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Floristic composition and phytogeography of an *Araucaria* Forest in the Serra da Mantiqueira, Minas Gerais, Brazil

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Abstract

The Parque Estadual da Serra do Papagaio (PESP) harbors some unusual fragments of mixed needle-broadleaved forest (MNF) of Minas Gerais state. This study aims to analyze the floristic composition and geographic distribution of the genera represented in the MNF of the PESP. Collections of fertile specimens of vascular plants (excluding epiphytes) were conducted monthly (March 2012–June 2013) in the alluvial and slope areas of MNF in the PESP, in altitudes ranging from 1,650–2,000 m above sea level. The genera were classified into seven phytogeographic groups that were delimited according to their current diversity centers available in the literature. We recorded 310 species belonging to 168 genera and 82 families of vascular plants. The richest families were Asteraceae (49 species), Melastomataceae (33 species) and Rubiaceae (16 species). We observed the presence of species often found in montane and high montane forests of southeastern region, besides of temperate genera, showing that low temperatures caused by high altitude influence the floristic composition of the area. The high richness found denotes the importance of altitude areas for diversity in Atlantic Forest and highlights the biogeographic importance of the region for presenting an unusual phytophysiognomy in the state with endemic and endangered species.

Key words: Altitude, Atlantic Forest, Mixed Ombrophilous Forest, Parque Estadual da Serra do Papagaio, *Araucaria angustifolia*.

Resumo

O Parque Estadual da Serra do Papagaio (PESP) possui fragmentos incomuns de Floresta Mista Latiaciculifoliada (MNF) do estado de Minas Gerais. Os objetivos deste trabalho foram analisar os aspectos florísticos e a distribuição geográfica dos gêneros presentes na MNF do PESP. Foram realizadas coletas mensais (de março de 2012 a junho de 2013) de exemplares férteis (excluindo-se as epífitas) nas áreas de MNF aluvial e de encosta do PESP, com altitudes entre 1.650–2.000 m. Os gêneros foram classificados em sete grupos fitogeográficos de acordo com seu centro de diversidade disponível na literatura. Foram registradas 310 espécies pertencentes a 168 gêneros e 82 famílias de plantas vasculares, sendo as famílias mais ricas: Asteraceae (49 espécies), Melastomataceae (33 espécies) e Rubiaceae (16 espécies). Foi observado a presença de espécies frequentes na floresta montana e alto-montana da Região Sudeste do Brasil, além de gêneros de origem temperada, mostrando que a baixa temperatura causada pela altitude influencia na composição florística da área. A elevada riqueza encontrada denota a importância das áreas de altitude para a diversidade da Floresta Atlântica e evidencia a importância biogeográfica da região por apresentar um fitofisionomia incomum no estado e com espécies endêmicas e ameaçadas.

Palavras-chave: Altitude, Floresta Atlântica, Floresta Ombrófila Mista, Parque Estadual da Serra do Papagaio, *Araucaria angustifolia*.

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Introduction

The Atlantic Forest is one of the 25 world-biodiversity hotspots (Myers *et al.* 2000) and harbors about 2.7% of the world flora, or ~12,000 plant species, of which a large percentage is endemic to this phytogeographic domain, highlighting its enormous diversity (MMA 2000). Minas Gerais state has an extensive land area, rugged terrain and abundant water resources, which enable the development of extremely rich and diverse vegetation (Drummond *et al.* 2009). The Serra da Mantiqueira is one of the largest and most important mountain chain of the southeastern region of Minas Gerais and contains several forest remnants of the Atlantic Domain (Costa & Herrmann 2006).

Currently, the most conserved forest fragments are found in regions of difficult access, such as mountain tops, and altitude is one of the main indirect environmental factors acting on the composition and structure of the vegetation (Whitmore 1998; Oliveira Filho & Fontes 2000). The vegetation at high altitudes often contains species with a narrow geographic distribution, harboring groups absent or with lower richness at lower altitude. Several of these groups have temperate origin and Andean centers of dispersal (Gentry 1988; Safford 2007).

We can find fragments of Araucaria forest at high altitudes in the Serra do Mar and Serra da Mantiqueira mountain ranges, in the states of São Paulo, Minas Gerais and Rio de Janeiro, a forest type whose main distribution area is in Southern Brazil. (Klein 1960; IBGE 2012). In Minas Gerais state, native Araucaria forests are unusual and in literature this type of physiognomy occurs only in Camanducaia and Parque Estadual da Serra do Papagaio (França & Stehmann 2004; Silva *et al.* 2008). According to Oliveira Filho (2009), this physiognomy is classified as mixed needle-broadleaved forest (MNF) due to the presence of *Araucaria angustifolia*, the only native species of the Araucariaceae family in the Brazilian flora. The other species are broadleaved, with the exception of *Podocarpus lambertii*, which also can be abundant. This species can account for more than 50% of the canopy, reaching up to 30 m in height. The main fragments of MNF are located in the Southern Region of Brazil (Klein 1960; Hueck 1972). Today, however, there are estimations that these remnants contain around only 5% of the original area (MMA 2000), so they are among the most endangered physiognomies of the Atlantic Forest domain.

In the Parque Estadual da Serra do Papagaio (PESP), located in the southern region of Minas Gerais, the occurrence of this physiognomy has high ecological value (Silva *et al.* 2008). The region of the PESP was visited in the 19th century by Saint Hilaire, who crossed Aiuruoca in 1822 and recorded several interesting plant species, which he did not find in any other place until then (Saint Hilaire 1932).

The goals of this study are to provide information about the floristic composition of a remnant of MNF in PESP, an unusual forest physiognomy in Minas Gerais state and evaluate the proportion of tropical and temperate elements. Our analyses were guided by the following questions: "Does the floristic composition of the MNF in PESP demonstrate a similar pattern to those observed in others southern MNF and montane and high montane forests of southeastern Brazil?"; "Is the altitude an important factor in floristic composition?"; and "What are the implications on floristic composition with the presence of genera from different origins?".

Materials and Methods

Study area

The Parque Estadual da Serra do Papagaio is located at the Planalto do Itatiaia, southern Mantiqueira range, at the southern limit of Minas Gerais state near the border with Rio de Janeiro and São Paulo states. It contains an area of 22,917 ha encompassing parts of the municipalities of Aiuruoca, Alagoa, Baependi, Itamonte, and Pouso Alto (IEF 2013) (Fig. 1) (22º8'33.5"S, 44º43'42.2"W - Datum: WGS84, at the administrative office of the park). The climate of the region is Cwb (highland tropical), according to the classification of Köppen, with warm and moist summers and cold and dry winters. The annual mean temperature is 18–19 ºC, and the mean annual rainfall is 1,500 mm (Simas *et al.* 2005). The altitude of PESP ranges from 1,200 m to 2,360 m a.s.l. The PESP integrates the "Corredor Ecológico da Serra da Mantiqueira" (Ecological Corridor of Mantiqueira) and is connected geographically with the northern part of the Parque Nacional do Itatiaia, which has high numbers of endemic species (Brade 1956). According to Silva *et al.* (2008), the PESP is a vegetation mosaic composed of MNF, broadleaved cloud forest, broadleaved seasonal forest and cloud grassland, using nomenclature according to the system of Oliveira Filho (2009).

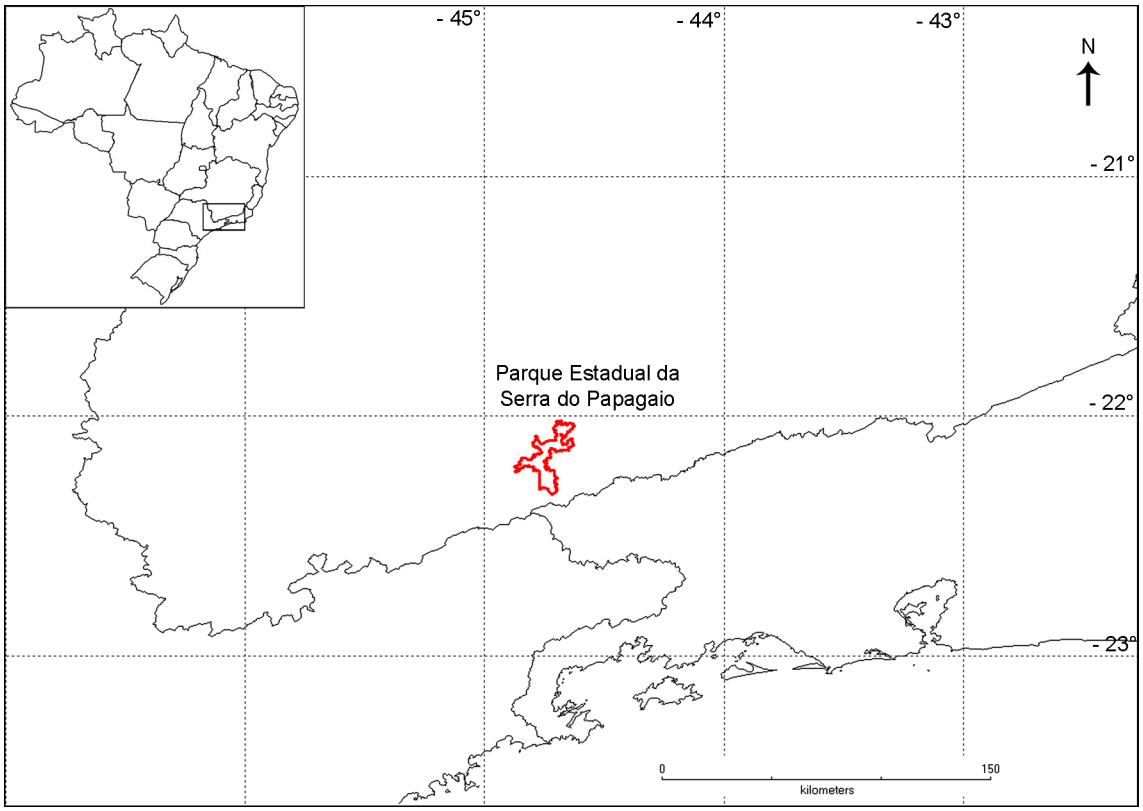

Figure 1 – Map showing the location of Parque Estadual da Serra do Papagaio, in southern Minas Gerais state, Brazil.

Floristic survey

The MNF of the PESP contain two types of formation (Fig. 2). The first is a forest along the Rio do Charco that has a moister soil, at an altitude around 1,650 m a.s.l., and named "mixed needle-broadleaved cloud evergreen tropical high montane talweg forest" (Oliveira Filho 2009) or "alluvial mixed ombrophilous forest" (IBGE 2012). The other type of forest formation occurs in the slopes where the altitude is 1,800–2,000 m, classified as "mixed needle-broadleaved cloud evergreen tropical high montane slope forest", according to Oliveira Filho (2009), or "high montane mixed ombrophilous forest" (IBGE 2012). In the latter formation, both *Araucaria angustifolia* and *Podocarpus lambertii* are represented by a lower number of individuals. Some patches of forest also occur interspersed with the "campos de altitude" adjacent to the slope formation. Hereafter, the acronym "MNF" is used for both formations.

Fertile specimens of vascular plants were collected, with the exception of the epiphytes, which were subject of another study (Furtado & Menini Neto 2015; Furtado & Menini Neto 2016). Data recorded to fertile specimens at the field were: habitat, habit, estimated height, and vegetative and reproductive features, according to Mori *et al.* (1989). The classifications of life forms followed Gonçalves & Lorenzi (2007). Fifteen collections were conducted monthly, from April 2012–June 2013, with mean durations of 3 days. An area of about 79 ha was covered via walking method (Filgueiras *et al.* 1994).

The collected specimens were herborized according to the protocol proposed by Mori *et al.* (1989) and deposited in the Herbarium CESJ of Universidade Federal de Juiz de Fora (acronym according Thiers, continuously updated). Identifications were conducted based on the literature, comparison with the herbarium collection, and assistance of specialists in the respective families. The names of angiosperm families are according to APG IV (2016), and fern families are according to PPG I (2016). The names of species and respective authors were conferred in the Brazilian list of the flora BFG (2015). Several

Figure 2 – a-d. Areas of mixed needle-broadleaved forest (MNF) in the Parque Estadual da Serra do Papagaio – a. View of the Rio do Charco valley; b. Transition between the alluvial MNF and the "campo de altitude"; c,d. Interior of the MNF. Photos: D.S. Santiago; J.H.C. Ribeiro; L. Menini Neto.

specimens from sporadic collections since 2010 and deposited in the Herbarium CESJ also were included in the floristic list.

Phytogeographic groups

The genera were classified into seven phytogeographic groups: Austral-antarctic, Holartic, Widespread Temperate, Cosmopolitan, Endemic to Brazil, Neotropical and Widespread Tropical, defined according to the current diversity centers presented in Safford (2007). The phytogeographic distribution of the genera was obtained based on the taxonomic literature and complemented with specialized sites (*e.g.*, <http://splink.cria.org.br> and <http://www.tropicos.org>).

Results

Floristic composition

We recorded 310 species distributed into 168 genera and 82 families, of which 290 were angiosperms, two were gymnosperms, and 18 were ferns. Of the total species, 255 were identified at the species level, 34 at the genus level, and 14 at family; seven were not identified (Tab. 1 in supplementary material <https://doi.org/10.6084/m9.figshare.7265741>). The richest families were Asteraceae (49 spp.), Melastomataceae (33 spp.), Rubiaceae (16 spp.), Solanaceae (15 spp.), Myrtaceae (13 spp.), Fabaceae (10 spp.), Orchidaceae (8 spp.) and Ericaceae (7 spp.) (Fig. 3). The richest genera were Leandra (14 spp.), Solanum (11 spp.), Baccharis (9 spp.), Myrcia (8 spp.), Tibouchina (8 spp.), Miconia (6 spp.) and Mimosa (5 spp.) (Fig. 4).

Were found 105 herbs, 98 trees, 68 shrubs, 33 lianas and 6 hemiparasites according to their habitat (Fig. 5). Among the trees, Melastomataceae contained 13 species, followed by Myrtaceae (12), Asteraceae (eight), and Solanaceae (six). Among the shrubs, Melastomataceae was also the richest with 15

species, followed by Asteraceae (14) and Ericaceae and Solanaceae (five species each). Among the herbs, Asteraceae was the richest family with 19 species, followed by Orchidaceae and Rubiaceae

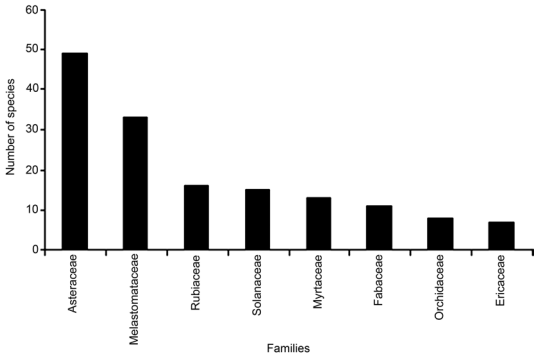

Figure 3 – Richest families in the mixed needle-broadleaved forest of the Parque Estadual da Serra do Papagaio.

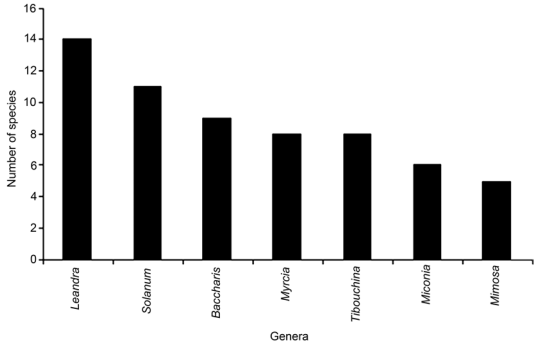

Figure 4 – Richest genera in the mixed needle-broadleaved forest of the Parque Estadual da Serra do Papagaio.

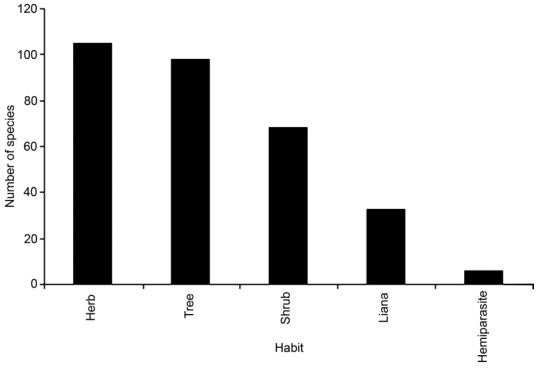

Figure 5 – Richest habits in the mixed needle-broadleaved forest of the Parque Estadual da Serra do Papagaio.

(eight species each) and Melastomataceae (six). Among the lianas, Asteraceae was the richest family with eight species, followed by Passifloraceae and Smilacaceae (four species each). Among the hemiparasites, only two families were recorded: Santalaceae (four species) and Loranthaceae (two).

Three species are endemic to Minas Gerais: *Gaylussacia salicifolia* (Fig. 6), *Myrsine glazioviana*, and *Serjania laxiflora*. Two new occurrences were recorded in the state: *Justicia plumbaginifolia* and *Wedelia hookeriana.*

Phytogeographic distribution

The genera of tropical distribution represented 73% of total, distributed among 45 wide tropical (27%), 68 Neotropical (40%), and 10 endemic to Brazil (6%). The genera of temperate origin corresponded to 27% of total, distributed as follows: 13 (8%) of Austral-Antarctic origin, three (2%) Holarctic, eight (5%) wide temperate, and 21 (12%) present cosmopolitan distribution (Tab. 2).

Discussion

Floristic composition

According to the red book of the Brazilian flora (Martinelli *et al.* 2013), Minas Gerais harbors a great number of threatened species. Despite this fact, in the MNF of the PESP, only two species are considered "endangered": *Araucaria angustifolia* (Fig. 6) and *Dicksonia sellowiana* (Carlucci *et al.* 2013; Santiago *et al.* 2013). Regarding the epiphytic species of the same area, some new records in Minas Gerais and threatened species at different scales also were noticed (Menini Neto *et al.* 2013; Furtado & Menini Neto 2015), which reinforce the need for conservation of the area. It is also important to highlight the presence of *Abutilon itatiaiae,* an endemic species to Serra da Mantiqueira. In São Paulo state it is restricted to 1,200 m a.s.l. (Takeuchi & Esteves 2012).

The new records contribute to the knowledge of state flora, as only a few floristic studies have been conducted in the PESP, which shows lack of knowledge of regional flora. These results point out that the PESP is a corridor in the Mantiqueira, protecting the fragments with connectivity of the landscape and avoiding the genetic erosion of several populations (Kageyama *et al.* 2003; Metzger 2003; Costa & Herrmann 2006), in addition to highlighting the need for conservation and an action plan for the protection of species.

Figure 6 – a-l. Some species of the mixed needle-broadleaved forest of the Parque Estadual da Serra do Papagaio – a. *Anemone sellowii*; b. *Araucaria angustifolia*; c. *Collaea speciosa*; d. *Drimys brasiliensis*; e. *Eremanthus erythropappus*; f. *Fuchsia regia*; g. *Gaylussacia salicifolia*; h. *Pavonia cf. schrankii*; i. *Pentacalia desiderabilis*; j. *Phoradendron fragile*; k. *Piptocarpha axillaris*; l. *Podocarpus lambertii*. Photos: L. Menini Neto; D.S. Santiago.

Table 2 – Phytogeographic groups of the collected genera in the formations of mixed needle-broadleaved forest in the Parque Estadual da Serra do Papagaio.

Phytogeographic groups	**Genera**	**Percentage**
Temperate		
Austral-antarctic: *Araucaria, Dicksonia, Drimys, Escallonia, Fuchsia, Gaultheria, Hydrocotyle, Myrceugenia, Podocarpus, Polygala, Polystichum, Sisyrinchium, Sticherus.*	13	8%
Holartic: *Berberis, Rhamnus, Valeriana.*	3	2%
Widespread Temperate: *Arenaria, Convolvulus, Hypericum, Plantago, Prunus, Ranunculus, Rubus, Senecio.*	8	5%
Cosmopolitan: *Anemone, Asplenium, Bidens, Blechnum, Borreria, Caamembeca, Dioscorea, Dryopteris, Eryngium, Galium, Ilex, Lathyrus, Lycopodium, Malaxis, Rhynchospora, Salvia, Selaginella, Solanum, Styrax* e *Thelypteris.*	20	12%
Tropical		
Endemic to Brazil: *Athenaea, Eremanthus, Huberia, Inulopsis, Macropeplus, Marcetia, Nematanthus, Peplonia, Pleroma, Trembleya.*	10	6%
Neotropical: *Adiantopsis, Aechmea, Aegiphila, Alchornea, Allophylus, Anchietea, Austroeupatorium, Baccharis, Billbergia, Bredemeyera, Brunfelsia, Byrsonima, Cabralea, Cestrum, Chaptalia, Chusquea, Cleistes, Coccocypselum, Collaea, Cordiera, Cranichis, Cuphea, Cyclopogon, Dasyphyllum, Declieuxia, Dendrophorbium, Dendrophthora, Eriosorus, Esterhazya, Galianthe, Gaylussacia, Hapalorchis, Hesperozygis, Ichnanthus, Lamanonia, Leandra, Lophosoria, Manettia, Mecardonia, Miconia, Microlicia, Mollinedia, Myrcia, Myrciaria, Orthosia, Passiflora, Paullinia, Peltodon, Pentacalia, Phoradendron, Piper, Piptocarpha, Prescottia, Psilochilus, Roupala, Rudgea, Sapium, Schefflera, Serjania, Serpocaulon, Siphocampylus, Siphoneugena, Tibouchina, Trichogonia, Trixis, Verbena, Vernonanthura, Vriesea.*	68	41%
Widespread Tropical: *Abutilon, Achyrocline, Agarista, Annona, Aspilia, Begonia, Buddleja, Cayaponia, Cinnamomum, Clethra, Croton, Cyathea, Desmodium, Dicranopteris, Erythroxylum, Gochnatia, Habenaria, Hypoxis, Hyptis, Jacaranda, Jacquemontia, Justicia, Lafoensia, Maytenus, Mikania, Mimosa, Myrsine, Ocotea, Pavonia, Peperomia, Persea, Pseudechinolaena, Psychotria, Scleria, Senna, Smilax, Strychnos, Symplocos, Ternstroemia, Tripogandra, Vernonia, Vigna, Wedelia, Zanthoxylum.*	44	26%
Total	**166**	**100%**

Asteraceae is one of the most diverse families at the global scale and can be found in several habitats around the world (Judd *et al.* 2009), although it is highly common in the tropical, mountainous regions of South America. Floristic studies conducted in the MNF of the Southern Region of Brazil also presented Asteraceae as the richest family (Britez *et al.* 1995; Kozera *et al.* 2006; Iurk *et al.* 2008; Gasper *et al.* 2013). This pattern is also found in the Southeasten Region, in the MNF of São Paulo state (Pereira Silva *et al.* 2007; Polisel *et al.* 2014). In the cloud broadleaved dwarf-forest of Serra Fina, Meireles & Shepherd (2015) highlighted the importance of this family in addition to other studies conducted in the upper highlands of the Atlantic Domain, where the abundance of Asteraceae species is associated with high elevation (Brade 1956; Falkenberg 2003; Meireles *et al.* 2014).

Baccharis is one of the richest genera in the MNF of the PESP. Meireles & Shepherd (2015) and Falkenberg (2003) also found this genus among the richest in forests of Serra Fina (in the triple border of Minas Gerais, Rio de Janeiro and São Paulo state) and Aparados da Serra (between Santa Catarina and Rio Grande do Sul), respectively. The Andes and mountainous regions of Southeastern Brazil are the main centers of diversity for *Baccharis* (Müller 2006).

Among the most common species of Asteraceae in the MNF of the PESP, *Piptocarpha*

axillaris (Fig. 6) must be highlighted, which is considered abundant in the Paraná state and typical of the MNF, but it also can be found in the cloud broadleaved forest of Serra do Mar and rarely found in the seasonal broadleaved forest (Grokoviski *et al.* 2009). The liana *Pentacalia desiderabilis* (Fig. 6) was found in the canopy at sites with light incidence and, according to Cabrera & Klein (1975), it is a common species in forest borders between 400–2,040 m a.s.l. *Eremanthus erythropappus* (Fig. 6) also was observed in the forest borders, although it is common in transition areas and in field physiognomies of the Cerrado Domain, occurring in the Atlantic Domain above 700 m a.s.l. (Macleish 1987). In Serra Negra, this species exists in large populations in the "campos rupestres" (Salimena *et al.* 2013), whereas in the Parque Estadual do Ibitipoca there is a monodominance in the cloud dwarf-forests (Oliveira Filho *et al.* 2013b).

Melastomataceae is the second-richest family with 33 species, corroborating the studies conducted in the MNF of Paraná (Liebsch & Acra 2004; Liebsch *et al.* 2009) and in the cloud forests of Aparados da Serra (Falkenberg 2003). This family also has high richness in the Atlantic Forest of the Southeastern Region, such as the Parque Nacional do Itatiaia, neighboring the PESP (Brade 1956; Pereira *et al.* 2006), and in the high montane forests of Monte Verde and Serra Fina (Meireles *et al.* 2008; Meireles *et al.* 2014).

The species of Melastomataceae are very common in the understory of the MNF in the studied area, especially *Leandra aurea*, *L. quinquenodis*, *Miconia budlejoides*, *M. hyemalis*, and *Tibouchina foveolata*. Goldenberg *et al.* (2012) reported that in forests of the Atlantic Domain, mainly at high altitudes, species of the tribe Miconiae are among the most common, especially those belonging to *Leandra* and *Miconia*, justifying their representation in the MNF of the PESP, as also indicated by Meireles & Shepherd (2015) in Serra Fina. *Leandra*, *Miconia*, and *Tibouchina* also are listed among the richest genera of mountainous areas both in the Atlantic Domain (Chiea 1990; Lima & Guedes Bruni 1997; Falkenberg 2003; Meireles *et al.* 2008) and other Neotropical forests (Gentry 1982, 1988, 1995).

Rubiaceae is the third-richest family of the MNF and owes its occurrence to understory environments (Carvalho *et al.* 2000; Liebsch & Acra 2004). Two species must be highlighted, *Coccocypselum condalia* and *Psychotria suterella*. The former is widely distributed in the forest interior, commonly found in moist and shade sites (Costa & Mamede 2002), while the latter is cited in the literature as frequent in the understory of such forest physiognomy (Liebsch & Acra 2004).

Myrtaceae is also a prominent family in the MNF of the PESP (Santana 2016), and it is known for its expressive participation in the floristic composition of the tree/shrub component in the Southern Region of Brazil (Rambo 1951), where it is cited as the richest in several studies (Nascimento *et al.* 2001; Rondon Neto *et al.* 2002; Budke *et al.* 2004; Klauberg *et al.* 2010; Selusniaki & Acra 2010; Higuchi *et al.* 2012, 2013; Lingner *et al.* 2013). In the Southeastern Region, it can be the richest family (*e.g.*, in the cloud broadleaved forest with elements of MNF in Camanducaia, southern region of Minas Gerais) (França & Stehmann 2004; Meireles *et al.* 2008). Fontes (1997) also noted the importance of Myrtaceae, Rubiaceae, and Melastomataceae in forests above 1,000 m a.s.l. in southeastern Brazil. Tabarelli & Peres (2002) showed that Myrtaceae are dispersed mainly by frugivorous animals, contributing to the high richness of species in the Neotropical forests.

Myrcia presented eight species, and it also exhibited significant richness in the MNF of Santa Catarina (Gasper *et al.* 2013). Some species were common: *Myrcia pulchra*, *M. splendens*, *M. laruotteana* and *M. obovata.* Andrade (2003) observed that *M. splendens*, among the tree species with zoocoric dispersal, exhibited one of the largest interaction frequencies, involving the consumption of fruits by birds, resulting in a "seed rain" of great importance to the dispersal and abundance of this species. The occurrence of *M. laruotteana* can be explained by its strict relationship with highly moist soils (Curcio *et al.* 2006).

Another representative genus was *Myrceugenia*, which is distributed along the east coast of Brazil, in areas above 1,000 m a.s.l., with moist and cold climates (Landrum 1981). In the Parque Nacional do Itatiaia, this genus has high richness in different montane physiognomies (Lima & Guedes Bruni 2004). Gasper *et al.* (2013) also report the importance of the genus in MNF of southern Brazil. In the present study, only three species were found, with emphasis on *Myrceugenia regnelliana*, locally known as "cambuí", which is widely distributed in the MNF of the PESP, especially along the valley of Rio do Charco, frequently forming dense groups in the moist understory. In the Southern Region of the

country, this species is cited in several studies in MNF, occurring at 900 m a.s.l. (Kozera *et al.* 2006; Liebsch *et al.* 2009; Martins Ramos *et al.* 2011; Higuchi *et al.* 2012, 2013). In the Southeastern Region, *M. regnelliana* also occurs in cold sites at high altitudes (Pereira *et al.* 2006; Meireles *et al.* 2008; CRIA 2014).

Mimosa scabrella is an important species of the Fabaceae family in the studied area, occurring at moist sites with high light incidence, frequently near the Rio do Charco. It is often found in southern Brazil (Kozera *et al.* 2006; Klauberg *et al.* 2010; Higuchi *et al.* 2012, 2013) and is a typical species of disturbed vegetation physiognomies above 800 m a.s.l. (Barneby 1992). In addition, dated pollen records of the Holocene show that this species already was present in association with *Araucaria* during the expansion of the MNF in southern Brazil (Behling *et al.* 2004). *Collaea speciosa* (Fig. 6) also was common along the Rio do Charco or the border of the forest, and it often is recorded in the literature in open areas and secondary vegetation. In Serra do Itatiaia, this species is found in transition areas between montane and high montane vegetation, around 2,000 m a.s.l. (Morim 2006).

Solanum is the second-richest genus, justified by the great number of species commonly found at high altitudes, as highlighted by Oliveira Filho & Fontes (2000), and corroborated by Meireles *et al.* (2014) in the Serra Fina above 1,500 m a.s.l. In the Southern Region, Gasper *et al.* (2013) recorded *Solanum* as the richest genus. In addition to the relationship with altitude, the occurrence of pioneer species and species commonly found in disturbed areas and forest borders (such as *Solanum sisymbriifolium* and *S. viarum*) can represent a regeneration after disturbance events, as fire was recorded in the studied area in 2011. Among the recorded species in the MNF of the PESP, *Solanum capoerum* is noteworthy, as previous records were known from Serra da Maria Comprida, in Petrópolis, state of Rio de Janeiro, and in Camanducaia, in southern Minas Gerais (CRIA 2016), above 1,500 m a.s.l.

Among the Lauraceae species, *Ocotea pulchella* should be highlighted, cited as "endangered" in the list of threatened species of Minas Gerais state (COPAM 1997), and common in the understory of the studied area. Klein (1960) pointed out the species as typical of the MNF, representing a pioneer stage. *O. pulchella* is also cited in several floristic studies of the Southern Region of Brazil (Budke *et al.* 2004; Eskuche 2007; Martins Ramos *et al.* 2011; Vibrans *et al.* 2011; Mognon *et al.* 2012).

Other genera recorded in the MNF of the PESP are cited as important in the floristic composition of the high montane forests and strongly related to the high altitudes of the Southeastern Region of Brazil, as follows: *Chusquea*, *Clethra*, *Drymis*, *Escallonia*, *Ilex*, *Mollinedia*, *Myrsine*, *Myrceugenia*, *Mikania*, *Podocarpus*, *Prunus*, *Roupala*, and *Tibouchina* (Holmes 1995; Webster 1995; Fontes 1997; Oliveira Filho & Fontes 2000; Meireles *et al.* 2008, 2009; França & Stehmann 2004). *Ilex* is common in montane and high montane forests of Paraná (Portes & Galvão 2002). *Roupala* has species typical of high altitudes and is cited as dominant in the high montane physiognomies of the Serra do Itatiaia (Segadas Viana & Dau 1965). *Mikania* has a dispersal center in the highlands of the Southeastern Region of Brazil (Holmes 1995). *Chusquea* is another genus related to altitude, commonly found in the montane and high montane forests of South America (Beard 1955) and important in the forest physiognomy of Monte Verde (Meireles *et al.* 2008). *Symplocos* also exhibits great floristic importance in the high montane forest, containing several endemic species of mountainous areas (Aranha Filho *et al.* 2007).

At the species level, *Drimys brasiliensis* (Fig. 6) is common in MNF and cited as an indicator species of altitude forests by Oliveira Filho & Fontes (2000), often associated with *A. angustifolia*, despite its occurrence in cloud broadleaved forests of Minas Gerais (França & Stehmann 2004; Meireles *et al.* 2008, 2014; Valente *et al.* 2011). Another noteworthy taxon is *Berberis laurina*, which represents an important Andean element in the MNF, endemic to this physiognomy, along with *Miconia hyemalis* and *Mimosa scabrella* (Bauermann & Behling 2009; Evaldt *et al.* 2009). *Podocarpus lambertii* (Fig. 6) is a dominant species of the canopy along the Rio do Charco associated with *A. angustifolia* (Santana 2016). These species may be present in regions of temperate climates where there is not a hydric deficit during the dry season [or it is moderated (Carvalho 2002)], and the water supply is provided by the common presence of fog. Furthermore, the majority of epiphytic species in the MNF of the PESP have *P. lambertii* as their main phorophyte (Furtado & Menini Neto 2015).

Terricolous ferns were represented by 18 species distributed in 14 genera and 11 families. Furtado & Menini Neto (unpublished data) found

42 species of epiphytic ferns, totaling 60 species in the MNF of the PESP. The Atlantic Forest is considered one of the largest centers of richness of ferns in the Neotropical region (Tryron 1972; Tryon & Tryon 1982; Moran 1995; Roos 1996).

Dicksonia sellowiana is a species found in the moist environments of the interior of MNF and is widely distributed in the Neotropical region. Mantovani (2004) stated the need of moisture for growth and development of this species, which occurs close to watercourses and in steep slopes with lower insolation. Behling *et al.* (2004) also noted that *D. sellowiana* is often found in gallery forests, occurring since the late Holocene. Popularly known as "xaxim", *D. sellowiana* experienced a significant reduction in population, since it is highly exploited as raw materials for the fabrication of vases and substrates for ornamental plants, and it is considered "endangered" in Brazilian flora (Santiago *et al.* 2013). Another fern found in highly humid habitats is *Cyathea corcovadensis*, recorded along the Rio do Charco. According to Oliveira Filho & Fluminhan Filho (1999), the Cyatheaceae family typically occurs in riparian environments of the altitude forests.

Melastomataceae, Myrtaceae, and Asteraceae were the richest in tree species. The first two families also were noted as the richest for the Atlantic Forest regarding this habit (Oliveira Filho & Fontes 2000). Among the most important families with shrubby habits in a MNF, Liebsch & Acra (2004) highlighted Melastomataceae and Solanaceae, which is corroborated in the present study. The herbaceous species contribute to the floristic increment of forest areas as well as soil composition, as they have shorter life cycles than arboreal species (Martin Ramos *et al.* 2011) but are often relegated to the background or even ignored in most previous studies (Kozera *et al.* 2006; Polisel *et al.* 2014).

In general, *A. angustifolia* occurs in altitudes above 200 m a.s.l. in the Southern Region and above 600 m in the Southeastern Region, between the latitudes 31º30'S at Canguçu (RS) and 19º15'S at Serra do Padre Ângelo, in Conselheiro Pena, Alto Rio Doce (MG) (Carvalho 2002). Thus, the decrease of latitude is compensated for by increased elevation, so the climatic features (*e.g.*, low temperature and high humidity) demanded by this species are maintained, allowing its presence in the MNF of Serra da Mantiqueira. Despite this, there is a greater similarity with the MNF of the Southern Region, at the family and genus levels, like discussed here. Regarding species, Jarenkow & Budke (2009) conducted a study with shrub and tree species of 38 areas of the MNF, of which 36 lie in the Southern Region and two in the Southeastern Region, observing only 16 species that exhibited relative constancy greater than 80%. Among those species, only six were recorded in the MNF of the PESP: *Allophylus edulis*, *Araucaria angustifolia*, *Myrsine umbellata*, *Prunus myrtifolia*, *Sapium glandulosum* and *Styrax leprosus*. In fact, some authors observed that the remnants of MNF in the Southeastern Region are different at the species level from those of the Southern Region (Jarenkow & Budke 2009; Oliveira Filho *et al.* 2013a), although Furtado & Menini Neto (unpublished data) showed that the flora of vascular epiphytes of the MNF of the PESP are more similar to that of areas in the southern region than with areas of dense ombrophilous forests in Southeastern and Southern regions of Brazil.

Some species of MNF in the Southern Region and in Minas Gerais are tolerant to low temperature and frost, which is one of the main physiological adaptations of plants from high altitudes (Safford 2007). According to Meireles & Shepherd (2015), the record of species with disjunct distribution in southern Brazil likely is due to the absence of a temperate climate in sites of intermediary elevation between the Serra da Mantiqueira and the Southern Plateau.

The relationship of MNF with seasonal broadleaved forests is demonstrated by some shared species such as *Aegiphila sellowiana*, *Cabralea canjerana*, *Clethra scabra*, *Drimys brasiliensis*, *Eremanthus* spp., *Miconia chartacea*, *M. theaezans*, *Myrcia laruotteana*, *Ocotea corymbosa*, *Psychotria suterella* and *Trembleya parviflora* (Oliveira Filho & Ratter 1995; Oliveira Filho & Fontes 2000; Scolforo & Carvalho 2006). Falkenberg & Voltolini (1995) considered the high montane forests of southern Brazil a transition between the coastal cloud broadleaved forests and the MNF or a transition with the "campos de altitude". The Serra da Mantiqueira is located in a predominantly seasonal matrix, and its high montane forests are in contact with the neighboring montane forests, with fragments of MNF or interspersed with the "campos de altitude" (Meireles & Shepherd 2015), justifying the presence of elements originating from other physiognomies. Oliveira Filho *et al.* (2013a) showed that the MNF and seasonal broadleaved forest have similar floras, occurring as a continuous transition of species, allowing a

high sharing index. In addition, the presence of elements from other vegetation physiognomies can be indicating that this area is an ecological corridor and transition region between these physiognomies. The presence of these floristic elements coming from neighboring physiognomies highlights the importance of vegetation matrix on the floristic composition of the MNF of the PESP, contributing to the increased diversity.

The presence of MNF at the top of Serra da Mantiqueira always has been discussed regarding the Quaternary Period expansion of forest toward to the Southeastern Region (Hueck 1972). Behling (1998) recorded the expansion of the southern MNF toward the southeast during the cold and moist periods of the Quaternary. Pollen records show that this expansion occurred only in the moist depressions and valleys of the Southeastern Region. This author concluded that the MNF remnants of the high-altitude areas of the Southeastern Region occupied these regions about 3,000 years ago. In addition, Behling *et al.* (2007) noted the occurrence of *A. angustifolia* since the later Pleistocene in the region of Serra da Bocaina (SP), about 50 km distance (in a straight line) from the PESP. According to these authors, the isolated patches of MNF acted as refugia, and they have been connected to other MNF fragments of the Southeastern Region since the last ice age, indicating that, in the past, the MNFs of this region were in contact. This substitution of vegetation by the MNF occurred during the drastic shifts in the climate and influenced the distribution of the species that were associated with this physiognomy. The presence of pollen grains of *Araucaria* and *Podocarpus* as well as those of Myrtaceae, *Myrsine*, *Mimosa scabrella*, and *Ilex*, in addition to spores of *Dicksonia sellowiana*, during the Middle and Higher Holocene (4,320–1,000 years ago), pointed to a floristic composition similar to that of the current MNF (Bauermann & Behling 2009).

Phytogeographic distribution

The high montane forests have floristic compositions different from those of lower-altitude forests, and the presence of endemic species is common, with much of them belonging to genera of high richness in montane forests of the Andes (Falkenberg & Voltolini 1995; Oliveira Filho & Fontes 2000; Meireles *et al.* 2008). Brade (1956) highlighted the remarkable presence of several Andean genera of ferns in the Itatiaia. According to Smith (1962), the flora of the Southeastern Region of Brazil has elements derived from other phytogeographic regions due to migrations of species that took place at different times. According to Safford (2007), there is a hybrid flora coming from the Andes and the Brazilian high-altitude mountains. Those plants are from different origins (*e.g.*, tropical, temperate, and cosmopolitan) that developed at these sites along the periods of environmental shifts, and migrations also play a role.

Araucaria, *Dicksonia*, *Drimys*, *Escallonia*, *Fuchsia*, *Gaultheria*, *Hydrocotyle*, *Myrceugenia*, *Podocarpus*, *Sticherus*, and *Sisyrinchium* are genera from Austral-Antarctic origin and are part of an ancient flora dispersed between Australia, Antarctica, and South America (Landrum 1981; Meireles & Shepherd 2015; Safford 2007). Safford (2007) reports that during the dry periods of the Tertiary Period, the Atlantic mountain chains acted as refugia for the species adapted to cold and humidity, especially the Austral-Antarctic taxa. During long periods of cold climate, the author suggested still that there was greater contact between the formations of eastern and western South America, favoring the colonization of Atlantic tropical forests by the Andean elements.

In the cloud broadleaved dwarf-forest of Serra Fina, the predominance of tropical genera was observed, but Austral-Antarctic taxa of trees also were well represented among the temperate genera (Meireles & Shepherd 2015). Species belonging to genera of Austral-Antarctic and tropical origins that speciated at sites of high altitude exhibited high conservation of their climatic niche, and several of them are restricted to the tops of the Atlantic mountains (Safford 2007; Meireles & Shepherd 2015). This speciation can be related to the drastic climatic shifts that occurred during the Late Quaternary (Behling 1998; Behling & Negrelle 2001).

Safford (2007) verified that at least 11% of the plant species of the Brazilian "campos de altitude" were shared with the Andean regions, and the majority belonged to the Asteraceae, of which several have a ruderal behavior. In the Serra da Mantiqueira, Fontes (1997) observed similarity between the shrubby/arborous flora of altitude forests in the Parque Estadual do Ibitipoca with the forests of the Andes, especially in species richness of Myrtaceae, Melastomataceae, Rubiaceae, and Solanaceae.

Oliveira Filho & Fontes (2000) described the enhancement of the relative importance of

Asteraceae, Melastomataceae, and Solanaceae to the Atlantic Forest of the Brazilian Southeastern Region, according to the elevation enhancement. A similar pattern was found by Gentry (1995) in the Andes, where Melastomataceae and Rubiaceae are the richest in woody species in altitudes above 1,500 m a.s.l., indicating that low temperature is not a limiting factor on the occurrence of these families. Escalloniaceae also has exclusive taxa from high-altitude and cold areas of South America (Safford 1999), including Serra do Itatiaia (Brade 1956; Pereira *et al.* 2006), but the genus is absent in the middle- and low-altitude forests of the Brazilian Southeastern Region.

Among the genera found, 40% are Neotropical, with emphasis on *Cabralea*, *Leandra*, *Miconia*, *Mollinedia*, *Myrcia*, *Myrciaria*, *Piptocarpha*, *Roupala*, *Siphoneugena*, *Tibouchina*, and *Vernonanthura*, that can contain exclusive species of the high montane forests and tolerate adverse conditions in higher altitude (Oliveira Filho & Fontes 2000; Meireles & Shepherd 2015). Among the Neotropical genera, some are commonly found in the Andes, such as *Baccharis*, *Chusquea*, *Dasyphyllum*, *Dendrophorbium*, *Gaylussacia*, and *Pentacalia*, and present great importance to the floristic composition of high montane vegetation of the Brazilian Southeastern Region (Brade 1956; Safford 1999; Müller 2006; Meireles *et al.* 2014).

Trembleya genera is the only endemic to Brazil in the Melastomataceae family (Lista do Brasil 2017). The Huberia genera, together with *Eremanthus*, *Inulopsis*, and *Macropeplus*, are common in high-altitude vegetation in the Atlantic Forest (Nakajima & Semir 2001; Santos & Peixoto 2001; Romero & Martins 2002; Baumgratz 2004).

Safford (2007) suggested that several species from temperate and cosmopolitan climates arrived first in the Southern Region of Brazil through migration using suitable habitats instead of long-distance dispersal. According to Brade (1956), the Holarctic elements used the Andes as a migration bridge going from North to South America and later advancing toward the eastern portion of the continent to the Serra do Mar and Mantiqueira. Those genera tolerate lower temperature, exhibiting physiological adaptations to their occurrence in high altitudes in mountain chains (Smith & Young 1987; Safford 1999, 2007); in the PESP, these are represented by *Berberis*, *Rhamnus* and *Valeriana*.

Thus, the results show similar floristic patterns at family level to the MNF of southern. At species level we observed a greater sharing with those found in montane and high montane forests of southern and southeastern Brazil. Besides that, the presence of temperate genera shows that the low temperatures caused by high altitude influence the floristic composition of the area.

The presence of elements from other vegetation physiognomies indicates that this area is an ecological corridor and transition region, highlighting its importance. Thus, floristic surveys in unexplored regions of Serra da Mantiqueira and others highland in the Brazilian Southeast may, in the future, extend the knowledge of the distribution of typical species of Atlantic Forest.

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