

# Diversity of vascular epiphytes in two high altitude biotopes of the Brazilian Atlantic Forest

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**Abstract** Montane environments create unique conditions that favour the development of remarkably rich and endemic biotas. The Serra da Mantiqueira is an important Brazilian mountain range and is recognised globally for certain groups of living organisms, whereas gaps in knowledge exist for other groups, such as epiphytes, which have been poorly studied in the region. The Serra da Mantiqueira contains rare fragments of a vegetation formation, the mixed ombrophilous forest (MOF), which is typical of the Southern Region of Brazil and is very threatened. The present study aimed to analyse the epiphytic communities occurring on individuals of *Podocarpus lambertii* Klotzsch ex Endl. (Podocarpaceae) in two biotopes: natural patches and continuous alluvial forest. We sampled 60 phorophytes, equally divided between the sites, and established five strata according to stem ramification. This phorophyte species is ecologically relevant, since it harbours 92 species and 19 families, and a single individual may support up to 30 % of the total richness of the studied community. The Shannon diversity index was 3.86, which is comparable to that found in other studies dealing with several phorophyte species and is the highest found to date for the MOF. The biotopes and strata did not

show significant differences in the calculated diversity indices, except in richness (80 species in the alluvial forest and 60 in the patches). The most representative ecological categories were characteristic holoeipiphytes (73 species) and accidental holoeipiphytes (nine species). The present study shows the importance that a single species can have in an ecosystem and contributes to our knowledge concerning epiphytic synusia in mountainous environments.

**Keywords** Community ecology · Mixed ombrophilous forest · Montane forest · *Podocarpus lambertii* · Serra da Mantiqueira · Taxonomic diversity

## Introduction

Mountainous regions possess features that make them environments with high indices of richness and endemism, and also represent vegetation islands that harbour important forest remnants, although these ecosystems are especially sensitive to anthropogenic disturbances (Martinelli 2007). The Serra da Mantiqueira, together with the Serra do Mar, represent the main highlands in the Atlantic Forest (AF), a geographic domain that contains 46 % of Brazilian flora (Stehmann et al. 2009; Forzza et al. 2012) and is therefore considered a world hotspot of biodiversity (Mittermeier et al. 2004). This mountainous range has a high biodiversity due to the occurrence of rare, endemic and threatened species of animals and plants (Drummond et al. 2005). However, its location in the Southeastern Region of Brazil, where 70 % of the Brazilian population is concentrated (Lino et al. 2007), places its astonishing biodiversity at risk, reinforcing the importance of enhancing knowledge that will support the conservation of this region (Drummond et al. 2009).

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Mixed ombrophilous forest (MOF) is one of the most threatened forest ecosystems of the Brazilian Atlantic Forest. It is estimated that only approximately 3 % of the original cover remains, including regenerating areas (Bauermann and Behling 2009). This forest formation occupies the highest areas of the Serra da Mantiqueira. One of the few surviving remnants lies within the Parque Estadual da Serra do Papagaio (PESP) (Ab'saber 2003; Backes 2009). In this protected area, the MOF comprises two gymnosperm species as the most common arboreal plants: *Araucaria angustifolia* (Bertol.) Kuntze (Araucariaceae) and *Podocarpus lambertii* Klotzsch ex Endl. (Podocarpaceae). The latter species occurs in two different biotopes [concept that combines the physical environment and the assemblage of conspicuous species (Olenin and Ducrotoy 2006)]: the continuous alluvial forest below the canopy composed of *A. angustifolia*, and the natural forest patches (locally named as “capões”) composed predominantly of one or several individuals of *P. lambertii* and/or with the presence of other tree species in the “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”).

Vascular epiphytes represent a functional group with high ecological importance that provides resources to a large number of animal and plant species and performs an essential role in maintaining biodiversity (Gentry and Dodson 1987; Benzing 1990). This synusia is highly sensitive to environmental variations such as temperature, humidity, luminosity and the substratum (Benzing 1990), and is continuously threatened due to habitat loss, especially in cloud forests, an environment where epiphytes are highly diverse but has been rapidly degraded in the past three decades (Scatena et al. 2010). It has also suffered from predatory collection due to the ornamental features of families such as Orchidaceae, Bromeliaceae, Gesneriaceae, Araceae and Cactaceae, which contain a great number of epiphytic species (Benzing 1990).

Brazil possesses an astonishing floristic richness, notably of epiphytes, especially due to the forest physiognomies of the Atlantic Domain. Studies regarding epiphytic communities have been conducted more intensively in the past 20 years and have concentrated in the Southern Region, of which several were done in MOF (e.g., Kersten and Silva 2002; Kersten et al. 2009; Waechter 2009; Bernardi and Budke 2010; Geraldino et al. 2010) but are scarce in other regions of the country (Kersten 2010). The present study is the first that aims to analyse the structure of the epiphytic community in the Serra da Mantiqueira, and the first conducted above 1600 m a.s.l. in Brazil.

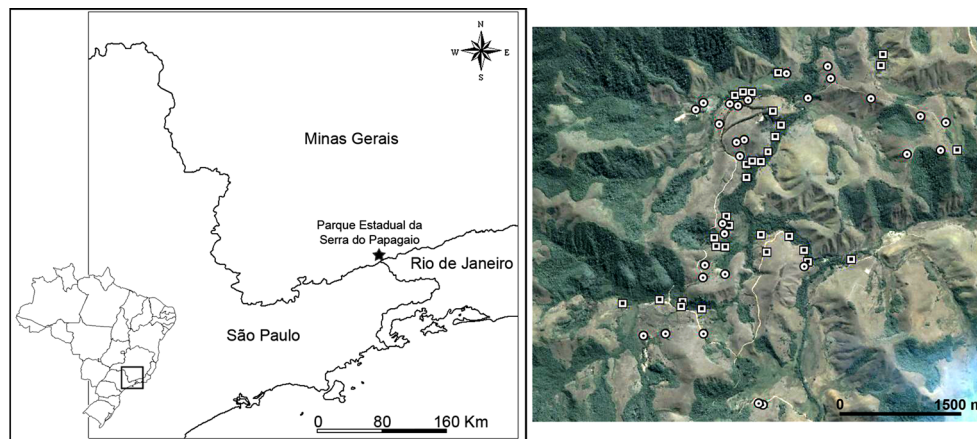
The main objective of this study was to broaden knowledge concerning the flora of the AF, especially the montane environments and the MOF. Thus, we evaluated the importance of *P. lambertii* as a phorophyte through analyses of richness, indices of diversity and the vertical structure of the epiphytic community. Furthermore, since epiphytes are sensitive to habitat variations, we also tested the hypothesis of differences existing in this community between the two biotopes, the continuous alluvial MOF and natural patches of forest vegetation in the “campo de altitude”.

## Materials and methods

### Study area

The Parque Estadual da Serra do Papagaio (PESP) is located in the southern region of Minas Gerais, in the Serra da Mantiqueira, neighbouring the Parque Nacional do Itatiaia (Fig. 1). It has an area of 22,917 ha, and lies between the municipalities of Aiuruoca, Alagoa, Baependi, Itamonte and Pouso Alto (22.1420S, 44.7328W). An important remnant of the AF is preserved within this protected area, which harbours a mosaic of cloud forests (high montane dense ombrophilous forest (DOF) and high montane MOF), and “campo de altitude”. In the studied area, the MOF occurs predominantly on humic and histic cambisols at altitudes between 1600 and 1700 m a.s.l., forming a transition area with the DOF at about 1900–2000 m a.s.l. in the southeast of the PESP, in the municipality of Baependi. The climate is Cwb (Köppen's classification), a temperate highland tropical climate with dry winters (Silva et al. 2008).

The main fragments of the MOF are alluvial (biotope 1) and are found along the Santo Agostinho brook, forming a continuous vegetation that is composed of three strata: a canopy of *A. angustifolia* (about 30 m high), a second stratum composed predominantly of *P. lambertii* (between 10 and 15 m high) and a third stratum (up to about 8–10 m high) composed of shrubs and treelets of the families Lauraceae, Myrtaceae, Primulaceae and Winteraceae, among others. *Podocarpus lambertii* also occurs in patches interspersed within the “campo de altitude” (biotope 2), adjacent to the alluvial forest. The patches comprise one to four individuals of *P. lambertii* (between 3 and 5 m high), sometimes surrounded by shrubs and treelets of several families (Asteraceae, Lauraceae, Melastomataceae, Myrtaceae, Primulaceae, etc.), but naturally without *A. angustifolia* (Figs. 1–13). Hereafter, these biotopes will be referred to as alluvial forest and patches.



**Fig. 1** Location of the studied area in the Parque Estadual da Serra do Papagaio, Minas Gerais, Brazil (source: modified from Pereira et al. 2013 and Google Earth®). □ Sampled individuals of Alluvial Forest; ● Sampled individuals of Patches

### Sampling

The sampling of phorophytes was conducted following a wide monthly survey of the vascular epiphytic flora of the MOF and the transition area with the DOF in the protected area, between April 2012 and September 2013, concerning its composition and, subsequently, a more precise identification of the observed specimens, even if they were sterile. The specimens were deposited in the CESJ herbarium of the Universidade Federal de Juiz de Fora (acronym according to Thiers 2014).

We sampled 60 individuals of *P. lambertii* equally divided between the two biotopes, and initially sampled 30 patches in an area of about 300 ha, between 1650 and 1750 m a.s.l. In each patch, we analysed only one individual of *P. lambertii* [when the patch contained two or more individuals, we chose the specimen with the largest diameter at breast height (1.3 m above the ground)]. In the alluvial forest, within the same area, we traversed existing tracks or opened new ones along the brook bank and sampled the largest phorophyte close to the trail. Starting from this individual, we then sampled the nearest and largest phorophyte at a distance of at least 50 m, covering the forest physiognomy in this systematic way until 30 individuals had been sampled (Fig. 1). Each phorophyte was divided into five strata: bole, first, second and third ramifications and external crown (the remainder of the crown). The epiphytes in each stratum were recorded and the ecological categories were classified according to Benzing (1990). The epiphytes were observed by the use of binoculars and through climbing the trees without ropes.

The evolutionary lineages of vascular plants were assigned according to Christenhusz et al. (2011) (lycophytes and monilophytes) and APG III (2009) (magnoliids, monocotyledons and eudicotyledons) (Table 2).

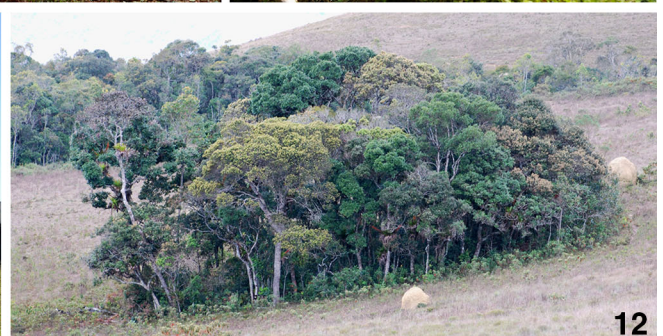
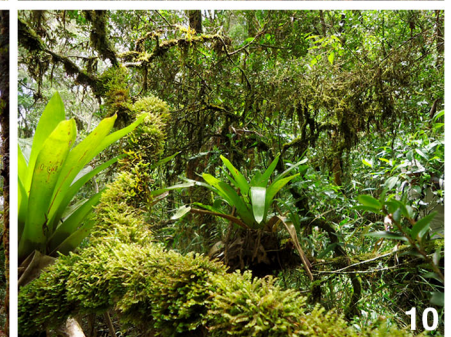
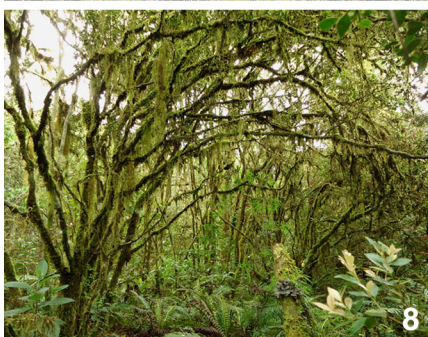
### Data analyses

The richness of the biotopes was compared through rarefaction curves with 95 % confidence intervals according to Colwell et al. (2012). The obtained data were used to calculate the relative and absolute frequencies as well as the diversity indices of Shannon ( $H'$ ) and Pielou ( $J$ ) for each strata, each biotope and in total. To calculate the Shannon's diversity index, we used the modification proposed by Waechter (1998), substituting abundance for frequency, due to the difficulty of identifying individuals in the epiphytic synusia. The  $J$  index is based on  $H'$  and estimates the uniformity of the community, estimating the obtained diversity ( $H'$ ) in relation to the maximum hypothetical diversity (Magurran 2004). The Hutcheson  $t$  test was used to compare the diversity between the biotopes as well as the diversity between the strata ( $\alpha > 0.05$ ) (Magurran 1988). The parameters of richness,  $H'$  and  $J$  in other studies about vascular epiphytes conducted in the Southern and Southeastern regions of Brazil are listed in Table 3 in order to compare them with the values obtained in the studied community.

We also calculated the indices of taxonomic distinctness ( $\Delta$ ), taxonomic diversity ( $\Delta^*$ ), average taxonomic distinctness ( $\Delta^+$ ) and variation in taxonomic distinctness ( $\Delta^+$ ), according to Clarke and Warwick (1998, 2001) for both biotopes (Table 4). In addition, the five most common species in this study were compared with those obtained in other studies performed in the MOF (Table 5) in order to evaluate if the most important species are similar in such physiognomy occurring in geographically distant sites.

We conducted a Kruskal–Wallis test to evaluate difference between the species richness in each stratum (Magurran 2004). A frequent close co-occurrence of *Aechmea distichantha* (Bromeliaceae) and *Pecluma pectinatifomis* (Polypodiaceae) was observed in the field and







◀ **Figs. 2–12** Environments of the studied area in the Parque Estadual da Serra do Papagaio, Minas Gerais, Brazil. **2.** General view of the vegetation mosaic formed by the “campo de altitude” and mixed ombrophilous forest; **3, 4.** General view of the alluvial forest canopy, with the presence of *Araucaria angustifolia*; **5–7.** Views of the alluvial forest. **8–10.** Interior of the alluvial forest; **11, 12.** Patches of *Podocarpus lambertii*

the potential correlation was tested through the Pearson coefficient.

The analyses were conducted using the software Past v. 3.01 (Hammer et al. 2001), EstimateS (Colwell 2013) and R (R Core Team 2014).

## Results

### Flora of vascular epiphytes

We found 92 species of vascular epiphytes on *P. lambertii*, distributed among 46 genera and 19 families. However, only 89 species were used in the analyses, since *Hadrolaelia coccinea* and *H. mantiqueirae* are considered as one morphospecies, as well as the taxon identified as *Octomeira* sp. (composed of three unidentified species with cylindrical leaves), due to the difficulty in identifying it when sterile (Table 1).

The evolutionary lineages of the vascular plants were represented by monocotyledons (45 spp., 50.5 %), followed by monilophytes (25 spp., 28.1 %), eudicotyledons (13 spp., 14.6 %), magnoliids (6 spp., 6.7 %) and lycophytes (3 spp., 3.4 %) (Table 2). The richest families were Orchidaceae (34 spp., 38 %), Polypodiaceae (17 spp., 19 %), Bromeliaceae (10 spp., 11 %) and Piperaceae (6 spp., 7 %), containing 75 % of the surveyed species (Table 1).

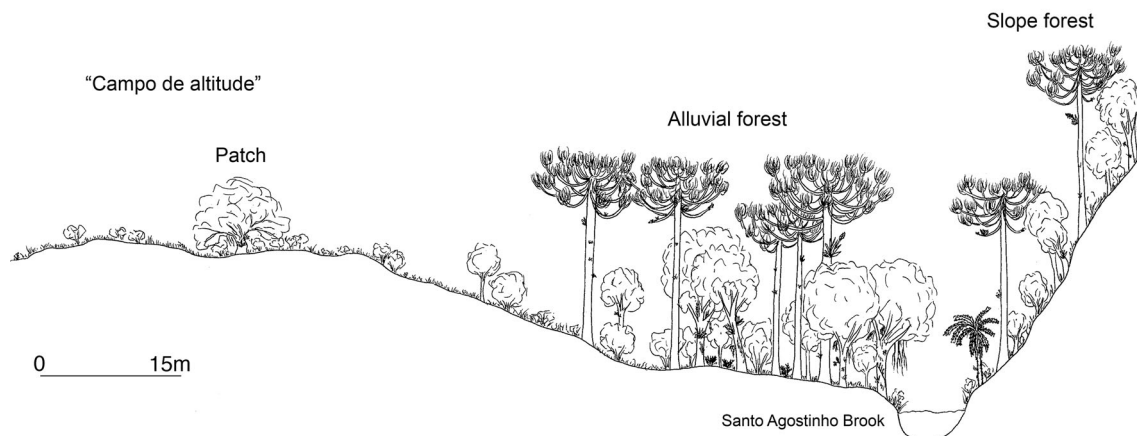
### Structure of the community and biotopes

The alluvial forest demonstrated a higher richness than the patches (80 vs. 60 species) (Fig. 14). The two biotopes presented 29 and nine exclusive species, respectively. The diversity index ( $H'$ ) for the whole area was 3.86 and the uniformity index ( $J$ ) was 0.86 (Table 3).

There was no difference between the diversity of the biotopes ( $t = -0.17$ ;  $df = 139.91$ ;  $P = 0.86$ ), and the higher value of  $J$  compared to the total value which showed an enhancement of uniformity within each environment separately. Similarly, the biotopes showed no difference in their indices of taxonomic diversity ( $P > 0.05$ ), although the forest showed slightly higher values. The variation in taxonomic distinction was higher in the patches, representing unevenness in the taxonomic composition of this biotope due to lower taxonomic spread (Table 4).

*Pleopeltis macrocarpa*, *Aechmea distichantha*, *Serpocaulon catharinae*, *Pecluma pectinatifomis* and *Rhipsalis floccosa* were the most frequent species in the whole community (above 80 %). The first three species were slightly more frequent in patches, and the latter two species were more frequent in the alluvial forest (Table 1). In general, these species were not found among the most frequent epiphytic vascular flora in the MOF as presented in Table 5.

The maximum number of occurrences of a single phorophyte was 64, and the richness ranged from 10 to 28 species. The phorophytes of the patches had greater amplitude between the minimum and maximum number of observed species, with a median of 18 species per phorophyte, whereas the richness of the phorophytes in the alluvial forest was less dispersed, with a lower median (17 spp.) (Fig. 15).



**Fig. 13** Vegetation profile of the studied area in the Parque Estadual da Serra do Papagaio, Minas Gerais, Brazil (drawn by L. Menini Neto)

**Table 1** List of vascular epiphytes recorded on *Podocarpus lambertii* in both biotopes, and analysed parameters

Species	Families	EC	TO	Biotopes (%)		Frequency		Strata					Voucher	
				Pat.	All. for.	AF	RF	A	B	C	D	E	CE	SJ
<i>Pleopeltis macrocarpa</i> (Bory ex Willd.) Kaulf	Polypodiaceae	CHL	57	52.6	47.4	95	5.23	17	32	41	45	44	Furtado 9	
<i>Aechmea distichantha</i> Lem.	Bromeliaceae	FHL	54	53.7	46.3	90	4.96	29	45	43	30	15	Furtado 234	
<i>Serpocaulon catharinae</i> (Langsd. & Fisch) A.R.Sm.	Polypodiaceae	CHL	53	54.7	45.3	88.3	4.87	21	40	31	32	18	Furtado 50	
<i>Pectuma pectinatifolium</i> (Lindm.) M.G.Price	Polypodiaceae	CHL	51	47.1	52.9	85	4.68	20	38	34	27	6	Souza 955	
<i>Rhipsalis floccosa</i> Salm-Dyck ex Pfeiff.	Cactaceae	CHL	50	48	52	83.3	4.59	14	23	32	32	19	Furtado 107	
<i>Vriesea scepterum</i> Mez	Bromeliaceae	FHL	48	47.9	52.1	80	4.41	14	27	35	32	23	Menini Neto 792	
<i>Pleopeltis hirsutissima</i> (Raddi) de la Sota	Polypodiaceae	CHL	44	61.4	38.6	73.3	4.04	6	26	28	32	33	Furtado 32	
<i>Pleopeltis pleopeltidis</i> (Fée) de la Sota	Polypodiaceae	CHL	38	50	50	63.3	3.49	5	13	22	23	24	Furtado 116	
<i>Campyloneurum angustifolium</i> (Sw.) Fée	Polypodiaceae	CHL	36	52.8	47.2	60	3.31	18	28	26	23	19	Menini Neto 965	
<i>Pleurothallis grobyi</i> Bateman ex Lindl.	Orchidaceae	CHL	36	38.9	61.1	60	3.31	17	28	28	24	27	Furtado 117	
<i>Peperomia tetraphylla</i> (G.Forst.) Hook & Am.	Piperaceae	CHL	32	56.3	43.8	53.3	2.94	14	19	20	16	10	Furtado 195	
<i>Octomeria crassifolia</i> Lindl.	Orchidaceae	CHL	31	71	29	51.7	2.85	3	10	16	18	24	Furtado 35	
<i>Microgramma squamulosa</i> (Kaulf) de la Sota	Polypodiaceae	CHL	28	75	25	46.7	2.57	17	24	27	23	23	Furtado 8	
<i>Oncidium longicornu</i> Mutel	Orchidaceae	CHL	27	33.3	66.7	45	2.48	14	15	10	7	7	Furtado 162	
<i>Maxillaria paranaensis</i> Barb.Rodr.	Orchidaceae	CHL	25	32	68	41.7	2.30	12	19	18	16	9	Furtado 36	
<i>Octomeria</i> sp.*	Orchidaceae	CHL	25	80	20	41.7	2.3	-	2	1	6	24	Furtado 167	
<i>Pleurothallis linearifolia</i> Cogn.	Orchidaceae	CHL	25	32	68	41.7	2.3	9	14	12	14	17	Furtado 163	
<i>Octomeria geraensis</i> Barb.Rodr.	Orchidaceae	CHL	23	60.9	39.1	38.3	2.11	-	2	2	4	20	Furtado 277	
<i>Tillandsia stricta</i> Cogn.	Bromeliaceae	CHL	22	86.4	13.6	36.7	2.02	4	12	9	12	18	Furtado 100	
<i>Sinningia douglasii</i> (Lindl.) Chautems	Gesneriaceae	CHL	21	19	81	35	1.93	5	12	13	13	8	Furtado 164	
<i>Leucotrichum organensis</i> (Gardner) Labiak	Polypodiaceae	CHL	19	21.1	78.9	31.7	1.74	7	11	9	6	1	Furtado 5	
<i>Oncidium gardneri</i> Lindl.	Orchidaceae	CHL	19	89.5	10.5	31.7	1.74	1	2	6	9	14	Furtado 215	
<i>Bulbophyllum regnellii</i> Lindl.	Orchidaceae	CHL	18	77.8	22.2	30	1.65	-	8	12	10	13	Furtado 242	
<i>Hadrolaelia coccinea</i> (Lindl.) Chiron & V.P.Castro/H mantiqueirae (Fowlie) Fowlie**	Orchidaceae	CHL	16	75	25	26.7	1.47	-	7	9	7	6	Furtado 79/80	
<i>Octomeria ochroleuca</i> Barb.Rodr.	Orchidaceae	CHL	15	66.7	33.3	25	1.38	-	-	-	-	15	Furtado 25	
<i>Rumohra adianthiformis</i> (G.Forst) Ching	Dryopteridaceae	CHL	15	20	80	25	1.38	2	7	11	4	2	Furtado 113	
<i>Peperomia hilariana</i> Miq.	Piperaceae	FHL	14	14.3	85.7	23.3	1.29	11	2	-	2	-	Menini Neto 814	
<i>Peperomia trineuroides</i> Dahlst.	Piperaceae	CHL	14	35.7	64.3	23.3	1.29	5	6	1	5	4	Furtado 172	
Polypodiaceae unidentified	Polypodiaceae	CHL	13	61.5	38.5	21.7	1.19	3	10	4	2	2	Furtado 45	
<i>Campyloneurum</i> sp.	Polypodiaceae	CHL	13	30.8	69.2	21.7	1.19	3	3	3	3	4	Furtado 216	
<i>Pleurothallis rubens</i> Lindl.	Orchidaceae	CHL	12	83.3	16.7	20	1.1	1	4	7	3	7	Furtado 87	
<i>Stelis papaquerensis</i> Rchb.f.	Orchidaceae	CHL	12	25	75	20	1.1	6	9	7	4	3	Furtado 186	
<i>Stelis</i> sp. 1	Orchidaceae	CHL	11	54.5	45.5	18.3	1.01	-	1	3	4	6	Furtado 196	

Table 1 continued

Species	Families	EC	TO	Biotopes (%)		Frequency		Strata				Voucher	
				Pat.	All. for.	AF	RF	A	B	C	D	E	CESJ
<i>Elaphoglossum gayanum</i> (Fée) T.Moore	Dryopteridaceae	CHL	10	20	80	16.7	0.92	7	1	4	–	–	Furtado 183
<i>Leellingeria apiculata</i> (Kunze ex Klotzsch) A.R.Sm.	Polypodiaceae	CHL	10	70	30	16.7	0.92	2	3	2	4	–	Furtado 110
<i>Zygophlebium longipilosa</i> (C. Chr.) L.E.Bishop	Polypodiaceae	CHL	10	20	80	16.7	0.92	5	5	2	1	–	Souza 1006
<i>Asplenium auritum</i> Sw.	Aspleniaceae	CHL	8	37.5	62.5	13.3	0.73	2	2	4	2	–	Furtado 37
<i>Hymenophyllum polyanthos</i> (Sw.) Sw.	Hymenophyllaceae	CHL	8	0	100	13.3	0.73	8	2	2	1	1	Furtado 64
<i>Myrsine umbellata</i> Mart.	Primulaceae	AHL	8	0	100	13.3	0.73	4	1	4	1	–	NC
<i>Billbergia distachia</i> (Vell.) Mez	Bromeliaceae	CHL	7	14.3	85.7	11.7	0.64	5	4	–	–	–	Furtado 91
<i>Epidendrum chlorinum</i> Barb.Rodr.	Orchidaceae	CHL	7	100	0	11.7	0.64	–	3	3	4	3	Furtado 214
<i>Maxillaria newwiedtii</i> Rchb.f.	Orchidaceae	CHL	6	50	50	10	0.55	3	3	3	2	1	Menini 1108
<i>Campyloneurum aglaolepis</i> (Alston) de la Sota	Polypodiaceae	CHL	5	80	20	8.3	0.46	2	2	2	1	1	Furtado 94
<i>Elaphoglossum vagans</i> (Mett.) Hieron.	Dryopteridaceae	FHL	4	0	100	6.7	0.37	3	–	–	1	–	Furtado 129
<i>Melpomene flabelliformis</i> (Poir.) A.R.Sm. & R.C.Moran	Polypodiaceae	CHL	4	50	50	6.7	0.37	–	2	–	2	1	Furtado 198
<i>Ocoteeria wawrae</i> Rchb.f.	Orchidaceae	CHL	4	100	0	6.7	0.37	–	–	–	1	3	Furtado 92
<i>Peperomia catharinae</i> Miq.	Piperaceae	CHL	4	50	50	6.7	0.37	2	1	1	–	–	Furtado 106
<i>Rhipsalis pulchra</i> Loefgr.	Cactaceae	CHL	4	25	75	6.7	0.37	–	1	–	2	1	Furtado 139
<i>Asplenium auriculatum</i> Sw.	Aspleniaceae	CHL	3	0	100	5	0.28	2	1	–	1	–	Furtado 37
<i>Asplenium incurvatum</i> Fée	Aspleniaceae	CHL	3	33.3	66.7	5	0.28	–	–	2	2	–	Furtado 93
<i>Capanemia adelaidae</i> Brade	Orchidaceae	CHL	3	66.7	33.3	5	0.28	–	–	–	1	3	Furtado 53
<i>Lankesterella gnoma</i> (Kraenzl.) Hoehne	Orchidaceae	CHL	3	66.7	33.3	5	0.28	–	3	1	1	–	Furtado 169
<i>Peperomia subternifolia</i> Yunek	Piperaceae	CHL	3	0	100	5	0.28	2	–	1	1	–	Furtado 98
<i>Phymatidium nello-barrettoi</i> Hoehne & Williams	Orchidaceae	CHL	3	66.7	33.3	5	0.28	–	–	1	–	2	Furtado 26
<i>Sinningia cooperi</i> (Paxton) Wiehler	Gesneriaceae	CHL	3	33.3	66.7	5	0.28	2	3	1	1	1	Furtado 49
<i>Stelis</i> sp. 2	Orchidaceae	CHL	3	33.3	66.7	5	0.28	–	2	–	–	1	Furtado 273
<i>Vriesea bituminosa</i> Wawra	Bromeliaceae	CHL	3	100	0	5	0.28	–	1	1	1	–	Furtado 250
<i>Dysochroa viridiflora</i> (Sims) Miers	Solanaceae	HEM	2	0	100	3.3	0.18	1	2	1	1	–	Furtado 244
<i>Fuchsia regia</i> (Vell.) Munz	Onagraceae	FHL	2	100	0	3.3	0.18	–	2	1	–	–	Furtado 165
<i>Hapalorchis micranthus</i> (Barb.Rodr.) Hoehne	Orchidaceae	AHL	2	0	100	3.3	0.18	1	1	–	–	–	Furtado 69
<i>Phlegmariurus biformis</i> (Hook.) BØllg	Lycopodiaceae	CHL	2	0	100	3.3	0.18	1	1	–	–	–	Furtado 75
<i>Phlegmariurus quadrifariatus</i> (Bory) BØllg	Lycopodiaceae	CHL	2	50	50	3.3	0.18	–	–	2	–	1	Furtado 66
Eudicot unidentified 2	–	AHL	2	0	100	3.3	0.18	–	–	–	2	–	NC
<i>Leucotrichum</i> sp.	Polypodiaceae	CHL	2	50	50	3.3	0.18	2	–	–	–	–	Furtado 44
<i>Maxillaria picta</i> Hook.	Orchidaceae	CHL	2	0	100	3.3	0.18	–	–	2	1	–	Furtado 174
<i>Melpomene pilosissima</i> (M.Martens & Galeotti) A.R.Sm. & R.C.Moran	Polypodiaceae	CHL	2	0	100	3.3	0.18	–	1	–	1	–	Furtado 127

Table 1 continued

Species	Families	EC	TO	Biotopes (%)		Frequency		Strata					Voucher	
				Pat.	All. for.	AF	RF	A	B	C	D	E	CE	SJ
<i>Oncidium cogniauxianum</i> Schltr.	Orchidaceae	CHL	2	0	100	3.3	0.18	1	-	-	-	-	1	Furtado 203
<i>Oncidium hookeri</i> Rolfe	Orchidaceae	CHL	2	100	0	3.3	0.18	-	-	1	-	-	2	Furtado 241
<i>Pleurothallis bocainensis</i> Porto & Brade	Orchidaceae	CHL	2	0	100	3.3	0.18	-	-	-	1	-	2	Furtado 68
<i>Pleurothallis pleurothalloides</i> (Cogn.) Handro	Orchidaceae	CHL	2	0	100	3.3	0.18	-	1	2	2	-	2	Furtado 1
<i>Vriesea gigantea</i> Gaudich.	Bromeliaceae	FHL	2	100	0	3.3	0.18	-	1	-	1	-	1	Furtado 146
<i>Anemone sellowii</i> Pritz	Ranunculaceae	AHL	1	0	100	1.7	0.09	1	-	-	-	-	-	Furtado 89
Asteraceae unidentified	Asteraceae	AHL	1	0	100	1.7	0.09	1	1	-	-	-	-	NC
<i>Campyloneurum nitidum</i> (Kaulf) C.Presl	Polypodiaceae	CHL	1	0	100	1.7	0.09	1	-	-	-	-	-	Furtado 236
<i>Dryadella lilliputiana</i> (Cogn.) Luer	Orchidaceae	CHL	1	0	100	1.7	0.09	-	-	-	-	-	1	Furtado 141
<i>Gomosa gomezoides</i> (Barb.Rodr.) Pabst	Orchidaceae	CHL	1	100	0	1.7	0.09	-	-	-	-	-	1	Furtado 210
<i>Hadrolaelia pygmaea</i> (Pabst) Chiron & V.P.Castro	Orchidaceae	CHL	1	100	0	1.7	0.09	-	-	-	-	-	1	Furtado 208
<i>Phlegmariurus acerossus</i> (Sw.) BØllg	Lycopodiaceae	CHL	1	0	100	1.7	0.09	-	-	1	-	-	-	Furtado 74
Eudicot unidentified 1	-	AHL	1	0	100	1.7	0.09	1	-	-	-	-	-	NC
<i>Miconia hyemalis</i> A St-Hil & Naudin	Melastomataceae	AHL	1	0	100	1.7	0.09	-	1	-	-	-	-	Furtado 246
<i>Myrceugenia ovata</i> (Hook & Arn) Oberg	Myrtaceae	AHL	1	0	100	1.7	0.09	1	1	-	-	-	-	NC
Orchidaceae unidentified	Orchidaceae	CHL	1	0	100	1.7	0.09	1	1	-	-	-	-	NC
<i>Peperomia</i> cf. <i>glabella</i> (Sw.) A.Dietr.	Piperaceae	CHL	1	0	100	1.7	0.09	-	1	1	-	-	-	Furtado 202
<i>Chusquea</i> sp.	Poaceae	AHL	1	0	100	1.7	0.09	1	-	-	-	-	-	Furtado 254
<i>Tillandsia gardneri</i> Lindl.	Bromeliaceae	CHL	1	0	100	1.7	0.09	-	1	1	1	1	1	NC
<i>Tillandsia recurvata</i> L.	Bromeliaceae	CHL	1	100	0	1.7	0.09	-	-	-	-	-	1	Furtado 222
<i>Tillandsia tenuifolia</i> L.	Bromeliaceae	CHL	1	0	100	1.7	0.09	-	-	1	-	-	-	Furtado 67
<i>Vittaria lineata</i> (L.) Sm.	Pteridaceae	CHL	1	0	100	1.7	0.09	-	-	1	1	1	-	Furtado 136
<i>Vriesea</i> sp.	Bromeliaceae	CHL	1	0	100	1.7	0.09	-	-	1	-	-	-	NC

The highest number of occurrences are highlighted in bold

The species are ordered according to the values of Frequency

Biotopes—Pat.: percentage of occurrence in the patches; All. For.: percentage of occurrence in the alluvial forest

Voucher: specimens deposited at Herbarium CESJ of Universidade Federal de Juiz de Fora (Thiers 2013)

EC ecological categories, AHL accidental holoepiphytes, CHL characteristic holoepiphytes, FHL facultative holoepiphytes, HEM hemiepiphytes, TO total of occurrences upon the phorophytes for each epiphytic species, AF absolute frequency, RF relative frequency, Strata occurrence of the vascular epiphytes in each stratum

\* *Octomeria* sp. encompasses three species, because it is not possible to identify when is sterile

\*\* *Hadrolaelia coccinea* and *H. mantiqueirae* also were considered as only one morphospecies due to the difficulty of delimitation when are sterile



**Table 2** Composition of vascular epiphytes on *Podocarpus lambertii* in the studied biotopes, according to evolutionary lineages and families

Biotopes	Evolutionary Lineages	<i>N</i>	%	Families	<i>NG</i>	<i>NS</i>	% spp.			
Patches	Lycophytes	1	1.7	Lycopodiaceae	1	1	1.7			
				Monillophytes	19	31.7	Aspleniaceae	1	2	3.3
							Dryopteridaceae	2	2	3.3
							Polypodiaceae	9	15	25
	Magnoliids	4	6.7	Piperaceae	1	4	6.7			
	Monocotyledons	31	51.7	Bromeliaceae	4	7	11.7			
				Orchidaceae	11	24	40			
				Eudicotyledons	5	8.3	Cactaceae	1	2	3.3
	Alluvial Forest	Lycophytes	3	3.8	Lycopodiaceae	1	3	3.8		
					Monillophytes	25	31.3	Aspleniaceae	1	3
		Magnoliids	6	7.5	Dryopteridaceae			2	3	3.8
					Hymenophyllaceae	1	1	1.3		
					Polypodiaceae	10	17	21.3		
		Eudicotyledons	12	15	Pteridaceae	1	1	1.3		
Piperaceae					1	6	7.5			
Bromeliaceae					4	7	8.8			
Orchidaceae					12	26	32.5			
<b>Poaceae</b>					1	1	1.3			
<b>Asteraceae</b>	1				1	1.3				
Cactaceae	1				2	2.5				
Gesneriaceae	1				2	2.5				
<b>Melastomataceae</b>	1	1	1.3							
<b>Myrtaceae</b>	1	1	1.3							
<b>Primulaceae</b>	1	1	1.3							
<b>Ranunculaceae</b>	1	1	1.3							
Solanaceae	1	1	1.3							
<b>Indeterminada</b>	2	2	2.5							
Total spp.						80				

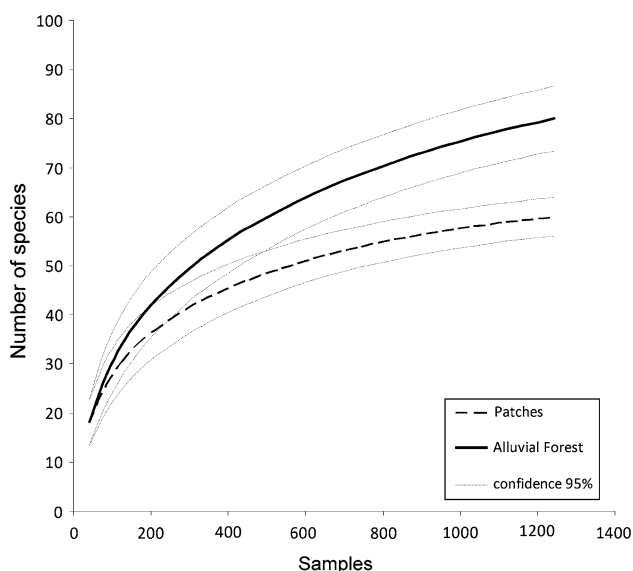
Families in bold are those represented only by accidental holoeipiphytes species

*N* number of species of evolutionary lineages, *NG* number of genera, *NS* number of species of each family

The richness between the strata ranged from 52 (stratum A) to 63 species (stratum B) and the Kruskal–Wallis test showed no difference between the strata ( $H = 2.357$ ,  $H_c = 2.483$ ,  $P = 0.6476$ ). Similarly, the Hutcheson *t* test showed no significant difference between the diversity indices of the strata ( $P > 0.05$  in all cases) (Fig. 16). However, some species were more frequent in only one stratum, such as *Hymenophyllum polyanthos*, with 62 % occurrence in stratum A, and *Octomeria* species, which in general were found more often in stratum E (*O. crassifolia* 51 %, *O. geraensis* 95 %, *O. ochroleuca* 94 %, *O. wawrae* 100 % and *Octomeria* sp. 41 %). Accidental holoeipiphytes occurred with a frequency of 68 % in strata A and B and 45 % in stratum A. The Pearson coefficient showed a strong positive correlation with the occurrence of *Aechmea*

*distichantha* and *Pecluma pectinatiformis* in each stratum ( $r = 0.98$ ,  $P = 0.004$ ).

The ecological categories of the species associated with the phorophytes were represented by 73 characteristic holoeipiphytes (CHL), nine accidental holoeipiphytes (AHL), six facultative holoeipiphytes (FHL) and only one hemiepiphyte (HEM) (Table 1). Notably, all recorded AHL were found in the alluvial forest and were dominated by eudicotyledons: Asteraceae, Melastomataceae, Myrtaceae, Poaceae, Primulaceae and Ranunculaceae, in addition to specimens of two unidentified families. The only exception was *Hapalorchis micranthus*, an Orchidaceae. These AHL species tended occur in strata A and B (except for *Myrsine umbellata* and unidentified Eudicot 2).



**Fig. 14** Rarefaction curves comparing the species richness in the alluvial forest (solid line) and patch (dashed line) biotopes. Dotted lines correspond to the confidence limit of 95 %

## Discussion

The richness and diversity found in this study are remarkable, even when compared to studies performed with more than one species of phorophyte. The values obtained are higher than those recorded in the MOF of the Southern Region, where equal or greater numbers of sampled phorophytes were analysed (Kersten and Silva 2002; Kersten et al. 2009; Waechter 2009; Bernardi and Budke 2010; Geraldino et al. 2010), or studies that evaluated only one species of phorophyte in different vegetation formations (Werneck and Espírito-Santo 2002; Gonçalves and Waechter 2003; Silva et al. 2008; Ferreira 2011). In general, only some areas of the DOF (Schütz-Gatti 2000; Petean 2009; Kersten and Waechter 2009) and the “Restinga” (Waechter 1992; Kersten and Silva 2006) showed higher values of richness and/or diversity. These data to some extent contradict the compilation of Kersten (2010), which asserts that the MOF is much more species-poor than other physiognomies, since Table 3 shows several areas poorer than we found in the present study. A reason for the observed richness could be the fact that the MOF in the PESP is probably much more conserved than those in the Southern Region, although the small extension of the surveyed area must also be highlighted.

However, the studied MOF areas were at altitudes below 1200 m. a.s.l.; thus, to date, the PESP is the studied area with the highest elevation (higher than 1600 m a.s.l.). This is one factor that is responsible for the higher richness and diversity values than those in the

MOF, since the mountainous ranges act as refugia for the regional flora, as well as hosting endemic species (Chaverri-Polini 1998; Safford 1999; Martinelli 2007), due to their discontinuous geographic distribution, which is responsible for the isolation of species and restriction of gene flow between populations (Barbará et al. 2007). Also, the cloud forests, like the studied area, have continuous or intermittent cloud cover, which is responsible for the horizontal precipitation, providing high humidity that is important for the occurrence of epiphytes (Hamilton et al. 1995; Nieder et al. 2001).

In addition, these observations suggest the contribution of altitude to the diversity of vascular epiphytes in montane cloud forests of the Neotropical Region, which frequently attain peaks of richness at similar altitudes (Hietz and Hietz-Seifert 1995; Krömer et al. 2005; Cardelús et al. 2006). Regarding the AF, Tonhasca Jr. (2005) highlights the occurrence of high richness and abundance of vascular and avascular epiphytes in cloud forests above 700 and 1500 m a.s.l. in the Southern and Southeastern regions, respectively. On the other hand, Blum et al. (2011) found the highest richness at altitudes between 400 and 500 m a.s.l. in the DOF of Serra da Prata (Paraná), and the lowest richness at 1000–1100 m.s.m., which were the highest altitudes of their study. However, it is possible that the high latitude and consequently low temperature of Serra da Prata, including the occurrence of frosts in winter, have restrained the development of vascular epiphytes, reducing their richness (Nieder et al. 2001). Another factor, suggested by Blum et al. (2011), is that the reduced size of phorophytes at highest elevations results in a reduced availability of substratum for epiphytes. Since this is the only study to deal with the elevation gradient of vascular epiphytes in the AF, more data are necessary to draw other conclusions about the existence in this phytogeographic domain of the same pattern observed in the Neotropical Region. Because large knowledge gaps exist concerning the flora of the extensive Serra da Mantiqueira mountain range that contains the study area (Stehmann and Sobral 2009), this diversity could potentially increase as more locations are studied.

The high richness of monocotyledons was expected, although the proportion was lower than that found in the AF by Kersten (2010) (50.5 vs. 65 %) due to the increased richness of other lineages, especially monilophytes (with 28.1 % of the recorded species in the PESP, compared with 15.4 % in the AF). Regarding the composition of the families, the observed result agrees to some extent with the pattern found for the Neotropical region (Gentry and Dodson 1987) and the AF (Kersten 2010), with the Orchidaceae, Polypodiaceae and Bromeliaceae being among the richest families. Two major differences were observed: the first concerns the

**Table 3** Comparison between the values of Shannon diversity index ( $H'$ ) recorded in studies conducted in the Southern and Southeastern regions of Brazil

Locality	State	Altitude (m)	Vegetation	NF	NS	$H'$	$J$	Source
Antonina	PR	20–50	DOF	55	138	4.54	0.92	Petean (2009)
Guaraqueçaba	PR	25–930	DOF	30	173	4.43	0.91	Schütz-Gatti (2000)
Piraquara	PR	900–1020	DOF	60	140	4.07	0.88	Kersten and Waechter (2009)
Torres	RS	0	RES	60	93	4.05	0.89	Waechter (1992)
<b>PESP*</b>	<b>MG</b>	<b>1600–1700</b>	<b>MOF</b>	<b>60</b>	<b>89</b>	<b>3.87</b>	<b>0.86</b>	<b>Present study</b>
Orleans/Grão-Pará	SC	400–1480	DOF	120	85	3.81	0.85	Padilha (2014)
Ilha do Mel	PR	0	RES	98	103	3.72	0.85	Kersten and Silva (2006)
Ilha do Mel	PR	0	RES	100	77	3.61	0.78	Kersten and Silva (2001)
Terra de Areia	RS	20	RES	60	77	3.52	–	Gonçalves and Waechter (2002)
Eldorado do Sul	RS	40	SSF	60	57	3.43	0.87	Giongo and Waechter (2004)
Criciúma	SC	30	DOF	60	65	3.33	0.86	Oliveira et al. (2013)
Campo Mourão*	PR	630	SSF, MOF	80	43	3.17	0.86	Geraldino et al. (2010)
Osório	RS	20	RES	60	53	2.99	0.87	Waechter (1998)
Arroio do Sal	RS	0	RES	8	25	2.93	0.91	Becker et al. (2013)
Taim	RS	0	RES	60	24	2.88	0.91	Waechter (1992)
Muitos Capões*	RS	930	MOF	60	31	2.88	0.83	Waechter (2009)
Ouro Preto	MG	920–1490	SSF	231	35	2.77	–	Ferreira (2011)
Guarapuava/Pinhão1*	PR	1100–1200	MOF	90	55	2.75	0.78	Kersten et al. (2009)
Araucária*	PR	900	MOF	110	49	2.71	0.77	Kersten and Silva (2002)
Guarapuava/Pinhão2*	PR	1100–1200	MOF	90	55	2.55	0.77	Kersten et al. (2009)
Erechim (borda)*	RS	770	SSF, MOF	228	20	2.38	0.78	Bernardi and Budke (2010)
Erechim (interior)*	RS	770	SSF, MOF	271	20	2.27	0.75	
FloNa de Ipanema	SP	550–970	SSF	270	21	2.27	0.71	Bataghin et al. (2010)
Ivinhema	MS	240	SSF	199	24	2.24	0.71	Tomazini (2007)
Maringá	PR	540	SSF	90	21	1.11	0.82	Dettke et al. (2008)

The present study is highlighted in bold

\* Areas whose vegetation is composed by Mixed Ombrophilous Forest States

MG Minas Gerais, MS Mato Grosso do Sul, PR Paraná, RS Rio Grande do Sul, SC Santa Catarina. Vegetation SSF seasonal semideciduous forest, DOF dense ombrophilous forest, MOF mixed ombrophilous forest, RES *Restinga* (sandy coastal forest), NF number of phorophytes, NS number of recorded species,  $H'$  Shannon diversity index,  $J$  Pielou evenness index

**Table 4** Diversity index calculated for biotopes

Indices	Expected value	Biotopes		$P$
		Patches	Forest	
$S$	–	60	80	–
$H'$	–	3.64	3.86	>0.05
$J$	–	0.88	0.89	–
$\Delta$	82.37	74.25	77.11	–
$\Delta^*$	75.84	76.62	79.18	–
$\Delta^+$	78.61	76.85	79.50	>0.05
$\Lambda^+$	–	643.06	552.66	–

$S$  species richness,  $H'$  Shannon index,  $J$  Pielou index,  $\Delta$  taxonomic distinction,  $\Delta^*$  taxonomic diversity,  $\Delta^+$  average taxonomic distinction,  $\Lambda^+$  variation in taxonomic distinction

ranking of the families, since the Bromeliaceae contains more epiphytic species than the Polypodiaceae, both in the AF and in the Neotropical region (Gentry and Dodson

1987; Kersten 2010), and the second concerns the absence of the Araceae among the richest families in the PESP, since no species were recorded in the present study. The reduced richness of Bromeliaceae and the absence of Araceae contributed to the reduction in monocotyledons among the lineages.

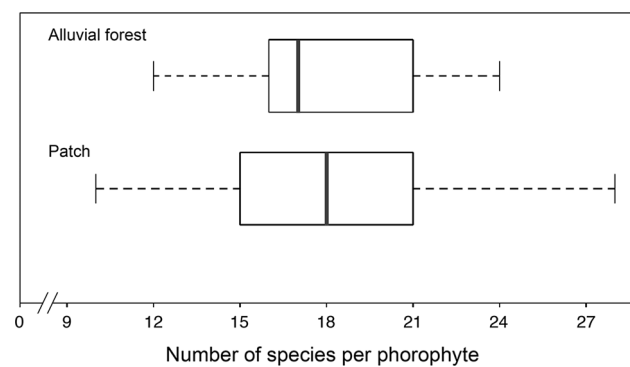
The first difference consists of a substitution in the second and third positions among the Bromeliaceae and Polypodiaceae between areas, as highlighted by Alves and Menini Neto (2014), whereas Piperaceae and Araceae commonly alternate as the fourth and fifth richest families. The second difference, the absence of the Araceae, is due to its low representation in the MOF, as highlighted by Kersten (2010), which positions it as the tenth-largest family in this physiognomy of the AF. The reduced richness of the Bromeliaceae in both biotopes and the absence of the Araceae also contributed to the smaller number of monocotyledon species.

**Table 5** Comparison between the five most frequent species in studies conducted in mixed ombrophilous forest in Brazil

Source	1st	2nd	3rd	4th	5th
1*	<i>Pleopeltis macrocarpa</i>	<i>Aechmea distichantha</i>	<i>Serpocaulon catharinae</i>	<i>Pecluma pectinatiformis</i>	<i>Rhipsalis floccosa</i>
2 <sup>+</sup>	<i>Microgramma squamulosa</i>	<i>Pleopeltis angusta</i>	<i>Capanemia australis</i>	<i>Peperomia catharinae</i>	<i>Pleopeltis hirsutissima</i>
3 <sup>+</sup>	<i>Microgramma squamulosa</i>	<i>Campyloneurum austrobrasillianum</i>	<i>Pleopeltis hirsutissima</i>	<i>Aechmea recurvata</i>	<i>Pleurothallis sonderana</i>
4 <sup>+</sup>	<i>Microgramma squamulosa</i>	<i>Pleopeltis pleopeltifolia</i>	<i>Pleopeltis hirsutissima</i>	<i>Peperomia catharinae</i>	<i>Capanemia australis</i>
5 <sup>+</sup>	<i>Vriesea friburgensis</i>	<i>Pleopeltis hirsutissima</i>	<i>Microgramma squamulosa</i>	<i>Serpocaulon catharinae</i>	<i>Hymenophyllum polyanthos</i>
6 <sup>#</sup>	<i>Campyloneurum austrobrasillianum</i>	<i>Pleopeltis angusta</i>	<i>Microgramma squamulosa</i>	<i>Tillandsia aeranthos</i>	<i>Pleopeltis hirsutissima</i>
7 <sup>#</sup>	<i>Peperomia trineuroides</i>	<i>Microgramma squamulosa</i>	<i>Lepismium cruciforme</i>	<i>Peperomia delicatula</i>	<i>Billbergia nutans</i>
8 <sup>+</sup>	<i>Microgramma squamulosa</i>	<i>Pleopeltis angusta</i>	<i>Tillandsia loliacea</i>	<i>Tillandsia recurvata</i>	<i>Pecluma sicca</i>

Source: 1) Present study; 2) Kersten and Silva (2002); 3) Kersten et al. (2009); 4) Kersten and Kuniyoshi (2009); 5) Kersten and Waechter (2009); 6) Waechter (2009); 7) Bernardi and Budke (2010); 8) Geraldino et al. (2010)

\* Minas Gerais (Southeastern Region); <sup>+</sup> Paraná, and <sup>#</sup> Rio Grande do Sul (Southern Region)



**Fig. 15** Comparison of parameters of species richness in the alluvial forest and patch biotopes. Box plots show median values (solid lines inside the boxes), 50th percentile values (box outline) and extreme values (whiskers)

The absence of the Araceae also implied a lower representation of the ecological category of HEM, since only *Dysochroma viridiflorum* (Solanaceae) was recorded. The AHL were more prominent and, as demonstrated by Kersten (2006), this result is consistent with those from more detailed surveys. Species without epiphytic adaptations establish in environments with a high humidity with relative ease (Benzing 1990), which might explain the representation of this category in the present study. Furthermore, all the AHL species were found in the alluvial forest, which is moister than the patches, because in addition to the occurrence of fog, it is located nearer to the brook.

The high value of  $J$  indicated a great uniformity in the analysed community, and 86 % of the hypothetical maximum diversity ( $H'$ ) was obtained. Additionally, the 92

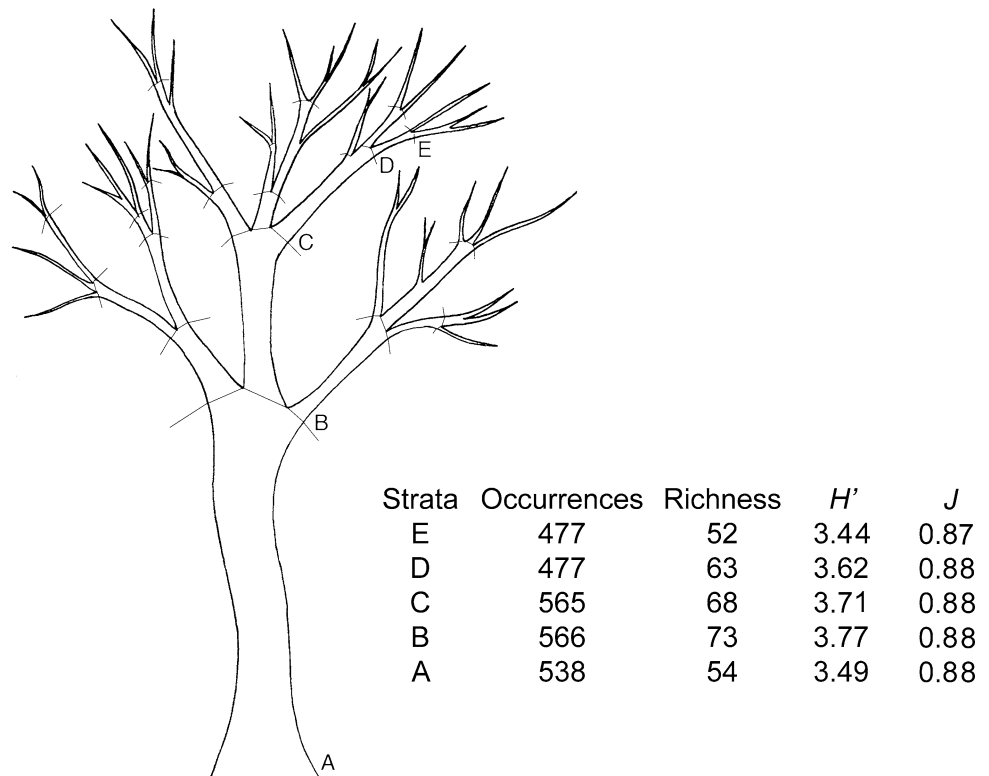
recorded species represented about 67 % of the diversity found in the floristic survey (138 spp.) (Furtado and Menini Neto, unpublished data) that was conducted on all phorophyte species. To date, no single phorophyte species that was studied in the Atlantic domain (Gonçalves and Waechter 2003; Ferreira 2011) has revealed such diversity and richness as *P. lambertii*, which highlights the ecological importance of this species.

The number of vascular epiphytes that a single specimen of *P. lambertii* can host is striking. The maximum value (28 spp.) represents 30 % of all species recorded in the present study and 20 % of the total found in the floristic survey (Furtado and Menini Neto, unpublished data). The extreme values of minimum and maximum richness found on a single phorophyte specimen were higher than those recorded by Kersten and Silva (2001) and Kersten (2006) in Ilha do Mel, Paraná, in DOF, “Restinga” and mangrove vegetation, by Kersten et al. (2009) in the Rio Iguaçu basin, Paraná in the MOF, and by Ferreira (2011), in the Serra da Brígida, Minas Gerais in a seasonal semideciduous forest.

Despite the absence of significant differences among the calculated diversity indices in both biotopes, variations in the microenvironment (for example, the higher humidity in the alluvial forest) probably influence the composition of epiphytic flora, since 38 out of 89 species occur exclusively in one of the biotopes, even on a single phorophyte species. In addition, several species that occur in both biotopes were recorded asymmetrically (with a much greater frequency in one biotope), indicating some sensitivity to microsite variations between the environments. Therefore, the biotopes are structurally similar, although they contain differences at the species level, but no major differences at



**Fig. 16** Distribution of strata and results of the parameters analysed for each stratum



other taxonomic levels, except in families, since the alluvial forest presented 18 families versus 10 families occurring in patches. This difference is to a large extent responsible for the higher value of variation in taxonomic distinction due to the concentration of species in two families, Orchidaceae and Polypodiaceae.

The most frequently occurring species often showed a higher frequency in one biotope, even when they were present in both biotopes. One example is *Oncidium gardneri*, an Orchidaceae species with well-developed pseudobulbs that can store large quantities of water and was present in the patches with a frequency of 89.5 %. These data reinforce the influence of variations in the microclimate on the richness (Cox and Moore 2011) and, consequently, on species conservation, by applying knowledge that can help to conserve species that show some habitat preferences. Another example is the morphotype *Hadrolaelia coccinea*/*H. mantiqueirae*, which suffers collection pressure due to its ornamental flowers. *H. coccinea* is threatened at the state level (Drummond et al. 2008) but showed a frequency of 75 % in the patches, which are isolated and more exposed to anthropic disturbances such as cattle and fire.

In general, the reason for differences among strata is the humidity and light gradient between the ground and the canopy (Benzing 1990). The analysis showed no difference in richness or diversity among the strata of the sampled phorophytes. Two reasons for this might be: (1) light is not

limiting in either biotope, since the density of the canopy in the alluvial forest is reduced and only slightly hinders the entrance of light; however, in the patches, which possess no canopy, the only barrier to light is the crown of the phorophyte; (2) there is no marked humidity gradient between the ground and canopy due to the presence of watercourses within the alluvial forest as well as the fog that results from the high altitude, which also provides humidity from the horizontal precipitation to the patches in the “campo de altitude”. The epiphytic community itself contributes to the maintenance of such humidity, according to Benzing (1990), especially tank bromeliads such as *Aechmea distichantha* and *Vriesea sceptrum*, two of the most common species in the present study.

With the exception of *Serpocaulon catharinae* (Polypodiaceae), the most frequent species differed from those found in other areas with the same physiognomy. This was also observed in the composition of genera, highlighting the uniqueness of the studied area regarding the epiphytic community. The presence of *Microgramma squamulosa* (Polypodiaceae) is notable, because it is among the three most frequent species in all other studies performed in the MOF and is also common in seasonal forests (Gonçalves and Waechter 2002; Giongo and Waechter 2004; Ferreira 2011). In the studied area, *M. squamulosa* occupies the thirteenth position in terms of frequency, although it occurs in all strata, and represents only 25 % of occurrences within the alluvial forest. It is widely distributed in South

America (Almeida 2014) and is often present in several communities of vascular epiphytes, regardless of their degree of conservation. The high richness and abundance of other species can influence and limit the occurrence of *M. squamulosa*, especially in the forest environment, and maintain this species at a lower frequency than that usually observed. Furthermore, *Microgramma* shows a lower richness and abundance at higher altitudes and is more frequent at intermediate altitude sites with high moisture content (T.E. Almeida, personal communication). Thus, although the humidity is high in the PESP, the high altitude limits the frequency of *M. squamulosa* as well as the size of the population.

*Pecluma pectinatiformis* (Polypodiaceae) and *Aechmea distichantha* (Bromeliaceae) were among the most frequent species and showed a close relationship, since almost all observed specimens of either species were found close to one another. The correlation for the occurrence of both species suggests that this relationship appears to be one of ecological facilitation. It is possible that *A. distichantha* may be responsible, playing a role commonly attributed to species of tank bromeliad, the so-called nurse plants (Benzing 1990), through retention of humidity or nutrients in the site of their fixation on the bark of phorophyte. A more specific study can elucidate this possibility.

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