

Diversity, vertical structure and floristic relationships of vascular epiphytes in an urban remnant of the Brazilian Atlantic Forest

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ABSTRACT - (Diversity, vertical structure and floristic relationships of vascular epiphytes in an urban remnant of the Brazilian Atlantic Forest). This study was conducted in a fragment of montane seasonal semi-deciduous forest (Minas Gerais State) with a history of anthropogenic disturbance. Our goals were to characterise the composition, structure and floristic diversity of vascular epiphytes and to investigate the floristic similarities of the community with other areas of urban seasonal forests in Brazil. We sampled 61 phorophytes with 47 epiphytic species. The richest families were Bromeliaceae (seven) and Polypodiaceae (seven). The most common ecological category was accidental holoepiphytes with 21 species - an unprecedented result for the Neotropical region. The Shannon index was 2.95 and the Pielou evenness index 0.77, showing a relatively high diversity with a few dominant species and numerous rare species. Similarity analyses showed a longitudinal gradient and strong influence of the distance from the ocean on floristic relationships as well as influence of dense ombrophilous forests on the composition of the vascular epiphytes of the surveyed area.

Keywords: accidental holoepiphytes, biodiversity hotspot, multivariate analyses, taxonomic diversity, urban forest

RESUMO - (Diversidade, estrutura vertical e relações florísticas de epífitas vasculares em um remanescente urbano da Floresta Atlântica brasileira). Este estudo foi realizado em um fragmento de floresta estacional semidecidual montana (Minas Gerais) com histórico de perturbação antrópica. Os objetivos foram caracterizar a composição, estrutura e diversidade florística das epífitas vasculares e investigar a similaridade florística da comunidade com outras áreas de florestas estacionais urbanas no Brasil. Foram amostrados 61 forófitos e registradas 47 espécies de epífitas. As famílias mais ricas foram Bromeliaceae (sete) e Polypodiaceae (sete). A categoria ecológica mais comum foi a de holoepífitas acidentais com 21 espécies - um resultado inédito na Região Neotropical. O índice de Shannon foi 2,95 e o índice de uniformidade de Pielou foi 0,77, mostrando diversidade relativamente alta com certa dominância de poucas espécies, enquanto as espécies raras foram numerosas. Análises de similaridade mostraram gradiente longitudinal e forte influência da distância do oceano sobre as relações florísticas, assim como influência das florestas ombrófilas densas sobre a composição das epífitas vasculares na área estudada.

Palavras-chave: análises multivariadas, diversidade taxonômica, floresta urbana, holoepífitas acidentais, “hotspot” de biodiversidade

Introduction

Tropical forests are characterised by warm and humid climates with little variation of temperature and marked stratification (Ricklefs 2011). In terms of epiphytes, they are the richest forests in the world, amassing more than 60% of all species (Biedinger & Fischer 1996). However, due to population growth and the need for territorial expansion, these forests are heavily fragmented, reinforcing the importance

of maintaining remnants in urban areas. Such urban forests are considered important agents of the local microclimate “by reducing the pollution and maintaining the temperature”, and they present great aesthetical value and importance to human welfare (Bolund & Hunhammar 1999, Bonametti 2003, Mckinney 2008). Urbanisation results in disturbance, and changes in the environmental conditions are evident and conducive to biotic modifications, for instance, in species composition (Mckinney 2008).

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However, few scientific studies have concentrated on urban environments (Marris 2009).

Vascular epiphytes are plants not connected to the soil or connected during only one life stage, using the phorophytes as support without parasitizing them through haustoria (Madison 1977). This synusia has great ecological importance, providing resources, such as fruits, nectar, pollen and water to the fauna and microhabitats to several animal groups (Benzing 1990). Vascular epiphytes are represented by about 29,000 species, or 10% of all vascular flora, distributed in 876 genera and 84 families (Zotz 2013). Globally seen, the Orchidaceae, Araceae and Bromeliaceae are the richest families (Gentry & Dodson 1987, Zotz 2013). The Brazilian Atlantic forest, an important global biodiversity hotspot (Myers *et al.* 2000), exhibits similar configuration of the richest epiphyte families, with about 2,256 species, mainly distributed in the Orchidaceae (46.5%), Bromeliaceae (26.2%), Polypodiaceae (4.3%) and Araceae (4.2%) (Freitas *et al.* 2016).

Knowledge about this synusia in Brazilian urban environments must still be considered as scarce, although a growing number of studies have been published in the last ten years, but concentrated in Brazil's South Region (*e.g.*, Dislich & Mantovani 1998, Dittrich *et al.* 1999, Gonçalves & Waechter 2003, Borgo *et al.* 2002, Fabricante *et al.* 2006, Hefler & Faustioni 2004, Dettke *et al.* 2008, Geraldino *et al.* 2010, Oliveira *et al.* 2013, Alves *et al.* 2014, Becker *et al.* 2015, Furtado & Menini Neto 2015). This reflects our knowledge about the epiphytic flora as a whole, since the majority of studies have also been conducted in South Brazil (Kersten 2010). Since a reduction of the anthropogenic pressure on the environment is rather unlikely in the near future (Hietz 1999), the composition of epiphytes needs to be investigated in different environments, such as isolated trees, plantations and urban forests, in order to develop effective conservation strategies.

Thus, the present study was conducted in order to expand our knowledge about the epiphytic flora in urban environments in Brazil's Southeastern Region. The municipality of Juiz de Fora, located southeast of Minas Gerais, represents a suitable area to perform such a study. It is well connected to the other regions of the Serra da Mantiqueira and integrates the Corredor Sudeste (southeastern corridor) of the Atlantic Forest, which characterises it as a region of "very high" biological importance (Drummond *et al.* 2005).

This study aimed to contribute to our knowledge about epiphytic synusia in an urban forest through characterisation of the composition, structure and floristic diversity of vascular epiphytes in a remnant of a seasonal semi-deciduous forest in the Atlantic domain. In addition, we investigated the floristic similarity of this community with other areas composed of urban seasonal forests in the same phytogeographic domain. Based on data available in the literature, we tested the following hypotheses: 1) the study area has low richness and diversity of epiphytic species, suggesting that urban areas tend to be more susceptible to human impacts (McKinney 2006, 2008); 2) the specific and generic composition and the proportion of ecological categories tend to be similar between urban areas as some species are more tolerant to anthropogenic stresses (Barthlott *et al.* 2001, Bermudez *et al.* 2009); 3) Because humidity is an important factor for the establishment of epiphytes (Johansson 1974, Benzing 1990), the areas closer to the ocean are clustered by separating those that are farther away from the ocean.

Materials and methods

Study area - The study was conducted at the edge of an urban fragment of secondary montane seasonal semi-deciduous forest (SSF) (Veloso *et al.* 1991) in altitudes ranging from 670-750 m.s.m. in an area of about 87 ha belonging to the Botanical Garden of the Federal University of Juiz de Fora in the municipality of Juiz de Fora, Zona da Mata of Minas Gerais (21°44'S, 43°22'W) (figure 1). This fragment is close to the environmental protection area Mata do Krambeck (MK) which encompasses about 300 ha and is composed of continuous secondary forest on a former coffee crop plantation. Regeneration processes have been taking place for the last 70 years, although the area is frequently under strong anthropogenic pressure from the surrounding municipalities, such as selective logging and introduction of exotic species (Fonseca & Carvalho 2012).

According to the Köppen classification, the climate in the region is Cwa, with dry and cold winters and rainy and warm summers. Mean annual rainfall is about 1,500 mm, with higher rates during January (~300 mm) (PMJF 2014). Mean annual temperature is about 18.9 °C, the hottest and coldest months are February (21.7 °C) and July (16.1 °C), respectively (PJF 2014).



Figure 1. Location of the Mata do Krambeck and the other 10 areas used in multivariate analyses.

Field and laboratory work - Field surveys were conducted from August to November 2013. We analysed the 61 largest phorophytes around a lake and marsh in an area of about 31,000 m². The phorophytes belonged to several species, both native and cultivated (exotic or native) (table 1). Plants were collected and herborised using common methodologies and were identified through analysis of previous collections deposited in the CESJ Herbarium of the Federal University of Juiz de Fora (acronym according to Thiers 2016), specialised literature and consultation with specialists.

The phorophytes were analysed using a methodology adapted from Johansson (1974) and the trees were divided into four strata: A) trunk base: from the base of the bole up to 50 cm from the soil; B) trunk top: from 50 cm up to the first ramification; C) internal crown: the first ramification of the crown; and D) external crown: the remaining part of the crown. The epiphytes were classified into four ecological categories according to the relationship with the phorophyte, as proposed by Benzing (1990): characteristic holoepiphytes (CHLs), facultative holoepiphytes (FHLs), accidental holoepiphytes (AHLs), and hemiepiphytes (HEMs).

Geographic distribution of the species was obtained by consulting the BFG's database (2015) and five patterns of distribution were observed: 1) endemic to the Atlantic forest; 2) occurring in the Cerrado and the Atlantic forest; 3) disjunct between the Amazon

and the Atlantic forest; 4) occurring in the three or more phytogeographic domains (wide distribution); and 5) exotic, invasive and/or cultivated.

Statistical analyses - The calculated parameters are relative and absolute frequencies (conducted in Microsoft Office Excel 2007), Shannon diversity index (H') and Pielou evenness (J) for the total and for each stratum [(in Past v. 3 (Hammer *et al.* 2001)]. In addition, we calculated indices of taxonomic diversity (Δ), taxonomic distinction (Δ^*), average taxonomic distinction (Δ^+) and variation in taxonomic distinction (Δ^+) for each stratum according to Clarke & Warwick (1998, 2001), using the R package (R Core Team 2014).

We constructed a matrix of presence (1) and absence (0) with 238 species of vascular epiphytes from 11 areas of seasonal forests of the Atlantic forest (figure 1, table 2). The matrix was used in cluster and ordination analyses, respectively, using UPGMA (Unweighted Pair Group Method with Arithmetic Mean) and PCoA (Principal Coordinate Analysis), both using the Jaccard index. Intraspecific, unidentified and accidental epiphytic taxa (given their occurrence was stochastic) were removed from multivariate analyses [conducted in Past v.3 (Hammer *et al.* 2001)].

A Mantel test, conducted in Past v.3 (Hammer *et al.* 2001), was applied to evaluate the correlation between floristic similarity (Jaccard index) and the geographic distances of the areas.

Table 1. Phorophytic species, origin and respective occurrences of epiphytic species.

Species	Families	Origin	NP	% P	NES
<i>Piptadenia gonoacantha</i> (Mart.) J.F. Macbr.	Fabaceae	native	13	21,3	19
<i>Cedrela fissilis</i> Vell.	Meliaceae	native	11	18,0	18
<i>Eryobotria japonica</i> (Thunb.) Lindl.	Rosaceae	exotic	8	13,1	11
Unidentified	-	-	5	8,2	22
<i>Ceiba speciosa</i> (A.St.-Hil.) Ravenna	Malvaceae	native	5	8,2	15
Fabaceae (unidentified)	Fabaceae	-	5	8,2	16
<i>Tibouchina granulosa</i> (Desr.) Cogn.	Melastomataceae	native	4	6,6	6
<i>Mangifera indica</i> L.	Anacardiaceae	exotic	1	1,6	5
<i>Syzygium cumini</i> (L.) Skeels	Myrtaceae	exotic	1	1,6	4
Arecaceae (unidentified)	Arecaceae	-	1	1,6	3
<i>Cupania emarginata</i> Cambess.	Sapindaceae	native	1	1,6	3
<i>Euterpe edulis</i> Mart.	Arecaceae	native	1	1,6	3
Sapindaceae (unidentified)	Sapindaceae	-	1	1,6	3
<i>Araucaria angustifolia</i> (Bertol.) Kuntze	Araucariaceae	native	1	1,6	2
<i>Alchornea triplinervia</i> (Spreng.) Müll.Arg.	Euphorbiaceae	native	1	1,6	1
<i>Syagrus</i> sp.	Arecaceae	-	1	1,6	1
<i>Syzygium jambos</i> Duthie	Myrtaceae	exotic	1	1,6	1

NP: number of phorophytic individuals; % P: percentage of total phorophytic individuals; NES: number of epiphytic species occurring upon the phorophytic species.

Results

We found 47 species belonging to 33 genera and 17 families (table 3). The richest families were Bromeliaceae and Polypodiaceae (seven species each), followed by Orchidaceae (five species) and Araceae (four species), which represented 23 species (about 48%) found in the study area. *Tillandsia* (Bromeliaceae) was the richest genus with four species, followed by *Pleopeltis* (Polypodiaceae) with three species. The majority of genera (26) were represented by only one species.

Geographic distribution of the identified species showed a predominance of widely distributed species occurring in two or more phytogeographic domains in Brazil (25 species, of which seven were restricted to the *Cerrado* and the Atlantic forest), while only seven species were endemic to the Atlantic forest and another seven were exotic (both cultivated and invasive, table 3).

The most common ecological category was the AHLs with 21 species, followed by the CHLs (19 species), HEMs (five species) and FHLs (two species) (table 3).

The Shannon index value (H') was 2.95 and the Pielou evenness index (J') 0.77. Both indices were

compared with those obtained in the SSF areas in southern and southeastern regions of Brazil (table 4).

Six species must be highlighted due to their occurrence on more than 10 phorophytes (figure 2). Table 5 shows the common occurrence of *Tillandsia*, *Microgramma* and *Pleopeltis* species in comparison with more frequent species found in studies conducted in SSF areas in the south and southeastern regions of Brazil.

We observed 432 occurrences in the strata distributed as follows: 49 in the trunk base, 101 in the trunk top, 115 in the internal crown and 167 in the external crown. Thus, the tree crown accounted for 65% of the records. The values of H' , J , Δ , Δ^* , Δ^+ and Λ^+ for each stratum are presented in table 6.

The presence and absence matrix showed that 11 species occurred in more than half of the areas: *Billbergia zebrina*, *Tillandsia recurvata*, *T. stricta* and *T. tricholepis* (Bromeliaceae); *Epiphyllum phyllanthus*, *Lepismium cruciforme* and *Rhipsalis cereuscula* (Cactaceae); *Miltonia flavescens*, *Oncidium pumilum* and *Polystachya estrellensis* (Orchidaceae); and *Microgramma squamulosa* (Polypodiaceae). Of these, only four were not recorded in the present study: *L. cruciforme*, *M. flavescens*, *O. pumilum* and *R. cereuscula*. We must highlight five species that were found in eight or more areas: *E. phyllanthus*,

Table 2. Localities used in the similarity analyses.

Areas (states)	Acronym	Altitude	Coordinates	N	Vegetation	Source
Mata do Krambeck, Juiz de Fora (MG)	mgmk	750 m	21°43'S, 43°22'W	24	SSF	Present study
Fazenda Fortaleza de Sant'Anna, Chácara (MG)	mgfs	850 m	22°00'S, 43°51'W	78	SSF	Barbosa <i>et al.</i> (2014)
Reserva Biológica da Represa do Gramma, Descoberto (MG)	mgrbrg	650 m	21°20'S, 42°55'W	69	SSF	Menini Neto <i>et al.</i> (2009b) Forzza <i>et al.</i> (2014)
Reserva da Cidade Universitária Armando de Salles Oliveira, São Paulo (SP)	spcuaso	750 m	23°33'S, 46°43'W	40	DOF/SSF	Dislich & Mantovani (1998) Gruppo & Pirani (2005)
Mata da Pavuna, Botucatu (SP)	sppav	700 m	22°54'S, 48°50'W	26	SSF	Biral & Lombardi (2012)
Estação Ecológica de Caetetus, Gália (SP)	spgal	600 m	22°24'S, 49°42'W	24	SSF	Breier (2005)
Parque Estadual do Rio Ivinhema, Ivinhema (MS)	msri	240 m	22°47'S, 53°32'W	25	SSF	Tomazini (2007)
Parque do Ingá, Maringá (PR)	prpi	550 m	23°25'S, 51°25'W	24	SSF	Detke <i>et al.</i> (2008)
Campo Mourão (PR)	prcm	480 m	23°57'S, 52°32'W	52	SSF/MOF	Geraldino <i>et al.</i> (2010)
Parque Estadual Vila Rica do Espírito Santo, Fênix (PR)	prpevr	440 m	23°54'S, 51°56'W	29	SSF	Borgo <i>et al.</i> (2002)
Estreito Augusto César, Marcelino Ramos (RS)	rsac	460 m	27°24'S, 51°27'W	59	SDF	Rogalski & Zanin (2003)

Vegetation - SSF: Seasonal Semideciduous Forest; DOF: Dense Ombrophilous Forest; MOF: Mixed Ombrophilous Forest; SDF: Seasonal Deciduous Forest.

L. cruciforme, *M. squamulosa*, *P. estrellensis* and *T. recurvata*.

Cluster analysis obtained a high cophenetic coefficient (0.91), exhibiting a good fit between the dendrogram and the presence and absence matrix. The dendrogram (figure 3) showed the formation of two groups, A and B. Group A was composed of the majority of areas located in Minas Gerais, except “spcuaso”, which is located in the State of São Paulo, and all four areas closer to the ocean compared to the areas of group B. The results of the PCoA (figure 4) reinforced the tendency of segregation between areas closer to the littoral (at the right hand side of the graphic, being the same group A of the dendrogram) from the inland areas (at the left hand side, which integrated group B of the dendrogram). The results of the Mantel test showed a weak non-significant, positive correlation between geographic distance and floristic similarity of the areas ($R = 0.139$; $p = 0.206$).

Discussion

Richness and geographic distribution - The most species-rich families in the MK (Bromeliaceae, Polypodiaceae, Araceae and Orchidaceae) share a common, similar status in several floristic and/or ecological surveys conducted on different forest physiognomies, both in the Atlantic forest (Waechter 1992, Dittrich *et al.* 1999, Kersten & Silva 2001, Kersten *et al.* 2009, Menini Neto *et al.* 2009a, Bianchi *et al.* 2012, Alves & Menini Neto 2014, Barbosa *et al.* 2014) and the Neotropical region (Catling & Lefkovitch 1989, Hietz & Hietz-Seifert 1995, Arévalo & Betancur 2004). These families are also the richest ones in terms of vascular epiphytes (Gentry & Dodson 1987, Benzing 1990, Zotz 2013).

However, the observed configuration in the Neotropical region, in which Orchidaceae is the richest family, often followed by Bromeliaceae (Linares 1999, Bussmann 2001, Rogalski & Zanin 2003, Arévalo & Betancur 2004, Giongo & Waechter 2004, Cervi & Borgo 2007, Menini Neto *et al.* 2009b, Ceja-Romero *et al.* 2010, Alves & Menini Neto 2014, Barbosa *et al.* 2014), is different in this study since Bromeliaceae and Polypodiaceae shared the first position (with seven species each) and Orchidaceae exhibited only five species.

Such results could be related to the anthropogenic disturbance in the studied area, since in urban environments of the Brazilian Atlantic forest, Orchidaceae often exhibit fewer species than

Table 3. List of vascular epiphytes recorded in this study, ecological category and analysed parameters.

Species	Families	EC	OP	Frequency		Strata				Voucher	
				AF	RF	GP	A	B	C		D
<i>Portea petropolitana</i> (Wawra) Mez	Bromeliaceae	FHL	45	73.77	16.36	1	7	16	25	31	Almeida 63
<i>Microgramma squamulosa</i> (Kaulf.) de la Sota	Polypodiaceae	CHL	36	59.01	13.09	1	3	18	27	27	Souza 346
<i>Billbergia horrida</i> Regel	Bromeliaceae	FHL	35	57.37	12.72	1	9	13	20	21	Silva 16
<i>Pleopeltis astrolepis</i> (Liebm.) E. Fourn.	Polypodiaceae	CHL	29	47.54	10.54	1	4	11	9	20	Menini Neto 1149
<i>Tillandsia stricta</i> Sol. ex Ker Gawl.	Bromeliaceae	CHL	19	31.14	6.90	4	0	3	10	18	Dias 12
<i>Polystachya estrellensis</i> Rchb.f.	Orchidaceae	CHL	13	21.31	4.72	4	2	1	1	12	Menini Neto 418
<i>Pleopeltis hirsutissima</i> (Raddi) de la Sota	Polypodiaceae	CHL	9	14.75	3.27	2	2	3	4	7	Menini Neto 1142
<i>Tillandsia recurvata</i> (L.) L.	Bromeliaceae	CHL	9	14.75	3.27	4	2	8	2	5	Menini Neto 417
<i>Billbergia zebrina</i> (Herb.) Lindl.	Bromeliaceae	CHL	8	13.11	2.90	1	2	2	3	3	Machado 74
<i>Tradescantia zebrina</i> Bosse	Commelinaceae	AHL	7	11.47	2.54	5	3	4	1	0	Silva 195
<i>Catasetum hookeri</i> Lindl.	Orchidaceae	CHL	6	9.83	2.18	4	0	1	1	5	CESJ 58803
<i>Ficus adhatodifolia</i> Schott	Moraceae	Hem	6	9.83	2.18	4	0	2	1	3	Silva 144
<i>Comparettia coccinea</i> Lindl.	Orchidaceae	CHL	4	6.55	1.45	2	0	0	0	4	Menini Neto 420
<i>Tillandsia tricholepis</i> Baker	Bromeliaceae	CHL	4	6.55	1.45	4	0	1	1	2	Dias 18
<i>Callisia repens</i> (Jacq.) L. *	Commelinaceae	AHL	3	4.91	1.09	5	3	0	0	0	Menini Neto 1144
<i>Epiphyllum phyllanthus</i> (L.) Haw.	Cactaceae	CHL	3	4.91	1.09	4	1	0	0	2	Gonzaga 39
<i>Phlebodium pseudoaureum</i> (Cav.) Lellinger	Polypodiaceae	CHL	3	4.91	1.09	4	0	1	1	1	Menini Neto 1154
<i>Impatiens walleriana</i> Hook.f. +	Balsaminaceae	AHL	2	3.27	0.72	5	1	1	0	0	Menini Neto 1141
<i>Microgramma vacciniifolia</i> (Langsd. & Fisch.) Copel.	Polypodiaceae	CHL	2	3.27	0.72	2	0	1	1	0	Menini Neto 1147
<i>Paspalum cf. nutans</i> Lam.	Poaceae	AHL	2	3.27	0.72	-	2	0	0	0	NC
<i>Serpocaulon catharinae</i> (Langsd. & Fisch.) A.R. SM.	Polypodiaceae	CHL	2	3.27	0.72	1	0	2	0	0	Souza 392
<i>Tillandsia polystachia</i> (L.) L.	Bromeliaceae	CHL	2	3.27	0.72	4	0	0	0	2	Machado 61
Unidentified 1	Asteraceae	AHL	2	3.27	0.72	-	0	2	0	0	NC
<i>Adiantopsis chlorophylla</i> (Sw.) Fée	Adiantaceae	CHL	1	1.63	0.36	2	0	1	0	0	Menini Neto 1146
<i>Hemionitis tomentosa</i> (Lam.) Raddi	Adiantaceae	AHL	1	1.63	0.36	2	0	0	1	0	Menini Neto 1145
<i>Alternanthera brasiliana</i> (L.) Kuntze	Amaranthaceae	AHL	1	1.63	0.36	4	0	1	0	0	Silva 155
<i>Epipremnum pinnatum</i> (L.) Engl. *	Araceae	Hem	1	1.63	0.36	5	1	1	0	0	Menini Neto 1153
<i>Monstera deliciosa</i> Liebm. *	Araceae	Hem	1	1.63	0.36	5	1	0	1	1	NC
<i>Syngonium angustatum</i> Schott *	Araceae	Hem	1	1.63	0.36	4	0	1	0	0	Silva 13

continue

Table 3 (continuation)

Species	Families	EC	OP	Frequency		Strata			Voucher									
				AF	RF	GP	A	B		C	D							
<i>Ageratum fastigiatum</i> (Gardn.) R.M. King & H. Rob.	Asteraceae	AHL	1	1.63	0.36	4	0	1	1	0	0	0	0	0	0	0	0	Memini Neto 1143
<i>Emilia sonchifolia</i> (L.) DC. ex DC.	Asteraceae	AHL	1	1.63	0.36	4	1	0	0	0	0	0	0	0	0	0	0	NC
<i>Drymaria cordata</i> (L.) Willd. ex Schult. +	Caryophyllaceae	AHL	1	1.63	0.36	5	0	1	0	0	0	0	0	0	0	0	0	Menini Neto 1150
<i>Commelina</i> sp.	Commelinaceae	AHL	1	1.63	0.36	-	0	1	0	0	0	0	0	0	0	0	0	NC
<i>Cedrela fissilis</i> Vell.	Meliaceae	AHL	1	1.63	0.36	4	0	0	1	0	0	0	0	0	0	0	0	Silva 57
<i>Campylocentrum linearifolium</i> Schltr. ex Mansf.	Orchidaceae	CHL	1	1.63	0.36	4	0	0	1	0	0	0	0	0	0	0	0	Souza 404
<i>Oncidium baueri</i> Lindl.	Orchidaceae	CHL	1	1.63	0.36	3	0	0	1	0	0	0	0	0	0	0	0	NC
<i>Dichantherium sciurotooides</i> (Zuloaga & Morrone) Davidse	Poaceae	AHL	1	1.63	0.36	2	1	0	0	0	0	0	0	0	0	0	0	NC
<i>Pleopeltis pleopeltifolia</i> (Raddi) Alston	Polypodiaceae	CHL	1	1.63	0.36	1	0	0	0	0	1	0	0	0	0	0	0	NC
<i>Solanum americanum</i> Mill.	Solanaceae	AHL	1	1.63	0.36	4	1	0	0	0	0	0	0	0	0	0	0	Almeida 69
<i>Solanum cernuum</i> Vell.	Solanaceae	AHL	1	1.63	0.36	2	0	1	0	0	0	0	0	0	0	0	0	Feliciano 15
<i>Thelypteris dentata</i> (Forssk.) E.P. St. John	Thelypteridaceae	AHL	1	1.63	0.36	4	0	1	0	0	0	0	0	0	0	0	0	Menini Neto 1148
<i>Urera baccifera</i> (L.) Gaudich.	Urticaceae	AHL	1	1.63	0.36	4	0	1	0	0	0	0	0	0	0	0	0	Menini Neto 1152
Unidentified 2	Araceae	Hem	1	1.63	0.36	-	1	1	1	1	1	1	1	1	1	1	1	NC
Unidentified 3	Poaceae	AHL	1	1.63	0.36	-	1	0	0	0	0	0	0	0	0	0	0	NC
Unidentified 4	Unidentified	AHL	1	1.63	0.36	-	0	0	0	0	1	0	0	0	0	0	0	NC
Unidentified 5	Unidentified	AHL	1	1.63	0.36	-	0	0	0	0	1	0	0	0	0	0	0	NC
Unidentified 6	Unidentified	AHL	1	1.63	0.36	-	1	0	0	0	0	0	0	0	0	0	0	NC

* Exotic cultivated species. + Naturalized species. EC, ecological category; CHL, characteristic holoeiphyte; AHL, accidental holoeiphyte; FHL, facultative holoeiphyte; HEM, hemieiphyte. OP, number of phorophytes with the presence of species; AF, absolute frequency; and RF, relative frequency. Strata: A, from the base of the bole up to 50 cm from soil; B, from 50 cm up to the first ramification, C, the first ramification of the crown; D, the rest of the crown. GP, patterns of geographic distribution: 1, endemic to Atlantic Forest; 2, occurring in "Cerrado" and the Atlantic Forest; 3, disjunct distribution between the Amazon and Atlantic Forests; 4, occurring in two or more phytogeographic domains; and 5, alien or cultivated species. Voucher deposited in the CESJ Herbarium (acronym according to Thiers [2014]). NC, not collected.

Table 4. Comparison between studies regarding vascular epiphytes conducted in areas of Seasonal Semideciduous Forest in the Atlantic Forest.

Locality	State	Vegetation	NP	NS	H'	J	Source
Campo Mourão	PR	SSF, MOF	80	43	3,17	0,86	Geraldino <i>et al.</i> (2010)
Krambeck	MG	SSF	61	47	2,95	0,77	Present study
Ouro Preto	MG	SSF	231	35	2,77	-	Ferreira (2011)
Erechim (borda)	RS	SSF, MOF	228	20	2,38	0,78	Bernardi & Budke (2010)
Erechim (interior)	RS	SSF, MOF	271	20	2,27	0,75	
FloNa de Ipanema	SP	SSF	270	21	2,27	0,71	Bataghin <i>et al.</i> (2010)
Ivinhema	MS	SSF	199	24	2,24	0,71	Tomazini (2007)
Maringá	PR	SSF	90	21	1,11	0,82	Dettke <i>et al.</i> (2008)

FloNa – National Forest. State – MG: Minas Gerais; MS: Mato Grosso do Sul; PR: Paraná; RS: Rio Grande do Sul; SP: São Paulo. Vegetation: SSF – Seasonal Semideciduous Forest; MOF – Mixed Ombrophilous Forest. NP: number of phorophytes. NS: number of species. H': Shannon diversity index. P: Pielou evenness index.

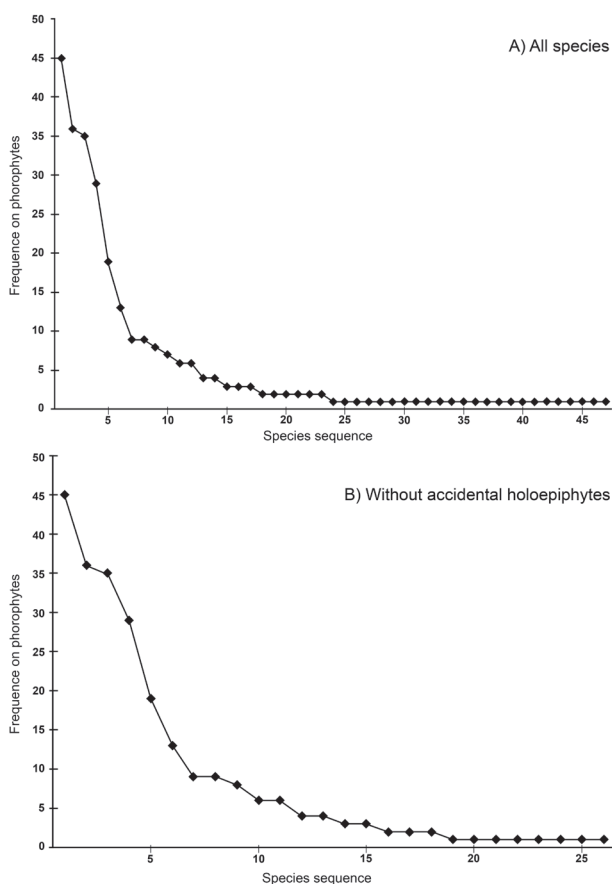


Figure 2. Species sequences from most common to rarest, expressed as the number of absolute occurrences in the 61 sampled phorophytes.

Bromeliaceae and Polypodiaceae (Dislich & Mantovani 1998, Fabricante *et al.* 2006, Dettke *et al.* 2008, Bataghin *et al.* 2010, Furtado & Menini Neto 2015). This pattern has also been observed in studies

conducted by Werner & Gradstein (2009) when analysing gradients of environmental disturbance in the Andes. Two main reasons could explain this pattern: several species of ornamental interest had been collected and/or those species that cannot tolerate the environmental changes had disappeared. Also, fragmentation could be responsible for this result since edge effects often influence the richness and abundance of species, leading to changes in community composition (Bierregaard *et al.* 1992, Metzger 1999).

In addition, a natural reduction in the proportion of occurrence of Orchidaceae compared to other families in SSFs of the Atlantic domain (Kersten 2010) could also be responsible for the observed configuration. This possibility is corroborated by Menini Neto *et al.* (2009a) who showed that the Bromeliaceae and Araceae are richer than the Orchidaceae in an area of SSF with reduced anthropogenic disturbance. However, the limited knowledge about vascular epiphytes in seasonal semi-deciduous forests impedes further conclusions.

Richness of the Polypodiaceae and Bromeliaceae both in MK and in other aforementioned studies is essentially due to the representation of *Microgramma* and *Pleopeltis* (in the first family) and *Tillandsia* (in the second family), whose species often occur in a wide range of environments, both in primary forests and urban centres. Regarding this subject, we must highlight the species of *Tillandsia*, known as biomonitors of air quality, due to their high tolerance to pollution in urban areas (Graciano *et al.* 2003, Alves *et al.* 2008, Bermudez *et al.* 2009). Thus, changes resulting from anthropogenic disturbances, such as

increases in luminosity and temperature, reduction of humidity, scarcity of pollinators and pollution, can act as environmental filters, turning the occurrence of species that cannot tolerate such changes and opening space for the establishment and proliferation of other

species in such environments, including accidental holoeiphytes, due to reduced competition.

The wide distribution of several species and the presence of exotic species point to a flora adapted to several natural environments as well as to disturbed urban environments. Changes caused by degradation of the environment also result from the predominance of accidental epiphytes, resulting in disequilibrium of the epiphytic community due to the reduction of competition with specialist species, such as the characteristic holoeiphytes (Barthlott *et al.* 2001, Bataghin *et al.* 2008, Dettke *et al.* 2008, Furtado & Menini Neto 2015). Such disturbance is the reason of the occurrence of typically terricolous species as epiphytic species, and that act as pioneer species in the epiphytic synusia, both in terms of exotics (*Drymaria cordata*, *Impatiens walleriana*, *Tradescantia zebrina*) and natives (*Ageratum fastigiatum*, *Emilia sonchifolia*, *Thelypteris dentata*, *Urera baccifera*). Some of these genera/species have already been recorded as accidental holoeiphytes in disturbed environments, reinforcing this possibility (Holzner & Numata 1982, Bhatt *et al.* 2015, Furtado & Menini Neto 2015).

Diversity and ecology - Richness and diversity values ($H' = 2.95$) were greater than expected when compared with other studies in areas of seasonal semi-deciduous forest and ecotones between this formation and mixed ombrophilous forests in the Atlantic domain. Even if accidental holoeiphytes were removed from the analysis, the MK would lose only one position in the rank and would still be among the three richest areas (with 26 species). The other three compared areas

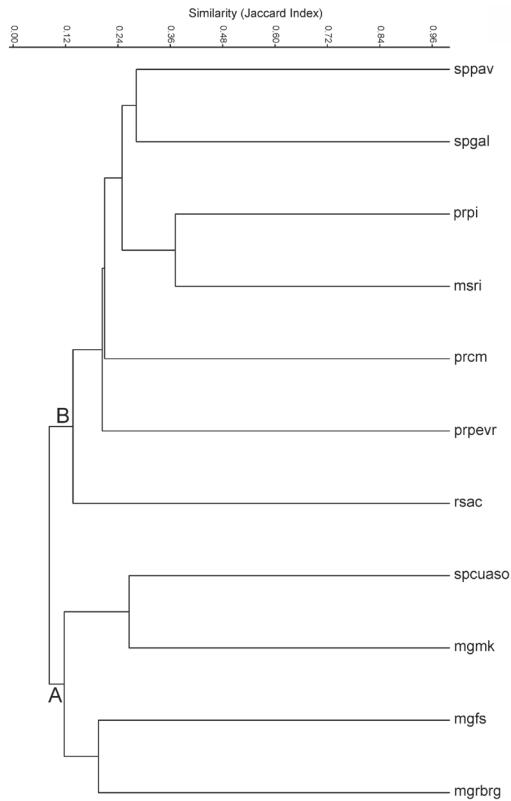


Figure 3. Dendrogram (Jaccard index) obtained from the cluster analysis of 238 species and 11 areas of seasonal forests of Brazil. Cophenetic correlation = 0.91. Acronyms according to table 1.

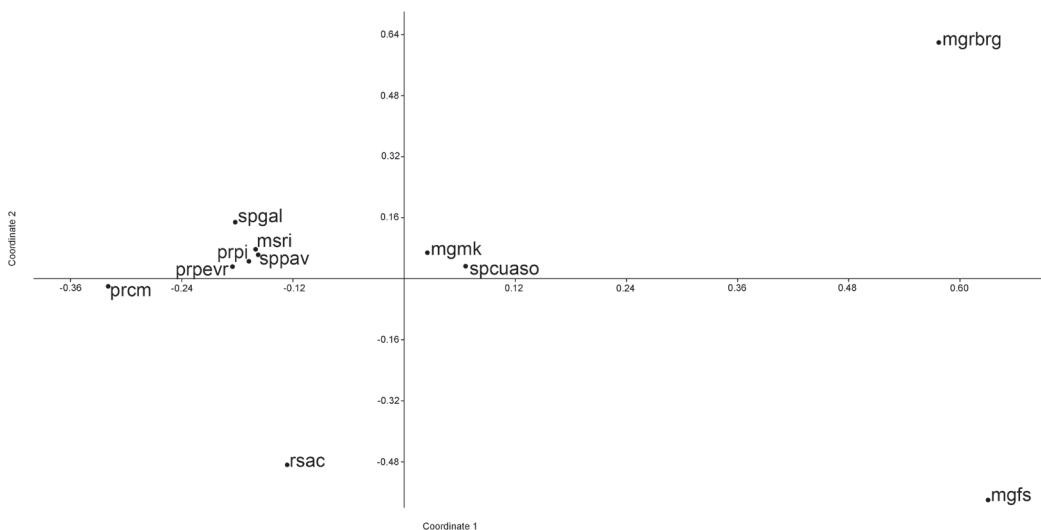


Figure 4. Principal coordinates analysis of 238 species and 11 areas of seasonal forests of Brazil. Acronyms according to table 1.

Table 5. Comparison between the five most frequent species in studies conducted in seasonal semi-deciduous forest in Brazil.

Source	1 st	2 nd	3 rd	4 th	5 th
Present study (MG)	<i>Portea petropolitana</i>	<i>Microgramma squamulosa</i>	<i>Billbergia horrida</i>	<i>Pleopeltis astrolepis</i>	<i>Tillandsia stricta</i>
Tomazini (2007) (MS)	<i>Microgramma vacciniifolia</i>	<i>Peperomia pereskiaefolia</i>	<i>Macradenia multiflora</i>	<i>Oncidium pumilum</i>	<i>Rhopsalis baccifera</i>
Dettke <i>et al.</i> (2008) (PR)	<i>Pleopeltis angusta</i>	<i>Pleopeltis polypodioides</i>	<i>Tillandsia tricholepis</i>	<i>Rhopsalis cereuscula</i>	<i>Lepismium cruciforme</i>
Bataghin <i>et al.</i> (2010) (SP)	<i>Tillandsia tricholepis</i>	<i>Tillandsia recurvata</i>	<i>Pleopeltis pleopeltifolia</i>	<i>Pleopeltis squalida</i>	<i>Tillandsia stricta</i>
Bernardi & Budke (2010) (RS)	<i>Peperomia trineuroides</i>	<i>Microgramma squamulosa</i>	<i>Lepismium cruciforme</i>	<i>Peperomia delicatula</i>	<i>Billbergia nutans</i>
Geraldino <i>et al.</i> (2010) (PR)	<i>Microgramma squamulosa</i>	<i>Pleopeltis angusta</i>	<i>Tillandsia loliacea</i>	<i>Tillandsia recurvata</i>	<i>Pecluma sicca</i>
Ferreira (2011) (MG)	<i>Microgramma squamulosa</i>	<i>Melpomene pilosissima</i>	<i>Cochlidium punctatum</i>	<i>Billbergia elegans</i>	<i>Serpocaulon catharinae</i>

Southeast Region: MG – Minas Gerais; SP – São Paulo. South Region: PR – Paraná; RS – Rio Grande do Sul. Central West Region: MS – Mato Grosso do Sul.

were characterised by low anthropogenic disturbances and one of them, Campo Mourão, is an ecotone area, which is often richer due to the presence of aggregate species of both formations (in some cases, involving seasonal semi-deciduous and mixed ombrophilous forests) (Geraldino *et al.* 2010). Thus, the richness and diversity of MK must be considered high, despite the degradation of its vegetation and relatively low number of sampled phorophytes. The proximity of a water body in the MK could be responsible for this, as humidity is one of the main features affecting the occurrence of epiphytes (Gentry & Dodson 1987, Benzing 1990, Barthlott *et al.* 2001) and, in general, this humidity is reduced in the seasonal forests (Oliveira-Filho *et al.* 2006). In addition, the forest fragment of the MK environmental protection area, which has been regenerating for the past 70 years, can be a source of epiphytic species for the studied area, enriching its composition despite intense anthropogenic activity.

However, the Pielou index ($J = 0.77$) revealed a relatively low evenness of the community, which is related to the higher frequency of a few species, while several species had just a few occurrences in the sampled area. Hietz (1999) and Bataghin *et al.* (2010) also found similar configuration in environments with different types of disturbances. Particularly, the structure of frequency distribution found in MK was similar to that observed by Hietz (1999) in an alder crop, showing a reduced number of dominant species, few species with intermediary frequencies and several rare species. Such configurations must have been caused by anthropogenic activity or even edge effects, since both of these effects are responsible for the reduction of population sizes (Terborgh 1992). In addition, some groups of epiphytes are less tolerant to environmental variations generated by disturbances (Sota 1971).

An analysis of the five most frequent species on phorophytes showed a similar composition of genera between MK and seven other areas composed of seasonal semi-deciduous forest. Some genera must be highlighted: *Microgramma* and *Pleopeltis* (Polypodiaceae) (found in five and four areas, respectively) and *Tillandsia* (Bromeliaceae) (four areas) and, to a lesser degree, *Billbergia* (Bromeliaceae) (found in two other areas). Conversely, species composition was quite distinct and only *Microgramma squamulosa* and *Tillandsia stricta* were shared between three and two areas, respectively.

Table 6. Conventional and taxonomic diversity indices of the vascular epiphytes in four strata in Mata do Krambeck.

Indices	Expected value	Strata				Levels of significance
		A	B	C	D	
S	-	21 (11)	29 (18)	23 (17)	20 (19)	-
H'	-	2.75 ^A	2.73 ^{Ab}	2.29 ^{abC}	2.44 ^{aBC}	0.05
J	-	0.90	0.81	0.73	0.81	-
Δ	72.35	68.47	68.41	64.40	68.71	0.05
Δ^*	67.96	76.40	76.47	76.25	77.22	0.05
Δ^+	79.64	80.01	79.23	78.62	77.64	0.05
Λ^+	-	545.51	623.04	624.16	619.79	-

S, number of species. Between parentheses are the numbers of species excluding accidental holoeiphytes. H' , Shannon diversity index; J , Pielou's evenness index; Δ , taxonomic distinctness; Δ^* , taxonomic diversity; Δ^+ , average taxonomic distinctness; and Λ^+ , variation in taxonomic distinctness. In the Shannon index, same upper-case letters represent non-significant differences, and same lower-case letters represent significant differences between the values. Strata: A, from the base of the bole up to 50 cm from soil; B, from 50 cm up to the first ramification, C, the first ramification of the crown; D, the rest of the crown.

Vertical stratification along the phorophytes resulted in lower values of H' (2.29) and J (0.73) for internal crown. Our results showed more unevenness in the distribution of occurrences (here used in substitution to abundance) compared to other strata, since only five species (out of 23) were dominant and occurred more than 10 times in such strata, while the other species were recorded less than four times. The lower values of Δ (64.40) and Δ^* (76.25) showed similar results for internal crown, although they were not significantly different from the expected values ($p > 0.05$). The higher value of Λ^+ (624.19) demonstrated strong unevenness in the frequency of taxa, since only two families (among nine recorded in the internal crown) and five genera (among 16) exhibited more than two occurrences (*Billbergia*, *Portea*, and *Tillandsia* in Bromeliaceae and *Microgramma* and *Pleopeltis* in Polypodiaceae).

It is likely that there were no microhabitats, because the surveyed trees were isolated (without a closed canopy) and near a water body. Thus, there were most probably no differences in light availability and humidity between the base and top of the phorophytes. We therefore assume that the inexistence of a typical stratification can be associated with the pressure of collections in the base and trunk top strata, mainly concerning the Bromeliaceae species (such as the

ornamentals *P. petropolitana* and *Billbergia horrida*), which were more representative in the internal and external crown strata (strata C and D, respectively), despite the large sizes of these plants. This possibility is supported by the fact that the Orchidaceae recorded in the analysed trees were concentrated in the external crown, whose populations already may have been reduced due to extraction in the area.

The characteristic holoeiphyte fern species were distributed more or less similarly across all strata (trunk base, three species; trunk top, seven species; internal crown, five species; external crown, five species). These results are different from those noted by Benzing (1990), who cited studies conducted in South America, Asia and Oceania, which stated that ferns typically were concentrated in the inferior levels of the phorophytes. However, some species of ferns could tolerate higher exposure to sunlight and/or seasonal dry environments, allowing their occurrence in superior strata. In MK, we recorded three species of *Pleopeltis* that exhibited poikilohydric features, such as strong rolling of the fronds during dry periods and tolerance to desiccation. Another two species belonged to *Microgramma*, a genus whose species have thick cuticles and suberified stems with water storage to avoid desiccation, as noted by Dubuisson *et al.* (2009).

Another observed pattern was the concentration of accidental holoepiphytes on the base and top trunk strata. This was an expected result, since the phorophyte base, nearer the soil, allows the development of species that lack adaptation to epiphytic environments due to higher humidity and, in many cases, the accumulation of organic matter. In addition, according to Benzing (1990), accidental holoepiphytes are commonly found in the humid forest, and although the MK is not a humid forest, the close proximity to a lake can contribute to these occurrences. Even the plants that occurred in the trunk top were nearer the trunk base than the crown.

By removing the accidental holoepiphytes and analysing the composition of other categories along the phorophyte, it is possible to notice that richness of the strata was similar (trunk top, 18; internal crown, 17; and external crown, 19), although with strong reduction in the richness of the trunk base (21 reduced to 11). However, the occurrences by strata with higher concentrations in the crown maintained this configuration (trunk base, 35; trunk top, 87; internal crown, 110; and external crown, 166). This proportion of occurrence (trunk base, 8.7%; trunk top, 21.85%; internal crown, 27.6%; and external crown, 41.7%) was, to a certain extent, similar to that observed by Johansson (1975) for epiphytic orchids; however, in this study, the percentage of trunk base was higher and that of external crown was lower. Thus, anthropogenic disturbances can be responsible for the strong change in composition and proportion of occurrence also in the epiphytic synusia, which is commonly observed in other groups (Mckinney 2008).

Similarity - Cluster analysis showed a clear longitudinal gradient, suggesting the influence of the distance to the ocean on the floristic relationships between the areas. Group A was composed of two areas whose distance to the ocean varied from 60 km (“spcuaso”) to 165 km (“mgrbrg”), isolating it from group B (whose area with the closest proximity to the ocean was about 250 km away from it), located in the transition with the Cerrado. Forzza *et al.* (2014) found a similar gradient when comparing the vascular flora of the Reserva Biológica da Represa do Grama (“mgrbrg”) with nine other areas of the southeastern region of Brazil, with strong segregation between littoral and inland areas.

Although the areas of Minas Gerais are composed of SSF, the influence of dense ombrophilous forest has been noted by Barbosa *et al.* (2014) in “mgfs” and by Forzza *et al.* (2014) in “mgrbrg”. Pifano *et al.*

(2007) also noticed such influence on the composition of the phanerogamic flora of Morro do Imperador, an area about 4 km from MK, and stated that milder temperatures of the region and geographic proximity to the littoral could be responsible for this relationship. Despite the geographic distance (between 400–460 km), the three areas of Minas Gerais were grouped together with “spcuaso” (in São Paulo), which is composed of dense ombrophilous and seasonal semi-deciduous forests (Dislich & Mantovani 1998), corroborating the influence of the first forest formation on its flora composition. The existence of water bodies associated with all areas of Minas Gerais could also collaborate through the establishment of plants typically found in ombrophilous environments, which could not tolerate the seasonality of semi-deciduous forests, influencing such observed relationships. The internal relationships of group B demonstrated a latitudinal gradient with initial segregation of the southernmost area (“rsac”), subsequent merging of two areas with similar latitude (“prpevr” and “prcm”) and formation of two other groups with closer latitudes (one composed of “prpi” and “msri” and another of “sppv” and “spgal”). Since the altitudes between the areas did not exhibit marked differences, it is likely that latitude influenced temperature, agreeing with what has been observed by Oliveira-Filho *et al.* (2006) regarding tree species in seasonal forests and, consequently, composition of species and similarity between the areas.

The PCoA corroborated the initial separation between the two groups (A and B), with a strong species turnover related to longitudinal gradient, although the latitudinal gradient observed in group B was not confirmed. The separation of “mgrbrg” and “mgfs” from the other areas was due to the richness of both areas (69 and 78 species, respectively), also reflecting the higher degree of conservation compared to the other areas of group A (“mgmk” and “spcuaso”), which are both located in an urban environment, subject to strong anthropogenic pressure and less species-rich (24 and 40 species, respectively).

Conclusions

This study presented the characterisation of the vascular epiphyte community in an urban forest environment, correlated it with environmental and geographical factors and compared it with similar studies conducted in Neotropical Region, seeking to evaluate the possible existence of a pattern in the structure of such a community in an anthropogenic environment.

In this sense, the observed proportion of ecological categories uncovered an enhancement of accidental holoepiphytes in a disturbed environment. The accidental holoepiphytes constituting the richest ecological category is unprecedented. However, this category has apparently been neglected in similar studies, even ignored several times. Regarding an environment undergoing regeneration, it is possible that the ecological role of accidental holoepiphytes is underestimated, as their occurrence could be important in the initial composition of the epiphytic flora, preparing the environment to the subsequent establishment of the specialists (*i.e.*, the characteristic holoepiphytes). More studies will need to be conducted to evaluate this possibility.

We observed some congruence in the composition of families and genera among the most frequent ecological studies conducted in the Atlantic domain. However, in a specific level, this composition was relatively distinct according to the locality, despite the prominence of *M. squamulosa* and *T. stricta*.

Taking into account the conditions of the environment and relatively small numbers of phorophytes sampled, the richness and diversity found in MK are impressive. However, if the anthropogenic disturbance does not cease, the number of rare species could decline due to local extinction, enhancing the dominance of a few taxa and reducing the diversity. Conversely, if the community continues to regenerate, the rare species can enhance their frequencies, compete with the most common species as well as with the accidental holoepiphytes, reduce their occurrence and establish a balance in the community. However, the importance of the occurrence of other components of the ecosystem, such as pollinators and dispersers, must be taken into consideration.

Therefore, it is important to encourage long-duration studies with epiphytic synusia in order to clarify how these changes occur in the communities located in urban environments in a temporal dynamic system.

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