

Fire effect on bamboo-dominated forests in Southwestern Amazon: impacts on tree diversity and forest structure

Efeito do fogo em florestas dominadas por bambu no sudoeste da Amazônia: impactos na diversidade de árvores e na estrutura da floresta

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ABSTRACT

Severe droughts increase the forest flammability, especially if fires are recurrent. Considering that fires tend to alter the forest structure and reduce biological diversity, we analyzed the fire effect on the tree plant community and forest structure over a 10-year post-fire period. The study was carried out in two tropical forest fragments located in the eastern Acre State in southwestern Brazilian Amazon. In each fragment, we established three plots of 250 × 10 m² in an unburned forest and three in a burned forest. In these plots, we collected all tree individuals with DBH ≥ 10 following the RAINFOR protocol, with censuses made in 2011, 2014, 2016, 2017, 2019, 2020 and 2021. The fire significantly reduced the abundance, basal area, and aboveground biomass of tree species, and altered the species composition along the post-fire temporal gradient. The absence of differences in the species richness and species diversity between unburned and burned forests is probably related to the life cycle of bamboo. The results suggest that, 10 years after the fire, the structure and phytosociology of the forest have not yet fully recovered.

Keywords: aboveground biomass; burned forests; tree species; tropical forests.

RESUMO

Secas severas aumentam a flamaabilidade da floresta, especialmente se os incêndios forem recorrentes. Considerando-se que as queimadas tendem a alterar a estrutura das florestas e reduzir a diversidade biológica, nós analisamos o efeito do fogo sobre a comunidade de plantas arbóreas e a estrutura florestal, em um gradiente temporal pós-fogo de dez anos. O estudo foi realizado em dois fragmentos de floresta tropical localizados no leste do estado do Acre, sudoeste da Amazônia Brasileira. Em cada fragmento, estabelecemos três parcelas de 250 × 10 m² em floresta não queimada e três em floresta queimada. Nessas parcelas, foram coletados todos os indivíduos arbóreos com DAP ≥ 10 cm seguindo o protocolo RAINFOR, com censos nos anos de 2011, 2014, 2016, 2017, 2019, 2020 e 2021. O fogo reduziu significativamente a abundância, a área basal e a biomassa acima do solo das espécies arbóreas e alterou a composição das espécies ao longo do gradiente temporal pós-fogo. A ausência de diferenças na riqueza e diversidade de espécies entre as florestas não queimada e queimada está provavelmente relacionada ao ciclo de vida do bambu. Os resultados deste estudo sugerem que, dez anos após o fogo, a estrutura e fitossociologia da floresta ainda não se recuperaram totalmente.

Palavras-chave: biomassa aérea; espécies arbóreas; florestas queimadas; florestas tropicais.

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Introduction

The use of fire in Amazonian ecosystems began more than 12 thousand years ago with the arrival of humans in the American continent (Magalhães et al., 2019). Initially, the fire was used on small scales to prepare land for agriculture (Pivello, 2011; Clement et al., 2015). Currently, this continues to be its main use, even though on a much larger scale of impacted areas (Fonseca-Morello et al., 2017). In recent decades, forest fires have become one of the greatest threats to tropical forests around the world (Juárez-Orozco et al., 2017; Tyukavina et al., 2022). Although some studies about this issue have already been published (Pontes-Lopes et al., 2022; Dutra et al., 2023), the understanding of fire frequency, severity and its impacts in different forest types is scarce and an open question (Fischer, 2021). Models proposed for the Amazon predict the intensification of forest fires in the coming years (Ferreira et al., 2023), associated with human impact on degradation and as an ignition source (Reis et al., 2022; Dutra et al., 2023).

Several studies demonstrate that extreme climate events, such as El Niño and the North Atlantic Oscillations, can favor the occurrence of severe droughts in the Amazon, which in turn tends to reduce the forest's resistance to fire (Haugaasen et al.; Marengo et al., 2008; Carvalho et al., 2020). The Amazonian forests are not easily flammable, due to their typical climatic conditions of high humidity (Morton et al., 2013); however, these forests can become vulnerable with increased moisture stress (Phillips et al., 2009). In severe drought events, its flammability increases significantly (Aragão et al., 2008; Marengo et al., 2008), and areas dominated by dense forests, which are resistant to fire, become susceptible (Alencar, 2015). This scenario is even more worrying in previously burned areas (Silva et al., 2020). This is because, after a forest fire, a significant amount of combustible material is deposited on the ground (Oliveira de Moraes et al., 2021). Furthermore, many living trunks and fallen dead trunks are partially charred, making even easier the recurrence of forest fires (Oliveira de Moraes et al., 2021).

A negative effect of forest fires related to severe drought events in the Amazon is the increase in carbon emissions into the atmosphere (Aragão et al., 2007; Phillips et al., 2009). In these extreme conditions, many trees die due to the scarcity of water in the soil, and due to the increase in the frequency of fire (Phillips et al., 2009). Unfortunately, there are still many uncertainties regarding the quantification of forest carbon in the Amazon and the impacts of climate change on these stocks (Vedovato et al., 2023).

Two other negative effects of forest fires are the loss of biological diversity (Horta et al., 2015), and the changes in the structure and dynamics of the forest (Balch et al., 2013). In the Amazon, depending on the intensity, these forest fires can reduce plant species richness by up to 30% (Cochrane, 2003; Araujo et al., 2013), as they cause mortality in all diameter classes of tree species (Balch et al., 2013). This increase in tree mortality tends to alter the vegetation structure by reducing basal area and forest biomass (Phillips et al., 2009; Andrade et al., 2020), with

consequent microclimatic changes and intensification of the edge effect (Barlow et al., 2020; Ritter et al., 2020). This set of fire effects makes the forest even more vulnerable to new fires (Silva-Junior et al., 2022), which tend to be more severe after each cycle (Barlow and Peres, 2008; Balch et al., 2013). In short, burned forests are subject to a decrease in their resilience and, due to a slower regeneration, they have a longer turnover time to a condition close to the pre-fire state (Andrade et al., 2019; Reis et al., 2022).

Southwestern Brazilian Amazon forests, more specifically in the State of Acre, have a high bamboo (*Guadua weberbaueri*) density (Silveira, 2005). In these bamboo dominated forests, throughout the life cycle of bamboo, changes occur in the floristic composition (Medeiros et al., 2013), with a reduction of up to 40% in the number of plant species. These changes in plant community tend to alter the forest structure, due to a decrease in tree density and biomass (Silveira, 2005; Barlow et al., 2012; McMichael et al., 2012). The presence of bamboo, for example, can reduce from 30 to 50% of the carbon storage potential in a tropical forest (Silveira, 2005). These changes tend to be more intense with the occurrence of forest fires (Smith and Nelson, 2011), making these environments even more vulnerable.

In order to contribute to knowledge about the impacts of fire in tropical forests, this study aimed to analyze the fire effect on the tree community and on the forest structure, in a 10-year post-fire temporal gradient, established in bamboo-dominated forests in southwestern Brazilian Amazon. More specifically, the hypotheses of this work are: 1. unburned forests present greater tree species richness and diversity, bigger tree abundance, and larger basal area and aboveground biomass, than burned forests, and 2. tree species composition differs between unburned and burned forests.

Methodology

Study areas

This work was carried out in two forest fragments affected by non-recurrent fires. The first is located in the Bonal Sustainable Development Project (10,500 ha), and the second is located in the Chico Mendes Extractive Reserve (971,000 ha), both located in the east of the State of Acre, southwest Brazilian Amazon (Figure 1). In the region, the average annual temperature is 25°C, the average relative humidity is 85%, and the average annual precipitation is 1,956 mm (Duarte, 2006). The prevailing forest types in both sites are Bamboo-dominated and Palm-dominated Forests (Silva et al., 2018).

Sampling designs

In each forest fragment, we selected a mature forest burned in 2010 and an unburned forest, at least 500 m apart. In each of these different environments, we established three 250 × 10 m (2,500 m²) plots, at least 300 m apart. We subdivided all plots into subplots of 50 × 10 m (500 m²).

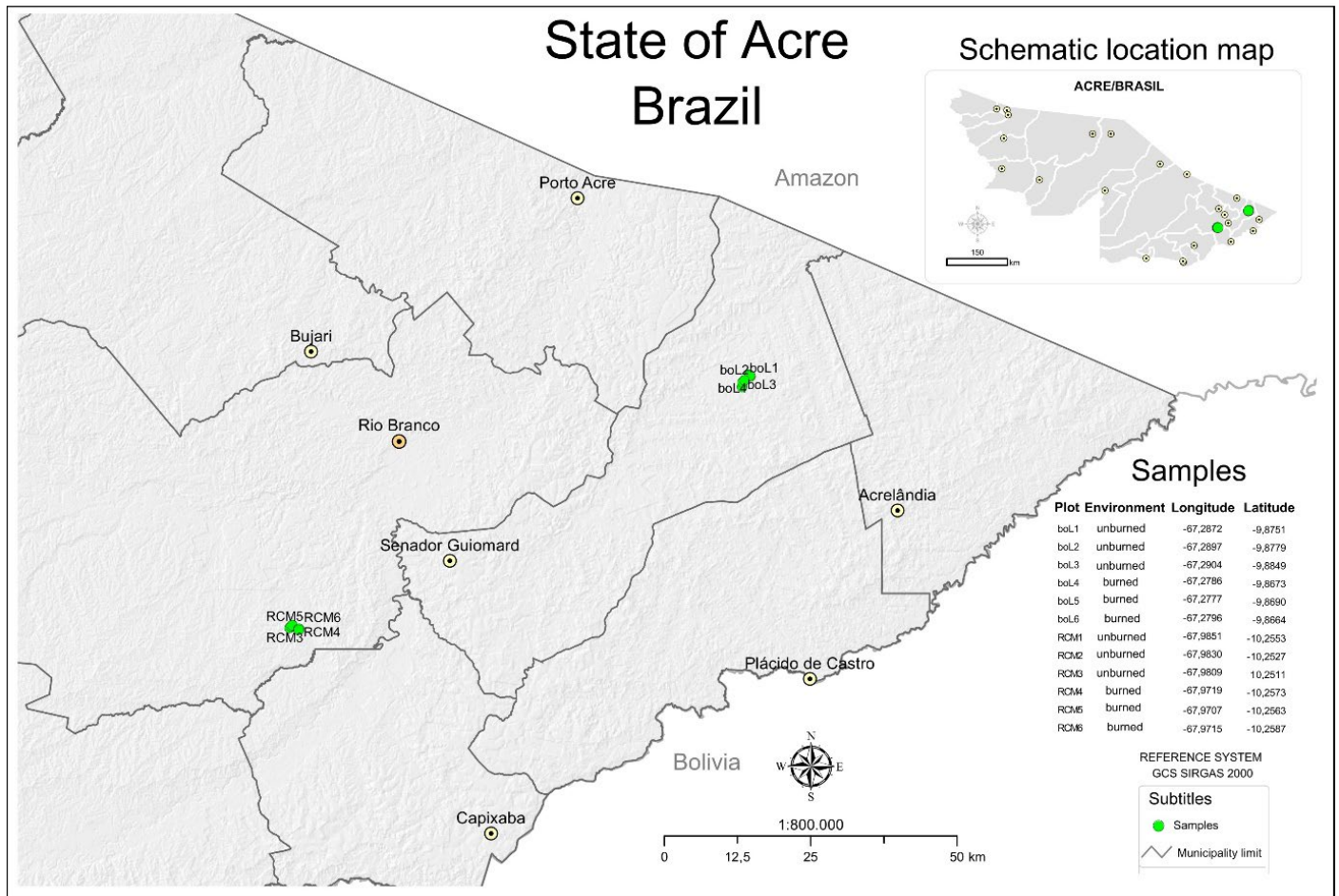


Figure 1 – Location of sampling plots established in burned and unburned environments in two forest fragments located in the east of the State of Acre, southwest Brazilian Amazon.

We plated, identified, measured and collected all trees with a diameter at breast height (1.30 m height from the ground) (DBH) ≥ 10 cm present in the subplots according to the RAINFOR protocol (RAINFOR, 2016), repeatedly in the years 2011, 2014, 2016, 2017, 2019, 2020, and 2021. In the field, the trees were preliminarily identified by a parataxonomist, with subsequent thorough identification in the Herbarium of the Universidade Federal do Acre (UFAC).

We calculated the forest biomass using the equation developed by Nascimento and Laurance (2002): $\text{Exp}((0.370+0.333) \cdot (\ln(\text{DAP})))$. The basal area was calculated using the formula: $A = 3.14 \cdot r^2$ (Martins, 1993), where r is the radius.

Data analysis

We quantified tree abundance, species richness, species diversity and species composition; and we measured the forest structure in terms of basal area and aboveground biomass. In order to assess the impact of fire of these variables along the post-fire period, we adopted a paired sampling design. Each sample pair consisted of the total data

from plots established in unburned and burned forests from the same annual sample census, totaling seven sampling units per environment.

We considered species tree abundance, species richness, species diversity, basal area, and aboveground biomass the response variables; and the environment (unburned and burned forest) the explanatory variable. We tested the models' significance by analysis of variance, and we performed residual analyzes and overdispersion tests (Crawley, 2012) to verify the adequacy of the models' prediction. We examined tree abundance and species richness using GLM with Poisson error distribution, and the species diversity, basal area, and aboveground biomass using LM with Gaussian error distribution. We created GLM and LM with the 'lme4' package (Bates et al., 2017), determined the analysis of variance between each model and the null model with the 'vegan' package (Oksanen et al., 2017), and the residual analysis of GLM and LM with the 'DHARMa' package (Florian, 2017) in R 3.2.3 software (R Development Core Team, 2016).

To assess whether species composition varies between unburned and burned forests, we carried out a non-metric multidimensional

scaling (NMDS) ordinations (Minchin, 1987) with tree abundance data, separately considering the data sampled in each year of the post-fire temporal gradient adopted in this study. To evaluate the species composition, we adopted the subplots 1, 3, and 5 of each plot of 2,500 m² as sampling units. Considering the two forest fragments sampled, there were a total of 18 sample units for the unburned forest and 18 sample units for the burned forest. To minimize the effects of subplots with high abundance, standardizations were carried out, in which we divided the abundance of each tree species by the total abundance of each subplot. From these standardizations, we used the Bray-Curtis quantitative index (Ludwig and Reynolds, 1988) to generate the similarity matrix applied in the ordination. For each year of the post-fire temporal gradient, we tested possible differences in

species composition between unburned and burned forests using the ADÔNIS - PERMANOVA (analysis of variance using distance matrices) (Anderson, 2001).

Results

In general, we sampled 160 tree species, distributed in 49 families and 147 genera (Table 1). The sampling carried out in the unburned forests resulted in 127 tree species, distributed in 42 families and 118 genera, with Fabaceae and Malvaceae being the families with the largest number of species (24 and 12 species, respectively) (Table 1). In the burned forests, we sampled 127 tree species, distributed in 45 families and 118 genera, with Fabaceae and Malvaceae being the families with the largest number of species (22 and 12 species, respectively) (Table 1).

Table 1 – List of tree species sampled in unburned and burned forest fragments in the State of Acre, southwest Brazilian Amazon.

Family	Species	Environment	
		Unburned	Burned
Anacardiaceae	<i>Astronium graveolens</i> Jacq.	X	0
	<i>Spondias testudinis</i> J.D.Mitch. & Daly	X	0
	<i>Thryrsodium bolivianum</i> J.D.Mitch. & Daly	X	X
Annonaceae	<i>Annona cordifolia</i> (Szyszyl.) R.E.Fr.	0	X
	<i>Duguetia odorata</i> (Diels) J.F.Macbr.	X	0
	<i>Ephedranthus amazonicus</i> R.E.Fr.	X	0
	<i>Onychopetalum periquino</i> (Rusby) D.M.Johnson & N.A.Murray	X	X
	<i>Rollinia</i> indet.	X	X
	<i>Xylopia</i> indet.	X	X
Apocynaceae	<i>Aspidosperma macrocarpon</i>	X	0
	<i>Aspidosperma megalocarpon</i> Müll. Arg.	0	X
	<i>Aspidosperma parvifolium</i> A.DC.	X	X
	<i>Geissospermum sericeum</i> Miers	X	X
	<i>Himatanthus sucubus</i> (Spruce ex Müll.Arg.) Woodson	0	X
	<i>Rauvolfia andina</i> Markgr.	X	X
	<i>Tabernaemontana heterophylla</i> Vahl	X	X
Araliaceae	<i>Schefflera morototoni</i> (Aubl.) Maguire et al.	X	X
Arecaceae	<i>Astrocaryum aculeatum</i> G.Mey.	X	X
	<i>Astrocaryum murumuru</i> Mart.	X	0
	<i>Attalea butyracea</i> (Muti sex L.f.) Wess Boer	0	X
	<i>Attalea maripa</i> (Aubl.) Mart.	X	X
	<i>Attalea phalerata</i> Mart. ex Spreng.	X	0
	<i>Bactris gasipaes</i> Kunth	X	0
	<i>Euterpe precatoria</i> Mart.	X	X
	<i>Iriarteia setigera</i> (Mart.) H. Wendl.	X	0
	<i>Mauritiella martiniana</i> (Mart.) Burret	0	X
	<i>Oenocarpus bataua</i> Mart.	0	X
Bignoniaceae	<i>Handroanthus impetiginosus</i> (Mart. ex DC.)	X	X
	<i>Handroanthus serratifolius</i> (Vahl) S.Grose	X	X
	<i>Jacaranda copaia</i> (Aubl.) D.Don	X	X

Continue...

Table 1 – Continuation.

Family	Species	Environment	
		Unburned	Burned
Bixaceae	<i>Cochlospermum orinocense</i> (Kunth) Steud.	0	X
Cordiaceae	<i>Cordia alliodora</i> (Ruiz & Pav.) Cham.	X	X
	<i>Cordia sellowiana</i> Cham.	X	X
Burseraceae	<i>Protium</i> indet.	X	X
	<i>Tetragastris altissima</i> (Aubl.) Swart	X	X
	<i>Trattinnickia boliviana</i> (Swart) Daly	X	0
Caricaceae	<i>Jacaratia digitata</i> (Poepp. & Endl.) Solms	X	X
Chrysobalanaceae	<i>Hirtella burchellii</i> Britton	X	0
	<i>Licania laevigata</i> Prance	X	X
Clusiaceae	<i>Vismia guianensis</i> (Aubl.) Choisy	0	X
Combretaceae	<i>Terminalia oblonga</i> (Ruiz & Pav.)	X	X
Dichapetalaceae	<i>Tapura acreana</i> (Ule) Rizzini.	0	X
Elaeocarpaceae	<i>Sloanea</i> indet.	X	0
Euphorbiaceae	<i>Euphorbiaaceae</i> indet.	X	0
	<i>Hevea brasiliensis</i> (Willd. ex A.Juss.) Müll.Arg.	X	X
	<i>Sapium glandulosum</i> (L.) Morong	X	X
	<i>Mabea nitida</i> Spruce ex Benth.	0	X
	<i>Pausandra Trianeae</i> (Müll.Arg.) Baill	X	0
Fabaceae	<i>Acacia paniculata</i> Willd.	X	X
	<i>Acacia polyphylla</i> D.C	X	X
	<i>Amburana acreana</i> (Ducke) A.C.Sm.	X	X
	<i>Andira surinamensis</i> (Bondt) Splitg. ex Amshoff	X	X
	<i>Apuleia leiocarpa</i> (Vogel) J.F.Macbr.	0	X
	<i>Barnebydendron riedelii</i>	X	0
	<i>Bauhinia acreana</i> Harms	0	X
	<i>Copaifera</i> indet.	X	X
	<i>Dalbergia</i> indet.	X	X
	<i>Dialium guianensis</i> (Aubl.) Sandwith	X	X
	<i>Diploptropis peruviana</i> J.F.Macbr.	0	X
	<i>Dipteryx ferrea</i> (Ducke) Ducke	X	X
	<i>Enterolobium barnebianum</i> Mesquita & M.F.Silva	X	0
	<i>Erythrina amazonica</i> Krukoff	0	X
	<i>Hymenaea courbaril</i> L. var. <i>courbaril</i>	X	0
	<i>Hymenaea parvifolia</i> Huber.	X	0
	<i>Inga</i> indet.	X	X
	<i>Lonchocarpus cultratus</i> (Vell.) A.M.G.Azevedo & H.C.Lima	X	X
	<i>Macrolobium</i> indet.	X	X
	<i>Myroxylon balsamum</i> (L.) Harms	X	X
	<i>Ormosia coccinea</i> Jacks.	X	0
	<i>Poeppigia procera</i> (Poepp. ex Spreng.) C. Presl	X	X
	<i>Pseudopiptadenia psilostachya</i> (DC.) G.P.Lewis & M.P.Lima	0	X
	<i>Pterocarpus rohrii</i> Vahl	X	X
	<i>Sclerolobium chrysophyllum</i> Poepp.	X	X
	<i>Senna silvestris</i> (Vell.) H.S.Irwin & Barneby.	0	X
	<i>Stryphnodendron</i> Indet	0	X
	<i>Swartzia</i> indet.	X	0
	<i>Tachigali formicarum</i> Harms	X	X
	<i>Vatairea fusca</i> (Ducke) Ducke	0	X

Continue...

Table 1 – Continuation.

Family	Species	Environment	
		Unburned	Burned
Humiriaceae	<i>Endopleura uchi</i> (Huber) Cuatrec.	0	X
Lauraceae	<i>Aniba williamsii</i> O.C.Schmidt	X	X
	<i>Mezilaurus</i> indet.	0	X
	<i>Mezilaurus itauba</i> (Meisn.) Taub. ex Mez	0	X
	<i>Nectandra cuspidata</i> Nees	X	X
	<i>Ocotea</i> indet.	X	X
Lecythidaceae	<i>Bertholletia excelsa</i> Bonpl.	X	X
	<i>Cariniana estrellensis</i> (Raddi) Kuntze	X	0
	<i>Couratari guianensis</i> Aubl.	X	X
	<i>Eschweilera</i> indet.	X	X
	<i>Gustavia augusta</i> L.	X	0
Loganiaceae	<i>Strychnos brasiliensis</i> (Spreng.) Mart.	X	0
Malpighiaceae	<i>Byrsonima crispa</i> A.Juss.	X	X
Malvaceae	<i>Apeiba membranacea</i> Spruce ex Benth.	X	X
	<i>Cavanillesia umbellata</i> Ruiz & Pav. LC	X	0
	<i>Ceiba pentandra</i> (L.) Gaertn.	X	X
	<i>Guazuma crinita</i> Mart	X	X
	<i>Heliocarpus americanus</i> L.	X	X
	<i>Huberodendron swietenoides</i> (Gleason) Ducke	0	X
	<i>Matisia bicolor</i> Ducke	X	X
	<i>Ochroma pyramidale</i> (Cav. ex Lam.) Urb.	X	X
	<i>Pseudobombax munguba</i> (Mart.) Dugand	X	X
	<i>Quararibea guianensis</i> Aubl.	X	X
	<i>Sterculia apeibophylla</i> Ducke	X	X
	<i>Theobroma cacao</i> L.	X	X
	<i>Theobroma speciosum</i> Willd. ex Spreng.	X	X
	<i>Cedrela odorata</i> L.	X	0
Meliaceae	<i>Guarea kunthiana</i> A.Juss.	X	X
	<i>Trichilia</i> indet.	X	X
Memecylaceae	<i>Mouriri myrtifolia</i> Spruce ex Triana	X	X
Menispermaceae	<i>Anomospermum reticulatum</i> (Mart.) Eichler	X	0
Moraceae	<i>Brosimum guianense</i> (Aubl.) Huber	X	X
	<i>Castilla ulei</i> Warb.	X	X
	<i>Clarisia racemosa</i> Ruiz & Pav.	X	X
	<i>Ficus</i> indet.	X	X
	<i>Maclura tinctoria</i> (L.)	X	X
	<i>Perebea mollis</i> (Poepp. & Endl.) Huber	X	X
Myristicaceae	<i>Iryanthera juruensis</i> Warb.	X	X
	<i>Virola surinamensis</i> (Rol. ex Rottb.) Warb.	X	X
Myrtaceae	<i>Eugenia</i> indet.	X	X

Continue...

Table 1 – Continuation.

Family	Species	Environment	
		Unburned	Burned
Nyctaginaceae	<i>Neea</i> indet.	X	X
Olaceae	<i>Heisteria ovata</i> Benth.	X	X
Opiliaceae	<i>Agonandra brasiliensis</i> Miers ex Benth. & Hook.f.	X	X
Polygonaceae	<i>Coccoloba mollis</i> Casar	X	X
Putranjivaceae	<i>Drypetes amazonica</i> Steyerm.	X	X
Quiinaceae	<i>Quiina</i> indet.	X	0
Rhamnaceae	<i>Colubrina glandulosa</i> Perkins	0	X
Rubiaceae	<i>Alibertia bertierifolia</i> K.Schum.	0	X
	<i>Alseis eggersii</i> Standl.	X	X
	<i>Calycophyllum spruceanum</i> (Benth.) K.Schum.	0	X
	<i>Faramea</i> indet.	0	X
	<i>Galipea trifoliata</i> Aubl.	X	X
	<i>Metrodorea flavida</i> K.Krause	X	X
Rutaceae	<i>Zanthoxylum rhoifolium</i> Lam.	0	X
Salicaceae	<i>Casearia gossypiosperma</i> Briq. LC	X	X
	<i>Casearia</i> indet.	X	X
Sapindaceae	<i>Matayba</i> indet.	0	X
	<i>Talisia cerasina</i> (Benth.) Radlk.	X	X
	<i>Toulicia reticulata</i> Radlk.	X	X
Sapotaceae	<i>Garcinia guacopary</i> S.Moore	X	X
	<i>Manilkara bidentata</i> (A.DC.) A.Chev.	X	X
	<i>Micropholis guyanensis</i> (A.DC.) Pierre	X	X
	<i>Pouteria glomerata</i> (Miq.) Radlk	X	X
	<i>Pouteria</i> indet.	X	X
Simaroubaceae	<i>Simaba cedron</i> Planch.	0	X
Siparaneaceae	<i>Siparuna</i> indet.	X	X
Olaceae	<i>Minquartia guianensis</i> Aubl.	X	X
Ulmaceae	<i>Celtis schippii</i> Standl.	X	X
Urticaceae	<i>Cecropia ficifolia</i> Warb. ex Snethl.	0	X
	<i>Cecropia sciadophylla</i> Mart.	X	X
	<i>Pourouma guianensis</i> Aubl.	X	0
	<i>Urera caracasana</i> (Jacq.) Griseb.	0	X
Verbenaceae	<i>Vitex triflora</i> Vahl	X	X
Violaceae	<i>Angostura longiflora</i> (K.Krause) Kallunki	0	X
	<i>Gloeospermum</i> indet.	X	0
	<i>Leonia racemosa</i> Mart.	X	X
	<i>Paypayrola</i> indet.	X	0
	<i>Rinorea lindeniana</i> (Tul.) Kuntze	0	X
	<i>Rinoreocarpus ulei</i> (Melch.) Ducke	X	X
Vochysiaceae	<i>Qualea brevipedicellata</i> Stafleu & Marc.-Berti.	X	0
	<i>Qualea grandiflora</i> Mart.	X	0
	<i>Vochysia</i> indet.	X	0

Regarding tree abundance, we detected higher values in the unburned forests compared to the burned forests, along the post-fire temporal gradient (ANOVA: $\chi^2=132.45$, d.f.=12, $p<0.001$) (Figure 2). The species richness (ANOVA: $\chi^2=0.23$, d.f.=12, $p=0.63$) and species diversity did not differ between environments (ANOVA: $F=1.09$, d.f.=12, $p=0.32$).

For all years of the post-fire temporal gradient, we detected significant differences in the species composition between the unburned and burned forests (Table 2 and Figure 3). A total of 32 and 33 tree species were exclusively found in the unburned and burned forests, respectively. In general, the tree species most associated with the unburned forests were *Guarea kunthiana* A.Juss., *Trichilia* indet., *Perebea mollis* (Poepp. & Endl.) Huber, *Metrodorea flavida* K.Krause, and *Vochysia* indet., and the tree species most associated with the burned forests were *Himatanthus sucubus* (Spruce ex Müll.Arg.) Woodson, *Jacaratia digitata* (Poepp. & Endl.) Solms, *Cochlospermum orinocense* (Kunth) Steud., *Sapium glandulosum* (L.) Morong, *Cecropia ficifolia*

Warb. ex Snethl., *Cecropia sciadophylla* Mart., and *Urera caracasana* (Jacq.) Griseb.

We found lower basal area (ANOVA: $F=26.07$, d.f.=12, $p<0.001$) (Figure 3) and also lower aboveground biomass (ANOVA: $F=46.73$, d.f.=12, $p<0.001$) in burned forests (Figure 2).

Table 2 – Non-metric multidimensional scaling ordinations carried out with the general data of tree species in unburned and burned forests, in each year of the post-fire temporal gradient, and results of the ADÓNIS – PERMANOVA.

Post-fire year	Stress	Attempts (best solution)	Variation (%) (2 axes)	PERMANOVA	
				pseudoF	p value
2011	0.25	34	52.66	1.99	<0.001
2014	0.25	52	52.59	1.99	<0.001
2016	0.25	155	50.9	2.81	<0.001
2017	0.25	51	50.82	2.41	<0.001
2019	0.23	36	53.88	2.55	<0.001
2020	0.23	105	54.08	2.58	<0.001
2021	0.26	19	53.05	1.66	<0.020

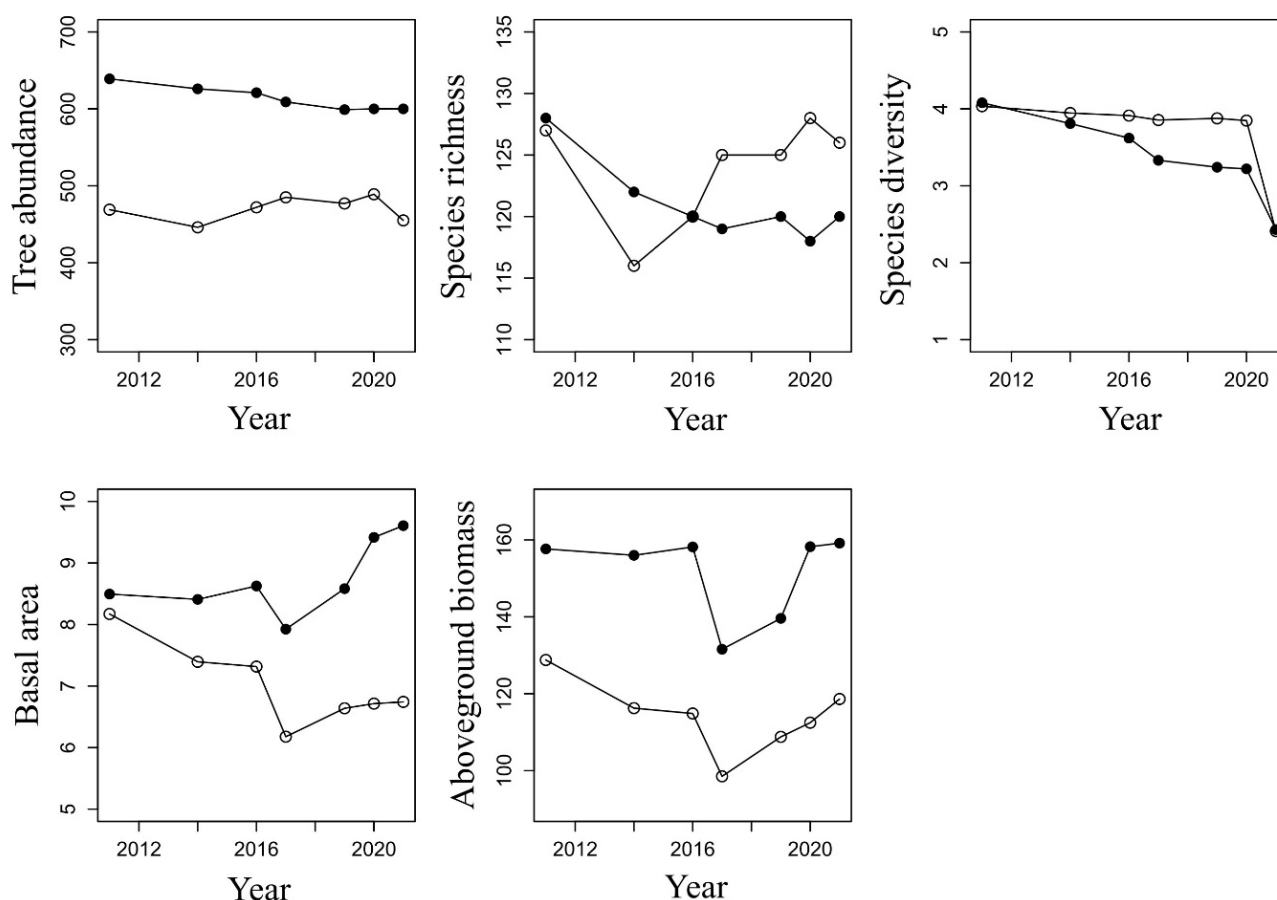


Figure 2 – Variation of the species richness, tree abundance, species diversity, basal area, and forest biomass in unburned and burned environments, along a 10-year post-fire temporal gradient. Black and white circles represent sampling units of unburned and burned environments, respectively.

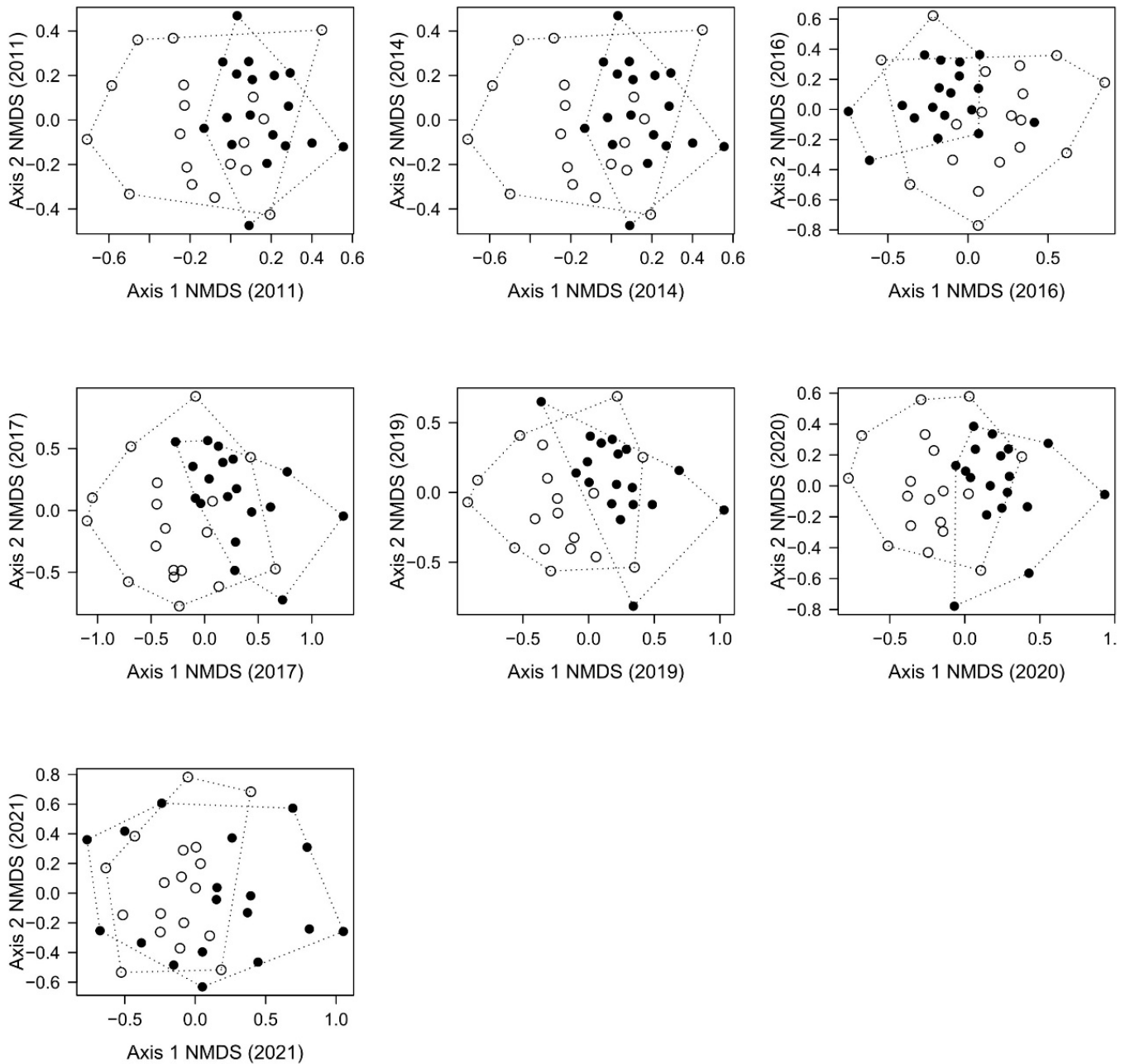


Figure 3 – Non-metric multidimensional scaling ordinations of the composition of tree species sampled in unburned and burned environments, located in the State of Acre, southwest Brazilian Amazon, with the black and white circles represent sampling units of unburned and burned environments, respectively.

Discussion

Although we found lower tree abundance in burned forests, species richness and diversity did not differ between burned and unburned forests. Nevertheless, species composition was different between burned and unburned forests in all years of the post-fire period. Finally, regarding the forest structure, we detected higher values of basal

area and aboveground biomass in the unburned forests in relation to the burned forests.

The lower abundance of trees detected in the burned forests corroborates other studies carried out in the Amazon (Resende et al., 2014), including other sites in southwestern Brazilian Amazon (Silva et al., 2020). The decrease in abundance is due to the pronounced

mortality of trees after fire, mainly of species of medium and small size (Balch et al., 2013; Pontes-Lopes et al., 2022). Four years after the fire event, we can see a slight recovery of the tree abundance, possibly related to the emergence of pioneer species (Xaud et al., 2013; Numata et al., 2017).

Contrary to expectations, we did not detect a reduction in species richness in burned forests, as reported in other studies also carried out in Amazon forests (Cochrane, 2003; Barlow et al., 2012; Nóbrega et al., 2019). Araujo et al. (2013), for example, detected a reduction of up to 30% in the number of plant species such as woody trees, palm trees, and vines, in the years following the fire event. Possibly, the absence of differences in tree species richness between unburned and burned forests detected is related to the life cycle of bamboo (*Gua-*dua weberbaure**). The dynamic of density and mortality of bamboo were recorded by Dalagnol et al. (2018) in the region, in many of the sampling years of the present study. In the first four years after the fire, we observed a reduction in species richness in burned forests; however, we also observed this reduction in unburned forests, but to a lesser extent. During this period, the life cycle peak of bamboo (i.e., the period of the life cycle of bamboo with the greatest density of culms) occurred, which possibly justifies the reduction in species richness in both environments, since the presence of bamboo tends to reduce the plant species richness in Amazon forests (Silveira, 2005). It is likely that the greater reduction in tree abundance in the burned forests is due to synergetic effects of fire and the bamboo expansion. After these first post-fire years, a rapid recovery of species richness was noticed in the burned forests, which can be explained by the emergence of a greater variety of fast growing pioneer species (Nascimento et al., 1999). These species were later replaced by late secondary species (small gap specialists) with a slower growth such as species of the genus *Cecropia* (Urticaceae), which are highly benefited in burned forests in the southwestern Amazon (Numata et al., 2017; Silva et al., 2021).

Just like species richness, species diversity did not differ between environments, contrary to expectations (Barlow and Peres, 2008; Xaud et al., 2013), and this result may be also related to the life cycle of bamboo. As reported in the scientific literature, the high density of bamboo in regions, called “tabocais”, can result in changes in the composition of plant species and forest structure, since bamboo directly affects forest structure and composition (Smith e Nelson, 2011; Barlow et al., 2012; Medeiros et al., 2013). For example, bamboo-dominated forests tend to have less species richness and higher dominance, that is, few tree species representing a high percentage of the total number of individuals (Silveira, 2005), which tends to directly affect the diversity indices. This is because bamboo mortality results in the opening of the canopy and colonization by pioneer species (Silveira, 2005). Therefore, the absence of difference in the species diversity between environments may be related to probable changes in tree community over time prior to the burning events, resulting from the life cycle of bamboo, as discussed

previously for species richness. In other words, the effect of the life cycle of bamboo may be masking the fire effect on richness and diversity of tree species, since natural clearings were opened in the forest due to the rotting and falling of its culms (Castro et al., 2013).

In all years of the post-fire studied period, species composition differed between environments, with a tree species transition throughout the succession process. The tree species most associated with the burned forests were pioneer species, such as *Urera caracasana* (Nascimento et al., 1999), which has a short life cycle, generally dying out after four years from the beginning of the succession process. Other pioneer species associated with the burned forests were *Cecropia ficifolia* and *Cecropia sciadophylla*. This genus is among the most abundant genera of tree species in Neotropical forests, with rapid growth and propensity to colonize large gaps and habitats in the initial stage of succession (Zalamea et al., 2013). On the contrary, the tree species most associated with the unburned forests were species considered shade tolerant, such as *Guarea kunthiana* (Debiasi et al., 2021) and *Trichilia* indet. (Calzavara et al., 2019).

The decrease in basal area and aboveground biomass in burned forests over time was expected (Aragão et al., 2018; Pontes-Lopes et al., 2022). As in the study carried out by Sato et al. (2016), the lowest biomass and basal area values in burned areas remained for more than a decade, probably due to the late mortality of large trees affected by fire (Barlow et al., 2002; Prestes et al., 2020). In forests dominated by bamboo, the post-fire period further favors the densification of bamboo, which in turn tends to reduce the abundance of large trees, and consequently the basal area (Prestes et al., 2020) and biomass (Ziccardi et al., 2019). It is important to note that, in the present study, from the post-fire fourth year onwards, biomass recovery noticeable, possibly due to the accentuated recruitment of fast-growing species such as *Colubrina glandulosa* and species of the genus *Cecropia*. These species spread after fire (Xaud et al., 2013; Numata et al., 2017; Silva et al., 2021), and remain in the area in constant cycles of mortality and growth of new individuals. Due to aboveground biomass decrease in burned areas and its committed emissions through decomposition, this process further increases carbon emissions to the atmosphere and climate warming (Aragão et al., 2018; Mataveli et al., 2023), which is an urgent topic of global interest.

Conclusion

The fire significantly reduced the abundance, basal area, and aboveground biomass of tree species, and altered the species composition along the post-fire temporal gradient, showing that the forest tends to a gradual recovery of its structure, which persists beyond the 10 years observed. The absence of differences in the species richness and species diversity between unburned and burned forests is probably related to the life cycle of bamboo. The dynamics of density and mortality of bamboo, with the consequent opening of

the canopy and colonization by pioneer species during the sampling years in both unburned and burned forests, may have masked the fire effect on species richness and species diversity.

Our results highlight the importance of long-term monitoring of these forests after fire events, to guarantee the observation of the tree community throughout a complete life cycle of bamboo, which is approximately 28 years. Finally, the fire impacts on the tree community detected in this work show the urgency of developing educational and inspection measures that seek to reduce forest fires in the Amazon, especially considering the alarming increase in av-

erage temperatures and the frequency of severe drought events in recent years.

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Contribution of the authors

SILVA, I.B.: conceptualization, investigation, methodology, data curation, formal analysis, writing – original draft, writing – review & editing. MIRANDA, P.N.: methodology, data curation, formal analysis, writing – original draft, writing – review & editing. ANDERSON, L.O.: conceptualization, funding, resources, project administration. JESUS, C. V. S.: investigation, writing – review & editing. ARAGÃO, L.E.O.C.: conceptualization, funding, resources, writing – review & editing. CAMPOS, C.A.: software, writing – review & editing. SALIMON, C.I.: supervision, validation, writing – review & editing. RODRIGUEZ, A.F.R.: methodology, supervision, validation, writing – review & editing. SILVEIRA, M.: investigation, supervision, validation, writing – review & editing.

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