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Structure and floristic similarities of upper montane forests in Serra Fina mountain range, southeastern Brazil[1]

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ABSTRACT

The upper montane forests in the southern and southeastern regions of Brazil have an unusual and discontinuous geographic distribution at the top of the Atlantic coastal mountain ranges. To describe the floristic composition and structure of the Atlantic Forest near its upper altitudinal limit in southeastern Brazil, 30 plots with 10 × 10 m were installed in three forest sites between 2,200 and 2,300 m.a.s.l. at Serra Fina. The floristic composition and phytosociological structure of this forest were compared with other montane and upper montane forests. In total, 704 individuals were included, belonging to 24 species, 15 families, and 19 genera. Myrsinaceae, Myrtaceae, Symplocaceae, and Cunoniaceae were the most important families, and *Myrsine gardneriana, Myrceugenia alpigena*, *Weinmannia humilis*, and *Symplocos corymboclados* were the most important species. The three forest sites revealed differences in the abundance of species, density, canopy height, and number of stems per individual. The upper montane forests showed structural similarities, such as lower richness, diversity, and effective number of species, and they tended to have higher total densities and total dominance per hectare to montane forests. The most important species in these upper montane forests belong to Austral–Antartic genera or neotropical and pantropical genera that are typical of montane areas. The high number of species shared by these forests suggests past connections between the vegetation in southern Brazilian high-altitude areas.

Keywords: Atlantic Rain Forest, cloud forest, Last Glacial Maximum, Mantiqueira mountain range, montane forest

Introduction

The Atlantic upper montane forest (AUMF) shows a distinct geographical distribution due to the spatial discontinuity of high-altitude areas in the Atlantic coastal mountain ranges of the south and southeastern regions of Brazil. This forest formation represents the upper altitudinal limit of the Atlantic Forest Domain and has a distinctive floristic composition and phytosociological structure in relation to forests located at intermediate and lower altitudes (Falkenberg & Voltolini 1995; Portes & Galvão 2002; Koehler *et al*. 2002; Meireles *et al.* 2008; Bertoncello *et al*. 2011; Scheer *et al*. 2011). These forests are equivalent to cloud forests, which typically occur in a narrow altitudinal zone, wherein topography and climate conditions favor the occurrence of clouds or fog. The clouds cover the forest belts by persistent, frequent, or seasonal frequency (Hamilton *et al.* 1995).

AUMF corresponds to "tropical ombrophilous cloud forest" (*sensu* UNESCO 1973), "tropical montane cloud forest" (*sensu* Hamilton *et al.* 1995), to "cloud forest" (*sensu* Stadmüller 1987). Cloud forests are extremely important for maintaining water resources by capturing water from fog, a process that is denominated "horizontal precipitation" (Bruijnzeel & Proctor 1995). This water, which could potentially be lost, is then retained and distinguishes cloud forests from other forest types (Stadtmüller 1987). The occurrence and extraction of water from cloud or fog increases atmospheric humidity, allowing these forests to occur in climatic regions where the matrix vegetation is predominantly drier or very seasonal (Gioda *et al*. 1995; Juvik & Nullet 1995).

In high-altitude areas, climate and physical conditions, such as strong winds, low temperatures, higher rainfall, higher incidence of UV-B light, and lower atmospheric pressure have been associated with the establishment, physiognomy, structure, and floristic composition of montane forests (Lawton 1982; Flenley 1995). The fog also affects the amount of energy received by changing the quality and intensity of light, reducing the solar radiation that creates a deficit in the suppression of evaporation and evapotranspiration from these forests (Flenley 1995; Hamilton *et*

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al. 1995). These conditions also favor the occurrence of avascular poikilohydric plants, such as bryophytes, lichens, and filmy ferns (Hymenophyllaceae) or arborescent ferns (Cyatheaceae and Dicksoniaceae). This is a typical feature shared by all cloud forests in the humid tropics (Stadtmüller 1987; Hamilton *et al.* 1995).

The physiognomic attributes of these forests include a reduction in canopy stature and number of tree layers, a high density of individuals and fewer species, a high proportion of avascular or vascular epiphytes, and a reduction of woody lianas. These are parameters that usually respond to higher altitudes in mountainous regions (Hamilton *et al.* 1995). In general, the trees are not tall, and they may present with a compact crown, branches, and trunks, which can be much branched. The leaves are usually simple, small, often thick, and leathery, with a smaller proportion of species containing compound leaves (Hamilton *et al.* 1995). In these forests, the growth of individuals is expected to be slower with shorter internodes, and the leaves often contain extra pigments, such as anthocyanins and flavonoids in their hypodermis (Flenley 1995).

AUMFs were largely ignored in the old Brazilian phytogeographical vegetation systems (Falkenberg & Voltolini 1995). Until the 1990s, no information was published about their floristic composition or their structural and ecophysiological characteristics (Falkenberg & Voltolini 1995; Carvalho *et al.* 2000; Portes & Galvão 2002; Koehler *et al.* 2002; França & Stehmann 2004; Meireles *et al.* 2008; Bertoncello *et al.* 2011; Scheer *et al.* 2011; Oliveira *et al.* 2014). This forest type in Brazil was first described by Rambo (1949) for the southern region (Falkenberg & Voltolini 1995). In the last two decades, some phytosociological surveys of AUMFs have been conducted in south and southeastern Brazil; however, till date, such studies have only been conducted at altitudes up to 1,900 m (see Koehler *et al.* 2002; Meireles *et al.* 2008).

Hueck (1972) mentioned that the lower altitudinal limit of AUMFs in the southeastern region of Brazil is at 1,200 m.a.s.l. in the Serra do Mar mountain range and between 1,300 and 1,400 m.a.s.l. in the Serra da Mantiqueira mountain range. Meireles *et al.* (2008) suggested that the lower altitudinal limit in the Serra da Mantiqueira is at 1.500 m.a.s.l. On the Itatiaia Plateau, AUMFs occur up to 2,300 m and within fragments of more protected areas at approximately 100–200 m above this elevation (Hueck 1972). In the southern region of Brazil, they occur at the top of the Serra do Mar mountain at altitudes above 1,200 m.a.s.l. They can also occur below this altitude in protected valleys in the states of Paraná and Santa Catarina and along the edge of Aparados da Serra Plateau, located in the south of Santa Catarina State along the northern boundary of the state of Rio Grande do Sul, at 700–1,700 m.a.s.l. (Falkenberg & Voltolini 1995; Koehler *et al.* 2002; Portes & Galvão 2002; Falkenberg 2003).

Falkenberg & Voltolini (1995) suggested that AUMFs do not form a homogeneous vegetation type, but instead form a set of plant communities with relatively similar physiognomies under the influence of altitude, degree of exposure to ocean winds, local topography, variable substrate, and local microclimatic. In the present study, our goal was to examine the floristic composition and phytosociological structure of the three forest sites of the upper montane forest at Pico do Capim Amarelo in the Serra Fina mountain range, located in southeastern Brazil. We conducted statistical comparisons between AUMF and montane forests (AMF) to verify if such forests differ in terms of horizontal and vertical phytosociological structure. Variations in floristic and phytosociological structure of AUMFs over its occurrences in the southern and southeastern Brazilian coastal mountains were also analyzed to help us identify and classify these forest formations within the Atlantic Forest Domain.

Material and Methods

The Serra Fina (SF) (22º20'–22º30'S, 44º45'–45º00'W) is one of the high-altitude areas of Serra da Mantiqueira mountain range in Itatiaia Plateau located at the triple-State geographical boundary of Minas Gerais, São Paulo, and Rio de Janeiro states in southeastern Brazil (Moreira & Camelier 1977). The SF has a very steep relief with altitudes in the central area that range markedly over 5 km between 1,000 to 2,798 m.a.s.l. on the Pedra da Mina peak, which is the fourth highest peak in Brazil (Chiesse 2004). The Pico do Capim Amarelo (PCAM) (22°59'25"S, 44°53'21"W; 2,392 m.a.s.l.) is located in the southern region of Serra Fina between the towns of Passa Quatro in Minas Gerais State and Lavrinhas in São Paulo State. The east side of PCAM has a long steep slope leading down to Vale do Paraíba (São Paulo State), and on the west side there is a gentle slope that leads down to Campo do Muro (Minas Gerais State).

The mean annual precipitation ranges from 1,500 to 1,700 mm, and can reach about 2,400 mm in higher areas (Nimer 1977a; Silva & Leite 2000). The rainfall has a seasonal distribution and is more intense in the warmer months (December–March), about 200 to 250 mm per month. The precipitation averages about 20 to 50 mm per month during the cold and dry months (June–August), but a severe drought has not been recorded (Nimer 1977a). The mean annual temperature above 1,500 m.a.s.l. ranges from 12 to 15°C, and in the coldest quarter it is around 5–8°C (Safford 1999). The absolute minimum temperature in the coldest months (June–July) may be less than 0°C, reaching between −4 to −6°C in the dry season (Safford 1999; Nimer 1977a). This region may have more than 100 cloudy days per year and has a high incidence of frost, with an average of 10–30 days per year of frost (Nimer 1977a; Tubelis & Nascimento 1980). Strong sporadic frosts may be observed, which completely freezes the forest formation. These climatic conditions correspond to subtropical climate of altitude, classified as Cwb in the Koeppen climatic system (Martins 2000).

The route to reach the PCAM begins at 1,500 m.a.s.l., where Montane forests, *candeia* scrub, and subsequently high-altitude grasslands in the quartzitic rocks are replaced by high-altitude grassland in the nifelina–sienito rock at approximately 2,000 m.a.s.l. At the top of PCAM there is a small flat area consisting of rocky outcrops and high-altitude grasslands dominated mainly by the giant tussock grasses *Cortaderia* sp. Forest formations surrounded by shrubs are distributed along steep or flat areas below the peak where moister soils are more developed. A phytosociological survey was conducted in three forest sites of the upper montane forest around PCAM from March to September 2007. Three independent forest sites (named VP, FO, and MN) were sampled by establishing 10 plots of 10 × 10 m at each site, representing a total area of 3,000 m^2. All individuals with a perimeter at breast height (PBH) of ≥15 cm were sampled and had their circumference (cm) and height (m) measured. Multi-stemmed individuals at breast height were sampled if at least one stem showed this minimal PBH criterion. Vouchers of specimens were deposited in the UEC Herbarium (Universidade Estadual de Campinas, São Paulo, Brazil).

The VP forest site (22°26’08”S, 44°51’27”W; 2,250 m.a.s.l.) was located in a steep area on the southeastern side, 200 meters below the PCAM summit, facing the Vale do Paraíba. The FO forest site (22°25’57”S, 44°53’24”W; 2,320 m.a.s.l.) was located in a small valley on the west side of the PCAM. The MN forest site (22°25’45”S, 44°52’46’”W; 2,280 m.a.s.l) was located about 1,000 meters to the north of the PCAM, in a region known as Maracanã. It is located in a relatively flat area and is continuous with forests that cover the east side of SF, facing the Vale do Paraíba. For more details about soil characteristics, herbaceous, and shrub strata see Meireles (2009).

To describe the forest structure, a floristic list was compiled with phytosociological parameters of the three sampling sites (Tables 1, 2). The calculated parameters for the species were absolute and relative frequency, relative values of density and dominance as well as cover and importance values for each sample area and for all sample areas together (Mueller-Dombois & Ellenberg 1974). The diversity index of Shannon–Wiener (H’), evenness (J), and Simpson index (D) were used to analyze the floristic heterogeneity (Magurran 1988). The phytosociological parameters and diversity index were calculated using Fitopac 1.6.4 (Shepherd 2006). A correspondence analysis (CA) (Hill 1973) was performed to analyze the indirect ordination of forest sites by species abundance in order to verify the horizontal structure similarities among PCAM forest sites. Those species observed at only one site were eliminated in this analysis because the CA is very sensitive to their presence (McCune & Grace 2002). This multivariate analysis was performed using Fitopac 1.6.4 (Shepherd 2006).

A non-parametric Kruskal–Wallis test was applied to verify statistical differences among forest sites on average tree height and diameter. A Chi-square test was performed to verify differences in the proportion of multi-stemmed individuals at breast height and the number of stems per individual among forest sites using Bioestat 5.0 (Ayres *et al.* 2007; Zar 1999). To verify the geographic distribution patterns of PCAM tree forest species, taxonomic literature and websites were checked and five patterns were described: (IP) species endemic to Itatiaia Plateau, (SE) species restricted to montane forests in southeastern Brazil, (SES) species that occur in the south and southeastern Brazilian coastal mountain ranges, (MA) species extending their occurrence area to montane areas in the Espinhaço Range or to the northeast and midwestern Brazilian regions, and (AN) species that occur in montane forest in the Andes.

To test for differences in horizontal and vertical structure between AMF and AUMF surveys, the structural parameters of species richness (S), Shannon-Wiener index (H’), total density per hectare (DE), total dominance per hectare (DO), and effective number of species (DH’) were listed among surveys with PBH ranging between 15 and 16 cm (Table 3). The AMF phytosociological parameters were compiled from Rodrigues *et al.* (1989) and Dilisch *et al.* (2001), and those from AUMF were compiled from Roderjan (1994), Rocha (1999), Falkenberg (2003), França & Stehmann (2004), and Meireles *et al.* (2008). The effective number of species corresponds to the exponential value of the Shannon–Wiener index (H’), representing the number of species expected if their abundances were equal within the sample (Jost 2006). An analysis of principal components was performed with those phytosociological parameters to verify the similarities between AUMF and AMF surveys using Fitopac 1.6.4 (Shepherd 2006).

To test for differences in structure between AUMFs and AMFs, statistical tests were performed. AMF parameters were obtained from Dislich *et al.* (2001). The eight AMF surveys were conducted in the Atlantic Plateau of São Paulo State and their altitudes ranged from 800 to 1,170 m.a.s.l. The AUMF surveys were conducted in southern and southeastern Brazil and their altitudes ranged from 1,200 to 1,710 m.a.s.l. in the southern region and 1,900 to 2,300 m.a.s.l. in the southeastern region (Fig. 1). Surveys conducted in different forest fragments in the same area were considered as separate for the analyses. The structural parameters that showed normal distribution were analyzed by the *t* tests, and by nonparametric Mann–Whitney tests (Zar 1999) for data that did not show normal distribution using Bioestat 5.0 (Ayres *et al.* 2007).

A second comparison was performed among AUMF surveys (Table 4). This set was composed of only AUMF forest sites to verify phytosociological structure differences between altitudinal extremes inside the same altitudinal regional gradients. Seven surveys along the extreme altitudinal gradient were conducted. One set consisting of

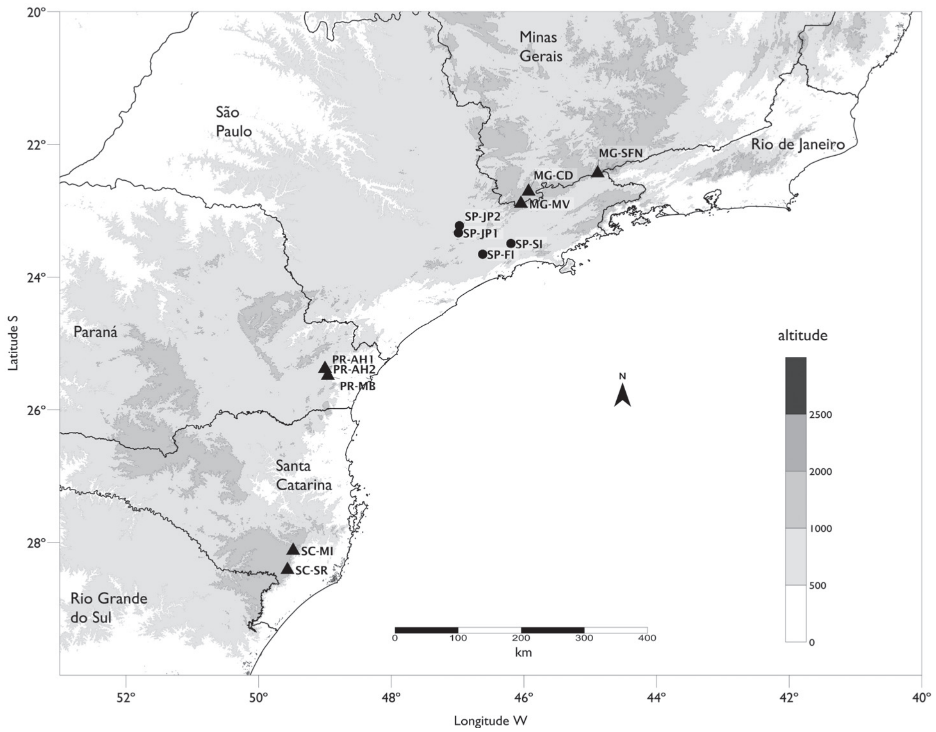

Figure 1. Geographical distribution of the Atlantic montane forest (AMF - ●) and Atlantic upper montane forests (AUMF - ▲) surveys in the southern and southeastern regions of Brazil. SC-SR and SC-MI: Falkenberg (2003), PR-MB: Rocha (1999), PR-AH1 and PR-AH2: Roderjan (1994), MG-MV: Meireles *et al.* (2008), MG-CD: França & Stehmann (2004), MG-SFN: this sample, SP-FI and SP-SI: Dilisch *et al.* (2003), SP-JP1 and SP-JP2: Rodrigues *et al.* (1989).

three surveys was dominated by AUMFs at higher altitudes (1,300–1,700 m.a.s.l. in the south and 2,300 m.a.s.l. in the southeast), while another set comprising four surveys was dominated by AUMFs at lower altitudes (1,200 m.a.s.l. in the south and 1,800–1,900 m.a.s.l. in the southeast). To analyze the variability of dominant species in AUMFs, we listed the five species with the highest values of importance (IV) in each survey and compared them with the floristic table composed by Dislich *et al.* (2001) and the AMF surveys (Table 5). AUMFs were also quantified using the most species rich families and genera, and using the complete floristic list of surveys.

Results

A total of 704 individuals belonging to 22 tree species and 2 woody lianas distributed in 15 families and 19 genera were sampled in three forest sites around the PCAM, including the standing dead individuals (Table 1). Asteraceae (07 spp.), Symplocaceae (03 spp.), and Myrtaceae (02 spp.) were the most species rich families. *Baccharis* (03 spp.) was the richest genera, while *Myrceugenia* and *Symplocos* were represented by two species. Myrsinaceae, Myrtaceae, Symplocaceae, and Cunoniaceae showed the highest IV and represented 60.3% of the total IV. Asteraceae, Solanaceae, Escalloniaceae, Winteraceae, Proteaceae, Celastraceae, and Melastomataceae accounted for 28.8% of the total IV. Aquifoliaceae, Onagraceae, and Clethraceae accounted for 1.6% of the total IV, whereas Fabaceae represented only 0.3% of the total IV.

The total density for the three forest sites was 2,346 individuals ha^{-1-} and the total dominance was 31.40 m^2 ha^{-1}. The Shannon-Wiener index (H') was 2.367 nat individual^{-1}, with an evenness (J) of 0.735 and Simpson index (D) of 0.146. *Myrsine gardneriana* had the highest IV (19.9% of the total), relative density, and relative frequency; but its relative dominance was lower than that of *M. alpigena* and *Weinmannia humilis*, which together represented 26.5% of the total IV (Table 1). *Escallonia laevis*, *Solanum itatiaiae*, *Symphyopappus itatiayensis*, and *Symplocos corymboclados* had more than 30 individuals, and obtained IV between 11.6 and 28.8, corresponding to 24.2% of the total IV. The standing dead biomass represented 8.9% of the total IV and 9.3% of the total individuals. Five species had more than 10 individuals, whereas 12 species had fewer than 10 individuals, and two species were represented by only one individual each.

Of the 24 species sampled, 13 (54%) were present in only one of the sample areas, three (12%) in two sample areas, and eight (33%) in three sample areas. The CA ordination of forest sites by species abundance indicated a greater similarity between VP and MN than FO. The inertia explained by the first two axes was 44.9% (Fig. 2). *M. gardneriana* was abundant in all sample areas, but was strongly associated with FO as well as *Baccharis dentata*

Table 1. Phytosociological parameters of individuals with CAP ≥15 cm sampled in three areas of upper montane forest of the Pico do Capim Amarelo, Serra Fina, and southeastern Brazil. AR., abbreviations used for sampled areas; C, all sample areas together; VP, facing toward to Vale do Paraíba; FO, west face below of the PCAM summit; MN, about 1,000 meters in the north of the PCAM; N.I., number of individuals; N.B., total number of stems; P.B., proportion of stems per individual; F.A., absolute frequency; De.R., relative density; Do.R., relative dominance; V.C., coverture value; F.R., relative frequency; V.I.; importance value; A.M., maximum height; D.M., maximum diameter; D.P., distribution patterns; IP, endemic to Itatiaia Plateau; SE, restricted to montane forest in southeastern Brazil; SES, species that occur in the southern and southeastern Brazilian coastal mountain ranges; MA, extend their occurrence area to montane areas in Espinhaço Range or to the northeast and midwestern Brazilian regions; and AN, species that occur in montane forest in Andes. In bold is AR where the species showed the greatest VI. In parenthesis, the species abbreviation and the collector number of Leonardo Dias Meireles.

Species	D.P.	AR.	N.I.	N.B.	P.B.	F.A.	De.R.	Do.R.	V.C.	F.R.	V.I.	A.M.	D. M.
Myrsine gardneriana A. DC.	MA	C	222	370	1.6	96.7	31.5	14.8	46.3	13.6	59.9	10.0	27.0
(M.gard. – LDM 1596)		VP	36	53	1.4	90.0	18.9	8.2	27.0	13.4	40.5	8.5	20.1
		FO	136	239	1.7	100.0	43.0	29.7	72.7	12.7	**85.4**	5.0	22.7
		MN	50	78	1.5	100.0	25.4	13.7	39.1	14.7	53.8	10.0	27.0
Myrceugenia alpigena (DC.) Landrum	MA	C	83	156	1.8	66.7	11.8	21.8	33.6	9.4	43.0	10.0	48.9
(M.alpig. – LDM 1661)		VP	17	26	1.5	80.0	8.9	7.4	16.3	11.9	28.3	9.0	25.3
		FO	3	19	6.3	30.0	1.0	4.1	5.0	3.8	8.8	5.0	23.3
		MN	63	111	1.7	90.0	32.0	52.0	84.0	13.2	**97.3**	10.0	48.9
Weinmannia humilis Engl.	SES	C	59	71	1.2	46.7	8.4	21.8	30.2	6.5	36.7	13.0	54.4
(W.hum. – LDM 1483)		**VP**	49	61	1.2	80.0	25.7	47.3	73.0	11.9	**84.9**	13.0	54.4
		FO	1	1	1.0	10.0	0.3	0.3	0.6	1.3	1.8	3.0	8.3
		MN	9	9	1.0	50.0	4.6	2.6	7.2	7.4	14.6	11.0	15.9
Symplocos corymboclados Brand	SES	C	50	56	1.1	60.0	7.1	13.3	20.4	8.4	28.8	11.0	31.9
(S.cory. – LDM 1697)		**VP**	35	38	1.1	100.0	18.3	22.3	40.6	14.9	**55.5**	11.0	31.9
		FO	14	17	1.2	70.0	4.4	13.7	18.1	8.9	27.0	7.0	26.3
		MN	1	1	1.0	10.0	0.5	1.3	1.8	1.5	3.3	7.0	22.9
Mortas	-	C	66	87	1.3	93.3	9.4	4.4	13.7	13.1	26.8	8.0	18.9
		VP	23	23	1.0	100.0	12.0	3.4	15.5	14.9	**30.4**	7.0	18.9
		FO	23	39	1.7	100.0	7.3	6.4	13.7	12.7	26.4	5.0	8.2
		MN	20	20	1.0	90.0	10.2	4.2	14.4	11.8	26.1	8.0	17.8
Symphyopappus itatiayensis (Hieron.)	SES	C	56	73	1.3	30.0	8.0	5.1	13.1	4.2	17.3	6.0	19.0
R.M. King & H. Rob. (Sy.itat. – LDM 2336)		**FO**	56	73	1.3	90.0	17.7	23.4	41.1	11.4	**52.5**	6.0	19.0
Solanum itatiaiae Glaz. ex Edmonds	IP	C	34	41	1.2	56.7	4.8	2.4	7.2	7.9	15.2	10.0	17.2
(So.itat. – LDM 2699)		VP	9	13	1.4	60.0	4.7	1.9	6.7	9.0	15.6	10.0	16.5
		FO	11	11	1.0	50.0	3.5	1.3	4.8	6.3	11.2	4.5	8.0
		MN	14	17	1.2	60.0	7.1	3.7	10.8	8.8	**19.6**	9.0	17.2
Escallonia laevis Sleumer	SE	C	31	51	1.6	33.3	4.4	2.5	6.9	4.7	11.6	6.0	23.6
(LDM 2337)		**FO**	31	51	1.6	100.0	9.8	11.5	21.3	12.7	**34.0**	6.0	23.6
Symplocos itatiaiae Wawra	SE	C	9	11	1.2	26.7	1.3	3.8	5.1	3.7	8.8	12.0	33.6
(LDM 2505)		VP	3	5	1.6	30.0	1.6	2.9	4.5	4.5	9.0	9.0	33.6
		FO	1	1	1.0	10.0	0.3	0.2	0.5	1.3	1.8	5.0	6.7
		MN	5	5	1.0	40.0	2.5	7.2	9.7	5.9	**15.6**	12.0	33.4
Drimys brasiliensis Miers	MA	C	14	17	1.2	33.3	2.0	1.8	3.8	4.7	8.5	9.0	21.6
(D.bras. – LDM 2422)		**VP**	8	8	1.0	50.0	4.2	2.8	7.0	7.5	**14.4**	9.0	21.6
		MN	6	9	1.5	50.0	3.1	1.8	4.8	7.4	12.2	9.0	16.5
Roupala rhombifolia Mart. ex Meisn.	MA	C	16	25	1.5	26.7	2.3	1.8	4.1	3.7	7.8	9.0	25.1
(R.rho. – NR)		VP	3	4	1.3	10.0	1.6	1.6	3.2	1.5	4.7	8.0	25.1
		FO	5	11	2.2	10.0	1.6	1.7	3.2	1.3	4.5	3.0	14.8
		MN	8	10	1.2	60.0	4.1	2.1	6.2	8.8	**15.0**	9.0	14.7

Continues

Table 1. Continuation.

Species	D.P.	AR.	N.I.	N.B.	P.B.	F.A.	De.R.	Do.R.	V.C.	F.R.	V.I.	A.M.	D. M.
Maytenus boaria Molina	AN	C	11	11	1.0	20.0	1.6	2.3	3.9	2.8	6.7	7.0	38.2
(M.boar. – LDM 1846)		VP	1	1	1.0	10.0	0.5	0.2	0.8	1.5	2.2	5.0	11.0
		FO	3	3	1.0	20.0	1.0	2.3	3.2	2.5	5.7	6.0	16.4
		MN	7	7	1.0	30.0	3.6	5.0	8.6	4.4	**13.0**	7.0	38.2
Tibouchina hospita Cogn.	SES	C	14	21	1.5	26.7	2.0	0.6	2.5	3.7	6.3	6.0	12.3
(T.hosp. – LDM 1481)		**FO**	12	18	1.5	60.0	3.8	2.1	5.9	7.6	**13.5**	4.5	12.3
		MN	2	3	1.5	20.0	1.0	0.3	1.3	2.9	4.2	6.0	8.9
Baccharis dentata (Vell.) G.M. Barroso	MA	C	10	11	1.1	26.7	1.4	0.4	1.8	3.7	5.5	7.0	9.2
(B.dent. – LDM 2989)		VP	1	2	2.0	10.0	0.5	0.2	0.7	1.5	2.2	7.0	9.2
		FO	9	9	1.0	70.0	2.9	1.3	4.1	8.9	**13.0**	5.0	8.6
Ilex taubertiana Loes.	SES	**C**	4	4	1.0	10.0	0.6	0.6	1.1	1.4	**2.5**	12.0	22.0
(LDM 3065)		**MN**	4	4	1.0	30.0	2.0	1.7	3.7	4.4	**8.1**	12.0	22.0
Dasyphyllum leptacanthum (Gardner) Cabrera	SE	C	4	10	2.5	6.7	0.6	0.6	1.2	0.9	2.1	10.0	20.4
(LDM 2295)		**MN**	4	10	2.5	20.0	2.0	1.9	3.9	2.9	**6.9**	10.0	20.4
Myrceugenia ovata (Hook. & Arn.) O. Berg	AN	C	3	8	2.6	10.0	0.4	0.2	0.6	1.4	2.0	3.0	10.8
(LDM 1681)		**FO**	3	8	2.6	30.0	1.0	0.8	1.8	3.8	**5.6**	3.0	10.8
Baccharis grandimucronata Teodoro	SES	C	5	8	1.6	6.7	0.7	0.1	0.8	0.9	1.8	3.2	7.3
(LDM 1635)		**FO**	5	8	1.6	20.0	1.6	0.6	2.2	2.5	**4.7**	3.2	7.3
Symplocos falcata Brand	SE	C	2	2	1.0	6.7	0.3	0.5	0.8	0.9	1.7	9.0	23.5
(LDM 2258)		**MN**	2	2	1.0	20.0	1.0	1.4	2.5	2.9	**5.4**	9.0	23.5
Piptocarpha organensis Cabrera	SES	C	2	2	1.0	6.7	0.3	0.4	0.7	0.9	1.6	9.0	17.2
(LDM 3172)		**MN**	2	2	1.0	20.0	1.0	1.2	2.2	2.9	**5.1**	9.0	17.2
Pentacalia desiderabilis (Velloso) Cuatrec.	MA	C	3	3	1.0	6.7	0.4	0.1	0.5	0.9	1.5	8.0	7.0
(LDM 2502)		**VP**	3	3	1.0	20.0	1.6	0.2	1.8	3.0	**4.8**	8.0	7.0
Fuchsia regia (Vell.) Munz	SES	C	2	2	1.0	6.7	0.3	0.2	0.5	0.9	1.4	7.0	15.2
(LDM 1471)		**VP**	2	2	1.0	20.0	1.1	0.5	1.5	3.0	**4.5**	7.0	15.2
Clethra scabra Pers.	AN	C	1	2	2.0	3.3	0.1	0.5	0.6	0.5	1.1	11.0	24.1
(LDM 1715)		**VP**	1	2	2.0	10.0	0.5	1.1	1.6	1.5	**3.1**	11.0	24.1
Senna itatiaiae H.S. Irwin & Barneby	IP	C	2	5	2.5	3.3	0.3	0.1	0.4	0.5	0.9	3.5	8.4
(LDM 2306)		**FO**	2	5	2.5	10.0	0.6	0.5	1.2	1.3	**2.4**	3.5	8.4
Baccharis glaziovii Baker	SES	C	1	1	1.0	3.3	0.1	0.0	0.2	0.5	0.6	2.8	6.4
(LDM 2563)		**FO**	1	1	1.0	10.0	0.3	0.2	0.5	1.3	**1.7**	2.8	6.4

and *Tibouchina hospita*. *Weinmannia humilis* and *Symplocos corymboclados* were associated with VP, *Maytenus boaria* and *M. alpigena* were associated with MN, whereas *Drimys brasiliensis* and *Symplocos itatiaiae* had similar abundances between them.

The FO site showed the highest density (316 individuals) and species-level richness (16 spp.) compared to the MN site (197 individuals and 14 spp.) and the VP site (191 individuals and 13 spp.). The density of individuals in FO was about 1.6 times higher than in VP and MN, but FO showed the lowest dominance (Table 2). The average height ($H = 311.9$, $P < 0.0001$) and diameter ($H = 126.2313$, $P < 0.0001$) of tree stems in FO were significantly lower than VP and MN, which had no significant differences between them. The MN and FO sites were similar in terms of the proportion of multi-stemmed individuals at breast height, 29.9% and 29.1% respectively, whereas in VP it was 21.4%. However, the proportion of multi-stemmed individuals at breast height among the sites did not show statistical differences ($\chi^2 = 2.647$, $P = 0.2663$, DF = 2), but FO showed a higher proportion of stems per individual than the other sites ($\chi^2 = 14.906$, $P = 0.0006$, DF = 2). The Shannon–Wiener (H') and evenness (J) were lower in FO than in VP and MN, whereas the Simpson index (D) was higher in FO.

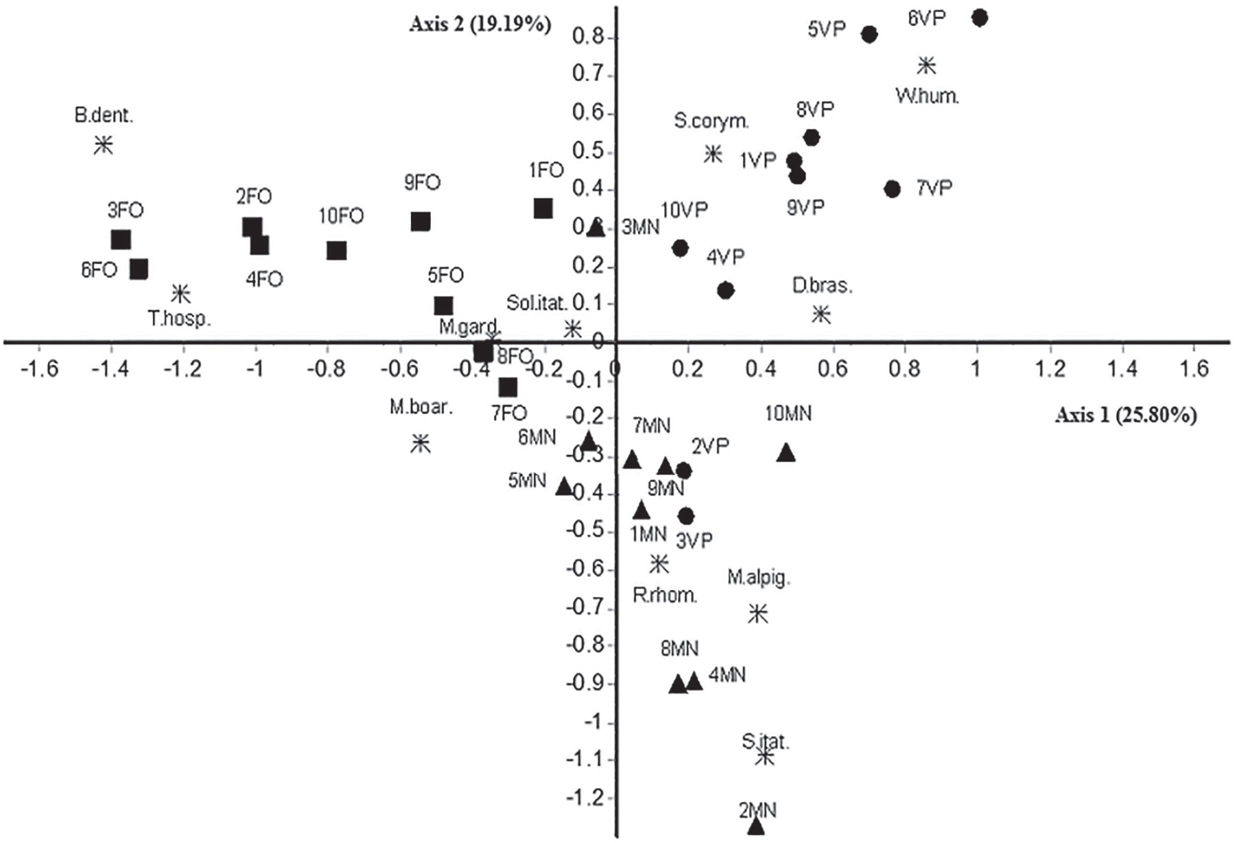

Figure 2. Correspondence analysis by the abundance of species in the upper montane forest for the three sample areas at Serra Fina, southeastern Brazil. VP (●), facing toward to Vale do Paraíba; FO (▲), west face below of the PCAM top; and MN (■), about 1,000 meters in the north of the PCAM. The species acronyms are in Table 1.

Table 2. Phytosociological parameters for the three sampled areas at the Pico do Capim Amarelo, Serra Fina, southeastern Brazil. VP, facing toward to Vale do Paraíba; FO, west face below of the PCAM summit; MN, about 1,000 meters the north of the PCAM at Maracanã; N.I., number of sampled individuals; I. Mstem, number of multi-stemmed individuals; N. Stem, total number of stems; M. Stem, median number of stems by individual; Density, individuals ha^{-1}; Dominance, m^2 ha^{-1}; H. Max., maximum height of individuals in meters; H.Med., average height of individuals in meters; CAP Max., cm CAP Med., cm; Shannon, Shannon–Weiner index; J, equability index; D, Simpson index.

Parameters	Total	VP (2,250 m)	FO (2,320 m)	MN (2,280 m)
Families	19	11	11	11
Genera	15	12	12	12
Species	24	13	16	14
N.I.	704	191	316	197
I. Mstem	192	41	92	59
N.Stem	1,144	310	514	320
M.Stem	1.62	1.28	1.62	1.40
Density	2,346	1,910	3,160	1,970
Dominance	31.40	41.55	20.67	32.0
H. Max.	13.0	13.0	7.0	12.0
H. Med.	5.38	7.04	3.64	6.58
CAP Max.	54.43	54.43	26.26	48.91
CAP Med.	11.15	14.46	8.29	12.51
H’	2.367	2.048	1.919	2.047
J	0.735	0.776	0.677	0.756
D	0.146	0.158	0.235	0.186

Table 3. Phytosociological parameters for the Atlantic montane forest (AMF) and Atlantic upper montane forests (AUMF) surveys in the southern and southeastern regions of Brazil. Abbr, abbreviation of sample area; PBH, perimeter at breast height; N, number of sampled individuals; S, species richness; H', Shannon–Weiner index; D_H, number of species expected by log of H'; DE, total density per hectare; DO, total dominance per hectare; Alt, altitude of sample area; and F.V.T., type of forest formation. MI–SC and RR–SC, Falkenberg (2003); MB–PR, Rocha (1999); AH1–PR and AH2–PR, Roderjan (1994); MV–MG, Meireles *et al.* (2008); CD–MG, França & Stehmann (2004); SF–MG, this sample; FI1–SP, FI2–SP, FI3–SP, SI1–SP, SI2–SP, and SI3–SP, Dilisch *et al.* (2003); and SJ1–SP and SJ2–SP, Rodrigues *et al.* (1989).

Surveys	Abbr.	PBH	N	S	H'	D_H'	DE	DO	Alt.	F.V.T.
Morro da Igreja	MI-SC	16.0	717	13	0.93	2.53	3,180	81.06	1710	AUMF
Rio do Rastro	RR-SC	16.0	719	16	1.58	4.85	2,824	56.70	1400	AUMF
Marumbi	MB-PR	10.0	321	29	2.91	18.36	4,012	35.24	1385	AUMF
Anhangava	AH1-PR	10.0	706	25	2.22	9.21	4,418	29.29	1350	AUMF
Anhangava	AH2-PR	10.0	564	43	3.18	24.05	2,169	41.28	1200	AUMF
Monte Verde	MV-MG	15.0	1,191	66	3.28	26.58	3,403	37.68	1940	AUMF
Camanducaia	CD-MG	15.0	1,501	58	2.90	18.17	2,001	48.12	1900	AUMF
Serra Fina	SF-MG	15.0	704	24	2.36	10.59	2,346	31.40	2300	AUMF
Fontes do Ipiranga	FI1-SP	15.7	500	123	4.28	72.24	1,604	20.00	800	AUMF
Fontes do Ipiranga	FI2-SP	15.7	508	123	4.14	62.80	1,506	33.50	800	AUMF
Fontes do Ipiranga	FI3-SP	15.0	360	85	3.85	47.00	1,488	26.00	800	AMF
Serra do Itapety	SI1-SP	15.0	480	97	3.80	44.70	1,731	41.10	NI	AMF
Serra do Itapety	SI2-SP	15.0	480	80	3.45	31.50	2,829	36.20	NI	AMF
Serra do Itapety	SI3-SP	15.0	480	67	3.30	27.12	1,914	9.20	NI	AMF
Serra do Japi	SJ1-SP	15.7	182	59	3.51	33.45	1,516	50.24	1170	AMF
Serra do Japi	SJ2-SP	15.7	464	57	3.41	30.26	3,866	68.67	870	AMF

AUMFs showed distinct horizontal structure when compared to AMFs (Table 3). AUMFs had lower richness (S) ($t = -4.5109$, $P = 0.0002$, GL = 14), lower effective number of species (DH') ($t = -3.5209$, $P = 0.0017$, GL = 14), and lower diversity according to the Shannon–Wiener index (H') ($U = 0.00$, Z(U) = 3.607, $P = 0.0004$); however, the total density per hectare was significantly higher when SJ2–SP (DE) was excluded ($t = 3.429$, $P = 0.0026$, GL = 14). For total dominance per hectare, no significant difference was observed ($t = 1.0677$, $P = 0.1518$, GL = 14). These parameters in the principal component analysis explained 85.2% of variance in the two first axes (Fig. 3).

Among AUMF surveys, a gradient was observed between AUMFs at lowest altitudes and AUMFs at higher altitudes. Statistically significant differences were observed for species richness, maximum height of the canopy, diversity index of Shannon–Wiener and maximum diameter. In AUMFs at higher altitudes, one or two tree strata were observed, whereas two or three strata were observed in AUMFs at lower altitudes (Table 4). The number of species (S) ranged from 13 to 29 for AUMFs at higher altitudes and from 43 to 58 for AUMFs at lower altitudes ($F = 63.5808$, $P < 0.00001$). The maximum height of the canopy (Amax) ranged from 7 to 13 m in the AUMFs at higher altitudes and from 12 to 22 m in AUMF at lower altitudes ($F = 9.5716$, $P = 0.0125$).

The diversity index of Shannon–Wiener (H') ranged from 0.93 to 2.91 nat individual^{-1} in AUMF at higher altitudes and 2.90 to 3.18 nat individual^{-1} in AUMF at lower altitudes and were significantly different in nonparametric tests ($H = 6.0357$, $P = 0.0140$). The maximum diameter (Dmax) ranged from 26.26 to 54.43 cm in AUMFs at higher altitude, and from 49.6 to 130 cm in AUMFs at lower altitude ($H = 4.3214$, $P = 0.0376$). The total density per hectare (DE) and the total dominance per hectare (DO) for AUMFs at lower altitudes ranged from 2,001 to 3,403 individuals ha^{-1} and 20.67 to 81.06 m^2 ha^{-1}, respectively, and 1,910 to 4,418 individuals ha^{-1} and 39.6 to 48.12 m^2 ha^{-1} in AUMFs at higher altitudes; but both were not different (DE: $F = 0.3460$, $P = 0.5761$; and DO: $H = 0.3214$, $P = 0.5708$).

AUMF at Serra da Mantiqueira mountain range, in the southeastern region, and Serra do Mar mountain range, in the south region, showed a strong floristic similarity in family, genera, and species level. In addition to the five species with the greatest IV in the upper montane forest surveys (Table 5), we observed 26 species belonging to 20 genera and 12 families. They represented 65% of the total number of species in the scenario of greater richness, which would correspond to 40 species. The most species-rich families with the greatest IV were Myrtaceae (10 spp.), Lauraceae (03 spp.), and Asteraceae and Winteraceae (02 spp.). The richest genera were *Myrceugenia* (05 spp.), *Ocotea* (03 spp.), and *Drimys* (02 spp.). Six species were present in more than one survey, representing 23% of the total species observed in the five classes with highest IV. Among the surveys of upper montane forest, 187 sampled tree species belong to 79 genera and 41 families, which were above 1,500 meters in the southeastern region and above 1,300 meters in the southern region. *Baccharis* (09 spp.), *Eugenia* (07 spp.), *Ilex* (05 spp.), *Ocotea* (09 spp.), *Maytenus* (05 spp.), *Miconia* (06 spp.), *Myrceugenia* (11 spp.), *Myrcia* (11 spp.), *Myrsine* (04

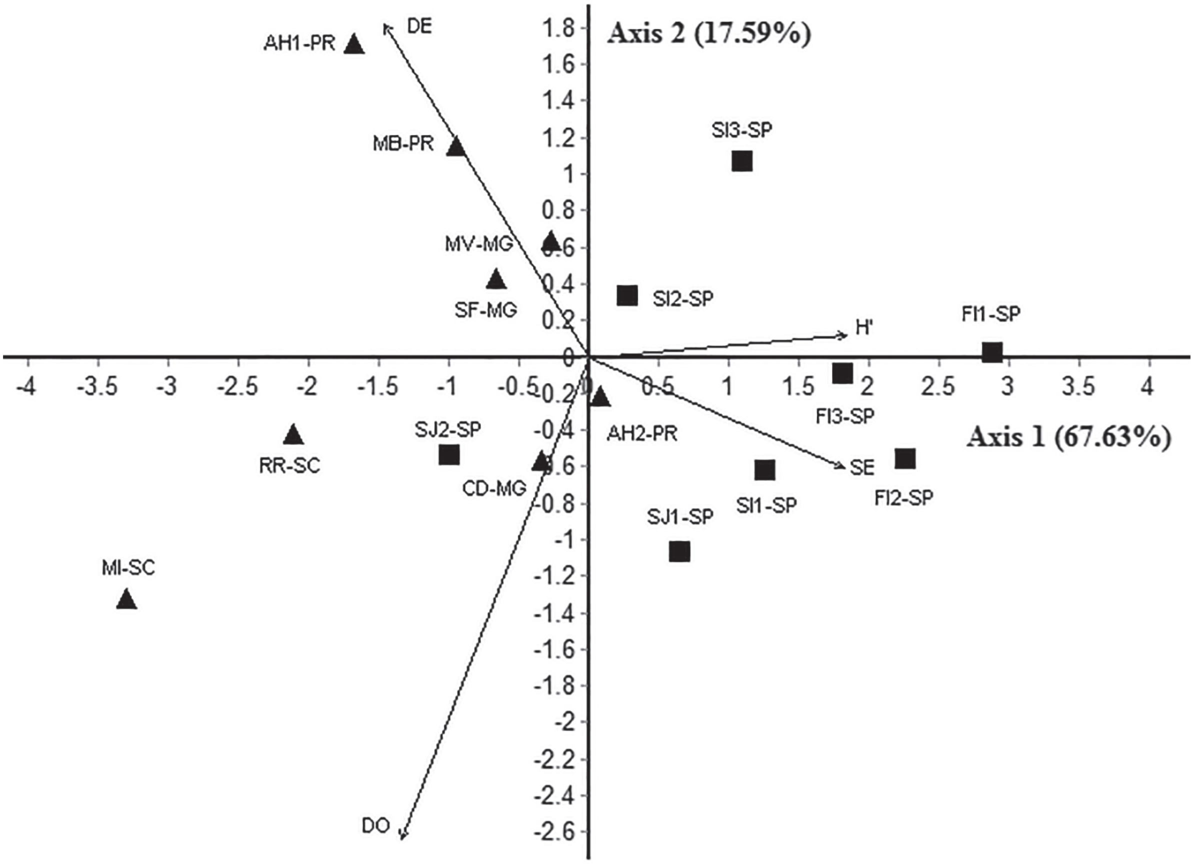

Figure 3. Principal component analysis of phytosociological parameters of the Atlantic montane forest (AMF ▲) and Atlantic upper montane forests (AUMF ■) surveys in the southern and southeastern regions of Brazil. H', Shannon-Wiener index; SE, number of species expected by log of H'; DE, total density per hectare; and DO, total dominance per hectare. MI–SC and RR–SC, Falkenberg (2003); MB–PR, Rocha (1999); AH1–PR and AH2–PR, Roderjan (1994); MV–MG, Meireles *et al.* (2008); CD–MG, França & Stehmann (2004); SF–MG, this sample; FI1–SP, FI2–SP, FI3–SP, SI1–SP, SI2–SP, and SI3–SP, Dilisch *et al.* (2003); SJ1–SP and SJ2–SP, Rodrigues *et al.* (1989).

Table 4. Phytosociological parameters for the Atlantic upper montane forests at higher altitude (AUMF at higher altitude, HA), and Atlantic upper montane forests at lower altitude (AUMF at lower altitude, LA) surveys in the southern and southeastern regions of Brazil. Area, sampled area; N, number of individuals sampled; S, species richness; H', Shannon–Weiner index; DE, total density per hectare; DO, total dominance per hectare; Dma, maximum diameter sampled; Dme, minimum diameter sampled; Ama, maximum height of individuals; Ame, median height of individuals; Str, number of forest strata; and Fr, type of forest formation. M. da Igreja and Rio do Rastro, Falkenberg (2003); Marumbi, Rocha (1999); Anhang. 1300 and Anhang. 1200, Roderjan (1994); Serra Fina VP, FO, MN, this sample; M. Verde 1900 and M. Verde 1800, Meireles *et al.* (2008); Camanducaia, França & Stehmann (2004).

Surveys	Area	N	S	H'	DE	DO	Dma	Dme	Ama	Ame	Str	Fr
M. da Igreja	0.20	717	13	0.937	3,180	81.1	51.0	15.0	8.0	6.3	1	HA
Rio do Rastro	0.22	719	16	1.584	2,824	56.7	42.0	13.0	9.0	7.3	1	HA
Marumbi	0.80	321	29	2.915	4,012	35.2	35.6	8.7	9.0	5.2	2	HA
Anhang. – 1300	0.16	706	25	2.220	4,418	29.3	31.9	8.0	7.0	3.5	1	HA
Anhang. – 1200	0.26	564	43	3.180	2,169	41.3	49.6	13.4	14.0	5.0	3	LA
Serra Fina – VP	0.10	191	14	2.048	1,910	41.5	54.4	14.7	13.0	7.0	1	HA
Serra Fina – FO	0.10	263	15	1.951	3,160	20.7	26.3	8.3	7.0	3.6	1	HA
Serra Fina – MN	0.10	197	14	2.047	1,970	32.0	48.9	12.5	12.0	6.6	1	HA
M. Verde – 1900	0.15	503	47	2.980	3,353	39.6	52.2	10.6	12.0	5.9	2 a 1	LA
M. Verde – 1800	0.20	688	53	3.110	3,440	38.9	84.3	10.0	14.0	6.6	3	LA
Camanducaia	0.75	1,501	58	2.900	2,001	48.1	130.0	-	22.0	11.0	3	LA

Table 5. Five species with the highest importance values in the Atlantic upper montane forests (AUMF) in the southern and southeastern regions of Brazil. MI–SC and RR–SC, Falkenberg (2003); MB–PR, Rocha (1999); AH1–PR and AH2–PR, Roderjan (1994); MV–MG, Meireles *et al.* (2008); CD–MG, França & Stehmann (2004); SF–MG: this sample.

Surveys	1ª IV	2ª IV	3ª IV	4ª IV	5ª IV
Morro da Igreja MI-SC	*Myrceugenia ovata*	*Drimys angustifolia*	*Crinodendron brasiliense*	*Maytenus boaria*	*Weinmannia humilis*
Rio do Rastro RR-SC	*Siphoneugena reitzii*	*Ilex microdonta*	*Ocotea pulchella*	*Myrceugenia alpigena*	*Myrceugenia glaucescens*
Marumbi MB-PR	*Ocotea catharinensis*	*Ilex microdonta*	*Myrceugenia seriato-ramosa*	*Siphoneugena reitzii*	*Eugenia neomyrtifolia*
Anhangava-1 AH1-PR	*Ilex microdonta*	*Siphoneugena reitzii*	*Blepharocalyx salicifolius*	*Drimys brasiliensis*	*Weinmannia humilis*
Anhangava-2 AH2-PR	*Ocotea catharinensis*	*Weinmannia humilis*	*Siphoneugena reitzii*	*Ilex microdonta*	*Critoniopsis quinqueflora*
Monte Verde MV-MG	*Pimenta pseudocaryophyllus*	*Roupala rhombifolia*	*Drimys brasiliensis*	*Miconia cinerascens*	*Myrceugenia myrcioides*
Camanducaia CD-MG	*Ocotea lancifolia*	*Cabralea canjerana*	*Psychotria velloziana*	*Myrcia fallax*	*Drimys brasiliensis*
Serra Fina SF-MG	*Myrsine gardneriana*	*Myrceugenia alpigena*	*Weinmannia humilis*	*Symplocos corymboclados*	*Symphyopappus itatiaiensis*

spp.), *Solanum* (07 spp.), *Symplocos* (08 spp.), *Vernonanthura* (06 spp.), *Tibouchina* (04 spp.), and *Weinmannia* (04 spp.) are the most species rich genera in AUMFs.

Discussion

AUMFs of PCAM demonstrated typical features of cloud forests, such as high stem density, less-developed stem diameter, low canopy height, low species richness, and a high proportion of multi-stemmed individuals at breast height (Hamilton *et al.* 1995; Falkenberg & Voltolini 1995; Meireles *et al.* 2008). Most of the sampled species in PCAM had narrow geographical distributions and occurred only in forest formations of high-altitude mountain ranges in the southern and southeastern region of Brazil, whereas other species were endemic to the Itatiaia Plateau, which is a typical feature of forests under the influence of clouds (Hamilton *et al.* 1995).

Regardless of the fact that the three PCAM forest sites were located at similar altitudes, they showed some physiognomic and structural differences. They showed low diversity, but the differences in diversity indices suggest that FO is be a more restrictive area for the occupation of some tree species than MN and VP. Some species were sampled in only one of these sites, but the greatest difference in horizontal structure between them was related to the abundance of the most important species. These differences could be associated with local abiotic conditions, occupation history, successional stages, and biotic factors related to the niche of species that influence the interspecific competition and the establishment of those tree species (Wright 2002).

The main physiognomic differences among the forest sites were related to canopy height and the number of stems per individual. FO had the lowest average and maximum height of trees. The height of the first trunk bifurcation was visually lower in FO than in VP and MN. Meireles *et al.* (2008) found a lower forest stature in areas most exposed to the winds in the same mountain range; however, the soil depth may be the main factor explaining the lower stature of trees in FO in the Serra Fina mountain range, although we do not have any information about soil depth in those areas to confirm this hypothesis. These forest sites did not display differences in the proportion of multi-stemmed individuals at breast height. However, in FO, the number of stems per individual was significantly higher than in VP and MN. In fact, the survey in FO included a forest site border that was in contact with high-altitude grassland areas, wherein some shrubs species occur, promoting the main floristic dissimilarities with VP and MN.

Physiognomic differences between PCAM forests sites could be associated with variations in the architecture of the most abundant species. The high abundance of multi-stemmed individuals in FO is partly related to the high abundance of *M. gardneriana*. The number of stems in individuals of *M. gardneriana* in FO was higher than in VP and in MN. This was observed more in *M. alpigena* and *Roupala rhombifolia* individuals in FO than in VP and MN. Architectural differences between species could be related to a growth trade-off between the gain in height and lateral diffusion (Archibald & Bond 2003). Species with a wide geographical distribution might display some architectural phenotypic plasticity in response to different environmental pressures (Pohlman *et al.* 2005). Abe & Yamada (2008) have found that *Symplocos* species occurring in high-altitude Asian montane forests had thinner stems, and crowns that were more closely arranged, possibly to obtain mechanical stability. Trees with multiple stems increase the possibility of obtaining more light and have advantages in the occurrence of physical damage (Falkenberg 2003). In AUMFs, the high incidence of multiple-stemmed trees may also be associated with mechanical stability in shallow soils or resistance to strong winds. In addition, multiple stems could be a strategy in response to the occurrence of frosts, which could affect the most exposed apical meristems.

The standing-up dead biomass usually has high importance values in AUMFs (Meireles *et al*. 2008; Falkenberg 2003). Falkenberg (2003) suggested that the persistence of standing-up dead individuals in the cloud forests is related to the low decomposition rate of organic matter compared to ombrophilous forests at lower altitudes. In another surveys of Serra Mantiqueira, the importance of standing dead biomass could be explained by the high amount of dead tree biomass, suggesting a mechanical limit for tree survival in high-altitude areas (Meireles *et al*. 2008). The greater exposure to mechanical and climate damage factors, such as differences in exposure to wind, soil depth, drainage patterns, and topography could be associated with mortality in high-altitude areas; however, these are generalizations that need to be tested (Arriaga 2000; Bellingham & Tanner 2000).

In PCAM forest sites, the massive mortality of bamboo clumps in the recent past has resulted in a large amount of dead biomass that has fallen into the understory and tree strata. This bamboo is most likely *Chusquea leptophylla,* for which there is no phenological information (Clark 2001). Some bamboo seedlings were observed in August 2007. The dead bamboo clumps fell onto the crowns of tree and shrubs, breaking or damaging some of the trees, and even falling into areas previously occupied by the same clumps. This promotes an increase in light in the forest understory and opening gaps of different sizes. The dynamic created by the dead clumps and the re-establishment of new bamboo individuals, and its effect on the tree seedling and understory species remains a phenomenon to be studied because of the phytosociological importance of bambusoides species in AUMFs (Stern *et al*. 1999; Meireles *et al*. 2008).

AUMF analyzed showed lower richness (S), effective number of species ($D_{H'}$), and diversity (H') than AMF in the Atlantic Plateau of São Paulo state and tended to have higher total density per hectare (DE) and total dominance per hectare (DO). Along altitudinal gradients, forests generally display both an increase in density of individuals and basal area and a decrease in species richness, canopy height, and tree diameter with an increase in elevation (Kitayama 1992; Givnish 1999). Rodrigues *et al*. (1989) related the structural changes of seasonal forests to physical and chemical soil characteristics along the altitudinal gradient. Some AMF studies conducted above 1,000 m.a.s.l. (Serra do Japi and Serra do Itapety) showed densities similar to those found in AUMF. However, AMFs at lower altitudes in more restrictive areas show greater tree species richness. Moreover, AUMFs had higher avascular or vascular epiphytism associated with the presence of fog and this could be another feature to differentiate them (Falkenberg & Voltolini 1995; Hamilton *et al*. 1995; Meireles *et al*. 2008).

The lower richness and diversity index in AUMFs suggest more restrictive environmental conditions in high-altitude areas than forests at middle altitudes (Scarano 2002). In more restrictive environmental conditions, the species that are best adapted to the local ecological conditions can dominate the community, showing a discrepancy in abundance in relation to other species (Kitayama 1992). The Simpson index was higher for PCAM surveys than for AUMF of Monte Verde in the same mountain range (Meireles *et al*. 2008). This suggests a higher concentration of individuals within a few species as altitude increases (Martins & Santos 1999). In PCAM forest sites (D = 0.146), three species accounted for 51.5% of the total standing individuals. In Monte Verde (D = 0.059), which is approximately 300 meters lower in altitude, six species accounted for 51.9% of individuals at 1,900 m.a.s.l., and eight species accounted for 49.9% of individuals at 1,800 m.a.s.l. (Meireles *et al*. 2008). This high concentration of individuals within a few species suggests an oligarchic community structure for AUMFs (Scarano 2002).

In MI–SC and RR–SC, only two species accounted for approximately 80% of the total density (Falkenberg 2003). The effective number of species among AUMFs showed that the "Aparados da Serra" (MI–SC) and "Serra do Rio do Rastro" (RR–SC) surveys had the lowest estimated richness, whereas AUMFs at lower altitudes (MV–MG and CD–MG, AH2–PR and MB–PR) had greater richness than surveys in the higher altitudes in Serra Fina (SF–MG) and Morro do Anhangava (AH1–PR). The lower richness that occured in "Aparados da Serra" and "Serra do Rio do Rastro" may be related to a decrease in tree species richness towards higher latitudes versus the regional altitudinal gradient, which is promoted by lower minimum temperatures and increasing frost events in the southern region (Nimer 1977b; Oliveira-Filho & Fontes 2000).

Among AUMF surveys, several of the analyzed structural parameters overlapped, which made it difficult to use a classification system based only on physiognomy and structural parameters. AUMFs showed high variation in canopy height, suggesting that this parameter alone should not be used to identify those forests. AUMFs at higher altitude with low canopy height had higher variation in dominance, whereas AUMFs at lower altitude with higher canopy height varied in density. Sub-divisions based on the physiognomy of montane forest formations have been related to the frequency and intensity of fog (Bruijnzeel & Veneklaas 1998). Grubb & Whitmore (1966) suggested that tropical montane forests with higher canopy have a lower frequency of fog than forests with lower canopy. AUMFs with low canopy height have been observed in the more restrictive areas with extreme altitudinal gradients (Meireles *et al*. 2008; Roderjan 1994; Bertoncello *et al*. 2011). But a gradual variation in the canopy height could be observed along the altitudinal gradients in the southern and southeastern coastal Brazilian mountain ranges along the same floristic belt (Meireles *et al*. 2008; Roderjan 1999).

Cloud forests could be regarded as a physiognomy of upper montane forest belts and their structural differences could be associated with a gradient of climatic changes related to altitude increase, topography, and soil depth characteristics (Segadas-Viana & Dau 1965; Whitmore & Burnham 1984; Cavalier & Goldstein 1989). The regional topographic conditions, length of altitudinal gradient, and distance to ocean could be the main factors associated with the variation of physiognomy observed between upper montane forests in the southern and southeastern regions of Brazil. Two situations have been described: (1) Typical cloud forests correspond to upper montane forest, with a reduced structure in flat areas in "Aparados da Serra" in the southern region (Falkenberg 2003). Alternatively (2), where typical cloud forests occur as a narrow belt inside an upper montane forest, such as occurs in the Serra da Mantiqueira mountain range and in the Serra do Mar in the states of Paraná and São Paulo (Roderjan 1999; Meireles *et al*. 2008; Bertoncello *et al*. 2011). A combination of the definitions by Veloso & Góes (1982) and Veloso (1992) for AUMF could be utilized to define forests that are influenced by clouds or fog in high-altitude areas. These definitions together described the upper montane or the "superomontane" belts in the Atlantic Forest (Oliveira-Filho 2009). Therefore, AUMFs analyzed in the present study correspond to ombrophilous forests composed of high density and dominance, with a high frequency of multi-stemmed individuals at breast height, and with a canopy height ranging from 7 to 20 meters.

On a global scale, tropical montane cloud forests show a significant variation in altitude; they can occur within the montane and sub-montane vegetation belts and do not have a fixed lower altitudinal limit for its occurrence (Stadtmüller 1987; Bruijnzeel & Veneklaas 1998; Hamilton *et al.* 1995; Doumenge *et al.* 1995). The classification in "Brazilian Vegetation Systems" provides an altitude range according to latitude to distinguish forest formations (Veloso 1992). However, the range of the upper montane forest belt and its lower altitudinal limit depends on the geographical position of mountain range, regional physiographic conditions, range of the regional altitudinal gradient, and distance to the ocean, which are factors that affect the occurrence and frequency of fog. The soil depth and micro topographical conditions allow for the establishment of forests inside mountain ranges, as occurs in Brazilian mountain ranges where a tree line is not observed (Hueck 1972).

In addition to structural similarities, AUMFs of the Serra da Mantiqueira mountain range in the southeastern region and AUMFs of the Serra do Mar mountain range in the southern region were very similar at the family, genera, and species levels (Meireles 2009). In the AMF of the Atlantic Plateau of São Paulo state, the species with the highest importance values belonged to 36 genera in the same geographical region (Dislich *et al*. 2001); and in AUMF, the most important species belonged to 20 genera. The most important families in AUMF usually are represented by few species or individuals in the tree strata of forest formations at middle and lower altitudes, like Asteraceae, Aquifoliaceae, Cunoniaceae, Escalloniaceae, Myrsinaceae, Proteaceae, Symplocaceae, and Winteraceae (Koehler *et al*. 2002; Meireles *et al*. 2008; Scheer *et al*. 2011).

Myrtaceae, the most species rich family in the Atlantic Rain Forest, is also one the most species rich in AUMF, with a high relatively density (Oliveira-Filho & Fontes 2000; Yamamoto *et al.* 2005; Meireles *et al.* 2008). The family Lauraceae, was absent from the PCAM forest sites, but some species from this family have been recorded in AUMF at intermediate altitudes. The families Proteaceae and Winteraceae had less phytosociologic importance in the Serra Fina, whereas Symplocaceae and Cunoniaceae had a higher importance. This is a very similar pattern with other tropical montane cloud forests (Madsen & Ollgaard 1994; Kelly *et al*. 1994; Hamilton *et al*. 1995). Fabaceae, one the most species rich families, mainly occurs in the seasonal and ombrophilous forests at lower altitudes, showed the lowest phytosociologic importance in AUMF (Yamamoto *et al*. 2005; Meireles *et al*. 2008; Punyasena *et al*. 2008).

At the genus level, AUMF showed similarities to the Andean montane forests and, shared some genera with Central American cloud forests (Falkenberg & Voltolini 1995; Luna-Vega *et al.* 2001). The most rich genera, or genera with the most phytosociological importance, may be not present in all areas where AUMF occur. Furthermore, this importance varies by regional scale and along altitudinal gradients. Some pantropical genera sampled in AUMF are present in tropical montane cloud forests around the world, like *Clethra*, *Myrsine*, *Prunus*, and *Symplocos* (Ohsawa 1991, Mabberley 1998; Madsen & Ollgaard 1994; Merlin & Juvik 1995; Kitayama 1995). Others are neotropical genera, with species that can either be unique to the upper montane forests, or be tolerant to adverse high-altitude environmental conditions and have a broad geographical distribution throughout Atlantic Forests, like *Euplassa*, *Leandra*, *Miconia*, *Pimenta*, *Roupala*, and *Siphoneugena* (Mabberley 1998; Oliveira-Filho & Fontes 2000; Meireles *et al.* 2008).

Some neotropical genera like *Baccharis*, *Chusquea*, *Crinodendron*, *Critoniopsis*, and *Dasyphyllum* are also the richest genera in the Andean Cordillera (Cabrera 1959; Smith & Smith 1970; King & Robinson 1987; Soderstrom *et al*. 1987; Müller 2006). *Azara, Drimys, Escallonia*, *Myrceugenia*, *Podocarpus*, and *Weinmannia* are Austral–Antarctic genera that represent the temperate element in the tree strata in AUMFs. These genera are the most rich in Andean forests, and most species are restricted to montane forests in the Atlantic Forest (Sleumer 1980; Giulietti & Pirani 1988; Lima *et al.* 2005; Landrum 1981; Safford 2007). *Macropeplus* and *Symphyopappus* are exclusive Atlantic genera and most of their species occur in montane forests or in high-altitude grasslands (King & Robinson 1987; Santos & Peixoto 2005).

Similarities in annual precipitation and annual mean temperatures, incidence of frosts, and high incidence of clouds may be observed among high-altitude areas of southern and southeastern Brazil are responsible for part of the floristic similarities in these AUMFs despite their discontinuous geographic distribution (Meireles 2009; Bertoncello *et al.* 2011). This floristic similarity is also influenced by the lower number of Atlantic Forest species that are able to tolerate the more restrictive conditions of high-altitude areas. In southeastern Brazil, the Serra da Mantiqueira mountain range plays a very important role in floristic placement along the altitudinal gradient in the Atlantic Forest, since this is an inland mountain range and it receives less influence from the Atlantic tropical flora. This is due to the more temperate climates of their high-altitude areas (Segadas-Viana & Dau 1965; Nimer 1977a). There is a similar occurrence in the coastal mountains of the southern region, which despite receiving greater influence from coastal air masses, their high-altitude areas are cooler due to the effect of latitude (Nimer 1977b).

Many species that belong to the Austral–Antarctic and tropical genera that occur mainly in high-altitude areas are related with these floristic similarities. The past climate change events in the late Quaternary period may also be involved in an explanation of this similarity. This has created particular phytogeographical patterns that are explained by the climatic niche of these species and Quaternary climate changes (Behling 1998; Behling 2002; Meireles 2009). Palynological records show that taxa currently restricted to high-altitude areas in the southeastern region occurred at middle altitudes and may have expanded via the Brazilian Plateau near the time of the Last Glacial Maximum (Pessenda *et al.* 2009; Oliveira *et al.* 2005). The cold and wet period that occurred near the time of the Last Glacial Maximum could have been the last time that the montane forest vegetation of the southern and southeastern regions of Brazil had greater contact (Meireles 2009). Additionally, this may have favored the dispersal of these species.

The distinctive climatic and physiographic conditions at the top of mountains strongly influence the forest structure that occurs there. The conditions along the altitudinal gradients gradually restrict the establishment of tree species, influencing the floristic composition and structure of these forests and the physiognomic variations that are related to density, dominance, canopy height, and the architecture and diameter of trees (Doumenge *et al.* 1995). Although the structure and physiognomy of mountain forests under the influence of fog are characteristic, there is no single environmental factor to explain the unmistakable characteristics of these forests, except the frequency of low cloud (Bruijnzeel & Veneklaas 1998). Abiotic, biotic, physiological, and forest dynamics hypotheses have been proposed to explain the structure and functioning of cloud forests, but they are not mutually exclusive (Stadtmüller 1987; Bruijnzeel & Veneklaas 1998).

AUMFs occupy a fragmented and small area, but they contain a large number of species that have a narrow geographic distribution and are restricted to adverse conditions of high-altitude areas. Despite the lower species richness in these forests, the specificity of the climate that the species are subjected to allows for the occurrence of endemic species throughout their geographic distribution range. There are still areas in upper montane forests where no floristic or phytosociological surveys have been conducted. The knowledge of the flora in these regions and other inland mountains ranges can bring new insights to the species distribution of forests under the influence of fog in the Atlantic Forest Domain.

Unfortunately, those forests are good candidates for studies involving changes in vegetation associated with global warming. Their unusual and discontinuous geographical distribution and the presence of endemic taxa emphasizes the biological and biogeographical importance of these forests. Due to the important role these forest ecosystems play, an effort to locate and describe new areas of upper montane forests in the Atlantic Forest Domain should be continued in an effort to contribute to the conservation of these forests.

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