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COMPOSITION, STRUCTURE AND BIODIVERSITY OF TREES IN TROPICAL MONTANE CLOUD FOREST PATCHES IN SERRA DO PAPAGAIO STATE PARK, SOUTHEAST BRAZIL

J. H. C. Ribeiro[1,2], L. D. Santana[3] & F. A. Carvalho[1,4]

Tropical montane cloud forests (TMCFs) are characterised principally by frequent immersion in ground-level clouds, which influences their structure. This study aimed to characterise TMCFs in Serra do Papagaio State Park, Minas Gerais State, Southeast Brazil, and to test the hypothesis that TMCF areas can be highly heterogeneous by comparing the tree species composition and structural parameters of 10 TMCF patches in the studied landscape. TMCFs of Serra do Papagaio State Park are of particular interest for conservation, because they contain important populations of threatened tree species.

Keywords. Atlantic Forest, phytosociology, Serra da Mantiqueira, threatened species, upper montane cloud forest.

Introduction

Tropical mountains are of great importance to biodiversity and natural resource conservation (Pratt & Preston, 1998; Price, 1998). They have great biological diversity, especially of plant species, with high levels of endemism (UNEP–CBD–AHTEG-MB, 2003; Martinelli, 2007). They also present different types of environments and phytophysiognomies, from open vegetation to various forest formations (Chaverri-Polini, 1998). One of the characteristic formations of tropical mountains, the tropical montane cloud forest (TMCF), is found usually between 1000 m and 2500 m above sea level and is characterised principally by frequent immersion in ground-level clouds (Hamilton *et al.*, 1995a; Fahey *et al.*, 2016). Cloud immersion can affect forest structures in different ways. Common features of these forests include low canopy height, high stem density and high density of epiphytes, but these features vary between different regions, and more studies are needed to characterise global relationships (Fahey *et al.*, 2016).

[1] Pós-graduação em Ecologia, Instituto de Ciências Biológicas, Universidade Federal de Juiz de Fora, 36036–900, Juiz de Fora, MG, Brazil. E-mail: jhugocampos@gmail.com
[2] Instituto Federal de Educação, Ciência e Tecnologia do Sudeste de Minas Gerais, 36884-036, Muriaé, MG, Brazil.
[3] Pós-graduação em Engenharia Florestal, Universidade Federal de Lavras, 37200-000, Lavras, MG, Brazil.
[4] Departamento de Botânica, Instituto de Ciências Biológicas, Universidade Federal de Juiz de Fora, 36036–900, Juiz de Fora, MG, Brazil.

Tropical montane cloud forests are found in more or less isolated areas in the landscape (Vázquez-Gárcia, 1995) and tend to have a different structure and floristic composition compared with lowland forests (Bertoncello *et al*., 2011). The transition between montane rain forests and TMCFs is not always evident and abrupt, but as elevation increases, three types of TMCF can be recognised: 1) above montane rain forests, trees become gradually smaller, bryophyte cover on stems increases and lower montane cloud forests are observed; 2) upper montane cloud forests (UMCFs) are found above lower montane cloud forests and are characteristically of shorter stature (2–20 m) and have high bryophyte density and diversity; and 3) at even higher elevations, where average maximum temperatures fall below 10°C, a subalpine cloud forest can be found, with smaller trees (1.5–9 m) and fewer tree species (Scatena *et al*., 2010).

Tropical montane cloud forests are distributed in the tropical regions of the world, conditioned by complex interactions between climatic conditions, topography and atmospheric circulation (Scatena *et al*., 2010). In Brazil, they are associated with large mountain ranges, such as the Aparados da Serra, Serra do Mar and Serra da Mantiqueira, and also occur in high-altitude areas on Guiana's plateau (Aldrich *et al*., 1997; Bruijnzeel *et al*., 2010; Pompeu, 2015). In the Atlantic Forest Domain, low temperatures, ground-level clouds and strong winds function as limiting factors for forest vegetation, and TMCFs tend to have a unique flora distinct from the flora of other forest areas of the domain (Scarano, 2009; Bruijnzeel *et al*., 2010; Bertoncello *et al*., 2011; Williams-Linera *et al*., 2013; Neves *et al*., 2017). Owing to their position on usually difficult terrains in mountainous areas, TMCFs have until recently remained well conserved in comparison with other tropical forests. The situation has changed over the past few decades as a result of expansion of human activity in these areas. In the early 1990s, TMCFs were already among the most threatened terrestrial ecosystems (Scatena *et al*., 2010). Conversion to agriculture and grazing lands, overharvesting, invasions by non-native species and construction of roads are the most prevalent threats to TMCFs worldwide (Scatena *et al*., 2010). Recent studies have shown that TMCFs could be severely affected by climate change (Martin & Bellingham, 2016). Changes in cloud formation, precipitation and temperature can be especially dangerous for TMCFs, but changes in other aspects, such as increasing dry seasons, droughts and intensity of rainstorms, can also severely damage these forests (Foster, 2001). However, climate change may affect TMCFs differently worldwide, making it necessary to investigate more sites of this phytophysiognomy (Martin & Bellingham, 2016).

To better understand the future consequences of climate change and other threats, it is important to know the current patterns of structure and floristic composition of these forests. Information about TMCFs has increased over the past few decades (see, for example, the revisions in Hamilton *et al*., 1995b, and Bruijnzeel *et al*., 2010). However, the structure, composition and floristic affinities of TMCFs are still poorly understood, and more investigations on this phytophysiognomy are greatly needed (Bertoncello *et al*., 2011).

Tropical montane cloud forests are usually very heterogeneous, even in small areas. They can show differences in richness, composition and structural parameters (Pereira *et al.*, 2006; Meireles *et al.*, 2008; Meireles & Shepherd, 2015). In this study, we aimed to analyse the composition, structure and biodiversity of trees in TMCFs in Serra do Papagaio State Park, Minas Gerais State, Southeast Brazil. We also tested the hypothesis that TMCF areas can be highly heterogeneous, by comparing tree species composition and structural parameters of 10 TMCF patches in the studied landscape.

Material and Methods

Study area

The Serra do Papagaio State Park protects a total area of 22,917 ha of the Atlantic Forest Domain in the south of Minas Gerais State, Brazil (IEF, 2009). It is located at 22°07′24.26″S, 44°44′51.15″W (Fig. 1), with a mean altitude of 1774 m and a maximum of 2359 m. The park is part of the Serra da Mantiqueira Environmental Protection Area, one of the world's most valuable protected areas for conservation (Le Saout *et al.*, 2013). Serra da Mantiqueira is characterised by an imposing escarpment facing the Paraíba Valley, with over 2000 m of altitude variability (Almeida & Carneiro, 1998). It forms the second step of the Brazilian Plateau, and together with Serra do Mar, represents one of the coldest and wettest regions of eastern South America (Moreira & Camelier, 1997). Two geomorphologic units can be recognised: 'Mantiqueira Meridional', where the study area is located, and 'Mantiqueira Setentrional' (Machado-Filho *et al.*, 1983).

The landscape is characterised by a rugged relief, with declivities of about 40% and large areas with over 75% declivity (IEF, 2009). The climate is Cwb, following the Köppen classification (Alvares *et al.*, 2013), with cold, dry winters and mild, wet summers. The temperature varies from 0°C to 10°C in the winter and can reach 30°C during some summer days. Mean annual precipitation is 1568 mm, concentrated between October and March (with 80% of annual precipitation), and there is no dry period (IEF, 2009).

The vegetation of the study area is a mosaic of Atlantic Forest (*Araucaria* mixed forest and dense ombrophilous forest) and open vegetation ('campos de altitude') (IEF, 2009). TMCFs (highland ombrophylous forests *sensu* IBGE, 2012) are located above 1800 m a.s.l. (IEF, 2009) (Fig. 2). The central portion of the park where this study was carried out is known locally as 'Chapadão' and is characterised by elevated hills and valleys, with altitudes ranging from 1800 m to 2000 m and 3–20% declivity. High-altitude fields exist in litholic soils, whereas cloud forest exists on patches of inceptisols and histosols in the valleys, usually associated with small rivers and springs (IEF, 2009).

Sampling and data collection

Tropical montane cloud forest patches with areas greater than 2 ha were mapped using satellite images and information gathered on field trips. Ten forest patches were selected

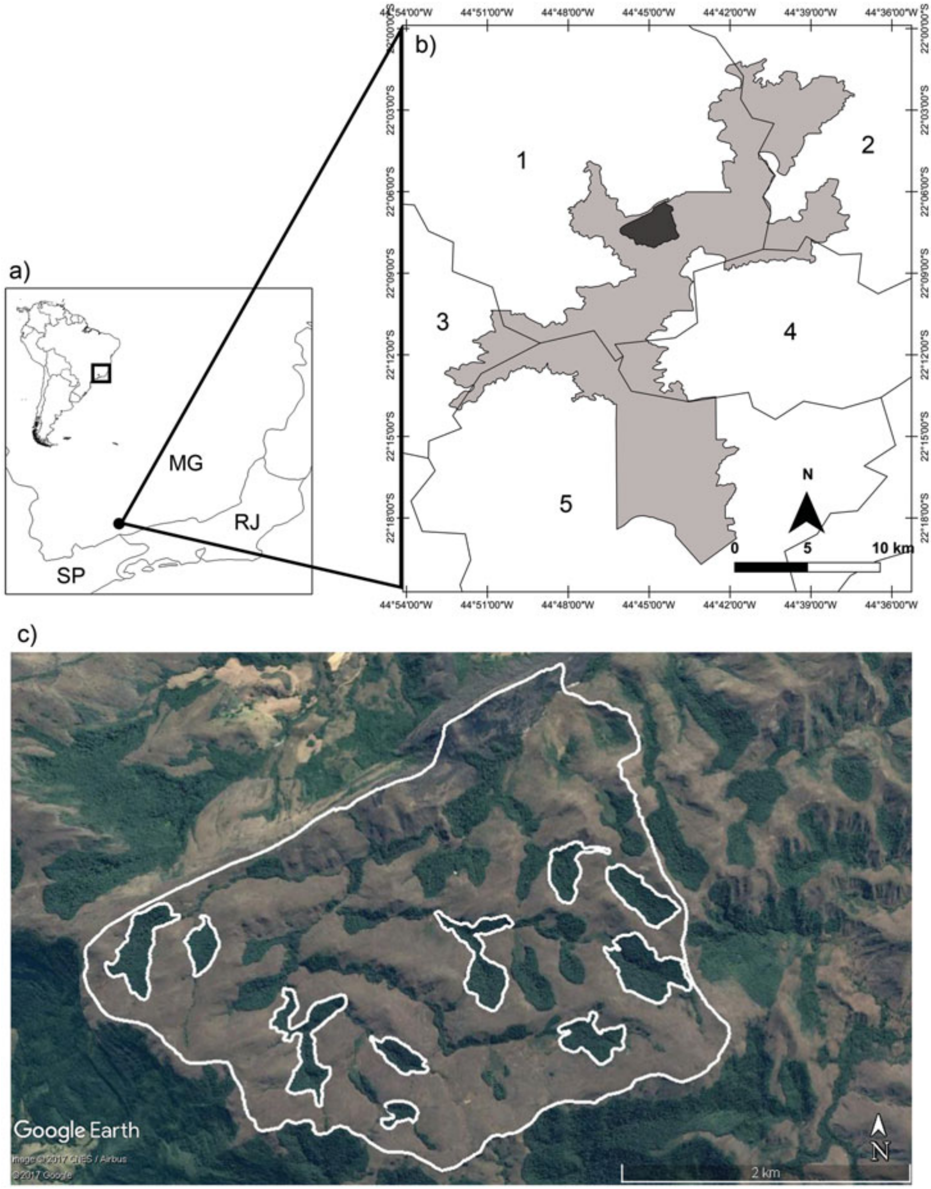

FIG. 1. A, Location of the Serra do Papagaio State Park, Minas Gerais, Brazil. B, Light grey area, Serra do Papagaio State Park; dark grey area, central portion of the park, known locally as 'Chapadão', where the study was conducted, in the municipalities of 1) Baependi, 2) Aiuruoca, 3) Pouso Alto, 4) Alagoa and 5) Itamonte. C, The 10 patches of tropical montane cloud forest selected for this study; the outer line delimits Chapadão. MG, Minas Gerais; RJ, Rio de Janeiro; SP, São Paulo. Sources: IBGE (no date) and Google Earth (Google Inc., no date).

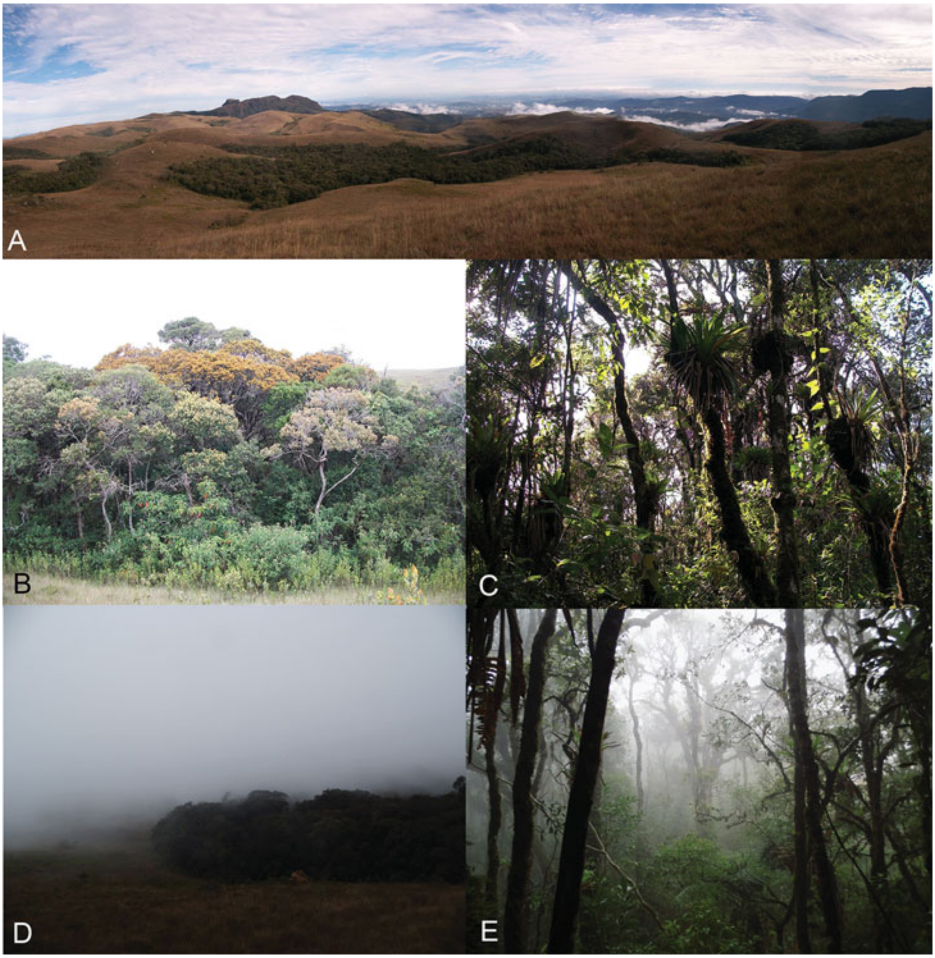

FIG. 2. Tropical montane cloud forest patches of Serra do Papagaio State Park, Minas Gerais, Brazil. A, Forest patches on a high-altitude field matrix. B, External view of a forest patch. C, Interior of a forest patch, showing the abundance of epiphytes. D, Formation of clouds at ground level. E, Interior of a forest patch, showing canopies immersed in clouds. Photographs from the authors' personal archives.

randomly from all the patches mapped (Fig. 1C). On each of the selected patches, we superimposed a 10 × 20 m grid. Using this grid, 10 permanent plots of 10 × 20 m were randomly chosen, covering 0.2 ha in each patch and 2 ha in total. Field data were collected between September 2014 and April 2016.

All trees with a circumference ≥ 15.5 cm at breast height (1.30 m) were marked with aluminium plates. Circumferences were measured at breast height, and total height was estimated for all individuals. Botanical material was collected for identification to species level. Identification of botanical material was performed by reference to the literature (identification keys, species descriptions and family monographs), consultation with experts, and comparison with material deposited in the Leopoldo Krieger Herbarium (CESJ; code following Thiers, continuously updated) of the Federal University of Juiz de Fora. Names of species and botanical synonyms were verified by consulting Brazilian Flora Group (2015) and the International Plant Names Index database (IPNI, continuously updated), and the classification of botanical families followed APG IV (Angiosperm Phylogeny Group, 2016) and PPG I (2016).

Data analysis

Structural parameters of species were evaluated according to formulas described by Kent and Coker (1992): absolute and relative frequency (*AF* and *RF*, respectively), absolute and relative density (*AD* and *RD*, respectively), absolute and relative dominance (*ADo* and *RDo*, respectively) and importance value (*IV*, calculated as the sum of *RF*, *RD* and *RDo*).

Histograms of diameter distribution for all live and dead individuals were generated. The class intervals were defined by an approximation of Spiegel's formula (Felfili & Resende, 2003), resulting in class intervals of 7 cm. To explore vertical structure, a histogram for height values of live individuals, with class intervals of 2 m, was prepared.

The average number of live individuals and basal areas per plot were compared between forest patches by using a one-way ANOVA test. Assumptions for the ANOVA test (i.e. homogeneity of variances and normality of residuals) were checked using Levene and Shapiro–Wilk normality tests. When these assumptions were not satisfied, a non-parametric Kruskal–Wallis test was performed. When a significant difference was observed, an *a posteriori* Tukey test was used to locate the differences. Tests were performed on R version 3.4.0 (R Core Team, 2017), using the packages CAR (Fox & Weisberg, 2011) and Vegan (Oksanen *et al.*, 2017).

To compare species richness between forest patches, individual-based rarefaction/extrapolation curves were used, following Colwell *et al.* (2012) and Hsieh *et al.* (2016a). Curves were generated on R version 3.4.0 (R Core Team, 2017), using the packages ggplot2 (Wickham, 2009) and iNEXT (Hsieh *et al.*, 2016b). Differences between rarefaction curves were tested following Cayuela *et al.* (2015), using the package rareNMtests (Cayuela & Gotelli, 2014).

Differences in species composition were analysed based on similarity matrices between all forest patches, using Jaccard (for incidence data) and Bray–Curtis (for abundance data) similarity indices. Multiresponse permutation procedures (MRPP) analysis was used to test for significant differences in similarity indices between the forest patches. The analysis was performed on R version 3.4.0 (R Core Team, 2017), using the Vegan package (Oksanen *et al.*, 2017).

Results

Floristic composition and structure

In all the forest patches, 4673 individuals were found, representing 89 morphospecies distributed across 32 families and 49 genera (Table 1). A total of 66 morphospecies

TABLE 1. Structural parameters for 89 morphospecies found in 10 tropical montane cloud forest patches in Serra do Papagaio State Park, Minas Gerais, Brazil[a]

Family	Species	*n*	*F*	*FP*	*AD* (individuals/ha)	*BA* (m^2/ha)	*RD* (%)	*RBA* (%)	*RF* (%)	*IV*	Voucher no.[b]
Myrtaceae	*Myrcia retorta* Cambess.	590	97	10	295	15.389	12.626	30.131	5.886	48.643	*J.H.C.Ribeiro* 561
Myrtaceae	*Myrceugenia* cf. *bracteosa* (DC.) D.Legrand & Kausel	293	83	10	146.5	5.375	6.269	10.523	5.036	21.829	*J.H.C.Ribeiro* 618
Myrtaceae	*Myrciaria floribunda* O.Berg	460	84	10	230	2.603	9.842	5.097	5.097	20.036	*J.H.C.Ribeiro* 583
Aquifoliaceae	*Ilex* sp. 1	235	82	10	117.5	3.428	5.028	6.712	4.976	16.715	*J.H.C.Ribeiro* 559
Melastomataceae	*Miconia pusilliflora* (DC.) Naudin	449	79	10	224.5	1.006	9.606	1.971	4.794	16.371	*J.H.C.Ribeiro* 582
Myrtaceae	*Myrcia pulchra* Kiaersk.	211	68	10	105.5	2.649	4.514	5.186	4.126	13.826	*K. Antunes* 596
Myrtaceae	*Myrcia splendens* DC.	285	84	10	142.5	1.145	6.098	2.242	5.097	13.437	*L.D. Santana* 21
Myrtaceae	*Siphoneugena crassifolia* (DC.) Proença & Sobral	170	70	10	85	1.115	3.637	2.184	4.248	10.069	*J.H.C.Ribeiro* 584
Malpighiaceae	*Byrsonima ligustrifolia* A.Juss.	127	57	10	63.5	1.633	2.717	3.197	3.459	9.373	*J.H.C.Ribeiro* 562
Rubiaceae	*Cordiera concolor* (Cham.) Kuntze	199	69	10	99.5	0.470	4.258	0.920	4.187	9.364	*J.H.C.Ribeiro* 644
Lauraceae	*Ocotea corymbosa* Mez	103	55	10	51.5	1.508	2.204	2.953	3.337	8.494	*J.H.C.Ribeiro* 599
Rubiaceae	*Psychotria vellosiana* Benth.	139	56	10	69.5	0.811	2.974	1.589	3.398	7.961	*J.H.C.Ribeiro* 619

TABLE 1. *(Continued)*

Family	Species	*n*	*F*	*FP*	*AD* (individuals/ha)	*BA* (m^2/ha)	*RD* (%)	*RBA* (%)	*RF* (%)	*IV*	Voucher no.[b]
Meliaceae	*Cabralea canjerana* (Vell.) Mart.	87	44	10	43.5	1.297	1.861	2.539	2.670	7.070	*J.H.C.Ribeiro* 523
Celastraceae	*Maytenus* sp. 1	79	40	10	39.5	1.263	1.690	2.472	2.427	6.590	*J.H.C.Ribeiro* 620
Primulaceae	*Myrsine gardneriana* A.DC.	94	43	10	47	0.876	2.011	1.715	2.609	6.335	*J.H.C.Ribeiro* 607
Myrtaceae	*Eugenia* cf. *widgrenii* Sond. ex O.Berg	95	33	8	47.5	1.088	2.033	2.131	2.002	6.166	*J.H.C.Ribeiro* 621
Proteaceae	*Roupala montana* Aubl.	61	35	10	30.5	0.952	1.305	1.864	2.124	5.293	*J.H.C.Ribeiro* 567
Rosaceae	*Prunus myrtifolia* (L.) Urb.	71	48	10	35.5	0.303	1.519	0.593	2.913	5.024	*J.H.C.Ribeiro* 622
Winteraceae	*Drimys brasiliensis* Miers	74	38	10	37	0.318	1.583	0.622	2.306	4.511	*J.H.C.Ribeiro* 605
Lauraceae	Lauraceae sp. 1	56	33	10	28	0.554	1.198	1.084	2.002	4.285	*J.H.C.Ribeiro* 560
Primulaceae	*Myrsine umbellata* Mart.	65	30	8	32.5	0.446	1.391	0.873	1.820	4.084	*J.H.C.Ribeiro* 579
Lauraceae	*Nectandra grandiflora* Nees & Mart.	42	22	8	21	0.658	0.899	1.289	1.335	3.523	*J.H.C.Ribeiro* 597
Myrtaceae	*Myrcia venulosa* DC.	45	27	8	22.5	0.224	0.963	0.439	1.638	3.040	*J.H.C.Ribeiro* 563
Symplocaceae	*Symplocos celastrinea* Mart.	38	26	9	19	0.288	0.813	0.565	1.578	2.955	*J.H.C.Ribeiro* 598
Araucariaceae	*Araucaria angustifolia* (Bertol.) Kuntze	11	11	3	5.5	1.021	0.235	1.998	0.667	2.901	*L.D.Santana* 96

TABLE 1. *(Continued)*

Family	Species	*n*	*F*	*FP*	*AD* (individuals/ha)	*BA* (m^2/ha)	*RD* (%)	*RBA* (%)	*RF* (%)	*IV*	Voucher no.[b]
Myrtaceae	*Myrceugenia regnelliana* (O.Berg) D.Legrand & Kausel	73	16	6	36.5	0.164	1.562	0.320	0.971	2.853	*J.H.C.Ribeiro* 581
Euphorbiaceae	*Alchornea triplinervia* (Spreng.) Müll.Arg.	38	20	7	19	0.360	0.813	0.706	1.214	2.732	*J.H.C.Ribeiro* 580
Melastomataceae	*Miconia sellowiana* Naudin	48	23	8	24	0.147	1.027	0.288	1.396	2.710	*J.H.C.Ribeiro* 596
Myrtaceae	*Pimenta pseudocaryophyllus* (Gomes) Landrum	33	21	9	16.5	0.251	0.706	0.492	1.274	2.472	*J.H.C.Ribeiro* 603
Asteraceae	*Vernonanthura discolor* (Less.) H.Rob.	21	19	9	10.5	0.411	0.449	0.804	1.153	2.406	*J.H.C.Ribeiro* 624
Myrtaceae	*Myrcia laruotteana* Cambess.	51	7	4	25.5	0.424	1.091	0.830	0.425	2.345	*J.H.C.Ribeiro* 565
Monimiaceae	*Macropeplus dentatus* (Perkins) I.Santos & Peixoto	31	18	9	15.5	0.230	0.663	0.451	1.092	2.207	*J.H.C.Ribeiro* 623
Clethraceae	*Clethra scabra* Pers.	17	15	8	8.5	0.244	0.364	0.477	0.910	1.751	*J.H.C.Ribeiro* 604
Bignoniaceae	*Jacaranda cuspidifolia* Mart.	12	11	6	6	0.405	0.257	0.794	0.667	1.718	*J.H.C.Ribeiro* 606

TABLE 1. *(Continued)*

Family	Species	*n*	*F*	*FP*	*AD* (individuals/ha)	*BA* (m^2/ha)	*RD* (%)	*RBA* (%)	*RF* (%)	*IV*	Voucher no.[b]
Euphorbiaceae	*Croton alchorneicarpus* Croizat	19	13	6	9.5	0.089	0.407	0.175	0.789	1.371	*J.H.C.Ribeiro* 625
Araliaceae	*Schefflera* cf. *calva* (Cham.) Frodin & Fiaschi	20	8	4	10	0.198	0.428	0.387	0.485	1.301	*J.H.C.Ribeiro* 564
Melastomataceae	*Miconia buddlejoides* Triana	15	11	7	7.5	0.044	0.321	0.085	0.667	1.074	*J.H.C.Ribeiro* 643
Cunoniaceae	*Lamanonia ternata* Vell.	6	6	4	3	0.242	0.128	0.473	0.364	0.966	*J.H.C.Ribeiro* 595
Symplocaceae	*Symplocos insignis* Brand	12	8	4	6	0.074	0.257	0.144	0.485	0.886	*J.H.C.Ribeiro* 639
Melastomataceae	*Leandra carassana* (DC.) Cogn.	13	8	4	6.5	0.059	0.278	0.115	0.485	0.879	*J.H.C.Ribeiro* 644
Myrtaceae	*Myrceugenia rufescens* (DC.) D.Legrand & Kausel	9	7	4	4.5	0.110	0.193	0.216	0.425	0.833	*J.H.C.Ribeiro* 608
Podocarpaceae	*Podocarpus lambertii* Klotzsch ex Endl.	8	7	3	4	0.105	0.171	0.206	0.425	0.802	*J.H.C.Ribeiro* 640
Lauraceae	*Ocotea odorifera* (Vell.) Rohwer	8	6	2	4	0.133	0.171	0.261	0.364	0.796	*J.H.C.Ribeiro* 600
Monimiaceae	*Mollinedia* sp. 1	9	8	4	4.5	0.051	0.193	0.100	0.485	0.778	*J.H.C.Ribeiro* 601
Rubiaceae	*Rudgea jasminoides* (Cham.) Müll.Arg.	7	7	4	3.5	0.012	0.150	0.023	0.425	0.598	*J.H.C.Ribeiro* 610

Table 1. *(Continued)*

Family	Species	*n*	*F*	*FP*	*AD* (individuals/ha)	*BA* (m^2/ha)	*RD* (%)	*RBA* (%)	*RF* (%)	*IV*	Voucher no.[b]
Ochnaceae	*Ouratea* sp. 1	6	5	4	3	0.042	0.128	0.083	0.303	0.515	*J.H.C.Ribeiro* 594
Undetermined	Undetermined 1	10	3	2	5	0.059	0.214	0.115	0.182	0.511	*J.H.C.Ribeiro* 566
Annonaceae	*Annona* sp. 1	13	3	3	6.5	0.023	0.278	0.045	0.182	0.506	*J.H.C.Ribeiro* 576
Melastomataceae	*Miconia latecrenata* Naudin	9	4	3	4.5	0.027	0.193	0.052	0.243	0.488	*J.H.C.Ribeiro* 634
Symplocaceae	*Symplocos falcata* Brand	9	4	3	4.5	0.026	0.193	0.052	0.243	0.487	*J.H.C.Ribeiro* 635
Melastomataceae	*Huberia nettoana* Brade	7	4	4	3.5	0.038	0.150	0.074	0.243	0.467	*J.H.C.Ribeiro* 611
Theaceae	*Laplacea fruticosa* (Schrad.) Kobuski	5	5	5	2.5	0.027	0.107	0.052	0.303	0.463	*J.H.C.Ribeiro* 578
Melastomataceae	*Miconia acutifolia* Ule	11	3	2	5.5	0.022	0.235	0.043	0.182	0.460	*J.H.C.Ribeiro* 609
Ochnaceae	*Ouratea* sp. 2	5	5	3	2.5	0.013	0.107	0.026	0.303	0.436	*J.H.C.Ribeiro* 636
Rhamnaceae	*Rhamnus sphaerosperma* Sw.	5	5	3	2.5	0.011	0.107	0.022	0.303	0.433	*J.H.C.Ribeiro* 593
Solanaceae	*Solanum pseudoquina* A.St.-Hil.	5	3	3	2.5	0.061	0.107	0.120	0.182	0.409	*J.H.C.Ribeiro* 568
Primulaceae	*Myrsine lancifolia* Mart.	6	4	2	3	0.017	0.128	0.032	0.243	0.404	*J.H.C.Ribeiro* 615
Undetermined	Undetermined 9	5	4	3	2.5	0.020	0.107	0.039	0.243	0.389	*J.H.C.Ribeiro* 585

TABLE 1. *(Continued)*

Family	Species	*n*	*F*	*FP*	*AD* (individuals/ha)	*BA* (m^2/ha)	*RD* (%)	*RBA* (%)	*RF* (%)	*IV*	Voucher no.[b]
Cunoniaceae	*Weinmannia paulliniifolia* Pohl ex Ser.	3	2	2	1.5	0.095	0.064	0.186	0.121	0.372	*J.H.C.Ribeiro* 569
Undetermined	Undetermined 2	2	2	1	1	0.104	0.043	0.204	0.121	0.368	*J.H.C.Ribeiro* 637
Celastraceae	*Maytenus evonymoides* Reissek	4	3	3	2	0.042	0.086	0.081	0.182	0.349	*J.H.C.Ribeiro* 642
Undetermined	Undetermined 3	3	3	2	1.5	0.010	0.064	0.021	0.182	0.267	*J.H.C.Ribeiro* 641
Annonaceae	*Guatteria australis* A.St.-Hil.	3	2	2	1.5	0.041	0.064	0.081	0.121	0.267	*J.H.C.Ribeiro* 638
Aquifoliaceae	*Ilex* sp. 2	2	2	1	1	0.050	0.043	0.098	0.121	0.262	*J.H.C.Ribeiro* 612
Solanaceae	*Solanum swartzianum* Roem. & Schult.	3	3	2	1.5	0.005	0.064	0.010	0.182	0.256	*J.H.C.Ribeiro* 633
Undetermined	Undetermined 8	2	2	2	1	0.030	0.043	0.058	0.121	0.222	*J.H.C.Ribeiro* 626
Dicksoniaceae	*Dicksonia sellowiana* Hook.	2	2	2	1	0.025	0.043	0.050	0.121	0.214	*J.H.C.Ribeiro* 571
Myrtaceae	*Eugenia handroana* D.Legrand	2	1	1	1	0.010	0.043	0.020	0.061	0.123	*J.H.C.Ribeiro* 632
Annonaceae	*Guatteria* sp. 1	1	1	1	0.5	0.019	0.021	0.037	0.061	0.119	*J.H.C.Ribeiro* 627
Lauraceae	Lauraceae sp. 2	2	1	1	1	0.007	0.043	0.014	0.061	0.118	*J.H.C.Ribeiro* 616

TABLE 1. *(Continued)*

Family	Species	*n*	*F*	*FP*	*AD* (individuals/ha)	*BA* (m^2/ha)	*RD* (%)	*RBA* (%)	*RF* (%)	*IV*	Voucher no.[b]
Cyatheaceae	*Cyathea corcovadensis* (Raddi) Domin	1	1	1	0.5	0.014	0.021	0.027	0.061	0.109	*J.H.C.Ribeiro* 591
Fabaceae	*Dalbergia villosa* Benth.	1	1	1	0.5	0.012	0.021	0.023	0.061	0.105	*J.H.C.Ribeiro* 570
Myrtaceae	*Myrcia montana* Cambess.	1	1	1	0.5	0.007	0.021	0.014	0.061	0.096	*J.H.C.Ribeiro* 630
Cyatheaceae	*Alsophila setosa* Kaulf.	1	1	1	0.5	0.005	0.021	0.010	0.061	0.092	*J.H.C.Ribeiro* 617
Undetermined	Undetermined 5	1	1	1	0.5	0.004	0.021	0.007	0.061	0.089	*J.H.C.Ribeiro* 586
Myrtaceae	*Myrcia guianensis* DC.	1	1	1	0.5	0.004	0.021	0.007	0.061	0.089	*J.H.C.Ribeiro* 592
Undetermined	Undetermined 7	1	1	1	0.5	0.003	0.021	0.007	0.061	0.089	*J.H.C.Ribeiro* 587
Myrtaceae	*Myrcia palustris* DC.	1	1	1	0.5	0.003	0.021	0.006	0.061	0.088	*J.H.C.Ribeiro* 613
Solanaceae	*Solanum capoerum* Dunal	1	1	1	0.5	0.003	0.021	0.006	0.061	0.088	*J.H.C.Ribeiro* 614
Lauraceae	*Cinnamomum* sp. 1	1	1	1	0.5	0.003	0.021	0.006	0.061	0.088	*J.H.C.Ribeiro* 631
Undetermined	Undetermined 4	1	1	1	0.5	0.003	0.021	0.005	0.061	0.087	*J.H.C.Ribeiro* 572
Myrtaceae	*Myrceugenia myrcioides* (Cambess.) O.Berg	1	1	1	0.5	0.003	0.021	0.005	0.061	0.087	*J.H.C.Ribeiro* 628

TABLE 1. *(Continued)*

Family	Species	*n*	*F*	*FP*	*AD* (individuals/ha)	*BA* (m^2/ha)	*RD* (%)	*RBA* (%)	*RF* (%)	*IV*	Voucher no.[b]
Asteraceae	*Piptocarpha axillaris* (Less.) Baker	1	1	1	0.5	0.002	0.021	0.005	0.061	0.087	*J.H.C.Ribeiro* 629
Vochysiaceae	*Vochysia magnifica* Warm.	1	1	1	0.5	0.002	0.021	0.005	0.061	0.087	*J.H.C.Ribeiro* 573
Apocynaceae	*Aspidosperma olivaceum* Müll.Arg.	1	1	1	0.5	0.002	0.021	0.004	0.061	0.087	*J.H.C.Ribeiro* 590
Myrtaceae	Myrtaceae sp. 1	1	1	1	0.5	0.002	0.021	0.003	0.061	0.086	*J.H.C.Ribeiro* 575
Solanaceae	Solanaceae sp. 1	1	1	1	0.5	0.002	0.021	0.003	0.061	0.086	*J.H.C.Ribeiro* 589
Celastraceae	*Maytenus* sp. 2	1	1	1	0.5	0.002	0.021	0.003	0.061	0.085	*J.H.C.Ribeiro* 588
Undetermined	Undetermined 6	1	1	1	0.5	0.001	0.021	0.002	0.061	0.084	*J.H.C.Ribeiro* 574
	Total	4673	1648		2336.5	51.074	–	–	–	–	
	Dead	615	97	10	307.5	4.315					

[a] Species ordered by decreasing importance value.
[b] The vouchers are deposited in the Leopoldo Krieger Herbarium (CESJ) and the Laboratory of Plant Ecology, Department of Botany, Federal University of Juiz de Fora, Minas Gerais, Brazil.
AD, absolute density; *BA*, basal area; *F*, frequency in the plots; *FP*, number of forest patches in which the species occurred; *IV*, importance value; *n*, number of individuals; *RBA*, relative basal area; *RD*, relative density; *RF*, relative frequency.

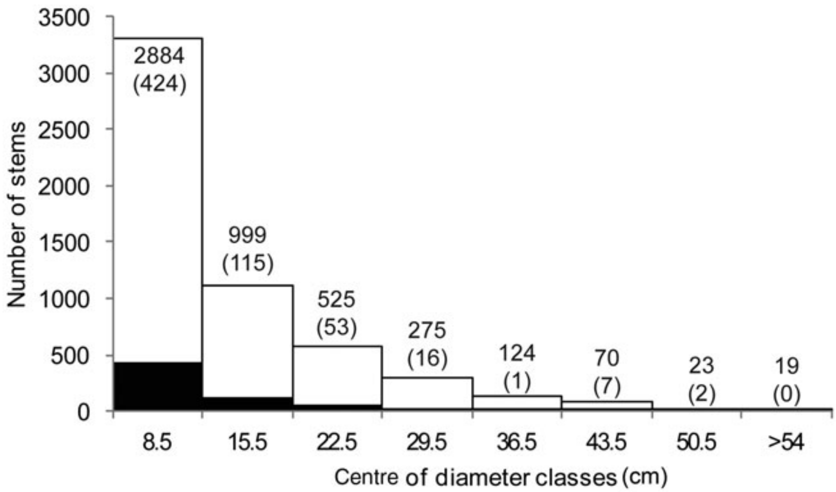

FIG. 3. Distribution of diameter classes for trees with a circumference at breast height ≥ 15 cm in Serra do Papagaio State Park, Minas Gerais, Brazil. White bars represent numbers of live stems, and black bars, numbers of dead stems. Numbers above the bars represent numbers of live stems in each class (the numbers of dead stems in each class are given in parentheses).

were identified at the species level, 10 at the genus level and 4 at the family level; 9 were not identified. Myrtaceae was the richest family, with 18 species, followed by Melastomataceae and Lauraceae (with 7 and 6 species, respectively). The most species-rich genus was *Myrcia* (with 8 species), followed by *Miconia* (5 species) and *Myrceugenia* (4 species).

Four species are considered endangered: *Araucaria angustifolia* (Bertol.) Kuntze, *Dicksonia sellowiana* Hook., *Ocotea odorifera* (Vell.) Rohwer and *Myrceugenia* cf. *bracteosa* (DC.) D.Legrand & Kausel (Martinelli & Moraes, 2013; CNCFlora, continuously updated). Two other species are considered near threatened: *Weinmannia paulliniifolia* Pohl ex Ser. and *Huberia nettoana* Brade (CNCFlora, continuously updated).

Species with higher *IV* in all forests were *Myrcia retorta* Cambess., *Myrceugenia* cf. *bracteosa* and *Myrciaria floribunda* O.Berg, all from the Myrtaceae family, which together account for 30% of *IV*, 29% of total density and 46% of total basal area (Tables 1 and 2). Myrtaceae was the most important family, with 18 species, almost 50% of total density and 61% of total basal area. The distribution of diameter classes shows a reversed-J pattern, with most individuals in the smaller classes (Fig. 3). The average height was 11.2 m, with emergent trees reaching a maximum of 26 m (Fig. 4).

Structure and composition heterogeneity

Densities and basal areas. Table 3 shows the parameters for 10 cloud forest patches. Densities varied from 1995 individuals/ha to 2665 individuals/ha. A Levene test showed

TABLE 2. Structural parameters for the 10 morphospecies with the highest importance values for each tropical montane cloud forest patch in Serra do Papagaio State Park, Minas Gerais, Brazil[a]

Forest patch	Morphospecies	*n*	*F*	*D* (individuals/ha)	*BA* (m^2/ha)	*RD* (%)	*RBA* (%)	*RF* (%)	*IV*
1	*Myrcia retorta*	102	10	510	20.63	19.14	35.60	6.54	61.27
	Myrceugenia cf. *bracteosa*	46	10	230	6.75	8.63	11.65	6.54	26.81
	Myrciaria floribunda	68	10	340	3.51	12.76	6.06	6.54	25.36
	Ilex sp. 1	41	10	205	3.20	7.69	5.53	6.54	19.76
	Miconia pusilliflora	53	8	265	1.10	9.94	1.90	5.23	17.07
	Myrcia pulchra	26	7	130	3.09	4.88	5.33	4.58	14.78
	Lauraceae sp. 1	12	5	60	3.30	2.25	5.69	3.27	11.21
	Psychotria vellosiana	17	7	85	1.34	3.19	2.32	4.58	10.08
	Maytenus sp. 1	14	7	70	1.42	2.63	2.44	4.58	9.65
	Byrsonima ligustrifolia	10	5	50	2.59	1.88	4.47	3.27	9.61
	Others	144	74	720	11.02	27.02	19.02	48.37	94.40
	Total	533	153	2665	57.96	–	–	–	–
2	*Myrcia retorta*	61	9	305	11.49	13.23	22.86	6.29	42.39
	Myrciaria floribunda	93	10	465	5.01	20.17	9.96	6.99	37.13
	Myrceugenia cf. *bracteosa*	35	7	175	4.89	7.59	9.74	4.90	22.22
	Miconia pusilliflora	53	8	265	1.11	11.50	2.21	5.59	19.30
	Ilex sp. 1	22	7	110	4.04	4.77	8.05	4.90	17.71
	Maytenus sp. 1	18	7	90	4.10	3.90	8.16	4.90	16.96
	Myrcia pulchra	18	8	90	1.47	3.90	2.93	5.59	12.43
	Byrsonima ligustrifolia	12	5	60	2.38	2.60	4.74	3.50	10.84
	Myrcia splendens	12	8	60	0.65	2.60	1.30	5.59	9.49
	Nectandra grandiflora	8	2	40	3.13	1.74	6.22	1.40	9.36
	Others	129	72	645	11.98	27.98	23.83	50.35	102.17
	Total	461	143	2305	50.25	–	–	–	–

TABLE 2. *(Continued)*

Forest patch	Morphospecies	*n*	*F*	*D* (individuals/ha)	*BA* (m^2/ha)	*RD* (%)	*RBA* (%)	*RF* (%)	*IV*
3	*Myrcia retorta*	59	10	295	19.09	14.46	38.70	6.33	59.49
	Myrceugenia cf. *bracteosa*	45	9	225	10.00	11.03	20.27	5.70	37.00
	Miconia pusilliflora	48	7	240	0.83	11.76	1.69	4.43	17.89
	Maytenus sp. 1	17	5	85	2.61	4.17	5.28	3.16	12.61
	Siphoneugena crassifolia	20	8	100	1.26	4.90	2.56	5.06	12.52
	Ilex sp. 1	16	7	80	1.58	3.92	3.21	4.43	11.56
	Psychotria vellosiana	24	6	120	0.61	5.88	1.24	3.80	10.92
	Myrcia splendens	20	7	100	0.68	4.90	1.38	4.43	10.71
	Myrcia pulchra	12	7	60	1.63	2.94	3.30	4.43	10.67
	Myrciaria floribunda	14	5	70	1.25	3.43	2.53	3.16	9.13
	Others	133	87	665	9.79	32.60	19.85	55.06	107.51
	Total	408	158	2040	49.34	–	–	–	–
4	*Myrcia retorta*	53	10	265	12.92	11.86	25.40	6.17	43.43
	Myrcia pulchra	47	9	235	6.68	10.51	13.14	5.56	29.21
	Miconia pusilliflora	77	10	385	1.72	17.23	3.38	6.17	26.78
	Myrceugenia cf. *bracteosa*	26	6	130	6.46	5.82	12.70	3.70	22.22
	Myrcia splendens	42	9	210	2.20	9.40	4.33	5.56	19.28
	Myrciaria floribunda	27	8	135	1.40	6.04	2.76	4.94	13.74
	Siphoneugena crassifolia	17	9	85	1.40	3.80	2.76	5.56	12.12
	Ocotea corymbosa	10	6	50	2.91	2.24	5.72	3.70	11.66
	Ilex sp. 1	12	7	60	2.04	2.68	4.02	4.32	11.02
	Alchornea triplinervia	14	6	70	1.51	3.13	2.96	3.70	9.80
	Others	122	82	610	11.62	27.29	22.84	50.62	100.75
	Total	447	162	2235	50.87	–	–	–	–

TABLE 2. *(Continued)*

Forest patch	Morphospecies	*n*	*F*	*D* (individuals/ha)	*BA* (m^2/ha)	*RD* (%)	*RBA* (%)	*RF* (%)	*IV*
5	*Myrcia retorta*	44	9	220	10.00	9.50	26.53	5.59	41.62
	Myrcia splendens	45	10	225	2.02	9.72	5.36	6.21	21.29
	Myrcia laruotteana	47	4	235	3.14	10.15	8.32	2.48	20.96
	Byrsonima ligustrifolia	35	10	175	2.33	7.56	6.19	6.21	19.96
	Myrcia pulchra	30	8	150	3.20	6.48	8.50	4.97	19.95
	Myrceugenia cf. *bracteosa*	25	8	125	3.31	5.40	8.79	4.97	19.16
	Siphoneugena crassifolia	25	9	125	1.52	5.40	4.02	5.59	15.01
	Miconia pusilliflora	31	7	155	0.64	6.70	1.71	4.35	12.75
	Myrceugenia regnelliana	35	4	175	0.90	7.56	2.39	2.48	12.44
	Myrciaria floribunda	13	7	65	1.26	2.81	3.34	4.35	10.49
	Others	133	85	665	9.36	28.73	24.85	52.80	106.37
	Total	463	161	2315	37.68	–	–	–	–
6	*Myrcia retorta*	56	10	280	15.93	12.61	30.42	6.10	49.13
	Myrceugenia cf. *bracteosa*	30	9	150	7.37	6.76	14.07	5.49	26.32
	Myrciaria floribunda	48	9	240	3.07	10.81	5.87	5.49	22.17
	Ilex sp. 1	25	8	125	4.39	5.63	8.38	4.88	18.89
	Miconia pusilliflora	49	7	245	1.28	11.04	2.44	4.27	17.74
	Myrcia splendens	39	9	195	1.59	8.78	3.03	5.49	17.30
	Myrsine gardneriana	19	8	95	1.31	4.28	2.50	4.88	11.66
	Psychotria vellosiana	21	6	105	1.61	4.73	3.08	3.66	11.46
	Cordiera concolor	21	9	105	0.48	4.73	0.91	5.49	11.12
	Siphoneugena crassifolia	14	6	70	1.10	3.15	2.09	3.66	8.90
	Others	122	83	610	14.25	27.48	27.22	50.61	105.31
	Total	444	164	2220	52.36	–	–	–	–

Table 2. *(Continued)*

Forest patch	Morphospecies	*n*	*F*	*D* (individuals/ha)	*BA* (m^2/ha)	*RD* (%)	*RBA* (%)	*RF* (%)	*IV*
7	*Myrcia retorta*	55	10	275	13.12	10.68	26.77	5.41	42.85
	Myrcia pulchra	36	7	180	3.97	6.99	8.10	3.78	18.87
	Ocotea corymbosa	22	9	110	3.83	4.27	7.82	4.86	16.96
	Siphoneugena crassifolia	29	10	145	2.12	5.63	4.32	5.41	15.36
	Miconia pusilliflora	44	9	220	0.85	8.54	1.73	4.86	15.14
	Psychotria vellosiana	34	10	170	1.47	6.60	3.00	5.41	15.01
	Myrciaria floribunda	38	7	190	1.88	7.38	3.83	3.78	15.00
	Myrcia splendens	31	10	155	1.24	6.02	2.53	5.41	13.96
	Ilex sp. 1	21	8	105	2.59	4.08	5.28	4.32	13.68
	Cordiera concolor	35	7	175	0.79	6.80	1.61	3.78	12.19
	Others	170	98	850	17.15	33.01	34.99	52.97	120.98
	Total	515	185	2575	49.00	–	–	–	–
8	*Myrcia retorta*	31	9	155	11.25	6.39	21.16	5.08	32.64
	Eugenia cf. *widgrenii*	48	8	240	4.88	9.90	9.18	4.52	23.59
	Araucaria angustifolia	7	7	35	9.19	1.44	17.28	3.95	22.68
	Myrceugenia cf. *bracteosa*	37	10	185	4.83	7.63	9.08	5.65	22.36
	Myrciaria floribunda	41	9	205	2.72	8.45	5.12	5.08	18.66
	Ilex sp. 1	22	9	110	3.48	4.54	6.55	5.08	16.17
	Myrcia splendens	34	9	170	1.21	7.01	2.28	5.08	14.37
	Cordiera concolor	34	9	170	0.70	7.01	1.33	5.08	13.42
	Byrsonima ligustrifolia	17	7	85	2.23	3.51	4.19	3.95	11.65
	Roupala montana	12	6	60	2.18	2.47	4.10	3.39	9.97
	Others	202	94	1010	10.49	41.65	19.73	53.11	114.48
	Total	485	177	2425	53.17	–	–	–	–

TABLE 2. *(Continued)*

Forest patch	Morphospecies	*n*	*F*	*D* (individuals/ha)	*BA* (m^2/ha)	*RD* (%)	*RBA* (%)	*RF* (%)	*IV*
9	*Myrcia retorta*	91	10	455	23.22	17.57	41.80	6.06	65.43
	Myrciaria floribunda	90	10	450	4.78	17.37	8.60	6.06	32.04
	Ilex sp. 1	36	10	180	5.04	6.95	9.08	6.06	22.09
	Miconia pusilliflora	46	9	230	1.39	8.88	2.51	5.45	16.84
	Siphoneugena crassifolia	25	10	125	1.79	4.83	3.23	6.06	14.11
	Cabralea canjerana	15	8	75	2.68	2.90	4.82	4.85	12.56
	Myrceugenia cf. *bracteosa*	11	8	55	2.74	2.12	4.94	4.85	11.91
	Myrcia splendens	26	7	130	0.89	5.02	1.61	4.24	10.87
	Cordiera concolor	21	5	105	0.64	4.05	1.16	3.03	8.24
	Psychotria vellosiana	11	8	55	0.40	2.12	0.71	4.85	7.69
	Others	146	80	730	11.97	28.19	21.55	48.48	98.22
	Total	518	165	2590	55.55	–	–	–	–
10	*Myrcia retorta*	38	10	190	16.24	9.52	29.77	5.56	44.85
	Ilex sp. 1	31	10	155	6.39	7.77	11.72	5.56	25.04
	Myrceugenia cf. *bracteosa*	23	9	115	6.16	5.76	11.29	5.00	22.06
	Myrcia pulchra	19	8	95	3.69	4.76	6.77	4.44	15.97
	Myrciaria floribunda	28	9	140	1.15	7.02	2.11	5.00	14.13
	Ocotea corymbosa	19	8	95	2.08	4.76	3.82	4.44	13.02
	Miconia pusilliflora	26	9	130	0.66	6.52	1.22	5.00	12.73
	Drimys brasiliensis	24	8	120	0.92	6.02	1.69	4.44	12.15
	Myrcia splendens	24	8	120	0.58	6.02	1.06	4.44	11.52
	Myrsine gardneriana	14	7	70	1.52	3.51	2.79	3.89	10.19
	Others	153	94	765	15.15	38.35	27.77	52.22	118.34
	Total	399	180	1995	54.55	–	–	–	–

[a] Species ordered by decreasing importance value.
BA, basal area; *D*, density; *F*, frequency in the plots; *IV*, importance value; *n*, number of individuals; *RBA*, relative basal area; *RD*, relative density (%); *RF*, relative frequency (%).

TABLE 3. Structural parameters of 10 cloud forest patches in Serra do Papagaio State Park, Minas Gerais, Brazil

Forest patch	Mean altitude (m a.s.l.)	No. of morphospecies	*n*	*D* (individuals/ha)	$\overline{D}$	*D* (SD)	*BA* (m^2/ha)	$\overline{BA}$	*BA* (SD)
All	1922	89	4673	2337	46.7	12.5	51.074	1.022	0.240
1	1909	39	533	2665	53.3	24.4	57.964	1.159	0.149
2	1902	37	461	2305	46.1	8.8	50.254	1.005	0.243
3	1893	46	408	2040	40.8	11.1	49.344	0.987	0.238
4	1919	42	447	2235	44.7	10.4	50.867	1.017	0.207
5	1931	45	463	2315	46.3	8.1	37.678	0.754	0.277
6	1909	38	444	2220	44.4	6.4	52.364	1.047	0.179
7	1898	49	515	2575	51.5	13.2	48.998	0.980	0.129
8	1965	45	485	2425	48.5	10.9	53.169	1.064	0.281
9	1941	39	518	2590	51.8	12.8	55.548	1.111	0.227
10	1955	45	399	1995	39.9	7.3	54.550	1.091	0.275

BA, basal area; $\overline{BA}$, mean basal area/plot; *BA* (SD), basal area/plot standard deviation; *D*, density; $\bar{D}$, mean density/plot; *D* (SD), density/plot standard deviation; *n*, number of individuals.

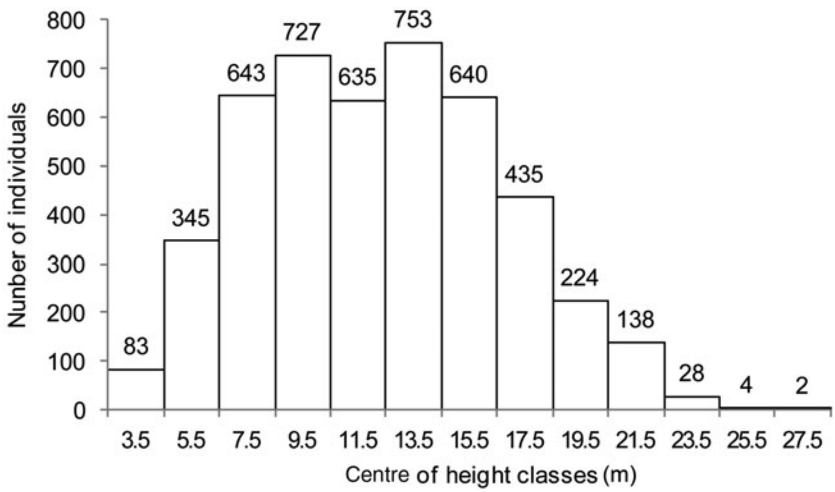

FIG. 4. Distribution of height classes for live trees with a circumference at breast height ≥ 15 cm in Serra do Papagaio State Park, Minas Gerais, Brazil. Numbers above the bars represent numbers of live trees in each class.

that the variances were not homogeneous ($F = 2.099$, $DF = 9$, $P = 0.037$). The Kruskal–Wallis test showed no significant differences between the 10 cloud forest patches (k = 9.773, $DF = 9$, $P = 0.369$).

Basal areas varied from 37.68 m^2/ha to 57.96 m^2/ha. A Levene test showed homogeneous variances ($F = 0.734$, $DF = 9$, $P = 0.676$), and residuals were normally distributed according to the Shapiro–Wilk normality test ($W = 0.987$, $DF = 9$, $P = 0.446$). The ANOVA test showed significant differences between at least two forest patches ($F = 2.371$, $DF = 9$, $P = 0.018$). The Tukey test showed that only forest patch 5 had significantly lower basal areas when compared with forest patch 1 ($P = 0.004$), forest patch 9 ($P = 0.038$) and forest patch 10 ($P = 0.021$). All other comparisons were not significantly different ($P > 0.05$).

Richness and composition. A total of 89 morphospecies were found in all forest patches. Richness varied from 37 to 49 morphospecies in each forest patch. Figure 5 shows rarefaction/extrapolation curves for all forest patches studied. The curves show a tendency towards stabilisation and are visually very similar. When comparing the rarefaction curves, the ecological null hypothesis (i.e. that samples were drawn from the same underlying assemblage and therefore have similar composition, species richness and relative abundance) was rejected (Z = 23,253.82, $P = 0.001$). However, the biogeographical null hypothesis (i.e. that samples were drawn from assemblages that share similar species richness and relative abundance but not necessarily the same composition) was accepted (Z = 59,916.09, $P = 0.291$).

Similarity indices were high for both incidence and abundance data (Table 4). Values for the Jaccard index varied from 0.42 to 0.65, and values for the Bray–Curtis index

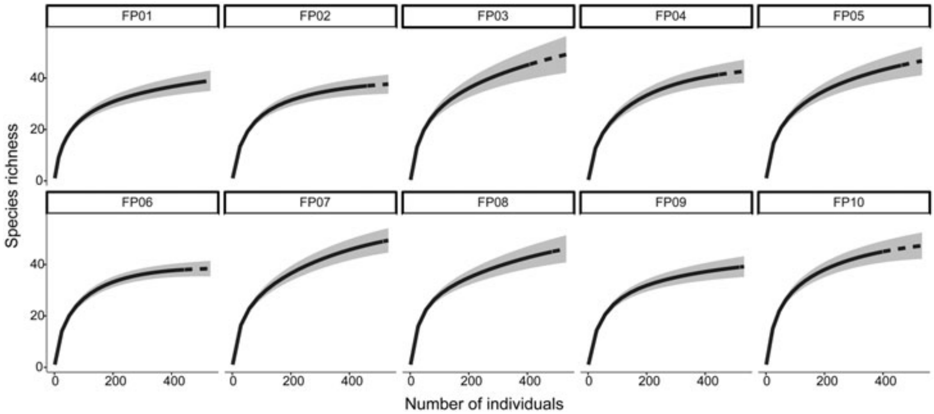

FIG. 5. Rarefaction/extrapolation curves for 10 tropical montane cloud forest patches in Serra do Papagaio State Park, Minas Gerais, Brazil. Curves were extrapolated to the number of individuals in the forest patch with the most individuals (i.e. 533 individuals). Solid line, rarefaction portion of the curve; dashed line, extrapolation portion of the curve; grey area, confidence interval.

TABLE 4. Similarity indices between 10 cloud forest patches in Serra do Papagaio State Park, Minas Gerais, Brazil[a]

	FP 1	FP 2	FP 3	FP 4	FP 5	FP 6	FP 7	FP 8	FP 9	FP 10
FP 1	–	0.75	0.70	0.63	0.50	0.70	0.65	0.51	0.73	0.60
FP 2	0.62	–	0.70	0.63	0.52	0.72	0.63	0.58	0.73	0.67
FP 3	0.57	0.54	–	0.66	0.58	0.73	0.66	0.52	0.62	0.64
FP 4	0.59	0.61	0.54	–	0.66	0.72	0.69	0.55	0.61	0.65
FP 5	0.42	0.55	0.54	0.55	–	0.59	0.57	0.53	0.51	0.58
FP 6	0.51	0.60	0.53	0.63	0.54	–	0.72	0.68	0.74	0.71
FP 7	0.57	0.56	0.53	0.60	0.47	0.55	–	0.60	0.67	0.65
FP 8	0.53	0.55	0.52	0.53	0.55	0.63	0.52	–	0.55	0.65
FP 9	0.53	0.62	0.55	0.65	0.58	0.60	0.57	0.56	–	0.63
FP 10	0.53	0.55	0.49	0.61	0.50	0.51	0.57	0.55	0.65	–

[a] Top right values correspond to Bray–Curtis similarity index for abundance data. Bottom left values correspond to Jaccard similarity index for incidence data.
FP, forest patch.

from 0.50 to 0.75. Although similarity indices were high, the MRPP analysis showed significant differences between forest patches for the Jaccard similarity index (delta = 0.567, $P = 0.001$, $A = 0.069$) and the Bray–Curtis similarity index (delta = 0.716, $P = 0.001$, $A = 0.046$).

DISCUSSION

Floristic composition and structure

The floristic composition of TMCFs in Serra do Papagaio State Park is similar to the patterns found in high-altitude forests in Southeast Brazil. The richest families found

(Myrtaceae, Melastomataceae and Lauraceae) were identified by Oliveira-Filho and Fontes (2000) as the most important families in terms of species numbers for high-altitude rain forests of the Atlantic Domain in Southeast Brazil. Myrtaceae was also found to be one of the most important families in other studies of cloud forests of Southeast Brazil (França & Stehmann, 2004; Carvalho *et al.*, 2005; Pereira *et al.*, 2006; Meireles *et al.*, 2008; Valente *et al.*, 2011; Pompeu *et al.*, 2014). The same pattern was observed for the richest genera, with *Myrcia*, *Miconia* and *Myrceugenia* among the most important genera for high-altitude rain forests of the Atlantic Domain (Oliveira-Filho & Fontes, 2000).

Of the species sampled, 10 were identified by Oliveira-Filho and Fontes (2000) as associated with high-altitude forests in the Atlantic Forest Domain: *Clethra scabra* Pers., *Drimys brasiliensis* Miers, *Laplacea fruticosa* (Schrad.) Kobuski, *Myrcia laruotteana* Cambess., *Myrsine lancifolia* Mart., *Nectandra grandiflora* Nees & Mart., *Pimenta pseudocaryophyllus* (Gomes) Landrum, *Schefflera* cf. *calva* (Cham.) Frodin & Fiaschi, *Symplocos celastrinea* Mart. and *Weinmannia paulliniifolia*. Bertoncello *et al*. (2011) also identified *Drimys brasiliensis* and *Weinmannia paulliniifolia* as indicator species for cloud forests in South and Southeast Brazil. They also indicated that *Pimenta pseudocaryophyllus*, *Rhamnus sphaerosperma* Sw. and *Symplocos falcata* Brand were preferential species of cloud forests.

Six species were considered to be under some degree of threat. Of these, five occurred at densities of less than 20 individuals/ha (see Table 1). The exception was *Myrceugenia* cf. *bracteosa*, which occurred at high densities and so deserves special attention. According to Martinelli and Moraes (2013) and CNCFlora (continuously updated), this species occurs at very low densities, about three individuals per hectare. Pompeu *et al*. (2014) also found *Myrceugenia bracteosa* at low densities, 13.3 individuals/ha, in an upper montane forest near Serra do Papagaio State Park (Itamonte, Minas Gerais). In contrast, in this study we found a density of 146.5 individuals/ha, and Santana *et al.* (in press) found a density of 498 individuals/ha in another mixed rain forest in Serra do Papagaio State Park. However, the identification of *Myrceugenia* species is very difficult, and the latest taxonomic revision was in 1981 (Landrum, 1981). It is possible that other populations, with more individuals, are still unknown or have been misidentified. Rather than casting doubt on the need to protect this species, our results show the importance of Serra do Papagaio State Park for its conservation and highlight the pressing need for more studies on the taxonomy and distribution of *Myrceugenia* species as well as other taxa typical of upper montane forests that are still poorly known.

The forest patch structure is similar to other TMCFs, especially UMCFs, with high stem densities, low canopy heights and few emergent trees (Scatena *et al.*, 2010; Fahey *et al.*, 2016). Species richness and density values were close to those observed in other high-altitude forests in Southeast Brazil, and basal area was among the highest observed (Table 5). Other features of UMCFs were observed in the field, such as abundant and diverse vascular and non-vascular epiphytes, very few climbers, and few species with compound leaves (only 9 of the 89 species found have compound leaves) (Scatena *et al.*, 2010). However, multistemmed and twisted trees, another typical

TABLE 5. Comparison of species richness and structural parameters between selected areas of high-altitude forests in Minas Gerais, Southeast Brazil

Location	Reference	Altitude (m)	*CBH* (cm)	Total sampled area (ha)	Species richness	*D* (individuals/ha)	*BA* (m^2/ha^{-1})
Bocaina de Minas	Carvalho *et al.* (2005)	1285	15.7	1.04	158	2475.00	33.27
Poços de Caldas	Costa *et al.* (2011)	1380	15.7	1.10	156	1784.55	29.85
Camanducaia	Meireles *et al.* (2008)	1880	15.0	0.35	64	3402.86	37.68
Camanducaia	França & Stehman (2004)	1900	15.0	0.75	58	1837.33	55.52
Itamonte	Pompeu *et al.* (2014)	1900	15.7	0.60	89	2083.33	33.00
Baependi	This work	1922	15.5	2.00	89	2337.00	51.07

BA, basal area; CBH, minimum circumference at breast height used; *D*, density.

feature of TMCFs (Fahey *et al.*, 2016), were rarely observed (only 120 individuals, 2.6% of all individuals sampled, had two or more stems at 1.3 m above ground). Bellingham and Sparrow (2009) explain that the prevalence of multistemmed trees in montane rain forests can be related to low soil nutrient content and disturbance (such as wind storms and fires). The positions of the forest patches studied, in valleys and associated with springs and small rivers, could favour the prevalence of single-stemmed trees by allowing accumulation of organic matter in the soil and providing protection against wind storms and fires.

Structure and composition heterogeneity

Tests showed no significant difference in densities and basal areas between forest patches. When comparing rarefaction/extrapolation curves, the two tests showed different results. Cayuela *et al.* (2015) explain that the ecological null hypothesis test is sensitive to floristic composition, whereas the biogeographical null hypothesis test is influenced only by richness and relative abundance. Therefore, there is no significant difference in richness between forest patches. Although MRPP showed significant differences between forest patches, the size effect measured by coefficient A was very small, and the differences observed between forest patches can be considered to be without ecological significance (McCune & Grace, 2002).

Therefore, we reject the initial hypothesis that TMCF patches could be highly heterogeneous even at the small geographical scale studied here, because the forest patches were very similar in terms of stem density, basal area, richness and composition. This could be due to the small distance between the forest patches and their similar environmental conditions (similar altitudes and position on the landscape). However, spatial structure could explain only 11% of tree community data, and spatial autocorrelation seems not to be a problem (Ribeiro, 2018). Other studies that showed heterogeneity between TMCFs usually compared areas on a broader geographical scale or at different altitudes with different environmental conditions (Pereira *et al.*, 2006; Meireles *et al.*, 2008; Meireles & Shepherd, 2015). Ongoing studies relating soil properties to the structure and composition of the 10 forest patches studied, as well as monitoring of the forest dynamics in the permanent plots established by the current study, may contribute to the elucidation of these patterns.

Final Considerations

The forest patches studied in Serra do Papagaio State Park showed a similar structure and composition to other TMCFs, especially UMCFs, of Southeast Brazil. Structurally, the 10 forest patches were uniform in terms of stem density, basal area, and species richness and composition. TMCFs of Serra do Papagaio State Park are of particular interest for conservation, because they contain important populations of threatened species. This study was the first to investigate tree composition and structure of TMCFs in Serra do Papagaio State Park, and the data can be used as a reference for conservation and restoration projects of TMCFs in the region. The monitoring of the permanent plots established by this study will contribute to a better understanding of TMCF dynamics and responses to incoming threats.

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