



Species diversity, community structure and ecological traits of trees in an upper montane forest, southern Brazil

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ABSTRACT

Upper montane ecosystems in Brazil are little known, and their structural and functional aspects poorly understood. Our goals were to describe tree species diversity and community structure, and to characterize tree species in relation to their ecological traits, phytogeographic history and conservation status in an upper montane araucaria forest remnant. A total of 26 species belonging to 18 families were found in a 1-hectare permanent plot. The tree community mainly comprised trees with diameters of less than 20 cm and heights of between 6.5 and 9.5 m. *Drimys angustifolia* and *Myrceugenia regnelliana* had the highest importance values. Most species were shade tolerant while most individuals were pioneers. Most species and individuals presented zoophily and zoochory. Most sampled species and individuals were related to araucaria forests. Seven species are threatened to some degree while one species, *Crinodendron brasiliensis*, besides threatened, is also endemic to the region. The presence of endemic and endangered species demonstrates that the studied area serves important conservation purposes. Furthermore, the present study demonstrates the important role that upper montane regions have for conservation and describes the structural patterns of still poorly studied habitats, reinforcing the importance such systems have in maintaining species diversity at high elevations.

Keywords: Araucaria forest, conservation, diversity, ecological traits, floristics, mixed rainforest, permanent plots, phytogeography, PPBio, upper montane

Introduction

Understanding aspects related to diversity, forest community structure and dynamics are essential for supporting conservation policies and monitoring biodiversity (Brito *et al.* 2007). Also, diversity-related aspects, such as species ecological traits and phytogeographic history, are key to comprehending ecological and organizational processes

of plant communities. Thus, combining information about diversity, structure and ecological traits may result in a better understanding of ecological systems than evaluating this information separately. However, baseline studies on diversity and structure are still lacking to properly characterize Brazilian ecosystems, especially those located in regions that are difficult to access, such as montane environments in southern Brazil.

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Montane environments occur globally, usually above 500 m a.s.l. (Meybeck *et al.* 2001). Of all tropical forests, these environments are among the most poorly known and most threatened, and usually have high levels of endemism (Gentry 1995). In subtropical Brazil, araucaria forests (mixed rainforests) occur mainly on the southern Brazilian plateau (Veloso *et al.* 1991), at altitudes ranging from 500 m to 1,800 m a.s.l. (Reitz & Klein 1966). In these forests, the conifer *Araucaria angustifolia* (hereafter “araucaria”) frequently abounds and dominates the tree stratum (Klein 1984). At higher altitudes (above 900 m a.s.l.), these forests frequently form mosaics with grasslands (Rambo 1994). Nowadays, araucaria forest occupies around 12 % of its original area (Ribeiro *et al.* 2009; Reis *et al.* 2014) and *Araucaria angustifolia* is at risk of extinction (Thomas 2013).

Processes and patterns that generate and maintain the biodiversity of Brazilian upper montane systems (above 1,200 m a.s.l.) are little known since structural and functional aspects of these areas are still poorly understood (Vibrans *et al.* 2008). Therefore, considering the idiosyncrasies of upper montane ecosystems, the high levels of endemism, the threats and the need to increase knowledge about these systems, our objectives were (1) to describe the species diversity and community

structure of trees, and (2) to characterize species in relation to their ecological traits, phytogeographic history (migration routes) and conservation status, in a permanent plot in an upper montane araucaria forest remnant.

Materials and methods

Study area

The study was conducted in the highlands of a subtropical rainforest in São Joaquim National Park, a protected area located in Santa Catarina State, southern Brazil (28°8'4”S 49°28'47” W) (Fig. 1). The park protects high-altitude grasslands, mixed rainforest (araucaria forest) and subtropical rainforest, all belonging to Atlantic Forest domain (Veloso *et al.* 1991). At higher elevations, the climate between 1961 and 2016, recorded by the nearest weather station (ca. 30 km), was characterized by an annual mean rainfall of 1,626.3 mm.yr⁻¹, equally distributed throughout the year, and an annual mean temperature of 13.3 °C. The average minimum temperature for the coldest month (July) was 6.0 °C and the average maximum temperature for the hottest month (January) was 22.9 °C (INMET 2017).

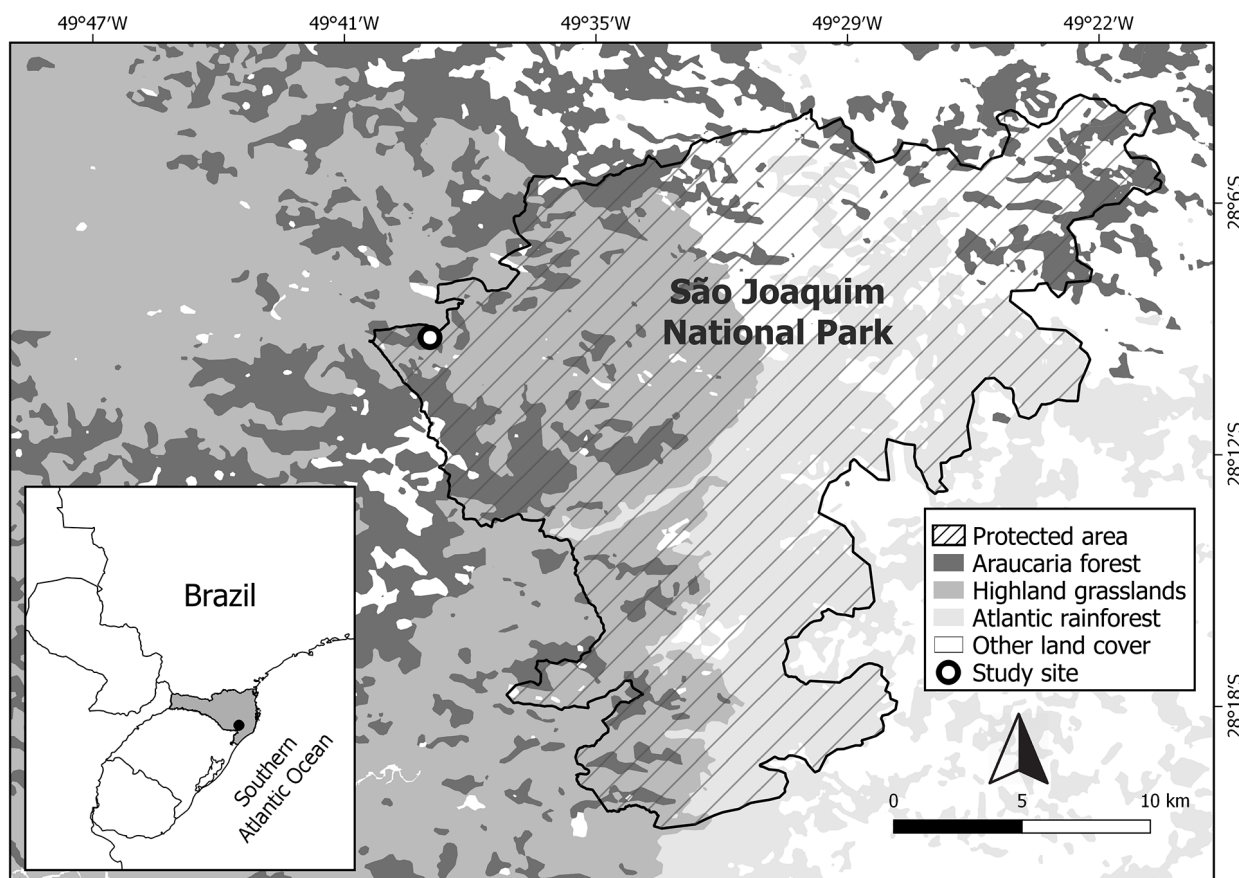


Figure 1. Location of the study area in an upper montane araucaria forest, southern Brazil.

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Due to its importance and uniqueness, permanent plots have been installed in this protected area to allow long-term ecological research (<http://ppbio.inpa.gov.br/Port/sitioscoleta>). These permanent plots and studies are linked to the Biodiversity Research Program (Programa de Pesquisa em Biodiversidade – PPBio) created in 2004 by the Brazilian Ministry of Science and Technology. The implemented methodology (more info at: Fernandes *et al.* 2017) has allowed for studies with different temporal and spatial scales and, thus, contributes to what is known about the ecological responses and degree of vulnerability of the biodiversity to effects of landscape changes over time. This study was conducted in the plot TN3500, in Module 1. The vegetation is characterized as upper montane araucaria forest and was possibly influenced by cattle until 2008, when the area was protected. Fire and cattle grazing are part of the common land management practices in the region (Sühs *et al.* 2018). There are, however, reports of cattle influencing the area after it was protected. In general, soils in this region are shallow and usually Cambisols and Litholic Neosols (Higuchi *et al.* 2013), which have low fertility and high aluminum saturation. The plot has an average inclination of ca. 22° and faces southwest.

Data collection

Species diversity and community structure

To describe the species diversity and community structure, a 1-hectare permanent plot was built from a central line 250 m long; permanent pickets were placed every 10 m. The line was set at a point with a known altitude (in this case 1,590 m a.s.l.) and held constant at the contour curve throughout its entire length. Data collection of community structure followed the methodology in Castilho *et al.* (2014), adapted to the Atlantic Forest domain. We measured diameter at breast height (DBH - 1.3 m height) and estimated the height of all individuals.

Two bands (2 and 3) were delimited upstream and downstream on both sides of the central line. Each band was 10 m wide and 250 m long (0.25 ha). The inclusion criterion for band 2 (0 to 10 m away from the central line) was DBH \geq 5 cm. For band 3 (10 to 20 m from the central line), the inclusion criterion was DBH \geq 10 cm. The total sampling area was 1 ha (0.5 ha for each band). For this study, the area within each demarked picket was considered a subplot, totaling 25 subplots of 10 x 20 m. (Fig. 2).

Sampled species were collected and incorporated into the herbarium FLOR (Federal University of Santa Catarina) if they were in a reproductive state. The classification of plant families follows the Angiosperm Phylogeny Group (APG IV 2016) for angiosperms, Christenhusz *et al.* (2011) for gymnosperms and Smith *et al.* (2006) for arborescent ferns (monilophytes). For the scientific nomenclature of species, we followed the Taxonomic Name Resolution

Service (<http://tnrs.iplantcollaborative.org/TNRSapp.html>).

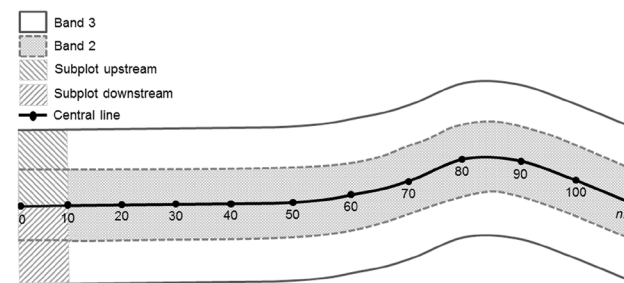


Figure 2. Schematic representation of the plot sampled in an upper montane araucaria forest, southern Brazil.

Ecological traits and phytogeographic history

To have a better understanding of the studied system, we characterized species in relation to their ecological traits, phytogeographic history and conservation status. We classified the species into ecological groups of vertical distribution, light requirement, pollen and diaspore dispersal and phytogeographic history. The classification of each species into these groups was based on observations during fieldwork (from 2015 to 2017), scientific literature and consultations with specialists.

Vertical distribution was based on the strata commonly reached by mature individuals of each species, as proposed by Swaine & Whitmore (1988), but slightly modified to adjust to lower average heights reached by individuals in upper montane araucaria forests (Oliveira-Filho *et al.* 1994). The categories were: “small tree species” (s), which includes trees < 6 m tall; “medium tree species” (m) \geq 6 < 11 m tall; “tall tree species” (t) \geq 11 < 16 m tall; and “emergent tree species” (e) \geq 16 m tall.

Regarding the light requirements for seed germination and establishment, species were classified into two main categories: “pioneer,” which includes species with an entirely heliophilous life cycle, forming a seed bank but no bank of juveniles; and “late successional,” which includes species that can germinate and become established under different shade levels to form a bank of juveniles (Swaine & Whitmore 1988). We divided the latter category into two subcategories, “shade tolerant” and “light-demanding late successional” species (Oliveira-Filho *et al.* 1994; Budke *et al.* 2010).

To determine the potential pollen dispersal agent based on flower and pollen morphology (Fægri & Pijl 1979), species were classified into two main groups of potential pollen dispersal agent: (a) abiotic (*e.g.*, wind, water) and biotic (*i.e.*, animals). Wind-pollinated species usually have flowers (angiosperms) / cones (conifers) without attractants and pollen adaptations (*e.g.*, lightweight, air-sacs), which differ from animal-pollinated species that usually have heavier, stickier and protein-rich pollen and colored flower parts for animal attraction (Fægri & Pijl 1979).



To determine diaspore dispersal strategy, species were grouped into categories based on diaspore morphology (Pijl 1982). The categories were the following: (a) “anemochorous” and “hydrochorous,” in which diaspores have winged structures or are small enough to be blown away by the wind or can float on water; (b) “autochorous,” which have diaspores dispersed by fruit explosion or by gravity; and (c) “zoochorous,” which have diaspores with attractants and/or food sources used to attract animals. The latter group was further classified into two subgroups based on diaspore size and color (Hoffmann *et al.* 1989), because small and dark colored diaspores (< 15 mm wide) may be preferentially dispersed by small animals (*e.g.*, frugivorous birds and bats) and larger and light-colored diaspores (>15 mm wide) may be preferentially dispersed by larger vertebrates (*e.g.*, medium-sized birds, bats, rodents and extinct megafauna). We emphasize that the absence of an obvious dispersal mechanism of a diaspore does not prevent other agents to act as dispersers (Howe & Smallwood 1982). Dispersal process studies are advisable to confirm such conjectures.

Species were categorized according to their phytogeographic history (migration routes to southern Brazil - Jarenkow & Waechter 2001) and were thus classified into four groups: Atlantic corridor (ATL), Paraná and Uruguai river basins (BPU), araucaria forests (ARA) and widely distributed (EAD). Categorization and species classification mainly follow Rambo (1951; 1961), Jarenkow & Waechter (2001), Budke *et al.* (2004), Lindenmaier & Budke (2006), Sühs *et al.* (2010) and Sühs & Budke (2011).

Additionally, species were classified according to their conservation status, based on regional (Consema 2014), national (Brazilian Official List- BRASIL 2014) and global (IUCN Red List - <http://www.iucnredlist.org/>) lists. We only focused on species with some degree of extinction risk, *i.e.*, those classified as data deficient (DD) or of least concern (LC), based on IUCN (2018) guidelines, were left out.

Data analysis

We used descriptive statistics to describe community structure and ecological characteristics. To evaluate the structure, we measured the density, dominance, frequency and importance value of the sampled species (Mueller-Dombois & Ellenberg 1974). We built histograms to express diameter and height classes (5 cm and 1 m intervals, respectively) of sampled individuals (Sühs & Budke 2011). Species diversity and evenness were evaluated through Shannon's diversity (entropy) index (H') and Pielou's evenness index (J'), respectively (Magurran 1988). Additionally, we exponentiated the value of H' to obtain the true diversity (effective number of species), which

allows for comparing diversities of different communities (Jost 2006). We used rarefaction curves to visualize the completeness of sampling and extrapolate species richness in our phytosociological subplots (Chao *et al.* 2014). For extrapolation, we used 95 % confidence intervals generated by 1,000 bootstrap resamplings (Colwell *et al.* 2012). Curves were extrapolated up to double our sample size. These analyses were performed with the iNEXT package (Hsieh & Chao 2016) in the R statistical programming language (R Development Core Team 2016).

Results

We sampled 1,208 trees (1,127 alive and 81 dead standing) belonging to 26 species within 20 genera and 18 families (one fern, two gymnosperms and 23 angiosperms) (Tab. 1). The most representative family was Myrtaceae (seven spp.), followed by Lauraceae (two spp.) and Symplocaceae (two spp.). The most representative genus was *Myrceugenia* (six spp.). The species with the highest importance values (IVs) were *Drimys angustifolia* (IV = 22.4), *Myrceugenia regnelliana* (IV = 15.3), *Myrceugenia myrcioides* (IV = 7.4), *Araucaria angustifolia* (IV = 7.2) and *Ilex microdonta* (IV = 6.7), which together account for 70 % of sampled individuals. These species are among the five with highest values of density and frequency. Only *I. microdonta* is not among the five most dominant species; it was surpassed by *Crinodendron brasiliense* for this parameter. Ten species had less than five individuals sampled, accounting together for 2 % of sampled individuals. The total basal area was 47.3 m².ha⁻¹ (\pm 0.05).

Regarding the diametric structure of the studied community, 20 % of individuals had a DBH < 10 cm, 60 % of individuals had a DBH < 20 cm and 2 % had a DBH > 50 cm (Fig. 3A). The average diameter value was 19.4 cm (\pm 11 cm) and the maximum recorded diameter was 62.7 cm. In relation to the frequency distribution of height classes, the average value was 7.7 m (\pm 2.6 m). Fifty percent of sampled individuals were between 6.5 and 9.5 m tall and the tallest individuals did not exceed 17 m (Fig. 3B).

Regarding the vertical distribution of species, small trees comprised 23 % of the species (2 % sampled individuals), medium and tall trees accounted for 35 % and 39 %, respectively (29 % and 64 % of sampled individuals, respectively), and one species was categorized as emergent (5 % of individuals) (Fig. 4A). *Dicksonia sellowiana* was the most abundant small tree species (nine individuals), *M. regnelliana* was the most abundant medium tree species (262 individuals) and *D. angustifolia* was the most abundant tall tree species (362 individuals). *Araucaria angustifolia* was the only species considered as emergent and had 60 sampled individuals.



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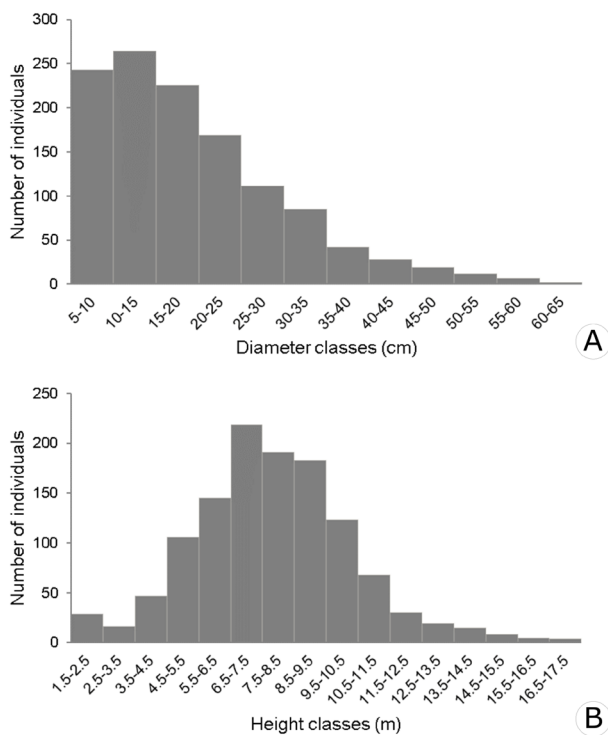


Figure 3. Diameter (A) and height classes (B) of trees in an upper montane araucaria forest, southern Brazil

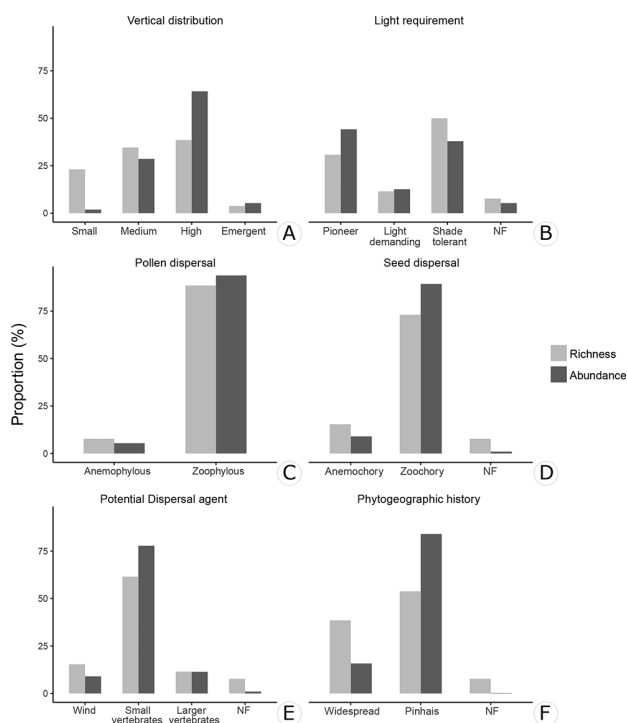


Figure 4. Ecological traits (A–E) and phylogeographic history (F) of trees in an upper montane araucaria forest, southern Brazil. Tree ferns were not included in the pollen transport and dispersal categories. Standing dead individuals were left out of this analysis. NF = not found.

Regarding light requirements for seed germination and establishment, eight species were classified as pioneers and three species as light demanding, corresponding to 43% and 57% of sampled individuals. Half of the sampled species (13) were classified as shade tolerant, corresponding to 38% of sampled individuals (Fig. 4B).

In relation to pollen dispersal, a larger part of the species has small flowers (< 20 mm in diameter) and the main visual structure (e.g., petals) is usually light colored. The colors white, beige and yellow were predominant (Tab. S1 in supplementary material). Thus, zoophily was the main pollen dispersal syndrome, represented by 23 species (89%) and 94% of the sampled individuals (Fig. 4C). Only *A. angustifolia* and *Baccharis* sp. (5% of sampled individuals) are wind pollinated. Similarly, 19 species (74%) represented by 90% of sampled individuals had fleshy diaspores and were classified as zoochorous species (Fig. 4D). Apart from *A. angustifolia* seeds, the fleshy diaspores are predominantly small (11.5 ± 5.3 mm x 7.78 ± 3.4 mm) and dark colored (purple to black when ripe). Sixteen species (62%) representing 78% of sampled individuals are potentially dispersed by small vertebrates, such as frugivorous birds and bats, while three species (12%) representing 11% of sampled individuals are potentially dispersed by larger vertebrates. Four species (15%) represented by 9% of sampled individuals had non-fleshy diaspores and are mainly dispersed by wind (Fig. 4E).

The evaluated community was composed mainly of species related to araucaria forests (54%), represented by 84% of sampled individuals, and widespread species (38%), represented by 16% of sampled individuals (Fig. 4F). We did not find any species from the Paraná River basin, Uruguai River basin and Atlantic contingents.

The rarefaction curve showed that when reaching the observed 26 species in 25 subplots, the lower and upper 95% confidence intervals were 23 and 29 species, respectively. The extrapolation demonstrates that by doubling the sample effort (50 subplots of 10 x 20 m), the expected number of species would be 30 species (lower and upper 95% confidence intervals of 24 and 35 species, respectively) (Fig. 5). Shannon's diversity (entropy) index (H') was 2.30 nats/ind⁻¹ and Pielou's evenness index (J') was 0.70. The true diversity of the sampled permanent plot is 10 species. The group of dead trees ranked fifth for the importance value (6.7%).

Seven species (17.6% of sampled individuals) are under some degree of threat. *Araucaria angustifolia* is considered critically endangered in Santa Catarina State (Consema 2014), endangered in Brazil (Brasil 2014) and classified as critically endangered on the world list (Thomas 2013). *Dicksonia sellowiana* is considered critically endangered in Santa Catarina State (Consema 2014) and endangered in



Table 1. Phytosociological parameters of the sampled species in an upper montane araucaria forest, southern Brazil. AD = absolute density (individuals.ha⁻¹); RD = relative density (%); ADo = absolute dominance (m².ha⁻¹); RDo = relative dominance (%); AF = absolute frequency (%); RF = relative frequency (%); IV = importance value (%); DBH max = maximum value of diameter at breast height (cm) and H max = maximum estimated height (m). Decreasing order of IV (alive individuals), followed by dead trees.

Family	Species	AD	RD	ADo	RDo	AF	RF	IV	DBH max	H max
Winteraceae	<i>Drimys angustifolia</i> Miers	362	29.97	13.35	28.23	100.00	9.00	22.40	58.78	14
Myrtaceae	<i>Myrceugenia regnelliana</i> (O.Berg) D. Legrand & Kausel	262	21.69	7.25	15.33	100.00	9.00	15.34	52.78	10.5
Myrtaceae	<i>Myrceugenia myrcioides</i> (Cambess.) O.Berg	65	5.38	4.09	8.64	92.31	8.30	7.44	62.71	12
Araucariaceae	<i>Araucaria angustifolia</i> (Bertol.) Kuntze	60	4.97	4.48	9.46	80.77	7.27	7.23	56.02	17
Aquifoliaceae	<i>Ilex microdonta</i> Reissek	90	7.45	2.25	4.76	88.46	7.96	6.73	48.29	16
Elaeocarpaceae	<i>Crinodendron brasiliense</i> Reitz & L.B.Sm.	59	4.88	3.71	7.84	73.08	6.57	6.44	57.33	16
Cunoniaceae	<i>Weinmannia humilis</i> Engl.	40	3.31	3.16	6.69	69.23	6.23	5.41	59.98	13
Lauraceae	<i>Ocotea pulchella</i> (Nees & Mart.) Mez	50	4.14	1.90	4.01	65.38	5.88	4.68	49.18	14
Celastraceae	<i>Maytenus boaria</i> Molina	29	2.40	0.95	2.00	53.85	4.84	3.08	36.99	15
Rosaceae	<i>Prunus myrtifolia</i> (L.) Urb.	15	1.24	0.66	1.41	38.46	3.46	2.04	34.7	12
Dicksoniaceae	<i>Dicksonia sellowiana</i> Hook.	9	0.75	0.97	2.06	26.92	2.42	1.74	59.62	5.5
Myrtaceae	<i>Myrceugenia oxysepala</i> (Burret) D. Legrand & Kausel	20	1.66	0.16	0.34	34.62	3.11	1.70	29.1	9
Myrtaceae	<i>Myrrhinium atropurpureum</i> Schott	12	0.99	0.28	0.59	34.62	3.11	1.57	46.03	11
Anacardiaceae	<i>Schinus polygamus</i> (Cav.) Cabrera	13	1.08	0.18	0.38	34.62	3.11	1.52	21.39	9
Symplocaceae	<i>Symplocos</i> cf. <i>tetrandra</i> Mart.	10	0.83	0.20	0.43	26.92	2.42	1.23	22.63	13
Berberidaceae	<i>Berberis laurina</i> Billb.	7	0.58	0.04	0.09	26.92	2.42	1.03	12.47	6
Cardiopteridaceae	<i>Citronella paniculata</i> (Mart.) R.A.Howard	4	0.33	0.20	0.43	15.38	1.38	0.71	29.28	10
Myrtaceae	<i>Myrceugenia acutata</i> D.Legrand	4	0.33	0.14	0.31	15.38	1.38	0.67	28.33	8
Primulaceae	<i>Myrsine coriacea</i> (Sw.) R.Br. ex Roem. & Schult.	4	0.33	0.11	0.23	15.38	1.38	0.65	27.15	11
Lauraceae	<i>Persea willdenovii</i> Kosterm.	4	0.33	0.09	0.20	7.69	0.69	0.41	24.54	12.5
Myrtaceae	<i>Myrceugenia pilotantha</i> (Kiaersk.) Landrum	2	0.17	0.02	0.05	7.69	0.69	0.30	12.71	5
Podocarpaceae	<i>Podocarpus lambertii</i> Klotzsch ex Endl.	2	0.17	0.03	0.06	3.85	0.35	0.19	17.63	11
Symplocaceae	<i>Symplocos</i> sp.	1	0.08	0.06	0.12	3.85	0.35	0.18	26.52	7
Escalloniaceae	<i>Escallonia bifida</i> Link & Otto	1	0.08	0.03	0.07	3.85	0.35	0.17	2	2
Asteraceae	<i>Baccharis</i> sp.	1	0.08	0.00	0.01	3.85	0.35	0.15	6.62	5.5
Myrtaceae	<i>Myrceugenia miersiana</i> (Gardner) D.Legrand & Kausel	1	0.08	0.00	0.00	3.85	0.35	0.14	5.1	5
Unclassified	Dead standing	81	6.71	2.94	6.23	84.62	7.61	6.85	40.11	10

Brazil (Brasil 2014). *Myrceugenia pilotantha* is classified as vulnerable on the world list (Pires O'Brien 1998). *Podocarpus lambertii* is classified as endangered in Santa Catarina State (Consema 2014). *Myrceugenia miersiana* and *M. myrcioides* are both classified as near threatened on the world list (Barroso 1998a; b). *Crinodendron brasiliense* is endemic to the highlands of Santa Catarina State (Smith Jr & Smith 1970) and is classified as endangered on the world list (Sühs 2018).

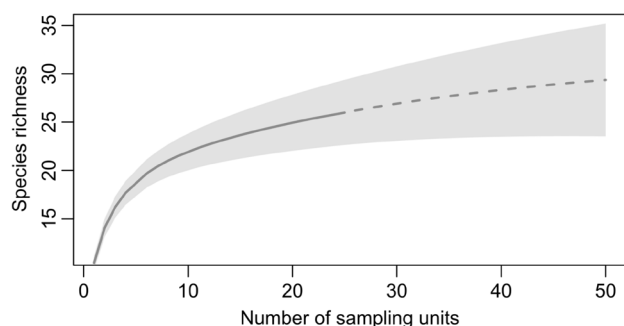


Figure 5. Sample-based rarefaction (solid lines) and extrapolation (dashed lines) curves of trees in an upper montane araucaria forest, southern Brazil. Shaded areas represent 95 % confidence intervals obtained by 1,000 resamplings through bootstrapping.

Discussion

The five species with the highest importance values comprised 70 % of sampled individuals, 68 % of the relative dominance and were highly frequent. This pattern of few dominant species and several subdominant to rare species is commonly found in araucaria forests (e.g., Vibrans *et al.* 2008; Higuchi *et al.* 2013; Silva *et al.* 2017). The five most important species in this study (*D. angustifolia*, *M. regnelliana*, *M. myrcioides*, *A. angustifolia* and *I. microdonta*) were reported as common in the few existing upper montane araucaria forest surveys (e.g. Martins-Ramos *et al.* 2010; Higuchi *et al.* 2013; Silva *et al.* 2017). Conversely, these species are not always the most important species in phytosociological surveys, which reinforces that araucaria forests, although visually alike, may vary in floristics and structure (Klein 1960; Jarenkow & Budke 2009). Only *I. microdonta* is not among the five most dominant species; it was surpassed by *Crinodendron brasiliense* for this parameter.

Among the surveyed families, Myrtaceae had the highest number of species. This family, in particular *Myrceugenia*, contributes the most species for the tree component in araucaria forests, including those from upper montane regions (Klauber *et al.* 2010; Gasper *et al.* 2013; Higuchi *et*

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al. 2013; Ferreira *et al.* 2016; Silva *et al.* 2017). About half of all *Myrceugenia* species that occur in Brazil are found in araucaria forests in Santa Catarina State (Gaspar *et al.* 2013), reinforcing the role of these forests as a center of endemism for this genus (Landrum 1981; Murillo-A *et al.* 2016). The tree fern *D. sellowiana*, like *A. angustifolia*, is frequently abundant in araucaria forests at high altitudes (Meyer *et al.* 2013; Sehnem 1978) and sometimes forms monodominant communities (Gaspar *et al.* 2011). However, although *D. sellowiana* grows in high densities in surrounding forests, it occurs in low density in the sampled area. This fact could be related to the humidity conditions of the area, since this species prefers sites with elevated levels of humidity and shade (Sehnem 1978), such as valleys and south-facing slopes.

The studied area had a Shannon's diversity (entropy) value (H') of 2.29 nats/individual (true diversity = 10 species), which is within the expected values for upper montane araucaria forests (from 1.01 to 2.81) (Meyer *et al.* 2013). However, this value is inferior compared to other studies carried out in similar systems (e.g. Higuchi *et al.* 2013 = 2.79; Ferreira *et al.* 2016 = 3.20; Klauberg *et al.* 2010 = 3.05; Silva *et al.* 2017 = 2.43). This could be attributed to higher altitudes in São Joaquim National Park, since species richness tends to be lower as altitude levels increase (Richards 1996; Givnish 1999). Moreover, the historical exploration of the area must also be taken into consideration because constant interventions in the understory, such as cattle grazing, can cause losses in total diversity of the community (Vibrans *et al.* 2013). The evenness value obtained ($J' = 0.70$) is common for upper montane araucaria forests (e.g., Higuchi *et al.* 2013; Ferreira *et al.* 2016; Silva *et al.* 2017), suggesting a high uniformity of individuals distributed among the sampled species.

Regarding vertical distribution, there was a predominance of species and individuals of the medium and tall height categories ($\geq 6 < 16$ m). We did not observe a continuous strata of emergent araucaria trees in the studied stand, which is commonly attributed to araucaria forests (Souza 2007). This fact could be the result of high species turnover in the area, evidenced by the high number of species and individuals that require light during development (57 % of sampled individuals). Moreover, the high number of dead standing individuals leads to gaps that allow more sunlight to reach the forest floor. On the other hand, 50 % of sampled species (38 % of sampled individuals) are shade tolerant and contribute to higher diametric classes. From a successional perspective, this could be indicative of an advanced stage of forest development (Budowisk 1965). Additionally, pioneer trees species, such as *A. angustifolia* and *D. angustifolia*, had elevated dominance (28.2 and 9.5, respectively), DBH and height values, indicating that they are not new arrivals.

Regarding pollen transport and seed dispersal, animals seem to play an important role for both processes in

the studied area. The majority of surveyed species and individuals have zoophilous pollen dispersal and seeds dispersed primarily by animals. Pollen transport and seed dispersal are both key mechanisms for ecological and evolutionary biology of plants (Okubo & Levin 1989; Howe & Smallwood 1982). These mechanisms underlie the transmission of genetic information, population growth, and migration of plant species (Kuparinen *et al.* 2007), affecting community structure and dynamics (Sinha & Davidar 1992). A great part of the surveyed species (and individuals) had small and light-colored flowers (< 20 mm in diameter) (Tab. S1 in supplementary material). These characteristics tend to attract small animals, such as insects, especially bees, wasps and beetles (Heithaus 1979; Somavilla *et al.* 2010), as the type of pollen transport is determined by attractants such as color, shape, presence of nectar and pollen (Fægri & Pijl 1979), contributing to the conservation of these groups.

Zoochory was the main diaspore dispersal syndrome (73 % of the species, 89 % of the individuals). These values match other studies in upper montane araucaria forests (e.g., Silva *et al.* 2017). In tropical forests, where zoochory prevails, birds and mammals are among the main dispersers (Howe & Smallwood 1982; Morellato *et al.* 2000). In this study, a large part of the zoochorous species sampled had small (< 20 mm diameter), dark-colored diaspores that tend to primarily attract small vertebrates (Hoffmann *et al.* 1989; Howe & Smallwood 1982), such as frugivorous birds. Species with lighter colors and/or larger diaspores, such as *A. angustifolia*, *Myrceugenia myrcioides* and *Citronella paniculata*, are potentially also dispersed by larger omnivore vertebrates, such as agoutis (Vieira & Iob 2009). In this context, *A. angustifolia* plays a crucial role as a food source for larger animals in these systems, since it has one of the largest and most nutritious diaspores. Moreover, araucaria diaspores are available during unfavorable seasons (i.e., autumn/winter, when most of the other tree species do not bear fruits). The predominance of zoochorous species for both pollen transport and seed dispersal reinforces the role of animal-plant interactions for the maintenance of these systems.

The rarefaction curve showed that the increment of species did not clearly stabilize with our sampling effort (25 subplots of 10 x 20 m). However, the extrapolation showed that even when doubling the sampling effort, the increment of species would be small, reaching a maximum of 35 species.

The studied forest is composed mainly of species and individuals that are characteristic of araucaria forests. Species such as *A. angustifolia* and *D. sellowiana* are associated with upper montane regions (Uhlmann *et al.* 2013), and *Weinmannia humilis* is found in forests above 1,200 m a.s.l. (Cuatrecasas & Smith 1971). We found no species from the Paraná and Uruguai river basins and, despite the geographical proximity, we found no species from the Atlantic contingent. araucaria forests have dynamic



relationships with adjacent vegetation formations, which results in floristic variation (Klein 1960; Jarenkow & Budke 2009). In our case, the lack of species from other regions may be attributed to the severe environmental conditions in the region, such as winter frosts and high thermal amplitude during the summer (Sühs *et al.* 2018). This may restrict other tree species from becoming established (Safford 2007; Scheer & Mocoinski 2009), especially those from regions of warmer climates. The species with the highest importance values belong to a floristic contingent (araucaria forests) that requires adaptations to cold temperatures and frosts. For example, the genus *Crinodendron* Molina is represented by four Andean species from southern South America, with geographical distributions restricted to cold environments (Reitz & Smith 1958). *Crinodendron brasiliense* is endemic to Santa Catarina cloud forests (Smith Jr & Smith 1970). Due to its restricted distribution and rarity, this species was not observed in the Floristic and Forest Inventory of Santa Catarina (Gasper *et al.* 2013), despite the high sampling effort carried out in the studied region. The presence of another six species under some degree of threat of extinction reinforces the importance of protecting and conserving these small and discontinuous forest fragments (Klein 1978).

The high number of individuals of endangered species, along with the presence of an endemic species, shows the studied region retains important peculiarities for conservation. The results of our study will contribute to long-term population monitoring, that may help explaining local phytogeographical patterns and the implications of climate change on them. Moreover, we demonstrate structural patterns from poorly studied upper montane regions and reinforce the role of these systems for maintaining species diversity at high elevations.

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