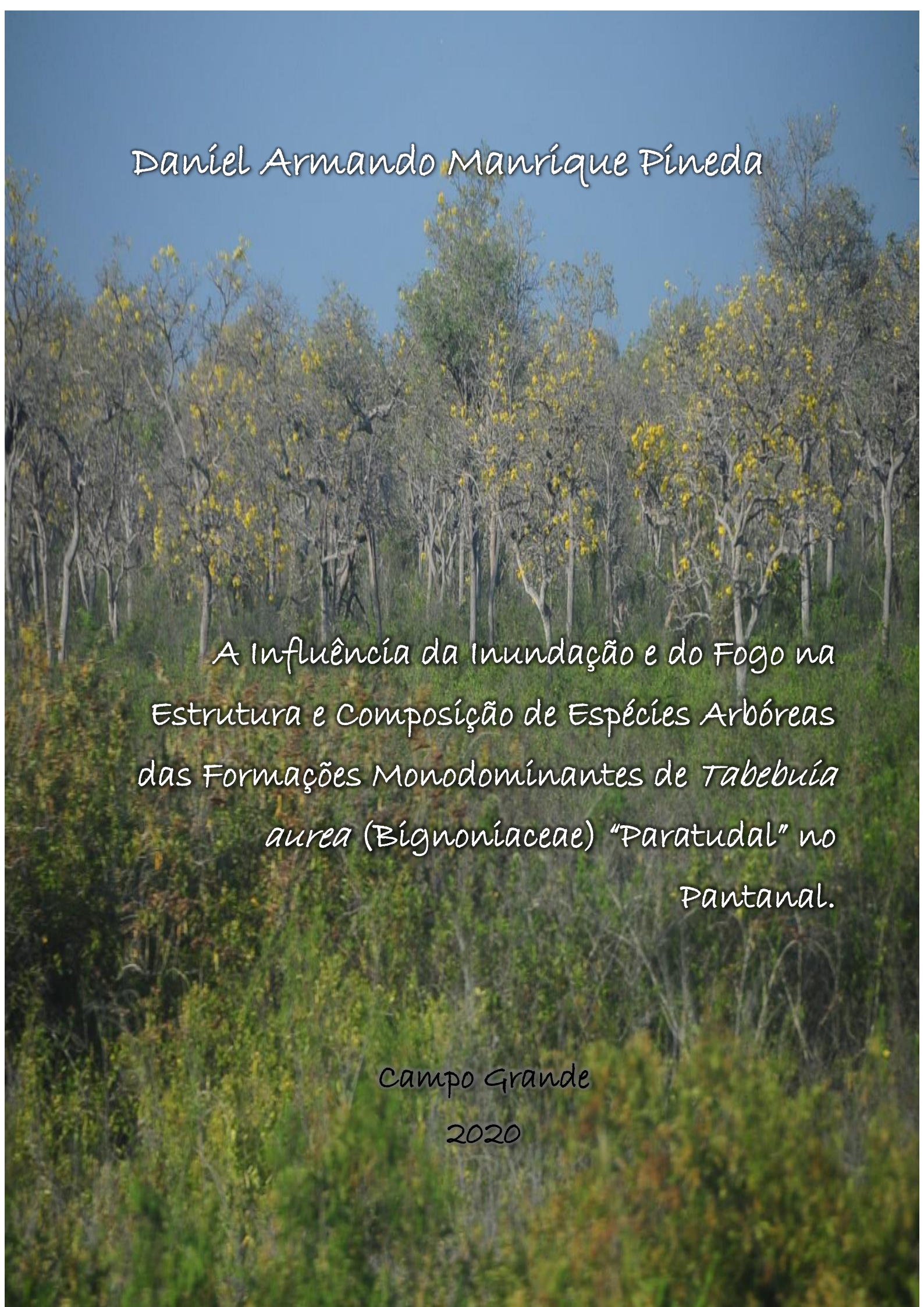




Daniel Armando Manríque Pineda

A Influência da Inundação e do Fogo na
Estrutura e Composição de Espécies Arbóreas
das Formações Monodominantes de *Tabebuia*
aurea (Bignoniaceae) "Paratudal" no
Pantanal.

Campo Grande

2020



MINISTÉRIO DA EDUCAÇÃO

FUNDAÇÃO UNIVERSIDADE FEDERAL DE MATO GROSSO DO SUL
CENTRO DE CIÊNCIAS BIOLÓGICAS E DA SAÚDE
PROGRAMA DE POS-GRADUAÇÃO EM BIOLOGIA VEGETAL



Daniel Armando Manrique Pineda

Dissertação de Mestrado

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Pós-graduação em Biologia Vegetal
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RESUMO

Os filtros ambientais afetam a diversidade de espécies. A compreensão da influência desses filtros na estruturação das comunidades vegetais são um dos principais desafios da ecologia na busca de ideias de manejo e conservação dos ecossistemas. As formações monodominantes do Pantanal estão sujeitas às fases de cheia e seca onde a inundação e o fogo atuam como filtros biológicos definindo a distribuição da flora e fauna. O objetivo deste trabalho foi verificar se a interação entre inundação e fogo influenciam na abundância, riqueza e área basal de espécies arbóreas; nas formações monodominantes de *Tabebuia aurea* e se esses fatores podem influenciar na monodominância. Por meio de imagens de satélite Landsat-5, -8 e Resourcesat-1, foram selecionadas 37 áreas com frequências de fogo de 2 até 9 anos, em 15 anos de investigação (2003 – 2017). Foram instaladas um total de 125 parcelas de 25m X 25m nas diferentes áreas. A descrição da comunidade foi feita por meio da coleta de todos os indivíduos com diâmetro à altura do peito igual ou maior a 3,18 cm e identificações. Dados da altura da marca da água em cada indivíduo foram usados para identificar o efeito da inundação. Foi comparada abundância, riqueza e área basal com o Modelo Linear Generalizado com distribuição Negativa Binomial, Poisson e Gaussian, respectivamente. Abundância e riqueza sob maior frequência de fogo foram maiores em número de indivíduos e de espécies nas áreas mais altas, diminuindo nas áreas sujeitas a maiores níveis de inundação. Enquanto áreas sob frequência de fogo menor o número de indivíduos foi constante com um incremento no número de espécies em relação ao aumento da altura da água. Área basal diminuiu com o aumento da altura da água independente da frequências de fogo, sendo maior em áreas sob frequência de fogo menor. Nossos resultados evidenciam que os indivíduos de *T. aurea* são beneficiados pela interação fogo e inundação, como também pela diminuição de outras espécies não tolerantes aos dois filtros ambientais.

Palavras-chave: Análises fitossociológicas, estrato arbóreo, fatores ecológicos, filtros ambientais, Pantanal brasileiro, sensoriamento remoto.

ABSTRACT

Environmental filters affect species diversity. Understanding the influence of these filters in the structuring of plant communities is one of the main challenges of the ecology in searching for ideas of management and conservation of the world ecosystems. Monodominant stands of the Pantanal are subject to the phases of flood and drought. Flood and fire act as biological filters defining the distributions of the plants and wildlife. The aim this work was to check if the interactions between flood and fire influence richness, abundance and basal area of the tree species in the monodominant stands of *Tabebuia aurea* and verify if these two filters can favor monodominance of this species. Through satellite images Landsat-5, -8 and Resourcesat-1, we selected 37 areas with annual fire frequency from 2 to 9 years in a period of 15 years (2003 - 2017). We set a total of 125 plots of 25m x 25m in the different area. We sampled all individuals with a diameter at breast height of 3,18 cm or more and identified all species. Watermark height data left by the last flooding on each individual were used to identify the flooding effect. Abundance, richness and basal area were compared with Generalized Linear Model and Negative binomial, Poisson and Gaussian distribution, respectively. Abundance and richness under higher fire frequency were high but decreased with increasing flood levels, while areas under lower fire frequency the number of individuals was constant with an increase in the number of species in relation to the increase of water height. Basal area decreased when height increase independent of fire frequencies, individuals with larger basal area were found in areas under lower fire frequency. Our results show that *T. aurea* individuals are benefited by the fire and flood interaction, as well as by the decrease of other species not tolerant to the two environmental filters.

Keyword: Arboreal stratum, Brazilian Pantanal, ecological factors, environmental filters, phytosociology, remote sensing.

INTRODUÇÃO

Os filtros ambientais são fatores ecológicos que atuam como selecionadores das espécies que podem sobreviver e se estabelecer em determinado local (Keddy, 1992; Poff, 1997). O processo de seleção atua sobre características intrínsecas das espécies restringindo o potencial biológico, onde só aquelas espécies que possuem as características adaptativas e competitivas adequadas vão resistir aos impactos dos filtros ambientais, sendo capazes de sobreviver sob condições específicas do ambiente e as interações inter e intraespecíficas (Cornwell et al., 2006; Hughes et al., 2008). Alguns dos filtros mais comuns são fogo, inundações, ação de herbívoros, revolvimento de solo, entre outros (Keddy, 1992). São considerados promotores das alterações nas estruturas dos sistemas naturais, pela redução na competição entre espécies e mudanças na disposição dos recursos que influenciam no equilíbrio dos ecossistemas (Sher et al., 2000). As espécies que tem as características necessárias para suportar os filtros ambientais competiram com as demais espécies que também passaram por esses filtros, podendo coexistir se suas características e estratégias de sobrevivência são diferentes umas das outras, caso contrário a espécie menos competitiva vai ser eliminada (Cornwell et al., 2006). Podemos assim dizer, que as comunidades são organizadas em relação aos filtros ambientais e relações inter e intraespecíficas, de forma que organismos mais especializados às condições do habitat vão a sobreviver e se estabelecer às diferentes mudanças das condições ambientais enquanto outras espécies iram a desaparecer (Costa and Melo, 2008; Poff, 1997).

Em tempos de mudanças climáticas globais a influência dos filtros ambientais resulta ser de bastante interesse para o entendimento das comunidades naturais, e compreender os processos que dão forma à comunidade vegetal em relação a esses filtros é um dos principais desafios da Ecologia (Mouillot et al., 2013). A frequência e intensidade dos filtros ambientais, podem influenciar a comunidade que por sua vez, depende da sua capacidade de resistência e resiliência, as quais determinam suas características, diversidade, riqueza e distribuição espacial; o entendimento das interações entre as espécies vegetais e sua relação com os filtros ambientais são importantes para o manejo e conservação de áreas naturais (Ives and Carpenter, 2007).

Um filtro ambiental como a inundação gera muitos efeitos e mudanças na estrutura e composição das comunidades vegetais. São ocasionadas pelo excesso de chuvas, transbordamento dos rios e/ou escoamento das águas, principalmente (Damasceno-Junior et al., 2004; Nunes Da Cunha and Junk, 2001). O ciclo de inundação é o principal filtro ecológico para as comunidades vegetais estabelecidas em uma área úmida (Junk et al., 2006), e pode ser prejudicial para as espécies arbóreas não adaptadas, induzem as disfunções na fotossíntese e na nutrição mineral o que leva à inibição do crescimento podendo levar à mortalidade das plantas (Kozłowski, 2002), principalmente em seus estádios iniciais (plântulas). Entretanto, espécies que crescem em zonas úmidas expostas a inundações sazonais e previsíveis, desenvolvem estratégias como a formação de lenticelas, aerênquima, suberização das raízes adventícias, entre outros, para tentar sobreviver a anóxia (Parolin et al., 2004). Mecanismos de proteção contra a falta de oxigênio e atividades fotossintéticas debaixo da água, que proporcionam adaptações metabólicas e influenciam na morfologia de indivíduos e na estrutura, riqueza e distribuição das espécies e comunidades (Nunes Da Cunha and Junk, 2001), além de influenciar nas suas atividades fisiológicas que possibilitam sua resistência e resiliência às condições do ambiente (Kozłowski, 2002).

Outro filtro que influencia a estrutura e composição das comunidades vegetais é o fogo, o qual ocorre em muitos ecossistemas do mundo (Bond and Parr, 2010). As principais causas estão relacionadas às condições climáticas, ciclo do carbono, atividades do uso da terra e secas de longa duração (Duffy et al., 2015; Morisette et al., 2005), e fenômenos como de El niño (Barbosa et al., 2018). É o principal filtro ambiental das savanas do mundo, no qual modela a paisagem, mantendo o predomínio herbáceo-arbustivo da vegetação e impedindo o avanço de florestas sobre a savana (Bond et al., 2005). Em savanas a presença de sistemas subterrâneos protege as árvores dos incêndios na superfície. Nesses sistemas as folhas rebrotam rapidamente após um evento de fogo, sendo fogo-dependentes (Bond, 2016). Geralmente, não sempre a presença de fogo é letal para a maioria das espécies de plantas, aquelas que estão sujeitas a frequente interação com o fogo desenvolvem características como cascas grossas, rápido crescimento, proteção de suas estruturas fotossintéticas e poder de germinação após um evento de fogo (Lukac et al., 2010). Porém, a resistência das plantas ao fogo é dependente da sua frequência, intensidade e severidade, que pode aumentar ou diminuir segundo a acumulação dos componentes herbáceos ou arbóreos que compõem a comunidade (Agee et al., 2002).

O efeito conjunto da inundação e fogo muda completamente a estrutura da comunidade de plantas, sendo um fenômeno regular em ambientes de savana. Por um lado, a inundação elimina espécies de plantas intolerantes afetando a riqueza, enquanto o fogo tem a capacidade de mudar a estrutura de nutrientes do solo, proporcionar uma abertura na paisagem e favorecer o rebrotamento das espécies mais tolerantes (Newman et al., 1998). Porém, frequentes inundações não permitem uma reocupação bem sucedida após eventos de fogo, promovendo uma diminuição na abundância das espécies (Lockwood et al., 2003). A intensidade do fogo pode ser controlada pela alta disponibilidade de água no solo das áreas úmidas (Schmidt et al., 2017). Quer dizer, que a inundação tem o papel mais importante ao determinar a composição de espécies da comunidade, pois aquelas espécies que têm a capacidade de rebrotamento após um evento de fogo morrem por hipóxia devido aos altos níveis da inundação, sobrevivendo só aquelas que tem as características morfológicas para suportar a inundação (Ishida et al., 2008). Qualquer mudança significativa no pulso de inundação das áreas úmidas alteraria por completo a frequência e intensidade do fogo, gerando drásticas mudanças no ecossistema (Mitsch et al., 2010), permitindo o avanço de gramíneas e morte de espécies arbóreas típico de savanas inundáveis com frequente interação de fogo (Armenterara et al., 2005).

Assim, o fogo e a inundação são considerados filtros ecológicos que podem formar ou modificar a estrutura e composição das comunidades vegetais, sendo um fenômeno interessante porque colocam em jogo dois eventos extremadamente opostos, o fogo e as inundações (Damasceno-Junior et al., 2005), de eventual regularidade nas savanas úmidas tropicais como no caso dos Everglades de Miami (Newman et al., 1998), Okavango Delta em Botswana (Heinl et al., 2008; Mitsch et al., 2010) e o Pantanal em Brasil (Nunes Da Cunha and Junk, 2004; Oliveira et al., 2014; Schmidt et al., 2017), de vital importância para o equilíbrio natural dos ecossistemas do mundo (Bond et al., 2005; Pott and Pott, 1994).

Deste modo, o Pantanal é uma das savanas sazonalmente inundáveis com maior biodiversidade no planeta, com aproximadamente 138.183 Km² no Brasil, localizada na bacia hidrográfica do alto Paraguai entre os estados de Mato Grosso e Mato Grosso do Sul (Silva and Abdon, 1998). É um dos locais ideais para testar as interações entre comunidades vegetais e filtros ambientais como a inundação e o fogo. A ocorrência de chuvas nos meses de outubro a março principalmente nas cabeceiras dos rios, fazem que o Pantanal inunde (Prado et al., 1994). A inundação junto com os diferentes tipos de solos, estruturas geológicas e ocorrência de

queimadas; definem os principais fatores que limitam o crescimento de espécies vegetais e influenciem na distribuição da flora e fauna (Pott et al., 2011).

As principais formações vegetais do Pantanal são as formações monodominantes, as quais são dominadas por uma determinada espécie de planta, sendo assim considerada quando 50% ou mais dos indivíduos pertencem a essa única espécie (Bueno et al., 2014; Hart et al., 1989). Nessas formações os filtros ambientais atuam mais pontualmente sobre espécies em regeneração ou menos adaptadas favorecendo as espécies monodominantes. No Pantanal, essas formações recebem nomes locais como “Cambarazal” (dominada por *Vochysia divergens* Pohl) (Arieira et al., 2018), “Carandazal” (de *Copernicia alba* Morong ex Morong e Britton) “Canjiqueiral” (de *Byrsonima cydioniifolia* A. Juss) “Pimenteiral” (*Licania parviflora* Benth.) “Babaçual” (*Attalea speciosa* Mart. Ex Spreng) e “Paratudal” (de *Tabebuia aurea* (Silva Manso) Benth e Hook.) (Bueno et al., 2014), dentre outros (Pott and Pott, 1994). Assim, a formação monodominante de *T. aurea* é a comunidade vegetal com maior interação do fogo e da inundação, por encontrar-se próximo aos rios Miranda e Paraguai e ter um estrato contínuo de gramíneas, que em épocas de seca se convertem em combustível para o fogo (Bueno et al., 2014; Riveiro and Brown 2002).

Neste sentido, devido à importância ecológica que tem *T. aurea* na região do Pantanal e a existência de poucos estudos sobre as comunidades de *T. aurea* (Bignoniaceae), o “Paratudo”. Este estudo tem como objetivo verificar qual é a relação entre os parâmetros estruturais das formações monodominantes de *T. aurea*, com os regimes de inundação e de fogo, e como estes fatores influenciam na sobrevivência da espécie e da comunidade. Utilizamos a seguinte pergunta de investigação: como a inundação e o fogo sob diferentes frequências (baixas e altas) influenciam na riqueza, abundância e área basal das comunidades monodominante da espécie *T. aurea*? A partir de três hipóteses: a primeira é que os indivíduos da espécie *T. aurea* vão manter-se estáveis ou pouco afetados nas áreas com maior frequência de fogo e inundação, esperando que os indivíduos de *T. aurea* ao ser uma espécie que cresce em áreas úmidas como o Pantanal (Bueno et al., 2014; Soares and Oliveira, 2009), e extremadamente secas como do Cerrado (Ribeiro and Brown, 2006, 2002, 1999), vai ser beneficiada pelo efeito conjunto e pela ausência de outras espécies não tolerantes ao fogo e à inundação.

A segunda hipótese é que a riqueza de espécies arbóreas vai diminuir nas áreas com maior frequência de fogo e com maior nível de inundação pela pouca capacidade que as espécies possuem de sobreviver a estes dois filtros ambientais. Pelo contrário os indivíduos de *T. aurea* vão aumentar em número de indivíduos. E uma terceira hipótese é que a área basal, vai ser menor nas áreas com maior nível de inundação e maior frequência de fogo devido à hipóxia produto do estresse que sofrem as plantas pelo excesso de água e falta de oxigênio e pela ação destrutiva do fogo, e vai aumentar em áreas de menor frequência de fogo e menor inundação pelo subsídio e condições adequadas para o crescimento das plantas na interação destes dois filtros ambientais.

Assim, a presente dissertação está escrita em um único capítulo intitulado: Environmental filters in the monodominant neotropical floodable savanna of *Tabebuia aurea*, que será submetido à revista *Forest Ecology and Management*, como produto do trabalho de investigação de conclusão de mestrado.

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Fire, flood and monodominance of *Tabebuia aurea* in Pantanal.

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Abstract

Environmental filters affect species diversity. Understanding their influence at plant communities is one of the main challenges of ecology in searching for ideas of both management and conservation of the floodable savannas. This work aimed to check if the interactions of flood and fire in monodominant stands of *Tabebuia aurea* favor the monodominant species with influences in abundance, richness and basal area of all tree species. Using satellite Landsat-5 and -8 and Resourcesat-1 data, we accessed the fire history in monodominant stands of *T. aurea* in the Pantanal from 2003 to 2017. We choose 37 areas with 2 to 9 annual fire episodes. A total of 125 25 X 25 m plots were established in the different areas, to sample arboreal strata. We sampled all individuals with > 3, 18 cm of diameter at breast height. In each plot, we measured the watermark height left by the last flooding on each individual as a proxy of inundation level. We applied generalized linear model analyses to compare effects of flood and fire on abundance, richness and basal area with Negative binomial,

Poisson and Gaussian distribution, respectively. We sampled 2411 individuals distributed among 19 families, 31 genera and 36 species. Abundance and richness under higher fire frequency were higher but dramatically decreased with water height but *T. aurea* individuals were so much than other species. Under lower fire frequency the abundance and richness was constant with a slight increase with water height. Basal area decreased with water height independent of fire frequencies, individuals with larger basal area were found under lower fire frequency. With the absence of earth-mound decreased abundance but increased basal area under low fire frequency to *T. aurea* individuals, in other species increased regardless of the fire frequency. Our results show that monodominance of *T. aurea* is benefited by the fire and flood interaction, as well as by the decrease of other species not tolerant to the two environmental filters.

Keywords: Environmental filters, monodominant stands, Pantanal of Miranda, phytosociology, remote sensing.

1. Introduction

Environmental filters are ecological factors that act as selectors of species that can establish in a particular habitat (Keddy, 1992; Poff, 1997). They act on inherent characteristics of species by restricting biological potential, where those that have the appropriate adaptive and competitive characteristics will resist environmental filters under specific conditions and inter and intraspecific interactions (Cornwell et al., 2006; Hughes et al., 2008). Some of the most common filters are fire, flood, herbivory, among others (Sher et al., 2000). Species that have the necessary characteristics to support the environmental filters competed with each other, and may coexist if their survival strategies are different, otherwise the less competitive species will be eliminated (Cornwell et al., 2006). Global climate changes influences environmental filters and are of great interest to the understanding of the natural communities, and their comprehension is a central challenge of ecology (Mouillot et al., 2013). The frequency and intensity of environmental filters may influence many aspects of the community. This influence depends on the ability of resistance and resilience of species which will determine characteristics such as diversity, richness and distribution (Agee et al., 2002; Stellmes, 2013). Understanding the interactions between plant species and their relationship with environmental

filters is essential for both management and conservation plans of natural areas (Ives and Carpenter, 2007).

Flooding causes many effects and changes in the structures and compositions of plant communities. The causes are excessive rainfall, river overflow and - or water runoff (Damasceno-Junior et al., 2004; Nunes da Cunha and Junk, 2001). Flood can be harmful to non-adapted species and lead to plant mortality (Kozłowski, 2002). Nevertheless, species that grow in wetland areas develop strategies such as reduced metabolism during the flood phase (aquatic) (Wittmann et al., 2004), hypertrophy of lenticels, adventitious roots, among others to survive anoxia (Bueno et al., 2014; Junk et al., 1989; Parolin et al., 2004). Extreme flood events decrease abundance, richness and diversity species, acting as a selective factor because can it eliminate seedlings and seeds (Bueno et al., 2014; Damasceno-Junior et al., 2004). Adult and adapted individuals can also survive by thickening the stem diameter as a strategy to generate resistance to hypoxia (Nunes da Cunha and Junk, 2004). It means that flooding acts as an environmental filter limiting diversity and species richness, being a selective force for tree species (Cianciaruso and Batalha, 2009; Damasceno-Junior et al., 2005; Silva and Batalha, 2008).

On the other hand, fire occurs in many ecosystems of the world especially in savannas (Bond and Parr, 2010), modeling the landscape and preventing the advance of forests by the flammable characteristics (Bond, 2016; Bond et al., 2005; Bond and Parr, 2010). Fire increases the density of herbaceous species and decreases richness of tree species, where fires occur with high frequency. It can generate permanent changes in structure, floristic and the shape of vegetation (Araújo et al., 2017). Interrelationships between climate conditions, carbon cycle, land use activities (Duffy et al., 2015; Morisette et al., 2005; Serrão et al., 2015) and El Niño phenomenon in some areas (20th Century) (Barbosa et al., 2018) potentiate long-term drought and fire frequency (Morisette et al., 2005; Serrão et al., 2015). Plant species undergoing fire occurrence developed, along with evolution, adaptations such as thick bark, fast growth, protection of photosynthetic structures and germination power after a fire event (Lukac et al., 2010). However, the resistance of plants to fire is dependent on its frequency, intensity and severity, such as the accumulation of the herbaceous or arboreal components that compose the community (Agee et al., 2002; Lukac et al., 2010). Savannah species resist many fire events, however generally young individuals are eliminated (Vander Yacht et al., 2017), but plant

propagules influence post-fire regeneration increasing richness and abundance of species after the fire event (Araújo et al., 2017).

The combined effect of flood and fire completely changes the structure of the plant community, being a regular phenomenon in seasonally flooded savanna environments. Flood eliminates intolerant plant species affecting species richness, on the other hand, fire can change the nutrient availability of the soil, provide an opening in the landscape and favor the regrowth of the most tolerant species (Newman et al., 1998). However, frequent flooding does not allow successful restore promoted by fire, suggesting an effect on species abundance (Lockwood et al., 2003). Flooding determines the species composition of the community (Ishida et al., 2008). Any significant change in the flood pulse of wetlands completely alters both fire frequency and intensity, generating drastic changes in ecosystems (Mitsch et al., 2010). It allows grass advance and death of tree species typical of flood savannas with frequent fire occurrence (Armenterasa et al., 2005). These ecological filters are of eventual regularity in tropical wet savannas as in the case of Everglades in Miami (Newman et al., 1998), Okavango Delta in Botswana (Heinl et al., 2008; Mitsch et al., 2010) and the Pantanal in Brazil (Nunes Da Cunha and Junk, 2004; Oliveira et al., 2014; Schmidt et al., 2017). These wetlands are of vital importance for the natural balance of the world's ecosystems (Bond et al., 2005; Pott and Pott, 1994).

The Pantanal is one of the most biodiverse seasonally flooded savanna of the planet, with approximately 138.183 Km² in Brazil, where fire and flood occur as, extremely opposite events (Bueno et al., 2014; Silva and Abdon, 1998; Damasceno et al., 2005; Prado et al., 1994; Pott and Pott, 1994). One of the main vegetal formations of the Pantanal are the monodominant stands, frequently associated with high levels of inundation (Pott and Pott, 1994; Soares and Oliveira, 2009). It is consider as monodominant when more than 50% of individuals belonging to a single species (Bueno et al., 2014; Hart et al., 1989).

Tabebuia aurea (Bignoniaceae) and its monodominant stands are a typical component of the landscape in the Miranda sub-region of the Pantanal. This sub-region is subject to regular events of fire and flood. We suspected that the interaction of fire and flood could be related to this monodominance.

This study has the objective to verify if the variation in fire and flood regime can be related to the monodominance of *Tabebuia aurea*. To investigate this we intend to answer the following questions: Do flood and fire at different frequencies influence variation in richness, abundance and basal area of the *T. aurea* monodominant communities? Do flood and fire at different frequencies influence or can benefit abundance and basal area of *T. aurea* monodominant stand? We hope that individuals of the species *T. aurea* will remain stable and benefit in the areas most frequently affected by fire and flood. We expect that *T. aurea* as a species that grows in wetlands like the Pantanal (Bueno et al., 2014; Soares and Oliveira, 2009) and extremely dry like the Cerrado (Ribeiro and Brown, 2006, 1999), will benefit from this joint effect. In addition, we also expect that abundance, richness and basal area of other tree species to diminish in high fire and flood high levels. Flood-tolerant species generally are sensitive to fire, i.e. die with the presence of fire (Pott and Pott, 1994). Moreover, fire tolerant species may regrow after fire event, however, young individuals tend to die quickly (Lukac et al., 2010) only those long-lived species and fire and flood-tolerant will survive (Ribeiro and Brown, 2002).

2. Materials and methods

2.1. Study area

The Miranda and Nabileque sub-region are located in the southern part of the Pantanal, corresponding to the Miranda River sub-basin (Upper Paraguay Basin), municipality of Corumbá-MS (Pott et al., 2011). These has the following limits: to the south with the Chaco forests in the municipality of Porto Murtinho, to the north with the Abobral sub-region, to the east with Aquidauana sub-region and to the west the highland of Bodoquena (Bueno et al., 2014). The main monodominant formations are “Cambarazal” (dominated by *Vochysia divergens* Pohl) (Arieira et al., 2018), “Carandazal” (by *Copernicia alba* Morong ex Morong & Britton), “Canjiqueiral” (by *Byrsonima cydioniifolia* A. Juss), “Paratudal” (by *Tabebuia aurea* (Silva Manso) Benth & Hook. F. ex S. Moore) (Bueno et al., 2014), and others (Pott and Pott, 1994). The monodominant stands of *Tabebuia aurea* are located mainly between the coordinates 19°18'44.30"S - 57°37'10.23"W, 19°17'03.09"S - 56°22'54.12"W, 20°12'05.09"S - 56°24'23.43"W and 20°15'59.88"S - 57°36'43.87"W (Soares and Oliveira, 2009) (Fig. 1).

The authorization to work in the areas was provided by SISBIO (Biodiversity Authorization and Information System).

The climate is Aw according to Köppen-Geiger classification (Alvares et al., 2014), with annual rainfall around 1,010mm, raining on average 100 days a year. The most intense period of rain occurs from December to March, the wettest month is January with 191mm, with water deficit from September to November, defining two seasons, rainy summer and dry winter (Soriano, 1997). In the Miranda and Nabileque sub-regions the maximum flooding peak occurs in April to June, when the Miranda river reaches 6 to 7 m above the low level and floods the whole plain (Hamilton, 1996).

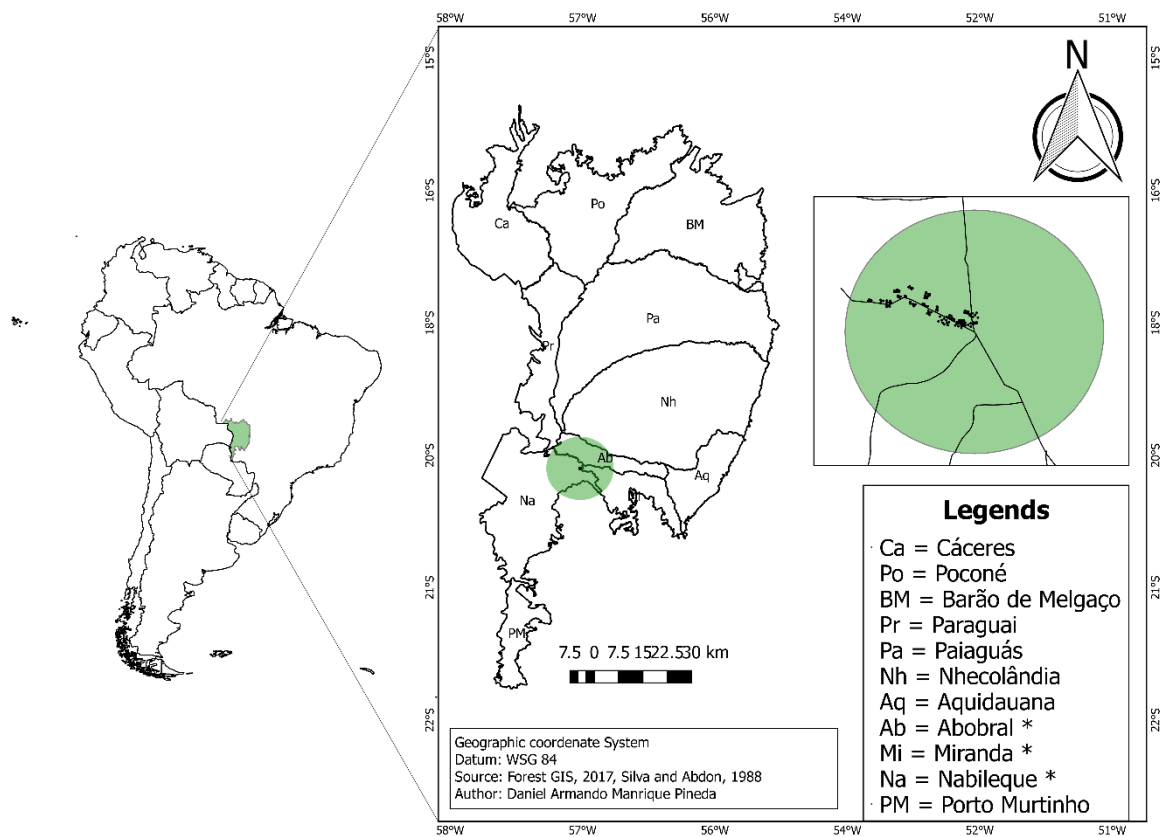


Fig. 1. Study area location: Map of Latin America with the Brazilian Pantanal. In the Pantanal, the circumference of 40 km in the Miranda and Nabileque sub-regions used to find the sampling plots (points), the lines inside the circumference are the access ways.

Tabebuia aurea (Bignoniaceae) is a tree with an average height between 5 and 16 m, with yellow flowers that bloom in August / September and grows on earth-mounds. These earth-mounds allow these trees to stay more time out of water during inundation in Pantanal. The

monodominant stands of *T. aurea* are found mainly in the southern part of the Pantanal of Miranda and are called Savana Park (Pott et al., 2011). There, the areas are mainly influenced by floods with alkaline pH waters and fire occurs in the dry season (Bueno et al., 2014; Soares and Oliveira, 2009) (Fig. 2).

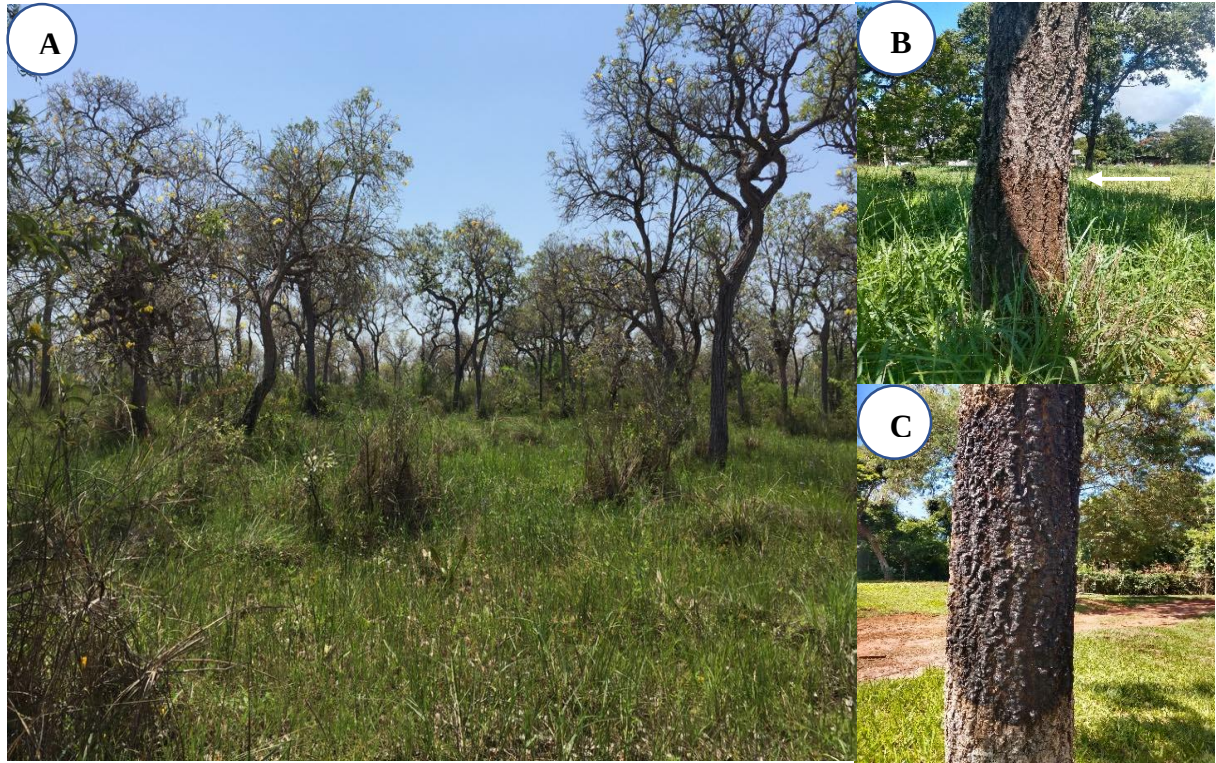


Fig. 2. Monodominant stand of *Tabebuia aurea* in the southern part of Pantanal. (A) Plot with *T. aurea* individuals and other tree species under high fire frequency; (B) Watermark on the stem of a *T. aurea* individual. (C) Firemark on the stem of a *T. aurea* individual. These photographs were taken in the dry season.

2.2. Area of sampling

We selected the areas of sampling tracing a circumference of 40km where monodominant stand of *T. aurea* are located. Posteriorly, downloaded heat spots obtained from the page of the National Institute for Space Research (INPE, 2017), for the recognition of areas with fire influence, already with the location of the heat spots we visualized them in Landsat-5, Landsat-8 and Resourcesat-1 (exclusive for 2012) satellite images, from July to November, when the most prolonged drought period occurred and indeed with the most extensive fire events in the Pantanal (Damasceno-Junior et al., 2005). The images were obtained from the United States Geological Survey (USGS, 2017), using the path 226/ row 074 to Landsat images;

and path/row 320/091, 320/092 and 321/092 to Resourcesat images, corresponding to the southern of Pantanal (Miranda and Nabileque subregions, mainly), and combination of bands 543, 752 (Landsat-5, -8) and 421 (Resourcesat-1). The images were processed through the Qgis 2.18 (Qgis Development Team, 2017), monitoring fire scars in the region (Fig. 3).



Fig. 3. Landsat 5 and Landsat 8 satellite images, scars indicate burned spots and black dots the heat spots, in the southern of Pantanal.

Thirty-seven areas were selected with monodominant stands of *T. aurea* with fire frequency, from 2 to 9 years in the region's last 15-year fire history (2003 to 2017). We selected 4 or sometimes 5 areas for each fire frequency well distributed from 2 years of repetitions to 9 years of fire repetitions. High-intensity fires occurred in 2005, 2007 and 2012, and low-intensity fires in the years 2006, 2011 and 2014.

2.3. Data Collection

We collected data between July and December 2018, using the sampling method suggested by Damasceno-Junior and Pott (2011) for studies in the Pantanal. In each one of the 37 areas, 25m x 25m square plots were sampled, systematically established from no less than 50 m from the edge and the same distance between plots, totaling 125 plots and around 5 ha sampled area. In each plot we sampled all individuals with a minimum diameter at breast height (dbh) of 3.18 cm, measuring their height, diameter and watermark from the last flood on each stem, using a tape (cm) and a rod 3 m long (Damasceno-Junior and Pott, 2011). The watermark measure was added to the height of the earth-mound when it was present. We collected fertile

specimens according to the usual procedures in botany, using pruning shears or high-pruning shears (Fidalgo and Bononi, 1984) and deposited them in the CGMS Herbarium of the Universidade Federal de Mato Grosso do Sul (UFMS).

The identifications of the plant specimens were undertaken by using specialized bibliography, comparing with exsiccates of the Herbarium and consulting with experts. APG IV (2016) was adopted (Chase et al., 2016), and species names were verified on the site <http://www.theplantlist.org> to confirm their nomenclature.

2.4. Data analyses

To analyze the influence of fire regime, we distributed the fire frequencies in different combinations to get data from areas with low (2 and 3 events), medium-low (4 and 5 events), medium-high (6 and 7 events) and high (8 and 9 events) frequencies of fire. The sampled trees were distributed into 3 categories: Total individuals (T), individuals on earth-mounds (M) and individuals without mounds (WM), performing test for the total of individuals, *T. aurea* individuals and individuals without *T. aurea* for each category. For inundation data, we used the average of the watermark (plus the height of the earth-mound when present) found on each individual per plot. Thus, we used the flooding as the continuous predictor variable, fire as categorical variable and abundance, richness and basal area as response variables.

We used general linear models (GLM) to verify the influence of fire and flooding in richness, abundance and basal area of the individuals (Turner, 2008). Using the *fitdistrplus* package, we found the appropriated distribution for each tested response variable (Delignette-Muller and Dutang, 2015). With the *fitdist* and *gofstat* functions, we determined the distributions as follows: Poisson distribution for richness, Negative Binomial for abundance and Gaussian for basal area, in the three categories for the total species test (Table 2) (Zeileis and Hothorn, 2002). In addition, we performed abundance and basal area tests exclusively for *T. aurea* individuals, and tests for the individuals of the total species except for the dominant specie (Tables 3, 4), for more accurate information on fire and flooding interaction, and their differences within the monodominant community. For the WM category, the Poisson Tweedie distribution was used to eliminate truncated zero in the plots due to the absence of individuals in the plots in this category (Table 3). We also used in testing total species without *T. aurea* in

all three categories (Table 4) (Dunn and Smyth, 2008). For graphical analysis, we used visreg package, all on the R platform (R Development Team, 2017).

3. Results

3.1. Species richness

We sampled a total of 2411 individuals distributed in 19 families, 31 genera and 36 species (Table 1).

Table 1. Species sampled in the monodominant stands of *Tabebuia aurea* the Miranda and Nabileque sub-regions of the Pantanal, Mato Grosso do Sul State, Brazil, with respective botanical families and fire frequency where they occurred.

Family	Scientific name	N. individuals	Firefrequency
Anacardiaceae	<i>Astronium fraxinifolium</i> Schott	1	8
Annonaceae	<i>Annona dioica</i> A.St.-Hil.	2	9
	<i>Annona nutans</i> (R.E.Fr.) R.E.Fr.	9	6,8,9
	<i>Annona</i> sp.	2	4,7
Arecaceae	<i>Copernicia alba</i> Morong	11	4,5,6,7,8
Bignoniaceae	<i>Handroanthus heptaphyllus</i> (Vell.) Mattos	12	2,3,4,5
	<i>Tabebuia aurea</i> (Silva Manso) Benth. & Hook.F. ex S.Moore	1795	All
Chrysobalanaceae	<i>Couepia uiti</i> (Mart. & Zucc.) Benth. ex Hook.F.	1	2
	<i>Licania parviflora</i> Benth.	1	2
Combretaceae	<i>Combretum lanceolatum</i> Pohl ex Eichler.	2	4
Erythroxylaceae	<i>Erythroxylum anguifugum</i> Mart.	175	All
Euphorbiaceae	<i>Sapium haematospermum</i> Müll.Arg.	29	All but 9
Fabaceae	<i>Albizia inundata</i> (Mart.) Barneby & J.W.Grimes	15	2,3,4,9
	<i>Albizia niopoides</i> (Spruce ex Benth.) Burkart.	1	6
	<i>Andira inermis</i> (W.Wright) DC.	2	6,9
	<i>Bauhinia bauhinioides</i> (Mart.) J.F.Macbr.	31	5,6,8,9
	<i>Inga vera</i> Willd.	24	All but 5

	<i>Pterocarpus santalinoides</i> L'Hér. ex DC.	1	2
	<i>Sesbania virgata</i> (Cav.) Pers.	5	6
Lauraceae	<i>Ocotea diospyrifolia</i> (Meisn.) Mez.	3	7
Malpighiaceae	<i>Byrsonima cydoniifolia</i> A.Juss.	110	All but 7
Moraceae	<i>Ficus luschnathiana</i> (Miq.) Miq.	1	3
Myrtaceae	<i>Eugenia egensis</i> DC.	5	2
	<i>Myrcia splendens</i> (Sw.) DC.	61	All
	<i>Psidium guajava</i> L.	1	4
	<i>Psidium guineense</i> Sw.	5	2,3,5,7
	<i>Psidium paranense</i> O. Berg	7	4,6,7
Nyctaginaceae	<i>Neea hermaphrodita</i> S.Moore	2	4,7
Phyllanthaceae	<i>Phyllanthus chacoensis</i> Morong	1	7
Polygonaceae	<i>Triplaris gardneriana</i> Wedd.	2	2
Rubiaceae	<i>Genipa americana</i> L.	27	All but 5
	<i>Randia armata</i> (Sw.) DC.	1	4
Rutaceae	<i>Zanthoxylum caribaeum</i> Lam.	1	9
Salicaceae	<i>Banara arguta</i> Briq.	12	4,6
	<i>Casearia aculeata</i> Jacq.	39	All but 2
	<i>Xylosma venosa</i> N.E.Br.	14	6,7,8,9

Trees in the surveyed plots displayed watermarks at heights ranging from 0.40 m to 2.25 m and a mean of 1.00 m per plot, while those on mounds ranged from 0.035 to 0.95 m with a mean of 0.32 m per plot. Not all individuals were present on a mound.

In all three categories (T, M, and WM), species richness increased with low fire frequency as flood height increased. I.e., a lower number of species in areas with low flooding levels and a higher number of species in areas with high flooding levels (Figs. 4, 5). Areas under high fire frequency had the opposite tendency. They showed the highest number of species when the flooding levels were lowest, and decreased gradually as the flooding levels increased (Figs. 4, 5).

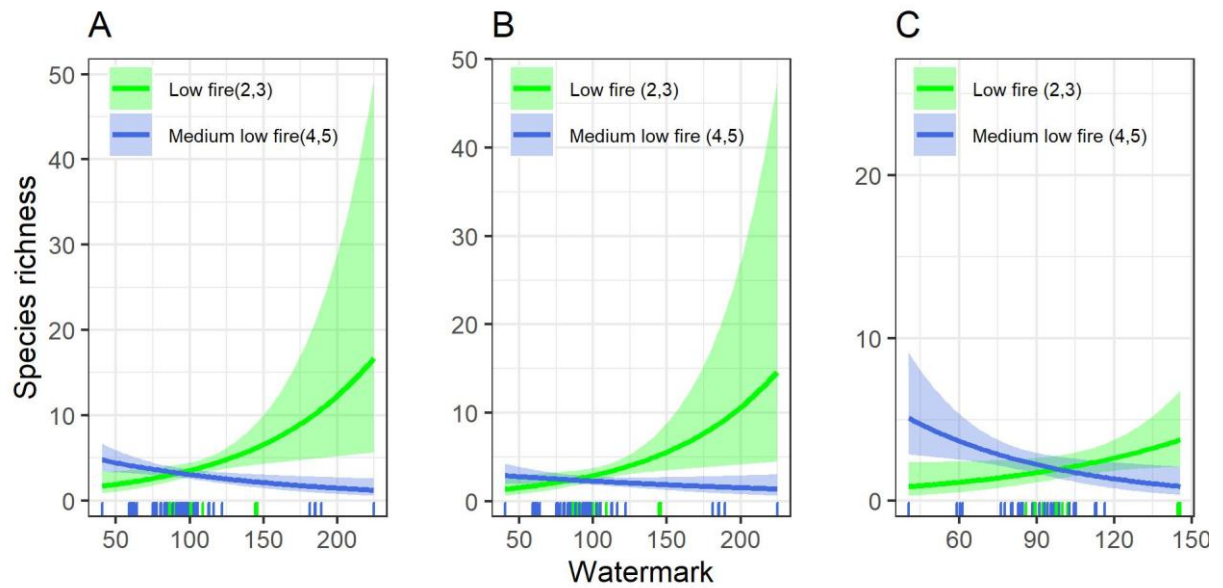


Fig. 4. Generalized linear models of Relationship between the three categories of richness (A= total of individuals, B= individuals on earth-mounds and C= only individuals without mounds) and the interaction levels of inundation and fire frequency in the monodominant stands of *Tabebuia aurea*. The green and blue lines are low fire frequency and medium-low fire frequency areas, respectively, with frequencies inside parentheses. The shaded areas in both lines are confidence intervals of 95%.

The differences in each combination and category were in the number of species; the highest number of species was in T category and the lowest in WM category (Fig. 4A, B, C) (Fig. 5A, B, C), but they showed the same trend, likewise in other significance tests of different combinations of fire. (Figs. 4, 5; Table 2).

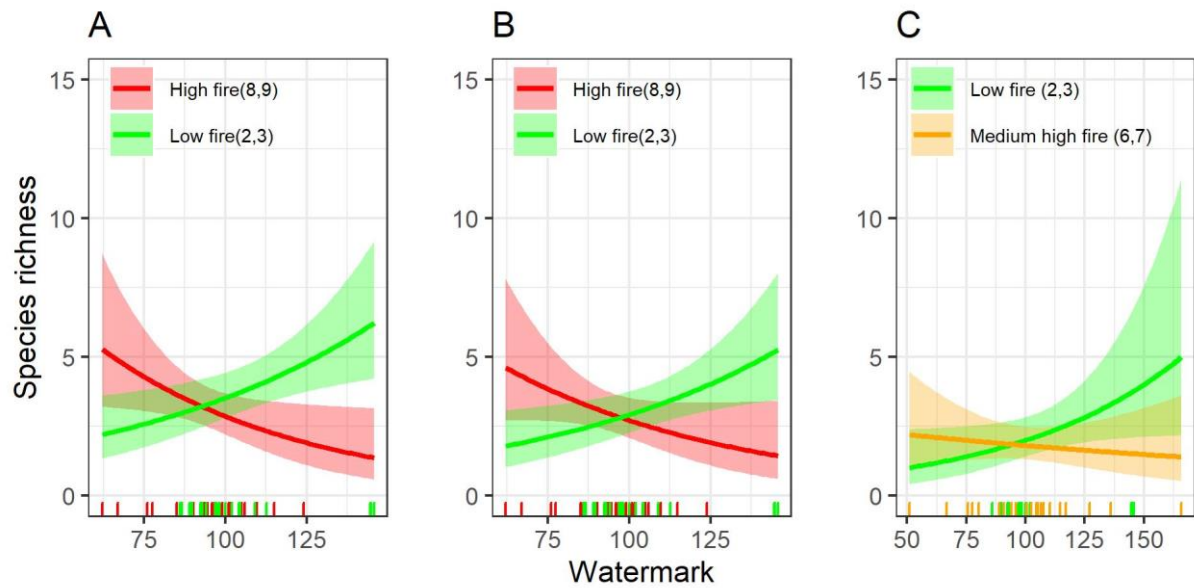


Fig. 5. Generalized linear models between the three categories of richness (A= total of individuals, B= individuals on earth-mounds and C= only individuals without mounds) and the interaction of levels of inundation and fire frequency in the monodominant stands of *Tabebuia aurea*. The green, red and brown lines are low, high and medium-high fire frequency areas, respectively, with frequencies inside parentheses. The shaded areas in both lines are confidence intervals of 95%.

3.4. Abundance

Abundance tests for individuals of all species (Fig. 6A; Table 2), exclusively *T. aurea* individuals (Fig. 6B; Table 3) and individuals except for the dominant species (Fig. 6C; Table 4), in the T category (plants over and without earth-mounds), decreased in number with high fire frequency as flood height increased (Fig. 6; Tables 2, 3, 4). Under high fire frequency, the highest number of individuals occurred in low flooding levels and the lowest number of individuals in high flooding levels. Areas under low fire frequency kept the number of individuals constant with a small increase in the highest flood level (Fig. 6A, B, C; Tables 2, 3, 4). We can see that the differences between abundance tests are in the number of individuals. Particularity *T. aurea* individuals are almost double compared to individuals of other species (Fig. 6B, C; Tables 3, 4). In addition, individuals of other species tend quickly to zero individuals at the highest flood levels and high fire frequency (Fig. 6C; Table 4). On the other hand, *T. aurea* individuals tend to gradually decrease as flood height increases, but do not tend

to zero in most flooded areas (Fig. 6B; Table 3). I.e., they had higher resistance to flooding in areas with high fire frequency. Thus, *T. aurea* individuals are affected by the highest flood levels, but they have more flood resistance than individuals of other species (Fig. 6; Tables 2, 3, 4). In general, the abundance was not affected for the low fire frequency areas, which showed constant abundance values independently of flood height.

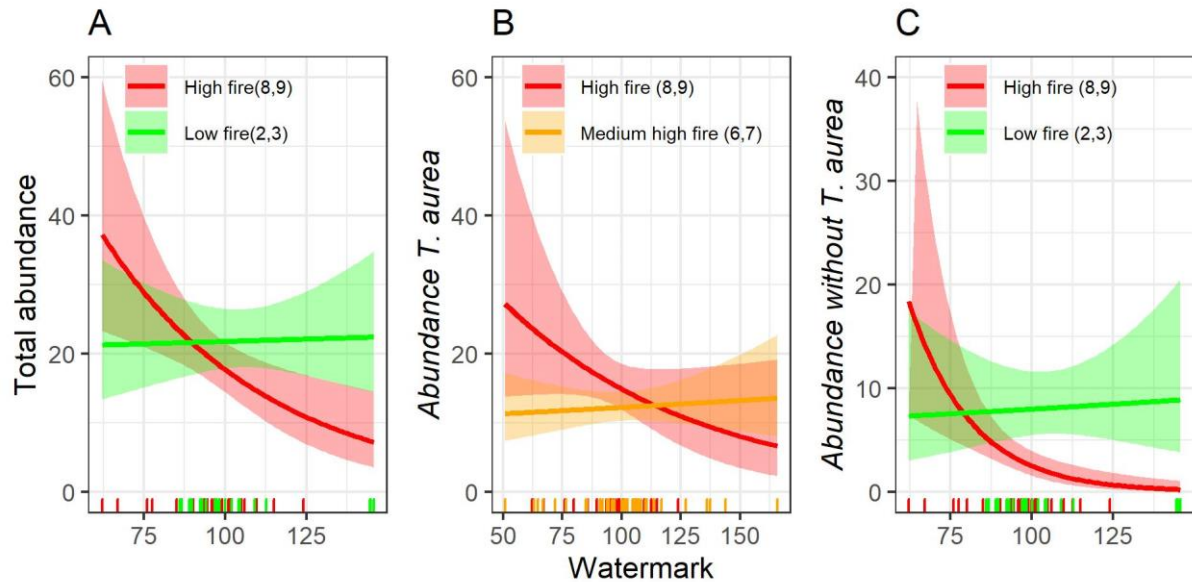


Fig. 6. Generalized linear models between different abundance groups over and without earth-mounds (T category) and the interaction of flood levels and fire frequency in the monodominant stands of *Tabebuia aurea*. The lines represent each fire frequency in the different areas, with frequencies inside parentheses. The shaded areas in both lines are confidence intervals of 95%.

In the M category (only plants over earth-mounds), the different abundance tests (A= Total abundance, B= abundance *T. aurea* and C= Abundance without *T. aurea*) were similar to the results already described to T category (Fig. 7; Tables 2, 3, 4). As well as we can see in figures 6 and 7, there is almost no difference between T and M categories because most individuals within the monodominant stand of *T. aurea* were found on earth-mounds (strategy to survive floods).

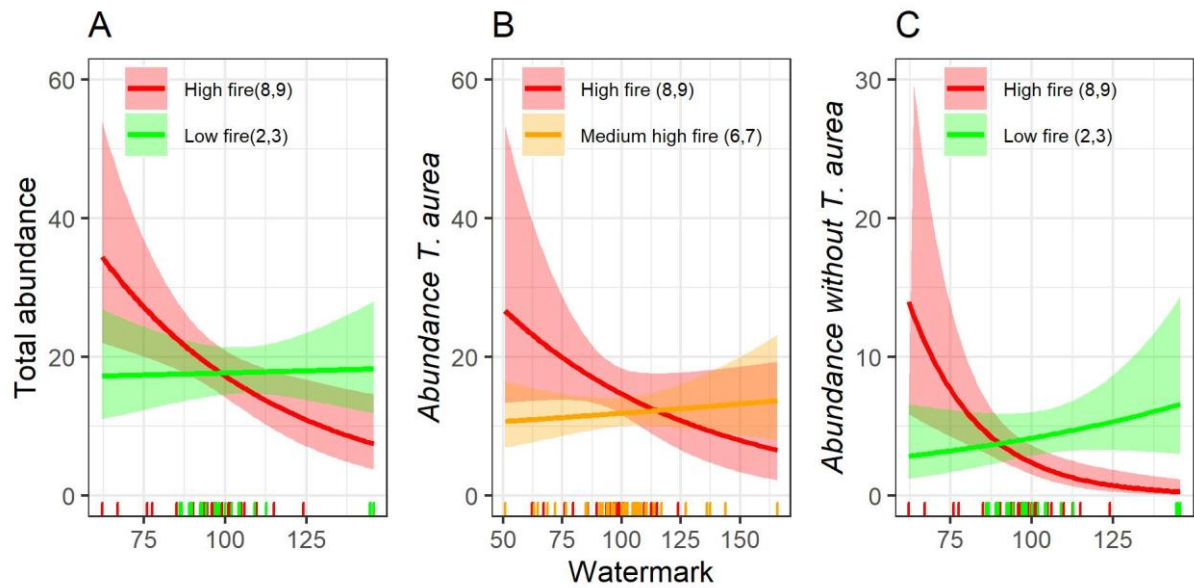


Fig. 7. General linear models between different abundance groups over earth-mounds (M category) and the interaction of flood levels and fire frequency in the monodominant stands of *Tabebuia aurea*. Graphic performed with Generalized Linear Model. The lines represent each fire frequency in the different areas, with frequencies inside parentheses. The shaded areas in both lines are confidence intervals of 95%.

Finally, in the WM category (category with only individuals out of earth-mounds - the least number of individuals), the Total abundance and Abundance of *T. aurea* tests maintain the trend shown in the T and M categories (Figs. 6, 7; Tables 2, 3, 4). However, *T. aurea* abundance tests showed the lowest number of individuals at lower flood levels under low fire frequency, with increased number of individuals from 1.00 m above water level; with medium-high fire frequency the abundance was lowest with a tendency to 0 individuals at the highest levels of flooding (Fig. 8B; Table 3). For the abundance without *T. aurea*, the highest occurred in the lower flood levels, being highest in the areas with lower fire frequency, drastically decreasing with high fire frequency as flood height increases, and decreasing slightly with low fire frequency (Fig. 8C; Table 4). In addition, our results indicate that individuals of *T. aurea* are resistant to high flood levels when without earth-mounds in areas with low fire frequency, while individuals of other species decreased. I.e., individuals of *T. aurea* are resistant to lower fire frequency at high flood levels where other species are not tolerant (Fig. 8B, C; Tables 3, 4).

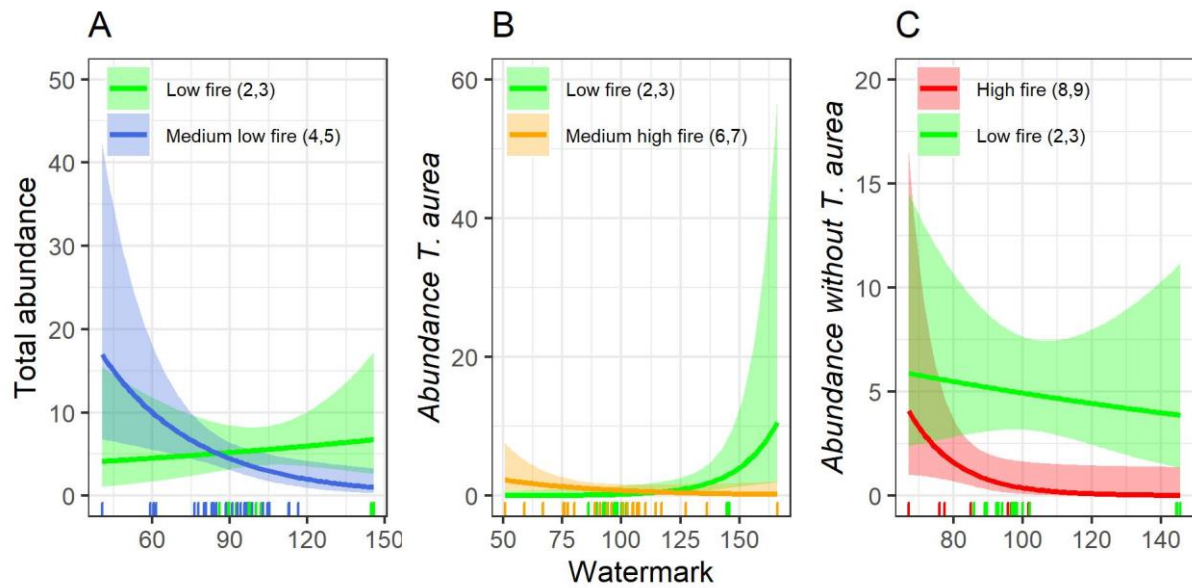


Fig. 8. Generalized linear models between different abundance groups for individuals without earth-mounds (WM category) and the interaction of flood levels and fire frequency in the monodominant stands of *Tabebuia aurea*. The lines represent each fire frequency in the different areas, with frequencies inside parentheses. The shaded areas in both lines are confidence intervals of 95%.

Besides the figures we tested many possibilities of combinations of fire frequency and flood levels and the trends were the same as of figures 6, 7 and 8 (Tables 2, 3, 4).

Table 2. Results for the three GLM models in the different categories and fire frequencies. Comp fire. = comparison between fire frequencies, T = total individuals, M = individuals on earth-mound and WM= only individuals without mound. The applied distribution type is listed under the name of the respective dependent variable. Numbers in brackets denote standard errors.

<i>Dependent variable:</i>										
Comp. fire		Abundance			Richness			Basal area [cm]		
		<i>Negative Binomial</i>			<i>Poisson</i>			<i>Gaussian</i>		
		T	M	WM	T	M	WM	T	M	WM
2,3 and 4,5	Intercept	<2e-16 *** (0.24)	2.27e-06*** (0.59)	0.2590 (1.08)	0.978789 (0.53)	0.70652 (0.58)	0.37220 (0.77)	2.1e-06 *** (0.25)	4.33e-07 *** (0.09)	0.00961 ** (0.05)
	Flood level	0.7727 (0.002)	0.901 (0.005)	0.6483 (0.01)	0.008696 ** (0.004)	0.01282 * (0.005)	0.04569 * (0.006)	0.00588 ** (0.002)	0.000985 *** (0.002)	0.0006 *** (0.0006)
	Fire	0.0898 . (0.26)	0.706 (0.63)	0.0488 * (1.36)	0.02185 ** (0.60)	0.02919 * (0.66)	0.00164 ** (0.95)	0.00222 ** (0.27)	0.000398 *** (0.27)	0.01543 * (0.08)
	Flood level * fire	0.0294 (0.002)	0.607 (0.005)	0.0246 * (0.01)	0.000321 *** (0.005)	0.00477 ** (0.006)	0.00138 ** (0.009)	0.03158 * (0.002)	0.006725 ** (0.002)	0.00618 ** (0.0008)
	Intercept	1.34e-12 *** (0.39)	4.43e-11 *** (0.39)	0.0371 * (0.84)	0.9788 (0.53)	0.7065 (0.58)	0.3722 (0.77)	1.11e-05 *** (0.27)	2.00e-07 *** (0.24)	0.1286 (0.11)

2,3 and 6,7	Flood level	0.973 (0.003)	0.791 (0.003)	0.4907 (0.008)	0.0087 ** (0.004)	0.0128 * (0.005)	0.0457 * (0.006)	0.01196 * (0.002)	0.000669 *** (0.002)	0.0417 * (0.001)
	Fire	0.781 (0.70)	0.762 (0.70)	0.6869 (1.35)	0.1323 (0.66)	0.3125 (0.75)	0.1063 (1.04)	0.00253 ** (0.32)	3.41e-05 **** (0.29)	0.2083 (0.13)
	Flood level * fire	0.910 (0.007)	0.963 (0.006)	0.4239 (0.01)	0.0404 * (0.006)	0.1642 (0.006)	0.0669 . (0.009)	0.00512 ** (0.003)	4.76e-05 **** (0.002)	0.2044 (0.001)
2,3 and 8,9	Intercept	6.5e-15*** (0.64)	2.77e-14 *** (0.61)	0.168 (2.64)	0.000177 *** (0.71)	0.00133 ** (0.74)	0.662 (2.16)	1.52e-05 *** (0.26)	2.5e-05 *** (0.27)	0.734 (0.15)
	Flood level	0.00277 ** (0.006)	0.0045 ** (0.006)	0.243 (0.03)	0.034203 * (0.007)	0.08018 . (0.007)	0.751 (0.02)	0.00431 ** (0.002)	0.00603 ** (0.002)	0.790 (0.001)
	Fire	0.02591 * (0.81)	0.0198 * (0.80)	0.399 (2.86)	0.002863 ** (0.89)	0.00582 ** (0.94)	0.475 (2.30)	0.95553 (0.34)	0.88052 (0.35)	0.204 (0.17)
	Flood level * fire	0.01356 * (0.008)	0.0185 * (0.008)	0.212 (0.03)	0.001455 ** (0.008)	0.00473 ** (0.009)	0.397 (0.02)	0.63562 (0.003)	0.69931 (0.003)	0.165 (0.001)
6,7	Intercept	1.85e-13 *** (0.65)	2.62e-12 *** (0.66)	0.00371 . (0.62)	0.000177 *** (0.71)	0.00133 ** (0.47)	0.153 (0.69)	0.000124 *** (0.31)	0.000154 *** (0.31)	0.964 (0.07)
	Flood level	0.00431 ** (0.006)	0.00900 ** (0.006)	0.31755 (0.006)	0.034204 * (0.007)	0.8018 . (0.007)	0.562 (0.006)	0.013690 * (0.003)	0.016198 * (0.003)	0.465 (0.0007)

and 8,9	Fire	0.00752 ** (0.75)	0.00657 ** (0.76)	0.40894 (2.08)	0.034552 * (0.83)	0.03787 * (0.88)	0.986 (2.27)	0.001726 ** (0.36)	0.002106 ** (0.36)	0.822 (0.22)
	Flood level * fire	0.01182 * (0.007)	0.01453 * (0.007)	0.24305 (0.02)	0.039547 * (0.008)	0.06162 . (0.009)	0.880 (0.02)	0.001128 ** (0.003)	0.001718 ** (0.003)	0.681 (0.002)
2,3,4 and 7,8,9	Intercept	<2e-16 *** (0.52)	3.88e-15*** (0.53)	0.00184 ** (1.04)	4.67e-06 *** (0.56)	0.000222*** (0.60)	0.289 (1.39)	0.0713 . (2.913e-01)	0.0341 * (0.30)	0.813 (1.35e-01)
	Flood level	0.0018 ** (0.005)	0.00733 ** (0.005)	0.03138 (0.01)	0.0119 * (0.005)	0.052360 . (0.006)	0.472 (0.01)	0.9836 (2.993e-03)	0.7062 (0.003)	0.963 (1.47e-03)
	Fire	0.0714 . (0.57)	0.02152 * (0.59)	0.78025 (1.09)	0.0952 . (0.62)	0.045363 * (0.67)	0.991 (1.48)	0.6786 (3.212e-01)	0.9891 (0.33)	0.415 (1.48e-01)
	Flood level * fire	0.0286 * (0.005)	0.01617 * (0.006)	0.62585 (0.01)	0.0571 . (0.006)	0.050189 . (0.006)	0.750 (0.01)	0.4798 (3.257e-03)	0.8169 (0.003)	0.411 (1.60e-03)

‘.’ P<0.1

‘*’ P<0.05

‘**’ P<0.01

‘***’ P<0.001

Table 3. Results for the two GLM models in the different categories and fire frequencies to *Tabebuia aurea* individuals. Comp fire = comparison between fire frequencies, T = total individuals, M = individuals on earth-mound and WM= only individuals without mound. Poisson Tweedie was use only in categorie without mound. The applied distribution type is listed under the name of the respective dependent variable. Numbers in brackets denote standard errors.

<i>Dependent variable:</i>							
Abundance				Basal area [cm]			
<i>Negative Binomial - Poisson Tweedie</i>				<i>Gaussian - Poisson Tweedie</i>			
Comp. fire		T	M	WM	T	M	WM
2,3 and 4,5	Intercept	6.27e-05 *** (0.68)	1.52e-05 *** (0.70)	0.007666 ** (2.88)	6.23e-08 *** (0.25)	5.83e-08 *** (0.25)	0.0111 * (2.87)
	Flood level	0.878 (0.006)	0.502 (0.006)	0.011510 * (0.024)	0.000118 *** (0.002)	0.000104 *** (0.002)	0.3697 (0.02)
	Fire	0.582 (0.72)	0.809 (0.75)	0.000351 *** (3.30)	8.25e-05 *** (0.27)	8.14e-05 *** (0.27)	0.0704 . (3.24)
	Flood level * fire	0.694 (0.006)	0.720 (0.007)	0.000728 *** (0.03)	0.001217 ** (0.002)	0.001176 ** (0.002)	0.0502 . (0.032)
2,3 and	Intercept	5.38e-08 *** (0.43)	5.15e-07 *** (0.44)	0.002787 * (3.35)	4.22e-07 *** (0.27)	3.37e-08 *** (0.24)	2.5e-06 (1.05)
	Flood level	0.704 (0.004)	0.617 (0.004)	0.01784 * (0.02)	0.000394 *** (0.002)	8.21e-05 *** (0.002)	0.00174 (0.01)
	Fire	0.631	0.336	0.01099 * (0.02)	0.000246 *** (0.002)	6.50e-06 *** (0.002)	0.66688 (0.01)

6,7		(0.78)	(0.82)	(3.60)	(0.31)	(0.29)	(2.11)
	Flood level * fire	0.731 (0.007)	0.396 (0.007)	0.00627 ** (0.02)	0.000311 *** (0.002)	6.91e-06 *** (0.002)	0.49695 (0.01)
2,3 and 8,9	Intercept	5.45e-08 *** (0.72)	1.92e-07 *** (0.74)	0.00529 (1.06)	8.55e-05 *** (0.25)	7.9e-05 *** (0.25)	0.0123 (2.99)
	Flood level	0.103 (0.007)	0.119 (0.007)	0.00403 (0.01)	0.0164 * (0.002)	0.0155 * (0.002)	0.3044 (0.03)
	Fire	0.205 (0.83)	0.388 (0.99)	0.48789 (1.36)	0.1950 (0.33)	0.1717 (0.33)	0.6987 (3.14)
	Flood level * fire	0.235 (0.009)	0.436 (0.009)	0.77389 (0.01)	0.3597 (0.003)	0.3336 (0.003)	0.7642 (0.03)
6,7 and 8,9	Intercept	1.17e-08 *** (0.68)	7.88e-08 *** (0.72)	0.149 (2.21)	0.000608 ** (0.33)	0.000512 *** (0.30)	0.171 (5.77)
	Flood level	0.0952 . (0.007)	0.1109 (0.007)	0.135 (0.02)	0.014662 (0.003)	0.037824 * (0.003)	0.591 (0.06)
	Fire	0.0841 . (0.76)	0.0539 . (0.83)	0.735 (2.37)	0.09670 . (0.37)	0.004233 ** (0.34)	0.718 (5.88)
	Flood level * fire	0.1461 (0.007)	0.1016 (0.008)	0.858 (0.02)	0.07686 . (0.003)	0.003219 ** (0.003)	0.970 (0.06)

‘.’ P<0.1

‘**’ P<0.05

‘***’ P<0.01

‘****’ P<0.001

Table 4. Results for the two GLM models in the different categories and fire frequencies without *T. aurea* individuals. Comp fire = comparison between fire frequencies, T = total individuals, M = individuals on earth-mound and WM= only individuals without mound. Negative binomial was use only in the category without mound in abundance. The applied distribution type is listed under the name of the respective dependent variable. Numbers in brackets denote standard errors.

<i>Dependent variable:</i>							
Abundance				Basal area [cm]			
<i>Poisson Tweedie - Negative Binomial</i>				<i>Poisson Tweedie</i>			
Comp. fire		T	M	WM	T	M	WM
2,3 and 4,5	Intercept	0.0843 . (1.022)	0.800 (0.95)	0.114 . (1.32)	4.41e-07 *** (0.95)	1.38e-06 *** (1.12)	0.011428 * (0.06)
	Flood level	0.7711 (0.009)	0.172 (0.008)	0.671 (0.010)	0.00131 ** (0.007)	0.00711 ** (0.009)	0.000964 *** (0.0005)
	Fire	0.4693 (1.24)	0.372 (1.14)	0.514 (1.62)	0.13536 (1.31)	0.18992 (1.48)	0.051397 . (0.07)
	Flood level * fire	0.1930 (0.012)	0.109 (0.01)	0.295 (0.017)	0.01243 * (0.011)	0.02774 * (0.013)	0.023206 * (0.0007)
	Intercept	0.106 (1.09)	0.801 (0.95)	0.138 . (1.41)	7.85e-05 *** (1.29)	1.25e-06 *** (1.11)	0.0719 . (1.64)

2,3 and 6,7	Flood level	0.786 (0.010)	0.174 (0.008)	0.691 (0.013)	0.0149 * (0.015)	0.00685 ** (0.009)	0.040654 * (0.13)
	Fire	0.945 (1.42)	0.421 (1.27)	0.735 (1.91)	0.5417 (1.83)	0.23375 (1.76)	0.901958 (2.37)
	Flood level * fire	0.582 (0.013)	0.243 (0.011)	0.978 (0.018)	0.2388 (0.015)	0.07975 . (0.016)	0.719682 (0.019)
2,3 and 8,9	Intercept	0.000149 *** (1.38)	5.85e-06 *** (1.05)	0.0417 * (3.05)	0.04828 * (0.09)	0.69262 (1.75)	0.908 (7.21)
	Flood level	0.004827 ** (0.016)	0.000530 *** (0.012)	0.0491 * (0.03)	0.08947 . (0.001)	0.02442 * (0.020)	0.461 (0.09)
	Fire	0.025207 * (1.70)	0.000529 *** (1.38)	0.2119 (3.27)	0.00199 ** (0.12)	0.00371 ** (2.19)	0.355 (7.35)
	Flood level * fire	0.009206 ** (0.018)	0.000304 *** (0.014)	0.0820 . (0.03)	0.00069 *** (0.001)	0.00276 ** (0.023)	0.300 (0.09)
6,7 and 8,9	Intercept	3.97e-06 *** (1.14)	9.29e-07 *** (0.99)	0.085 . (2.99)	0.6655 (2.04)	0.61270 (1.37)	0.904 (6.92)
	Flood level	0.00064 *** (0.013)	0.000196 *** (0.011)	0.108 (0.037)	0.0454 * (0.024)	0.00415 ** (0.015)	0.442 (0.086)
	Fire	0.00516 ** (1.33)	0.001520 ** (1.24)	0.224 (3.10)	0.0292 * (2.35)	0.01595 * (1.86)	0.355 (7.06)
	Flood level * fire	0.00528 ** (0.015)	0.002429 ** (0.013)	0.148 (0.037)	0.0328 * (0.026)	0.03069 * (0.020)	0.317 (0.087)
	Intercept	4.16e-06 *** (1.02)	3.52e-07 *** (0.87)	0.0107 * (1.93)	0.78514 (1.49)	0.90546 (1.58)	0.7302 (4.11)

2,3,4 and 7,8,9	Flood level	0.00103 ** (0.011)	0.000142 **** (0.009)	0.0238 * (0.021)	0.01190 * (0.017)	0.01837 * (0.018)	0.1772 (0.05)
	Fire	0.02168 * (1.17)	0.000262 **** (1.006)	0.2276 (2.07)	0.00233 ** (1.63)	0.00636 ** (1.76)	0.0600 . (4.25)
	Flood level * fire	0.00771 ** (0.013)	0.000304 **** (0.010)	0.0885 . (0.023)	0.00107 ** (0.018)	0.00635 ** (0.019)	0.0515 . (0.05)

‘.’ P<0.1

‘*’ P<0.05

‘**’ P<0.01

‘***’ P<0.001

3.5 Basal area

The total basal area was 12172.85 cm².ha (mean 486.91 cm²; SD 268.26; min 7.76 cm²/plot; max 1122.56 cm²/plot) for the total individuals. 11608.83 cm².ha (mean 464.35 cm²; SD 264.73; min 7.73 cm²/plot; max 1122.56 cm²/plot) for the individuals on earth-mound; and 564.02 cm².ha (mean 39.16 cm²; SD 69.97; min 0.41 cm²/plot; max 374.28 cm²/plot) only individuals without mound.

Tests of total basal area for all species and exclusively *T. aurea* individuals in T and M categories; showed a decrease with low and high fire frequencies as flood height increased (Figs. 9A, B, 10A, B; Tables 2, 3). I.e., the largest basal area in low flooding levels and lowest basal area in high flooding levels. However, the basal area values for *T. aurea* individuals were the same independent of fire frequency in the highest flood levels (Figs. 9B, 10B; Table 3). In contrast, the basal area without *T. aurea* (Fig. 9C; Table 4), decreased with high fire frequency as flood height increased and increased with low fire frequency as flood height increased.

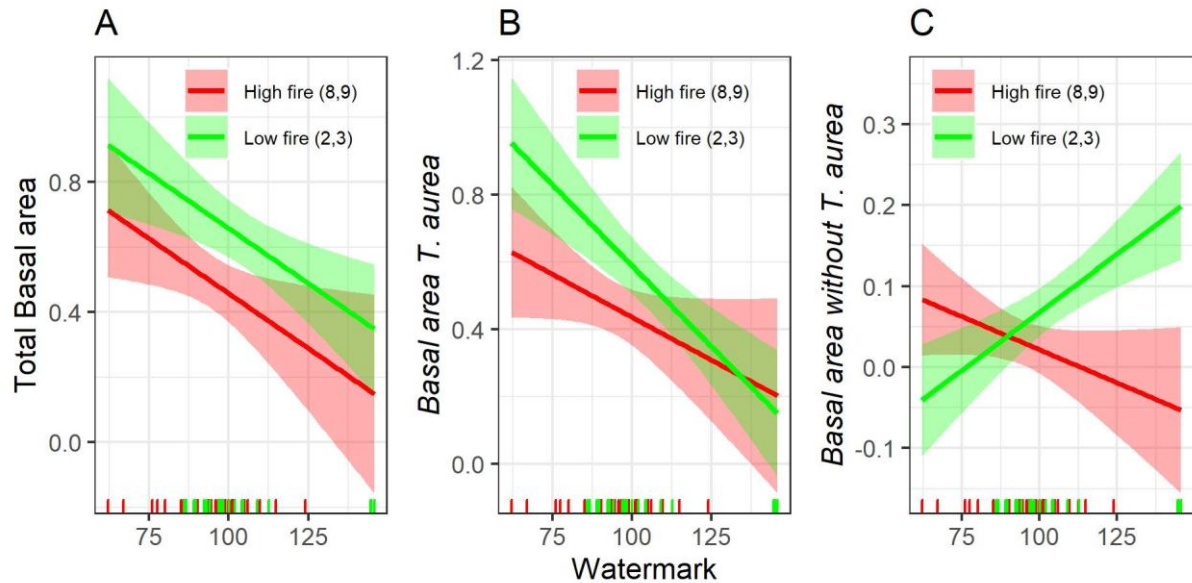


Fig. 9. Generalized linear models between different basal area groups for individuals with and without earth-mounds (T category) and the interaction of flood levels and fire frequency in the monodominant stands of *Tabebuia aurea*. The lines represent each fire frequency in the different areas, with frequencies inside parentheses. The shaded areas in both lines are confidence intervals of 95%.

The largest basal area per category was in T compared with M (Figs. 9C, 10C; Table 4). Furthermore, the basal area values for *T. aurea* individuals tended to be larger than the total basal area and basal area without *T. aurea* (Figs. 9, 10; Tables 2, 3, 4).

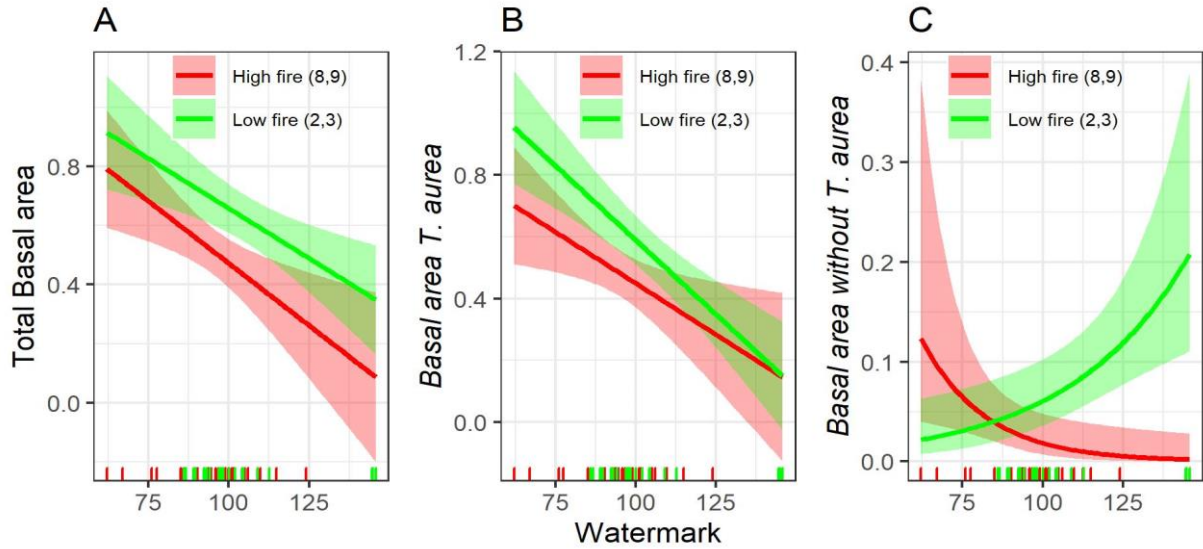


Fig. 10. Generalized linear models between different basal area groups for individuals on earth-mounds (M category) and the interaction of flood levels and fire frequency in the monodominant stands of *Tabebuia aurea*. The lines represent each fire frequency in the different areas, with frequencies inside parentheses. The shaded areas in both lines are confidence intervals of 95%.

In the WM category, the results were different for total basal area and abundance of *T. aurea* test compared with abundance without *T. aurea*. These two first tests had a constant trend with high fire frequency at different flood levels but with a decrease as flood height increased (Fig. 11A, B; Tables 2, 3), and with low fire frequency increased as flood height increased. The graph of the total basal area has negative values at the lowest flood levels, but all diameter values were above zero (Fig. 11A; Table 2). On the other hand, the basal area without *T. aurea* also increased as flood height increased, regardless of fire frequency; however, the basal area values with high fire frequency were very low, being almost constant and very close to zero under the highest flood levels (Fig. 11 C; Table 4). I.e., that high fire frequency benefits *T. aurea* individuals but in low flood levels, and low fire frequency favors all individuals in high flood levels, benefiting from the flood.

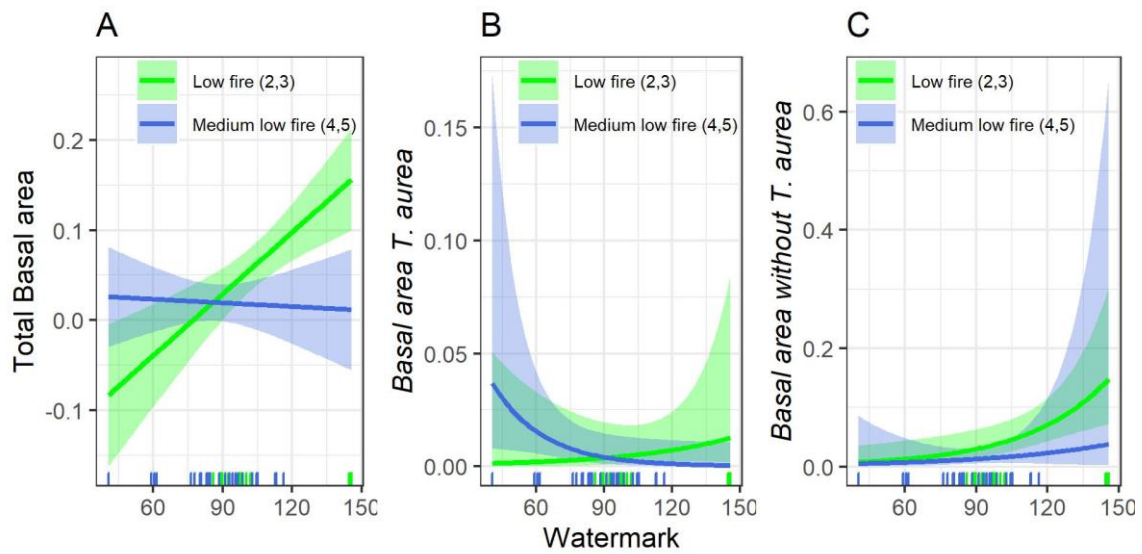


Fig. 11. Generalized linear models between different basal area groups for individuals without earth-mounds (WM category) and the interaction of flood levels and fire frequency in the monodominant stands of *Tabebuia aurea*. The lines represent each fire frequency in the different areas, with frequencies inside parentheses. The shaded areas in both lines are confidence intervals of 95%.

As described in the results of the abundance tests, the basal area tests in each T, M and WM categories (Figs. 8, 9, 10) were different, being described in tables 2, 3 and 4, respectively. Moreover, they show the same trend as figures 9, 10 and 11.

4. Discussion

Our results show that the relatively low number of species found for the tree stratum in monodominant stands of *T. aurea* is consistent with earlier reports (Bueno et al., 2014; Soares and Oliveira, 2009). However, as we suspected, our results revealed that the synergistic action of fire and flood gives significant advantage to *T. aurea* individuals. It diminishes species richness, under both high fire frequency and high flood levels. Under high fire frequency and low flood levels, the species richness is high but decreasing as flood levels increase. I.e., recurrent fire events in dry seasons can partly top-kill and remove the vegetation and provide gaps, thus promoting a selection and increasing the density of fire-resistant species, or with regrowth traits, depending on fire intensity (Arruda et al., 2016; Pott and Pott, 1994; Ribeiro and Brown, 1999; Viganó et al., 2018). However, species that do not tolerate high levels of

flooding or probably the young individuals are young when flooding increases (Heinl et al., 2008), leading most to disappear.

On the other hand, some tree species in low fire frequency areas benefit from high levels of flooding, because they are wetland species with characteristics that allow them to settle in areas of prolonged flooding (Pott and Pott, 1994). However, they lack fire-resistance. In these areas with low fire frequency and high flood levels, species richness tends to increase. Many tree species colonize there, affecting or decreasing the proportional density *T. aurea*, which could directly affect the monodominance.

The abundance of species in the T and M categories, maintained the same trend of results shown for species richness under high fire frequency as flood level increased. Flooding effect on areas with high fire frequency causes a decreasing species richness as well as in *T. aurea* individuals and individuals of other species. However, the density of *T. aurea* is still more than twice the total of individuals of the other species because it can succeed in flooded areas where other species tend to die. In addition, the abundance of all species drastically decreased as flood level increased, tending to zero individual in the highest flood levels. Although *T. aurea* individuals also decreased, they steadily decreased along the flood gradient, with an average of 8 individuals in the highest flood levels. I.e., our results demonstrate that *T. aurea* is more resistant to the combination of flood and fire than other tree species within the community. Abundance in low fire frequency remained constant throughout the flood gradient, increasing slightly in areas with highest flood levels for all species, where *T. aurea* individuals showed an adaptive advantage to the interaction of fire and flood over other tree species. In the WM category, the abundance of all species also decreased with high fire frequency as flood levels decreased; however, with low fire frequency, the abundance of *T. aurea* increased as flood levels increased. Moreover, other species abundance decreased regardless of fire frequency, with lower abundance in high than low fire frequency. Once again *T. aurea* proves to be better adapted to flooding compared with other species. Perhaps both massive seed dispersal and fast growing capacities (Ribeiro and Brown, 2002) help tolerate and survive environmental filters to dominate the landscape. Despite of species richness increase, the abundance of these species decreased under high fire frequency and increased flood levels. It is also relevant to highlight that only *T. aurea* was present in all sampled plots.

T. aurea success in settling as a dominant species where trees tend to diminish is a typical phenomenon of savannas, where most species have a high mortality rate; however, adult trees may survive because the flames little reach the canopy (Heinl et al., 2008). Thus, *T. aurea* individuals, as well as the other species, die due to flooding or severe fire events, needing to settle on earth-mounds in drier years to reach the adult stage (Oliveira and Gualtieri, 2017). These earth-mounds are fundamental for survival since most species grow there. Once established, *T. aurea* can support both environmental filters. In this context, a savannization phenomenon occurs, with the presence of many herbaceous species that tend to be combustible and a discontinuous tree stratum, as in *T. aurea* individuals sampled in our plots. However, long-established *T. aurea* individuals will survive outside earth-mounds. Other characteristics of the savannization phenomenon are tree bark thickness, grass cover, discontinuous open-canopy shrubs with great abundance of reprofing plants, except recurrent fires that can increase juvenile mortality, reducing tree cover, and increasing grass cover that enhances further fire events (Sansevero et al., 2020). Here the savannization has been promoted by the combination of fire and flood.

Environmental filters like fire and flood influence the presence or absence of species, continuously modifying the structure of the communities, also influencing in ecological succession processes (Chang and Turner, 2019). It means that vegetation evolves to tolerate fire and even need fire for reproductive activities. However, where flooding is prolonged, succession is too slow or may not happen (Lockwood et al., 2003), generating a decrease in species abundance as observed in our abundance tests. Thus, the seasonal changes that characterize the Nabileque and Miranda subregions, with a marked period of flooding and another of fires, define a constant switch of species. When flood levels are high and fire frequencies are low, the colonizing species are flood-resistant, and in the dry season when flood levels are low, fire-resistant species are established (Pott and Pott, 1994). It happens in the second half of the year when fire events are more frequent. *T. aurea* individuals will always dominate because they may support the fire and flood interaction, where other species can only resist fire or flood but not their interaction, as observed in our results. Tree species may increase their abundance depending on time post-fire (Bell and Koch, 1980). Besides, flooding can reduce the pool of species mainly restricted by anoxia in the root and leaf system in the early stage when they are trying to establish down again (Ferreira and Stohlgren, 1999; Parolin et al.,

2010; Wittmann et al., 2006). In this way the succession process is controlled by this interaction in our *T. aurea* savanna.

Arruda et al. (2016) also found influence in tree species composition on riparian forest with the effect of environmental filters (fire and flood). Indeed, with the same tendency of succession, richness and abundance were also limited in low areas close to the Paraguay River where flooding is highest, and most tree species cannot establish themselves.

Studies in the Everglades also evidenced that under fire and flood interaction: the shorter the flooding period, the more abundance of a given species (those most resistant to environmental filters), and less altered the plant community will be. However, when the flooding period increases, occur variations in the community and - or species diversity and loss of species abundance (Lockwood et al., 2003).

For the total species, there was a decrease in tree basal area with the increase of flood level regardless of fire frequency. That is also true for the *T. aurea* individuals. Basal area of other species decreased with high fire frequency with the same trend of species richness and abundance described above. I.e., waterlogged soil generates anoxia in plants (Rodríguez-González et al., 2010), leading them to death for lack of oxygen. Nascimento and Nunes da Cunha (1989) found the same relationship in the monodominant stand of *V. divergens* in the northern part of the Pantanal, where the stem diameter of tree species decreased with increased flooding. In dry areas prone to flood events, water may be a limiting resource affecting species by scarcity (those adapted to flood), or it can be a stressor. It can also cause a limitation of soil nutrient availability, interfering in plant gas exchange, generating soil toxicity (Mitsch and Gosselink, 2007). As shown by our results, the higher the water level, the smaller the stem diameter. Thus, high flood levels can also affect plant growth and influence the regrowth processes (Rodríguez-González et al., 2010), being a contrast to typical savanna species exposed to high fire frequency which generally have high regrowth rates (Pettit and Naiman, 2007).

On the other hand, our results evidenced that the thickest diameter occurred in areas with the lowest level of flooding, where water generates a positive influence and - or subsidy, because it increases soil nutrient availability plants compared with more flooded areas

(Rodríguez-González et al., 2010). In the WM category, the basal area of *T. aurea* individuals in areas with high fire frequency also decreased as flood levels increased; however, with low fire frequency, it increased only slightly. Particularly in these areas with high fire frequency and the highest flood levels attained by these individuals without the help of earth-mounds, we observed that *T. aurea* individuals increased in abundance, as described above. However, they were young individuals with yet thin stems.

Without earth-mounds, individuals of other species increased in basal area, as flood level increased, regardless of fire frequency. However, the values of basal area under high fire frequency were extremely low, very close to zero, so we could not recognize that there was a significant increase in diameter. Species adapted to constant flood interaction can generate branched growth systems, i.e. multiple stems (observed in the sampled species) to withstand water stress, but species continuing with a single stem will tend to decrease or even die (Pott et al., 2011; Rodríguez-González et al., 2010). Moreover, second, because species that survive constant fire events generate resistance in their young phase known as the "Gulliver" effect, whereby shrubs became stunted after a fire event but can quickly spread after being burned, as well as generating multiple stems (Heinl et al., 2008; Higgins et al., 2000).

The earth-mounds may have a key-function within the tree community because they act as a basis for maintaining diversity, protecting seeds and regenerating individuals, without the risk of being eliminated by flooding (Marimon et al., 2015). Our tests show a clear difference between species on earth-mounds and species without earth-mounds, the latter with the lowest values in abundance, basal area and species richness, thus, corroborating the key-function of the earth-mounds.

The earth-mounds function as an escape mechanism that abbreviates the longer-lasting flood occurring among mounds, establishing a difference concerning microhabitat, where those species without association with earth-mounds and are unadapted to flooding will soon die.

At last, we point out that fire effect causes an increase in abundance, species richness. *T. aurea* has better condition than other species to survive the recurrent fire and extreme flood conditions, proven by our results. In our study, areas with greater diversity were those with the highest flood level but the lowest fire frequency, i.e., the joint action of fire and flood modifies

the plant species composition continuously in the monodominant stands community of *T. aurea*. If any of the environmental filters does not occur, more they would change the behavior of the community.

5. Conclusion

We verified that the synergistic action of fire and flood significantly benefits the position of *T. aurea* as a monodominant species within the community, as it survives high levels of flood and recurrent fire where species richness, abundance and basal area tend to decrease. However, frequent fire, prolonged floods or absence of any of the environmental filters, will completely alter the dynamics of *T. aurea* within the community and in fact the monodominance.

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Considerações finais

Características morfológicas observadas nas espécies amostradas em este estudo, apresentaram múltiplos caules como estratégia de sobrevivência aos filtros ambientais descritas neste trabalho. As únicas espécies que não apresentaram caules ramificados foram *Tabebuia aurea*, *Handroanthus heptaphyllus* and *Byrsonima cydoniifolia*. Assim, a comunidade arbórea da monodominância de *Tabebuia aurea* é formada principalmente por espécies arbustivas ou arbóreas com alturas relativamente baixas.

As Imagens de satélite podem fornecer informações sobre o teor de água e/ou inundação presente na superfície através do índice de diferença normalizada da água NDWI e informações sobre relevos na superfície, dados adicionais para o entendimento do posicionamento de espécies na comunidade monodominante.

A interação do fogo e a inundação especialmente na região de Miranda, condicionam o posicionamento das espécies arbóreas presentes no Pantanal.