The effect of fire on the structure and composition of the plant community in paleo-levees, Pantanal, Brazil

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Keywords: Resilience; forest fire; Pantanal; cordilleira; rebrote.

ABSTRACT – The Pantanal is a fire-dependent Brazilian biome. Both the annual flood pulse and fire events are important drivers that condition the structure of its vegetation formations. Among the biome's physiognomies are paleo-levees, which are ancient formations of riparian vegetation associated with abandoned river channels known as cordilleiras. When affected by fire, these environments can have their structure and species composition altered. Many trees in the Pantanal are adapted to fire and flooding, but high-intensity fires can result in additional impacts on vegetation structure. Therefore, we conducted a study in levees areas in the Refúgio Ecolóogico Caiman in the Pantanal after the 2019 fire. We investigated how species structure and composition might be affected by fire. The study showed differences in species composition between burned and unburned areas, attributed to the history of fires in the zones analyzed. The unburned area has been unburned for more than 25 years, while the burned area experienced fires in 2007 and 2019. Although no significant differences were observed in richness, abundance, basal area, and diversity, fire does affect species composition. Resilience was observed in species such as Curatella americana and Attalea phalerata, which show the ability to regenerate after fires. The results indicate that the vegetation of the paleo-levees in the Refúgio Ecológico Caiman is resilient to fire, highlighting the importance of these areas in integrated fire management since, even if affected, they will not suffer major structural changes.

Efeito do fogo sobre a estrutura e composição da comunidade vegetal em paleo-levees, Pantanal, Brasil

Palavras-chave: Resiliência; incêndio florestal; pantanal; cordilheira; rebrote.

RESUMO – O Pantanal é um bioma brasileiro dependente do fogo. Tanto o pulso de inundação anual como os eventos de fogo são importantes drivers que condicionam a estrutura das suas formações vegetais. Dentre as fisionomias do bioma encontram-se os paleo-levees, que são antigas formações de vegetação ciliares associadas a canais de rios abandonados conhecidas como cordilheiras. Esses ambientes, quando atingidos por fogo, podem ter estrutura e composição de espécies alteradas. Muitas árvores do Pantanal são adaptadas ao fogo e às inundações, entretanto, incêndios de alta intensidade podem resultar em impactos adicionais na estrutura da vegetação. Dessa forma, conduzimos um estudo em áreas de levees no Refúgio Ecológico Caiman após o incêndio de 2019. Investigamos como a estrutura e composição das espécies podem ser afetadas pelo fogo. O estudo mostrou que há diferenças na composição das espécies entre áreas queimadas e não queimadas, atribuídas ao histórico de incêndios nas áreas analisadas. A área não queimada está sem queimadas há mais de 25 anos, enquanto a área queimada passou por incêndios em 2007 e 2019. Embora não tenha sido observado diferenças significativas em riqueza, abundância, área basal e diversidade, constatamos que o fogo afeta a composição das espécies. Foi observada resiliência em espécies como Curatella americana e Attalea phalerata, que mostram capacidade de regeneração após incêndios. Os resultados indicam que a vegetação das áreas de cordilheiras do Refúgio Ecológico Caiman é resiliente ao fogo, destacando a importância dessas áreas no manejo integrado do fogo, já que, mesmo se afetadas, não sofrerão grandes mudanças estruturais.

Efecto del fuego sobre la estructura y composición de la comunidad vegetal en los paleo-levees, Pantanal, Brasil

Palabras clave: Resiliencia; incendio forestal; Pantanal; cordillera; rebrote.

RESUMEN – El Pantanal es un bioma brasileño dependiente del fuego. Tanto el pulso anual de inundaciones como los incendios son importantes factores que condicionan la estructura de sus formaciones vegetales. Entre las fisionomías del bioma se encuentran los Páleo Levees, que son antiguas formaciones de vegetación ribereña asociadas a canales fluviales abandonados conocidos como cordillera. Cuando se ven afectados por el fuego, estos ambientes pueden ver alterada su estructura y composición de especies. Muchos árboles del Pantanal están adaptados al fuego y a las inundaciones, pero los incendios de alta intensidad pueden provocar impactos adicionales en la estructura de la vegetación. Por lo tanto, realizamos un estudio en las áreas de Páleo Levees en el Refúgio Ecológico Caiman en el Pantanal después del incendio de 2019. Investigamos cómo la estructura y la composición de las especies podrían verse afectadas por el fuego. El estudio mostró que existen diferencias en la composición de especies entre las áreas quemadas y no quemadas, atribuidas a la historia de los incendios en las áreas analizadas. La zona no quemada lleva más de 25 años sin arder, mientras que la area quemada sufrió incendios en 2007 y 2019. Aunque no se observaron diferencias significativas en riqueza, abundancia, área basal y diversidad, el fuego sí afecta a la composición de especies. Se observó resiliencia en especies como Curatella americana y Attalea phalerata, que muestran capacidad de regeneración tras los incendios. Los resultados indican que la vegetación de las zonas de Páleo Levees del Refúgio Ecológico Caiman es resiliente al fuego, destacando la importancia de estas zonas en la gestión integral del fuego, ya que, aunque se vean afectadas, no sufrirán grandes cambios estructurales.

Introduction

Fire is an important biological filter that selects species, promotes adaptations of these organisms over time, and affects the variability of traits in neotropical savannas, acting more as an external filter than an internal factor [1]. It can be considered as one of the main factors responsible for variations in species richness, providing conditions for species endemism and thus influencing the composition and structure of terrestrial ecosystems [2]. In the Pantanal, together with flooding, it acts as a powerful environmental filter that modulates the distribution of species and promotes the monodominance of some groups [3][4].

Although positive for certain groups, different terrestrial ecosystems respond differently to the presence of fire, depending primarily on the environment's relationship to fire in its evolutionary history [5]. In this sense, there are thought to be fire-sensitive environments in which fire is not part of their evolutionary history, and other fire-dependent environments in which fire has historically shaped their evolution over time [6]. In general, savannas around the world are fire-dependent environments [7].

The Brazilian Pantanal is a humid area situated within the savanna zone, where the cerrado physiognomy is prevalente [8]. Despite the annual flood pulse that sustains it, it is considered one of the Brazilian biomes with the highest number of annual fire events relative to its total area. The Pantanal presents a paradoxical relationship between fire and flooding. Although they are opposite phenomena, fire events are more frequent in the most flooded areas, which occur along the main rivers of the region, forming "fire and flood corridors". (9). Although 95% of ignition is attributed to human causes, studies that analyzed sedimentary records of pollen and charcoal [10] indicate the presence of fires in the Pantanal 12,000 years ago. This evidence suggests that the biome evolved with fire and may be dependent on this fire regime to maintain its structure.

The Pantanal has a wide variety of vegetation formations in a gradient of grassland, savanna and forest formations, according to topographic nuances and corresponding flood levels, the grassland areas are predominant and more prone to fire [9]. However, in recent years, large-scale fires have affected forested environments, which are considered to be more sensitive to fire [5][11]. In the Pantanal, forested environments are represented by alluvial seasonal semi-deciduous forests (riparian forests), capões (which are circular or elliptical forest formations that occur in the middle of the grassland matrix) and formations known locally as cordilheiras (Páleo Levees). Cordilheiras are paleo-levees that originate from old formations of riparian vegetation in abandoned river channels, which are no longer subject to flooding [12][13] and have a different composition than riparian forests [14], is a contact formation between the Seasonal forest and the Cerrado.

In the Cerrado, transitional forests exhibit high post-fire resilience due to low tree mortality and high growth rates of resprouting trees [15]. In the Pantanal, only riparian forests have been assessed for fire resilience [16][17], and it was found that riparian forests, when affected by fire, can decrease tree species richness and abundance in more flooded areas and increase richness and abundance in areas that remain flooded for shorter periods of time with little change in basal area. Because fire is very common in the region, it is important to know its effects on forest formations, especially those that have been little studied.

The Pantanal has recently been affected by large forest fires. The main causes of these high-intensity fires are related to a combination of human activities and climate change [18][19]. Changes in land use and land cover are increasing rapidly [20], climate change scenarios predict a warmer biome [21], so there is a possibility that forested environments will continue to be affected by high-intensity fires. Thus, given the lack of baseline data in the Pantanal that includes the effects of fire on paleo-levees, our objective was to assess the effects of fire on paleo-levees vegetation structure to support integrated fire management in the region.

Material and Methods

Study area

The study was conducted out on a private rural property called the Refúgio Ecológico Caiman (REC). Established in 1987, the REC is located in the Southern Pantanal (Pantanal de Aquidauana), in the municipality of Miranda/MS (Figure 1).

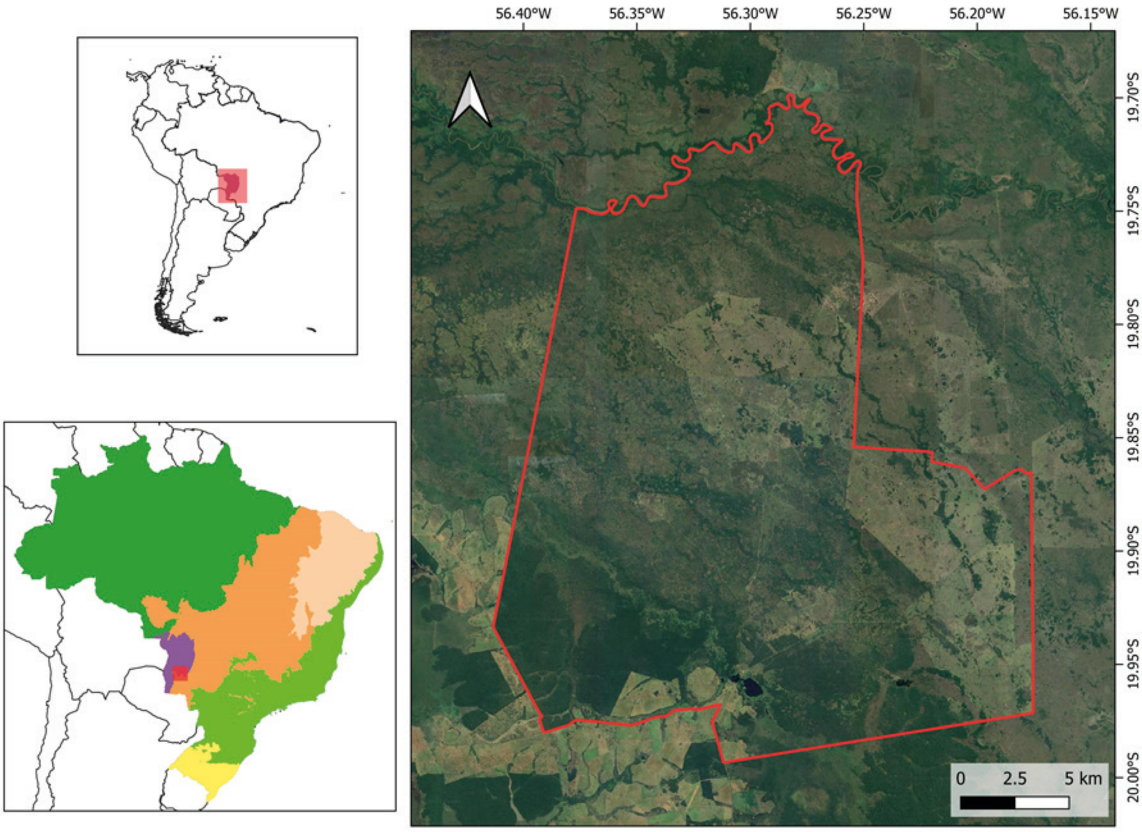

Figure 1 – Location of the Refúgio Ecológico Caiman in the Pantanal of Aquidauana, Miranda/MS. Source: Biome boundaries: Brazilian Institute of Geography and Statistics; Satellite image: Google Image Base.

The climate of the reghion is classified as Awa [22]. With an area of 53,000 ha, the REC is part of a matrix dominated by cultivated and native pastures, where there are currently around 35,000 head of cattle in livestock and nature integration [23].

The vegetation is characterized by the presence of formations of seasonal deciduous and semi-deciduous forest (lowland and alluvial), wooded savanna, wooded savanna and grassy savanna, distributed in phytophysiognomies known locally as cordilheiras, riparian forest, flooded fields, capões and lixeiral (monodominance of Curatella americana). Associated with these phytophysiognomies are water bodies, vazantes, corixos, baias and the Aquidauana River, which cuts through the northern side of the property [23]. Fire is most frequent in the region between July and October. During the winter, a combination of low relative humidity, high temperatures, low rainfall, constant winds, and reduced flooding of the plains creates favorable conditions for flames to advance [24][25].

Data collection

Areas were selected based on field visits to burned and unburned areas previously identified from 2019 satellite imagery. Vegetation structure was sampled in eight fragments of the range, four in areas burned in 2019 (B) and four in areas unburned in that event (UB). Six rectangular plots measuring 10 m×5 m were established in each fragment, for a total of 48 plots and 2,400 m^2 (Figure 2).

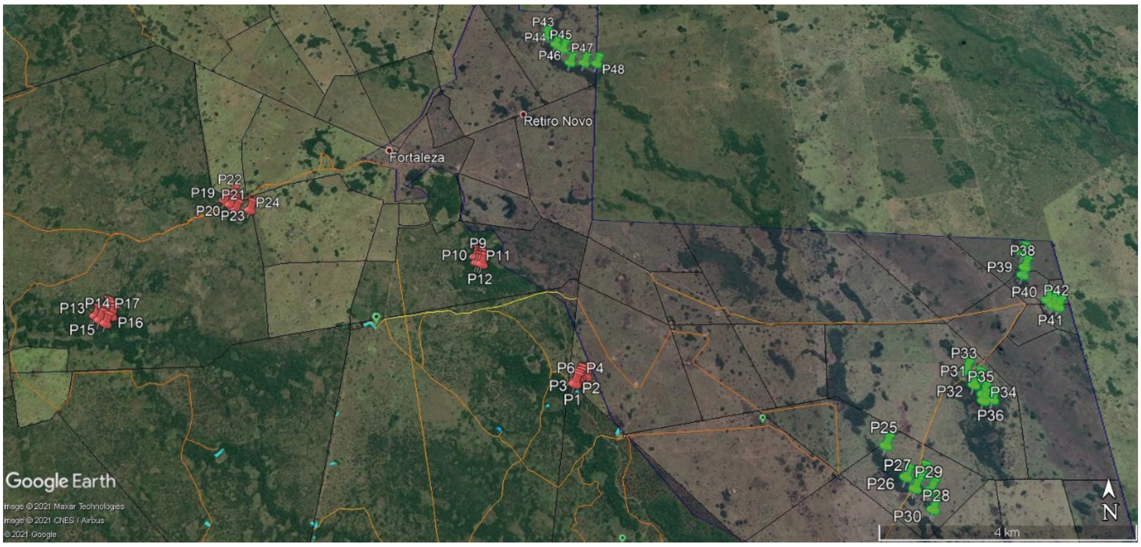

Figure 2 – Distribution of plots in the evaluated areas of the Refúgio Ecológico Caiman. The red icons indicate burned areas and the green icons unburned areas. Source: Google Earth.

MapBiomas data was used to assess the last fire event in the areas evaluated [26]. The unburn area has remained fire-free since 1999, a period of 25 years without burning. Area burned experienced a fire event in 2007 and a subsequent fire interval of twelve years in 2019 (Figure 3).

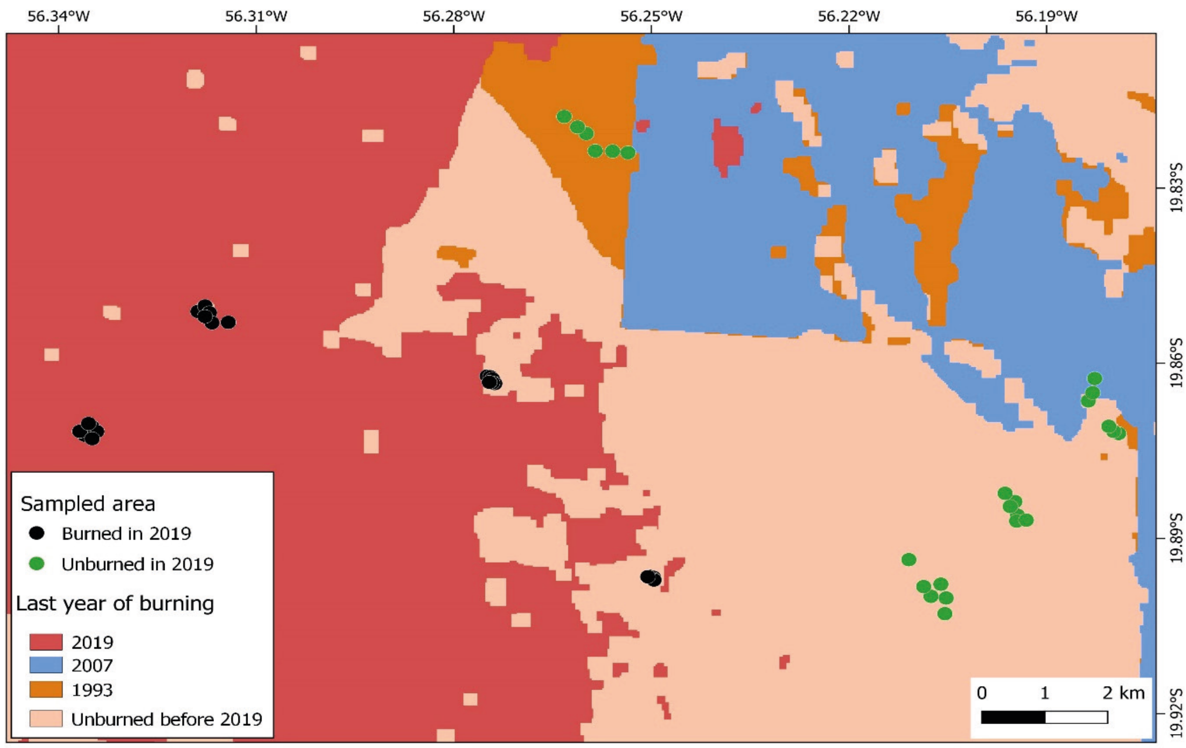

Figure 3 – Fire history of the areas assessed after the 2019 fire, Refúgio Ecológico Caiman in the Pantanal of Aquidauana, Miranda, MS. Source: MapBioma, 2024.

Sampling units were stablished following the slope of the land towards the Aquidauana River (Figure 2). Then, all the individuals with a CBH (Circumference at Breast Height) greater than or equal to 10 cm were sampled, and the total height of each individual was also noted by comparing it to a stick of known size. The horizontal structural parameters assessed were abundance, richness, density, frequency, basal area, dominance and the importance value index [27].

The floristic survey was carried out using the walking method [28], which consists of walking around the study area identifying, collecting and writing down the species found in order to complement the phytosociological plots. All sterile and reproductive material was collected, herborized and identified with the help of specialized literature [29] and specialists, as well as compared with exsiccates from the CGMS herbarium at the Federal University of Mato Grosso do Sul. Scientific and family names were checked against the Flora and Fungi of Brazil website (http://floradobrasil.jbrj.gov.br/2024) [30]; Missouri Botanical Garden (http://www.mobot.org// Research/APweb/welcome.html) and the Angiosperm Phylogeny IV website [31]. Information on the popular names, economic potential and traditional use of the species was obtained through a literature review [29][32].

Data analysis

To assess the horizontal structure of the vegetation, calculations were performed using the FITOPAC program [33] and the R environment [34]. In the R environment, we first constructed rarefaction and extrapolation curves for species in the tree community based on Hill's series (iNEXT function, iNEXT package, [35][36]). Rarefaction indicates the observed richness as a function of sampling effort, and extrapolation indicates the expected richness if sampling effort is doubled. We constructed two curves separating species by burned and unburned area.

To determine possible variation in plant community attributes in burned and unburned areas, we built general linearized mixed models (GLMM function glmmPQL, MASS package, [37]). We chose this type of model because there is a correlation structure in the equation to control for the possible effect of spatial autocorrelation, since the plots are arranged in a block design. For the attributes richness and abundance (total number of individuals in the plots) we used the Poisson distribution, and for the attribute basal area we used the gamma error distribution. The test of statistical significance was calculated by type II analysis of squared deviations (Anova function, package car. 38).

To graphically represent the spatial distribution of the sampling units according to whether the area had been burned or not, we ordered the species composition by non-metric multidimensional scaling (NMDS, metaMDS function, vegan package, 39). To do this, we used a presence-absence matrix to perform the ordering, and we recovered the first two-dimensional solutions ($r2adj = 0.37$, $P \leq 0.001$). To determine whether the composition varied according to the burned and unburned areas, we built a multivariate analysis of variance model (MANOVA, manova function, stats package, 34), and to test for possible differences we used the Pillai-trace statistic.

Results and Discussion

Species composition

In the floristic composition recorded by walking and in the phytosociological plots, 508 individuals were recorded, distributed in 83 species, 53 genera and 28 families (Table 1). Of these, 77 were identified to the taxonomic level of species, six to genus, one to family and 11 were undetermined due to the burning of its external parts (leaves and bark).

Three families stood out for having a large number of species in the burned area (Figure 4a)

Table 1 – List of species recorded in the levees burning and unburning in 2019, Refúgio Ecológico Caiman (REC), Miranda-MS.

Familia	Nome científico	Nome popular	Burned	Unburned
Anacardiaceae	Astronium fraxinifolium Schott	gonçalo-alves	x	x
	Astronium urundeuva (M. Allemão) Engl.	aroeira-preta		x
	Spondias mombin L.	cajá	x	x
	Lithraea molleoides (Vell.) Engl.	aroeira-brava		

Familia	Nome científico	Nome popular	Burned	Unburned
Annonaceae	Annona emarginata (Schltdl.) H.Rainer	araticum-mirim	x	x
	Annona sylvatica A.St.-Hil.	araticum-do-mato	x	x
Apocynaceae	Aspidosperma australe Müll.Arg.	guatambu	x	
	Aspidosperma sp.		x	
Arecaceae	Acrocomia aculeata (Jacq.) Lodd. ex Mart.	macaúba	x	
	Attalea phalerata Mart. ex Spreng.	acuri	x	x
	Copernicia alba Morong	carandá	x	x
Bignoniaceae	Handroanthus chrysotrichus (Mart. ex DC.) Mattos	ipê-amarelo-miúdo	x	
	Handroanthus heptaphyllus (Vell.) Mattos	piúva	x	
	Handroanthus impetiginosus (Mart. ex DC.) Mattos	ipê-roxo	x	x
	Handroanthus serratifolius (Vahl) S.Grose	ipê-amarelo-da-mata		x
	Jacaranda cuspidifolia Mart.	jacarandá	x	x
	Tabebuia aurea (Silva Manso) Benth. & Hook.f. ex S.Moore	paratudo	x	
	Tabebuia roseoalba (Ridl.) Sandwith	ipê-branco	x	x
Boraginaceae	Cordia glabrata (Mart.) A.DC.	louro-branco	x	x
Cactaceae	Cereus bicolor Rizzini & A.Mattos	cacto	x	
Cannabaceae	Celtis iguanaea (Jacq.) Sarg.	jameri	x	
Combretaceae	Combretum laxum Jacq.	pombeiro-branco	x	
	Combretum leprosum Mart.	carne-de-vaca		x
	Terminalia argentea Mart. & Zucc.	capitão		x
Dilleniaceae	Curatella americana L.	lixeira	x	x
Fabaceae	Albizia niopoides (Spruce ex Benth.) Burkart	farinha-seca		x
	Anadenanthera colubrina (Vell.) Brenan	angico	x	
	Bauhinia ungulata L.	mororó		x
	Cenostigma pluviosum (DC.) Gagnon & G.P.Lewis	sibipiruna	x	x
	Dipteryx alata Vogel	baru		x
	Diptychandra aurantiaca Tul.	carvão-vermelho	x	
	Enterolobium contortisiliquum (Vell.) Morong	orelha-de-negro	x	x
	Hymenaea courbaril L.	jatobá-mirim		x
	Hymenaea martiana Hayne	jatobá-da-mata	x	
	Hymenaea stigonocarpa Mart. ex Hayne	jatobá	x	x
	Inga vera Willd.	ingá-4-quinas		x
	Machaerium acutifolium Vogel.	bico-de-pato		x
	Machaerium hirtum (Vell.) Stellfeld	barreiro	x	x
	Senegalia tenuifolia (L.) Britton & Rose		x	
Lamiaceae	Vitex cymosa Bertero ex Spreng.	tarumã	x	x
Lauraceae	Ocotea diospyrifolia (Meisn.) Mez	canela-louro	x	
Malvaceae	Guazuma ulmifolia Lam.	mutamba-preta	x	
	Luehea candicans Mart.	açoita-cavalo	x	x
Meliaceae	Trichilia catigua A. Juss	catiguá	x	x
	Trichilia pallida Sw.		x	x
	Trichilia elegans A.Juss.	catiguazinho	x	
	Trichilia stellato-tomentosa Kuntze	guaranizinho		x
Moraceae	Brosimum gaudichaudii Trécul	maminha-cadela	x	x

Familia	Nome científico	Nome popular	Burned	Unburned
	Ficus luschnathiana (Miq.) Miq.	figueira	x	x
	Ficus pertusa L.f.	figueira-grande	x	x
	Ficus sp.		x	x
Myrtaceae	Myrcia splendens (Sw.) DC.	coração-tinto	x	
	Myrcia sp.		x	x
	Psidium guineense Sw.	araçá	x	
Opiliaceae	Agonandra brasiliensis Miers ex Benth. & Hook.f.	tinge-cuia		x
Polygonaceae	Coccoloba cujabensis Wedd.		x	
	Coccoloba obtusifolia Jacq.	azedinha	x	x
	Coccoloba parimensis Benth.	cipó-ponte	x	x
	Coccoloba ochreolata Wedd.		x	
	Coccoloba sp.1		x	
	Triplaris americana L.	novateiro	x	
	Triplaris gardneriana Wedd.	novateiro-preto	x	
Rhamnaceae	Rhamnidium elaeocarpum Reissek	cafezinho	x	x
Rubiaceae	Calycophyllum multiflorum Griseb.	castelo	x	
	Calycophyllum sp.		x	
	Chomelia obtusa Cham. & Schltdl.	arbustinho	x	x
	Genipa americana L.	jenipapo	x	x
	Randia armata (Sw.) DC.	limoeiro	x	x
	Tocoyena formosa (Cham. & Schltdl.) K.Schum.		x	x
Rutaceae	Zanthoxylum caribaeum subsp. rugosum (A.St.-Hil. & Tul.) Reynel	cera-cozida		x
	Zanthoxylum rigidum Humb. & Bonpl. ex Willd.			x
	Zanthoxylum rhoifolium Lam.	mamica-de-porca		x
Salicaceae	Casearia aculeata Jacq.		x	x
	Casearia cf. arborea (Rich.) Urb.		x	
	Casearia gossypiosperma Briq.	espeteiro		x
	Casearia rupestris Eichler	pruruca	x	
Sapindaceae	Allophylus edulis (A.St.-Hil., A.Juss.&Cambess.) Hieron. ex Niederl.	chal-chal		x
	Dilodendron bipinnatum Radlk.	maria-pobre	x	x
	Matayba elaeagnoides Radlk.	camboatã-branco		x
	Sapindus saponaria L.	saboneteira	x	
Sapotaceae	Pouteria gardneri (Mart. & Miq.) Baehni			x
Simaroubaceae	Simarouba versicolor A.St.-Hil.	perdiz	x	
Urticaceae	Cecropia pachystachya Trécul	imbaúba	x	x
	Indeterminada 1,2,3,4,5,6,7,8,9,10 e 11		x	
	Indeterminada 3		x	x
	Morto		x	

and the unburned areas (Figure 4b): Fabaceae, Bignoniaceae and Rubiaceae.

These families have already been observed in studies carried out at the Refúgio Ecológico Caiman

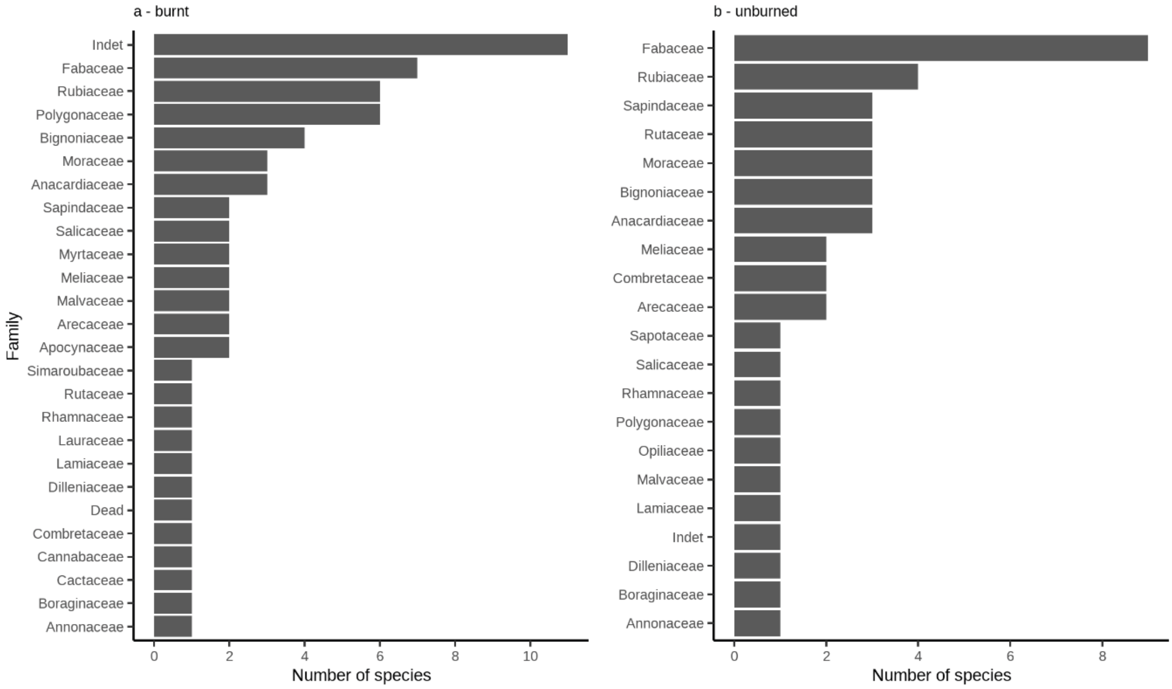

Figure 4 – Family richness by species recorded in mountain ranges with burning and unburning in 2020, Refúgio Ecológico Caiman, Miranda-MS. Where: a) area with burning, b) area without burning.

(21) and in the Abobral Pantanal region [40]. The species richness of the Fabaceae family is explained by its wide distribution. In addition to the large number of species, the family has approximately 727 genera and 19,325 species, and is considered the third largest Angiosperm family in the world [41]. Considering the differences between burned and unburned areas, the families occurring are practically the same in both situations. Fabaceae is cosmopolitan, Rubiaceae is a rich family in the of forest areas [42] and Bignoniaceae is generally successful in dry neotropical formations [43].

The ability of Fabaceae to persist in a post-fire environment after fire depends on several factors [44] Studied the fire survival of seedlings of woody Fabaceae species in the Cerrado and concluded that young plants as young as six months old have the ability to regrow after fire. This occurs from buds, using a source of carbohydrates present in the underground structures of these species. The family has also been tested for its fire-retardant potential and found to be effective [45]. This is probably a trait that favors the family and makes it resilient in fire-prone environments.

Structural parameters

Regard the richness of species found in the plots, out of a total of 77 species recorded, 66 occurred in the burned areas and 45 species in the unburned areas (Figure 5). Statistically terms, richness did not differ between the burned and unburned plots (Poisson PQL GLMM: $\chi^2=0.93$, $P=0.336$ (Figure 6a). Similarly, abundance, represented by comparing the number of individuals per plot, also did not vary between the burned and unburned areas (Poisson PQL GLMM: $\chi^2=0.36$, $P=0.549$ (Figure 6b). Finally, the basal area also did not vary between the burned and unburned areas (Poisson PQL GLMM: $\chi^2=1.61$, $P=0.204$ (Figure 6c).

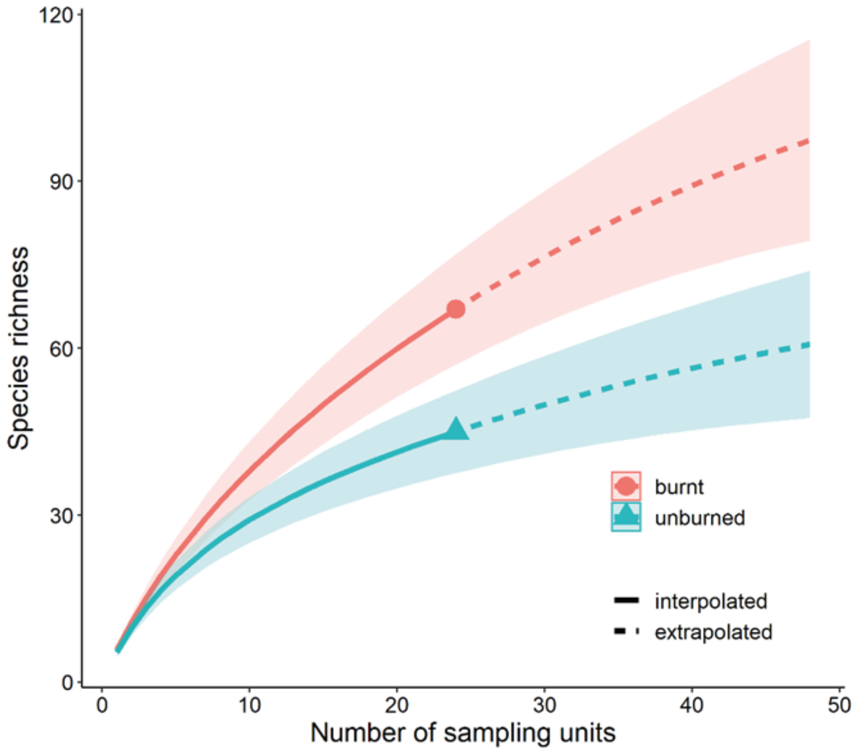

Figure 5 – Rarefaction and estimation of total species richness of arboreal shrubs and palms in burned and unburned areas of the Refúgio Ecológico Caiman, Pantanal Miranda-MS. Collected in the field (solid line) in burned and unburned areas. The dotted line represents the estimated species richness in the study area if the sampling effort were doubled.

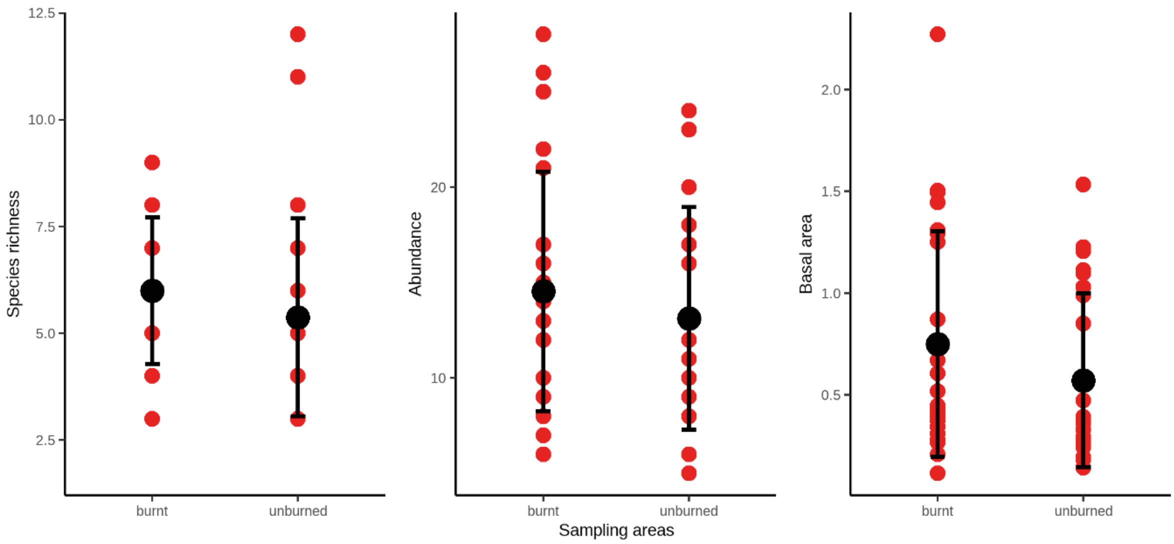

Figure 6 – Comparison of the structural parameters of burned and unburned areas of mountain ranges in the Refúgio Ecológico Caiman, Miranda, MS. Each point on the graphs represents a sample plot. a) total number of species in each plot (red circles) and mean (± SD) of species richness (black circle). b) Total abundance in each plot (red circles) and means (± SD) of abundance (black circle). c) Total basal area in each plot (red circles) and mean (± SD) of basal area (black circle).

In contrast to herbaceous species, which respond immediately to the disturbance caused by fire, in tree species the loss of leaves and the death of the aerial part are the most visible damages. Nevertheless, there was no variation in these parameters one year after the fire, indicating the resilience of the vegetation to fire. The paleo-levees are dominated by species often found in the Cerrado, such as Curatella americana and Handroanthus serratifolius, which have fire-resistant mechanisms such as thick bark [46][47]. Even some of the riparian forest trees recorded in the area are fire resistant due to the phenolic compounds present in their bark [48]. Thus, because there are species that are resistant or even favored by fire [3][49][50], we understand that the passage of fire did not promote changes in basal area, richness and abundance, mainly due to the large number of fire-resistant species in the two situations evaluated. It is possible that in the long term some opportunistic species will succeed in occupying the burned environment and structural differences will be established.

In terms of composition, only 27 species occurred in both plots, forty were exclusive to the burned plots and 18 were exclusive to the unburned plots (Figure 4). The results of NMDS ordination showed that there was a difference in species composition between the burned and unburned plots (MANOVA: $F_{1,46} = 5.34$, Pillai-Trace=0.19, P≤0.001 (Figure 7).

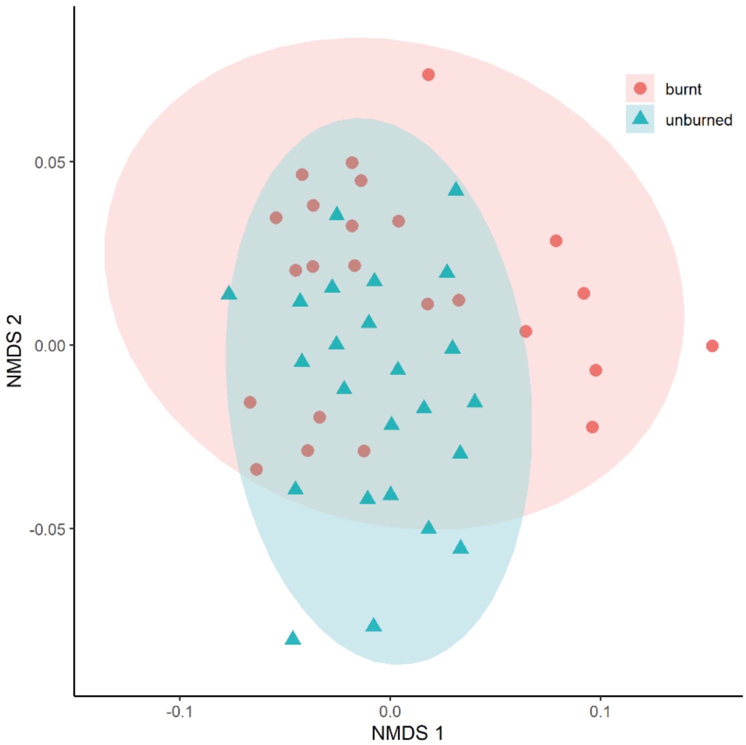

Figure 7 – NMDS-type ordination of the composition of plant species sampled in the levee plots of the Refúgio Ecológico Caiman in the Pantanal, based on the presence/absence matrix. The first two-dimensional solutions recovered 37% of the original variability of the data ($r2adj = 0.37$, P≤0.001).

This type of difference has also been observed in the regeneration of riparian forests along the Paraguay River with a history of fire and in other flooded areas [16][51]. Areas in the Pantanal show slight differences related to the regional species assemblage and how these species are positioned in the landscape [52].

A specific point in relation to these differences in species composition is the proximity of the burned areas to the Aquidauana River. The vegetation closest to the riverbank is influenced by the overflow of the river during the flood season, and in some sections there are channels that remain wet during the drought, influencing the composition of the vegetation.

Some species that occur exclusively in the burned area are indicative of riparian vegetation, such as Combretum laxum, Handroanthus heptaphyllus, Myrcia splendens, Ocotea diospyrifolia, Trichilia elegans, Triplaris gardneriana, or those that have a certain affinity with water, such as Tabebuia aurea (paratudo). In the unburned areas, species exclusive to the Cerrado sensu lato are common, such as Astronium urundeuva, Handroanthus serratifolius, Combretum leprosum and Terminalia argentea. Therefore, we understand that the differences recorded may be the result of edaphic variations and flooding, or an interaction between fire and flooding.

In studies of savanna areas, the results show that gains in number of individuals and basal area were driven by characteristics related to water availability in lower regions, i.e., close to drainage lines and with higher humidity, and the greatest losses in number of individuals and basal area were greater in regions bordering the cerrado vegetation, i.e., regions of higher elevation and consequently lower humidity [53].

In the burned areas, Attalea phalerata was the species with the highest values for all phytosociological parameters, followed by Curatella americana, Randia armata and Cenostigma pluviosum (Table 2). Overall, the ten most important species in the burned area represented about 59.82% of the total IV (importance value). Attalea phalerata contributed about 20.13% of the total IV, followed by Curatella americana with 12% of the IV. Attalea phalerata was also among the main species with the highest IV found in the phytosociological survey carried out in the fire-ravaged grasslands of the Abobral Pantanal [54]. Curatella americana was the most abundant species in a Páleo Levees formation in the Poconé Pantanal [55].

In unburned areas, Astronium fraxinifolium and Chomelia obtusa were the species with the highest density and frequency, while Attalea phalearata and Ficus sp. were the most dominant species (Table 3). Overall, the ten most important species in the unburned area accounted for about 66.24% of the total IV (importance value). Attalea phalerata contributed about 12.85% of the total IV, followed by Astronium fraxinifolium with 9.57% of the IV. The species Astronium fraxinifolium and Attalea phaleratta are characteristic of the Pantanal formations and have also been recorded in the mountain ranges of the Abobral and Poconé Pantanal [55][56].

Table 2 – Phytosociological parameters of the 20 most representative species recorded in the Páleo Levees with burning and unburning in 2020, in the Refúgio Ecológico Caiman, Miranda-MS, ordered by importance value (IV). Where: AD = absolute density of species i, RD = relative density of species i, AF = absolute frequency of species i, RF = relative frequency of species i, ADo = absolute dominance of species i, RDo = relative dominance of species i, IV = importance value of species i. CV = cover value of species.

Burning								
Species	**AD**	**RD**	**AF**	**RF**	**ADo**	**RDo**	**IV**	**CV**
Attalea phalerata	417	14	54	9	48	37	60	51
Curatella americana	558	19	25	4,2	16	12	36	32
Cenostigma pluviosum	142	4,9	29	4,9	9,4	7,2	17	12
Randia armata	267	9,3	38	6,3	0,6	0,5	16	9,7
Coccoloba obtusifolia	250	8,7	13	2,1	1,4	1,1	12	9,8
Enterolobium contortisiliquum	50	1,7	21	3,5	8,2	6,3	12	8
Vitex cymosa	42	1,5	13	2,1	5,3	4	7,6	5,5
Ficus luschnathiana	8,3	0,3	4,2	0,7	7,8	5,9	6,9	6,2
Chomelia obtusa	100	3,5	17	2,8	0,3	0,3	6,5	3,7
Spondias mombin	67	2,3	17	2,8	0,8	0,6	5,7	3
Combretum leprosum	58	2	21	3,5	0,3	0,2	5,7	2,3
Hymenaea martiana	8,3	0,3	4,2	0,7	6,2	4,7	5,7	5
Handroanthus impetiginosus	42	1,5	21	3,5	0,8	0,6	5,6	2,1
Handroanthus heptaphyllus	8,3	0,3	4,2	0,7	5,5	4,2	5,2	4,5
Anadenanthera colubrina	33	1,2	17	2,8	1,2	0,9	4,9	2,1
Myrcia sp.	33	1,2	17	2,8	0,5	0,4	4,3	1,5
Genipa americana	50	1,7	8,3	1,4	1,5	1,1	4,3	2,9

Species	AD	RD	AF	RF	ADo	RDo	IV	CV
Zanthoxylum rigidum	42	1,5	13	2,1	0,3	0,3	3,8	1,7
Zanthoxylum sp.	2,3	0,2	0	0,2	0,1	0,1	3,8	1,7
Ficus sp.	8,3	0,3	4,2	0,7	3	2,3	3,3	2,6

Unburning								
Species	**AD**	**RD**	**AF**	**RF**	**ADo**	**RDo**	**IV**	**CV**
Attalea phalerata	217	8,3	46	8,5	29	22	39	30
Astronium fraxinifolium	375	14	42	7,8	8,9	6,7	29	21
Cenostigma pluviosum	183	7	33	6,2	9	6,7	20	14
Chomelia obtusa	367	14	29	5,4	1,2	0,9	20	15
Coccoloba obtusifolia	258	9,8	33	6,2	2,2	1,6	18	11
Ficus sp.	33	1,3	13	2,3	19	15	18	16
Vitex cymosa	33	1,3	17	3,1	17	13	17	14
Astronium urundeuva	200	7,6	29	5,4	5,3	4	17	12
Enterolobium contortisiliquum	25	1	13	2,3	11	8,3	12	9,2
Trichilia sp.	100	3,8	25	4,7	2	1,5	9,9	5,3
Rhamnidium elaeocarpum	92	3,5	25	4,7	1,1	0,8	9	4,3
Inga vera	83	3,2	8,3	1,6	3,6	2,7	7,4	5,9
Casearia gossypiosperma	75	2,9	17	3,1	0,7	0,5	6,5	3,4
Hymenaea courbaril	8,3	0,3	4,2	0,8	6,6	4,9	6	5,3
Randia armata	58	2,2	17	3,1	0,1	0,1	5,4	2,3
Cordia glabrata	42	1,6	13	2,3	1,8	1,3	5,2	2,9
Luehea candicans	50	1,9	13	2,3	0,7	0,5	4,8	2,4
Acrocomia aculeata	33	1,3	13	2,3	0,7	0,5	4,1	1,8
Zanthoxylum caribaeum	25	1	8,3	1,6	2,2	1,6	4,1	2,6
Annona emarginata	33	1,3	13	2,3	0,3	0,2	3,8	1,5

The Attalea phalerata palm is very common in the Pantanal and is one of the plants known to form monodominant formations in areas subject to the double stress of fire and flooding [57]. Thus, the presence of this palm with greater expression in burned areas is expected, since it survives fire, especially due to the resistance offered by the remnants of the leaf sheaths (Figure 8). This structure can offer protection to the buds during fire events and resistance and tolerance to the stem. Heat tolerance is the ability of plant organs to withstand high temperatures, while fire resistance is the ability to survive a fire [58].

Tomlinson [59] compares palm trunks to reinforced concrete columns, where the vascular bundles are like steel rods and the parenchyma cells are like concrete. The fiber cells near the phloem in the vascular bundles continue to deposit lignin and cellulose throughout their lives, strengthening the older parts of the trunk. In contrast, in the stems of dicotyledons and conifers, the cells of the xylem vessels die and lose their contents before becoming functional as water-conducting tissue, and new phloem is continually produced to replace the old. In palms, however, xylem, phloem, and even parenchyma cells remain alive throughout the life of the plant, which can be hundreds of years in some species [60]. Outside the central cylinder is a region of sclerotized tissue known as the cortex and a very thin epidermis, sometimes collectively called the pseudobark [60].

Figure 8 – Regrowth of Attalea phalerata (acuri), seven days after a fire in 2019, at Refúgio Ecológico Caiman, Miranda, MS.

Another plant species that benefits from fire is Curatella americana, which is characterized by vegetative reproduction and underground shoots that remain active after fire events. The double protection afforded of species offers a degree of resilience to extreme fire events, whereby the crown may be killed off, but the underground buds remain undamaged. In less extreme fire events, the aerial buds can be utilised to promote growth, particularly in terms of height. This was observed fifteen days after a fire in 2019 at the Refúgio Ecológico Caiman in the Pantanal (Figure 9). This growth is supported by underground storage systems, Hoffmann et al. [15] conclude that after top-kill, root carbohydrate reserves are essential to sustain regrowth until sufficient leaf area has developed to sustain net plant growth. Curatella americana, also forms large monodominant patches under fire and flood conditions [6] and, together with other species such as Annona coriacea, Dimorphandra mollis and Styrax ferrugineus, forms a specific group of fire-adapted plants [61][62].

Figure 9 – The species Curatella americana (lixeira) offers dual protection against extreme fire events that may result in top kill. In such instances, the plant's underground buds remain undamaged, while the aerial buds, which are exposed to the flames, are destroyed. However, if the fire event does not reach such extremes, the aerial buds can be utilized, promoting growth in height. Image 15 days after a fire in 2019, at Refúgio Ecológico Caiman, Pantanal of Aquidauana, Miranda, MS.

Unlike Attalea phalerata and Curatella americana, Astronium fraxinifolium can be considered sensitive to fire, as it does not have thick bark or other characteristics that protect it from flames. In burned areas in the Abobral region, this species has been found with large numbers of dead individuals (GA Damasceno-Junior obs pess).

In general, adaptations to fire include structural and physiological changes. Structurally, the thick, corky rhytidome provides greater thermal protection to the vascular cambium [63][64], and the bark of fire-susceptible and fire-intolerant species differs in both structure and chemical composition [48]. Fire stress can also affect plant phenology, stimulating rapid regrowth and promoting both morphological and physiological variation [65][66]. Thermal insulation and the ability to regrow are considered post-fire attributes [67], so we understand that the species listed in the burned areas have high fire resistance and post-fire resilience.

Although the Pantanal is considered a fire-dependent ecosystem [9], many species respond differently to the effects of fire. Fire-resistant species can establish rapidly under frequent and intense fire disturbance [3]. In contrast, many species tend to be less abundant in areas with frequent fire. However, there are exceptions: some species typical of the region's riparian forests, found in the Paraguay River levees [48], which would theoretically be more sensitive to fire, have adaptations such as higher amounts of phenolic compounds in the bark and lower amounts of parenchyma, which in a sense replace the adaptation of thick bark to fire in these environments [48].

The results of studies conducted in forest-savanna transition zones [15] indicate that savanna trees do not exhibit higher survival rates or greater regrowth than forest tree species. The high survival rate of forest trees can be attributed to their occasional exposure to fire, either through natural selection or the elimination of fire-sensitive species from the community. The trees in these forests tend to have thicker bark than those measured in an Amazon rainforest, for example, which suggests that fire plays a role in shaping the tree community. Greater bark thickness results in lower topkill rates (total aerial stem loss) compared to the tropical rainforest. However, this alone does not explain the greater ability to survive fire, as even individuals with topkill exhibited high survival rates in the gallery forests studied [15].

Diversity

The burned area showed a value of 3.1 nats. ind.-1 for the Shannon-Weaver Diversity Index (H`) and the unburned area showed a value of 3.0 nats. ind.-1, which are practically coincident values. The index value is lower than other studies in mountainous areas, which ranged from 3.9 to 4.72 [68], but within the range expected for this type of environment. When compared to other fire-exposed forests, the results are similar [69][70]. Relatively diverse natural ecosystems have a Shannon Diversity Index between 3 and 4, which classifies the areas assessed as diverse [71].

The estimated value of the Pielou index for both areas was J'=0.7, indicating that 70% of the theoretical maximum diversity was obtained by the sampling carried out. This value was similar to that found in a mountain range in Mato Grosso [55].

The similarity of the equitability values in the two plots is striking, suggesting that little has changed in the structural parameters of the plots after fire. Fire generally causes an immediate decrease in biodiversity, resulting in lower local diversity [72][73]. In our study, the diversity values were very similar and follow the trend that there are no differences between burned and unburned areas, indicating the resistance and resilience of the vegetation studied in relation to fire. Although forest formations are always indicated as more sensitive than grasslands, a caveat must be made as these are vegetations with many fire-resistant species. In addition, these areas are elongated strands of forest vegetation and therefore have a lot of contact with the grassland matrix, which makes them more likely to be exposed to fire over the years and consequently select species that are typical of the boundaries between grassland and forest vegetation [74].

Conclusion

The results of the structural parameters showed that there are differences in the species composition of the burned and unburned areas, which can be explained by the fire history of the studied areas. The unburned area has not been burned for more than 25 years, while the burned area has been burned in 2007 and 2019. Although there were no significant differences in richness, abundance, basal area and diversity, our results show that fire events affect species composition.

Resilience has been observed through the detection of species that regrow after fire, such as Curatella americana, and with new leaves emerging from the apical bud (observed in Attalea phalerata), indicating that the presence or persistence of this species are not limited by fire as an environmental filter. Taking into account specific measures related to the conservation of the environment, the results show that the vegetation of the Levess of the Refúgio Ecológico Caiman is resilient after fire. These results show that areas of *Levees* vegetation are important in the context of integrated fire management, because they are formations that, if eventually affected by the management fire used in grassland formations, will not have major structural changes.

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