

Original Article

## Fire effects on Atlantic Forest sites from a composition, structure and functional perspective

Efeitos do fogo na Mata Atlântica por meio de uma abordagem de composição, estrutura e funcional

L. Z. G. Carvalho<sup>a</sup> , K. G. Massi<sup>a,b\*</sup> , M. P. Coutinho<sup>c</sup>  and V. D. Magalhães<sup>d</sup> 

<sup>a</sup>Universidade Estadual Paulista "Júlio de Mesquita Filho" – UNESP, Centro Nacional de Monitoramento e Alertas de Desastres Naturais – CEMADEN, Programa de Pós-graduação em Desastres Naturais, São José dos Campos, SP, Brasil

<sup>b</sup>Universidade Estadual Paulista "Júlio de Mesquita Filho" – UNESP, Departamento de Engenharia Ambiental, Instituto de Ciência e Tecnologia, São José dos Campos, SP, Brasil

<sup>c</sup>Centro Paula Souza, Faculdade de Tecnologia – FATEC, Jacaré, SP, Brasil

<sup>d</sup>Bolsista FAPESP, São Paulo, SP, Brasil

### Abstract

Recently, some portions of the Atlantic Forest biome have been suffering an increase in forest fires, possibly changing its vegetation cover, composition, structure and functioning. Understanding these changes is critical to evaluate the present and future response of tropical forests to fire. Thus, the purpose of our study was to evaluate how diversity, structure and functioning of tree communities differed between burned and unburned sites. Two unburned and two burned forest patches were selected for floristic and phytosociological surveys. Then, we calculated species richness, Shannon diversity index, tree density and basal area, Importance Value Index for trees in each site and we assessed community weighted mean of six functional traits (maximum tree height, wood density, leaf length, leaf deciduousness, shade tolerance and dispersal mode). Diversity, species richness, tree density and basal area were similar between sites. We found changes in floristic composition, but did not verified variations in functional traits. Results indicate that recovery may be fast and that pioneer and early secondary species are occupying post burned sites (nine years old). One-time anthropogenic, superficial and low intensity fires might disrupt advanced stages of succession and start again the dynamics of species substitution.

**Keywords:** burning, diversity, flora, functional traits, tropical rainforest.

### Resumo

Recentemente, algumas regiões do bioma Mata Atlântica têm sofrido com um aumento de incêndios, possivelmente modificando sua cobertura vegetal, composição, estrutura e funcionalidade. Compreender essas mudanças é imprescindível para avaliar as respostas, no presente e futuro, das florestas tropicais ao fogo. Assim, o objetivo do nosso estudo foi avaliar como a diversidade, estrutura e funcionamento das comunidades arbóreas diferem entre áreas queimadas e não queimadas. Dois fragmentos queimados e dois fragmentos não queimados foram selecionados para os levantamentos florísticos e fitossociológicos. Depois, foram calculadas a riqueza de espécies, o Índice de diversidade de Shannon, densidade da árvore e área basal, Índice de valor de importância para as espécies em cada uma das áreas e avaliamos a média de seis características funcionais (altura máxima da árvore, densidade da madeira, comprimento da folha, deciduidade foliar, tolerância a sombra e síndrome de dispersão). Diversidade, riqueza, densidade e área basal foram similares entre as áreas analisadas. Nós encontramos mudanças na composição florística, mas não foram verificadas variações nas características funcionais. Os resultados indicam que a recuperação pode ser rápida e que espécies pioneiras e secundárias iniciais estão ocupando as áreas queimadas cerca de nove anos depois. Um único incêndio antrópico, superficial e de baixa intensidade, pode interromper estágios avançados de sucessão e iniciar a nova dinâmica de substituição de espécies.

**Palavras-chave:** queimadas, diversidade, flora, traços funcionais, floresta tropical.

## 1. Introduction

The Atlantic Forest biome is a biodiversity hotspot (Myers et al., 2000). The biome presents great diversity of habitats, among which evergreen and seasonal forests,

mangroves and highland grasslands (IBGE, 2012). Due to intense deforestation and human disturbance that mostly occurred in the first half of the 19th century (Dean, 1996),

\*e-mail: klecia.massi@unesp.br

Received: September 26, 2022 – Accepted: 13 December, 2022



This is an Open Access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original work is properly cited.

only about 13% of Atlantic Forest biome native vegetation cover remains in Brazil (Fundação SOS Mata Atlântica, 2018). Nature reserves protect only 9% of the remaining forest (Ribeiro et al., 2009). Recently, some portions of the Atlantic Forest biome have been experiencing an increase in area burned by anthropogenic wildfires (INPE, 2021).

Every year, wildfires burn more than 400 million hectares worldwide (Andela et al., 2017) and shape the structure and diversity of all biomes (Bond and Keeley, 2005). Fires in tropical forests generally cause extensive top-kill in small trees (Hoffmann et al., 2009) and leaf-fall in larger trees, allowing increased light to the forest floor and the establishment of grasses, changing the local fire regime (Veldman and Putz, 2011). This results in lowered humidity, increased forest environment dryness, decreased tree cover, and altered species richness (Fu et al., 2013), changing likelihood of recurrent fires. Edge environments are specially more exposed to the action of strong winds, lower humidity, higher air temperatures and to fires (Magnago et al., 2015; Guedes et al., 2020). When subjected to such conditions, non-adapted species can be selectively excluded from the community, generating a drastic change in species composition of the forest environment, which may come to be dominated by few species tolerant to drought and fire conditions (Silvério et al., 2013; Brancalion et al., 2019; Sansevero et al., 2020).

In some forest fragments, these impacts can initiate the process of biotic homogenization and forest secundarization (although both phenomena are independent and happen in different ways: Nobre et al., 1991; Salazar et al., 2007; Nobre and Borma, 2009; Flores et al., 2016; Veldman and Putz, 2011; Staal et al., 2018), i. e. high proportion of species requiring undisturbed forest tend to experience intense degradation of their forest habitats, while secondary forest stands face a form of arrested succession supporting impoverished communities (Jolly et al., 2015; Mata et al., 2022). In general, it is verified higher species richness, diversity and basal area for unburned sites and lowest for recurrent burned areas in Amazon forests (Mena et al., 2020; Prestes et al., 2020).

Species response to fires has been associated with functional traits by different mechanisms, such as bark thickness, wood density and leaf area providing structural protection against fire or related to an avoidance strategy of water loss (Hoffmann et al., 2004; Hoffmann et al., 2009; Armenteras et al., 2021). In addition, in forest areas subject to fire, it would be expected to find a greater number of species with leaf deciduousness (deciduous and semideciduous species), dispersal syndromes by abiotic agents, and shadow intolerance, among other functional traits (Massi et al., 2017).

Despite the importance of the Atlantic Forest and its potential threat to fires, studies on the impacts of disturbances such as fires over these ecosystems are scarce (Guedes et al., 2020; Sansevero et al., 2020; Mata et al., 2022). Thus, the objective of our study is to contribute to filling this knowledge gap by investigating how fire shapes composition, diversity, structure and functioning of the Atlantic Forest. Here, we evaluated the extent to which diversity (richness and Shannon diversity index), structure (tree density, basal area and importance value), and functioning (community weighted mean of five

vegetative and one reproductive traits) of tree communities differ between burned and unburned Atlantic Forest sites. Considering fire as an anthropogenic disturbance in humid tropical forests, we predicted that tree density, basal area, richness and diversity would be lower in the burned sites. Additionally, we predict that burned sites would be dominated by species with traits associated with small leaf length, low maximum height and wood density, shade intolerant, leaf deciduousness and abiotic dispersal. Finally, we predicted that the importance value of species of burned sites (higher for pioneer species) would differ from unburned forests (lower for pioneer species).

## 2. Material and Methods

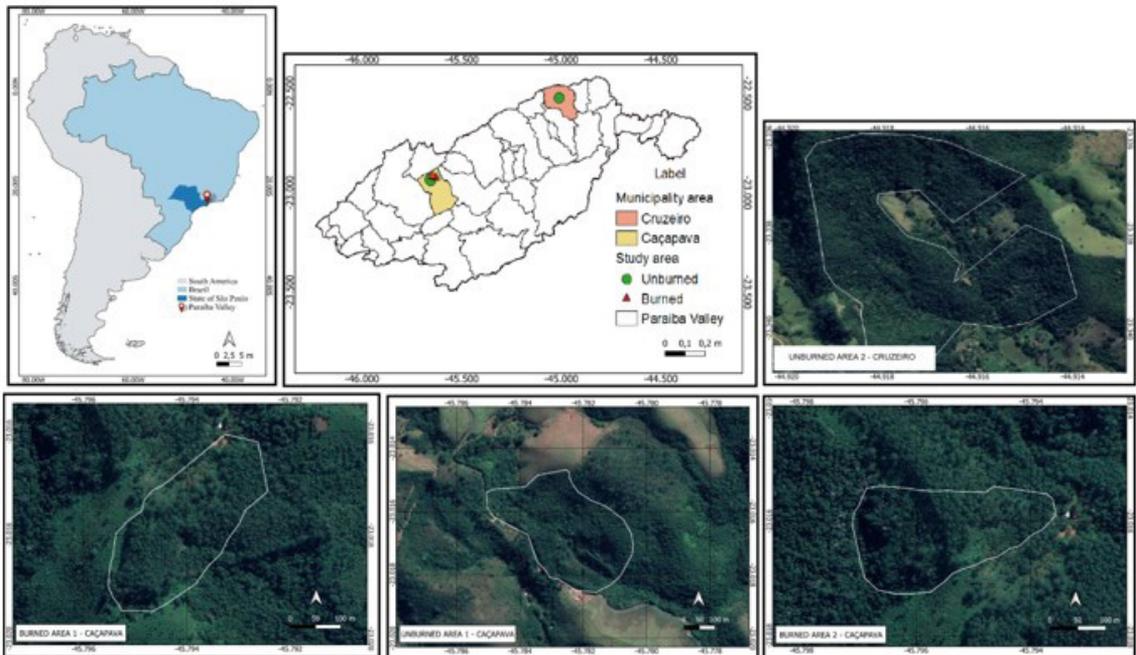
### 2.1. Study area

The study was conducted in forest patches in Paraíba do Sul river basin, southeast Brazil (Figure 1 and Supplementary Information 1). The region is located between São Paulo and Rio de Janeiro, both Brazilian biggest cities and with a current population estimated at 2 million inhabitants along the basin (IBGE, 2017). The Paraíba do Sul river basin region has a hilly relief (between 20% to 45% slope: Embrapa, 1979), located between two large mountain ranges, the Serra da Mantiqueira and the Serra do Mar, soil is red-yellow latosol (Brasil, 1960), vegetation is Atlantic Forest biome (transition between evergreen and seasonal forests) and disjoint savanna areas (Radam Brasil, 1983), climate is classified as dry-winter subtropical (Cwa: Alvares et al., 2013), average annual temperature is 21 °C, with a relative humidity of approximately 70% (INPE, 2022), landscape is dominated by pasture, small fragments of secondary forest and silviculture (*Eucalyptus* species: Sapucci et al., 2021).

Historically, sugar cane in the 17th century, coffee in the 19th and urban-industrial expansion along the road-railway axis (1950) gave rise to an anthropogenic landscape (Dean, 1996). Years later, industrial production, especially linked to pulp and paper, and low intensity pasture took over the region land. Since then, the region has become a focus of natural regeneration of the Atlantic Forest, having its vegetation cover increased to more than 35% by 2015 (Numata et al., 2017; Silva et al., 2017). Despite that, deforestation actions, including anthropogenic fires in secondary and regenerating forests, still represent 95% of the damage caused to these environments between the years 2003 and 2021 (INPE, 2021). Furthermore, fire has negative implications for regeneration areas, for restoration projects and for the conservation of remnants (Guedes et al., 2020). We do not have information on fires that occurred in these forests, but tropical rainforests are fire-sensitive ecosystems, where fire is usually superficial and low-intensity, due to humidity, but it may cause extensive damage (Pivello et al., 2021).

### 2.2. Floristic and phytosociological inventory

Two unburned (U1: Caçapava and U2: Cruzeiro municipality) and two burned (B1 and B2: Caçapava municipality) forest patches were selected for floristic and phytosociological surveys, which we inventoried



**Figure 1.** Paraíba do Sul river basin study site, Southeast Atlantic Forest biome, inside São Paulo state, Brazil and South America. Red and blue pins represent burned and unburned forest sites where field inventory was performed, with satellite images of each.

in the beginning of 2021 (U2 was inventoried in 2019; Figure 1 and Table S1: Silva et al., 2021). All patches were located in private properties, but U1 site was also inside a municipal protected area of sustainable use (Área de Proteção Ambiental da Serra do Palmital), covered with plateau evergreen to seasonal tropical rainforest, 20 years without disturbance; U2 was covered by evergreen to seasonal tropical rainforest, with no history of significant disturbance. B1 and B2 sites were located inside the same municipal protected area (Área de Proteção Ambiental da Serra do Palmital), covered with plateau evergreen to seasonal tropical rainforest, which burned in 2012.

Floristic and phytosociological surveys in U1, B1 and B2 were performed using the quadrant point sampling method (Durigan, 2003), with the sampling units being distributed approximately 10 to 30 meters apart, covering the entire study area. U1 had 76 sampled quadrant points; B1, 62; and B2, 50 (forest gaps were avoided). The four individuals closest to the center of the crosshead with stem diameter  $\geq 5$  cm at breast height had their species identified and diameter measured. For data collection in U2, we randomly installed 34 plots of 25 x 4 m (100 m<sup>2</sup>, plots were distant 100 m from each other) and we identified and measured all individuals with stem diameter  $\geq 5$  cm at breast height (Silva et al., 2021). Plant material was identified using botanical identification references (Lorenzi, 2016). For plant family classification, we used the Angiosperm Phylogeny Group IV (APG IV, 2016) and the Brazil Flora List (JBRJ, 2020).

### 2.3. Taxonomic evaluation

For each of the four sites, we calculated the following parameters: species richness, Shannon diversity index

( $H' = -\sum pi \cdot \ln pi$ ; being  $pi = ni / N$ , where  $ni$  is number of individuals of a species  $i$  and  $N$  is the total number of individuals), tree density and basal area. We also determined the Importance Value Index (IVI; Kent, 2012) for trees in each site. By aggregating three important ecological parameters (abundance, dominance and frequency), this index is an indication of which species are ecologically more important in sites with and without fire.

### 2.4. Functional evaluation

The functional traits considered in this study are related to species strategies to cope with fire (resistance or avoidance) (Cornelissen et al., 2003; Sobral and Cianciaruso, 2012; Massi et al., 2017). These included five vegetative traits: maximum tree height, wood density, leaf length, leaf deciduousness (evergreen and deciduous) and shade tolerance (tolerant and not tolerant) and one reproductive trait: dispersal mode (biotic and abiotic). Successional status of species obtained from Barbosa et al. (2017). The information on species functional traits was obtained from data compilation (JBRJ, 2020). Finally, we calculated community weighted mean (CWM: Garnier et al., 2004) trait values, weighted by species abundance (CWM height, CWM leaf length, CWM wood density, CWM deciduousness, CWM dispersal mode, CWM shade tolerance).

### 2.5. Data analysis

To evaluate whether species richness, diversity, tree density and basal area (by area: m<sup>2</sup>/ha) and CWM values of traits differed between the burned and unburned sites, we used T test. Analyses were performed in R version 3.6.3 (R Core Team, 2019).

### 3. Results

#### 3.1. Forest structure and composition

The four studied communities were characterized by distinctive plant communities as shown in Table 1 (richness of U1 and U2 were 20 and 47; while B1 and B2 were, 16 and 17). Only a few species were common to burned and unburned forest sites: *Casearia sylvestris* Sw., *Cecropia pachystachya* Trécul, *Cedrela fissilis* Vell., *Euterpe edulis* Mart., *Piptadenia gonoacantha* (Mart.) J.F. Macbr. and *Pleroma granulosum* (Desr.) D. Don. Despite that, *C. fissilis*, *E. edulis* and *P. gonoacantha* had higher IVI on unburned sites; while *C. pachystachya* and *P. granulosum* had higher IVI on burned sites (Table 1: *C. sylvestris* was found equally in burned and unburned sites). Fifty-eight species were exclusive to unburned sites (mostly late secondary species) and ten to burned ones (Table 1). *Schizolobium parahyba* (Vell.) Blake (IVI = 14.17) and *L. grandiflora* (IVI = 34.88) dominated unburned sites 1 and 2, respectively while *X. aromatica* (IVI = 34.93) and *C. pachystachya* (IVI = 14.30) dominated burned sites 1 and 2, respectively (Table 1).

#### 3.2. Taxonomic and functional evaluation

Richness and Shannon diversity did not differ between burned and unburned sites among burned and unburned sites (Table 2 and Figures 2A and C). Tree density and Basal area were not significantly different between burned and unburned sites (Table 2 and Figures 2B and D).

Regarding the functional composition metrics for vegetative traits, species of burned sites had the

same maximum height, leaf length and wood density compared to unburned sites nine years ago (Table 2 and Figures 2E to G). CWM deciduousness was higher in burned areas, representing a higher proportion of evergreen individuals in burned and a higher percentage of deciduous individuals in unburned areas (Table 2 and Figures 2H). CWM shade tolerance and CWM dispersal mode did not differ between burned and unburned communities (Table 2 and Figures 2I and J).

### 4. Discussion

We examined how forest structure, taxonomic diversity and functional composition, differ between the tree component of burned and unburned Atlantic Forest sites. Diversity, species richness, tree density and basal area were similar between fire regimes. We found changes in floristic composition (as shown by IVI), but not significant shifts in functional composition between fire regimes (except for leaf deciduousness). The results of field data indicates that forest recovery was very fast and that in nine years after fire functional changes are not perceived. Results might also indicate that fire intensity was not strong enough to make substantial damage.

We found 58 and 10 species exclusive to unburned and burned sites, respectively, indicating two different plant communities according to fire regime, as verified by Ribeiro et al. (2019) for savanna ecosystems. Only a few species (six) were common between burned and unburned fragments, but with dissimilar IVI. *C. pachystachya* and *T. granulosa*, which showed higher

**Table 1.** Family, species and Importance Value index (IVI, %) in unburned (U1 and U2) and burned (B1 and B2) forest patches in Paraíba do Sul river basin, Southeast Atlantic Forest biome, Brazil.

Family	Species	U1	U2	B1	B2
Anacardiaceae	<i>Schinus terebinthifolia</i> Raddi			1.05	2.51
Annonaceae	<i>Guatteria australis</i> A.St.-Hil.		0.71		
Apocynaceae	<i>Xylopia aromatica</i> (Lam.) Mart.			34.93	5.81
	<i>Aspidosperma discolor</i> var. <i>parvifolium</i> Müll.Arg.		0.81		
	<i>Tabernaemontana hystrix</i> Steud.		3.28		
Arecaceae	<i>Astrocaryum aculeatissimum</i> (Schott) Burret	2.62			
	<i>Euterpe edulis</i> Mart.	8.15	8.58	0.91	1.32
	<i>Syagrus romanzoffiana</i> (Cham.) Glassman	2.68	4.82		
Bignoniaceae	<i>Sparattosperma leucanthum</i> (Vell.) K.Schum.		8.63		
	<i>Zeyheria tuberculosa</i> (Vell.) Bureau ex Verl.		1.40		
Boraginaceae	<i>Cordia trichotoma</i> (Vell.) Arráb. ex Steud		1.66		
Cannabaceae	<i>Trema micrantha</i> (L.) Blume		2.35	4.2	
Dicksoniaceae	<i>Dicksonia sellowiana</i> Hook	3.75		0.89	1.53
Euphorbiaceae	<i>Alchornea glandulosa</i> Poepp. & Endl.		0.77		
	<i>Croton floribundus</i> Spreng.		1.71		
	<i>Croton urucurana</i> Baill.		1.60		
	<i>Sapium glandulatum</i> (Vell.) Pax		2.67		

Table 1. Continued...

Family	Species	U1	U2	B1	B2
Fabaceae	<i>Acacia plumosa</i> Mart. ex Colla			4.55	
	<i>Albizia niopoides</i> (Spruce ex Benth.) Burkart			5.45	3.33
	<i>Anadenanthera colubrina</i> (Vell.) Brenan	5.42			
	<i>Anadenanthera peregrina</i> (L.) Speg.		3.19		
	<i>Bauhinia forficata</i> Link		7.19		
	<i>Dalbergia nigra</i> (Vell.) Allemão ex Benth.			12.04	
	<i>Erythrina verna</i> Vell.			1.58	
	<i>Inga marginata</i> Willd.	1.02			
	<i>Inga sessilis</i> (Vell.) Mart.			2.66	
	<i>Inga striata</i> Benth.			2.03	
	<i>Inga uruguensis</i> Hook. & Arn.	2.36			
	<i>Leucochloron incuriale</i> (Vell.) Barneby & J.W.Grimes			1.72	
	<i>Libidibia ferrea</i> (Mart. ex Tul.) L.P.Queiroz	3.52			
	<i>Machaerium hirtum</i> (Vell.) Stellfeld			6.10	
	<i>Machaerium nyctitans</i> (Vell.) Benth.			18.21	
	<i>Machaerium stipitatum</i> Vogel			7.30	3.59
	<i>Machaerium villosum</i> Vogel	3.65			5.27
	<i>Paubrasilia echinata</i> (Lam.) Gagnon, H.C.Lima & G.P.Lewis	1.53			
	<i>Piptadenia gonoacantha</i> (Mart.) J.F.Macbr.	5.60	26.14	3.26	3.03
	<i>Platypodium elegans</i> Vogel			8.41	
	<i>Pterogyne nitens</i> Tul.				4.81
	<i>Senna macranthera</i> (DC. Ex Collad.) H.S.Irwin & Barneby			1.50	
	<i>Schizolobium parahyba</i> (Vell.) Blake	14.17			2.83
<i>Aegiphila integrifolia</i> (Jacq.) Moldenke			0.73		
<i>Vitex polygama</i> Cham.			1.79		
Lauraceae	<i>Endlicheria paniculata</i> (Spreng.) J.F.Macbr.			0.94	
	<i>Nectandra oppositifolia</i> Nees			10.00	
	<i>Ocotea velutina</i> (Nees) Rohwer	6.51	1.63		
Lecythidaceae	<i>Cariniana estrellensis</i> (Raddi) Kuntze	1.90			
Malvaceae	<i>Apeiba tibourbou</i> Aubl.		1.94		
	<i>Ceiba speciosa</i> (A.St.-Hil.) Ravenna	7.95	1.12		
	<i>Guazuma ulmifolia</i> Lam.			5.00	6.70
	<i>Luehea divaricata</i> Mart.	4.97			
	<i>Luehea grandiflora</i> Mart. & Zucc.			34.88	
	<i>Pseudobombax grandiflorum</i> (Cav.) A.Robyns			0.99	
Melastomataceae	<i>Miconia cabucu</i> Hoehne			4.13	7.75
	<i>Miconia cinnamomifolia</i> (DC.) Naudin		2.43		
	<i>Miconia sellowiana</i> Naudin		0.71		
	<i>Pleroma granulosum</i> (Desr.) D. Don	4.16	5.72	7.39	12.53
	<i>Pleroma mutabile</i> (Vell.) Triana			2.9	2.06
Meliaceae	<i>Cabralea canjerana</i> (Vell.) Mart.		1.98		
	<i>Cedrela fissilis</i> Vell.	4.50	2.20	0.91	1.57
	<i>Guarea kunthiana</i> A.Juss.		16.14		

**Table 1.** Continued...

Family	Species	U1	U2	B1	B2
Moraceae	<i>Ficus adhatodifolia</i> Schott in Spreng.		0.98		
	<i>Maclura tinctoria</i> (L.) D.Don ex Steud.		2.52		
Myrtaceae	<i>Myrcia splendens</i> (Sw.) DC.		12.40		
	<i>Pimenta pseudocaryophyllus</i> (Gomes) Landrum		0.96		
	<i>Psidium sartorianum</i> (O.Berg) Nied.	2.71			
Phytolaccaceae	<i>Gallsia integrifolia</i> (Spreng.) Harms	1.85			
Primulaceae	<i>Myrsine coriacea</i> (Sw.) R.Br. ex Roem. & Schult.			3.40	5.70
	<i>Myrsine gardneriana</i> A.DC.			3.37	7.22
	<i>Randia armata</i> (Sw.) DC.		1.51		
Rutaceae	<i>Zanthoxylum rhoifolium</i> Lam.	2.53	3.45		1.84
Salicaceae	<i>Casearia decandra</i> Jacq.		1.39		
	<i>Casearia sylvestris</i> Sw.	3.30	21.98	2.03	4.41
Sapindaceae	<i>Cupania racemosa</i> (Vell.) Radlk.		1.21		
	<i>Cupania vernalis</i> Cambess.		6.47		
Siparunaceae	<i>Siparuna guianensis</i> Aubl.		12.48		
Cecropiaceae	<i>Cecropia glaziovii</i> Sneathl.		1.19		
	<i>Cecropia hololeuca</i> Miq.	1.37			
	<i>Cecropia pachystachya</i> Trécul	3.78	2.59	9.21	14.30
Vochysiaceae	<i>Vochysia tucanorum</i> Mart.		0.67		

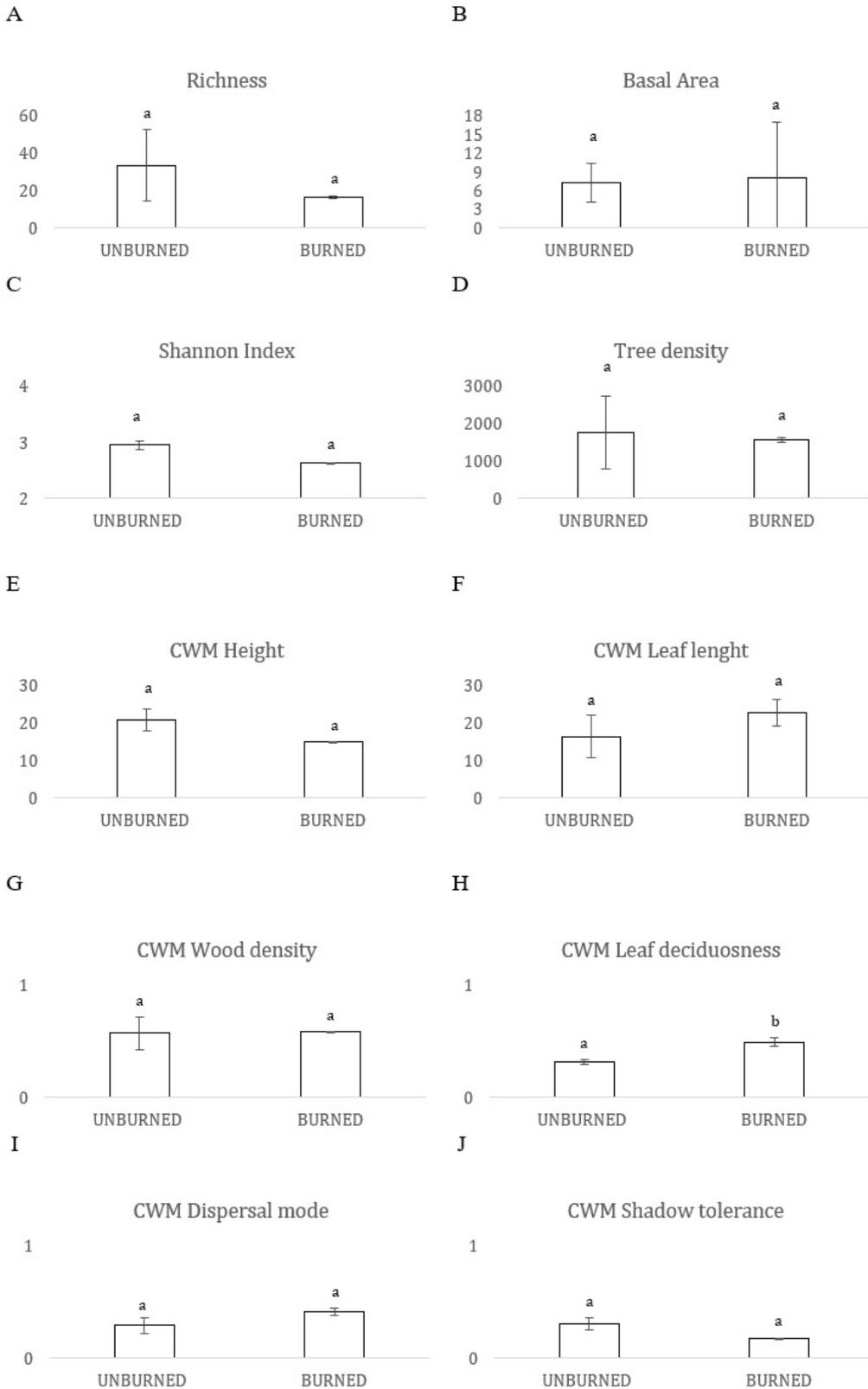
**Table 2.** Mean values and standard deviations, differences between burned and unburned sites and results of T tests and p-value of the taxonomic and structure variables and the community-weighted mean (CWM) of vegetative and reproductive traits in the four sites (two unburned and two burned).

Variables	Burned	Unburned	(B-U)/U %	T	p-value
Richness	16.5 ± 0.7	33.5 ± 19.1	-50.7	1.258	0.427
Shannon	2.6 ± 0.0	2.9 ± 0.1	-10.3	-0.122	0.919
Density	1563.4 ± 56.8	1754.1 ± 983.3	-10.9	5.689	0.108
Basal area	8.1 ± 8.9	7.3 ± 3.2	9.9	0.274	0.830
CWM height	14.9 ± 0.1	20.9 ± 3.0	-28.7	2.872	0.213
CWM leaf length	22.9 ± 3.6	16.4 ± 5.7	28.4	-1.354	0.329
CWM wood density	0.6 ± 0.0	0.6 ± 0.1	0	-0.135	0.915
CWM deciduousness	0.5 ± 0.0	0.3 ± 0.0	66.7	-6.132	<b>0.044</b>
CWM dispersal mode	0.4 ± 0.0	0.3 ± 0.1	33.3	-2.150	0.213
CWM shade tolerance	0.2 ± 0.0	0.3 ± 0.1	-33.3	3.572	0.174

B = burned site; U = unburned site in Paraíba do Sul river basin, Southeast Atlantic Forest biome, Brazil. Data were averaged between the two sites per fire regime. Values in bold indicate statistical differences ( $p < 0.05$ ) between sites.

IVI in burnt sites, are early successional species (São Paulo, 1994). On the other side *C. fissilis* and *E. edulis*, that had higher IVI on unburned sites, are late successional species. In fact, most species of the burned patches were pioneers and early secondary, while most species of unburned sites were mid to late secondary (Barbosa et al., 2017). The same results were found in burned tropical forests in the Atlantic Forest Biome in Rio de Janeiro (Sansevero et al., 2020).

We hypothesized that tree density, basal area, species richness and diversity would be lower in the burned sites compared to unburned ones. Indeed, diversity was 10% lower in burned sites, but no significant differences were found for richness, tree density and basal area. Studies have verified highest species richness, diversity and basal area for unburned sites and lowest for recurrent burned areas (Mena et al., 2020; Prestes et al., 2020). Fires generally cause high tree mortality, may locally extinguish fire-sensitive



**Figure 2.** Average of species richness (A), basal area (B), Shannon index (C), tree density (D), CWM Height (E), CWM Leaf length (F), CWM wood density (G), CWM Leaf deciduousness (H), CWM dispersal mode (I), CWM shade tolerance (J) for tree species inventoried in burned and unburned sites in Paraíba do Sul river basin, Southeast Atlantic Forest biome, Brazil. Same letters represent no statistical difference.

species (Hoffmann and Solbrig, 2003; Leblanc et al., 2005) and cause arrested succession in communities subjected to recurrent fires. However, one-time fires, as other small-intensity disturbances in tropical forests, might disrupt advanced stages of succession and start the dynamics of species substitution (as verified for some sites in the Amazon basin: Massi et al., 2017). In addition, fire in these forests could induce sprouting of fire-resistant species trunks and roots. Genera such as *Cecropia*, *Trema*, *Croton*, *Solanum* and *Piper*, mostly pioneers, found in the present study, especially in burned sites, are known by the ability of rapidly establishing and occupying habitats in natural dynamics of regeneration (Gómez-Pompa, 1971; Whitmore, 1989). Nevertheless, this potential resilience should be evaluated with care, e.g. long-term studies, more inventoried burnt sites and evaluating pre-fire conditions of forest remnants are crucial (Andrade et al., 2020).

Additionally, we predicted that burned sites would be dominated by species with vegetative traits associated with high light incidence (small leaf length, low maximum height and wood density and less shade tolerant species) and strategies of leaf deciduousness that represent water economy (more deciduous and semideciduous species) and with reproductive traits associated to abiotic agents to seed dispersal. Contrary to our expectations functional traits were not different according to burning influence. Nine years after fires, succession might be driving burned sites to an early secondary stage, making differences with late secondary stage studied areas (with 20 and 45 years old) subtle. The presence of more deciduous trees was also expected to be higher in burned sites, but we found the opposite, which can be explained by the fact that most evergreen species were short life cycle pioneers occupying the burnt communities.

Finally, we did not evaluate the presence of invasive species inside burned sites, but *Pteridium* ssp. was abundant in these areas. They vigorously regrow after fire and are favored by increased light (Castellani and Stubblebine, 1993). This study evaluated composition, structure and functional impacts of fire on forest patches in the Atlantic Forest biome. The Atlantic Forest is an important focus of conservation and restoration at a global level (Brançalion et al., 2019) and an understanding of the susceptibility and responses of this biome to fire, especially within the context of current fragmentation and future climate change (Scarano and Ceotto, 2015), are important for the success of its conservation and restoration efforts (Guedes et al., 2020).

## Acknowledgements

V.D.M. would like to thank the Research project (FAPESP Process 2019/19529-8) for the TT-3 scholarship (Process 2020/15218-5). Conflict of interest: none.

## References

ALVARES, C.A., STAPE, J.L., SENTELHAS, P.C., MORAIS, J.L. and SPAROVEK, G., 2013. Koppen's climate classification map for

Brazil. *Meteorologische Zeitschrift*, vol. 22, no. 6, pp. 711-728. <http://dx.doi.org/10.1127/0941-2948/2013/0507>.

ANDELA, N., MORTON, D.C., GIGLIO, L., CHEN, Y., VAN DER WERF, G.R., KASIBHATLA, P.S., DEFRIES, R.S., COLLATZ, G.J., HANTSON, S., KLOSTER, S., BACHELET, D., FORREST, M., LASSLOP, G., LI, F., MANGEON, S., MELTON, J.R., YUE, C. and RANDERSON, J.T., 2017. A human-driven decline in global burned area. *Science*, vol. 356, no. 6345, pp. 1356-1362. <http://dx.doi.org/10.1126/science.aal4108>. PMID:28663495.

ANDRADE, D.F.C., RUSCHELB, A.R., SCHWATZ, J., CARVALHO, O.P., HUMPHRIES, J. and GAMA, R.V., 2020. Forest fire resilience in eastern Amazon depends on pre-fire disturbance intensity. *Forest Ecology and Management*, vol. 472, pp. 118258. <http://dx.doi.org/10.1016/j.foreco.2020.118258>.

ANGIOSPERM PHYLOGENY GROUP IV – APG IV, 2016. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. *Botanical Journal of the Linnean Society*, vol. 181, no. 1, pp. 1-20. <http://dx.doi.org/10.1111/boj.12385>.

ARMENTERAS, M.C.M., GONZÁLEZ, T.M., OLIVEIRAS, I., BALCH, J.K. and RENATA, J., 2021. Fire threatens the diversity and structure of tropical gallery forests ecosphere. *Ecosphere*, vol. 19, pp. 179-188. <http://dx.doi.org/10.1016/2021.03.005>.

BARBOSA, L.M., SHIRASUNA, R.T., LIMA, F.C., ORTIZ, P.R.T., BARBOSA, K.C. and BARBOSA, T.C., 2017. *Lista de espécies recomendadas para restauração ecológica em diferentes regiões do Estado de São Paulo*. São Paulo: Instituto de Botânica, 344 p.

BOND, W.J. and KEELEY, E.J., 2005. Fire as a global 'herbivore': the ecology and evolution of flammable ecosystems. *Trends in Ecology & Evolution*, vol. 20, no. 7, pp. 387-394. <http://dx.doi.org/10.1016/j.tree.2005.04.025>. PMID:16701401.

BRANÇALION, P.H.S., NIAMIR, A., BROADBENT, E., CROUZEILLES, R., BARROS, F.S.M., ZAMBRANO, A.M.A., BACCINI, A., ARONSON, J., GOETZ, S., REID, J.L., STRASSBURG, B.B.N., WILSON, S. and CHAZDON, R.L., 2019. Global restoration opportunities in tropical rainforest landscapes. *Science Advances*, vol. 5, no. 7, pp. eaav3223. <http://dx.doi.org/10.1126/sciadv.aav3223>. PMID:31281881.

BRASIL. CENTRO NACIONAL DE ENSINO E PESQUISAS AGRONÔMICAS E RECONHECIMENTO DE SOLOS, 1960. *Levantamento e reconhecimento de solos do Estado de São Paulo*. Rio de Janeiro: Serviço Nacional de Pesquisas Agronômicas.

CASTELLANI, T.T. and STUBBLEBINE, W.H., 1993. Sucessão secundária em floresta tropical após perturbação por fogo. *Revista Brasileira de Botânica*, vol. 16, pp. 181-203.

CORNELISSEN, J.H.C., LAVOREL, S., GARNIER, E., DÍAZ, S., BUCHMANN, N., GURVICH, D.E., REICH, P.B., STTEGE, H., MORGAN, H.D., HEIJDEN, M.G.A., PAUSAS, J.G. and POORTER, H., 2003. A handbook of protocol manual for standardized and easy measurement of functional characteristics of plants worldwide. *Australian Journal of Botany*, vol. 51, no. 4, pp. 335-380. <http://dx.doi.org/10.1071/BT02124>.

DEAN, W.A., 1996. *Ferro e fogo: a história e a devastação da Mata Atlântica brasileira*. Trans. C.K. Moreira. São Paulo: Cia. das Letras.

DURIGAN, G., 2003. Métodos de análise de vegetação arbórea. In: L. CULLEN JUNIOR, R. RUDRAN and C. VALLADARES-PADUA, eds. *Métodos de estudos em biologia da conservação e gestão da vida silvestre*. Curitiba: UFPR, Fundação Boticário de Proteção à Natureza, pp. 455-479.

EMPRESA BRASILEIRA DE PESQUISA AGROPECUÁRIA – EMBRAPA, 1979 [viewed 12 July 2021]. *Resumo da 10ª Reunião Técnica de Levantamento de Solo* [online]. Rio de Janeiro: Serviço Nacional

- de Pesquisa e Conservação do Solo. Available from: <https://edepot.wur.nl/480004>
- FLORES, B.M., FAGOAGA, R., NELSON, B.W., HOLMGREN, M. and BARLOW, J., 2016. Repeated fires trap Amazonian blackwater floodplains in an open vegetation state. *Journal of Applied Ecology*, vol. 53, no. 5, pp. 1597-1603. <http://dx.doi.org/10.1111/1365-2664.12687>.
- FU, R., YIN, L., LI, W., ARIAS, P.A., DICKINSON, R.E., HUANG, L., CHAKRABORTY, S., FERNANDES, K., LIEBMANN, B., FISHER, R. and MYNENI, R.B., 2013. Increased dry-season length over southern Amazonia in recent decades and its implication for future climate projection. *Proceedings of the National Academy of Sciences of the United States of America*, vol. 110, no. 45, pp. 18110-18115. <http://dx.doi.org/10.1073/pnas.1302584110>. PMID:24145443.
- FUNDAÇÃO SOS MATA ATLÂNTICA. Instituto Nacional de Pesquisas Espaciais – INPE, 2018. *Atlas dos Remanescentes Florestais da Mata Atlântica, período 2016-2017*. São Paulo.
- GARNIER, E., CORTEZ, J., BILLÈS, G., NAVAS, M.-L., ROUMET, C., DEBUSSCHE, M., LAURENT, G., BLANCHARD, A., AUBRY, D., BELLMANN, A., NEILL, C. and TOUSSAINT, J.P., 2004. Plant functional markers capture ecosystem properties during secondary succession. *Ecology*, vol. 85, no. 9, pp. 2630-2637. <http://dx.doi.org/10.1890/03-0799>.
- GOMEZ-POMPA, A., 1971. Posible papel de la vegetación secundaria en la evolución de la flora tropical. *Biotropica*, vol. 3, no. 2, pp. 125-135. <http://dx.doi.org/10.2307/2989816>.
- GUEDES, B.J., MASSI, K.G., EVERS, C. and NIELSEN-PINCUS, M., 2020. Vulnerability small forest patches to fire in the Paraíba do Sul River Valley, southeast Brazil: implications for restoration of the Atlantic Forest biome. *Forest Ecology and Management*, vol. 465, pp. 118095. <http://dx.doi.org/10.1016/j.foreco.2020.118095>.
- HOFFMANN, W. and SOLBRIG, O.T., 2003. The role of topkill in the differential response of savanna woody species to fire. *Forest Ecology and Management*, vol. 180, no. 1-3, pp. 1273-1286. [http://dx.doi.org/10.1016/S0378-1127\(02\)00566-2](http://dx.doi.org/10.1016/S0378-1127(02)00566-2).
- HOFFMANN, W.A., ADASME, R., HARIDASAN, M., CARVALHO, M.T., GEIGER, E., PEREIRA, M.A.B., GOTSCH, S.G. and FRANCO, A.C., 2009. Tree topkill, not mortality, governs the dynamics of savanna-forest boundaries under frequent fire in Central Brazil. *Ecology*, vol. 90, no. 5, pp. 1326-1337. <http://dx.doi.org/10.1890/08-0741.1>. PMID:19537552.
- HOFFMANN, W.A., LUCATELLI, V.M.P.C., SILVA, F.J., AZEVEDO, I.N.C., MARINHO, M.S., ALBUQUERQUE, A.M.S., LOPES, A.P. and MOREIRA, S.P., 2004. Impact of the invasive alien grass *Melinis minutiflora* at the savanna-forest ecotone in the Brazilian Cerrado. *Diversity & Distributions*, vol. 10, no. 2, pp. 99-103. <http://dx.doi.org/10.1111/j.1366-9516.2004.00063.x>.
- INSTITUTO BRASILEIRO DE GEOGRAFIA E ESTATÍSTICA – IBGE, 2012. *Manual técnico da vegetação brasileira*. Brasília: IBGE.
- INSTITUTO BRASILEIRO DE GEOGRAFIA E ESTATÍSTICA – IBGE, 2017 [viewed 12 August 2020]. *Cidades, São Paulo*. Available from: <https://cidades.ibge.gov.br/brasil/sp/sao-paulo/panorama>
- INSTITUTO NACIONAL DE PESQUISAS ESPACIAIS – INPE, 2021 [viewed 22 July 2021]. Available from: <http://www.inpe.br/>
- INSTITUTO NACIONAL DE PESQUISAS ESPACIAIS – INPE. Centro de Previsão de Tempo e Estudos Climáticos – CPTEC, 2022 [viewed 12 December 2022]. Available from: <https://www.cptec.inpe.br/>
- JARDIM BOTÂNICO DO RIO DE JANEIRO – JBRJ, 2020 [viewed 22 July 2012]. *Reflora* [online]. Available from: <http://www.floradobrasil.jbrj.gov.br>
- JOLLY, W.M., COCHRANE, M.A., FREEBORN, P.H., HOLDEN, Z.A., BROWN, T.J., WILLIAMSON, G.J. and BOWMAN, D.M.J.S., 2015. Climate-induced variations in global wildfire danger from 1979 to 2013. *Nature Communications*, vol. 6, no. 1, pp. 7537. <http://dx.doi.org/10.1038/ncomms8537>. PMID:26172867.
- KENT, M., 2012. *Vegetation description and data analysis. A practical approach*. Oxford: Wiley & Sons.
- LEBLANC, S.G., CHEN, J.M., FERNANDES, R., DEERING, D.W. and CONLEY, A., 2005. Methodology comparison for canopy structure parameters extraction from digital hemispherical photography in boreal forests. *Agricultural and Forest Meteorology*, vol. 129, no. 3-4, pp. 187-207. <http://dx.doi.org/10.1016/j.agrformet.2004.09.006>.
- LORENZI, H., 2016. *Árvores Brasileiras*. Nova Odessa: Plantarum.
- MAGNAGO, L.F.S., ROCHA, M.F., MEYER, L., MARTINS, S.V. and MEIRANETO, J.A.A., 2015. Microclimatic conditions at forest edges have significant impacts on vegetation structure in large Atlantic Forest fragments. *Biodiversity and Conservation*, vol. 24, no. 9, pp. 2305-2318. <http://dx.doi.org/10.1007/s10531-015-0961-1>.
- MASSI, K.G., BIRD, M., MARIMON, B.S., MARIMON JUNIOR, B.H., NOGUEIRA, D.S., OLIVEIRA, E.A., PHILLIPS, O.L., QUESADA, C.A., ANDRADE, A.S., BRIENEN, R.J.W., CAMARGO, J.L.C., CHAVE, J., CORONADO, N.H., FERREIRA, L.V., HIGUCHI, N., LAURANCE, S.G., LAURANCE, W.F., LOVEJOY, T., MALHI, Y., MARTINEZ, R.V., MONTEAGUDO, A., NEILL, D., PIETRO, A., RAMÍREZ-ÁNGULO, H., STEEGE, H., VILANOVA, E. and FELDPAUSCH, T.R., 2017. Does soil pyrogenic carbon determine plant functional traits in Amazon Basin forests? *Plant Ecology*, vol. 218, no. 9, pp. 1047-1062. <http://dx.doi.org/10.1007/s11258-017-0751-9>.
- MATA, S., BRAGA, J.M.A., MOSER, P., SARTORI, R.A., SÁNCHEZ-TAPIA, A. and SANSEVERO, J.B.B., 2022. Forever young: arrested succession in communities subjected to recurrent fires in a lowland tropical forest. *Plant Ecology*, vol. 223, no. 6, pp. 659-670. <http://dx.doi.org/10.1007/s11258-022-01239-4>.
- MENA, C.F., ARSEL, M., PELLEGRINI, L., ORTA-MARTINEZ, M., FAJARDO, P., CHAVEZ, E., GUEVARA, A. and ESPÍN, P., 2020. Community-based monitoring of oil extraction: lessons learned in the Ecuadorian Amazon. *Society & Natural Resources*, vol. 33, no. 3, pp. 406-417. <http://dx.doi.org/10.1080/08941920.2019.1688441>.
- MYERS, N., MITTERMEIER, R.A., MITTERMEIER, C.G., FONSECA, G.A.B. and KENT, J., 2000. Biodiversity hotspots for conservation priorities. *Nature*, vol. 403, no. 6772, pp. 853-858. <http://dx.doi.org/10.1038/35002501>. PMID:10706275.
- NOBRE, C.A. and BORMA, L.D.S., 2009. 'Tipping points' for the Amazon Forest. *Current Opinion in Environmental Sustainability*, vol. 1, no. 1, pp. 28-36. <http://dx.doi.org/10.1016/j.cosust.2009.07.003>.
- NOBRE, C.A., SELLERS, P. and SHUKLA, J., 1991. Amazonian deforestation and regional climate change. *Journal of Climate*, vol. 4, no. 10, pp. 957-988. [http://dx.doi.org/10.1175/1520-0442\(1991\)004<0957:ADARCC>2.0.CO;2](http://dx.doi.org/10.1175/1520-0442(1991)004<0957:ADARCC>2.0.CO;2).
- NUMATA, I., SILVA, S.S., COCHRANE, M.A. and D'OLIVEIRA, M.V.N., 2017. Fire and edge effects in a fragmented tropical forest landscape in the southwestern Amazon. *Forest Ecology and Management*, vol. 401, pp. 135-146. <http://dx.doi.org/10.1016/j.foreco.2017.07.010>.
- PIVELLO, V.R., VIEIRA, I., CHRISTIANINI, A.V., RIBEIRO, D.B., MENEZES, L.S., BERLINCK, C.N., MELO, F.P.L., MARENGO, J.A., TORNQUIST, C.G., TOMAS, W.M. and OVERBECK, G.E., 2021. Understanding Brazil's catastrophic fires: Causes, consequences and policy needed to prevent future tragedies. *Perspectives in Ecology and Conservation*, vol. 19, no. 3, pp. 233-255. <http://dx.doi.org/10.1016/j.pecon.2021.06.005>.
- PRESTES, N.C.C.S., MASSI, K.G., SILVA, E.A., NOGUEIRA, D.S., OLIVEIRA, E.A., FREITAG, R., MARIMON, B.S., MARIMON-JUNIOR,

- B.H., KELLER, M. and FELDPAUSCH, T.R., 2020. Fire effects on understory forest regeneration in southern Amazonia. *Frontiers in Forests and Global Change*, vol. 3, pp. 10. <http://dx.doi.org/10.3389/ffgc.2020.00010>.
- R CORE TEAM, 2019 [viewed 12 July 2021]. *R: a language and environment for statistical computing. Version 3.6.1* [online]. Vienna: R Foundation for Statistical Computing. Available from: <http://www.r-project.org>
- RADAM BRASIL, 1983 [viewed 12 August 2020]. *Levantamento das regiões fitoecológicas do Estado de São Paulo*. Instituto Florestal. Available from: <https://biblioteca.ibge.gov.br/visualizacao/livros/liv24027.pdf>
- RIBEIRO, M.C., METZGER, J.P., MARTENSEN, A.C., PONZONI, F.J. and HIROTA, M.M., 2009. The Brazilian Atlantic Forest: how much is left, and how is the remaining forest distributed? Implications for conservation. *Biological Conservation*, vol. 142, no. 6, pp. 1141-1153. <http://dx.doi.org/10.1016/j.biocon.2009.02.021>.
- RIBEIRO, N., RUECKER, G., GOVENDER, N., MACANDZA, V., PAIS, A., MACHAVA, D., CHAUQUE, A., LISBOA, S.N. and BANDEIRA, R., 2019. The influence of fire frequency on the structure and botanical composition of savanna ecosystems. *Ecology and Evolution*, vol. 9, no. 14, pp. 8253-8264. <http://dx.doi.org/10.1002/ece3.5400>. PMID:31380087.
- SALAZAR, L.F., NOBRE, C.A. and OYAMA, M.D., 2007. Climate change consequences on the biome distribution in tropical South America. *Geophysical Research Letters*, vol. 34, no. 9, pp. L09708. <http://dx.doi.org/10.1029/2007GL029695>.
- SANSEVERO, J.B.B., GARBIN, M.L., SÁNCHEZ-TAPIA, A., VALLADARES, F. and SCARANO, F.R., 2020. Fire drives abandoned pastures to a savanna-like state in the Brazilian Atlantic Forest. *Perspectives in Ecology and Conservation*, vol. 18, no. 1, pp. 31-36. <http://dx.doi.org/10.1016/j.pecon.2019.12.004>.
- SÃO PAULO, 1994 [viewed 12 July 2021]. *Resolução Conjunta SMA IBAMA/ SP nº 01 de 17 de fevereiro de 1994* [online]. Diário Oficial do Estado de São Paulo, São Paulo. Available from: [https://www.cetesb.sp.gov.br/licenciamento/documentos/1994\\_Res\\_Conj\\_SMA\\_IBAMA\\_1.pdf](https://www.cetesb.sp.gov.br/licenciamento/documentos/1994_Res_Conj_SMA_IBAMA_1.pdf)
- SAPUCCI, G.R., NEGRI, R.G., CASACA, W. and MASSI, K.G., 2021. Analyzing Spatio-temporal Land Cover Dynamics in an Atlantic Forest Portion Using Unsupervised change detection techniques. *Environmental Modeling and Assessment*, vol. 26, no. 4, pp. 581-590. <http://dx.doi.org/10.1007/s10666-021-09758-6>.
- SCARANO, F.R. and CEOTTO, P., 2015. Brazilian Atlantic Forest: impact, vulnerability, and adaptation to climate change. *Biodiversity and Conservation*, vol. 24, no. 9, pp. 2319-2331. <http://dx.doi.org/10.1007/s10531-015-0972-y>.
- SILVA, L.G.P., MASSI, K.G., MARTINS, M.G., NOGUEIRA, T.P., GUISSARD, J.B., SANTOS, R.L.M., BUZATI, J.R., DAMETTO, R., PAIVA, J.M., RODRIGUES, A.H.J., SILVA, N.R.F.M., LEITE, M.A.S., COUTINHO, M.P., BARROS, D.A. and BOTELHO, S.A., 2021. Phytosociological assessment of a natural regeneration site in the southeast Atlantic Forest Biome. *Revista do Instituto Florestal*, vol. 33, pp. 182-191. <http://dx.doi.org/10.24278/2178-5031.202133207>.
- SILVA, R.F.B., BATISTELLA, M. and MORAN, E.F., 2017. Socioeconomic changes and environmental policies as dimensions of regional land transitions in the Atlantic Forest, Brazil. *Environmental Science & Policy*, vol. 74, pp. 14-22. <http://dx.doi.org/10.1016/j.envsci.2017.04.019>.
- SILVERIO, D.V., BRANDO, P.M., BALCH, J.K., PUTZ, F.E., NEPSTAD, D.C., OLIVEIRA-SANTOS, C. and BUSTAMANTE, M.M.C., 2013. Testing the Amazon savannization hypothesis: fire effects on invasion of a neotropical forest by native cerrado and exotic pasturegrasses. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, vol. 368, no. 1619, pp. 20120427. <http://dx.doi.org/10.1098/rstb.2012.0427>. PMID:23610179.
- SOBRAL, F.L. and CIANCARUSO, M.V., 2012. Phylogenetic and functional structure of assemblages: (re)assembling Community Ecology at different spatial scales. *Bioscience Journal*, vol. 28, pp. 617-631.
- STAAL, A., VAN NES, E.H., HANTSON, S., HOLMGREN, M., DEKKER, S.C., PUEYO, S., XU, C. and SCHEFFER, M., 2018. Resilience of tropical tree cover: the roles of climate, fire and herbivory. *Global Change Biology*, vol. 24, no. 11, pp. 5096-5109. <http://dx.doi.org/10.1111/gcb.14408>. PMID:30058246.
- VELDMAN, J.W. and PUTZ, F.E., 2011. Grass-dominated vegetation, not species-diverse natural savanna, replaces degraded tropical forests on the southern edge of the Amazon Basin. *Biological Conservation*, vol. 144, no. 5, pp. 1419-1429. <http://dx.doi.org/10.1016/j.biocon.2011.01.011>.
- WHITMORE, T.C., 1989. Canopy gaps and the two main groups of forest trees. *Ecology*, vol. 70, no. 3, pp. 536-538. <http://dx.doi.org/10.2307/1940195>.

## Supplementary Material

Supplementary material accompanies this paper.

**Table S1.** Characterization of the study areas where field inventory was performed, Paraíba do Sul river basin, Southeast Atlantic Forest biome, Brazil.

This material is available as part of the online article from <https://doi.org/10.1590/1519-6984.268185>