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Vascular epiphytic flora of a high montane environment of Brazilian Atlantic Forest: composition and floristic relationships with other ombrophilous forests

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ABSTRACT

Only a few studies regarding vascular epiphytes have been conducted in mixed ombrophilous forests (MOF) in Serra da Mantiqueira, a mountainous environment in the Brazilian Atlantic Forest, where the relationships of epiphytic flora with other physiognomies are unknown. This study aimed to survey the epiphytes of a MOF remnant located in Serra da Mantiqueira, and to analyze the floristic relationships with ombrophilous forests of the Southern and Southeastern regions of Brazil. The checklist was compared with 51 other areas composed of ombrophilous forests and/or ecotones with other physiognomies using UPGMA (with Sørensen index), and canonical correspondence analysis (CCA). We recorded 138 species, and Orchidaceae and Polypodiaceae were the richest families (51 and 23 species, respectively). The UPGMA showed the importance of physiognomy and elevation in the floristic relationships, and CCA reinforced the influence of elevation, in addition to the shortest distance to the ocean and minimum annual temperature; however, in this analysis, the physiognomies showed little influence on the relationships. The epiphytic flora of MOF of Southern and Southeastern regions of Brazil has different relationships compared with the data available for shrubs and trees, suggesting a greater importance of phorophytic species than geographical distance and, to some extent, environmental variables.

Keywords: biodiversity, conservation, endangered species, environmental variables, epiphytism, mixed ombrophilous forest, Serra da Mantiqueira, similarity

Introduction

Brazilian Atlantic Forest exhibits high diversity, harbouring approximately 16000 plant species, totalling about 46% of the country flora, of which approximately 7500 are endemic (Stehmann *et al*. 2009; Forzza *et al*. 2012). These numbers, together with intense anthropogenic degradation, earned it the status of the world hotspot of biodiversity (Mittermeier *et al*. 2004). However, there are great gaps in knowledge about the native flora, especially in places of difficult access, such as the mountainous environments (Martinelli 2007; Rapini *et al*. 2009), as well as for some functional groups, such as epiphytes (Kersten 2010).

Mountainous regions are environments with high indices of richness and endemism, in addition to representing islands of vegetation with important forest remnants (Martinelli 2007), maintained due to the barrier represented by the relief, which avoids direct anthropogenic action.

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The Serra da Mantiqueira covers the borders of Minas Gerais, São Paulo, Rio de Janeiro, and Espírito Santo states, forming together with the Serra do Mar a mountainous range consisting primarily of Atlantic Forest (Rizzini 1997). It is considered a priority for conservation and study due to its biotic and abiotic features (Drummond *et al.* 2005; Lino *et al.* 2007; Saout *et al.* 2013).

Serra do Papagaio is one of the natural areas that must be highlighted in the Serra da Mantiqueira in Minas Gerais. It is protected by a state park (Parque Estadual da Serra do Papagaio [PESP], composed of approximately 23000 ha, and is geographically connected with the Parque Nacional do Itatiaia, representing a continuous montane environment. Despite the importance of this region, only a few floristic/ecologic studies have been conducted to date (Scolforo *et al.* 2008; Pereira *et al.* 2013; Santiago 2013; Furtado & Menini Neto 2015a; Santana 2016).

The PESP harbours one of the rare fragments of mixed ombrophilous forest (MOF) (or araucaria forest) of Minas Gerais (Ab'Saber 2003; Backes 2009), interspersed with "campo de altitude" and dense ombrophilous forest (DOF). This is the only protected MOF fragment by a conservation unity of integral protection in Minas Gerais (Furtado & Menini Neto 2015a). It is one of the most threatened forest ecosystems of the country. It is estimated that only about 3% of the original cover of this physiognomy remains, including exploited and regeneration areas (Bauermann & Behling 2009). This forest formation reaches the highest elevation in the Serra da Mantiqueira (Backes 2009), and, in PESP, this elevation can reach 2000 m a.s.l. (SG Furtado & L Menini Neto unpubl. res.).

Several studies were carried out in Neotropical Region showing the astonishing diversity of vascular epiphytes (*e.g.***,** Gentry & Dodson 1987; Catchpole 2004; Benavides *et al.* 2005; Blum *et al.* 2011; Alves & Menini Neto 2014; Leitman *et al.* 2014), as well as the importance of elevation gradient on this diversity, especially in the Andes and Central America (*e.g.*, Krömer *et al.* 2005; Cardelús *et al.* 2006; Watkins Jr. *et al.* 2006; Furtado 2016). However, despite the increasing number of studies on flora and ecology of epiphytes, especially in recent years, there is still a shortage, when considering their ecological importance in the tropical forests (Nadkarni 1984; Nieder *et al.* 2000). Although Brazil has a considerable richness of epiphytes, mainly due to the forest physiognomies of the BAF (Freitas *et al.* 2016; Menini Neto *et al.* 2016), studies of the epiphytic synusia only have been intensive during the past 30 years, mainly concentrating in the Southern Region of the country (Kersten 2010). In order to contribute to the reduction of knowledge gaps regarding this functional group in the Atlantic Forest, the goals of this study were: 1) to evaluate the richness and composition of the vascular epiphytes in the physiognomy of MOF and in the ecotone with DOF in the PESP; 2) to analyse the floristic relationships, and respective influence of environmental variables, between areas of the Southeastern and Southern regions of Brazil with similar vegetation; 3) to test whether the pattern of floristic relationships of trees and shrubs found in MOF of Serra da Mantiqueira and those of Southern Region is corroborated by epiphytic flora.

Materials and methods

Study area

The PESP is located in the southern region of Minas Gerais in Serra da Mantiqueira (Fig. 1), comprising 22917 ha, between the municipalities of Aiuruoca, Alagoa, Baependi, Itamonte, and Pouso Alto (22.1420S, 44.7328W). The elevations are mainly above 1800 m a.s.l., and the climate is classified as Cwb (according to the Köppen classification), a temperate, highland, tropical climate with dry winters (Silva *et al.* 2008).

The park harbours important remnants of Atlantic Forest, composed of a mosaic of high montane DOF, high montane MOF, and "campo de altitude" (which is a vegetation predominantly composed of open fields with grasses, sometimes with rocky outcrops, also named by Safford (1999) as "Brazilian páramos"). In the studied area, the MOF occurs mainly as fragments of alluvial forest, predominantly on humic and histic cambisols, at elevations ranging from 1600-1700 m a.s.l., along the Santo Agostinho brook (Silva *et al.* 2008). It forms continuous vegetation that is composed of three strata: a canopy of *Araucaria angustifolia* (Bertol.) Kuntze (Araucariaceae) (about 30 m high); a second stratum composed predominantly of *Podocarpus lambertii* Klotzsch ex Endl. (Podocarpaceae) (10-15 m high); and a third stratum (up to approximately 8–10 m high) composed of shrubs and treelets of the families Lauraceae, Myrtaceae, Primulaceae, and Winteraceae, among others. This physiognomy exhibits transition areas, with the DOF at 1900-2000 m a.s.l., with few individuals of *A. angustifolia* and near complete absence of *P. lambertii*. *Podocarpus lambertii* also occurs in patches interspersed within the "campo de altitude", adjacent to the alluvial forest (Furtado & Menini Neto 2015a).

Floristic survey

The floristic survey was conducted through monthly expeditions between April 2012 and September 2013 using the walking method ("método de caminhamento") (Filgueiras *et al.* 1994) in order to cover the largest possible area of MOF and transition with DOF in each expedition. The fertile specimens were collected, herborised, and deposited in the Herbarium CESJ (acronym according to Thiers [2015]). The plants were photographed in the field and published as a rapid colour guide (Furtado & Menini Neto 2013). The species were classified according to their relationships with

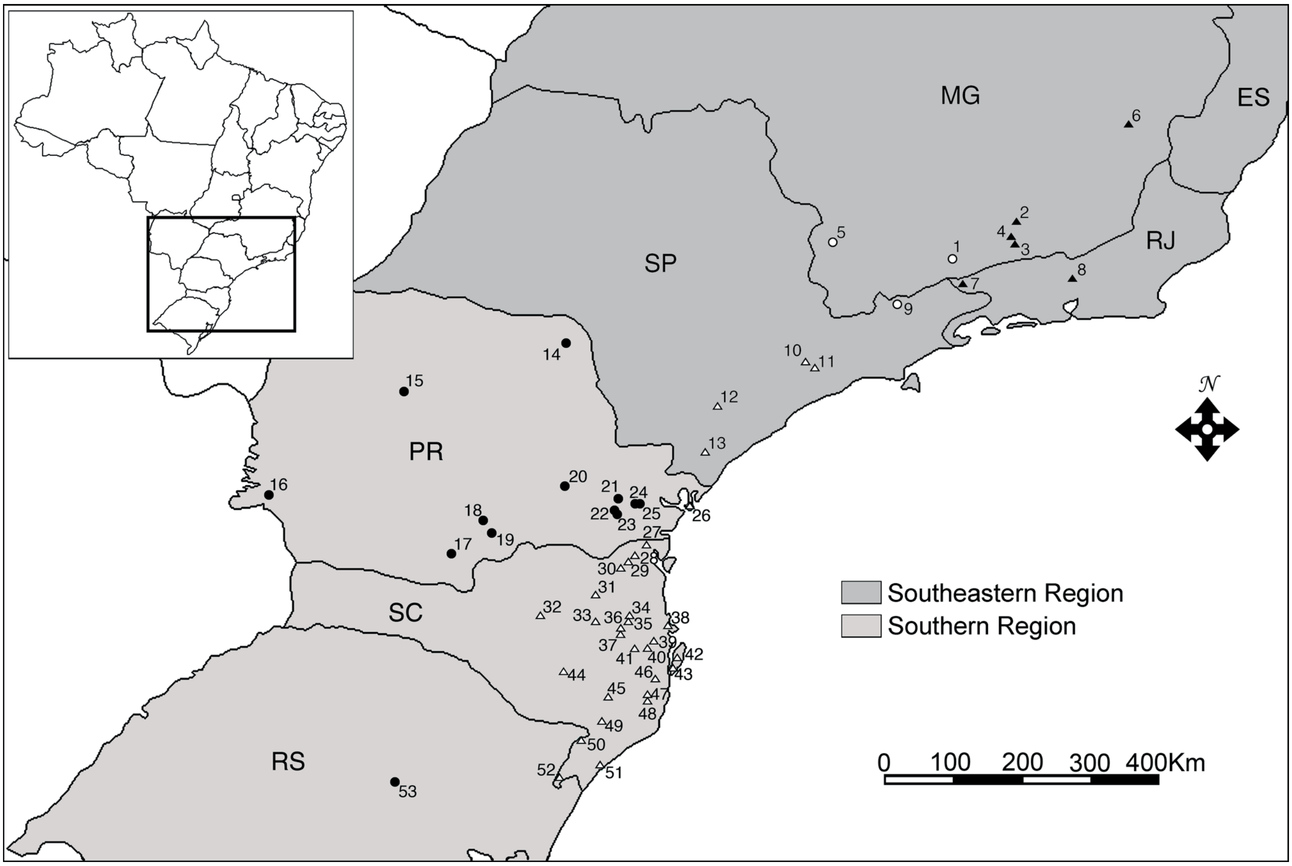

Figure 1. Figure 1. Location of Parque Estadual da Serra do Papagaio (1) and other 52 areas used in multivariate analyses. The numbers of localities are presented in Tab. S1 in supplementary material. ● areas composed by mixed ombrophilous forest from Planalto Meridional (Southern Region), ○ areas composed by mixed ombrophilous forest from Serra da Mantiqueira (Southeastern Region), ▲ areas composed by dense ombrophilous forest from Serra do Mar or Serra da Mantiqueira (Southeastern Region), Δ areas composed by dense ombrophilous forest from Serra do Mar (Southern Region).

phorophytes (Benzing 1990) and identified according to the specialised bibliography, consultation with the herbarium material collection, and specialists.

Evolutionary lineages are according to the APG IV (2016) for angiosperms (eudicotyledons, magnoliids, and monocotyledons) and Christenhusz *et al.* (2011) for the ferns (lycophytes and monilophytes). Orchidaceae genera *Maxillaria*, *Oncidium*, and *Pleurothallis* were considered in a broad sense due to the lack of consensus regarding their delimitations and due to several recent proposals of segregation in several smaller genera.

Multivariate analyses

The composition of vascular epiphytes of the PESP was compared to areas with available lists of vascular epiphytes and some areas with extensive vascular flora surveys that discriminated each life form. We used 52 areas of MOF or DOF, and, in some cases, ecotones with other physiognomies occurring in Southern and Southeastern regions of Brazil, in addition to areas of the Serra da Mantiqueira with elevations similar to the PESP (Tab. S1 in supplementary material). The data were obtained from published studies and the database of herbaria collections available at the site Specieslink of "Centro de Referência em Informação Ambiental" (CRIA) (http://www.splink.org.br). All unidentified species were excluded, resulting in a matrix of presence (1) and absence (0), with 910 species.

The similarity between the aforementioned areas was evaluated through cluster analysis using the unweighted pair-group method with arithmetic mean (UPGMA) and similarity index of Sørensen. The cophenetic coefficient was calculated to test the fit between the matrix and resulting dendrogram. A Mantel test was conducted to evaluate the correlation between the geographic distance and calculated similarity among the areas. These analyses were conducted using the software PAST v. 3.01 (Hammer *et al.* 2001).

In order to evaluate the correlation among the environmental variables and composition of vascular epiphytes, a canonical correspondence analysis (CCA) was conducted (ter Braak 1986; Palmer 1993). Previous analyses were performed with a set of 19 climatic variables (annual mean temperature, mean monthly temperature range, isothermality, temperature seasonality, max temperature of warmest month, min temperature of coldest month, temperature annual range, mean temperature of wettest quarter, mean temperature of driest quarter, mean temperature of warmest quarter, mean temperature of coldest quarter, annual precipitation, precipitation of wettest month, precipitation of driest month, precipitation seasonality, precipitation of wettest quarter, precipitation of driest quarter, precipitation of warmest quarter, precipitation of coldest quarter). The variables were presented by Hijmans *et al.* (2005), and are available in the site WorldClim (www.worldclim.org). These variables were complemented with other considered important to the epiphytic flora (Benzing 1990): minimal and maximal elevations and minimal and maximal annual means of temperature obtained in the respective articles, and the shortest distance to the Atlantic Ocean, which was calculated for each area using the software DIVA-GIS v. 7.5 (Hijmans *et al.* 2001), which is used to represent a seasonality gradient.

After this preliminary analysis, the redundant variables, with high values of inflation, were discarded (ter Braak 1986). Three variables resulted as the most representative and correlated with the two first ordination axes: shortest distance to the ocean, elevation, and minimal annual temperature. The permutation test of Monte Carlo was conducted a posteriori in order to evaluate the significance of the canonical correlations at a significance level of 95% ($p < 0.05$) (ter Braak 1986; Palmer 1993). These analyses were conducted with the software CANOCO v. 4.5 (ter Braak & Smilauer 2002).

Results

Floristic survey

We recorded 25 families, 66 genera, and 138 species in the studied area. The ferns were represented by 43 species (31.16% of total) and the angiosperms by 95 species (68.84%). Orchidaceae was the richest family (51 species, 37%), followed by Polypodiaceae (23 species, 17%), Bromeliaceae, and Piperaceae (10 species, 7% each). *Pleurothallis s.l.* was the richest genus with 11 species, followed by *Peperomia*, with 10 species (Tab. 1). The majority of species occurred in the MOF (122 species), of which 62 were exclusive, and 60 were shared with the ecotone with the DOF, with 16 being exclusive to the ecotone.

The richest evolutionary lineages were the monocotyledons (63 species) and the monilophytes (39 species), being Orchidaceae and Polypodiaceae the richest families, respectively. Characteristic holoepiphytes were the most well represented ecological category (107 species), but the number of accidental holoepiphytes families and species, 10 (40% of total) and 19 (14% of total), respectively,

Table 1. List of vascular epiphytes recorded in the Parque Estadual da Serra do Papagaio, Minas Gerais, Brazil.

Families and species	EC	Habitat	Voucher
Ferns			
Licophytes – Vinícius A.O. Dittrich (CESJ)			
Lycopodiaceae (1/4)			
Phlegmariurus acerosus (Sw.) B.Øllg.	CHL	F	Furtado 74
Phlegmariurus biformis (Hook.) B.Øllg.	CHL	F	Furtado 75
Phlegmariurus fontinaloides (Spring) B.Øllg.	CHL	F/E	Furtado 114
Phlegmariurus quadrifariatus (Bory) B.Øllg.	CHL	F	Furtado 66
Monilophytes – Vinícius A.O. Dittrich, Filipe S. Souza (CESJ), A. Salino (BHCB)			
Anemiaceae (1/1)			
Anemia phyllitidis (L.) Sw.	AHL	F	Furtado 88
Aspleniaceae (1/5)			
Asplenium aff. *inaequilaterale* Willd.	AHL	F	Furtado 221
Asplenium auriculatum Sw.	CHL	F/E	Furtado 46
Asplenium auritum Sw.	CHL	F/E	Furtado 37
Asplenium incurvatum Fee	CHL	F/E	Furtado 93
Asplenium serra Langsd. & Fisch.	CHL	E	Souza 960
Dryopteridaceae (2/3)			
Elaphoglossum gayanum (Fée) T.Moore	CHL	F/E	Furtado 183
Elaphoglossum vagans (Mett.) Hieron.	FHL	F/E	Furtado 129
Rumohra adiantiformis (G.Forst.) Ching	CHL	F/E	Furtado 113
Hymenophylaceae (3/4)			
Hymenophyllum polyanthos (Sw.) Sw.	CHL	F/E	Furtado 64
Polyphlebium angustatum (Carmich.) Ebihara & Dubuisson	CHL	F	Furtado 97
Trichomanes anadromum Rosenst	CHL	F	Furtado 276
Trichomanes polypodioides Raddi	CHL	F	Furtado 90
Ophioglossaceae (1/1)			
Ophioglossum palmatum L.	CHL	E	Furtado 267

Table 1. Cont.

Families and species	EC	Habitat	Voucher
Polypodiaceae (12/23)			
Campyloneurum aglaolepis (Alston) de la Sota	CHL	F	Furtado 94
Campyloneurum angustifolium (Sw.) Fée	CHL	F/E	Menini Neto 965
Campyloneurum nitidum (Kaulf.) C.Presl	CHL	F	Furtado 236
Campyloneurum sp.	CHL	F/E	Furtado 216
Ceradenia albidula (Baker) L.E.Bishop	CHL	E	Furtado 132
Cochlidium punctatum (Raddi) L.E.Bishop	CHL	F/E	Furtado 137
Lellingeria aff. pumila Labiak	CHL	E	Furtado 198
Lellingeria apiculata (Kunze ex Klotzsch) A.R.Sm. & R.C.Moran	CHL	F/E	Furtado 110
Leucotrichum organense (Gardner) Labiak	CHL	F/E	Furtado 5
Leucotrichum sp.	CHL	F	Furtado 44
Melpomene flabelliformis (Poir.) A.R.Sm. & R.C.Moran	CHL	F/E	Furtado 198
Melpomene pilosissima (M.Martens & Galeotti) A.R.Sm. & R.C.Moran	CHL	F/E	Furtado 127
Microgramma percussa (Cav.) de la Sota	CHL	F	Salimena 2836
Microgramma squamulosa (Kaulf.) de la Sota	CHL	F/E	Furtado 8
Micropolypodium achilleifolium Labiak & F.B.Matos	CHL	F	Furtado 150
Pecluma pectinatiformis (Lindm.) M.G.Price	CHL	F/E	Souza 955
Pecluma sp.	CHL	F	Furtado 7
Pleopeltis hirsutissima (Raddi) de la Sota	CHL	F/E	Furtado 32
Pleopeltis macrocarpa (Bory ex Willd.) Kaulf.	CHL	F/E	Furtado 9
Pleopeltis pleopeltidis (Fée) de la Sota	CHL	F/E	Furtado 116
Serpocaulon catharinae (Langsd. & Fisch.) A.R.Sm.	CHL	F/E	Furtado 50
Zygophlebia longipilosa (C.Chr.) L.E.Bishop	CHL	F	Souza 1006
Polypodiaceae indet.	CHL	F	Furtado 45
Pteridaceae (1/2)			
Vittaria graminifolia Kaulf.	CHL	F/E	Souza 979
Vittaria lineata (L.) SM	CHL	F/E	Furtado 136
Angiosperms			
Magnoliids			
Piperaceae (1/10) – Daniele Monteiro (RB)			
Peperomia campinasana C.DC.	CHL	F	Furtado 73
Peperomia catharinae Miq.	CHL	F	Furtado 106
Peperomia cf. glabella (Sw.) A.Dietr.	CHL	F	Furtado 202
Peperomia hilariana Miq.	FHL	F/E	Menini Neto 814
Peperomia hispidula (Sw.) A. Dietr.	CHL	F	Furtado 72
Peperomia mandioccana Miq.	CHL	F/E	Furtado 99
Peperomia subternifolia Yunck.	CHL	F/E	Furtado 98
Peperomia tetraphylla (G.Forst.) Hook. & Arn.	CHL	F/E	Furtado 195
Peperomia trineura Miq.	CHL	F/E	Menini Neto 841
Peperomia trineuroides Dahlst.	CHL	F/E	Furtado 172
Monocotyledons			
Araceae (1/1)			
Philodendron sp.	HEM	E	Nardy 2
Bromeliaceae (5/10) – Rafaela C. Forzza (RB)			
Aechmea aiuruocensis Leme	FHL	E	Furtado 259
Aechmea distichantha Lem.	FHL	F	Furtado 234
Billbergia distachia (Vell.) Mez	CHL	F/E	Furtado 91
Nidularium marigoi Leme	FHL	F/E	Furtado 228
Tillandsia recurvata (L.) L.	CHL	F	Furtado 222
Tillandsia stricta Sol.	CHL	F/E	Furtado 100
Tillandsia tenuifolia L.	CHL	F	Furtado 67
Vriesea bituminosa Wawra	FHL	F/E	Furtado 250
Vriesea gigantea Gaudich.	FHL	F/E	Furtado 146
Vriesea sceptrum Mez	FHL	F/E	Menini Neto 792

Table 1. Cont.

Families and species	EC	Habitat	Voucher
Orchidaceae (18/51) – Luiz Menini Neto, Samyra G. Furtado, Camila Nardy (CESJ)			
Bifrenaria stefanae V.P.Castro	CHL	E	Furtado 124
Bulbophyllum granulosum Barb.Rodr.	CHL	F	Furtado 207
Bulbophyllum regnellii Rchb.f.	CHL	F	Furtado 242
Capanemia adelaidae Brade	CHL	F	Furtado 53
Cryptophoranthus jordanensis Brade	CHL	E	Furtado 274
Dryadella lilliputiana (Cogn.) Luer	CHL	F/E	Furtado141
Encyclia patens Hook.	CHL	F	Furtado 275
Epidendrum chlorinum Barb.Rodr.	CHL	F/E	Furtado 214
Epidendrum mantiqueiranum Porto & Brade	CHL	F/E	Furtado 85
Gomesa gomezoides (Barb.Rodr.) Pabst	CHL	F/E	Furtado 210
Grobya amherstiae Lindl.	CHL	E	Furtado 255
Hadrolaelia coccinea (Lindl.) Chiron & V.P.Castro	CHL	F/E	Furtado 79
Hadrolaelia mantiqueirae (Fowlie) Fowlie	CHL	F/E	Furtado 80
Hadrolaelia pygmaea (Pabst) Chiron & V.P.Castro	CHL	F	Furtado 208
Hapalorchis lineatus (Lindl.) Schltr.	AHL	E	Furtado 252
Hapalorchis micranthus (Barb.Rodr.) Hoehne	AHL	F/E	Furtado 69
Lankesterella gnoma (Kraenzl.) Hoehne	CHL	F/E	Furtado 169
Loefgrenianthus blanche-amesii (Loefgr.) Hoehne	CHL	F/E	Furtado 176
Maxillaria neuwiedii Rchb.f.	CHL	F	Menini Neto 1108
Maxillaria notylioglossa Rchb.f.	CHL	E	Furtado 243
Maxillaria paranaensis Barb.Rodr.	CHL	F	Furtado 36
Maxillaria picta Hook.	CHL	F/E	Furtado174
Octomeria crassifolia Lindl.	CHL	F/E	Furtado 35
Octomeria geraensis Barb.Rodr.	CHL	F/E	Furtado 277
Octomeria ochroleuca Barb.Rodr.	CHL	F	Furtado 25
Octomeria wawrae Rchb.f.	CHL	F	Furtado 92
Octomeria sp1	CHL	F	Furtado167
Octomeria sp2	CHL	F	Furtado168
Octomeria sp3	CHL	F	Furtado 213
Oncidium cogniauxianum Schltr.	CHL	F	Furtado 203
Oncidium divaricatum Lindl.	CHL	F	Furtado 220
Oncidium forbesii Hook.	CHL	E	Menini Neto 776
Oncidium gardneri Lindl.	CHL	F/E	Furtado 215
Oncidium hookeri Rolfe	CHL	F/E	Furtado 241
Oncidium longicornu Mutel	CHL	F/E	Furtado 162
Phymatidium mellobarretoi Hoehne & Williams	CHL	F/E	Furtado 26
Pleurothallis adenochila Loefgr.	CHL	E	Furtado 119
Pleurothallis bocainensis Porto & Brade	CHL	F/E	Furtado 68
Pleurothallis cf. corticicola Schltr. ex Hoehne	CHL	F	Furtado 251
Pleurothallis grobyi Bateman ex Lindl.	CHL	F/E	Furtado 117
Pleurothallis linearifolia Cogn.	CHL	F	Furtado 163
Pleurothallis pleurothalloides (Cogn.) Handro	CHL	F	Furtado 1
Pleurothallis pterophora Cogn.	CHL	E	Furtado 226
Pleurothallis radialis Porto & Brade	CHL	E	Furtado 253
Pleurothallis rostellata Barb.Rodr.	CHL	F	Furtado 161
Pleurothallis rubens Lindl.	CHL	F/E	Furtado 87
Pleurothallis uniflora Lindl.	CHL	F	Menini Neto 1068
Stelis intermedia Poepp. & Endl.	CHL	F	Menini Neto 1059
Stelis papaquerensis Rchb.f.	CHL	F/E	Furtado 186
Stelis sp1	CHL	F/E	Furtado 196
Stelis sp2	CHL	F	Furtado 273
Eudicotyledons			
Araliaceae (1/1)			
Hydrocotyle cf. *bonariensis* Lam.	AHL	F	Furtado 22

Table 1. Cont.

Families and species	EC	Habitat	Voucher
Asteraceae (2/6)			
Ageratum fastigiatum (Gardner) R.M.King & H.Rob.	AHL	F	Furtado 247
Baccharis crispa Spreng.	AHL	F	Furtado 237
Asteraceae sp1	AHL	F	Furtado 268
Asteraceae sp2	AHL	F	Furtado 269
Asteraceae sp3	AHL	F	Furtado 270
Asteraceae sp4	AHL	F	Furtado 271
Cactaceae (1/2) – Diego R. Gonzaga (CESJ)			
Rhipsalis floccosa Salm-Dyck ex Pfeiff.	CHL	F/E	Furtado 107
Rhipsalis pulchra Loefgr.	CHL	F/E	Furtado 139
Caryophyllaceae (1/1)			
Arenaria lanuginosa (Michx.) Rohrb.	AHL	F	Furtado 23
Ericaceae (1/1) – Andressa Cabral (CESJ)			
Agarista oleifolia (Cham.) G.Don	AHL	F	Santiago 604
Gesneriaceae (2/3) – Luciana C. Pereira (CESJ)			
Nematanthus fornix (Vell.) Chautems	FHL	E	Furtado 160
Sinningia cooperi (Paxton) Wiehler	CHL	F	Furtado 49
Sinningia douglasii (Lindl.) Chautems	CHL	F	Furtado 164
Melastomataceae (3/3) – Luciana L. Justino (CESJ)			
Leandra carassana (DC.) Cogn.	AHL	F	Furtado 248
Miconia hyemalis A.St.-Hil. & Naudin	AHL	F	Furtado 246
Pleiochiton blepharodes (DC.) Reginato *et al.*	CHL	F	Furtado 201
Onagraceae (1/1)			
Fuchsia regia (Vell.) Munz	FHL	F	Furtado 165
Plantaginaceae (1/1)			
Plantago sp.	AHL	F	Furtado 272
Poaceae (1/1)			
Chusquea sp.	AHL	F/E	Furtado 254
Polygalaceae (1/1)			
Polygala lancifolia A.St.-Hil. & Moq.	AHL	F	Furtado 65
Ranunculaceae (1/1)			
Anemone sellowii Pritz.	AHL	F	Furtado 89
Solanaceae (1/1)			
Dyssochroma viridiflorum (Sims) Miers	HEM	F/E	Furtado 244

Numbers between parentheses after the families names represent the number of genera and species, respectively. Names after families represent the specialists that collaborate in the taxa identification. EC: Ecological categories – HEM: hemiepiphyte; AHL: accidental holoepiphyte; CHL: characteristic holoepiphyte; FHL facultative holoepiphyte. Habitat – F: Mixed Ombrophilous Forest; E: ecotone.

must be highlighted, with Asteraceae being the richest family with six species. Also, Melastomataceae must be noted, exhibiting one characteristic holoepiphyte and two accidental holoepiphytes species (Tab. 2).

Multivariate analyses

The cluster analysis resulted in the dendrogram presented in the Fig. 2, which obtained a cophenetic coefficient of 0.86, showing little distortion between the matrix and graphic. The Mantel test resulted in a positive correlation between the geographic distance and similarity matrix (r = 0.55, p = 0.0001).

Two main clusters were formed (1 and 2). The first (1) is composed mainly of DOF and shows a division in two other groups, with areas of Serra do Mar and Serra da Mantiqueira at elevations ranging from 500-2879 m a.s.l. in a group (▲) and areas of Southern and Southeastern regions at elevations ranging from 0-1000 m a.s.l. in the other group (∆). Cluster 2 grouped together the MOF but shows a segregation of the southern areas at elevations ranging from 340-1200 m a.s.l. (●) from those of Serra da Mantiqueira (including the PESP) at elevations ranging from 1000-2010 m a.s.l. (○).

Despite the existence of a branch composed only of MOF areas, the similarity can be considered low among

Table 2. Evolutionary lineages and respective ecological categories.

Evolutionary lineages and families	Ecological categories							
	CHL (107/78%)		FHL (10/7%)		AHL (19/14%)		HEM (2/1%)	
	N	%	N	%	N	%	N	%
Licophytes (4)								
Lycopodiaceae (4)	4	100%	-	-	-	-	-	-
Monilophytes (39)								
Anemiaceae (1)*	-	-	-	-	1	100%	-	-
Aspleniaceae (5)	4	80%	-	-	1	20%	-	-
Dryopteridaceae (3)	2	66.6%	1	33.3%	-	-	-	-
Hymenophyllaceae (4)	4	100%	-	-	-	-	-	-
Ophioglossaceae (1)	1	100%	-	-	-	-	-	-
Polypodiaceae (23)	23	100%	-	-	-	-	-	-
Monilophytes (39)								
Pteridaceae (2)	2	100%	-	-	-	-	-	-
Magnoliids (10)								
Piperaceae (10)	9	90%	1	10%	-	-	-	-
Monocotyledons (63)								
Araceae (1)	-	-	-	-	-	-	1	100%
Bromeliaceae (10)	4	40%	6	60%	-	-	-	-
Orchidaceae (51)	49	96.1 %	-	-	2	3.%	-	-
Poaceae (1)*	-	-	-	-	1	100%	-	-
Eudicotyledons (22)								
Araliaceae (1)*	-	-	-	-	1	100%	-	-
Asteraceae (6)*	-	-	-	-	6	100%	-	-
Cactaceae (2)	2	100%	-	-	-	-	-	-
Caryophyllaceae (1)*	-	-	-	-	1	100%	-	-
Ericaceae (1)*	-	-	-	-	1	100%	-	-
Gesneriaceae (3)	2	66.6%	1	33.3%	-	-	-	-
Melastomataceae (3)	1	33.3%	-	-	2	66.6%	-	-
Onagraceae (1)	-	-	1	100%	-	-	-	-
Plantaginaceae (1)*	-	-	-	-	1	100%	-	-
Polygalaceae (1)*	-	-	-	-	1	100%	-	-
Ranunculaceae (1)*	-	-	-	-	1	100%	-	-
Solanaceae (1)	-	-	-	-	-	-	1	100%

The number of species of each family or evolutionary lineage is between parentheses after their names. CHL – characteristic holoepiphytes; FHL – facultative holoepiphytes; AHL – accidental holoepiphytes; HEM – hemiepiphytes. N – number of species, % – percentage of species of each family distributed in the ecological categories.

* Families with species typically terricolous and represented in this study only by accidental holoepiphytes.

the two aforementioned subsets (around 0.25). Even the subset composed only of the remnants of MOF in the Serra da Mantiqueira exhibited low similarity and shared only 11 species (Fig. 3).

The results of the CCA, highlighted in the Tab. 3, showed eigenvalues higher than 0.3, which is considered high according to Felfili *et al.* (2011), representing a strong gradient in both axes. The values of species-environment correlations also are considered high (0.985 and 0.947 for axes 1 and 2, respectively). The Monte Carlo test showed a significant correlation between the distribution of species and the environmental variables used in the analysis ($p < 0.05$) (Tab. 3). The variables elevation and minimum annual temperature showed higher correlations with axis 1, while the shortest distance to the ocean was more correlated with axis 2 (Tab. 4).

The ordination diagram (Fig. 4) did not show a clear group among the areas with same physiognomy, as presented in the dendrogram (Fig. 2), especially regarding the MOF; only a tendency of grouping among them was observed. However, the area surveyed in the present study, 'mgpesp', was closely related to at least one of the MOF areas in the Serra da Mantiqueira, 'sppecj' (Parque Estadual de Campos do Jordão, in São Paulo state), and both were more correlated with the areas of DOF at high elevations than those of MOF occurring in the Southern Region of Brazil (Fig. 4).

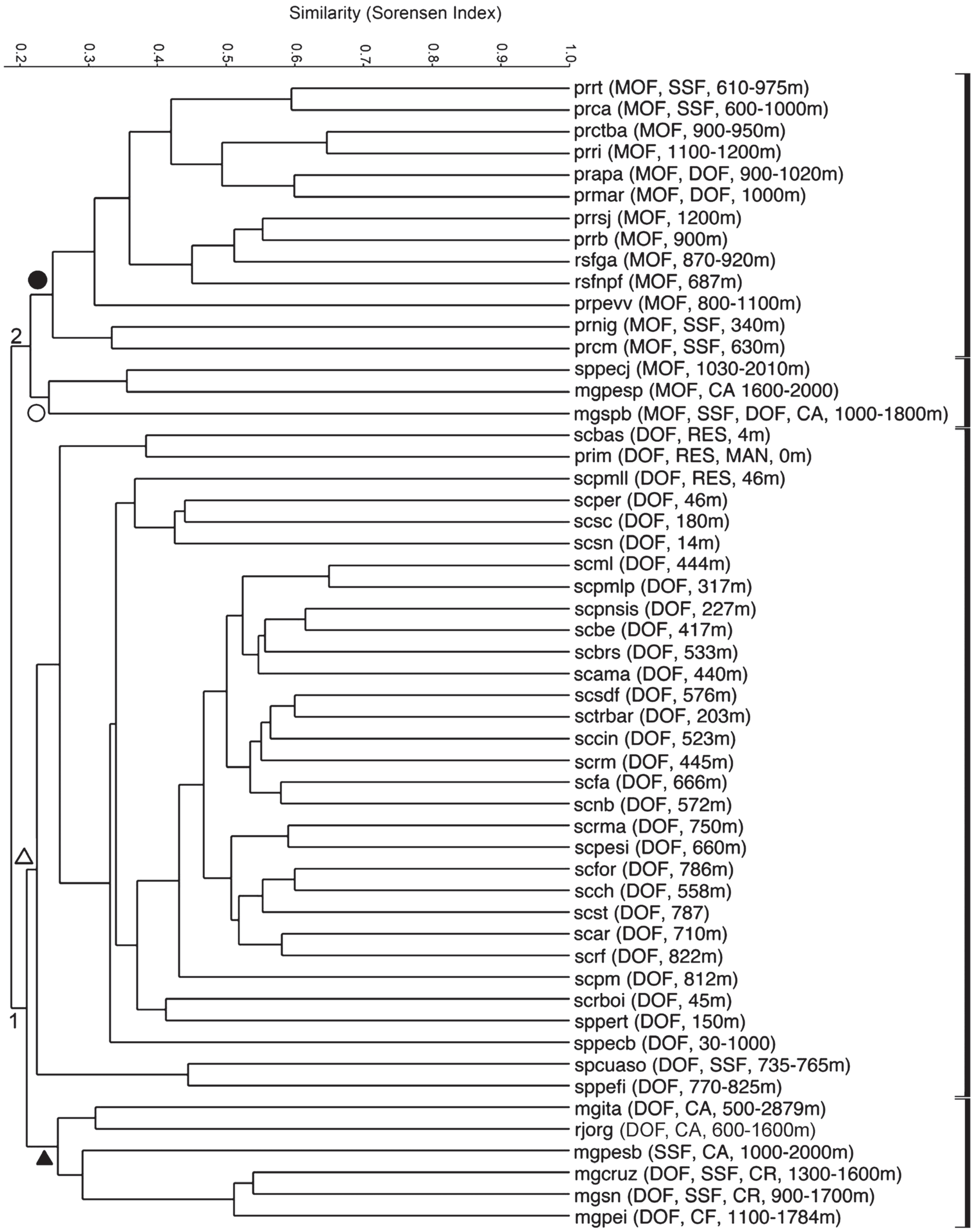

Figure 2. Dendrogram (Sørensen similarity index) obtained in the similarity analysis with 53 localities of the Southeastern and Southern regions of Brazil based on a binary matrix of 910 species of vascular epiphytes. Cophenetic coefficient = 0.86. Numbers in the branches are explained in the text. DOF: dense ombrophilous forest; MOF: mixed ombrophilous forest; CR: 'campo rupestre'; CA: 'campo de altitude'; SSF: seasonal semi-deciduous forest; RES: 'restinga' (coastal vegetation); MAN: Mangrove. ● areas composed by mixed ombrophilous forest from Planalto Meridional (Southern Region), ○ areas composed by mixed ombrophilous forest from Serra da Mantiqueira (Southeastern Region), ▲ areas composed by dense ombrophilous forest from Serra do Mar or Serra da Mantiqueira (Southeastern Region), Δ areas composed by dense ombrophilous forest from Serra do Mar (Southern Region).

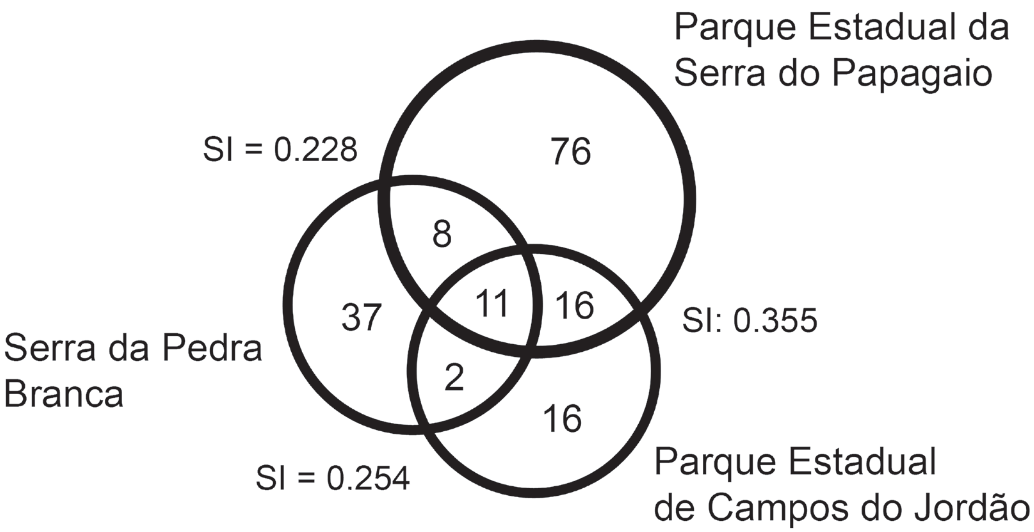

Figure 3. Venn diagram with the superposition of vascular epiphytic species of areas with mixed ombrophilous forest (MOF) of Serra da Mantiqueira: Parque Estadual da Serra do Papagaio; Serra da Pedra Branca; and Parque Estadual de Campos do Jordão. SI: Similarity index of Sørensen.

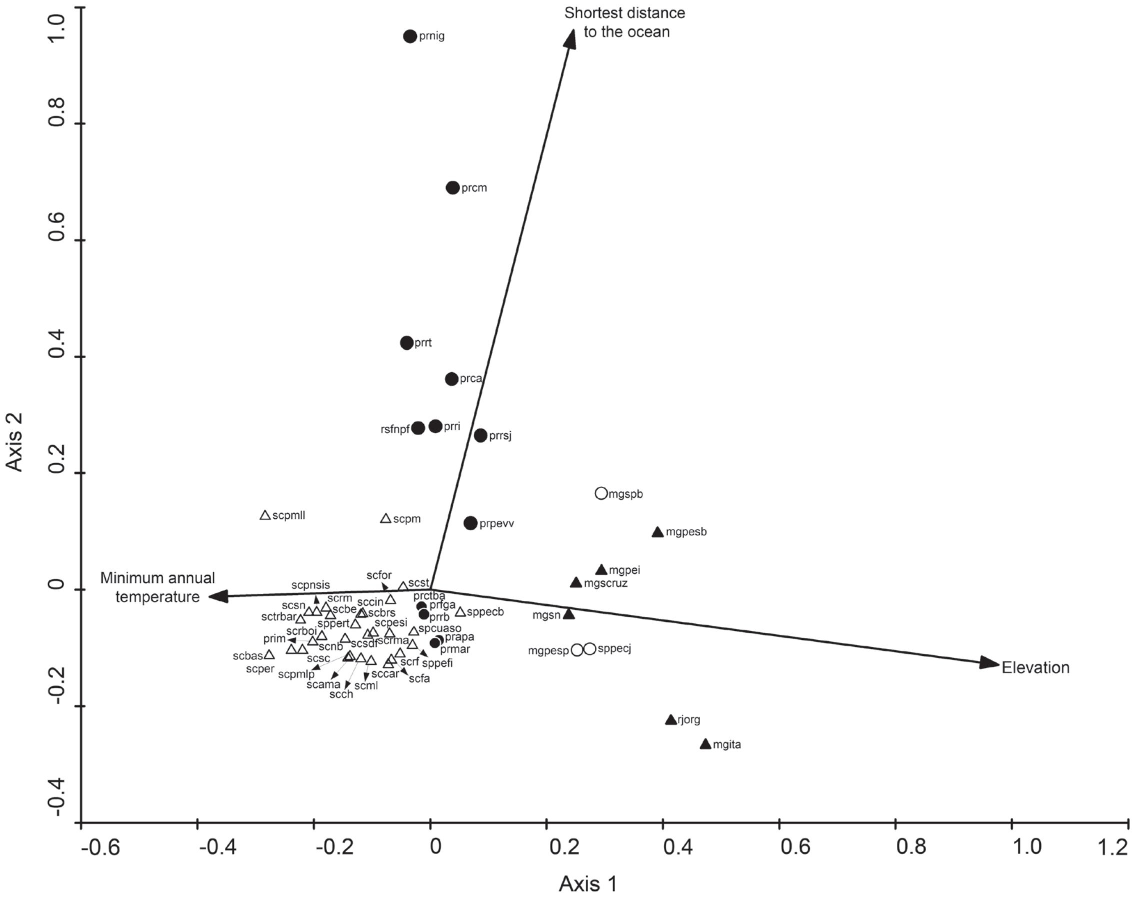

Figure 4. Bi-plot diagram results of the canonical correspondence analysis showing the relationships of 53 areas of the Southeastern and Southern regions of Brazil based on a binary matrix of 910 species of vascular epiphytes and the main environmental variables. The diagram shows the ordination of the first two axes. ● areas composed by mixed ombrophilous forest from Planalto Meridional (Southern Region), ○ areas composed by mixed ombrophilous forest from Serra da Mantiqueira (Southeastern Region), ▲ areas composed by dense ombrophilous forest from Serra do Mar or Serra da Mantiqueira (Southeastern Region), Δ areas composed by dense ombrophilous forest from Serra do Mar (Southern Region).

Table 3. Estimators of the two first axes of canonical ordination of vascular epiphytes of 53 areas of Southeastern and Southern regions as well as the most important environmental variables.

Estimators	Axis 1	Axis 2
Eigenvalues	0.448	0.373
Species-environment correlations	0.985	0.947
Cumulative percentage variance of species-data	5.3	9.8
Cumulative percentage variance of species-environment relation	42.2	77.4
Monte Carlo test (p)	0.002	0.002*

*All canonical axes.

Table 4. Correlations of the environmental variables with the two first axes of canonical ordination of vascular epiphytes of 53 areas of Southeastern and Southern regions.

Environmental variables	Correlation coefficients	
	Axis 1	Axis 2
Shortest distance to the ocean	0.2431	0.9098
Elevation	0.9626	-0.1219
Minimum annual temperature	-0.3739	-0.0116

Discussion

Floristic survey

The species richness of each evolutionary lineage is similar to that observed in the Atlantic Forest (Kersten 2010; Freitas *et al*. 2016), although the proportion of representation of each is different. We found a lower percentage of monocotyledons (approximately 46% in the PESP versus approximately 64% for the Atlantic Forest) and a higher percentage of monilophytes (approximately 29% in the PESP versus approximately 16% for the Atlantic Forest). This lower representation of monocotyledons is due to the reduced number of species of Bromeliaceae (10 species) and Araceae (only one species). The monilophytes exhibited a larger contribution to the species composition, as the group is recognisably rich in the MOF, especially due to the Polypodiaceae, according to Kersten (2010).

Despite Orchidaceae, Polypodiaceae, Bromeliaceae, Araceae and Piperaceae are the five richest families in epiphytes in Atlantic domain (Kersten 2010; Freitas *et al*. 2016) and Neotropical region (Gentry & Dodson 1987) as well as at the global level (Zotz 2013), the contribution of each family in this study was different. When considering the physiognomy of MOF only, the first three families also are the richest. However, the Piperaceae contribution increases, being the fourth richest, and the Araceae contribution considerably decreases, according to Kersten (2010). In the present study, this fact is corroborated, since Araceae is represented only by *Philodendron* sp., found in the ecotone between MOF and DOF.

The two richest genera (*Pleurothallis s.l.* and *Peperomia*) are prominent in the Atlantic domain as well as in the Neotropical region. *Pleurothallis s.l.* is one of the richest genera of Orchidaceae and the largest among the epiphytic plants, and the Brazilian Atlantic Forest is one of the centres of diversity especially in areas of high elevations (Pridgeon 1982; Luer 1986; Gentry & Dodson 1987), such as the PESP. *Peperomia* is one of the largest genera of Piperaceae and exhibits high richness in the Brazilian Atlantic Forest (Menini Neto *et al*. 2016), especially in the ombrophilous forest (Carvalho-Silva 2008), and it is the richest genus among epiphytes if the large genera of Orchidaceae are excluded (Zotz 2013), justifying the number of species.

The richness of vascular epiphytes of the PESP is higher than that of other studied areas in the MOF of the Southern Region (*e.g.*, Cervi & Dombrowski 1985; Cervi *et al*. 1988; Dittrich *et al*. 1999; Kersten & Silva 2002; Borgo & Silva 2003; Kersten 2006: Kersten *et al*. 2009) and in the MOF of Parque Estadual de Campos do Jordão (located at the Serra da Mantiqueira) (Mania 2013), even if we consider only the richness found in the araucaria forests of the PESP (122 species). The PESP exhibits higher richness than that found in several studies conducted in seasonal semi-deciduous forest (Aguiar *et al*. 1981; Dislich & Mantovani 1998; Borgo *et al*. 2002; Rogalski & Zanin 2003; Giongo & Waechter 2004). This contradicts the data gathered by Kersten (2010), who found this physiognomy richer compared to the MOF of Southern Region of Brazil, although this author suggests that status of conservation of the MOF could be the responsible for this result. Thus, the degree of conservation of the PESP must be responsible, in part, for these results, although other features, such as elevation, could influence observed richness (Furtado & Menini Neto 2015a), once a richness peak for epiphytes in altitudinal gradients is common among 1000-2000 m (Madison 1977; Gentry e Dodson 1987; Benzing 1990; Krömer *et al*. 2005; Cardelús *et al*. 2006).

Two other aspects can also influence the richness and must be addressed. The lower latitude of PESP compared with other areas composed by MOF, also can be important due to the influence of latitude on the temperature, which is a relevant feature regarding the epiphyte richness (Benzing

1990). Montane environment itself is another possible influence on the richness found in the present study. Such environment is often found to be a refuge to species and, consequently, shows remarkable richness and endemism if compared with lowland vegetation (Körner 2004; Martinelli 2007).

On the other hand, the ecotone between the MOF and DOF exhibited lower richness (76 species) when compared to the study conducted by Kersten (2006) in a similar environment of transition, in which 143 species were recorded. The same situation occurs when comparing the PESP with areas of DOF, which are typically richer (Breier 2005; Petean 2009; Bonnet *et al.* 2013a, b). However, in some cases, the PESP exhibits a higher richness (Hertel 1950; Petean 2002). Such result must be related to the absence of *Podocarpus lambertii* in the ecotone area. This tree species represents an important phorophyte in the PESP, harbouring 89 of the epiphyte species or 75% of the total recorded in this study (Furtado & Menini Neto 2015a).

Results confirm that characteristic holoepiphyte is the most common ecological category, corroborating similar studies conducted in MOF (Dittrich *et al.* 1999; Hefler & Faustioni 2004; Buzatto *et al.* 2008; Bonnet *et al.* 2011). However, accidental holoepiphytes, as the second-most representative category, is unusual (Bonnet *et al.* 2011) and must be noted. In the PESP, the majority of accidental holoepiphytes was found in some parts of the forest that suffered from fire in the year 2011 that had their entire or almost entire epiphytic communities destroyed.

Anthropogenic disturbances (as fire) are often responsible to alter the community composition, opening space to the establishment of opportunist and/or ruderal species that tolerate the new disturbed environment (Hobbs *et al***.** 1992) and occupy the earliest stages of succession (Monaco *et al*. 2002). Thus, such disturbances can be related with the establishment of accidental holoepiphytes in the studied site, consequently enhancing their proportion in comparison with characteristic holoepiphytes. Some weed/ruderal species were already recorded as accidental holoepiphytes in disturbed environments (*e.g.*, *Ageratum conyzoides*, *Drymaria cordata*, *Erechtites valerianaefolius*, *Plantago major*, *Setaria palmifolia*) (Holzner & Numata 1982). Species of these genera were also found as accidental holoepiphytes in the present study (*Ageratum* and *Plantago*) and in some other studies dealing with vascular epiphytes in disturbed environment (for example, Bhatt *et al*. 2015; Furtado & Menini Neto 2015b). It is necessary to conduct more accurate studies in addition to better sampling of this ecological category of epiphytes, which is neglected in several studies regarding epiphyte synusia, and deserves more attention as pointed out by Zotz (2013). Moreover, Benzing (1990) emphasised that environments with high moisture facilitate the occurrence of accidental species, which can explain, in part, the representativeness of this category in the present study.

Multivariate analyses

Importance of vegetation formation and elevation in the composition and distribution of vascular epiphytes showed in the dendrogram is similar to the pattern found for angiosperm epiphytes by Menini Neto *et al***.** (2009) although these authors used fewer areas than the present study. In the graphic, there is a tendency of grouping the areas that share DOF but segregation of the MOF of Southern and Southeastern regions.

The scatter plot of the CCA reinforced the influence of elevation but added the shortest distance to the ocean and the minimum annual temperature as important in calculation of the relationships. The set of variables of this study were also showed to be relevant in studies dealing with biogeography and floristic relationships of angiosperm epiphytes in Atlantic Forest (Menini Neto *et al*. 2009; 2016; Leitman *et al*. 2015).

Variables such moisture, light availability, temperature, and seasonality have direct influence in the distribution of epiphytes in the environment (Benzing 1990). Thus, complex variables that are composed by the first ones, for instance in a wide scale, elevation, latitude, continentality and, in a narrow scale, distance from water bodies, stratification on the phorophyte, and relief, also interfere on the epiphyte community.

Low temperature and frost are pointed as limiting to the richness of vascular epiphytes in different scales (Gentry & Dodson 1987; Krömer *et al***.** 2005; Blum *et al*. 2011; Hsu *et al*. 2014), which is corroborated in this study, once we found that minimum annual temperature is one of the important variables regarding the obtained floristic relationships. Elevation is directly related with temperature, atmospheric pressure and cloud cover and indirectly related with moisture, sun hours, wind, geology and seasonality (Körner 2004), that is, adds both positive and negative variables to the development of epiphytes, inclusive showing a variation depending upon the epiphytic group. For instance, Orchidaceae and monilophytes present a relative enhancement in the richness following the elevation, reaching a diversity peak in higher altitudes than found in other groups (Moran 1995; Krömer *et al*. 2005).

Positive correlation between geographic distance and Sørensen similarity index is due to the grouping in a cluster of distant areas composed by MOF (since the areas of ‘Planalto Meridional’, in the Southern Region, grouped together with those present in the Serra da Mantiqueira, in the Southeastern Region of Brazil). This cluster, albeit with a reduced similarity index, contradicts the rare studies that deal with the floristic relationships of the MOF. For instance, studies concerning the flora of shrubs and trees showed great dissimilarities between the areas of MOF of the Southern and Southeastern regions of Brazil (Jarenkow & Budke 2009; Ribeiro 2011).

During the Middle and Upper Holocene (between 4,320 and 1,000 years before the present) the typical tree species of MOF expanded, especially due to the enhancement of moisture, forming forests along the rivers (Bauermann & Behling 2009). Therefore, the MOF of Serra da Mantiqueira took refuge in patches and became isolated from the southern forests, forming islands among the 'campo de altitude', likely due to the dynamic between the field and forest (Behling & Pillar 2007). This isolation, although sufficient for some recognition of distinct floristic sets, as the case of shrubs and trees, seems too weak for homogenisation of the vascular epiphytic flora of MOF with other surrounding physiognomies.

Regarding the environmental variables, the study of Oliveira-Filho *et al.* (2013) also stressed the shortest distance to the ocean, elevation, and variation in the temperature throughout the year, among others, as important in determining the relationships among the forest physiognomies of the Southern Region of Brazil based on flora of trees.

It is possible that the composition of typical tree species in the MOF and, consequently, the probability of being the main phorophytes contribute to higher frequency and sharing of several epiphytic species, explaining the similarity between the areas of the Southern and Southeastern regions, despite the distance between them. Therefore, species like *A. angustifolia* and *P. lambertii*, which are dominant trees in the studied area (Santana 2016), often emphasised among the species of the prominent importance value index in phytosociological studies conducted on MOF of the Southern and Southeastern regions (Geraldi *et al.* 2005; Seger *et al.* 2005; Ribeiro *et al.* 2007; Araujo *et al.* 2010; Silva *et al.* 2012; Souza *et al.* 2012), can possibly be a determinant for the occurrence of epiphytic species shared by areas with this physiognomy, regardless of geographic distance or environmental variables.

Wilberger *et al.* (2009) and Furtado & Menini Neto (2015a) evaluated the vascular epiphytes on *A. angustifolia* and *P. lambertii*, respectively, showing their importance as support for the epiphytic synusia. However, the lack of studies that correlated the occurrence of epiphytes and respective phorophytes in the MOF, regardless of species, impede deeper conclusions about this subject.

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