UNIVERSIDADE FEDERAL DE UBERLÂNDIA

INSTITUTO DE BIOLOGIA

PROGRAMA DE PÓS GRADUAÇÃO EM ECOLOGIA E CONSERVAÇÃO DE RECURSOS NATURAIS

Padrões de diversidade e composição funcional de espécies arbóreas no Cerrado: o papel do clima, fogo e adensamento arbóreo

Diego Raymundo Nascimento

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Orientador: Dr. Paulo Eugênio Alves Macedo de Oliveira

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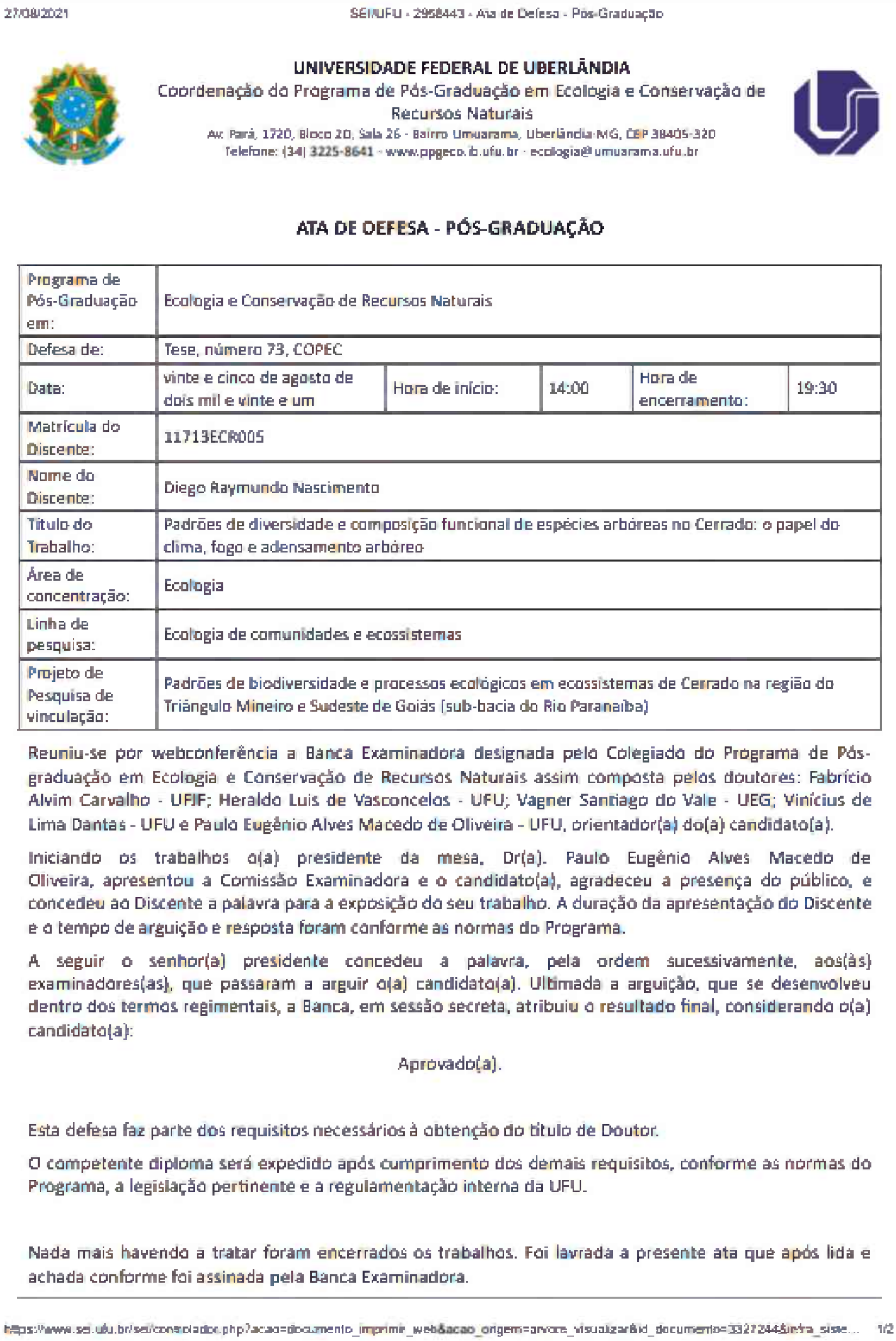

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Resumo

O processo de adensamento da vegetação lenhosa tem sido associado com mudanças nas funções ecossistêmicas de savanas, seja aumentando o estoque de carbono ou causando perdas na biodiversidade. Esta tese busca entender como o processo de adensamento da vegetação pode estar relacionado com a estrutura, diversidade e características funcionais no Cerrado. Assim, cada um dos três capítulos apresentados teve uma pergunta principal: 1) Como o adensamento arbóreo afeta as características florísticas e funcionais de indivíduos arbóreos adultos e regenerantes em um Cerrado típico? 2) Como a diversidade de espécies, e a composição florística e funcional mudam ao longo do tempo em uma área que apresenta adensamento arbóreo? 3) Como os fatores climáticos, o fogo e o adensamento arbóreo influenciam na diversidade de espécies e composição funcional de comunidades arbóreas em larga escala no Cerrado? No primeiro capítulo, nosso estudo mostrou que em um Cerrado sentido restrito que está sob o processo de adensamento da vegetação, árvores jovens e adultas não são floristicamente similares. Além disso, os indivíduos jovens apresentaram maior riqueza de espécies, e maior proporção de espécies com cascas finas e com sementes dispersas pela fauna. No segundo capítulo, nossos resultados mostram que as estratégias de história de vida das espécies estão mudando através de um aumento na dominância de espécies com uma estratégia de uso de recursos aquisitiva (aquisição de recursos mais rápida e taxas de crescimento mais rápidas). No terceiro capítulo, nossos resultados indicam que no cenário de mudanças climáticas com aumento de temperatura e diminuição da pluviosidade pode causar um declínio na diversidade de espécies e uma mudança na composição funcional através de uma diminuição na abundância tanto de espécies de árvores especialistas de floresta quanto espécies especialistas de savana, favorecendo espécies com estratégias de vida que permitem a

persistência em temperaturas mais quentes (assim como espécies com alta SLA e densidade de madeira). Além das mudanças climáticas e parcialmente sendo causada por ela,
Nós demonstramos que um alto sequestro de carbono pode causar um declínio na biodiversidade e favorecer espécies com estratégias adaptadas à alta produtividade do ecossistema mesmo considerando só espécies arbóreas. Além disso, o fogo não teve efeito na biodiversidade ou na composição funcional.

Palavras-chave: Características funcionais, dinâmica da vegetação, sensoriamento remoto, grupos funcionais, Cerrado sentido restrito

Abstract

The process of woody plant encroachment has been associated with changes in the ecosystem functions of savannas, either increasing carbon stock or causing losses in biodiversity. This thesis aimed to understand how the process of woody plant encroachment may be related to the structure, diversity and functional characteristics of the Cerrado sentido restrito plant community. Thus, each of the three chapters presented had a main question: 1) How does woody plant encroachment affects the floristic and functional characteristics of adult and regenerating tree individuals in a typical Cerrado? 2) How does the diversity of species, and the floristic and functional composition change over time in an area that are under woody plant encroachment? 3) How do woody plant encroachment, climatic factors and fire influence the species diversity and functional composition of tree communities in large-scale in the Cerrado? In the first chapter, our study showed that in a Cerrado sentido restrito that is under the process of woody plant encroachment, young and adult trees are not floristically similar. In addition, young individuals showed higher species richness, and a higher proportion of species with thin bark and seeds dispersed by the animals. In the second chapter, our results showed that species life history strategies are changing through an increase in species dominance with an acquisitive resource use strategy (faster resource acquisition and faster growth rates). In the third chapter, our results indicated that in the climate change scenario, an increase in temperature and a decrease in rainfall can cause a decline in species diversity and a change in functional composition through a decrease in the abundance of both specialist forest and savanna specialist species, favoring species with life strategies that allow persistence in warmer temperatures (as well as species with high SLA and wood density). In addition to and partially caused by climate change, we also demonstrated that woody plant encroachment can cause a decline in biodiversity and favor species with strategies adapted to the high productivity of the ecosystem even considering only arboreal species. In addition, fire had no effect on biodiversity or functional composition.

Palavras-chave: Functional traits, Vegetation dynamics, remote sensing, functional groups, Cerrado sentido restrito

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Sumário

Introdução geral

O processo de adensamento da vegetação lenhosa tem sido associado com mudanças nas funções ecossistêmicas de savanas, seja aumentando o estoque de carbono ou causando perdas na biodiversidade (Honda and Durigan, 2016; Parr et al., 2014), e alterando regimes hidrológicos e ciclos de carbono e nitrogênio no solo (Boutton and Liao, 2010; Honda and Durigan, 2016; Jackson et al., 2002; Mureva et al., 2018). O processo de adensamento da vegetação lenhosa é definido como um aumento na biomassa ou na densidade de árvores em um ecossistema aberto e pode ser produto de uma variedade de mudanças ambientais, tais como uso do solo, regimes de fogo e chuva, e concentração de CO_2 atmosférico (Van Auken, 2009; Zhang et al., 2016). No Cerrado, a mais diversa savana no mundo e um hotspot de biodiversidade global (Strassburg et al., 2017), o adensamento da vegetação lenhosa está ocorrendo em 19% das áreas nativas de Cerrado remanescentes (Durigan, 2020; Rosan et al., 2019) e o impacto negativo desse processo na diversidade e composição de espécies herbáceas pode ser extremo (Giles et al., 2021; Pellegrini et al., 2016b; Pilon et al., 2021). Apesar disso, ainda existe uma carência de estudos empíricos avaliando as relações entre o adensamento da vegetação e as variáveis bióticas e climáticas no Cerrado, e esses estudos são fundamentais para entender como essa vegetação pode ser afetada por esse processo nos cenários de mudanças climáticas e outros impactos antrópicos.

O adensamento da vegetação lenhosa pode diminuir a disponibilidade local de luz que no sistema, aumentar a retenção de água no solo e a quantidade de nutrientes em suas camadas mais profundas (Leitner, Davies, Parr, Eggleton, & Robertson, 2018; Throop & Archer, 2007), e pode diminuir a temperatura local do ar (Thomas et al., 2018). Essas mudanças nas condições ambientais locais podem reduzir a diversidade de árvores com adaptações às condições das savanas, que são altamente dependentes de luz e resistentes ao fogo. Apesar disso, essas mudanças também pode aumentar a diversidade de espécies arbóreas que tem uma melhor adaptação em ambientes sombreados e menos quentes, com menor frequência e intensidade de fogo (Abreu et al., 2017). Uma maneira eficiente de quantificar essas características de adaptação de espécies, é avaliando suas características funcionais. Algumas características vegetativas como área foliar específica (SLA), densidade de madeira (WD), espessura de casca e altura máxima da espécie são comumente utilizadas para avaliar respostas das espécies à mudanças nas condições ambientais (Dantas & Pausas, 2013; Flake, Abreu, Durigan, & Hoffmann, 2021; Hoffmann et al., 2012).

A SLA é positivamente relacionada com taxas fotossintéticas e transpiração (Lohbeck et al., 2013; Poorter, Niinemets, Poorter, Wright, & Villar, 2009) e espécies com alta SLA teóricamente otimizam seus arranjos foliares para uma maior interceptação de luz e maior captação de água e nutrients, aumentando a produtividade da planta em ambientes com sem fogo e sombreados (Poorter, 2009; Raymundo et al., 2019). A WD é negativamente relacionada com a aquisição de água e a vulnerabilidade à seca. Espécies com uma menor densidade de madeira são comumente beneficiadas com o aumento da disponibilidade de água no solo (Raymundo et al., 2019; Zanne et al., 2009). Em ambientes savânicos, a espessura de casca é positivamente relacionada com a proteção dos vasos condutores contra o fogo, e devido ao alto investimento de carbono, a espessura de casca é uma alocação de energia pouco vantajosa em ambientes livres de fogo (Loram-Lourenço et al., 2020). A altura máxima da espécie é positivamente relacionada com a competição das espécies por luz e em ambientes com muita luz como ambientes savânicos, espécies tendem a focar seus recursos em estratégias para resistir ao fogo e captar água e nutrientes (Dantas & Pausas, 2013; Moles et al., 2009).

Outro fator é a diversidade de espécies e diversidade funcional, que podem ser alterados com o adensamento da vegetação no Cerrado. A riqueza de espécies é o método mais intuitivo para avaliar a diversidade taxonômica (Gotelli and Colwell, 2001), e tem uma ampla gama de estudos examinando as relações entre a diversidade e as funções ecossistêmicas (Abreu et al., 2017; Flake et al., 2021; Poorter et al., 2015). Da mesma forma, mas ainda menos comumente utilizada, os índices de diversidade funcional (como dispersão funcional e riqueza funcional) também desempenham um importante papel evidenciando a dissimilaridade de características entre as espécies de um ambiente (Cooke et al., 2019; Laliberté et al., 2010). Estudos sugerem que a diversidade de árvores pode aumentar com o adensamento da vegetação em ambientes savânicos, uma vez que esse processo pode favorecer espécies menos suscetíveis às queimadas (devido principalmente à redução do estrato herbáceo) e menos suscetíveis às condições estressantes de alta temperatura e menor disponibilidade de água no ambiente aberto.

Esta tese busca entender como o processo de adensamento da vegetação pode estar relacionado com a estrutura, diversidade e características funcionais no Cerrado. Para isso, um capítulo foi dedicado ao estudo em escala local e unitemporal (capítulo 1), um capítulo foi dedicado ao estudo em escala local e multitemporal (capítulo 2) e um capítulo foi dedicado ao estudo em larga escala e multitemporal (capítulo 3). Assim, cada capítulo teve uma pergunta principal: 1) Como o adensamento arbóreo afeta as características florísticas e funcionais de indivíduos arbóreos adultos e regenerantes em um Cerrado típico? 2) Como a diversidade de espécies, e a composição florística e funcional mudam ao longo do tempo em uma área que apresenta adensamento arbóreo? 3) Como os fatores climáticos, o fogo e o adensamento arbóreo influenciam na diversidade de espécies e composição funcional de comunidades arbóreas em larga escala no Cerrado?

Para responder a primeira pergunta, estabelecemos uma amostragem de 1 hectare (distribuída em 10 parcelas permanentes de 20x50m) em ambientes de cerrado típico na Estação Ecológica do Panga (EEP). Nessas parcelas além de mensurar todos os indivíduos arbóreos adultos, também alocamos sub-parcelas (10x10m) para amostragem do estrato regenerante. O adensamento vegetal na EEP está ocorrendo em todas as fitofisionomias do parque e esse primeiro capítulo mostra que além da dissimilaridade florística entre o estrato adulto e regenerante, as espécies regenerantes são mais sensíveis ao fogo e são representadas principalmente por espécies florestais. Esses resultados mostram que o adensamento vegetal pode ser detectado comparando-se a composição de espécies e funcional do componente adulto e juvenil no Cerrado, utilizando-se ferramentas e trabalho de campo já amplamente desenvolvidos na ecologia vegetal.

Para responder a segunda pergunta, aliamos dados de dinâmica arbórea coletados em 2003 e 2010 por integrantes do Laboratório de Ecologia Vegetal da UFU, com um banco de dados de características funcionais disponíveis na literatura. Esse capítulo mostrou que ao longo do processo de adensamento arbóreo, existe uma grande mudança das características funcionais, mas nenhum ganho na diversidade de espécies. A composição funcional mudou ao longo do tempo, favorecendo espécies com características aquisitivas em relação à luz, disponibilidade de água e nutrientes, e fogo.

A terceira pergunta visou abordar padrões ecológicos em escala no bioma. Foram compilados dados climáticos, funcionais, de diversidade de espécies e estruturais de diversas áreas de Cerrado sentido restrito ao longo do bioma Cerrado. Foram registradas 340 espécies distribuídas em 33 áreas. Nesse capítulo mostramos que o adensamento vegetal pode reduzir a diversidade de espécies arbóreas e favorecer espécies com características florestais. Além disso, mostramos que altas temperaturas e a seca podem também reduzir a diversidade.

CAPÍTULO 1

Assessing woody plant encroachment by comparing adult and juvenile trees in a Brazilian savanna

Assessing woody plant encroachment by comparing adult and juvenile trees in a Brazilian savanna

Abstract

Brazilian Cerrado is a threatened biome due to the intensive agricultural activities and besides the direct effect of these human activities, the absence of an established policy of conservation can also lead to the transformation of savanna environments into forests, in a process referred as woody plant encroachment (WPE). Here, we compared the adult (trees with DGL ≥ 5cm) and juvenile (trees with DGL < 5cm) components in a Cerrado *sensu strictu* in Brazil to assess changes in a plant formation under a process of woody encroachment. We found that the tree and juvenile components had the mean Jaccard similarity index of 19% and PERMANOVA analysis showed a separation of two clusters (species of the adult component and species of the juvenile component), indicating a higher species dissimilarity between both components. We also found a higher percentage of forest species, with lower bark thickness and dispersed by animals in the juvenile component compared to the adult component. Our results indicate that under a process of WPE, forest species less adapted to stressful conditions can establish in the juvenile component and may reflect environmental changes as increasing shade and reducing fire and high temperatures. This approach is useful to detect further encroachment in Cerrado throughout short-term plant inventories.

Keywords: Functional traits, bark thickness, maximum tree height, Cerrado

INTRODUCTION

The Brazilian Cerrado is the savanna holding the highest diversity of plants in the world and more than 44% of its plant species are endemic (Deus Vidal et al., 2019; Klink and Machado, 2005). The vegetation types in the Cerrado range from grasslands to forest vegetation and the spatial heterogeneity and the mosaic of vegetational types is a determining factor of the great biodiversity found (Bridgewater et al., 2004; Vitorino et al., 2020). Besides the higher biodiversity, Cerrado has an important role in conserving water resources in Brazil, due to the core position in Brazilian territory, the deep soils and the higher elevation (Klink et al., 2020). These characteristics allow the occurrence of the main Brazilian hydrographic basins and, consequently, a wide network of rivers that provide water and energy to Cerrado and other regions (Oliveira et al., 2019). The remained native vegetation covers 56% of Cerrado territory and pastures, planted forests and cash crops account for 40% (Scaramuzza et al., 2017; Souza et al., 2020). The ecosystem services and economic importance put Cerrado at the same time as one of the last major agricultural frontiers and one of the most threatened biomes in the world (Spera, 2017; Spera et al., 2016). Therefore, it is fundamental to inventory and understand the dynamics of the remained Cerrado flora, to be able to predict how the native vegetation will respond to human activities and how to restore already degraded areas.

Besides Cerrado degradation by agricultural activities, other factor that can contribute to change its vegetation is the way that these remaining native areas are protected (Durigan and Ratter, 2016). Cerrado is not mentioned in the environmental section of Brazilian Constitution and conservation policies are focused on forest recovery, neglecting the Cerrado intrinsic factors such as dominance of grasses and fire occurrence maintaining the higher endemism and diversity (Bond and Keeley, 2005; Durigan and Ratter, 2016; Pausas et al., 2006). The main vegetation type occurring in the Cerrado domain is the cerrado *sensu stricto* a typical savanna habitat that depends on fire to maintain its vegetation structure (Dantas and Pausas, 2013; Lehmann et al., 2014). The fire suppression can facilitate the establishment of fire-intolerant species and cause a woody plant encroachment that have been reported to be increasing in Cerrado (Goncalves et al., 2021; Rosan et al., 2019; Sühs et al., 2020). Under new local environmental conditions modified during the woody plant encroachment (i.e. increased shaded conditions and reduction in local temperature), forest-adapted species can establish in the system with a strong competitive ability compared to savanna species (Archer et al., 2017). This increase in tree cover can reduce grasses density and diversity changing the vegetation structure, the ecosystem functioning and services over the time (Auken, 2009). Despite several studies have evaluated the effects of woody plant encroachment in savanna areas, they are based on chronosequence or dynamic data (Altomare et al., 2021; Maracahipes-Santos et al., 2018) which demand time and resources to obtain the results; or are based on remote sensing data (Goncalves et al., 2021; Rosan et al., 2019), that does not provide data on species diversity and composition which are important metrics to evaluate encroachment effects (Abreu et al., 2017; Pellegrini et al., 2021). Since evaluating changes in vegetation in Cerrado are an urgent matter, the development of other methods to detect changes in vegetation using a single-time plant inventory can help to improve the management plans and conservation policies.

The comparison of adult and juvenile trees can be a good method to evaluate shifting in species composition due to fire absence over time (Geiger et al., 2011; Morris and Watson, 2020; Saha and Howe, 2003), since the juvenile component represents the species that are growing and trying to establish in the system. Thus, if the juvenile component differs from the adult component, it would indicate that the community are experiencing a turnover of species over time (Guariguata and Ostertag, 2001). Specially in savanna habitats where the main type of plant reproduction strategy is resprouting, juvenile species should be floristically dissimilar to adult species in an encroachment scenario due to the arrival of new forest species. These floristic dissimilarity between juvenile and adult individuals can also be assessed throughout looking at some characteristics of the species in the community, such as the predominant type of vegetation that species occur (forest or savanna habitats) and their functional traits.

Forest species usually can establish and grow faster in shaded and fireless environments compared to savanna species (Rossatto et al., 2009; Xavier et al., 2019). Generally, savanna species have fire-adapted structures, such as thicker barks, which despite protecting the plant from fire may slowdown plant growth (Hoffmann et al., 2009; Lawes et al., 2011; Lehmann et al., 2009). The lower allocation of resources to bark thickness investments and other fire-protecting structures allow forest species to grow faster and occupy wider areas. Forest species also tend to be animal dispersed and the fauna in savannas areas are attracted to less harsh environments with a more complex vegetation structure (Loggins et al., 2019; Stanton et al., 2021; Tassicker et al., 2006). Thus, it is expected that woody encroachment would favor plant species dependent of animals to seed dispersal.

Here we aimed to evaluate how juvenile tree component differ from the adult tree component considering the species composition and functional traits in a cerrado "*sensu strictu*" under a process of woody plant encroachment. We sampled 10 plots and compared the species composition, dispersion mode and the vegetation type of species occurrence of both components in a Brazilian savanna located in a conservation unit. We hypothesized that juvenile and adult tree components would have a higher species dissimilarity, and the juveniles would have a higher percentage of forest and biotic-dispersed species with lower bark thickness and higher maximum stem height compared to the adult component.

METHODS

Study area

This study was conducted in a Cerrado "*strictu sensu*" in the Panga Ecological Station (PES), a conservation unit that comprises 409.5 ha in the south of the Uberlândia municipality, Minas Gerais state, Brazil (Figure 1). The station is geographically positioned at an average altitude of 800m, presenting an excellent representation of the different vegetation types found in the Cerrado region of Central Brazil (Schiavini and Araújo, 1989). The climate is the Aw type according to the Köppen classification, with hot and humid summers, and cold and dry winters (Alvares et al., 2013). Recent remote sensing studies have shown that all vegetation types in PES are under a process of woody plant encroachment, with a reduction in cerrado *sensu strictu* areas and an increase in vegetation cover over time (Goncalves et al., 2021). Although the area is a conservation unit, fire events eventually occur due to the frontier with agricultural lands, pastures and public road. The last fire events occurred in 2015 and 2017 (Goncalves et al., 2021).

Sampling design

To sample the adult component, we established 10 plots of 20x50m (a total of 1ha) (Felfili et al., 2005) and measured the diameter of all trees with diameter at ground level (DGL) ≥ 5 cm. To sample the juvenile component, we established 10 x 10 m subplots, located inside the plots of the adult component at right corner. All the juvenile trees (DGL < 5cm and height > 1m) had their DGL measured and identified. This classification of adult and juvenile components was based on the protocol for sampling tree communities in Cerrado (Felfili et al., 2005). The species were identified using the collection at HUFU (Federal University of Uberlândia Herbarium). The species synonyms were standardized following the species list of the Brazilian flora (http://floradobrasil.jbrj.gov.br/). The classification of botanical families followed the APG IV system (APG 2016).

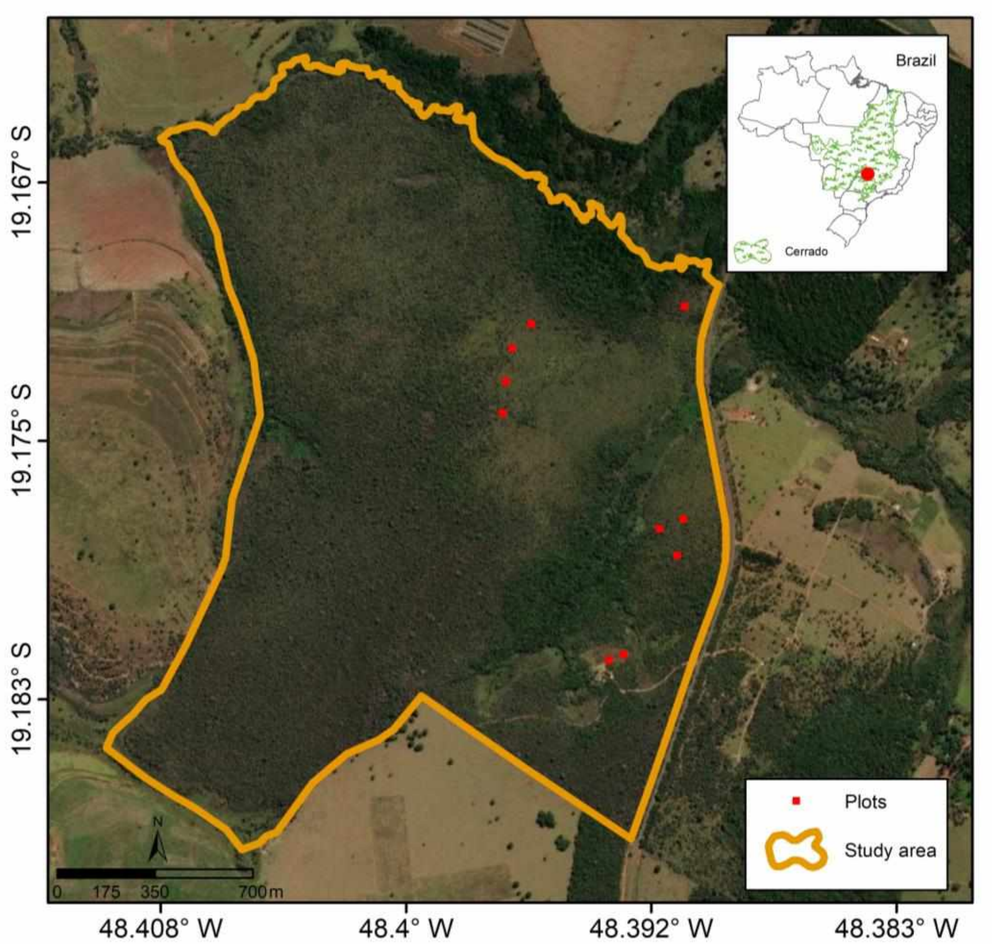

Figure 1 – Study area (Panga Ecological Station) and sample sites in the Cerrado in Brazil.

Tree community assessment

To describe community structure in the juvenile and adult components, we calculated the phytosociological parameters for each species in each component (Kent and Coker, 1992): tree density (TD), species basal area (BA), species relative frequency in the plots (RF%), species relative density (RD, %), species relative basal area (RBA, %), and the importance value (IV, %). The importance value reflects the ecological importance of the species in the study area, by combining the relative tree density, basal area and frequency (IV= (RD+ RBA+RF)/3). Species diversity was estimated using the number of species in each component.

To assess seed dispersal mode (SD, %), we classified the species with seeds dispersed by either wind (abiotic dispersal) or animals (biotic dispersal) (Peres, 2016). We also classified the species as savanna or forest species based on the species common occurrence in different vegetation types in the Cerrado biome (Bueno et al., 2018). To assess differences in functional composition between juvenile and adult components, we calculated the Community-Weighted Mean (CWM) of two important traits related to the establishment of tree species in the savannas: total bark thickness and maximum tree height (Dantas and Pausas, 2020). The CWM's were calculated per plot for the juvenile and adult components by summing the species trait value weighted by species stem density of all species in the plot, and dividing it by total stem density in the plot (Laliberté et al., 2014). Mean bark thickness for each species was compiled using data from the literature (Batalha et al., 2011b, 2011a; Carvalho, 2013; Cianciaruso et al., 2012; Miatto, 2011; Oliveira, 2013; Pellegrini et al., 2017; Santos, 2018). When a species was found in more than one database, we calculated the mean bark thickness of all studies to include in the analyses. When species bark thickness was not found in any database, we considered an average value for the genus. Maximum tree height was compiled from NeoTropTree dataset (Oliveira-Filho, 2017). When maximum tree height was not available at species level, we considered the average of the genus as in bark thickness data. We calculated CWM values using the “FD” package in R (Laliberté et al., 2014). Additional information on CWM's per plot can be found in Appendix S1.

Data analyses

To verify whether there is a floristic similarity between the adult and juvenile components, we performed a NMDS (Non-metric Multidimensional Scale) analysis based on Jaccard index (species presence/absence) (Holland, 2008). After that, we tested the difference between the formed groups using a PERMANOVA with 999 permutations (Anderson, 2005). The analyzes were performed in R (R Development Core Team, 2014), using the adonis function and the argument strata (to account for adult and sapling dependence within each plot) in “*Vegan*” package (Oksanen et al., 2013)

To compare (1) the abundance of species with biotic dispersal mode, (2) the relative abundance of forest species, (3) the community weighted mean (CWM) of bark thickness, and (4) the CWM of maximum stem height between tree and sapling components, we performed four linear mixed models, including each metric as a response variable in each model. In all models, we used the vegetation component (adult or juvenile component) as a fixed factor and plot as random factor. We used plot as random factor in all models to account for the possible dependence of adults and juveniles in the same plot. Specifically for the model (3), we performed Generalized Linear Mixed models with Gamma family (link=log) due to logarithmic distribution of the model residuals. The analyses were performed in R 4.0.5 (Team, 2016), using lmer function (linear mixed models) and glmer function (generalized linear mixed models) in “lme4” package (Bates et al., 2015). All data met the assumptions of homcedasticity, normality and linearity.

Results

In the adult component, we found a total of 617 trees with a total basal area of 7.7 m².ha^{-1}. These trees were from 75 species of 32 families (Table 1). The three species with the highest importance value (IV) were *Caryocar brasiliense* (9,63%), *Qualea parviflora* (7.44%), and *Qualea grandiflora* (6.21%). The juvenile component had 252 trees (2520 trees per hectare), distributed in 59 species and 29 families (Table 1). The species with the highest importance value (IV) were *Miconia albicans* (8.34%), *Davilla elliptica* (6.73%), and *Byrsonima coccolobifolia* (6.33%). We found that 50% of the species in the adult component were exclusive and did not occur in juvenile component. In the juvenile component, 38% of the species were exclusive and did not occur in the adult component.

Table 1. Species and their respective relative density (RD, %), relative basal area (RBA, %), relative frequency in the plots (RFr,%) and the importance value index (IVI, %) in the adult and juvenile tree components. The classification of the species with seeds dispersed (SD) by biotic vectors (B) and abiotic vectors (A), and the main vegetation type of occurrence (VT) of the species (forest – F or cerrado sensu stricto – C) are given.

Species	**Adult component**				**Juvenile component**				**SD**	**VT**
	RD	**RBA**	**RFr**	**IVI**	**RD**	**RBA**	**RFr**	**IVI**		
Aegiphila verticillata	0.16	0.03	0.37	0.19	-	-	-	-	B	C
Agonandra brasiliensis	-	-	-	-	0.79	0.89	0.73	0.80	B	C
Andira sp1	-	-	-	-	0.40	0.34	0.73	0.49	B	NA

Species	Adult component				Juvenile component				SD	VT
	RD	RBA	RFr	IVI	RD	RBA	RFr	IVI		
Andira vermifuga	0.80	0.74	1.49	1.01	-	-	-	-	B	C
Annona crassiflora	4.15	5.06	2.60	3.94	1.19	0.90	1.46	1.19	B	C
Aspidosperma macrocarpon	0.48	0.39	0.74	0.54	-	-	-	-	A	C
Aspidosperma tomentosum	1.75	0.69	1.49	1.31	-	-	-	-	A	C
Bauhinia rufa	-	-	-	-	3.57	0.57	2.19	2.11	A	C
Bauhinia sp1	-	-	-	-	0.40	0.23	0.73	0.45	A	C
Bowdichia virgilioides	0.64	1.36	1.49	1.16	-	-	-	-	A	C
Brosimum gaudichaudii	0.48	0.20	1.12	0.60	1.59	0.92	2.19	1.57	B	C
Byrsonima affinis	0.80	1.39	1.86	1.35	-	-	-	-	B	C
Byrsonima coccolobifolia	4.31	3.06	3.35	3.57	5.95	8.67	4.38	6.33	B	C
Byrsonima pachyphylla	1.91	1.17	2.60	1.90	1.19	0.72	1.46	1.12	B	C
Byrsonima sp1	-	-	-	-	1.19	0.29	0.73	0.74	B	C
Byrsonima verbascifolia	0.80	0.58	1.12	0.83	-	-	-	-	B	C
Caryocar brasiliense	9.89	15.95	2.60	9.48	5.56	6.50	4.38	5.48	B	C
Casearia sylvestris	0.80	0.20	1.12	0.70	0.40	0.26	0.73	0.46	B	C
Coccoloba mollis	0.16	0.05	0.37	0.19	-	-	-	-	B	F
Coussarea hydrangeifolia	0.16	0.09	0.37	0.21	0.79	0.49	0.73	0.67	B	F
Curatella americana	1.12	0.91	1.86	1.30	0.40	0.48	0.73	0.54	B	F
Dalbergia miscolobium	1.75	2.20	1.49	1.81	-	-	-	-	A	C
Davilla elliptica	3.67	2.16	2.97	2.94	5.95	10.58	3.65	6.73	B	C
Dead trees	1.59	1.28	2.60	1.83	-	-	-	-	NA	NA
Didymopanax macrocarpus	0.64	0.21	1.12	0.66	0.79	1.29	0.73	0.94	B	C
Dimorphandra mollis	2.87	1.71	2.60	2.39	0.79	0.99	1.46	1.08	A	C
Diospyros lasiocalyx	2.07	1.23	2.23	1.85	4.37	7.66	2.19	4.74	B	C
Duguetia furfuracea	-	-	-	-	0.40	0.14	0.73	0.42	B	C
Enterolobium gummiferum	0.64	0.34	1.49	0.82	1.98	1.07	2.19	1.75	B	C
Eriotheca gracilipes	0.48	0.30	0.37	0.38	-	-	-	-	A	C
Eriotheca pubescens	0.16	0.14	0.37	0.22	-	-	-	-	A	C
Erythroxylum deciduum	0.80	0.69	1.12	0.87	1.98	1.91	3.65	2.51	B	F
Erythroxylum sp1	0.16	0.06	0.37	0.20	-	-	-	-	B	C
Erythroxylum suberosum	0.32	0.20	0.74	0.42	0.79	0.86	1.46	1.04	B	C
Erythroxylum tortuosum	1.28	0.46	1.86	1.20	1.19	0.90	2.19	1.43	B	C
Guapira graciliflora	0.64	0.30	0.74	0.56	0.79	0.18	1.46	0.81	B	F
Guapira noxia	0.80	0.23	1.12	0.72	-	-	-	-	B	C
Hancornia speciosa	0.32	0.28	0.74	0.45	-	-	-	-	B	C
Handroanthus ochraceus	2.39	1.29	2.23	1.97	3.17	3.95	2.19	3.10	A	C
Himatanthus bracteatus	0.16	0.06	0.37	0.20	-	-	-	-	A	C
Himatanthus obovatus	-	-	-	-	1.59	1.41	1.46	1.48	A	C
Kielmeyera coriacea	5.74	4.53	3.35	4.54	1.19	0.52	2.19	1.30	A	C
Kielmeyera rubriflora	0.16	0.14	0.37	0.22	-	-	-	-	A	C

Species	Adult component				Juvenile component				SD	VT
	RD	RBA	RFr	IVI	RD	RBA	RFr	IVI		
Lafoensia pacari	0.32	0.08	0.74	0.38	-	-	-	-	A	C
Leptolobium dasycarpum	0.64	0.52	1.12	0.76	0.40	1.05	0.73	0.73	A	C
Leptolobium elegans	2.23	3.78	1.86	2.62	1.19	1.76	2.19	1.71	A	C
Licania apetala	0.16	0.10	0.37	0.21	-	-	-	-	B	F
Lithraea molleoides	-	-	-	-	0.40	0.40	0.73	0.51	B	F
Machaerium acutifolium	0.48	0.23	0.74	0.49	1.19	0.32	1.46	0.99	A	F
Machaerium opacum	1.28	2.25	1.86	1.79	-	-	-	-	A	C
Malpighiaceae sp1	-	-	-	-	1.19	0.17	0.73	0.70	B	NA
Matayba guianensis	-	-	-	-	1.98	1.23	2.19	1.80	B	F
Miconia albicans	0.32	0.14	0.37	0.28	8.33	11.58	5.11	8.34	B	C
Myrcia splendens	-	-	-	-	4.37	4.21	4.38	4.32	B	F
Myrcia tomentosa	0.80	0.18	1.12	0.70	1.98	1.56	1.46	1.67	B	C
Myrcia variabilis	0.32	0.08	0.74	0.38	0.40	0.42	0.73	0.52	B	C
Myrtaceae sp1	0.16	0.19	0.37	0.24	0.79	0.41	0.73	0.64	B	NA
Nectandra sp1	-	-	-	-	0.40	0.05	0.73	0.39	B	F
Neea theifera	0.16	0.12	0.37	0.22	-	-	-	-	B	C
Ocotea sp1	-	-	-	-	0.40	0.05	0.73	0.39	B	F
Ouratea spectabilis	0.64	0.42	1.49	0.85	-	-	-	-	B	C
Palicourea rigida	0.16	0.06	0.37	0.20	-	-	-	-	B	C
Piptocarpha rotundifolia	2.55	1.25	2.60	2.13	0.79	0.61	1.46	0.95	A	C
Plathymenia reticulata	0.80	0.55	1.12	0.82	-	-	-	-	A	C
Platypodium elegans	0.64	0.64	1.12	0.80	1.59	2.68	2.92	2.39	A	F
Pouteria ramiflora	0.64	2.94	1.49	1.69	-	-	-	-	B	C
Protium heptaphyllum	-	-	-	-	1.19	0.12	2.19	1.17	B	F
Psidium laruotteanum	0.16	0.08	0.37	0.20	-	-	-	-	B	C
Qualea dichotoma	0.16	0.30	0.37	0.28	-	-	-	-	A	F
Qualea grandiflora	7.50	8.24	2.60	6.11	1.59	0.76	1.46	1.27	A	C
Qualea multiflora	1.59	0.47	1.49	1.18	-	-	-	-	A	C
Qualea parviflora	6.06	12.56	3.35	7.32	2.78	3.82	2.19	2.93	A	C
Roupala montana	1.28	1.71	1.86	1.61	2.78	0.70	2.19	1.89	A	C
Rourea induta	-	-	-	-	0.40	0.28	0.73	0.47	B	C
Rudgea viburnoides	-	-	-	-	1.98	1.97	0.73	1.56	B	C
Strychnos pseudoquina	0.64	0.33	1.12	0.69	-	-	-	-	B	C
Stryphnodendron adstringens	0.80	0.28	1.12	0.73	-	-	-	-	B	C
Stryphnodendron polyphyllum	2.71	1.10	1.86	1.89	3.17	3.36	2.19	2.91	B	C
Stryphnodendron rotundifolium	1.28	0.60	1.49	1.12	1.59	2.98	2.19	2.25	B	C
Styrax ferrugineus	1.75	0.76	1.86	1.46	1.19	0.36	0.73	0.76	B	C
Symplocos nitens	0.16	0.03	0.37	0.19	1.19	0.46	1.46	1.04	B	NA
Tabebuia aurea	1.12	1.03	1.86	1.33	-	-	-	-	A	F

Species	Adult component				Juvenile component				SD	VT
	RD	**RBA**	**RFr**	**IVI**	**RD**	**RBA**	**RFr**	**IVI**		
Tachigali aurea	2.23	3.11	2.23	2.52	-	-	-	-	A	C
Tachigali sp1	-	-	-	-	0.40	0.31	0.73	0.48	A	F
Tachigali vulgaris	-	-	-	-	0.40	0.31	0.73	0.48	A	F
Tapirira guianensis	0.16	0.05	0.37	0.19	-	-	-	-	B	F
Terminalia argentea	0.48	0.59	1.12	0.73	-	-	-	-	A	F
Tocoyena formosa	0.32	0.18	0.74	0.41	2.38	1.88	2.92	2.40	B	C
Unidentified sp1	0.16	0.39	0.37	0.31	-	-	-	-	NA	NA
Vatairea macrocarpa	0.16	0.50	0.37	0.34	-	-	-	-	A	C
Vernonanthura polyanthes	0.64	0.19	1.12	0.65	-	-	-	-	A	C
Vernonia sp1	-	-	-	-	0.40	0.13	0.73	0.42	A	C
Virola sebifera	0.16	0.03	0.37	0.19	1.98	0.34	2.19	1.51	B	C
Vochysia rufa	2.55	3.16	2.23	2.65	0.79	1.37	1.46	1.21	A	C
Vochysia tucanorum	0.64	1.11	0.74	0.83	0.40	0.19	0.73	0.44	A	F
Xylopia aromatica	-	-	-	-	1.59	1.46	1.46	1.50	B	C
TOTAL	100	100	100	100	100	100	100	100	-	-

The mean Jaccard similarity index between adult and juvenile tree components were 19% (Standard deviation = 7.1%) and the NMDS analysis divided two clusters (adult and juvenile groups) (Figure 2). PERMANOVA test indicates a significant dissimilarity in species composition between juvenile and adult components within each plot (F-model= 2.73, p= 0.002).

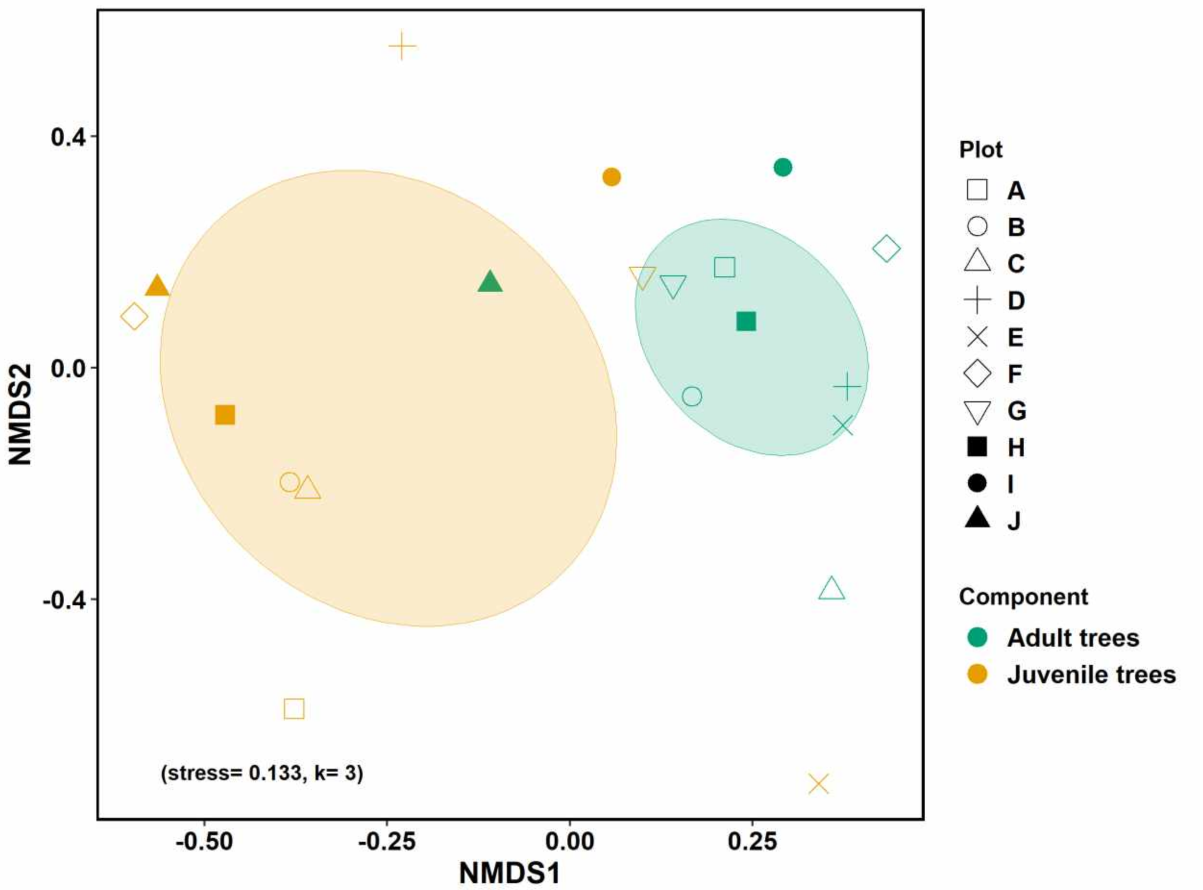

Figure 2. Non-metric Multidimensional Scale (NMDS) analysis, clustering two main different groups: adult and juvenile components. A – J = Sampling plot identification.

We found that the mean percentage of forest species was 444% higher in juvenile component than in adult component (mean percentage for juvenile component = 15.08 %, standard deviation for juvenile component = 8.63; mean percentage for the adult component = 2.77, standard deviation for the adult component = 2.46; p=0,001) (Figure 3a, Appendix S2). The mean percentage of species with biotic dispersal mode was 50% higher in juvenile component than in adult component ($\text{Mean}_{\text{adult}}$= 70.56, SD_{juv} =17.64; $\text{Mean}_{\text{adult}}$ = 47.01, SD_{juv} = 14.06; p=0,004) (Figure 3b, Appendix S2). The community weighted mean (CWM) of bark thickness (mm) was 15% lower in juvenile component than in adult component (Mean_{juv}= 10.39, SD_{juv} =2.55; $\text{Mean}_{\text{adult}}$ = 12.26, SD_{adult} = 1.50; p=0,007) (Figure 3c, Appendix S2). The CWM of maximum stem height was not significant different comparing both components (Figure 3d, Appendix S2).

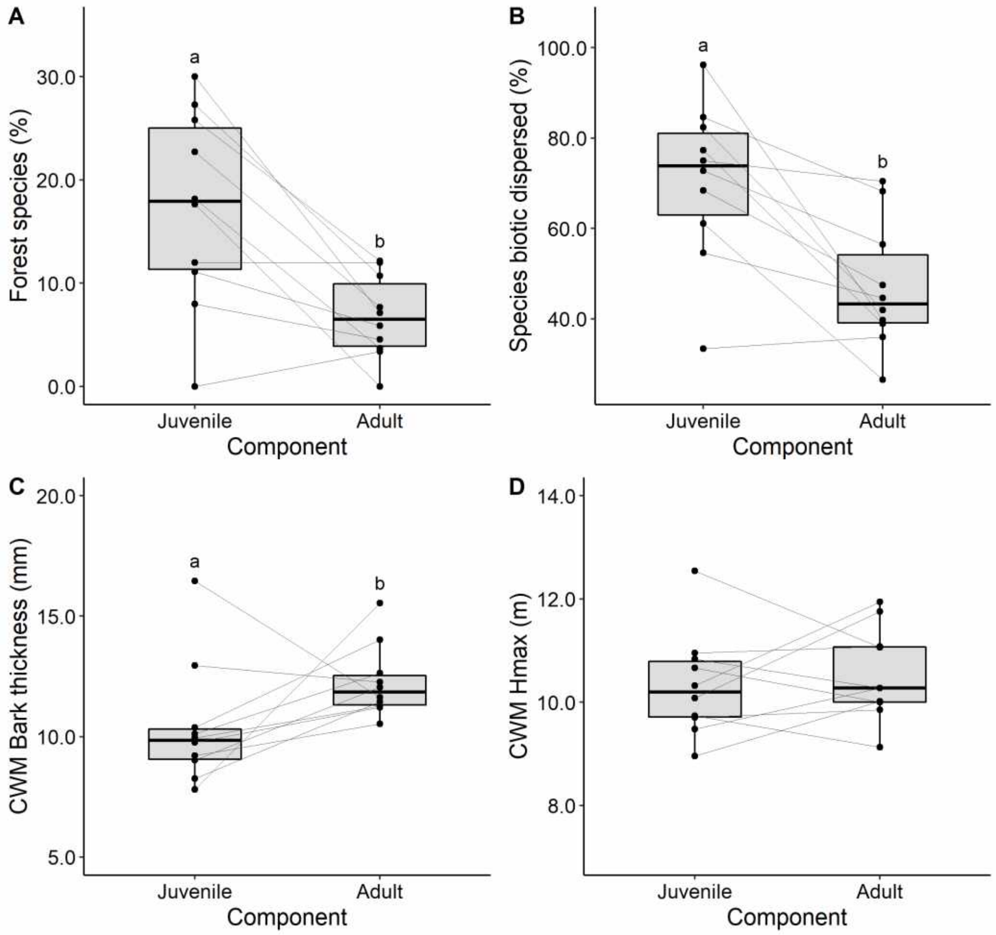

Figure 3. Linear mixed models comparing (A) the percentage of species indicators of forest habitats (%), (B) the percentage of individuals with biotic seed dispersal mode (%), (C) the community weighted mean (CWM) of bark thickness (mm), and (D) the CWM of maximum tree height (m).

DISCUSSION

Here we showed that the comparison of adult and juvenile trees is an efficient tool to detect and evaluate the effects of woody encroachment process in the Brazilian savanna. We found that under encroachment, juvenile tree species had dominance of fire-intolerant forest individuals dispersed by fauna species, while the adult tree species had dominance of fire-resistant savanna individuals, dispersed by wind.

We expected that the adult component would have a floristic dissimilarity with the juvenile component, with higher percentage of forest species with seeds dispersed by fauna species. Indeed, we found a separation between two clusters (adults and juveniles) when comparing species similarity and the mean Jaccard similarity index was only 19%. In savannas, the density of juveniles can be higher close to the adults of the same species mainly due to resprouting reproduction, where established adult individuals can resprout after disturbance even in belowground organs (e.g. roots, bulbs and rhizomes) (Klimešová et al., 2018; Zupo et al., 2021). In a scenario of woody plant encroachment without frequent fires, new woody species are constantly arriving and growing in the system, changing species composition over the time (Gonzaga et al., 2013) as occurs in forest successional process (Santos et al., 2018). The juveniles represent the species that are germinating and trying to establish in the system. Thus, if the juveniles differ of the adults, it is a signal that the community is changing, shifting species composition (Guariguata and Ostertag, 2001). For example, species that are present in the adult tree component tend to disappear within a few years, because it does not have recruiting trees in juvenile component. On the other hand, the presence of species only in juvenile tree component indicates a possible increase in local diversity, because juveniles can become an adult tree in the future. The species *Agonandra brasiliensis*, *Lithraea molleoides*, *Matayba guianensis*, *Ocotea* sp1, and *Protium heptaphyllum* are examples of species found only in the juvenile component, which are tree species occurring mainly in forest habitats. Among species found exclusively in the adult component were *Aspidosperma macrocarpon*, *Aspidosperma tomentosum*, *Bowdichia virgilioides*, *Byrsonima affinis*, *Plathymenia reticulata* and *Stryphnodendron adstringens,* all typical species of open savanna areas (cerrado *sensu strictu*) (Bueno et al., 2018). In fact, we found that the juvenile component had more forest species compared to the adult component In open savanna areas, denser clusters of larger individuals tend to reduce the extreme environmental conditions such as the air temperature and drought, and increase shading (Arantes et al., 2014). Those changes in environmental conditions allow the arriving and establishment of forest species not adapted to survive in open savannas or grasslands, under higher insolation, drought and temperatures which prevails before woody plant encroachment. Further arrival of forest species feedbacks the process, contributing to change the vegetation type into a new woodland/forest environment. Other factor that can contribute to the colonization of forest species is the absence or lower frequency of fire events. Even with shaded conditions provided by tree individuals, saplings of forest species often cannot persist after fire events (Hoffmann, 2000). Although the last fire events occurred at 2015 and 2017 (Goncalves et al., 2021), our results indicate that the juveniles of forest species are establishing themselves in the system, reinforcing the idea that after encroachment, the system takes a long time to back to the previous stage before encroachment, if it ever does (Hoffmann et al., 2012).

In addition to the higher percentage of forest species in juvenile component, we also found a higher percentage of species with seeds dispersed by animals when compared to the adult component, which had a higher percentage of wind-dispersed species. Abiotic dispersal is a common type of seed dispersal in open areas, mainly because greater wind flow and absence of denser vegetation which usually prevent seed dispersal (Collevatti et al., 2020). In an encroached environment, clustered trees could attract animals (i.e. birds and small mammals) providing shelter and perching, and also refuges from predators, nesting places and other attractants, functioning as a focal point in open savanna environments, and leading to increasing seed dispersal (González-Castro et al., 2021). Animal dispersers can also be contributing to the arrival of forest species, once they can move for long distances and use different vegetation types (Wandrag et al., 2017; Wunderle, 1997). Proximity to the forest patches can increase animal dispersers of forest species (Cubiña and Mitchell Aide, 2001) as the case of our plots. Panga Ecological Station is characterized by having a mosaic of Cerrado vegetation types and forest patches are relatively close to cerrado *sensu strictu* (Goncalves et al., 2021; Lopes and Schiavini, 2007). This may favor the movement of different animals that can feed in forest areas and disperse seeds into open cerrado *sensu strictu* areas.

We found that the abundance of species with higher bark thickness was higher in the adult component than in juvenile ones, as expected. Bark thickness is a trait related to fire resistance, and species that need to persist in a fire-prone environment, need to allocate more resources in these structures (Dantas et al., 2013; Gignoux et al., 1997). A thicker bark could protect the vascular tissues and meristems from the fire, allowing the individuals to survive even burning its leaves (Pausas, 2015; Pellegrini et al., 2017; Schafer et al., 2015). On the other hand, species with thinner barks, are not able to survive in fire-prone environments (Staver et al., 2020), and take advantage in a scenario of woody plant encroachment once the habitat become more similar to forest environments where plants need to allocate more resources in structures to compete for light. The juvenile component did not have the expected dominance of species that reach higher maximum stem heights. Although the dominance of juveniles of forest species, maximum tree height is less adaptative in open areas because to grow taller, it is required a higher cost to maintain the leaf production, water transport and the maintenance of the individual stand (Moles et al., 2009). Moreover, the colonization during woody plant encroachment is mainly by generalist species that can occurs either in open savannas or forest systems (Flake et al., 2021) and do not reach high maximum heights.

Our results reinforce that the woody plant encroachment is occurring in Panga Ecological Station (PES) (Goncalves et al., 2021) and that the floristic composition are changing towards the dominance of forest juveniles in open savanna areas. This arrival of forest species can have direct consequences on herb and grasses communities that dominate the ground of the cerrado *sensu strictu* vegetation. Moreover, the reduction of open savanna habitats could lead to the reduction of local water retention in the soil and streams (Honda and Durigan, 2016), and the absence of fire events in PES could also contribute to changes in hydrological regimes at landscape scale. Finally, we can note that the actual fire regime (last fire in 2017) is not sufficient to maintain the open savanna habitats over time (Goncalves et al., 2021) and because PES is a conservation unit, a widely discussion should be rise towards the need to implement policies of fire management to conserve open savannas. Studies have shown that the absence of fire events for prolonged times can lead to more intense fire events if it does, due to the accumulation of the organic matter of dead grasses and trees that are fuel to fire (Steel et al., 2015).

FINAL CONSIDERATIONS

Our study showed that Panga Ecological Station is a Cerrado with a higher species diversity in Central Brazil, and it can act as a natural laboratory to ecological studies in different ecological topics. We also showed that under a process of woody plant encroachment, juveniles and adults are not floristically similar, and juvenile component harbors more forest species, with lower bark thickness and dispersed by fauna. These differences highlight the potential of comparing adult and juvenile components to detect and predict vegetation changes and successional process in Cerrado, once juveniles can be the trees of the system in the future. These comparisons could be done by using only one field inventory, optimizing time and resources. Although the potential of these comparisons, we know that juvenile trees not necessarily will reach the adult component and a large percentage will die before to become adult (Nguyen et al., 2019). Thus, it is fundamental to evaluate if these patters remain the same over time, by assessing vegetation dynamic data. Our results also indicates that woody plant encroachment can reduce the importance of wind and increase the importance of biotic vectors to seed dispersal. Although it could increase resource for fauna species, it also can be a risk especially to endemic grasses species that are highly dependent of wind to disperse it seeds and can have its populations restricted by woody cover. Finally, woody plant encroachment can favor species with low bark thickness and the juvenile component can be more vulnerable in case of a fire event.

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Appendix S1. Information about plot community weighted mean (CWM) of forest species (CWMforest, %), CWM of biotic dispersal (CWMbio, %), CWM of bark thickness (CWMbark, mm), and CWM of maximum tree height (CWMhmax, m) for the tree adult and sapling components.

Component	Plot	CWMforest	CWMbio	CWMBark	CWMhmax
Sapling	A	25,00	75,00	9,94	10,66
Sapling	B	22,73	72,73	8,27	10,95
Sapling	C	11,11	61,11	9,21	9,71
Sapling	D	19,35	82,35	10,12	10,83
Sapling	E	27,27	54,55	12,95	12,55
Sapling	F	13,64	77,27	9,02	8,95
Sapling	G	0,00	68,42	10,38	9,74
Sapling	H	15,69	96,23	7,81	9,48
Sapling	I	8,00	84,62	9,76	10,08
Sapling	J	8,00	33,33	16,45	10,32
Adult	A	1,02	70,41	11,26	10,00
Adult	B	5,13	56,41	11,44	11,07
Adult	C	2,94	26,47	10,53	9,85
Adult	D	4,05	41,89	12,63	10,27
Adult	E	7,14	44,64	12,28	11,06
Adult	F	0,00	38,89	12,06	10,02
Adult	G	3,39	47,46	14,02	9,13
Adult	H	0,00	39,71	15,54	10,28
Adult	I	0,00	68,18	11,21	11,76
Adult	J	4,00	36,00	11,63	11,94

Appendix S1. Mean and standard deviation, linear mixed models p-value and mean percentage of difference in community weighted mean (CWM) of forest species (Forest, %), CWM of biotic dispersal (Biotic disp, %), CWM of bark thickness (Bark, mm) and CWM of maximum tree height (Hmax, m) between juvenile and adult tree component.

Metric	**Sapling component**		**Tree component**		**p-value**	**% of difference**
	Mean	**SD**	**Mean**	**SD**		
Forest	15,08	8,63	2,77	2,46	0,001	445
Biotic disp	70,56	17,64	47,01	14,06	0,003	50
Bark	10,39	2,55	12,26	1,50	0,007	15
Hmax	10,33	1,00	10,54	0,89	0,380	2

CAPÍTULO 2

Temporal changes in the dominance of tree functional traits, but no changes in species diversity and composition during woody plant encroachment in a Brazilian savanna

Temporal changes in the dominance of tree functional traits, but no changes in species diversity and composition during woody plant encroachment in a Brazilian savanna

Abstract

1. Woody encroachment in savannas has been associated with both changing taxonomic composition and ecosystem function. Curiously, it remains unknown how encroachment impacts plant functional diversity and how those changes relate to plant demography, a crucial mediator between taxonomic composition and ecosystem function.

2. Using a landscape scale fire suppression experiment in a diverse Brazilian savanna, we quantify how change in species composition over seven years impacted the functional diversity of vegetative and reproductive characters determined by new recruits, dead and surviving trees.

3. Over the seven years, tree aboveground biomass increased by 15%, while total species richness did not change and species composition was 82% similar. For the vegetative traits, we found an increase in the community weighted mean (CWM) of maximum tree height (2.1%) and specific leaf area (5,3%), and a decrease in CWM of wood density (1.3%). For the reproductive traits, we found larger changes than in vegetative traits, with an increasing in the CWM of monoecy (32.6%), dioecy (44.2%), large seeds (20,3%), seed dispersal by animals (4,9%) and pollination by very small insects (45.5%).

4. Net changes in functional traits were largely driven by the recruits and dead trees. The overall decrease in CWM of bark thickness and increase in CWM of monoecy and dioecy were mainly driven by the lower bark thickness and higher monoecy and dioecy of recruits, respectively. The overall increase in CWM of SLA and decrease in CWM of small seeds were mainly driven by the lower SLA and small seeds of dead trees, respectively.

5. Woody encroachment leads to ecosystem changes making savannas more vulnerable to fire and drought, and compositional changes are marked in reproductive traits, indicating increasing dependence of plants on animals for dispersal and reproduction. Understanding post-hoc encroachment impacts in an era of widespread pervasive encroachment is fundamental to reconciling ecosystems functions such as nutrient cycling and pollination services, and it is also a tragic process of documenting the loss of species with open ecosystem life history strategies. There remains an urgent need to understand relationships between woody cover and ecosystem function to determine thresholds in woody cover promoting resilient savanna ecosystems.

Key Words: Functional composition, demographic groups, tree community dynamics, functional diversity, community weighted mean, vegetative traits, reproductive traits

INTRODUCTION

Woody encroachment has been associated with changing savanna ecosystem functions via increasing carbon stocks or causing biodiversity losses (Honda and Durigan, 2016; Parr et al., 2014), and changing hydrological regimes and soil carbon and nitrogen cycles (Boutton and Liao, 2010; Honda and Durigan, 2016; Jackson et al., 2002; Mureva et al., 2018). Woody encroachment is defined as an increase in biomass or tree density in an ecosystem, and can be a product of a multitude of environmental changes such as land use, fire and rainfall regimes, and atmospheric CO_2 concentrations (Van Auken, 2009; Zhang et al., 2016). In Brazilian savannas (Cerrado), the most diverse savanna in the world and a global biodiversity hotspot (Strassburg et al., 2017), woody encroachment is occurring across 19% of remaining savannas (Durigan, 2020; Rosan et al., 2019). The negative impacts of encroachment on herbaceous diversity and composition can be extreme (Giles et al., 2021; Pellegrini et al., 2016b; Pilon et al., 2021). However, the impact of encroachment will vary among species due to their functional traits and relative sensitivity to changing environmental conditions (Ding et al., 2020; Eldridge and Ding, 2021). Hence, understanding of how encroachment relates to ecosystem function is contingent on understanding how functional diversity and demographic change are inter-related (Pellegrini et al., 2021).

With increasing tree cover, Cerrado ground layer environments change, reducing both ground layer light availability and decomposition rates, consequently altering nutrient cycling (Leitner et al., 2018; Throop and Archer, 2007) via a reduction in the grass component and an increase in water and nutrients in deeper soil layers, favouring the recruitment and reproduction of woody species (Dantas, Pausas, Batalha, Loiola, & Cianciaruso, 2013; Pausas et al., 2004; Shiflett, Zinnert, & Young, 2017). Such local scale environmental change would likely increase the relative abundance of species with life history strategies centred around resource competition (light, water and nutrients) rather than stress and disturbance (higher temperatures and fire) (Dantas, Batalha, & Pausas, 2013). Vegetative traits such as specific leaf area (SLA), wood density (WD), bark thickness, maximum tree height and phenology are commonly used to evaluate species responses to changing environmental conditions (Dantas & Pausas, 2013; Flake, Abreu, Durigan, & Hoffmann, 2021; Hoffmann et al., 2012). For instance, SLA is positively related to photosynthetic rates, plant transpiration (Lohbeck et al., 2013; Poorter, Niinemets, Poorter, Wright, & Villar, 2009) and species with higher SLA theoretically optimize leaf arrangements for light interception and water and nutrients acquisition, increasing plant productivity in fire-absent and shaded habitats (Poorter, 2009; Raymundo et al., 2019). Wood density is related to water acquisition and drought resistance and species with low wood density are reported to be benefited with increasing water availability (Raymundo et al., 2019; Zanne et al., 2009). In savannas, bark thickness is positively related to stem protection from fire and given the carbon investment, thick bark is a less advantageous allocation strategy in fire-free environments (Loram-Lourenço et al., 2020). Maximum tree height is positively related to species competition for light, and where in high light savanna ecosystems, constraints on maximum tree height generally centre on allocation strategies related to fire resistance and water use (Dantas & Pausas, 2013; Moles et al., 2009). Therefore, with encroachment and the development of more shaded environments we should expect an increase in mean maximum height of species. In savanna ecosystems, deciduousness is associated with drought resistance (Poorter & Markesteijn, 2008) due to dry season length, whereas in shaded environments, with increased water in deeper soil layers, we would expect an increasing proportion of evergreen species in encroached environments.

While it has been little investigated, reproductive traits are likely sensitive to encroachment. With encroachment and changes in tree density, habitat structure changes substantially and is likely to directly impact the faunal composition of ecosystems (Dirks et al., 2017). Encroachment increases habitat complexity that might lead to an increase in forest-dependent animals that can hide from predators in tree canopies, and favouring tree species that depend on animals for seed dispersal and reproduction (Andersen and Steidl, 2019). Hence, pollination and sexual systems of plants would be expected to change in response changing suites of animals (or not) involved in pollination and dispersal. For example, in open savanna ecosystems with high ground layer temperatures and with limited buffering of ground layer environments by an overstorey, woody and herbaceous species tend to have less specific pollination and reproduction systems (i.e. pollination by wind and hermaphrodite sexual system). In comparison, in closed habitats, plants species are more likely to have specific pollination and reproductive systems (i.e. pollination by very small insects, and dioicy and monoicy) (Deus & Oliveira, 2016). Moreover, seed size can be a proxy for a species investment in reproduction (Kuhlmann and Ribeiro, 2016) and where tree species characterising open savanna habitats tend towards production of large seeds with structures to tolerate heat and fire (Daibes et al., 2019; Ribeiro and Borghetti, 2014). In contrast, in closed forest habitats, and where environmental stress is relatively less, tree species tend towards smaller seeds (Lahoreau et al., 2006; Ribeiro et al., 2015).

Species richness is the most intuitive method to assess taxonomic diversity as the total number of species (Gotelli and Colwell, 2001), and there is a wide body of literature examining relationships between diversity and ecosystem function (Abreu et al., 2017; Flake et al., 2021; Poorter et al., 2015). However, indices such as functional dispersion that quantify trait dissimilarity among species and functional richness that quantify the diversity of traits within a community (Laliberté et al., 2015; Villéger et al., 2008) are useful to understand how the profiles of communities respond to changing environmental conditions (Cooke et al., 2019;

Laliberté et al., 2010). The demographic processes of such functional change should be driven by the growth of resident tree species and the recruitment of new individuals with different ensembles of traits (Brudvig et al., 2011; Passos et al., 2018). However, rapid growth and competitive ability of new recruits could also increase mortality of individuals with traits less adaptative in encroached conditions (Catford et al., 2018).

One effective way to characterize species responses to environmental changes and their effects on ecosystem functions is evaluating community level changes in functional traits (Eldridge and Ding, 2021; Öckinger et al., 2010; Osborne et al., 2018; Raymundo et al., 2019) and species and functional diversity (van der Sande et al., 2017; Villéger et al., 2008). Linking species trait data with demographic changes in species relative abundances over time, can help determine at a community level the plant traits most responsive to encroachment. Such information could also be useful in identifying species and life history strategies vulnerable to encroachment and those most likely to be lost from ecosystems. These data could increase our understanding on the effects of woody encroachment and lead to improvements in ecosystem management and public policies, providing insights into which species should be removed or maintained to reach the aimed ecosystem service in restoration and conservation plans (Ding et al., 2020; Eldridge and Ding, 2021). Surprisingly, most temporal analyses of woody encroachment on vegetation focus on structure and taxonomic diversity (Abreu et al., 2017; Maracahipes-Santos et al., 2018; Moreira, 2000), and few studies look at the changes in functional traits and diversity over time (but see Pellegrini et al. 2021). Here, we used data of nine functional traits to evaluate how the functional diversity and composition of tree species changes over seven years where fire suppression had been implemented for 30 years. We address two questions: 1) How did overall community species and functional diversity change over time? We hypothesized that tree species and functional diversity increased, alongside an increase in the community weighted mean (CWM) of functional traits associated with closed versus open environments (Table 1). 2) What was the relative importance of new recruits, surviving trees, and mortality changing functional diversity and composition? We hypothesized that new recruits and surviving trees would be associated with functional changes towards an increasing in forest-adapted characteristics, while dead trees would be associated with functional change towards a reduction in savanna-adapted characteristics.

Table 1. Functional traits, abbreviation, units and description. The expected results of changes along 7 years of woody plant encroachment are given. Up arrows indicate an expected increase and down arrows indicate an expected decrease in the metric over time. WD = wood density, Bark = bark thickness, SLA = specific leaf area, Hmax = maximum height, Dec = deciduousness, VSI = pollination by very small insects, SMI = pollination by small insects, LI = pollination by large insects, VE = pollination by vertebrates, D = dioic species, H = hermaphrodite species, Mon = monoic species, Bio = biotic seed dispersion, Abi = abiotic seed dispersion, SS = species with small seeds, MS = species with medium seeds, LS = species with large seeds.

Trait	**Abbreviation**	**Units**	**Indicator**	**Hypothesis**
Wood density	WD	g/cm^3	Plant defense and growth	↓
Bark thickness	BT	cm	Fire resistance	↓
Specific leaf area	SLA	cm^2/g	Light interception efficiency and photosynthetic rates	↑
Maximum height	Hmax	m	Plant growth and light interception	↑
Deciduousness	Dec	%	Drought avoidance	↓
Pollination system	VSI	%	Very small flowers	↑
	SMI	%	Small flowers	↑
	LI	%	Flowers adapted to large insects pollination	↓
	VE	%	Flowers adapted to vertebrates pollination	↑
Sexual system	H	%	Generalist reproductive strategies	↓
	Mon	%	Specialist reproductive strategies	↑

	Dio	%	Specialist reproductive strategies	↑
Seed dispersion	Bio	%	Dependence of fauna to seed dispersion	↑
Seed size	SS	%	Low resources investments per seed	↑
	MS	%	Medium resources investment per seed	↑
	LS	%	High resources investment per seed	↓

METHODS

Study area and sampling

The conservation unit where this study was conducted is located in Parque Municpal Victório Siquierolli (-18.87 S, -48.28 W), a conservation unity in the outskirts of Uberlândia city in Minas Gerais state, Southeastern Brazil. To evaluate vegetation change, 24 permanent plots (10 x 10m) were established in three transects in 2003 (T0) distributed throughout the conservation unit (15 ha of overall site). All trees with stem diameter at ground level (DGL, 30cm above ground) $\geq$ 3cm diameter were permanently tagged and stem diameter recorded at 30cm above ground (accurate to 1 millimeter) using a measuring tape. Tree height was estimated using a clinometer. Tree identity was recorded at a species level, even for sapling recruits and dead trees, based on vegetative features. After seven years (T7, 2010) a second census of all previously marked trees along with new recruits was undertaken.

The site has a tropical seasonally dry climate of wet summers (October to March) and dry winters (April to September) with a mean annual rainfall of 1524 mm. The dry season length can vary from 4 to 6 months (i.e. a cumulative period with <100 mm rainfall). The mean annual temperature is 21 ºC with a mean maximum of 22.7 ºC in February and a mean minimum of 17.8 in July (Alvares et al., 2013). In the conservation site, there was no evidence of either cattle grazing or logging over the census period. Further, there is no record of fire at the site at least since 1998 (Instituto Nacional de Pesquisas Espaciais - INPE, http://www.inpe.br/queimadas). As INPE have data available only since 1998, we also assembled a times series of Landsat 5 and 7 satellites images since 1984 (Thematic Mapper and Enhanced Thematic Mapper, 30m resolution) and could find no sign of fire from 1984 - 1998. As such, we consider that the area has been fire free for more than 30 years.

To evaluate compositional and functional change related to demography, we divided trees into three groups: 1) New recruits, individuals which were not present in T0 census but were recorded at T7 census; 2) Dead trees, individuals recorded as alive in T0 census but recorded as dead in T7 census; and, 3) Surviving trees, recorded as alive in both T0 and T7.

Woody plant encroachment and species diversity metrics

All metrics explained below were calculated both for 1) the plant community at a plot level for both T0 and T7 census periods; and, 2) for each demographic group. Plot level aboveground biomass for each plot in both T0 and T7 was estimated by calculating the aboveground biomass (AGB, Mg) of each individual combining tree diameter (cm), height (H, m), and species wood density (WD, g/cm^3) using the equation: $AGB = 0.0673 \times (WD \times DGL^2 \times H)^{0.976}$ (Chave et al., 2014). On a plot basis, AGB was calculated by summing the AGB of all trees in a plot and divided by 0.01 (the area of each plot in hectares) to have a per hectare value. To determine species diversity per plot, we calculated species richness as the total number of species in a plot. Additional information on community structure and species diversity per plot for the overall community and demographic groups can be found in Table S1 and Table S2.

Functional traits

We evaluated five vegetative and four reproductive functional traits known to be associated with fire, drought and shade tolerance that could indicate species responses to increasing tree density and tree cover (Deus & Oliveira, 2016; Raymundo et al., 2019; Van Der Sande et al., 2016) (Table 1). Vegetative traits are: 1) wood density (WD, g/cm^3) (Zanne et al., 2009); 2) bark thickness (BT, mm); 3) specific leaf area (SLA, cm^2/g); 4) deciduousness (Dec, %) (Batalha et al., 2011; Prado-Junior et al., 2016); and, 5) maximum tree height (Hmax, m) (Calculated from the database of this study). Wood density values were obtained for 98% of the species and 2% were calculated using the average of the genus. BT, SLA, Dec and Hmax were obtained for all species at species level.

Reproductive traits were: 1) Sexual system (SSy, %) where species were classified as dioeciuos, monoecious and hermaphrodite; 2) Pollination system (PS, %) were classified as species pollinated by vertebrates (birds or bats), large insects (moths, large bees, butterflies or beetles), small insects (bees, flies and wasps), and very small insects (micro-Hymenopteran, Lepidoptera, and small beetles) (Barbosa & Sazima, 2008; Deus & Oliveira, 2016); 3) Mode of seed dispersal (SD, %) was classified as species with seeds dispersed by either wind (abiotic dispersion) or fauna (biotic dispersion); and, 4) Seed size (SSi, %) was classified categorically with species with small (<10 mm), medium (10 to 20mm) and large seeds (>20mm) (Peres, 2016). The reproductive trait data were obtained for all species used in this study. Additional information on functional traits per species can be found in Table S3.

Community-weighted mean traits and functional diversity indices

To assess changes in functional composition, we calculated the community-weighted mean (CWM) values for the quantitative (WD, BT, SLA, Hmax) and categorical traits (Dec, SSy, PSy, SD and SSi). These indices were calculated per plot for the overall community (at T0 and T7) and for each demographical group (recruits, surviving and dead trees, only at T7). The CWM of quantitative traits were calculated in two ways (Laliberté et al., 2015): 1) Summing the species trait value weighted by species basal area of all species in the plot, and dividing it by total basal area in the plot; and 2) Summing the species trait value weighted by species stem density of all species in the plot, and dividing it by total stem density in the plot. We calculated CWM weighting species by relative basal area because it is related with actual ecosystem processes (e.g., productivity) and reflects species performance. Thus, CWM weighted by basal area mainly reflects the role of large surviving and dead trees. To account for the effect of small and recruit trees, we also calculated the CWM weighted by tree density giving equal weights to recruits, dead and surviving trees. CWM for categorical traits were calculated as the percentage of individuals (weighted by species abundance) and percentage of basal area (weighted by basal area).

To assess functional diversity related to all vegetative and reproductive traits we calculated functional richness (F_{ric}) and functional dispersion (F_{dis}) indices per plot for the overall community (at T0 and T7) and for each demographical group (recruits, surviving and dead trees, only at T7). F_{ric} is a measure of the volume of multivariate trait space that the species of the community occupy, and does not account for species basal area (Villéger et al., 2008). F_{dis} is a measure of multivariate trait diversity weighted by species basal area or tree density, and it is based on the mean distance in multidimensional trait space of individual species to the centroid of the whole community (Laliberte and Legendre, 2010). We calculated functional diversity metrics (CWM and FD indices) using the "FD" package in R (Laliberté et al., 2015). Additional information on CWM and Functional diversity indices per plot can be found in Table S1 and Table S2.

Data analysis

To quantify woody plant encroachment, we used a linear mixed model (LMM) with AGB as response variable, census (T0 and T7) as fixed effect and plot as a random effect. Plot was a random effect to account for the dependence of plots over time. To test for changes in overall community species diversity (S'), functional diversity (Fric and Fdis), and trait composition (CWM of WD, BT, SLA, Hmax, Dec, PS, SSy, SD, and SSi) over time, a LMM was analysed for each metric following the same model structure with census (T0 and T7) as a fixed effect and plot as a random effect. Linear mixed models were analysed with the lmer function in "lme4" package (Bates et al., 2015) in R (Team, 2016). To evaluate changes in species composition in overall community (beta diversity) over time, we calculated the Jaccard similarity index for each plot between census in T0 and T7. Then, we calculated the mean Jaccard similarity index for all plots. The analyzes were performed using the *vegdist* function in "Vegan" package (Oksanen et al., 2013) in R (Team, 2016).

To evaluate the contribution of the recruits, dead and surviving trees in the overall changes in the community metrics, we performed one linear model (LM) per metric. including overall changes of each metric per plot as response variable, and metrics calculated by each demographical group (recruit and dead trees, and surviving trees at the second census) as fixed factor. In this second analysis, we used LM instead of LMM because the metrics for demographical groups are calculated only in T7 and plot did not need to be included as random effect. We selected the best model based on the lower Akaike Information Criteria (AIC) values. To compare the relative importance of each demographic group in overall changes in community metrics, we compared their standardized regression coefficients in each model. Generalized linear models were performed in R 3.1.2 (Team, 2016) using *lm* function (Team, 2016).

To test for spatial autocorrelation between plots, we performed Moran's I test in all LM and LMM models, based on plot coordinates (Kissling and Carl, 2008). No models showed spatial autocorrelation (Moran's I p-value<0.05) and we continued the analyses using the results of the LM and LMM models. Moran's I test were performed using *moran.test* function in "spdep" package (Bivand, 2015) in R. When necessary, data were square root transformed prior to analysis to meet the assumptions of normality, homoscedasticity, to control for the effect of outliers, and to account for possible nonlinear relationships between variables.

RESULTS

Species richness and composition

We found 70 species of 56 genus and 37 families in first census (T0), and 68 species of 54 genus and 35 families in the second census (T7) (Table S5). Rare species with only one individual accounted for 30% (21 species) of the total species at T0. We found 19 species of 17 genus and 13 families that recruited, but only two species (3% of the total species present in T0) were new species (belonging two genus and two families) that were not present in T0 (*Cardiopetalum calophyllum* and *Myrcia tomentosa*) (Table S5). We found 32 species of 29 genus and 19 families that died, and four of those tree species (6% of the total species present in T0) of four genus and four families were and were not present in the second census (*Piptocarpha rotundifolia*, *Dimorphandra mollis*, *Kielmeyera coriacea* and *Miconia ligustroides*) (Table S5). The four species locally extinct were rare species with only one individual in the T0. The mean Jaccard similarity index between our plots in T0 and T7 was 82% (Standard Error = 0.02) and we did not find significant differences in mean species richness over time (Figure 1b, Table S4).

Community change in structure and function

We found a total of 812 trees with 36.03 Mg.ha^{-1} of aboveground biomass (AGB) in the first census (T0) and 794 trees with 41.63 Mg.ha^{-1} of AGB in the second census (T7). The five most abundant species, with higher aboveground biomass and frequency in the plots at T0 (Figure 2, Table S6) were *Miconia albicans* (184 individuals, 7.43 Mg.ha^{-1}, and present in 23 plots), *Virola sebifera* (121 individuals, 1.64 Mg.ha^{-1}, and present in 18 plots), *Xylopia aromatica* (111, 2.28 Mg.ha^{-1}, and present in 24 plots), *Qualea grandiflora* (48, 3.95 Mg.ha^{-1}, and present in 20 plots) and *Ouratea hexasperma* (32, 1.52 Mg.ha^{-1}, and present in 15 plots). The five most abundant species, with higher aboveground biomass and frequency in the plots at T7 (Figure 2, Table S5) were *Virola sebifera* (174 individuals, 3.29 Mg.ha^{-1}, and present in 21 plots), *Xylopia aromatica* (122, 3.77 Mg.ha^{-1}, and present in 23 plots), *Miconia albicans* (84 individuals, 5.32 Mg.ha^{-1}, and present in 23 plots), *Qualea grandiflora* (46, 4.25 Mg.ha^{-1}, and present in 20 plots), and *Siparuna guianensis* (39 individuals, 0.59 Mg.ha^{-1}, and present in 17 plots). Recruits accounted for 21.6% (172 individuals) of the total tree density and 6.5% (2.74 Mg.ha^{-1}) of total AGB in T7. The three species that recruited more individuals with more aboveground biomass were *Virola sebifera* (36% of the recruit individuals and 31.6% of the recruit AGB), *Xylopia aromatica* (20.35% of the recruit individuals and 19.23% of the recruit AGB) and *Siparuna guianensis* (17.44% of the recruit individuals and 15.84% of the recruit AGB). Dead trees accounted for 24% (190 individuals) of the total tree density and 12% (4.98 Mg.ha^{-1}) of aboveground biomass in T7. The three species that had a higher mortality of individuals with more aboveground biomass were *Miconia albicans* (54.2% of the dead individuals and 57.2% of the dead AGB), *Xylopia aromatica* (12.63% of the dead individuals and 7.14% of the dead AGB) and *Virola sebifera* (4.74% of the dead individuals and 2.9% of the dead AGB).

Mean AGB increased 15.5% over time (Mean in T0 = 36.04 $Mg.ha^{-1}$, Standard Error in T0 = 0.93; Mean in T7 = 41.63 $Mg.ha^{-1}$ ± Standard Error in T7 = 0.98) indicating significant encroachment over seven years (Figure 1a). The overall changes in functional trait and diversity metrics over time followed the same pattern for both species weighted by basal area and tree density, and we focused on the results of metrics weighted by basal area either in the overall and demographic analyses (but see all results on Table S4). We found an increase of 4.3% (T0= 0.24 ± 0.002; T1= 0.25 ± 0.002, Figure 1d) in Functional dispersion index (F_{dis}), and an increase of 3.9% (T0= 0.53 ± 0.01; T1= 0.55 ± 0.01; marginally significant, p=0.055) in Functional richness index (F_{ric}) (Figure 1c).

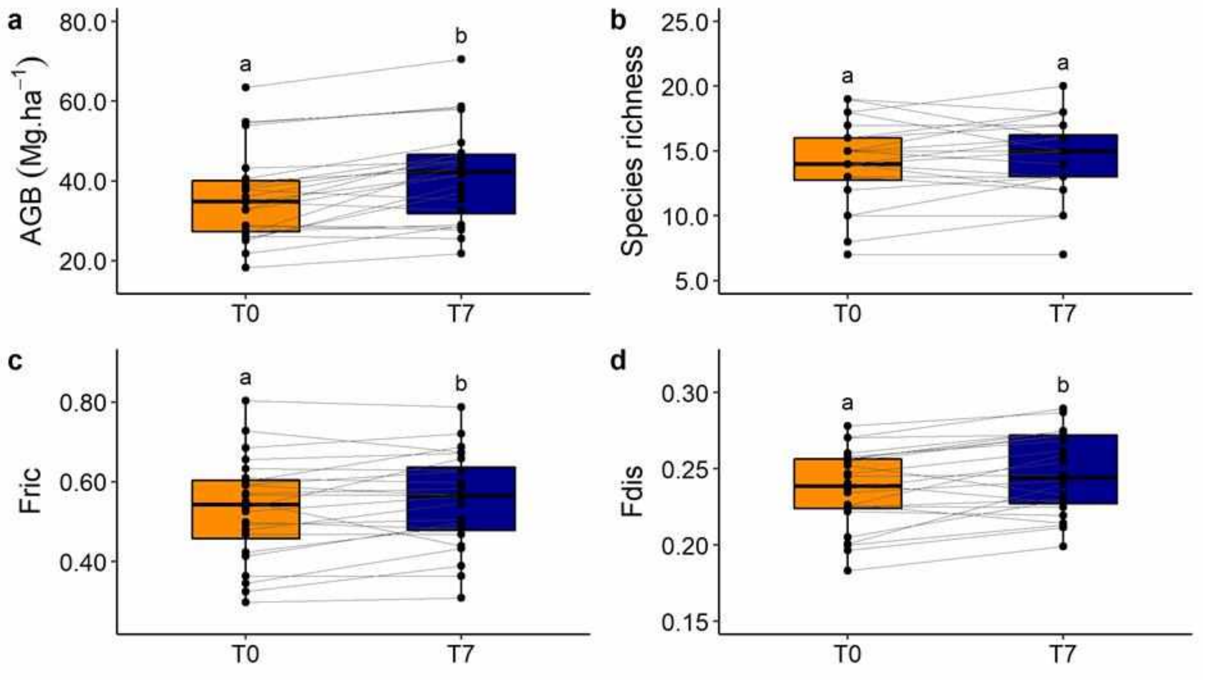

Figure 1. Changes in community metrics weighted by species basal area during woody plant encroachment in 7 years of monitoring. (a) AGB = Tree aboveground biomass; (b) Species richness; (c) Fric = functional richness index; (d) Fdis = functional dispersion index. Different letters indicate significant changes. Lines indicates the increase or decrease of each metric per plot over time.

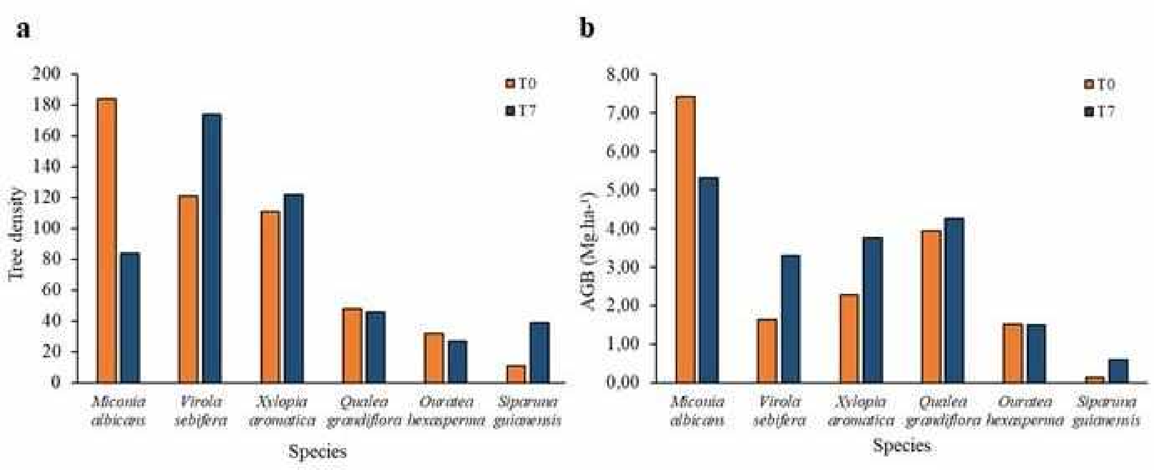

Figure 2. Tree density (a) and aboveground biomass (b) of the six most abundant species in the first census (t0) and second census (t7).

Turnover in vegetative and reproductive functional traits

We found an increase of 5.2% (T0= 9.21 ± 0.05; T1= 9.70 ± 0.05, Figure 3d) in CWM of specific leaf area (CWM_{sla}); 2.1% (T0= 7.10 $cm^2.g^{-1}$ ± 0.04; T1= 7.26 $cm^2.g^{-1}$ ± 0.04, Figure 3c) in CWM of maximum tree height (CWM_{Hmax}); 45.5% (T0= 13.80 m ± 0.97; T1= 20.08 m ± 1.06, Figure 3g) in CWM of species pollinated by very small insects (CWM_{vsi}); 44.2% (T0= 13.62% ± 1.11; T1= 19.64% ± 1.27, Figure 3j) in CWM of dioecy (CWM_{dio}); 32.6% (T0= 4.12% ± 0.59; T1= 5.47% ± 0.76, Figure 3k) in CWM of monoecy (CWM_{mon}); 5% (T0= 57.77% ± 1.36; T1= 60.63% ± 1.44; marginally significant, p=0.06) in CWM of biotic seed dispersal (CWM_{bio}) (Figure 3f); and 20.3% (T0= 11.07% ± 0.79; T1= 13.32% ± 0.79, Figure 3o) in CWM of large-seeded species (CWM_{ls}). We found a decrease of 1.3% (T0= 0.56 g/cm^3 ± 0.002; T1= 0.55 g/cm^3 ± 0.002, Figure 3a) in CWM of wood density (CWM_{wd}); 9.4% (T0= 9.85 mm ± 0.27; T1= 8.92 mm ± 0.26, Figure 3b) in CWM of bark thickness (CWM_{bt}); 12.5% (T0= 39.94% ± 1.18; T1= 34.93% ± 1.20, Figure 3h) in CWM of species pollinated by small insects (CWM_{smi}); 9% (T0= 82.26% ± 1.11; T1= 74.89% ± 1.29; Figure 3l) in CWM of hermaphrodite species (CWM_{h}), and 6.8% (T0= 55.01% ± 1.28; T1= 51.25% ± 1.28; Figure 3m) in CWM of species with small seeds (CWM_{ss}). We did not find significant changes in CWM of deciduousness (CWM_{dec}, Figure 3e), CWM of species pollinated by large insects (CWM_{li}, Figure 3i), vertebrates (CWM_{ve}, Table S4), and CWM of species with medium seed size (CWM_{ms}, Figure 3n).

Demography and trait turnover

When analyzing the demographic drivers of net changes in community metrics (Figure 4, Table S6), we found that the overall increase in AGB, CWM_{Hmax}, and CWM_{ls} were positively related to these metrics for the recruits (Standardized regression coefficient $\beta_{AGB} = 0.46$ and Standard Error $SE_{AGB} = 0.12$; $\beta_{Hmax} = 0.5$, $SE_{Hmax} = 0.18$; $\beta_{ls} = 0.44$, $SE_{ls} = 0.17$) and negatively related to these metrics for the dead trees ($\beta_{AGB} = -0.61$, $SE_{AGB} = 0.12$; $\beta_{Hmax} = -0.74$, $SE_{Hmax} = 0.18$; $\beta_{ls} = -0.38$, $SE_{ls} = 0.17$). Overall increase in CWM_{dio} and CWM_{mon} were only positively related with these metrics for the recruits ($\beta_{dio} = 0.36$, $SE_{dio} = 0.2$; $\beta_{mon} = 0.68$, $SE_{mon} = 0.2$). Overall increase in CWM_{sla} was only related to this metric for dead trees ($\beta_{sla} = -0.54$, $SE_{sla} = 0.18$), and overall increase in CWM_{bio} was only related to this metric for surviving trees ($\beta_{bio} = -0.63$, $SE_{bio} = 0.16$). Overall increase in CWM_{vsi} was positively related to this metric for recruits ($\beta_{vsi} = 0.51$, $SE_{vsi} = 0.17$) and negatively related to this metric for dead ($\beta_{vsi} = -0.42$, $SE_{vsi} = 0.16$) and surviving trees ($\beta_{vsi} = -0.41$, $SE_{vsi} = 0.18$). Overall decrease in CWM_{wd} was positively related to this metric for recruits ($\beta_{wd} = 0.48$, $SE_{wd} = 0.13$) and negatively related to this metric for dead trees ($\beta_{wd} = -0.62$, $SE_{wd} = 0.13$). Overall decrease in CWM_{bt} was only positively related to this metric for recruits ($\beta_{bt} = 0.40$, $SE_{bt} = 0.19$), and overall decrease in CWM_{ss} was only negatively related to this metric for dead trees ($\beta_{ss} = -0.74$, $SE_{bt} = 0.14$). Overall decrease in CWM_{smi} was positively related to this metric for surviving trees ($\beta_{smi} = 0.35$, $SE_{smi} = 0.14$) and negatively related to this metric for dead trees ($\beta_{smi} = -0.74$, $SE_{smi} = 0.14$). Overall decrease in CWM_{h} was positively related to this metric for recruits ($\beta_{h} = 0.39$, $SE_{h} = 0.13$) and surviving trees ($\beta_{h} = 0.60$, $SE_{h} = 0.13$) and negatively related to this metric for dead trees ($\beta_{h} = 0.39$, $SE_{h} = 0.13$). The non-significant change in CWM_{dec} was positively related to this metric only for recruits ($\beta_{dec} = 0.43$, $SE_{dec} = 0.19$). The non-significant change in CWM_{ms} was negatively related to this metric only for surviving trees ($\beta_{ms} = 0.45$, $SE_{ms} = 0.19$). The non-significant change in $\mathrm{CWM}_{\mathrm{li}}$ was positively related to this metric for surviving trees (β_{li}= 0.43, $\mathrm{SE}_{\mathrm{li}}$ = 0.16) and negatively related with this metric for dead trees (β_{li}= 0.51, $\mathrm{SE}_{\mathrm{li}}$ = 0.16). The non-significant overall changes in species richness and $\mathrm{CWM}_{\mathrm{ve}}$ were reflected in no relationship of these metrics to recruits, surviving or dead trees. Overall increases in Fdis and Fric were also not related to any demographic group, indicating that increases in functional diversity is not dependent to functional diversity of recruits, dead or surviving trees.

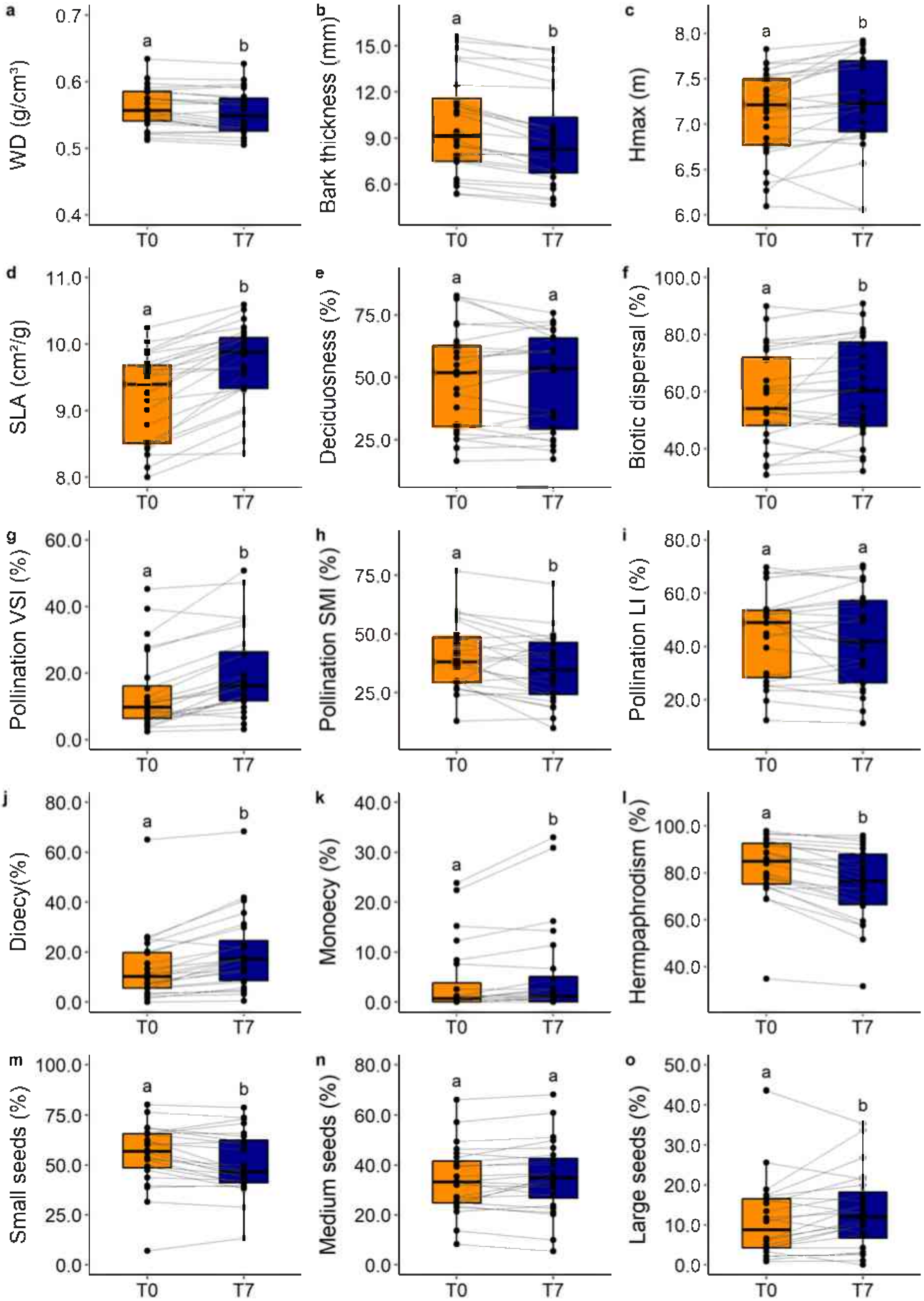
a
WD (g/cm³)
0.4
0.5
0.6
0.7
a
b
T0
T7
b
Bark thickness (mm)
6.0
9.0
12.0
15.0
a
b
T0
T7
c
Hmax (m)
6.0
6.5
7.0
7.5
8.0
a
b
T0
T7
d
SLA (cm²/g)
8.0
9.0
10.0
11.0
a
b
T0
T7
e
Deciduosness (%)
25.0
50.0
75.0
a
a
T0
T7
f
Biotic dispersal (%)
40.0
60.0
80.0
100.0
a
b
T0
T7
g
Pollination VSI (%)
0.0
20.0
40.0
60.0
a
b
T0
T7
h
Pollination SMI (%)
25.0
50.0
75.0
a
b
T0
T7
i
Pollination LI (%)
20.0
40.0
60.0
80.0
a
a
T0
T7
j
Dioecy(%)
0.0
20.0
40.0
60.0
80.0
a
b
T0
T7
k
Monoecy (%)
0.0
10.0
20.0
30.0
40.0
a
b
T0
T7
l
Hermpaphrodism (%)
40.0
60.0
80.0
100.0
a
b
T0
T7
m
Small seeds (%)
0.0
25.0
50.0
75.0
100.0
a
b
T0
T7
n
Medium seeds (%)
0.0
20.0
40.0
60.0
80.0
a
a
T0
T7
o
Large seeds (%)
0.0
10.0
20.0
30.0
40.0
50.0
a
b
T0
T7

Figure 3. Changes in functional traits weighted by species basal area during woody plant encroachment in 7 years of monitoring. (a) WD = CWM of wood density; (b) CWM of bark thickness; (c) Hmax = CWM of maximum tree height; (d) SLA = CWM of specific leaf area; (e) Deciduosness = CWM of deciduousness; (f) Biotic dispersal = CWM of biotic seed dispersal; (g) Pollination VSI = CWM of species pollinated by very small insects; (h) Pollination SMI = CWM of species pollinated by small insects; (i) Pollination LI = CWM of species pollinated by large insects; (j) Dioecy = CWM of dioecious species; (k) Monoecy = CWM of monoecious species; (l) Hermphroditism = CWM of hermaphrodite species; (m) Small seeds = CWM of species with small seed size; (n) Medium seeds = CWM of species with medium seed size; (o) Large seeds = CWM of species with large seed size. Different letters indicate signifficant changes. Lines indicates the increase or decrease of each metric per plot over time.

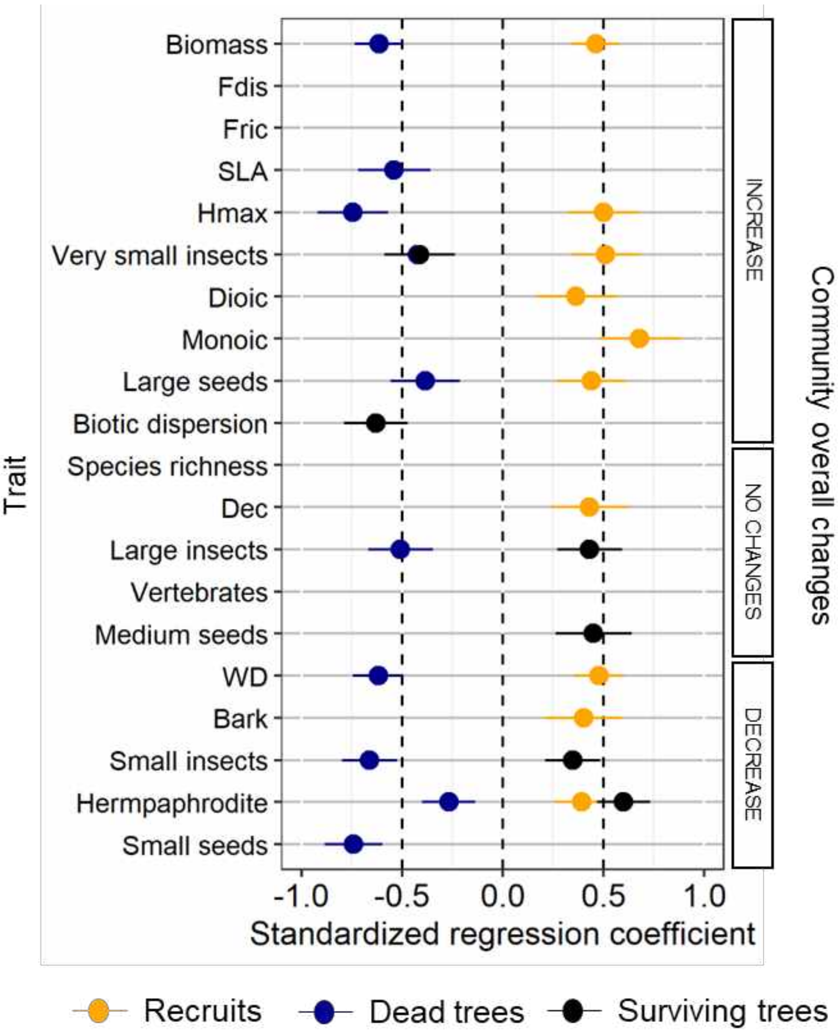

Figure 4. Demographic drivers (recruits, dead and surviving trees) of overall changes in community metrics over seven years. Community weighted mean (CWM) and functional diversity indices were weighted by species basal area. Fric = functional richness, Fdis= functional dispersion, WD = CWM of wood density, Bark = CWM of bark thickness, SLA = CWM of specific leaf area, Hmax = CWM of maximum tree height, Dec = CWM of deciduousness, Very small insects = CWM of pollination by very small insects, Small insects = CWM of pollination by small insects, Large insects = CWM of large insects, Vertebrates = CWM of pollination by vertebrates, Dioic = CWM of dioecious species, Hermpahrodite = CWM of hermaphrodite species, Monoic = CWM of monoecious species, Biotic dispersion = CWM of species with biotic seed dispersion, Small seeds = CWM of species with small seeds,

Medium seeds = CWM of species with medium seeds, Large seeds = CWM of species with large seeds. Regression coefficients values were standardized to compare the effects of each demographic group in the overall metrics. Metrics were grouped by overall changes in community trait dominance (increase, decrease or non-significant changes). Fric, Fdis, species richness and CWM of pollination by vertebrates have no significant demographic drivers.

DISCUSSION

Our study is the first to evaluate temporal change in tree functional diversity as a product of encroachment in a tropical savanna and our results mirror patterns in early stage secondary tropical forest succession, where functional diversity tends to increase with reduced environmental filtering and high tree aboveground biomass (Craven et al., 2018; Lohbeck et al., 2012). Although few changes in overall species composition, we found substantial change in functional traits that support an increase in dominance of forest adapted tree species, with higher maximum tree height, lower bark thickness, lower woody density, higher SLA, large seeds dispersed by animals, and higher relative abundance of species utilizing more specialized pollination (by very small insects) and sexual systems (monoecy and dioecy). These overall changes were explained by the growth and recruitment of forest tree species, and the mortality of individuals conservative traits, less adapted to encroached conditions. Recruits were the main drivers of decreased bark thickness and increased monoecy and dioecy, indicating that the new individuals have thinner barks and specialized reproductive strategies. On the other hand, dead trees had a higher contribution on the increased abundance of higher SLA species and decreased abundance of species with small seed size, indicating a mortality of species with lower SLA and small seeds. We discussed these trends and their consequences in detail below.

Encroachment is a worldwide phenomenon and product of global change (Stevens et al., 2017; Wigley et al., 2010) and specifically in the Cerrado, changing fire regimes and fire suppression policies are leading to rapidly changing savanna ecosystems via encroachment (Andela et al., 2017; Rosan et al., 2019). However, the understanding of the impacts of encroachment remains surprisingly limited and our results suggest life history strategies vulnerable and resistant to encroachment. Both functional richness and dispersion increased over time, but with no change in mean species richness. We found that encroachment can benefit tree species that had the establishment and growth restricted by stressful environmental conditions in open savannas. Consequently, a changing in dominance of species can increase functional diversity that are directly related to the response of the species to resource availability and environmental filtering. Although higher functional diversity is related to the capacity of the forest systems to adapt, rearrange and maintain ecosystems functions in disturbances scenarios (Laliberté et al., 2010; Oliver et al., 2015), savannas are already a system adapted to disturbances (e.g. fire, temperature and drought) and an increase in functional diversity can mean a reduced dominance of savanna-adapted species, suggesting that encroachment can reduce the resilience potential of tree communities in open habitats.

Previously, encroachment has been found to reduce species richness when considering both tree and herbaceous species (Abreu et al., 2017; Alofs and Fowler, 2013; Giles et al., 2021; Price and Morgan, 2008). We found that savanna tree species are more resistant to increasing vegetation cover than grasses, as there was no net gain in species richness, and is likely related to the generation times and ages of woody plants in comparison to grasses. In addition to no net gain in species richness, we found a higher similarity in species composition over time, indicating that is not occurring a species replacement. Only two new species (3%) arrived in the system over time (*Cardiopetalum calophyllum* and *Myrcia tomentosa*) and four tree species (6%) were locally extinct in the second census (*Piptocarpha rotundifolia, Dimorphandra mollis, Kielmeyera coriacea* and *Miconia ligustroides*), indicating that changes in functional composition are not due to species replacement, but probably related to changing in the abundance of constituent species. In fact, the most abundant species in first census (*Miconia albicans*) showed a high mortality, while other abundant species (e.g. *Virola sebifera, Xylopia aromatica*) showed a higher recruitment. Besides the higher recruitment of abundant species, *Siparuna guianensis* (that was not abundant in the first census) also increased either in tree density and aboveground biomass in T7. The most abundant recruit species are common from woodland savannas and forests and the most abundant dead species is common from open cerrado (Bueno et al., 2018). Furthermore, our results revealed different patterns in species composition and functional diversity when compared to more arid systems where a dominance of few species leads to encroachment (Connell et al., 2021; Throop and Archer, 2007; Zhou et al., 2017). These different patterns could be due to higher mean annual precipitation of savannas in Cerrado (Lehmann et al., 2014) that can allow the development of species with a large range of strategies, compared to more arid systems where water is a limiting resource and can act as an environmental filter. The different patterns also can be due to the mosaic of vegetation present in Cerrado, allowing the coexistence of different species in landscape level.

We found an increase in importance of most vegetative and reproductive functional traits adapted to forest conditions. Overall, the results showed higher percentages of net changes in reproductive traits than vegetative traits (see Figure 2 and Results section), which indicates that reproductive strategies are more responsive to changes in environmental conditions than vegetative strategies (Dirks et al., 2017). The dominance of species with higher SLA increased over time, as expected, and this net change were mainly due to the mortality of individuals with low SLA values. Higher SLA values represents lower investments in leaf structures, but higher assimilation rates, increasing plant reproductive ability but reducing plant defense to high temperatures and fire events (Poorter & Bongers, 2006; Rossatto, de Araújo, da Silva, & Franco, 2018). In an encroached environment, species that can invest more in fast-growth strategies (e.g. higher SLA) than in early reproduction are able to easily reach the early formed canopy and optimize light capture (Valladares et al., 2016). Consequently, species that invest more in leaf structure may have lower competitive potential, negatively affecting tree survival over time (Pillay and Ward, 2014). Moreover, SLA is positively related to water and soil nutrient availability, that are reported to increase in the deeper soil layers of encroached areas (Blaser, Shanungu, Edwards, & Olde Venterink, 2014; Oliveira et al., 2005). The absence of grasses to retain soil and nutrients in the upper soil layers can increase their percolation into deeper soil layers, where it is more available for tree species than grasses. This could also help to explain the pattern of changes in community woody density and maximum tree height.

As expected, we found a decrease in community woody density and an increase in community maximum tree height over time. These changes were mainly due to the mortality of individuals with high wood density and low maximum height, and the recruitment of individuals with low wood density and high maximum tree height. Summarizing, the community are changing into the recruitment of taller and soft-wood species at expense of mortality of shorter and dense-wood species. Lower wood density and maximum tree height are commonly reported to be positively related to soil water and nutrient availability (Dantas & Pausas, 2020; Quesada et al., 2012; Raymundo et al., 2019). To have an adaptative gain in encroached environments, species needs to grow taller to have access to better light conditions. This fast growth is allowed by the large stem vessels (i.e lower wood density), that conduct more water to the upper parts of the tree (Thomas et al., 2004), favoring the recruitment of taller and soft-wood species. On the other hand, high wood density and low maximum tree height are common traits of species adapted to drought and nutrient limitation and can have a less adaptative potential, leading to mortality by competitive exclusion (Pillay and Ward, 2014). As we hypothesized, the CWM of bark thickness decreased over time, mainly due to the recruitment of individuals with low bark thickness. Bark thickness is a trait that confers protection to plant xylem and phloem against fire incidence and can increase tree survival (Dantas & Pausas, 2013; Pellegrini et al., 2017). In an encroached scenario, invest in thicker barks can be less adaptative, since species with thinner barks can grow faster (Hoffmann et al., 2012; Rossatto et al., 2009). Our results show that under encroachment process, savanna systems can become less resilient to climate change effects, due to increasing in dominance of species more vulnerable to extreme drought and fire events that are predicted to be more common in the future (Abatzoglou et al., 2019; Grillakis, 2019; Kirchmeier-Young et al., 2019).

For the reproductive traits, we indeed found an increase in CWM of animal dispersed species indicating an increasing dependence of interactions to seed dispersion, which is common for forest species (DeMattia et al., 2004; Paine et al., 2016). The increase in animal dispersed species occurs in detriment of species dispersed by wind, that is a characteristic of species occurring in open habitats. In comparison to open habitats as savannas, forest habitats are commonly associated with a high species diversity of birds (Chapman and Reich, 2007), which could be the main factor contributing to plant dispersal in the study area. Moreover, a closed-canopy habitat could reduce the wind flow, consequently reducing the success of dispersion of species with wind-dispersed and small seeds (Lohbeck et al., 2013). Against our expectation, we found an increase in CWM of large seeds. Large seeds are associated to heat and fire resistance in savannas (Ribeiro et al., 2015) and in a scenario of woody encroachment, it would expected an increase in trees that produce many small seeds. Our contrary results could be due to the time of sampling, that was done in the last third of 30 years of fire suppression. The greater time since fire suppression could allow a good performance of forest species with larger seeds that are expected to increase during forest secondary succession (Lai et al., 2020; Westoby et al., 2002). We evidence that encroachment increase the plant dependence of animals even to seed dispersion and reproduction. Although for one side this dependence could benefit specific animal communities under encroachment providing habitat and resources, this dependence can make plant communities more vulnerable to local animal extinctions. Animal local extinction is increasing around the world due to climate changes (Román-Palacios and Wiens, 2020) and fragmentation effects (Crooks et al., 2017). Many savannas under encroachment in Brazil are located in a fragmented landscape within farms (Rosan et al., 2019), which can restrict animal locomotion and cause local extinctions. Consequently, in a system high dependent of plant-animal interactions, animal extinctions may reduce plant reproduction and dispersion over time.

We also found an increase in the importance of dioecious (CWM_{dio}) and monoecious (CWM_{mon}) species, and a decrease in hermaphrodite (CWM_{h}) species, indicating that more specialist reproductive strategies could be benefited by the woody plant encroachment conditions. It may be due to a more structurally complex environment, increasing the reproduction success of forest species. Forest species have more obligate allogamous reproductive strategies (such as dioecy) when compared to open savanna areas (Hoffmann, 1998; Oliveira, 1996). We also found an increase in representativeness of species pollinated by very small insects (CWM_{vsi}) in detriment of species pollinated by small insects (CWM_{smi}). Very small insects have few body structures and defenses to persist in higher temperatures and low air moisture (Jourdan et al., 2019; Pureswaran et al., 2018) as in open savannas, and they have been associated to pollination of dioecious forest trees (Oliveira, 1996). Thus, these very small insects may improve their growth performance and reproductive success in encroached habitat (Estay et al., 2014), favoring the reproductive success of the plants pollinated by these animals.

Our results suggest that the study area may have surpassed savanna-forest threshold (Dantas et al., 2013), and are following the successional processes of secondary forests as we found that the life history strategies of the species are shifting toward dominance of species with acquisitive performance (fast resource acquisition and growth rates) (Báez and Homeier, 2018; Díaz et al., 2013; Kunstler et al., 2016), except for seed size. Changes in trait dominance can have direct effects on ecosystem processes such as water, nutrients and carbon cycle. Although acquisitive traits can indicate a carbon gain in short-term, it can be reduced in long term in a fire event or changing climatic conditions, due to the increasing dominance of species less resistant to fire and drought (e.g. low woody density and bark thickness) (Pellegrini et al., 2016a). Regarding to nutrient cycles, acquisitive traits can increase decomposition rates and consequently the availability of soil nutrients over time (Szefer et al., 2017). The increasing availability in soil nutrients can feedback the process, contributing to a higher representativeness of acquisitive species over time. Regarding to hydrological cycle, acquisitive species could act as a drain, since these species commonly have higher transpiration rates (Honda & Durigan, 2016; Oliveira et al., 2005). Moreover, the dominance of trees with reproductive functional traits adapted to forest (e.g. monoecious and dioecious plant species pollinated by very small insects) also can contribute to maintain resources for fauna species that are more vulnerable to harsh environmental conditions.

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CAPÍTULO 3

Woody plant encroachment and hotter and drier climates reduce tree species diversity and change functional composition in Cerrado

Woody plant encroachment and hotter and drier climates reduce tree species diversity and change functional composition in Cerrado

Abstract:

Tree species diversity and functional traits are related with important ecosystem functions as productivity and nutrient cycling in savanna environments. Surprisingly, we do know yet how the main factors that drive species diversity and functional composition (i.e. climate, fire and woody plant encroachment) act simultaneously in the Brazilian savanna, the most diverse savanna in the world. Using data of relative basal area of more than 40.000 trees, of 340 species in Cerrado, we disentangle the effects of mean annual temperature, mean annual precipitation, fire frequency and wood plant encroachment on species diversity and functional composition. Moreover, we look at the mediator effects of species diversity on functional composition. Species diversity was negatively related to mean annual temperature and woody plant encroachment and positively related to mean annual temperature. Mean annual temperature was negatively related to the abundance of species with both higher and lower values of maximum tree height, and to the abundance of species with higher bark thickness values. Moreover, mean annual temperature was positively related to the abundance of species with higher specific leaf area and wood density values. Tree species diversity was positively related to the abundance of species with higher maximum tree height values and negatively related to the abundance of species with lower maximum tree height and higher bark thickness values. Fire frequency was not related to species diversity or functional composition. We demonstrate that hotter and drier climates, predicted to be increasing in Cerrado, can decline species diversity and abundance of trees with forest or savanna specialist strategies. Moreover, woody encroachment also can decline species diversity, but cause an increase in the abundance of forest specialist trees.

Key Words: species richness, biodiversity, functional traits, mean annual temperature, mean annual precipitation, fire, specific leaf area, wood density, maximum tree height, bark thickness, structural equation model

INTRODUCTION

Ecologists have widely discussed the role of species diversity as an important ecosystem component, mainly because species diversity have been related to primary productivity (Ammer, 2019), and invasion or pest and diseases resistance (Byun et al., 2018; Jactel et al., 2021), contributing to the resilience of ecosystems. Moreover, species diversity is also a political and social concern, since human activities and climate changes are causing an increasing in the species extinction rates (Román-Palacios and Wiens, 2020). Evaluate the drivers of species diversity is a challenge mainly in high diverse environments as Brazilian savanna (Cerrado), where there is a large variation in climate, vegetation structure and fire regimes, that are important factors influencing species diversity and composition (Dantas et al., 2013; Scheiner and Rey-Benayas, 1994). Several studies have been developed to understand the drivers of plant species diversity in savannas (Abreu et al., 2017; Durigan et al., 2020; Flake et al., 2021; Maracahipes-Santos et al., 2018; Pellegrini et al., 2016b), but they are single-factor studies and do not integrate the abiotic (climate and disturbance factors) and biotic (species and functional) parameters, which are essential to understand species diversity (Pausas and Austin, 2001a). Since Cerrado is the main agricultural frontier in Brazil, is becoming hotter and drier (Hofmann et al., 2021), and several areas are suffering the process of woody plant encroachment (Goncalves et al., 2021; Rosan et al., 2019) it is fundamental to understand how species diversity and functions are affected simultaneously by these variables, to be able to prevent the negative impacts of extreme climate and anthropic changes (Pausas and Austin, 2001b).

Among the drivers of plant species diversity in Cerrado, the increasing in the vegetation cover (woody plant encroachment process, hereafter referred as WPE) in open savanna areas has been studied in the last decade. WPE can be caused by fire suppression (Durigan, 2020a), increasing atmospheric CO2 (Zhang, Li, Zhang, Zhang, & Chen, 2016) and precipitation (Archer et al., 2017). These changes in the local environmental conditions increase shade, water and nutrients availability in the deep soil layers (Leitner, Davies, Parr, Eggleton, & Robertson, 2018; Throop & Archer, 2007), and decrease local temperature (Thomas et al., 2018). These changes in local environmental conditions can reduce the diversity of grasses and specialist savanna species that are highly light-dependent and fire-resistant, but can increase the diversity of tree species that have a higher performance in shadier and cooler environments, with lower fire frequency (Abreu et al., 2017). Another important factor driving tree species diversity in Cerrado is water availability. Mean annual precipitation (MAP) is commonly reported to increase species productivity globally (Lehmann et al., 2014), allowing the development mainly of seedlings and saplings that depend on the precipitation to increase water availability in the firsts soil layers. Mean annual temperature (MAT) also can positively influence species diversity at global scale because MAT increase species metabolic rates. Despite that, global results consider very low temperatures (i.e. very high latitudes) (Moles et al., 2009). In Cerrado, hotter temperatures are the environmental filter, and colder temperatures should increase species diversity (Chapungu et al., 2020), favoring tree species that can germinate their seeds in colder temperatures than grasses (Borghetti et al., 2021). Additionally, fire is the most important environmental filter in Cerrado maintaining vegetation structure in open habitats.

Although favor grasses and shade-intolerant species (Durigan et al., 2020; Pausas and Ribeiro, 2017), fire events can cause large damages in plant structure and higher fire frequency can reduce tree species diversity (Makumbe et al., 2020).

Rarefied species richness is a commonly used metric to evaluate species diversity, mainly because it uses the number of species, which is the main composite of species diversity; and weight for the number of individuals that is very useful to compare species richness among different areas (Durigan et al., 2020; Gotelli and Colwell, 2001; Poorter et al., 2015). Although it is important to look at changes in species diversity, in high diverse environments species diversity alone can not necessarily reflect changes in ecosystem proprieties. For example, after disturbance events tree communities can recover the number of species after short time, but with large changes in species and functional composition compared to the time before disturbance (Raymundo et al., 2019; Zhang et al., 2017). Thus, it is necessary to understand how climate and local environmental changes are related to both species diversity and functional composition.

Functional traits are a good tool to assess functional composition, since some functional traits can represent the response of the species to the environmental conditions. Some traits such as specific leaf area, woody density, maximum tree height and bark thickness are common traits used to evaluate ecosystem changes in savannas (Dantas and Pausas, 2020, 2013; Flake et al., 2021; Hoffmann et al., 2012; Pellegrini et al., 2016a). SLA is positively related to plant investments in light interception and heat dissipation, and negatively related to drought (Poorter & Bongers, 2006). Wood density reflects a trade-off between hydraulic efficiency vs. safety and is positively related to drought resistance (Bucci et al., 2004), temperature (Martínez-Cabrera et al., 2009; Thomas et al., 2007, 2004; Wiemann and Williamson, 2002), and negatively related to water availability (Swenson and Enquist, 2007; Wiemann and

Williamson, 2002) and fire (Altomare et al., 2021). Maximum tree height is positively associated to species competition for light (Dantas & Pausas, 2013; Moles et al., 2009) and escape from fire (Makumbe et al., 2020). Maximum height is also increased by water availability (Gorgens et al., 2021; Scholes et al., 2002) and temperature (Klein et al., 2015). Bark thickness is a common adaptation of savanna species to climate and fire, and higher bark thickness is related to xylem protection to fire (Loram-Lourenço et al., 2020), hotter temperatures and drought (Gashaw et al., 2002; Rosell, 2016).

Although the knowledge about the effects of species diversity on ecosystem processes such as primary productivity (Poorter et al., 2015) or nutrient cycling (Hooper et al., 2005), the effects of species diversity on functional composition receive little attention (Roscher et al., 2011), and this relationship is important since the change in ecosystem proprieties are mediated by functional traits (Díaz et al., 2013; Lienin and Kleyer, 2012). In species-rich environments, species with functional traits more adapted to resource acquisition are predicted to be more adaptive than species with functional traits more adapted to stressful environmental conditions (Roscher et al., 2011), since competition can represent an important factor in high diversity ecosystems. Thus, higher species diversity should favor species more adapted to forest conditions with higher SLA and maximum tree height, but lower WD and bark thickness.

Here we aim to evaluate how the climate, fire and woody plant encroachment drive species diversity and functional composition in the Cerrado. We used data on more than 40,000 trees distributed in 340 species and we classified these species in functional groups based on important functional traits related to fire, water availability, temperature and light availability. We ask three main questions: 1) how encroachment, temperature, precipitation and fire are related to tree species diversity? We expected that temperature and fire should be negatively related to tree species diversity, and precipitation and WPE should be positively related to species diversity; 2) how encroachment, temperature, precipitation and fire are related to the abundance of functional traits? We expected that precipitation would be positively related to the abundance of species with higher SLA and maximum tree height, and lower wood density and bark thickness. Temperature would be positively related to the abundance of species with higher SLA, WD and bark thickness, and with lower maximum tree height. WPE should be positively related to the abundance of species with higher SLA and maximum tree height and lower WD and bark thickness. Finally, we expected that fire occurrence should be positively related to the abundance of species with higher bark thickness and WD, and lower SLA and maximum tree height.

METHODS

Study areas

This study is based on previously tree inventories in 33 savanna areas in the Brazilian Cerrado biome (Figure 1) (Abreu et al., 2012, 2014; Araújo et al., 2012; Assunção and Felfili, 2004; Borges, 2009; Brant, 2011; Cardoso et al., 2016; Carielo et al., 2012; Casella, 2014; Cerqueira et al., 2017; Costa et al., 2010; de Moura et al., 2010; Giácomo et al., 2013; Leal, 2015; Lehn, 2008; Lemos, 2013; Lima, 2015; Lopes et al., 2009; Medeiros et al., 2008, 2012; Miranda, 2008; Mota et al., 2014; Oestreich-Filho, 2014; Oliveira et al., 2015; W. F. da Silva, 2007; Teixeira, 2015). Specifically, the vegetation type of the study sites is called “Cerrado strictu sensu”, a typical and most representative savanna vegetation type in Cerrado. In the 33 study areas, 18 sites had sampling size of 1ha, eight sites had the sampling size higher than 1ha, and seven sites had the sampling size <1ha. All sites were sampled by using sub-plots where all trees and shrubs with diameter at ground level (DGL, 0.30m) ≥ 5 cm were measured and species identified. The mean annual precipitation varied from 1088 to 1731 mm, and the mean annual temperature varied from 20.1 to 25.9ºC. The data compilation shows a sum of more than 40.000 trees, belonging to 340 species.

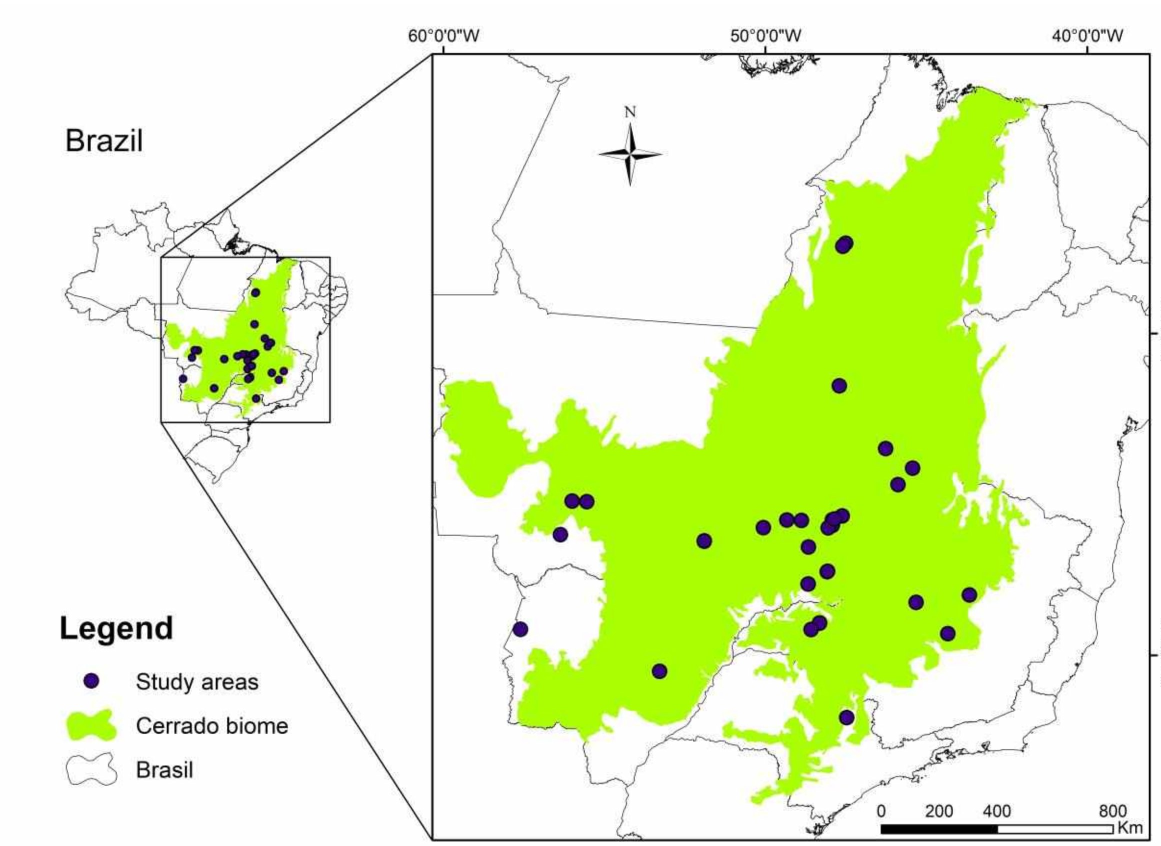

Figure 1. Location of the 33 study areas in Brazilian Cerrado.

Environmental metrics and woody plant encroachment

To assess the water availability, we used the mean annual precipitation (MAP) and to assess local temperature we used mean annual temperature (MAT). Temperature and precipitation metrics were obtained for each area using WorldClim data (Fick and Hijmans, 2017). The data of fire frequency was also obtained for each area using data of fire frequency (presence/absence) between 2000 and 2020 from the MODIS product MCD14ML collection 6 v.3 (Giglio, 2015). To assess woody plant encroachment, we calculated the relative difference in Normalized Difference Vegetation Index (Δ_{NDVI}, %) for each area between 2000 and 2020.

To calculate NDVI, we used surface reflectance derived from Landsat satellite images obtained from the USGS (United State Geological Survey). To obtain NDVI from 2000, we used the Landsat 5 Thematic Mapper (TM) scenes that have information about the earth surface reflectance in pixels with 30m of resolution. To obtain NDVI from 2020, we used the Landsat 8 Operational Land Imager (OLI) extracting values in 30m-resolution pixels. We used imageries from Landsat collection 2 level 2 (on demand) that already have the appropriate corrections to temporal analyses. We used imageries from the wet season (between November and May) that had no cloud presence in the study areas. We clipped the NDVI composite images based on the polygons drawn for each area and then we calculated the mean NDVI. Therefore, each area had a mean NDVI value for 2000 and 2020. The relative difference in NDVI was calculated as: $\Delta_{NDVI} = ((NDVI_{2020} - NDVI_{2000}) / NDVI_{2000}) * 100$. $NDVI_{2000}$ is the mean NDVI value calculated in 2000 for each area. $NDVI_{2020}$ is the mean NDVI value calculated in 2020 for each area. Additional information on WPE, MAP, MAT and fire frequency per plot per plot can be found in Appendix S1.

Functional traits

We compiled from the literature four vegetative functional traits that can be associated to changes in species diversity, climate, fire and woody plant encroachment: 1) wood density (WD, g/cm^3) (Zanne et al., 2009); 2) bark thickness (BT, mm) (Batalha et al., 2011b, 2011a; G. Carvalho, 2013; Cianciaruso et al., 2012; Miatto, 2011a; Oliveira, 2013; Pellegrini et al., 2017; Santos, 2018); 3) specific leaf area (SLA, cm^2/g) (Abe et al., 2016; Araújo, 2006; Batalha et al., 2011b, 2011a; Capuzzo et al., 2012; Carvalho, 2005; Carvalho, 2013; Cianciaruso et al., 2013, 2012; Dantas, 2010; Franco et al., 2005; Jardim, 2006; Jardim and Batalha, 2008; Loiola et al., 2010; Meira-Junior, 2015; Miatto, 2011b; Miatto et al., 2016; Oliveira, 2005, 2013; Peixoto, 2007; Pringle et al., 2011; Rosado and Mattos, 2010; Rossatto et al., 2009; Saboya, 2014; Santos, 2017; Silva and Batalha, 2011; Silva, 2007); and 4) maximum stem height (Hmax, m) (NeotropTree, 2020). Trait data were obtained for the species that cover more than 90% of the total basal area for each site.

Species diversity and functional groups

To assess species diversity, we used rarefied species richness for each plot. Rarefied species richness is the most intuitive method evaluate species diversity, because it allows to evaluate species richness considering the same tree density for all areas. We assessed species richness based on 380 individuals, since it was the minimum tree density considering all sites. Functional groups were classified using hierarchical clustering on principal components (HCPC), based on a multivariate matrix with the value of each trait (bark thickness, maximum tree height, wood density, and specific leaf area). We used the HCPC function in FactoMineR package in R to define the optimal number of functional groups. Because 95 species were classified as unidentified (without information on family, genus or species identity), we considered only 245 species in functional group analyses. Cluster analyses indicate the separation of four functional groups (Figure 2, Appendix 1) and we used these groups as a proxy for functional composition in further analyses described below.

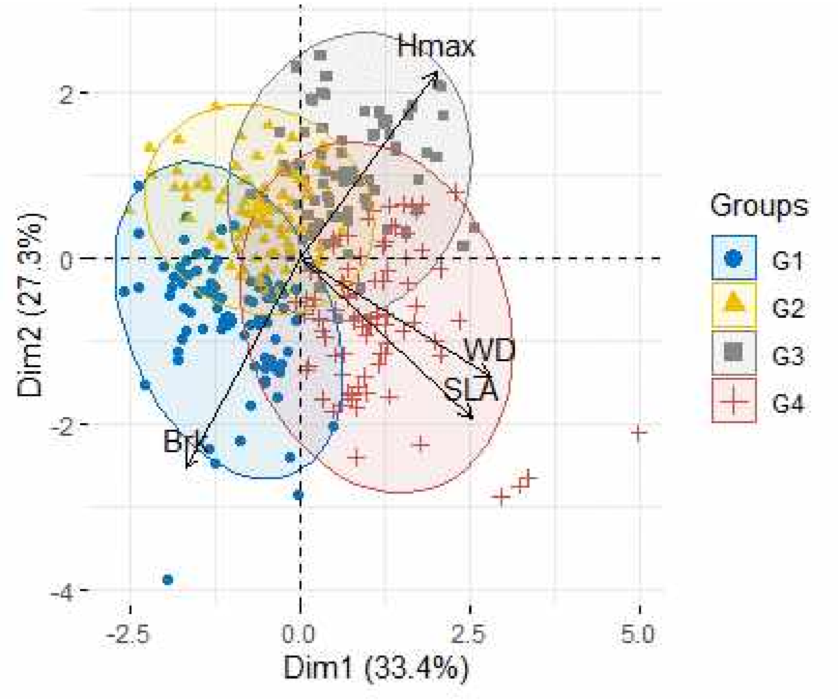

Figure 2. Biplot of the first and second PCA axis with the group classification of hierarchical clustering on principal components using HCPC function using *FactoMineR* package. Axis 1 explained 33.4% of the variance and axis 2 explained 27.3% of the variance. Ellipses represent the 95% interval confidence for each group. Species names and their functional groups are given in Appendix S2.

Community-weighted mean of functional groups

We calculated the community-weighted mean (CWM) values of each functional group (functional group 1, 2, 3 and 4) per site. We calculated CWM weighting species by relative basal area, summing the species trait value weighted by species basal area of all species in each site, and dividing it by total basal area in each site. We calculated CWM weighting species by relative basal area because it is related with actual ecosystem processes (e.g., productivity) and reflects species performance. We calculated CWM using the "FD" package in R (Laliberté et al., 2015). Additional information on CWM of functional groups per plot can be found in Appendix S1.

Statistical analysis

To evaluate how the values of each functional trait (SLA, WD, maximum tree height and bark thickness) per species differed among functional groups, we performed four linear models. The first model included SLA of each species as the response variable and the functional group that the species were classified (functional group 1, 2, 3, and 4) as fixed factors. The second model included WD of each species as the response variable and the functional group that the species were classified as fixed factors. The third model included maximum tree height of each species as the response variable and the functional group that the species were classified as fixed factors. The fourth model included bark thickness of each species as the response variable and the functional group that the species were classified as fixed factors.

To evaluate the relative abundance of each functional group based on the representativeness of basal area of each group per plot, we performed a linear mixed model including the CWM of each functional group as a response variable, the functional group as a fixed factor, and each site as a random factor. We included site as random factor to compare the differences in the CWM of functional groups within each site.

To evaluate how tree species diversity and functional groups are related to woody plant encroachment and climate, we used Piecewise Structural Equation models, considering the pairwise relationship between our variables, and the non-linear distribution of the linear model residuals. We used rarefied species richness as a mediator variable, CWM of functional groups as endogenous variables, and mean annual temperature (MAT), mean annual precipitation (MAP), woody plant encroachment (WPE) and fire frequency as exogenous variables. Thus, we performed the pSEM model including five linear mixed models. The first model included the CWM of functional group 1 per plot as a response variable and fire frequency, rarefied species richness, MAP, MAT, and WPE as fixed factors. The second model included the CWM of functional group 2 per plot as a response variable and fire frequency, rarefied species richness, MAP, MAT, and WPE as fixed factors. The third model the CWM of functional group 3 per plot as a response variable and fire frequency, rarefied species richness, MAP, MAT, and WPE as fixed factors. The fourth model included the CWM of functional group 4 per plot as a response variable and fire frequency, rarefied species richness, MAP, MAT, and WPE as fixed factors. The fifth model included the rarefied species richness per plot as a response variable and fire frequency, MAP, MAT, and WPE as fixed factors.

All statistical analyses were performed in software R (Team, 2016). Linear models were performed using *lm* function in “stats” package. Linear mixed model were performed using *lmer* function in “lme4” package (Bates et al., 2015). Piecewise SEM model were performed using psem function in “piecewiseSEM” package (Lefcheck et al., 2019; Lefcheck, 2016).

RESULTS

Species dominance and diversity

The databases provided a total of 47,797 individuals of 340 species, 163 genus and 59 families. The five species with higher relative abundance were *Qualea parviflora, Qualea grandiflora, Davilla elliptica, Ouratea hexasperma and Kielmeyera coriacea,* representing 22% of the total individuals. The five species with higher relative basal area were *Qualea parviflora, Qualea grandiflora, Pouteria ramiflora, Caryocar brasiliense* and *Kielmeyera coriacea* representing 24.82% of the total basal area. The number of species per plots ranges from 23 to 91 species (mean = 56.81; SD = 15.79), the tree density ranges from 380 to 4720 individuals (mean = 1448.39; SD = 964.79), and basal area ranges from 2.7 to 33.5 m^2/ha (mean = 12.24; SD = 5.92).

Characterization of functional groups

Linear models indicate that mean bark thickness was 222% higher in functional group 1 (FGR 1, mean = 11.2 mm, Standard deviation, SD = 3.56mm) than in functional group 2 (FGR 2, mean = 3.47mm, SD = 2.13 mm), 104% higher than functional group 3 (FGR 3, mean = 5.47mm, SD = 3.29 mm), and 114% higher than functional group 4 (FGR 4, mean = 5.23 mm, SD = 3.19 mm) (Figure 3A, Appendix S3). Mean bark thickness was 57.5% higher in FGR 3 than FGR 2, and 50.5% higher in FGR 4 than FGR2 (Figure 3A, Appendix S3). Mean bark thickness of FGR 3 and FGR 4 were not significantly different (Figure 3A, Appendix S3). Maximum tree height in FGR 3 (mean = 28.64 m, SD = 6.29 m) was 224% higher than FGR 1 (mean = 8.8 m, SD = 4.8 m), 182% higher than FGR 2 (mean = 10,1 m, SD = 4.99 mm), and 122,4% higher than FGR 4 (mean = 12.9 m, SD = 6.28 m) (Figure 3B, Appendix S3). Maximum tree height in FGR 4 was higher than FGR 1 and FGR 2, and it was not significantly different between FGR 1 and FGR 2 (Figure 3B, Appendix S3). Specific leaf area in FGR 4 (mean = 16.72 cm^2/g, SD = 6.79 cm^2/g) was 79.3% higher than in FGR 1 (mean = 9.32 cm^2/g, SD = 3.02 cm^2/g), 79.8% higher than FGR 2 (mean = 9.3 cm^2/g, SD = 2.77 cm^2/g) and 69.2% higher than FGR 3 (mean = 9.88 cm^2/g, SD = 2.4 cm^2/g), and SLA did not differ significantly among FGR 1, FGR 2 and FGR 3 (Figure 3C, Appendix S3). Wood density in FGR 4 (mean = 0.78 g/cm^3, SD = 0.14 g/cm^3) was 34.9% higher than FGR 1 (mean = 0.58 g/cm^3, SD = 0.16 g/cm^3), 56.9% higher than FGR 2 (Mean = 0.5 g/cm^3, SD = 0.13 g/cm^3) and 16.9% higher than FGR 3 (mean = 0.67 g/cm^3, SD = 0.15 g/cm^3). Wood density in FGR 3 was 15.4% higher than FGR 1 and 34.2% higher than FGR 2. Wood density in FGR 1 was 16.3% higher than FGR 2 (Figure 3D, Appendix S3).

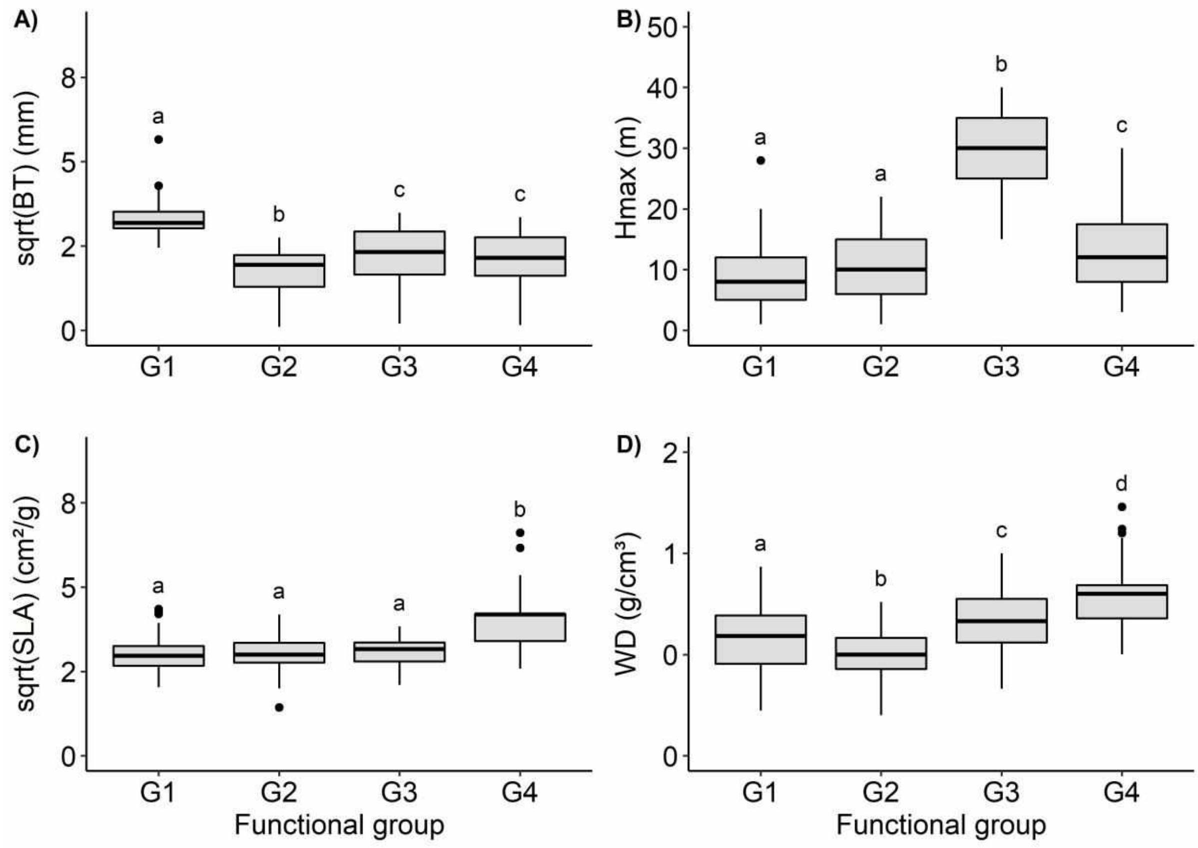

Figure 3. Distribution of mean values of (A) bark thickness (BT), (B) maximum tree height (Hmax), (C), specific leaf area (SLA), and (D) wood density (WD) for functional group 1 (G1, n=86), functional group 2 (G2, n=84), functional group 3 (G3, n=73), functional group 4 (G4, n=83). Different letters indicate significant differences (linear model p-value<0,05) among groups. Bark

The FGR 1 had 73 species (30.4% of total species) and its mean relative basal area varied from 17% to 81% (mean = 55.94; SD = 17.32) of total basal per plot. In FGR 1, 15 species represented 50% of the total basal area of the group. The FGR 2 had 66 species (27.5% of total species) and its relative basal area varied from 3.4% to 47.7% (mean = 21.03; SD = 11.63) of total basal area per plot. In FGR 2, 13 species represented 51% of the total basal area of the group. The FGR 3 had 49 species (20.4% of total species) and its relative basal area varied from 1.4% to 50.8% (mean = 12.56; SD = 10.65) of total basal per plot. In FGR 3, six species represented 49% of the total basal area of the group. The FGR 4 had 57 species (23.7% of total species) and its relative basal area varied from 17% to 81% (mean = 55.94; SD = 17.32) of total individuals per plot. In FGR 4, nine species represented 51% of the total basal area of the group. We found that mean relative basal area in FGR 1 was 163% higher than FGR 2, 398% higher than FGR 3, and 399% higher than FGR 4 (Figure 4). FGR 2 was 89% higher than FGR 3 and 89% higher than FGR 4 (Figure 4). Relative basal area of FGR 3 and FGR 4 were not significantly different (Figure 4).

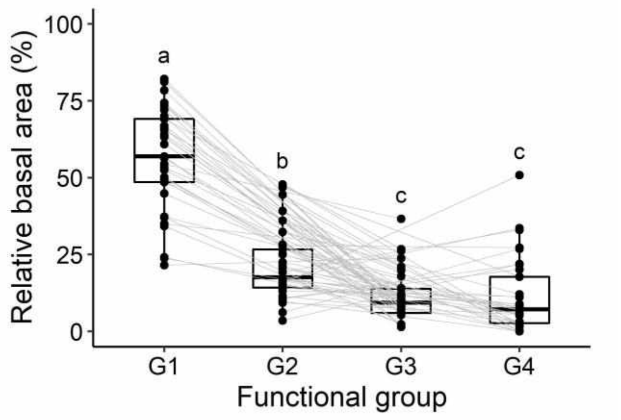

Figure 4. Distribution of relative basal area values in each functional group per plot. G1= functional group 1; G2= functional group 2; G3= functional group 3; G4= functional group 4. Different letters indicate significant differences.

Climate and woody encroachment effects on species diversity and functional groups

Piecewise Structural Equation Models showed a strong relationship between climate and encroachment on species diversity and functional groups (Figure 5, Appendix S4) and the results are described below. We found that woody plant encroachment (WPE) had a negative direct effect on species diversity and a positive effect on the abundance of the functional group of forest specialist species. Mean annual temperature (MAT) had a negative effect on species diversity, on the abundance of the functional group 1, and on the abundance of functional group 3. MAR also had a positive direct effect on the abundance of the functional group 4. Mean annual precipitation (MAP) had a positive effect on species diversity. Species diversity had a positive effect on the abundance of functional group of forest specialist species and had a negative effect on the abundance of functional group of savanna specialist species. Moreover, WPE also had a negative indirect effect on forest species and a positive indirect effect on the abundance of functional group of savanna species once it reduced species diversity. MAT also had a positive indirect effect on the abundance of functional group of savanna species and a negative indirect effect on the abundance of functional group of forest species, once MAT reduced species diversity. Fire frequency was not related to species diversity or any functional groups.

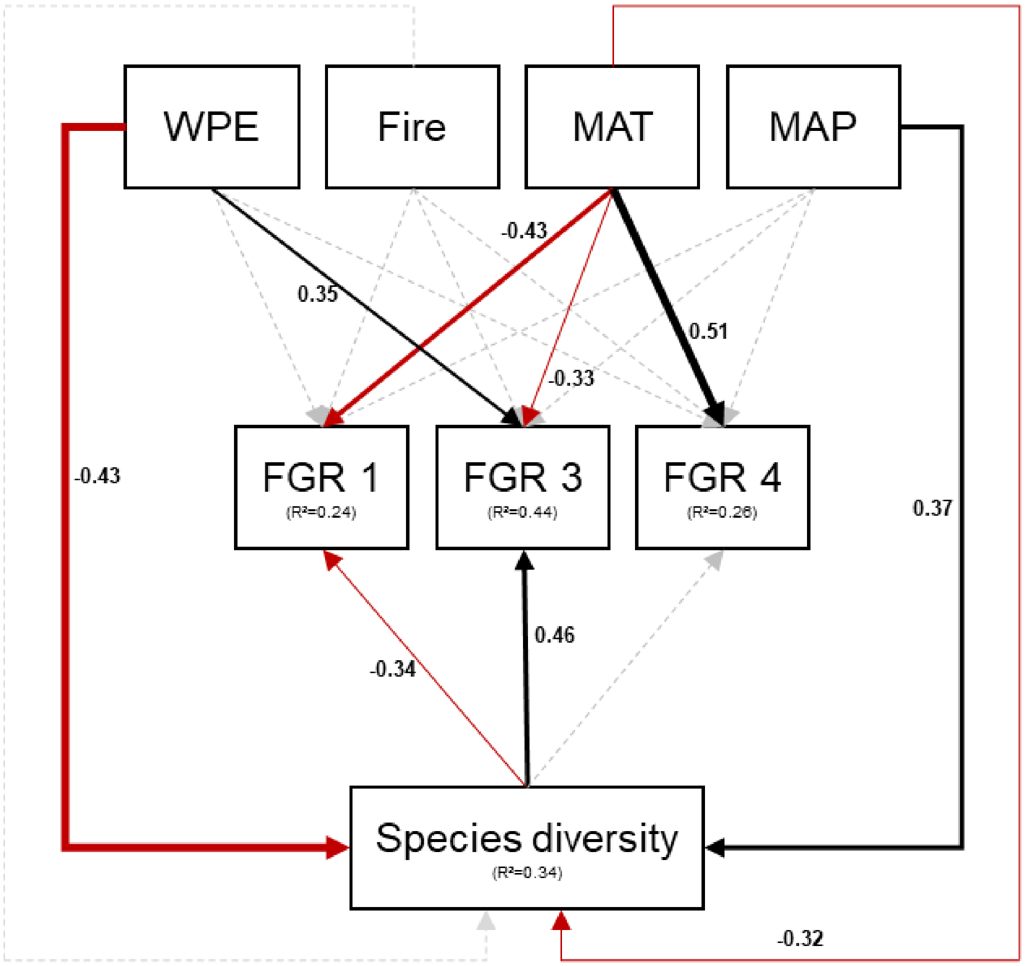

Figure 5. Piecewise Structural Equation Model showing the relationships among mean annual precipitation (MAP), mean annual temperature (MAT), fire frequency (Fire), woody plant encroachment rates represented by Δ_{NDVI} (WPE), rarefied species richness (Species diversity), and functional group 1 (FGR 1), functional group 2 (FGR 2), functional group 3 (FGR 3), and functional group 4 (FGR 4). Continuous lines indicate significative relationships. Dashed arrows indicate non-significative relationships. Regression coefficients are given for each

relationship, where positive values indicate positive relationships (black arrows) and negative values indicate negative relationships (red arrows). Thicker arrows indicate a stronger relationship (higher standardized beta coefficient). R² values from each linear model was included inside the box where the variable was the response variable. Species in Functional group 1 had the higher values of bark thickness and lower values of maximum height. Species in functional group 2 had the lower values of bark thickness, maximum height and wood density. Species in functional group 3 had the higher values of maximum height. Species in functional group 4 had the higher values of wood density and specific leaf area. Functional group 2 were not significantly related to any variable and was removed from the best model.

DISCUSSION

Here we provided the first exploration of the drivers of biodiversity in large scale in Brazilian Cerrado. We found that woody plant encroachment (WPE) and mean annual temperature (MAT) were the main drivers negatively affecting species diversity, while mean annual precipitation (MAP) was the main driver positively affecting species diversity. Moreover, MAT negatively affected the abundance of both species adapted to savanna (high fire and less shade) and forest (low fire and high shade), and positively affected the abundance of species with high SLA and WD, with intermediate values of maximum tree height and bark thickness. On the other hand, WPE positively affected the abundance of species adapted to forest conditions. MAT, MAP and WPE also had indirect effects on functional groups, since species diversity positively explained the variation in the abundance of forest specialist species and negatively explained the variation in savanna specialist species. Thus, MAT can indirectly intensify the reduction in forest specialist species, but also can buffer the direct negative effect on savanna specialist species, by reducing species diversity. Finally, WPE had a positive indirect effect on the abundance of savanna specialist species and a negative effect on the abundance of forest specialist species, by reducing species diversity.

Effects of woody plant encroachment and climate on species diversity, but no fire influence

We expected that woody plant encroachment (WPE) would be positively related to tree species diversity and we did not find that. Forests contain a more complex vertical structure and provide more opportunities for species with different life-history strategies (Scheiner and Rey-Benayas, 1994). Usually, WPE allow the establishment and growth of forest species less adapted to stressful environmental conditions in open savannas, and several studies have found that tree basal area or biomass stocks are positively related to tree species diversity (Abreu et al., 2017; Pellegrini et al., 2016b). Despite that, these studies do not measure WPE as a metric that represent quantitatively the changes in vegetation cover, only local measures of aboveground biomass. In forest systems, although biomass stocks are positively related to species diversity, net changes in AGB were not related to species diversity (Poorter et al., 2017). Our results reveal that in Cerrado tree species diversity is vulnerable to higher encroachment rates, which can be an indicative that although increasing forest adapted species, higher WPE rates can also cause high mortality of savanna specialist related species, less adapted to encroached environments.

Mean annual temperature (MAT) was negatively related to species diversity, as expected. In temperate zones, temperature is positively related to species diversity, since the minimum temperatures can affect the tree physiology, reducing species productivity and fitness (Jonas et al., 2015; Rohde, 1992). In the case of our data, the minimum temperature of the sites (20ºC) was not an extreme low temperature and in an environment as savannas, where plants need to deal with naturally hotter conditions, a cooler temperature can favor the establishment and growth of forest species, increasing tree species diversity (Chapungu et al., 2020). We hypothesized that mean annual rainfall (MAP) should be positively related to species diversity and we indeed found that. Water availability is one of the main factors driving species productivity in savannas (Lehmann et al., 2014) and a higher annual precipitation could allow the development of a higher species diversity, since water can represent an ecological filter. Several studies have related water availability to species diversity in forest environments (Poorter et al., 2017; Raymundo et al., 2019) or African savannas (Godlee et al., 2021) but to our acknowledge our results are the first relating an increase in species diversity in wetter Brazilian savannas.

We did not find any relationship between fire and species diversity, contrary to our expectations. Fire can represent a direct damage to plant tissue, representing a barrier to tree establishment and growth. Although fire tend to reduce species diversity in forests, recent studies have found that in fire did not decline species diversity in fire-prone environments as savannas (Bond and Parr, 2010; Durigan et al., 2020; Makumbe et al., 2020). Tree species in open savannas had life-story strategies adapted to fire (i.e. thicker barks and resprouting) (Pausas et al., 2006; Simon and Pennington, 2012; Zupo et al., 2021), which can buffer the fire impacts on plant survival, and consequently, in species diversity. Our results highlight that fire is not a constrain for tree species diversity even at a biome scale in Cerrado.

Mean annual temperature and encroachment effects on functional composition

Mean annual temperature (MAT) was the main factor explaining the variation in functional composition. MAT was positively related to the abundance of species with higher SLA and WD values, but medium values of maximum tree height and bark thickness. Specific leaf area is associated to plant heat dissipation, and higher SLA values allow a greater heat dissipation. This higher SLA strategy is favored in high temperatures, where higher temperatures can damage the leaf tissue, affecting tree survival. Higher temperatures also can decrease the water viscosity in the xylem, which increase the water flow rates (Roderick and Berry, 2001). The lower water viscosity at lower temperatures require large diameter vessels (low woody density), and at higher temperatures there is not necessary large diameter vessels, allowing plants to invest in higher carbon allocation and increasing wood density (Thomas et al., 2007, 2004). We found that MAT was negatively related to the abundance of species with higher bark thickness and lower maximum tree height, and negatively related to the abundance of species with higher values of maximum tree height. The results indicate that extreme strategies in plant height (taller or shorter) are not favored at higher temperatures. Moreover, plants that allocate resources to create thicker barks could reduce the investments in woody density (Poorter et al., 2014), increasing tree vulnerability to higher temperatures. Woody plant encroachment rates were positively related to the abundance of species with higher maximum height values, as expected. Encroachment environments usually favor species with strategies to deal with light limitation provided by new trees arriving in the system (Flake et al., 2021; Pellegrini et al., 2016a). Thus, species tend to growth at higher heights to intercept the light in the canopy.

Species diversity mediated encroachment and climate effects on functional composition

As hypothesized, species diversity was positively related to the abundance of species with higher competitive strategies (higher maximum tree height; functional group 3) than conservative strategies (lower maximum tree height and higher bark thickness; functional group 1). Species diversity favor niche complementarity, but at higher diversity environments also can cause functional redundance and increase competition. Thus, species that had life-story traits associated to fast resource acquisition as maximum tree height can be more adaptative in diverse habitats, compared to species that invest in structures to resist higher temperatures, fire and drought (Roscher et al., 2011; Zuppinger-Dingley et al., 2014). Besides the negative effect of MAT on the functional group 3 (higher maximum tree height), MAT can also have an indirect negative effect by reducing species diversity, since species diversity is positively related to functional group 3. On the other hand, lower species diversity can have a positive effect on conserving savanna specialist species (functional group 1, higher bark thickness and lower species maximum height), since MAT reduces species diversity but species diversity also reduces the abundance of this group. It means that at higher temperatures, although savanna specialist species are reduced, MAP also can reduce the number of species that are able to persist in hotter conditions. Therefore, the reduced diversity can reduce the local competition for limiting resources, allowing a better performance of savanna specialist species which, consequently, increase the abundance of these species.

Implications under climate changes and woody encroachment scenarios

Recent studies have alert for the increasing in hotter and drier climates in Cerrado due to climate changes, with a 2.2-4 ºC monthly increase in maximum temperature and 2.4-2.8ºC increasing in minimum temperature, and a reducing in relative humidity by 15% over the past 60 years (Hofmann et al., 2021). Our results indicate that this climate change scenario may cause a decline in species diversity and change functional composition towards the decreasing in abundance of either forest and savanna specialist tree species, favoring species with strategies that allow the persistence under hotter temperatures (i.e. higher SLA and WD). In addition to climate changes and partially being cause by that (Archer et al., 2017; Van Auken, 2009), woody plant encroachment is occurring in 19% of total vegetation cover in Cerrado (Rosan et al., 2019). We demonstrate that higher carbon sequestration may cause a decline in biodiversity and favor species with higher traits that reflects higher ecosystem productivity even considering only tree species in Brazilian savanna. Moreover, fire had no effect on biodiversity or functional composition. These results reinforce that conservation strategies that focus on carbon accumulation and fire exclusion to theoretically increase biodiversity should be urgently reviewed to avoid species losses (Abreu et al., 2017; Durigan, 2020b). The historical conception that forest is a climax ecosystem and savannas are disturbed forests, and the visible impact of extreme fire events lead to the resistance of politicians and even the scientific community to deal with fires as an ecological component of Cerrado. This resistance results in fire suppression policies that leads to woody plant encroachment even in important conservation units in Cerrado (Abreu et al., 2017; Goncalves et al., 2021). Thus, besides the loss of these savanna reminiscent areas to agriculture, policies that intend to protect can be acting as a disturbance.

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Appendix 1 – Site information. Site coordinates in decimal degrees (X – Longitude; Y – Latitude), mean annual precipitation (MAP, mm), mean annual temperature (MAT, ºC), the relative basal area of functional group 1 (FGR 1, %), the relative basal area of functional group 2 (FGR 2, %), the relative basal area of functional group 3 (FGR 3, %), the relative basal area of functional group 4 (FGR 4, %), rarefied species richness (S), number of fire occurrence per year between 2000 and 2020, relative changes in vegetation cover between 2000 and 2020 (WPE, %).

Site	Y	X	MAT	MAP	FGR1	FGR2	FGR3	FGR4	S	Fire	WPE
C045	-18,13	-43,66	20,07	1243	37,27	14,97	36,64	11,12	32,51	1	159,76
C091	-15,96	-47,92	20,18	1529	70,01	14,25	13,82	1,92	30,05	1	156,22
C008	-19,33	-44,33	20,71	1316	53,28	20,59	17,97	8,16	34,72	0	130,24
C051	-15,79	-47,92	20,76	1519	65,51	17,57	11,25	5,68	31,79	0	155,62
C014	-15,67	-47,61	20,82	1477	48,97	16,86	26,76	7,4	33,26	1	145,68
C046	-15,81	-48,88	20,82	1636	21,57	25,02	26,22	27,19	35,55	2	165,81
C010	-16,05	-48,05	20,84	1525	54,39	16,57	23,78	5,26	36,79	1	156,24
C007	-15,77	-47,86	21,15	1489	56,38	32,39	10,94	0,29	31,23	0	155,17
C080	-17,79	-48,67	21,2	1545	81,17	10,63	8,16	0,03	29,69	1	151,3
C038	-17,79	-48,67	21,2	1545	78,39	13,15	8,46	0	28,34	1	161,85
C011	-17,41	-48,08	21,38	1510	35,03	28,01	10,13	26,82	31,5	1	136,77
C035	-21,94	-47,47	21,54	1344	52,55	36,05	8,31	3,08	28,02	0	121,81
C006	-16,64	-48,66	21,61	1578	82,13	15,54	2,32	0	35,37	0	118,98
C083	-19	-48,31	21,72	1552	72,09	19,28	5,99	2,64	25,56	1	145,95
C082	-19,01	-48,31	21,72	1552	73,99	10,74	12,08	3,19	28,33	1	147,45
C012	-17,39	-48,07	21,77	1495	63,86	9,29	21,02	5,83	26	0	140
C058	-19,21	-48,58	22,15	1530	69,08	26,67	2,2	2,04	27,4	0	168,96
C049	-14,7	-45,88	22,57	1437	74,29	6,21	14,01	5,49	25,45	0	183,61
C003	-15,8	-49,33	22,59	1648	63,32	20,81	7,12	8,75	31,96	4	133,19
C001	-16,46	-51,9	22,6	1634	66,82	21,22	10,29	1,66	28,5	0	123,38
C002	-16,45	-51,9	22,63	1633	66,22	16,63	5,85	11,29	26,84	0	128,25
C062	-18,36	-45,32	22,67	1134	49,72	22,46	10,1	17,72	36,15	0	123,38
C036	-19,2	-57,61	22,77	1133	73,38	25,11	1,46	0,05	16,76	1	149,77
C015	-14,19	-45,43	22,84	1088	37,05	47,77	8,04	7,14	18,92	2	139,82
C042	-16,03	-50,06	23,03	1697	44,89	28,29	19,87	6,95	36,83	0	125,87
C013	-20,5	-53,28	23,28	1363	60,88	14,88	2,33	21,9	27,94	0	131,63
C024	-15,23	-55,55	23,5	1503	48,6	11,47	6,93	33	36,8	0	114,02
C023	-15,22	-56	23,73	1384	63,2	9,79	5,32	21,69	28,81	3	107,8
C057	-13,58	-46,27	23,95	1364	56,93	3,49	5,96	33,62	22,24	3	203,04

C031	-11,63	-47,7	25,08	1498	50,13	39,15	1,86	8,86	33,57	0	101,88
C020	-16,25	-56,37	25,35	1347	23,77	46,84	9,31	20,08	31,43	0	140,8
C041	-7,2	-47,51	25,46	1731	34,2	44,45	9,28	12,06	26,47	4	178,86
C040	-7,29	-47,59	25,93	1682	24,08	17	8,11	50,82	29,02	0	132,66

Appendix S2. Species and their functional groups. G1 = Functional group 1; G2 = functional group 2; G3 = functional group 3; G4 = functional group 4.

FGR	Species
G1	*Anadenanthera peregrina*
G1	*Andira fraxinifolia*
G1	*Andira humilis*
G1	*Annona crassiflora*
G1	*Aspidosperma multiflorum*
G1	*Aspidosperma nobile*
G1	*Aspidosperma pyrifolium*
G1	*Aspidosperma tomentosum*
G1	*Bauhinia longifolia*
G1	*Bauhinia pulchella*
G1	*Byrsonima coccolobifolia*
G1	*Byrsonima cydoniifolia*
G1	*Byrsonima salzmanniana*
G1	*Byrsonima sericea*
G1	*Byrsonima verbascifolia*
G1	*Caraipa densifolia*
G1	*Caryocar brasiliense*
G1	*Caryocar coriaceum*
G1	*Caryocar cuneatum*
G1	*Connarus perrottetii*
G1	*Connarus suberosus*
G1	*Copaifera coriacea*
G1	*Dalbergia miscolobium*
G1	*Dimorphandra gardneriana*
G1	*Dimorphandra mollis*
G1	*Diospyros brasiliensis*
G1	*Diospyros coccolobifolia*
G1	*Diptychandra aurantiaca*
G1	*Enterolobium gummiferum*
G1	*Eremanthus erythropappus*

FGR	Species
G1	*Eriotheca gracilipes*
G1	*Erythroxylum anguifugum*
G1	*Erythroxylum buxus*
G1	*Erythroxylum campestre*
G1	*Erythroxylum daphnites*
G1	*Erythroxylum engleri*
G1	*Erythroxylum suberosum*
G1	*Erythroxylum tortuosum*
G1	*Eugenia aurata*
G1	*Eugenia biflora*
G1	*Eugenia inundata*
G1	*Ferdinandusa elliptica*
G1	*Guapira noxia*
G1	*Handroanthus ochraceus*
G1	*Himatanthus drasticus*
G1	*Kielmeyera coriacea*
G1	*Kielmeyera lathrophyton*
G1	*Kielmeyera petiolaris*
G1	*Kielmeyera rubriflora*
G1	*Kielmeyera speciosa*
G1	*Leptolobium dasycarpum*
G1	*Leptolobium elegans*
G1	*Leptobalanus humilis*
G1	*Machaerium acutifolium*
G1	*Machaerium hirtum*
G1	*Machaerium opacum*
G1	*Machaerium villosum*
G1	*Mouriri elliptica*
G1	*Myrcia guianensis*
G1	*Neea theifera*
G1	*Ouratea hexasperma*
G1	*Ouratea spectabilis*
G1	*Palicourea rigida*
G1	*Piptocarpha rotundifolia*
G1	*Pouteria ramiflora*
G1	*Psidium guineense*
G1	*Pterocarpus villosus*
G1	*Qualea cordata*
G1	*Qualea cryptantha*
G1	*Qualea grandiflora*
G1	*Qualea parviflora*

FGR	Species
G1	*Salvertia convallariodora*
G1	*Solanum lycocarpum*
G1	*Strychnos pseudoquina*
G1	*Stryphnodendron coriaceum*
G1	*Stryphnodendron rotundifolium*
G1	*Styrax ferrugineus*
G1	*Tabebuia aurea*
G1	*Terminalia argentea*
G1	*Tibouchina papyrus*
G1	*Vatairea macrocarpa*
G1	*Vochysia cinnamomea*
G1	*Vochysia divergens*
G1	*Vochysia gardneri*
G1	*Vochysia thyrsoidea*
G1	*Zeyheria montana*
G2	*Aegiphila verticillata*
G2	*Aiouea trinervis*
G2	*Alibertia edulis*
G2	*Allophylus semidentatus*
G2	*Anacardium humile*
G2	*Anacardium occidentale*
G2	*Annona coriacea*
G2	*Bauhinia rufa*
G2	*Blepharocalyx salicifolius*
G2	*Brosimum gaudichaudii*
G2	*Byrsonima crassifolia*
G2	*Byrsonima pachyphylla*
G2	*Callisthene fasciculata*
G2	*Callisthene minor*
G2	*Cardiopetalum calophyllum*
G2	*Casearia grandiflora*
G2	*Casearia sylvestris*
G2	*Cecropia pachystachya*
G2	*Clusia burchellii*
G2	*Cnidoscolus vitifolius*
G2	*Coccoloba latifolia*
G2	*Coccoloba mollis*
G2	*Combretum mellifluum*
G2	*Cordia naidophila*
G2	*Cordia superba*
G2	*Croton blanchetianus*

FGR	Species
G2	*Cupania racemosa*
G2	*Curatella americana*
G2	*Davilla elliptica*
G2	*Diospyros lasiocalyx*
G2	*Duguetia furfuracea*
G2	*Eriotheca pubescens*
G2	*Guapira graciliflora*
G2	*Guazuma ulmifolia*
G2	*Hancornia speciosa*
G2	*Heisteria citrifolia*
G2	*Himatanthus obovatus*
G2	*Hymenaea stigonocarpa*
G2	*Hyptidendron canum*
G2	*Jacaranda cuspidifolia*
G2	*Jacaranda micrantha*
G2	*Kielmeyera grandiflora*
G2	*Lacistema hasslerianum*
G2	*Lafoensia pacari*
G2	*Lithraea molleoides*
G2	*Miconia albicans*
G2	*Miconia ferruginata*
G2	*Miconia ligustroides*
G2	*Miconia rubiginosa*
G2	*Myrcia obovata*
G2	*Myrcia splendens*
G2	*Myrcia tomentosa*
G2	*Myrsine coriacea*
G2	*Myrsine umbellata*
G2	*Ocotea pulchella*
G2	*Ocotea spixiana*
G2	*Ouratea castaneifolia*
G2	*Plenckia populnea*
G2	*Pseudobombax tomentosum*
G2	*Rourea induta*
G2	*Rudgea viburnoides*
G2	*Sapium argutum*
G2	*Sapium glandulosum*
G2	*Didymopanax macrocarpus*
G2	*Simarouba versicolor*
G2	*Sterculia striata*
G2	*Stryphnodendron adstringens*

FGR	Species
G2	*Stryphnodendron polyphyllum*
G2	*Styrax camporum*
G2	*Symplocos nitens*
G2	*Symplocos pubescens*
G2	*Symplocos revoluta*
G2	*Symplocos rhamnifolia*
G2	*Tabernaemontana catharinensis*
G2	*Tachigali aurea*
G2	*Tachigali vulgaris*
G2	*Tocoyena formosa*
G2	*Vochysia elliptica*
G2	*Vochysia rufa*
G2	*Vochysia tucanorum*
G2	*Xylopia aromatica*
G2	*Xylopia sericea*
G2	*Zanthoxylum rhoifolium*
G2	*Zanthoxylum rigidum*
G3	*Aegiphila integrifolia*
G3	*Agonandra brasiliensis*
G3	*Albizia niopoides*
G3	*Alchornea triplinervia*
G3	*Anadenanthera colubrina*
G3	*Andira anthelmia*
G3	*Andira inermis*
G3	*Andira nitida*
G3	*Andira vermifuga*
G3	*Aspidosperma australe*
G3	*Aspidosperma cylindrocarpon*
G3	*Aspidosperma discolor*
G3	*Aspidosperma macrocarpon*
G3	*Aspidosperma polyneuron*
G3	*Aspidosperma spruceanum*
G3	*Astronium graveolens*
G3	*Bocageopsis mattogrossensis*
G3	*Bowdichia virgilioides*
G3	*Terminalia corrugata*
G3	*Cabralea canjerana*
G3	*Calophyllum brasiliense*
G3	*Campomanesia guazumifolia*
G3	*Cenostigma tocantinum*

FGR	Species
G3	*Chloroleucon acacioides*
G3	*Combretum glaucocarpum*
G3	*Copaifera langsdorffii*
G3	*Copaifera martii*
G3	*Cupania vernalis*
G3	*Dalbergia brasiliensis*
G3	*Diospyros sericea*
G3	*Ecclinusa ramiflora*
G3	*Ephedranthus pisocarpus*
G3	*Eriotheca pentaphylla*
G3	*Eschweilera coriacea*
G3	*Eugenia pyriformis*
G3	*Ficus americana*
G3	*Ficus citrifolia*
G3	*Ficus insipida*
G3	*Genipa americana*
G3	*Guarea kunthiana*
G3	*Guatteria australis*
G3	*Handroanthus serratifolius*
G3	*Heisteria ovata*
G3	*Hirtella glandulosa*
G3	*Hymenaea courbaril*
G3	*Licania kunthiana*
G3	*Astronium urundeuva*
G3	*Myrsine guianensis*
G3	*Nectandra membranacea*
G3	*Pera glabrata*
G3	*Plathymenia reticulata*
G3	*Platonia insignis*
G3	*Platypodium elegans*
G3	*Pouteria torta*
G3	*Protium heptaphyllum*
G3	*Protium spruceanum*
G3	*Pseudobombax grandiflorum*
G3	*Qualea multiflora*
G3	*Roupala montana*
G3	*Didymopanax morototoni*
G3	*Tabebuia insignis*
G3	*Tabebuia roseoalba*
G3	*Tachigali guianensis*
G3	*Tachigali paniculata*

FGR	Species
G3	*Tachigali subvelutina*
G3	*Tapirira guianensis*
G3	*Tapirira obtusa*
G3	*Terminalia fagifolia*
G3	*Terminalia glabrescens*
G3	*Virola sebifera*
G3	*Vitex flavens*
G3	*Vochysia haenkeana*
G3	*Zanthoxylum riedelianum*
G4	*Andira cujabensis*
G4	*Aspidosperma subincanum*
G4	*Astronium fraxinifolium*
G4	*Callisthene major*
G4	*Myrcia glomerata*
G4	*Campomanesia aromatica*
G4	*Casearia gossypiosperma*
G4	*Cenostigma macrophyllum*
G4	*Chrysophyllum marginatum*
G4	*Combretum leprosum*
G4	*Cordia glabrata*
G4	*Couepia grandiflora*
G4	*Coussarea hydrangeifolia*
G4	*Coutarea hexandra*
G4	*Cybistax antisyphilitica*
G4	*Cyclolobium brasiliense*
G4	*Dilodendron bipinnatum*
G4	*Dipteryx alata*
G4	*Duguetia lanceolata*
G4	*Emmotum nitens*
G4	*Erythroxylum deciduum*
G4	*Erythroxylum pelleterianum*
G4	*Eschweilera nana*
G4	*Esenbeckia grandiflora*
G4	*Eugenia dysenterica*
G4	*Exellodendron cordatum*
G4	*Guettarda angelica*
G4	*Guettarda viburnoides*
G4	*Handroanthus chrysotrichus*
G4	*Handroanthus vellosoi*
G4	*Hirtella ciliata*
G4	*Hirtella gracilipes*

FGR	Species
G4	*Lafoensia vandelliana*
G4	*Leptobalanus parvifolius*
G4	*Leptobalanus sclerophyllus*
G4	*Luehea candicans*
G4	*Luehea divaricata*
G4	*Luehea grandiflora*
G4	*Mabea fistulifera*
G4	*Magonia pubescens*
G4	*Maprounea guianensis*
G4	*Martiodendron mediterraneum*
G4	*Matayba guianensis*
G4	*Mezilaurus crassiramea*
G4	*Mezilaurus vanderwerffii*
G4	*Miconia nervosa*
G4	*Miconia pepericarpa*
G4	*Miconia prasina*
G4	*Mimosa claussenii*
G4	*Mimosa laticifera*
G4	*Mouriri cearensis*
G4	*Mouriri guianensis*
G4	*Mouriri pusa*
G4	*Myrcia fenzliana*
G4	*Myrcia glabra*
G4	*Myrcia hebepetala*
G4	*Myrcia multiflora*
G4	*Myrcia ochroides*
G4	*Myrcia palustris*
G4	*Myrcia variabilis*
G4	*Myrciaria cuspidata*
G4	*Myrocarpus fastigiatus*
G4	*Ocotea felix*
G4	*Ocotea lancifolia*
G4	*Ocotea nutans*
G4	*Ocotea pomaderroides*
G4	*Oxandra sessiliflora*
G4	*Parkia platycephala*
G4	*Peltogyne confertiflora*
G4	*Physocalymma scaberrimum*
G4	*Psidium cattleyanum*
G4	*Psidium guyanense*
G4	*Psidium myrsinites*

FGR	Species
G4	*Pterodon emarginatus*
G4	*Pterodon pubescens*
G4	*Qualea dichotoma*
G4	*Randia armata*
G4	*Rhamnidium elaeocarpum*
G4	*Schinopsis brasiliensis*
G4	*Schinus terebinthifolia*
G4	*Siparuna guianensis*
G4	*Siphoneugena densiflora*
G4	*Trichilia catigua*

Appendix S3. Mean and standard deviation (SD) of bark thickness (BT, mm), specific leaf area (SLA, cm²/g), wood density (g/cm³) and maximum tree height (Hmax, m) per functional group. G1 = Functional group 1; G2 = functional group 2; G3 = functional group 3; G4 = functional group 4.

Functional group	Mean BT	SD BT	Mean SLA	SD SLA	Mean WD	SD WD	Mean Hmax	SD Hmax
G1	11,20	3,56	9,32	3,02	0,58	0,16	8,84	4,81
G2	3,47	2,13	9,30	2,77	0,50	0,13	10,13	4,99
G3	5,47	3,29	9,88	2,40	0,67	0,15	28,64	6,29
G4	5,23	3,19	16,72	6,79	0,78	0,14	12,88	6,28

Appendix S4. Results from piecewise Structural Equation Model. Response variables (FGR 1 = functional group 1; FGR 3 = functional group 3; FGR 4 = functional group 4; and rarefied species richness = Diversity) and predictor variables (mean annual temperature = MAT, mean annual precipitation = MAP, rarefied species richness = Diversity, and relative changes in vegetation cover between 2000 and 2020 = WPE).

Response	Predictor	Regression coefficient	Std.Error	P.Value	Standardized coefficient
FGR 1	MAT	-4,7158	1,7805	0,0128	-0,43
FGR 1	Diversity	-1,1683	0,5632	0,0467	-0,34
FGR 3	MAT	-0,2501	0,1121	0,0336	-0,33
FGR 3	Diversity	0,1093	0,0374	0,0066	0,46
FGR 3	WPE	0,0185	0,0082	0,0308	0,35
Diversity	MAT	-1,0109	0,4864	0,0467	-0,32
Diversity	MAP	0,0111	0,0046	0,0218	0,37
Diversity	WPE	-0,0943	0,0337	0,0091	-0,43
FGR 4	MAT	0,5972	0,182	0,0026	0,51

Considerações finais da tese

No primeiro capítulo, nosso estudo mostrou que em um Cerrado sentido restrito que está sob o processo de adensamento da vegetação, árvores jovens e adultas não são floristicamente similares. Além disso, os indivíduos jovens apresentaram maior riqueza de espécies, e maior proporção de espécies com cascas finas e com sementes dispersas pela fauna. Essas diferenças evidenciam o potencial de comparar os estratos adultos e jovens em uma comunidade para detectar e predizer mudanças na vegetação no Cerrado sentido restrito, uma vez que os indivíduos jovens podem ser as árvores que estarão no sistema no futuro. Essas comparações podem ser feitas usando apenas um inventário de campo, otimizando tempo e recursos. Nossos resultados também indicam que o processo de adensamento arbóreo pode reduzir a importância de espécies com sementes dispersas pelo vento, em detrimento de espécies com sementes dispersas pela fauna.

No segundo capítulo, nossos resultados sugerem que a área de estudo pode ter ultrapassado o limite do ambiente savânico para o ambiente florestal (Dantas et al., 2013) e está seguindo o processo sucessional semelhante ao de florestas secundárias. Isso, porque no nosso sistema as estratégias de história de vida das espécies estão mudando através de um aumento na dominância de espécies com uma estratégia de uso de recursos aquisitiva (aquisição de recursos mais rápida e taxas de crescimento mais rápidas) (Báez and Homeier, 2018; Díaz et al., 2013; Kunstler et al., 2016). A mudança na dominância das características funcionais tem efeitos diretos nos processos ecossistêmicos tais quais o ciclo da água, do carbono e de nutrientes. Apesar de características funcionais aquisitivas indicarem um ganho de carbono em curto prazo, isso pode ser reduzido no longo prazo em um evento de fogo ou mudando as condições climáticas, devido ao aumento da dominância de espécies menos resistentes ao fogo e seca (ex. espécies com baixa densidade de madeira e espessura de casca)

(Pellegrini et al., 2016a). Em relação à aquisição de nutrientes, características aquisitivas podem aumentar as taxas de decomposição e, consequentemente, a disponibilidade de nutrientes no solo ao longo do tempo (Szefer et al., 2017). O aumento da disponibilidade de nutrientes no solo pode influenciar positivamente o processo, contribuindo para uma maior representatividade de espécies aquisitivas ao longo do tempo. Em relação ao ciclo hidrológico, espécies aquisitivas poderiam agir como um dreno, uma vez que essas espécies comumente tem altas taxas de respiração (Honda & Durigan, 2016; Oliveira et al., 2005). Além disso, a dominância de árvores com características reprodutivas relacionadas à ambientes florestais (e.g. monoicia, dioicia e polinização por insetos muito pequenos) também podem contribuir para manter os recursos para espécies da fauna que estão mais vulneráveis às condições estressantes.

No terceiro capítulo avaliamos possíveis direcionadores da diversidade de espécies no Cerrado. Estudos recentes tem alertado para o aumento de climas quentes e secos no Cerrado devido às mudanças climáticas, com um aumento mensal de 2.2-4 ºC na temperatura máxima e um aumento de 2.4-2.8ºC na temperatura mensal mínima, e uma redução na umidade relativa do ar em 15% nos últimos 60 anos (Hofmann et al., 2021). Nossos resultados indicam que esse cenário de mudanças climáticas pode causar um declínio na diversidade de espécies e uma mudança na composição funcional através de uma diminuição na abundância tanto de espécies de árvores especialistas de floresta quanto espécies especialistas de savana, favorecendo espécies com estratégias de vida que permitem a persistência em temperaturas mais quentes (assim como espécies com alta SLA e densidade de madeira). Além das mudanças climáticas e parcialmente sendo causada por ela (Archer et al., 2017; Van Auken, 2009), o adensamento arbóreo está ocorrendo em aproximadamente 19% da vegetação nativa no domínio do Cerrado

(Rosan et al., 2019). Nós demonstramos que um alto sequestro de carbono pode causar um declínio na biodiversidade e favorecer espécies com estratégias adaptadas à alta produtividade do ecossistema mesmo considerando só espécies arbóreas. Além disso, o fogo não teve efeito na biodiversidade ou na composição funcional. Esses resultados reforçam que as estratégias de conservação que focam na acumulação de carbono e exclusão do fogo para, teoricamente, aumentar a biodiversidade devem ser urgentemente revistas para evitar a perda de espécies (Abreu et al., 2017; Durigan, 2020b). A concepção histórica que a floresta é o climax ecossistêmico e savanas são florestas degradadas, e o visível impacto de eventos extremos de fogo leavam à resistência de políticos e até a comunidade científica para lidar com os eventos de fogo como um componente ecológico das savanas. Essa resistência resulta em políticas de supressão total do fogo que podem causar o adensamento arbóreo, mesmo em importantes áreas de conservação públicas no Brasil (Abreu et al., 2017; Goncalves et al., 2021). Assim, além da perda áreas nativas de Cerrado para a agricultura e pecuária, políticas que pretendem proteger também podem atuar como mais um meio de degradação.