UNIVERSIDADE ESTADUAL PAULISTA
"JÚLIO DE MESQUITA FILHO"
INSTITUTO DE BIOCIÊNCIAS – RIO CLARO

PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA, EVOLUÇÃO E BIODIVERSIDADE

# DINÂMICA DE COMUNIDADES VEGETAIS DE CAMPO SUJO DE CERRADO SOB DIFERENTES REGIMES DE FOGO

CASSY ANNE DOS SANTOS RODRIGUES

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**CASSY ANNE DOS SANTOS RODRIGUES**

Tese apresentada ao Instituto de Biociências do Câmpus de Rio Claro, Universidade Estadual Paulista, como parte dos requisitos para obtenção do título de Doutora em Ecologia, Evolução e Biodiversidade.
Orientadora: Profa. Assoc. Alessandra Tomaselli Fidelis.

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TÍTULO DA TESE: DINÂMICA DE COMUNIDADES VEGETAIS DE CAMPO SUJO DE CERRADO SOB DIFERENTES REGIMES DE FOGO

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*À pessoa a quem todas as minhas conquistas também pertence, mãe.*

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## RESUMO

Ecossistemas abertos, como as savanas tropicais são estruturados e mantidos por diversos fatores bióticos e abióticos. Entre eles, um fator que exerce enorme influência na montagem, dinâmica e funcionalidade das comunidades vegetais é a ocorrência do fogo. O regime de fogo descreve padrões de frequência, época, extensão e intensidade da ocorrência do fogo em um determinado local. Portanto, o regime de fogo pode influenciar a regeneração das comunidades vegetais devido a sua influência no comportamento do fogo; de acordo com a fase fenológica e de crescimento das plantas durante o evento de fogo; e devido às condições pós-fogo que impõem as plantas. Deste modo, o principal objetivo deste estudo foi analisar como diferentes regimes de queimadas influenciam a médio-longo prazo a estrutura, composição, produtividade e a diversidade de espécies e funcional das comunidades vegetais de ecossistemas abertos de Cerrado, bem como as condições microclimáticas pós-queima. Para isso, foram realizados levantamentos da vegetação e coleta de biomassa aérea em áreas com diferentes frequências de fogo (11 anos sem queima, queimadas anuais e bienais por nove anos) e época de fogo (queimadas bienalmente no início, meio e fim da estação seca por nove anos). Os levantamentos da vegetação consistiram na estimativa visual da cobertura de cada uma das espécies, da biomassa morta e da porcentagem de solo descoberto e foram realizados em subparcelas de 1x1m (10 subparcelas/parcela, 3-4 parcelas/tratamento). Também foram medidos na estação chuvosa de 2022, atributos funcionais relacionados à resposta das plantas ao regime de fogo em três indivíduos das espécies que correspondiam a 80% da comunidade em cada tratamento. As amostragens da biomassa aérea foram realizadas dentro de cinco subparcelas de 0.5x0.5m nas bordas de cada parcela experimental, nas estações chuvosa e seca. Em laboratório as amostras de biomassa foram separadas nos seguintes componentes: graminóides, herbáceas não-graminóides, arbustos e biomassa morta. Para avaliar como as condições microclimáticas são influenciadas pela frequência de fogo foram instalados *data loggers* com sensores de umidade relativa do ar, luminosidade e temperatura nas parcelas sob tratamentos com diferentes frequências de queimas. Em relação a influência do regime do fogo no microclima de savanas abertas, o presente estudo observou que a frequência

de fogo afeta os parâmetros microclimáticos ao longo do tempo através das diferenças na cobertura vegetal entre as parcelas queimadas e não queimadas e que seus efeitos perduram por pelo menos 12 meses após a queimada, sendo potencializados pela estação seca. Quanto à riqueza de espécies, produtividade e dinâmica da biomassa aérea, a exclusão do fogo teve o impacto mais negativo nas comunidades vegetais, afetando a riqueza e cobertura de herbáceas não-graminóides e graminóides, a riqueza total de espécies, diversidade taxonômica e funcional e a produtividade do estrato herbáceo. O tratamento de queimadas precoces também representou prejuízos às comunidades de campo sujo, resultando em menor riqueza de espécie total e de graminóides e menor diversidade taxonômica do que os demais tratamentos. As comunidades do estrato herbáceo de savanas abertas se mostraram resilientes ao fogo anual, mantendo sua diversidade e produtividade estáveis. Os dados obtidos através deste estudo trazem informações inéditas acerca dos efeitos de diferentes regimes de fogo a médio-longo prazo em fisionomias abertas de Cerrado e devem orientar o desenvolvimento de ações de manejo e políticas públicas de fogo que assegurem a conservação das savanas tropicais.

Palavras-chave: dinâmica de comunidades vegetais; época de fogo; estrato herbáceo; frequência de fogo; microclima; produtividade; riqueza de espécies; savanas abertas.

## ABSTRACT

Open ecosystems, such as tropical savannas, are shaped and maintained by various biotic and abiotic factors. Fire is a crucial element that influences the plant communities' assembly, dynamics, and functionality. Fire regime describes patterns of frequency, season, extent, and intensity of fire occurrence in a particular location. Therefore, fire regimes can influence the post-fire regeneration of plant communities due to their influence on fire behavior; according to plants' phenological and growth stage during the fire event; and due to the post-fire conditions imposed on plants. We aimed to analyze how different fire regimes influence the structure, composition, productivity, and taxonomic and functional diversity of plant communities in open Cerrado, as well as their post-fire microclimatic conditions. We performed vegetation surveys and aboveground biomass samples in areas with different fire frequencies (fire exclusion for 11 years, annual and biennial fires for 9 years) and fire seasons (biennial burnings at early, mid, and late the dry season). Functional traits of fire response were also measured in the 2022 rainy season in three individuals of the species that corresponded to 80% of the community in each treatment. To evaluate how microclimatic conditions are influenced by fire frequency, data loggers were installed with relative humidity, illuminance, and temperature sensors in plots under treatments with different fire frequencies. We found that fire frequency affects microclimatic parameters over time through differences in vegetation cover between burned and unburned plots. The changes in microclimate last for at least 12 months after the fire, being enhanced by the dry season. Regarding species richness, productivity, and aboveground biomass dynamics, fire exclusion had the most negative impact on plant communities, affecting the richness and cover of forbs and graminoids, total species richness, taxonomic and functional diversity, and the productivity of the herbaceous layer. The treatment of early fires also resulted in lower total and graminoid species richness and lower taxonomic diversity than the other fire treatments. Communities in the

herbaceous layer of open savannas showed to be resilient to annual fire, maintaining stable diversity and productivity. The findings obtained through this study provide new information about the medium-long-term effects of different fire regimes in open savannas and may guide the development of management actions and public fire policies that ensure the conservation of tropical savannas.

Key-words: fire frequency; fire season; herbaceous layer; microclimate; plant communities dynamic; productivity; open savannas; species richness.

**SUMÁRIO**

## 1. INTRODUÇÃO GERAL

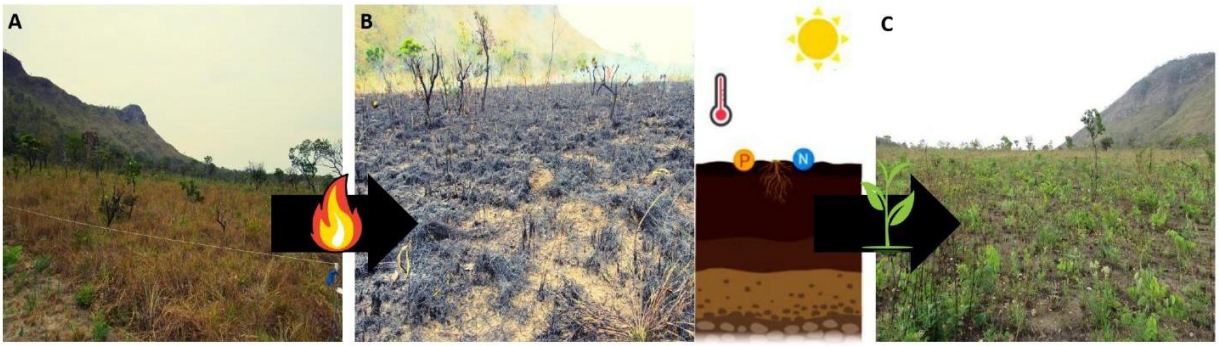
Ecossistemas abertos sustentam uma alta biodiversidade e fornecem serviços ecossistêmicos essenciais, como regulação do ciclo de água e nutrientes, armazenamento de carbono, regulação do clima e serviços culturais (Myers et al., 2000; Parr et al., 2014; Zhao et al., 2020). No entanto, os ecossistemas abertos como as savanas, em especial seu estrato herbáceo-arbustivo, são constantemente negligenciadas, mesmo por pesquisadores e tomadores de decisão, que historicamente têm dado mais atenção às fisionomias savânicas densas e florestais ou somente ao componente lenhoso das savanas abertas (Parr et al., 2014; Overbeck et al., 2015; Lahsen et al., 2016; Sawyer & Lahsen, 2016; Oliveira et al., 2017; Strassburg et al., 2017). O desinteresse por campos e savanas, comparado ao esforço dedicado a ecossistemas florestais, explica-se em parte pelo equívoco em se considerar estes ambientes como degradados, sendo resultado da ação antrópica (Bond et al., 2008; Bond & Parr, 2010).

Na realidade, campos e savanas são sistemas complexos, com particularidades na sua história evolutiva, ecologia e funcionalidade (Cerling, et al., 1997; Bond & Parr, 2010; Edwards et al., 2010; Hoffman et al., 2012, Parr et al., 2014; Veldman, et al., 2015). Diversos fatores bióticos e abióticos podem afetar a estruturação das comunidades, a riqueza e composição de espécies, a diversidade funcional, a produtividade e a dinâmica da biomassa do estrato herbáceo em ecossistemas abertos. Por exemplo, a duração e intensidade da estação chuvosa, recursos disponíveis no solo, condições microclimáticas e, principalmente distúrbios como herbivoria e fogo (Sarmiento, 1984; Briggs & Knapp, 1995; Sankaran et al., 2005; Bond, 2008; Bustamante et al., 2012; Fidelis et al., 2013; Lehmann et al., 2014; Rodrigues & Fidelis, 2022).

O fogo é um fator ecológico presente em diversos ecossistemas ao redor do mundo, moldando as comunidades vegetais e influenciando sua estrutura e funcionalidade (Whelan, 1995; Keeley et al., 2011). A própria distribuição de ecossistemas é influenciada pelo fogo há centenas de milhões de anos (Bond & Keeley, 2005; Pausas, 2012). No entanto, é nos campos e savanas que observamos a maior frequência e impacto do fogo (Lehmann et al., 2011; Archibald et al., 2013). Como uma força seletiva, o fogo afeta desde indivíduos, até comunidades e ecossistemas (Whelan, 1995; Bond & van Wilgen, 1996), alterando as condições

ambientais, bem como as relações interespecíficas das plantas e consequentemente a dinâmica das comunidades vegetais (Laterra & Solbrig, 2001; Marcos et al., 2004). As queimadas removem uma grande quantidade de biomassa aérea, tanto viva quanto morta das plantas, expondo o solo (Bond & van Wilgen, 1996; Fidelis et al., 2012), promovendo assim, um aumento na disponibilidade de nutrientes, na incidência da luz solar e espaço (Figura 1, Whelan, 1995; Fidelis & Blanco, 2014). As novas condições do ambiente pós-fogo podem resultar em maiores taxas de crescimento e produtividade das plantas (Whelan,1995), bem como em mudanças na riqueza, composição e abundância de diferentes formas de crescimento após queimas (Whelan, 1995; Fidelis et al., 2012; Boughton et al., 2013; Rodrigues & Fidelis, 2022). Estas mudanças se dão pelas respostas das plantas à passagem do fogo e às novas condições ambientais, através das adaptações selecionadas pelos regimes de fogo sob o qual evoluíram (Whelan, 1995; Pivello & Norton, 1996).

**Figura 1 -** Esquema ilustrando a vegetação de uma área de savana aberta A - antes de ser queimada, em seguida a B - remoção da biomassa aérea após a passagem do fogo, expondo o solo e aumentando a disponibilidade de nutrientes, espaço e luz solar e C - finalmente a regeneração da comunidade impulsionada pelas novas condições do ambiente pós-fogo.




O regime do fogo descreve o padrão de ocorrência do fogo num determinado local em termos de frequência (intervalo de retorno do fogo), época (período/estação do ano em que ocorre a queimada), extensão, intensidade (calor liberado durante a queimada) e severidade (impacto biológico do fogo). A época e a frequência das queimadas podem levar a grandes mudanças nas populações e comunidades vegetais (Bond & Van Wilgen,1996), uma vez que afetam o recrutamento de plântulas, a regeneração dos diferentes grupos funcionais, e até processos ecossistêmicos, como a ciclagem de nutrientes (Pivello et al., 2010; Oliveras et al., 2013). Portanto, o

regime de fogo pode influenciar a produtividade e o acúmulo de biomassa nas comunidades de savana.

A exclusão do fogo por períodos longos, leva a um grande acúmulo de serapilheira e biomassa morta, reduzindo a produtividade das plantas (Knapp & Seastedt, 1986), uma vez que os nutrientes ficam imobilizados na biomassa morta (Frost & Robertson, 1987). Por outro lado, em áreas frequentemente queimadas, grande parte dos nutrientes é alocada nos órgãos subterrâneos das plantas (Oliveras et al., 2013) e parte dos nutrientes da biomassa queimada retorna à comunidade através das cinzas, aumentando a disponibilidade de nutrientes nas camadas mais superficiais ao serem incorporados pelo solo (Pivello & Coutinho, 1992; Miranda et al., 2002; Knox & Clarke, 2005). No entanto, intervalos curtos entre incêndios podem reduzir a produtividade ao esgotar os nutrientes do solo e das plantas, afetando a produção de novos caules e folhas (Pivello et al., 2010; Savadogo et al., 2009). A época de fogo também pode afetar a produtividade da comunidade vegetal, uma vez que, ao longo da estação seca as plantas apresentam diferentes estágios fenológicos, que podem ser distintamente afetados pela ocorrência do fogo (Knapp et al., 2009), em especial devido a alocação de recursos em cada fase (Oliveras et al., 2013). Além disso, nas savanas, a disponibilidade de água no solo é um fator chave na regeneração da biomassa herbácea e varia ao longo das estações (Quesada et al., 2004; Oliveras et al., 2013). Igualmente, a duração do período de restrição hídrica após uma queimada também varia dependendo da época de fogo (Quesada et al., 2004). Deste modo, o fogo durante o início da estação seca impõe às plantas um período mais longo sem água até à próxima estação chuvosa, o que pode afetar a regeneração pós-fogo da comunidade.

As queimadas em diferentes frequências e épocas influenciam não apenas a produtividade e a dinâmica da biomassa aérea vegetal, mas também causam mudanças significativas na fisionomia e na composição de espécies da vegetação (Moreira, 2000; Rodrigues & Fidelis, 2022). Comunidades abertas ao serem excluídas do fogo tendem a apresentar um aumento na cobertura lenhosa o que pode acarretar na perda de espécies herbáceas não-graminóides e em drásticas mudanças na fisionomia (Moreira, 2000; Abreu et al., 2017). Por outro lado, frequências altas de fogo, como queimadas anuais, podem levar ao aumento de solo descoberto e mudanças nos padrões de composição de espécies (Rodrigues & Fidelis, 2022). A

época em que ocorre a queimada pode influenciar o recrutamento e persistência de espécies, afetando a composição de espécies e estrutura da comunidade. Isto porque, a queimada em cada época ocorre em diferentes condições ambientais (e.g. teor de água no solo e na vegetação) e diferentes estágios fenológicos das espécies (e.g. variação na alocação de recursos para a produção de novos ramos, folhas, flores e frutos) (Quesada et al., 2004; Knapp et al., 2009; Oliveras et al., 2013). As alterações na estrutura da vegetação e na composição de espécies promovidas por diferentes frequências e épocas de fogo podem impactar a diversidade funcional da comunidade e sua funcionalidade (Diaz e Cabido, 2001).

Como em diversos ecossistemas no mundo, o fogo pode ser considerado como um dos fatores determinantes na estruturação e manutenção do Cerrado (Coutinho, 1982). O fogo está presente há pelo menos quatro milhões de anos no Cerrado, indicado pelas linhagens de espécies com atributos relacionados ao fogo nesse sistema (Simon et al., 2009). No entanto, foi o grande aumento da população humana que ocorreu durante o Holoceno, que intensificou a ocorrência do fogo e provocou, portanto, alterações no regime de fogo no Cerrado (Pivello, 2011; Fidelis & Pivello, 2011). As atividades humanas de manejo do fogo para limpar áreas, renovar o pasto para pecuária e para fins agrícolas aumentaram a frequência, extensão e mudaram a época de ocorrência das queimadas (Coutinho, 1990; Pivello, 2011).

Estas alterações no regime no fogo pelo homem, muitas vezes, trazem resultados nocivos ao ambiente, como esgotamento e erosão do solo, eliminação do estrato arbóreo, perda de diversidade, infestação por espécies ruderais, dentre outros (Pivello, 2006). Contudo, é necessário compreender que estes são os resultados do mau uso do fogo e que sua exclusão traz tanto ou mais prejuízos para ecossistemas que evoluíram na presença do fogo (Moreira 2000, Abreu et al. 2017). Nas savanas, o uso adequado e planejado do fogo pode proporcionar diversos benefícios do ponto de vista ecológico, como por exemplo, manutenção de ecossistemas abertos e da biodiversidade (Abreu et al., 2017). Além disso, é um bom instrumento de manejo e com custos baixos, para ser utilizado em unidades de conservação (UCs) que se destinam à conservação dos ecossistemas do Cerrado (Moraes et al., 2016).

O Manejo Integrado do Fogo (MIF) foi estabelecido inicialmente em poucas UCs de Cerrado em 2014 (Schmidt et al., 2018) e seu uso tem aumentado gradualmente em outras UCs (Schmidt & Eloy, 2020). Nestes locais, as queimadas

precoces são utilizadas para controle do material combustível, evitando-se dessa maneira, os grandes incêndios do final da estação seca (Schmidt et al., 2018). Experimentos de longa-duração, como o projeto FOGO em Brasília trouxeram grandes avanços ao conhecimento sobre o comportamento do fogo e seus efeitos, sendo realizado em diferentes épocas do ano e frequências na vegetação (Miranda, 2010). Porém, este experimento não contava com réplicas e também trouxe resultados principalmente relacionados ao estrato lenhoso. Portanto, há poucos dados de experimentos de longa-duração que mostram os efeitos do fogo em diferentes épocas e frequências no estrato herbáceo do Cerrado, onde a maior parte da diversidade se encontra (Mendonça et al., 2008).

Informações sobre como regimes de fogo afetam as espécies herbáceas são escassas e geralmente voltadas para o acúmulo do material combustível, deixando lacunas acerca dos impactos de cada regime de fogo sobre a composição de espécies e diversidade funcional das comunidades vegetais. Estas lacunas no conhecimento sobre a influência da frequência e época de fogo na resiliência e funcionalidade dos sistemas abertos do Cerrado tornam estas vegetações vulneráveis à degradação. Portanto, estudos que avaliem como o regime de fogo afeta a montagem de comunidades (estrutura, composição e diversidade), a produtividade e a resiliência de ecossistemas abertos de Cerrado, através de experimentos com queimadas em diferentes épocas e frequências, são fundamentais para orientar processos regulatórios do uso do fogo, assim como o desenvolvimento de estratégias de manejo em UCs que preservem a variedade de ecossistemas e a biodiversidade do Cerrado e consequentemente, sua funcionalidade e serviços ecossistêmicos. O experimento na Reserva Natural Serra do Tombador, iniciado em 2013, com tratamentos de queima em diferentes épocas do ano e frequência (Rissi et al., 2017, Rodrigues et al., 2021), foi um dos primeiros a avaliar os efeitos do fogo no estrato herbáceo-arbustivo do Cerrado. E para que as informações geradas possam contribuir efetivamente para o planejamento de ações de uso de fogo para fins de conservação da vegetação das áreas abertas de Cerrado, os experimentos com queimadas foram estabelecidos levando em consideração as épocas de ocorrência de fogo natural (início e final da estação seca) e antrópico (exclusão do fogo, queimadas anuais e meio da estação seca). Além disso, foram estabelecidos experimentos com diferentes frequências de

fogo para avaliar as respostas da vegetação de campo sujo de Cerrado à intervalos menores ou maiores entre as queimadas.

Deste modo, este estudo buscou gerar informações inéditas e robustas quanto aos impactos de diferentes regimes de fogo sobre a vegetação do estrato herbáceo-arbustivo de sistemas abertos de Cerrado a médio-longo prazo. O que deve contribuir para o entendimento avançado da dinâmica das comunidades vegetais sujeitas ao distúrbio, indicando em que momento sob um determinado regime de fogo iniciam-se as alterações na composição de espécies, estrutura, e produtividade das comunidades. Além disso, foi possível determinar se após anos sob um determinado regime de fogo ocorreram alterações na riqueza de espécies e na diversidade funcional das comunidades vegetais e nas condições microclimáticas. Todo este conhecimento deve elucidar como se dá a relação entre a época e frequência de fogo e a resiliência das comunidades vegetais de campo sujo, o que é determinante para a conservação de savanas.

O estudo foi conduzido na Reserva Nacional da Serra do Tombador (RNST), utilizando dados coletados entre 2014 (maioria a partir de 2016) a 2022. A RNST está localizada no município de Cavalcante, Goiás. Trata-se de uma Reserva Particular de Proteção da Natureza (RPPN) de Cerrado, com uma área total de 8900 ha. O clima é tropical, com estação seca de inverno, a precipitação anual média varia entre 1300-1500 mm e temperaturas médias máximas entre 26 e 36°C e mínimas entre 8 e 14°C (Antonelli-Filho 2011). Diferentes fisionomias de Cerrado compõem a vegetação da RNST, como campo limpo, campo sujo, cerrado rupestre, cerrado *sensu stricto*, veredas, além de florestas de vale (Antonelli-Filho, 2011).

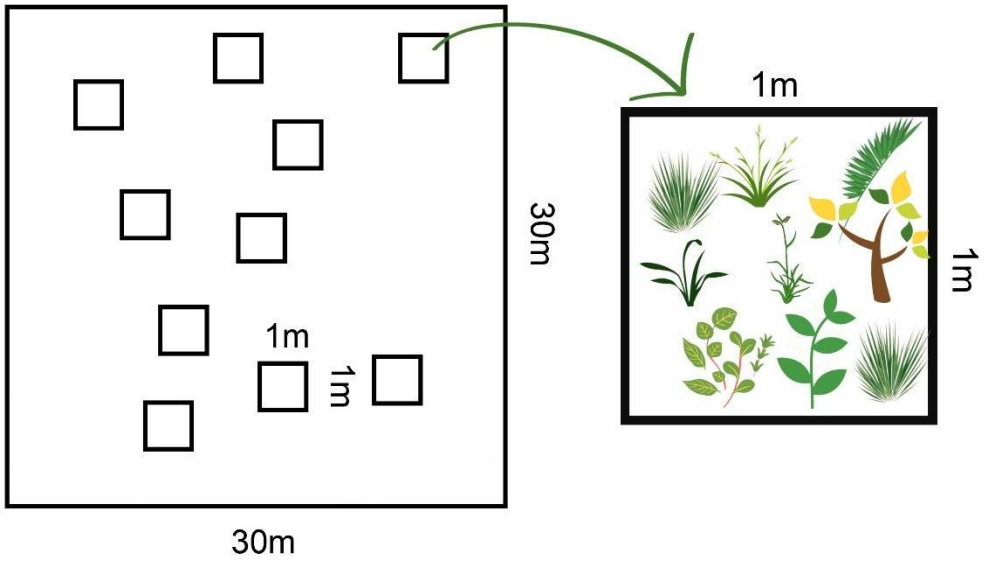
Com o objetivo de avaliar os efeitos da época e da frequência de fogo na dinâmica da vegetação do estrato herbáceo-arbustivo, utilizamos parcelas experimentais de 30x30m estabelecidas numa área de campo sujo na RNST. Estas parcelas foram estabelecidas em uma área sem presença de espécies invasoras e que havia queimado pela última vez em 2011. A frequência de fogo na área antes ao estabelecimento dos experimentos era alta, queimando a cada 2-3 anos (Daldegan et al., 2014). Diferentes tratamentos com queimas experimentais são aplicados desde 2013: exclusão do fogo (sem queima desde 2011), queima bienal precoce (a cada dois anos no início da estação seca, maio), bienal modal (a cada dois anos no meio da seca, julho), bienal tardia (a cada dois anos no final da seca, outubro) e queima

anual (queimadas anualmente no meio da estação seca, julho), com quatro réplicas/tratamento, totalizando 20 parcelas (Figura 2).

**Figura 2 -** Distribuição de parcelas com diferentes tratamentos de fogo na área de campo sujo de Cerrado selecionada na RNST. A: queimada anual; E: exclusão do fogo desde 2011; P: queimada precoce bienal; M: queimada modal bienal; T: queimada tardia bienal. *parcelas queimadas acidentalmente em outubro de 2017 e **parcela substituta a partir de janeiro de 2018.

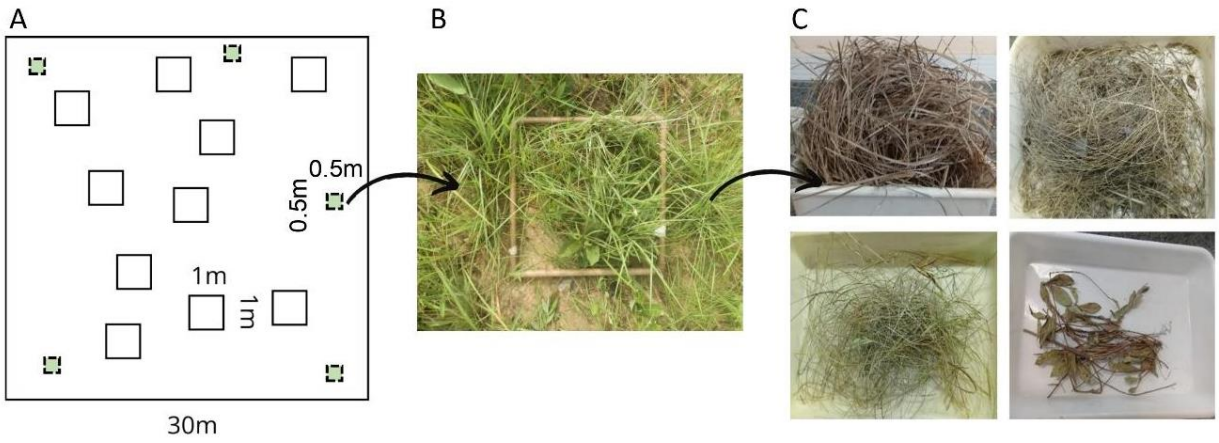

Dentro de cada parcela experimental foram estabelecidas 10 subparcelas permanentes de 1x1m para levantamento da comunidade vegetal e avaliação de parâmetros estruturais das comunidades (porcentagem de solo descoberto e biomassa morta) a cada seis meses (estação chuvosa (janeiro) e seca (julho), Figura 3). Os parâmetros microclimáticos das comunidades sob diferentes frequências de fogo também foram mensurados dentro das subparcelas de 1x1m para que fosse possível relacioná-los com a cobertura da vegetação. Para isso, foram instalados conjuntos de sensores de temperatura, umidade relativa do ar e de iluminância dentro de cinco subparcelas/parcela num período de um ano (após as queimas de julho de 2017 até julho de 2018).

**Figura 3 -** Distribuição das subparcelas permanentes de 1x1m utilizadas para levantamento da vegetação do estrato herbáceo de campo sujo de Cerrado dentro das parcelas de 30x30m com queimadas experimentais (queimada anual, exclusão do fogo desde 2011, queimadas bienias precoce, modal e tardia).




As amostragens da biomassa aérea foram realizadas dentro de subparcelas de 0.5x0.5m nas bordas das parcelas experimentais (Figura 4A). Nas estações chuvosa e seca de cada ano foram coletadas cinco amostras de biomassa por parcela, sempre posicionando as subparcelas de forma aleatória, mas evitando a coleta em um mesmo ponto através do uso de um mapa indicando pontos já coletados (Figura 4B). Em laboratório as amostras de biomassa foram separadas nos seguintes componentes: graminóides, herbáceas não-graminóides, arbustos e biomassa morta (Figura 4C). Para calcular a diversidade funcional das comunidades, foram medidos atributos funcionais de resposta ao fogo em indivíduos das espécies que correspondem a 80% das comunidades em cada tratamento durante a estação chuvosa de 2022.

**Figura 4 -** A - Distribuição das subparcelas de 0.5x0.5m utilizadas para amostragem da biomassa aérea do estrato herbáceo de campo sujo de Cerrado dentro das parcelas de 30x30m com queimadas experimentais (queimada anual, exclusão do fogo desde 2011, queimadas bienais precoce, modal e tardia); B - imagem de uma subparcela durante a coleta; C - separação da biomassa nos diferentes componentes.




As queimadas de cada parcela foram realizadas sempre separadamente, a fim de evitar pseudoreplicação, na direção do vento e buscando condições (velocidade do vento, temperatura e período do dia) semelhantes entre todos os tratamentos. Maiores detalhes do delineamento amostral e da metodologia utilizada em todo o trabalho são descritos nos capítulos que compõem a tese.

A tese foi organizada em três capítulos, apresentados em formato de artigos científicos e ao final foram elaboradas as conclusões gerais acerca da influência dos diferentes regimes de fogo no microclima, riqueza e composição de espécies, produtividade e dinâmica da biomassa aérea de comunidade do estrato herbáceo de fisionomias abertas do Cerrado.

No primeiro capítulo "**Fire frequency affects microclimate in open savannas communities distinctly across the seasons",** investigamos os efeitos de diferentes frequências de fogo (queimadas anuais, bienais e exclusão do fogo desde 2011) nos parâmetros microclimáticos em comunidades vegetais de campo sujo de Cerrado. Nós avaliamos mudanças na umidade relativa, nas temperaturas da superfície do solo e à 3 cm de profundidade e na iluminância a nível do solo durante um ano após a realização das queimadas experimentais e as relacionamos com a cobertura do solo pela vegetação. Nossos resultados elucidam como é o microclima nas savanas abertas após o fogo e nas comunidades excluídas do fogo, e como o microclima de áreas sob diferentes frequências de fogo é afetado pela sazonalidade.

No segundo capítulo “**Fire exclusion and early dry-season fires negatively impact plant communities in tropical open savannas in the Cerrado”,** abordamos a influência de diferentes frequências (queimadas anuais, bienais e exclusão do fogo desde 2011) e épocas de fogo (queimadas bienais precoces, modais e tardias) na riqueza de espécies, na cobertura das diferentes formas de crescimento (herbáceas não-graminóides, graminóides e arbustos) e na estrutura das comunidades do estrato herbáceo de campo sujo ao longo do tempo. Também avaliamos os efeitos de cada regime de fogo após nove anos de experimentos na riqueza de espécies, cobertura das formas de crescimento, estrutura e diversidade taxonômica e funcional das comunidades. Nossos resultados permitiram compreender os aspectos positivos e negativos de cada regime de fogo e assim orientar ações de manejo para utilizá-los de forma eficiente e segura para garantir a conservação das savanas.

No terceiro e último capítulo “**Fire frequency, not fire season matters for aboveground biomass dynamics in open savannas of the Cerrado”** novamente avaliamos a influência de diferentes frequências (queimadas anuais, bienais e exclusão do fogo desde 2011) e épocas de fogo (queimadas bienais precoces, modais e tardias) nas comunidades do estrato herbáceo de campo sujo, mas desta vez investigando como a produtividade e a dinâmica da biomassa aérea é afetada pelos diferentes regimes de fogo ao longo do tempo e após nove anos de experimentos. Analisamos os diferentes componentes da biomassa aérea (biomassa total, morta e viva, esta última dividida em biomassa de graminóides e não graminóides) a fim de identificar mudanças nas quantidades e quais fatores seriam os responsáveis por possíveis mudanças. O conhecimento gerado por este estudo poderá contribuir para estabelecer o regime de fogo indicado para cada objetivo de manejo de forma consciente sobre os efeitos nas comunidades do estrato herbáceo de savanas abertas de Cerrado.

## REFERÊNCIAS BIBLIOGRÁFICAS

Abreu, R. C., Hoffmann, W. A., Vasconcelos, H. L., Pilon, N. A., Rossatto, D. R., & Durigan, G. (2017). The biodiversity cost of carbon sequestration in tropical savanna. Science advances, 3(8), e1701284.

Antonelli-Filho, R. 2011. Plano de Manejo da Reserva Natural Serra do Tombador, Cavalcante - Goiás.

Archibald, S., Lehmann, C. E., Gómez-Dans, J. L., & Bradstock, R. A. (2013). Defining pyromes and global syndromes of fire regimes. Proceedings of the National Academy of Sciences, 110(16), 6442-6447.

Bond, W. J. (2008). What limits trees in C4 grasslands and savannas?. Annual review of ecology, evolution, and systematics, 39, 641-659.

Bond, W. J., & Keeley, J. E. (2005). Fire as a global 'herbivore': the ecology and evolution of flammable ecosystems. Trends in ecology & evolution, 20(7), 387-394.

Bond, W. J., & Parr, C. L. (2010). Beyond the forest edge: ecology, diversity and conservation of the grassy biomes. Biological conservation, 143(10), 2395-2404.

Bond, W. J., Silander Jr, J. A., Ranaivonasy, J., & Ratsirarson, J. (2008). The antiquity of Madagascar's grasslands and the rise of C4 grassy biomes. Journal of Biogeography, 35(10), 1743-1758.

Bond WJ & van Wilgen BW (1996) Fire and plants. 263.

Boughton, E. H., Bohlen, P. J., & Steele, C. (2013). Season of fire and nutrient enrichment affect plant community dynamics in subtropical semi-natural grasslands released from agriculture. Biological conservation, 158, 239-247

Briggs, J. M., & Knapp, A. K. (1995). Interannual variability in primary production in tallgrass prairie: climate, soil moisture, topographic position, and fire as determinants of aboveground biomass. American journal of botany, 82(8), 1024-1030.

Bustamante, M. M., de Brito, D. Q., Kozovits, A. R., Luedemann, G., de Mello, T. R., de Siqueira Pinto, A., ... & Takahashi, F. S. (2012). Effects of nutrient additions on plant biomass and diversity of the herbaceous-subshrub layer of a Brazilian savanna (Cerrado). Plant Ecology, 213, 795-808.

Castro, E.A. de & Kauffman J.B. (1998) Ecosystem structure in the Brazilian Cerrado: a vegetation gradient of aboveground biomass, root mass and consumption by fire. Journal of Tropical Ecology 14, 263-283.

Cerling, T. E., Harris, J. M., MacFadden, B. J., Leakey, M. G., Quade, J., Eisenmann, V., & Ehleringer, J. R. (1997). Global vegetation change through the Miocene/Pliocene boundary. Nature, 389(6647), 153-158.

Coutinho, L. M. (1982). Ecological effects of fire in Brazilian cerrado. In Ecology of tropical savannas (pp. 273-291). Berlin, Heidelberg: Springer Berlin Heidelberg.

Coutinho, L. M. (1990). Fire in the ecology of the Brazilian cerrado. In Fire in the tropical biota (pp. 82-105). Springer Berlin Heidelberg.

Díaz, S., & Cabido, M. (2001). Vive la différence: plant functional diversity matters to ecosystem processes. Trends in ecology & evolution, 16(11), 646-655.

Edwards, E. J., Osborne, C. P., Strömberg, C. A., Smith, S. A., C4 Grasses Consortium, Bond, W. J., ... & Tipple, B. (2010). The origins of C4 grasslands: integrating evolutionary and ecosystem science. science, 328(5978), 587-591.

Fidelis, A., Alvarado, S. T., Barradas, A. C. S., & Pivello, V. R. (2018). The year 2017: megafires and management in the Cerrado. Fire, 1(3), 49.

Fidelis A, & Blanco C (2014) Does fire induce flowering in Brazilian subtropical grasslands?Appl Veg Sci17:690-699.

Fidelis A, Blanco CC, Müller SC, et al. (2012) Short-term changes caused by fire and mowing in Brazilian Campos grasslands with different long-term fire histories. J Veg Sci 23:552-562.17

Fidelis A, Lyra M, Pivello V (2013) Above and below ground biomass and carbon dynamics in Brazilian Cerrado wet grasslands. J Veg Sci 24:356-364.

Fidelis, A., & Pivello, V. R. (2011). Deve-se usar o fogo como instrumento de manejo no Cerrado e Campos Sulinos?. Biodiversidade brasileira, (2), 12-25.

Filgueiras TS (2002) Herbaceous plant communities. In: Oliveira PS, Marquis RJ (eds) Cerrados Brazil Ecol. Nat. Hist. a Neotrop. savanna. Columbia University Press, New York, pp 121-139

Hoffmann, W. A., Geiger, E. L., Gotsch, S. G., Rossatto, D. R., Silva, L. C., Lau, O. L., ... & Franco, A. C. (2012). Ecological thresholds at the savanna-forest boundary: how plant traits, resources and fire govern the distribution of tropical biomes. Ecology letters, 15(7), 759-768.

Keeley, J. E., J. G. Pausas, P. W. Rundel, W. J. Bond, And R. A. Bradstock. 2011. Fire as an evolutionary pressure shaping plant traits. Trends Plant Sci. 16: 406–411.

Keeley, J. E., & Rundel, P. W. (2005). Fire and the Miocene expansion of C4 grasslands. Ecology Letters, 8(7), 683-690.

Knox KJE & Clarke PJ (2005) Nutrient availability induces contrasting allocation and starch formation in resprouting and obligate seeding shrubs. Funct Ecol 19:690-698.

Laterra P, Solbrig O. T (2001) Dispersal strategies, spatial heterogeneity and colonization success in firemanaged grasslands. Ecol Modell 139:17-29.

Lehmann, C. E., Anderson, T. M., Sankaran, M., Higgins, S. I., Archibald, S., Hoffmann, W. A., ... & Bond, W. J. (2014). Savanna vegetation-fire-climate relationships differ among continents. Science, 343(6170), 548-552.

Lehmann, C. E., Archibald, S. A., Hoffmann, W. A., & Bond, W. J. (2011). Deciphering the distribution of the savanna biome. New Phytologist, 191(1), 197-209.

Marcos E, Tárrega R, Luis-Calabuig E (2004) Interactions between mediterranean shrub species eight years after experimental fire. Plant Ecol 170:235-241.

Mendonça, R. D., Felfili, J. M., Walter, B. M. T., Silva-Júnior, M. D., Rezende, A. V., Filgueiras, T. S., ... & Ribeiro, J. F. (2008). Cerrado: ecologia e flora. Brasília, DF: EMBRAPA Informação e Tecnologia, 2.

Moraes Falleiro, R., Santana, M. T., & Berni, C. R. (2016). As contribuições do Manejo Integrado do Fogo para o controle dos incêndios florestais nas Terras Indígenas do Brasil. Biodiversidade brasileira, 6(2), 88-105.

Moreira, A. G. (2000). Effects of fire protection on savanna structure in Central Brazil. Journal of biogeography, 27(4), 1021-1029.

Oliveras I, Meirelles ST, Hirakuri VL, et al. (2013) Effects of fire regimes on herbaceous biomass and nutriente dynamics in the Brazilian savanna. Int J Wildl Fire 22:368.

Overbeck, G. E., Vélez-Martin, E., Scarano, F. R., Lewinsohn, T. M., Fonseca, C. R., Meyer, S. T., ... & Pillar, V. D. (2015). Conservation in Brazil needs to include non-forest ecosystems. Diversity and distributions, 21(12), 1455-1460.

Parr, C. L., Lehmann, C. E., Bond, W. J., Hoffmann, W. A., & Andersen, A. N. (2014). Tropical grassy biomes: misunderstood, neglected, and under threat. Trends in ecology & evolution, 29(4), 205-213.

Pausas J. G., Schwilk D. (2012) Fire and plant Evolution. New Phytologist 193 : 301–303

Pivello, V. R. (2006). Fire management for biological conservation in the Brazilian cerrado. Savannas and Dry Forests: Linking people with Nature. Aldershot, England: Ashgate Publishing, 129-154.

Pivello, V. R., & Norton, G. A. (1996). FIRETOOL: an expert system for the use of prescribed fires in Brazilian savannas. Journal of Applied Ecology, 348-356.

Pivello, V.R.; Oliveras, I; Miranda, H.S.; Haridasan, M.; Sato, M.N. & Meirelles, S.T. 2010. Effect of fires on soil nutrient availability in an open savanna in Central Brazil. Plant and Soil, 337(1-2): 111–123

Quesada CA, Miranda AC, Hodnett MG, et al. (2004) Seasonal and depth variation of soil moisture in a burned open savana (campo sujo) in Central Brazil. Ecol Appl 14:33-41. doi: 10.1890/01-6017

Rissi, M. N., Baeza, M. J., Gorgone-Barbosa, E., Zupo, T., & Fidelis, A. (2017). Does season affect fire behaviour in the Cerrado?. International Journal of Wildland Fire, 26(5), 427-433.

Rodrigues, C. A., & Fidelis, A. (2022). Should we burn the Cerrado? Effects of fire frequency on open savanna plant communities. Journal of Vegetation Science, 33(6).

Rodrigues, C. A., Zirondi, H. L., & Fidelis, A. (2021). Fire frequency affects fire behavior in open savannas of the Cerrado. Forest Ecology and Management, 482.

Sankaran, M., Hanan, N. P., Scholes, R. J., Ratnam, J., Augustine, D. J., Cade, B. S., ... & Zambatis, N. (2005). Determinants of woody cover in African savannas. Nature, 438(7069), 846-849.

Sarmiento, G. (1984). The ecology of neotropical savannas. Harvard University Press.

Schmidt, I. B., & Eloy, L. (2020). Fire regime in the Brazilian Savanna: Recent changes, policy and management. Flora, 151613.

Schmidt, I. B., Moura, L. C., Ferreira, M. C., Eloy, L., Sampaio, A. B., Dias, P. A., & Berlinck, C. N. (2018). Data from: Fire management in the Brazilian savanna: First steps and the way forward. Dryad Digital Repository,

Simon, M. F., Grether, R., de Queiroz, L. P., Skema, C., Pennington, R. T., & Hughes, C. E. (2009). Recent assembly of the Cerrado, a neotropical plant diversity hotspot, by in situ evolution of adaptations to fire. Proceedings of the National Academy of Sciences, 106(48), 20359-20364.19

Veldman, J. W., Buisson, E., Durigan, G., Fernandes, G. W., Le Stradic, S., Mahy, G., ... & Bond, W. J. (2015). Toward an old-growth concept for grasslands, savannas, and woodlands. Frontiers in Ecology and the Environment, 13(3), 154-162.

Whelan, R. J. (1995). The ecology of fire. Cambridge university press.

Zhao, Y., Liu, Z., & Wu, J. (2020). Grassland ecosystem services: A systematic review of research advances and future directions. Landscape Ecology, 1-22.

# 1. CAPÍTULO 1

## Microclimate is affected by fire frequency and seasonality in tropical open savannas of the Cerrado

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### Abstract

Fire promotes shifts in the environmental conditions, such as in microclimate in fire-prone ecosystems. Fire frequency affects the cover of growth forms, dead biomass accumulation, and bare soil percentage. Consequently, microclimate may be affected. Since microclimate can influence several processes and properties of plant communities, we aimed to evaluate how microclimate differs among open savanna areas under different fire frequencies. Moreover, we asked how microclimate varies through time in each fire frequency, and thus if it is affected by seasonality. We used experimental plots of 30x30m with different fire frequencies since 2013: fire exclusion, biennial, and annual fires. We sampled the microclimate data after the prescribed fires of July 2017 for one year. Data loggers with sensors of soil temperature (at the surface and 3 cm below the surface), relative humidity, and illuminance were arranged in each plot. We found that the microclimate of open savanna differed among areas under distinct fire frequencies in all periods evaluated, with major differences being observed just after the fire. Higher temperatures and illuminance and lower relative humidity were recorded in burned plots. Changes in microclimate across time were also different among fire frequencies. Burned sites had a higher variation in microclimate than unburned ones until the end of the rainy season. However, at the beginning of the dry season, fire exclusion plots displayed a higher decrease in relative humidity and illuminance than burned plots. Our results describe the microclimate in open savannas after the fire and in fire-excluded communities, and how microclimate is affected by seasonality.

**Keywords**: annual fire, biennial fire, fire exclusion, illuminance, soil temperature.

## Introduction

In fire-prone ecosystems, fire promotes several alterations in the environmental conditions of plant communities, such as an increase in gaps and available nutrients, as well as changes in the microclimate (Coutinho, 1982; Whelan, 1995; Bond & Van Wilgen, 1996; Fidelis et al., 2012; Fidelis & Blanco, 2014; Daibes et al., 2017). Fire consumes the aboveground biomass, thus reducing the vegetation cover temporarily, which, along with the deposition of an ash layer on the soil surface, reduces the albedo (Castro-Neves & Miranda, 1996). The reduction in albedo, in turn, affects other microclimate parameters, such as the soil heat flux, and the range of soil temperature (Castro-Neves & Miranda, 1996).

Fire frequency is an important factor of the fire regime since it influences species composition, structure, and productivity of plant communities (Moreira, 2001; Abreu et al., 2017; Rodrigues & Fidelis, 2022). In tropical savannas, fire frequency is high, with a fire return of 1 to 5 years (Hoffmann et al., 2012; Trollope et al., 1982), due to the high production of biomass that accumulates rapidly during the rainy season and is converted into dead biomass in the prolonged dry season (Govender et al., 2006). Fires are characterised as surface fires, with high combustion rates, consuming almost all the fine fuel load of the herbaceous layer (Rissi et al., 2017; Santos et al., 2021; Rodrigues et al., 2021). Most herbaceous species are fire-adapted and resprout after fire (Pilon et al., 2021b, Zupo et al., 2021). However, the interval of fire return can affect the cover of different growth forms, dead biomass accumulation, and consequently, bare soil percentage (Rodrigues & Fidelis, 2022). As a consequence, microclimate parameters may be altered (Wolf et al., 2021). For example, the incidence of light and soil temperatures increase in response to the reduction of vegetation cover, while relative humidity decreases (Fidelis & Blanco, 2014; Davies et al., 2013).

Illuminance is an important driver of soil water evaporation (Smits et al., 2012), plant evapotranspiration (Saugier & Katerji, 1991), and a determinant of photosynthetic efficiency (Rossato et al., 2017). Thereby, the illuminance can promote direct and indirect variation in plant traits, such as plant height (Zheng et al., 2021), leaf area and length (Rossato et al., 2017; Carlos & Rossato, 2017; Pilon et al., 2021a), and root length (Cabal & Rubenstein, 2018). Moreover, it may also influence plant species diversity, community composition, structure, competition hierarchy (Lloyd, 1968;

Knapp, 1984; Hulbert, 1988; Pilon et al., 2021a), flowering (Fidelis & Blanco, 2014), and productivity (Amundson et al., 1995).

Relative humidity affects the decomposition of organic matter in savannas: the lower the relative humidity, the slower the decomposition (Silveira et al., 2009; Davies et al., 2013). Flammability of open savannas may also be influenced by humidity since lower relative air humidity leads to lower fuel moisture, thus increasing the flammability of the system (Hoffmann et al., 2012; Zanzarini et al., 2022). Temperature, on the other hand, can affect the productivity of plant communities if extreme temperatures are reached (Larcher, 1981; Scanlon & Albertson, 2004; Chidumayo, 2001). Likewise, soil temperatures can influence flowering, fruiting (Le Maitre & Brown, 1992), and germination of savanna species (Daibes et al., 2017; Daibes et al., 2020), and thus, changes in soil temperature range can have a significant effect on post-fire vegetation regeneration.

Despite the influence of microclimate on plant communities, knowledge about its parameters in open savannas is scarce, especially how microclimate parameters change after a fire event over time. Microclimate was described for woody vegetation in the Cerrado (Hoffman et al., 2011; Dodonov et al., 2013) and less is known about the effects of fire frequency on the microclimate of open savannas.

Therefore, we aimed to evaluate (i) how microclimate parameters differ among open savannas areas under different fire frequencies; (ii) how microclimate parameters vary over time among areas with different fire frequencies; (iii) how microclimate would be influenced by changes in the vegetation cover in open savannas. We hypothesised that (i) fire-excluded areas would have the highest relative air humidity, lower illuminance, and soil and soil surface temperatures, as well as lower temperature fluctuation, due to the greatest vegetation cover; (ii) fire-excluded areas would display lower variability of microclimate parameters over time. Among burned areas, biennially burned ones would regenerate faster and thus, with time since fire, we would expect to find less variation in microclimate parameters. On the other hand, annually burned plots would regenerate slower, having more open gaps within the vegetation and thus, we would still observe higher variation of microclimate parameters with time since last fire; (iii) as vegetation cover increases, illuminance and temperatures decrease, while relative humidity increases, since vegetation recovery after fire reduces bare soil

percentages. Thus, there is lower light incidence directly on the soil surface, leading to lower heating and water evaporation of the soil.

## Material and Methods

*Study area*

The study was conducted at the Reserva Natural Serra do Tombador (RNST, 13°35-38'S and 47°45-51'W, 8900 ha, 560–1118 m a.s.l., Central Brazil), where the climate is tropical, with a marked dry season (from May to October, Appendix S1), average annual rainfall of 1300 - 1500 mm, maximum average temperatures between 26 and 36°C, and minimum temperatures between 8 and 14°C (Antonelli-Filho, 2011).

At the RNST, different vegetation types of the Cerrado can be found, from grasslands (e.g., campo limpo) to savannas (e.g., campo sujo) and forests (e.g., Dense Ombrophilous and Seasonal Semideciduous Forest, Antonelli-Filho, 2011). These open savannas comprise a dominant herbaceous layer (mostly C4 grasses and forbs) with scattered shrubs and small trees (Coutinho, 1978; Ribeiro & Walter, 1998). The main component of the species-rich herbaceous stratum in the site is C4 grasses, mainly composed of *Oncorachis ramosa* (Zuloaga & Soderstr.) Morrone & Zuloaga, *Axonopus aureus* P. Beauv., *Elionurus muticus* (Spreng.) Kuntze, *Aristida setifolia* Kunth, *Mesosetum ferrugineum* (Trin.) Chase *and Paspalum pectinatum* Nees ex Trin. (Rodrigues & Fidelis, 2022). The fuel load bed is continuous, composed mostly of fine fuel (graminoids, Rissi et al., 2017; Rodrigues et al., 2021), and fire frequency was high until the creation of the protected area, in 2006 (every 3 years, Daldegan et al., 2014). Fire was excluded in the area until 2011 when there was a wildfire at the end of the dry season. A fire experiment was established in 2013, two years after the wildfire, with different fire treatments related to frequency and season (Rissi et al., 2017, Rodrigues et al., 2021).

### 1.1.1. *Experimental design*

To characterise the microclimate after a fire in open savanna communities under different fire frequencies (fire exclusion, biennial and annual fires), we used fire experimental plots of 30x30m. Treatments with different fire frequencies have been performed since 2013: fire exclusion (FE - three plots, fire exclusion since 2011),

biennial (BF - four plots, burned biennially in July, a total of three fires), and annual (AF - four plots, burned annually, in July, a total of five fires). We sampled the data after the prescribed fires of July 2017 until July 2018. Biennial burns showed fire intensity three times higher than annual burns, reaching 1850 Kw·m−1. Besides, flames were taller and hotter, and their residence time was longer in biennially burned plots compared to annually burned. However, burn efficiency rates were similar between both treatments, consuming around 90% of the plant biomass in both areas (Rodrigues et al., 2021, Figure 1).

**Figure 1**. Images of plots under different fire frequency treatments to show the vegetation cover of each treatment at the time of installation of microclimate sensors in an area of the campo sujo of Cerrado. From left to right: fire exclusion, biennial fires, and annual fire plots.

Within each experimental plot, we randomly established 10 subplots (1m²) to visually estimate the bare soil percentage of the plant community every six months (rainy and dry season). Four to five data loggers with temperature sensors (temperature measured at the soil surface; and soil temperature: measured 3 cm below the surface), relative humidity, and illuminance at ground level were arranged in each experimental plot with different fire frequencies. Technical information and specifications for all data loggers and sensors are presented in Appendix S2. The sensors were placed inside four to five subplots, randomly set, to establish a relationship between the ground cover and the microclimate parameters (4 to 5 sensors of every microclimate parameter x 3-4 plots x 3 fire frequencies). Data was recorded every 60 minutes. It is important to highlight that before the experimental fires and one year after (July 2018), all treatments showed a similar cover of forbs, shrubs, and graminoids (Rodrigues & Fidelis, 2022). Differences in ground cover among treatments were found only in bare soil and dead biomass percentage. The highest

dead biomass coverages were observed in fire exclusion and biennial fire areas, 56 ± 2.5% and 34 ± 1.9%, respectively, compared to 23 ± 1.7% in annual fire ones. Consequently, the highest percentage of bare soil was observed in the annual fire areas, 48 ± 2.8%, while in fire exclusion and biennial fire areas, they were 12 ± 2.3% and 15 ± 2.1%, respectively (Rodrigues & Fidelis, 2022). Thus, we decided to use only bare soil and dead biomass percentage to relate to microclimate parameters.

*Data analysis*

We evaluated the following microclimate parameters: hourly and daily average of relative air humidity, illuminance, and soil and soil surface temperatures; daily amplitude of soil and soil surface temperatures, which correspond to the variation from the minimum to the maximum temperatures recorded during the day. For the daily illuminance average, we used only values of the diurnal period (from 6h to 18h) when there is solar light. We grouped and analyzed the microclimate data according to five periods related to the rainy and dry season and time since last fire: from mid to late-dry season (0 - 3 months after fire), early-rainy season (3 - 5 months after fire), mid-rainy season (5 - 7 months after fire), late-rainy season (7 - 9 months after fire), and from early to the mid-dry season (9 -12 months after fire). Since the microclimate parameters may respond to vegetation cover, we chose these periods to group microclimate data considering the stage of plant growth. During the dry season, plant growth is minimal. Plant growth increases until it peaks at the end of the rainy season (Oliveiras et al., 2012).

To assess differences in microclimate parameters (average of diurnal illuminance, temperatures, relative air humidity and temperature amplitude, and maximum temperatures) among areas under different fire frequencies in each period analyzed, we used generalized linear mixed models (GLMM, family: Gaussian). To compare variations in microclimate parameters over periods (Δ) between treatments, we calculated the variation for each microclimate parameter, obtained by the difference between the value observed in one period and the next one. Then, we compared these differences among each fire frequency treatment using generalized linear models (GLM, family: Gaussian). We performed all analyses using the glmer function, available at the lme4 package version 1.1-27.1 (Bates et al., 2015). The F and p values and degrees of freedom were accessed through the drop1 function of stats package

version 4.1.1 (R Core Team, 2021). Significant differences among treatment pairs were assessed by performing Tukey test using the emmeans function, available at the emmeans package version 1.6.3 (Lenth, 2021).

Finally, we performed linear models using the lm function (lme4 package version 1.1-27.1, Bates et al., 2015) to analyze the relationship between bare soil and dead biomass percentage and microclimate parameters. We used survey data from the rainy season of 2018, six months after fire experiments.

## Results

We found differences in illuminance, relative air humidity, and soil and soil surface temperatures among areas under different fire frequencies in all the analyzed periods (Appendix S3). These differences were more evident during the hottest period of the day, from 12 pm to 5 pm (Figs 2 and 3). However, the largest differences among treatments, mainly between burned and unburned plots, were observed during the first three months after fire (from the mid to late-dry season). In this period, the average illuminance exceeded 44000 lx in the AF and BF plots, whilst FE plots had values < 37000 lx (Table 1).

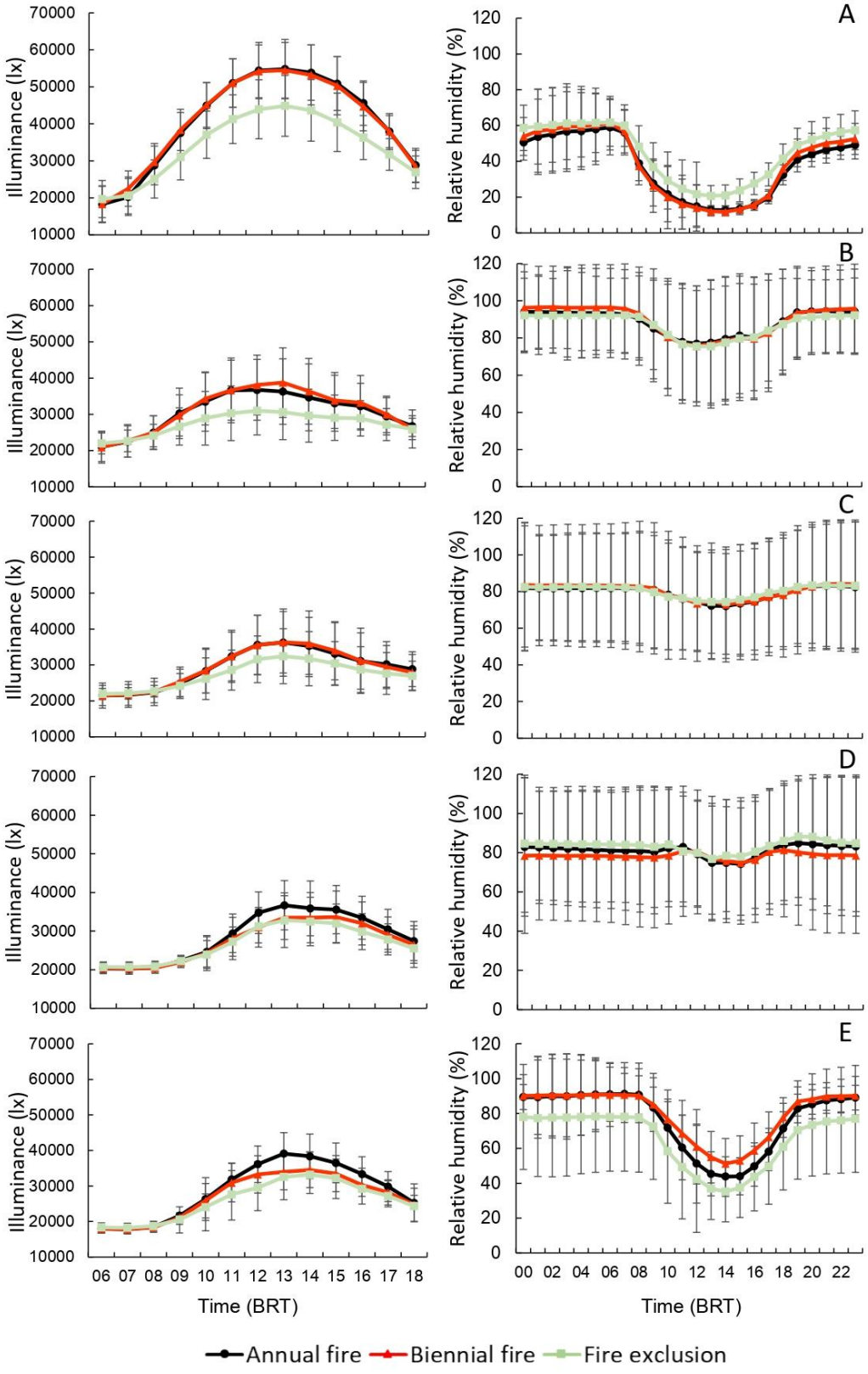



**Figure 2.** Daily patterns (mean and standard deviation) of illuminance and relative air humidity in open savanna plant communities of the Cerrado, under different fire frequency treatments: annual fires, biennial fires, and fire exclusion. Data were recorded in: (A) from mid to the late-dry season, (B) early-rainy season, (C) mid-rainy season, (D) late-rainy season, and (E) from early to the mid-dry season.

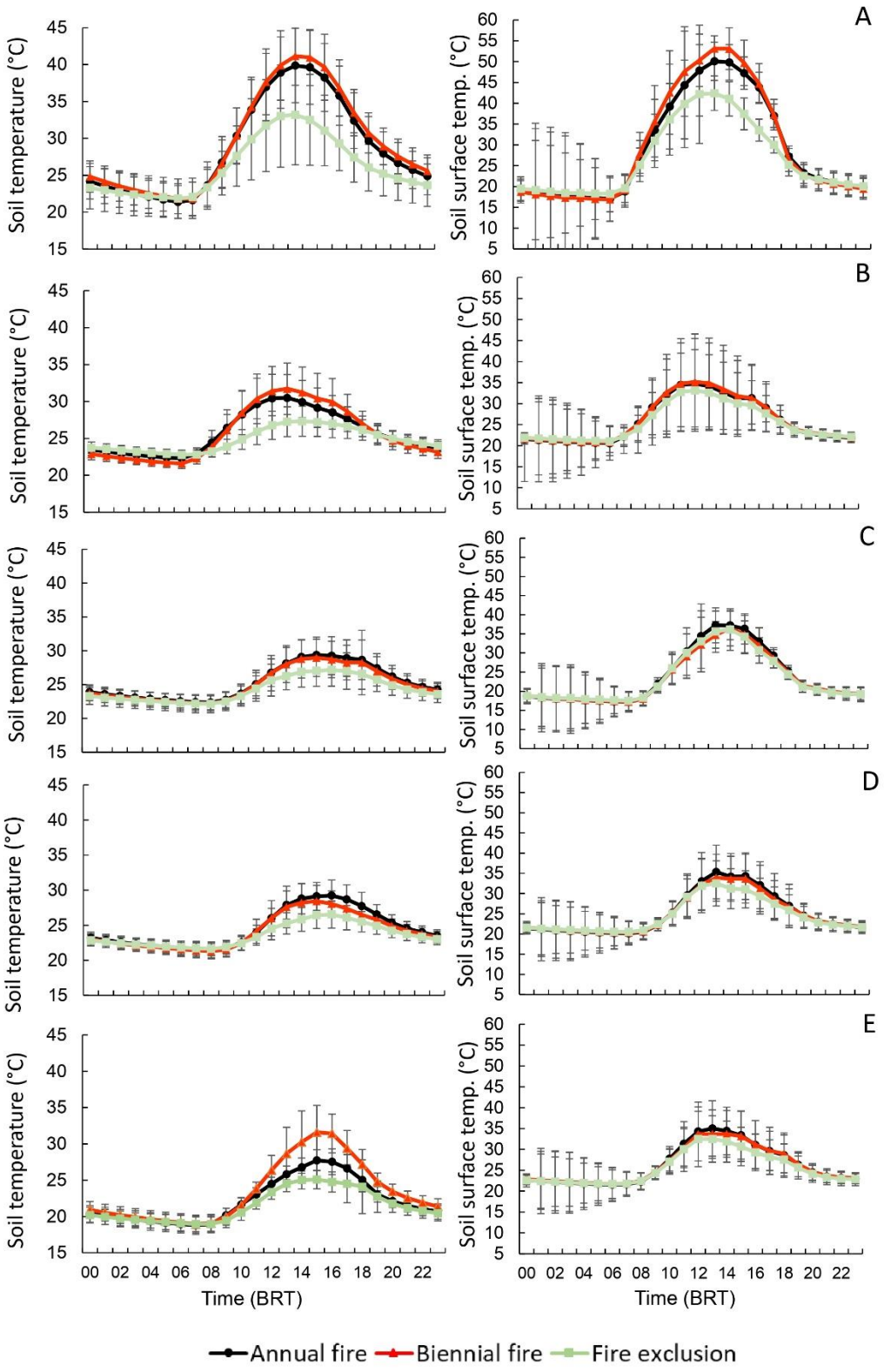



**Figure 3.** Daily patterns (mean and standard deviation) of soil (buried 3 cm below ground) and soil surface temperatures in open savannas plant communities of the Cerrado, under different fire frequency treatments: annual fires, biennial fires, and fire exclusion. Data were recorded in: (A) from mid to the late-dry season, (B) early-rainy season, (C) mid-rainy season, (D) late-rainy season, and (E) from early to the mid-dry season.

**Table 1.** Microclimate parameters (mean ± standard error) recorded from July 2017 to July 2018 in open savanna plant communities of the Cerrado under different fire frequencies: AF - annual fires, BF - biennial fires, and FE - fire exclusion. The microclimate data recorded were grouped in five periods related to the rainy and dry seasons and time since the last fire: from mid to the late-dry season (0 - 3 months after fire), early-rainy season (3 - 5 months after fire), mid-rainy season (5 - 7 months after fire), late-rainy season (7 - 9 months after fire), and from early to the mid-dry season (9 -12 months after fire). Different letters represent significant differences among fire frequencies for each analyzed period (P ≤ 0.05) determined by the Tukey test.

| Period | Fire frequency | Illuminance (lx) | Relative humidity (%) | Soil temperature (°C) | | Soil surface temperature (°C) | |
|---|---|---|---|---|---|---|---|
| | | | | Average | Amplitude | Average | Amplitude |
| Mid/late-dry season | AF | 44312 ± 226$^{a}$ | 38.1 ± 0.8$^{a}$ | 28.8 ± 0.1$^{a}$ | 18.5 ± 0.1$^{a}$ | 28.8 ± 0.4$^{a}$ | 33.0 ± 0.4$^{a}$ |
| | BF | 44259 ± 231$^{a}$ | 39.5 ± 0.8$^{b}$ | 29.5 ± 0.1$^{b}$ | 19.3 ± 0.1$^{b}$ | 29.5 ± 0.5$^{b}$ | 36.2 ± 0.5$^{b}$ |
| | FE | 36472 ± 276$^{b}$ | 45.2 ± 1.1$^{c}$ | 26.2 ± 0.1$^{c}$ | 11.3 ± 0.1$^{c}$ | 26.6 ± 0.4$^{c}$ | 24.1 ± 0.4$^{c}$ |
| Early-rainy season | AF | 32209 ± 417$^{a}$ | 88.3 ± 1.1$^{a}$ | 25.7 ± 0.3$^{a}$ | 8.2 ± 0.3$^{a}$ | 25.9 ± 0.2$^{a}$ | 14.1 ± 0.2$^{a}$ |
| | BF | 32852 ± 454$^{b}$ | 89.3 ± 0.9$^{b}$ | 25.7 ± 0.3$^{a}$ | 10.1 ± 0.3$^{b}$ | 26.2 ± 0.2$^{b}$ | 14.3 ± 0.2$^{a}$ |
| | FE | 28404 ± 330$^{c}$ | 87.1 ± 1.2$^{c}$ | 24.8 ± 0.1$^{b}$ | 4.5 ± 0.1$^{c}$ | 25.4 ± 0.2$^{c}$ | 12.1 ± 0.2$^{b}$ |
| Mid-rainy season | AF | 30656 ± 331$^{a}$ | 79.5 ± 1.4$^{a}$ | 25.3 ± 0.1$^{a}$ | 7.0 ± 0.1$^{a}$ | 26.2 ± 0.2$^{a}$ | 13.5 ± 0.2$^{a}$ |
| | BF | 30750 ± 401$^{a}$ | 80.3 ± 1.6$^{a}$ | 25.0 ± 0.1$^{b}$ | 6.7 ± 0.1$^{b}$ | 26.1 ± 0.2$^{a}$ | 12.0 ± 0.2$^{b}$ |
| | FE | 28242 ± 221$^{b}$ | 80.3 ± 1.5$^{a}$ | 24.3 ± 0.1$^{c}$ | 5.0 ± 0.1$^{c}$ | 25.5 ± 0.2$^{b}$ | 10.8 ± 0.2$^{c}$ |
| Late-rainy season | AF | 30028 ± 249$^{a}$ | 81.1 ± 1.4$^{a}$ | 24.5 ± 0.1$^{a}$ | 7.8 ± 0.1$^{a}$ | 25.1 ± 0.1$^{a}$ | 15.2 ± 0.1$^{a}$ |
| | BF | 28527 ± 293$^{b}$ | 78.5 ± 1.7$^{b}$ | 24.2 ± 0.1$^{b}$ | 7.1 ± 0.1$^{b}$ | 24.9 ± 0.1$^{a}$ | 13.6 ± 0.1$^{b}$ |
| | FE | 27793 ± 262$^{c}$ | 83.4 ± 1.5$^{c}$ | 23.6 ± 0.1$^{c}$ | 4.9 ± 0.1$^{c}$ | 24.9 ± 0.1$^{a}$ | 12.0 ± 0.1$^{c}$ |
| Early/Mid-dry season | AF | 30587 ± 212$^{a}$ | 76.3 ± 1.1$^{a}$ | 22.2 ± 0.2$^{a}$ | 8.9 ± 0.2$^{a}$ | 23.7± 0.3$^{a}$ | 20.1 ± 0.3$^{a}$ |
| | BF | 28634 ± 193$^{b}$ | 79.7 ± 1.1$^{b}$ | 23.4 ± 0.2$^{b}$ | 12.6 ± 0.2$^{b}$ | 23.2 ± 0.3$^{a}$ | 19.2 ± 0.3$^{b}$ |
| | FE | 27166 ± 234$^{c}$ | 65.2 ± 2.4$^{c}$ | 24.5 ± 0.1$^{c}$ | 6.1 ± 0.1$^{c}$ | 23.2 ± 0.3$^{a}$ | 18.6 ± 0.3$^{b}$ |

Likewise, just after fire (from the mid to late-dry season), relative humidity average in FE plots was 7.1% and 5.7% higher than AF and BF, respectively (Table 1), with differences reaching up to 12% at 5 pm (Fig 1). Differences in the soil and soil surface temperatures average among burned and unburned plots were 3°C (Table 1). However, the temperature amplitude varied greatly among fire frequencies, mainly due to differences observed in maximum temperature (Fig. 3 and Table 1). In AF and BF plots, the amplitude of soil temperature recorded was 8°C higher than in FE. Regarding soil surface temperature, the differences in amplitude between burned and unburned plots were even greater, with records in burned plots being 12°C higher than in fire-excluded plots (Table 1). The main difference between burned plots (AF and BF) was

in soil surface temperatures, with BF plots displaying maximum temperatures 4°C higher than AF ones (Fig. 3).

Throughout the rainy season, the differences in microclimate parameters among areas under different fire frequencies decreased (Table 1). AF and BF plots showed values of relative humidity and soil surface temperature at the early and mid-rainy seasons similar to those observed in FE plots (Figs. 2 and 3). However, the average and amplitude of soil temperature differed among treatments, mainly between burned and unburned areas (Fig. 3). Also, soil temperatures remained unchanged for a longer time in FE plots compared to AF and BF plots, from the early to late-rainy season (Fig.3). The illuminance was similar between AF and BF plots until the mid-rainy season. However, during the late-rainy season, illuminance decreased by 8% in the BF plots thus it became similar between BF and FE plots and different only in AF ones (Table 1 and Fig. 2).

Nevertheless, from the early to the mid-dry season (9 to 12 months after fire), changes were observed in microclimate parameters. Relative humidity of the air was different among areas with different fire frequencies, both for the average and for daily fluctuation (Table 1). Minimum relative humidity values of 33%, 41%, and 51% were recorded in the FE, AF, and BF plots, respectively, and maximum values of 79% in the FE plots and 91% in both burned plots (Table 1 and Fig. 2). The average of Illuminance did not change in all fire frequencies and remained higher in AF plots. However, AF plots increased its fluctuation, with average values ranging from 18000 to 49000lx during the day (Fig.2). Both average and amplitude soil surface temperatures were similar among treatments (Table 1). Even during the hottest hour of the day, the differences recorded did not reach 2°C (Fig. 3). However, soil temperatures showed large differences among all treatments. Fire-excluded plots displayed the lowest average and fluctuation of soil temperature, while biennial fire ones displayed the largest values of these parameters. Differences larger than 3°C were observed for more than six hours among biennial fire plots and the other treatments (Fig 3).

In general, the variation of microclimate parameters (Δ) over time in burned plots (AF and BF) had greater fluctuation than in FE ones (Fig. 4 and Appendix S4). Except for the late-rainy season to early/mid-dry season, when illuminance and relative humidity varied more in fire-excluded than in burned plots. Differences between the

burned plots were observed mainly in transitions from dry to rainy and rainy to dry seasons (Fig. 4 and Appendix S4).

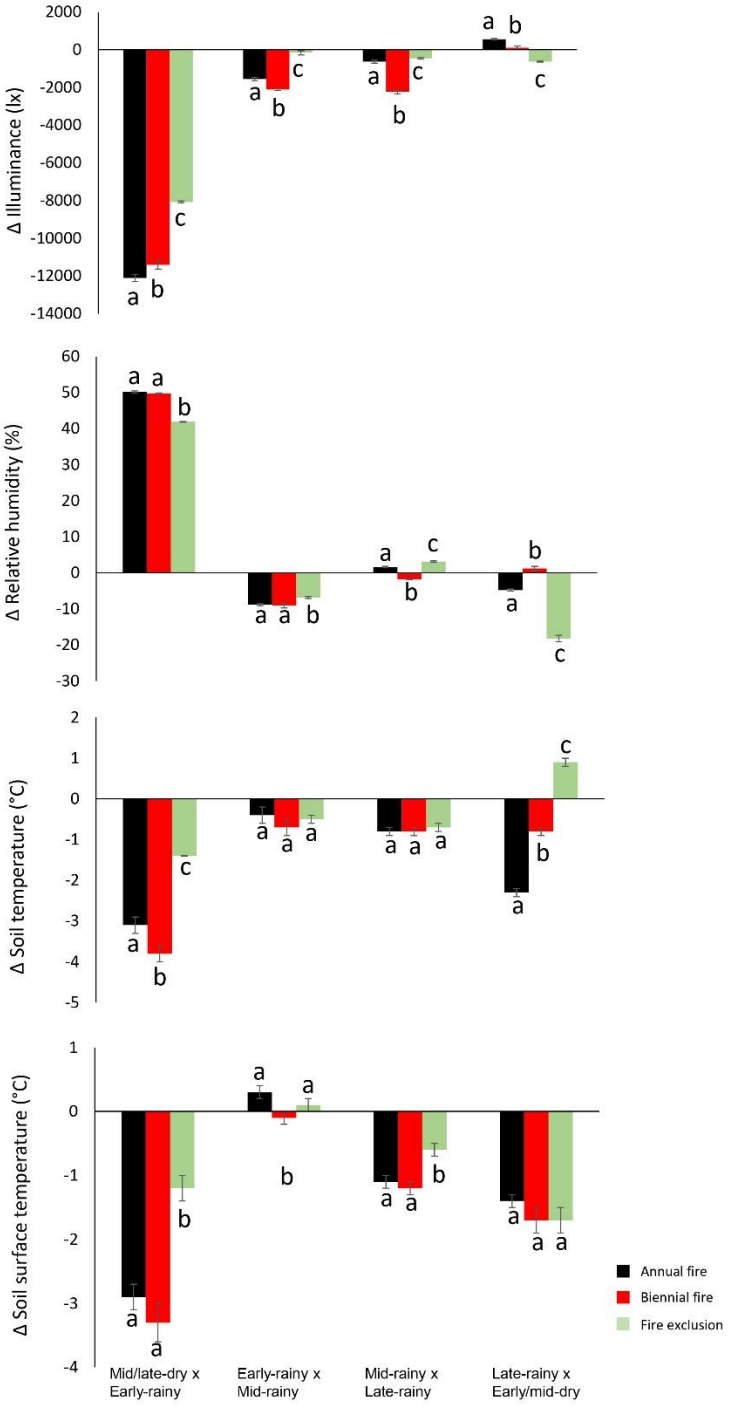



**Figure 4.** Changes in microclimate parameters (Δ) over periods sampled (from mid to the late-dry season, early-rainy season, mid-rainy season, late-rainy season, and from early to the mid-dry season), among plots under different fire frequencies (AF - annual fires, BF - biennial fires, and FE - fire exclusion), in open savanna plant communities of the Cerrado. Letters represent significant differences between treatments ($P \leq 0.05$) determined by the Tukey test.

Bare soil percentage was related to all the microclimate parameters. Illuminance, soil and soil surface temperatures increased as the bare soil percentage increased. Conversely, relative air humidity decreased as bare soil percentage increased (Fig. 5). Dead biomass percentage was not related to microclimate parameters ($p > 0.05$).

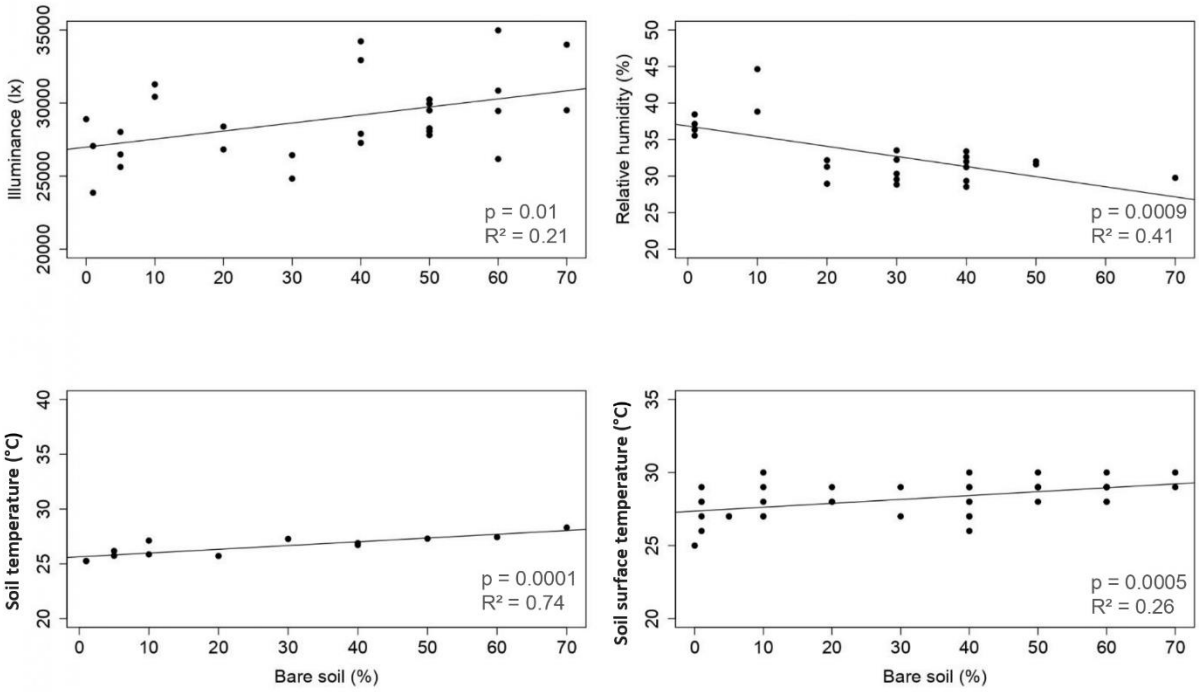



**Figure 5.** Relationship between bare soil percentage and microclimate parameters in open savannas of the Cerrado obtained by data of mid-rainy season of 2018. p- values were obtained by linear models.

## Discussion

Microclimate parameters of open savanna communities differed among plots under distinct fire frequencies in all periods evaluated during one year after fire. However, the major differences were observed just after fire (from mid to the late-dry season, 0 to 3 months after fire) between burned and unburned plots. During the rainy season, the differences decreased and increased again with the beginning of the next dry season (from the early to the mid-dry season, 9 to 12 months after fire), showing that not only time since the last fire but also season is an important factor affecting microclimate parameters. Differences found are related to the vegetation cover in all plots with different fire frequencies, since bare soil cover was correlated with all measured parameters. Changes in microclimate parameters over time also were

different among plots under different fire frequencies: burned sites had a higher variation in microclimate parameters than unburned ones until the late-rainy season. However, in the early/mid-dry season, FE plots displayed higher relative air humidity and illuminance variation than AF and BF plots.

Fire removes the aboveground biomass of the herbaceous layer, opening the vegetation and exposing the soil (Bond & Van Wilgen, 1996; Fidelis et al., 2012). Changes in vegetation cover alter the microclimate, increasing the illuminance, soil and air temperatures and decreasing the relative air humidity (Wolf et al., 2021). Biennial fires are more intense, hotter, and with higher flames than annual ones (Rodrigues et al., 2021). Therefore, plant communities in BF plots may have been more severely affected than in AF plots, which led to a higher bare soil percentage in BF just after the fire (mid/late-dry season, 0-3 months after fire). Conversely, fire exclusion leads to a high accumulation of dead biomass, which remains attached to the tussock grasses for longer periods, reducing thus, gaps in the herbaceous layer (Rodrigues et al,. 2021).

Higher temperatures and illuminance, low relative air humidity, and high fluctuations of temperature recorded during the mid/late-dry season (0-3 months after fire) can influence several processes and properties of plant communities in open savannas, such as species composition, competition status, structure, and post-fire regeneration. These microclimate parameters can affect the establishment and persistence of species by influencing the germination of savanna seeds and the survival of seedlings after a fire (Auld & Bradstock, 1996; Santana et al., 2010, 2013; Daibes et al., 2017; Daibes et al., 2021). High soil temperature (>40°C, Fig. 3) along with daily soil temperature fluctuations (from 25°C to 42°C, Fig. 3), recorded just after fire in burned plots, may be sufficient to alleviate the physical dormancy of seeds, enabling them to germinate with the start of the rainy season (Daibes et al., 2017). However, high soil temperatures can also have negative effects on plant communities, such as lower soil water availability due to higher evaporation affecting several physiological plant processes like germination, resource allocation for the production of branches or roots, and productivity (Gleeson & Tilman, 1992; Silveira et al,. 2012; Furquim et al., 2018).

Illuminance is also a critical factor influencing species composition of plant communities. High illuminance, recorded in recently burned areas, promotes the

establishment of shade-intolerant species that were previously being suppressed by high vegetation cover (Pilon et al., 2021a; Rodrigues & Fidelis, 2022). Besides, an increase in illuminance, as observed in AF and BF plots just after fire (mid/late-dry season, 0-3 months after fire), may stimulate flowering (Norden & Kirkman, 2004; Lamont & Downes, 2011) which is an important response to fire in tropical savannas (Coutinho, 1976; Fidelis & Zirondi, 2021; Zirondi et al., 2021). Flowering just after fire is more advantageous than during fire intervals since, at this moment, the availability of nutrients is high and vegetation cover and competition are low, reducing the cost of reproducing and increasing the success rate of seedling recruitment (Gowe & Brewer, 2005).

Relative air humidity, in turn, has a strong effect on the system's flammability (Hoffmann et al., 2012). The lower humidity recorded in FE plots during the early/mid-dry season (9 to 12 months after fire) may have led to a higher rate of biomass curing, turning FE plots more flammable than AF and BF during this period. Fuel moisture, along with the system's flammability, drives fire behavior by influencing fire intensity, residence time, and temperatures (Rissi et al., 2017; Rodrigues et al., 2021; Zanzarini et al., 2022). Recently resprouted plants of burned plots retain more humidity than unburned vegetation (Matthews, 2013), which may explain why FE plots have displayed lower relative humidity than AF and BF in the early/mid-dry season. Furthermore, the higher proportion of dead than live biomass in the unburned plots promotes greater absorption of moisture from the environment by the vegetation. In the absence of rain, the moisture of dead biomass depends exclusively on the exchange of water vapour between the fuel and the environment, while the moisture of living biomass depends more on the physiological characteristics of the plants (Matthews, 2013).

Changes in microclimatic parameters observed over one year at all plots under different fire frequencies are mainly related to two factors: i) seasonality and ii) the progressive increase in vegetation cover in the burned areas. Such microclimate variation over time requires adaptations by plants to survive and have good fitness under several environmental conditions. Leaf area and mass per area, for example, vary according to illuminance (Rossato et al., 2017; Carlos & Rossato, 2017). Leaf traits like these determine several aspects of plant function, such as rates of photosynthesis, transpiration and investment costs for leaf construction (Dong et al.,

2020). Root traits also respond to changes in microclimate conditions (e.g., root tissue density, specific root length, and root C content vary according to illuminance (Cabal & Rubenstein, 2018; Vetaas, 1992), and are involved in many ecosystem processes like carbon and nutrient cycling, community productivity, and soil formation (Bardgett et al., 2014; Czarnes et al., 2000; Orwin et al., 2010). Therefore, variations in microclimate can affect plants, which in turn will affect processes at the ecosystem level. Microclimatic changes over time were more accentuated in burned plots during all periods except in the transition from rainy to the dry season (9 months after fire), when FE plots had more decrease in illuminance and relative air humidity than BF and AF.

In conclusion, as we hypothesized, the frequency of fires influences the microclimatic parameters over time, both through the differences in vegetation cover between burned and unburned plots. However, seasonality also plays a major role in influencing local microclimate and should be further considered. Our study showed that the effects of fire frequency on the microclimate of open savannas persist for at least 12 months after fire, being enhanced by the dry season. We describe the microclimate after annual and biennial fires, which can support understanding post-fire processes such as flowering, germination, seedling recruitment and establishment, community assembly, and plant productivity, among others. Furthermore, our description of microclimate in fire exclusion areas in different periods is important to comprehend plant community dynamics according to seasonality.

## References

Abreu, R. C., Hoffmann, W. A., Vasconcelos, H. L., Pilon, N. A., Rossatto, D. R., & Durigan, G.(2017). The biodiversity cost of carbon sequestration in tropical savanna. Science advances, 3(8), e1701284.

Amundson, R. G., Ali, A. R., & Belsky, A. J. (1995). Stomatal responsiveness to changing light intensity increases rain-use efficiency of below-crown vegetation in tropical savannas. *Journal of Arid Environments*, *29*(2), 139-153.

An, N., Lu, N., Fu, B., Chen, W., Keyimu, M., & Wang, M. (2021). Root trait variation of seed plants from China and the primary drivers. *Journal of Biogeography*, *48*(10), 2402-2417.

Antonelli-Filho, R. (2011). Plano de Manejo da Reserva Natural Serra do Tombador.

Auld, T. D., & O'Connell, M. A. (1991). Predicting patterns of post-fire germination in 35 eastern Australian Fabaceae. *Australian Journal of Ecology*, 16(1), 53-70.

Bates, D., Maechler, M., Bolker, B., Walker, S. (2015). Fitting Linear Mixed- Effects Models Using lme4. Journal of Statistical Software,67(1),1-48.

Bond, W. J., & Van Wilgen, B. W. (1996). Plants and fire. Chapman, New York.

Cabal, C., & Rubenstein, D. I. (2018). Above-and below-ground allocation and functional trait response to soil water inputs and drying rates of two common savanna grasses. Journal of Arid Environments, 157, 1-12.

Carlos, N. A., & Rossatto, D. R. (2017). Leaf traits combinations may explain the occurrence of savanna herbaceous species along a gradient of tree encroachment. Theoretical and Experimental Plant Physiology, 29(3), 155-163.

Chidumayo, E. N. (2001). Climate and phenology of savanna vegetation in southern Africa. Journal of Vegetation Science, 347-354.

Coutinho, L. M. (1976). Contribuição ao conhecimento do papel ecológico das queimadas na floração de espécies do Cerrado (Tese (Livre Docência). Universidade de São Paulo, São Paulo. Recuperado de http://www.teses.usp.br/teses/disponiveis/livredocencia/41/tde-04092014-095647/.

Coutinho, L. M. (1978). O conceito do cerrado. Revista brasileira de Botânica, 1, 17-23ri

Coutinho, L. M. (1982). Ecological effects of fire in Brazilian cerrado. In Ecology of tropical savannas (pp. 273-291). Springer, Berlin, Heidelberg.

Daibes, L. F., Zupo, T., Silveira, F. A., & Fidelis, A. (2017). A field perspective on effects of fire and temperature fluctuation on Cerrado legume seeds. Seed Science Research, 27(2), 74-83.

Daibes, L. F., Martins, A. R., Silveira, F. A., & Fidelis, A. (2021). Seed tolerance to post-fire temperature fluctuation of Cerrado legume shrubs with micromorphological implications. Flora, 275, 151761.

Daldegan, G., de Carvalho, O., Guimarães, R., Gomes, R., Ribeiro, F., & McManus, C. (2014). Spatial patterns of fire recurrence using remote sensing and GIS in the Brazilian savanna:Serra do Tombador Nature Reserve, Brazil. Remote Sensing, 6(10), 9873- 9894.

Davies-Colley, R. J., Payne, G. W., & Van Elswijk, M. (2000). Microclimate gradients across a forest edge. New Zealand Journal of Ecology, 111-121.

Davies, A. B., van Rensburg, B. J., Eggleton, P., & Parr, C. L. (2013). Interactive effects of fire, rainfall, and litter quality on decomposition in savannas: frequent fire leads to contrasting effects. Ecosystems, 16(5), 866-880.

Dodonov, P., Harper, K. A., & Silva-Matos, D. M. (2013). The role of edge contrast and forest structure in edge influence: vegetation and microclimate at edges in the Brazilian cerrado. Plant ecology, 214(11), 1345-1359.

Dong, N., Prentice, I. C., Wright, I. J., Evans, B. J., Togashi, H. F., Caddy-Retalic, S., ... & Lowe, A. J. (2020). Components of leaf-trait variation along environmental gradients. New Phytologist, 228(1), 82-94.

Eiten, G. (1972). The cerrado vegetation of Brazil. The Botanical Review, 38(2), 201-341

Fidelis, A., Blanco, C. C., Müller, S. C., Pillar, V. D., & Pfadenhauer, J. (2012). Short-term changes caused by fire and mowing in Brazilian Campos grasslands with different long-term fire histories. Journal of Vegetation Science, 23(3), 552-562.

Fidelis, A., & Blanco, C. (2014). Does fire induce flowering in B razilian subtropical grasslands?. Applied Vegetation Science, 17(4), 690-699.

Fidelis, A., & Zirondi, H. L. (2021). And after fire, the Cerrado flowers: A review of post-fire flowering in a tropical savanna. Flora, 280, 151849.

Furquim, L. C., dos Santos, M. P., de Andrade, C. A. O., de Oliveira, L. A., & Evangelista, A. W. P. (2018). Relação entre plantas nativas do Cerrado e água. Científic@-Multidisciplinary Journal, 5(2), 146-156.

Gleeson, S. K., & Tilman, D. (1992). Plant allocation and the multiple limitation hypothesis. The American Naturalist, 139(6), 1322-1343.

Gorgone-Barbosa, E., Pivello, V. R., Bautista, S., Zupo, T., Rissi, M. N., & Fidelis, A. (2015). How can an invasive grass affect fire behavior in a tropical savanna? A community and individual plant level approach. Biological Invasions, 17(1), 423-431.

Govender, N., Trollope, W. S., & Van Wilgen, B. W. (2006). The effect of fire season, fire frequency, rainfall and management on fire intensity in savanna vegetation in South Africa. Journal of Applied Ecology, 43(4), 748-758.

Gowe, A. K., & Brewer, J. S. (2005). The evolution of fire-dependent flowering in goldenasters (Pityopsis spp.) 1. The Journal of the Torrey Botanical Society, 132(3), 384-400.

Hoffmann, W. A., Jaconis, S. Y., Mckinley, K. L., Geiger, E. L., Gotsch, S. G., & Franco, A. C. (2012). Fuels or microclimate? Understanding the drivers of fire feedbacks at savanna–forest boundaries. Austral Ecology, 37(6), 634-643.

Hulbert, L.C. (1988). Causes of fire effects in tallgrass prairie. Ecology 69: 46–58.

Knapp, A.K. (1984). Post-burn differences in solar radiation, leaf temperature and water stress influencing production in a lowland tallgrass prairie. American Journal of Botany 71: 220–227.

Lamont, B. B., & Downes, K. S. (2011). Fire-stimulated flowering among resprouters and geophytes in Australia and South Africa. Plant Ecology, 212(12), 2111-2125.

Larcher, W. (1981). Effects of low temperature stress and frost injury on plant productivity. Physiological processes limiting plant productivity, 253-269.

Le Maitre, D. C., & Brown, P. J. (1992). Life cycles and fire-stimulated flowering in geophytes. In Fire in South African mountain fynbos (pp. 145-160). Springer, Berlin, Heidelberg.

Lenth, R.V. (2021). emmeans: Estimated Marginal Means, aka Least-Squares Means. R package version 1.5.5-1. https://CRAN.R-project.org/package=emmeans

Lloyd, P.S. 1968. The ecological significance of fire in limestone grassland communities of the Derbyshire Dales. Journal of Ecology 56: 811–826.

Matthews, S. (2013). Dead fuel moisture research: 1991–2012. International Journal of Wildland Fire, 23(1), 78-92.

Miranda, A. C., Miranda, H. S., Dias, I. D. F. O., & de Souza Dias, B. F. (1993). Soil and air temperatures during prescribed cerated fires in Central Brazil. Journal of tropical ecology, 9(3), 313-320.

Miranda, H. S., Sato, M. N., Neto, W. N., & Aires, F. S. (2009). Fires in the cerrado, the Brazilian savanna. In Tropical fire ecology (427-450). Springer, Berlin, Heidelberg.

Moreira, F., Rego, F. C., & Ferreira, P. G. (2001). Temporal (1958–1995) pattern of change in a cultural landscape of northwestern Portugal: implications for fire occurrence. Landscape Ecology, 16(6), 557-567.

Norden, A. H., & Kirkman, L. K. (2004). Factors controlling the fire-induced flowering response of the federally endangered Schwalbea americana L.(Scrophulariaceae). Journal of the Torrey Botanical Society, 16-22.

Oliveras, I., Meirelles, ST, Hirakuri, VL, Freitas, CR, Miranda, HS, & Pivello, VR (2012). Efeitos dos regimes de fogo sobre a biomassa herbácea e a dinâmica de nutrientes no cerrado brasileiro. International Journal of Wildland Fire , 22 (3), 368-380.

Pilon, N. A., Durigan, G., Rickenback, J., Pennington, R. T., Dexter, K. G., Hoffmann, W. A., ...Lehmann, C. E. (2021a). Shade alters savanna grass layer structure and function along a gradient of canopy cover. Journal of Vegetation Science, 32(1), e12959.

Pilon, N. A., Cava, M. G., Hoffmann, W. A., Abreu, R. C., Fidelis, A., & Durigan, G. (2021b). The diversity of post-fire regeneration strategies in the cerrado ground layer. Journal of Ecology, 109(1), 154-166.

R Core Team (2021). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/

Ribeiro, J. F., & Walter, B. M. T. (1998). Fitofisionomias do bioma Cerrado. Embrapa Cerrados-Capítulo em livro científico (ALICE).

Rodrigues, C. A., & Fidelis, A. (2022). Should we burn the Cerrado? Effects of fire frequency on open savanna plant communities. Journal of Vegetation Science, e13159.

Rodrigues, C. A., Zirondi, H. L., & Fidelis, A. (2021). Fire frequency affects fire behavior in open savannas of the Cerrado. Forest Ecology and Management, 482, 118850.

Rossatto, D. R., de Araújo, P. E., da Silva, B. H. P., & Franco, A. C. (2018). Photosynthetic responses of understory savanna plants: Implications for plant persistence in savannas under tree encroachment. Flora, 240, 34-39.

Santos, A. C., da Rocha Montenegro, S., Ferreira, M. C., Barradas, A. C. S., & Schmidt, I. B. (2021). Managing fires in a changing world: Fuel and weather determine fire behavior and safety in the neotropical savannas. Journal of environmental management, 289, 112508.

Sarmiento, G. (1992). Adaptive strategies of perennial grasses in South American savannas. Journal of Vegetation Science, 3(3), 325-336

Saugier, B., & Katerji, N. (1991). Alguns fatores vegetais que controlam a evapotranspiração. Meteorologia Agrícola e Florestal , 54 (2-4), 263-277.

Scanlon, T. M., & Albertson, J. D. (2004). Canopy scale measurements of CO2 and water vapor exchange along a precipitation gradient in southern Africa. Global Change Biology, 10(3), 329-341.

Silveira, J. M., Barlow, J., Krusche, A. V., Orwin, K. H., Balch, J. K., & Moutinho, P. (2009). Effects of experimental fires on litter decomposition in a seasonally dry Amazonian forest. Journal of Tropical Ecology, 25(6), 657-663.

Silveira, F. A., Ribeiro, R. C., Oliveira, D. M., Fernandes, G. W., & Lemos-Filho, J. P. (2012). Evolution of physiological dormancy multiple times in Melastomataceae from Neotropical montane vegetation. Seed Science Research, 22(1), 37-44.

Smits, K. M., Ngo, V. V., Cihan, A., Sakaki, T., & Illangasekare, T. H. (2012). An evaluation of models of bare soil evaporation formulated with different land surface boundary conditions and assumptions. Water Resources Research, 48(12).

Trollope, W. S. W. (1982). Ecological effects of fire in South African savannas. In Ecology of tropical savannas (292-306). Springer, Berlin, Heidelberg.

Vetaas, O. R. (1992). Micro-site effects of trees and shrubs in dry savannas. Journal of vegetation science, 3(3), 337-344.

Zanzarini V., Andersen AN, Fidelis, A. 2022. Flammability in tropical savannas: variation among growth-forms and seasons in Cerrado. Biotropica.

Zheng, S., Webber, B. L., Didham, R. K., Chen, C., & Yu, M. (2021). Disentangling biotic and abiotic drivers of intraspecific trait variation in woody plant seedlings at forest edges. Ecology and evolution, 11(14), 9728-9740.

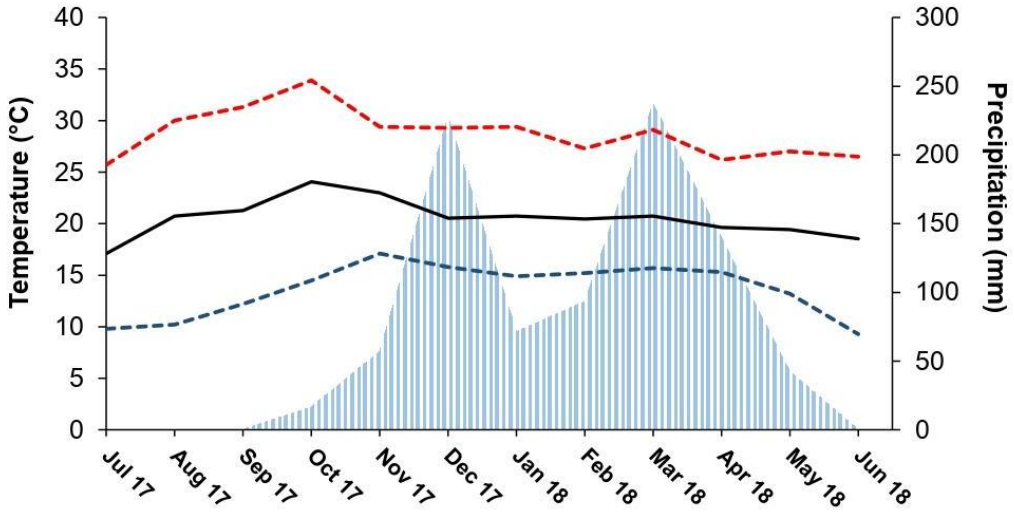
Zirondi, H., Ooi, M. K., & Fidelis, A. (2021). Fire-triggered flowering is the dominant post-fire strategy in a tropical savanna. Journal of Vegetation Science, 32(2), e12995.

Whelan, R. J. (1995). The ecology of fire. Cambridge university press.

Wolf, K. D., Higuera, P. E., Davis, K. T., & Dobrowski, S. Z. (2021). Wildfire impacts on forest microclimate vary with biophysical context. Ecosphere, 12(5), e03467.

**Supporting information**: Rodrigues & Fidelis. Microclimate is affected by fire frequency and seasonality in tropical open savannas of the Cerrado.

**Appendix S1.** Climatic diagram for Alto Paraíso de Goiás - GO (weather station closest to the study area), showing monthly mean temperature (black line), monthly mean maximum temperature (dotted red line), monthly mean minimum temperature (dotted blue line), and precipitation monthly total (area with vertical blue bands) during the study period (July 2017 to June 2018).




**Appendix S2.** Technical information and specifications for data loggers and sensors used to measure microclimate parameters. Information extracted from: https://www.onsetcomp.com/products?f%5B0%5D=product_type%3A931

| Microclimate parameter | Model | Operation Range |
|---|---|---|
| Illuminance | HOBO Pendant Temperature/Light 64K/UA-002-64 | 0 to 320,000 lux |
| Relative humidity | HOBO U23 Pro v2 External/U23-002A | 0 to 100% RH |
| Temperature | HOBO 2x External/U23-002A | -40 to 70°C |

**Appendix S3.** Results of Tukey test and pairwise comparisons from generalized linear mixed models (GLMM, family: Gaussian) analysis of open savanna plant communities of the Cerrado, under different fire frequency treatments: AF = annual fires, BF = biennial fires, and FE = fire exclusion by microclimate parameters recorded from July 2017 to July 2018.

| | | | | | Pairwise | | |
|---|---|---|---|---|---|---|---|
| Response | Period | npar | F-value | p | AF - BF | AF - FE | BF - FE |
| Illuminance | Mid/late-dry season | 2 | 1054.6 | <0.0001 | 0.9 | <0.0001 | <0.0001 |
| | Early-rainy season | | 291.7 | <0.0001 | 0.003 | <0.0001 | <0.0001 |
| | Mid-rainy season | | 123.8 | <0.0001 | 0.78 | <0.0001 | <0.0001 |
| | Late-rainy season | | 92.3 | <0.0001 | <0.0001 | <0.0001 | 0.0001 |
| Relative humidity | Early/mid-dry season | 2 | 274.7 | <0.0001 | <0.0001 | <0.0001 | <0.0001 |
| | Mid/late-dry season | | 434.8 | <0.0001 | <0.0001 | <0.0001 | <0.0001 |
| | Early-rainy season | | 20.7 | <0.0001 | 0.02 | 0.0008 | <0.0001 |
| | Mid-rainy season | | 10.9 | 0.01 | 0.12 | 0.17 | 0.09 |
| | Late-rainy season | | 26.1 | <0.0001 | 0.04 | <0.0001 | <0.0001 |
| Soil tempature | Early/mid-dry season | 2 | 912.8 | <0.0001 | <0.0001 | <0.0001 | <0.0001 |
| | Mid/late-dry season | | 1124.6 | <0.0001 | <0.0001 | <0.0001 | <0.0001 |
| | Early-rainy season | | 78.8 | <0.0001 | 0.9 | <0.0001 | <0.0001 |
| | Mid-rainy season | | 155.0 | <0.0001 | 0.0016 | <0.0001 | <0.0001 |
| | Late-rainy season | | 79.7 | <0.0001 | <0.0001 | <0.0001 | <0.0001 |
| Soil surface temperature | Early/mid-dry season | 2 | 150.5 | <0.0001 | <0.0001 | <0.0001 | <0.0001 |
| | Mid/late-dry season | | 172.9 | <0.0001 | <0.0001 | <0.0001 | <0.0001 |
| | Early-rainy season | | 25.5 | <0.0001 | 0.04 | <0.0001 | <0.0001 |
| | Mid-rainy season | | 29.1 | <0.0001 | 0.8 | <0.0001 | <0.0001 |
| | Late-rainy season | | 25.6 | 0.05 | 0.4 | 0.4 | 0.4 |
| Soil temperature amplitude | Early/mid-dry season | 2 | 10.3 | 0.001 | 0.07 | 0.2 | 0.2 |
| | Mid/late-dry season | | 172.8 | <0.0001 | 0.003 | <0.0001 | <0.0001 |
| | Early-rainy season | | 234.7 | <0.0001 | 0.001 | <0.0001 | <0.0001 |
| | Mid-rainy season | | 159.3 | <0.0001 | 0.001 | <0.0001 | <0.0001 |
| | Late-rainy season | | 136.9 | <0.0001 | 0.003 | <0.0001 | <0.0001 |
| Air temperature amplitude | Early/mid-dry season | 2 | 896.4 | <0.0001 | <0.0001 | <0.0001 | <0.0001 |
| | Mid/late-dry season | | 1002.3 | <0.0001 | <0.0001 | <0.0001 | <0.0001 |
| | Early-rainy season | | 86.3 | <0.0001 | 0.4 | <0.0001 | <0.0001 |
| | Mid-rainy season | | 796.9 | <0.0001 | <0.0001 | <0.0001 | <0.0001 |
| | Late-rainy season | | 804.6 | <0.0001 | <0.0001 | <0.0001 | <0.0001 |
| | Early/mid-dry season | | 63.4 | <0.0001 | 0.02 | 0.001 | 0.08 |

| Response | Period | npar | F-value | p | Pairwise | | |
|---|---|---|---|---|---|---|---|
| | | | | | AF - BF | AF - FE | BF - FE |
| Maximum soil temperature | Mid/late-dry season | 2 | 167.1 | <0.0001 | 0.001 | <0.0001 | <0.0001 |
| | Early-rainy season | | 65.3 | <0.0001 | 0.03 | <0.0001 | <0.0001 |
| | Mid-rainy season | | 98.3 | <0.0001 | 0.4 | 0.003 | 0.003 |
| | Late-rainy season | | 102.1 | <0.0001 | 0.08 | 0.001 | 0.001 |
| | Early/mid-dry season | | 726.4 | <0.0001 | >0.0001 | >0.0001 | >0.0001 |
| Maximum soil surface temperature | Mid/late-dry season | 2 | 679.3 | <0.0001 | <0.001 | <0.001 | <0.001 |
| | Early-rainy season | | 59.1 | <0.0001 | 0.2 | 0.007 | 0.006 |
| | Mid-rainy season | | 43.9 | <0.0001 | 0.07 | 0.01 | 0.2 |
| | Late-rainy season | | 74.7 | <0.0001 | 0.01 | 0.001 | 0.009 |
| | Early/mid-dry season | | 12.1 | 0.1 | 0.4 | 0.4 | 0.9 |

**Appendix S4.** Results of Tukey test and pairwise comparisons from generalized linear mixed models (GLMM, family: Gaussian) analysis of open savanna plant communities of the Cerrado, under different fire frequency treatments: AF = annual fires, BF = biennial fires, and FE = fire exclusion by variation in microclimate parameters over time.

| | | | | | Pairwise | | |
|---|---|---|---|---|---|---|---|
| Response | Period | npar | F-value | p | AF - BF | AF - FE | BF - FE |
| Δ Illuminance | Mid/late-dry x Early-rainy | 2 | 732.6 | <0.0001 | 0.003 | <0.0001 | <0.0001 |
| | Early-rainy x Mid-rainy | | 542.3 | <0.0001 | 0.002 | <0.0001 | <0.0001 |
| | Mid-rainy x Late-rainy | | 222.9 | <0.0001 | <0.0000 | 0.01 | <0.0001 |
| | Late-rainy x Early/mid-dry | | 304.5 | <0.0001 | <0.0001 | 0.05 | 0.0001 |
| Δ Relative humidity | Mid/late-dry x Early-rainy | 2 | 122.9 | <0.0001 | 0.1 | 0.001 | 0.001 |
| | Early-rainy x Mid-rainy | | 201.7 | <0.0001 | 0.6 | 0.007 | 0.009 |
| | Mid-rainy x Late-rainy | | 100.9 | 0.01 | 0.02 | 0.01 | 0.009 |
| | Late-rainy x Early/mid-dry | | 216.1 | <0.0001 | 0.01 | <0.0001 | <0.0001 |
| Δ Soil temperature | Mid/late-dry x Early-rainy | 2 | 457.3 | <0.0001 | 0.01 | <0.0001 | <0.0001 |
| | Early-rainy x Mid-rainy | | 11.2 | 0.07 | 0.6 | 0.8 | 0.8 |
| | Mid-rainy x Late-rainy | | 20.1 | 0.09 | 0.1 | 0.1 | 0.1 |
| | Late-rainy x Early/mid-dry | | 88.9 | <0.0001 | 0.003 | 0.003 | 0.02 |
| Δ Soil surface temperature | Mid/late-dry x Early-rainy | 2 | 60.2 | <0.0001 | 0.09 | 0.001 | 0.001 |
| | Early-rainy x Mid-rainy | | 25.5 | 0.07 | 0.05 | 0.08 | 0.05 |
| | Mid-rainy x Late-rainy | | 302.5 | 0.002 | 0.4 | 0.01 | 0.01 |
| | Late-rainy x Early/mid-dry | | 10.3 | 0.08 | 0.1 | 0.2 | 0.2 |

# 2. CAPÍTULO 2

## Fire exclusion and early dry-season fires negatively impact plant communities in tropical open savannas in the Cerrado

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### Abstract

In tropical savannas, fire influences assembling plant communities. Species richness, composition, and abundance of different growth forms may be affected by fire events and new environmental conditions post-fire, which can impact the functional diversity of the community and its functionality. Thus, we aimed to compare the influence of different fire regimes (seasons and frequencies) on plant communities of the herbaceous layer in open savanna over time. Further, we compared the effect of fire regimes on growth form cover, structure, and taxonomic and functional diversity after nine years of fire experiments. In 2013, we established a fire experiment with four 30x30m plots per treatment, including FE: fire exclusion since 2011, AF: annual fires, and biennial fires in EDF: early-, MDF: mid-, and LDF: late-dry seasons. Vegetation samplings were conducted in subplots (1m²x10subplots/ three - four plots/ five treatments = 180 total subplots) during the rainy and dry seasons from 2016 to 2022. We found that both frequency and season of fire influenced the species richness of plant communities. Fire regimes affected differently the richness of the growth forms. Fewer species of forb and graminoids were found in fire exclusion and early dry-season fires in all periods observed. EDF plots had the lowest graminoid and forb covers over time. The species composition of plant communities was also influenced by fire frequency and season. Species turnover drove changes among treatments and within each treatment over time. After nine years of experiments, we found a higher richness of forb, graminoids, and total species in AF, MDF, and LDF treatments. FE treatment presented lower total and forb richness, and together with EDF, the lowest richness of graminoids. The Shannon-Wiener index was lower in FE and EDF treatments. Functional diversity was highest in the AF treatment. In conclusion, plant communities

of the herbaceous layer in open savannas responded differently to distinct fire regimes. Differences among communities have appeared since the initial years of the experiment and were consolidated over time. Fire exclusion has had the most negative impact on plant communities, indicating that prescribed fire is essential not only for controlling fuel load accumulation but also for preserving the diversity of tropical savannas. Despite early dry-season fires being the most used for fire management in protected areas, they reduce the diversity of open savanna communities. Therefore, understanding the positive and negative aspects of each fire regime is crucial to use them efficiently and safely to ensure the conservation of the savannas.

**Keywords:** Cerrado, community dynamic, community structure, fire frequency, fire season, functional diversity, savannas, and taxonomic diversity.

## Introduction

In fire-prone ecosystems, like tropical savannas, species richness, composition, and abundance of different growth forms may be affected by fire events and new environmental conditions post-fire, which can impact the functional diversity and functionality of the community (Diaz & Cabido, 2001). Changes in plant communities after burnings occur due to distinct responses of species to fire directly and to alterations in the availability of space, nutrients, and light (Laterra & Solbrig, 2001). These responses include post-fire flowering (Pilon et al., 2018; Fidelis & Zirondi, 2021; Zirondi et al., 2021), resprouting (Bond & Midgley, 2001; Clarke et al., 2013; Zupo et al., 2020), seed dormancy break (Moreira et al., 2010; Keeley et al., 2011; Lamont and He, 2017; Zirondi et al., 2019), etc. Plant fire responses are adaptations selected by fire regimes under which the species evolved (Whelan, 1995; Pivello & Norton, 1996). Fire regime is a key driver in the vegetation of tropical savannas (Whelan, 1995; Bond & van Wilgen, 1996), varying in terms of frequency and season of occurrence, intensity (energy released), severity (the biological impact), and spatial extension (Whelan, 1995; Keeley, 2009). Fire frequency and season may influence post-fire seedling recruitment and resprouting of different growth forms (Whelan, 1995; Bond & van Wilgen, 1996), through the influence on fire behavior parameters such as intensity, flame temperatures, and fire residence time (Govender et al. 2006; Rissi et al. 2017; Rodrigues et al. 2021), which are important factors in plant survival and recovery.

Furthermore, depending on the frequency and season of fire, there may be changes in the functional traits of species in the community related to recruitment and persistence, such as bud bank size (Bombo et al., 2022), seed viability and dormancy (Zupo et al., 2020), resprouting capacity (Clarke et al., 2013), plant height (Dantas & Pausa, 2013), etc. Changes in functional traits can impact not only the persistence of species in the community but also ecosystem functionality, such as productivity and carbon storage (Diaz & Cabido, 2001; Parr et al., 2014; Zhao et al., 2020).

Burning in different seasons can distinctly affect plant communities in tropical savannas since they are modulated by seasonality. Biomass growth and production occur mainly during the rainy season, and during the dry season, such material dries and is converted into dead biomass (Sarmiento et al., 1985; Oliveira et al., 2013). After a fire event, vegetation recovery depends on water availability, which varies according to season (Quesada et al., 2004; Oliveras et al., 2013). Extended periods of water shortage can delay or even impact the ability of vegetation to regrow after fire (Quesada et al., 2004; Oliveras et al., 2013). Further, the species display different phenological stages, both reproductive and vegetative, to deal with such water availability across seasons (Knapp et al., 2009). Therefore, fires can affect plant species differently depending on the season in which they occur. Consequently, fires in different seasons can result in distinct plant communities due to their impact on post-fire community assembly.

In tropical open savannas, the return interval of fire is short (1 - 5 years) (Eiten, 1972; Russell-Smith & Yate, 2007; Archibaldi et al., 2013; Pivello, 2011). Plants in open savannas are resilient to frequent fires, resprouting quickly, flowering, and increasing productivity after fire (Rodrigues & Fidelis, 2022; Rodrigues et al. in prep.a). Hence, longer intervals between fires can alter the structure of vegetation and the species composition of plant communities (Abreu et al., 2017; Rodrigues & Fidelis, 2022). Extended periods without fire can cause woody encroachment, leading to a change from open to closed ecosystems and herbaceous layer species loss (Moreira, 2000; Abreu et al., 2017; Wieczorkowski & Lehmann, 2022). Moreover, when fire is excluded from the system, a substantial amount of dead biomass accumulates in the vegetation, altering the environmental conditions, such as a reduction in space availability and illuminance in the herbaceous layer (Fidelis et al., 2012; Rodrigues & Fidelis, in prep.b). All these changes caused by fire exclusion can lead to the

replacement of fire-adapted by fire-sensitive species, which tend to dominate the community (Abreu et al., 2017; Rodrigues & Fidelis, 2022). Despite the vegetation of open savannas is highly resilient to frequent fires (Rodrigues & Fidelis, 2022), high fire frequency can have negative long-term effects on the ecosystem, due to the depletion of plant storage and soil nutrients, impacting regeneration, productivity, and resource allocation (Pivello & Coutinho, 1996; Pivello, 2011). It can also cause changes in community structure, such as an increase in bare soil percentage (Rodrigues & Fidelis, 2022), which may open space to invasive species (Damasceno et al., 2018), affect the spread of fire in vegetation (Rodrigues et al., 2021), impact the seeds' survival (Daibes et al., 2018), etc.

In the Cerrado, like other tropical savannas, human activities have altered fire regimes (Pivello, 2011; Archibald et al., 2013). Agricultural practices have resulted in more frequent anthropogenic than natural fires (Pivello, 2011; Pivello et al., 2021). On the other hand, fire has been suppressed in protected areas of Cerrado for years, leading to wildfires (Fidelis et al., 2018) and loss of species diversity of the herbaceous layer, converting the open into closed ecosystems (Abreu et al., 2017). Fortunately, changes have occurred gradually, and integrated fire management (IFM) has been implemented to control fuel loads and maintain biodiversity (Schmidt et al., 2018; Schmidt & Eloy, 2020). However, it is crucial to understand the impact of different fire regimes on plant communities in open savannas to plan fire management actions effectively.

Thus, (i) we aimed to compare the influence of different fire frequencies and seasons on species richness, composition, growth forms cover, and structure of plant communities of the herbaceous layer in open savanna over time from 2016 to 2022. Complementarily, (ii) we compared the effect of fire regimes on these community variables, and on both taxonomic and functional diversity after nine years of fire experiments. (i) We hypothesize that annual fires will reduce the cover of graminoids and shrubs over time compared to biennial fires and fire exclusion. This is due to the depletion of resprouting resources and increased shrub mortality from extremely frequent burnings. However, species richness, mostly of forbs, increases under annual and biennial fires compared to fire exclusion, since there is less cover of dead biomass and graminoids of dense tussock in burned areas. For the same reason species composition differs among fire frequency treatments, with fire exclusion promoting

fewer forb and more shrub species than annual and biennial fires. Among fire season treatments, fire in the early-dry season will reduce the cover of all growth forms and species richness and increase bare soil percentage over time compared to mid and late dry season fires, due to the longer water restriction time after fire occurrence. Species composition will also differ among fire season treatments, with species more sensitive to longer hydric restriction decreasing in communities burned in the early dry season and species sensitive to more intense fire decreasing in communities burned in the late dry season. (ii) After nine years of fire experiments, plant communities under different fire regimes exhibit differences in structure, taxonomic diversity, and functional diversity. Annual fires will result in the highest taxonomic and functional diversity, followed by late and mid-dry season fires, then early dry-season fires, and last by fire exclusion treatment since the lower the cover of dead biomass and the dominance of dense tussock graminoids increase the richness of forbs and small graminoids and shrubs. Conversely, fire exclusion will result in higher ground cover by dead biomass and graminoids. Among the treatments with experimental fires, early dry-season fires will promote the lowest richness and cover of growth forms due to longer hydric restriction post-fire which may delay or even damage the regrowth of plants. We expect that the results of this study will contribute to data-driven management actions to conserve the biodiversity of tropical open savannas.

## Material and methods

### *Study area*

This study was conducted at the Reserva Natural Serra do Tombador (RNST, 13° 35-38 'S and 47 ° 45-51' W, 8900 ha, 560–1118m a.s.l., Central Brazil). The climate is tropical, with dry winters and rainy summers, average annual rainfall between 1300-1500 mm, maximum average temperatures between 26 and 36°C, and minimum temperatures between 8 and 14°C (Antonelli-Filho, 2011). Fire experiments were installed in an area of open savanna (*campo sujo*), in which the fuel load bed is continuous and mainly consists of graminoids (Ribeiro & Walter, 1998). Before the creation of the protected area in 2006, fires occurred every three years (Daldegan et al., 2014). In 2011, during the dry season, a wildfire occurred at the location where fire

experiments were to be conducted. As a result, the experiments had to be postponed until 2013, when the vegetation had recovered enough to support the experiments. Therefore, before the experiments began, all the plots had the same fire frequency and time since the last fire.

C4 grasses are the dominant growth form in the species-rich herbaceous layer. The most common species are *Mesosetum ferrugineum* (Trin.) Chase, *Oncorachis ramosa* (Zuloaga & Soderstr.) Morrone & Zuloaga, *Axonopus aureus* P. Beauv., *Elionurus muticus* (Spreng.) Kuntze, *Aristida setifolia* Kunth, and *Paspalum pectinatum* Nees ex Trin. (Rodrigues & Fidelis, 2022). There is a great richness of forbs and shrubs (Rodrigues & Fidelis, 2022), including several endemic species of the RNST, such as *Harpalyce tombadorensis* São-Mateus et al. (São-Mateus et al., 2019), *Mimosa cavalcantina* T.P.Mendes, Marc.F.Simon & M.J.Silva (Mendes et al., 2022), and *Microlicia rubra* Ferreira-Alves & R.Romero (Ferreira-Alves & Romero, 2020).

*Experimental design*

Experimental plots (30x30m) were established with four plots for each treatment. A minimum distance of four meters was maintained between the plots. Soil, climate conditions, and vegetation structure were consistent across all plots before the beginning of the experiments (Rissi, 2016). We have plots with different fire frequencies: annual (AF, burned annually since July 2013, a total of nine fires), biennial (BF, burned biennially since July 2013, a total of five fires), and exclusion (FE, fire exclusion since 2011), and fire seasons: early (EDF, burned biennially in May, early-dry season fires), mid (MDF, burned biennially in July, mid-dry season fires), and late (LDF, burned biennially in October, late-dry season fires). Table 1 displays the years in which each treatment was burned, from 2013 to 2021, and the data of vegetation surveys available for each treatment. Experimental fires could not be conducted in May 2017, resulting in the postponement of the EDF plots' burning to May 2018. The COVID-19 pandemic further delayed the planned AF and EDF treatments in 2020, which were rescheduled to 2021. The mid- and late-dry season fires remained unaffected by the pandemic. Thus, we have collected data from 2016 to 2022, every rainy (January) and dry season (July). However, in some periods, vegetation surveys were not conducted for some fire treatments (See Table 1).

**Table 1.** Years in which experimental fires were carried out in open savannas of the Cerrado (Central Brazil) from 2013 to 2021, and the data of vegetation surveys available for each treatment (from 2016 to 2022). AF - annual fires; EDF - Early dry season fires; MDF - mid dry season fires; LDF - late dry season fires; and FE - fire exclusion).

| Treatment | Fires | Vegetation surveys data | |
|---|---|---|---|
| | | Rainy season | Dry season |
| AF | 2013, 2014, 2015, 2016, 2017, 2018, 2019, and 2021 | 2018, 2019, 2020, and 2022 | 2016, 2017, 2018, 2019, 2021, and 2022 |
| EDF | 2013, 2015, 2018, and 2021 | 2017, 2018, 2019, 2020, and 2022 | 2016, 2018, 2019, 2021, and 2022 |
| MDF | 2013, 2015, 2017, 2019, and 2021 | 2017, 2018, 2019, 2020, and 2022 | 2016, 2017, 2018, 2019, 2021, and 2022 |
| LDF | 2013, 2015, 2017, 2019, and 2022 | 2017, 2018, 2019, 2020, and 2022 | 2016, 2017, 2018, 2019, 2021, and 2022 |
| FE | - | 2017, 2018, 2019, 2020, and 2022 | 2016, 2017, 2018, 2019, 2021, and 2022 |

Within each experimental plot, 10 fixed subplots of 1 m² were randomly established in a grid (of 100x100m) for vegetation surveys. We visually estimated the cover (%) for bare soil, dead biomass (standing + litter), and for each species up to 150 cm in height. All plants were identified until the highest taxonomic level possible. We grouped species according to their growth form: graminoids (Poaceae and Cyperaceae), forbs (subshrubs were included in forbs), and shrubs. Vegetation was sampled every six months until July 2022 (in the rainy and mid-dry seasons).

To determine community taxonomic diversity, we used species richness, Shannon-Winner, Simpson, and evenness (J) index metrics. To determine functional diversity, we measured ten plant functional traits on the dominant species from every treatment to calculate the functional diversity (FD) index. We measured functional fire-related traits: growth form, height, branching architecture, belowground organ type, and concentration in leaves of the following elements: Nitrogen, Phosphor, Potassium, Calcium, Magnesium, and Sulfur (Appendix S1, Cornelissen et al., 2003; Pérez-Harguindeguy et al., 2013). We considered as dominant plant species those plants that represented 80% of vegetation cover in the community in each fire treatment. Functional traits have been measured in three different individuals for each species in

each treatment (Cornelissen et al., 2003; Perez-Harguindeguy et al., 2016). To avoid measuring the same plant, each individual was sampled at least three meters from the nearest neighbor of the same species, given that clonal growth is common in savannas (Lamont et al., 2011; Pausas et al., 2018). Measurements were performed in the rainy season of 2022.

*Statistical analysis*

(i) Compare communities under different fire frequencies and seasons over time.

We used generalized additive mixed modeling (GAMM) to investigate the effects of fire frequency and season across time on total and growth forms species richness, as well as the cover of dead biomass, bare soil, forb, graminoids, and shrubs over time. We proceeded to model selection based on the restricted maximum likelihood criteria (REML). We performed the analysis using the “gam” function.

To investigate the dissimilarity level of plant communities under different fire frequencies and seasons, we used two data matrices: the first with sampling units described by species cover (Bray–Curtis as resemblance measurement), and the other described by species presence/absence (Jaccard as resemblance measurement). To compare plant community composition among fire treatments, we performed permutational multivariate variance analysis (PERMANOVA), considering the values of the dissimilarity indices, using the “adonis” function. We compared the pairwise plot level species composition among plant communities with distinct treatments using pairwise post hoc tests of HSD Tukey type, including Bonferroni corrections for multiple comparisons, by “pairwise.adonis” function. Further, we calculated beta-diversity components (nestedness and turnover) among treatments using the “beta.pair” function and we identified significant ($p < 0.05$) indicator species for each fire frequency and season using the “multipart” function, considering frequency and abundance of the species.

(ii) Compare the effects of all different fire regimes after nine years of experiments.

Shannon-Winner, Simpson, and J index were obtained by the “diversity” function using the July 2022 survey data. FD index was obtained by using the “pd” function. To evaluate the effect of fire seasons and frequencies on growth form covers,

community structure, and taxonomic and functional diversity of plant communities after nine years of fire experiments, we performed General linear mixed models (GLMMs) using the “glmer” function. Significant differences among treatments were assessed by performing the Tukey test using the “emmeans” function.

All statistical analyses were performed using the R software (R Core Team, 2023) with the packages *mgcv* (Wood, 2011), *ggeffects* (Lüdecke, 2018), *ggplot2* (Wickham & Wickham, 2009), *vegan* version 2.5-7 (Oksanen et al., 2020), *pairwiseAdonis* (version 0.0.1, R Core Team, R Foundation for Statistical Computing, Vienna, AT), *betapart* version 1.5.4 (Baselga et al., 2020), *indicspecies* (Cáceres & Legendre, 2009), *picante* (Kembel et al., 2010), *lme4* version 1.1-27.1 (Bates et al., 2015), *emmeans* (Lenth, 2023), and *stats* version 4.1.1 (R Core Team, 2023).

## Results

Influence of fire frequency and season on plant communities over time

We found that both fire frequency and season influenced both total and growth form species richness of plant communities (Appendix S2). The total species richness presented a variation similar to forb richness, increasing in AF and BF plots and decreasing in FE ones over time (Figure 1a). Growth form richness was affected differently by fire treatments. After three years of experiments, in July 2016, we found that AF plots already had a higher forb richness than BF and FE treatments, which had the same forb richness. After that, forb richness increased in BF plots, becoming similar to AF plots, whereas it decreased in FE plots (Figure 1b). Over time, species richness of graminoids increased in all fire frequency treatments. However, it remained higher in AF plots compared to other fire frequencies throughout time (Figure 1c). Shrub richness was not influenced by fire frequency, not changing over time or among treatments (Figure 1d).

Fire season also influenced both the total and growth form species richness of plant communities (Appendix S2). Total species richness was lower in EDF than MDF and LDF plots during all periods observed (1e). EDF plots also had a lower richness of both graminoids and forbs during all periods observed, while mid and LDF plots had the same forb and graminoid richness (1f and g). Nevertheless, forb and graminoid

richness increased over time independently of fire season. Fire season did not influence shrub richness (Figure 1h).

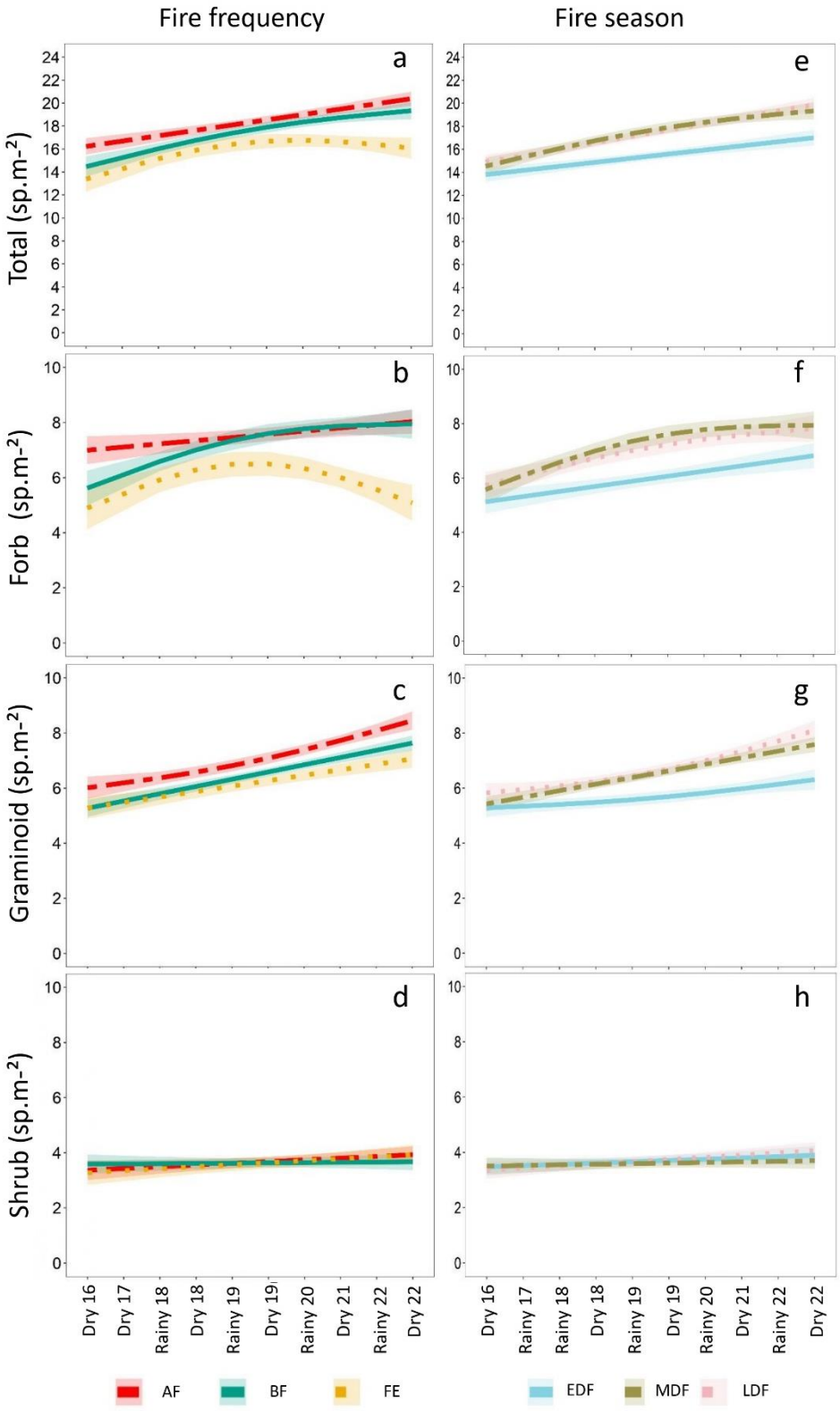


**Figure 1.** Total (a-e), forb (b-f), graminoid (c-g), and shrub (d-h) species richness (spp.m$^{-2}$) by fire frequency (AF: annual fires, BF: biennial fires, and FE: fire exclusion since 2011) and fire season (EDF: early, MDF: mid, and LDF: late-dry season fires) treatments in an open savanna area of Cerrado from 2016 to 2022. Lines are predicted values by the best-fitted model, and the shaded areas are the corresponding 95% confidence intervals.

Cover of growth forms and dead biomass, as well as bare soil, were influenced by fire frequency and season. Over time, forb, graminoid, and shrub cover decreased in all treatments. In fire frequency treatments, forb cover was initially higher in AF and BF plots, but the differences reduced over time, and by July 2022, all treatments had the same forb cover (Figure 2a). Graminoid and shrub cover increased in FE plots, then decreased, and became equal to AF and BF plots (Figure 2b-c). Bare soil percentage remained relatively stable over time in fire frequency treatments, prevailing the highest percentage in AF plots and twice as low in FE plots (Figure 2d). Opposite of bare soil percentage, dead biomass cover was 2-fold higher in FE plots and predominantly lower in AF plots (Figure 2e). Among the fire season treatments, during the initial years of the experiments, forb and graminoid cover were higher in MDF and LDF plots, then decreased and became similar to the cover found in EDF plots (Figure 2f-g). Shrub cover was equal among treatments in all surveys (Figure 2h). The percentage of bare soil changed little over time and was similar among all treatments in most observations (Figure 2i). On the other hand, the cover of dead biomass was lower in the MDF and LDF plots at the beginning of the experiment. However, it increased over time and surpassed the values of the EDF plots, only to decrease again and become the same as in EDF plots (Figure 2 j).

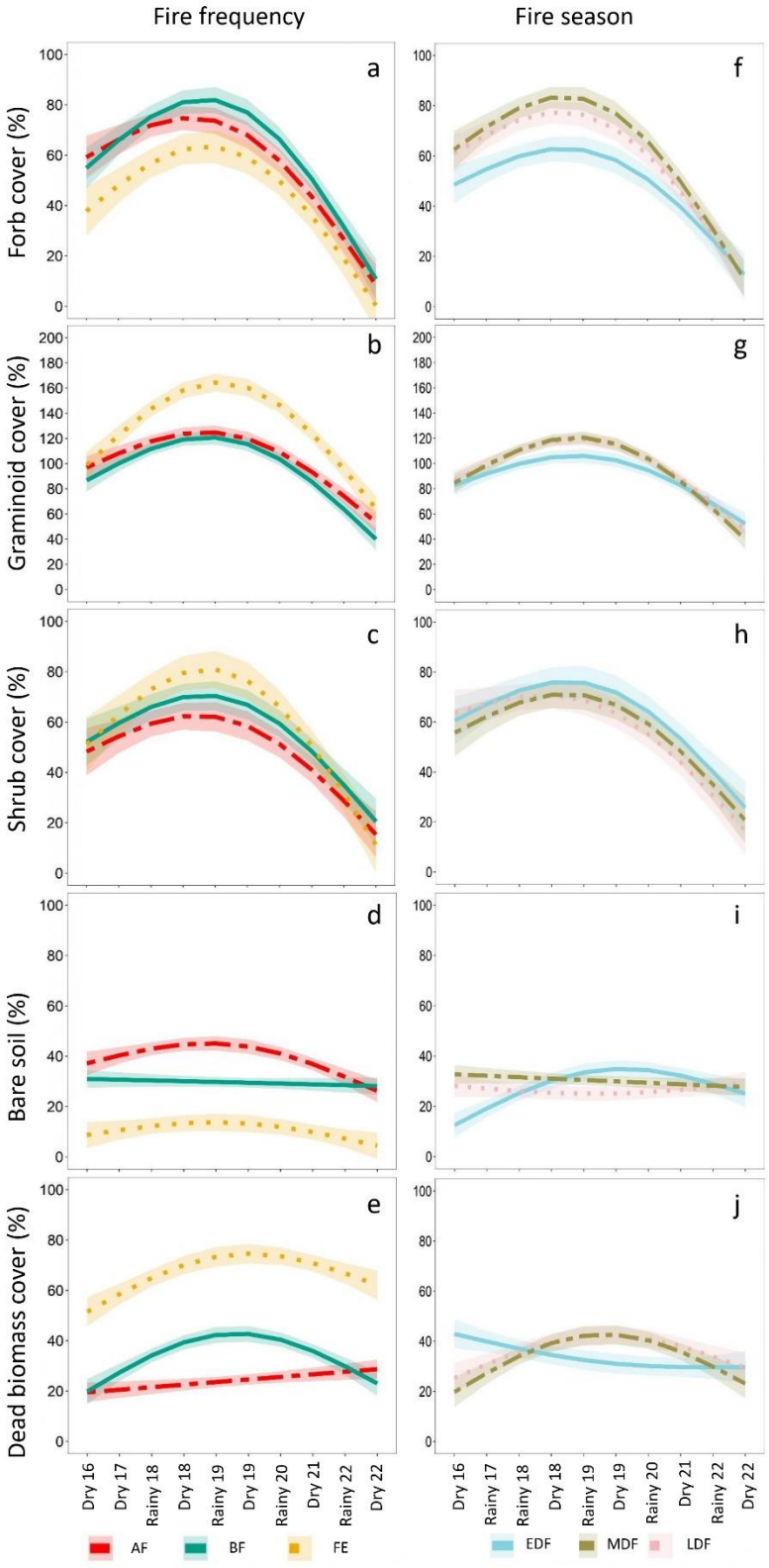


**Figure 2.** Forb (a-f), graminoid (b-g), shrub (c-h), bare soil (d-i), and dead biomass (e-j) cover (%) by fire frequency (AF: annual fires, BF: biennial fires, and FE: fire exclusion since 2011) and fire season (EDF: early, MDF: mid, and LDF: late-dry season fires) treatments in an open savanna area of Cerrado from 2016 to 2022. Lines are predicted values by the best-fitted model, and the shaded areas are the corresponding 95% confidence intervals.

Furthermore, we found that the species composition of plant communities was influenced by fire frequency and season. However, the communities of each treatment changed over time mostly due to the alterations in the abundance of species (Figure 3 A-C) rather than the presence/absence of particular species (Figure 3 B-D). On the other hand, the species composition of communities under different treatments differed more in presence/absence than in the abundance of species. Regarding fire frequency, FE plots had a distinct plant community from AF and BF plots ($p = 0.0001$). As for fire season, EDF plots differed from MDF and LDF plots ($p = 0.003$). The dissimilarity analysis of plant communities revealed that the differences in species composition were mainly a result of species turnover rather than loss. Species turnover drove changes among treatments and within each treatment over time (Tables 2 and 3).

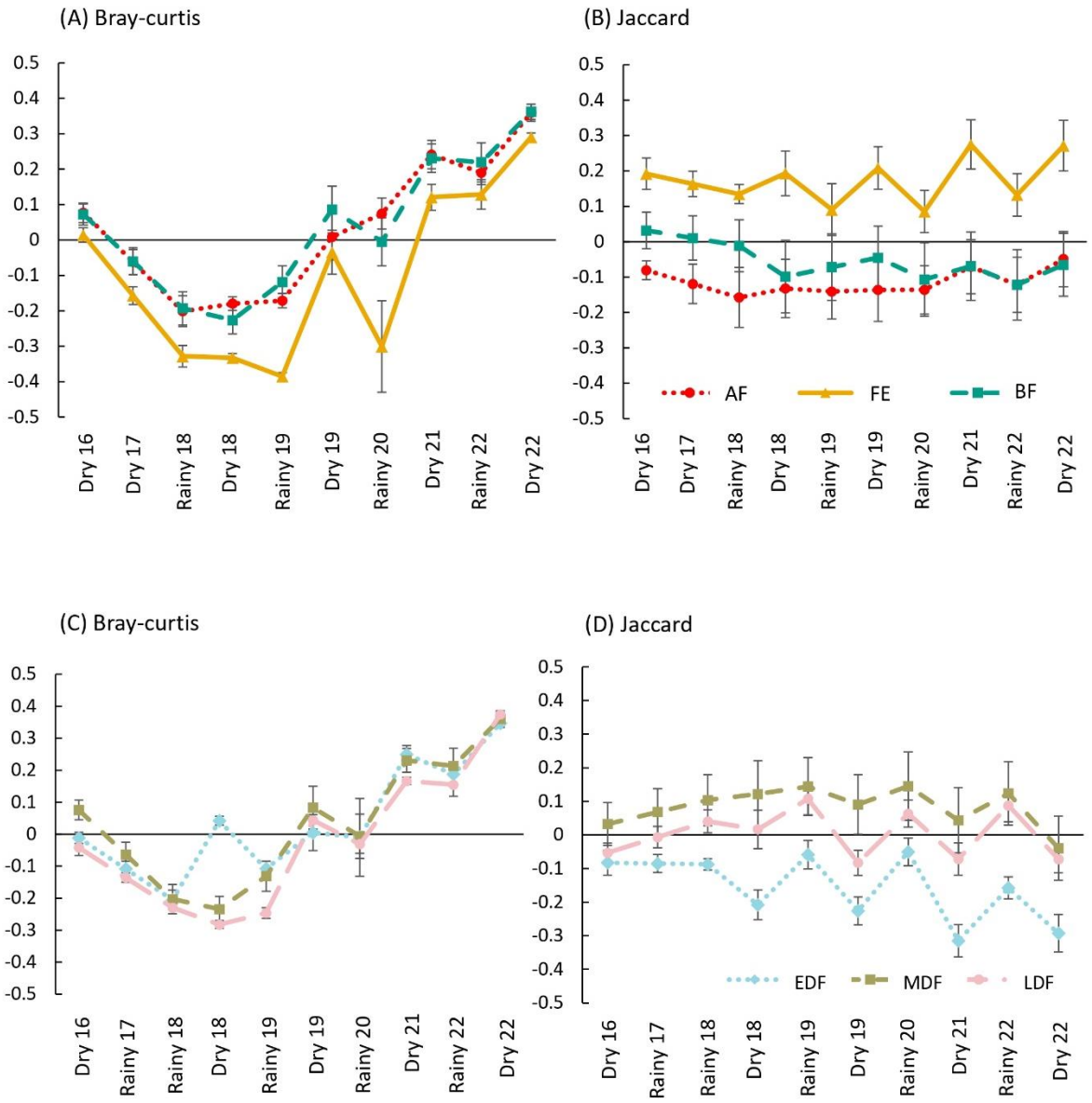


**Figure 3.** Principal coordinate analysis (PCoA) species cover (%, Bray-Curtis distance); presence/absence (Jaccard distance) at the different fire frequencies (annual, biennial, and exclusion since 2011) and seasons (early, mid, and late- dry season fires) from 2016 to 2022. Lines are the mean values and error bars are the standard error of PCoA scores.

**Table 2.** Betapart partitioning of beta-diversity (Jaccard) into nestedness and turnover components, between fire frequency treatments in all sampling times.

| Time | Pairs | Turnover | Nestedness | Total |
|---|---|---|---|---|
| | Annual - Exclusion | 0.425 | 0.033 | 0.458 |
| Dry 2016 | Annual - Biennial | 0.363 | 0.053 | 0.416 |
| | Biennial - Exclusion | 0.3 | 0.017 | 0.317 |
| | Annual - Exclusion | 0.298 | 0.108 | 0.406 |
| Rainy 2018 | Annual - Biennial | 0.219 | 0.134 | 0.353 |
| | Biennial - Exclusion | 0.359 | 0.007 | 0.366 |
| | Annual - Exclusion | 0.253 | 0.151 | 0.404 |
| Dry 2018 | Annual - Biennial | 0.22 | 0.007 | 0.227 |
| | Biennial - Exclusion | 0.207 | 0.169 | 0.376 |
| | Annual - Exclusion | 0.224 | 0.085 | 0.309 |
| Rainy 2019 | Annual - Biennial | 0.252 | 0.051 | 0.303 |
| | Biennial - Exclusion | 0.336 | 0.026 | 0.362 |
| | Annual - Exclusion | 0.309 | 0.098 | 0.407 |
| Dry 2019 | Annual - Biennial | 0.301 | 0.042 | 0.343 |
| | Biennial - Exclusion | 0.309 | 0.06 | 0.369 |
| | Annual - Exclusion | 0.313 | 0.006 | 0.319 |
| Rainy 2020 | Annual - Biennial | 0.206 | 0.031 | 0.237 |
| | Biennial - Exclusion | 0.28 | 0.034 | 0.314 |
| | Annual - Exclusion | 0.273 | 0.123 | 0.396 |
| Dry 2021 | Annual - Biennial | 0.289 | 0.055 | 0.344 |
| | Biennial - Exclusion | 0.342 | 0.062 | 0.404 |
| | Annual - Exclusion | 0.268 | 0.1 | 0.368 |
| Rainy 2022 | Annual - Biennial | 0.239 | 0.024 | 0.263 |
| | Biennial - Exclusion | 0.289 | 0.076 | 0.365 |
| | Annual - Exclusion | 0.281 | 0.157 | 0.438 |
| Dry 2022 | Annual - Biennial | 0.233 | 0.046 | 0.279 |
| | Biennial - Exclusion | 0.358 | 0.104 | 0.462 |

**Table 3.** Betapart partitioning of beta-diversity (Jaccard) into nestedness and turnover components, between fire season treatments in all sampling times.

| Time | Pairs | Turnover | Nestedness | Total |
|---|---|---|---|---|
| | Early - Late | 0.222 | 0.031 | 0.253 |
| Dry 2016 | Early - Mid | 0.222 | 0.059 | 0.281 |
| | Late - Mid | 0.189 | 0.031 | 0.22 |
| | Early - Late | 0.194 | 0.123 | 0.317 |
| Rainy 2018 | Early - Mid | 0.333 | 0.062 | 0.395 |
| | Late - Mid | 0.321 | 0.036 | 0.357 |
| | Early - Late | 0.305 | 0.113 | 0.418 |
| Dry 2018 | Early - Mid | 0.231 | 0.227 | 0.458 |
| | Late - Mid | 0.192 | 0.123 | 0.315 |
| | Early - Late | 0.307 | 0.055 | 0.362 |
| Rainy 2019 | Early - Mid | 0.326 | 0.041 | 0.367 |
| | Late - Mid | 0.288 | 0.014 | 0.302 |
| | Early - Late | 0.26 | 0.093 | 0.353 |
| Dry 2019 | Early - Mid | 0.309 | 0.145 | 0.454 |
| | Late - Mid | 0.372 | 0.059 | 0.431 |
| | Early - Late | 0.211 | 0.097 | 0.308 |
| Rainy 2020 | Early - Mid | 0.211 | 0.118 | 0.329 |
| | Late - Mid | 0.291 | 0.02 | 0.311 |
| | Early - Late | 0.387 | 0.149 | 0.536 |
| Dry 2021 | Early - Mid | 0.387 | 0.155 | 0.542 |
| | Late - Mid | 0.352 | 0.007 | 0.359 |
| | Early - Late | 0.38 | 0.041 | 0.421 |
| Rainy 2022 | Early - Mid | 0.256 | 0.106 | 0.362 |
| | Late - Mid | 0.238 | 0.058 | 0.296 |
| | Early - Late | 0.328 | 0.087 | 0.415 |
| Dry 2022 | Early - Mid | 0.352 | 0.097 | 0.449 |
| | Late - Mid | 0.37 | 0.015 | 0.385 |

Both in July 2016 and July 2022, exclusive species were observed in all treatments. Among fire frequency treatments, AF plots had the highest number of exclusive species (14 in both years), followed by BF plots (10 in 2016 and 12 in 2022) and FE plots with only seven in 2016 and five in 2022. However, species in common among treatments were changed from 2016 to 2022. In July 2016 FE and BF had more common species each other than with AF. Then, in July 2022 the AF and BF plots had more species in common with each other than with the exclusion plots (Figure 4A-B and Appendix S3). Among fire season treatments, MDF plots had the highest number of exclusive species (11 in 2016 and 12 in 2022), followed by EDF (six in 2016 and 10 in 2022), and LDF fire plots with only four in 2016 and five in 2022. MDF and LDF had more species in common with each other than with the EDF plots in both years (Figure 4C-D and Appendix S3).

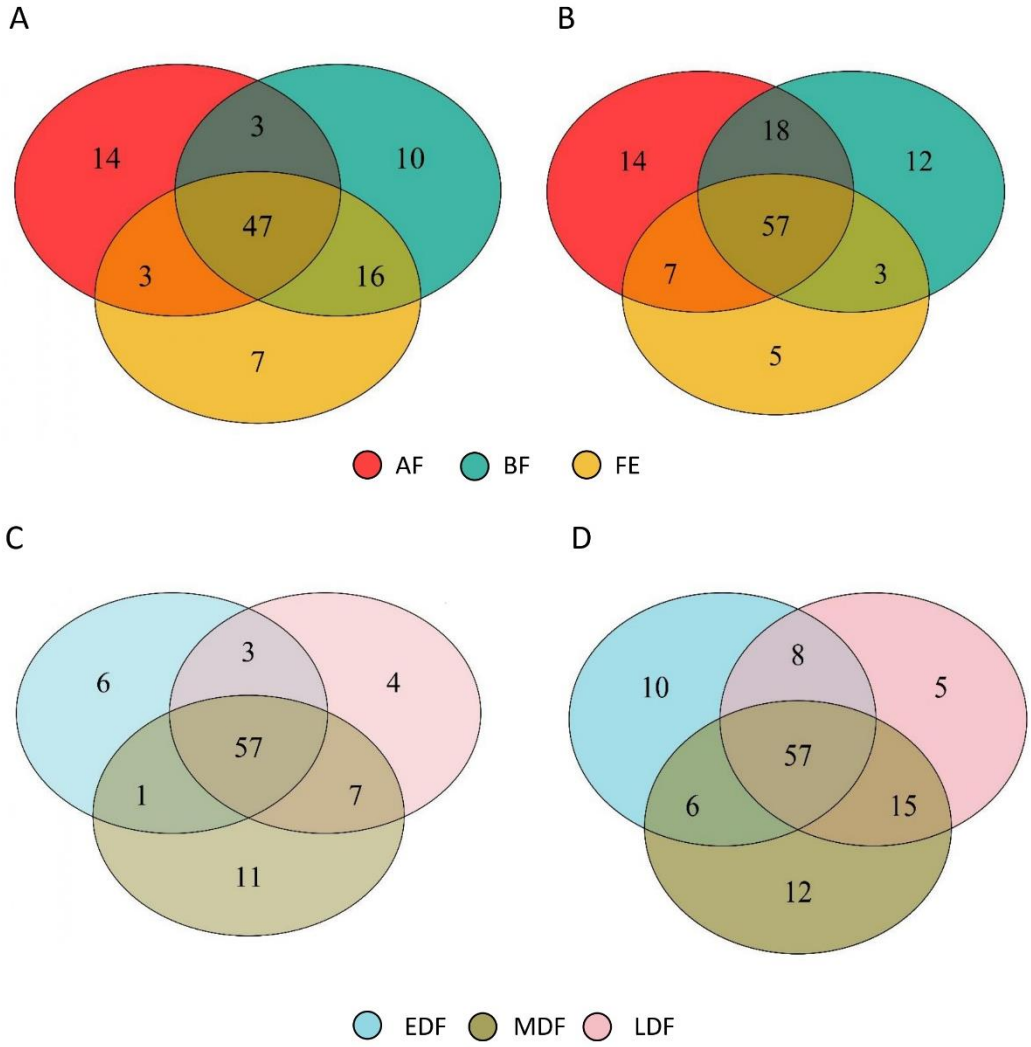


**Figure 4.** Venn diagram of shared and exclusive species in the plant communities A - fire frequency treatments in July 2016 (AF: annual fires, BF: biennial fires, and FE: fire exclusion since 2011), and B – in July 2022; C - fire season treatments in July 2016 (EDF: early, MDF: mid, and LDF: late-dry season fires), and D - in July 2022.

Moreover, we found changes in indicator species of each plant community between July 2016 and July 2022 (Table 4). Not only the identity of indicator species in each treatment was changed, but the growth form was also changed (Table 4). In FE plots, for example, during July 2016 one graminoid of small tussock, one of dense tussock, and one forb were the indicator species. In July 2022 one shrub and two graminoids of dense tussocks were indicator species in FE.

**Table 4.** Indicator species for each fire frequency and season considering frequency and abundance of the species in plant communities of open savanna on Cerrado in Central Brazil in July 2016 and 2022. AF: annual fires, EDF: early, MDF: mid, LDF: late dry season fires, and FE: fire exclusion since 2011.

| Date | Treatment | Species | Growth form | stat | p.value |
|---|---|---|---|---|---|
| July 2016 | AF | *Borreria poaya* | Forb | 0.861 | 0.013 |
| | | *Mesosetum loliiforme* | Graminoid of small tussock | 0.773 | 0.037 |
| | BF | *Ouratea lanceolata* | Shrub | 0.935 | 0.019 |
| | | *Chamaecrista ochrosperma* | Forb | 0.809 | 0.029 |
| | FE | *Bulbostylis paradoxa* | Graminoid of small tussock | 0.902 | 0.01 |
| | | *Oncorachis ramosa* | Graminoid of dense tussock | 0.87 | 0.01 |
| | | *Hypenia sp* | Forb | 0.866 | 0.023 |
| | AF + BF | *Chamaecrista claussenii* | Forb | 0.727 | 0.041 |
| | BF + FE | *Heteropterys pannosa* | Shrub | 0.757 | 0.05 |
| July 2022 | AF | *Declieuxia lancifolia* | Forb | 0.905 | 0.003 |
| | BF | *Chamaecrista ochrosperma* | Forb | 0.632 | 0.015 |
| | FE | *Annona tomentosa* | Shrub | 0.897 | 0.008 |
| | | *Mesosetum ferrugineum* | Graminoid of dense tussock | 0.866 | 0.008 |
| | | *Oncorachis ramosa* | Graminoid of dense tussock | 0.854 | 0.008 |
| | AF + BF | *Elionurus muticus* | Graminoid of small tussock | 0.786 | 0.016 |
| | | *Trachypogon spicatus* | Graminoid of small tussock | 0.759 | 0.041 |
| July 2016 | LDF | *Anemopaegma arvense* | Forb | 0.765 | 0.048 |
| | EDF + LDF | *Gymneia chapadensis* | Forb | 0.763 | 0.039 |
| | | *Harpalyce tombadorensis* | Shrub | 0.728 | 0.021 |
| July 2022 | EDF | *Ouratea lanceolata* | Shrub | 0.796 | 0.015 |
| | | *Paspalum pectinatum* | Graminoid of small tussock | 0.778 | 0.024 |
| | | *Ichthyothere hirsuta* | Forb | 0.67 | 0.04 |

Effects of the different fire regimes on plant communities after nine years.

After nine years of fire experiments, we observed differences in plant communities according to the different fire regimes. Structure and growth form cover significantly differed among the treatments. Significant differences were observed mainly in bare soil and dead biomass cover. Bare soil percentage was four to six times lower in FE in comparison to the other treatments. FE treatment had the highest percentage of dead biomass, followed by EDF, LDF, MDF, and AF treatments (Table 5 and Appendix S4). Forb cover was lowest in exclusion plots. Graminoid cover differed only among exclusion plots and MDF and LDF plots, with higher cover in exclusion ones. Shrub cover differed only in EDF and AF plots, with higher cover in EDF plots.

Overall, we found higher species richness in AF, MDF, and LDF treatments. Total and graminoid richness were lower in FE and EDF plots than in other treatments. Forb richness was lowest in FE plots. Shrub richness was similar among all treatments (Table 5 and Appendix S4).

**Table 5.** Species richness of forbs, graminoids, shrubs, and total (mean ± se, sp.m$^{-2}$) and bare soil, dead biomass, forbs, graminoids, and shrubs cover (mean ± se, %) of plant communities of open savannas under different fire regimes (AF: annual fires, EDF: early, MDF: mid, and LDF: late dry season fires, and FE: fire exclusion since 2011) in July 2022.

| | | Treatments | | | | |
|---|---|---|---|---|---|---|
| | | **AF** | **EDF** | **MDF** | **LDF** | **FE** |
| Richness (sp.m$^{-2}$) | Forb | 7.5 ± 0.3 | 6.6 ± 0.3 | 7.7 ± 0.3 | 7.1 ± 0.3 | 4.7 ± 0.3 |
| | Graminoid | 8.9 ± 0.2 | 7 ± 0.2 | 8 ± 0.2 | 8.5 ± 0.2 | 7.1 ± 0.3 |
| | Shrub | 4 ± 0.3 | 4 ± 0.3 | 3.4 ± 0.3 | 4.2 ± 0.3 | 3.54 ± 0.3 |
| | Total | 20.5 ± 0.5 | 17.7 ± 0.6 | 19.2 ± 0.5 | 19.8 ± 0.5 | 15.5 ± 0.6 |
| Cover (%) | Bare soil | 36.7 ± 2 | 26.7 ± 2 | 32.2 ± 2 | 34.4 ± 2 | 6 ± 2 |
| | Dead biomass | 33.6 ± 3.9 | 55 ± 4.5 | 37 ± 3.9 | 43.3 ± 3.9 | 78 ± 3.9 |
| | Forb | 17.6 ± 1.5 | 18.2 ± 2 | 23.9 ± 1.5 | 17.9 ± 1.5 | 9.3 ± 2 |
| | Graminoid | 67 ± 3 | 67 ± 3 | 57 ± 3 | 58 ± 3 | 78 ± 3 |
| | Shrub | 18.6 ± 3 | 30.4 ± 3 | 23 ± 3. | 20 ± 3 | 18 ± 3 |

The species diversity index differs only to the Shannon-Wiener index, which was significantly higher in AF than FE and EDF treatments (Figure 5a-b-c and Appendix S5). Functional diversity was highest in the AF treatment, followed by the LDF treatment, then the MDF and EDF treatment, and lowest in the FE treatment (Figure 5d and Appendix S5).

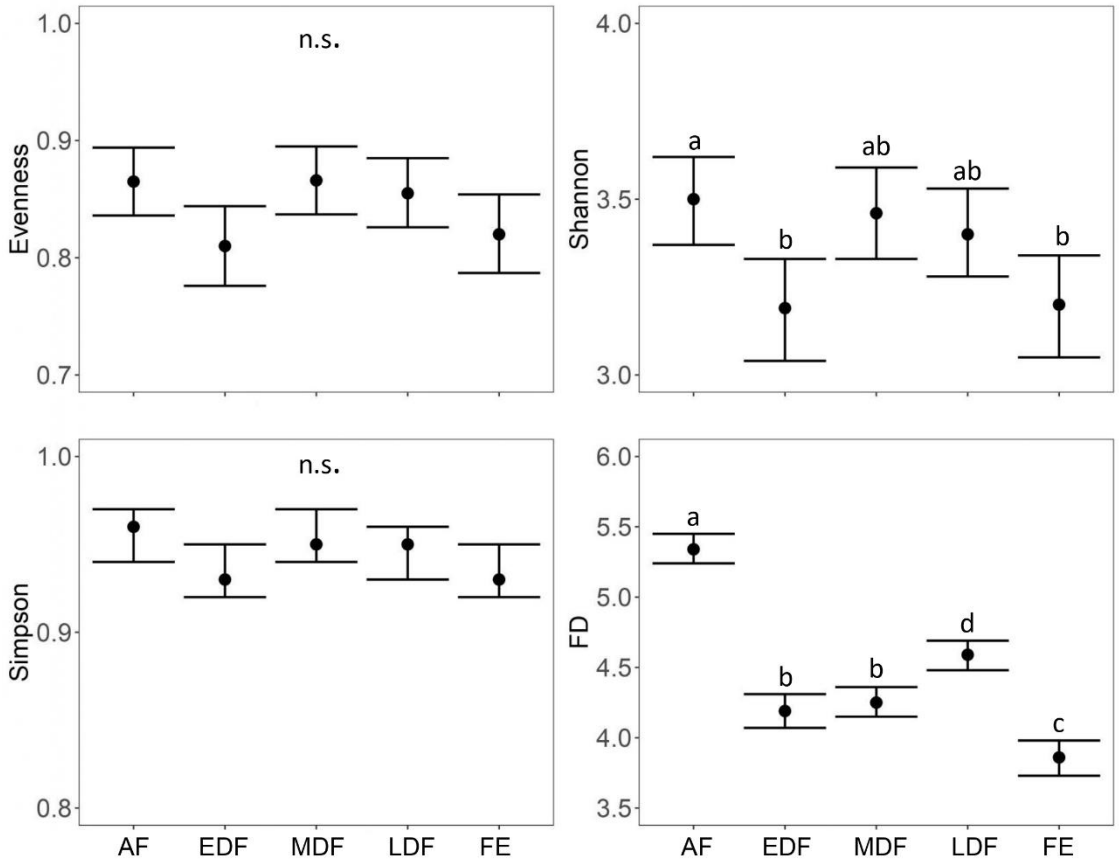


**Figure 5.** a – Evenness index; b – Shannon-Winner index; c – Simpson index; d – Functional diversity index in áreas of open savanna under different fire treatments (AF: annual fire, EDF: early, MDF: mid, LDF: late dry season fire, and FE: fire exclusion since 2011) in 2022. Values are mean and error bars correspond to standard error.

## Discussion

Fire frequency and season influenced open savanna plant communities, not only by affecting taxonomic and functional diversity but also community structure, composition, and abundance of species. Our comparison of fire frequency treatments revealed that fire exclusion in open savannas prejudiced the herbaceous layer. The FE plots exhibited the lowest species richness of forb, graminoid, and total, as well as lower forb cover, since the first years of fire exclusion and across all observed periods. Also, the species composition of FE communities differed from burned communities over time. Differences in species composition between burned and unburned increased from 2016 to 2022, with FE plots having fewer species in common with AF and BF plots, due mainly to the high dominance of a few species of graminoids of dense tussocks in FE plots. Likewise, among fire season treatments, early dry season

fires negatively impact plant communities. In EDF plots we found the lowest forb, graminoid, and total species richness, and lower forb cover since 2016 (three years of fire experiments).

The evaluation of the effects of all treatments after nine years of fire experiments reinforces the negative impact of fire exclusion and early dry season fires in open savanna communities. Both treatments led to plant communities with lower species diversity (species richness and Shannon diversity index), and low forb cover. Fire exclusion affected even functional diversity. As hypothesized, fire exclusion led to communities with a large cover of dead biomass and graminoids, which increased over time. As previously observed by Rodrigues & Fidelis (2022) in short-term analyses, large amounts of dead biomass accumulated and graminoid dominance may prevent the establishment of small species, mainly forbs and smaller grasses, by space and light competition (Rodrigues & Fidelis, 2022). Illuminance is significantly lower in fire exclusion plots than in burned ones (Rodrigues & Fidelis, in prep.b), affecting more shade-sensitive species. In the present study, FE plots displayed communities dissimilar from AF and BF, with different species composition, where large tussock grasses such as *Mesosetum ferrugineum* dominated. Despite being the dominant species in all treatments, *Mesosetum ferrugineum* is less abundant in burned plots, since it has its biomass constantly removed by fire. Thus, when their tussocks are smaller, there is more open space for other species to grow. Therefore, to compare burned and unburned communities, we observed that while most of the dissimilarity among communities is explained by species turnover, there was a suppression of forbs and small graminoid species in fire exclusion, such as *Anemopegma arvenses* (Vell.) Stellfeld ex de Souza, *Ipomoea fiebrigii* Hassl. ex O'Donell, *Declieuxia lancifolia, Lippia* horridula (Epling) Salimena, Múlgura & Harley, *Rhynchospora consanguínea* (Kunth) Boeckeler*, Rhynchospora elatior* Kunth, etc.

Early-dry season fires showed similar negative effects of fire exclusion on plant communities, affecting mainly graminoid and forb. Further, among ten exclusive species, five were shrubs and two trees (Appendix S5). The hydric restriction post-fire is longer in EDF plots (ca. 3 - 5 months) and may have harmed the regeneration of the community, affecting sensitive species. Drought affects the water status of species of plants, influencing nutrient absorption and carbon exchange, fundamentals for plant growth (Franco et al., 2005; Prior et al, 2004; Rossato et al., 2013). Graminoids, forbs,

and shrubs deal differently with water deficit (Eamus et al., 1999; Franco, 2002; Goldstein et al., 1998; Quesada et al., 2014; Rossatto & Franco, 2017), by uptaking water from different depths of the soil in the rainy and dry season (Rossato et al., 2012). Woody plants (shrubs and trees) uptake water from deeper soil layers (40 - 80 cm in the dry season), whereas graminoids and forbs uptake water from shallow soil layers (0 - 20 and 0 - 40 cm, respectively, during the dry season) (Rossato et al., 2012). Water storage is lower in shallower layers during the dry season (Quesada et al., 2004), and water potential suffers strong seasonal changes compared to the water availability at deeper soil layers, which is much more constant throughout the year (Scholes & Archer, 1997; Franco, 2002). Hence, shrubs and trees minimize better the effects of hydric restriction than forbs and mainly graminoids, maintaining their physiological activities, such as leaf expansion, flowering, and fructification (Oliveira & Gibbs, 2000). Besides, during the dry season, the evapotranspiration of soil, particularly the topsoil, is reduced (Quesada et al., 2004). This is due to the conversion of vegetation into dry biomass, which serves as a protective layer that prevents water loss in the soil (Dunin et al., 1997; Quesada et al., 2004). However, a fire event removes dead biomass, exposing the soil, increasing soil temperature, and decreasing relative air humidity (Rodrigues & Fidelis, in prep.b). Consequently, evapotranspiration increases (Quesada et al., 2004), which may deplete more quickly the water storage of soil. Thus, early dry season fires may cause more severe hydric restriction to communities impacting the persistence of more sensitive species resulting in plant community diversity.

A decrease in species diversity is a serious issue, particularly in areas with high levels of endemism, such as the Cerrado. Added to this is a loss of functional diversity that may compromise the functioning of the plant community (Díaz & Cabido, 2001; Tilman et al., 2001). Lower functional diversity may result in decreased productivity, soil carbon and nitrogen accumulation, root biomass, and resistance to invasive species (Tilman et al., 1997; Prieu-Richard & Lavorel, 2000; Dukes, 2001; Fornara & Tilman, 2008). Teixeira et al. (2022) also found less functional diversity in fire-excluded areas, associated with reduced net ecosystem carbon dioxide exchange and total soil organic C. Conversely, Loiola et al. (2010) did not observe differences in functional diversity between areas frequently burned and fire-excluded ones. We found that the exclusion plots had lower functional diversity compared to the other treatments,

corroborating our hypothesis. We also found differences in functional diversity among treatments with burnings. Annual fires promoted the highest functional diversity of open savanna communities. This can be explained by every fire event promoting new environmental conditions, such as increased light incidence and higher temperature fluctuations (Fidelis & Blanco, 2014; Rodrigues & Fidelis, in prep.b), changes in water availability, elevated nutrient levels (Whelan, 1986; Neary et al., 1999), more space (Fidelis et al., 2012), resulting in a reduction of species competition and higher environmental heterogeneity (Pausas et al., 2003; Krawchuk & Moritz, 2011; Pivello et al., 2010; He et al., 2019). These factors provide niches for species establishment and increase plant coexistence, leading to greater diversity (Noble & Slatyer, 1980).

In conclusion, plant communities of the herbaceous layer in open savannas responded differently to distinct fire regimes. Differences among communities have appeared since the initial years of the experiment and were consolidated over time. Among all the treatments, fire exclusion has had the most negative impact on plant communities, indicating that prescribed fire is essential not only for controlling fuel load accumulation but also for maintaining the taxonomic and functional diversity of tropical savannas. In addition, we showed that early dry-season fires can be harmful to communities, since a reduction in forb, graminoid, and overall species richness, as well as functional diversity was observed. However, early-dry season fires are the most used in fire management programs. In protected areas, early-dry season fire is used to control fuel load due to the higher moisture content vegetation and milder environmental conditions in this period, resulting in fires of lower intensity and easier to control (Schmidt et al., 2018; Eloy et al., 2019). On the other hand, fires during the mid- and late-dry seasons may help to maintain species and functional diversity, even though they may be of higher intensity and more difficult to control (Dos Santos et al., 2021). Unlike expected, plant communities in the herbaceous layer of open savannas maintained their stable growth forms cover and richness. Annual fires, even, resulted in the highest diversity of species and functional diversity. However, annual burnings may be unpracticable in large areas. Besides, some areas may not be able to accumulate enough fuel to burn annually. Therefore, a recommendation for fire management actions consists of observing the fuel load in the areas to avoid dense accumulation and performing burnings with different fire frequencies and seasons to increase biodiversity.

## References

Abreu, R. C., Hoffmann, W. A., Vasconcelos, H. L., Pilon, N. A., Rossatto, D. R., & Durigan, G. (2017). The biodiversity cost of carbon sequestration in tropical savanna. Science advances, 3(8), e1701284.

Antonelli-Filho, R. (2011). Plano de Manejo da Reserva Natural Serra do Tombador, Cavalcante - Goiás.

Archibald, S., Lehmann, C. E., Gómez-Dans, J. L., & Bradstock, R. A. (2013). Defining pyromes and global syndromes of fire regimes. Proceedings of the National Academy of Sciences, 110(16), 6442-6447.

Baselga, A., Orme, D., Villeger, S., Bortoli, J., Leprieur, F. & Logez, M. (2020) Betapart: partitioning Beta diversity into turnover and Nestedness components. R package version, 1(5), 2. Available from: https://CRAN.R-project.org/package=betapart

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software, 67(1), 1-48. doi:10.18637/jss.v067.i01.

Bombo, A. B., Appezzato-da-Glória, B., & Fidelis, A. (2022). Fire exclusion changes belowground bud bank and bud-bearing organ composition jeopardizing open savanna resilience. Oecologia, 199(1). https://doi.org/10.1007/s00442-022-05172-1

Bond, W. J., & Keeley, J. E. (2005). Fire as a global “herbivore”: The ecology and evolution of flammable ecosystems. In Trends in Ecology and Evolution (Vol. 20, Issue 7). https://doi.org/10.1016/j.tree.2005.04.025

Bond, W.J. & Midgley, J.J. (2001) Ecology of sprouting in woody plants: the persistence niche. Trends in Ecology & Evolution, 16(1), 45–51

Bond, W. J., & van Wilgen, B. W. (1996). Fire and Plants.,(Chapman: New York, NY, USA).

Bond, W. J., Woodward, F. I., & Midgley, G. F. (2005). The global distribution of ecosystems in a world without fire. New phytologist, 165(2), 525-538.

Cáceres M, Legendre P (2009). “Associations between species and groups of sites: indices and statistical inference.” _Ecology_, *90*, 3566-3574. doi:10.1890/08-1823.1 <https://doi.org/10.1890/08-1823.1>.

Clarke, P.J., Lawes, M.J., Midgley, J.J., Lamont, B.B., Ojeda, F., Burrows, G.E. et al. (2013) Resprouting as a key functional trait: how buds, protection, their and resources drive persistence after fire. New Phytologist, 197(1), 19–35.

Cornelissen, J. H., Lavorel, S., Garnier, E., Díaz, S., Buchmann, N., Gurvich, D. E., ... & Poorter, H. (2003). A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. Australian journal of Botany, 51(4), 335-380.

Daibes, L.F., Gorgone-Barbosa, E., Silveira, F.A., Fidelis, A., 2018. Gaps critical for the survival of exposed seeds during Cerrado fires. Aust. J. Bot. 66 (2), 116–123.

Daldegan, G. A., de Carvalho Júnior, O. A., Guimarães, R. F., Gomes, R. A. T., de Figueiredo Ribeiro, F., & McManus, C. (2014). Spatial patterns of fire recurrence

using remote sensing and GIS in the Brazilian savanna: Serra do Tombador Nature Reserve, Brazil. Remote Sensing, 6(10), 9873-9894.

Damasceno, G., Souza, L., Pivello, V. R., Gorgone-Barbosa, E., Giroldo, P. Z., & Fidelis, A. (2018). Impact of invasive grasses on Cerrado under natural regeneration. Biological Invasions, 20(12), 3621-3629.

Dantas VD, Pausas JG. The lanky and the corky: fire-escape strategies in savanna woody species. Journal of Ecology. 2013 Sep;101(5):1265-72.

Díaz, S., & Cabido, M. (2001). Vive la différence: plant functional diversity matters to ecosystem processes. Trends in ecology & evolution, 16(11), 646-655.

Dos Santos, A. C., da Rocha Montenegro, S., Ferreira, M. C., Barradas, A. C. S., & Schmidt, I. B. (2021). Managing fires in a changing world: Fuel and weather determine fire behavior and safety in the neotropical savannas. Journal of environmental management, 289, 112508.

Dukes, J. S. (2001). Biodiversity and invasibility in grassland microcosms. Oecologia, 126, 563-568.

Dunin, F. X., Miranda, H. S., Miranda, A. C., & Lloyd, J. (1997). Evapotranspiration responses to burning of campo sujo savanna in Central Brasil. In Bushfire'97: Australian bushfire conference 8-10 July 1997 (pp. 146-151). CSIRO Tropical Ecosystems Research Centre.

Eamus D., Hutley L.B., O'Grady A.P. (2001) Daily and seasonal patterns of carbon and water fluxes above a north Australian savanna. Tree Physiology, 21, 977–988.

Eiten, G. (1972.). The Cerrado Vegetation of Brazil. In Source: Botanical Review (Vol. 38, Issue 2).

Eloy, L., Schmidt, I. B., Borges, S. L., Ferreira, M. C., & Dos Santos, T. A. (2019). Seasonal fire management by traditional cattle ranchers prevents the spread of wildfire in the Brazilian Cerrado. Ambio, 48, 890-899.

Ferreira-Alves, R., & Romero, R. (2020). Microlicia rubra (Melastomataceae), a remarkable new species from Goiás, Brazil. Phytotaxa, 458(4), 294-300.

Fidelis, A., Alvarado, S. T., Barradas, A. C. S., & Pivello, V. R. (2018). The year 2017: Megafires and management in the Cerrado. Fire, 1(3), 49.

Fidelis, A., Blanco, C.C., Müller, S.C., Pillar, V.D. & Pfadenhauer, J. (2012) Short-term changes caused by fire and mowing in Brazilian Campos grasslands with different long-term fire histories. Journal of Vegetation Science, 23(3), 552–562

Fidelis, A., & Blanco, C. (2014). Does fire induce flowering in Brazilian subtropical grasslands?. Applied Vegetation Science, 17(4), 690-699.

Fidelis, A. & Zirondi, H.L. (2021) And after fire, the Cerrado flowers: a review of post-fire flowering in a tropical savanna. Flora, 280, 151849.

Fornara, D. A., & Tilman, D. (2008). Plant functional composition influences rates of soil carbon and nitrogen accumulation. Journal of Ecology, 96(2), 314-322.

Franco A.C.. (2002) Ecophysiology of woody plants. In: P.S. Oliveira, R.J. Marquis (Eds) The cerrados of Brazil: ecology and natural history of a Neotropical savanna. Columbia University Press, New York, pp. 178–197.

Franco AC, Bustamante M, Caldas LS, Goldstein G, Meinzer FC, Kozovits AR, Rundel P, Coradin VTR (2005) Leaf functional traits of neotropical savanna trees in relation to seasonal water deficit. Trees 19:326–335

Goldstein G., Meinzer F.C., Bucci S.J., Scholz F.G., Franco A.C., Hoffmann W.A. (2008) Water economy of Neotropical savanna trees: six paradigms revisited. Tree Physiology, 28, 395–404.

Govender, N., Trollope, W. S., & Van Wilgen, B. W. (2006). The effect of fire season, fire frequency, rainfall and management on fire intensity in savanna vegetation in South Africa. Journal of Applied Ecology, 43(4), 748-758.

He, T., Lamont, B. B., & Pausas, J. G. (2019). Fire as a key driver of Earth's biodiversity. Biological Reviews, 94(6), 1983-2010.

Krawchuk, M. A., & Moritz, M. A. (2011). Constraints on global fire activity vary across a resource gradient. Ecology, 92(1), 121-132.

Keeley, J. E. (2009). Fire intensity, fire severity and burn severity: A brief review and suggested usage. International Journal of Wildland Fire, 18(1), 116–126. https://doi.org/10.1071/WF07049

Keeley, J. E., Pausas, J. G., Rundel, P. W., Bond, W. J., & Bradstock, R. A. (2011). Fire as an evolutionary pressure shaping plant traits. In Trends in Plant Science (Vol. 16, Issue 8). https://doi.org/10.1016/j.tplants.2011.04.002

Kembel, S.W. , Cowan, P.D., Helmus, M.R. , Cornwell, W.K. , Morlon, H. , Ackerly, D.D., Blomberg, S.P. & Webb, C.O. (2010). Picante: R tools for integrating phylogenies and ecology. Bioinformatics 26:1463-1464.

Knapp, E. E., Estes, B. L., & Skinner, C. N. (2009). Ecological effects of prescribed fire season: a literature review and synthesis for managers.

Laliberté, E., Legendre, P., and B. Shipley. (2014). FD: measuring functional diversity from multiple traits, and other tools for functional ecology. R package version 1.0-12.2.

Lamont, B. B., Enright, N. J., & He, T. (2011). Fitness and evolution of resprouters in relation to fire. Plant Ecology, 212, 1945-1957.

Laterra, P., & Solbrig, O. T. (2001). Dispersal strategies, spatial heterogeneity and colonization success in fire-managed grasslands. In Ecological Modelling (Vol. 139). www.elsevier.com/locate/ecolmodel

Lenth, R. (2023). _emmeans: Estimated Marginal Means, aka Least-Squares Means_. R package version 1.8.8, <https://CRAN.R-project.org/package=emmeans>.

Loiola, P. P., Cianciaruso, M. V., Silva, I. A., & Batalha, M. A. (2010). Functional diversity of herbaceous species under different fire frequencies in Brazilian savannas. Flora-Morphology, Distribution, Functional Ecology of Plants, 205(10), 674-681.

Lüdecke, D. (2018). “ggeffects: Tidy Data Frames of Marginal Effects from Regression Models.” _Journal of Open Source Software_, *3*(26), 772. doi:10.21105/joss.00772 <https://doi.org/10.21105/joss.00772>.

Mendes, T. P., Simon, M. F., & da Silva, M. J. (2022). Three New Species of Mimosa L.(Leguminosae) from the Brazilian Cerrado Hotspot of Biodiversity. Brittonia, 74(4), 361-380.

Moreira, A. G. (2000). Effects of fire protection on savanna structure in Central Brazil. Journal of biogeography, 27(4), 1021-1029.

Moreira, B., Tormo, J., Estrelles, E., Pausas, J.G., 2010. Disentangling the role of heat and smoke as germination cues in Mediterranean Basin flora. Ann. Bot. 105 (4), 627–635.

Neary, D. G., Klopatek, C. C., DeBano, L. F., & Ffolliott, P. F. (1999). Fire effects on belowground sustainability: a review and synthesis. Forest ecology and management, 122(1-2), 51-71.

Noble, I. R., & Slatyer, R. O. (1980). The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. Vegetatio, 43, 5-21.

Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R, O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.M., Szoecs, E. & Wagner, H. (2020) Vegan: community Ecology package. R package version 2.5–7. https://CRAN.R-project.org/package=vegan

Oliveira, P. E., & Gibbs, P. E. (2000). Reproductive biology of woody plants in a cerrado community of Central Brazil. Flora, 195(4), 311-329.

Oliveira, P. T. S., Nearing, M. A., Moran, M. S., Goodrich, D. C., Wendland, E., & Gupta, H. V. (2014). Trends in water balance components across the Brazilian Cerrado. Water Resources Research, 50(9), 7100-7114.

Parr, C.L., Lehmann, C.E., Bond, W.J., Hoffmann, W.A., Andersen, A.N., 2014. Tropical grassy biomes: misunderstood, neglected, and under threat. Trends Ecol. Evol. 29 (4), 205–213

Pausas, J. G., Lamont, B. B., Paula, S., Appezzato-da-Glória, B., & Fidelis, A. (2018). Unearthing belowground bud banks in fire-prone ecosystems. New Phytologist, 217(4), 1435-1448.

Perez-Harguindeguy, N., Diaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., ... & Cornelissen, J. H. C. (2016). Corrigendum to: New handbook for standardised measurement of plant functional traits worldwide. Australian Journal of botany, 64(8), 715-716.

Pilon, N.A.L., Cava, M.G., Hoffmann, W.A., Abreu, R.C., Fidelis, A. & Durigan, G. (2021) The diversity of post-fire regeneration strategies in the cerrado ground layer. Journal of Ecology, 109(1), 154–166.

Pilon, N.A.L., Hoffmann, W.A., Abreu, R.C.R. & Durigan, G. (2018) Quantifying the short-term flowering after fire in some plant communities of a cerrado grassland. Plant Ecology and Diversity, 11, 259–266.

Pivello, V. R. (2011). The use of fire in the Cerrado and Amazonian rainforests of Brazil: past and present. Fire ecology, 7, 24-39.

Pivello, V. R., & Coutinho, L. M. (1996). A qualitative successional model to assist in the management of Brazilian cerrados. Forest Ecology and Management, 87(1-3), 127-138.

Pivello, V. R., & Norton, G. A. (1996). FIRETOOL: an expert system for the use of prescribed fires in Brazilian savannas. Journal of Applied ecology, 348-356.

Pivello, V. R., Oliveras, I., Miranda, H. S., Haridasan, M., Sato, M. N., & Meirelles, S. T. (2010). Effect of fires on soil nutrient availability in an open savanna in Central Brazil. Plant and Soil, 337(1). https://doi.org/10.1007/s11104-010-0508-x

Pivello, V. R., Vieira, I., Christianini, A. V., Ribeiro, D. B., da Silva Menezes, L., Berlinck, C. N., ... & Overbeck, G. E. (2021). Understanding Brazil's catastrophic fires: Causes, consequences and policy needed to prevent future tragedies. Perspectives in Ecology and Conservation, 19(3), 233-255.

Prieur-Richard, A. H., & Lavorel, S. (2000). Invasions: the perspective of diverse plant communities. Austral Ecology, 25(1), 1-7.

Prior, L. D., Bowman, D. M., & Eamus, D. (2004). Seasonal differences in leaf attributes in Australian tropical tree species: family and habitat comparisons. Functional Ecology, 18(5), 707-718.

Quesada, C. A., Miranda, A. C., Hodnett, M. G., Santos, A. J. B., Miranda, H. S., & Breyer, L. M. (2004). Seasonal and depth variation of soil moisture in a burned open savanna (campo sujo) in central Brazil. Ecological Applications, 14(4 SUPPL.). https://doi.org/10.1890/01-6017

R Core Team (2023). _R: A Language and Environment for Statistical Computing_. R Foundation for Statistical Computing, Vienna, Austria.<https://www.R-project.org/>.

Ribeiro, J. F., & Walter, B. M. T. (1998). Fitofisionomias do bioma Cerrado.

Rissi, M. N., Baeza, M. J., Gorgone-Barbosa, E., Zupo, T., & Fidelis, A. (2017). Does season affect fire behaviour in the Cerrado? International Journal of Wildland Fire, 26(5), 427–433. https://doi.org/10.1071/WF14210

Rodrigues, C. A., & Fidelis, A. (2022). Should we burn the Cerrado? Effects of fire frequency on open savanna plant communities. Journal of Vegetation Science, 33(6). https://doi.org/10.1111/jvs.13159

Rodrigues, C. A., & Fidelis, A.(in preparation)a. Fire frequency, not fire season matters for aboveground biomass dynamics in open savannas of the Cerrado

Rodrigues, C. A., & Fidelis, A.(in preparation)b. Microclimate is affected by fire frequency and seasonality in tropical open savannas of the Cerrado

Rodrigues, C. A., Zirondi, H. L., & Fidelis, A. (2021). Fire frequency affects fire behavior in open savannas of the Cerrado. Forest Ecology and Management, 482. https://doi.org/10.1016/j.foreco.2020.118850

Rossatto, D. R., & Franco, A. C. (2017). Expanding our understanding of leaf functional syndromes in savanna systems: the role of plant growth form. Oecologia, 183, 953-962.

Rossatto, D. R., Hoffmann, W. A., de Carvalho Ramos Silva, L., Haridasan, M., Sternberg, L. S., & Franco, A. C. (2013). Seasonal variation in leaf traits between congeneric savanna and forest trees in Central Brazil: implications for forest expansion into savanna. Trees, 27, 1139-1150.

Rossatto, D. R., Silva, L. D. C. R., Villalobos-Vega, R., Sternberg, L. D. S. L., & Franco, A. C. (2012). Depth of water uptake in woody plants relates to groundwater level and vegetation structure along a topographic gradient in a neotropical savanna. Environmental and Experimental Botany, 77, 259-266.

Russell-Smith, J., & Yates, C. P. (2007). Australian savanna fire regimes: context, scales, patchiness. Fire ecology, 3(1), 48-63.

São-Mateus, W. M., Simon, M. F., de Queiroz, L. P., Jardim, J. G., & Cardoso, D. B. (2019). Two new species of Harpalyce (Leguminosae, Papilionoideae) from the Cerrado hotspot of biodiversity in Brazil. Kew bulletin, 74, 1-11.

Sarmiento, G., Goldstein, G., & Meinzer, F. (1985). Adaptive strategies of woody species in neotropical savannas. Biological Reviews, 60(3), 315-355.

Schmidt, I.B. & Eloy, L. (2020) Fire regime in the Brazilian savanna: recent changes, policy and management. Flora, 268, 151613.

Schmidt, I.B., Moura, L.C., Ferreira, M.C., Eloy, L., Sampaio, A.B., Dias, P.A. et al. (2018) Fire management in the Brazilian savanna: first steps and the way forward. Journal of Applied Ecology, 55(5), 2094–2101.

Scholes R.J., Archer S.R. (1997) Tree–Grass interactions in Savannas. Annual Review of Ecology and Systematics, 28, 517–544.

Staver, A. C., Archibald, S., & Levin, S. (2011). Tree cover in sub-Saharan Africa: rainfall and fire constrain forest and savanna as alternative stable states. Ecology, 92(5), 1063-1072.

Teixeira, J., Souza, L., Le Stradic, S., & Fidelis, A. (2022). Fire promotes functional plant diversity and modifies soil carbon dynamics in tropical savanna. Science of The Total Environment, 812, 152317.

Tilman, D., Reich, P. B., Knops, J., Wedin, D., Mielke, T., & Lehman, C. (2001). Diversity and productivity in a long-term grassland experiment. Science, 294(5543), 843-845.

Whelan, R.J. (1986) Seed dispersal in relation to fire. Seed dispersal, 237–271

Whelan, R. J. (1995). The ecology of fire. Cambridge University press.

Wickham, H., & Wickham, H. (2016). Data analysis (pp. 189-201). Springer International Publishing.

Wieczorkowski, J. D., & Lehmann, C. E. (2022). Encroachment diminishes herbaceous plant diversity in grassy ecosystems worldwide. Global Change Biology, 28(18), 5532-5546.

Wood, S.N. (2011) Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. Journal of the Royal Statistical Society (B) 73(1):3-36

Zanzarini, V., Andersen, A. N., & Fidelis, A. (2022). Flammability in tropical savannas: Variation among growth forms and seasons in Cerrado. Biotropica, 54(4), 979-987.

Zirondi, H., Ooi, M.K. & Fidelis, A. (2021) Fire-triggered flowering is the dominant post-fire strategy in a tropical savanna. Journal of Vegetation Science, 32(2), e12995

Zhao, Y., Liu, Z., Wu, J., 2020. Grassland ecosystem services: A systematic review of research advances and future directions. Landscape Ecol. 1–22.

Zirondi, H.L., Silveira, F.A., Fidelis, A., 2019. Fire effects on seed germination: Heat shock and smoke on permeable vs impermeable seed coats. Flora 253, 98–106.

Zupo, T., Daibes, L. F., Pausas, J. G., & Fidelis, A. (2021). Post-fire regeneration strategies in a frequently burned Cerrado community. Journal of Vegetation Science, 32(1). https://doi.org/10.1111/jvs.12968

**Supporting information:** Rodrigues & Fidelis. Fire exclusion and early dry-season fires negatively impact plant communities in tropical open savannas in the Cerrado.

**Appendix S1.** Description of the functional traits related to the plants response to fire and their respective functional importance and methods used for the measurement.

| Trait | Functional importance | Method |
|---|---|---|
| Growth form | Plant growth and persistence, influencing biomass distribution and accumulation | Functional classification in the field using reference bibliography[1;2] |
| Height | Competitive vigor to grow in the interval between disturbances | Field measurement (cm) [1;2] |
| Branching architecture | Post-fire growth strategy (height x branching) | Field measurement and calculation of the apical dominance index[1] |
| Underground organ | Regeneration and persistence after disturbance | Field collection and underground organ classification[3] |
| Leaf macronutrients content | Availability and use of soil resources | Leaf chemical analysis[1;2] |

**Appendix S2.** Pairwise comparisons from GAMM analysis of plant communities under different fire frequencies and seasons by the variation in their species richness and vegetation cover observed over time (2016 – 2022) in communities of the herbaceous layer of open savannas in the Cerrado. AF: annual fires, BF: biennial fires, FE: fire exclusion since 2011, EDF: early, MDF: mid, and LDF: late dry season fires.

| | **Richness** | | | | | | **Cover** | | |
|---|---|---|---|---|---|---|---|---|---|
| **Pairs** | **F** | **G** | **S** | **T** | **BS** | **DB** | **F** | **G** | **S** |
| AF x FE | **<0.001** | **<0.001** | 0.7 | **<0.001** | **< 0.001** | **< 0.001** | **0.03** | **< 0.001** | **<0.001** |
| AF x BF | 0.8 | **<0.001** | 0.7 | 0.08 | **< 0.001** | **< 0.001** | **0.02** | 0.3 | **0.04** |
| FE x BF | **< 0.001** | 0.009 | 0.9 | **0.002** | **< 0.001** | **< 0.001** | **< 0.001** | **<0.001** | **0.03** |
| Model | **< 0.0001** | **< 0.0001** | 0.9 | **< 0.0001** | **< 0.0001** | **< 0.0001** | **< 0.0001** | **< 0.0001** | **0.002** |
| EDF x LDF | **<0.001** | **<0.001** | 0.7 | **<0.001** | **<0.001** | **<0.001** | **<0.001** | **<0.001** | 0.1 |
| EDF x MDF | **< 0.001** | **< 0.001** | 0.6 | **< 0.001** | **0.02** | **<0.001** | **< 0.001** | **<0.001** | 0.3 |
| LDF x MDF | 0.1 | 0.06 | 0.4 | 0.2 | **0.002** | 0.9 | 0.06 | 0.754 | 0.5 |
| Model | **< 0.0001** | **< 0.0001** | 0.8 | **< 0.0001** | **< 0.0001** | **< 0.0001** | **< 0.0001** | **< 0.0001** | **0.25** |

**Appendix S3.** List of families and species occurring in areas with annual and biennial fires, as well as fire exclusion nine years after treatments in the dry season of 2022 in open savannas in Central Brazil. AF: annual fires, EDF: early, MDF: mid, LDF: late dry season fires, and FE: fire exclusion since 2011.

| Species | Family | Growth form | AF | EDF | FE | LDF | MDF |
|---|---|---|---|---|---|---|---|
| *Justicia lanstyakii* Rizzini | Acanthaceae | Forb | x | x | x | x | x |
| *Ruellia angustior (Nees) Lindau* | Acanthaceae | Shrub | | x | x | | |
| *Ruellia nitens* (Nees) Wassh. | Acanthaceae | Forb | x | x | x | x | x |
| *Anacardium* sp | Anacardiaceae | Shrub | | x | | | |
| *Annona tomentosa* R.E.Fr. | Annonaceae | Shrub | x | x | x | x | |
| *Hemipogon acerosus* Decne. | Apocynaceae | Forb | x | x | x | x | x |
| *Syagrus acaulis* (Drude) Becc. | Arecaceae | Palm | x | | x | | x |
| *Aldama grandiflora* (Gardner) E.E.Schill. & Panero | Asteraceae | Forb | | | | | |
| *Asteraceae n.id.* | Asteraceae | Shrub | x | x | | x | |
| *Ayapana amygdalina* (Lam.) R.M.King & H.Rob | Asteraceae | Forb | | x | | x | |
| *Eremanthus goayzesnsis* (Gardner) Sch.Bip. | Asteraceae | Shrub | x | | | | |
| *Ichthyothere hirsuta* Gardner | Asteraceae | Forb | x | x | x | x | x |
| *Lessingianthus durus* (Mart. ex DC.) H.Rob. | Asteraceae | Forb | x | | | | |
| *Porophyllum obscurum (Spreng.) DC* | Asteraceae | Forb | x | x | | | |
| *Trixis glutinosa* D. Don | Asteraceae | Forb | | | | | x |
| *Adenocalymma axillare* (K.Schum.) L.G.Lohmann | Bignoniacea | Shrub | | x | | | |
| *Anemopaegma arvense* (Vell.) Stellfeld ex de Souza | Bignoniacea | Forb | x | x | | x | |
| *Kielmeyera abdita* Saddi | Calophyllaceae | Forb | | x | | | x |
| *Kielmeyera rubriflora* Cambess. | Calophyllaceae | Shrub | | | x | | |
| *Caryocar brasiliense* Cambess. | Caryocaraceae | Tree | | | | | x |
| *Connarus suberosus* Planch. | Connaraceae | Tree | | | x | x | |
| *Ipomoea echioides* Choisy | Convolvulaceae | Forb | x | x | x | x | x |
| *Ipomoea fiebrigii* Hassl. ex O'Donell | Convolvulaceae | Forb | x | x | | | x |
| *Merremia ericoides* (Meisn.) Hallier f. | Convolvulaceae | Forb | | x | | x | |
| *Bulbostylis junciformis* (Kunth) C.B.Clarke | Cyperaceae | Graminoid | x | | x | x | |
| *Bulbostylis paradoxa* (Spreng.) Lindm. | Cyperaceae | Graminoid | x | x | x | | x |
| *Rhynchospora consanguinea* (Kunth) Boeckeler | Cyperaceae | Graminoid | x | x | | | x |
| *Rhynchospora elatior Kunth* | Cyperaceae | Graminoid | x | x | | x | x |
| *Rhynchospora globosa* (Kunth) Roem. & Schult. | Cyperaceae | Graminoid | x | x | x | x | x |
| *Erythroxylum suberosum* A.St.-Hil. | Erythroxylaceae | Shrub | x | | | x | |
| *Bernardia hirsutissima* (Baill.) Müll.Arg. | Euphorbiaceae | Forb | x | x | x | x | x |
| *Croton gracilescens* Müll.Arg. | Euphorbiaceae | Forb | x | x | x | x | x |
| *Croton megalocalyx* Müll.Arg. | Euphorbiaceae | Shrub | | x | | | |
| *Dalechampia linearis* Baill. | Euphorbiaceae | Forb | x | | x | | |
| *Euphorbia potentilloides* Boiss. | Euphorbiaceae | Forb | x | x | x | x | x |
| *Manihot kalungae* M.J. Silva & R.C. Sodré | Euphorbiaceae | Forb | | x | x | | |
| *Aeschynomene* sp | Fabaceae | Forb | | x | | x | x |
| *Ancistrotropis firmula* (Mart. ex Benth.) A. Delgado | Fabaceae | Shrub | | | | | x |
| *Bauhinia dumosa* Benth. | Fabaceae | Shrub | x | x | x | x | x |

| Species | Family | | AF | EDF | FE | LDF | MDF |
|---|---|---|---|---|---|---|---|
| *Calliandra dysantha* Benth. | Fabaceae | Shrub | x | x | x | x | x |
| *Chamaecrista claussenii* (Benth.) H.S.Irwin & Barneby | Fabaceae | Forb | x | x | x | x | x |
| *Chamaecrista fagonioides* (Vogel) H.S.Irwin & Barneby | Fabaceae | Forb | | | | | x |
| *Chamaecrista isidorea* (Benth.) H.S.Irwin & Barneby | Fabaceae | Forb | x | x | x | x | x |
| *Chamaecrista ochrosperma* (H.S.Irwin & Barneby) H.S.Irwin & Barneby | Fabaceae | Forb | x | x | x | x | x |
| *Desmodium platycarpum* Benth. | Fabaceae | Forb | | x | | x | |
| *Eriosema congestum* Benth. | Fabaceae | Shrub | x | | x | x | x |
| *Harpalyce tombadorensis São-Mateus et al.* | Fabaceae | Shrub | x | x | x | x | |
| *Mimosa cavalcantina* T.P.Mendes, Marc.F.Simon & M.J.Silva | Fabaceae | Forb | x | x | x | | |
| *Mimosa gracilis* Benth. | Fabaceae | Forb | x | | x | x | x |
| *Mimosa leiocephala* Benth. | Fabaceae | Shrub | x | | x | x | x |
| *Mimosa macrocephala* Benth. | Fabaceae | Forb | | | | | x |
| *Mimosa pteridifolia* Benth. | Fabaceae | Shrub | x | x | x | x | x |
| *Senna corifolia* (Benth.) H.S.Irwin & Barneby var. *corifolia* | Fabaceae | Shrub | x | x | x | x | x |
| *Calolisianthus speciosus* (Cham. & Schltdl.) Gilg | Gentianacea | Forb | | | | x | |
| *Deianira pallescens* Cham. & Schltdl. | Gentianacea | Forb | | | | x | |
| *Cipura xanthomelas* Klatt | Iridaceae | Forb | | | x | | |
| *Sisyrinchium luzula* Klotzsch ex Klatt | Iridaceae | Forb | x | | | x | x |
| *Trimezia juncifolia* (Klatt) Benth. & Hook. | Iridaceae | Forb | | | x | x | |
| *Eriope glandulosa* (Harley) Harley | Lamiaceae | Forb | x | x | x | x | x |
| *Gymneia chapadensis* Harley | Lamiaceae | Forb | x | x | x | x | x |
| *Hypenia* sp | Lamiaceae | Forb | | | x | x | |
| *Hyptis remota* Pohl ex Benth. | Lamiaceae | Forb | x | x | x | x | x |
| *Medusantha mollissima* (Benth.) Harley & J.F.B.Pastore | Lamiaceae | Forb | x | x | x | x | x |
| *Spigelia schlechtendaliana* | Loganiaceae | Forb | | | | | x |
| *Cuphea ericoides* Cham. & Schltdl. | Lythraceae | Forb | x | x | x | x | x |
| *Cuphea spermacoce* A.St.-Hil. | Lythraceae | Forb | | | | x | x |
| *Diplusodon paraisoensis* Lourteig | Lythraceae | Shrub | x | | | | x |
| *Diplusodon punctatus* Pohl | Lythraceae | Shrub | x | | x | x | x |
| *Byrsonima* sp | Malpighiaceae | Shrub | | x | | | |
| *Camarea ericoides* A.St.-Hil. | Malpighiaceae | Forb | x | | | | x |
| *Heteropterys pannosa Griseb* | Malpighiaceae | Shrub | x | x | x | x | x |
| *Byttneria jaculifolia* Pohl | Malvaceae | Forb | x | | | x | x |
| *Pavonia grandiflora* A.St.-Hil. | Malvaceae | Shrub | | | | | x |
| *Peltaea macedoi* Krapov. & Cristóbal | Malvaceae | Shrub | | x | x | | |
| *Stenodon suberosus* Naudin | Melastomataceae | Shrub | | | | | x |
| *Tibouchina melastomoides* (Naudin) Cogn. | Melastomataceae | Forb | x | x | x | x | x |
| *Brosimum gaudichaudii* Trécul | Moraceae | Shrub | x | x | x | x | x |
| *Myrcia* sp | Myrtaceae | Shrub | x | x | x | x | x |
| *Ouratea* sp | Ochnaceae | Tree | | x | | | |
| *Ouratea lanceolata (Pohl) Engl.* | Ochnaceae | Shrub | x | x | | | x |
| *Buchneria* sp | Orobanchaceae | Forb | | | | x | |
| *Oxalis goyazensis* Turcz. | Oxalidaceae | Forb | x | | | x | x |
| *Oxalis pyrenea var. macrochaeta* Lourteig | Oxalidaceae | Forb | | | | | x |

| Species | Family | | AF | EDF | FE | LDF | MDF |
|---|---|---|---|---|---|---|---|
| *Andropogon lateralis* Nees | Poaceae | Graminoid | x | x | x | x | x |
| *Anthaenantia lanata* (Kunth) Benth. | Poaceae | Graminoid | x | x | x | x | x |
| *Aristida setifolia* Kunth | Poaceae | Graminoid | x | | | x | x |
| *Arthropogon villosus* Nees | Poaceae | Graminoid | x | x | x | x | x |
| *Axonopus aureus* P. Beauv. | Poaceae | Graminoid | x | x | x | x | x |
| *Elionurus muticus* (Spreng.) Kuntze | Poaceae | Graminoid | x | x | x | x | x |
| *Mesosetum ferrugineum* (Trin.) Chase | Poaceae | Graminoid | x | x | x | x | x |
| *Mesosetum loliiforme* (Hochst.) Chase | Poaceae | Graminoid | x | x | x | x | x |
| *Oncorachis ramosa* (Zuloaga & Soderstr.) Morrone & Zuloaga | Poaceae | Graminoid | x | x | x | x | x |
| *Paspalum gardnerianum* Nees | Poaceae | Graminoid | x | | | | |
| *Paspalum pectinatum* Nees ex Trin. | Poaceae | Graminoid | x | x | x | x | x |
| *Poaceae* n.id. | Poaceae | Graminoid | | x | | | |
| *Schizachyrium tenerum* Nees | Poaceae | Graminoid | x | x | x | x | x |
| *Sporobulus cubensis* Hitchc. | Poaceae | Graminoid | x | x | x | x | x |
| *Trachypogon spicatus* (L.f.) Kuntze | Poaceae | Graminoid | x | x | x | x | x |
| *Trichanthecium cyanescens* (Nees ex Trin.) Zuloaga & Morrone | Poaceae | Graminoid | x | x | x | x | x |
| *Asemeia marquesiana* (J.F.B.Pastore & T.B.Cavalc.) J.F.B.Pastore & J.R.Abbott | Polygalacea | Forb | x | | | | |
| *Senega* sp | Polygalacea | Forb | x | | | | x |
| *Crumenaria choretroides* Mart. ex Reissek | Rhamnaceae | Forb | | x | | x | |
| *Borreria poaya (A.St.-Hil.) DC.* | Rubiaceae | Forb | | | | x | |
| *Declieuxia lancifolia* J.H.Kirkbr. | Rubiaceae | Forb | x | | | x | x |
| *Palicourea rigida* Kunth | Rubiaceae | Shrub | | | x | | |
| *Spermacoce tenella Kunth* | Rubiaceae | Forb | x | x | x | x | x |
| *Casearia sylvestris* Sw. | Salicaceae | Tree | x | x | x | x | x |
| *Serjania trichomisca* Radlk. | Sapindacea | Shrub | | | x | x | |
| *Solanum lycocarpum* A.St.-Hil. | Solanaceae | Tree | x | | | | |
| *Turnera emendata* Arbo | Turneraceae | Forb | x | | | | x |
| *Vellozia squamata* Pohl | Velloziaceae | Shrub | x | x | | x | |
| *Lippia horridula (Epling) Salimena, Múlgura & Harley* | Verbenaceae | Forb | x | x | | x | x |
| *Stachytarpheta villosa* (Pohl) Cham. | Verbenaceae | Forb | | | | x | x |
| *Verbenaceae n.id.* | Verbenaceae | Forb | | x | | | |
| *Vochysia pumila* Pohl | Vochysiaceae | Shrub | x | | x | x | x |
| *Vochysia* sp | Vochysiaceae | Tree | | x | | | |
| *Xyris* sp | Xyridacea | Graminoid | x | | | | |
| *Climber* n.id. 1 | - | Climber | x | | | | |
| *Shrub* n.id. | - | Shrub | x | | | | |
| *Forb* n.id. | - | Forb | | | x | | |
| *Climber* n.id. 2 | - | Climber | | x | | | |

**Appendix S4.** Pairwise comparisons from GLMM analysis of plant communities under different fire treatments by their species richness, vegetation cover, evenness, Simpson, Shannon, and FD index observed in the dry season of 2022, in communities of the herbaceous layer of the campo sujo on Cerrado. AF: annual fires, EDF: early, MDF: mid, LDF: late dry season fires, and FE: fire exclusion since 2011.

| | Pairs | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | **AF x EDF** | **AF x FE** | **AF x LDF** | **AF x MDF** | **EDF x FE** | **EDF x LDF** | **EDF x MDF** | **FE x LDF** | **FE x MDF** | **LDF x MDF** | **p - Model** | **AIC** |
| **F richness** | > 0.05 | **<0.0001** | > 0.05 | > 0.05 | **0.002** | > 0.05 | > 0.05 | **<0.0001** | **<0.0001** | > 0.05 | **<0.0001** | 758.16 |
| **G richness** | **<0.0001** | **<0.0001** | > 0.05 | > 0.05 | 1 | **0.001** | **0.04** | **0.0004** | 0.07 | 0.4 | **<0.0001** | 631.72 |
| **S richness** | > 0.05 | > 0.05 | > 0.05 | > 0.05 | > 0.05 | > 0.05 | > 0.05 | > 0.05 | > 0.05 | > 0.05 | **<0.0001** | 694.44 |
| **T richness** | **0.004** | **<0.0001** | 0.9 | 0.4 | 0.07 | 0.06 | 0.3 | **<0.0001** | **<0.0001** | 0.9 | **<0.0001** | 923.12 |
| **BS cover** | **0.01** | **<0.0001** | > 0.05 | > 0.05 | **<0.0001** | > 0.05 | > 0.05 | **<0.0001** | **<0.0001** | > 0.05 | **<0.0001** | 1409.4 |
| **DB cover** | **<0.0001** | **<0.0001** | 0.006 | > 0.05 | **<0.0001** | 0.0009 | **<0.0001** | **<0.0001** | **<0.0001** | > 0.05 | **<0.0001** | 1399.9 |
| **F cover** | 1.0 | **0.01** | 1.0 | 0.05 | **0.01** | 1.00 | 0.14 | **0.004** | <.0001 | 0.0664 | **<0.0001** | 1348.5 |
| **G cover** | > 0.05 | > 0.05 | > 0.05 | > 0.05 | > 0.05 | > 0.05 | > 0.05 | **0.0002** | **0.0001** | >0.05 | **<0.0001** | 1581.2 |
| **S cover** | 0.06 | > 0.05 | > 0.05 | > 0.05 | 0.0500 | > 0.05 | > 0.05 | > 0.05 | > 0.05 | > 0.05 | **<0.0001** | 1547.2 |
| **Evenness** | > 0.05 | > 0.05 | > 0.05 | > 0.05 | > 0.05 | > 0.05 | > 0.05 | > 0.05 | > 0.05 | > 0.05 | **<0.0001** | -72.721 |
| **Simpson** | >0.05 | >0.05 | >0.05 | >0.05 | >0.05 | >0.05 | >0.05 | >0.05 | >0.05 | >0.05 | **<0.0001** | -104.14 |
| **Shannon** | **0.02** | **0.03** | >0.05 | >0.05 | >0.05 | >0.05 | >0.05 | >0.05 | >0.05 | >0.05 | **<0.0001** | -19.738 |
| **FD** | **<0.0001** | **<0.0001** | **<0.0001** | **<0.0001** | **0.009** | **0.001** | 0.9 | **<0.0001** | **0.001** | **0.003** | **<0.0001** | -25.826 |

## References

1. Perez-Harguindeguy, N., Diaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., ... & Cornelissen, J. H. C. (2016). Corrigendum to: New handbook for standardised measurement of plant functional traits worldwide. Australian Journal of botany, 64(8), 715-716.

2. Cornelissen, J. H., Lavorel, S., Garnier, E., Díaz, S., Buchmann, N., Gurvich, D. E., ... & Poorter, H. (2003). A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. Australian journal of Botany, 51(4), 335-380.

3. Pausas, J. G., Lamont, B. B., Paula, S., Appezzato-da-Glória, B., & Fidelis, A. (2018). Unearthing belowground bud banks in fire-prone ecosystems. New Phytologist, 217(4), 1435-1448.

# 3. CAPÍTULO 3

## Fire frequency, not fire season matters for aboveground biomass dynamics in open savannas of the Cerrado

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### Abstract

Aboveground biomass quantity and dynamics in open ecosystems are modulated by seasonality and influenced by fire regime. Thus the present study aims to analyze the effects of different fire regimes on aboveground biomass dynamics and productivity of open savanna communities over time. In a long-term fire experiment (4 replicates/treatment, 30x30 m plots), established in 2013 with different fire frequencies (annual, biennial fires and fire exclusion since 2011) and seasons (biennial burns in early-dry, mid-dry, and late-dry seasons) we sampled aboveground biomass in each plot (0.5×0.5m, five samples/plot x four plots/treatment = 100 per observation time) in the rainy and mid-dry seasons from 2013 to 2022. Total biomass showed a distinct amount among fire frequency treatments over time, driven by the variation in dead biomass. Fire frequency did not affect total live biomass changes throughout time. However, fire exclusion plots had more graminoid and less non-graminoid biomass compared to other treatments. The productivity was affected by fire frequency. Fire exclusion plots displayed an average productivity five times lower than biennial plots and seven times lower than annual plots. Fire season did not affect neither the biomass component nor productivity of plant communities in open savannas. In conclusion, our study showed that open savanna plant communities in the Cerrado, regarding biomass regrowth, are resilient to frequent fires, no matter the fire season, but not to fire exclusion.

**Keywords:** aboveground biomass, fire exclusion, fire frequency, fire season, productivity, resilience, tropical savannas.

## Introduction

The productivity and dynamics of aboveground biomass in open ecosystems, like savannas and grasslands, are influenced by several biotic and abiotic factors, for example, rainy season duration and intensity, available soil resources, species composition, and mostly the fire regime (Briggs & Knapp, 1995; Bustamante et al., 2012; Sarmiento, 1984; Rodrigues & Fidelis, 2022; Fidelis et al., 2013). Fire is an important ecological disturbance in open ecosystems, consuming and controlling biomass accumulation (Bond, 2005; Bond & Keeley, 2005) since grasslands expansion during the Miocene, when large areas of C3 species were replaced by C4 species, increasing the fire occurrence (Keeley & Rundel, 2005). Fire removes an expressive amount of aboveground biomass (80 to 95%) in open savannas (Rissi et al., 2017; Rodrigues et al., 2021; Dos Santos et al., 2021). However, vegetation may recover rapidly, reaching the fire's previous biomass quantity in about two years (Rissi, 2016; Oliveira et al., 2021). This is because savanna plants are resilient to fire and respond fast to fire events and post-fire conditions through adaptations to the fire regimes under which they evolved (Coutinho, 1982; Keeley et al., 2011; Clarke et al., 2013 ). For example, graminoids can assimilate available nutrients rapidly from the soil since their roots are shallow, and most of the nutrients are concentrated in the first centimeters of the soil layers (Coutinho, 1990; Le Stradic et al., 2021), allowing them to rapidly regrowth after a fire.

Contrarily, when the fire is suppressed for longer periods, there is a large accumulation of litter and dead biomass, reducing plant productivity (Knapp & Seastedt, 1986). This occurs because nutrients become immobilized in dead biomass (Frost & Robertson, 1987). Additionally, the dense layer of dead biomass alters microclimatic conditions, such as decreasing illuminance (Rodrigues & Fidelis, in prep.). Shading reduces the photosynthetic capacity of plants, comprising communities' productivity (ZIMMERMANN et al., 2010) However, short intervals between fires may also reduce productivity by depleting soil and plant nutrients, affecting new stem and leaf production (Pivello et al., 2010; Savadogo et al., 2009). Thus, fire frequency can influence productivity and biomass accumulation in savanna communities.

Likewise, fire season may affect the plant community's productivity since, in each season, plants will be in different phenological stages (Knapp et al., 2009). In savannas, the availability of soil water is a key factor in the regrowth of herbaceous aboveground biomass, and it varies throughout the seasons (Quesada et al., 2004; Oliveras et al., 2013). Additionally, the duration of hydric restriction following a fire varies depending on the fire season (Quesada et al., 2004). For example, fire during the early dry season imposes on plants a longer time without water until the next rainy season, which can affect the post-fire regeneration of the community. The season also impacts biomass composition and properties, since the proportion of dead biomass within total biomass increases across the dry season and moisture content decreases (Rissi et al., 2017). Dead biomass amount and fuel load moisture content are important factors influencing fire intensity, fire spread, and flame height (Rissi et al., 2017; Rodrigues et al., 2021; Dos Santos et al., 2021). These fire behavior parameters may be related to fire severity, and thus, can influence plant post-fire regeneration (Keeley, 2009).

As in several ecosystems in the world, fire can be considered as one of the factors determinants in the structuring and maintenance of the Cerrado (Coutinho, 1978). Cerrado is characterized by a seasonal climate, with a well-marked dry season (Eiten, 1972), from May to September (Coutinho, 1982). Natural fires in Cerrado are caused by lightning and occur mainly during the rainy season, from September to May (Ramos-Neto & Pivello, 2000). In the open ecosystems of the Cerrado, the continuous herbaceous layer and the dominance of grasses favor high-frequency fires with a return time of 1 to 5 years (Eiten, 1972). They are surface fires with high combustion rates, essentially consuming all the fine fuel of the herbaceous stratum that was converted into dead biomass in the dry season (Rissi et al., 2017, Rodrigues et al., 2021).

Although fire is an important factor affecting productivity in open ecosystems, it is not the only driver. Annual precipitation also plays a significant role in biomass growth, with higher productivity observed during years with higher precipitation (Briggs & Knapp, 1995). Therefore, it is crucial to understand how fire and annual precipitation interact to regulate productivity in open savannas. Hence, this study aims to examine the long-term impact of fire frequency and season on the dynamics of aboveground biomass and productivity of open savannas in the Cerrado. Complementary, we

investigated if there is a relationship between annual rainfall and biomass productivity for each treatment. We predict that annual fires will lead to a decrease in total biomass and productivity over time compared to other fire frequencies. Fire exclusion, on the other hand, will promote an increase in biomass over time, driven mostly by the accumulation of dead biomass. However, productivity in fire-excluded sites will be low due to the absence of fire and the large accumulation of biomass. Regarding fire season, burning in the early- dry season can hinder vegetation regeneration in the following months due to water restrictions. On the other hand, burning in the late-dry season can lead to faster regeneration with higher productivity, because rains occur right after these fires, promoting biomass regrowth. However, late-dry fires are hotter and more intense, which can cause more harm to shrubs. Finally, we expect to find a relationship between rainfall and productivity: in years of lower rainfall, productivity will be lower independently of the fire regime.

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## Methods

*Study area*

This study was conducted at the Reserva Natural Serra do Tombador (RNST, 13° 35-38 'S and 47 ° 45-51' W, 8900 ha, 560–1118m a.s.l., Central Brazil, Brazil). The climate is tropical, with dry winters and rainy summers, with an average of annual rainfall between 1300-1500 mm, maximum average temperatures between 26 and 36°C, and minimum temperatures between 8 and 14°C (Antonelli-Filho, 2011). Fire experiments were established in an area of open savannas (*campo sujo*) (Figure 1A-B), characterized by the dominance of graminoids (mostly C4 grasses) and forbs, with scattered small trees and shrubs (Coutinho, 1978). The fuel load bed is continuous, composed mostly of fine fuel (graminoids) and fire frequency was high until the protected area was created in 2006 (every 3 years, Daldegan et al., 2014). A wildfire occurred in the area in 2011 at the end of the dry season. Fire experiments began in 2013, two years after the wildfire; therefore, all experimental plots had the same fire frequency and time since the last fire at the beginning of the fire experiments (Daldegan et al., 2014).

The herbaceous layer is species-rich, and its main component is C4 grasses, with a dominance of *Mesosetum ferrugineum* (Trin.) Chase, *Oncorachis ramosa* (Zuloaga

& Soderstr.) Morrone & Zuloaga, *Axonopus aureus* P. Beauv., *Elionurus muticus* (Spreng.) Kuntze, *Aristida setifolia* Kunth, and *Paspalum pectinatum* Nees ex Trin. (Rodrigues & Fidelis, 2022). Grasses are the most important flammable component of the vegetation and their flammability varies according to the season due to the moisture content and amount of dead biomass (Zanzarini et al 2022). There is also a high diversity of forbs and shrubs that display belowground bud-bearing organs (Rodrigues & Fidelis, 2022; Bombo et al., 2022). Therefore the most important post-fire regeneration strategy is resprouting from basal and belowground structures (Zupo et al., 2021).


**Figure 1.** Open savannas in Central Brazil, with the (A) general view of the study site selected for the establishment of the experimental plots; (B) a detailed view of the vegetation structure of open savannas; (C) distribution of plots with different fire treatments in the selected area. AF: annual fire; EDF: biennial early-dry fire; FE: fire exclusion; LDF: biennial late-dry fire; MDF: biennial mid-dry fire. * accidentally burned and ** substitute plot.

*Experimental design*

We established 30x30m plots in an area of open savanna (four plots for each treatment), respecting a distance of at least 4m plots (Figure 1C). All plots had the same soil, climate conditions, and vegetation structure before the establishment of the experiments (Rissi, 2016). Fire treatments began in 2013, with different fire frequencies: annual (AF, burned annually from July 2013), biennial (BF, burned biennially from July 2013), and fire exclusion (FE, fire exclusion since 2011) and fire seasons: early- (EDF, burned biennially in May), mid- (MDF, burned biennially in July), and late-dry season (LDF, burned biennially in October). Each of the experimental fires was performed separately to avoid pseudoreplication. Table 1 shows the years in which each treatment was burned from 2013 to 2021. Due to impediments to performing experimental fires in the study area, the EDF treatment plots could not be burned in 2017, with the burning of this treatment delayed to 2018. In 2020, due to the COVID-19 pandemic, it was impossible to carry out the burnings planned for the AF and EDF treatments, which were delayed until 2021. The other treatments (MDF and LDF) were not affected by the pandemic.

**Table 1.** Years in which experimental fires were carried out in open savannas of the Cerrado (Central Brazil) under different fire regimes. AF: annual fires, EDF: early, MDF: mid, and LDF: late dry season fires.

| Year | AF | EDF | LDF | MDF |
|---|---|---|---|---|
| 2013 | x | x | x | x |
| 2014 | x | | | |
| 2015 | x | x | x | x |
| 2016 | x | | | |
| 2017 | x | | x | x |
| 2018 | x | x | | |
| 2019 | x | | x | x |
| 2020 | | | | |
| 2021 | x | x | x | x |

Within each experimental plot, we randomly sampled all aboveground biomass and litter (0.5 × 0.5 m, five samples/plot) in the rainy (from January to March) and mid-dry seasons (July or August), since 2013. We sorted biomass into graminoids, non-graminoids (forbs and shrubs), and dead biomass in the laboratory. Samples were then

dried in an oven at 80 ◦C for 48 h and weighed to obtain the amount ($g \cdot m^{-2}$) according to each biomass category.

To evaluate the relationship between the productivity of communities and annual precipitation we used precipitation data from the closest station to the experimental plots (14° 8 'S and 47 ° 31 W, 1260m a.s.l., Central Brazil, Brazil), which is situated 179 km away from the RNST. We related, for every treatment, total rainfall data of the previous year to annual productivity data from 2016 to 2022 (Appendix S1).

*Statistical analysis*

We have in our database biomass data from 2016 to 2022. We obtained data from July 2015 on fire frequency treatments from Zupo et al. (2022) and data from January and July 2014 on fire season from Rissi (2016) (Appendix S2).

We used generalized additive mixed modeling (GAMM) to investigate the effects of fire frequency and season across time on every category of biomass (total biomass, total live and total dead biomass, graminoid, non-graminoid) over time. We proceeded to model selection based on the restricted maximum likelihood criteria (REML). We performed the analysis using the “gamm” function.

To assess the productivity of plant communities ($g.m^{-2}.year^{-1}$), we measured the total biomass that accumulated over one year following the fires. For treatments that experience fires every two years, we determined the productivity of the second post-fire year by calculating the difference in biomass from the previous year. We used the same method to calculate the productivity of each year for plots where fires were excluded. The average of plant communities' productivity during the evaluated period was compared among treatments using generalized linear models (GLMM, family: Gaussian). We performed the analysis using the “glmer” function. The F and p values and degrees of freedom were accessed through the "drop1" function. Significant differences among treatments were assessed by performing the Tukey test using the “emmeans” function. To compare productivity over time among treatments we also used generalized additive modeling (GAMM).

Linear regressions were conducted to determine whether there was a significant relationship ($P < 0.05$) between productivity and total rainfall ($mm.\ yr^{-1}$). All statistical analyses were performed using the R software (R Core Team, 2023) with the packages

*mgcv* (Wood, 2011), *ggeffects* (Lüdecke, 2018), *ggplot2* (Wickham & Wickham, 2016), lme4 version 1.1-27.1 (Bates et al., 2015), *emmeans* (Lenth, 2023), and stats version 4.1.1 (R Core Team, 2023).

## Results

Biomass of plant communities over time

Fire frequency influenced biomass dynamics of plant communities of open savannas (Appendix S3). The total biomass was different among communities under distinct fire frequencies over time ($p < 0.0001$, Fig. 2a), driven by the dead biomass dynamics ($p < 0.0001$, Fig 2b), which is the major biomass component in all treatments (Appendix S4). FE plots had the highest biomass amount, with values three-fold the ones found for AF and BF plots. When we analyzed the burned plots, in the first year after each burning, the amounts of total biomass were similar. However, in the following year (second-year post-fire for BF plots), the total biomass of BF plots was higher than AF plots ($p < 0.001$, Fig. 2a).

Total live biomass was similar across all fire frequency treatments ($p = 0.8$, Fig. 2c) over time. Nevertheless, fire frequency had an impact on graminoids and non-graminoid biomass (Fig. 3a and b, respectively): they differed between fire exclusion and burned plots ($p \leq 0.01$) over time. FE plots had the highest graminoid and lowest non-graminoid biomass from the dry season of 2017 until the rainy season of 2020 compared to burned plots. Live biomass was similar between AF and BF plots ($p > 0.05$) over time.

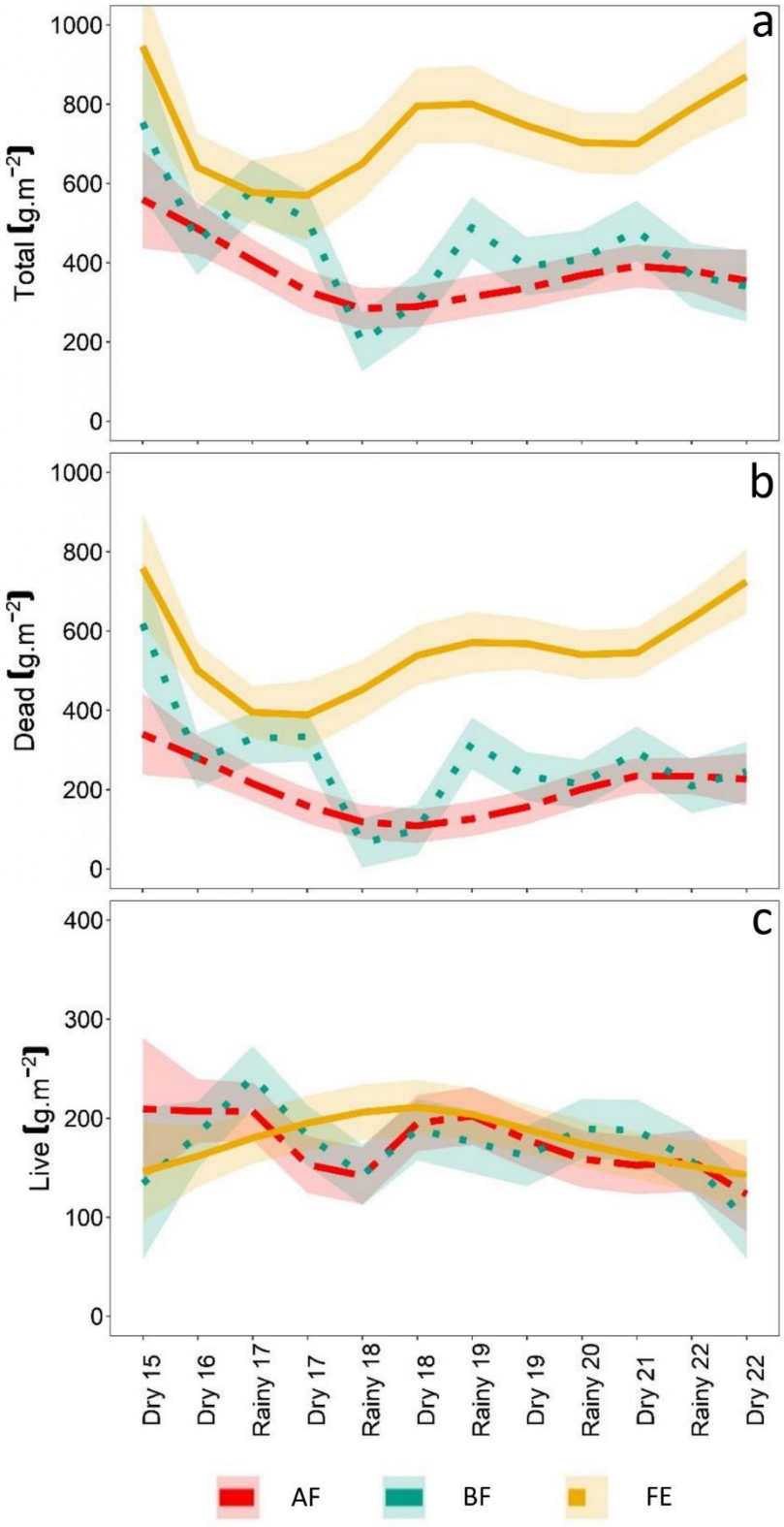


**Figure 2.** Total (a), dead (b), and live (c) biomass (g.m$^{-2}$) in plots with different fire frequencies, AF: annual fires, BF: biennial fires, and FE: fire exclusion since 2011, in an open savanna area of the Cerrado, sampled during the dry and rainy season from 2016-2022. Lines are predicted values by the best-fitted model, and the shaded areas are the corresponding 95% confidence intervals.

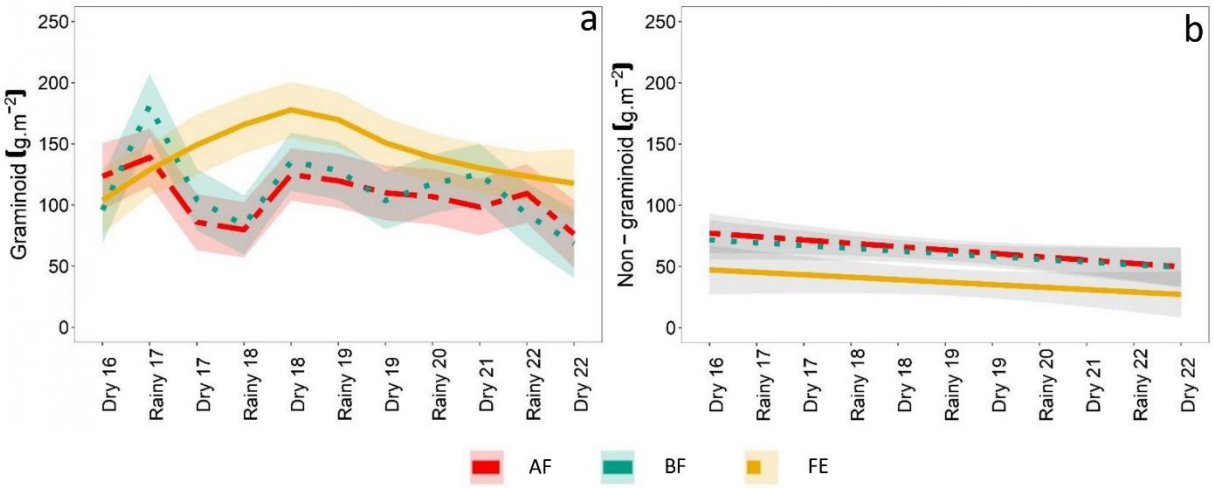


**Figure 3.** Graminoid (a) and non-graminoid (b) biomass ($g.m^{-2}$) over time by fire frequency treatments, AF: annual fires, BF: biennial fires, and FE: fire exclusion since 2011, in an open savanna area of Cerrado. Lines are predicted values by the best-fitted model, and the shaded areas are the corresponding 95% confidence intervals.

We observed that the biomass of plant communities was not impacted by the fire season over time (see Appendix S3). In the first rainy season after each fire, all treatments had already exhibited the same total biomass. Total biomass varied over time in all treatments due to the dead biomass amount, affected by the fire occurrence. The live biomass showed minor variations over time, which were not related to seasonality. The biomass amounts, including total, dead, and live biomass, were similar among communities under different fire seasons ($p > 0.05$, Fig. 4a, b, and c). However, the graminoid biomass of LDF plots was higher than EDF and MDF ones (Fig. 5a, $p > 0.005$ and $p > 0.009$, respectively), while the non-graminoid biomass did not differ among fire season plots over time ($p< 0.05$, Fig. 5b).

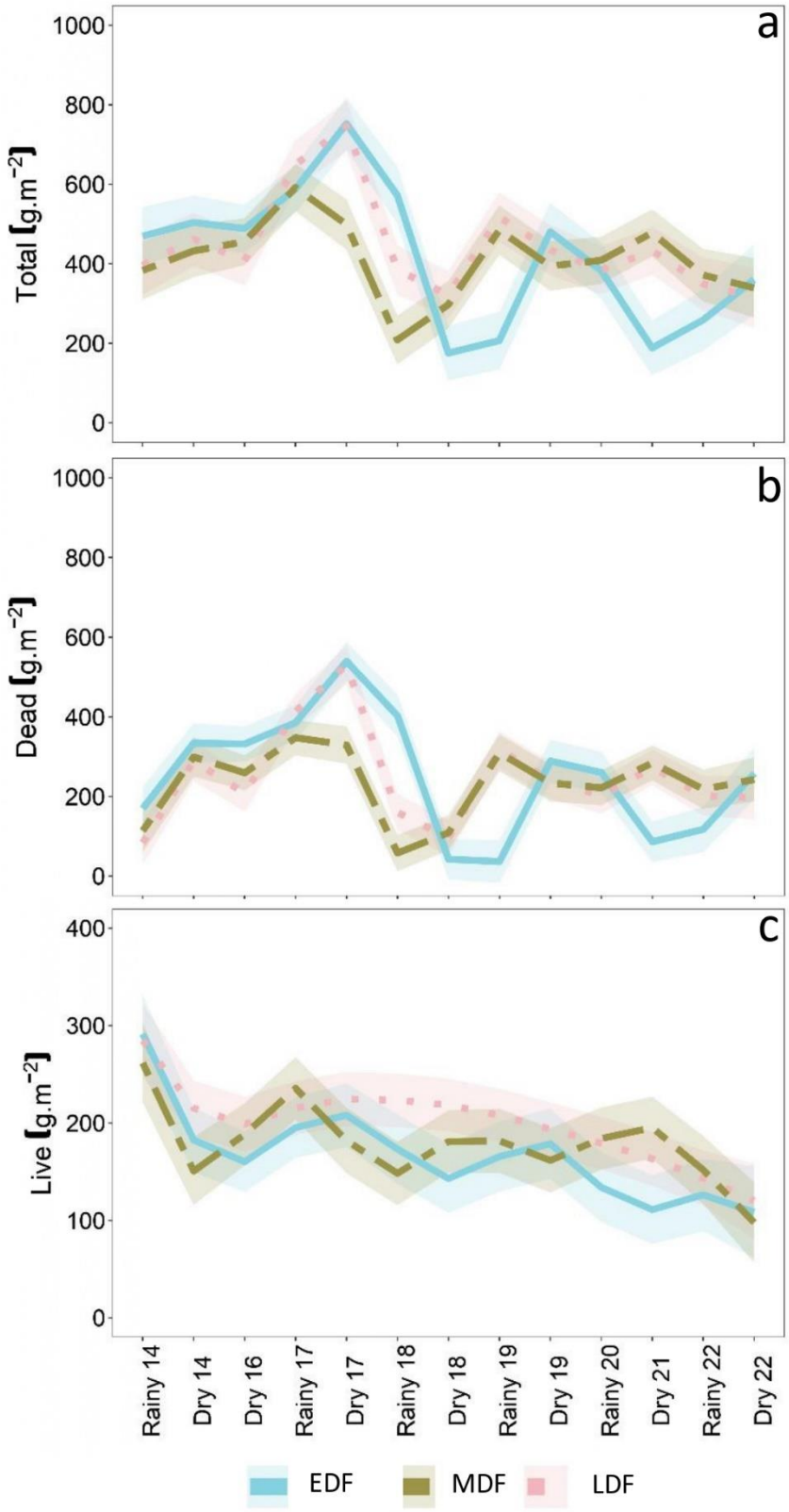


**Figure 4.** Live (a), dead (b), and total (c) biomass (g.m$^{-2}$) by fire season treatments (EDF: early, MDF: mid, and LDF: late-dry season fires) in an open savanna area of Cerrado. Lines are predicted values by the best-fitted model, and the shaded areas are the corresponding 95% confidence intervals.

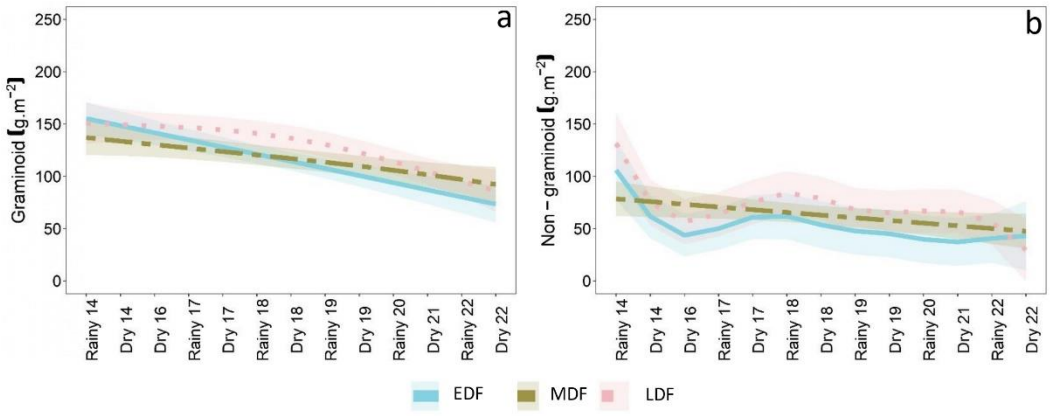


**Figure 5.** Graminoid (a) and non-graminoid (b) biomass (g.m$^{-2}$) over time by fire season treatments (EDF: early, MDF: mid, and LDF: late-dry season fires) in an open savanna area of Cerrado. Lines are predicted values by the best-fitted model, and the shaded areas are the corresponding 95% confidence intervals.

Productivity of plant communities under different fire frequencies and seasons

The productivity of aboveground biomass was affected by fire frequency: FE plots displayed average productivity five times lower than BF plots and seven times lower than AF plots ($p < 0.0001$ and $p = 0.0005$, Fig. 6a). There was no difference in productivity between burned communities, with averages of 286 ± 29 g.m$^{-2}$.yr$^{-1}$ and 369 ± 28 g.m$^{-2}$.yr$^{-1}$ in BF and AF fire plots, respectively ($p > 0.05$). On the other hand, fire season had no impact on the productivity of plant communities, with mean values between 286 ± 29 (MDF plots) and 355 ± 38 g.m$^{-2}$.yr$^{-1}$ (EDF plots, $p > 0.05$, Fig. 6b).

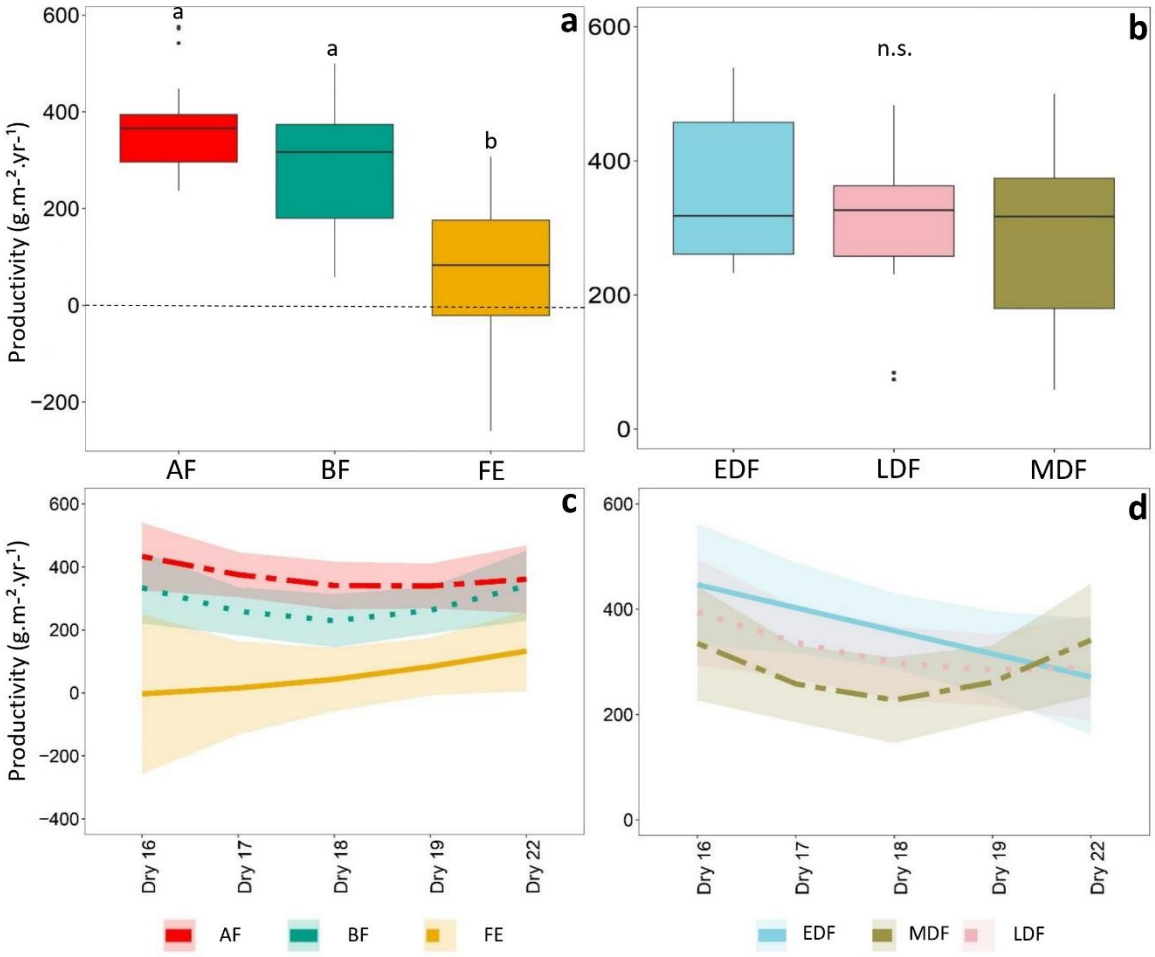


**Figure 6**. a and b - Average of productivity of biomass (g.m-$^{2}$.yr.-$^{1}$) and c and d – productivity over time (g.m-$^{2}$.yr.-$^{1}$) in plant communities under different fire frequencies (AF: annual and BF: biennial fires , and FE: fire exclusion since 2011) and fire seasons (EDF: early, MDF: mid, and LDF: late-dry season fires) of open savannas. a and b - Letters represent significant differences among treatments (P ≤ 0.05) determined by the Tukey test, and c and d - lines are predicted values by the best-fitted model, and the shaded areas are the corresponding 95% confidence intervals.

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The productivity remained stable over time in all fire frequency treatments (Fig. 6c). However, productivity was lower in FE plots than in burned plots ($p > 0.01$, Fig. 6c, Appendix S3). On the other hand, productivity over time was similar among fire season treatments ($p > 0.05$, Fig. 6d, Appendix S3). Nevertheless, we observed a tendency for a decrease in productivity in communities under early-dry season fires (Fig. 6d).

We found a positive relationship between productivity and precipitation of the previous year only in FE ($p = 0.01$, $r^2 = 0.78$). For burned plots, there was no significant relationship between productivity and precipitation ($p > 0.05$).

## Discussion

Overall, fire occurrence itself seems to be the primary factor influencing aboveground biomass in open savannas. In burned areas, the biomass is reduced by fire and then accumulates quickly until the next fire. After one year, there is already enough accumulated biomass to fuel a new fire. In unburned areas, biomass accumulation stabilized after the first years of fire exclusion due the decrease in productivity. In all treatments biomass dynamics was driven by variation in the amount of dead biomass, since live biomass dynamics was not affected by the fire regimes. Fire season influences neither biomass dynamics nor productivity. However, the frequency of fires affected both. Longer intervals between fires resulted in greater amounts of dead biomass and, consequently, total biomass. Furthermore, annual and biennial fires promoted an average productivity twice as high as fire exclusion. Therefore, contrary to our initial hypothesis, annual fires did not decrease biomass after eight consecutive fires. Plant communities not only maintained their amount of live biomass over time from 2016 to 2022 but also displayed high productivity over time. This could be attributed to fires promoting productivity by accelerating nutrient cycling (Pivello & Coutinho, 1992; Miranda et al., 2002). Rapid nutrient turnover favors herbaceous species with superficial roots, such as graminoids, which are the dominant group in open savannas and compose the majority of aboveground biomass (Coutinho, 1990; Le Stradict et al., 2021).

In addition to nutrient availability and superficial roots, the bud bank and belowground organs of reserve are crucial factors in the rapid regrowth of plants in savannas (Clarke et al., 2013; Moraes et al., 2016; Bombo et al., 2022). Through diverse types of bud bear below-ground organs, for example, xylopodia in woody and forbs and rhizomes in graminoids plants, whose presence is an adaptation to fire, savanna vegetation may resprout after fire events (Clarke et al., 2013; Bombo et al., 2022). All these factors explain the high productivity in burned areas, mainly in the first year after a fire observed in our study. Conversely, long-term fire exclusion can cause nutrients to be immobilized in dead biomass, resulting in a depletion of the surface soil

layer, less nutrient allocation in belowground organs (Frost & Robertson, 1987; Oliveras et al., 2013), and lower absorptive root biomass production (Le Stradict et al., 2021), explaining the lower productivity observed in FE plots.

However, the main differences between plant communities under distinct fire frequencies were driven mostly by the accumulation of dead biomass over time. The average percentage of dead biomass in FE plots was significantly higher (76 ± 3%) than in burned plots (63 ± 2% in AF, and 64 ± 2% in BF). High accumulation of dead biomass, like the ones found in FE plots, may cause small species suppression aboveground due to competition for resources, such as light and space, preventing species recruitment and persistence in communities (Zimmermann et al.,2010; Fidelis et al., 2012; Pilon, 2019; Rodrigues & Fidelis, 2022).

Our findings contradict our initial hypothesis regarding the effects of fire season on productivity and biomass dynamics in open savanna communities, which predicted lower productivity in communities under early dry-season fires and less non-graminoid biomass in communities under late dry-season fires. However, they are consistent with other studies showing no differences in biomass among fire seasons (for example, Oliveras et al., 2013; Rissi et al., 2017). It was expected that fires occurring early in the dry season would lead to a reduction in biomass and productivity due to the longer dry period after the fire. However, Rissi (2016) demonstrated that despite the delay in biomass regrowth compared to other fire season treatments, the EDF treatment already had the same amount of biomass as the MDF and LDF treatments in the first rainy season after the fire, as well we observed in our study. Likewise, it was expected that late-dry season fires could be more harmful to vegetation, especially for non-graminoid species, because it may be more severe. Nevertheless, LDF plots showed the same non-graminoid biomass as other treatments at all sampled times and also displayed higher graminoid biomass than EDF and MDF plots at some years. It is possible that the lack of differences in biomass among fire season treatments can be explained by the fact that Cerrado plants are adapted to fires. These plants have reserve structures that ensure their regrowth after early dry-season fires, as well as buds that are protected at the base or below the ground (Chiminazzo et al. 2021, Zupo et al., 2021) that ensure their regeneration after late dry-season, even with more severe fires with the arrival of rains.

Biomass decreases just after fire, followed by an increase, especially in the first year post-fire, until the next fire comes. Therefore, regardless of fire season, changes

that occur due to fire, such as in microclimate (Dhillion & Anderson, 1994), increased nutrient availability (Wan et al., 2001), alterations in the plant nutrient use and carbon mobilization (Ojima et al., 1994), rejuvenation in plant tissue (Van de Vijver et al., 1999), seems to be the most important factors that influence productivity and modulate biomass dynamics of burned plant communities in savannas. On the other hand, in unburned savannas, precipitation is the key factor of productivity, with increased productivity associated with greater annual precipitation.

In conclusion, our study showed that open savanna plant communities in the Cerrado are resilient to frequent fires due to the rapid recovery, independent of when fire occurs. Both recurrent annual and biennial fires maintain stable live biomass across the years and high productivity. On the other hand, fire exclusion results in substantially lower productivity over the years. Another crucial point is the variation that fire frequency promotes in dead biomass, a parameter guide to fire management actions. Regarding the drivers of biomass dynamics, evaluating long-term temporal series data, we display that in unburned areas, the annual precipitation influences how productivity varies over time. In burned areas, biomass dynamics are mainly driven by fire occurrence.

## References

Antonelli-Filho, R. (2011). Plano de Manejo da Reserva Natural Serra do Tombador, Cavalcante - Goiás.

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software, 67(1), 1-48. doi:10.18637/jss.v067.i01.

Bombo, A. B., Appezzato-da-Glória, B., & Fidelis, A. (2022). Fire exclusion changes belowground bud bank and bud-bearing organ composition jeopardizing open savanna resilience. Oecologia, 199(1). https://doi.org/10.1007/s00442-022-05172-1

Bond, W. J., & Keeley, J. E. (2005). Fire as a global “herbivore”: The ecology and evolution of flammable ecosystems. In Trends in Ecology and Evolution (Vol. 20, Issue 7). https://doi.org/10.1016/j.tree.2005.04.025

Bond, W. J. (2005). ‘Large parts of the world are brown or black : A different view on the “Green World” hypothesis’, Journal of Vegetation Science, 16, pp. 261–266.

Bova, A. S., and Dickinson, M. B. (2005). Linking surface-fire behavior, stem heating, and tissue necrosis. Canadian Journal of Forest Research, 35(4), 814-822.

Briggs, J. M., & Knapp, A. K. (1995). Interannual variability in primary production in tallgrass prairie: climate, soil moisture, topographic position, and fire as determinants of aboveground biomass. American journal of botany, 82(8), 1024-1030.

Bustamante, M. M., de Brito, D. Q., Kozovits, A. R., Luedemann, G., de Mello, T. R., de Siqueira Pinto, A., ... & Takahashi, F. S. (2012). Effects of nutrient additions on plant biomass and diversity of the herbaceous-subshrub layer of a Brazilian savanna (Cerrado). Plant Ecology, 213, 795-808.

Chiminazzo, M. A., Bombo, A. B., Charles-Dominique, T., & Fidelis, A. (2021). Your best buds are worth protecting: variation in bud protection in a fire-prone cerrado system. Functional Ecology, 35(11), 2424-2434.

Clarke, P. J., Lawes, M. J., Midgley, J. J., Lamont, B. B., Ojeda, F., Burrows, G. E., ... & Knox, K. J. E. (2013). Resprouting as a key functional trait: how buds, protection and resources drive persistence after fire. New phytologist, 197(1), 19-35.

Coutinho, L. M. (1978). O conceito de Cerrado. Rev. Brasil. Bot, 1(1), 17-23
Coutinho, L. M. (1990). Fire in the Ecology of the Brazilian Cerrado (J. G. Goldammer, Ed.; pp. 82–105). Springer Berlin Heidelberg.

Coutinho, L. M. (1982). Ecological effects of fire in Brazilian cerrado. In Ecology of tropical savannas (pp. 273-291). Berlin, Heidelberg: Springer Berlin Heidelberg.

Coutinho, L. M. (1990). Fire in the ecology of the Brazilian cerrado. In Fire in the tropical biota: ecosystem processes and global challenges (pp. 82-105). Berlin, Heidelberg: Springer Berlin Heidelberg.

Daldegan, G. A., de Carvalho Júnior, O. A., Guimarães, R. F., Gomes, R. A. T., de Figueiredo Ribeiro, F., & McManus, C. (2014). Spatial patterns of fire recurrence using remote sensing and GIS in the Brazilian savanna: Serra do Tombador Nature Reserve, Brazil. Remote Sensing, 6(10), 9873-9894.

Dhillion, S. S., & Anderson, R. C. (1994). Production on burned and unburned sand prairies during drought and non-drought years. Vegetation, 115, 51-59.

Dos Santos, A. C., da Rocha Montenegro, S., Ferreira, M. C., Barradas, A. C. S., & Schmidt, I. B. (2021). Managing fires in a changing world: Fuel and weather determine fire behavior and safety in the neotropical savannas. Journal of environmental management, 289, 112508.

Eiten, G. (1972.). The Cerrado Vegetation of Brazil. In Source: Botanical Review (Vol. 38, Issue 2).

Fidelis, A., Blanco, C. C., Müller, S. C., Pillar, V. D., & Pfadenhauer, J. (2012). Short-term changes caused by fire and mowing in Brazilian Campos grasslands with different long-term fire histories. Journal of Vegetation Science, 23(3), 552-562.

Fidelis, A., Lyra, M. F. D. S., & Pivello, V. R. (2013). Above-and below-ground biomass and carbon dynamics in B razilian Cerrado wet grasslands. Journal of Vegetation Science, 24(2), 356-364.

Fidelis, A., & Pivello, V. (2011). Deve-se usar o fogo como instrumento de manejo no Cerrado e Campos Sulinos? Biodiversidade Brasileira, 1(2).

Frost, P. H. G., & Robertson, F. (1987). The ecological effects of fire in savannas. In 'Determinants of Tropical Savannas'.(Ed. BH Walker) pp. 93–141.

Keeley, J. E. (2009). Fire intensity, fire severity and burn severity: a brief review and suggested usage. International journal of wildland fire, 18(1), 116-126.

Keeley, J. E., Pausas, J. G., Rundel, P. W., Bond, W. J., & Bradstock, R. A. (2011). Fire as an evolutionary pressure shaping plant traits. Trends in plant science, 16(8), 406-411.

Keeley, J. E., & Rundel, P. W. (2005). Fire and the Miocene expansion of C4 grasslands. Ecology Letters, 8(7), 683-690.

Knapp, E. E., Estes, B. L., & Skinner, C. N. (2009). Ecological effects of prescribed fire season: a literature review and synthesis for managers.

Knapp, A. K., & Seastedt, T. R. (1986). Detritus Accumulation Limits Productivity of Tallgrass Prairie (Vol. 36, Issue 10).

Lenth, R. (2023). _emmeans: Estimated Marginal Means, aka Least-Squares Means_. R package version 1.8.8, <https://CRAN.R-project.org/package=emmeans>.

Le Stradic, S., Roumet, C., Durigan, G., Cancian, L., & Fidelis, A. (2021). Variation in biomass allocation and root functional parameters in response to fire history in Brazilian savannas. Journal of Ecology, 109(12), 4143-4157.

Lüdecke, D. (2018). "ggeffects: Tidy Data Frames of Marginal Effects from Regression Models." _Journal of Open Source Software_, *3*(26), 772. doi:10.21105/joss.00772 <https://doi.org/10.21105/joss.00772>.

Miranda, H. S., Bustamante, M. M., & Miranda, A. C. (2002). The fire factor. In The cerrados of Brazil: ecology and natural history of a neotropical savanna (pp. 51-68). Columbia University Press.

Moraes, M. G., de Carvalho, M. A. M., Franco, A. C., Pollock, C. J., & Figueiredo-Ribeiro, R. D. C. L. (2016). Fire and drought: soluble carbohydrate storage and survival mechanisms in herbaceous plants from the Cerrado. BioScience, 66(2), 107-117.

Ojima, D. S., Schimel, D. S., Parton, W. J., & Owensby, C. E. (1994). Long-and short-term effects of fire on nitrogen cycling in tallgrass prairie. Biogeochemistry, 24, 67-84.

Oliveras, I., Meirelles, S. T., Hirakuri, V. L., Freitas, C. R., Miranda, H. S., & Pivello, V. R. (2013). Effects of fire regimes on herbaceous biomass and nutrient dynamics in the Brazilian savanna. International Journal of Wildland Fire, 22(3). https://doi.org/10.1071/WF10136

Oliveira, U., Soares-Filho, B., de Souza Costa, W. L., Gomes, L., Bustamante, M., & Miranda, H. (2021). Modeling fuel loads dynamics and fire spread probability in the Brazilian Cerrado. Forest Ecology and Management, 482, 118889.

Pilon, N.A.L. (2019). Efeitos de distúrbios naturais e da supressão do fogo na diversidade e estrutura do estrato herbáceo-arbustivo do Cerrado. Tese (Doutorado

em Ecologia) – Instituto de Biologia, Universidade Estadual de Campinas, Campinas, 2019.

Pivello, V. R., & Coutinho, L. M. (1992). Transfer of macro-nutrients to the atmosphere during experimental burnings in an open cerrado (Brazilian savanna). Journal of tropical ecology, 8(4), 487-497.

Pivello, V. R., Oliveras, I., Miranda, H. S., Haridasan, M., Sato, M. N., & Meirelles, S. T. (2010). Effect of fires on soil nutrient availability in an open savanna in Central Brazil. Plant and Soil, 337(1). https://doi.org/10.1007/s11104-010-0508-x

Quesada, C. A., Miranda, A. C., Hodnett, M. G., Santos, A. J. B., Miranda, H. S., & Breyer, L. M. (2004). Seasonal and depth variation of soil moisture in a burned open savanna (campo sujo) in central Brazil. Ecological Applications, 14(4 SUPPL.). https://doi.org/10.1890/01-6017

Ramos-Neto, M. B., & Pivello, V. R. (2000). Lightning fires in a Brazilian savanna national park: rethinking management strategies. Environmental management, 26, 675-684.

R Core Team (2023). _R: A Language and Environment for Statistical Computing_. R Foundation for Statistical Computing, Vienna, Austria.<https://www.R-project.org/>.

Rissi, M. N. (2016). Efeito da época da queima na dinâmica de campo sujo de Cerrado. Tese (Doutorado em Ciência Biológicas - Biologia Vegetal) – Instituto de Biociências, Universidade Estadual Paulista, Rio Claro, 2016.

Rissi, M. N., Baeza, M. J., Gorgone-Barbosa, E., Zupo, T., & Fidelis, A. (2017). Does season affect fire behaviour in the Cerrado? International Journal of Wildland Fire, 26(5), 427–433. https://doi.org/10.1071/WF14210

Rodrigues, C. A., & Fidelis, A. (2022). Should we burn the Cerrado? Effects of fire frequency on open savanna plant communities. Journal of Vegetation Science, 33(6). https://doi.org/10.1111/jvs.13159

Rodrigues, C. A., Zirondi, H. L., & Fidelis, A. (2021). Fire frequency affects fire behavior in open savannas of the Cerrado. Forest Ecology and Management, 482. https://doi.org/10.1016/j.foreco.2020.118850

Sarmiento, G. (1984). The ecology of neotropical savannas. Harvard University Press.

Savadogo, P., Tigabu, M., Sawadogo, L., & Odén, P. C. (2009). Herbaceous phytomass and nutrient concentrations of four grass species in Sudanian savanna woodland subjected to recurrent early fire. African Journal of Ecology, 47(4), 699-710.

Van de Vijver, C. A. D. M., Poot, P., & Prins, H. H. (1999). Causes of increased nutrient concentrations in post-fire regrowth in an East African savanna. Plant and Soil, 214, 173-185.

Wan, S., Hui, D., & Luo, Y. (2001). Fire effects on nitrogen pools and dynamics in terrestrial ecosystems: a meta-analysis. Ecological Applications, 11(5), 1349-1365.

Wickham, H., & Wickham, H. (2016). Data analysis (pp. 189-201). Springer International Publishing.

Whelan, R. J. (1995). The ecology of fire. Cambridge University press.

Wood, S.N. (2011) Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. Journal of the Royal Statistical Society (B) 73(1):3-36

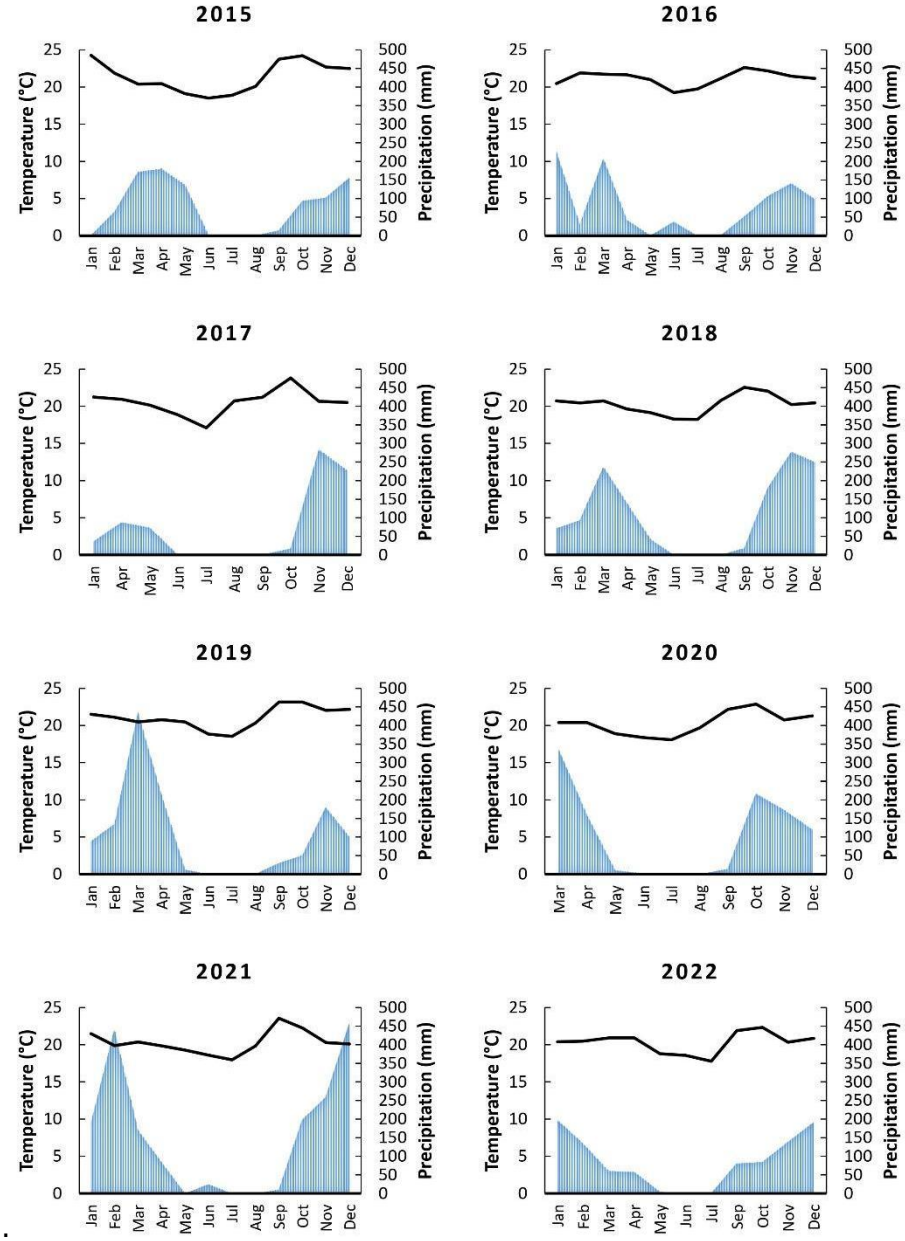
Zimmermann, J., Higgins, S. I., Grimm, V., Hoffmann, J., & Linstädter, A. (2010). Grass mortality in semi-arid savanna: the role of fire, competition and self-shading. Perspectives in Plant Ecology, Evolution and Systematics, 12(1), 1-8.

Zupo, T., Daibes, L. F., Pausas, J. G., & Fidelis, A. (2021). Post-fire regeneration strategies in a frequently burned Cerrado community. Journal of Vegetation Science, 32(1). https://doi.org/10.1111/jvs.12968

Zupo, T., Gorgone-Barbosa, E., Ninno Rissi, M., & Daibes, L. F. (2022). Experimental burns in an open savanna: Greater fuel loads result in hotter fires. Austral Ecology, 47(5), 1101-1112.

**Supporting Information**: Fire frequency, not fire season matters for aboveground biomass dynamics in open savannas of the Cerrado

**Appendix S1.** Climatic diagram for Alto Paraíso de Goiás - GO (weather station closest to the study area), showing monthly mean temperature (black line) and monthly total precipitation (area with vertical blue bands) for every year of the study period (2015 - 2022).



**Appendix S2.** Data sampled and data origin of biomass for each treatment (AF: annual fires, BF: biennial fires, FE: fire exclusion, EDF: early, MDF: mid, and LDF: late dry season fires) in the rainy and dry season from 2014 to 2022 in open savannas in Central Brazil. * indicating available data only to total, dead, and live biomass (unsorted in graminoid and non-graminoid biomass).

| Year | Season | AF | BF/MDF | EDF | LDF | FE |
|---|---|---|---|---|---|---|
| 2014 | Rainy | No sampling | Rissi, 2016 | Rissi, 2016 | Rissi, 2016 | No sampling |
| | Dry | No sampling | Rissi, 2016 | Rissi, 2016 | Rissi, 2016 | No sampling |
| 2015 | Rainy | No sampling | No sampling | No sampling | No sampling | No sampling |
| | Dry | Zupo et al., 2020* | Zupo et al., 2020* | No sampling | No sampling | Zupo et al., 2020* |
| 2016 | Rainy | No sampling | No sampling | No sampling | No sampling | No sampling |
| | Dry | Sampled data | Sampled data | Sampled data | Sampled data | Sampled data |
| 2017 | Rainy | Sampled data | Sampled data | Sampled data | Sampled data | Sampled data |
| | Dry | Sampled data | Sampled data | Sampled data | Sampled data | Sampled data |
| 2018 | Rainy | Sampled data | Sampled data | Sampled data | Sampled data | Sampled data |
| | Dry | Sampled data | Sampled data | Sampled data | Sampled data | Sampled data |
| 2019 | Rainy | Sampled data | Sampled data | Sampled data | Sampled data | Sampled data |
| | Dry | Sampled data | Sampled data | Sampled data | Sampled data | Sampled data |
| 2020 | Rainy | Sampled data | Sampled data | Sampled data | Sampled data | Sampled data |
| | Dry | No sampling | No sampling | No sampling | No sampling | No sampling |
| 2021 | Rainy | No sampling | No sampling | No sampling | No sampling | No sampling |
| | Dry | Sampled data | Sampled data | Sampled data | Sampled data | Sampled data |
| 2022 | Rainy | Sampled data | Sampled data | Sampled data | Sampled data | Sampled data |
| | Dry | Sampled data | Sampled data | Sampled data | Sampled data | Sampled data |

**Appendix S3.** Pairwise comparisons from GAMM analysis of plant communities under different fire frequencies (AF: annual fires, BF: biennial fires, and FE: fire exclusion since 2011) and seasons (EDF: early, MDF: mid, and LDF: late dry season fires) by the variation in their total, dead, live, graminoid, and non-graminoid biomass, and productivity observed over time (2016 – 2022) in communities of the herbaceous layer of the open savannas of Cerrado.

| Pairs | Total | Dead | Live | Graminoid | Non-graminoid | Productivity |
|---|---|---|---|---|---|---|
| FE x AF | < 0.001 | < 0.001 | 0.95 | 0.002 | <0.001 | < 0.001 |
| FE x BF | < 0.001 | < 0.001 | 0.212 | 0.012 | 0.001 | 0.007 |
| AF x BF | < 0.001 | < 0.001 | 0.25 | 0.635 | 0.625 | 0.06 |
| Model | < 0.0001 | < 0.0001 | 0.782 | < 0.0001 | 0.0004 | < 0.0001 |
| EDF x LDF | 0.144 | 0.665 | < 0.001 | 0.005 | 0.076 | 0.3 |
| EDF x MDF | 0.508 | 0.739 | 0.165 | 0.813 | 0.463 | 0.04 |
| LDF x MDF | 0.384 | 0.912 | 0.036 | 0.009 | 0.101 | 0.2 |
| Model | < 0.0001 | < 0.0001 | 0.002 | < 0.0001 | < 0.0001 | < 0.0001 |

**Appendix S4.** Composition of biomass of plant communities of open savannas of Cerrado under different fire frequencies (AF: annual fires, BF: biennial fires, and FE: fire exclusion since 2011) and seasons (EDF: early, MDF: mid, and LDF: late dry season fires). Percentage (mean ± se) of dead biomass, graminoids, and non-graminoids biomass in total biomass observed in rainy and dry from 2016 to 2002.

| Season | Treatment | Dead (%) | Graminoid (%) | Non-graminoid (%) |
|---|---|---|---|---|
| Rainy | EDF | 55.1 ± 79 | 31.6 ± 34 | 13.3 ± 26 |
| | AF | 33.3 ± 56 | 42.6 ± 43 | 24.1 ± 59 |
| | FE | 73.4 ± 90 | 20.9 ± 24 | 5.6 ± 10 |
| | LDF | 44 ± 70 | 36.6 ± 37 | 19.4 ± 34 |
| | MDF | 46 ± 70 | 36.8 ± 32 | 17.2 ± 25 |
| Dry | EDF | 70.2 ± 80 | 20.2 ± 19 | 9.6 ± 12 |
| | AF | 64.3 ± 83 | 21.9 ± 31 | 13.8 ± 41 |
| | FE | 77.7 ± 85 | 17.5 ± 28 | 4.7 ± 15 |
| | LDF | 67.5 ± 81 | 21.3 ± 18 | 11.2 ± 25 |
| | MDF | 65.5 ± 80 | 21.3 ± 32 | 13.2 ± 38 |

## 4. CONSIDERAÇÕES FINAIS

O presente estudo buscou identificar os efeitos de diferentes regimes de fogo sobre importantes aspectos das comunidades vegetais do estrato herbáceo de campo sujo de Cerrado a fim de apoiar ações de manejo para conservação das fisionomias abertas de savana. A conservação de ecossistemas abertos, transcende a proteção da biodiversidade, o que por si só já seria fundamental (Parr et al., 2012). De sua conservação dependem a manutenção de serviços ecossistêmicos valiosíssimos, como a regulação do ciclo da água e nutrientes, armazenamento de carbono, regulação do clima, subsistência de populações humanas através de recursos da biodiversidade, além de diversos serviços culturais (Russell-Smith & Cooke, 2009; Richards & Andersen, 2012; Olsson & Ouattara, 2013; Parr et al., 2014; Zhao et al., 2020). Para além da degradação de campos e savanas para sua conversão em áreas de cultivo e pastagens, ecossistemas abertos têm sofrido com o manejo de fogo inadequado, mesmo em áreas de proteção (Hoekstra et al., 2005; Sano et al., 2010; Durigan & Ratter, 2016, Fidelis et al., 2018). A falta de entendimento de como o fogo atua na estruturação, manutenção e funcionalidade das comunidades, tem levado a decisões de manejo equivocadas e prejudiciais à conservação de campos e savanas tropicais.

Assim, é crucial intensificar os esforços para preencher as lacunas no entendimento de como o fogo afeta as comunidades vegetais dos ecossistemas abertos tropicais. Isso inclui investigar a influência do fogo na montagem das comunidades, nas adaptações e respostas das espécies e nas condições ambientais. Embora tenham sido estabelecidas conexões valiosas com a ocorrência do fogo em si, havia pouca compreensão dos efeitos de diferentes regimes de fogo no estrato herbáceo-arbustivo das savanas do Cerrado, especialmente em uma perspectiva de longo prazo. Neste sentido, são compartilhadas a seguir as principais conclusões de cada tópico avaliado neste estudo esperando-se contribuir para futuras pesquisas e políticas baseadas em dados para conservação das savanas tropicais.

Os principais resultados deste estudo quanto aos efeitos de diferentes regimes de fogo no microclima das comunidades vegetais de campo sujo, apresentados no primeiro capítulo desta tese, indicaram que a frequência de fogo influencia os

parâmetros microclimáticos ao longo do tempo através das diferenças na cobertura vegetal entre as parcelas queimadas e não queimadas. Maiores temperaturas e iluminância e menor umidade relativa foram registradas nas parcelas queimadas. Os efeitos da frequência do fogo no microclima das savanas abertas persistem por pelo menos 12 meses após a queimada, sendo potencializados pela estação seca. Portanto, a sazonalidade também desempenha um papel importante nas mudanças do microclima local e deve ser considerada mais minuciosamente. A descrição do microclima após queimadas anuais e bienais, neste estudo, pode apoiar a compreensão dos processos pós-fogo, como floração, germinação, recrutamento e estabelecimento de mudas, montagem da comunidade e produtividade das plantas, entre outros. Além disso, a descrição do microclima em áreas excluídas do fogo ao longo de um ano é importante para compreender a dinâmica da comunidade vegetal de acordo com a sazonalidade.

As análises realizadas no segundo e terceiro capítulos acerca dos efeitos a longo prazo dos diferentes regimes de fogo na estrutura, produtividade, dinâmica da biomassa aérea, diversidade e composição de espécies, bem como na diversidade funcional das comunidades de campo sujo, revelaram que as comunidades vegetais respondem diferentemente à frequência e época do fogo. As diferenças entre as comunidades sob queimadas anuais, bienais no início, meio e final da estação seca e exclusão do fogo surgiram desde os primeiros anos de experimentos e foram consolidadas ao longo do tempo. Entre todos os tratamentos, a exclusão do fogo teve o impacto mais negativo nas comunidades vegetais. A exclusão do fogo afetou a riqueza e cobertura de herbáceas e graminóides, a riqueza total de espécies, diversidade taxonômica e funcional e a produtividade do estrato herbáceo de savanas abertas. Isto indica que o fogo é essencial não apenas para controlar o acúmulo de material de combustível, mas também para preservar a biodiversidade e funcionalidade das savanas tropicais. Do mesmo modo, queimadas no início da estação seca podem ser prejudiciais para as comunidades vegetais. O fogo nesta época, apesar de não afetar a produtividade e a dinâmica da biomassa aérea da vegetação, pode reduzir a riqueza de graminóides, a riqueza total de espécies e a diversidade taxonômica do estrato herbáceo em savanas abertas. Contudo, as queimadas precoces são as mais utilizadas em programas de manejo de fogo em áreas protegidas para controlar a carga de combustível. A escolha por esta época

para realizar as queimadas prescritas justifica-se devido à teor de umidade da vegetação ser mais elevado no início da seca comparado ao meio e final e às condições ambientais serem mais amenas nesse período (Rissi et al., 2017; Dos Santos et al., 2021), resultando em fogo menos intenso e mais fácil de controlar. Por outro lado, as queimadas durante o meio e o final da estação seca promovem maior diversidade de espécies, mas são difíceis de controlar. Alta diversidade de espécies e funcional também foi observada em comunidades sob fogo anual, que se mostraram resilientes às queimadas recorrentes, mantendo a cobertura das formas de crescimento e a produtividade semelhantes aos outros tratamentos. De fato, ambas frequências de fogo recorrentes (anual e bienal) mantêm uma quantidade estável de biomassa viva e alta produtividade.

Em resumo, diante dos resultados obtidos, concluiu-se que manter o fogo nas savanas abertas é essencial para sua conservação. E a adoção de práticas de manejo utilizando diferentes frequências e épocas de fogo, como queimadas em mosaico, além de evitar incêndios descontrolados, permite se beneficiar dos aspectos positivos de cada regime de fogo, mitigar os negativos e promover uma maior pirodiversidade.

## REFERÊNCIAS BIBLIOGRÁFICAS

Dos Santos, A. C., da Rocha Montenegro, S., Ferreira, M. C., Barradas, A. C. S., & Schmidt, I. B. (2021). Managing fires in a changing world: Fuel and weather determine fire behavior and safety in the neotropical savannas. Journal of environmental management, 289, 112508.

Durigan, G., & Ratter, J. A. (2016). The need for a consistent fire policy for Cerrado conservation. Journal of Applied Ecology, 53(1), 11-15.

Fidelis, A., Alvarado, S. T., Barradas, A. C. S., & Pivello, V. R. (2018). The year 2017: megafires and management in the Cerrado. Fire, 1(3), 49.

Hoekstra, J. M., Boucher, T. M., Ricketts, T. H., & Roberts, C. (2005). Confronting a biome crisis: global disparities of habitat loss and protection. Ecology letters, 8(1), 23-29.

Olsson, E. G. A., & Ouattara, S. (2013). Opportunities and challenges to capturing the multiple potential benefits of REDD+ in a traditional transnational savanna-woodland region in West Africa. Ambio, 42, 309-319.

Parr, C. L., Gray, E. F., & Bond, W. J. (2012). Cascading biodiversity and functional consequences of a global change–induced biome switch. Diversity and Distributions, 18(5), 493-503.

Parr, C. L., Lehmann, C. E., Bond, W. J., Hoffmann, W. A., & Andersen, A. N. (2014). Tropical grassy biomes: misunderstood, neglected, and under threat. Trends in ecology & evolution, 29(4), 205-213.

Richards, A. E., Andersen, A. N., Schatz, J. O. N., Eager, R., Dawes, T. Z., Hadden, K., ... & Van Der Geest, M. (2012). Savanna burning, greenhouse gas emissions and indigenous livelihoods: Introducing the Tiwi Carbon Study. Austral Ecology, 37(6), 712-723.

Russell-Smith, J., Whitehead, P., & Cooke, P. (Eds.). (2009). Culture, ecology and economy of fire management in North Australian savannas: rekindling the Wurrk tradition. Csiro Publishing.

Sano, E. E., Rosa, R., Brito, J. L., & Ferreira, L. G. (2010). Land cover mapping of the tropical savanna region in Brazil. Environmental monitoring and assessment, 166, 113-124.

Zhao, Y., Liu, Z., & Wu, J. (2020). Grassland ecosystem services: A systematic review of research advances and future directions. Landscape Ecology, 1-22.