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OUT OF THE FRYING PAN INTO THE FIRE: THE COMMUNITY STRUCTURE OF EPIPHYTES IN BRAZILIAN SAVANNA AFTER THE PASSAGE OF FIRE

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Cerrado sensu stricto (a physiognomy of the Cerrado domain, the Brazilian savanna) is subject to the annual occurrence of fire. Data on the epiphytic community in this physiognomy is scarce, as is evaluation of the influence of fire on its structure and composition. The aim of this study was to describe the structure of the vascular epiphyte community and its relationships with phorophytes in the Cerrado domain, Southeast Region of Brazil, after the passage of fire. We found the greatest abundance of epiphytes in the upper strata (65% of the individuals occurring above 3 m in height) and the dominance of three generalist species (*Tillandsia streptocarpa*, *T. recurvata* and *Epiphyllum phyllanthus*), suggesting that fire has an influence on the structure and composition of the epiphytic community.

Keywords. Abundance, Cerrado, *cerrado sensu stricto*, dead phorophytes, epiphyte stratification.

Introduction

The Cerrado phytogeographic domain (Brazilian savanna) is an important global biodiversity hotspot (Mendonça *et al.*, 1998; Myers *et al.*, 2000; Silva & Bates, 2002); however, there is little information on its epiphytic synusia (Bataghin *et al.*, 2012; Joanitti *et al.*, 2017), probably due to the markedly seasonal nature of the vegetation. Our knowledge is much more concentrated in ombrophilous environments (Benzing, 1990), where studies in the Neotropical region are common and for which we currently have a better understanding of epiphyte ecology (e.g. Sugden & Robins, 1979; Bittner & Trejos-Zelaya, 1997; Tremblay & Castro, 2009; Kersten, 2010; Blum *et al.*, 2011; Furtado & Menini Neto, 2015, 2016, 2018).

There is climatic seasonality in the Cerrado domain, with a mean annual precipitation of 1500 mm, of which 90% is concentrated between October and March, resulting in rainy summers and dry winters (Malheiros, 2016). The absence of a canopy in the vegetation physiognomy,

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which is mainly composed of isolated trees (IBGE, 2012), further limits water availability, presenting a hostile environment for epiphytes. This feature probably affects the vertical distribution of epiphytes along phorophytes (stratification), as this is conditioned by gradients of light and humidity (Johansson, 1974; ter Steege & Cornelissen, 1989; Parker, 1995; Krömer *et al.*, 2007; Dislich & Mantovani, 2016). According to Benzing (1990), vertical stratification in such an environment is reduced or absent, due to little variation in luminosity and humidity between soil level and the canopy of the trees. Conversely, in physiognomies subject to the occurrence of fire, such as those of the Cerrado (Mistry, 1998), its influence could be a disturbing feature impeding or decreasing the establishment and maintenance of epiphytes in the inferior strata of phorophytes, especially on trunks (Adams & Lawson, 1984; Bartareau & Skull, 1994; Zotz, 2016), resulting in a concentration of individuals in the canopy of the trees, far away from fire.

Studies dealing with the influence of fire on epiphytes are scarce, for both vascular (Adams & Lawson, 1984; Cook, 1991; Robertson & Platt, 1992; Bartareau & Skull, 1994; Robertson & Platt, 2001) and non-vascular communities (Brasell & Mattay, 1984; Benscoter, 2006; Saxena *et al.*, 2009; Pharo *et al.*, 2013). There are no studies to date on the influence of fire on the epiphytic synusia in Brazilian Cerrado, and knowledge is poor even in other ecosystems (Robertson & Platt, 2001), justifying and reinforcing the relevance of the present study.

Our aims were therefore to describe the structure of the vascular epiphyte community and its relationships with phorophytes in the Cerrado domain, Southeast Region of Brazil. Because the community was studied after a fire event, we also seek to provide data that could be useful for studies on the influence of fire on epiphytes in the Cerrado.

Materials and Methods

Study area and sampling

The study was conducted in August 2014 in the Parque Estadual do Rio Preto, Diamantina Plateau, which is part of the Serra do Espinhaço, located in the Cerrado domain, north central Minas Gerais, Brazil (Fig. 1). The park has an area of 12,000 ha and is delimited by the Rio Preto basin (43°18′–43°21′W, 18°14′–18°03′S), between 700 m and 1826 m in altitude. The vegetation comprises a mosaic of *campo rupestre*, *cerrado sensu stricto* and seasonal semideciduous forest (Versieux *et al.*, 2010). The climate is Cwb according to the Köppen classification, with precipitation and temperature means of 1250–1500 mm and 18–19°C, respectively (Neves *et al.*, 2005; Versieux *et al.*, 2010).

The *cerrado sensu stricto* (woodland) is one of the savanna physiognomies of the Cerrado domain and is characterised by the presence of short, inclined and tortuous trees with irregular and twisted branching, subject to the annual occurrence of fire (Ribeiro & Walter, 1998; IBGE, 2012). Within the study area, it is represented by trees with an average height of about 5 m, frequently in contact with areas of *campo rupestre*, and occurring on rocky outcrops in some places (personal observation).

For sampling, we considered an existing trail to represent a transect 5 km long and 10 m wide at an altitude of between 750 and 800 m, near to the ecotone of *cerrado sensu stricto*

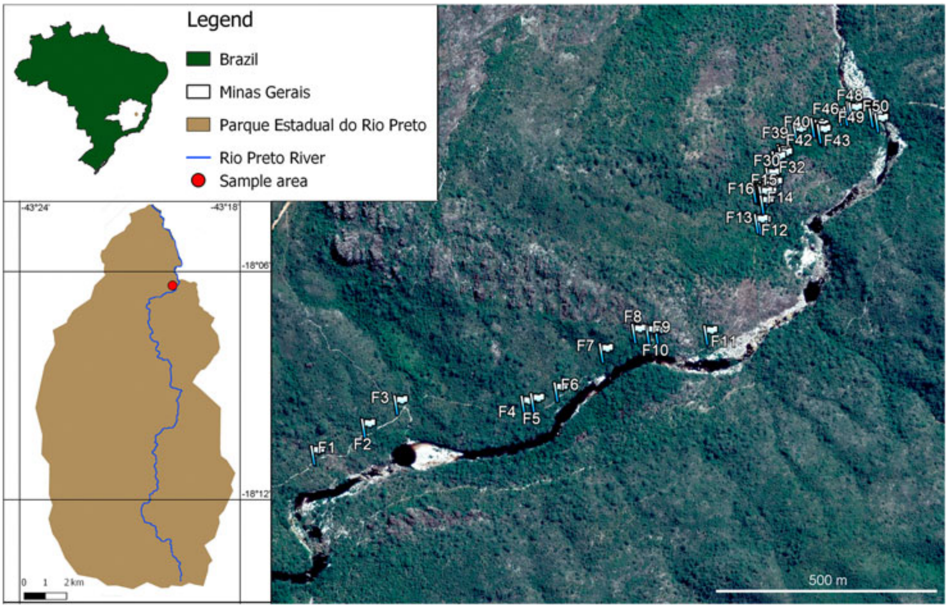

FIG. 1. Location of the study area, Parque Estadual do Rio Preto, Minas Gerais, Brazil, and distribution of the studied phorophytes (modified from Google Earth).

and *campo rupestre* on the western margin of Rio Preto. This area presented evidence of fire, such as carbonised wood and resprouted plants; according to park employees, the fire had occurred in the previous year (2013). All trees along the track with vascular epiphytes present and a diameter at base height > 10 cm (named phorophytes) were recorded. Fifty phorophytes were sampled; the vascular epiphytes were identified and counted, and the height of epiphytes on phorophytes was measured with a graduated stick.

We established five height categories: A, 0–0.99 m; B, 1–1.99 m; C, 2–2.99 m; D, 3–3.99 m; and E, ≥ 4 m. We chose this method for division of strata, because the phorophytes had very irregular branching.

Data analysis

To describe the structure of the vascular epiphytic community, we calculated abundance (number of individuals in each strata) as well as absolute frequency (*AF*) and relative frequency (*RF*), according to Waechter & Batista (2004):

$$AF_{\mathrm{i}} = (Nph_{\mathrm{i}}/Nph_{\mathrm{a}}).100$$

$$RF_{\mathrm{i}} = (Nph_{\mathrm{i}}/\Sigma Nph_{\mathrm{i}})$$

In these equations, Nph_{i} is the number of phorophytes occupied by epiphyte species i and Nph_{a} the total number of phorophytes in the sample.

The ecological categories adopted were characteristic epiphyte (plants genuinely epiphytic, with one to several modifications for epiphytism), facultative epiphyte (plants presenting such modifications but inhabiting trees and the ground interchangeably) and accidental epiphyte (plants possessing no special modifications for epiphytism) (Benzing, 1990; Zotz, 2016).

Analysis of stratification was performed with the five most abundant species (totalling nearly 95% of the sampled specimens). The other species were accidental epiphytes or had sporadic occurrences. To evaluate differences in the abundance of epiphytes between phorophyte strata (height categories), we used the non-parametric test of Kruskal–Wallis, because the data did not present a normal distribution (Magurran, 2011).

Statistical analysis was performed using the PAST 3 software (Hammer *et al.*, 2001).

Results

We recorded 273 specimens of vascular epiphytes, belonging to six families, 10 genera and 12 species (data summarised in Table 1). We found only angiosperms, with the richest families being Bromeliaceae (four species) and Orchidaceae (three species). Cactaceae was represented by two species (of which one was an accidental epiphyte), and the remaining families (Araceae, Gesneriaceae and Portulacaceae) were represented by only one species each, the last being accidental. There was a strong dominance of three species: *Tillandsia streptocarpa* Baker and *T. recurvata* (L.) L. (Bromeliaceae), with 121 and 71 individuals, respectively, and *Epiphyllum phyllanthus* (L.) Haw. (Cactaceae), with 35 observed individuals (totalling 83.5%).

The epiphytes were found on 12 species of phorophyte (data summarised in Table 2), of which *Aspidosperma dispermum* Müll. Arg. (Apocynaceae) was the most frequent, with 21 individuals, hosting 10 of the 12 recorded species of epiphyte. It was also noteworthy that seven individuals of dead, unidentified phorophytes hosted specimens of 58% of the epiphyte species sampled in this study.

The five most abundant species (*Tillandsia streptocarpa*, *T. recurvata*, *Epiphyllum phyllanthus*, *Catasetum barbatum* (Lindl.) Lindl. and *Billbergia zebrina* (Herb.) Lindl.) represented the highest concentration of individuals above 3 m, where more than 65% of sampled epiphyte specimens occurred (Fig. 2). The Kruskal–Wallis test showed a significant difference in abundance between the two highest strata (D and E) and the lowest stratum (A), and between the highest (E) and second highest (B) strata ($H = 9.92$, $H_c = 10.03$, $P = 0.04$).

Discussion

Composition and structure of the community

The families recorded (Araceae, Bromeliaceae, Cactaceae, Gesneriaceae, Orchidaceae and Portulacaceae), except for the Portulacaceae with a single accidental species, are often the most important for vascular epiphytes, both in the Neotropical region (Gentry & Dodson, 1987) and globally (Benzing, 1990; Zotz, 2013, 2016). In the Cerrado domain specifically, Bataghin *et al.* (2012) and Joanitti *et al.* (2017) also found the Bromeliaceae and

TABLE 1. Species of vascular epiphytes recorded in the study area of Parque Estadual do Rio Preto, Minas Gerais, Brazil, and evaluated parameters

								Height category				
Species	Family	EC	Dispersal	Abundance	*AF*	*RF*	No. of phorophytes	A (0–0.99 m)	B (1–1.99 m)	C (2–2.99 m)	D (3–3.99 m)	E (≥ 4)
Tillandsia streptocarpa Baker	Brom	FE	Ane	121	44	28.21	22	0	13	23	41	44
Tillandsia recurvata (L.) L.	Brom	CE	Ane	71	20	12.82	10	0	4	26	16	25
Epiphyllum phyllanthus (L.) Haw.	Cact	CE	Zoo	35	34	21.80	17	4	3	3	15	10
Catasetum barbatum (Lindl.) Lindl.	Orch	CE	Ane	19	18	11.54	9	1	0	2	1	15
Billbergia zebrina (Herb.) Lindl.	Brom	CE	Zoo	13	20	12.82	11	0	3	3	3	4
Bulbophyllum cf. *weddelii* Rchb.f.	Orch	FE	Ane	4	4	2.56	2	0	0	0	0	4
Bulbophyllum sp.	Orch	CE	Ane	4	4	2.56	2	0	3	1	0	0
Aechmea bromeliifolia (Rudge) Baker	Brom	FE	Zoo	2	4	2.56	2	0	1	0	0	1
Anthurium aff.*minarum* Sakur. & Mayo	Arac	FE	Zoo	1	2	1.28	1	0	0	1	0	0
Cipocereus minensis (Werderm.) F.Ritter	Cact	AE	Zoo	1	2	1.28	1	0	0	1	0	0
Portulaca hirsutissima Cambess.	Port	AE	Zoo	1	2	0.02	1	0	1	0	0	0
Sinningia sp.	Gesn	CE	Ane	1	2	1.28	1	0	1	0	0	0

AE, accidental epiphyte; *AF*, absolute frequency; Ane, anemochory; Arac, Araceae; Brom, Bromeliaceae; Cact, Cactaceae; CE, characteristic epiphyte; EC, ecological category; FE, facultative epiphyte; Gesn, Gesneriaceae; Orch, Orchidaceae; Port, Portulacaceae; *RF*, relative frequency; Zoo, zoochory.

TABLE 2. Phorophyte species and families, and parameters of richness and abundance of epiphytes recorded in the study area of Parque Estadual do Rio Preto, Minas Gerais, Brazil

Phorophyte species	Phorophyte family	No. of phorophytes[a]	No. of epiphytes[b]	Richness[c]
Aspidosperma dispermum Müll. Arg.	Apocynaceae	21	108	10
Dead	–	7	18	7
Senegalia polyphylla (DC.) Britton	Fabaceae	5	13	3
Amaioua guianensis Aubl.	Rubiaceae	4	41	2
Caryocar brasiliense Cambess.	Caryocaraceae	3	8	3
Kielmeyera coriacea Mart. & Zucc.	Calophyllaceae	2	41	2
Unidentified species 1	–	2	13	1
Eremanthus sp.	Asteraceae	1	4	2
Hymenaea stigonocarpa Mart. ex Hayne	Fabaceae	1	1	1
Qualea dichotoma (Mart.) Warm.	Vochysiaceae	1	3	1
Schefflera macrocarpa (Cham. & Schltdl.) Frodin	Araliaceae	1	1	1
Unidentified species 2	–	1	21	3
Unidentified species 3	–	1	1	1

[a] Number of phorophytes belonging to the species.
[b] Number of epiphyte specimens found on the phorophyte specimens.
[c] Number of epiphyte species found on the phorophyte species.

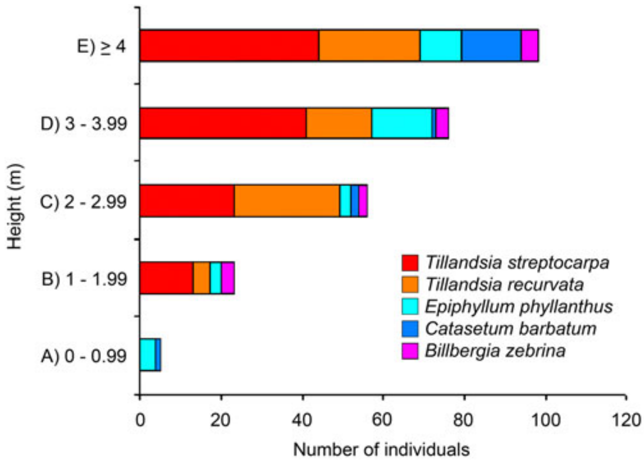

FIG. 2. Height distribution in the phorophytes of the five most abundant species of epiphyte in the study area of Parque Estadual do Rio Preto, Minas Gerais, Brazil.

Orchidaceae to be the richest families of angiosperms. The absence of the Polypodiaceae in our area is noteworthy, because it is one of the richest families of vascular epiphytes and includes several species adapted to dry or seasonal environments, in particular the genus *Pleopeltis*, which includes poikilohydrous species, or at least species with high desiccation tolerance (Kessler & Siorak, 2007; Zotz, 2016). Both Bataghin *et al.* (2012) and Joanitti *et al.* (2017) listed Polypodiaceae as among the three richest families of vascular epiphytes, although in both cases they were studying forest Cerrado physiognomies rather than savanna ones. It is possible that seasonality has stronger effects in a more open vegetation, such as the savanna physiognomy, limiting the occurrence of Polypodiaceae in the studied area.

The three dominant species (*Tillandsia streptocarpa*, *T. recurvata* and *Epiphyllum phyllanthus*), which together accounted for 83.5% of the sampled abundance, have a wide distribution throughout the Neotropical region and are adapted to a broad spectrum of habitats (Taylor & Zappi, 2004; Paixão-Souza, 2016; BFG, 2018). Both *Tillandsia* species are part of a lineage composed of atmospheric plants adapted to adverse conditions and a high hydric deficit. *Epiphyllum phyllanthus* is a widely distributed Cactaceae species in eastern Brazil, and one of the few epiphytic species of the family that occurs in the Cerrado domain (Taylor & Zappi, 2004; BFG, 2018). Its seedlings have a high capacity to survive without water, and this feature is presumably responsible for its prominent occurrence in this limiting habitat.

The high frequency of *Aspidosperma dispermum* as a phorophyte is probably associated with its profound rhytidomal fissures, facilitating the retention of resources such as humidity and nutrients, and consequently the establishment of epiphytes (Benzing, 1990; Zotz, 2016). The occurrence of seven species of epiphyte on dead phorophytes (totalling more than half of the species recorded) is noteworthy, because there is an expected reduction of substrate after the death of a tree, due to the loss of branches and detachment of the rhytidoma, this often being followed by a decrease in epiphyte richness (Taylor & Burns, 2015). However, this result suggests that standing dead trees are capable of maintaining part of the epiphytic community, depending on the resistance of the wood to putrefaction. This is especially important for epiphytes in savannas, which are characterised by low tree density (Ribeiro & Walter, 1998), consequently reducing substrate availability.

Vertical stratification as a response to fire?

Benzing (1990) states that a lack or reduction of stratification of epiphytes in woodlands is due to intrinsic features of this vegetation physiognomy. Thus, our result (elevated abundance above 3 m in height, totalling more than 65% of individuals) suggests that fire can influence the distribution of plants and that they have greater success when established in the upper strata of phorophytes in this type of environment that is prone to fire. A similar result was found by Bartareau & Skull (1994) for epiphytic orchids on *Melaleuca viridiflora* Sol. ex Gaertn. (Myrtaceae) in woodlands in Australia. In our study, the height at which most individuals occur seems to be sufficient for the epiphytes to avoid direct fire, because Castro & Kauffman (1998) indicated that the fire height limit in *cerrado sensu stricto* varies between 2.7 and 2.9 m.

The flames consume the herbaceous stratum but seldom the arboreal plants (Miranda *et al.*, 1993), and the intensity, speed and height of the fire vary according to the physiognomy (field, savanna or forest), with larger values in field environments that decrease with an increase in the height of vegetation (Miranda *et al.*, 2010). Thus, epiphytes that are distributed in the higher strata of phorophytes maintain their substrate and are protected from the direct or even indirect action of the fire, because the temperature and duration of the heat pulse vary according to height (Miranda *et al.*, 1993). The greater the height at which it is established, the less likely it is that the epiphyte will be affected, although the flow of hot air is still a potential source of damage (Kayll, 1968; Wright, 1970), and different species of epiphyte would be expected to respond to this in different ways.

Stocker & Mort (1981) and Bartareau & Skull (1994) indicated that the intensity, frequency and season of occurrence of fire present short- and long-term effects on the plant community, drastically shifting the succession process. This is very apparent in the area studied here, because all individuals found at heights under 1 m were seedlings (four specimens of *Epiphyllum phyllanthus* and one of *Catasetum barbatum*), having seemingly germinated during the previous year, that is, after the fire had been recorded in the area.

The five most abundant species represent three of the richest epiphyte families (Bromeliaceae, Cactaceae and Orchidaceae) (Benzing, 1990; Zotz, 2013, 2016). These species have functional traits that reflect their adaptation to epiphytism (Benzing, 1990; Zotz, 2016), such as absorptive and reflective hairs (*Billbergia zebrina*, *Tillandsia recurvata* and *T. streptocarpa*), phytotelmata (*B. zebrina*), water-storage parenchyma in the leaves (*T. recurvata* and *T. streptocarpa*) or stems (*Catasetum barbatum* and *Epiphyllum phyllanthus*), leaf loss in dry seasons and trash-basket roots with velamen (*C. barbatum*). Because these species establish themselves in the upper strata (thus surviving fire), such adaptations allow them to survive in a stress environment such as the tree canopy of *cerrado sensu stricto* under strong insolation, desiccant winds, marked seasonality and reduced water availability, these conditions representing a strong environmental filter.

Conclusions

The results presented here strongly suggest the influence of fire on the structure of the epiphytic community in the *cerrado sensu stricto*. The majority of individuals that survive in an environment prone to the occurrence of fire are concentrated in upper phorophyte strata, thus avoiding the direct or indirect effects of flames and their intense heat. Future studies comparing areas with and without the regular occurrence of fire could help to shed further light on this issue.

To survive in environments of marked seasonality, several adaptations are necessary to resist the high hydric deficit present for at least half of the year, in addition to the intense insolation and the desiccation caused by wind due to the absence of a canopy in this savanna environment. Such an environmental filter selects generalist species that are mostly capable of living in a broad range of habitats and of being abundant in this limiting environment.

Lastly, it is interesting to note the importance of standing dead phorophytes, which can host a relatively high diversity of epiphytes in an environment known to be poor in this life form. This is even more relevant given the reduced arboreal density in savanna environments such as the *cerrado sensu stricto*.

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References

Adams, P. B. & Lawson, S. D. (1984). The effects of bushfire on Victorian epiphytic and lithophytic orchids. *Orchadian* 7(12): 282–286.

Bartareau, T. & Skull, S. (1994). The effects of past fire regimes on the structural characteristics of coastal plain *Melaleuca viridiflora* Sol. ex Gaert. woodlands and the distribution patterns of epiphytes (*Dendrobium canaliculatum* R.Br., *Dischidia nummularia* R.Br.) in Northeastern Queensland. *Biotropica* 26(2): 118–123.

Bataghin, F. A., Muller, A., Pires, J. S. R., Barros, F., Fushita, A. T. & Scariot, E. C. (2012). Riqueza e estratificação vertical de epífitas vasculares na Estação Ecológica de Jataí – área de Cerrado no Sudeste do Brasil. *Hoehnea* 39(4): 615–626.

Benscoter, B. W. (2006). Post-fire bryophyte establishment in a continental bog. *J. Veg. Sci.* 17(5): 647–652.

Benzing, D. H. (1990). *Vascular Epiphytes*. Cambridge: Cambridge University Press.

BFG [Brazil Flora Group] (2018). Brazilian Flora 2020: innovation and collaboration to meet Target 1 of the Global Strategy for Plant Conservation (GSPC). *Rodriguésia* 69(4): 1513–1527.

Bittner, J. & Trejos-Zelaya, J. (1997). Analysis of the vascular epiphytes of tree ferns in a montane rain forest in Costa Rica. *Revista Mat. Teoría y Aplicaciones* 4(2): 63–73.

Blum, C. T., Roderjan, C. V. & Galvão, F. (2011). Composição florística e distribuição altitudinal de epífitas vasculares da Floresta Ombrófila Densa na Serra da Prata, Morretes, Paraná, Brasil. *Biota Neotrop.* 11(4): 141–159.

Brasell, H. M. & Mattay, J. P. (1984). Colonization of bryophytes of burned eucalyptus forest in Tasmania, Australia: changes in biomass and element content. *Bryologist* 87(4): 302–307.

Castro, E. A. de & Kauffman, J. B. (1998). Ecosystem structure in the Brazilian Cerrado: a vegetation gradient of aboveground biomass, root mass and consumption of fire. *J. Trop. Ecol.* 14(3): 263–283.

Cook, G. D. (1991). Effects of fire regimen on two species of epiphytic orchids in tropical savannas of the Northern Territory. *Austral. Ecol.* 16(4): 537–540.

Dislich, R. & Mantovani, W. (2016). Vascular epiphytes assemblages in a Brazilian Atlantic Forest fragment: investigating the effect of host tree features. *Plant Ecol.* 217(1): 1–12.

Furtado, S. G. & Menini Neto, L. (2015). Diversity of vascular epiphytes in two high altitude biotopes of the Brazilian Atlantic Forest. *Brazil. J. Bot.* 38(2): 295–310.

Furtado, S. G. & Menini Neto, L. (2016). Vascular epiphytic flora of a high montane environment of Brazilian Atlantic Forest: composition and floristic relationships with other ombrophilous forests. *Acta Bot. Brasil.* 30(3): 422–436.

Furtado, S. G. & Menini Neto, L. (2018). Elevational and phytophysiognomic gradients influence the epiphytic community in a cloud forest of the Atlantic phytogeographic domain. *Plant Ecol.* 219(6): 677–690.

Gentry, A. H. & Dodson, C. H. (1987). Diversity and biogeography of Neotropical vascular epiphytes. *Ann. Missouri Bot. Gard.* 74(2): 205–233.

Hammer, Ø., Harper, D. A. T. & Ryan, P. D. (2001). Past: paleontological statistics software package for education and data analysis. *Palaeontol. Electronica* 4(1): 1–9.
IBGE (2012). *Manual Técnico da Vegetação Brasileira*, 2nd edition. Rio de Janeiro: Instituto Brasileiro de Geografia e Estatística.
Joanitti, S. A., Weiser, V. L., Cavassan, O. & Giles, A. L. (2017). Vascular epiphytes in a woodland savanna forest in southeastern Brazil. *J. Torrey Bot. Soc.* 144(4): 439–449.
Johansson, D. (1974). Ecology of vascular epiphytes in West African rain forest. *Acta Phytogeogr. Suec.* 59: 1–136.
Kayll, A. J. (1968). Heat tolerance of tree seedlings. In: *Proceedings: 8th Tall Timbers Fire Ecology Conference 1968*, pp. 9–15.
Kersten, R. A. (2010). Epífitas vasculares – histórico, participação taxonômica e aspectos relevantes, com ênfase na Mata Atlântica. *Hoehnea* 37(1): 9–38.
Kessler, M. & Siorak, Y. (2007). Desiccation and rehydration experiments on leaves of 43 pteridophyte species. *Amer. Fern J.* 97(4): 175–185.
Krömer, T., Kessler, M. & Gradstein, S. R. (2007). Vertical stratification of vascular epiphytes in submontane and montane forest of the Bolivian Andes: the importance of the understory. *Plant Ecol.* 189(2): 261–278.
Magurran, A. E. (2011). *Medindo a Diversidade Biológica. Tradução de Dana Moiana Vianna*. Curitiba: Editora UFPR.
Malheiros, R. (2016). A influência da sazonalidade na dinâmica da vida no bioma Cerrado. *Revista Brasil. Climatol.* 19: 113–128.
Mendonça, R. C., Felfili, J. M., Walter, B. M. T., Silva Júnior, M. C., Rezende, A. V., Filgueiras, T. S. & Nogueira, P. E. (1998). Flora vascular do cerrado. In: Almeida, M. S. & Almeida, S. P. (eds) *Cerrado: Ambiente e Flora*, pp. 287–556. Planaltina: Embrapa – CPAC.
Miranda, A. C., Miranda, H. S., Dias, I. F. O. & Dias, B. F. S. (1993). Soil and air temperatures during prescribed cerrado fires in Central Brazil. *J. Trop. Ecol.* 9(3): 313–320.
Miranda, H. S., Neto, W. N. & Neves, B. M. C. (2010). Capítulo 2 – Caracterização das queimadas de cerrado. In: Miranda, H. S. (org.) *Efeitos do Regime de Fogo Sobre a Estrutura de Comunidades do Cerrado: Projeto Fogo*, pp. 23–33. Brasília: Ibama [Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis]. Online. Available: http://www.ibama.gov.br/sophia/cnia/livros/efeitosdoregimedefogopaginarevisadasparaprovadigital.pdf (accessed 27 March 2018).
Mistry, J. (1998). Fire in the cerrado (savannas) of Brazil: an ecological review. *Progr. Phys. Geogr. Earth Environm.* 22(4): 425–448.
Myers, N., Mittermeier, R. A., Mittermeier, C. G., Fonseca, G. A. B. da & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature* 403: 853–858.
Neves, S. C., Abreu, P. A. A. & Fraga, L. M. S. (2005). Fisiografia. In: Silva, A. C., Pedreira, L. C. V. S. F. & Abreu, P. A. A. (eds) *Serra do Espinhaço Meridional: Paisagens e Ambientes*, pp. 47–58. Belo Horizonte: Editora O Lutador.
Paixão-Souza, B. (2016). *Filogenia e evolução de Tillandsia subgênero Anoplophytum (Beer) Baker (Bromeliaceae – Tillandsioideae)*, 105 pp. Tese de doutorado, Museu Nacional – UFRJ, Rio de Janeiro.
Parker, G. G. (1995). Structure and microclimate of forest canopies. In: Lowman, M. D. & Nadkarni, N. M. (eds) *Forest Canopies*, pp. 73–106. San Diego: Academic Press.
Pharo, E. J., Meagher, D. A. & Lindenmayer, D. B. (2013). Bryophyte persistence following major fire in eucalypt forest of southern Australia. *Forest Ecol. Managem.* 296: 24–32.
Ribeiro, J. F. & Walter, B. M. T. (1998). Capítulo III – fitofisionomias do bioma Cerrado. In: Sano, S. M. & Almeida, S. P. (eds) *Cerrado: Ambiente e Flora*, pp. 89–166. Planaltina: Embrapa – CPAC.

ROBERTSON, K. & PLATT, W. (1992). Effects of fire on bromeliads in subtropical hammocks of Everglades National Park, Florida. *Selbyana* 13: 39–49.

ROBERTSON, K. & PLATT, W. (2001). Effects of multiple disturbances (fire and hurricane) on epiphyte community dynamics in a subtropical forest, Florida, USA. *Biotropica* 33(4): 573–582.

SAXENA, D. K., ARFEEN, M. S. & KAUR, H. (2009). Effects of fire on bryocommunity of Kausani, India. *Indian J. Forest.* 32(1): 13–22.

SILVA, J. M. C. & BATES, J. M. (2002). Biogeographic patterns and conservation in the South American Cerrado: a tropical savanna hotspot. *BioScience* 52(3): 225–233.

STOCKER, G. C. & MORT, J. J. (1981). Fire in tropical forests and woodlands of northern Australia. In: GILL, A. M., GROVES, R. H. & NOBLE, J. R. (eds) *Fire and the Australian Biota*, pp. 427–439. Canberra: Australian Academy of Science.

SUGDEN, A. M. & ROBINS, R. J. (1979). Aspects of the ecology of vascular epiphytes in Colombian cloud forests, I. The distribution of the epiphytic flora. *Biotropica* 11(3): 173–188.

TAYLOR, A. & BURNS, K. C. (2015). Epiphyte community development throughout tree ontogeny: an island ontogeny framework. *J. Veg. Sci.* 26(5): 902–910.

TAYLOR, N. & ZAPPI, D. (2004). *Cacti of Eastern Brazil*. Richmond: Royal Botanic Gardens, Kew.

TER STEEGE, H. & CORNELISSEN, J. H. C. (1989). Distribution and ecology of vascular epiphytes in lowland rain forest of Guyana. *Biotropica* 21(4): 331–339.

TREMBLAY, R. L. & CASTRO, J. V. (2009). Circular distribution of an epiphytic herb on trees in a subtropical rain forest. *Trop. Ecol.* 50(2): 211–217.

VERSIEUX, L. M., LOUZADA, R. B., VIANA, P. L., MOTA, N. & WANDERLEY, M. G. L. (2010). An illustrated checklist of Bromeliaceae from Parque Estadual do Rio Preto, Minas Gerais, Brazil, with notes on phytogeography and one new species of *Cryptanthus*. *Phytotaxa* 10(1): 1–16.

WAECHTER, J. L. & BATISTA, L. R. M. (2004). Abundância e distribuição de orquídeas epifíticas em uma floresta turfosa do Brasil Meridional. In: BARROS, F. & KERBAUY, G. B. (eds) *Orquideologia sul Americana: Uma Compilação Científica*, pp. 135–145. São Paulo: Secretaria do Meio Ambiente, Instituto de Botânica.

WRIGHT, S. J. (1970). A method to determine heat-cause mortality in bunchgrass. *Ecology* 51(4): 582–587.

ZOTZ, G. (2013). The systematic distribution of vascular epiphytes – a critical update. *Bot. J. Linn. Soc.* 171(3): 453–481.

ZOTZ, G. (2016). *Plants on Plants – the Biology of Vascular Epiphytes*. Geneva: Springer.

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