Iheringia
Série Botânica
ISSN ON-LINE 2446-8231

Jardim Botânico de Porto Alegre

Small forest fragments and their importance for conservation of tree communities in Atlantic Semideciduous Forest

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Received 12.X.2020
Accepted 05.VI.2023

DOI 10.21826/2446-82312023v78e2023019

ABSTRACT - It is important to consider the ecological relevance of small forest fragments, especially in areas that have high deforestation rates and few inventories. We aim to describe two stratum of tree communities from small fragments of Atlantic Semideciduous Forest in a highly fragmented landscape. We inventoried all woody individuals taller than 1.3 m in nine fragments, in ten 10 x 20 m plots per fragment. We sampled 8323 individuals and 303 species. Large numbers of species (33.66%) and families (20.7%) occurred only in the understory, while two families (16.4%) and 38 (12.21%) species occurred only in the tree stratum. Sampling two forest stratum was important because we found different species, due the inclusion of permanent wood species of the understory, in addition to young and adult tree individuals. Moreover, we could demonstrate the regeneration potential of the forest and that small forest fragments could present high diversity, with many rare and threatened species. Therefore, small fragments could be valuable to preserve biodiversity in highly fragmented landscapes.

Keywords: floristic composition, forest structure, tree diversity.

RESUMO - Fragmentos florestais pequenos e sua importância para a conservação das comunidades arbóreas da Mata Atlântica Semidecidual. É importante considerar a relevância ecológica dos pequenos fragmentos florestais, especialmente em áreas que apresentam altas taxas de desmatamento e poucos inventários. Nosso objetivo é descrever dois estratos de comunidades arbóreas de pequenos fragmentos em uma paisagem altamente fragmentada de Mata Atlântica Semidecidual. Nós inventariamos todos os indivíduos lenhosos com mais de 1,3 m em nove fragmentos, em dez parcelas de 10 x 20 m por fragmento. Encontramos 8.323 indivíduos e 303 espécies. Um grande número de espécies (33,66%) e famílias (20,7%) ocorreram apenas no sub-bosque, enquanto duas famílias (16,4%) e 38 (12,21%) espécies ocorreram apenas no estrato arbóreo. A amostragem dos dois estratos florestais foi importante porque encontramos espécies diferentes, devido à inclusão de espécies lenhosas permanentes do sub-bosque, além de indivíduos arbóreos jovens e adultos. Além disso, pudemos demonstrar o potencial de regeneração da floresta e que pequenos fragmentos florestais podem apresentar grande diversidade, com muitas espécies raras e ameaçadas de extinção. Portanto, pequenos fragmentos podem ser valiosos para preservar a biodiversidade em paisagens altamente fragmentadas.

Palavras-chave: composição florística, diversidade arbórea, estrutura florestal.

INTRODUCTION

The Atlantic Forest is one of the most endangered forests of the world due to the expansion of agricultural activity (Ribeiro *et al.* 2009, Lopes *et al.* 2012, Santo-Silva *et al.* 2016). The anthropic activities expansion in this biome are continually reducing and fragmenting the remnant forests (Silva *et al.* 2006). Fragmentation has multiple negative effects on forest ecosystems, altering their diversity, species composition and impacting the ecological processes of the remnant communities (Laurance *et al.* 2011, Silva *et al.* 2019). Many direct and indirect factors could continually change the species richness, abundance and size structure of plant communities from forest fragments, such as edge effect, biological interaction, invasion of exotic species and stochastic demographic drift (Fahrig *et al.* 2019). Accordingly, several studies have shown that fragmentation leads to impoverished communities with few dominant and generalist species, and have few rare and/or threatened taxa (Laurance *et al.* 2007, Arroyo-Rodriguez *et al.* 2013, Santo-Silva *et al.* 2016). However, these effects may be stronger in small forest fragments (Arroyo-Rodriguez *et al.* 2009).

While some studies demonstrate that small forest fragments show difficulty to flora regeneration, invasions from plant exotic species and dominance from tree pioneer species (e.g. Tabarelli *et al.* 1999, Salles & Schiavini 2007, Fonseca *et al.* 2013, Paiva *et al.* 2015, Rotmeister *et al.* 2015), others studies show that small forest fragments could retain high plant diversity and have importance to conserve the regional flora biodiversity (e.g. Augusto *et al.* 2000, Pither & Kellman 2002, Faria *et al.* 2007, Franco *et al.* 2007, Brito & Carvalho 2014, Toledo-Aceves *et al.* 2014). These findings are very important for Atlantic Forest conservation decisions, since most of their biodiversity currently resides within small forest fragments (Ribeiro *et al.* 2009, Lima *et al.* 2015), despite these fragments being historically marginalized in conservation initiatives (Gibson *et al.* 2011). Therefore, an assessment of community structure (richness, diversity, evenness, floristic composition) in small fragments are important, especially in tropical biodiversity hotspots that have some of their forest physiognomies with large sampling gaps (e.g. Deciduous Forests; Hernadez-Ruedas *et al.* 2014, Lima *et al.* 2015). The biodiversity acknowledgment is not only important for botanical and ecological investigations, but is primordial for understanding biogeographical patterns and subsidize management and conservation programs (ter Steege 1998, Bergamin *et al.* 2017). Therefore, tree diversity knowledge is an indispensable tool in order to help the elaboration of efficient conservation decisions, especially urgent in the current scenario of forest destruction (Melo *et al.* 2013, Terra *et al.* 2017).

The Semidecidual Atlantic Forest from the south of Minas Gerais are a highly threatened landscape by fragmentation with few representative areas preserved (SOS Mata Atlântica /INPE/ISA 1998, Durigan *et al.* 2000, Silva *et al.* 2006, Souza *et al.* 2006). Additionally, most of the tree community studies in Atlantic Forest emphasize only the arboreal component (DBH > 5cm) (Souza *et al.* 2006, Caiafa & Martins 2007, Lima *et al.* 2015). Plant community studies on lower stratum are necessary, because they could give us important information, such as tree species regeneration or successional trajectory (Meira Neto & Martins 2003, Santos *et al.* 2015, Santana *et al.* 2020). Therefore, in this study we aim to describe two stratum of tree communities from small fragments of Atlantic Semideciduous Forest (< 100 ha), on a highly fragmented landscape in the south of Minas Gerais. We intended to (i) know the diversity contribution that small fragments provide to the Semideciduous Forest and (ii) provide information concerning the regional flora, increasing our knowledge about the geographical distributions and abundances of species.

METHODS

Study area

Our study was undertaken in nine montane Semideciduous Atlantic Forest fragments (Veloso 1992) in Alfenas and Machado rural areas, southern of Minas Gerais State, Brazil (Tab. 1). All studied sites had forest since 1979, the oldest register for the area (ESRI 2016), however there is no information about their anthropic use or perturbation over the years. The land use around these nine forest fragments were agriculture and pasture (MapBiomas 2019). The region soil is the dystrophic Red Latosol (Olivetti *et al.* 2015). The distance between fragments ranged from 3.1 to 49.6 km and the area of fragments ranged from 20.9 to 87.2 ha (Tab. 1).

Table 1. Description of sampling sites in Seasonal Semideciduous Forest analyzed.

Fragment	City	Site ID	Area (ha)	Coordinates	m.a.s.l
1	Alfenas	Matão	20,91	S 21°30'16.8" W 045°52'38.5"	802
2	Alfenas	Gaspar Lopes	81,55	S 21°22'43.8" W 045°55'46.7"	835
3	Alfenas	M	56,05	S 21°27'24.6" W 046°10'07.1"	827
4	Alfenas	Paraíso	36,85	S 21°21'46.5" W 045°50'26.4"	813
5	Alfenas	I	37,05	S 21°25'35.1" W 046°05'39.4"	820
6	Machado	Cemitério	22,99	S 21°33'34.5" W 045°56'15.8"	877
7	Alfenas	Porto	87,18	S 21°25'16.3" W 046°07'22.3"	833
8	Alfenas	N	24,80	S 21°28'07.2" W 046°09'46.2"	856
9	Alfenas	São José	28,57	S 21°26'02.4" W 046°08'57.6"	828

The regional climate is classified as Cwa with average winter temperature 16.9 ºC and 21.5 ºC in summer, and the monthly average precipitation is 26 mm in the winter and 290 mm in the summer (1500 mm annually) (Alvares *et al.* 2014). Regional elevations vary from 720 to 1350 m a.s.l. in a predominantly hilly landscape associated with mountains. The region retains, since 1986, only about 9% of its native forest cover, with the most common matrix types being pasture (51%), permanent cultivation (mainly coffee - 17%), and temporary crops (mainly sugar cane and corn - 7%) (Olivetti *et al.* 2015).

Phytosociological survey

Ten randomly 10 x 20 m plots (0.2 ha per fragment) were installed in each forest fragment at least 10 m from the edge into the fragment interior. All woody individuals alive taller than 1.3 m were sampled and measured within each plot. For practical reasons, the individuals were divided into two classes: those with diameters at breast height (DBH) ≥ 5 cm (hereafter referred to as tree stratum) and those with DBH < 5 cm (hereafter referred to as understory stratum). Although many young trees in the understory strata will achieve forest canopy height, and there were many tall adult shrubs placed in the tree stratum, we established these two classes to facilitate the interpretation of our results. We used the Brazilian Flora 2020 classifications available in the "flora" package to get the species life-form occupying each investigated stratum (Carvalho 2020). We categorized our life-forms in three classes based on Flora 2020 classification: those species that are exclusively (i) trees, (ii) shrubs, or (iii) treelets (which are classified both as tree/shrub). Our procedures were made inside the R environment version 3.6.3 (R Core Team 2020).

Botanical identifications were made in the field; when this was not possible, samples were collected for posterior identification by specialists and deposited in UALF herbarium (Federal University of Alfenas). We used the Angiosperm Phylogeny Group IV (APG IV 2016). The "get.taxa" function from the "flora" package was subsequently used to update and correct misspelling synonyms according to Brazilian Flora 2020 (Carvalho 2020, R Core Team 2020). We considered as rare those species with one or two individuals in our sampling, and those found in only one forest fragment were considered as exclusive species (sensu Martins 1991). We classified the endangered species according to Biodiversitas (2007) and Martinelli & Moraes (2013).

Statistical analyses

Phytosociological parameters were calculated for all forest fragments using the Fitopac software (Shepherd 2010), according to formulation presented by Kent & Coker (1992). In order to account for the sampling effort, we estimated the species richness using rarefaction curves and employing the Bootstrap estimator in the Estimate software (Colwell 2013). This estimator is indicated for samples with large numbers of rare species (e.g. low abundance species; Magurran 2004). We calculate the pairwise dissimilarity index both using species abundance (Bray-Curtis) and presence-absence (Jaccard) among all the forest fragments using the function "vegdist" in the "vegan" package available in R environment (Oksanen *et al.* 2011).

Size structures (heights and diameters) were verified using the Gini coefficient and the Lorenz curve (Weiner & Solbrig 1984). The Gini coefficient (G) is a measure of inequality, which can vary from 0 to 1; values near 0 indicate that individuals in the community are of similar dimensions, while values near 1 indicate large differences between them. In the Lorenz curve, the data (cumulative size x cumulative number of individuals) is ordered from the lowest to the highest (height or diameter) in a cumulative manner. If all individuals are of the same size/diameter, the resulting plot will be a diagonal line; if the individuals are of unequal sizes/diameters the curve will fall below the diagonal. Greater spacing between the sizes/diameters reflects more unequal sizes/diameters (Wiener & Solbrig 1984). These analyses were made using the "redist" (Fifield *et al.* 2016) and "boot" (Canty & Ripley 2019) packages in R environment.

RESULTS

We sampled 8338 individuals belonging to 60 families, 159 genera, and 303 species, only 3% of individuals were not identified. Among those species we found that 174 (57.42%) were exclusively trees, 105 (34.65%) treelets, 20 (6.6%) shrubs, 3 (0.99%) palm trees and only one was not identified (*Croton* L.). We also found that 164 (54.12%) species and 46 (76.67%) families were common between both stratum: tree and woody understory. Large numbers of species (102, 33.66%) and families (20.7%) occurred only in the understory stratum, while two families (16.4%) (Caricaceae and Rhamnaceae) and 37 (12.21%) species occurred only in the tree stratum. The families Anacardiaceae, Annonaceae, Euphorbiaceae, Fabaceae, Lauraceae, Meliaceae, Myrtaceae, Salicaceae, and Rubiaceae, as well as the species *Duguetia lanceolata* A. St.-Hil. and *Copaifera langsdorffii* Desf. occurred in both stratum and in all fragments (Supplemental Tab. 1). Few species are dominant and many of them are rare. We found some exotic species: one sampled (*Coffea arabica* L.) and others that were not sampled, such as banana (*Musa sp.*). In turn, these fragments presented very high wood plant density, with very low basal area. We found this result after removing two species, with only one individual each in the total sample, which presented very large DBH: *Ficus trigona* L. f and *F. gomelleira* Kunth.

Tree stratum (Individuals with DBH ≥ 5 cm)

We sampled 1981 individuals with DBH ≥ 5 cm, distributed among 201 species, 111 genera, and 48 families, from the tree stratum in the nine fragments. The total estimated species richness was 239.05 (Fig. 1), ranging from 46.5 to 105.3 in the plots, while Shannon's diversity index was 4.38, and Pielou's evenness index was 0.82. (Supplemental Tab. 2). The richness estimated by Bootstrap for each plot (0.2 ha) ranged from 46.5 to 105.3, while Shannon's diversity index (H') from 3.17 to 4.03, and Pielou's evenness (J') index from 0.82 to 0.91 (Supplemental tab. 2). Twenty families (41.6%) were represented by only a single species, while the richest families were Fabaceae (12.91%), Myrtaceae (10.94%), Lauraceae (9.45%), Meliaceae (5.97%), and Euphorbiaceae (5.47%). These five families greatly contributed to regional tree diversity, comprising 44.7% of all species (Supplemental tab. 1). Anacardiaceae, Annonaceae, Euphorbiaceae, Fabaceae, Lauraceae, Meliaceae, Myrtaceae, Rubiaceae, and Salicaceae (18.7%) were the most frequent families, occurring in almost all fragments (Supplemental tab. 1). We sampled 126 (62.8%) trees, 61 (30.3%) treelets, 10 (4.97%) shrubs and 3 (1.49%) palm tree species (Tab. 2).

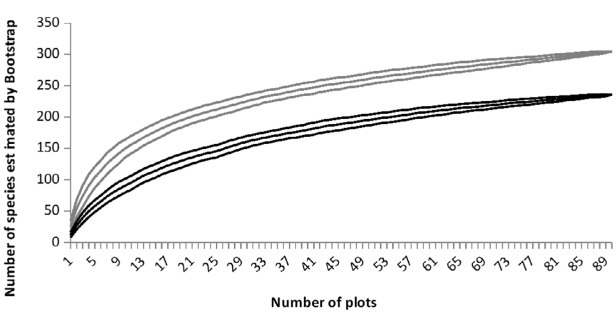

Figure 1. Species accumulation curve designed by Bootstrap estimator for the nine sites of seasonal semideciduous forest in southeastern Brazil. Gray lines: Species with DAP < 5.0 cm. Black lines: Species with DAP > 5.0 cm. Dashed line: standard deviation.

Table 2. Total number of species of each life form in each studied stratum. Stratum exclusive species are presented inside parenthesis of their respective life-form.

Life-form	Total	Tree stratum	Understory stratum
Trees	174	126 (24)	150 (48)
Treelet	105	61 (8)	97 (44)
Shrub	20	10 (3)	17 (10)

The species *Copaifera langsdorffii*, *Ocotea odorifera* (Vell.) Rohwer, *Cryptocarya aschersoniana* Mez, *Metrodorea stipularis* Mart., and *Miconia willdenowii* Klotzsch ex Naudin had the highest VI (Supplemental Tab. 3); *Duguetia lanceolata, Cryptocarya aschersoniana, Copaifera langsdorffii, and Ocotea corymbosa* (Meisn.) Mez were the most frequent species in all the nine fragments, representing 1.99% of the total richness and 13.5% of the total number of individuals sampled. The most abundant species were also the most frequent ($rPearson_{203}$ = 0.94; $p < 0.0001$) one. Some species, however, had high abundances but low frequencies, such as *Vernonanthura divaricata* (Spreng.) H. Rob*, Platypodium elegans Vogel* and *Piptadenia gonoacantha* (Mart.) J.F. Macbr., while others had low abundances and high frequencies, such as *Dalbergia villosa* (Benth.) Benth.*, Tapirira obtusa* (Benth.) J.D. Mitch*, and Guatteria australis* A. St-Hil. (Supplemental Tab. 3).

All forest fragments presented higher tree dissimilarity, ranging from 0.43 to 0.71, considering species abundance; and from 0.60 to 0.83, considering species presence/absence. Fragments 2 and 7 showed the highest dissimilarity, while 5 and 9 the lowest one, from both indexes. Forty percent of the species were found in only one forest fragment, and the fragments had 26,86% of rare species (only one individual, Supplemental Tab. 2). In addition to retaining large numbers of species, the areas held many endangered species. *Euterpe edulis* Mart.*, Ficus cyclophylla* (Miq.) Miq. and *Cedrela fissilis* Vell. are classified as vulnerable to extinction, while *Ocotea odorifera* (Vell.) Rohwer is endangered in Brazil, and *Persea rufotomentosa* Nees & Mart. and *Ocotea odorifera* are classified as vulnerable in Minas Gerais State (Tab. 3). In addition to its vulnerability to extinction, *Euterpe edulis* was also exclusive to tree stratum.

We found 126 tree species in the tree stratum, distributed among 31 families (Tab. 2), with Fabaceae (21 species), Lauraceae (16), Myrtaceae (15) being the richest ones. Two families (Caricaceae and Rhamnaceae) and 24 tree species were exclusive in this stratum, with most part of them (75%) considered as rare (presenting only one individual sampled). *Copaifera langsdorffii*, *Ocotea odorifera*, *Cryptocarya aschersoniana* showed the highest VI for trees in this stratum. However, we highlight the importance of some rare and exclusive species such as those of *Ficus* genera (e.g. *Ficus trigona* and *Ficus gomelleira*), which presented high VI due to their very large basal area (Supplemental Tab. 3). We also found in tree stratum 61 treelet species among 29 families, being Euphorbiaceae (6) and Myrtaceae (6) the richest ones. Only 8 treelet species, in 7 families, were exclusive in tree stratum. *Trichilia emarginata* (Turcz.) C.DC.*, Mabea fistulifera* Mart. and *Casearia sylvestris* Sw. had the highest VI for this life-form, while *Roupala montana* Aubl. presented the highest VI among the exclusive ones. In turn, we only found 10 shrub species in the tree stratum, being only 3 of them exclusive, in 7 families (Rubiaceae being the richest one). *Faramea latifolia* (Cham. & Schltdl.) DC., *Cordiera sessilis* (Vell.) Kuntze (exclusive), *Aspidosperma olivaceum* Müll. Arg., *Cordiera elliptica* (Cham.) Kuntze (exclusive) were shrub species presenting the highest VI.

Table 3. Endangered species sampled in nine sites of seasonal semideciduous forest of southeastern Brazil. VU = Vulnerable, EN = Endangered, F = Frequency, A = Abundance, AT = Total Abundance.

Families/Species	Brasil	Minas Gerais	F > 5 cm	F < 5 cm	A > 5 cm	A < 5 cm	AT
Arecaceae							
Euterpe edulis	VU	-	2	0	3	0	3
Lauraceae							
Ocotea odorifera	EN	VU	8	9	130	134	264
Persea rufotomentosa	VU	-	2	1	4	5	
Lecythidaceae							
Cariniana legalis	EN	-	0	3	0	3	3
Meliaceae							
Cedrela fissilis	VU	-	4	4	11	11	22
Moraceae							
Ficus cyclophylla	VU	-	1	2	2	4	6
Myrtaceae							
Eugenia malacantha	EN	-	0	3	0	9	9
Myrcia diaphana	VU	-	0	1	0	2	2
Rubiaceae							
Rudgea jasminoides	VU	-	0	5	0	9	9

The total area studied (1.8 ha) had a mean total basal area of 28.10 m^2 ha^{-1} and an overall density of 1102.78 ind ha^{-1}. Among the different fragments, basal areas ranged from 17.8 to 46.2 m^2 ha^{-1}, while their densities ranged from 845 to 1400 ind ha^{-1} (Supplemental Tab. 2). The sampled individuals were generally short (mean = 9.2±3.9 m tall) and thin (mean = 13.8±11.6 cm in diameter). In turn, there were no large variations among individuals either in terms of their heights (G = 0:26; CI = 0.22 to 0.24) or diameters (G = 0.36; IC = 0.34 to 0.37) (Supplemental Fig. 1).

Understory woody stratum (trees, treelets and shrubs less than 5 cm DBH)

The 6342 individuals sampled in the understory (individuals with DBH ≤ 5 cm), belonged to 266 species, 145 genera and 58 families. Eighteen families (31%) were represented by single species. The total estimated species richness was 304.5 (Fig. 1), ranging from 96.8 to 147.3 in each plot (Supplemental Tab. 2). Shannon's diversity index was 4.26, and Pielou's evenness index was 0.76. Richness, as estimated by Bootstrap, for each fragment (0.2 ha) ranged from 96.8 to 147.3, Shannon's diversity (H') ranged from 3.18 to 4.15, and Pielou's evenness (J') ranged from 0.67 to 0.85 (Supplemental Tab. 2). Conversely, 39.47% of the species belonged to five families: Myrtaceae (13.9%), Fabaceae (9.77%), Rubiaceae (5.63%), Lauraceae (5.26%), and Melastomataceae (4.88%; Supplemental tab. 1). Fabaceae, Myrtaceae, and Rubiaceae were the most frequent families, occurring in almost every fragment (Supplemental Tab. 1). Twenty seven percent of the species in this stratum occurred in only one fragment. We sampled 150 (56.39%) of sapling trees, 97 (36.46%) treelets, 17 (6.39%) shrubs and 1 (0.37%) palm tree species (Tab. 2).

Siparuna guianensis Aubl., *Palicourea sessilis* (Vell.) C.M. Taylor, *Trichilia emarginata, Cupania zanthoxyloides* Radlk., and *Ocotea odorifera* had the highest VI (Supplemental tab. 4). *Duguetia lanceolata, Croton floribundus* Spreng., *Copaifera langsdorffii, Ocotea odorifera, Mollinedia widgrenii* A.DC., *Amaioua guianensis* Aubl., *Palicourea sessilis, Casearia decandra Jacq., Casearia sylvestris Sw.,* and *Siparuna guianensis* were the most frequent species in the nine fragments, representing 3.75% of the total species richness and 33.03% of the total number of individuals surveyed. The most abundant species were also the most frequent ($rPearson_{270}$ = 0.73; $p < 0.0001$). Some species showed high abundance, but low frequency, including *Trichilia clausseni* C. DC., *Piper amalago L., Galipea jasminiflora* (A.St.-Hil.) Engl., and *Trichilia elegans* A. Juss.; others showed low abundance and high frequency, such as *Tapirira obtusa, Cordia sellowiana* Cham., *Eugenia florida* DC., and *Ilex cerasifolia* Reissek (Supplemental Tab. 4).

The tree dissimilarity among the fragments ranged from 0.36 to 0.69 considering species abundance; and from 0.53 to 0.81 considering only species presence/absence. Fragments 2 and 7 showed the higher dissimilarity, while 4 and 6 the lowest one from both indexes. Approximately 21.8% of the species present only one individual and, in general, 34.2% of the total number of species are exclusive of only one fragment. Among the large numbers of species, the fragments showed species in a vulnerable (*Apuleia* *leocarpa* (Vogel) J.F. Macbr., *Cedrela fissilis*, *Ficus cyclophylla* and *Myrcia diaphana* (O. Berg) N. Silveira) and endangered conservation status in Brazil (*Cariniana legalis* (Mart.) Kuntze, *Eugenia malacantha* D. Legrand and *Ocotea odorifera*), according to Biodiversitas (2007) and Martinelli & Moraes (2013) (Tab. 3). In addition, *Persea rufotomentosa* and *Ocotea odorifera* are classified as vulnerable in Minas Gerais State (Biodiversitas 2007).

We found 150 tree species in the understory wood stratum, distributed among 31 families (Myrtaceae and Fabaceae were the richest ones, with 29 and 20 species respectively; Tab. 2). Forty eight of these trees were exclusive of this stratum, predominantly from Myrtaceae (15 species). In addition, we found that some exclusive tree species are classified as endangered (EN) in this stratum, such as *Cariniana legalis* and *Eugenia malacantha*, and one vulnerable (VU): *Myrcia diaphana* (Tab. 3). *Cupania zanthoxyloides*, *Ocotea odorifera* and *Metrodorea stipularis* had the highest VI among trees from the understory stratum; while *Galipea jasminiflora*, *Myrcia pubiflora* DC. and *Eugenia paracatuana* O. Berg. were the most important among the exclusive ones. We also found 97 treelet species in the understory stratum, among 40 families, with Melastomataceae and Rubiaceae being the richest ones (8 species each). Forty four treelet species were exclusive, being *Siparuna guianensis* and *Palicourea sessilis* exclusive species from this stratum presenting the highest VI (Supplemental Tab. 4). In addition, this life-form also presented the *Rudgea jasminoides* (Cham.) Müll. Arg. as an exclusive vulnerable (VU) species (Tab. 3). On the other hand, we found 17 shrub species (10 exclusive) occurring in the understory stratum. These shrub species were distributed among 10 families, with Rubiaceae (5 species, 4 exclusive) being the richest one. *Piper amalago* and *Psychotria subtriflora* Müll. Arg., exclusive shrub species in this stratum, showed the highest VI among shrub species. However, it is worth mentioning that we found a high VI and abundance of *Coffea arabica*, an exclusive exotic shrub species in this stratum.

The study area (1.8 ha) had a mean basal area of 1.38 m^2 ha^{-1} area and total density of 3529.4 ind ha-1. The basal areas of the fragments ranged from 0.85 m^2 ha^{-1} to 2.2 m^2 ha^{-1}, while plant density at each site (0.2 ha) ranged from 2085 ind ha^{-1} to 5770 ind ha^{-1} (Supplemental tab. 2). The individuals surveyed were generally short (mean = 3.3 ± 1.9 m tall) and thin (mean = 2.0 ± 0.98 cm in diameter) and there were no large variations between individuals either in terms of height (G = 0.23; CI = 0.23 to 0.24) or diameter (G = 0.26; IC = 0.25 to 0.26) (Supplemental Fig. 2).

DISCUSSION

The fragments studied presented high species richness and diversity compared with well-preserved areas (see detail below). Many species are rare and/or exclusive, as well as vulnerable or endangered. However, few species were very abundant and some exotic ones were found. Although it is not possible to assure it without the fragments' disturbance history, the low basal areas, with high densities of short and thin individuals found, could indicate that these areas may be in a recuperation phase following a recent disturbance (*sensu* Oliveira-Filho *et al.* 2004). The woody understory stratum contributed with large numbers of exclusive species to the total species richness of the fragments, and the inclusion of this stratum in the sampling increased richness by 33.66%. Most of the tree species (86.2%) were found in the understory stratum, being almost ⅓ of them exclusive of this stratum. These findings may indicate that the forest fragments presenting the regeneration base, being capable of preserving a high diversity over time if no new anthropic event disturb them (Lawton & Putz 1988, Okuda *et al.* 1997).

The small forest fragments in the present study showed high diversity and richness, compared with those in well-preserved areas or large fragments (Meira Neto & Martins 2000, Botrel *et al.* 2002, Dalanesi *et al.* 2004, Spósito & Stehmann 2006, Maragon *et al.* 2008, Torres *et al.* 2017, Silva *et al.* 2019). The fragments studied here showed large numbers of rare (only one sampled individual) and exclusive species (present in only a single fragment) that contributed to their high diversity. The fragments preserved many families and species known from the regional semideciduous forests. The families Myrtaceae, Fabaceae, and Lauraceae showed the highest numbers of species in both strata in almost all the fragments. In the canopy stratum the highest richness was represented by Fabaceae, Myrtaceae, Lauraceae, Meliaceae and Euphorbiaceae families. The same pattern of species richness among families was pointed out by other floristic surveys in semideciduous Atlantic Forest (van den Berg & Oliveira-Filho 2000, Filho & Santin 2002, Carvalho *et al.* 2005, Oliveira-Filho 2006, Silva *et al.* 2009, Naves & Berg 2012, Torres *et al.* 2017, Reis *et al.* 2015, Cunha & Junior 2018, Silva *et al.* 2019). Even in understory strata, the families that showed the highest richness were represented by Myrtaceae, Fabaceae, Rubiaceae, Melastomataceae and Lauraceae; all of them are commonly found in the mature stage of Semideciduous Atlantic forests (Oliveira Filho & Fontes 2000, Estevan *et al.* 2016, Torres *et al.* 2017). Interestingly, the richest genera (*Aspidosperma*, *Casearia*, *Eugenia*, *Machaerium*, *Myrcia*, *Ocotea*, *Trichilia*), with few exceptions (*Ficus* as the richest only in the tree stratum, while *Miconia* only in the understory one), were very similar between both stratum and have almost 50% of all species, being also the richest genera in other studies from semideciduous forest fragments (Meira-Neto & Martins 2002, Machado *et al*. 2004, Santana *et al.* 2019).

The species with the highest VI in our fragments were *Copaifera langsdorffii*, *Ocotea odorifera*, *Cryptocarya aschersoniana*, *Metrodorea stipularis* and *Miconia willdenowii*. The first four species were found with high importance in other studies at semideciduous Atlantic Forest (Filho & Santin 2002, Rocha *et al.* 2005, Souza *et al.* 2012, Naves & Berg 2012). On the other hand, *Miconia willdenowii* did not appear with high importance in other phytosociology studies of semideciduous Forest. Likewise, *Ocotea odorifera* and *Copaifera langsdorffi* are found in large numbers in other large and well-preserved semideciduous forests (Werneck *et al.* 2000, Dalanesi *et al.* 2004, Marangon *et al.* 2008). The fragments studied here still preserved nine endangered species (Biodiversitas 2007, Martinelli & Moraes 2013) in both their canopies and understories, demonstrating the importance of these fragments to the conservation of regional biodiversity. As example, *Cedrella fissilis* and *Ocotea odorifera* (which also presented high VI) are vulnerable tree species considered as indicators of preserved areas that have a large number of individuals in both stratum (Franco *et al.* 2007). On the other hand, the vulnerable species *Euterpe edulis* and *Ficus cyclophylla* showed few individuals, with the first presenting individuals only in the tree stratum. These endangered species are likewise found in large numbers in other large and well-preserved Semideciduous Atlantic Forests (Dalanesi *et al.* 2004, Marangon *et al.* 2008), but not always as important and frequent as in the present study. The species we found in the understory stratum with greater VI, mainly from the treelet and tree life forms, are also commonly found, mainly in the semideciduous forests fragments, such as the treelet species: *Casearia sylvestris, Mabea fistulifera, Roupala montana* and *Trichilia emarginata*; as some of our highest VI shrub species *Cordiera elliptica*, *Cordiera sessilis* and *Faramea latifolia* (Pinheiro *et al*. 2012, Franco *et al*. 2007, Pedreira & Sousa 2011, Lopes *et al*. 2012, Paiva *et al*. 2015, Rotmeister *et al*. 2015, Silva & Mazine 2016, Silva *et. al*. 2019). We also found some species that are indicators from mature forest (according Franco *et al*. 2007), such as the tree species: *Campomanesia guazumifolia* (Cambess.) O. Berg., *Campomanesia simulans* M.L. Kawas., *Campomanesia xanthocarpa* (Mart.) O. Berg, *Cariniana estrellensis* (Raddi) Kuntze (exclusive in the understory stratum), *Cariniana legalis* (exclusive in the understory stratum), *Cryptocarya aschersoniana*, *Hymenaea courbaril* L. (exclusive in the tree stratum) and *Ocotea odorifera;* the treelet species: *Chrysophyllum marginatum* (Hook. & Arn.) Radlk; and the shrub species *Aspidosperma olivaceum*.

However, the size structure of the plant community, or its DBH and height pattern, studied here could indicate some disturbance impact (Nunes *et al.* 2003, Lorenzoni-Paschoa *et al.* 2019). We noticed that the density was very high and the basal area was very low. These results were very similar to other disturbed areas (Oliveira-Filho *et al.* 1994, Botrel *et al.* 2002, Souza *et al.* 2003, Dalanesi *et al.* 2004, Oliveira-Filho *et al.* 2004, Pinto *et al.* 2008, Dias Neto *et al.* 2009, Lopes *et al.* 2011). The high tree densities with low basal areas found in our study indicate the densification of thinner individuals – characteristic of environments that have suffered recent disturbances and are in the process of regeneration (Nunes *et al.* 2003, Lorenzoni-Paschoa *et al.* 2019). Two other aspects of this study reinforce this conclusion: (i) the average height of all individuals was 9.2±3.9 m, and only two fragments had taller individuals (more than 20 m tall), and (ii) most individuals had thin stems (mean: 13.8±11.6 cm). Some authors have argued that it is possible to infer the regeneration status of a plant community based on its size structure (Clark *et al.* 1994, Hutchings 1997, Condit *et al.* 1998), as size structure reflects the biotic and abiotic factors influencing the plant populations. Areas studied (Atlantic Forest) by Nunes *et al.* (2003), that had suffered recent disturbances, had basal areas, densities, heights and diameters similar to those observed in the present study. Neves & Peixoto (2008) studying Atlantic Forest fragments found that the canopy stratum of recently disturbed fragments (< 20 years) had thinner and shorter trees than older disturbed sites (> 40 years). However, it is important to highlight that relief and soil variations can also influence the size structure of the plant community in fine-scales (Guerra *et al.* 2013, Gonçalves *et al.* 2018).

While many studies have reported fragmented plant communities with low diversity and that were dominated by pioneers species (Laurance *et al.* 2006, Santos *et al.* 2008, Santo-Silva *et al.* 2016, Ibanez *et al.* 2017), we found that our forest remnants had high levels of diversity, high species dissimilarity among them, with many rare, exclusive and threatened species. Some studies showed that even small forest fragments, most of them in private areas, could maintain high diversity or, at least some plant species from mature forest stage (e.g. Santin 1999, Franco *et al.* 2007, Reis *et al.* 2007, Carvalho & Felfili 2011, Brito & Carvalho 2014, Rotmeister *et al.* 2015). Even small secondary forest fragments are important for conservation, since they present high floristic heterogeneity resulting from environmental variations and the different disturbance degrees to which these forests have been submitted (Sansevero *et al.* 2017). Therefore, our study corroborates that forest fragments could show high dissimilarity, even if they are near each other (Bergamin *et al.* 2017). In addition, the high number of indicator species suggest that the studied fragments may passively be restored and reach later successional trajectories in the future, depending on the disturbances of/and their adjacent land uses (Sansevero *et al.* 2017, Mangueira *et al.* 2021). This indicates that we should consider both public and private areas for conservation actions and management of environmental quality, such as seed collection, seedling production, and specimen reintroduction from different sites to improve genetic variability in these areas.

There are two possible explanations for the high diversity from the studied forest fragments. First, the heterogeneous landscape mosaic and land-use history of the matrix may be helping to maintain species diversity. Matrices that are structurally heterogeneous (in terms of plant sizes and crown coverage), with some similarity to forest fragments, could mitigate the edge effects providing shelter and food for wildlife, while facilitate dispersal, survival and maintenance of species among fragments (Mesquita *et al.* 1999). These forest fragments may have been used as stepping stones, permitting the local fauna locomote through the highly fragmented landscape, helping maintain the diversity, or at least, reducing the probability of regional extinction through metapopulation processes (e.g. propagules arrival; Alves & Metzger 2006). Our fragments did not show evidence of severe disturbance, such as selective logging or the passage of fire, although cattle had apparently grazed some areas. However, they presented invasions by exotic species, such as the abundant *Coffea arabica* (coffee) in the understory stratum (Nunes *et al.* 2003, Borges & Azevedo 2017). The coffee is a biological problem also observed in other semideciduous Atlantic Forest sites (Durigan *et al.* 2000, Martins & Rodrigues 2002, Borges & Azevedo 2017), raising concern how this species interferes with the natural succession processes (Raymundo *et al.* 2018), and may suggest that probably there were coffee plantations in nearby areas or in the same area in the past.

The Atlantic Forest currently has few portions of large extensions of continuous habitat (Ribeiro *et al.* 2009). The preservation and restoration of forest fragments is currently a central issue in discussions of biodiversity conservation, as most tropical biodiversity is now located in these types of environments (Melo *et al.* 2013). Despite the great importance of understory stratum to better understand the long-term effects of fragmentation and the regeneration of the biodiversity, most studies has focused only in adult trees (Salles & Schiavini 2007, Lima *et al.* 2015, Matínez-Ramos *et al.* 2018). Younger trees and treelets represent the regenerative potential of the forest, making it possible to construct inferences about forest regeneration and the maintenance of biodiversity in the medium and long term (Alves & Metzger 2006, Salles & Schiavini 2007, Crouzeilles *et al.* 2017). We have shown that even small forest fragments can maintain high plant species richness, with important floristic regionalism, and threatened species, therefore, have high conservation ecological value compared with well-preserved areas or some large forest fragments. These forest fragments are representative of regional landscape, help maintain ecosystem services, serve as stepping stones, and provide resources for wildlife by increasing landscape connectivity (Arroyo-Rodriguez *et al.* 2009, Hernández-Ruedas *et al.* 2014, Barbosa *et al.* 2017, Wintle *et al.* 2019). The ecological value of large reserves for biodiversity conservation is unquestionable, however, in areas highly fragmented without conservation units, healthy small forest fragments could act as a valuable option to conservation actions and preserve a high tree diversity (Machado *et al.* 2016).

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