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THE IMPORTANCE OF HETEROGENEITY OF HABITATS FOR THE SPECIES RICHNESS OF VASCULAR EPIPHYTES IN REMNANTS OF BRAZILIAN MONTANE SEASONAL SEMIDECIDUOUS FOREST

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Epiphytes are an important component of the diversity of tropical forests, and they also have several ecological functions. Vegetation heterogeneity is one of the features responsible for the high biodiversity of the Atlantic Forest, especially in the domain's seasonal semideciduous forest (SSF). This biodiversity presents as high endemism and species richness. Owing to the seasonal nature of SSF, organisms that require high humidity (e.g. epiphytes) would be expected to show low species richness in these forests. The aims of this study were to conduct a survey of the vascular epiphytes in remnants of montane SSF in the Serra do Ibitipoca, Brazil, and to evaluate the importance of habitat heterogeneity for the richness and composition of species in these areas. We also evaluated whether the intrinsic characteristics of the SSF phytophysiognomy and fragmentation could result in low species richness and a high number of accidental epiphyte species. The study was conducted in the course of 18 expeditions undertaken between September 2013 and December 2016, covering five fragments of montane SSF (totalling 23.6 ha). We recorded 96 species (only one of which is an accidental epiphyte), distributed across 41 genera and 10 families. This is the highest epiphytic species richness recorded in Brazilian SSF to date. The results refuted the initial hypothesis and reinforce the importance to the epiphytic community of conservation of fragments with different structures.

Keywords. Atlantic Forest, ferns, Orchidaceae, Serra da Mantiqueira, Serra do Ibitipoca.

Introduction

Epiphytes are an important component of the diversity of tropical forests (Kitching, 2006). Additionally, they have vital ecological functions and play key roles in hydrological and nutrient dynamics (Coxson & Nadkarni, 1995; Stanton *et al.*, 2014). They are considered "biodiversity amplifiers" (Gonçalves-Souza *et al.*, 2010) providing several resources to fauna, such as microenvironments, shelter and food (Benzing, 1990; Richter, 1998; Cruz-Angón & Greenberg, 2005). According to Zotz (2016), epiphytes comprise c.27,600 species, equivalent to 9% of the known global vascular flora. In the Atlantic

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Forest, this proportion increases to c.15% of the vascular flora, represented by 2256 species, of which 78% are endemic to Brazil and 11.3% are threatened with extinction (Freitas *et al.*, 2016).

The high biodiversity of the Brazilian Atlantic Forest is influenced by, among other features, vegetation heterogeneity (Oliveira-Filho & Fontes, 2000). Seasonal semideciduous forest (SSF) is the second-ranked phytophysiognomy in terms of both species richness and number of endemic species (Stehmann *et al.*, 2009), and it is probably home to c.25% of the vascular epiphytic species of the Atlantic Forest Domain (Kersten, 2010). However, floristic knowledge of SSF is low compared with that of other formations, such as rain forests, and this phytophysiognomy has only recently been delineated as an integral part of the Atlantic Forest (Oliveira-Filho & Fontes, 2000). In Minas Gerais, SSF occupies the largest extension of Atlantic Forest. However, it is currently represented only by remnants, often secondary forests, consequent to severe fragmentation (predominantly due to mining activities but also urban and crop expansion) (Stehmann & Sobral, 2009).

Owing to the seasonal nature of SSF, which undergoes a dry period during winter (IBGE, 2012), organisms that require high humidity, such as epiphytes, would be expected to show low species richness in these forests (Gentry & Dodson, 1987; Kersten, 2010). Moreover, the disturbances caused by fragmentation can also contribute to low species richness and alteration of the composition of the epiphyte community. They would increase the proportion of accidental epiphytes (i.e. species of plants growing as epiphytes but without adaptations to an epiphytic lifeform), for instance due to a decrease in humidity and edge effects (Barthlott *et al.*, 2001; Furtado & Menini Neto, 2015; Santana *et al.*, 2017).

Studies of epiphytic synusia in SSF can be considered scarce, especially when compared with those conducted in rain forests (Kersten, 2010). To date, only three articles specifically regarding epiphytes in the SSF of Minas Gerais have been published (Barbosa *et al.*, 2015; Furtado & Menini Neto, 2015; Santana *et al.*, 2017), despite the large area of SSF in this state (Stehmann & Sobral, 2009). Given the scarcity of studies of the SSF of the Atlantic Forest (SSF/AF), the aims of the present study were to survey the vascular epiphytes in five fragments of montane SSF in Serra do Ibitipoca, Brazil, and to evaluate the importance of habitat heterogeneity for the richness and composition of species in these areas. The findings were to answer the following question: in these fragments, is species richness low and the number of accidental epiphyte species high as a result of intrinsic characteristics of the SSF phytophysiognomy as well as disturbances caused by fragmentation?

Material and Methods

Study area

Serra do Ibitipoca is in the southeast of Minas Gerais State, between the municipalities of Lima Duarte, Bias Fortes and Santa Rita do Ibitipoca, in the Serra da Mantiqueira, Zona da Mata. It is considered a region of special biological importance and one of the priority areas for flora conservation in Minas Gerais (Drummond *et al.*, 2005). The study was conducted on a private property named Fazenda do Tanque (FT) (21°41′S, 43°54′W), located in the

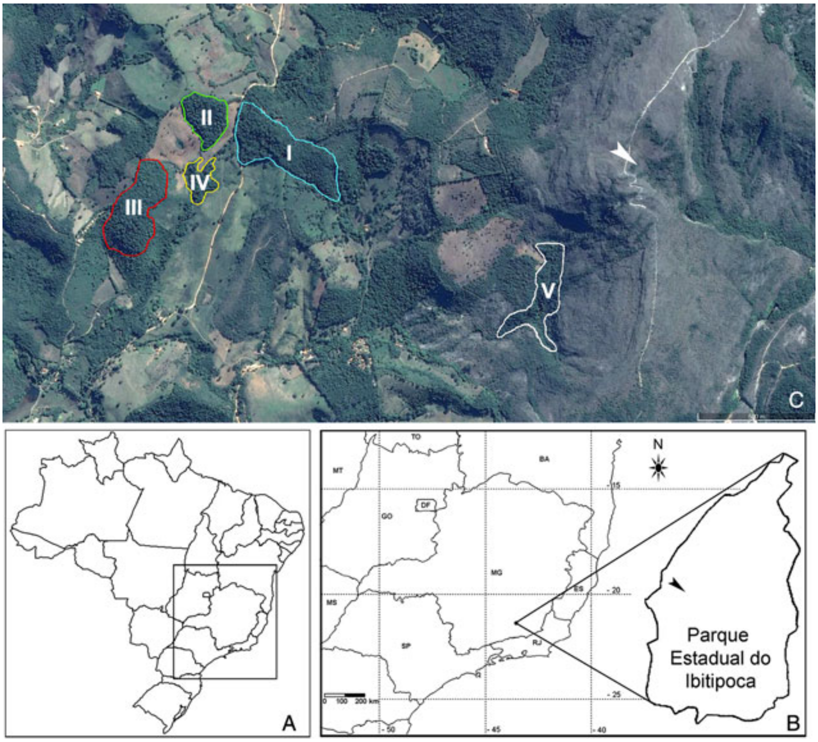

FIG. 1. Location of the study area. A, States of Brazil; the area within the square is shown at a larger scale in panel B. B, Minas Gerais (MG) and neighbouring states; the inset map shows the Parque Estadual do Ibitipoca (PEIB). C, The five fragments of montane seasonal semideciduous forest surveyed at Fazenda do Tanque, a private property contiguous to the PEIB. The arrowhead in panels B and C indicates the location of the landmark cross, Cruzeiro, in the PEIB. BA, Bahia; DF, Distrito Federal; ES, Espírito Santo; GO, Goiás; MS, Mato Grosso do Sul; MT, Mato Grosso; RJ, Rio de Janeiro; SP, São Paulo; TO, Tocantins.

village of Conceição de Ibitipoca in the municipality of Lima Duarte. The property is contiguous to the Parque Estadual do Ibitipoca (PEIB), an important conservation unit of Minas Gerais (Drummond *et al.*, 2005; Forzza *et al.*, 2013) (Fig. 1), and is predominantly composed of montane SSF (IBGE, 2012) with patches of cloud dwarf-forest (Valente *et al.*, 2013) (Fig. 2). The relief of the site ranges from wavy to strongly undulating, with altitudes between 1200 and 1430 m a.s.l. Mean annual precipitation and temperature are c.1532 mm and 18.9°C, respectively. The climate of the region is Cwb according to the Köppen classification, with dry winters and rainy and mild summers (CETEC, 1983).

The five fragments surveyed were in a matrix of crops and pastures used for cattle farming (see Fig. 2). They ranged in extent from c.2 to c.8 ha, totalling 23.6 ha. The largest fragment (c.8 ha) included a patch of cloud dwarf-forest (c.0.4 ha) (see Fig. 2E). Two other fragments had temporary or permanent watercourses. The characteristics of the fragments are summarised in Table 2.

FIG. 2. Fragments of montane seasonal semideciduous forest surveyed at Fazenda do Tanque, Serra do Ibitipoca, Zona da Mata, Minas Gerais, Brazil. A, Fragments I (on right) and II (on left); B, fragments III (top) and IV (bottom); C, fragment V; D, seasonal semideciduous forest; E, a patch of cloud dwarf-forest in fragment I.

Fieldwork

The walking method (Filgueiras *et al.*, 1994) was used to conduct a survey of vascular epiphytes in the five fragments of montane SSF, in the course of 18 expeditions undertaken between September 2013 and December 2016.

Photographs of fertile specimens were taken for use in a field guide. The specimens were then vouchered and deposited at CESJ, the herbarium of the Universidade Federal de Juiz de Fora (herbarium name abbreviated according to Thiers, continuously updated). Specimens were identified by comparison with the whole herbarium collection, reference to specialist literature and consultation with family specialists. The spelling of species names and authors was taken from the International Plant Names Index (Royal Botanic Gardens, Kew, *et al.*, continuously updated). Angiosperms were classified according to APG IV (Angiosperm Phylogeny Group, 2016), and ferns and lycophytes according to PPG I (Pteridophyte Phylogeny Group, 2016). Because of frequent changes and lack of consensus regarding the delimitation of the genera *Maxillaria* Ruíz & Pav., *Oncidium* Sw. and *Pleurothallis* R.Br. (Orchidaceae), they were considered in a broad sense.

The species recorded were classified into ecological categories according to their relationship with phorophytes, based on categories defined by Benzing (1990). However, no distinction was made between primary and secondary hemiepiphytes. Species are listed as Threatened in accordance with Drummond *et al.* (2008) and *Livro Vermelho da Flora do Brasil* (the *Red Book of the Flora of Brazil*) (Martinelli & Moraes, 2013).

Results

We recorded 96 species of vascular epiphytes distributed across 41 genera and 10 families (Table 1). The most common ecological category was characteristic holoepiphyte (82 spp.), followed by facultative holoepiphyte (11 spp.), hemiepiphyte (two spp.) and accidental epiphyte (one species).

Angiosperms were represented by 66 species across 25 genera and six families (Table 1 and Fig. 3). The most species-rich angiosperm families, with percentage of the total number of species recorded given in parentheses, were Orchidaceae, with 30 species (c.31%) across 13 genera; Bromeliaceae, with 19 species (c.20%) across five genera; and Piperaceae, with eight species (c.8%) in one genus. *Peperomia* Ruíz & Pav. was the most species-rich genus, with eight species, followed by *Pleurothallis* R.Br. *sensu lato* (*s.l.*) (seven spp.), *Vriesea* Lindl. (six spp.), *Tillandsia* L. (five spp.), and *Aechmea* Ruíz & Pav. and *Oncidium* Sw. *s.l.* (four spp. each).

Ferns were represented by 30 species across 16 genera and four families (see Table 1 and Fig. 3). Polypodiaceae was the most species-rich of the fern families, with 18 species (60% of the total number of fern species recorded) across 10 genera, followed by Dryopteridaceae, with five species in two genera, and Aspleniaceae, with four species in one genus. The most species-rich of the fern genera were *Asplenium* L., *Elaphoglossum* Schott ex J.Sm. and *Pleopeltis* Humb. & Bonpl. ex Willd. (four spp. each). The 12 species in these three genera represented 40% of the fern species recorded in this study.

A comparison of the distribution of species across the five fragments is provided in Table 2. A total of 45 species (c.47% of the total number of species recorded) were exclusive to an individual fragment. Some species, such as *Epidendrum chlorinum* Barb. Rodr. and *Lellingeria apiculata* (Kunze ex Klotzsch) A.R.Sm. & R.C.Moran, were

TABLE 1. Vascular epiphytes recorded at Fazenda do Tanque, Serra do Ibitipoca, Zona da Mata, Minas Gerais, Brazil[a]

Family and species	Ecological category	Fragment I	II	III	IV	V	Voucher no.[b]
Araceae (2 genera, 4 spp.)							
Anthurium comtum Schott	CHL		+				245
Anthurium minarum Sakur. & Mayo	FHL	+				+	155
Philodendron cordatum Kunth ex Schott[c]	Hem	+	+			+	355
Philodendron sp.	Hem			+			195
Aspleniaceae (1 genus, 4 spp.)							
Asplenium feei Kunze ex Fée	CHL		+				252
Asplenium praemorsum Sw.	CHL	+			+	+	168
Asplenium sp. 1[c]	CHL		+				232
Asplenium sp. 2[c]	CHL	+					197
Bromeliaceae (5 genera, 19 spp.)							
Aechmea bromeliifolia (Rudge) Baker var. *albobracteata* Philcox	CHL	+	+	+		+	257
Aechmea lamarchei Mez[c]	CHL	+					216
Aechmea nudicaulis (L.) Griseb.	FHL	+					170
Aechmea sp.[c]	FHL			+			263
Billbergia alfonsijoannis Reitz	CHL	+		+			210
Billbergia distachia (Vell.) Mez	FHL	+		+	+	+	201
Nidularium ferdinandocoburgii Wawra	CHL			+			248
Nidularium marigoi Leme	FHL	+					181
Tillandsia gardneri Lindl.	CHL	+	+		+		147
Tillandsia geminiflora Brongn	CHL	+	+		+	+	186
Tillandsia recurvata (L.) L.	CHL	+			+	+	141
Tillandsia stricta Sol.	CHL	+	+	+	+	+	146
Tillandsia usneoides (L.) L.	CHL	+					154
Vriesea bituminosa Wawra	FHL	+	+	+	+	+	152
Vriesea friburgensis Mez	FHL	+				+	266
Vriesea guttata Linden & André	CHL					+	224
Vriesea heterostachys (Baker) L.B.Sm.	CHL	+				+	150
Vriesea lubbersii (Baker) E.Morren[c]	CHL				+		243
Vriesea sp.[c]	CHL		+				246
Cactaceae (3 genera, 4 spp.)							
Hatiora salicornioides (Haw.) Britton & Rose	FHL	+	+		+		153
Lepismium cruciforme (Vell.) Miq.	FHL	+					175
Rhipsalis cf. *floccosa* Salm-Dyck ex Pfeiff.	CHL	+	+	+		+	194
Rhipsalis pulchra Loefgr.	CHL	+	+		+		229
Dryopteridaceae (2 genera, 5 spp.)							
Ctenitis aspidioides (C.Presl) Copel.[c]	AE				+		239
Elaphoglossum gayanum (Fée) T.Moore	CHL					+	234
Elaphoglossum lingua (C.Presl) Brack.	CHL					+	226
Elaphoglossum sp. 1[c]	CHL					+	203
Elaphoglossum sp. 2[c]	CHL					+	269

TABLE 1. *(Continued)*

Family and species	Ecological category	Fragment I	II	III	IV	V	Voucher no.[b]
Gesneriaceae (1 genus, 1 sp.)							
Nematanthus strigillosus (Mart.) H.E.Moore	FHL					+	223
Hymenophyllaceae (3 genera, 3 spp.)							
Hymenophyllum polyanthos (Sw.) Sw.	CHL	+	+	+			198
Polyphlebium angustatum (Carmich.) Ebihara & Dubuisson	CHL				+		196
Trichomanes anadromum Rosenst.[c]	CHL					+	225
Orchidaceae (13 genera, 30 spp.)							
Campylocentrum robustum Cogn.	CHL	+	+				177
Campylocentrum sp.	CHL				+		167
Capanemia gehrtii Hoehne[c]	CHL	+					187
Capanemia thereziae Barb. Rodr.[c]	CHL	+					142
Dichaea cogniauxiana Schltr.	CHL	+				+	158
Encyclia patens Hook.	CHL	+	+	+	+		211
Epidendrum chlorinum Barb. Rodr.	CHL	+					173
Epidendrum pseudodifforme Hoehne & Schltr.	CHL					+	264
Eurystyles actinosophila cf (Barb. Rodr.) Schltr.	CHL	+					253
Eurystyles cotyledon Wawra[c]	CHL	+		+			178
Gomesa glaziovii Cogn.	CHL	+					149
Gomesa recurva R.Br.	CHL	+	+				261
Isochilus linearis (Jacq.) R.Br.	CHL	+	+		+		193
Maxillaria gracilis Lodd.	CHL		+				303
Maxillaria notylioglossa Rchb.f.	CHL		+				259
Oncidium gravesianum Rolfe	CHL				+	+	237
Oncidium hookeri Rolfe	CHL	+				+	172
Oncidium longipes Lindl.	CHL		+	+			247
Oncidium truncatum Pabst	CHL	+	+	+			159
Pleurothallis adenochila Loefgr.[c]	CHL	+					354
Pleurothallis hygrophila Barb. Rodr.[c]	CHL				+		242
Pleurothallis luteola Lindl.	CHL	+	+		+		171
Pleurothallis malachantha Rchb.f.	CHL	+	+	+	+	+	157
Pleurothallis recurva Lindl.	CHL	+	+		+		176
Pleurothallis rubens Lindl.	CHL					+	265
Pleurothallis saurocephala Lodd.	CHL	+	+				218
Polystachya estrellensis Rchb.f.	CHL	+	+		+		156
Polystachya hoehneana Kraenzl.	CHL	+					183
Prosthechea allemanoides (Hoehne) W.E.Higgins	FHL	+					148
Prosthechea pachysepala (Klotzsch) Chiron & V.P.Castro	CHL	+	+				185

TABLE 1. *(Continued)*

Family and species	Ecological category	Fragment I	II	III	IV	V	Voucher no.[b]
Piperaceae (1 genus, 8 spp.)							
Peperomia alata Ruiz & Pav.[c]	CHL		+				165
Peperomia corcovadensis Gardner	CHL	+	+				238
Peperomia diaphanoides Dahlst.	CHL	+			+		161
Peperomia cf. *mandioccana* Miq.	CHL	+	+				262
Peperomia quadrifolia (L.) Kunth[c]	CHL	+	+				251
Peperomia tetraphylla (G.Forst.) Hook. & Arn.	CHL	+	+	+	+		160
Peperomia sp. 1	CHL	+	+				258
Peperomia sp. 2	CHL	+	+				268
Polypodiaceae (10 genera, 18 spp.)							
Campyloneurum angustifolium (Sw.) Fée	CHL	+				+	192
Campyloneurum nitidum (Kaulf.) C.Presl	CHL			+		+	166
Campyloneurum rigidum Sm.[c]	CHL	+		+			231
Cochlidium punctatum (Raddi) L.E.Bishop	CHL	+	+				207
Cochlidium serrulatum (Sw.) L.E.Bishop	CHL	+					233
Lellingeria apiculata (Kunze ex Klotzsch) A.R.Sm. & R.C.Moran	CHL	+					199
Leucotrichum schenckii (Hieron.) Labiak[c]	CHL		+				256
Melpomene pilosissima (M.Martens & Galeotti) A.R.Sm. & R.C.Moran	CHL					+	235
Microgramma squamulosa (Kaulf.) de la Sota	CHL	+	+	+	+	+	140
Pecluma pectinatiformis (Lindm.) M.G. Price	CHL		+	+		+	169
Pecluma sp.[c]	CHL	+					254
Phlebodium pseudoaureum (Cav.) Lellinger	CHL	+					163
Pleopeltis astrolepis (Liebm.) E.Fourn.	CHL		+		+		145
Pleopeltis hirsutissima (Raddi) de la Sota	CHL	+	+	+	+	+	144
Pleopeltis macrocarpa (Bory ex Willd.) Kaulf.	CHL	+	+		+	+	182
Pleopeltis pleopeltifolia (Raddi) Alston[c]	CHL				+		338
Serpocaulon catharinae (Langsd. & Fisch.) A.R.Sm.	CHL	+	+		+	+	162
Serpocaulon fraxinifolium (Jacq.) A.R.Sm.	CHL		+				244

+, present; AE, accidental epiphyte; CHL, characteristic holoepiphyte; FHL, facultative holoepiphyte; Hem, hemiepiphyte.

[a] The names of the specialists who collaborated with the authors on the identification of species are, by family, as follows: Araceae, Marcus Nadruz (RB); Aspleniaceae, Vinicius A. O. Dittrich (CESJ); Bromeliaceae, Rafaela C. Forzza (RB) and Ana Paula Gelli de Faria (CESJ); Cactaceae, Diego R. Gonzaga (RB); Dryopteridaceae, Vinicius A. O. Dittrich (CESJ); Hymenophyllaceae, Vinicius A. O. Dittrich (CESJ); Orchidaceae, Luiz Menini Neto (CESJ); Polypodiaceae, Vinicius A. O. Dittrich (CESJ).

[b] Voucher name: *D.E.F. Barbosa* (deposited at CESJ).

[c] Species not recorded in the Parque Estadual do Ibitipoca by Furtado & Menini Neto (2018).

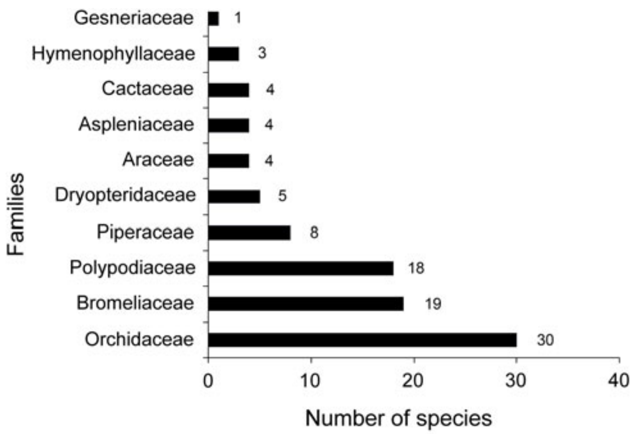

FIG. 3. Number of species in each family of vascular epiphytes recorded at Fazenda do Tanque, Serra do Ibitipoca, Zona da Mata, Minas Gerais, Brazil.

restricted to fragment I, the only fragment in transition with cloud dwarf-forest. *Vriesea guttata* Linden & André was recorded only in fragment V, the fragment with a mean altitude higher than 1400 m a.s.l. The Dryopteridaceae species, as well as two species of Hymenophyllaceae (*Polyphlebium angustatum* (Carmich.) Ebihara & Dubuisson and *Trichomanes anadromum* Rosenst.) were exclusive to fragments IV and V, which had temporary or permanent watercourses.

Discussion

Species richness at family level

The distribution of vascular epiphyte species at FT, with the most species-rich families being Orchidaceae, Bromeliaceae, Polypodiaceae and Piperaceae, follows the general trend observed in similar studies conducted in the Neotropical region (i.e. Waechter, 1992; Hietz & Hietz-Seifert, 1995; Wolf & Alejandro, 2003; Giongo & Waechter, 2004; Küper *et al.*, 2004; Breier, 2005; Kersten *et al.*, 2009; Alves & Menini Neto, 2014; Barbosa *et al.*, 2015; Furtado & Menini Neto, 2016, 2018). In all these studies, as in the present study, Orchidaceae was found to be the most species-rich family. Indeed, it is the richest family in terms of representation of epiphyte species both in the Atlantic Forest (c.47% of the total; Freitas *et al.*, 2016) and globally (c.68% of the total; Zotz, 2016).

The families of the vascular epiphyte species recorded at FT are generally also the most species-rich families of vascular epiphytes found across the SSF/AF (Kersten, 2010). However, there are several differences in representation, as expressed in terms of percentage of the total number of vascular epiphyte species recorded (Table 3). Among the angiosperms, Orchidaceae, Araceae and Cactaceae are generally better represented across the SSF/AF than at FT specifically. Piperaceae has similar values for across the SSF/AF and at FT. Gesneriaceae is poorly represented both across the SSF/AF and at FT.

TABLE 2. Characteristics of and distribution of species in five fragments of montane seasonal semideciduous forest surveyed at Fazenda do Tanque, Serra do Ibitipoca, Zona da Mata, Minas Gerais, Brazil

	Fragment				
Variable	I	II	III	IV	V
Extent (ha)	8.1	3.0	6.5	1.8	4.2
Occurrence of watercourse	No	No	No	Yes (temporary)	Yes (permanent)
Latitude S	21°41′56″	21°41′52″	21°42′05″	21°42′02″	21°42′15″
Longitude W	43°54′52″	43°54′53″	43°55′07″	43°54′59″	43°54′07″
Mean altitude (m)	1325	1275	1265	1240	1405
No. of species	64	44	21	29	33
No. of species exclusive to the individual fragment	18	9	3	6	9

TABLE 3. Distribution across families of vascular epiphyte species recorded at Fazenda do Tanque, Serra do Ibitipoca, Zona da Mata, Minas Gerais, Brazil (data from the present study) and other areas of seasonal semideciduous forest of the Atlantic Forest (data from previous studies)

	Percentage of total number of species recorded	
Family	Fazenda do Tanque (%)	Seasonal semideciduous forest of the Atlantic Forest (%)
Angiosperms		
Orchidaceae	31.3	39.8
Bromeliaceae	19.8	13.8
Piperaceae	8.3	8.6
Araceae	4.2	7.4
Cactaceae	4.2	6.7
Gesneriaceae	1.0	1.5
Ferns		
Polypodiaceae	18.8	8.2
Dryopteridaceae	5.2	0.4
Aspleniaceae	4.2	3.3
Hymenophyllaceae	3.1	1.1

Bromeliaceae is the only angiosperm family for which the value for FT is higher than that for across the SSF/AF. In contrast, each of the four families of fern are generally better represented at FT than across the SSF/AF. Dryopteridaceae is much more prominent at FT; in terms of percentage of the total number of vascular epiphyte species recorded, the value for Dryopteridaceae at FT is 13 times higher than the equivalent value for across the SSF/AF. For Polypodiaceae, the value for FT is more than double that for across the SSF/AF; for Hymenophyllaceae, it is almost three times higher; and for Aspleniaceae, it is slightly higher.

Species richness and elevation

Some researchers have reported a decrease in the number of Araceae species at higher elevations (Krömer *et al*., 2005; Cardelús *et al*., 2006; Furtado & Menini Neto, 2016), a finding that is probably related to the lower temperatures in these areas. In the South Region of Brazil, which has a lower average temperature than the Southeast Region (which includes Minas Gerais), the family is poorly represented among epiphytes in the SSF (Borgo *et al*., 2002; Cervi & Borgo, 2007; Dettke *et al*., 2008), and its members are sometimes not even recorded (Giongo & Waechter, 2004; Perleberg *et al*., 2013). These findings of previous studies are reinforced by our finding of low species richness for Araceae at FT, which is in a high-elevation area with a low mean temperature.

For ferns, an inverse relationship has been reported, with several authors describing high species richness at higher elevations (Hietz & Hietz-Seifert, 1995; Moran, 1995; Krömer *et al*., 2005; Cardelús *et al*., 2006). Such a relationship seems possible when the results of the present study are interpreted alongside those of Barbosa *et al*. (2015). In the earlier study, carried out in an area of SSF c.90 km from FT but with altitudes between 800 and 900 m a.s.l. (versus 1200 and 1430 m a.s.l. in the present study), less than half the number of fern species were recorded (13 spp. versus 30 spp.) despite a similar total number of species found (91 spp. versus 96 spp.). New surveys of SSF, distributed along an elevation gradient, would help to confirm if this pattern of higher species richness at higher elevations applies generally for ferns growing in this phytophysiognomy.

Species-rich genera at Fazenda do Tanque

Asplenium (Kersten *et al*., 2009; Menini Neto *et al*., 2009, Perleberg *et al*., 2013) and *Pleopeltis* (Kersten & Silva, 2001; Cervi & Borgo, 2007; Buzatto *et al*., 2008; Furtado & Menini Neto, 2015) are often cited as the most species-rich of epiphytic fern genera. However, at FT, the number of *Asplenium* and *Pleopeltis* species is matched by the number of *Elaphoglossum* species, making them the three most species-rich fern genera in the present study. *Elaphoglossum* had not previously been recorded in studies carried out in the SSF/AF. This genus is often found in rain forests (Blum *et al*., 2011; Alves & Menini Neto, 2014; Furtado & Menini Neto, 2016), and its presence in the area studied is probably related to increased humidity (resulting from high altitude) and proximity to the PEIB, where it is represented by eight species (Furtado & Menini Neto, 2018). The same explanation must be valid for two other Hymenophyllaceae genera, *Hymenophyllum* Sm. and *Polyphlebium* Copel., which contributed one species each.

The genus *Peperomia* is well known to be richly represented in rain forests (Carvalho-Silva & Guimarães, 2008; Menini Neto *et al*., 2009). It is also the most species-rich epiphytic genus in SSF, according to reports of several studies conducted in these areas (Cervi & Borgo, 2007; Barbosa *et al*., 2015; Marcusso & Monteiro, 2016). *Pleurothallis s.l.* is the second most species-rich genus at FT. It has previously been reported to be the most species-rich genus in SSF (Barbosa *et al*., 2015) and is also often found to be highly diverse in rain forests (Luer, 1986; Furtado & Menini Neto, 2016).

Influence of rain forests

The influence of rain forests on the composition of epiphytes in SSF in the Reserva Biológica da Represa do Grama (ReBio do Grama), located in the municipality of Descoberto, Minas Gerais, has been described by Forzza *et al.* (2014). Considering the importance of typical rain forest species or genera in areas of SSF studied by Forzza *et al.* (2014) and Barbosa *et al.* (2015), the occurrence of watercourses in these areas is probably the feature responsible for their finding of decreased influence of climatic seasonality on species composition. In the present study, a similar effect is probably due primarily to the high elevation at FT (minimum, 1200 m), because it provides a mild climate and greater humidity, although two of the fragments of montane SSF surveyed have a watercourse (temporary or permanent).

Ecological categories

The predominance of characteristic holoepiphytes is a pattern often found in studies of the epiphytic flora of Brazil (e.g. Kersten & Silva, 2002; Giongo & Waechter, 2004; Buzatto *et al.*, 2008; Alves & Menini Neto, 2014; Barbosa *et al.*, 2015; Furtado & Menini Neto, 2016). Bromeliaceae is the most well-represented genus among the facultative holoepiphytes found at FT (c.55% of the total number of facultative holoepiphytes recorded), a finding that shows the plasticity of this family (Zotz, 2016). The two hemiepiphytes recorded in the present study are both members of *Philodendron* Schott in Araceae, a family that often predominates in this ecological category (Blum *et al.*, 2011).

Areas subject to anthropogenic disturbance are commonly suitable for colonisation by accidental epiphytes, due to environmental changes caused by degradation, such as decreased humidity and increased incident light (Barthlott *et al.*, 2001; Bataghin *et al.*, 2008; Furtado & Menini Neto, 2015, 2016; Santana *et al.*, 2017). However, in the present study we recorded only one accidental epiphyte species, suggesting that the fragments are relatively well conserved despite being surrounded by an anthropogenic matrix. Alternatively, the finding may be due to the absence of a propagule source for opportunist species.

Conservation status of species recorded

Five of the species recorded in the present study are cited in floristic lists of species threatened with extinction (Drummond *et al.*, 2008; Martinelli & Moraes, 2013). For Minas Gerais, *Pleurothallis malachantha* Rchb.f. and *Polystachya hoehneana* Kraenzl. (Orchidaceae) are cited as Vulnerable (VU). For Brazil, *Nematanthus strigillosus* (Mart.) H.E.Moore (Gesneriaceae) is cited as Near Threatened (NT) and *Oncidium truncatum* Pabst (Orchidaceae) as Critically Endangered (CR). *Nidularium marigoi* Leme is cited in both lists as VU (Minas Gerais) and NT (Brazil).

Comparison with species richness in other areas

The number of vascular epiphyte species recorded is lower at FT than in the adjacent PEIB, where Furtado & Menini Neto (2018) recorded 223 species of vascular epiphytes. This result was expected because the PEIB has c.300 ha of cloud forest; cloud forest is favourable to colonisation by epiphytes, owing to the high humidity and more pronounced elevation gradient (1000 to c.1800 m). However, although the PEIB has one of the richest epiphytic floras ever recorded in Brazil, 22 species recorded at FT (see Table 1) were not found in the PEIB conservation unit. This must be related to differences in phytophysiognomy between the two areas, because the PEIB is home to only cloud forest.

Compared with records of species richness available as checklists of vascular epiphytes found in SSF to date, the species richness recorded at FT is the highest in Brazil (Table 4). Although the studies are unequal in terms of collection effort, in several surveys it is similar to or greater than that of the present study (Rogalski & Zanin, 2003; Dettke *et al.*, 2008; Laurenti-Santos, 2008; Bonnet *et al.*, 2011; Perleberg *et al.*, 2013; Furtado & Menini Neto, 2015), and some of the areas surveyed in these studies covered an area larger than FT. Our finding of high species richness at FT is inconsistent with the expectation of low species richness in disturbed areas. However, it supports the designation by Drummond *et al.* (2005) of the Serra do Ibitipoca as an area of special biological importance, the highest level adopted in their classification, in the context of the Minas Gerais flora.

A similar richness of vascular epiphyte species to that found in the present study has been reported by Barbosa *et al.* (2015), who recorded 91 species in only 1 ha of SSF, also in Minas Gerais. They attributed the high species richness to the local microclimate, because a watercourse provides constant humidity to the epiphytes in the area studied. Similar species richness has also been recorded by Rogalski & Zanin (2003) and Giongo & Waechter (2004) in the same type of forest formation in the South Region of Brazil.

In two of the fragments surveyed in the present study, the occurrence of a permanent or temporary watercourse may influence species richness by contributing to the maintenance of local humidity. Species richness also seems to be influenced by other factors. These include altitude, which favours higher humidity (Rahbek, 1995; Ding *et al.*, 2016); several studies have found the species richness of vascular epiphytes to be highest between 1000 and 2000 m a.s.l. (Madison, 1977; Gentry & Dodson, 1987; Benzing, 1990; Küper *et al.*, 2004; Krömer *et al.*, 2005; Ding *et al.*, 2016). Other factors are the transition of one fragment to the phytophysiognomy of cloud dwarf-forest, and microclimatic characteristics related to elevation gradient (c.200 m) (Körner, 2004). These observations highlight the complexity of interactions between plants and their habitat.

Habitat heterogeneity and biodiversity

Our findings reinforce the importance to biodiversity of habitat heterogeneity. Almost half the total number of species recorded in the present study were found to be exclusive to an individual fragment. They include species commonly found in more humid environments, such as *Epidendrum chlorinum* and *Lellingeria apiculata* (BFG, 2018; SpeciesLink, no date), which are restricted to the fragment in transition with cloud dwarf-forest. Additionally, *Vriesea guttata*, a species typically found at high altitudes, was recorded only in the fragment with the highest mean altitude. The Dryopteridaceae species and two of the three Hymenophyllaceae species were found to be always associated with the occurrence of watercourses.

TABLE 4. Comparison of the number of vascular epiphyte species recorded at Fazenda do Tanque, Serra do Ibitipoca, Zona da Mata, Minas Gerais, Brazil (data from the present study) and other areas of seasonal semideciduous forest of the Atlantic Forest (data from previous studies)

Locality, state	Coordinates	Elevation (m a.s.l.)	Mean temperature (°C)	Mean precipitation (mm)	Extent	Duration of sampling	No. of species	Source
Conceição do Ibitipoca, MG	21°41′–43°54′	1200–1430	18.9	1500	23.6 ha	18 months	96	Present study
Chácara, MG	22°01′–43°86′	800–900	21	1581	1 ha	9 months	91	Barbosa *et al.* (2015)
Marcelino Ramos, RS	27°24′–51°27′	NA	18	1400	5.5 km^2	24 months	70	Rogalski & Zanin (2003)
Vários, PR	23°18′–50°58′	NA	17–21.2	1602	NA	2006–2008[a]	63	Bonnet *et al.* (2011)
Pelotas, RS	31°22′–52°29′	100–300	22.9	1367	3 ha	38 months	63	Perleberg *et al.* (2013)
Eldorado do Sul, RS	30°04′–51°40′	NA	19.2	1310	NA	12 months	57	Giongo & Waechter (2004)
Foz do Iguaçu, PR	25°23′–53°47′	168	22.1	1728	170,000 ha	NA	56	Cervi & Borgo (2007)
Botucatu, SP	22°55′–48°27′	850	20.7	1359	14 ha	13 months	56	Marcusso & Monteiro (2016)
Alegre, ES	20°40′–41°29′	220	24	1450	NA	12 months	55	Couto *et al.* (2016)
Juiz de Fora, MG	21°44′–43°22′	670–750	18	1500	87 ha	4 months	47	Santana *et al.* (2017)
Juiz de Fora, MG	21°43′–43°22′	800–900	18.9	1536	83 ha	19 months	43	Furtado & Menini Neto (2015)
São Paulo, SP	23°38′–46°36′	770–825	19	1540	357 ha	18 months	40	Laurenti-Santos (2008)
Fênix, PR	23°54′–51°56′	440	21	1500	354 ha	22 months	32	Borgo *et al.* (2002)
Maringá, PR	23°25′–51°25′	550	21	1600	47.3 ha	2003–2007[a]	29	Dettke *et al.* (2008)
Gália, SP	22°24′–49°42′	520–590	22.1	1401	10.2 ha	1 month	25	Breier (2005)
Iperó, SP	23°21′–47°45′	550–971	20	1400	5179.9 ha	12 months	21	Bataghin *et al.* (2010)

ES, Espírito Santo; MG, Minas Gerais; NA, data not available; PR, Paraná; RS, Rio Grande do Sul; SP, São Paulo.
[a] Number of months not stated in reference.

Species richness in Minas Gerais

Vascular epiphytes have a lower species richness in SSF than in rain forests (Gentry & Dodson, 1987; Kersten, 2010). However, it is worth noting the high richness of epiphyte species recorded in Minas Gerais compared with other areas in the Southeast and South Regions of Brazil. Furtado & Menini Neto (2015) and Santana *et al*. (2017) have conducted studies in urban forest under strong anthropogenic pressure; the results showed reduced species richness compared with more conserved areas surveyed in the other two studies done in Minas Gerais (see Table 4). Even in general floristic studies, in which the number of vascular epiphytes is often underestimated due to differences in methodology and sampling effort (Cervi *et al*., 2007; Lima *et al*., 2011), 75 species of vascular epiphytes were recorded in ReBio do Grama, representing a higher species richness than that recorded in specific studies of epiphytes in the South Region of Brazil (Forzza *et al*., 2014). Variables such as relief, climate and availability of hydrological resources have been suggested as being responsible for Minas Gerais having the most species-rich flora in Brazil (Drummond *et al*., 2005, Stehmann & Sobral, 2009; BFG, 2018).

Study limitations

It must be borne in mind that knowledge of epiphytic synusia in the SSF of Minas Gerais is incipient (Barbosa *et al*., 2015; Furtado & Menini Neto, 2015; Santana *et al*., 2017; the present study), that previous studies were conducted using different methodologies, and that the forest fragments surveyed were subject to different degrees of disturbance. New studies of the SSF phytophysiognomy in Minas Gerais are needed to verify if the high species richness found in the present study is a local phenomenon or a finding that can be generalised to other areas of SSF.

Conclusions

Fazenda do Tanque has the highest epiphytic species richness of SSF fragments surveyed in Brazil to date, despite being surrounded by a matrix of land subject to anthropogenic disturbance, and even when compared with larger areas surveyed with equal or greater collection effort. This finding confirms the biological importance of the Serra do Ibitipoca to the Brazilian flora. It also highlights the importance of habitat heterogeneity for species richness and conservation of the flora, as well as the maintenance of fragments, regardless of extent, disturbance or altitude, especially under the present-day scenario of ongoing degradation of the Atlantic Forest.

The predominance of characteristic holoepiphytes reinforces the importance of this ecological category to the formation of epiphytic communities. The record of only one species considered to be an accidental epiphyte is contrary to what we had expected for a disturbed area and is probably related to the conservation status of the fragments.

The presence of 22 species not recorded in the neighbouring PEIB, and of species threatened with extinction, highlights the importance of conservation and surveys conducted in areas that are not protected by conservation units. Such areas deserve attention because they can represent important sanctuaries for flora and fauna. Therefore, the execution of more studies in such areas is imperative for conserving the entire biodiversity of the Atlantic Forest. Given the current fragmentation of the Atlantic Forest, the findings of the present study reinforce the importance of private properties (even small ones, because 80% of Atlantic Forest remnants are less than 50 ha in extent; Ribeiro *et al.*, 2009). Our findings also reinforce the need for actions implemented jointly by environmental organisations and landowners, with the aim of protecting the remaining remnants of the Atlantic Forest, regardless of their extent.

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