



Atlantic Forest meets the Cerrado: floristic, structure and species distribution of an ecotonal tree community

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ABSTRACT: We evaluated the floristic and structural composition of a tree community in an ecotone between Cerrado (cerradão) and Atlantic Forest (seasonal semideciduous forest) domains located in Porto Ferreira State Park (PFSP), southeastern Brazil. We compared the floristic relationships of this ecotone with those of previous surveys carried out on the same vegetation types and checked the species distribution among the Brazilian biomes. We sampled all living trees with PBH \geq 10 cm in 64 10x10 m plots (0.64 ha), totaling 1,755 individuals belonging to 101 species and 37 families. The richest families were Myrtaceae (13 spp.) and Fabaceae (11 spp.), and *Siparuna guianensis* was the most abundant species (188 individuals). We reported two threatened species. A great number of species are widely distributed, occurring in different Brazilian biomes. Floristic similarity values were low among the selected studies, but our sampled community clustered with communities of cerradão and ecotone areas of previous surveys. Our results corroborate that ecotonal areas have great tree diversity and the predominance of widely distributed species. This fact, combined with the vegetation thickening verified through historical photographs, reinforces that the study area belongs to an under-changing ecotone.

Keywords: ecotone; cerradão; seasonal semideciduous forest; phytogeography; floristic similarities.

Mata Atlântica encontrando o Cerrado: florística, estrutura e distribuição de espécies de uma comunidade arbórea ecotonal

RESUMO: No presente estudo, avaliamos a composição florística e estrutura de uma comunidade arbórea de um ecótono entre o Cerrado (cerradão) e a Floresta Atlântica (floresta estacional semidecidual) localizado no Parque Estadual de Porto Ferreira (PEPF), sudeste do Brasil. Verificamos também as relações florísticas com outros levantamentos realizados nestas fitofisionomias, e analisamos a distribuição das espécies nos domínios fitogeográficos brasileiros. Para isso amostramos todos os indivíduos vivos com PAP \geq 10cm em 64 parcelas de 10x10m (0,64 ha), totalizando 1755 indivíduos pertencentes a 101 espécies e 37 famílias. As famílias mais ricas em espécies foram Myrtaceae (13 espécies) e Fabaceae (11) sendo *Siparuna guianensis* a espécie mais abundante (188 indivíduos). Registramos duas espécies ameaçadas de extinção e verificamos um grande número de espécies com ampla distribuição entre os domínios fitogeográficos do Brasil. Encontramos baixos valores de similaridade florísticas entre as áreas analisadas, e a comunidade amostrada apresentou maior similaridade com levantamentos realizados em área de cerradão e ecótonos. Em síntese, os resultados corroboram a grande diversidade arbórea de áreas ecotonais, e o predomínio de espécies com ampla distribuição. Esse fato associado ao adensamento da vegetação verificado em série fotográfica histórica, reforçam que a área do estudo pertence a um ecótono em transformação.

Palavras-chave: ecótono; cerradão; floresta estacional semidecidual; fitogeografia; similaridade florísticas.

1. INTRODUCTION

Ecotones (gr. tonus = tension) are transitional areas between ecological communities that commonly occur along environmental gradients (ORCZEWSKA; GLISTA, 2005). Studies have reported high species richness and abundance tendency for ecotonal areas (e.g., KARK; van RENSBURG, 2006). Ecotones play an important role since environmental gradients are important speciation and diversification sites (SCHILTHUIZEN, 2000; SCHLUTER, 2000; SMITH et al., 2001). The preservation of such areas can guarantee adaptive responses of species to climate change (SMITH et al., 2001).

Savannah and forest ecotones play an important ecological role in the tropics (HOFFMANN, 2005). Mosaics

of savannah-forest transitions occupy about 24% of the Cerrado domain in Brazil (SILVA; BATES, 2002), and several studies have pointed to edaphic factors as decisive drivers of the establishment of Cerrado (savannah) and Atlantic Forest physiognomies (FURLEY, 1992; RATTER, 1992; DURIGAN; RATTER, 2006; PINHEIRO; MONTEIRO, 2008; BARROS et al. 2018; PINHEIRO et al. 2021). Furley (1992) concluded that soil moisture is a determining factor in savannah-forest transitions. For Ratter (1992), the soil is the main factor that influences the geographic distribution of vegetation. Furthermore, fire suppression can change the Cerrado vegetation types, since

forest vegetation types can replace open vegetations over the years (DURIGAN; RATTER, 2006; PINHEIRO et al., 2021). On the other hand, the presence of fire can facilitate the invasion of savannah species in seasonal semideciduous forests (PINHEIRO; MONTEIRO, 2008).

Sauer (1988) claims that there is a balance in savannah-forest ecotones in South America. However, several studies have shown a movement of these phytocenoses and an expansion of forest formations over areas previously occupied by Cerrado vegetation types (COUTINHO, 1990; RATTER, 1992; PIVELLO; COUTINHO, 1996; DURIGAN; RATTER, 2006; PINHEIRO; MONTEIRO, 2021).

Floristic and structural studies have been carried out on Cerrado and seasonal semideciduous forests of southeastern Brazil (DURIGAN et al., 1994; IVANAUSKAS et al. 1999; DURIGAN et al. 2002; TEIXEIRA et al. 2004; NETO et al., 2009; PINHEIRO & DURIGAN, 2012; HENCKER et al., 2012; GARCIA et al., 2015), but few of them have encompassed transitional areas (e.g., PINHEIRO; MONTEIRO, 2008; GUILHERME; NAKAJIMA, 2007; GOMES et al., 2004). Thus, we still do not understand this complex mosaic completely. Data about transitional areas are the basis for restoration projects, considering their importance for legal activities for environmental adaptations and licensing processes (e.g., Degraded Areas Recovery Plan – PRAD). Furthermore, floristic relationships of these ecotonal areas are important for characterizing and contextualizing vegetations under its transitional condition.

In this study, we evaluate the composition, structure, species distribution, and phytogeographic relationships of the tree community of an ecotonal area to support recovery, restoration and conservational actions in Cerrado-Atlantic Forest ecotones in São Paulo state.

2. MATERIALS E METHODS

2.1. Study area

The study was conducted in an area with a *cerradão* (CER) vegetation, a forested savannah, in transition with a seasonal semideciduous forest (SSF) in Porto Ferreira State Park (PFSP), municipality of Porto Ferreira, São Paulo state, southeastern Brazil (Figure 1). Plots were placed in an area at the north of “Lagoa do Cerrado” (21°50'49”S, 47°25'39”W), where the average altitude was 600 m. The region’s climate is classified as Cwa, or mesothermal dry winter, according to the Köppen-Geiger scale (Alvares et al., 2013). The annual mean temperature and precipitation are 22°C and 1470 mm, respectively, with a well pronounced dry winter (INMET, 2020).

The PFSP is composed of different vegetation types. CER is predominant in the north and SSF in the south of PFSP (Rossi et al., 2005). At the southernmost limit of the PFSP, parallel to the Mogi Guaçu River, the predominant vegetation type is the riparian forest (KONOPCZYK, 2014). CER occupies an area of about 180 ha, where the topography is higher (Bertoni et al., 2001). The study area has a secondary vegetation that has greatly recovered its structure, as evidenced by the sequential aerial photographs taken in the 1960s, 1970s, and 1980s (Figure 2).

2.2. Sampling and species distribution

We sampled 64 plots with 10x10 m (totalizing 0.64 ha), alternately placed along eight transects (with eight plots each).

The delimitation of transects and plots was made by using timber stakes and cotton strings. We sampled all living trees and palms with a perimeter at breast height (PBH) \geq 10 cm. The botanical material was identified by consulting specialized bibliography and taxonomic specialists and by comparing it with materials deposited in the Herbario Rioclarense (HRCB) collection. Fertile material was deposited in the HRCB collection. Taxa classification followed APG IV (2016) and the nomenclature was updated according to Flora do Brasil (Flora do Brasil, 2020), The Plant List (2020), and Tropicos (2020). We assessed the threatened status of the species sampled following the Livro Vermelho da Flora do Brasil (MARTINELLI; MORAES, 2013).

For phytosociological analysis, we recorded the PBH values and the height of each individual sampled. We assessed the natural distribution of the species in Brazilian biomes according to Flora do Brasil 2020 (2020). Species occurring in four or more biomes were classified as “widely distributed”.

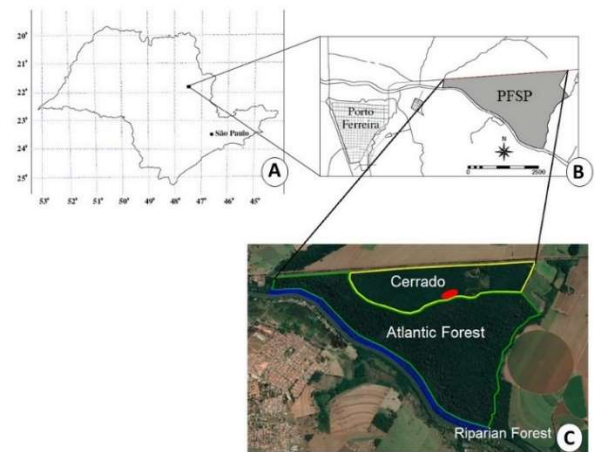


Figure 1. Location of Porto Ferreira State Park (PFSP), Porto Ferreira, São Paulo state. A- study site in São Paulo state map; B- PFSP; C- vegetation types of PFSP. Red ellipse indicates the site of the study plots.

Figura 1. Localização do Parque Estadual de Porto Ferreira (PEPF), Porto Ferreira, estado de São Paulo. A- Local de estudo no mapa do estado de São Paulo; B - PEPF; C- fitofisionomias do PEPF. A elipse vermelha indica a localização das parcelas do estudo.



Figura 2. Fotografias aéreas do Parque Estadual de Porto Ferreira. A- de 1962; B- de 1971; C- de 1983; D- imagem de satélite de 2020 (Google Earth©). Retângulos vermelhos indicam a localização das parcelas do estudo.

Figure 2. Aerial photographs of Porto Ferreira State Park. A- from 1962; B- from 1971; C- from 1983; D- satellite image from 2020 (Google Earth©). Red rectangles indicate the site of the study plots.

We compiled 19 studies previously carried out on CER, cerrado *sensu stricto*, SSF, and ecotones including one of these vegetation types (Table 1). Only native shrub and tree taxa identified at the species level were considered (if the study included more life forms).

2.3. Data analysis

Phytosociological parameters such as relative frequency, dominance, and importance value were calculated following Shepherd (2008). We also estimated the Shannon diversity index (H') and Pielou equability (J'). Finally, to assess sample sufficiency, we performed a species accumulation curve (SAC) to compute the mean SAC and its standard deviation

from 999 random permutations of the data (GOTELLI; COLWELL, 2001).

We conducted a cluster analysis to assess floristic similarity among the compiled studies and the present study. We built a binary matrix with the presence (1) and absence (0) of all species and conducted an agglomerative hierarchical cluster analysis (UPGMA) using the Jaccard dissimilarity index (LEGENDRE; LEGENDRE, 2012). Then, we verified exclusive and shared species among the studies carried out on ecotones.

All analyses were conducted in R software (R Development Core Team, 2020) using the 'vegan' package (OKSANEN et al., 2013).

Table 1. Selected studies for the floristic similarity analysis. Co: Code; Ph: physiognomy; N: number of taxons included in similarity analysis; Nt: total number of taxons; St. R. do P. Quatro: Santa Rita do Passa Quatro; S.B. do Campo: São Bernardo do Campo; Ssf: seasonal semideciduous forest; Eco: ecotone; Cd: cerrado; C ss: cerrado *sensu stricto*.

Tabela 1. Estudos selecionados para a análise de similaridade florística. Co: Código; Ph: fisionomia; N: número de táxons utilizados na análise de similaridade; Nt: Número total de táxons; St. R. do P. Quatro: Santa Rita do Passa Quatro; S.B. do Campo: São Bernardo do Campo; Ssf: floresta estacional semidecidual; Eco: ecótono; Cd: cerrado; C ss: cerrado *sensu stricto*.

Co	Study Site	Ph.	N / Nt	REFERENCE
A	Porto Ferreira – SP	Eco	87/ 101	Present study
B	Bauru – SP	Eco	223/ 264	Pinheiro & Monteiro, 2008
C	Brotas – SP	Eco	116/ 125	Gomes et al., 2004
D	Uberlândia – MG	Eco	121/ 141	Guilherme & Nakajima, 2007
E	Viçosa – MG	Ssf	93/ 107	Ribas et al., 2003
F	Campinas – SP	Ssf	132/ 362	Bernacci & Leitão, 1996
G	Campinas – SP	Ssf	135/ 201	Guaratini et al., 2008
H	St. R. do P. Quatro – SP	Ssf	56/ 56	Bertoni et al., 1988
I	St. R. do P. Quatro – SP	Ssf	59/ 81	Vieira et al., 1989
J	Itatinga – SP	Ssf	87/ 97	Ivanauskas et al., 1999
K	S. B. do Campo – SP	Ssf	70/ 75	Pastore et al., 1992
L	São Carlos – SP	Ssf	123/ 146	Silva & Soares, 2003
M	Águas da Prata – SP	Ssf	117/ 126	Toledo Filho et al., 1993
N	Uberlândia – MG	Cd	73/ 74	Alves et al., 2013
O	St. R. do P. Quatro – SP	Cd	81/ 148	Batalha & Mantovani, 2001
P	Luís Antonio – SP	Cd	89/ 121	Silva et al., 2004
Q	Bauru – SP	Cd	126/ 135	Pinheiro & Monteiro, 2006
R	Mogi mirim – SP	Cd	88/ 104	Toledo Filho et al., 1989
S	Uberlândia – MG	Cd, C ss	103/ 107	Costa & Araújo, 2001
T	Paraopeba – MG	Cd, C ss	81/ 91	Campos et al., 2006

3. RESULTS

We surveyed 1,755 trees and palms. We reported 101 species distributed in 37 botanical families and 69 genera (Table 2). *Enterpe edulis* Mart. (Arecaceae) and *Cedrela fissilis* Vell. (Meliaceae) were classified as “vulnerable” according to the list of threatened species of the Livro Vermelho da Flora do Brasil (Martinelli & Moraes, 2013). The Shannon-Wiener diversity index was 3.65 nats/ind., and the Pielou equability index was 0.79.

The richest species families were Myrtaceae (13 spp.), Fabaceae (11 spp.), Annonaceae (6 spp.), Anacardiaceae (5 spp.), Melastomataceae, Rubiaceae, Euphorbiaceae, and Lauraceae (4 spp. each). Altogether, these families comprised 50.4% of the species recorded and 54.3% of the individuals sampled. Fifteen families were represented by a single species, and 27 species were represented by a single individual. Lauraceae was the family with the highest importance value (IV= 28.9), followed by Anacardiaceae (IV= 28.5), and Fabaceae (IV= 24.7).

Among the species, *Tapirira guianensis* Aubl. showed the highest importance value (IV= 20), followed by *Miconia affinis*

DC. (IV= 18.7) and *Siparuna guianensis* Aubl. (IV= 18.4). *Siparuna guianensis* was the most abundant species (188 individuals, 10.7% of the total amount of species) followed by *M. affinis* (154 individuals, 8.7%), and *Xylopia aromatica* (Lam.) Mart. (113 individuals, 6.4%). According to the species accumulation curve, the sample size of our study was sufficient to discuss differences among the areas (Figure 3).

The total basal area of the individuals was 11.65 m². The mean height was 6.6 m (standard deviation= 2.9), with minimum and maximum values of 1.9 and 22 m, respectively. The mean diameter was 7.4 cm (standard deviation= 5.3), with minimum and maximum values of 3.18 cm and 58.27 cm, respectively.

Out of the 101 species reported in this study, 87 (1,703 individuals) were identified at the species level and classified based on their distribution among the Brazilian biomes. Of this total, 38 species (44%) were classified as “widely distributed”, and together they included 713 individuals (41.8%). Only five species (6%) and 31 individuals (1.8%) are restricted to the Atlantic Forest. Likewise, six species (7%) and 147 individuals (8.6%) are restricted to

Cerrado. Also, 31 species (36%) and 670 individuals (39.3%) are reported for both Cerrado and Atlantic Forest.

The total amount of 644 species were sampled from the 20 lists chosen for the floristic similarity, of which 244 (37.8%) have been reported exclusively in a single study (appendix 1). Only 26 species (4%) occurred in 50% or more of the lists (Appendix 2), and no species were recorded for all areas.

Among the ecotonal lists (A-D, Table 1), 341 species were reported, of which 215 (63%) has exclusive occurrence

(appendix 3), 126 (36.9%) occur in 50% or more of the 4 lists, and 19 species were reported for all areas (appendix 4).

The similarity analysis showed a high coefficient of cophenetic correlation (0.91), and floristic similarities were higher among closer areas. The cluster analysis segregated two major floristic groups (Figure 4). The first group (1) clustered the studies carried out on CER and ecotones, including the present study; the second (2) clustered the studies carried out on SSF.

Table 2. Floristic list, structural parameters, and biomes of occurrence of an ecotonal tree community, Porto Ferreira State Park, municipality of Porto Ferreira, São Paulo State, southeastern Brazil. Abd: abundance; RelDo: relative dominance; RelFr: relative frequency; IV: importance value; WD: widely distributed; Cer: Cerrado; AF: Atlantic Forest; Am: Amazon; Pa: Pampa; Caa: Caatinga; Pn: Pantanal; “\”: not evaluated; asterisks indicate threatened species according to “Livro Vermelho da Flora do Brasil” by CNCFlora (Martinelli & Moraes, 2013).

Tabela 2. Lista florística, parâmetros estruturais e ocorrência das espécies nos domínios fitogeográficos de uma comunidade arbórea ecotonal, Parque Estadual de Porto Ferreira, cidade de Porto Ferreira, Estado de São Paulo, Sudeste do Brasil. Abd: abundância; RelDo: dominância relativa; RelFr: frequência relativa; IV: valor de importância; WD: ampla distribuição; Cer: Cerrado; AF: Mata Atlântica; Am: Amazônia; Pa: Pampa; Caa: Caatinga; Pn: Pantanal; “\”: não avaliado; asteriscos indicam espécies ameaçadas de acordo com o “Livro Vermelho da Flora do Brasil”, CNCFlora (Martinelli & Moraes, 2013).

Family	Species	Abd	RelDo	RelFr	IV	Biomes
Anacardiaceae	<i>Astronium graveolens</i> Jacq.	7	0.21	0.71	1.32	WD
	<i>Astronium urundeuva</i> (M.Allemão) Engl.	1	0.04	0.1	0.2	WD
	<i>Litbraea molleoides</i> (Vell.) Engl.	1	0.02	0.1	0.18	WD
	<i>Tapirira guianensis</i> Aubl.	82	11.01	4.34	20.02	WD
	<i>Tapirira obtusa</i> (Benth.) J.D.Mitch.	26	4.34	1.72	7.53	Cer, AF, Am
Annonaceae	<i>Annona syriatica</i> A.St.-Hil.	1	0.02	0.1	0.18	WD
	<i>Annona</i> sp.	1	0.05	0.1	0.21	\
	<i>Duguetia lanceolata</i> A.St.-Hil.	4	0.16	0.4	0.79	Cer, AF
	<i>Xylopia aromatica</i> (Lam.) Mart.	113	4.13	4.34	14.91	Cer, Am
	<i>Xylopia brasiliensis</i> Spreng.	2	0.11	0.2	0.42	AF
Apocynaceae	<i>Xylopia sericea</i> A.St.-Hil.	25	1.15	1.72	4.29	Cer, AF, Am
	<i>Aspidosperma</i> sp.	1	0.04	0.1	0.2	\
Araliaceae	<i>Dendropanax cuneatus</i> (DC.) Decne. & Planch.	1	0.04	0.1	0.19	WD
	<i>Didymopanax morototoni</i> (Aubl.) Decne. & Planch.	17	0.7	1.41	3.08	WD
Arecaceae	<i>Acrocomia aculeata</i> (Jacq.) Lodd. ex Mart.	1	0.3	0.1	0.46	Cer, AF
	<i>Euterpe edulis</i> Mart. *	1	0.03	0.1	0.19	Cer, AF
	<i>Syagrus romanzoffiana</i> (Cham.) Glassman	27	5.34	1.92	8.8	Cer, AF, Pa
Asteraceae	<i>Piptocarpha macropoda</i> (DC.) Baker	2	0.04	0.2	0.35	Cer, AF
Bignoniaceae	<i>Handroanthus ochraceus</i> (Cham.) Mattos	3	0.07	0.2	0.44	WD
	<i>Handroanthus vellosii</i> (Toledo) Mattos	11	0.91	1.01	2.55	AF
Burseraceae	<i>Protium heptaphyllum</i> (Aubl.) Marchand	4	0.17	0.2	0.6	WD
Calophyllaceae	<i>Calophyllum brasiliense</i> Cambess.	1	0.02	0.1	0.17	WD
Clethraceae	<i>Clethra scabra</i> Pers.	2	0.12	0.2	0.43	Cer, AF, Caa
Combretaceae	<i>Terminalia argentea</i> Mart. & Zucc.	3	0.19	0.3	0.66	WD
	<i>Terminalia glabrescens</i> Mart.	42	1.88	2.02	6.29	WD
Euphorbiaceae	<i>Alchornea glandulosa</i> Poepp. & Endl.	2	0.7	0.2	1.02	Cer, AF, Am
	<i>Croton floribundus</i> Spreng.	10	0.9	0.91	2.38	AF
	<i>Maprounea guianensis</i> Aubl.	59	2.44	3.63	9.44	Cer, AF, Am
	<i>Sebastiania</i> sp.	3	0.15	0.3	0.62	\
Fabaceae	<i>Andira anbelmia</i> (Vell.) Benth.	4	0.13	0.2	0.56	Cer, AF
	<i>Andira humilis</i> Mart. ex Benth.	1	1	0.1	1.15	Cer
	<i>Copaifera langsdorffii</i> Desf.	61	9.27	2.72	15.47	WD
	<i>Dimorphandra mollis</i> Benth.	1	0.21	0.1	0.36	Cer, Am, Pn
	<i>Inga striata</i> Benth.	1	0.09	0.1	0.25	WD
	<i>Leptolobium dasy carpum</i> Vogel	1	0.06	0.1	0.22	Cer
	<i>Machaerium aculeatum</i> Raddi	6	0.3	0.61	1.25	Cer, AF, Pn
	<i>Machaerium villosum</i> Vogel	5	0.29	0.5	1.08	WD
	<i>Peltophorum dubium</i> (Spreng.) Taub.	1	0.01	0.1	0.17	WD
	<i>Platy podium elegans</i> Vogel	9	1.88	0.71	3.09	WD
Lacistemataceae	<i>Senegalia polyphylla</i> (DC.) Britton & Rose	12	0.22	0.81	1.72	WD
	<i>Lacistema hasslerianum</i> Chodat	6	0.07	0.61	1.02	Cer
Lamiaceae	<i>Aegiphila integrifolia</i> (Jacq.) Moldenke	3	0.2	0.3	0.67	WD

Family	Species	Abd	RelDo	RelFr	IV	Biomes
Lauraceae	<i>Ocotea corymbosa</i> (Meisn.) Mez	77	7.47	4.24	16.1	Cer, AF
	<i>Ocotea nutans</i> (Nees) Mez	24	0.66	1.92	3.94	Cer, AF
	<i>Ocotea pulchella</i> (Nees & Mart.) Mez	59	4.22	3.83	11.42	Cer, AF, Pa
	<i>Ocotea velutina</i> (Nees) Rohwer	1	0.29	0.1	0.45	Cer, AF
Malpighiaceae	<i>Byrsonima intermedia</i> A.Juss.	85	3.93	4.04	12.81	Cer
	<i>Byrsonima</i> sp.	3	0.13	0.3	0.6	\
Malvaceae	<i>Luebea divaricata</i> Mart.	2	0.03	0.2	0.35	WD
	<i>Luebea grandiflora</i> Mart.	4	0.92	0.4	1.55	WD
	<i>Pseudobombax grandiflorum</i> (Cav.) A.Robyns	7	0.42	0.4	1.22	AF
Melastomataceae	<i>Miconia affinis</i> DC.	154	4.86	5.15	18.78	Cer, AF, Am
	<i>Miconia ligustroides</i> (DC.) Naudin	3	0.12	0.3	0.6	Cer, AF, Caa
	<i>Miconia rubiginosa</i> (Bonpl.) DC.	1	0.02	0.1	0.17	Cer, Am
	<i>Tibouchina</i> sp.	1	0.01	0.1	0.17	\
Meliaceae	<i>Cedrela fissilis</i> Vell. *	2	0.11	0.2	0.42	WD
	<i>Trichilia casaretti</i> C.DC.	5	0.07	0.3	0.66	Cer, AF
	<i>Trichilia pallida</i> Sw.	44	1.19	2.22	5.92	Cer, AF, Am
Moraceae	<i>Ficus guaranitica</i> Chodat	6	0.14	0.61	1.08	Cer, AF
	<i>Maclura tinctoria</i> (L.) D.Don ex Steud.	1	0.01	0.1	0.17	WD
Myristicaceae	<i>Virola sebifera</i> Aubl.	17	0.73	1.41	3.11	Cer, AF, Am
Myrtaceae	<i>Eugenia florida</i> DC.	6	0.09	0.61	1.04	WD
	<i>Eugenia</i> sp.	1	0.42	0.1	0.58	\
	<i>Myrcia bella</i> Cambess.	35	2.01	2.02	6.03	Cer
	<i>Myrcia guianensis</i> (Aubl.) DC.	19	0.69	1.31	3.08	WD
	<i>Myrcia</i> sp.	24	0.41	1.51	3.29	\
	<i>Myrcia splendens</i> (Sw.) DC.	11	0.19	1.01	1.82	WD
	<i>Myrcia tomentosa</i> (Aubl.) DC.	20	0.72	1.61	3.47	WD
	<i>Myrcia venulosa</i> DC.	10	0.22	1.01	1.8	Cer, AF
	<i>Myrciaria</i> sp.	2	0.03	0.2	0.34	\
	Myrtaceae 1	1	0.01	0.1	0.16	\
	Myrtaceae 2	2	0.02	0.1	0.23	\
	Myrtaceae 3	1	0.02	0.1	0.18	\
	Ochnaceae	<i>Psidium rufum</i> Mart. ex DC.	15	0.79	1.11	2.75
<i>Ouratea castaneifolia</i> (DC.) Engl.		2	0.2	0.2	0.51	WD
Peraceae	<i>Pera glabrata</i> (Schott) Baill.	45	2.69	2.42	7.67	WD
Primulaceae	<i>Myrsine coriacea</i> (Sw.) R.Br. ex Roem. & Schult.	16	0.5	1.61	3.03	Cer, AF, Pa
	<i>Myrsine umbellata</i> Mart.	100	3.33	4.54	13.57	WD
Proteaceae	<i>Rouppala montana</i> Aubl.	1	0.01	0.1	0.17	WD
Rosaceae	<i>Prunus myrtifolia</i> (L.) Urb.	3	0.06	0.3	0.54	WD
Rubiaceae	<i>Amaioa guianensis</i> Aubl.	21	0.47	1.72	3.38	Cer, AF, Am
	<i>Cordia sessilis</i> (Vell.) Kuntze	11	0.16	0.91	1.7	Cer, Caa
	<i>Ixora brevifolia</i> Benth.	15	1.38	1.31	3.55	Cer, Caa
	<i>Rudgea viburnoides</i> (Cham.) Benth.	1	0.02	0.1	0.18	Cer, Caa, Am
Rutaceae	<i>Zanthoxylum rhoifolium</i> Lam.	2	0.14	0.2	0.46	WD
Salicaceae	<i>Casearia gossypiosperma</i> Briq.	4	0.19	0.3	0.72	Cer, AF, Am
	<i>Casearia</i> sp.	1	0.01	0.1	0.16	\
	<i>Casearia sylvestris</i> Sw.	29	0.79	1.92	4.36	WD
Sapindaceae	<i>Allophylus semidentatus</i> (Miq.) Radlk.	1	0.02	0.1	0.18	Cer, AF, Am
	<i>Cupania vernalis</i> Cambess.	9	0.2	0.81	1.52	WD
	<i>Matayba</i> sp.	10	0.77	0.81	2.15	\
Sapotaceae	<i>Chrysophyllum marginatum</i> (Hook. & Arn.) Radlk.	9	0.41	0.71	1.63	WD
	<i>Pouteria</i> sp.	1	0.03	0.1	0.19	\
Siparunaceae	<i>Siparuna guianensis</i> Aubl.	188	2.18	5.55	18.44	WD
Styracaceae	<i>Styrax acuminatus</i> Pohl	1	0.03	0.1	0.19	AF
	<i>Styrax camporum</i> Pohl	16	0.71	1.51	3.13	Cer, AF, Caa
	<i>Styrax ferrugineus</i> Nees & Mart.	2	0.06	0.2	0.38	Cer
Urticaceae	<i>Cecropia pachystachya</i> Trécul	5	0.19	0.4	0.88	WD
Vochysiaceae	<i>Qualea cordata</i> Spreng.	7	0.54	0.71	1.64	Cer, AF, Caa
	<i>Qualea grandiflora</i> Mart.	17	1.67	1.41	4.06	Cer
	<i>Vochysia tucanorum</i> Mart.	31	3.32	1.31	6.4	Cer, AF

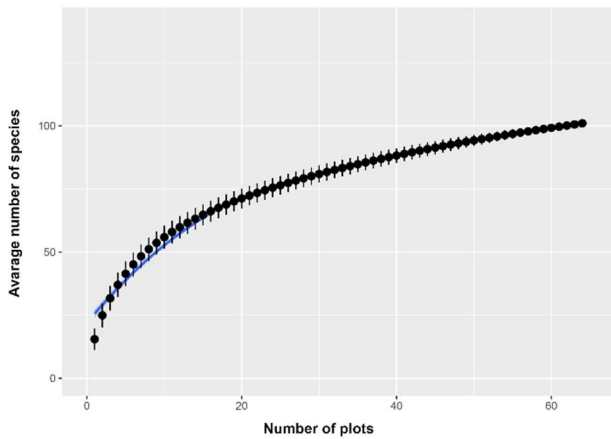


Figure 3. Species accumulation curve generated by using the sampling random method for the tree community surveyed in the ecotonal area of Porto Ferreira State Park, Porto Ferreira, Brazil. Figura 3. Curva de acumulação de espécies geradas para a comunidade arbórea amostrada em área ecotonal, Parque Estadual de Porto Ferreira, Porto Ferreira, Brasil.

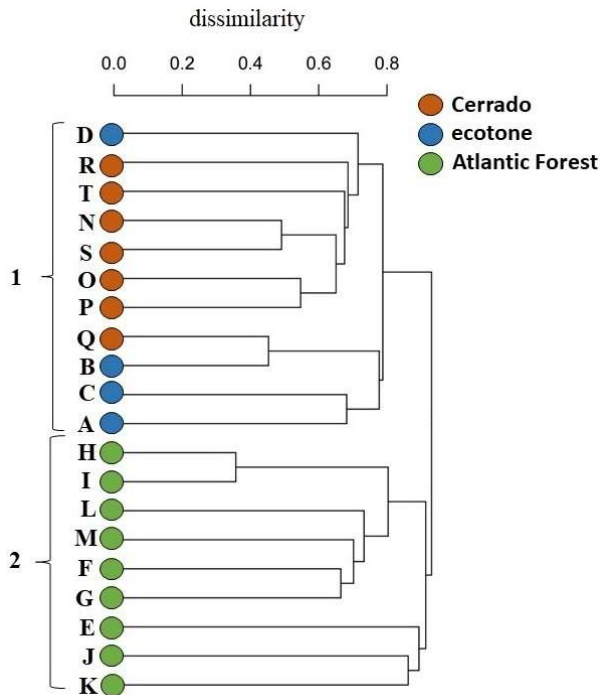


Figure 4. Cluster analysis (UPGMA), using Jaccard's index, of 20 studies carried out on Cerrado, Atlantic Forest, and ecotones. A – the present study. A-T – previous selected studies. The list of the selected studies is given in Table 1. Figura 4. Análise de agrupamento (UPGMA) usando o índice de Jaccard entre 20 estudos conduzidos no Cerrado, Mata Atlântica e ecótonos. Letra A- presente estudo. Estudos (identificados pelas letras A-T) estão disponíveis na tabela 1.

4. DISCUSSION

The tree diversity we found in this survey was similar from what was found in previous studies carried out on Cerrado (Toledo Filho et al., 1989; Costa & Araújo, 2001; Silva et al., 2004), SSF (Vieira et al., 1989; Ivanauskas et al., 1999), and ecotones (Gomes et al., 2004; Guilherme; Nakajima, 2007). However, diversity comparisons should be made with caution, given the differences in inclusion criteria and sample sizes among the studies. Studies encompassing a

big range of life forms (e.g., Bernacci; Leitão, 1996; Batalha; Mantovani, 2001; Guaratini et al., 2008; Pinheiro; Monteiro, 2008) naturally show a greater number of species.

The diversity value (3.65) found in the present study site is higher than those of studies on CER (which range from 2.46 to 3.54) (Costa; Araújo, 2001; Alves et al., 2013) and higher than the expected for SSF (ranging from 3.45 to 3.77) (Ivanauskas, 1999; Silva; Soares, 2003), and ecotone sites (ranging from 3.37 to 3.99) (Gomes et al., 2004; Guilherme; Nakajima, 2007). This shows that the diversity in transitional areas can be greater than what has been found in underlying vegetation types.

The richest families of tree species corroborate the results found for CER (Silva et al., 2004; Campos et al., 2006), SSF (Bernacci; Leitão, 1996; Ivanauskas et al., 1999; Guaratini et al., 2008), and ecotones (Gomes et al., 2004; Guilherme; Nakajima, 2007; Pinheiro; Monteiro, 2008). In SSF surveys, Fabaceae and Myrtaceae are often the richest families (Vieira et al., 1989; Bernacci; Leitão, 1996; Ivanauskas et al., 1999; Guaratini et al., 2008). Anacardiaceae is the only family of our list rarely ranked among the most diverse family in other studies. In Atlantic Forest, Myrtaceae, Fabaceae, Melastomataceae, Rubiaceae, and Euphorbiaceae are among the 10 richest families (BFG, 2015). These families are also among the richest families in Cerrado, except for Myrtaceae (BFG, 2015).

Lauraceae was the family with the highest importance value (IV= 9.64%) due to the large dimensions of the individuals and the abundance of *Ocotea corymbosa* and *Ocotea pulchella*. Likewise, Anacardiaceae showed the second highest IV (9.5%) due to the great number of individuals of *Tapirira guianensis* and *Tapirira obtusa* surveyed and their big sizes.

Many species were represented by a few individuals, corroborating the distribution pattern of individuals of tropical forest species (HUBBEL, 2013). In that sense, 45 species were represented by three or fewer individuals, 27 of which were represented by a single individual (e.g., *Andira humilis*, *Acrocomia aculeata*, *Calophyllum brasiliense*, and *Ocotea velutina*). The presence of rare or naturally low-density species indicates that new taxa tend to be found as the sample area increases, as demonstrated by Condit et al. (1996).

Regarding the most important species, *Tapirira guianensis*, has been reported in several studies carried out on different vegetation types and is considered a generalist species (Oliveira-Filho; Fontes, 2000). *Siparuna guianensis*, the most abundant species in the present study, has been frequently sampled in CER vegetation (e.g., Fina; Monteiro, 2009; Pereira-Silva et al., 2004) and reported in studies carried out on SSF (e.g., Joly, 1994; Silva et al., 2004; Yamamoto et al., 2005).

The basal area of the individuals we found was low (e.g., Toledo Filho et al., 1989; Vieira et al., 1989; Ivanauskas et al., 1999; Costa; Araújo, 2001; Guilherme; Nakajima, 2014). This fact may be related to anthropic disturbances suffered in the past, such as selective cutting, as showed in Figure 2 for the area of the present study. This supports that low basal area values are found in areas with selective cutting history (ALVES et al., 2013).

Many species of our study have wide distribution, occurring in different Brazilian biomes, which was also reported by Gomes et al. (2004) for another ecotonal area. Durigan et al. (2012) highlighted that generalist species with high ecological plasticity are generally abundant in ecotonal

areas. The predominance of species with wide distribution and the presence of species occurring in both Cerrado and Atlantic Forest reinforce that the area we studied is, in fact, an ecotone. On the other hand, few species are restricted to the Cerrado domain, e.g., *Qualea grandiflora*, *Byrsonima intermedia*, and *Myrcia bella*; and to the Atlantic Forest, e.g., *Xylopia brasiliensis*, *Handroanthus vellosi*, and *Pseudobombax grandiflorum* (Flora do Brasil, 2020).

The shared species among ecotonal studies (Appendix 4), such as *Copaifera langsdorffii*, *Ocotea corymbosa*, *Platypodium elegans*, *Terminalia glabrescens*, and *Vochysia tucanorum*, can be indicator species of Cerrado-Atlantic Forest ecotones from southeastern Brazil (DURIGAN et al., 2012).

Changes in the vegetation type of the study site over time (e.g., Figure 2), with a putative replacement of species of SSF over those of CER, indicate that fire suppression and soil conditions allowed the development of both floristics unities. The ecotonal area, was composed of savannah physiognomies with species of Cerrado (BERTONI et al., 2001; MATTOS; ROCHA, 2002). Currently, it is mainly composed of CER and SSF. Studies have indicated that fire is an important modelling agent in the physiognomies of Cerrado (HENRIQUES, 2005; HOFFMAN; MOREIRA, 2002; PINHEIRO et al., 2021). Fire suppression can replace areas initially occupied by open forms of Cerrado by CER and SSF over the years (DURIGAN et al., 1987; DURIGAN; RATTER 2006). A common action taken in protected areas in Brazil is to extinguish fire events (Monteiro, personal communication), which naturally occur in Cerrado (FIDELIS, 2020).

The analysis of floristic relationships among the compared areas showed a marked distinction between Cerrado and SSF, but placed ecotonal areas closer to the Cerrado or as a subgroup. Although, species of the SSF can colonize areas with fire suppression in Cerrado, the transformation of the vegetation type can be constrained by the soil type (HARIDASSAN, 1992; ROSSI et al., 2005; RODRIGUES et al., 2016; BARROS et al., 2018). Furthermore, we observed a great floristic heterogeneity among the analyzed areas, which included many exclusive and few shared species. Even though communities were sampled in geographically close areas and had the same vegetation types, they had few shared species. Our results support the hypothesis that tropical tree communities have a great floristic heterogeneity over short geographic distances (HUBBEL, 2013; BUENO et al., 2018). In addition, our results indicate that ecotonal tree communities may shelter a heterogeneous species composition and have species from different vegetation types. However, geographically closer communities share more species.

5. CONCLUSIONS

In this study, we provided important data about a poorly known vegetation type, corroborating the importance of preserving ecotonal areas for maintaining the high diversity of tropical tree communities. Our data can also help to recognize ecotones between Cerrado and Atlantic Forest from southeastern Brazil and can be used as a floristic reference for future conservation and restorative measures.

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8. APPENDIX

Appendix 1. Numbers of species reported exclusively in this and each one of the previous studies. Co: code; Vt: vegetation type; E spp.: number of exclusive species; Ssf: seasonal semideciduous forest; Cd: cerrado; C ss: cerrado *sensu stricto*.

Apêndice 1. Número de espécies exclusivas entre os estudos selecionados para a análise de similaridade florística. Co: código; Vt: Fitofisionomia; E spp: número de espécies exclusivas; Ssf: floresta estacional semidecidual; Cd: cerrado; C ss: cerrado *sensu stricto*.

Co	Reference	Vt	E spp.
A	Present study	Ecotone	5
B	Pinheiro & Monteiro 2008	Ecotone	30
C	Gomes et al. 2004	Ecotone	10
D	Guilherme & Nakajima 2007	Ecotone	14
E	Ribas et al. 2003	Ssf	32
F	Bernacci & Leitão 1996	Ssf	21
G	Guaratini et al. 2008	Ssf	22
H	Bertoni et al. 1988	Ssf	1
I	Vieira et al. 1989	Ssf	0
J	Ivanauskas et al. 1999	Ssf	16
K	Pastore et al. 1992	Ssf	24
L	Silva & Soares 2003	Ssf	18
M	Toledo Filho et al. 1993	Ssf	20
N	Alves et al. 2013	Cd	1
O	Batalha & Mantovani, 2001	Cd	6
P	Silva et al. 2004	Cd	4
Q	Pinheiro & Monteiro 2006	Cd	1
R	Toledo Filho et al. 1989	Cd	7
S	Costa & Araújo 2001	Cd, C ss	5
T	Campos et al. 2006	Cd, C ss	7

Appendix 2. Species occurring in 10 (50%) or more lists among the compared studies and PFSP. N: number of lists in which the species occurs.

Apêndice 2. Espécies com ocorrência igual ou superior a 10 listas (50%) entre os estudos selecionados para a análise de similaridade florística. N: número de listas com ocorrência.

Species	N	%
<i>Roupala montana</i> Aubl.	18	90
<i>Copaifera langsdorffii</i> Desf.	16	80
<i>Qualea multiflora</i> Mart.	16	80
<i>Tapirira guianensis</i> Aubl.	14	70
<i>Casearia sylvestris</i> Sw.	13	65
<i>Myrcia splendens</i> (Sw.) DC.	13	65
<i>Ocotea corymbosa</i> (Meisn.) Mez	13	65
<i>Vochysia tucanorum</i> Mart.	13	65
<i>Siparuna guianensis</i> Aubl.	12	60
<i>Dimorphandra mollis</i> Benth.	11	55
<i>Lafoensia pacari</i> A.St.-Hil.	11	55
<i>Miconia albicans</i> (Sw.) Triana	11	55
<i>Myrcia tomentosa</i> (Aubl.) DC.	11	55
<i>Myrsine umbellata</i> Mart.	11	55
<i>Pera glabrata</i> (Schott) Baill.	11	55
<i>Plathymentia reticulata</i> Benth.	11	55
<i>Platypodium elegans</i> Vogel	11	55
<i>Qualea grandiflora</i> Mart.	11	55
<i>Rudgea viburnoides</i> (Cham.) Benth.	11	55
<i>Xylopia aromatica</i> (Lam.) Mart.	11	55
<i>Bowdichia virgilioides</i> Kunth	10	50
<i>Brosimum gaudichaudii</i> Trécul	10	50
<i>Caryocar brasiliense</i> Cambess.	10	50
<i>Croton floribundus</i> Spreng.	10	50
<i>Protium heptaphyllum</i> (Aubl.) Marchand	10	50
<i>Terminalia glabrescens</i> Mart.	10	50

Appendix 3. Numbers of exclusive species among the studies carried out on ecotonal vegetation. Co: code; Vt: vegetation type; E spp.: number of exclusive species; Ssf: seasonal semideciduous forest; Cd: cerrado; C ss: cerrado *sensu stricto*.

Apêndice 3. Número de espécies exclusivas entre os estudos selecionados para a análise de similaridade florística. Co: código; Vt: fitofisionomia; E spp: número de espécies exclusivas; Ssf: floresta estacional semidecidual; Cd: cerrado; C ss: cerrado *sensu stricto*.

Co	REFERENCE	Vt	E spp.
A	Present study	Ecotone	18
B	Pinheiro & Monteiro 2008	Ecotone	125
C	Gomes et al. 2004	Ecotone	30
D	Guilherme & Nakajima 2007	Ecotone	46

Appendix 4. Shared species among ecotonal vegetation lists.

Apêndice 4. Espécies compartilhadas nas listas de vegetação ecotonal.

Species
<i>Casearia sylvestris</i> Sw.
<i>Copaifera langsdorffii</i> Desf.
<i>Dimorphandra mollis</i> Benth.
<i>Myrcia tomentosa</i> (Aubl.) DC.
<i>Myrsine umbellata</i> Mart.
<i>Ocotea corymbosa</i> (Meisn.) Mez
<i>Pera glabrata</i> (Schott) Baill.
<i>Platypodium elegans</i> Vogel
<i>Protium heptaphyllum</i> (Aubl.) Marchand
<i>Qualea grandiflora</i> Mart.
<i>Roupala montana</i> Aubl.
<i>Rudgea viburnoides</i> (Cham.) Benth.
<i>Siparuna guianensis</i> Aubl.
<i>Styrax camporum</i> Pohl
<i>Tapirira guianensis</i> Aubl.
<i>Terminalia glabrescens</i> Mart.
<i>Vochysia tucanorum</i> Mart.
<i>Xylopia aromatica</i> (Lam.) Mart.
<i>Zanthoxylum rhoifolium</i> Lam.