmariurus flexibilis* (Fée) B.Øllg.	CH	LK 5604 (MBML)		
Lycopodiaceae	*Phlegmariurus heterocarpon* (Fée) B.Øllg.	CH	RRV 1351 (MBML)		
Lycopodiaceae	*Phlegmariurus martii* (Wawra) B.Øllg.	CH	GMM 1276 (HRCB)	EN	
Melastomataceae	*Clidemia fluminensis* Baumgratz & D'El Rei Souza	FH	LK 5654 (RB)		VU
Melastomataceae	*Pleiochiton blepharodes* (DC.) Reginato et al.	SH	HQB 3372 (MBML)		
Melastomataceae	*Pleiochiton setulosum* Cogn.	CH	RRV 1596 (MBML)		
Orchidaceae	*Acianthera auriculata* (Lindl.) Pridgeon & M.W.Chase	CH	GMM 1460 (HRCB)		
Orchidaceae	*Acianthera bidentula* (Barb.Rodr.) Pridgeon & M.W.Chase	CH	RRV 2245 (MBML)		
Orchidaceae	*Acianthera glanduligera* (Lindl.) Luer	CH	GMM 1769 (HRCB)		
Orchidaceae	*Acianthera luteola* (Lindl.) Pridgeon & M.W.Chase	CH	GMM 1130 (HRCB)		
Orchidaceae	*Acianthera nemorosa* (Barb.Rodr.) F.Barros	CH	GMM 892 (HRCB)		
Orchidaceae	*Acianthera ramosa* (Barb. Rodr.) F.Barros	CH	GMM 889 (HRCB)		
Orchidaceae	*Acianthera saundersiana* (Rchb.f.) Pridgeon & M.W.Chase	CH	RRV 438 (MBML)		
Orchidaceae	*Acianthera tricarinata* (Poepp. & Endl.) Pridgeon & M.W.Chase	CH	GMM 1289 (HRCB)		
Orchidaceae	*Anathallis adenochila* (Loefgr.) F.Barros	CH	GMM 1148 (HRCB)		
Orchidaceae	*Anathallis aristulata* (Lindl.) Luer	CH	GMM 1637 (HRCB)		

Family	Species	Ecological categories	Voucher	Threatened status	
				National	State
Orchidaceae	*Anathallis gehrtii* (Hoehne & Schltr.) F.Barros	CH	LK 5080 (MBML)	VU	EN
Orchidaceae	*Anathallis graveolens* (Pabst) F.Barros	CH	LK 5163 (MBML)		VU
Orchidaceae	*Anathallis linearifolia* (Cogn.) Pridgeon & M.W.Chase	CH	GMM 1645 (HRCB)		VU
Orchidaceae	*Anathallis microphyta* (Barb.Rodr.) C.O.Azevedo	CH	GMM 1552 (HRCB)		
Orchidaceae	*Anathallis obovata* (Lindl.) Pridgeon & M.W.Chase	CH	GMM 1150 (HRCB)		
Orchidaceae	*Anathallis sclerophylla* (Lindl.) Pridgeon & M.W.Chase	CH	GMM 1732 (HRCB)		
Orchidaceae	*Anathallis tigridens* (Loefgr.) F.Barros & Barberena	CH	LK 6676 (MBML)		VU
Orchidaceae	*Aspasia lunata* Lindl.	CH	RRV 2041 (MBML)		
Orchidaceae	*Barbosella gardneri* (Lindl.) Schltr.	CH	GMM 1405 (HRCB)		
Orchidaceae	*Barbosella macaheensis* (Cogn.) Luer	CH	RRV 712 (MBML)		
Orchidaceae	*Barbosella miersii* (Lindl.) Schltr.	CH	GMM 1126 (HRCB)		
Orchidaceae	*Bifrenaria calcarata* Barb.Rodr.	CH	LK 4715 (MBML)		VU
Orchidaceae	*Bifrenaria clavigera* Rchb.f.	CH	GMM 1280 (HRCB)		VU
Orchidaceae	*Bifrenaria mellicolor* Rchb.f.	CH	GMM 1533 (HRCB)		CR
Orchidaceae	*Bifrenaria racemosa* (Hook.) Lindl.	CH	RRV 1000 (MBML)		EN
Orchidaceae	*Brasiliorchis gracilis* (Lodd.) R.B.Singer et al.	CH	GMM 1640 (HRCB)		
Orchidaceae	*Brasiliorchis kautskyi* (Pabst) R. Singer, S.Koehler & Carnevali	CH	GMM 1619 (HRCB)		VU
Orchidaceae	*Brasiliorchis ubatubana* (Hoehne) R.B.Singer et al.	CH	JR 363 (MBML)		
Orchidaceae	*Bulbophyllum micropetaliforme* J.E.Leite	CH	LK 4735 (MBML)		VU
Orchidaceae	*Bulbophyllum napellii* Lindl.	CH	LK 4639 (MBML)		
Orchidaceae	*Campylocentrum brachycarpum* Cogn.	CH	RRV 2182 (MBML)		
Orchidaceae	*Campylocentrum crassirhizum* Hoehne	CH	GMM 1278 (HRCB)		
Orchidaceae	*Campylocentrum ornithorrhynchum* (Lindl.) Rolfe	CH	GMM 1383 (HRCB)		
Orchidaceae	*Campylocentrum spannagelii* Hoehne	CH	RRV 2488 (MBML)		
Orchidaceae	*Catasetum hookeri* Lindl.	CH	LK 5548 (MBML)		VU

Family	Species	Ecological categories	Voucher	Threatened status	
				National	State
Orchidaceae	*Cattleya harpophylla* (Rchb.f.) Van den Berg	CH	GMM 1270 (HRCB)	VU	CR
Orchidaceae	*Cattleya pumila* Hook.	CH	LK 5641 (MBML)	VU	CR
Orchidaceae	*Cattleya pygmaea* (Pabst) Van den Berg	CH	RRV 2068 (MBML)	EN	EN
Orchidaceae	*Cattleya wittigiana* (Barb.Rodr.) Van den Berg	CH	RRV 302 (MBML)	EN	CR
Orchidaceae	*Cattleya xanthina* (Lindl.) Van den Berg	CH	RRV 147 (MBML)	EN	EN
Orchidaceae	*Christensonella paranaensis* (Barb.Rodr.) S.Koehler	CH	GMM 1639 (HRCB)		VU
Orchidaceae	*Christensonella subulata* (Lindl.) Szlach. et al.	CH	GMM 1734 (HRCB)		
Orchidaceae	*Cirrhaea nasuta* Brade	CH	GMM 1746 (HRCB)		EN
Orchidaceae	*Cirrhaea seidelii* Pabst	CH	GMM 1507 (HRCB)		EN
Orchidaceae	*Comparettia coccinea* Lindl.	CH	GMM 1150 (HRCB)		EN
Orchidaceae	*Dichaea brevicaulis* Cogn.	CH	RRV 848 (MBML)		
Orchidaceae	*Dichaea cogniauxiana* Schltr.	CH	GMM 1156 (HRCB)		VU
Orchidaceae	*Dichaea mosenii* Cogn.	CH	LK 4842 (MBML)	VU	
Orchidaceae	*Dichaea pendula* (Aubl.) Cogn.	CH	GMM 1743 (HRCB)		
Orchidaceae	*Elleanthus brasiliensis* (Lindl.) Rchb.f.	CH	LK 5628 (MBML)		
Orchidaceae	*Elleanthus crinipes* Rchb.f.	FH	RRV 2628 (MBML)		
Orchidaceae	*Elleanthus linifolius* C.Presl	CH	GMM 1468 (HRCB)		
Orchidaceae	*Encyclia patens* Hook.	CH	GMM 1735 (HRCB)		
Orchidaceae	*Epidendrum armeniacum* Lindl.	CH	GMM 1158 (HRCB)		
Orchidaceae	*Epidendrum avicula* Lindl.	CH	GMM 1483 (HRCB)		
Orchidaceae	*Epidendrum campaccii* Hágsater & L.Sánchez	CH	RRV 621 (MBML)		
Orchidaceae	*Epidendrum carpophorum* Barb.Rodr.	CH	GMM 1754 (HRCB)		
Orchidaceae	*Epidendrum chlorinum* Barb.Rodr.	CH	RRV 2569 (MBML)		
Orchidaceae	*Epidendrum densiflorum* Hook.	CH	RRV 1182 (MBML)		
Orchidaceae	*Epidendrum geniculatum* Barb.Rodr.	CH	GMM 1445 (HRCB)		VU

Family	Species	Ecological categories	Voucher	Threatened status	
				National	State
Orchidaceae	*Epidendrum henschenii* Barb.Rodr.	CH	GMM 1551 (HRCB)	EN	
Orchidaceae	*Epidendrum paranaense* Barb.Rodr.	CH	LK 4857 (MBML)		VU
Orchidaceae	*Epidendrum patentifolium* Fraga, A.P.Fontana & L.Kollmann	CH	RRV 708 (MBML)		EN
Orchidaceae	*Epidendrum proligerum* Barb.Rodr.	CH	GMM 1541 (HRCB)		
Orchidaceae	*Epidendrum ramosum* Jacq.	CH	GMM 1750 (HRCB)		
Orchidaceae	*Epidendrum rigidum* Jacq.	CH	GMM 1761 (HRCB)		
Orchidaceae	*Epidendrum saxatile* Lindl.	CH	GMM 1439 (HRCB)		
Orchidaceae	*Epidendrum strobiliferum* Rchb.f.	CH	LK 5561 (MBML)		
Orchidaceae	*Epidendrum vesicatum* Lindl.	CH	GMM 1721 (HRCB)		VU
Orchidaceae	*Eurystyles actinosophila* (Barb.Rodr.) Schltr.	CH	GMM 1636 (HRCB)		
Orchidaceae	*Gomesa damacenoi* (Chiron & V.P.Castro) M.W.Chase & N.H.Williams	CH	GMM 1628 (HRCB)		VU
Orchidaceae	*Gomesa imperatoris-maximiliani* (Rchb.f.) M.W.Chase & N.H.Williams	CH	GMM 1914 (HRCB)		EN
Orchidaceae	*Gomesa jucunda* (Rchb.f.) M.W.Chase & N.H.Williams	CH	GMM 1768 (HRCB)		
Orchidaceae	*Gomesa ranifera* (Lindl.) M.W.Chase & N.H.Williams	CH	GMM 1546 (HRCB)		
Orchidaceae	*Gomesa recurva* R.Br.	CH	GMM 1610 (HRCB)		
Orchidaceae	*Grandiphyllum auricula* (Vell.) Docha Neto	CH	GMM 1738 (HRCB)		
Orchidaceae	*Grandiphyllum edwallii* (Cogn.) Docha Neto	CH	GMM 1915 (HRCB)		
Orchidaceae	*Heterotaxis brasiliensis* (Brieger & Illg) F.Barros	CH	GMM 1726 (HRCB)		
Orchidaceae	*Heterotaxis valenzuelana* (A.Rich.) Ojeda & Carnevali	CH	LK 6530 (MBML)		VU
Orchidaceae	*Hoehneella heloisae* Ruschi	CH	RRV 1806 (MBML)		CR
Orchidaceae	*Huntleya meleagris* Lindl.	CH	GMM 1415 (HRCB)		VU
Orchidaceae	*Isochilus linearis* (Jacq.) R.Br.	CH	GMM 1655 (HRCB)		
Orchidaceae	*Lepanthopsis floripecten* (Rchb.f.) Ames.	CH	RRV 151 (MBML)		
Orchidaceae	*Leptotes tenuis* Rchb.f.	CH	GMM 1136 (HRCB)		VU
Orchidaceae	*Mapinguari desvauxianus* (Rchb.f.) Carnevali & R.Singer	CH	GMM 1427 (HRCB)		

Family	Species	Ecological categories	Voucher	Threatened status	
				National	State
Orchidaceae	*Masdevallia infracta* Lindl.	CH	GMM 1249 (HRCB)		
Orchidaceae	*Maxillaria imbricata* Barb.Rodr.	CH	GMM 1745 (HRCB)		
Orchidaceae	*Maxillaria johannis* Pabst	CH	TBF 1078 (ESA)		EN
Orchidaceae	*Maxillaria crocea* Lindl.	CH	LK 6533 (MBML)		
Orchidaceae	*Maxillaria milenae* V.P.Castro & Chiron	CH	GMM 1756 (HRCB)		
Orchidaceae	*Maxillaria ochroleuca* Lodd. ex Lindl.	CH	GMM 1101 (HRCB)		
Orchidaceae	*Maxillaria spiritusanctensis* Pabst	CH	LK 5394 (MBML)		EN
Orchidaceae	*Mormolyca cleistogama* (Brieger & Illg) M.A.Blanco	CH	GMM 1767 (HRCB)		
Orchidaceae	*Mormolyca rufescens* (Lindl.) M.A.Blanco	CH	GMM 1506 (HRCB)		
Orchidaceae	*Myoxanthus punctatus* (Barb.Rodr.) Luer	CH	GMM 1097 (HRCB)		
Orchidaceae	*Myoxanthus ruschii* Fraga & L.Kollmann	CH	GMM 1662 (HRCB)	CR	EN
Orchidaceae	*Nitidobulbon nasutum* (Rchb.f.) Ojeda & Carnevali	CH	GMM 1426 (HRCB)		EN
Orchidaceae	*Notylia hemitricha* Barb.Rodr.	CH	RRV 1644 (MBML)		
Orchidaceae	*Octomeria alexandri* Schltr.	CH	GMM 1772 (HRCB)	EN	
Orchidaceae	*Octomeria concolor* Barb.Rodr.	CH	LK 4932 (MBML)		
Orchidaceae	*Octomeria crassifolia* Lindl.	CH	GMM 1725 (HRCB)		
Orchidaceae	*Octomeria diaphana* Lindl.	CH	MB 650 (MBM)		
Orchidaceae	*Octomeria gracilis* Lodd. ex Lindl.	CH	GMM 1159 (HRCB)		
Orchidaceae	*Octomeria grandiflora* Lindl.	CH	GMM 1098 (HRCB)		
Orchidaceae	*Octomeria juncifolia* Barb.Rodr.	CH	GMM 1157 (HRCB)		
Orchidaceae	*Octomeria linearifolia* Barb.Rodr.	CH	LK 5187 (MBML)		
Orchidaceae	*Octomeria praestans* Barb.Rodr.	CH	LK 5162 (MBML)		
Orchidaceae	*Octomeria rotundiglossa* Hoehne	CH	GMM 1135 (HRCB)		VU
Orchidaceae	*Octomeria sagittata* (Rchb.f.) Garay	CH	RRV 1463 (MBML)		
Orchidaceae	*Octomeria tricolor* Rchb.f.	CH	GMM 1252 (HRCB)		

Family	Species	Ecological categories	Voucher	Threatened status	
				National	State
Orchidaceae	*Octomeria warmingii* Rchb.f.	CH	LK 5326 (MBML)		VU
Orchidaceae	*Ornithidium rigidum* (Barb.Rodr.) M.A.Blanco & Ojeda	CH	GMM 1545 (HRCB)		
Orchidaceae	*Ornithocephalus myrticola* Lindl.	CH	LK 5640 (MBML)		
Orchidaceae	*Pabstia viridis* (Lindl.) Garay	CH	GMM 927 (HRCB)		EN
Orchidaceae	*Pabstiella fusca* (Lindl.) Chiron & Xim.Bols.	CH	JAL 9848 (HRCB)		
Orchidaceae	*Pabstiella henrique-aragonii* (Pabst) Chiron & Xim.Bols.	CH	RRV 145 (MBML)		
Orchidaceae	*Pabstiella hians* (Lindl.) Luer	CH	EL 36 (MBML)		
Orchidaceae	*Pabstiella lingua* (Lindl.) Luer	CH	GMM 1795 (HRCB)	EN	VU
Orchidaceae	*Pabstiella lueriana* Fraga & L.Kollmann	CH	GMM 1800 (HRCB)		VU
Orchidaceae	*Pabstiella matinhensis* (Hoehne) Luer	CH	GMM 1677 (HRCB)		
Orchidaceae	*Pabstiella nymphalis* Luer & Toscano	CH	GMM 1661 (HRCB)		EN
Orchidaceae	*Pabstiella pterophora* (Cogn.) Chiron	CH	GMM 1744 (HRCB)		
Orchidaceae	*Pabstiella punctatifolia* (Barb.Rodr.) Luer	CH	GMM 1584 (HRCB)		
Orchidaceae	*Pabstiella seriata* (Lindl.) Luer & Toscano	CH	GMM 1386 (HRCB)		
Orchidaceae	*Pabstiella trifida* (Lindl.) Luer	CH	GMM 1147 (HRCB)		
Orchidaceae	*Pabstiella villosisepala* Fraga & L.Kollmann	CH	GMM 1111 (HRCB)		VU
Orchidaceae	*Phloeophila nummularia* (Rchb.f.) Garay	CH	GMM 1638 (HRCB)		
Orchidaceae	*Phymatidium hysteranthum* Barb.Rodr.	CH	JR 494 (MBML)		
Orchidaceae	*Platystele oxyglossa* (Schltr.) Garay	CH	RRV 1087 (MBML)		VU
Orchidaceae	*Polystachya concreta* (Jacq.) Garay & Sweet	FH	GMM 1409 (HRCB)		
Orchidaceae	*Prescottia lancifolia* Lindl.	CH	RRV 1147 (MBML)		
Orchidaceae	*Promenaea guttata* (Rchb.f.) Rchb.f.	CH	GMM 1921 (HRCB)		VU
Orchidaceae	*Prosthechea bulbosa* (Vell.) W.E.Higgins	CH	RRV 2359 (MBML)		
Orchidaceae	*Prosthechea calamaria* (Lindl.) W.E.Higgins	CH	RRV 419 (MBML)		
Orchidaceae	*Prosthechea kautzkii* (Pabst) W.E.Higgins	CH	GMM 1828 (HRCB)		

Family	Species	Ecological categories	Voucher	Threatened status	
				National	State
Orchidaceae	*Prosthechea pachysepala* (Klotzsch) Chiron & V.P.Castro	CH	GMM 1302 (HRCB)		
Orchidaceae	*Prosthechea pygmaea* (Hook.) W.E.Higgins	CH	RRV 1177 (MBML)		
Orchidaceae	*Rhetinantha notylioglossa* (Rchb.f.) M.A.Blanco	CH	GMM 1464 (HRCB)		
Orchidaceae	*Scaphyglottis brasiliensis* (Schltr.) Dressler	CH	RRV 657 (MBML)		
Orchidaceae	*Scaphyglottis modesta* (Rchb.f.) Schltr.	CH	GMM 1739 (HRCB)		
Orchidaceae	*Scuticaria hadwenii* (Lindl.) Planch.	CH	GMM 1404 (HRCB)		
Orchidaceae	*Specklinia grobyi* (Batem. ex Lindl.) F.Barros	CH	RRV 1996 (MBML)		
Orchidaceae	*Specklinia marginalis* (Rchb.f.) F.Barros	CH	GMM 1400 (HRCB)		
Orchidaceae	*Specklinia subpicta* (Schltr.) F.Barros	CH	GMM 1128 (HRCB)		VU
Orchidaceae	*Stelis amoena* Pridgeon & M.W.Chase	CH	GMM 1742 (HRCB)		
Orchidaceae	*Stelis aprica* Lindl.	CH	GMM 1160 (HRCB)		
Orchidaceae	*Stelis argentata* Lindl.	CH	GMM 1367 (HRCB)		
Orchidaceae	*Stelis deregularis* Barb.Rodr.	CH	GMM 1762 (HRCB)		
Orchidaceae	*Stelis intermedia* Poepp. & Endl.	CH	GMM 1382 (HRCB)		
Orchidaceae	*Stelis megantha* Barb.Rodr.	CH	GMM 1414 (HRCB)		
Orchidaceae	*Stelis papaquerensis* Rchb.f.	CH	GMM 1384 (HRCB)		
Orchidaceae	*Thysanoglossa organensis* Brade	CH	GMM 898 (HRCB)		
Orchidaceae	*Trichopilia fragrans* (Lindl.) Rchb.f.	CH	RRV 2133 (MBML)		
Orchidaceae	*Trichosalpinx montana* (Barb.Rodr.) Luer	CH	LK 5475 (MBML)		VU
Orchidaceae	*Vanilla edwallii* Hoehne	SH	RRV 1668 (MBML)		VU
Orchidaceae	*Xylobium pallidiflorum* (Hook.) G.Nicholson	CH	RRV 133 (MBML)		VU
Piperaceae	*Peperomia alata* Ruiz & Pav.	CH	GMM 1141 (HRCB)		
Piperaceae	*Peperomia choroniana* C.DC.	FH	GMM 1465 (HRCB)		EN
Piperaceae	*Peperomia corcovadensis* Gardner	CH	GMM 886 (HRCB)		
Piperaceae	*Peperomia glabella* (Sw.) A.Dietr.	CH	GMM 894 (HRCB)		

Family	Species	Ecological categories	Voucher	Threatened status	
				National	State
Piperaceae	*Peperomia glazioui* C.DC.	CH	GMM 1255 (HRCB)		
Piperaceae	*Peperomia obtusifolia* (L.) A.Dietr.	CH	RRV 83 (MBML)		
Piperaceae	*Peperomia pilicaulis* C.DC.	CH	GMM 893 (HRCB)		VU
Piperaceae	*Peperomia pseudoestrellensis* C.DC.	CH	GMM 917 (HRCB)		
Piperaceae	*Peperomia tetraphylla* (G.Forst.) Hook. & Arn.	CH	GMM 921 (HRCB)		
Piperaceae	*Peperomia turbinata* Dahlst.	CH	LK 5497 (MBML)		VU
Piperaceae	*Peperomia urocarpa* Fisch. & C.A.Mey.	CH	GMM 1624 (HRCB)		
Polypodiaceae	*Alansmia reclinata* (Brack) Moguel & M. Kessler	CH	LK 5498 (MBML)		
Polypodiaceae	*Campyloneurum angustifolium* (Sw.) Fée	CH	GMM 1621 (HRCB)		
Polypodiaceae	*Campyloneurum herbaceum* (Christ) Ching	CH	GMFA 351 (MBML)		
Polypodiaceae	*Campyloneurum nitidum* (Kaulf.) C.Presl	FH	GMM 1314 (HRCB)		
Polypodiaceae	*Cochlidium punctatum* (Raddi) L.E.Bishop	CH	GMM 1281 (HRCB)		
Polypodiaceae	*Cochlidium serrulatum* (Sw.) L.E.Bishop	CH	GMM 916 (HRCB)		
Polypodiaceae	*Lellingeria brevistipes* (Mett. ex Kuhn) A.R.Sm. & R.C.Moran	CH	JAL 9814 (HRCB)		
Polypodiaceae	*Leucotrichum schenckii* (Hieron.) Labiak	CH	GMM 1127 (HRCB)		
Polypodiaceae	*Melpomene melanosticta* (Kunze) A.R.Sm. & R.C.Moran	CH	GMM 1287 (HRCB)		
Polypodiaceae	*Microgramma lycopodioides* (L.) Copel.	CH	RRV 2431 (MBML)		
Polypodiaceae	*Microgramma percussa* (Cav.) de la Sota	CH	GMM 1687 (HRCB)		
Polypodiaceae	*Microgramma squamulosa* (Kaulf.) de la Sota	CH	GMM 1104 (HRCB)		
Polypodiaceae	*Microgramma tecta* (Kaulf.) Alston	CH	AS 13979 (BHCB)		
Polypodiaceae	*Microgramma vacciniifolia* (Langsd. & Fisch.) Copel.	CH	GMM 1116 (HRCB)		
Polypodiaceae	*Moranopteris gradata* (Baker) R.Y. Hirai & J. Prado	CH	GMM 938 (HRCB)		
Polypodiaceae	*Niphidium crassifolium* (L.) Lellinger	FH	GMM 1656 (HRCB)		
Polypodiaceae	*Pecluma pectinatiformis* (Lindm.) M.G.Price	CH	GMM 1413 (HRCB)		
Polypodiaceae	*Pecluma pilosa* (A.M.Evans) M.Kessler & A.R.Sm.	FH	GMM 935 (HRCB)		

Family	Species	Ecological categories	Voucher	Threatened status	
				National	State
Polypodiaceae	*Pecluma robusta* (Fée) M.Kessler & A.R.Sm.	FH	AS 13976 (BHCB)		
Polypodiaceae	*Pecluma truncorum* (Lindm.) M.G.Price	CH	GMM 888 (HRCB)		
Polypodiaceae	*Phlebodium pseudoaureum* (Cav.) Lellinger	CH	GMM 1606 (HRCB)		
Polypodiaceae	*Pleopeltis astrolepis* (Liebm.) E.Fourn.	CH	GMM 1308 (HRCB)		
Polypodiaceae	*Pleopeltis desvauxii* (Klotzsch) Salino	CH	RRV 596 (MBML)		
Polypodiaceae	*Serpocaulon catharinae* (Langsd. & Fisch.) A.R.Sm.	FH	GMM 1831 (HRCB)		
Polypodiaceae	*Serpocaulon fraxinifolium* (Jacq.) A.R.Sm.	SH	GMM 925 (HRCB)		
Polypodiaceae	*Serpocaulon laetum* (C. Presl) A. R. Sm. & Schwartsb.	FH	RRV 2365 (MBML)		
Polypodiaceae	*Serpocaulon latipes* (Langsd. & Fisch.) A.R.Sm.	FH	AS 13974 (BHCB)		
Polypodiaceae	*Serpocaulon triseriale* (Sw.) A.R.Sm.	FH	GMM 1607 (HRCB)		
Pteridaceae	*Polytaenium lineatum* (Sw.) Kaulf.	CH	RRV 1931 (MBML)		
Pteridaceae	*Vittaria graminifolia* Kaulf.	CH	GMM 1429 (HRCB)		
Pteridaceae	*Vittaria lineata* (L.) Sm.	CH	GMM 1423 (HRCB)		
Rubiaceae	*Hillia parasitica* Jacq.	SH	RRV 1857 (MBML)		
Solanaceae	*Dyssochroma atlanticum* (Stehmann & Giacomin) A. Orejuela & C.I. Orozco	SH	GMM 1627 (HRCB)		VU
Solanaceae	*Dyssochroma viridiflorum* (Sims) Miers.	SH	JR 497 (MBML)		

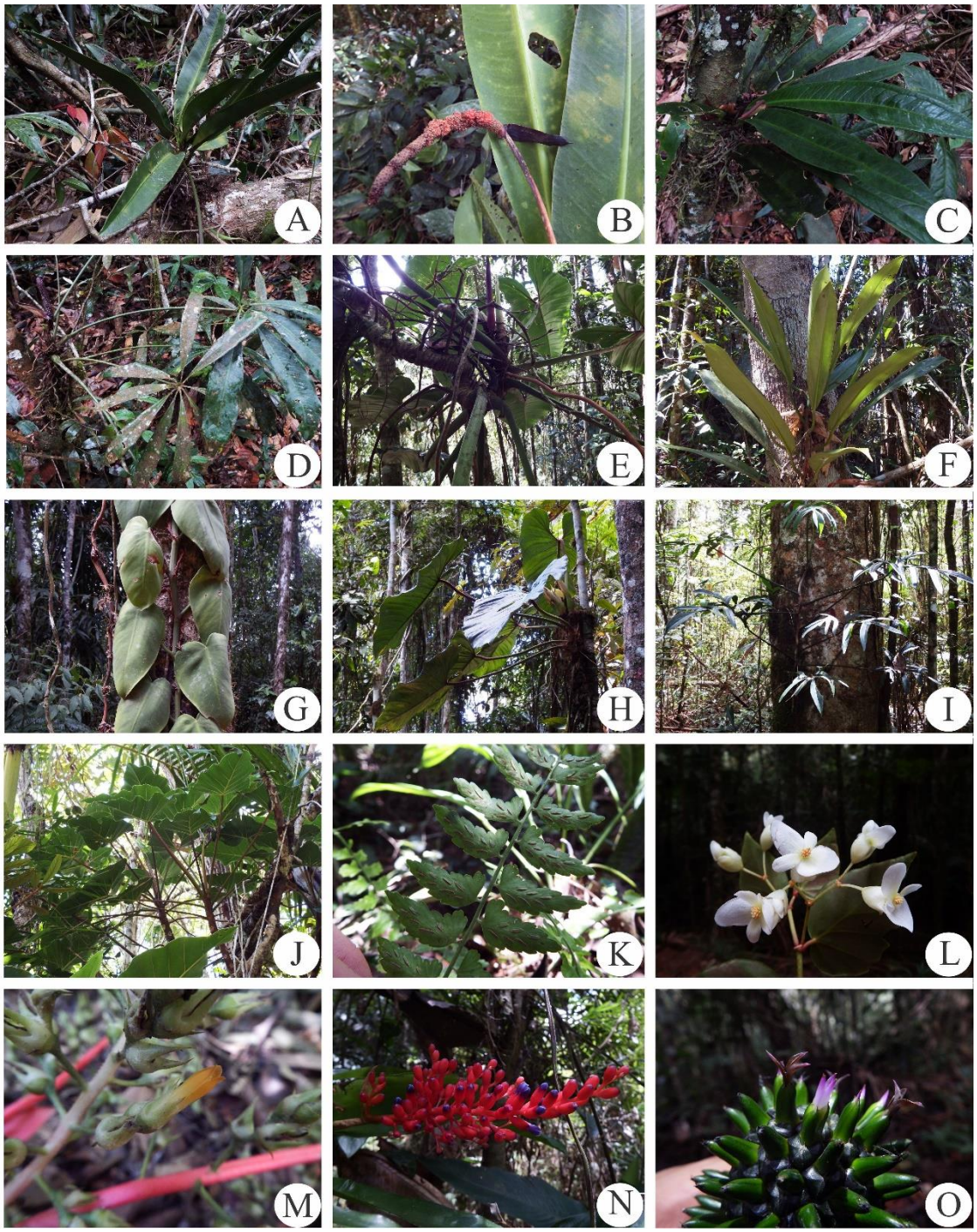


Fig. 2 Vascular epiphytes representatives of the Augusto Ruschi Biological Reserve, Santa Teresa, Espírito Santo, Brazil. **a–j** Araceae: **a–b** *Anthurium angustifolium*. **c** *Anthurium longifolium.* **d** *Anthurium pentaphyllum*. **e** *Philodendron bernardopazii.* **f** *Philodendron hatschbachii.* **g** *Philodendron hederaceum*. **h** *Philodendron ornatum*. **i** *Philodendron pedatum.* **j** *Thaumatophyllum corcovadense.* **k** *Asplenium auriculatum* (Aslpeniaceae). **l** *Begonia solananthera.* Bromeliaceae: **m** *Aechmea araneosa*. **n** *Aechmea capixabae*. **o** *Aechmea castanea*.



Fig. 3 Vascular epiphytes representatives of the Augusto Ruschi Biological Reserve, Santa Teresa, Espírito Santo, Brazil. **a–o** Bromeliaceae: **a** *Aechmea lamarchei*. **b** *Aechmea pineliana*. **c** *Billbergia euphemiae*. **d** *Billbergia lymanii*. **e** *Billbergia vittata*. **f** *Neoregelia guttata*. **g** *Nidularium cariacicaense*. **h** *Nidularium longiflorum*. **i** *Nidularium procerum*. **j** *Portea fosteriana*. **k** *Quesnelia strobilispica*. **l** *Tillandsia kautskyi*. **m** *Vriesea breviscapa*. **n** *Vriesea ensiformis*. **o** *Vriesea longicaulis*.



Fig. 4 Vascular epiphytes representatives of the Augusto Ruschi Biological Reserve, Santa Teresa, Espírito Santo, Brazil. **a–g** Bromeliaceae: **a** *Vriesea poenulata*. **b** *Vriesea pulchra*. **c** *Vriesea racinae*. **d** *Vriesea rhodostachys.* **e** *Vriesea simplex*. **f** *Vriesea tijucana.* **g** *Vriesea vagans.* **h** *Thoracocarpus bissectus* (Cyclanthaceae). **i–j** Dryopteridaceae: **i** *Elaphoglossum luridum.* **j** *Elaphoglossum plumosum.* **k–n** Gesneriaceae: **k** *Codonanthe devosiana.* **l** *Nematanthus albus*. **m** *Nematanthus crassifolius*. **n** *Nematanthus kautskyi*. **o** *Hymenophyllum caudiculatum* (Hymenophyllaceae).



Fig. 5 Vascular epiphytes representatives of the Augusto Ruschi Biological Reserve, Santa Teresa, Espírito Santo, Brazil. **a–c** Hymenophyllaceae: **a** *Hymenophyllum polyanthos*. **b** *Polyphlebium angustatum*. **c** *Trichomanes polypodioides*. **d** *Phlegmariurus martii* (Lycopodiaceae). **e–o** Orchidaceae: **e** *Acianthera auriculata*. **f** *Acianthera glanduligera*. **g** *Acianthera nemorosa*. **h** *Acianthera ramosa*. **i** *Acianthera tricarinata*. **j** *Anathallis adenochila*. **k** *Anathallis aristulata*. **l** *Anathallis linearifolia*. **m** *Anathallis microphyta*. **n** *Anathallis sclerophylla*. **o** *Barbosella gardneri*.

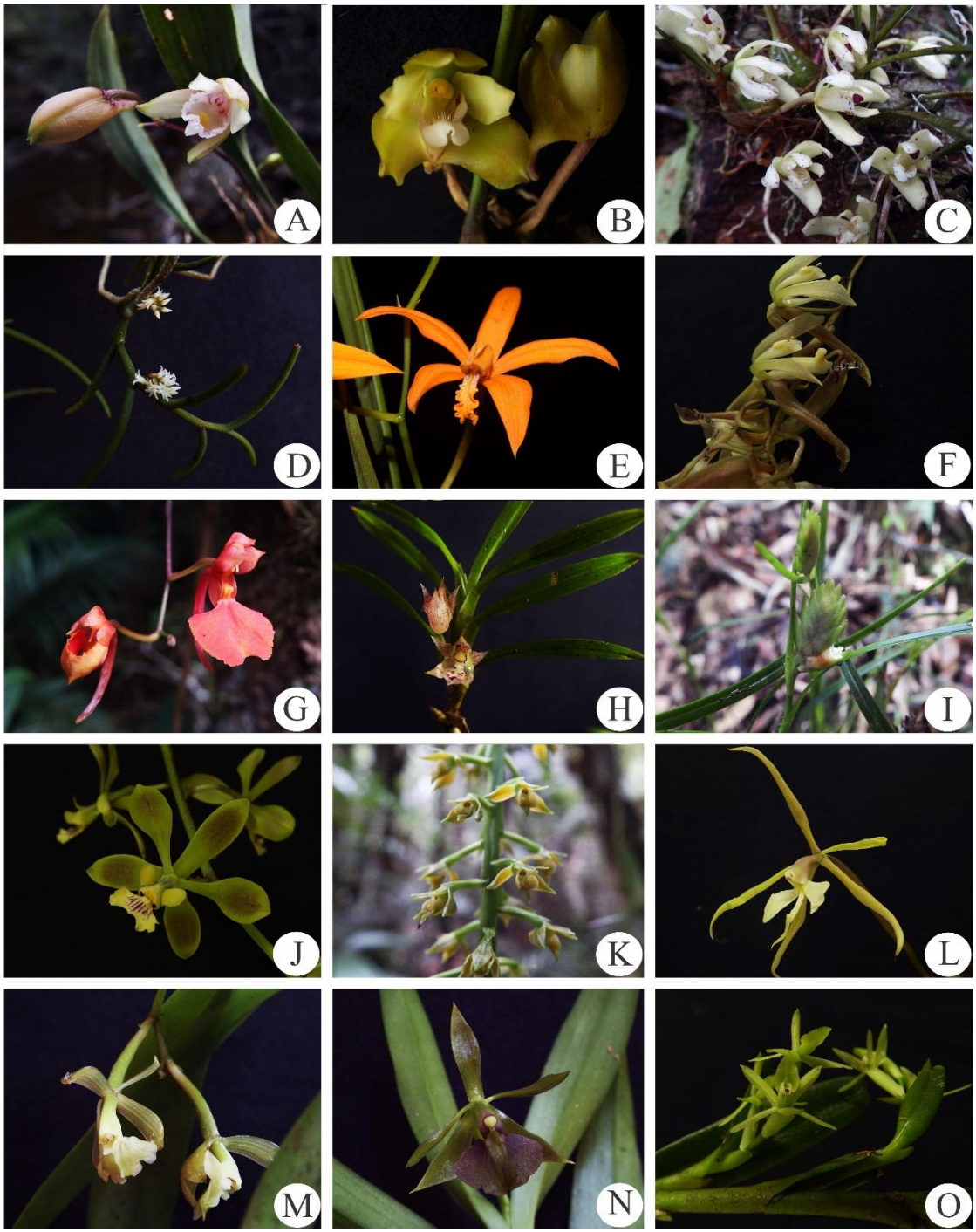


Fig. 6 Vascular epiphytes representatives of the Augusto Ruschi Biological Reserve, Santa Teresa, Espírito Santo, Brazil. **a–o** Orchidaceae: **a** *Bifrenaria clavigera*. **b** *Bifrenaria mellicolor*. **c** *Brasiliorchis kautskyi*. **d** *Campylocentrum ornithorrhynchum.* **e** *Cattleya harpophylla*. **f** *Cirrhaea nasuta*. **g** *Comparettia coccínea*. **h** *Dichaea cogniauxiana.* **i** *Elleanthus linifolius.* **j** *Encyclia patens.* **k** *Epidendrum armeniacum.* **l** *Epidendrum carpophorum*. **m** *Epidendrum henschenii*. **n** *Epidendrum proligerum.* **o** *Epidendrum ramosum.*

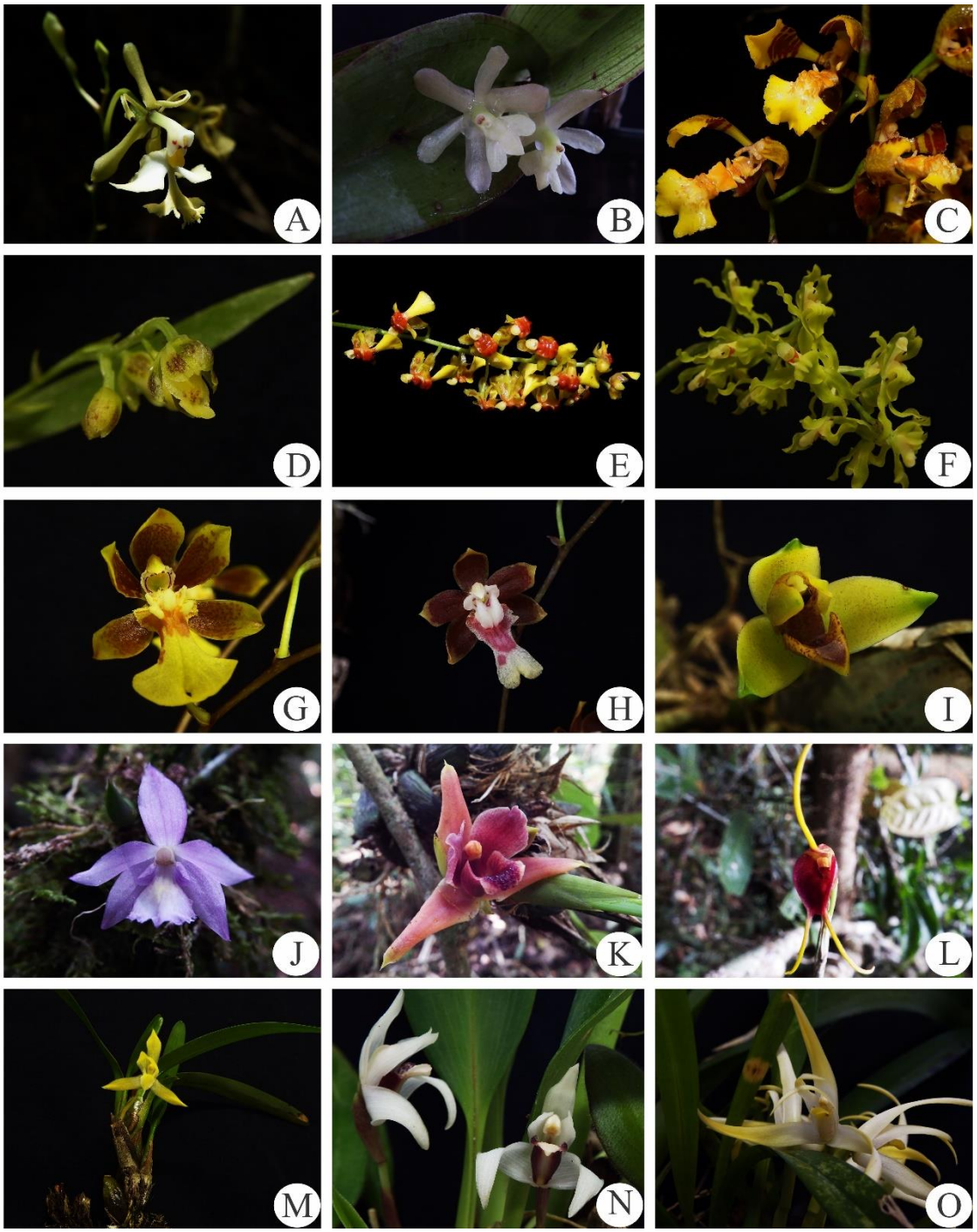


Fig. 7 Vascular epiphytes representatives of the Augusto Ruschi Biological Reserve, Santa Teresa, Espírito Santo, Brazil. **a–o** Orchidaceae: **a** *Epidendrum saxatile*. **b** *Epidendrum vesicatum*. **c** *Gomesa damacenoi*. **d** *Gomesa jucunda*. **e** *Gomesa ranifera*. **f** *Gomesa recurva*. **g** *Grandiphyllum auricula*. **h** *Grandiphyllum edwallii*. **i** *Heterotaxis brasiliensis*. **j** *Leptotes tenuis*. **k** *Mapinguari desvauxianus*. **l** *Masdevallia infracta*. **m** *Maxillaria imbricata*. **n** *Maxillaria milenae*. **o** *Maxillaria ochroleuca*.



Fig. 8 Vascular epiphytes representatives of the Augusto Ruschi Biological Reserve, Santa Teresa, Espírito Santo, Brazil. **a–o** Orchidaceae: **a** *Myoxanthus punctatus*. **b** *Myoxanthus ruschii.* **c** *Nitidobulbon nasutum*. **d** *Octomeria alexandri.* **e** *Octomeria crassifolia*. **f** *Octomeria gracilis.* **g** *Octomeria juncifolia*. **h** *Octomeria rotundiglossa*. **i** *Ornithidium rigidum.* **j** *Pabstia viridis.* **k** *Pabstiella lingua.* **l** *Pabstiella lueriana*. **m** *Pabstiella matinhensis*. **n** *Pabstiella nymphalis.* **o** *Pabstiella pterophora.*

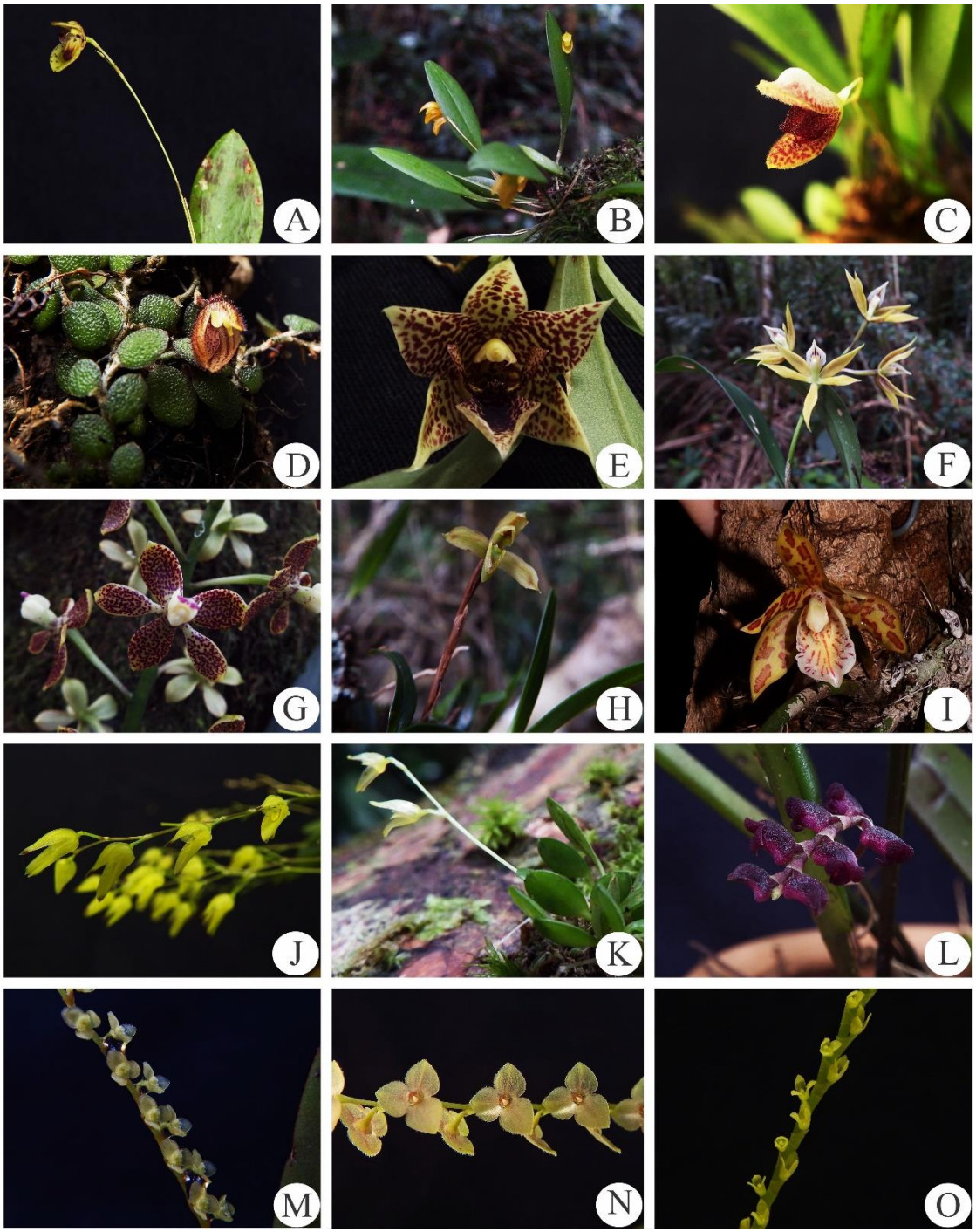


Fig. 9 Vascular epiphytes representatives of the Augusto Ruschi Biological Reserve, Santa Teresa, Espírito Santo, Brazil. **a–o** Orchidaceae: **a** *Pabstiella seriata*. **b** *Pabstiella trifida*. **c** *Pabstiella villosisepala*. **d** *Phloeophila nummularia*. **e** *Promenaea guttata*. **f** *Prosthechea kautzkii*. **g** *Prosthechea pachysepala*. **h** *Rhetinantha notylioglossa*. **i** *Scuticaria hadwenii*. **j** *Specklinia marginalis*. **k** *Specklinia subpicta*. **l** *Stelis amoena*. **m** *Stelis aprica*. **n** *Stelis argentata*. **o** *Stelis deregularis*.



Fig. 10 Vascular epiphytes representatives of the Augusto Ruschi Biological Reserve, Santa Teresa, Espírito Santo, Brazil. **a–c** Orchidaceae: **a** *Stelis intermedia*. **b** *Stelis papaquerensis.* **c** *Thysanoglossa organensis*. **d–j** Piperaceae: **d** *Peperomia alata*. **e** *Peperomia choroniana*. **f** *Peperomia glaziou.* **g** *Peperomia pilicaulis.* **h** *Peperomia pseudoestrellensis.* **i** *Peperomia tetraphylla.* **j–m** Polypodiaceae: **j** *Cochlidium punctatum.* **k** *Cochlidium serrulatum*. **l** *Melpomene melanosticta*. **m** *Pecluma truncorum*. **n** *Vittaria lineata* (Pteridaceae). **o** *Dyssochroma atlanticum* (Solanaceae).

Discussion

Overall, 82,3% of the species recorded in the ARBR belong to the five richest families. The results recorded here follow the pattern, with some level of substitutions among the richest families worldwide (Kress 1986; Zotz 2013; 2016). Epiphytism evolved in about 80 families (Kress 1986; Zotz 2013; 2016). However, few demonstrate high diversification rates, like Orchidaceae and Bromeliaceae (Givnish *et al*. 2014; 2015). The richest genera also belong to these families, supporting the values reported to the Atlantic Forest (Kersten 2010; Freitas *et al.* 2016).

The great majority of the species are endemic to the Atlantic Forest (231 species, 64% of overall) - of that, 39 are endemic to ES (according to BFG 2018) - especially among Bromeliaceae and Orchidaceae, corroborating the previous results for the AF which indicated high levels of endemism for these families (Stehmann *et al.* 2009; Freitas *et al.* 2016). The same trend occurs regarding threatened species which, at the national level, comprises 20 species cited in the Red Book of Brazilian Flora (Martinelli and Moraes 2013), and, at the state level, 97 species (Fraga *et al.* 2019). This supports ES ranking second among the Brazilian States with the high number of threatened species (Martinelli & Moraes 2013) and Santa Teresa as a Key Biodiversity Area to the conservation of plant biodiversity (Giulietti *et al.* 2009).

The richness of vascular epiphytes recorded in this study for the ARBR is outstanding so far for the Atlantic Forest, Brazil, and even the Neotropical Region (Table 2). The richness recorded corroborates the high number of species and endemism in this area (Werneck *et al.* 2011; Menini Neto *et al.* 2016; Lima *et al.* 2020; Furtado 2020). The number of species recorded corresponds to approximately 16% of the vascular epiphytic flora of the Atlantic Forest (Freitas *et al.* 2016), in an area of 0,002 % of the whole geographical area of the referred domain (Ribeiro *et al.* 2009). This represents 25,5 % of the entire vascular flora of the ARBR (Amaral & Kollmann unpublished data), which fits it in a number above the average for the Atlantic Forest (Kersten 2010; Freitas *et al.* 2016), and the Neotropical Region (Wolf & Flamenco-S 2003).

The top Brazilian richness, considering local surveys exclusively of vascular epiphytes, are from mountainous sites with several years of collections (Table 2). Regarding the first aspect, ARBR stands out as one of the smallest elevational ranges and the small average precipitation values (Table 2). To give an idea, even compared with surveys considering broad sites in the AF, as the upper Iguaçu river, in Southern Brazil

(Kersten & Kunyioshi 2006), the richness recorded in the ARBR is outstanding. When comparing with the Amazon, the epiphyte richness of the ARBR is higher than the entire Acre state (Obermüller *et al.* 2014). However, the epiphyte-richness in the Amazon can be high in some areas, as Benavides *et al.* (2005) demonstrated. The comprehensive survey of vascular epiphytes of ARBR was possible to give the high number of collections performed in the last 20 years in the area, added with the fieldwork carried, that allowed us to record 31 taxa for the first time in the ARBR, two of them, *Epidendrum henschenii* Barb. Rodr. (Figure 6 m) and *Thysanoglossa organensis* Brade (Figure 10 c), are recorded for the first time in ES.

Table 2 Local floristic surveys exclusively of vascular epiphytes in the Neotropical Region, organized in descending order of species richness. (Spp = number of species; Gen = number of genera; Fam = number of families; NI Data not informed in the source; * excluded mistletoes; ** including only angiosperms).

Country	Location	Spp	Gen	Fam	Elevation (m)	Precipitation (mm)	Temperature (Cº)	Area (hectares)	Source
Ecuador	San Francisco	641	118	20	1800-3150	2500-5000	11-17	1000	Bussmann (2001)
Panama	Río Changuinola	476	124	32	110-550	4000	NI	400	Wester *et al.* (2011)
Mexico	El Triunfo	465	131	31	0-4060	2152	21.2	119.000	Martínez-Meléndez *et al.* (2009)
Ecuador	Otonga	456	93	30	1400-2200	2600	NI	1000	Küper *et al.* (2004)
Brazil	**Augusto Ruschi**	**360**	**116**	**20**	**780-1150**	**1258**	**20**	**3560**	**Present study**
Ecuador	Yasuni	313	103	26	230	3200	25	650	Kreft *et al.* (2004)
Brazil	Macaé de Cima	312	87	26	880-1720	2128	17,9	7200	Fontoura *et al.* (1997)*
Ecuador	Cotapata (Tunquini)	291	76	24	1650-2200	2500	13-19	3	Krömer (2003)
Brazil	Serra da Prata	278	109	30	300-1100	2290	NI	6,3	Blum *et al.* (2011a)
Bolivia	Mosetenes	274	83	24	1250-1600	NI	NI	2	Krömer *et al.* (2008); Kessler *et al.* (2008)
Brazil	Serra das Lontras	256	87	18	400-1000	1300-1600	24	11000	Leitman *et al.* (2014)**
Costa Rica	Monteverde	256	105	27	1500-1550	2500	NI	4	Ingram *et al.* (1996)
Ecuador	Guajalito	256	70	29	1800-2200	2700	NI	400	Küper *et al.* (2004)
Ecuador	Sapecho	255	87	23	600-1200	2000	24-25	5	Krömer (2003)
Brazil	Ibitipoca	224	81	22	1000-1800	1532	18,9	300	Furtado & Menini Neto (2018)
Colombia	Caquetá	213	73	27	150	3060	25.7	0,75	Benavides *et al.* (2005)

The diversification in the AF may be due to its complex biogeography history (climatically and geologically), helping us to understand the high species richness and endemism found in the ARBR. Historically, the vicariance events seem to have played an important role in the diversification. The rise of the dry diagonal in South America during the Oligocene/Miocene made the AF isolated from the Amazon (Prado & Gibbs 1993; Fiaschi & Pirani 2009; Zanella 2011), a period when the diversification of several plant groups occurred in the Brazilian coast (e.g., Perret *et al.* 2006; 2013; Givnish *et al.* 2014; Moreno *et al.* 2015). The erosive dynamics that shaped eastern Brazil's mountains occurred in the same period of biota diversification in the AF, perhaps a consequence of the habitat heterogeneity created, providing several new niches for plant lineages to evolve (Almeida & Carneiro 1998; Ribeiro 2006). Together, the climatic stability - probably since the Miocene - in the Brazilian coast may have acted in the high species accumulation and endemism currently found in the AF (Prance 1982; Carnaval & Moritz 2008; Staggemeier *et al.* 2015; Fiaschi *et al.* 2016).

Regarding the local conditions, the intermediate elevational position of the ARBR in the mountainous region of Espírito Santo, which ranges from sea level to about 2050 m (*Forno Grande* summit), may justify this result. One of the explanations is the high species overlap from both ends of the altitudinal gradient at mid-elevations (Colwell *et al.* 2004; Cardelús *et al.* 2006), mainly driven by humidity and intermediate temperature conditions (Kluge *et al.* 2006), *e.g.*, in the high elevation the temperature is low, and at lower elevations is the opposite (Körner 2007; INCAPER 2020). Regarding the humidity, in the studied area, the precipitation is unusually high to the ES mountains (INCAPER 2020), a factor that comprises one of the main drives favouring the VE richness and distribution (Gentry & Dodson 1987a; Zotz & Hietz 2001; Cardelus *et al.* 2006; Ding *et al.* 2016). The precipitation (annual average and seasonality) in the ARBR is unusual. It is mainly influenced by the orographic rains occurring in the eastern side of the mountain slopes, demonstrating the importance of the relief in the unequal rainfall distribution (Nascimento & Vale 2019), and, consequently, in the vegetation distribution (*e.g.*, Blum *et al.* 2011).

Comparing with the Atlantic Forest as a whole, this is a state with intermediated climatic conditions (Alvares *et al.* 2013) and one of the biodiversity hotspots (Werneck *et al.* 2011; Menini Neto *et al.* 2016), supporting the high species richness recorded in this study, as well as in the northern Espírito Santo and the southern coast of Bahia (Rolim *et al.* 2016a). These results disagree with the general patterns of vascular epiphytes

species richness. An unexpectedly high number of species was registered in an area with low precipitation average and seasonal climate (Gentry & Dodson 1987a; Zotz 2016). On the other hand, it agrees with the patterns of greatest diversity at intermediate precipitation regimes (Wolf & Flamenco-S 2003; Neves *et al.* 2020).

This is the first comprehensive checklist of vascular epiphytes of the ARBR, and we could demonstrate that this protected area holds the high species richness recorded until now in the AF. This data corroborates the previous studies about the floristic richness of ES mountains and reinforces this synusia as one of the main functional groups of the taxonomic composition in tropical forests (Gentry & Dodson 1987b). Furthermore, the high number of species recorded in an area with low precipitation average and seasonal climate is a distinctive feature regarding the Neotropical Region's general patterns. A factor of noteworthy importance is the vegetation conservation level in the ARBR, which mainly comprises pristine forest, which helps understand this high richness in the area. Finally, we encourage further studies in poorly studied remnants of the Atlantic Forest in the state of Espírito Santo, mainly focused on specific habits such as the epiphytic.

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Capítulo 4

Plants in the clouds: Vascular epiphytes of Pedra Azul, a mountain top in Espírito Santo, Southeastern Brazil

Abstract

Cloud forests usually occur at high-altitude sites of the Atlantic Forest in eastern Brazil, albeit scattered and fragmented along the mountain tops. In this habitat, the vegetation occurs at low-temperature conditions and is usually provided by additional water sources that arise due to the horizontal precipitation of the frequent fogs. Together with the more considerable air movement and higher luminosity, these factors are conditioning for singular floras at high elevations, mainly the vascular epiphytes, which are macro and microclimate dependent. In the mountains range at the center of the Espírito Santo State, Southeastern Brazil, some mountain tops such as *Pedra Azul* (PA) hold these environmental features. Here, we aimed to present the first checklist of vascular epiphytes in the Pedra Azul State Park and surroundings based on fieldwork and herbarium specimens. The checklist comprises 152 species, 65 genera, and 17 families, the main families being Orchidaceae, Bromeliaceae, and Polypodiaceae, with the main genera represented by *Vriesea*, *Acianthera*, and *Peperomia*. The holoepiphytes were the main category among the epiphytes, although an unusually high number of facultative epiphytes were recorded. *Asplenium theciferum* and *Octomeria cucullata* are recorded in Espírito Santo for the first time, and we confirmed the occurrence of *Rhipsalis cereuscula* in the state. Overall, the richness recorded in PA is amongst the highest of the Atlantic Forest cloud forests. Six species are threatened at the national level and 32 at the state level. These results support the importance of the protected area for conserving the flora; however, several species - including threatened - were only recorded in the surroundings, demonstrating that the buffer zone of the Pedra Azul State Park must be included in the management plans.

Key words: Atlantic Forest, cloud forest, endangered species, floristic, inselberg, Pedra Azul State Park.

Introduction

The Atlantic Forest, which occurs in eastern Brazil, northern Argentina, and eastern Paraguay, is a phytogeographic domain comprising the second largest forest massif of South America, only smaller than the Amazon (Oliveira-Filho & Fontes 2000; Fiaschi & Pirani 2009). It occurs in the most mountainous region of Brazil, thus having a rugged relief and, consequently, a physiognomy conditioned by several environmental factors (e.g., climatic and edaphic), resulting in different types of vegetation (e.g., Semideciduous and Deciduous Seasonal Forests, Dense and Mixed Rain Forest, and Coastal Plain Forest (*Restinga*) (Oliveira-Filho & Fontes 2000; Fiaschi & Pirani 2009).

At high altitudes, primarily in southern and southeastern Brazil, some particular vegetation types occur in the Atlantic Forest, such as the cloud forests, *Araucaria* forests, and high-altitude grasslands (Safford *et al.* 1999; Costa *et al.* 2018). The main mountain ranges are the *Serra da Mantiqueira* and the *Serra do Mar*, with elevations reaching nearly 3,000 m above sea level (e.g., *Pico da Bandeira*, at 2,890 m) (Costa *et al.* 2018). Besides these, in the state of Espírito Santo, southeastern Brazil, there is a mountain range locally called *Montanhas Capixabas* or *Serra do Castelo* (Chiron & Bolsanello 2015). Although it does not reach elevations as high as the former ones, with the highest peak reaching about 2,000 m on the highest mountain top of the *Serra do Castelo* (Chiron & Bolsanello 2015; Garbin *et al.* 2017), it is one of the least botanically studied of the Atlantic Forest mountain ranges, with few floristic studies available.

The vegetation of these highlands, nowadays restricted and scattered on mountain tops, was likely widespread in the past due to the cold climate during the Pleistocene glaciations, forcing them to occur at lower elevations and latitudes (Luna-Vega *et al.* 2001; Behling *et al.* 2002). Thus, this vegetation represents vestiges of the past cold climate physiognomies that are nowadays reduced to fragments on the mountain tops (Koehler *et al.* 2002; Bertoncello *et al.* 2011) and harbor important and threatened species with restricted distributions and which may disappear with the increase of global temperatures (Foster 2001; Colwell *et al.* 2008).

High-altitude environments hold peculiar environmental conditions such as the presence and persistence of clouds and mist, influencing edaphic and microclimatic conditions (Bertoncello *et al.* 2011) and, consequently, the distribution of the flora and vegetation (Gentry & Dodson 1987; Oliveira-Filho & Fontes 2000; Blum *et al.* 2011b; Leitman *et al.* 2015).

At the Serra do Castelo, high-altitude vegetation, like occurs in the Pedra Azul, is associated with the granite-gneiss dome-shaped rock massifs (inselberg) (Garbin *et al.* 2017; de Paula *et al.* 2020). In such environments, according with the topography, in the rock slopes occurs scattered mats with herbaceous plants, and with where patches of shallow soil are formed, a shrub vegetation occurs; also, where the deepest soils are formed, scattered dwarf cloud forests developed (Rizzini 1997; Garbin et al. 2017; de Paula et al. 2020). Furthermore, surrounding the inselbergs, taller montane and high-montane cloud forests may occur (Magnago *et al.* 2007; Thomaz 2010). Such forests are characterized by low temperatures and abundant fog that substantially increase the humidity and may provide water during drought periods (Stadtmüller 1987; Bruijnzeel *et al.* 2010; Bertoncello *et al.* 2011; Arcova *et al.* 2016). Hence, vascular epiphytes, which are greatly dependent of humidity, are favored by the horizontal precipitation provided by the clouds, resulting in great diversity and biomass of epiphytes in cloud forests (Nadkarni 1984; Clark *et al.* 1998; Freiberg & Freiberg 2000; Köhler *et al.* 2007).

In Brazil, few floristic surveys of vascular epiphytes have been carried out in cloud forests (e.g., Bianchi *et al.* 2012; Bonnet *et al.* 2013; Alves & Menini Neto 2014; Furtado & Menini Neto 2016; 2018). In Espírito Santo, only two studies of vascular epiphytes were performed in high-altitude sites (Couto *et al.* 2016; Francisco *et al.* 2019). Gaps in biodiversity knowledge are one of the biggest problems for conservation (e.g., Almeida & Mamede 2014; Giaretta *et al.* 2015). Therefore, it is essential to carry out floristic studies in areas that have been little studied and present environmental heterogeneity, aiming to direct the conservation efforts (Kessler 2001), besides the great relevance of understanding the origin, maintenance, distribution patterns, and processes to which biodiversity is subject (Werneck *et al.* 2011; Santos *et al.* 2014; Zizka & Antonelli 2018).

Here, we aim to present the first checklist of the composition of vascular epiphytes at a mountain top in the center of the state of Espírito Santo *(Serra do Castelo)*, Southeastern Brazil, specifically in the Pedra Azul State Park and surroundings.

Material and Methods

Study site

The Pedra Azul (PA) is situated in the mountainous region of Espírito Santo, which occupies the central-south portion of the state (IPEMA 2005). These mountains

are known locally as *Serra do Castelo* (Castelo Mountain Chain) (Chiron & Bolsanello 2015) and delimited to the North by the Doce River valley, to the East by the coastal plain, to the South by the Itapemirim River valley, to the Southwest by the *Serra do Caparaó*, and to the Northwest by the state of Minas Gerais and the *Serra da Chibata*, with an average altitude of 700 m reaching up to 2,050 m (Chiron & Bolsanello 2015). In the collection sites of the PA, the elevation ranges between 1,100 m and 1,600 m.

According to the Köppen classification, the climate in the PA is Cfb, with an average temperature from 14 °C to 16 °C, average precipitation of 1,200 mm to 1500 mm, and seasonal drought in the winter (May to October), with six months with less than 100 mm of rain (Alvares *et al.* 2013; INCAPER 2020). In the PA, the occurrence of fogs is usual (pers. obs.), with an estimated mean annual cloud cover of 80 % (Wilson & Jetz 2016).

In PA, the vegetation is usually classified as montane to high-montane cloud rainforest (dense ombrophilous forest) (Magnago *et al.* 2007; Garbin *et al.* 2017). However, there are six months of drought (Alvares *et al.* 2013; INCAPER 2020), so it is better fitted as a seasonal forest (IBGE 2012). In the collection sites, the vegetation ranges from tall montane and high-montane cloud forests to dwarf high-montane cloud forests, including riverine formations of both. The first occur in the deep valleys, slopes, and some patches among the inselberg drainages, while the latter in the high-altitude inselbergs, between *Pedra das Flores* and *Pedra Azul*.

The study site comprises part of the Pedra Azul State Park (PASP) and a valley in the Buffer Zone (BF) (central coordinate 20° 25' 05" S and 41° 00' 25" W) (Figure 1), situated in the district of Aracê, which belongs to the municipality of Domingos Martins, in the state of Espírito Santo (ES), Southeastern Brazil. The PASP was created in 1960 originally named Pedra Azul Forest Reserve (State Decree No. 312, of October 31st, 1960), comprising the steepest areas usually with little or no interest for crop cultivation or pastures (IDAF 2004). Consequently, the protected area includes the high-altitude inselbergs (*Pedra Azul* at 1,822 m, *Pedra das Flores* at 1,909 m) and adjacent mountain tops, comprising about 1,240 hectares, surrounded by private properties. The PASP has a well-developed tourism activity.

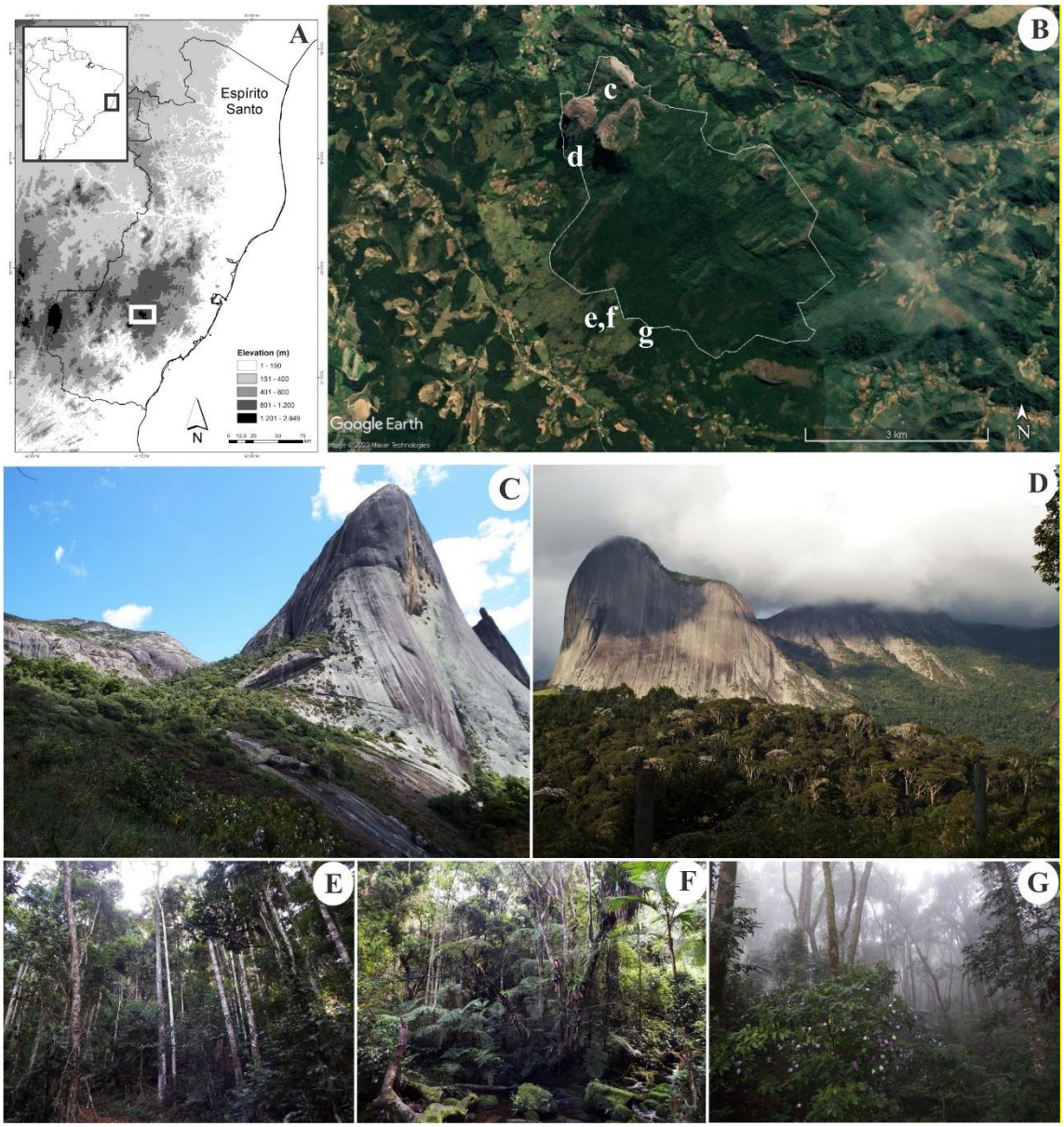


Figure 1. Geographical location of Pedra Azul and the delimitation of the Pedra Azul State Park (PASP) in white, in Domingos Martins municipality, Espírito Santo, Brazil. **a** Espírito Santo state, highlighting the location of Pedra Azul. **b** Delimitation of PASP. The letters are according to the photos. **c-d** Showing the interior of the PASP. **c** Pedra Azul, dwarf cloud forest and Pedra das Flores in the background. **d** Pedra Azul and Pedra das Flores covered by the clouds showing the tall montane forest in the slopes. **e-g** The buffer zone sampled in this study. **e** Tall montane cloud forest. **f** Alluvial cloud montane forest**. g** Secondary montane cloud forest. (a: prepared by Henrique Lauand Ribeiro; b: adapted from Google Earth Pro; c–g: photos of Gabriel Mendes Marcusso).

Collections were made on the touristic trail from the natural pools up to the foothill of *Pedra das Flores* and *Pedra Azul* (ranging from 1,350 m to 1,600 m a.s.l., covering about 12 hectares of dwarf cloud forest), in the secondary forest surrounding the research lodge (1,300 m to 1,400 m, covering about 20 ha), and in an area contiguous to the Park, in the slopes and riverine forests, in the headwaters of the Jucu River, which crosses a private property (1,100 m to 1,230 m, covering about 5 ha) (Figure 1).

Data collection

The floristic inventory of vascular epiphytes was carried out over seven expeditions lasting about one to three days each, in January, May, and September of 2018, February, August, and October of 2019, and November of 2020. Fertile specimens were deposited at the Herbarium Rioclarense (HRCB), and duplicates were sent to the herbaria BHCB, CESJ, RB, and UNOP (acronyms follow Thiers, 2020). Sterile specimens collected mainly from fallen trees and branches were kept at a greenhouse in Rio Claro until flowering and subsequently processed. To complement the floristic inventory, we used the SpeciesLink network (CRIA 2020) and Reflora - Virtual Herbarium (2020) to analyze previous collections carried out within the Park and deposited at the herbaria MBML, RB, and VIES (acronyms follow Thiers, 2020).

During the expeditions to the field, we observed the habits of the epiphytes and classified them into ecological categories according to their relationship with the phorophytes, following Benzing (1990): characteristic holoepiphytes, facultative holoepiphytes, primary hemiepiphytes, and secondary hemiepiphytes. It was preferred to use this classification instead of that of Zotz (2013a) to facilitate comparison with other studies since most used the former. Terrestrial species occasionally found growing as epiphytes were not considered in this study, as they are deemed ephemeral epiphytes (Kersten 2010; Zotz 2016).

Taxonomic identification was made using taxonomic literature and herbarium collections at HRCB and MBML, as well as by consulting specialists (mentioned in the acknowledgments). The taxonomic classification is according to APG IV (2016) for angiosperms and PPG I (2016) for monilophytes and lycophytes. Species names, synonymy, authors, and distributions are used according to Flora do Brasil 2020 (BFG 2018). The conservation statuses were obtained at national (Martinelli & Moraes 2013; CNC Flora 2020) and, at the state level (Fraga *et al.* 2019).

Results

In the PA, we recorded 152 species of vascular epiphytes belonging to 65 genera and 17 families (Table 1; Figures 2 and 3). Ferns and Lycophytes account for 37 of the recorded species, and flowering plants represent the vast majority (115 species). In the PASP 104 species were recorded, in the BF, of the 73 species, 48 were not recorded inside the protected area; 25 of them were recorded in both (Table 1). Overall, the richest families were Orchidaceae (56 species), Bromeliaceae (29), Polypodiaceae (16), Cactaceae and Piperaceae (9 each), and Araceae (7). The richness genera were *Vriesea* (11 species), *Acianthera* and *Peperomia* (9 each), *Gomesa* (7), *Asplenium* (6), and *Hymenophyllum*, *Nidularium*, *Octomeria*, *Rhipsalis*, and *Tillandsia* (5 each). The main ecological category is the characteristic holoepiphytes (88 species), followed by the facultative holoepiphytes (58) and the secondary hemiepiphytes (6).

Six species are reported as threatened at the national level, one critically endangered, two endangered, and three vunerable. At state level 32 are cited in the list, four are critically endangered, six endangered, and 22 vunerable (Table 1). Furthermore, 10 species are Data Deficient (DD) at the state level.

Table 1 List of vascular epiphyte species recorded in the Pedra Azul State Park and the neighboring area, Domingos Martins, Espírito Santo, Brazil. CH = characteristic holoepiphyte, FH = facultative holoepiphyte, SH = secondary hemiepiphyte. PASP = Pedra Azul State Park, BF = buffer zone. Voucher: APF = A. P. Fontana, GC = G. Chiron, GMM = G. M. Marcusso, GM = G. Martinelli, LCV = L. C. Vargas, LK = L. Kollmann, RR = R. Ramaldes. The acronyms HRCB, MBML, RB, and VIES. Threatened species were classified at the national level according to Martinelli & Moraes (2013) and CNC Flora (2021), and at state level according to Fraga *et al.* (2019), respectively, using the following criteria: VU = vulnerable, EN = endangered, CR = critically endangered, and DD = Data Deficient.

Families	Species	Ecological categories	Ocurrence		Voucher	Threatened status	
			PASP	BF		National	State
Araceae	*Anthurium comtum* Schott	FH		x	GMM 1048 (HRCB)		
Araceae	*Anthurium fragae* Nadruz	FH	x	x	GMM 1033 (HRCB)		VU
Araceae	*Anthurium scandens* (Aubl.) Engl.	CH	x	x	GMM 1017 (HRCB)		
Araceae	*Philodendron appendiculatum* Nadruz & Mayo	SH	x		GMM 884 (HRCB)		
Araceae	*Philodendron cordatum* Kunth ex Schott	SH	x	x	GMM 1359 (HRCB)		
Araceae	*Philodendron hatschbachii* Nadruz & Mayo	CH		x	GMM 1695 (HRCB)		
Araceae	*Philodendron propinquum* Schott	CH	x	x	GMM 1044 (HRCB)		
Aspleniaceae	*Asplenium auriculatum* Sw.	FH	x	x	GMM 1056 (HRCB)		
Aspleniaceae	*Asplenium feei* Kunze ex Fée	CH	x		GMM 994 (HRCB)		DD
Aspleniaceae	*Asplenium harpeodes* Kunze	CH	x		GMM 1001 (HRCB)		
Aspleniaceae	*Asplenium praemorsum* Sw.	FH	x	x	GMM 1090 (HRCB)		
Aspleniaceae	*Asplenium serra* Langsd. & Fisch.	FH		x	GMM 1053 (HRCB)		
Aspleniaceae	*Asplenium theciferum* (Kunth.) Mett.	FH		x	GMM 1501 (HRCB)		
Begoniaceae	*Begonia convolvulacea* (Klotzsch) A.DC.	SH		x	GMM 1074 (HRCB)		
Blechnaceae	*Lomaridium plumieri* (Desv.) C. Presl.	SH	x		GMM 993 (HRCB)		
Bromeliaceae	*Aechmea coelestis* (K.Koch) E.Morren	CH	x	x	GMM 1035 (HRCB)		
Bromeliaceae	*Billbergia amoena* (Lodd.) Lindl.	CH		x	GMM 1494 (HRCB)		
Bromeliaceae	*Billbergia euphemiae* E.Morren	FH		x	GMM 1073 (HRCB)		

Families	Species	Ecological categories	Ocurrence		Voucher	Threatened status	
			PASP	BF		National	State
Bromeliaceae	*Billbergia horrida* Regel	FH		x	GMM 1696 (HRCB)		
Bromeliaceae	*Billbergia zebrina* (Herb.) Lindl.	CH	x	x	GMM 1876 (HRCB)		VU
Bromeliaceae	*Neoregelia diversifolia* E.Pereira	FH	x		GMM 1014 (HRCB)		EN
Bromeliaceae	*Neoregelia farinosa* (Ule) L.B.Sm.	FH		x	GMM 1505 (HRCB)		VU
Bromeliaceae	*Nidularium bicolor* (E.Pereira) Leme	FH		x	GMM 1047 (HRCB)		VU
Bromeliaceae	*Nidularium cariacicaense* (W.Weber) Leme	FH	x		LK 8303 (MBML)		
Bromeliaceae	*Nidularium* cf. *espiritosantense* Leme	FH		x	GMM 1095 (HRCB)		
Bromeliaceae	*Nidularium longiflorum* Ule	FH	x		GM 15721 (RB)		
Bromeliaceae	*Nidularium* cf. *procerum* Lindm.	FH	x		GMM 1032 (HRCB)		
Bromeliaceae	*Quesnelia kautskyi* C.M.Vieira	FH	x		GMM 1015 (HRCB)	VU	
Bromeliaceae	*Tillandsia geminiflora* Brongn.	CH	x		GMM 878 (HRCB)		
Bromeliaceae	*Tillandsia recurvata* (L.) L.	CH		x	GMM 1597 (HRCB)		
Bromeliaceae	*Tillandsia stricta* Sol.	CH	x		GMM 1024 (HRCB)		
Bromeliaceae	*Tillandsia tenuifolia* L.	CH	x		GMM 1690 (HRCB)		
Bromeliaceae	*Tillandsia usneoides* (L.) L.	CH	x	x	GMM 877 (HRCB)		
Bromeliaceae	*Vriesea capixabae* Leme	CH	x		GMM 883 (HRCB)		VU
Bromeliaceae	*Vriesea carinata* Wawra	CH	x		GMM 1002 (HRCB)		
Bromeliaceae	*Vriesea friburgensis* Mez	FH	x		GMM 882 (HRCB)		DD
Bromeliaceae	*Vriesea guttata* Linden & André.	CH	x		RR 20 (MBML)		DD
Bromeliaceae	*Vriesea hydrophora* Ule	CH		x	GMM 1046 (HRCB)		
Bromeliaceae	*Vriesea longicaulis* (Baker) Mez	FH	x		GMM 1027 (HRCB)		
Bromeliaceae	*Vriesea lubbersii* (Baker) E.Morren	FH	x		GMM 1088 (HRCB)		
Bromeliaceae	*Vriesea* aff. *pabstii* McWill. & L.B.Sm.	FH	x		GMM 1013 (HRCB)		
Bromeliaceae	*Vriesea pereirae* L.B.Sm.	FH	x		GM 15730 (RB)		VU

Families	Species	Ecological categories	Ocurrence		Voucher	Threatened status	
			PASP	BF		National	State
Bromeliaceae	*Vriesea poenulata* (Baker) Mez	CH	x	x	GMM 1352 (HRCB)		
Bromeliaceae	*Vriesea vagans* (L.B.Sm.) L.B.Sm.	CH	x		GMM 1591 (HRCB)		
Cactaceae	*Hatiora salicornioides* (Haw.) Britton & Rose	FH	x		GMM 860 (HRCB)		
Cactaceae	*Lepismium cruciforme* (Vell.) Miq.	CH		x	GMM 1324 (HRCB)		
Cactaceae	*Lepismium warmingianum* (K.Schum.) Barthlott	CH		x	GMM 1323 (HRCB)		
Cactaceae	*Rhipsalis cereuscula* Haw.	FH		x	GMM 1641 (HRCB)		
Cactaceae	*Rhipsalis clavata* F.A.C.Weber	CH		x	GMM 1049 (HRCB)		EN
Cactaceae	*Rhipsalis floccosa* Salm-Dyck ex Pfeiff.	CH	x	x	GMM 1083 (HRCB)		
Cactaceae	*Rhipsalis hoelleri* Barthlott & N.P.Taylor	CH	x		GMM 1484 (HRCB)		EN
Cactaceae	*Rhipsalis teres* (Vell.) Steud.	CH	x	x	GMM 1043 (HRCB)		
Cactaceae	*Schlumbergera kautskyi* (Horobin & McMillan) N.P.Taylor	FH		x	GMM 1534 (HRCB)	EN	CR
Dryopteridaceae	*Elaphoglossum glaziovii* (Fée) Brade	FH		x	GMM 1051 (HRCB)		
Dryopteridaceae	*Elaphoglossum vagans* (Mett.) Hieron.	CH	x		GMM 1472 (HRCB)		
Dryopteridaceae	*Olfersia cervina* (L.) Kunze	SH		x	GMM 1599 (HRCB)		
Dryopteridaceae	*Rumohra adiantiformis* (G.Forst.) Ching	FH	x		GMM 1034 (HRCB)		
Gesneriaceae	*Codonanthe cordifolia* Chateums	FH	x		GMM 846 (HRCB)		VU
Gesneriaceae	*Sinningia douglasii* (Lindl.) Chautems	FH		x	GMM 1363 (HRCB)		CR
Hymenophyllaceae	*Hymenophyllum caudiculatum* Mart.	CH	x		GMM 1347 (HRCB)		
Hymenophyllaceae	*Hymenophyllum hirsutum* (L.) Sw.	FH	x		GMM 1000 (HRCB)		
Hymenophyllaceae	*Hymenophyllum myriocarpum* Hook.	CH	x		GMM 998 (HRCB)		
Hymenophyllaceae	*Hymenophyllum polyanthos* (Sw.) Sw.	CH	x		GMM 1490 (HRCB)		
Hymenophyllaceae	*Hymenophyllum tunbrigense* (L.) Sm.	FH	x		GMM 1007 (HRCB)		DD

Families	Species	Ecological categories	Ocurrence		Voucher	Threatened status	
			PASP	BF		National	State
Hymenophyllaceae	*Polyphlebium angustatum* (Carmich.) Ebihara & Dubuisson	CH	x	x	GMM 1050 (HRCB)		
Lomariopsidaceae	*Lomariopsis marginata* (Schrad.) Kuhn	FH		x	GMM 1599 (HRCB)		
Lycopodiaceae	*Phlegmariurus biformis* (Hook.) B.Øllg.	CH	x		GMM 1350 (HRCB)		
Lycopodiaceae	*Phlegmariurus quadrifariatus* (Bory) B. Øllg.	CH	x		GMM 1860 (HRCB)		DD
Onagraceae	*Fuchsia regia* (Vell.) Munz	FH	x	x	GMM 1079 (HRCB)		
Orchidaceae	*Acianthera binotii* (Regel) Pridgeon & M.W.Chase	CH	x		GMM 1164 (HRCB)		VU
Orchidaceae	*Acianthera fenestrata* (Barb.Rodr.) Pridgeon & M.W.Chase	CH	x		GMM 868 (HRCB)		
Orchidaceae	*Acianthera heringeri* (Hoehne) F.Barros	CH		x	GMM 1070 (HRCB)	CR	VU
Orchidaceae	*Acianthera maculiglossa* Chiron & Sanson	CH		x	GMM 1398 (HRCB)		
Orchidaceae	*Acianthera montana* (Barb.Rodr.) F.Barros & L.Guimarães	CH	x	x	GMM 871 (HRCB)		
Orchidaceae	*Acianthera octophrys* (Rchb.f.) Pridgeon & M.W.Chase	CH		x	GMM 1045 (HRCB)		
Orchidaceae	*Acianthera recurva* (Lindl.) Pridgeon & M.W.Chase	FH		x	GMM 1535 (HRCB)		
Orchidaceae	*Acianthera rostellata* (Barb.Rodr.) Luer	CH	x		LK 103 (MBML)		DD
Orchidaceae	*Acianthera tricarinata* (Poepp. & Endl.) Pridgeon & M.W.Chase	FH	x	x	GMM 1863 (HRCB)		
Orchidaceae	*Anathallis adenochila* (Loefgr.) F.Barros	CH		x	GMM 1066 (HRCB)		
Orchidaceae	*Anathallis obovata* (Lindl.) Pridgeon & M.W.Chase	CH	x	x	GMM 1163 (HRCB)		
Orchidaceae	*Anathallis radialis* (Porto & Brade) Pridgeon & M.W.Chase	CH	x		GMM 999 (HRCB)		VU

Families	Species	Ecological categories	Ocurrence		Voucher	Threatened status	
			PASP	BF		National	State
Orchidaceae	*Brasiliorchis gracilis* (Lodd.) R.B.Singer et al.	FH	x		GMM 1861 (HRCB)		
Orchidaceae	*Brasiliorchis marginata* (Lindl.) R.B.Singer et al.	FH	x		GMM 870 (HRCB)		
Orchidaceae	*Cattleya coccinea* Lindl.	CH	x		APF 2226 (RB)		CR
Orchidaceae	*Centroglossa macroceras* Rchb.f.	CH		x	GMM 1389 (HRCB)		VU
Orchidaceae	*Dichaea cogniauxiana* Schltr.	CH	x		GMM 1162 (HRCB)		VU
Orchidaceae	*Epidendrum armeniacum* Lindl.	CH		x	GMM 1499 (HRCB)		
Orchidaceae	*Epidendrum chlorinum* Barb.Rodr.	CH	x		GMM 876 (HRCB)		EN
Orchidaceae	*Epidendrum latilabrum* Lindl.	CH	x		GMM 1760 (HRCB)		
Orchidaceae	*Epidendrum proligerum* Barb.Rodr.	CH	x		GMM 858 (HRCB)		
Orchidaceae	*Eurystyles actinosophila* (Barb.Rodr.) Schltr.	CH		x	GMM 1325 (HRCB)		
Orchidaceae	*Gomesa cruciata* (Rchb.f.) M.W.Chase & N.H.Williams	CH	x	x	GMM 1486 (HRCB)		
Orchidaceae	*Gomesa gardneri* (Lindl.) M.W.Chase & N.H.Williams	FH	x		LK 108 (MBML)		VU
Orchidaceae	*Gomesa gomezoides* (Barb.Rodr.) Pabst	CH	x		GMM 1406 (HRCB)		VU
Orchidaceae	*Gomesa imperatoris-maximiliani* (Rchb.f.) M.W.Chase & N.H.Williams	FH	x		GMM 874 (HRCB)		EN
Orchidaceae	*Gomesa praetexta* (Rchb.f.) M.W.Chase & N.H.Williams	FH	x		GMM 1479 (HRCB)		EN
Orchidaceae	*Gomesa recurva* R.Br.	CH		x	GMM 1401 (HRCB)		
Orchidaceae	*Gomesa uhlii* (Chiron & V.P.Castro) M.W.Chase & N.H.Williams	CH	x		GMM 1030 (HRCB)		DD
Orchidaceae	*Grandiphyllum divaricatum* (Lindl.) Docha Neto	CH	x	x	GMM 873 (HRCB)		

Families	Species	Ecological categories	Ocurrence		Voucher	Threatened status	
			PASP	BF		National	State
Orchidaceae	*Grandiphyllum edwallii* (Cogn.) Docha Neto	CH		x	GMM 1733 (HRCB)		DD
Orchidaceae	*Grobya amherstiae* Lindl.	CH	x	x	GMM 1488 (HRCB)		
Orchidaceae	*Hadrolaelia pumila* (Hook.) Chiron & V.P.Castro	CH	x		GMM 945 (HRCB)	VU	CR
Orchidaceae	*Isabelia virginalis* Barb.Rodr.	CH		x	GMM 1092 (HRCB)	VU	
Orchidaceae	*Isochilus linearis* (Jacq.) R.Br.	FH	x		GMM 1028 (HRCB)		
Orchidaceae	*Lankesterella ceracifolia* (Barb.Rodr.) Mansf.	CH	x		GMM 1482 (HRCB)		VU
Orchidaceae	*Masdevallia infracta* Lindl.	CH		x	GMM 1064 (HRCB)		
Orchidaceae	*Miltonia clowesii* Lindl.	CH		x	GMM 1492 (HRCB)		
Orchidaceae	*Miltonia spectabilis* Lindl.	CH		x	GMM 1741 (HRCB)		VU
Orchidaceae	*Notylia hemitricha* Barb.Rodr.	CH	x		GMM 1719 (HRCB)		
Orchidaceae	*Octomeria crassifolia* Lindl.	FH	x		GMM 1029 (HRCB)		
Orchidaceae	*Octomeria cucullata* Porto & Brade	CH	x		GMM 1161 (HRCB)		
Orchidaceae	*Octomeria diaphana* Lindl.	CH	x		GMM 1093 (HRCB)		
Orchidaceae	*Octomeria gracilis* Lodd. Ex Lindl.	CH	x		GMM 1588 (HRCB)		VU
Orchidaceae	*Octomeria palmyrabellae* Barb. Rodr.	CH	x		GMM 1555 (HRCB)		VU
Orchidaceae	*Pabstia jugosa* (Lindl.) Garay	CH	x		GMM 1344 (HRCB)	EN	VU
Orchidaceae	*Pabstiella fusca* (Lindl.) Chiron & Xim.Bols.	CH		x	GMM 1060 (HRCB)		
Orchidaceae	*Pabstiella leucopyramis* (Rchb.f.) Luer	CH	x		GMM 864 (HRCB)		VU
Orchidaceae	*Polystachya estrellensis* Rchb.f.	FH		x	GMM 1504 (HRCB)		
Orchidaceae	*Promenaea xanthina* (Lindl.) Lindl.	CH	x		GMM 865 (HRCB)		
Orchidaceae	*Prosthechea fragrans* (Sw.) W.E.Higgins	CH		x	LCV s.n. (VIES)		
Orchidaceae	*Prosthechea pygmaea* (Hook.) W.E.Higgins	CH		x	GC 9929 (MBML)		

Families	Species	Ecological categories	Ocurrence		Voucher	Threatened status	
			PASP	BF		National	State
Orchidaceae	*Rhetinantha notylioglossa* (Rchb.f.) M.A.Blanco	FH	x		GMM 1737 (HRCB)		
Orchidaceae	*Specklinia grobyi* (Batem. ex Lindl.) F.Barros	CH		x	GMM 1062 (HRCB)		
Orchidaceae	*Stelis aprica* Lindl.	CH		x	GMM 1063 (HRCB)		
Orchidaceae	*Stelis papaquerensis* Rchb.f.	CH	x	x	GMM 1379 (HRCB)		DD
Piperaceae	*Peperomia alata* Ruiz & Pav.	FH	x	x	GMM 851 (HRCB)		
Piperaceae	*Peperomia catharinae* Miq.	CH	x		GMM 1087 (HRCB)		VU
Piperaceae	*Peperomia corcovadensis* Gardner	FH	x		GMM 1349 (HRCB)		
Piperaceae	*Peperomia glabella* (Sw.) A.Dietr.	CH		x	GMM 1071 (HRCB)		
Piperaceae	*Peperomia mandioccana* Miq.	CH	x		GMM 1078 (HRCB)		
Piperaceae	*Peperomia martiana* Miq.	FH	x	x	GMM 1055 (HRCB)		
Piperaceae	*Peperomia pilicaulis* C.DC.	CH		x	GMM 1042 (HRCB)		VU
Piperaceae	*Peperomia tetraphylla* (G.Forst.) Hook. & Arn.	FH	x		GMM 867 (HRCB)		
Piperaceae	*Peperomia urocarpa* Fisch. & C.A.Mey.	FH		x	GMM 1068 (HRCB)		
Polypodiaceae	*Campyloneurum aglaolepis* (Alston) de la Sota	FH		x	GMM 1040 (HRCB)		
Polypodiaceae	*Campyloneurum angustifolium* (Sw.) Fée	FH	x		GMM 1694 (HRCB)		
Polypodiaceae	*Campyloneurum atlanticum* R.C.Moran & Labiak	FH	x		GMM 1006 (HRCB)		
Polypodiaceae	*Campyloneurum nitidum* (Kaulf.) C.Presl	CH	x		GMM 848 (HRCB)		
Polypodiaceae	*Cochlidium punctatum* (Raddi) L.E.Bishop	CH	x		GMM 1865 (HRCB)		
Polypodiaceae	*Melpomene pilosissima* (M.Martens & Galeotti) A.R.Sm. & R.C.Moran	CH	x		GMM 1864 (HRCB)		
Polypodiaceae	*Microgramma squamulosa* (Kaulf.) de la Sota	FH	x	x	GMM 854 (HRCB)		
Polypodiaceae	*Microgramma tecta* (Kaulf.) Alston	CH		x	GMM 1502 (HRCB)		

Families	Species	Ecological categories	Ocurrence		Voucher	Threatened status	
			PASP	BF		National	State
Polypodiaceae	*Moranopteris achilleifolia* (Kaulf.) R.Y. Hirai & J. Prado	FH	x		GMM 1008 (HRCB)		
Polypodiaceae	*Niphidium crassifolium* (L.) Lellinger	FH	x	x	GMM 1023 (HRCB)		
Polypodiaceae	*Pecluma robusta* (Fée) M.Kessler & A.R.Sm.	CH	x		GMM 1857 (HRCB)		DD
Polypodiaceae	*Pleopeltis astrolepis* (Liebm.) E.Fourn.	CH		x	GMM 1041 (HRCB)		
Polypodiaceae	*Pleopeltis hirsutissima* (Raddi) de la Sota	FH	x		GMM 1086 (HRCB)		
Polypodiaceae	*Pleopeltis macrocarpa* (Bory ex Willd.) Kaulf.	CH	x		GMM 849 (HRCB)		
Polypodiaceae	*Serpocaulon catharinae* (Langsd. & Fisch.) A.R.Sm.	FH	x		GMM 1019 (HRCB)		
Polypodiaceae	*Serpocaulon fraxinifolium* (Jacq.) A.R.Sm.	SH	x		GMM 1018 (HRCB)		
Pteridaceae	*Vittaria lineata* (L.) Sm.	FH	x		GMM 997 (HRCB)		
Rubiaceae	*Hillia parasitica* Jacq.	FH	x		GMM 861 (HRCB)		

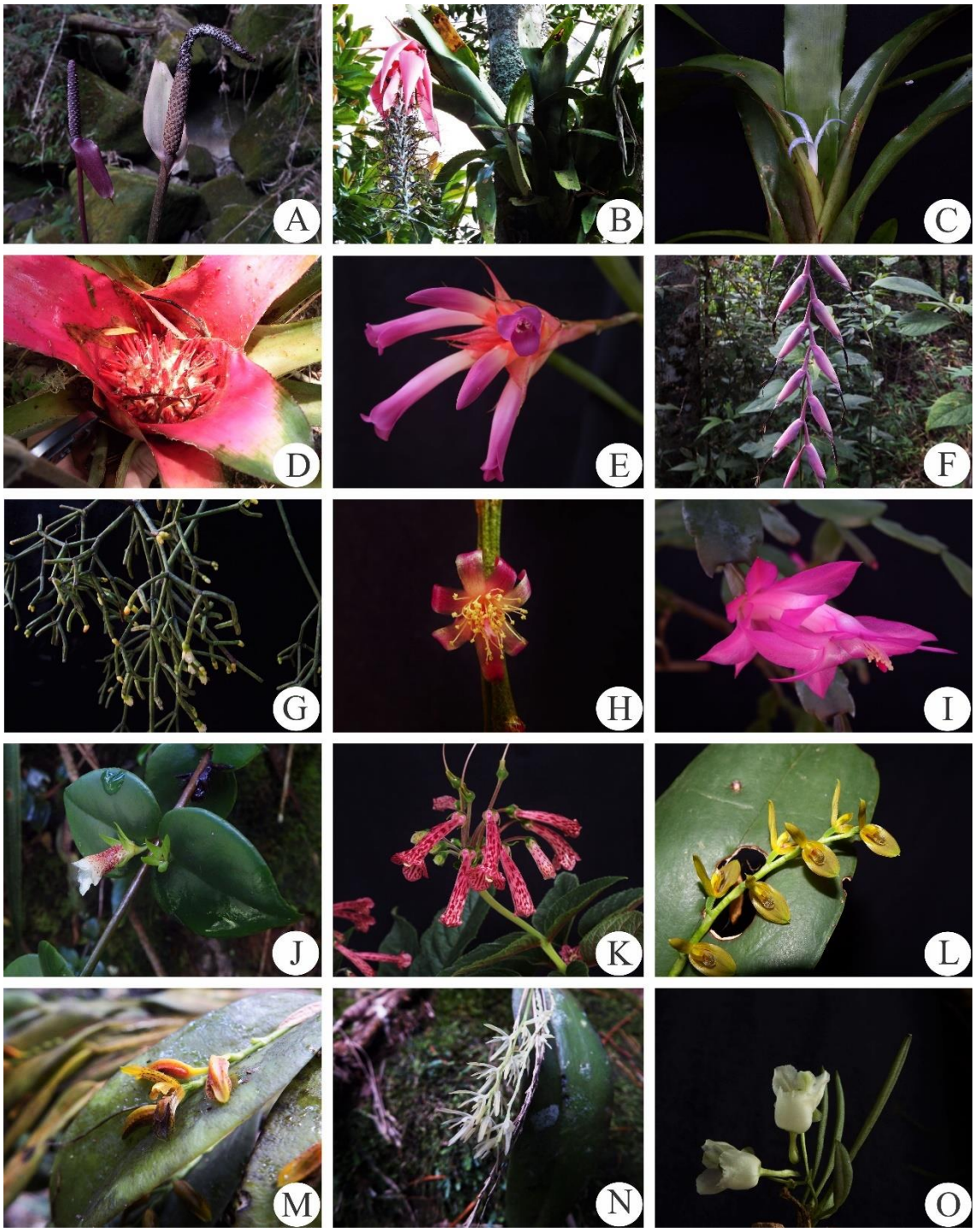


Figure 2. Vascular epiphytes representatives of Pedra Azul State Park and a neighbor particular area, Domingos Martins, Espírito Santo, Brazil, highlighting new records to Espírito Santo, threatened and data deficient species. **a** *Anthurium fragae* (Araceae). **b-f** Bromeliaceae: **c** *Neoregelia diversifolia.* **d** *Neoregelia farinosa*. **e** *Quesnelia kautskyi.* **f** *Vriesea capixabae.* **g-i** Cactaceae: **g** *Rhipsalis cereuscula.* **h** *Rhipsalis hoelleri.* **i** *Schlumbergera kautskyi*. **j-k** Gesneriaceae: **j** *Codonanthe cordifolia.* **k** *Sinningia douglasii*. **l-o** Orchidaceae: **l** *Acianthera binotii.* **m** *Acianthera heringeri.* **n** *Anathallis radialis*. **o** *Centroglossa macroceras.*

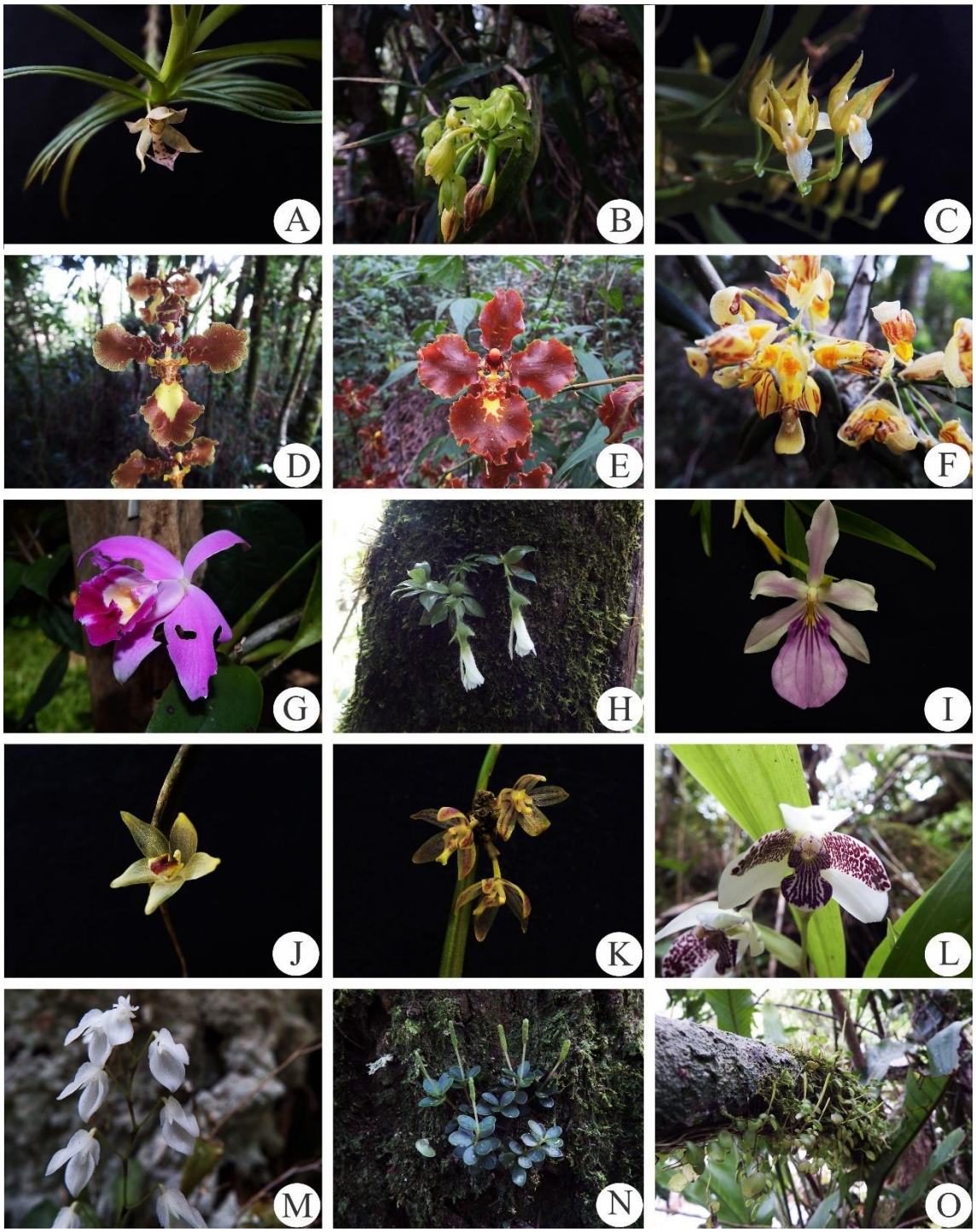


Figure 3. Vascular epiphytes representatives of Pedra Azul State Park and a neighbor particular area, Domingos Martins, Espírito Santo, Brazil, highlighting new records to Espírito Santo, threatened and data deficient species. **a-m** Orchidaceae: **a** *Dichaea cogniauxiana*. **b** *Epidendrum chlorinum*. **c** *Gomesa gomezoides*. **d** *Gomesa imperatoris-maximiliani*. **e** *Gomesa praetexta*. **f** *Gomesa uhlii* **g** *Hadrolaelia pumila*. **h** *Lankesterella ceracifolia*. **i** *Miltonia spectabilis*. **j** *Octomeria cucullata.* **k** *Octomeria palmyrabellae*. **l** *Pabstia jugosa*. **m** *Pabstiella leucopyramis*. **n-o** Piperaceae: **n** *Peperomia catharinae.* **o** *Peperomia pilicaulis.*

Discussion

We presented the first checklist of the vascular epiphytes of the Pedra Azul, including part of the Pedra Azul State Park and a river valley in the buffer zone. We found new records for the state and species threatened of extinctions at both state and national level. Overall, the number of species is outstanding for the cloud forests of the AF. The great number of facultative epiphytes is a characteristic feature of forest in rockiness matrix, like the mountain's summits. Furthermore, the peculiar climatic conditions -with the prevalence of cloud cover inputting water in the vegetation and the low temperature- are the main drive for the singular flora found in this high-altitude site.

In Brazil, few floristic studies regarding vascular epiphytes have been carried out in mountainous sites above 1,000 m of elevation (Table 2). These studies registered a richness ranging from 50 to 312 species, although they used different sample efforts and areas (Table 2). The richness recorded in the PA agrees with the data on vascular epiphytes in mountainous sites of the Atlantic Forest. The PA only stands below studies that carried out more comprehensive sampling, considering several years of collections, and those in areas with a wider altitude range (e.g., Fontoura *et al.* 1997; Furtado & Menini Neto 2016). Furthermore, considering the area sampled in the present study (about 37 hectares) and the entire area of the State Park (1,240 hectares), we may consider that the PA harbors a rich vascular epiphyte flora. Undoubtedly, additional species are expected to occur in the area since most pristine forest patches of the PA are of difficult access due to the mountainous relief and there being few trails that cross such areas. Some species are not mentioned in the list because they were not found fertile (e.g., *Acianthera nemorosa*, *Epidendrum paranaense* (Orchidaceae), *Spirotheca rivieri* (Malvaceae), and *Nematanthus* sp. (Gesneriaceae)).

Table 2 Local floristic surveys exclusively of vascular epiphytes in the high-altitude (above (880-)1,000 m) pluvial to seasonal cloud forests in the Brazilian Atlantic Forest organized in descending order of species richness. (Spp = number of species; Gen = number of genera; Fam = number of families; m = meters above sea level; mm = millimeters, ha = hectares; NI = Data not informed at the source; * = excluded mistletoes).

Location	State	Spp.	Gen.	Fam.	Altitude (m)	Precipitation (mm)	Area (ha)	Source
Macaé de Cima	RJ	312	87	26	880-1720	2128	7200	Fontoura et al. (1997)*
Ibitipoca	MG	224	81	22	1000-1800	1532	300	Furtado & Menini Neto (2018)
Pedra Azul	**ES**	**152**	**65**	**17**	**1100-1600**	**1200-1500**	**37**	**Present study**
Serra do Papagaio	MG	138	66	25	1800-2000	NI	NI	Furtado & Menini Neto (2016)
Serra do Cruz	MG	135	62	16	1100-1500	1200-1500	NI	Alves & Menini Neto (2014)
Marumbi	PR	127	59	21	1000	1384	1	Bianchi et al (2012)
Serra da Prata	PR	121	64	23	1000-1100	2290	0,2	Blum et al. (2011)
Ponte Alta	SC	84	47	16	1131	NI	2,01	Bonnet et al. (2013)
Cubatão, Joinville	SC	73	44	16	1168	NI	2,01	Bonnet et al. (2013)
Pedra dos Pontões	ES	66	34	10	1150	NI	1	Francisco et al. (2019)
Pedra Roxa	ES	62	46	15	1114	1391	2	Couto et al. (2016)
Guarapuava	PR	54	32	13	1100-1200	NI	NI	Kersten et al. (2009)
Campos do Jordão	SP	51	31	11	1030-2007	NI	NI	Mania (2013)
Nova Trento	SC	50	34	13	1097	NI	2,01	Bonnet et al. (2013)

Low temperatures and frost are constraining factors that affect vascular epiphyte diversity in high-altitude habitats (Gentry & Dodson 1987; Krömer *et al.* 2005; Blum *et al.* 2011b; Hsu *et al.* 2014). In turn, the occurrence of fogs acts as a source of humidity (Arcova *et al.* 2012) and is positively associated with the epiphytic assemblage, thus being one of the most important factors conditioning the occurrence of vascular epiphytes (Gentry & Dodson 1987; Laube & Zotz 2003; Ding *et al.* 2016). This additional humidity has great importance in the driest periods, mitigating the drought due to the 'horizontal precipitation' (Vogelmann, 1973; Arcova *et al.* 2012). Unfortunately, quantitative climatic data (e.g., on water input by cloud condensation) are scarce in the Brazilian mountains, mainly in Espírito Santo. In the PA, fog at the mountain is common, especially from nightfall to morning (pers. obs.).

In the PA, the richest families reported follow the expected for cloud forests of eastern Brazil (Alves & Menini Neto 2014; Furtado & Menini Neto 2016; 2018), for the Atlantic Forest in particular (Kerstern 2010; Freitas *et al.* 2016), and to the global patterns, except for the more considerable importance of the Bromeliaceae family, which is a near endemic Neotropical family (Zotz 2013b; 2016). About 80 % of the vascular epiphytes are concentrated in the greatly diversified Orchidaceae family, resulting in the significant taxonomic importance of this family in this synusia (Kersten 2010; Zotz 2013b; 2016). The low representativity of the Araceae family in high-altitude habitats is expected in the Neotropical Region (Krömer *et al.* 2005; Ortiz *et al.* 2019), and the Atlantic Forest (Menini Neto *et al.* 2009; Rogalski *et al.* 2016), with a better contribution in lowland forests (Coelho 2010), mainly in the Amazon (Irume *et al.* 2013; Obermuller *et al.* 2014).

Few ferns and lycophytes were recorded in the PA (21.7 % of the total). This pattern is not usually observed in higher-altitude forests in the Neotropical Region, which usually is richer at high-altitude sites (Krömer *et al.* 2005; 2013; Cardelús *et al.* 2006). The pattern appears to be different in the Atlantic Forest, with lycophytes and ferns decreasing in richness when the altitude increases (Paciencia 2008; Blum *et al.* 2011b; Nóbrega 2013; Couto *et al.* 2016).

Regarding the distribution, the vast majority of the identified species (95 spp., 62.5% overall) are endemic of the Atlantic Forest, and seven are restricted to Espírito Santo (*Anthurium fragae*, *Gomesa uhlii*, *Neoregelia diversifolia*, *Nidularium cariacicaense*, *Vriesea capixabae*, *V. pereirae*, and *Rhipsalis hoelleri*). *Octomeria cucullata* and *Asplenium theciferum* are being reported for the first time in Espírito Santo and represent the first collections for Brazil after over 50 years, according to Dutra *et al.*

(2015), CRIA (2020), and REFLORA (2020). We recorded the occurrence of *Rhipsalis cereuscula* in Espírito Santo; the only collection previously reported of it (Dutra *et al.* 2015) was in the city of Espírito Santo do Pinhal, in the state of São Paulo. Furthermore, 22 species are being recorded in cloud forests of the Southeastern Brazil for the first time (Furtado 2020).

The predominance of holoepiphyte characteristics is an expected pattern (Freitas et al. 2016; Zotz 2016). On the other hand, the great number of facultative holoepiphytes recorded is outstanding (38.1 % overall) when compared with some sites of the Atlantic Forest (Bonnet *et al.* 2011; Padilha *et al.* 2015; Couto *et al.* 2016; Marcusso & Monteiro 2016; Rolim *et al.* 2016). This different pattern could be explained by the abundance of rock outcrops in the studied area (Biral & Lombardi 2012; Perleberg *et al.* 2013; Couto *et al.* 2016). The rocks show a level of ecological equivalence with the trunks and branches of trees, such as the few nutrients available and the higher water drainage (Zotz 2016). Also, when situated below the forest cover, they may hold light conditions similar to those of the lower trunk and inner tree crown (Zotz 2016). These features have demonstrated a high habitat equivalence, allowing the occurrence of epiphytes, mainly accidental, in the trees (Perleberg *et al.* 2013; Couto *et al.* 2019). In our study, few accidental epiphytes' species, not included in the checklist, were observed in forks and horizontal branch (e.g. *Bifrenaria tyrianthina* (Lodd. ex Loudon) Rchb.f., *Epidendrum secundum* Jacq. and the exotic Crassulaceae, *Kalanchoe fedtschenkoi* Raym.-Hamet & H.Perrier). However, several of the facultative species recorded, grows on the rocks. The presence of trees with horizontal and exposed roots perhaps is a determinant factor for the colonization of a high number of typical rupicolous species, like *Pseudobombax* (Couto *et al.* 2019), not observed in the PA.

The hemiepiphytes were represented by few species in the PA, in agreement with the low representativity of families with a great prevalence of this habit, such as the Araceae, corroborating the previous data on vascular epiphytes at high altitudes or in rocky outcrop habitats (Alves & Menini Neto 2014; Couto *et al.* 2016; Furtado & Menini Neto 2016; 2018; Rogalski *et al.* 2016).

The records of 31,6 % of the species only outside the protected area argue for the conservation issues in the BZ of the PASP, which must be considered in conservationist policies. Special attention regarding the threatened species recorded only outside the PASP are need: three of them are threatened at national level - *Acianthera heringeri* (Hoehne) F.Barros being critically endangered – and nine at state level - *Schlumbergera*

kautskyi (Horobin & McMillan) N.P.Taylor and *Sinningia douglasii* (Lindl.) Chautems being critically endangered. On the other hand, the sampling of the inaccessible areas inside the PASP could locate these threatened taxa inside its area. Therefore, a first step is to reach the inaccessible areas of the PASP by means of trails, to monitor and allow new studies in the areas not visited by tourists. Plus, monitoring the populations inside the PASP and the BF is needed, to avoid the illegal collections, the illegal suppression of the vegetation and the occurrence of the fire. In this way, we encourage more botanical collections and studies within the boundaries of this protected area.

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Capítulo 5

Elevational distribution of the vascular epiphytes of the mountainous region of Espírito Santo, Southeastern Brazil

Abstract

The mountains of central Espírito Santo State (ES), Southeastern Brazil, harbor high species richness and endemism levels, however, is one of the few know floristically region of eastern Brazil. In these mountains, occurs the Atlantic Forest (AF), a biogeographical entity that occurs in eastern Brazil, a region with broad topographical heterogeneity. Based on recently floristic surveys of vascular epiphytes (VE) in the mountainous region of ES (200 to 1550 m a.s.l.), we investigate the distributional patterns of vascular epiphytes of three protected areas along the altitudinal gradient, investigating the changes in the composition of the species, assessing the beta diversity (BD) and the taxonomic distinctness (TD) of this synusia. In the three areas, 507 species belonging to 139 genus and 22 families of VE were recorded. We found the high species richness in the intermediary elevation (ca. 700 to 1100 m a.s.l.), and the distributional pattern of families followed the observed pattern to the whole community, with few exceptions. The beta diversity was strongly represented by the turnover of the species, in which the highest and significant contribution was found to the highland area. Moreover, the TD was equally in both areas, demonstrating which the taxonomic lineages are diverse in the three altitudinal belts. In summary, we analyzed the broader altitudinal range (ca. 1350 m) in the AF regarding the VE distribution. We demonstrated that the epiphytes present different composition in each altitudinal level, mainly drive by climatic and, putatively, historical conditions. Our results also support the great importance to consider the different altitudinal belts in conservationist initiatives, as the creation of new protected areas.

Keywords
Altitudinal gradient, Atlantic Forest, Beta Diversity, hotspot, latitudinal gradient, phytogeography, Serra do Castelo, Taxonomic Distinctiveness

Introduction

The vascular epiphytes are plants that live on other plants using it just like supports (Benzing 1990; Zotz 2016), accounting globally with about 10% of the vascular plants, with a huge diversity in the mountains of the Neotropical Region, represented mainly by the families Orchidaceae, Bromeliaceae, Polypodiaceae, Araceae and Piperaceae (Gentry and Dodson 1987; Kersten 2010; Zotz 2013; 2016). Mountains are the habitat of half of the world's biodiversity hotspots and harbour one-third of the terrestrial species (Martinelli 2007; Körner 2004; Spehn et al. 2011). One of these hotspots is the Atlantic Forest (Myers et al. 2000), which is associated with the main mountain's ranges of eastern Brazil (Fiaschi and Pirani 2009, Guedes et al. 2020). This biogeographical unit holds the richest vascular plant diversity of Brazil, harbouring about 16,000 species (Stehmann et al. 2009; BFG 2018), of which, 2,200 are vascular epiphytes, with near 80% being endemic (Freitas et al. 2016). The Atlantic Forest spread in a broad latitudinal (3°S to 30ºS) and longitudinal gradients (35ºW to 55ºW), furthermore, experienced several altitudinal influences (ranging from the sea level to near 3,000 m a.s.l.), due to the occurrence in the most mountainous region of Brazil (Oliveira-Filho and Fontes 2000; Stehmann et al. 2009; Guedes et al. 2020).

In eastern Brazil are situated the main mountains chains of the country (e.g. Serra do Castelo or Montanhas Capixabas (Espírito Santo State), Serra Geral (Southern Region), Serra da Mantiqueira (Southeastern) and Serra do Mar (South and Southeastern)), with intermittent and/or parallels position each other (Costa et al. 2018; Guedes et al. 2020). In Espírito Santo State, the main mountain ranges are the Serra do Caparaó (the northern portion of the Serra da Mantiqueira, in the border with Minas Gerais State), and the Serra do Castelo. The last one reaches about 2,000 m (e.g. Forno Grande 2039 m, Pedra das Flores 1909 m, Pedra Azul 1822 m) (Chiron and Bolsanello 2015; Garbin et al. 2017). This mountain range is floristically important, harbouring a high species richness and endemism (Werneck et al. 2011; Saiter and Thomaz 2014; Reginato and Michelangeli 2020). However, comprehensive floristic studies including several altitudinal ranges were not made until now in the Serra do Castelo.

In mountains ranges, along elevational variations, the atmospheric pressure, temperature, solar radiation, and UV-B radiation are abiotic factors related to altitude in mountainous regions, and precipitation, wind speed and seasonality are indirectly related factors (Körner 2007). Among these factors, the best known and traditionally associated

with conditioning of forest physiognomies and distribution of vascular epiphytes are temperature and precipitation (average and annual distribution) (Gentry and Dodson 1897; Oliveira-Filho and Fontes 2000; Blum et al. 2011b; Leitman et al. 2015; Furtado and Menini Neto 2021).

In tropical mountain systems, one of the main recorded distributional patterns of epiphytes is the richness peak at medium altitudes (Gentry and Dodson 1987; Hietz and Hietz-Seifert 1995; Küper et al. 2004; Zotz 2016). This pattern is traditionally attributed to the overlap of species of both ends of the gradient at intermediary altitudes, resulting in a peak of richness caused by the geographical constraints (the mid domain effect), as one of the main causes (Rahbek 1995; Colwell et al. 2004; Cardelus et al. 2006). However, it must play a secondary role (Zotz 2016), with the climatic factors acting strongly in the distribution and diversity (Currie and Kerr 2008; Zhang et al. 2015). Rainfall is positively related to the richest areas, usually both shows highest values at intermediary altitudes (Gentry and Dodson 1987; Küper et al. 2004; Krömer et al. 2005; Cardelús et al. 2006; Zotz 2016). In the slopes of Serra do Mar, in the South and Southeast coast of Brazil, a higher precipitation average (Milanesi and Galvani 2011) and lower temperatures (Blum et al. 2011b) occurring in the highest elevational belts. Additionally, the presence of fog tends to increase the relative humidity of high-altitude areas, supplying the humidity in the driest months (Arcova et al. 2016). However, the low temperature in the high elevations could be a constraint factor, even in these moister sites (Furtado 2020). Furthermore, some biotic factors, like the structure of the arboreal community (basal area), is also known to influence the diversity of vascular epiphytes in environmental gradients; in this case associated with a decrease at high altitudes (Krömer et al. 2005; Ding et al. 2016). One of the possible explanations would be the fact that the arboreal flora is incipient or even absent in areas located at high altitudes (Krömer et al. 2005; Ding et al. 2016).

In the Atlantic Forest, studies with tree flora along the altitudinal gradient also found high species richness at intermediary altitudes (e.g. Eisenlohr et al. 2013; Sanchez et al. 2013; Kamimura et al. 2017), a monotonic decrease (Ferreira et al. 2015; Caglioni et al. 2018) or a monotonic increase for the family Lauraceae (Kamimura et al. 2017). For vascular epiphytes, also different results were recorded: Menini Neto et al. (2009) and Furtado and Menini Neto (2018), found richer areas at high altitudes in the Serra da Mantiqueira; Blum et al. (2011a), in the lowest sites in Serra do Mar and Furtado (2020) in the intermediary to low sites in the cloud forest of the Serra da Mantiqueira; and Couto

et al. (2016a), recorded high richness at intermediary elevations in granitic outcrops (inselbergs) in Espírito Santo. Thus, there is no consensus on the altitudinal distribution of vascular epiphytes in the Atlantic Forest. However, the number of studies that explored this topic is still incipient; this fact demonstrates the relevant contribution of the present study in elucidating these patterns. In addition, the present study includes a greater altitudinal range (about 1350 m) than those considered in previous studies carried out in the Atlantic Forest.

Furthermore, to understanding the effects of elevation on epiphyte´s diversity, in terms of species turnover (Anderson et al. 2010) and evolutionary aspects (Ricotta 2005) we assessed the changes in beta diversity and taxonomic distinctness along the altitudinal gradient. The assessment of beta diversity allows us to demonstrate how the species composition change along environmental gradients and evaluate if the species are replaced along the sites (turnover) or if they are widespread (nestedness) (Baselga 2010). Regarding the evolutionary aspects, changes on phylogenetic relationship among the taxa can be evaluate in the matter of taxonomic diversity (Warwick and Clarke 1998). This measure expresses the evolutionary history of the species and could present a different pattern in comparison to traditional indices (Warwick and Clarke 1998; Warwick and Clarke 2001). Since the evaluation of taxonomic diversity, by means of taxonomic distinctiveness, does not require an equally sample (Warwick and Clarke 1998), it is relevant for comparing flora with different habitat and historical conditions, also presenting a huge relevance to the conservationist purposes (Roque et al. 2014).

Here we aim to assess the distribution of the vascular epiphytes along an altitudinal gradient (200 to 1550 m a.s.l.) in the mountains of the central region of Espírito Santo state, in Southeast Brazil, exploring the changes in species richness, phylogenetic diversity (taxonomic distinctiveness) and species turnover (beta diversity).

Material and Methods

Study sites

The present study comprises the data from the floristic survey of the vascular epiphytes carried out in three protected areas in the south-central mountainous region of the Espírito Santo state (ES hereafter), in Southeast Brazil, ranging from 200 to 1550 m a.s.l. (Duas Bocas Biological Reserve, Augusto Ruschi Biological Reserve and Pedra Azul State Park and neighbour) (see Table 1 for details). The ES is divided into two geomorphological compartments: the Barreiras formation, which occurs in the narrow coastal plain of the south of the state, becoming wider in the north; and the mountainous region, which occupies the interior portion of the state, with the altitude varying from sea level to 2987 m, in Serra do Caparaó (IPEMA 2005). The predominant climate, according to the Köppen classification in the plain is Aw and Am and in the mountain region, Cfa and Cfb (Alvares et al. 2013). The entire state of Espírito Santo is inserted in the Atlantic Forest domain, represented by several types of vegetation, such as Mangroves, Restingas, Seasonal Semideciduous Forests, high altitude grasslands (campos de altitude), and Ombrophilous Dense Forest (Simonelli and Fraga 2007; Garbin et al. 2017). In the mountainous region occurs the Ombrophilous Dense Forest (Simonelli and Fraga 2007; Garbin et al. 2017), however, a seasonal climate occurs in these areas, with a dry season in the winter (Alvares et al. 2013). The fog is usual in the Pedra Azul, in the highest belts (pers. obs.).

The current study was carried out in the mountainous region in the south-central portion of Espírito Santo, known locally as Serra do Castelo (Chiron and Bolsanello 2015) or Montanhas Capixabas. These mountains are considered by some authors as part of Serra do Mar (Scaramuzza et al. 2011), and by other as Serra da Mantiqueira (Silva et al. 2018). In ES these mountains spread by 140 km length and 100 km wide. It is bounded in the north by the Doce River valley, in the east by the coastal plain, to the south by the Itapemirim River valley, to the southwest by Serra do Caparaó and to the northwest by the state of Minas Gerais and Serra da Chibata, its average altitude is 700 meters, ranging from sea level to about 2050 meters (Chiron and Bolsanello 2015).

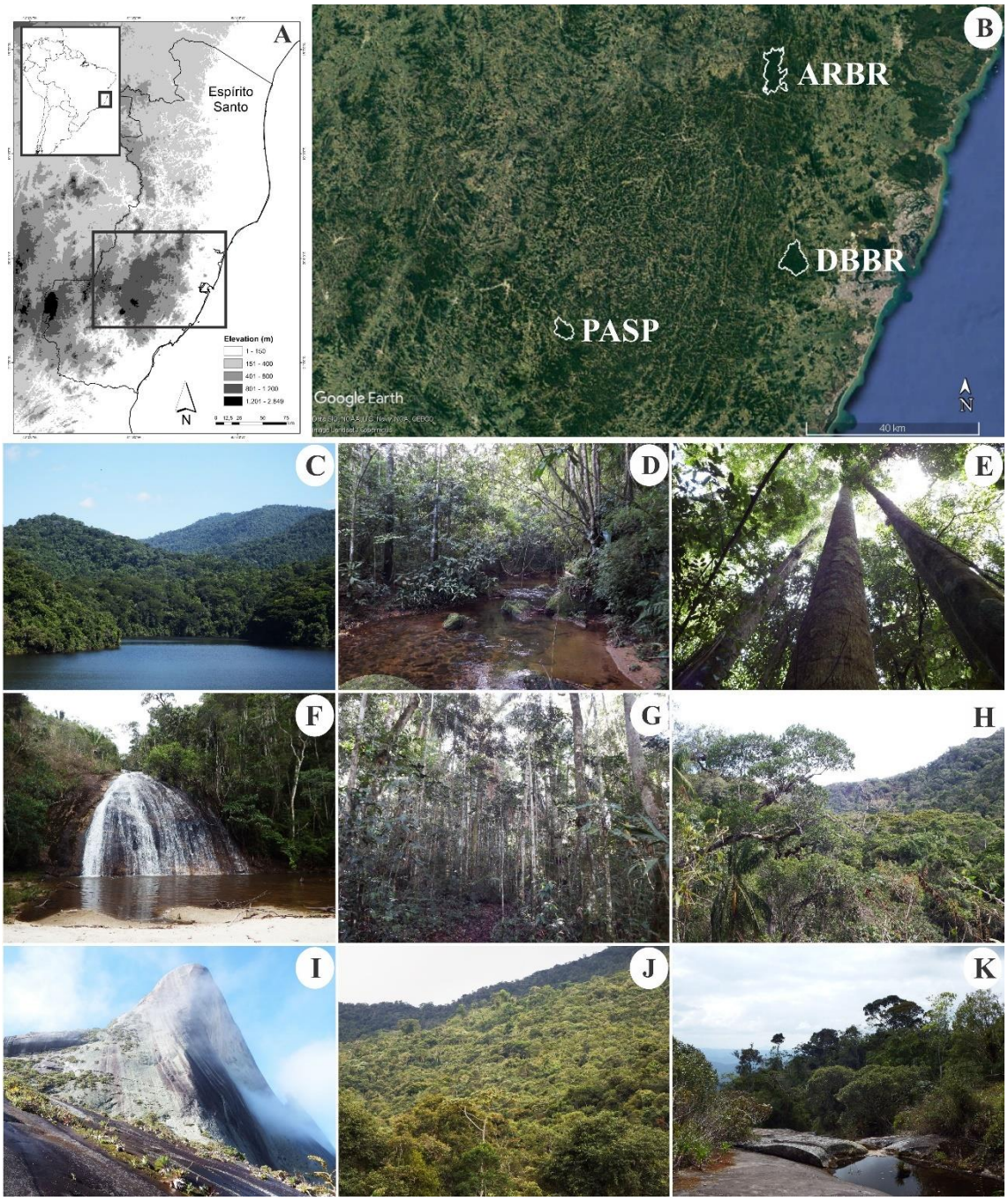


Fig. 1 Geographical location of the mountain region of the Espírito Santo, Southeastern Brazil. **a** Elevational profile of the mountainous region. **b** Delimitation of the Augusto Ruschi Biological Reserve (ARBR), Duas Bocas Biological Reserve (DBBR), and Pedra Azul State Park (PASP). **c–e** Vegetation in the DBBR. **f–h** Vegetation in the ARBR. **i–k** Vegetation on the PASP.

Table 1. Geographical, climatic and vegetational characteristics of the three analysed sites in the mountainous region of the central Espírito Santo State, Southeastern Brazil.

	Duas Bocas Biological Reserve (DBBR)	**Augusto Ruschi Biological Reserve (ARBR)**	**Pedra Azul State Park (PASP)**
Latitude	20º18'05"/20º19'08" S	19º45'00"/20º00'00"S	20º23´32"/20º29´24"S
Longitude	40º28'06"/40º32'28" W	40º27'00"/40º38'00"W	40º00´25"/40º59´29"W
Municipallity	Cariacica	Santa Teresa	Domingos Martins
Area (hectares)	2910	3598	1240
Altitudinal range	200-800 m	780-1143 m	1100-1550 m
Temperature average (ºC)	21,1	20	15,5
Precipitation average (mm)	1260	1320	1487
Forest types	Submontane to Montane	Montane	Montane to uppermontane

Data collection

The floristic inventory of vascular epiphytes was carried out on seven expeditions for collection of botanical material, lasting about three days on each trip, in January, May and September 2018, February, August and October 2019, and November 2020. Collections were made along the trails and in the roads, which crosses the protected areas. The collections were deposited at the Herbarium Rioclarense (HRCB), and duplicates were sent to the herbaria BHCB, CESJ, RB, and UNOP (acronyms according to Index Herbariorum 2020). Herbarium specimens were assessed firstly using SpeciesLink network (CRIA 2018) and Reflora - Virtual Herbarium (2018) for specimens deposited at the herbaria BHCB, HRCB, MBM, MBML, and RB (acronyms according to Index Herbariorum 2020) from previous collections in the study sites.

During the expeditions to the field, we observed the epiphytes' habits, and classified them in ecological categories according to their relationship with the phorophytes, following Benzing (1990): characteristic holoepiphytes, facultative holoepiphytes, primary hemiepiphytes, and secondary hemiepiphytes. It was preferred to use this classification instead of that of Zotz (2016) to facilitate comparison with other studies since most used the first one. Terrestrial species occasionally found growing in

forks, hollows or cavities with an accumulation of organic matter were not considered in the study, as they are considered ephemeral epiphytes (Kersten 2010; Zotz 2016).

Taxonomic identification was made using taxonomic literature (classical works, floras, taxonomic revisions, etc.), herbarium collections of the HRCB and MBML, and consultations of specialists. The taxonomic classification is according to APG IV (2016) for angiosperms and PPG I (2016) for monilophytes and lycophytes. The nomenclatural determination of species and the distribution is according to BFG (2018) and Flora do Brasil 2020 (under construction).

Data analyses

For all analyses, we only used the identified species, excluding the records in genus or family level from the matrix of species. To understanding the floristic dissimilarity among areas, we conducted an agglomerative hierarchical clustering analysis (UPGMA; Legendre & Legendre 2012), by means of a binary matrix with the presence (1) and absence (0) and Jaccard dissimilarity. in the vegan package (Oksanen et al. 2020). We also built a Venn diagram to assess the number of exclusive and common species among study areas.

The phylogenetic diversity was computed by means of the indices of taxonomic distinctness (Clarke & Warwick 1998, 2001). For this purpose, we built a matrix of all epiphytes recorded in all sites, classifying them by Species, Genus, Family, Order, Superorder and Subclass, according to Tropicos.org (2021). The taxonomic diversity was (Δ +) was estimated by the equation: $\Delta^{*} = (\sum\sum_{i<j} \omega_{ij} x_i x_j)/(\sum\sum_{i<j} x_i x_j)$. The equations give the index value for a single site, and summation goes over species i and j, in which ω are taxonomic distances among taxa, and x are species abundances for a site (Clarke & Warwick 1998, 2001).

To investigate the total beta diversity among samples and Local Contribution to Beta Diversity (LCBD) of each site, we built a matrix with all species collected from all sites and computed Sorensen´s dissimilarity coefficient (Legendre & De Caceres 2013). We first assessed the total beta diversity, as the sum of spatial turnover measure and nestedness-resultant dissimilarity among sites (Baselga 2010). We then computed LCBD of each site, to represent the degree of uniqueness of the sites in terms of their species

compositions. LCBD indices were tested for significance by 999 independent permutations of the data (Legendre & De Caceres, 2013).

The analyses were conducted in the software R (R Development Core Team, 2020), using the 'adespatial' (Dray et al. 2020), 'betapart' (Orme et al. 2020) and 'vegan' (Oksanen et al. 2020), packages.

Results

The overall richness recorded in the three analysed areas comprises 507 identified species, belonging to 139 genera and 22 families, 15 orders, and three subclasses. By means of cluster analysis, we found the segregation of the upper sites from the other sites, in which we found a high coefficient of cophenetic correlation of 0.92 (Figure 2a). Only 43 species occurred in the three areas, 131 in two of them, and the great majority (333 species) were exclusively from a single locality (Figure 2b). The ARBR holds the greatest number of species (360), followed by the DBBR (215) and PASP (149). The ARBR also holds the greatest number of exclusively species, sharing more species with the DBBR. The elevational extremes of the gradient shared the small number of species (Figure 2b).

Overall, the families' richness followed the patterns of VE community, with few exceptions (Figure 3). The overall richest families were Orchidaceae (297 species or 58,6%), Bromeliaceae (128 or 32,2%), Polypodiaceae (65 or 12,8%), Araceae (52 or 10,2%), Piperaceae (32 or 6,3%) and Dryopteridaceae (30 or 5,9%). The richest genera were *Vriesea* (44 species or 31,6%), *Peperomia* (32 or 23%), *Aechmea* and *Epidendrum* (25 or 18% each), *Acianthera* and *Octomeria* (24 or 17,3% each), *Pabstiella* (23 or 16,5%), *Philodendron* (21 or 15,1%), and *Elaphoglossum* (20 or 14,3%).

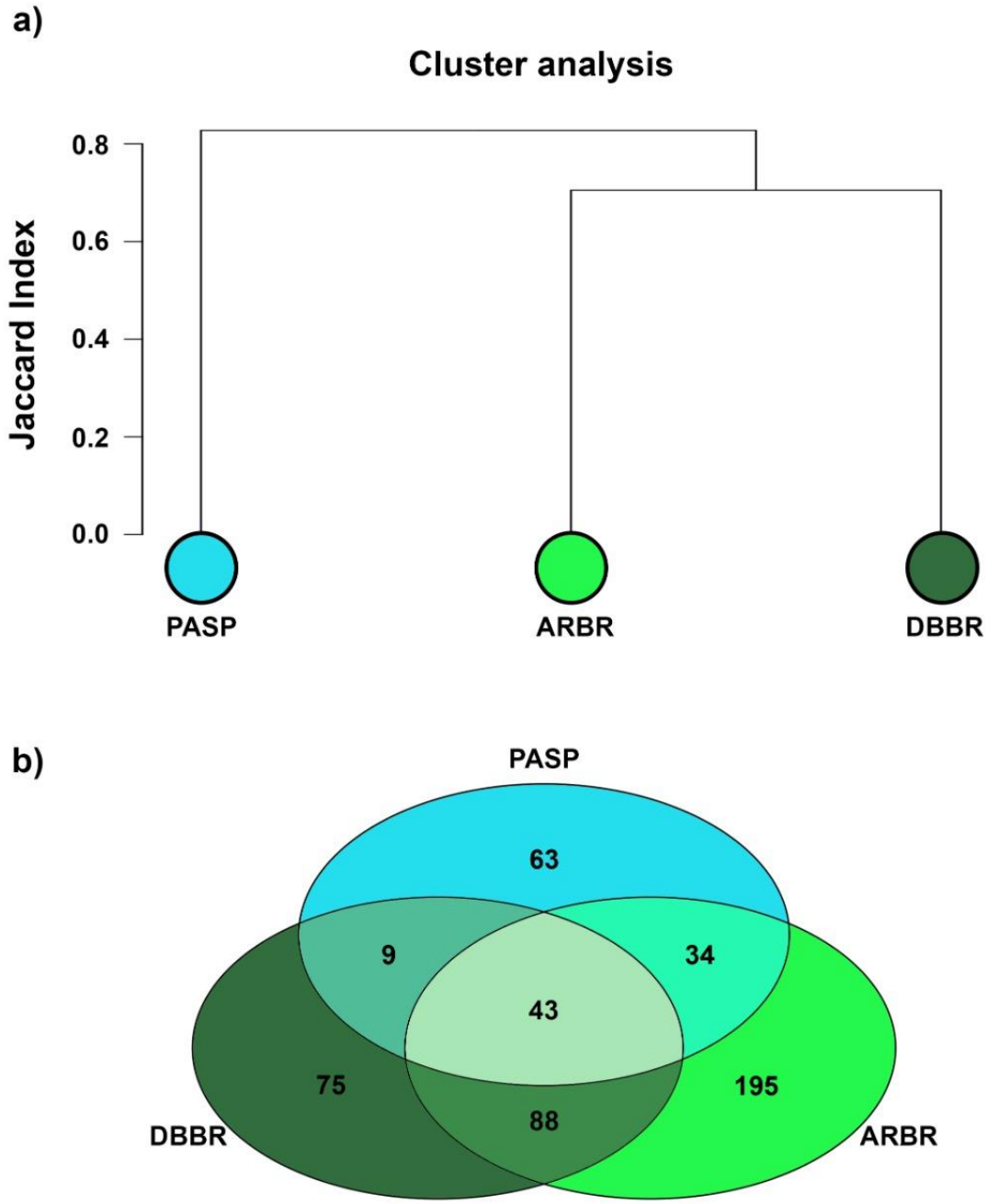


Fig. 2 Floristic relationships and shared vascular epiphyte's species recorded in three areas distributed along an elevational gradient in the mountainous region of the central Espírito Santo state, Southeastern Brazil. **a** Dendrogram of the similarity, generated by means of UPGMA, for vascular epiphytes' species. **b** Venn diagram showing the shared species among the areas. ARBR: Augusto Ruschi Biological Reserve; DBBR: Duas Bocas Biological Reserve; PASP: Pedra Azul State Park.

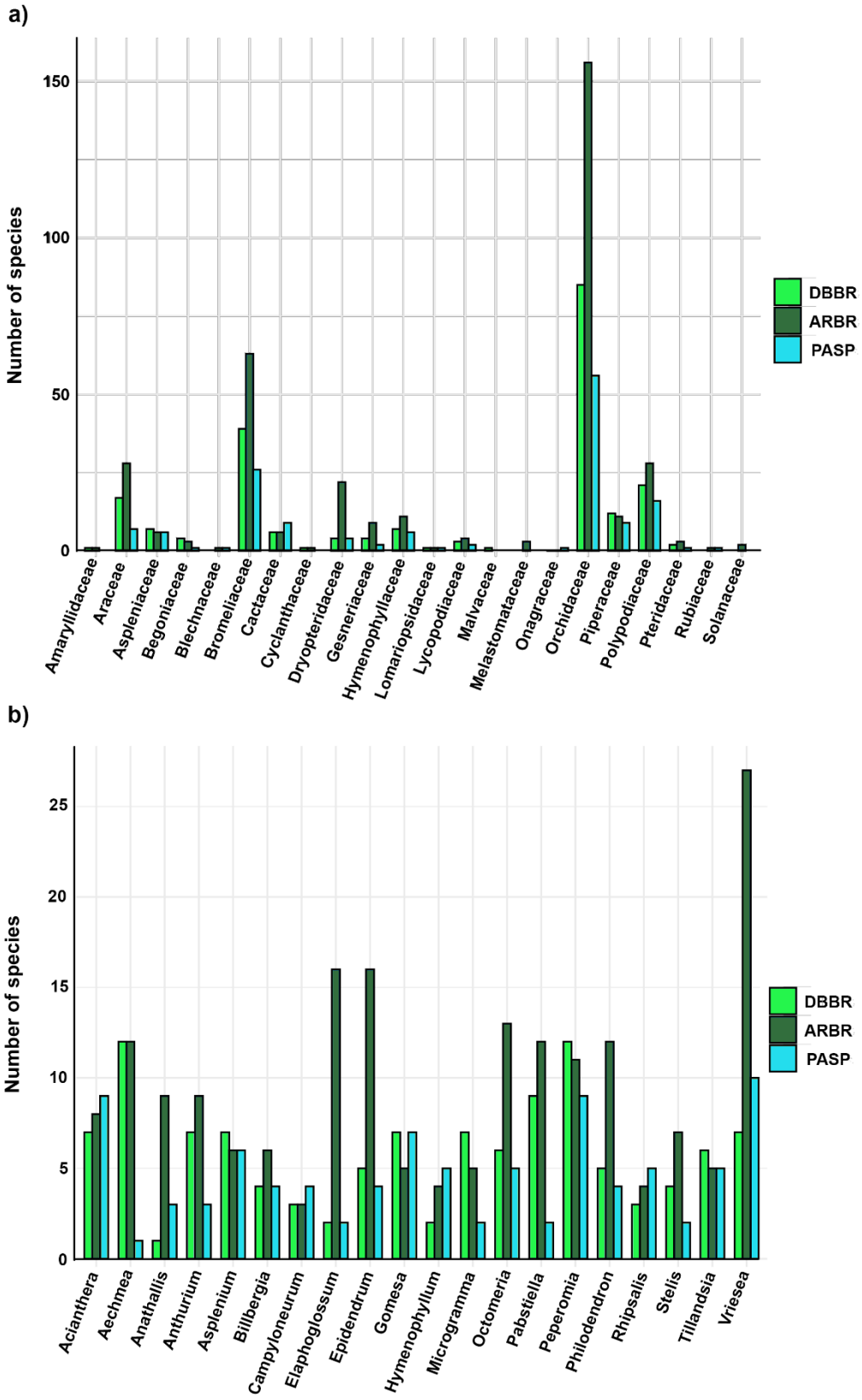


Fig. 3 The families and richest genera recorded in the three analysed sites in the mountainous region of the central Espírito Santo state, Southeastern Brazil. **a** Species richness per families in the three analysed sites. **b** Species richness of the richest genus. ARBR: Augusto Ruschi Biological Reserve; DBBR: Duas Bocas Biological Reserve; PASP: Pedra Azul State Park.

The total beta diversity was mainly generated by species turnover (Sorensen pair-wise dissimilarity = 1.95) than species nestedness (nestedness-fraction of Sorensen pair-wise dissimilarity = 0.43). Regarding LCBD, we found the highest values for sites located in the extreme elevations of the gradient evaluated (Figure 4a). The highland site presents the higher and only one significant value of LCBD. In the matter of phylogenetic diversity, all areas presented values of TD lower than expected (Figure 4b), but inside the confidence interval. The expected Taxonomic Distinctness (TD, Delta+) was 88.60, in which the highest value of TD was found for the site at intermediary elevation (Delta+ of ARBR = 88.40), followed by TD values of the DBBR (Delta+ = 88.17), and the PASP (Delta+ = 87.32).

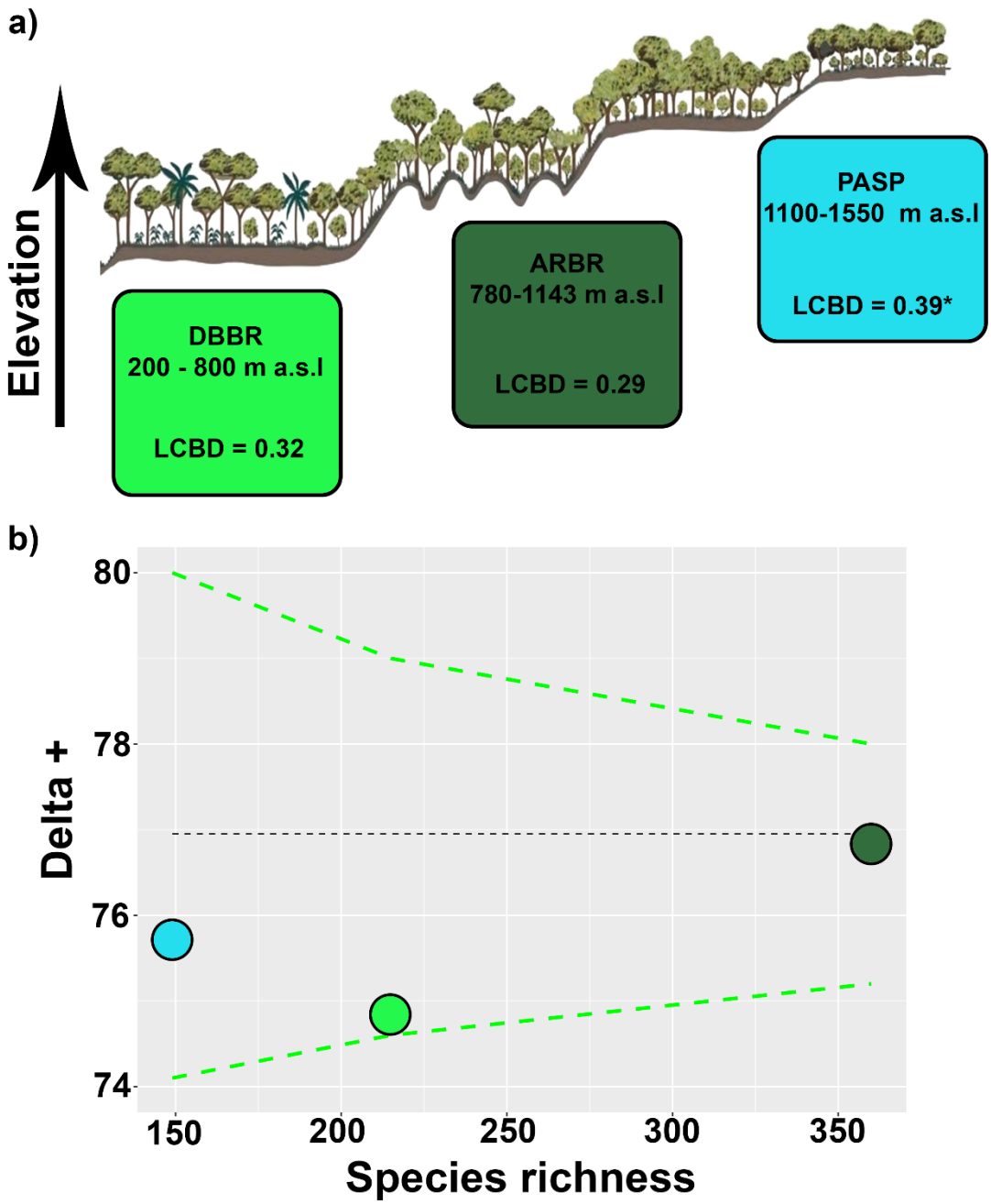


Fig. 4 a Local Contribution to Beta Diversity (LCBD). **b** Average taxonomic distinctness index (Delta+) for the vascular epiphytes' species in the three analysed sites in the mountain region of the central Espírito Santo state, Southeastern Brazil. ARBR: Augusto Ruschi Biological Reserve; DBBR: Duas Bocas Biological Reserve; PASP: Pedra Azul State Park. * $P < 0.05$.

Discussion

The overall richness of the analysed areas in the central mountain region of ES is remarkable, comprising about 22 % of the vascular epiphytes of the AF (Freitas et al. 2016), in about 0,005 % of the whole geographical area of the domain (Ribeiro et al. 2009). Floristic studies with VE in the AF which included large scale sampled areas but not in mountainous relief registered a small number of species than we found here (e.g. Kersten and Kunioshyi 2006). This result highlights the importance of the mountainous relief for the floristic diversity (Ferraz et al. 2004; Kreft and Jetz 2007). Furthermore, even when compared with studies that included a broad latitudinal and altitudinal range in the pluvial forest of Santa Catarina state, Southern Brazil, which recorded 491 species (Vibrans et al. 2013) and the Acre State, in the Amazon, where 331 species were recorded (Obermuller et al. 2014), the mountains of ES standing out. However, the 278 species recorded by Blum et al. (2011a) in a single slope along an altitudinal gradient in Paraná, suggests that other mountain ranges in the Serra do Mar are also rich in VE. When comparing with other countries like the Veracruz state in Mexico, which has a geographical area almost twice the size of the ES, the whole state has 750 species of VE (Krömer et al. 2020), a small difference considering the broader geographical area.

The distribution of the richness patterns of VE in large altitudinal ranges in the Neotropical Region is mainly the hump-shaped (peak of richness at intermediary altitudinal levels) in cloud forests (Gentry and Dodson 1987, Hietz and Hietz-Seifert 1995; Bussmann 2001; Wolf and Flamenco-S 2003, Küper et al. 2004; Krömer et al. 2005; Cardelús et al. 2006; Zotz 2016). However, in some gradients, a monotonic decline (Ibisch et al. 1996; Zotz 2016; Krömer et al. 2020) or a monotonic increase of species richness (Krömer et al. 2013) are also observed. Besides, idiosyncratic patterns may also occur, like Guzmán-Jacob et al. (2019) which found two peaks of richness in Veracruz, Mexico.

In the AF a small altitudinal range is found (up to about 3000 m a.s.l.), when compared with other Neotropical mountains (reaching 6000 m a.s.l.) (Guedes et al. 2020). The few studies which analysed the distribution of VE along elevational gradient registered a high richness in the low elevations range (monotonic declines), in a subtropical latitude (Blum et al. 2011), and at tropical latitudes, both the intermediary elevational (hump-shaped pattern) (Couto et al. 2016; Furtado 2020) and monotonic increase (Furtado and Menini Neto 2018) was found. Here, our results also supported the

hump-shaped patterns at tropical areas in the mountains of ES. The ARBR holds the small altitudinal range (780 to 1150 m a.s.l.), in comparison with both extremes, but, on the other hand, has the larger area. In this way, the different methods (sample area) could bias this result at a point. However, in ES a low richness of VE in low altitude forest is supported by the results found for the lowland seasonal forest (30-60 m a.s.l.) (Rolim et al. 2016a).

Orchidaceae and Bromeliaceae usually are amongst the richest families of VE inventories in the Neotropical Region (Zotz 2013), and its distribution is also influenced by the altitude (Fontoura et al. 2012; Zhang et al. 2015), usually corroborating the distributional patterns of the whole assemblage (Wolf and Flamenco-S 2003; Kromer et al. 2005; Cardelús et al. 2006) or showing a monotonic increase (Kromer et al. 2013). For this families in the AF, it may show a monotonic decrease (Blum et al. 2011a), or a hump shaped pattern (Couto et al. 2016). Here we corroborate a peak of richness at intermediary elevations, supporting the distribution of this families, perhaps due to the climatic constraints (Kromer et al. 2005; Cardelús et al. 2016).

The Araceae distribution patterns usually fit at a monotonic decline in large altitudinal ranges (Kessler 2001; Krömer et al. 2005; 2013; Zotz 2016). However, this appears to not be universal, where a hump-shaped (Cardelús et al. 2006), a monotonic increase in epiphytic (Ortiz et al. 2019) or a stable richness (Wolf and Flamenco-S 2003) also were recorded for the family. Here we also supported the hump-shaped pattern, however, a great number is also found at lower elevations, as found by Rolim et al. (2016a) in the lowland seasonal forest in the north of Espírito Santo.

In broader elevation ranges, like in the Andes and Costa Rica mountains, the ferns and lycophytes usually show higher richness in the highest belts (Krömer et al. 2005; 2013; Cardelús et al. 2006; Zotz 2016; Jiménez-Lopez et al. 2020). However, in some broad ranges also a peak of richness at intermediary elevations is found (Wolf and Flamenco-S 2003; Suisa and Sundue 2020), like in the AF, in which a hump-shaped patterns is observed (Paciencia 2008; Blum et al. 2011a; Nóbrega 2013; Couto et al. 2016). On the other hand, in other sites of eastern Brazil, a high richness in the upper ranges (Nervo et al. 2016; Furtado and Menini Neto 2018), and an equally distribution along the gradient (Damasceno 2010) were recorded. The ferns and lycophytes are impressive part of this synusia of temperate forests in high latitudes, in comparison with angiosperm families VE (Díaz et al. 2010; Zotz 2005; 2016; Mai et al. 2019). It argues that the climate could influence the distribution of this plants, as well as along both

latitudinal and altitudinal gradients (Zotz 2016). This helps us to explain the strong differentiation of the VE along the elevational ranges analysed.

Although the mid domain effect usually is attributed to the high number of species at intermediary elevations (Wolf and Flamenco-S, 2003; Cardelus et al. 2006), the main causes are probably driven by climatic factors, which act as predictors of the distribution of the VE (Wolf and Flamenco-S 2003; Küper et al. 2004; Zotz 2016), rather than geographical constraints (Currie and Kerr 2008; Zhang et al. 2015). This result is also suggested in the present study by small number of species shared between the belts.

The humidity usually is the most important factors for the distribution of richness and composition of the VE (Gentry and Dodson 197; Kreft et al. 2004; Zotz 2016). In the mountains, cloud forests are usually associated with the peak of richness of VE, and the settlement of these forests can vary according to the altitudinal ranges of the gradient in each mountain system and latitude (e.g. Gentry and Dodson 1987; Wolf and Flamenco-S 2003; Cardelús et al. 2006; Furtado and Menini Neto 2018; Jiménez-López et al. 2020). The intermediary richness belts usually received more humidity provided by the water input and low evapotranspiration from the frequent clouds and fogs (Bussmann 2001; Stadtmüller 1987). In the AF of Southeastern Brazil, the cloud forest usually occurs above 1100 meters a.s.l. (Bertoncello et al. 2011), with a higher cloud formation in the upper parts of the gradients (Blum et al. 2011b; Milanesi and Galvani 2011; Arcova *et al.* 2016), where it is replaced, above 1000, until the tree line, about 2000 m a.s.l., for the highlands grasslands (Safford 1999), and not in the intermediary altitudes, like in large gradients (e.g. Bussmann 2001; Wolf and Flamenco-S 2003). Our results did not corroborate the high richness in the cloud forests, which occurs only in the upper belts of the studied gradient (1100 to 1550 m), even with the highest precipitation average (Table 1). Although a high abundance of epiphytes (pers. obs.), a small number of species was recorded in the PASP. One of the causes could be the low temperature average, filtering the settlement and colonization of several species (Gentry and Dodson 1987; Kromer et al. 2005; Hsu et al. 2014; Zotz 2016; Furtado 2020), but, in the tropical latitude and low altitude of the present study site, it could not be a satisfactory explanation (Zotz 2016).

Another factor that could help to explain the low richness of VE in the moist cloud forest is the climatic and vegetational history of the regions. The dry and cold conditions of the Quaternary strongly marked the vegetation of the highlands (Behling et al. 2002; Veríssimo et al. 2012). In the highlands, the widespread grassland became replaced by the forest formations when the temperature and humidity increase, in the late Holocene,

allowing the upward of the tropical forest that later occurred at lower elevations maintained by the orographic rain (Behling et al. 2002; Veríssimo et al. 2012). On the other hand, in the lowland's dry vegetation perhaps widespread in these areas (Buso Jr. et al. 2016; 2019). In this way, the intermediary belts could not experience strong constraints conditions, with forest vegetation maintenance even in the glacial periods, with intermediary temperature and humidity in these altitudinal belts, due to the orographic rain, in comparison with the grassland, cold and dry in the highlands (Veríssimo et al. 2012), and the open vegetation (savanna) to the seasonal forest under higher temperatures and dry conditions in the lowlands (Buso Jr. et al. 2016; 2019). Further studies in the intermediary belts in the mountains of ES are necessary to support this idea, but it can be a reasonable explanation to the high richness of trees found (Saiter and Thomaz 2014; Rolim et al. 2016b) and in the present study.

The species richness was higher at the intermediate elevation; however, it was not reflected in the contribution to beta diversity. Beyond the effects of elevational variation on distributions of species diversity, changes in the composition of species are also related to abiotic conditions, in which limitations on species distribution can be led by resource constraints (Gentry and Dodson 1987; Ding et al. 2016; Zotz 2016). In this way, we found a high level of species turnover among sites, and the higher LCBD for the highland site, which meets the hypothesis of species cooccurrences being a result of species interactions and their dispersal limitations related to the environmental conditions (Levine and HilleRisLambers 2009; Krishnadas et al. 2016). This fact can be associated with local mechanisms, for instance, elevated temporal turnover of lineages, driving great species diversity but low phylogenetic diversity (Oommen and Shanker 2005).

We also found that the number of species did not reflect the phylogenetic diversity of the VE along the altitudinal gradient. This pattern has been reported in studies carried out in other regions for other vegetation components (e.g., Manish and Pandit 2018; Qian et al. 2019). In our cause, this fact can be related to the life history and niche conservatism of the species along (Losos 2008). These findings are especially important since the variation patterns of species and phylogenetic diversities can be different along elevational gradients, and the loss of phylogenetic diversity may have negative effects on ecosystem function and stability (Cadotte et al. 2010; Gerhold et al. 2015; Knapp et al. 2017). This fact reinforces the importance of the protected areas in different altitudinal belts and to considering the altitudinal gradient in conservationists' purposes (Rezende et al. 2015).

In summary, this is the study that considered the broad altitudinal gradient to evaluate the distribution of the VE in the AF and explored the beta diversity and phylogenetic diversity between the different altitudinal belts. We found an outstanding richness of vascular epiphytes in the mountainous central Espírito Santo, demonstrating the importance of the heterogeneity to the diversity, and which the taxonomic beta diversity is mainly generated by turnover, with small overlap of species in the intermediary belts. Perhaps the actual optimum climatic conditions and the paleoclimate of this areas are responsible for the observed patterns. Otherwise, besides the changes and differences in the composition and richness along the altitudinal gradient, we found a high phylogenetic diversity (measured by the taxonomic distinctiveness) in the three areas. This reinforces the conservation and importance of the protected areas considering the altitudinal belts. Finally, we encourage more studies in the several forest remnants of the mountains of Espírito Santo, to improve the assembly of the whole picture of the biodiversity of this megadiverse Brazilian state, as well as subsiding the creation of new protected areas, considering the elevational and compositional changes of the species.

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CONCLUSÃO GERAL

O presente estudo apresentou a mais abrangente compilação e síntese fitogeográfica das epífitas vasculares na Região Neotropical. Com isso, foi possível identificar os principais padrões de distribuição para a Região, sobretudo em localidades com maior número de estudos. Por outro lado, padrões gerais foram detectados para as áreas com menos estudos (e.g. Amazônia e Andes). Os padrões de substituições florísticas foram corroborados por dados climáticos, demonstrando o potencial bioindicador das epífitas vasculares como grupo modelo para bioregionalizações.

Em menor escala, levantamos dados sobre a flora epifítica de um dos estados mais ricos, e ainda com muitas lacunas de coletas e publicações florísticas, do Brasil. Este levantamento possibilitou registrar a maior riqueza de epífitas vasculares para uma determinada localidade na Floresta Atlântica. Assim como trouxe dados inéditos sobre a composição e diversidade de áreas montanas e alto montanas, consideradas relictos de vegetações amplamente distribuídas nos períodos glaciais e que se encontram restritas e ameaçadas a poucos maciços montanhosos. Ademais, as florestas das encostas serranas, em altitudes inferiores demonstrou ser detentora de relevante diversidade florística. Esses levantamentos também permitiram que sete novos registros para a flora capixaba fossem feitos. Várias espécies consideradas com dados deficientes também foram documentadas, auxiliando no aumento do conhecimento sobre essas espécies no estado.

Por fim, também demonstramos o efeito das mudanças altitudinais na composição das espécies, com um expressivo número de espécies exclusivas para cada faixa, com poucas espécies ocorrendo em todo o gradiente. Destaca-se que mesmo áreas com um menor número de espécies a diversidade taxonômica e a contribuição com espécies exclusivas é alta. Estes resultados justificam e reforçam o papel das Unidades de Conservação em todas as faixas de elevação, para que uma proteção mais efetiva da biodiversidade possa ocorrer.

Appendix 1.

Qualitative/quantitative surveys exclusively on vascular epiphytes carried out in the Neotropical Region up to 2017 used in the compilation for the meta-analysis.

Nº area	Province	Country	Location	Latitude	Longitude	Species total	Species Included
1	Araucaria/Paraná Forest	Argentina	Cruce Caballero	26°31'17"S	53°59'26"O	57	55
2	Araucaria/Paraná Forest	Argentina	La Araucaria	26°37'53"S	54°06'08"O	24	24
3	Yungas/Chacoan	Argentina	El Rey	24°48'41"S	64°41'21"O	53	16
4	Yungas	Bolivia	Sehuencas	17°30'00"S	65°15'59"O	204	93
5	Yungas	Bolivia	Sapecho	15°32'29"S	67°20'18"O	255	195
6	Yungas	Bolivia	Cotapata (Tunquini)	16°11'59"S	67°51'59"O	291	172
7	Yungas	Bolivia	Mosetenes	16°13'58"S	66°24'54"O	274	161
8	Yungas/Rondônia	Bolivia	Madidi	14°26'00"S	67°55'00"O	152	113
9	Araucaria Forest	Brasil	Médio Rio Tibagi	24°22'45"S	50°35'04"O	142	118
10	Araucaria Forest	Brasil	Estreito de Augusto César	27°24'22"S	51°58'09"O	70	59
11	Araucaria Forest	Brasil	Campo Mourão	24°00'01"S	52°20'31"O	61	52
12	Araucaria Forest	Brasil	Marumbi	25°27'29"S	49°00'46"O	127	116
13	Araucaria Forest	Brasil	Corredor Araucária	26°07'59"S	51°35'21"O	125	101
14	Araucaria Forest	Brasil	Alto Iguaçu	25°37'25"S	49°18'36"O	114	105
15	Araucaria Forest	Brasil	Curitiba	25°24'05"S	49°14'45"O	105	94
16	Araucaria Forest	Brasil	Alto Tibagi	25°05'09"S	49°57'32"O	78	64
17	Araucaria Forest	Brasil	Barigui	25°25'08"S	49°18'32"O	74	68
18	Araucaria Forest	Brasil	Guarapuava	25°39'33"S	51°25'47"O	54	50
19	Araucaria Forest	Brasil	São Franciso de Paula	29°25'21"S	50°23'29"O	54	48
20	Araucaria Forest	Brasil	Araucária	25°35'00"S	49°21'38"O	51	46

Nº area	Province	Country	Location	Latitude	Longitude	Species total	Species Included
21	Araucaria Forest	Brasil	Fazenda Experimental Gralha Azul	25°39'37"S	49°16'54"O	48	43
22	Araucaria Forest	Brasil	Parque São Cristóvão	25°24'25"S	49°19'57"O	17	16
23	Atlantic	Brasil	Morro do Baú	26°48'12"S	48°56'15"O	168	166
24	Atlantic	Brasil	Montante rio Sorocaba	23°38'54"S	47°22'34"O	139	124
25	Atlantic	Brasil	Fontes do Ipiranga	23°38'22"S	46°37'09"O	40	39
26	Atlantic	Brasil	Cidade Universitária	23°33'49"S	46°43'47"O	37	36
27	Atlantic	Brasil	Macaé de Cima	22°23'59"S	42°30'00"O	312	307
28	Atlantic	Brasil	Serra da Prata	25°37'45"S	48°40'43"O	278	245
29	Atlantic	Brasil	Serra das Lontras	15°10'46"S	39°23'18"O	256	221
30	Atlantic	Brasil	Cananéia	25°04'39"S	47°55'44"O	178	165
31	Atlantic	Brasil	Salto Morato	25°10'20"S	48°17'54"O	173	152
32	Atlantic	Brasil	Sete Barras	24°11'55"S	47°55'16"O	161	154
33	Atlantic	Brasil	Antonina	25°25'33"S	48°46'39"O	159	143
34	Atlantic	Brasil	Serra do Itajaí	27°03'35"S	49°04'50"O	159	127
35	Atlantic	Brasil	Pedra dos Pontões	20°56'18"S	41°32'38"O	105	81
36	Atlantic	Brasil	Pedra Roxa	20°23'43"S	41°44'05"O	62	42
37	Atlantic	Brasil	Piraquara	25°31'59"S	49°00'36"O	140	132
38	Atlantic	Brasil	Torres	29°21'09"S	49°45'21"O	120	120
39	Atlantic	Brasil	Serra Furada	28°10'54"S	49°23'21"O	115	90
40	Atlantic	Brasil	Ilha do Mel 1	25°32'52"S	48°18'01"O	77	68

Nº area	Province	Country	Location	Latitude	Longitude	Species total	Species Included
41	Atlantic	Brasil	Ilha do Mel 2	25°32'52"S	48°18'01"O	103	95
42	Atlantic	Brasil	Mangaratiba	23°03'01"S	43°57'07"O	93	72
43	Atlantic	Brasil	Serra dos Órgãos	22°29'21"S	43°00'31"O	85	38
44	Atlantic	Brasil	Barra do Turvo	24°56'05"S	48°09'59"O	78	77
45	Atlantic	Brasil	Criciúma	28°41'25"S	49°25'54"O	65	56
46	Atlantic	Brasil	Ubatuba	23°21'22"S	44°51'06"O	64	55
47	Atlantic	Brasil	Balneário Arroio do Silva	29°02'00"S	49°31'00"O	62	53
48	Atlantic	Brasil	Ilha Anchieta	23°32'26"S	45°04'03"O	43	38
49	Atlantic	Brasil	Arroio do Sal	29°29'22"S	49°50'39"O	40	35
50	Atlantic	Brasil	Iguape	24°25'25"S	47°07'52"O	15	10
51	Atlantic	Brasil	Campos do Jordão	22°39'19"S	45°26'33"O	51	44
52	Atlantic	Brasil	Cubatão, Joinville	26º06'00"S	49º03'00"O	73	60
53	Atlantic	Brasil	Ponte Alta	27º16'30"S	50º07'56"O	84	67
54	Atlantic	Brasil	Nova Trento	27º15'49"S	49º01'38"O	50	40
55	Atlantic	Brasil	Faxinal, Praia Grande	29º10'45"S	50º01'23"O	50	40
56	Atlantic	Brasil	Angelina	27º27'00"S	49º03'00"O	82	71
57	Atlantic	Brasil	Taió	27º00'02"S	50º07'46"O	108	85
58	Atlantic	Brasil	Benedito Novo	26º54'36"S	49º29'52"O	125	86
59	Atlantic	Brasil	Rio do Sul	27º05'24"S	49º35'24"O	114	91
60	Atlantic	Brasil	Doutor Pedrinho	26°43'40"S	49°35'06"O	115	92
61	Atlantic	Brasil	Rio Manso, Joinville	26º16'48"S	49º08'24"O	130	105
62	Atlantic	Brasil	Antônio Carlos	27º27'00"S	48º52'12"O	101	79
63	Atlantic	Brasil	Imaruí	28º09'54"S	48º52'11"O	102	83
64	Atlantic	Brasil	Blumenau	27º05'49"S	49º08'22"O	155	125

Nº area	Province	Country	Location	Latitude	Longitude	Species total	Species Included
65	Atlantic	Brasil	Vitor Meireles	26º43'47"S	49º51'33"O	61	46
66	Atlantic	Brasil	Dona Francisca, Joinville	26°11'33"S	49°02'52"O	155	126
67	Atlantic	Brasil	Treviso	28º26'38"S	49º29'55"O	108	87
68	Atlantic	Brasil	São Martinho	28º04'48"S	48º52'13"O	123	90
69	Atlantic	Brasil	Presidente Nereu	27º10'53"S	49º13'54"O	143	106
70	Atlantic	Brasil	Botuverá	27º16'12"S	49º13'48"O	150	109
71	Atlantic	Brasil	Siderópolis	28º37'12"S	49º35'24"O	57	51
72	Atlantic	Brasil	Orleans	28º10'12"S	49º24'37"O	96	80
73	Atlantic	Brasil	Morro da Lagoa, Florianópolis	27º34'36"S	48º28'32"O	97	80
74	Atlantic	Brasil	Biguaçu	27º21'36"S	48º46'48"O	107	93
75	Atlantic	Brasil	São Bento do Sul	26°21'54"S	49º14'08"O	147	123
76	Atlantic	Brasil	Rio do Boi, Praia Grande	29º12'19"S	50º04'28"O	94	57
77	Atlantic	Brasil	Lagoa Peri, Florianópolis	27º43'27"S	48º32'07"O	98	81
78	Atlantic	Brasil	Spitzkopf, Blumenau	27º00'26"S	49º07'05"O	135	116
79	Atlantic	Brasil	Vargem Grande, Florianópolis	27º28'46"S	48º25'48"O	67	47
80	Atlantic	Brasil	Morro Grande	28°42'36"S	49°46'12"O	129	102
81	Atlantic	Brasil	Paulo Lopes	27º52'44"S	48º45'44"O	112	87
82	Atlantic	Brasil	Lagoinha do leste, Florianópolis	27°46'31"S	48°29'33"O	74	57
83	Atlantic	Brasil	Garuva	26º03'19"S	48°43'30"O	95	72
84	Atlantic	Brasil	Porto Belo	27º08' 58"S	48º36'07"O	89	65
85	Atlantic	Brasil	Grumari	23º02’30"S	43º31’00"O	37	29
86	Atlantic	Brasil	Reserva da Vale	19°08'35"S	40°01'35"O	184	183
87	Atlantic	Brasil	Santa Maria de Jetibá	20º00’44"S	40º36’53"O	29	17
88	Atlantic	Brasil	Alegre	20°40'12"S	41°29'45"O	55	45

Nº area	Province	Country	Location	Latitude	Longitude	Species total	Species Included
89	Atlantic	Brasil	Jacarepiá	22°54'47"S	42°25'49"O	34	29
90	Atlantic	Brasil	Rio dos Sinos 1	29°43'42"S	50°21'59"O	30	28
91	Atlantic	Brasil	João Pessoa	07°08'53"S	34°51'34"O	9	9
92	Atlantic	Brasil	Parque Curió	22°35'02"S	43°42'07"O	43	32
93	Cerrado	Brasil	Central rio Sorocaba	22°40'14"S	48°08'31"O	56	52
94	Cerrado	Brasil	Botucatu	22°55'26"S	48°27'27"O	87	82
95	Cerrado	Brasil	Jataí	21°36'15"S	47°48'38"O	29	28
96	Cerrado	Brasil	Assis	22°35'07"S	50°22'30"O	15	15
97	Cerrado	Brasil	Bauru	22°20'38"S	49°01'22"O	21	21
98	Cerrado	Brasil	Brasília	15°54'23"S	48°00'41"O	38	36
99	Cerrado	Brasil	Borebi	22°34'13"S	48°58'06"O	27	18
100	Imerí	Brasil	Parque Nacional Jaú	02°00'25"S	62°00'00"O	37	29
101	Imerí	Brasil	Mamirauá	02°55'04"S	64°56'50"O	73	45
102	Imerí/Roraima	Brasil	Manaus	03°01'09"S	60°13'05"O	36	31
103	Madeira	Brasil	Coari	04°51'59"S	65°20'07"O	165	127
104	Madeira	Brasil	Humaitá	07°31'18"S	63°05'02"O	7	4
105	Pampean	Brasil	Pelotas	31°22'53"S	52°29'28"O	62	60
106	Pampean	Brasil	Itapuã	30°23'06"S	50°58'14"O	62	58
107	Pampean	Brasil	Eldorado do Sul	30°04'39"S	51°38'53"O	57	52
108	Pampean	Brasil	Viamão	30º05'00"S	50º50'00"O	54	51
109	Pampean	Brasil	Osório	29°58'07"S	50°14'35"O	53	53
110	Pará	Brasil	Maracanã	00°36'39"S	47°34'25"O	11	11
111	Parana Forest	Brasil	Médio rio Tietê	22°43'04"S	48°22'57"O	64	59

Nº area	Province	Country	Location	Latitude	Longitude	Species total	Species Included
112	Parana Forest	Brasil	Chácara	22º36'30"S	43º12'48"O	91	80
113	Parana Forest	Brasil	Porto Ferreira	21°51'02"S	47°25'48"O	66	66
114	Parana Forest	Brasil	Baixo Rio Tibagi	23°33'47"S	50°56'07"O	62	50
115	Parana Forest	Brasil	Descoberto	21°22'21"S	42°56'11"O	59	57
116	Parana Forest	Brasil	Foz do Iguaçu	25°29'48"S	53°58'47"O	56	54
117	Parana Forest	Brasil	Barroso	21°11'02"S	43°55'19"O	40	39
118	Parana Forest	Brasil	Ouro Preto	20°21'36"S	43°30'11"O	35	33
119	Parana Forest	Brasil	Fênix	23°55'01"S	51°57'04"O	32	29
120	Parana Forest	Brasil	Jateí	22°47'00"S	53°31'52"O	29	25
121	Parana Forest	Brasil	Rio dos Sinos 2	29°40’54”S	51°06’56”O	25	22
122	Parana Forest	Brasil	Maringá	23°25'41"S	51°55'45"O	25	23
123	Parana Forest	Brasil	Gália	22°24'11"S	49°41'37"O	24	24
124	Parana Forest	Brasil	Iperó	23°26'21"S	47°38'10"O	21	18
125	Parana Forest	Brasil	Pedra Lisa	20°41'55"S	41°18'28"O	24	15
126	Parana Forest	Brasil	Serra do Cruz	21°54'3"S	44°04'39"O	135	122
127	Parana Forest	Brasil	Ibitipoca	21º40'21"S	43º52'43"O	224	201
128	Parana Forest	Brasil	Mato Castelhano	28°17'17"S	52°11'15"O	44	39
129	Parana Forest	Brasil	Erechim	27°37'54"S	52°16'52"O	21	18
130	Parana Forest	Brasil	Juiz de Fora	21°43'50"S	43°22'13"O	42	25
131	Paraná Forest/ Atlantic	Brasil	Serra do Papagaio	22°08'31"S	44°43'58"O	138	106
132	Rondônia/Madeira	Brasil	Acrelândia	10°00'09"S	66°46'40"O	77	42
133	Roraima	Brasil	Reserva Ducke	02°55′00 S	59°59′00"O	122	115
134	Xingu-Tapajós	Brasil	Caxiuãna	01°42'300"S	51°31'45"O	85	60

Nº area	Province	Country	Location	Latitude	Longitude	Species total	Species Included
135	Caatinga	Brasil	Areia	06°57'46"S	35°41'31"O	12	12
136	Pampean	Brasil	Palmares do Sul	30°22'21"S	50°20'43"O	24	23
137	Cauca/Magdalena	Colombia	Antioquía	06°34'59"N	75°45'00"O	64	36
138	Cauca/Magdalena	Colombia	Córdoda	07°57’37"N	76º05'04"O	73	48
139	Guajira	Colombia	Sierra Nevada	10°48'59"N	73°46'20"O	68	17
140	Guajira	Colombia	Serrania de Macuira	12°09'30"N	71°20'15"O	25	17
141	Imerí	Colombia	Caquetá	01°01'46"S	71°40'24"O	213	140
142	Imerí	Colombia	Amacayacu	03°00'51"S	69°58'59"O	161	98
143	Imerí	Colombia	Chiribiquete 1	00°13'06"S	72°28'34"O	154	106
144	Imerí	Colombia	Chiribiquete 2	00°04'16"N	72°26'48"O	183	119
145	Puntarenas-Chiriquí	Costa Rica	Monteverde	10°18'00"N	84°47'59"O	256	229
146	Cauca	Equador	Loja	04°05'58"S	79°11'34"O	138	35
147	Cauca	Equador	San Francisco	03°58'40"S	79°04'32"O	641	640
148	Cauca	Equador	Otonga	00°42'00"S	79°00'00"O	456	244
149	Cauca	Equador	Guajalito	00°14'00"S	78°48'59"O	256	173
150	Napo	Equador	Yasuni	00°38'21"S	76°08'53"O	313	255
151	Chiapas Highlands	Guatemala	San Lorenzo 1	15°07'04"N	89°40'38"O	68	52
152	Guianan Lowlands	Guiana	Mabural Hill	05°19'59"N	58°09'59"O	176	148
153	Guianan Lowlands	Guiana Francesa	Saül	03º37'59"N	53º12'00"O	140	121
154	Guianan Lowlands	Guiana Francesa	Aratai Station	03°59'24"N	52°35'27"O	74	60
155	Mosquito	Honduras	Cusuco	15°32'31"N	88°15'49"O	207	170
156	Jamaica	Jamaica	Hog House Hill	18º04'59"N	76º21'59"O	91	87
157	Pacific Lowlands	México	El Triunfo	15º39'08"N	92º49'52"O	465	458

Nº area	Province	Country	Location	Latitude	Longitude	Species total	Species Included
158	Veracruzan	México	Veracruz 1a	19°21'54"N	96°47'44"O	42	41
159	Veracruzan	México	Veracruz 1b	19°25'07"N	96°48'00"O	41	39
160	Veracruzan	México	Veracruz 1c	19°36'55"N	96°52'51"O	21	20
161	Veracruzan	México	Veracruz 1d	19°28'34"N	96°57'37"O	52	47
162	Veracruzan	México	Veracruz 1e	19°41'02"N	96°51'15"O	39	34
163	Veracruzan	México	Veracruz 1f	19°36'58"N	97°04'46"O	23	20
164	Veracruzan	México	Veracruz 2	19°30'56"N	96°59'50"O	118	94
165	Veracruzan	México	Rio Uxpanapa	17°32'31"N	94°14'9"O	212	146
166	Veracruzan	México	Otonpec	21°15'30"N	97°53'10"O	99	86
167	Guatuso-Talamanca	Panamá	Barro Colorado	09º09'18"N	79º50'33"O	80	79
168	Guatuso-Talamanca	Panamá	San Lorenzo 2	09°21'20"N	79°58'06"O	125	117
169	Guatuso-Talamanca	Panamá	Río Changuinola	09°05'00"N	82°28'00"O	476	316
170	Puntarenas-Chiriquí	Panamá	Fortuna Forest Reserve	08º45'40"N	82º14’22"O	155	76
171	Guajira	Venezuela	La Carbonera	08°37'00"N	71°20'59"O	191	170
172	Guajira	Venezuela	Mérida	08°32'23"N	71°08'32"O	133	115
173	Imerí	Venezuela	Surumoni	03º10'30"N	65º40'29"O	53	41

Appendix 2.

Bibliographical references of the 109 studies performed in 173 sites considering qualitative/quantitative surveys exclusively on vascular epiphytes carried out in the Neotropical Region up to 2017.

Nº area	Reference	Author	Title	Journal/Book	Year
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2	Kersten, R.A.; Rios, R.C. Epífitas vasculares em áreas de ecótono entre Floresta Ombrófila Mista e Estacional Semidecidual em Missiones, Argentina. Estudos de Biologia 35(84): 49-57. 2013.	Kersten, R.A.; Rios, R.C.	Epífitas vasculares em áreas de ecótono entre Floresta Ombrófila Mista e Estacional Semidecidual em Missiones, Argentina.	Estudos de Biologia 35 (84): 49-57.	2013
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6	Krömer, T. Diversität und Ökologie der vaskulären Epiphyten in primären und sekundären Bergwäldern Boliviens. Dissertation zur Erlangung des Doktorgrades der Mathematisch-Naturwissenschaftlichen Fakultäten der Georg-August-Universität zu Göttingen. 171p. 2003.	Krömer , T.	Diversität und Ökologie der vaskulären Epiphyten in primären und sekundären Bergwäldern Boliviens.	Dissertation zur Erlangung des Doktorgrades, Fakultäten der Georg-August-Universität zu Göttingen. 171p. 2003.	2003
7	Kessler, M.; Jimenez, I.; Krömer T. Diversity and endemismo of six plant groups in the Cordillera Mosetenes, Cochabamba, Bolívia. Revista Boliviana de Ecología y Conservación Ambiental 23: 15-25. 2008.	Kessler, M.; Jimenez, I.; Krömer T.	Diversity and endemismo of six plant groups in the Cordillera Mosetenes, Cochabamba, Bolívia.	Revista Boliviana de Ecología y Conservación Ambiental 23: 15-25. 2008.	2008
7	Krömer T.; Jimenez, I.; Kessler, M. Diversity and vertical distribution patterns of vascular epiphytes in the Cordillera Mosetenes, Cochabamba, Bolivia. Revista Boliviana de Ecología y Conservación Ambiental (26): 27-38. 2008.	Krömer T.; Jimenez, I.; Kessler, M.	Diversity and vertical distribution patterns of vascular epiphytes in the Cordillera Mosetenes, Cochabamba, Bolivia.	Revista Boliviana de Ecología y Conservación Ambiental (26): 27-38. 2008.	2008
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Nº area	Reference	Author	Title	Journal/Book	Year
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Nº area	Reference	Author	Title	Journal/Book	Year
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Nº area	Reference	Author	Title	Journal/Book	Year
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Nº area	Reference	Author	Title	Journal/Book	Year
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Nº area	Reference	Author	Title	Journal/Book	Year
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Nº area	Reference	Author	Title	Journal/Book	Year
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Nº area	Reference	Author	Title	Journal/Book	Year
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Nº area	Reference	Author	Title	Journal/Book	Year
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Appendix 3.

Bioclimatic variables used in the ordination analyses for the 173 qualitative/quantitative surveys exclusively on vascular epiphytes carried out in the Neotropical Region up to 2017. The data were extracted from WorldClim dataset (Fick & Hijmans, 2007), at a resolution of 30 arc-seconds, except the cloud cover which was extracted from Earthenv (Wilson & Jetz, 2016). (BIO1 = Annual Mean Temperature; BIO2 = Mean Diurnal Range (Mean of monthly (max temp - min temp); BIO3 = Isothermality (BIO2/BIO7) (* 100); BIO4 = Temperature Seasonality (standard deviation *100); BIO5 = Max Temperature of Warmest Month; BIO6 = Min Temperature of Coldest Month; BIO7 = Temperature Annual Range (BIO5-BIO6); BIO8 = Mean Temperature of Wettest Quarter; BIO9 = Mean Temperature of Driest Quarter; BIO10 = Mean Temperature of Warmest Quarter; BIO11 = Mean Temperature of Coldest Quarter; BIO12 = Annual Precipitation; BIO13 = Precipitation of Wettest Month; BIO14 = Precipitation of Driest Month; BIO15 = Precipitation Seasonality (Coefficient of Variation); BIO16 = Precipitation of Wettest Quarter; BIO17 = Precipitation of Driest Quarter; BIO18 = Precipitation of Warmest Quarter; BIO19 = Precipitation of Coldest Quarter; Cloud = Mean annual cloud cover).

Nº area	BIO.1	BIO.2	BIO.3	BIO.4	BIO.5	BIO.6	BIO.7	BIO.8	BIO.9	BIO.10	BIO.11	BIO.12	BIO.13	BIO.14	BIO.15	BIO.16	BIO.17	BIO.18	BIO.19	Cloud
1	18.192	11.867	55.1938	353.076	28.2	353.08	21.5	22.35	14.83	22.35	13.87	1859	189	125	12.1397	503	415	503	448	59.2
2	18.629	12.408	54.1849	366.95	29.3	366.95	22.9	22.95	15.08	22.95	14.12	1822	186	121	12.3638	487	393	487	397	58.6
3	15.613	11.608	52.2898	377.125	26	377.13	22.2	19.75	12.22	19.75	10.67	655	144	5	98.8909	395	16	395	17	67.5
4	15.342	17.3	76.2115	187.445	25.8	187.44	22.7	16.77	12.8	17.2	12.73	920	175	16	78.479	485	56	293	65	87.2
5	24.65	10.45	70.1342	147.355	31.5	147.36	14.9	25.8	22.58	25.92	22.57	1799	278	51	55.3091	785	170	710	189	69.2
6	18.842	13.733	80.7843	99.7687	26.9	99.769	17	19.6	17.45	19.65	17.45	1155	192	17	65.1597	554	73	465	73	78.5
7	21.004	12.542	74.6528	153.57	28.8	153.57	16.8	22.13	18.82	22.4	18.82	2078	320	62	55.4767	910	218	635	218	86.7
8	24.642	9.85	68.8811	152.566	31	152.57	14.3	25.92	23.18	25.97		1876	286	67	53.4121	803	210	698	214	65
9	18.608	12.8	61.5385	298.525	28.6	298.53	20.8	22.02	14.88	22.02	14.8	1365	154	69	25.5268	445	244	445	257	59.7
10	18.588	10.975	54.064	352.286	28.3	352.29	20.3	16.9	18.57	22.78	14.3	1762	194	123	15.6629	517	388	445	426	49.7
11	19.567	12.233	62.735	282.741	29	282.74	19.5	22.87	16.17	22.87	16.02	1499	183	74	27.9688	504	269	504	311	54.6
12	16.792	10.3	57.5419	269.257	25.7	269.26	17.9	19.98	13.52	19.98	13.52	1899	242	94	31.4931	666	301	666	301	72.7
13	15.992	11.317	56.8677	317.36	25.4	317.36	19.9	14.58	15.97	19.75	12.08	1796	180	119	14.2922	488	409	483	421	59.5
14	17.387	10.492	57.0199	293.94	26.4	293.94	18.4	20.83	13.77	20.83	13.77	1384	178	67	30.099	485	247	485	247	66.4
15	17.675	11.283	58.7674	290.826	27.2	290.83	19.2	21.1	14.12	21.1	14.12	1580	210	81	29.8967	550	271	550	271	69.4
16	16.954	11.775	57.7206	291.153	27.1	291.15	20.4	20.33	13.42	20.43	13.4	1586	199	87	26.3322	541	304	518	324	64.5
17	17.483	11.283	58.1615	294.467	27.1	294.47	19.4	20.95	13.87	20.95	13.87	1525	203	79	29.0328	529	269	529	269	67.9
18	15.613	11.408	59.4184	285.172	24.8	285.17	19.2	15.73	12.12	19	12.12	1704	182	98	19.4734	493	350	485	350	66.6
19	14.942	9.4667	52.8864	314.135	23.7	314.14	17.9	12.85	16.1	18.85	11.2	2083	200	135	10.0864	553	477	551	526	66.5
20	17.408	11.05	58.1579	294.964	26.8	294.96	19	20.88	13.8	20.88	13.8	1419	188	70	30.0254	499	253	499	253	69
21	17.067	10.617	57.6993	290.832	26.1	290.83	18.4	20.48	13.48	20.48	13.48	1435	184	71	29.9937	502	256	502	256	68.3
22	17.258	11.2	58.3333	292.931	26.8	292.93	19.2	20.7	13.67	20.7	13.67	1556	211	78	29.9446	546	272	534	272	68.3
23	18.125	8.9	51.4451	308.961	26.9	308.96	17.3	21.92	14.85	21.92	14.35	1713	218	91	27.7519	594	299	594	308	72.3
24	17.487	9.625	59.4136	240.644	25.5	240.64	16.2	20.22	14.42	20.3	14.42	1384	237	44	57.2572	617	146	585	146	63.1
25	18.521	10.308	60.6373	241.411	27.1	241.41	17	21.37	15.58	21.43	15.58	1471	244	41	59.6101	665	134	634	134	66.6
26	18.892	10.55	61.6959	235.727	27.5	235.73	17.1	21.63	15.98	21.68	15.98	1442	244	38	61.2418	663	128	633	128	67.1
27	17.017	9.85	57.2674	243.388	25.7	243.39	17.2	19.73	13.92	19.92	13.92	1360	244	26	68.7328	637	88	564	88	74
28	16.479	8.925	54.7546	274.958	24.6	274.96	16.3	19.83	13.18	19.83	13.18	2106	269	106	32.0998	766	339	766	339	82.3

Nº area	BIO.1	BIO.2	BIO.3	BIO.4	BIO.5	BIO.6	BIO.7	BIO.8	BIO.9	BIO.10	BIO.11	BIO.12	BIO.13	BIO.14	BIO.15	BIO.16	BIO.17	BIO.18	BIO.19	Cloud
29	20.063	7.4917	65.7164	146.739	25.5	146.74	11.4	18.57	19.03	21.72	18.12	1552	159	107	13.339	422	338	375	419	75.5
30	22.313	7.2917	47.3485	285.372	30.2	285.37	15.4	25.83	18.88	25.83	18.88	2208	327	78	45.4101	912	279	912	279	62.6
31	21.654	7.5083	47.8238	297.432	29.7	297.43	15.7	25.37	18.12	25.37	18.12	2092	304	74	45.1592	868	270	868	270	75.8
32	21.779	9.4583	53.7405	284.393	30.6	284.39	17.6	25.1	18.25	25.13	18.25	1466	227	54	49.0233	611	182	609	182	74.6
33	20.979	7.975	48.9264	304.687	29.3	304.69	16.3	24.88	17.47	24.88	17.47	1783	249	69	43.2365	727	240	727	240	67.2
34	18.142	9.3167	52.0484	313.498	27.2	313.5	17.9	21.97	14.75	21.97	14.28	1670	202	91	26.0572	562	295	562	311	71.6
35	18.804	11.708	62.2784	226.239	28.2	226.24	18.8	20.67	15.83	21.45	15.83	1270	212	32	62.0125	598	102	443	102	75.8
36	17.192	12.55	63.3838	221.696	27	221.7	19.8	19	14.23	19.75	14.23	1324	227	25	66.6988	645	87	475	87	74.1
37	17.292	10.233	57.8154	267.869	26.1	267.87	17.7	20.48	14.03	20.48	14.03	1857	236	90	31.6597	656	297	656	297	70.2
38	19.308	7.6833	46.5657	333.677	27.8	333.68	16.5	23.45	20.37	23.45	15.25	1414	146	93	15.0827	408	313	408	332	56
39	17.313	10.292	55.6306	305.191	26.7	305.19	18.5	21.08	14.05	21.08	13.62	1523	191	89	26.0551	519	273	519	297	73.3
40	20.979	7.0083	46.1075	298.774	29.1	298.77	15.2	24.9	17.65	24.9	17.65	2090	288	86	42.2846	857	294	857	294	59.7
41	20.979	7.0083	46.1075	298.774	29.1	298.77	15.2	24.9	17.65	24.9	17.65	2090	288	86	42.2846	857	294	857	294	59.7
42	23.175	10.183	60.2564	200.72	32	200.72	16.9	25.55	20.95	25.8	20.95	1430	203	53	44.6577	549	163	510	163	57.3
43	19.083	9.65	57.4405	226.338	27.7	226.34	16.8	21.7	16.3	21.92	16.3	1632	255	40	61.9043	731	134	704	134	77.6
44	20.829	7.9417	49.6354	295.431	28.9	295.43	16	24.37	17.23	24.37	17.23	1930	283	65	45.6249	798	245	798	245	77
45	19.542	10.95	54.4776	335.077	29.6	335.08	20.1	23.63	16.02	23.63	15.43	1346	165	78	25.5297	457	246	457	259	66.1
46	22.429	9.525	55.7018	234.845	31.3	234.84	17.1	25.42	19.62	25.42	19.62	2544	316	107	39.5128	932	333	932	333	69.8
47	19.396	9.425	50.9459	340.764	28.9	340.76	18.5	23.57	15.93	23.57	15.23	1325	149	84	20.231	414	266	414	286	54.6
48	22.429	9.525	55.7018	234.845	31.3	234.84	17.1	25.42	19.62	25.42	19.62	2544	316	107	39.5128	932	333	932	333	61.6
49	19.271	7.825	47.1386	331	27.7	331	16.6	23.38	20.28	23.38	15.25	1434	145	93	14.1831	405	319	405	342	56.9
50	22.142	8.4167	52.6042	262.374	30.4	262.37	16	25.38	18.95	25.38	18.95	2039	284	78	44.0042	813	248	813	248	77.6
51	13.804	11.925	51.6234	307.205	26.2	307.2	23.1	17.3	9.9	17.3	9.9	1804	322	34	66.2607	867	143	867	143	69.1
52	15.188	9.625	55.3161	286.508	23.9	286.51	17.4	18.62	11.72	18.63	11.72	1750	214	91	28.5461	606	310	599	310	74.5
53	14.996	9.8417	53.4873	313.423	23.8	313.42	18.4	18.72	11.45	18.77	11.18	1647	173	102	15.3971	466	349	466	381	70.9
54	15.213	9.2417	53.42	296.84	23.8	296.84	17.3	18.85	12.05	18.85	11.62	1761	214	102	24.6478	590	322	590	352	73.8
55	15.5	8.9667	52.4366	300.273	24.1	300.27	17.1	19.28	12.45	19.28	11.97	1850	184	127	12.8302	528	415	528	440	76.4
56	16.237	9.8583	54.4659	303.526	25.4	303.53	18.1	19.97	13	19.97	12.55	1692	214	93	26.3377	577	302	577	331	72.8
57	16.213	10.692	54.8291	327.963	25.6	327.96	19.5	20.13	12.45	20.13	12.18	1607	170	98	16.5359	467	339	467	363	68.3
58	16.096	10.108	54.9366	308.858	25.1	308.86	18.4	19.8	12.63	19.8	12.33	1625	185	91	23.07	523	306	523	324	72.6
59	16.308	9.95	54.0761	315.86	25.4	315.86	18.4	20.07	14.35	20.08	12.43	1671	183	105	18.6058	512	340	510	371	66.4
60	16.129	10.325	55.2139	310.318	25.3	310.32	18.7	19.87	12.62	19.87	12.35	1569	180	84	24.3726	510	287	510	303	71.5
61	16.929	9.4917	53.6252	301.266	25.8	301.27	17.7	20.57	13.55	20.57	13.27	1617	204	82	28.8246	563	284	563	290	76.2
62	16.742	9.5667	53.7453	302.488	25.9	302.49	17.8	20.5	13.6	20.5	13.08	1703	221	94	28.0558	597	300	597	324	73.1
63	16.95	9.6	54.5455	295.389	25.9	295.39	17.6	20.68	14.02	20.68	13.45	1628	205	92	26.0242	560	297	560	321	70.6
64	16.671	9.775	54.3056	305.313	25.7	305.31	18	20.4	13.37	20.4	12.95	1687	202	92	25.6194	567	301	567	322	73.6
65	17.846	10.475	54.2746	330.34	27.3	330.34	19.3	21.77	14.03	21.77	13.77	1534	166	89	20.6342	480	307	480	319	63.2
66	17.267	9.1667	52.9865	297.859	26	297.86	17.3	20.88	13.95	20.88	13.67	1660	214	83	30.3854	591	287	591	290	74.9
67	17.3	10.183	55.3442	305.011	26.7	305.01	18.4	21.08	14.08	21.08	13.62	1509	184	88	24.5606	505	277	505	300	75.1
68	17.367	9.6333	54.4256	298.324	26.5	298.32	17.7	21.12	14.37	21.12	13.8	1601	208	87	28.0872	564	284	564	306	69.2
69	17.021	9.9417	54.326	313.198	26.2	313.2	18.3	20.82	13.6	20.82	13.18	1668	198	94	24.0053	549	308	549	334	70.6

Nº area	BIO.1	BIO.2	BIO.3	BIO.4	BIO.5	BIO.6	BIO.7	BIO.8	BIO.9	BIO.10	BIO.11	BIO.12	BIO.13	BIO.14	BIO.15	BIO.16	BIO.17	BIO.18	BIO.19	Cloud
70	17.317	9.9667	54.1667	315.273	26.6	315.27	18.4	21.15	13.87	21.15	13.45	1648	199	93	24.7158	546	300	546	329	67.5
71	17.296	10.158	55.2083	307.951	26.4	307.95	18.4	21.12	14.07	21.12	13.58	1506	173	95	21.0706	484	293	484	318	71.6
72	17.471	10.308	55.4211	305.915	26.9	305.91	18.6	21.23	14.18	21.23	13.75	1521	194	86	26.7817	522	271	522	291	76
73	18.263	9.2083	52.9215	304.729	27	304.73	17.4	22.1	15.28	22.1	14.6	1677	213	100	26.5857	588	309	588	327	61.4
74	18.033	9.15	51.6949	309.548	27.2	309.55	17.7	21.88	14.85	21.88	14.28	1680	215	92	28.0576	591	298	591	310	73.4
75	17.667	9.55	53.6517	307.633	26.4	307.63	17.8	21.37	14.22	21.37	13.92	1566	198	80	28.5431	539	274	539	283	69.5
76	17.612	8.7417	50.8236	316.466	26.4	316.47	17.2	21.55	14.38	21.55	13.8	1620	166	109	13.7775	466	361	466	377	71.5
77	18.667	9.2833	53.0476	304.424	27.4	304.42	17.5	22.5	15.7	22.5	15.02	1617	213	93	28.1124	575	296	575	312	61.6
78	18.683	9.25	51.9663	318.522	27.6	318.52	17.8	22.57	15.22	22.57	14.77	1670	202	92	25.337	553	295	553	315	68
79	19.25	9.35	52.5281	310.374	28.4	310.37	17.8	23.15	16.22	23.15	15.5	1636	193	103	23.004	554	319	554	324	60.5
80	17.637	9.8083	53.8919	311.084	26.8	311.08	18.2	21.5	14.37	21.5	13.88	1497	171	95	20.3456	473	291	473	317	73.8
81	18.983	9.1667	52.3809	305.832	28.2	305.83	17.5	22.83	15.95	22.83	15.32	1573	224	81	32.7116	583	271	583	291	71.6
82	19.125	8.9833	52.2287	303.394	27.8	303.39	17.2	22.98	16.23	22.98	15.5	1579	198	95	25.6371	548	297	548	314	60.5
83	20.75	7.85	49.0625	296.257	29.1	296.26	16	24.55	17.32	24.55	17.32	1813	262	84	39.3498	725	268	725	268	71.7
84	20.013	9.275	51.5278	322.66	29.3	322.66	18	24.02	16.08	24.02	16.08	1581	199	87	26.9911	548	279	548	279	61.2
85	23.204	9.5083	58.6934	202.074	31.7	202.07	16.2	25.85	20.93	25.85	20.93	1231	167	46	44.6645	467	148	467	148	55.6
86	23.529	8.9083	61.016	192.087	31	192.09	14.6	24.98	21.62	25.82	21.08	1193	180	42	50.0552	510	146	351	148	66.9
87	19.167	11.383	65.0476	201.114	28	201.11	17.5	20.73	16.57	21.57	16.57	1320	202	50	50.3875	573	161	390	161	74.6
88	22.525	12.067	64.1844	218.824	31.9	218.82	18.8	24.27	19.68	25.13	19.68	1127	200	23	67.9574	557	74	393	74	57.4
89	23	8.4667	57.9909	213.776	30.7	213.78	14.6	25.73	20.65	25.73	20.48	1093	162	27	51.9773	449	104	449	114	50.4
90	17.462	8.425	49.5588	322.223	26	322.22	17	15.13	18.52	21.48	13.6	1726	166	108	10.8964	462	386	454	442	64.4
91	25.642	7.6333	73.3974	91.4985	30.4	91.498	10.4	24.78	26.12	26.53	24.3	1902	315	40	62.6563	845	142	416	754	60.8
92	21.742	10.683	58.3789	232.719	31	232.72	18.3	24.4	18.83	24.57	18.83	1619	254	40	57.8718	711	140	648	140	62.2
93	20.687	11.542	60.4276	243.433	29.9	243.43	19.1	23.28	17.5	23.3	17.5	1266	231	29	68.4955	623	100	580	100	51.8
94	19.025	12.15	63.9474	237.769	28.4	237.77	19	21.68	16.03	21.68	16.03	1325	226	35	62.5755	622	121	622	121	61.1
95	21.529	11.575	61.2434	222.674	30.3	222.67	18.9	23.62	18.5	23.65	18.43	1374	245	23	72.7961	681	80	600	107	53.4
96	20.588	12.525	62.3134	268.778	30.2	268.78	20.1	23.48	18.37	23.48	16.97	1211	197	38	51.6672	520	143	520	165	56.7
97	21.288	12.175	64.0789	218.29	30.5	218.29	19	23.63	18.62	23.63	18.35	1164	206	25	63.9868	562	107	502	121	56.7
98	20.663	11.492	70.9362	118.708	28.1	118.71	16.2	21.25	19.03	21.62	18.9	1526	260	9	77.9097	728	31	430	51	62.4
99	20.692	12.483	65.0174	227.145	30	227.14	19.2	23.17	17.88	23.17	17.7	1214	211	25	62.147	575	113	575	128	56.6
100	26.463	9.025	87.6213	29.5516	31.7	29.552	10.3	26.35	26.62	26.85	26.08	2560	319	133	29.6468	897	433	518	678	74.7
101	26.779	8.375	87.2396	22.3056	31.6	22.306	9.6	26.68	26.8	27.07	26.52	3180	356	174	23.3006	1004	542	681	744	69.1
102	26.567	8.7667	85.1133	45.9908	32	45.991	10.3	26.15	26.78	27.22	26.12	2243	302	56	50.009	885	219	373	865	73.2
103	26.429	8.725	88.1313	28.6403	31.3	28.64	9.9	26.42	26.45	26.77	26.07	2429	315	87	41.4615	902	295	495	407	74.2
104	26.15	10.85	88.9344	46.27	31.9	46.27	12.2	25.92	25.93	26.77	25.65	2303	329	27	53.4023	900	157	382	241	74.2
105	18.058	8.9667	46.4594	398.633	27.1	398.63	19.3	13.77	22.05	22.6	13.15	1455	144	89	15.0634	414	304	347	409	63.8
106	19.496	8.3417	46.8633	355.339	28	355.34	17.8	15.13	20.85	23.78	15.13	1439	140	89	11.7724	386	317	367	386	50
107	19.738	9.575	49.8698	373.668	28.7	373.67	19.2	24.02	15.73	24.05	15.12	1410	144	102	11.7456	413	322	397	323	57.8
108	19.417	9.0833	49.6357	348.61	28.3	348.61	18.3	15.12	20.77	23.63	15.12	1511	147	92	12.139	406	335	381	406	55.5
109	19.371	8.4083	48.3238	340.25	28	340.25	17.4	16.83	20.5	23.57	15.23	1521	147	93	12.2462	410	332	396	396	54.6
110	26.554	7.125	82.8488	52.8918	31	52.892	8.6	25.98	27.23	27.27	25.98	2611	512	15	81.6949	1370	57	109	1370	46

Nº area	BIO.1	BIO.2	BIO.3	BIO.4	BIO.5	BIO.6	BIO.7	BIO.8	BIO.9	BIO.10	BIO.11	BIO.12	BIO.13	BIO.14	BIO.15	BIO.16	BIO.17	BIO.18	BIO.19	Cloud
111	21	11.533	62.0072	243.908	30	243.91	18.6	23.65	17.87	23.67	17.87	1259	226	28	67.7576	617	101	571	101	52.5
112	21.754	9.7417	56.6376	232.286	30.6	232.29	17.2	24.67	18.93	24.67	18.93	1789	256	51	56.2031	765	168	765	168	64.2
113	21.779	12.592	62.335	230.291	31.2	230.29	20.2	23.93	18.68	23.97	18.55	1346	255	19	76.3369	688	76	624	96	53.3
114	20.292	11.833	61.9546	270.486	29.4	270.49	19.1	23.3	16.9	23.3	16.72	1449	192	60	34.5025	539	232	539	267	55.2
115	17.25	10.333	60.0775	216.889	25.8	216.89	17.2	19.03	14.45	19.8	14.45	1555	282	28	73.3024	772	88	646	88	69.1
116	19.529	11.492	54.206	352.275	29.5	352.27	21.2	23.7	15.22	23.7	15.22	1801	217	115	20.5165	526	376	526	387	55
117	18.783	11.017	62.5947	202.668	27.4	202.67	17.6	20.45	16.13	21.07	16.13	1453	281	16	80.0024	748	54	619	54	65.5
118	16.563	10.492	62.8243	202.834	24.7	202.83	16.7	18.27	13.8	18.77	13.8	1611	313	21	78.5325	842	76	671	76	70.8
119	20.179	12.792	62.3984	300.208	29.9	300.21	20.5	23.58	17.57	23.58	16.33	1479	204	67	38.3643	528	248	528	295	52
120	22.175	12.217	63.2988	266.718	31.4	266.72	19.3	23.8	19.75	25.1	18.73	1338	189	36	40.0305	492	182	455	225	48.5
121	19.696	10.025	51.6753	358.37	28.9	358.37	19.4	23.95	17.62	23.97	15.28	1549	155	103	10.7146	432	363	422	375	57.9
122	18.3	14.083	61.2319	304.996	29.3	305	23	21.77	15.57	21.77	14.37	1262	160	43	35.6321	457	179	457	180	60.1
123	20.479	12.442	62.2083	259.575	30.1	259.58	20	23.28	17.22	23.28	17.02	1274	210	33	60.5766	598	129	598	152	56.5
124	18.004	9.7583	60.2366	238.542	25.9	238.54	16.2	20.67	14.93	20.72	14.93	1230	214	35	60.1289	565	122	527	122	60.3
125	23.054	10.792	62.7422	217.741	31.7	217.74	17.2	24.77	20.25	25.68	20.25	1110	193	24	65.1816	541	83	369	83	58.2
126	16.45	10.333	60.0775	213.712	25	213.71	17.2	18.87	13.7	18.9	13.7	1682	309	23	74.5568	834	83	726	83	69.3
127	16.558	10.05	60.5422	202.112	24.8	202.11	16.6	18.85	13.98	18.93	13.98	1662	303	24	74.5435	819	83	710	83	74.2
128	17.037	11.592	54.421	350.87	27.4	350.87	21.3	15.03	17.15	21.23	12.87	1753	200	122	14.3597	522	378	439	444	59.8
129	17.204	11.792	56.6907	343.468	27.2	343.47	20.8	15.52	17.15	21.32	13.1	1861	201	127	12.698	544	412	463	457	58.4
130	19.667	10.15	60.4167	215.979	28.1	215.98	16.8	22.1	16.95	22.28	16.95	1427	268	17	77.5277	713	60	631	60	66.7
131	15.083	12.85	58.945	235.742	26.1	235.74	21.8	17.73	12.02	17.73	12.02	1875	338	28	74.0718	937	100	937	100	72.8
132	26.058	10.517	81.5246	70.7374	32.1	70.737	12.9	26.28	25.12	26.75	25.05	1813	267	19	60.3321	774	91	454	152	69.4
133	26.442	8.8667	84.4444	48.6095	32	48.609	10.5	26	26.65	27.13	25.97	2311	305	67	46.8655	888	248	389	861	79.3
134	26.071	10.175	86.2288	49.1962	32.1	49.196	11.8	25.8	26.67	26.7	25.48	2239	326	48	57.7775	964	185	190	825	68.9
135	21.604	8.775	63.1295	137.253	28	137.25	13.9	21.37	22.25	22.98	19.7	1264	181	27	56.2055	498	96	316	454	70.5
136	19.183	7.8333	46.3511	342.765	27.5	342.77	16.9	16.55	20.27	23.42	15.02	1491	146	88	13.5968	405	316	375	404	53.2
137	21.096	9.3583	88.2862	45.8485	26.5	45.848	10.6	20.55	20.97	21.57	20.47	2493	340	96	37.6279	808	339	453	684	82.4
138	21.908	8.4333	89.7163	30.8835	26.8	30.883	9.4	21.6	22	22.3	21.6	2411	288	64	34.2448	752	289	622	688	94.6
139	2.4292	13.008	83.9247	86.7719	10.3	86.772	15.5	3.35	1.267	3.4	1.267	1978	364	6	75.5391	906	40	821	40	93.9
140	26.658	8.9167	74.93	108.687	32.3	108.69	11.9	26.25	25.87	27.85	25.25	642	116	10	67.5781	305	69	129	209	88.1
141	26.137	8.275	76.6204	53.5607	31.2	53.561	10.8	26.27	26.53	26.6	25.35	2860	314	191	17.4566	893	581	659	727	78.1
142	26.688	7.7417	80.6424	39.2616	31.4	39.262	9.6	26.68	26.62	27.17	26.15	2972	306	168	18.5956	880	564	654	694	75.2
143	26.158	8.4	76.3636	66.1209	31.2	66.121	11	26	26.73	26.83	25.2	2728	312	120	28.1771	880	416	489	831	80.6
144	26.438	8.275	75.9174	68.4279	31.4	68.428	10.9	26.28	27.02	27.18	25.47	2706	322	105	30.9214	891	389	453	843	73.3
145	18.587	9.0583	79.4591	78.0479	24.3	78.048	11.4	18.42	19.03	19.6	17.72	2521	419	24	67.5666	1129	122	318	421	87.3
146	14.942	11.15	81.3869	36.3589	21.6	36.359	13.7	15.12	14.52	15.27	14.4	1124	151	55	32.2905	413	187	256	199	90.1
147	16.879	11.108	81.0827	41.9664	23.6	41.966	13.7	17.08	17.15	17.28	16.27	827	103	49	23.7651	265	160	164	211	84.4
148	15.271	8.0083	92.0498	22.5084	19.6	22.508	8.7	15.53	15.08	15.62	15.08	1635	268	24	69.2883	791	118	678	118	96.9
149	16.417	8.5833	92.2939	22.1906	21.2	22.191	9.3	16.62	16.38	16.75	16.22	2066	316	36	58.0347	927	205	825	380	97.7
150	25.233	8.7333	78.6787	55.6504	30.6	55.65	11.1	24.87	25.75	25.85	24.47	3198	346	189	20.3202	998	578	643	875	80.8
151	15.85	8.85	72.541	124.408	22	124.41	12.2	16.82	15.82	17.28	14.35	1762	286	48	61.0607	766	159	508	198	76.4

Nº area	BIO.1	BIO.2	BIO.3	BIO.4	BIO.5	BIO.6	BIO.7	BIO.8	BIO.9	BIO.10	BIO.11	BIO.12	BIO.13	BIO.14	BIO.15	BIO.16	BIO.17	BIO.18	BIO.19	Cloud
152	26.633	8.95	80.6306	65.0291	32.6	65.029	11.1	26.48	27.52	27.52	25.87	2070	299	79	44.3845	861	310	310	416	68.2
153	24.942	9.8167	82.493	49.6732	31.1	49.673	11.9	24.9	25.55	25.55	24.32	2649	389	83	44.8661	1020	285	285	801	66.2
154	25.737	9.4917	81.1254	47.9642	31.8	47.964	11.7	25.67	26.35	26.35	25.18	3025	423	74	46.7397	1191	325	325	916	70.4
155	20.817	9.3167	66.0756	147.16	27.7	147.16	14.1	21.8	21	22.43	18.85	1768	259	40	51.8176	676	147	432	384	95.9
156	22.254	8.525	72.8632	120.236	28	120.24	11.7	22.03	21.23	23.53	20.65	2238	306	91	38.3747	847	313	499	553	80.3
157	17.783	11.433	78.3105	118.27	24.8	118.27	14.6	18.57	16.15	18.97	16.15	1567	333	4	98.6033	845	19	480	19	91.8
158	22.483	10.35	61.2426	224.827	30.5	224.83	16.9	23.93	20.1	24.77	19.35	1153	222	23	84.9957	612	78	310	80	66.7
159	20.937	9.2417	59.6237	213.596	28.4	213.6	15.5	22.2	20.42	23.2	17.97	1305	239	34	77.1917	646	108	354	118	71.6
160	20.413	10.442	60.7074	231.115	28.6	231.12	17.2	22.27	17.92	22.73	17.2	1542	266	50	66.7386	694	159	441	160	70.7
161	19.025	10.817	62.8876	221.949	27.2	221.95	17.2	20.52	16.62	21.23	15.92	1608	305	44	70.3565	741	139	429	146	74.6
162	16.042	9.15	64.8936	193.307	22.8	193.31	14.1	17.33	15.5	18	13.35	1513	276	43	66.2051	707	150	351	171	79.3
163	11.454	11.142	70.0734	174.466	19.1	174.47	15.9	12.35	9.917	13.42	9.1	1116	218	28	74.3436	550	93	284	93	70.8
164	17.229	10.225	64.7152	208.146	24.7	208.15	15.8	18.68	14.98	19.27	14.32	1529	284	43	71.1898	738	135	389	141	77.6
165	25.45	9.85	55.9659	230.346	34	230.35	17.6	26.88	24.95	27.88	22.28	2914	543	49	77.2742	1550	188	496	320	66.9
166	20.275	8.7833	53.2323	262.12	27.9	262.12	16.5	22.32	19.28	22.92	16.62	2397	481	70	68.7731	1124	225	779	275	76.7
167	26.05	6.1167	74.5935	67.0481	30.4	67.048	8.2	25.68	26.2	27	25.35	2210	330	11	64.4832	869	65	396	648	76.3
168	26.4	6.3333	78.1893	54.0202	30.7	54.02	8.1	26.02	26.38	27.15	25.8	2179	361	10	66.1822	950	55	328	486	70.7
169	24.075	8.5167	81.891	54.2511	29.3	54.251	10.4	24.17	24.35	24.77	23.42	2918	318	135	25.8217	924	478	605	701	94.1
170	18.758	9.1333	82.2823	60.8961	24.4	60.896	11.1	18.22	19.02	19.5	18.03	3664	463	112	33.3001	1239	496	637	856	96.6
171	14.971	9.3917	83.1121	59.2935	20.4	59.294	11.3	15.38	14.35	15.45	14.12	1183	186	23	58.3755	445	86	439	91	94.8
172	17.125	8.8167	83.9682	52.9794	22.2	52.979	10.5	17.22	16.67	17.53	16.38	1240	179	21	51.3479	476	106	360	114	93.4
173	27.029	10.008	82.0355	50.1116	32.9	50.112	12.2	26.37	27.37	27.52	26.32	2711	381	87	44.9117	1062	304	327	986	58.8

Appendix 4.

Correlations between the bioclimatic variables considering all the 173 qualitative/quantitative surveys in the Neotropical Region carried out up to 2017.

	BIO.1	BIO.2	BIO.3	BIO.4	BIO.5	BIO.6	BIO.7	BIO.8	BIO.9	BIO.10	BIO.11	BIO.12	BIO.13	BIO.14	BIO.15	BIO.16	BIO.17	BIO.18	BIO.19	cloud
BIO.1	1	-0.7	0.63	-0.69	0.91	-0.69	-0.78	0.95	0.98	0.94	0.98	0.35	0.64	-0.03	0.23	0.68	0.03	-0.49	0.73	0
BIO.2	-0.7	1	-0.4	0.5	-0.52	0.5	0.74	-0.63	-0.73	-0.67	-0.7	-0.24	-0.57	-0.43	0.17	-0.61	-0.48	0.11	-0.85	-0.21
BIO.3	0.63	-0.4	1	-0.99	0.28	-0.99	-0.91	0.39	0.72	0.33	0.77	0.7	0.85	-0.35	0.58	0.84	-0.27	-0.45	0.57	0.7
BIO.4	-0.69	0.5	-0.99	1	-0.35	0.98	0.95	-0.48	-0.78	-0.41	-0.82	-0.67	-0.89	0.34	-0.59	-0.89	0.26	0.41	-0.61	-0.67
BIO.5	0.91	-0.52	0.28	-0.35	1	-0.35	-0.44	0.97	0.83	0.98	0.81	0.08	0.33	0.04	0.08	0.38	0.06	-0.43	0.53	-0.4
BIO.6	-0.69	0.5	-0.99	0.98	-0.35	1	0.95	-0.48	-0.78	-0.41	-0.82	-0.67	-0.89	0.34	-0.59	-0.89	0.26	0.41	-0.61	-0.67
BIO.7	-0.78	0.74	-0.91	0.95	-0.44	0.95	1	-0.58	-0.86	-0.55	-0.88	-0.62	-0.88	0.09	-0.37	-0.89	0.01	0.37	-0.78	-0.61
BIO.8	0.95	-0.63	0.39	-0.48	0.97	-0.48	-0.58	1	0.88	0.98	0.88	0.15	0.48	0.01	0.15	0.53	0.04	-0.36	0.59	-0.23
BIO.9	0.98	-0.73	0.72	-0.78	0.83	-0.78	-0.86	0.88	1	0.89	0.99	0.45	0.7	-0.01	0.24	0.74	0.06	-0.54	0.8	0.13
BIO.10	0.94	-0.67	0.33	-0.41	0.98	-0.41	-0.55	0.98	0.89	1	0.86	0.13	0.4	0.15	0.01	0.45	0.18	-0.43	0.66	-0.3
BIO.11	0.98	-0.7	0.77	-0.82	0.81	-0.82	-0.88	0.88	0.99	0.86	1	0.46	0.75	-0.1	0.34	0.78	-0.04	-0.5	0.75	0.19
BIO.12	0.35	-0.24	0.7	-0.67	0.08	-0.67	-0.62	0.15	0.45	0.13	0.46	1	0.48	-0.14	0.29	0.48	-0.08	-0.46	0.45	0.62
BIO.13	0.64	-0.57	0.85	-0.89	0.33	-0.89	-0.88	0.48	0.7	0.4	0.75	0.48	1	-0.29	0.59	1	-0.22	-0.08	0.58	0.59
BIO.14	-0.03	-0.43	-0.35	0.34	0.04	0.34	0.09	0.01	-0.01	0.15	-0.1	-0.14	-0.29	1	-0.94	-0.26	1	0.12	0.48	-0.22
BIO.15	0.23	0.17	0.58	-0.59	0.08	-0.59	-0.37	0.15	0.24	0.01	0.34	0.29	0.59	-0.94	1	0.56	-0.91	-0.09	-0.22	0.39
BIO.16	0.68	-0.61	0.84	-0.89	0.38	-0.89	-0.89	0.53	0.74	0.45	0.78	0.48	1	-0.26	0.56	1	-0.19	-0.09	0.61	0.56
BIO.17	0.03	-0.48	-0.27	0.26	0.06	0.26	0.01	0.04	0.06	0.18	-0.04	-0.08	-0.22	1	-0.91	-0.19	1	0.08	0.55	-0.16
BIO.18	-0.49	0.11	-0.45	0.41	-0.43	0.41	0.37	-0.36	-0.54	-0.43	-0.5	-0.46	-0.08	0.12	-0.09	-0.09	0.08	1	-0.41	0
BIO.19	0.73	-0.85	0.57	-0.61	0.53	-0.61	-0.78	0.59	0.8	0.66	0.75	0.45	0.58	0.48	-0.22	0.61	0.55	-0.41	1	0.24
cloud	0	-0.21	0.7	-0.67	-0.4	-0.67	-0.61	-0.23	0.13	-0.3	0.19	0.62	0.59	-0.22	0.39	0.56	-0.16	0	0.24	1

Appendix 5.

Correlations between the bioclimatic variables considering the qualitative/quantitative surveys of the group 1, performed in Amazon, Andes, Caribe, Central America, and México.

	BIO.1	BIO.2	BIO.3	BIO.4	BIO.5	BIO.6	BIO.7	BIO.8	BIO.9	BIO.10	BIO.11	BIO.12	BIO.13	BIO.14	BIO.15	BIO.16	BIO.17	BIO.18	BIO.19	cloud
BIO.1	1	-0.87	0.42	-0.61	0.98	-0.61	-0.76	0.99	0.99	0.99	0.99	-0.22	0.62	0.71	-0.69	0.7	0.71	-0.25	0.89	-0.71
BIO.2	-0.87	1	-0.55	0.73	-0.78	0.73	0.9	-0.83	-0.9	-0.84	-0.9	0.45	-0.77	-0.79	0.76	-0.83	-0.81	-0.08	-0.92	0.43
BIO.3	0.42	-0.55	1	-0.97	0.23	-0.97	-0.86	0.3	0.5	0.31	0.54	-0.09	0.4	0.62	-0.77	0.46	0.67	0.11	0.7	0.21
BIO.4	-0.61	0.73	-0.97	1	-0.44	1	0.95	-0.51	-0.69	-0.51	-0.72	0.17	-0.53	-0.75	0.87	-0.6	-0.8	-0.09	-0.84	-0.03
BIO.5	0.98	-0.78	0.23	-0.44	1	-0.44	-0.61	0.99	0.95	0.99	0.94	-0.16	0.54	0.61	-0.56	0.62	0.59	-0.34	0.78	-0.81
BIO.6	-0.61	0.73	-0.97	1	-0.44	1	0.95	-0.51	-0.69	-0.51	-0.72	0.17	-0.53	-0.75	0.87	-0.6	-0.8	-0.09	-0.84	-0.03
BIO.7	-0.76	0.9	-0.86	0.95	-0.61	0.95	1	-0.68	-0.82	-0.68	-0.84	0.33	-0.68	-0.81	0.87	-0.75	-0.85	-0.1	-0.93	0.16
BIO.8	0.99	-0.83	0.3	-0.51	0.99	-0.51	-0.68	1	0.97	1	0.97	-0.21	0.58	0.66	-0.62	0.66	0.65	-0.28	0.83	-0.77
BIO.9	0.99	-0.9	0.5	-0.69	0.95	-0.69	-0.82	0.97	1	0.98	1	-0.23	0.65	0.75	-0.74	0.73	0.76	-0.22	0.92	-0.65
BIO.10	0.99	-0.84	0.31	-0.51	0.99	-0.51	-0.68	1	0.98	1	0.97	-0.21	0.59	0.66	-0.61	0.67	0.65	-0.29	0.83	-0.77
BIO.11	0.99	-0.9	0.54	-0.72	0.94	-0.72	-0.84	0.97	1	0.97	1	-0.22	0.64	0.76	-0.76	0.72	0.77	-0.21	0.93	-0.62
BIO.12	-0.22	0.45	-0.09	0.17	-0.16	0.17	0.33	-0.21	-0.23	-0.21	-0.22	1	-0.58	-0.19	0.1	-0.56	-0.2	-0.41	-0.25	0.17
BIO.13	0.62	-0.77	0.4	-0.53	0.54	-0.53	-0.68	0.58	0.65	0.59	0.64	-0.58	1	0.6	-0.49	0.99	0.62	0.24	0.77	-0.43
BIO.14	0.71	-0.79	0.62	-0.75	0.61	-0.75	-0.81	0.66	0.75	0.66	0.76	-0.19	0.6	1	-0.96	0.67	1	0.34	0.85	-0.17
BIO.15	-0.69	0.76	-0.77	0.87	-0.56	0.87	0.87	-0.62	-0.74	-0.61	-0.76	0.1	-0.49	-0.96	1	-0.57	-0.97	-0.26	-0.85	0.04
BIO.16	0.7	-0.83	0.46	-0.6	0.62	-0.6	-0.75	0.66	0.73	0.67	0.72	-0.56	0.99	0.67	-0.57	1	0.69	0.2	0.84	-0.46
BIO.17	0.71	-0.81	0.67	-0.8	0.59	-0.8	-0.85	0.65	0.76	0.65	0.77	-0.2	0.62	1	-0.97	0.69	1	0.34	0.87	-0.13
BIO.18	-0.25	-0.08	0.11	-0.09	-0.34	-0.09	-0.1	-0.28	-0.22	-0.29	-0.21	-0.41	0.24	0.34	-0.26	0.2	0.34	1	-0.03	0.51
BIO.19	0.89	-0.92	0.7	-0.84	0.78	-0.84	-0.93	0.83	0.92	0.83	0.93	-0.25	0.77	0.85	-0.85	0.84	0.87	-0.03	1	-0.44
cloud	-0.71	0.43	0.21	-0.03	-0.81	-0.03	0.16	-0.77	-0.65	-0.77	-0.62	0.17	-0.43	-0.17	0.04	-0.46	-0.13	0.51	-0.44	1

Appendix 6.

Correlations between the bioclimatic variables considering the qualitative/quantitative surveys of the group 2 and 3, performed in the southeastern South America, mainly in Brazil.

	BIO.1	BIO.2	BIO.3	BIO.4	BIO.5	BIO.6	BIO.7	BIO.8	BIO.9	BIO.10	BIO.11	BIO.12	BIO.13	BIO.14	BIO.15	BIO.16	BIO.17	BIO.18	BIO.19	cloud
BIO.1	1	0.02	0.41	-0.59	0.98	-0.59	-0.5	0.93	0.94	0.95	0.98	-0.57	0.17	-0.63	0.55	0.2	-0.63	0.05	-0.6	-0.71
BIO.2	0.02	1	0.79	-0.38	0.17	-0.38	0.66	0.03	-0.12	-0.16	0.07	-0.66	0.06	-0.54	0.45	0.01	-0.53	-0.16	-0.51	-0.24
BIO.3	0.41	0.79	1	-0.86	0.47	-0.86	0.05	0.46	0.19	0.15	0.53	-0.71	0.44	-0.9	0.85	0.4	-0.9	0.18	-0.89	-0.2
BIO.4	-0.59	-0.38	-0.86	1	-0.56	1	0.43	-0.68	-0.34	-0.33	-0.72	0.47	-0.73	0.95	-0.97	-0.72	0.95	-0.54	0.96	0.06
BIO.5	0.98	0.17	0.47	-0.56	1	-0.56	-0.31	0.91	0.92	0.93	0.96	-0.67	0.11	-0.65	0.55	0.13	-0.64	-0.03	-0.62	-0.79
BIO.6	-0.59	-0.38	-0.86	1	-0.56	1	0.43	-0.68	-0.34	-0.33	-0.72	0.47	-0.73	0.95	-0.97	-0.72	0.95	-0.54	0.96	0.06
BIO.7	-0.5	0.66	0.05	0.43	-0.31	0.43	1	-0.53	-0.44	-0.46	-0.54	-0.2	-0.45	0.23	-0.31	-0.49	0.24	-0.49	0.26	-0.13
BIO.8	0.93	0.03	0.46	-0.68	0.91	-0.68	-0.53	1	0.77	0.85	0.95	-0.49	0.36	-0.7	0.66	0.38	-0.7	0.26	-0.7	-0.51
BIO.9	0.94	-0.12	0.19	-0.34	0.92	-0.34	-0.44	0.77	1	0.97	0.88	-0.52	-0.1	-0.39	0.29	-0.06	-0.38	-0.18	-0.35	-0.82
BIO.10	0.95	-0.16	0.15	-0.33	0.93	-0.33	-0.46	0.85	0.97	1	0.89	-0.47	-0.06	-0.38	0.29	-0.02	-0.37	-0.11	-0.35	-0.78
BIO.11	0.98	0.07	0.53	-0.72	0.96	-0.72	-0.54	0.95	0.88	0.89	1	-0.58	0.31	-0.74	0.68	0.33	-0.74	0.17	-0.72	-0.61
BIO.12	-0.57	-0.66	-0.71	0.47	-0.67	0.47	-0.2	-0.49	-0.52	-0.47	-0.58	1	0.19	0.64	-0.46	0.22	0.63	0.44	0.58	0.66
BIO.13	0.17	0.06	0.44	-0.73	0.11	-0.73	-0.45	0.36	-0.1	-0.06	0.31	0.19	1	-0.63	0.78	1	-0.64	0.96	-0.68	0.41
BIO.14	-0.63	-0.54	-0.9	0.95	-0.65	0.95	0.23	-0.7	-0.39	-0.38	-0.74	0.64	-0.63	1	-0.98	-0.61	1	-0.4	1	0.24
BIO.15	0.55	0.45	0.85	-0.97	0.55	-0.97	-0.31	0.66	0.29	0.29	0.68	-0.46	0.78	-0.98	1	0.77	-0.98	0.59	-0.99	-0.08
BIO.16	0.2	0.01	0.4	-0.72	0.13	-0.72	-0.49	0.38	-0.06	-0.02	0.33	0.22	1	-0.61	0.77	1	-0.63	0.97	-0.67	0.4
BIO.17	-0.63	-0.53	-0.9	0.95	-0.64	0.95	0.24	-0.7	-0.38	-0.37	-0.74	0.63	-0.64	1	-0.98	-0.63	1	-0.42	1	0.22
BIO.18	0.05	-0.16	0.18	-0.54	-0.03	-0.54	-0.49	0.26	-0.18	-0.11	0.17	0.44	0.96	-0.4	0.59	0.97	-0.42	1	-0.47	0.52
BIO.19	-0.6	-0.51	-0.89	0.96	-0.62	0.96	0.26	-0.7	-0.35	-0.35	-0.72	0.58	-0.68	1	-0.99	-0.67	1	-0.47	1	0.17
cloud	-0.71	-0.24	-0.2	0.06	-0.79	0.06	-0.13	-0.51	-0.82	-0.78	-0.61	0.66	0.41	0.24	-0.08	0.4	0.22	0.52	0.17	1