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**PROGRAMA DE PÓS-GRADUAÇÃO EM CIÊNCIAS BIOLÓGICAS  
(BIOLOGICA VEGETAL)**

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**COMO O FOGO E A INVASÃO BIOLÓGICA AFETAM A DINÂMICA DE CARBONO  
EM ECOSISTEMAS CAMPESTRES E SAVÂNICOS DO CERRADO?**

**JULIANA MACEDO GITAHY TEIXEIRA**

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**JULIANA MACEDO GITAHY TEIXEIRA**

Tese apresentada ao Instituto de Biociências do Câmpus de Rio Claro, Universidade Estadual Paulista, como parte dos requisitos para obtenção do título de Doutor em Ciências Biológicas – Biologia Vegetal.

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**CERTIFICADO DE APROVAÇÃO**

**TÍTULO DA TESE: "Como o fogo e a invasão biológica afetam a dinâmica de carbono em ecossistemas campestres e savânicos do Cerrado"**

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*"Poderoso para mim não é aquele que descobre ouro.  
Para mim poderoso é aquele que descobre as insignificâncias  
(do mundo e as nossas)"*

Manoel de Barros  
(Tratado geral das grandezas do ínfimo)

## RESUMO

Promover o estoque de carbono torna-se uma ferramenta importante para a mitigação de mudanças climáticas. Os ecossistemas neotropicais campestres e savânicos são ambientes inflamáveis, com alta diversidade de espécies e alto potencial para a provisão de serviços ecossistêmicos, como o estoque de carbono. Porém, a provisão deste serviço ecossistêmico pode ser modificada por mudanças no regime de fogo e pela invasão biológica, que são grandes ameaças a estes ecossistemas. O papel da mudança de regime de fogo (*i.e.*, diferentes frequências) e da invasão biológica na dinâmica de carbono dos ecossistemas campestres e savânicos precisam ser analisados. O objetivo principal desta tese foi entender como o fogo e a invasão biológica afetam a dinâmica de carbono em ecossistemas campestres e savânicos do Cerrado. Para isso, avaliamos: (i) como o fogo afeta os fluxos de entrada e de saída de carbono (C) analisando os processos e os caminhos de mudanças destes fluxos (*i.e.*, biomassa, diversidade); (ii) como o fogo afeta a biomassa subterrânea e a composição dos órgãos subterrâneos; e (iii) como diferentes frequências de fogo e gramíneas africanas invasoras afetam os fluxos de entrada e saída do C. Para responder essas perguntas, utilizamos: áreas de campo sujo nas quais o fogo foi manipulado com diferentes frequências de fogo (pergunta i, ii e iii), em um experimento na região central do Brasil (Reserva Natural Serra do Tombador, RNST); quatro outras áreas que compreendem ecossistemas campestres e savânicos ocorrendo do limite norte até a região sudeste do Cerrado (pergunta ii) ; e áreas invadidas por *Urochloa brizantha* e não invadidas (pergunta iii), localizadas também na região central do Cerrado (RNST). Foram mensurados a troca líquida de dióxido de carbono do ecossistema (NEE), a eficiência do uso de água no ecossistema (eWUE), e o carbono orgânico do solo (SOC), representando o fluxo de entrada de C no sistema. Medimos também a evapotranspiração do ecossistema (ET) e a respiração do solo, representando a saída de carbono do ecossistema. Coletamos atributos funcionais aéreos (área foliar específica, forma de crescimento, altura) e subterrâneos (área específica de raiz, matéria seca de raiz, densidade do tecido de raiz) relacionados com a dinâmica do C nas comunidades de campo sujo, além da biomassa aérea e subterrânea, incluindo raízes e órgãos. Os órgãos subterrâneos foram classificados de acordo com as suas funções relacionadas ao banco de gemas. No capítulo 1, demonstramos que o fogo aumenta o SOC, a diversidade funcional, e o investimento em biomassa de raízes. Porém, a relação entre o fogo e as modificações dos processos ligados ao fluxo de entrada de carbono (SOC e NEE) e a diversidade funcional não foi evidenciada em nosso estudo. No capítulo 2, evidenciamos que o fogo aumentou a biomassa total de raízes e a proporção de xilopódios. Também demonstramos que sem o fogo a biomassa de órgãos subterrâneos se manteve mesmo após 12 anos de exclusão, porém, houve variação na composição dos órgãos subterrâneos. No capítulo 3, demonstramos que áreas submetidas a alta frequência de fogo recuperam rapidamente as taxas de entrada de carbono (NEE), e que a presença de espécies invasoras leva a ausência de variação sazonal no fluxo de C como foi observado em áreas não invadidas. Os resultados desta tese ajudam a entender melhor como a dinâmica do C acontece no Cerrado, ajudando a criação de modelos e ações que contemplem o potencial serviço de estoque de C destes ecossistemas.

**Palavras-chave:** dinâmica do carbono, regime de fogo, invasões biológicas, diversidade funcional, alocação de biomassa, Cerrado.

## ABSTRACT

Increasing carbon stocks become an important tool for mitigating climate change. Neotropical grassland and savanna ecosystems are fire-prone ecosystems, with high species diversity and a high potential for the provision of ecosystem services, such as carbon stock. However, the provision of this ecosystem service can be strongly modified by changes in the fire regime and by biological invasion, which are two of the major threats to these ecosystems. The role of fire (in the context of changes in fire regime, i.e., different frequencies) and biological invasion on carbon dynamics of grassland and savanna ecosystems needs to be analyzed. The main goal of this work was to understand how fire and biological invasion can affect carbon dynamics in Cerrado grassland and savanna ecosystems. We assessed: (i) how fire affects carbon (C) fluxes (outputs and inputs) by analyzing the pathways between fire and C fluxes (i.e., biomass, diversity); (ii) how fire affects belowground biomass and belowground organ composition; and (iii) how different fire frequencies and biological invasion by African grass affect C fluxes. To answer these questions, we used: areas of *campo sujo* where fire was manipulated according to different fire frequencies (question i, ii and iii), in an experiment in central Brazil (*Reserva Natural Serra do Tombador*, RNST); four other areas comprising grassland and savanna ecosystems occurring from the northern limit to the southeastern region of the Cerrado (question ii); and areas invaded by *Urochloa brizantha* and uninvaded areas (question iii), also located in the central region of the Cerrado (RNST). Net ecosystem exchange carbon dioxide (NEE), ecosystem water use efficiency (eWUE), and soil organic carbon (SOC) were measured, representing ecosystem C input. We also measured ecosystem evapotranspiration (ET) and soil respiration, representing ecosystem C output. We collected aerial (i.e. specific leaf area, growth form, height) and belowground (i.e. specific root area, root dry matter content, root tissue density) functional traits related to the dynamics of C in the *campo sujo* communities, as well as the aerial and belowground biomass (including roots and organs). The belowground organs were classified according to their bud-bearing functions. In Chapter 1, we demonstrated that fire increased SOC, functional diversity, and root biomass investment. However, the pathways between C input (SOC and NEE) and the functional diversity were not evidenced in our study. In chapter 2, we showed that fire increased the total root biomass and the proportion of xylopodia. We also demonstrated that 12 years of fire exclusion were not enough to change total belowground organs biomass. However, fire exclusion led to variation in the composition of belowground organs. In Chapter 3, we demonstrated that areas subjected to high fire frequencies quickly recovered C input rates (NEE). The presence of invasive species led to the absence of seasonal variation in C flux as observed in non-invaded areas. The results of this thesis help to better understand how C dynamics can be modified in the Cerrado, thus assisting the creation of models and actions implementation that addresses the potential C stock service of the Cerrado grassland and savanna ecosystem.

**Keywords:** carbon dynamics, fire regime, biological invasion, functional diversity, biomass allocation, Cerrado.

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## SUMÁRIO

|                                                                                                                                                                                                    |     |
|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-----|
| <b>INTRODUÇÃO GERAL</b>                                                                                                                                                                            | 14  |
| Contextualização                                                                                                                                                                                   | 14  |
| 1. Dinâmica do Carbono                                                                                                                                                                             | 16  |
| 1.1. Efeito do fogo na dinâmica do carbono em ecossistemas<br>campestres e savânicos                                                                                                               | 17  |
| 1.2. Atividades antrópicas e a dinâmica do carbono em<br>ecossistemas campestres e savânicos                                                                                                       | 19  |
| 2. Importância de estruturas subterrâneas em ecossistemas campestres e<br>savânicos                                                                                                                | 20  |
| 3. Fogo, diversidade funcional e a dinâmica de carbono em<br>ecossistemas campestres e savânicos                                                                                                   | 24  |
| 4. Ecossistemas campestres e savânicos do Cerrado                                                                                                                                                  | 26  |
| 5. Objetivos                                                                                                                                                                                       | 30  |
| 6. Estrutura da Tese                                                                                                                                                                               | 31  |
| <br><b>CAPÍTULO I</b>                                                                                                                                                                              |     |
| Fire promotes functional plant diversity and modifies soil<br>carbon dynamics in tropical savanna<br>(Teixeira, J., Souza, L., Le Stradic, S., Fidelis, A.)                                        | 49  |
| <br><b>CAPÍTULO II</b>                                                                                                                                                                             |     |
| Does fire affect belowground biomass composition and<br>allocation in tropical grasslands and savannas open?<br>(Teixeira, J., Le Stradic, S., Souza, L., Bombo, A.B., Dairel,<br>M., Fidelis, A.) | 99  |
| <br><b>CAPÍTULO III</b>                                                                                                                                                                            |     |
| Ecosystem dynamics in response to fire frequency and<br>biological invasion in the Cerrado<br>(Teixeira, J., Souza, L., Le Stradic, S., Damasceno, G.,<br>Gorgone-Barbosa, E., Fidelis, A.)        | 136 |
| <br><b>CONSIDERAÇÕES FINAIS</b>                                                                                                                                                                    | 171 |





Vista geral de um campo sujo do Brasil central  
(Reserva Natural Serra do Tombador, Goiás).

## INTRODUÇÃO GERAL

Um dos grandes desafios da atualidade é a mitigação das mudanças climáticas. As emissões de carbono atmosférico chegaram na última década (2010-2019) a marcas equivalentes a  $59 \pm 6.6$  giga toneladas de gás carbônico equivalente por ano ( $\text{GtCO}_2\text{-eq yr}^{-1}$ ), valores nunca registrados na história humana (Dhakal et al. 2022). Mesmo com a redução de 5,8% do total de emissões em 2020 devido a pandemia de COVID-19, em 2021 as emissões se igualaram as de 2019, com previsões de novos aumentos para os anos subsequentes (Friedlingstein et al. 2022). Este aumento está associado, entre outros, a queima de combustíveis fósseis e mudanças no uso da terra em regiões tropicais do globo, representando juntos a emissão de  $39.3 \text{ GtCO}_2\text{-eq yr}^{-1}$  no ano de 2021, o que corresponde a 76% do total de emissões (IPCC 2022; Friedlingstein et al. 2022). Assim, segundo os recentes acordos e cooperações globais, como o Acordo de Paris (UNFCCC 2015) e o Pacto Climático de Glasgow (UNFCCC 2021), são essenciais a implementação de medidas que diminuam essas emissões. Especificamente, estima-se que essas emissões devem ser reduzidas a taxas de  $1.4 \text{ GtCO}_2$  ao ano (Friedlingstein et al. 2022), para assegurar que as taxas de entrada e saída de carbono (i.e., balanço de carbono) limitem o aumento da temperatura da Terra a  $1.5^\circ\text{C}$  (IPCC 2022; Lecocq et al. 2022).

Promover o estoque de carbono através da conservação e da restauração de ecossistemas, inclusive ecossistemas abertos pode ser uma importante ferramenta para ajudar a solucionar este problema (Griscom et al. 2017; Yang et al. 2019). Estima-se que com a restauração de ecossistemas campestres pode-se alcançar o sequestro anual de  $3.4 \text{ GtCO}_2\text{-eq}$  de carbono no solo (Bai & Cotrufo 2022). E assim, potencialmente reduzindo as emissões até 2100 em magnitudes de até  $248.7 \pm 154.6 \text{ GtCO}_2\text{eq}$ , se somente forem incluídos os ecossistemas campestres úmidos (Zou et al. 2022). Já a conservação de ecossistemas savânicos pode acumular anualmente de 52 a 26 giga toneladas de carbono ( $\text{GtC}$ ) (Grace et al. 2006). Isso acontece porque ecossistemas campestres e savânicos representam 40% da cobertura terrestre (Dixon et al. 2014) e tem alto potencial para o armazenamento de carbono no solo (Jobbagy & Jackson 2000; Lloyd et al. 2008; Wigley et al. 2020; Bai & Cotrufo 2022) e em biomassa, este último representando 17% do total de carbono estocado em biomassa no mundo (Spawn et al. 2020). Aproximadamente 85% do carbono armazenado em ecossistemas savânicos está embaixo da terra na forma de biomassa de raízes,

carbono orgânico do solo (SOC) (Bardgett et al. 2021; Zhou et al. 2022) e em estruturas de reservas portadoras de gemas (*i.e.*, órgãos subterrâneos) (Fidelis et al. 2013; Bombo et al. 2022).

Apesar destes ecossistemas armazenarem muito carbono no solo, eles representam regiões com altas emissões de carbono atmosférico (IPCC 2022). As emissões de carbono atmosférico estão relacionadas à alta conversão de áreas naturais abertas em áreas agricultáveis ou de pastagens plantadas (Conant et al. 2017; Bonanomi et al. 2019; IPBES 2019), e a um dos fatores naturais que mantém esses ecossistemas abertos: o fogo (Bond & Keeley 2005; Bond & Parr 2010; Hoffmann et al. 2012; Veldman, Buisson, et al. 2015; Pausas & Bond 2019). Anualmente a queima de ecossistemas campestres e savânicos representa 80% do total de áreas queimadas no planeta (Strömberg & Staver 2022). Assim, acordos mundiais focados na redução dos gases de efeito estufa através da conservação e restauração de ecossistemas (Jørgensen 2015), não incluem os ecossistemas campestres e savânicos como prioridade em suas ações, ou até mesmo priorizam o plantio de árvores em áreas nativas campestres e savânicas (Parr et al. 2014; Dudley et al. 2020; Buisson et al. 2022). Isto foi inicialmente promovido devido a identificação histórica dos ecossistemas campestres e savânicos como áreas sem funcionalidade e degradadas, com aptidão para o plantio de árvores (Veldman, Overbeck, et al. 2015; Veldman et al. 2017; Bastin et al. 2019; Stevens et al. 2022), porém desconsiderando e subestimando o serviço de armazenamento de carbono no solo (Fidelis et al. 2013; Bai & Cotrufo 2022; Zhou et al. 2022).

Dentro deste contexto, identificar o papel dos ecossistemas abertos para a mitigação das mudanças climáticas torna-se essencial. Porém ainda não é claro quais são os mecanismos que regulam a dinâmica de carbono (*i.e.* entrada e saída de carbono) (Grace et al. 2006), e como as grandes ameaças destes sistemas (por exemplo, alteração dos distúrbios naturais e a invasão biológica) podem alterar estes mecanismos (Bond 2022). Principalmente em relação aos ecossistemas tropicais savânicos, que são ecossistemas inflamáveis caracterizados por clima sazonal (Staver et al. 2011; Buisson et al. 2019; Keeley & Pausas 2019). Isso porque, a dinâmica do carbono em ecossistemas savânicos depende não só da sazonalidade, mas da interação e feedback com o fogo, tornando-se ainda mais complexa (Pausas & Bond 2020b; Strömberg & Staver 2022).

## 1. Dinâmica do Carbono

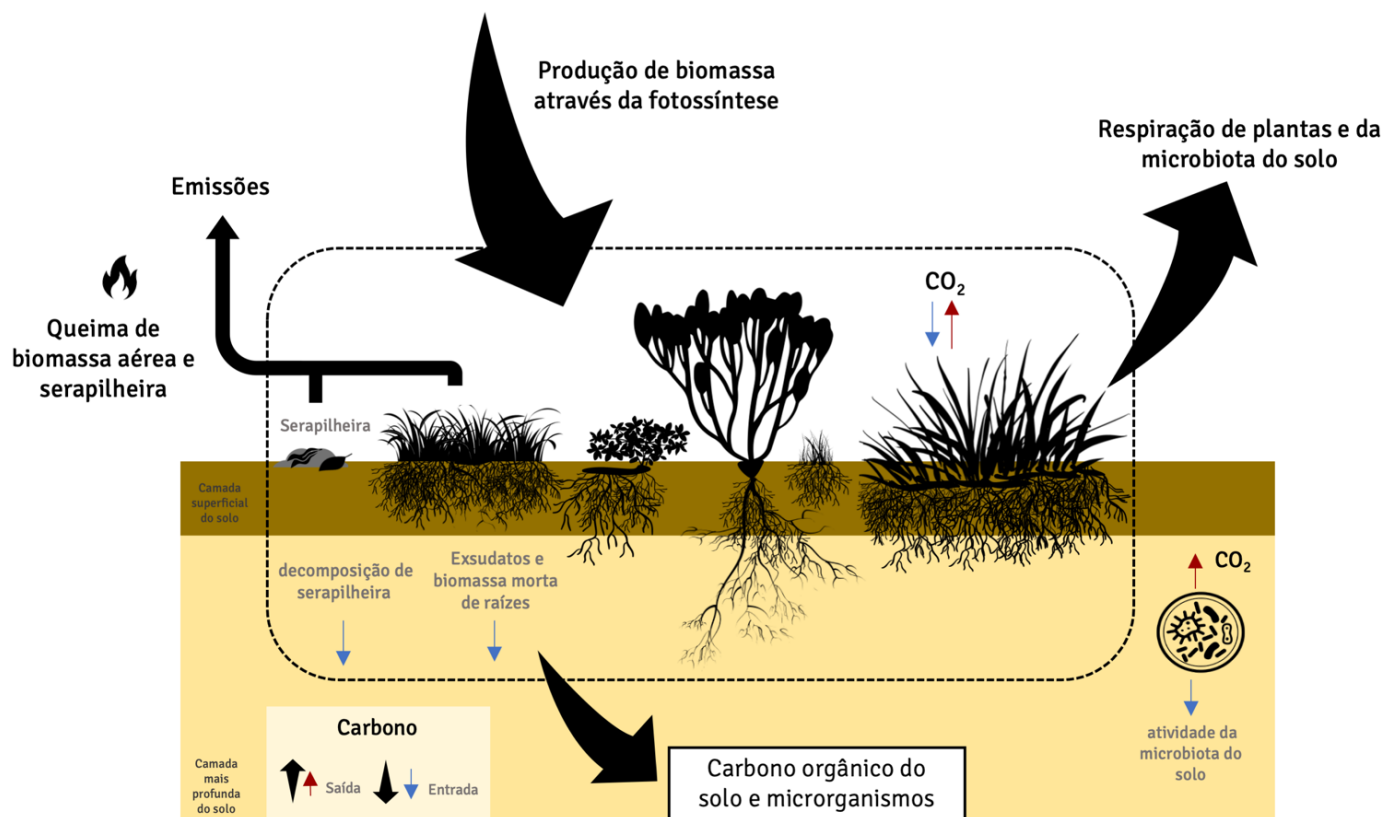
A dinâmica do carbono dos ecossistemas pode ser entendida como uma medida de fluxos de entrada (*e.g.*, fotossíntese, produção primária líquida, do inglês *net primary production*, NPP, entre outros), e de saída (*e.g.*, respiração, decomposição e consumo de plantas) de carbono (Baldocchi 2008). A fotossíntese fixa energia nos ecossistemas e suporta diretamente o crescimento das plantas. A fotossíntese produz material orgânico (*i.e.*, serapilheira, exsudação de raízes, morte de raízes) que é consumido por animais e a microbiota do solo, movendo o carbono das plantas para o solo (*i.e.*, SOC) (Norby & Jackson 2000; Chapin et al. 2011a). A perda de carbono nos ecossistemas acontece através da respiração de plantas, de sua morte total ou parcial, da secreção de compostos orgânicos voláteis, como também da transferência do carbono das plantas para microrganismos simbioticamente associados ou pelo consumo das plantas por distúrbios, *e.g.*, fogo (Chapin et al. 2011b). Uma forma de mensurar esses processos se dá através da estimativa de NEE (do inglês *net ecosystem exchange of carbon dioxide*), que representa a diferença entre o dióxido de carbono (CO<sub>2</sub>) que as plantas conseguem assimilar pela fotossíntese, e a perda de CO<sub>2</sub> pela respiração de plantas e da atividade microbiana (NEE, do inglês *net ecosystem exchange of carbon dioxide*) (Law 2005); de ET (do inglês *evapotranspiration*) que representa a perda de água pela transpiração das plantas e do solo; e da eficiência do uso de água (eWUE, do inglês *ecosystem water use efficiency*) que é a relação entre a assimilação de carbono e perda de água entre a superfície terrestre e a atmosfera (Tubiello et al. 1999).

Todos esses processos ecossistêmicos são diretamente dependentes do clima (por exemplo variação interanual da temperatura e precipitação, sazonalidade), da estrutura, da composição e dos atributos funcionais presentes nas comunidades, já que esses fatores podem alterar tanto a disponibilidade como a eficiência no uso de diferentes recursos (*i.e.*, água, incidência de luz e nutrientes) no sistema, limitando ou não o ganho de carbono ecossistêmico (Chapin et al. 2011b). Por exemplo, por muitas vezes serem mais eficientes no uso de recursos, ecossistemas com alta diversidade (funcional e taxonômica) tendem a apresentar maior capacidade em ganho de carbono em comparação aos menos diversos (Tilman et al. 1997; De Deyn et al. 2011; Chen et al. 2018; Yang et al. 2019). Em ecossistemas campestres e savânicos, no início da época chuvosa há um aumento de ET e NEE como consequência das altas taxas fotossintéticas no sistema (Miranda et al. 1997; Giambelluca et al. 2009). Isso acontece, devido ao aumento da área foliar produzida

durante a produção de biomassa, que encontra recursos favoráveis (água) para o seu crescimento (Giambelluca et al. 2009). Já durante o período seco, há a diminuição da ET como uma estratégia de conservação de água (Miranda et al. 1997; Giambelluca et al. 2009).

## **1.1. Efeito do fogo na dinâmica do carbono em ecossistemas campestres e savânicos**

A dinâmica do carbono em ecossistemas campestres e savânicos é fortemente influenciada pela presença de distúrbios, como por exemplo o fogo (Weng et al. 2012; Beringer et al. 2015). O fogo é um distúrbio natural em ecossistemas savânicos e nos ecossistemas campestres tropicais, e um dos principais responsáveis pela manutenção do estado aberto destes ecossistemas, especialmente em regiões que as características climáticas suportam a existência de florestas (Buisson et al. 2019). Em ecossistemas inflamáveis abertos, o fogo atua reciclando o carbono e nutrientes (Pivello et al. 2010), assim seu regime influencia fortemente a entrada e a saída do carbono no sistema (Chapin et al. 2011b; Weng et al. 2012; Pellegrini et al. 2018). A saída de carbono nesses sistemas também acontece devido a queima da biomassa aérea e da serrapilheira (Figura 1). O consumo da biomassa pelo fogo, leva a emissão direta de carbono na atmosfera, e, para estes ecossistemas, é uma medida conhecida como ‘fluxo natural’ (*i.e.*, fluxo de combustão, Grace et al. 2006). A emissão de carbono atmosférico, proferido pela queima destes ambientes inflamáveis, representa uma fonte de emissões da grandeza de 2.2 GtC o que equivale a 65.3% das emissões globais provenientes de queimadas (Van Der Werf et al. 2017). Porém, devido aos ecossistemas inflamáveis serem resilientes ao fogo (Keeley et al. 2011), eles rapidamente compensam a saída de carbono em magnitudes iguais ou superiores a sua condição antes da queima (Santos et al. 2003; Jones et al. 2019), através da rápida regeneração da vegetação (Keeley et al. 2011; McLauchlan et al. 2020; Bowman et al. 2020; Simpson et al. 2021).



**Figura 1.** Visão geral dos maiores fluxos de carbono que compõem a dinâmica de carbono de ecossistemas savânicos. O carbono entra nos ecossistemas através da produção de biomassa (área e subterrânea) pela fotossíntese das plantas. Grande parte da biomassa é transferida para matéria orgânica do solo na forma de biomassa morta de raízes, exsudatos de raízes e serapilheira. A saída de carbono acontece através da respiração de plantas (folhas e raízes) e de microrganismos, e do consumo da biomassa através de distúrbios. No caso dos ecossistemas inflamáveis, a saída de carbono através do consumo da biomassa aérea, é uma medida conhecida como fluxo natural (i.e. fluxo de combustão), que representa a emissão de carbono atmosférico como resultado de queimas (Grace et al. 2006), rapidamente compensada através da rápida regeneração pós fogo. Nestes ecossistemas todos estes processos são influenciados pelo regime de fogo e sazonalidade. As setas azuis e vermelhas representam a entrada e saída de C respectivamente, mais específicas. Figura baseada em Chapin (2011b) e Bai e Cotrufo (2022). Os ícones utilizados são do *thenoun.project.com*: grass (Milena Zanotelli, Jhonatan, Angel Santos Freya), drought (Adrien Coquet), Flowers (Travis Bird), microbes (Dima Lagunov), roots (Guilhem and Julia Amadeo), shrub (Sofscase).



## **1.2. Atividades antrópicas e a dinâmica do carbono em ecossistemas campestres e savânicos**

Atividades antrópicas podem modificar a dinâmica do carbono de ecossistemas campestres e savânicos (Scholze et al. 2006). A alteração do regime natural do fogo, através do aumento ou diminuição da frequência do fogo (Keeley & Pausas 2019; McLauchlan et al. 2020; Bowman et al. 2020), e/ou invasões biológicas (Ehrenfeld 2010; Simberloff et al. 2013) são umas destas atividades. Porém cada uma delas pode afetar diferentemente a dinâmica do carbono. O aumento da frequência do fogo em savanas tropicais promove a diminuição do material combustível, o aumento do solo descoberto (Rodrigues et al. 2021), e o aumento da mortalidade da vegetação lenhosa, levando a diminuição da evapotranspiração do solo e das taxas de NEE, comprometendo o sequestro de carbono do sistema (Quesada et al. 2004; Medeiros & Miranda 2008; Gomes et al. 2020; Santos et al. 2021). Em seu outro extremo, a supressão do fogo pode levar ao adensamento lenhoso e substituições de espécies de savana por florestais (Abreu et al. 2017; Zhou et al. 2022). A mudança de composição e estrutura destes ecossistemas, pode levar a um aumento de ET (Honda & Durigan 2016; Schreiner-McGraw et al. 2020), a diminuição de eWUE do sistema (Scott et al. 2014), e a possível diminuição de SOC, principalmente por que o crescimento subterrâneo da vegetação é desproporcionalmente menor do que o crescimento aéreo (February et al. 2020; Zhou et al. 2022).

Por sua vez, a invasão por gramíneas, pode gerar modificação na dinâmica do carbono (Ens et al. 2015) mas seus efeitos em ecossistemas neotropicais são pouco conhecidos (Chong et al. 2021). Processos relacionados ao uso de água e nutrientes, decomposição e produtividade, apesar de serem fortemente dependentes de condições ambientais (Ricciardi et al. 2021), podem ser mais eficientes em sistemas invadidos (Cavaleri and Sack 2010; Fei et al. 2014, Vila et al. 2011). Isso pode acontecer principalmente porque gramíneas invasoras quando comparadas a gramíneas nativas acumulam mais biomassa, crescem mais rápido, investem em folhas mais amplas e, em alguns casos, o investimento também pode ocorrer na biomassa subterrânea (Musso et al. 2021; Willians and Baruch 2000). Estas características podem influenciar positivamente os processos de assimilação de carbono na biomassa e no solo (Funk & Vitousek 2007; Garcia et al. 2022),

favorecendo a persistência e ocorrências das invasoras no sistema (Williams & Baruch 2000; Ehrenfeld 2010).

Assim, apesar de representarem importantes ameaças a conservação de savanas abertas tropicais (Buisson et al. 2019), o efeito de diferentes frequências de fogo, e dos níveis de cobertura de espécies invasoras na dinâmica de carbono nestes ecossistemas são pouco avaliados (porém veja Garcia et al. 2022).

## **2. Importância de estruturas subterrâneas em ecossistemas campestres e savânicos**

Em ecossistemas campestres e savânicos, as comunidades vegetais investem grande parte de sua biomassa nas partes subterrâneas (Figura 2, De Castro & Kauffman 1998; Poorter et al. 2012; Oliveras et al. 2013; Jackson et al. 2017; Ottaviani et al. 2020). O alto investimento em biomassa subterrânea, em conjunto com o carbono orgânico do solo, representa os principais componentes de estoque de carbono em ecossistemas abertos inflamáveis (Bai & Cotrufo 2022; Zhou et al. 2022). A alocação de biomassa subterrânea nestes ecossistemas, caracteriza-se como uma importante estratégia adaptativa em ambientes inflamáveis (Veldman, Buisson, et al. 2015; Buisson et al. 2019; Ottaviani et al. 2020; Buisson et al. 2022). Este investimento acontece, em parte, através de órgãos subterrâneos, que são estruturas protetoras de gema e/ou com capacidade de reserva (Clarke et al. 2013; Klimešová et al. 2018), e de raízes (Figura 2, Gill & Jackson 2000; Mokany et al. 2006; Jackson et al. 2016). A presença de órgãos portadores de gemas e de reserva permite às comunidades de plantas destes sistemas persistir, através do rápido rebrotamento pós-fogo (Clarke et al. 2013; Pausas et al. 2018). Por sua vez, alguns tipos de órgãos permitem aumentar a habilidade de colonização através do crescimento clonal (Klimešová et al. 2018; Pausas & Paula 2020). Já o investimento em produção de raízes, proporciona as espécies de plantas a rápida aquisição de recursos (Kramer-Walter et al. 2016; Hodge 2004). Esta rápida aquisição é tanto necessária para a regeneração pós-fogo, como para o alcance da maturidade reprodutiva

durante os períodos de condições ambientais favoráveis (Kramer-Walter et al. 2016; Simpson et al. 2019).

A forma cuja biomassa subterrânea é alocada (*i.e.*, tipo de órgãos subterrâneos e tipo de raízes) também pode determinar as respostas das plantas ao fogo, devido às diferenças funcionais (*i.e.*, persistência, resistência, propagação lateral), morfológicas (*i.e.*, número e localização de gemas, diâmetro de raízes) e anatômicas (*i.e.*, meristemas de reserva, tipos de componente de reserva) destas estruturas (Fidelis et al. 2014; Pausas et al. 2018; Klimešová et al. 2019; Pilon et al. 2021; Zupo et al. 2021). Por exemplo, os rizomas proporcionam o crescimento clonal e a rápida regeneração de várias espécies herbáceas. Tais funções são relacionadas à ocupação do espaço e regeneração pós-fogo (Ottaviani et al. 2017; Pausas et al. 2018). Os rizomas produzem ramos horizontais subterrâneos, têm moderada quantidade de gemas (~10 a 100 gemas) protegidas por catafilos, e são estruturas de reserva de carboidratos, água e nutrientes (Lamont & Downes 2011; de Moraes et al. 2016; Pausas et al. 2018). Bulbos e cormos não têm capacidade clonal e possuem baixa quantidade de gemas (< 10) que são por sua vez altamente protegidas (Pausas et al. 2018). Assim essas estruturas proporcionam rápido rebrotamento pós-fogo, pois são relacionadas com o grande acúmulo de material de reserva (Al-Tardeh et al. 2008; Rodrigues & Estelita 2009; Pausas et al. 2018). Órgãos como *root crowns* não possuem capacidade clonal, mas tem banco de gemas localizados na superfície do solo, sendo associadas ao rebrotamento pós-fogo de raízes de espécies lenhosas (Pausas et al., 2018). Já os xilopódios são órgãos lenhosos de estrutura complexa, com alto potencial gemífero (muitas gemas, localizadas próximo ao solo), dependentes de estruturas de reserva adicionais como raízes com acúmulo de reservas (Appezato-da-Glória et al. 2008; Pausas et al. 2018). Xilopódios e *root crowns* são característicos de plantas associadas a ecossistemas com alta frequência de fogo, principalmente as savanas tropicais da América do Sul (Appezato-da-Glória et al. 2008; Pausas et al. 2018).



**Figura 2.** Estruturas subterrâneas encontradas em ecossistemas campestres e savânicos. A- Rebrotamento pós fogo, a partir de órgãos subterrâneos portadores de gemas. Foto de Alessandra Fidelis. B- Xilopódio de *Ichthyothere hirsuta* Gardner. Foto de Alessandra Fidelis. C- Diversidade de órgãos subterrâneos portadores de gemas e/ou reserva coletados em área de campo sujo no centro do Brasil (reserva Natural Serra do Tombador, RNST, Góias). D- Xilopódio de *Brosimum gaudichaudii* Trécul. Foto de Aline Bombo. E- Sub amostra de raízes finas coletadas em área de campo sujo no centro-oeste do país (Parque Nacional Chapada dos Guimarães, PNCG, Mato Grosso do Sul).

O investimento em biomassa de raízes de ecossistemas campestres e savânicos, acontece na forma de raízes grossas ( $> 2\text{mm}$ , *coarse roots*) e finas ( $< 2\text{mm}$ ) (Tomlinson et al. 2012; Wigley et al. 2019), nas camadas mais superficiais do solo, entre 0-30 cm de profundidade (De Castro & Kauffman 1998; Le Stradic et al. 2021). O investimento em raízes grossas, está relacionado com o suporte da rede de raízes finas e das estruturas da planta, e com o transporte de nutrientes e água aos ramos (Oliveira et al. 2005; Tobin et al. 2007). Mas é o investimento em raízes finas que está relacionado à aquisição e absorção de nutrientes (McCormack et al. 2015). O fogo estimula a produção de raízes finas principalmente de espécies graminóides nas camadas mais superficiais do solo ( $< 20\text{ cm}$  de profundidade), caracterizando-se como uma estratégia eficiente para a o uso de recursos pós-fogo destes ecossistemas (Oliveras et al. 2013; Pellegrini et al. 2020; Le Stradic et al. 2021), em que há um incremento de nutrientes no solo devido às cinzas provenientes da biomassa consumida durante a queima (Pivello et al. 2010). Por sua vez, é a biomassa de raízes que contribui mais do que a biomassa aérea para o carbono no solo em ecossistemas campestres e savânicos (Schenk & Jackson 2002; Wang et al. 2019). Também é a deposição de biomassa morta de raízes uma das formas mais comumente incorporadas em SOC nestes ecossistemas (Jackson et al. 2017; Bai & Cotrufo 2022).

Alterações no regime de fogo nos ecossistemas campestres e savânicos, como por exemplo a diminuição da frequência de fogo, podem ocasionar a perda da resiliência e mudança de seu estado campestre e savânico para, por exemplo um estado florestal (Buisson et al. 2019). Isso acontece porque há a substituição de espécies herbáceas por lenhosas, levando a perda das estruturas subterrâneas das espécies herbáceas (Bombo et al. 2022), e a diferenças em alocação de biomassa (Le Stradic et al. 2021), em que o investimento é proporcionalmente maior na biomassa aérea do que na subterrânea (Zhou et al. 2022). Essas modificações podem levar a alterações na dinâmica de carbono, em especial em seu sequestro (Bai & Cotrufo 2022), levando a menores quantidades de carbono estocado em forma de biomassa subterrânea nestes ecossistemas (Zhou et al. 2022). Além do mais, devido a perda das estruturas subterrâneas das espécies herbáceas e graminóides, a regeneração pós-fogo desta vegetação, que é característica dos ecossistemas campestres e savânicos, pode não acontecer (Buisson et al. 2019; Buisson et al. 2022). Porém, apesar de já existirem estudos que quantificaram a relação do fogo com a alocação de biomassa subterrânea, considerando seus diferentes componentes (Fidelis et al. 2013; Fidelis et al. 2014; Bombo et al. 2021; Le Stradic et al. 2021; Bombo et al. 2022), essa relação não é necessariamente linear, e pode

variar de acordo com o regime de fogo e fatores ambientais (como tipo de solo, e precipitação). Assim, é de suma importância compreender como a alocação de biomassa nestes ecossistemas é afetada pelo fogo, afetando a capacidade de regeneração e o investimento em carbono no solo, na forma de biomassa subterrânea.

### **3. Fogo, diversidade funcional e a dinâmica de carbono em ecossistemas campestres e savânicos**

O fogo é o agente de seleção dominante em vários ecossistemas abertos (Cowling 1987; He et al. 2019; Lamont et al. 2019), estimulando a diversificação de espécies ao longo dos últimos 6-8 milhões de anos (Simon et al. 2009; He et al. 2011; He et al. 2016). O fogo gera um aumento da biodiversidade, especialmente de plantas que possuem atributos selecionados pelo fogo (i.e., banco de gemas em órgãos subterrâneos, e rápido rebrotamento pós-fogo) (Coutinho 1990; Bond et al. 2005; Bond & Parr 2010; Keeley et al. 2011; Pivello 2011; Buisson et al. 2019). Esses atributos garantem a persistência destas espécies em ambientes inflamáveis (Archibald et al. 2019). Em contrapartida, sem o fogo a biodiversidade destes ecossistemas é afetada com a diminuição de espécies de plantas (Abreu et al. 2017), resultando em uma mudança de estado em que a vegetação florestal substitui a campestre e savânica (Bond et al. 2005; Buisson et al. 2019).

A variação na composição de comunidades de plantas em resposta ao fogo é associada com a variação de atributos funcionais (Loreau 2000; Keeley et al. 2011; Lamont et al. 2013). A variação de atributos funcionais é relacionada com a medida de diversidade funcional (Petchey & Gaston 2002). Por sua vez, esta variação de atributos é importante para determinar as diferentes funções de um ecossistema (Díaz & Cabido 2001; Tilman 2001; Garnier et al. 2016), como por exemplo, a provisão do estoque de carbono no solo (Petchey & Gaston 2006; Chen et al. 2018). Já se sabe que a diversidade de plantas é importante para a formação e o estoque de carbono no solo (Yang et al. 2019). A alta diversidade de plantas em ecossistemas campestres e savânicos aumenta o estoque de carbono no solo por elevar a entrada de carbono na forma de biomassa subterrânea (i.e., biomassa de raízes), promover o crescimento microbiano, turnover e deposição de necromassa

(Lange et al. 2015; Chen et al. 2018; Prommer et al. 2020). Isto acontece devido a atributos das plantas que são chave para a dinâmica de carbono: os atributos de raízes (De Deyn et al. 2008; Laughlin et al. 2021; Freschet et al. 2021; Carmona et al. 2021).

Por exemplo, alto comprimento específico de raízes finas (SRL, *specific root length*, comprimento de raiz fina por unidade de massa investida), baixa densidade do sistema de raízes (RTD, *root tissue density*), e baixo diâmetro de raízes de espécies graminóides nas camadas superficiais do solo, promovem a estas plantas eficiência na aquisição de recursos (Freschet et al. 2018; Linder et al. 2018; Case et al. 2020), e alta taxa de crescimento (Kramer-Walter et al. 2016; Simpson et al. 2020). Estas características se relacionam com o input de carbono (i.e., SOC e biomassa) na camada mais superficial do solo, devido ao maior crescimento, inclusive nas raízes, que leva ao investimento em biomassa de raízes finas (Jobbagy & Jackson 2000; De Deyn et al. 2008; Pellegrini et al. 2020; Weemstra et al. 2020). Já alta profundidade de raízes e grande diâmetro, são atributos mais relacionados com o crescimento da vegetação lenhosa e ao uso de água em camadas profundas do solo (Case et al. 2020; Zhou et al. 2020). Espécies com estes atributos, podem estar relacionadas com o aumento de SOC nas camadas mais profundas do solo (Pellegrini et al. 2020; Pellegrini et al. 2021).

Alterações no regime de fogo, podem produzir diferentes paisagens e selecionar diferentes atributos (Bond & Keeley 2005; Keeley et al. 2011; Enright et al. 2014). Por exemplo, menores frequências de fogo em ambientes inflamáveis, como as savanas do Cerrado (Pivello 2011), podem levar a uma mudança na composição de espécie (*e.g.*, espécies arbóreas substituindo espécies graminóides e herbáceas). Com isso, esta alteração da frequência do fogo pode selecionar majoritariamente atributos relacionados com a maior alocação em biomassa aérea do que subterrânea (*e.g.*, maiores valores para altura da planta, largura e comprimento de folhas), ao uso de recurso em camadas mais profundas do solo (*e.g.*, altos valores para a profundidade de raízes), e com semelhante estratégia de regeneração (*e.g.*, atributos com baixos valores para habilidade clonal e rebrotamento, ver Klimešová et al. 2019). Por sua vez, estas mudanças de atributos, podem resultar em alterações na dinâmica do carbono, através do comprometimento da entrada de carbono no solo (Chen et al. 2018). Isso acontece, por que os atributos selecionados a partir da diminuição da frequência de fogo, não estão relacionados a maior alocação de biomassa subterrânea (*e.g.*, alta habilidade clonal e de rebrotamento, altos valores para densidade do sistema de raízes), como é



característico de ecossistemas campestres e savânicos do Cerrado (Pausas et al. 2018; Ottaviani et al. 2020; Le Stradic et al. 2021).

Desse modo, a avaliação da diversidade funcional passa a ser fundamental para entender os mecanismos de modificação da dinâmica do carbono em resposta ao fogo, mas continua sendo ainda pouco explorada.

#### **4. Ecossistemas campestres e savânicos do Cerrado**

A vegetação do Cerrado é dominante no centro do Brasil e originalmente representava 23% do território nacional, mas atualmente representa apenas 12% do território (MapBiomas 2022). Essa vegetação é composta por diferentes fisionomias que formam um gradiente estrutural indo de ecossistemas campestres, savânicos até florestais (Oliveira-Filho & Ratter 2002). Os ecossistemas campestres no Cerrado (Figura 3), abrigam uma grande variedade de plantas intolerantes à sombra, com alta dominância de gramíneas perenes C4, formando um estrato graminóides contínuo (Eiten 1972; Overbeck et al. 2022). Os filtros ambientais que limitam o crescimento de árvores nestas regiões são responsáveis pela formação e manutenção das diferenças destes ecossistemas campestres. Estes filtros são variáveis e podem ocorrer de forma conjunta, como por exemplo o fogo, e fatores edáficos (*e.g.*, baixa fertilidade e características físicas do solo), ou até mesmo em resposta ao regime hidrológico (Overbeck et al. 2022; Villalobos-Veja et al. 2014). Por exemplo, campos rupestres representam um dos ecossistemas campestres do Cerrado com o maior grau de endemismo no Brasil (BFG 2015), e seus principais filtros são: substrato pobre em nutrientes, grande proporção de afloramentos rochosos, baixa capacidade de retenção de água no solo (Silveira et al. 2016). Essa vegetação ocorre majoritariamente em altitudes superiores a 800-900 m acima do mar, com grande proporção de afloramentos rochosos (Silveira et al. 2016).

Já os ecossistemas savânicos são os ecossistemas dominantes no Cerrado, mas também ocorrem na Amazônia, Pantanal, Mata Atlântica e Caatinga (Figura 3, Overbeck et al. 2022). Os ecossistemas savânicos do Cerrado são caracterizadas por serem um ecossistema com seu estrato herbáceo composto majoritariamente por gramíneas C4, sob clima tropical sazonal (5 a 7 meses de estação seca), com a presença de arbustos e árvores esparsas, que variam em diferentes

densidades (menor densidade de árvores, campo sujo, cobertura arbórea < 5%) até fechadas (maior densidade de árvores, cerrado denso, cobertura arbórea de 50% a 70%) (Oliveira-Filho & Ratter 2002; Ribeiro & Walter 2008). Estes ecossistemas savânicos do Cerrado possuem altos níveis riqueza, sendo considerada a savana mais rica em espécies de plantas do mundo (mais de 12 mil espécies plantas), em que a maior diversidade de plantas está no substrato herbáceo (~ 64%, Myers et al. 2000; Mendonça et al. 2008). O fogo interagindo com o clima, regime hidrológico e solo, é um filtro importante para definir e manter a heterogeneidade dos ecossistemas savânicos e campestres do Cerrado (Eiten 1972; Eiten 1978; Coutinho 1990).

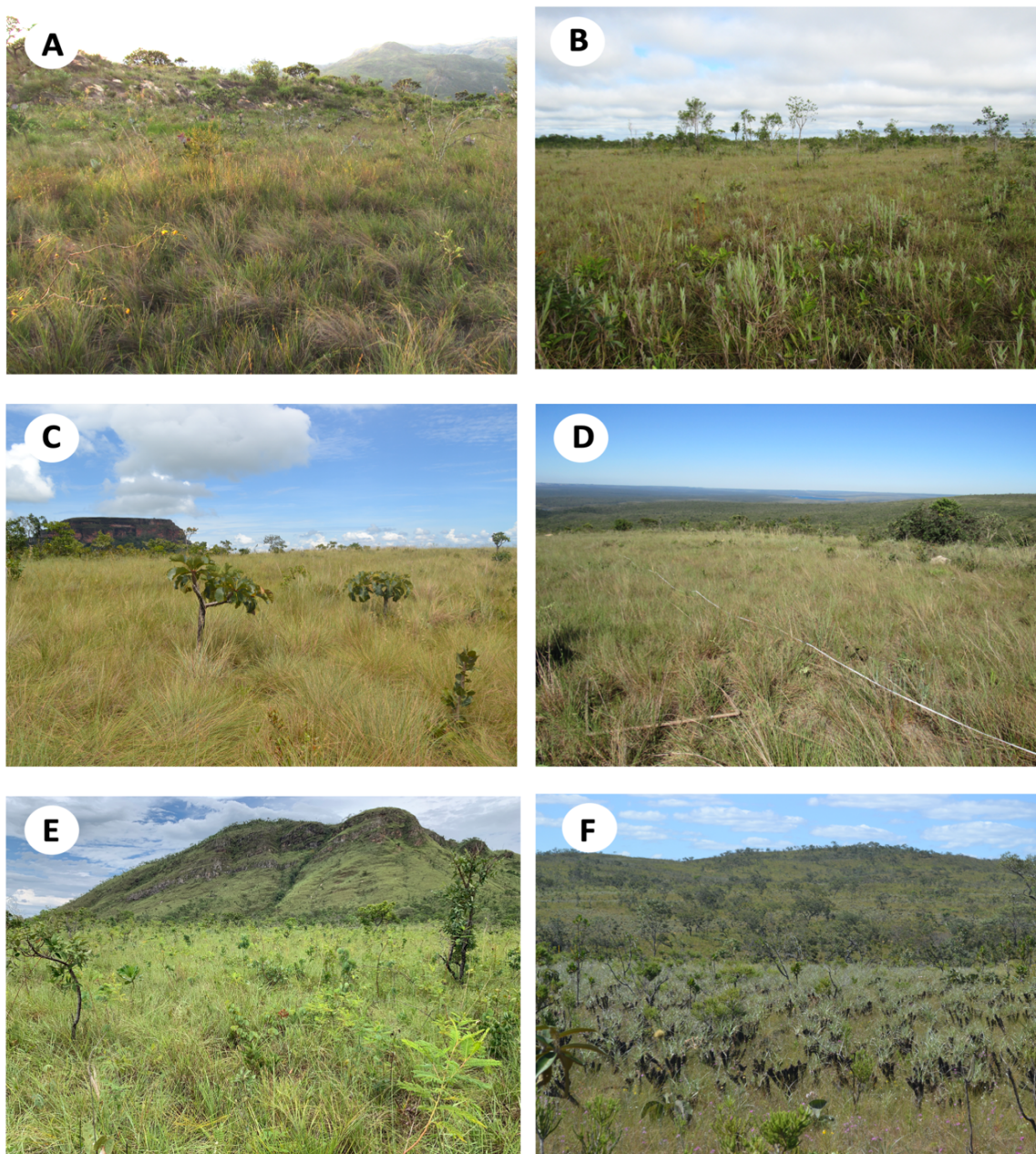
O fogo tem um papel chave para a definição desses ecossistemas savânicos do Cerrado (Bond & Keeley 2005; Bond et al. 2005), pois a condição climática onde eles estão localizados, com precipitação anual acima de 1000mm (Eiten 1972; Alvares et al. 2013), geralmente está associada à florestas (Whittaker 1965). Assim, de acordo com a frequência e a intensidade do fogo há a limitação ou não do estabelecimento e o crescimento de árvores (Bond & Keeley 2005; Pausas & Bond 2020a). Os ecossistemas savânicos abertos são presentes quando há maior frequência de fogo, enquanto as formações mais florestais ocorrem com menor frequência de fogo (Bond & Keeley 2005). Assim, a variação no regime de fogo possibilita que ecossistemas campestres ocorram com ecossistemas savânicos abertos até os mais lenhosos ou florestais (Oliveira-Filho & Ratter 2002; Staver et al. 2011; Bueno et al. 2017).

Porém, o inadequado manejo do fogo nestes ecossistemas (*e.g.*, políticas de fogo zero) promoveu historicamente a sua degradação levando à homogeneização da vegetação através da diminuição de espécies herbáceas, e a mudança de seu estado aberto para um florestal (Pivello 2011; Abreu et al. 2017; Durigan 2020). Essas políticas de fogo zero tiveram como consequência a ocorrência de grandes incêndios, com características muito distintas dos fogos naturais, que são fogos superficiais, rápidos e de baixa severidade (Pivello 2011; Durigan & Ratter 2016; Fidelis et al. 2018). Em consequência aos impactos destas políticas de fogo zero, desde 2014 iniciaram-se políticas do Manejo Integrado do Fogo (MIF) em áreas protegidas, que buscam criar um mosaico de diferentes regimes de fogo na escala da paisagem através de queimas prescritas, para reduzir a prevalência de incêndios, proteger a vegetação sensível ao fogo e reduzir os conflitos entre gestores de áreas protegidas e comunidades locais (Schmidt et al. 2018; Schmidt & Eloy 2020)(Schmidt et al. 2018; Schmidt & Eloy 2020). Contudo, para que estas políticas avancem, mais estudos são

necessários, em especial os relacionados a entender qual é o efeito de diferentes regimes de fogo na dinâmica do carbono (Schmidt et al. 2018).

As invasões biológicas também podem ser uma ameaça para estes ecossistemas (Buisson et al. 2019; Buisson et al. 2022; Stevens et al. 2022). Em especial, as gramíneas invasoras africanas, utilizadas como pastagem de gado, como as espécies do gênero *Urochloa*, como *U. brizantha* (Hochst. ex A.Rich.) R.D.Webster e *U. decumbens* (Stapf) R.D.Webster (Pivello et al. 1999; Durigan et al. 2007; Souza et al. 2020). Estas espécies foram escolhidas para a implementação de pastagens, pois elas apresentam maior produtividade e palatabilidade em comparação com as gramíneas nativas, além de se adaptarem bem ao clima do Cerrado (tolerância a seca) (Kornelius et al. 1979). Assim, por apresentarem atributos que conferem vantagens competitivas, como rápido crescimento e acúmulo de biomassa, alta capacidade de dispersão, altas taxas de reprodução e sobrevivência (Pyšek & Richardson 2007; Funk et al. 2008), estas espécies expandem sua área de ocorrência, e já se encontram por todos os ecossistemas campestres e savânicos do Brasil (Pivello et al. 1999; Assis et al. 2021; Overbeck et al. 2022). Estas espécies competem com as espécies nativas de gramíneas alterando a composição e a dinâmica da vegetação (Damasceno et al. 2018), podendo alterar o regime de fogo (Gorgone-Barbosa et al. 2015), e impactar a dinâmica de carbono destes ecossistemas (Garcia et al. 2022). Por fim, a mudança no regime de fogo também pode favorecer o processo de invasão nestes ecossistemas (Buisson et al. 2019).

Os ecossistemas campestres e savânicos do Cerrado são excelentes modelos para entender os impactos das mudanças antrópicas na dinâmica do carbono em ecossistemas abertos inflamáveis, pois além de sua grande relevância para a conservação da biodiversidade, tem como uma das principais ameaças as mudanças no regime de fogo e invasões biológicas (Fidelis et al. 2018; Buisson et al. 2019; Souza et al. 2020; Bond 2022; Stevens et al. 2022).

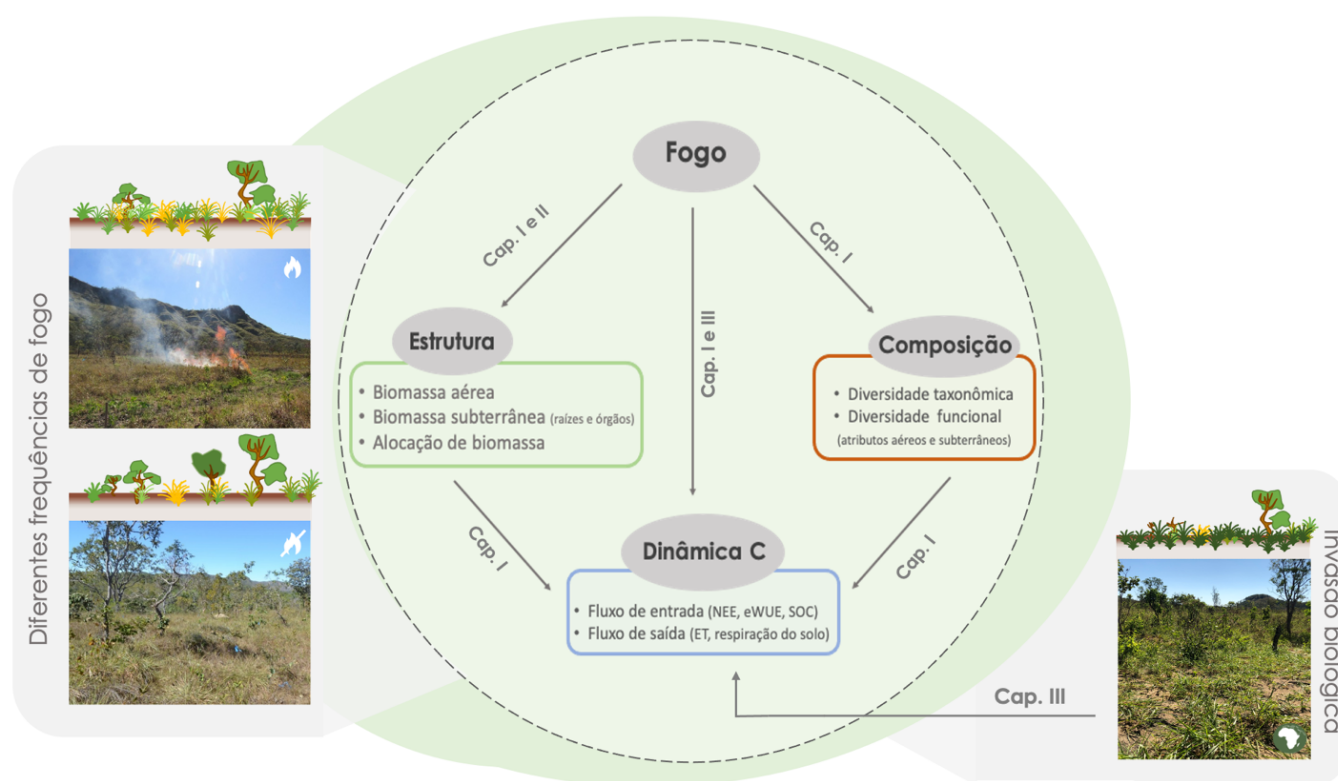


**Figura 3.** Ecossistemas campestres e savânicos do Cerrado. A- Parque Nacional Serra do Cipó, Minas Gerais, campo rupestre. B- Parque Nacional Campos Amazônicos, Rondônia, porção norte do Cerrado; C- Parque Nacional Chapada dos Guimarães, Mato Grosso do Sul, porção centro-oeste; D- Parque Nacional de Brasília, Distrito Federal, e E e F- Reserva Natural Serra do Tombador, Goiás, representam a porção central do Cerrado. B-F: representam fisionomias de campo sujo. E: Fotografia de Alessandra Fidelis.

## 5. Objetivos

O objetivo geral desta tese foi investigar como o fogo (diferentes frequências de fogo) e invasões biológicas afetam a dinâmica do carbono (fluxo de entrada e saída de carbono) em savanas tropicais, utilizando o Cerrado como nosso modelo de estudo (Figura 4). Para isso, buscamos entender:

- (i) como o fogo afeta a entrada (i.e., NEE, eWUE, SOC) e a saída (i.e. ET, e respiração do solo) de carbono analisando processos ligados a esses fluxos, e avaliando os potenciais mecanismos de mudanças (i.e., variação da diversidade funcional e biomassa) desses fluxos (Capítulo 1);
- (ii) como o fogo afeta a alocação de biomassa e os diferentes componentes da biomassa subterrânea em diversos ecossistemas campestres e savânicos (Capítulo 2);
- (iii) como o fogo e a invasão biológica afetam a entrada (i.e., NEE, eWUE) e saída (i.e. ET) de carbono, e como estes fluxos interagem com a variação sazonal destes ecossistemas (Capítulo 3).



**Figura 4.** Resumo esquemático da estruturação geral desta tese com base nos pontos de investigação realizados em savanas abertas do Cerrado. As setas representam os possíveis efeitos e interações estudadas

neste trabalho. O círculo pontilhado representa o conjunto de interações estudadas. O efeito da invasão biológica foi testado diretamente na dinâmica de carbono

## 6. Estrutura da Tese

Para atingir os objetivos desta tese, elaboramos três capítulos (Figura 5), em que no primeiro capítulo ***“Fire promotes functional plant diversity and modifies soil carbon dynamics in tropical savanna”*** (“O fogo promove a diversidade funcional de plantas e modifica a dinâmica do carbono no solo em savanas tropicais”) buscamos entender como o fogo impactou as funções ecossistêmicas ligadas a dinâmica do carbono além da estrutura e da diversidade do sistema (objetivos i). Hipotetizamos que o fogo promove a entrada de carbono no sistema e reduz a sua saída, através do aumento de alocação em biomassa subterrânea e da promoção da diversidade taxonômica e funcional. Para responder a esta pergunta comparamos uma área de savana frequentemente queimada (queimas bienais) com uma área excluída do fogo há mais de 16 anos no centro do Brasil, onde mensurados atributos funcionais, biomassa e NEE, ET, eWUE e SOC, em parcelas pertencentes a um experimento de fogo de longo-prazo (Projeto FAPESP 2015/06743-0, *“How does fire season affects Cerrado Vegetation?”*) (Figura 5).

No segundo capítulo, ***“Does fire affect belowground biomass allocation and composition in tropical grasslands and savannas?”*** (“O fogo afeta a alocação e composição de biomassa subterrânea em formações tropicais campestres e savânicas”) buscamos entender como o fogo afeta a alocação e a composição da biomassa subterrânea analisando tanto as raízes e os órgãos subterrâneos (objetivo ii). Hipotetizamos que o fogo aumenta a alocação de biomassa subterrânea através do investimento em órgãos subterrâneos e de raízes finas e promove diferenças na composição de órgãos subterrâneos. Analisamos biomassa subterrânea incluindo raízes e órgãos além de avaliar a composição em órgãos subterrâneos portadores de gemas e reserva em cinco diferentes áreas que compreendem ecossistemas campestres e savânicos do Cerrado, comparando áreas frequentemente queimadas com áreas excluídas do fogo há pelo menos mais de 12 anos.





**Figura 5.** Experimentos de fogo de longo prazo parte do projeto “*How does fire season affects Cerrado Vegetation?*”, coordenado pela Profa. Dra. Alessandra Fidelis. Neste experimento, foram estabelecidas parcelas de 30m x 30m em uma área de campo sujo onde se manejam os seguintes tratamentos de queima

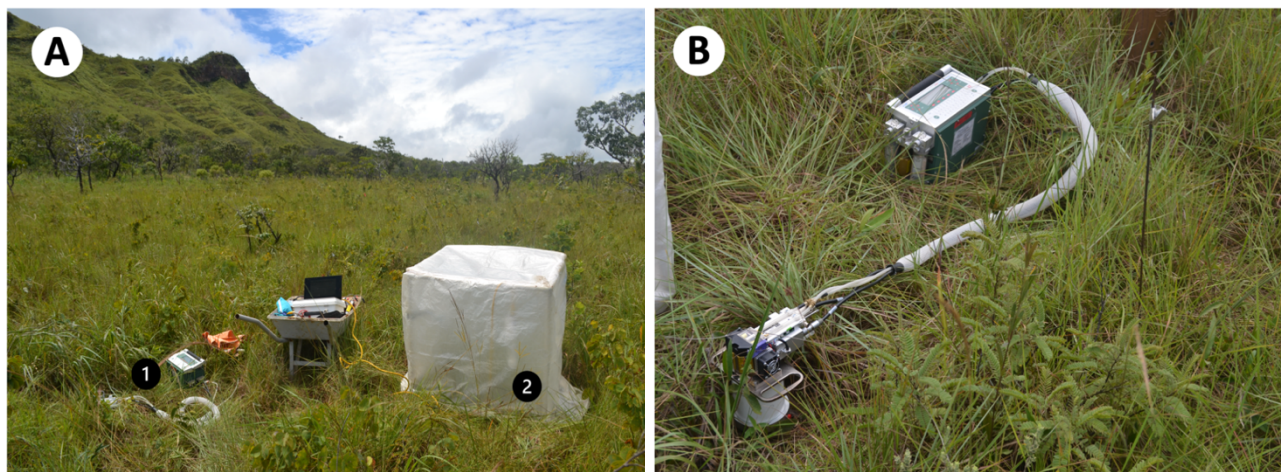


com quatro réplicas cada: anuais, bienais, trienais (desde 2011 queimas em Maio, Julho e Outubro representando o período prévio, o meio e o final da estação seca) e controles (excluídas do fogo desde 2011) para mais detalhes veja Rissi et al (2017) e Rodrigues et al. (2021). A- Parcelas experimentais estabelecidas desde 2011 na Reserva Natural Serra do Tombador (RNST), no município de Cavalcante, Goiás. Foto de Marco Chiminazzo. B-Equipe de brigadistas da RNST durante uma das queimas experimentais. C-Medições dos parâmetros do fogo realizadas durante a queima experimental em julho de 2021 pelos cientistas do Laboratório de Ecologia da Vegetação (LEVeg), da Universidade Estadual Paulista (UNESP, Rio Claro). D- Pós-queima imediato. E- Três meses após a queima experimental realizada em maio de 2021. Do lado esquerdo parcela bienal não queimada.

No terceiro capítulo “*Ecosystem dynamics in response to fire frequency and biological invasion in the Cerrado*” (“A dinâmica do ecossistema em resposta a frequência de fogo e a invasão biológica no Cerrado”) investigamos como distintas frequências de fogo e invasão biológica podem afetar a dinâmica do carbono durante as estações seca e chuvosa em formações campestres do Cerrado (objetivo iii). Nós esperamos que a diminuição da frequência de fogo irá diminuir a entrada de carbono do sistema quando comparada a altas frequências de fogo. Durante a estação chuvosa, esperávamos um aumento nas taxas de entrada de carbono nas áreas recentemente queimadas, porque a produção de biomassa viva é estimulada (rebrotamento da vegetação). Nas áreas em que houve a diminuição da frequência de fogo, esperávamos maiores taxa de saída de carbono durante a estação chuvosa, devido a maiores taxas de transpiração das plantas. Na estação seca, esperávamos a redução nas taxas de entrada de carbono nos sistemas sob altas frequências de fogo, e maiores taxas na entrada de carbono no sistema com a diminuição da frequência de fogo, devido o maior acúmulo de biomassa deste sistema. Em relação à invasão biológica, esperamos que áreas invadidas promovam maior entrada e saída de carbono no sistema quando comparadas a áreas não invadidas, principalmente na estação seca. Isso acontece porque as espécies invasoras podem apresentar alta eficiência no uso da água para o investimento em carbono (i.e., biomassa) quando comparadas as nativas. Para que pudéssemos responder essa pergunta, mensuramos NEE, ET e eWUE durante a estação seca e a chuvosa em uma área experimental de savana no centro do Brasil (Figura 6), onde se é manipulada queimas anuais, bienais e exclusão do fogo, e onde existem áreas invadidas pela gramínea africana *Urochloa brizantha* (Hochst. ex A.Rich.).

Ao final apresentamos as **Considerações Finais** deste trabalho. Nesta sessão retomamos os principais resultados encontrados, suas aplicações para o avanço da ciência e precedentes para estudos potenciais. Também indicamos como os achados desta tese podem subsidiar ações de

manejo e tomadores de decisões que reconheçam e conservem os potenciais serviços ecossistêmicos promovidos pelos ecossistemas campestres e savânicos que, por sua vez, podem auxiliar o controle das mudanças climáticas.



**Figura 6.** Mensuração dos processos relacionados aos fluxos de entrada e saída de carbono. A- Detalhamento de medições realizadas em campo, através do rastreamento: (1) da respiração do solo; (2) da diferença entre o dióxido de carbono ( $\text{CO}_2$ ) que as plantas conseguem assimilar pela fotossíntese, e a perda de  $\text{CO}_2$  pela respiração das plantas e da atividade microbiana (NEE, do inglês *net ecosystem exchange of carbono dioxide*); e da perda de água de transpiração das plantas e do solo (ET). As medidas de NEE e ET demonstradas nessa figura, foram realizadas através da utilização de um equipamento que registra ao longo do tempo as taxas de  $\text{CO}_2$  e vapor de água. Para que isso aconteça, o equipamento é colocado preso a um tripé, em conjunto com dois ventiladores elétricos de 15 cm de diâmetro, e coberto por uma câmara de polietileno *rip-stop* ( $0.49 \text{ m}^2$  de área total e  $0.37 \text{ m}^3$  de volume). A ventilação artificial tem a função de misturar o ar dentro da câmara, para que não haja um aumento de temperatura dentro da câmara. O polietileno *rip-stop* mantém as temperaturas constantes durante as medições (*e.g.*, o aumento da temperatura durante a medição não excede  $1^\circ\text{C}$ ). Como o NEE integra a absorção de  $\text{CO}_2$  pelas plantas via fotossíntese, e a liberação de  $\text{CO}_2$  pela respiração do solo (respiração de raízes e microrganismos), estima-se individualmente a liberação média de  $\text{CO}_2$  do solo. B- Equipamento utilizado para estimar as taxas de  $\text{CO}_2$  do solo.

## REFERÊNCIAS

- Abreu, R.C.R., 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: 1–8.
- Abreu, R.C.R., 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: 1–8.
- Al-Tardeh, S., Sawidis, T., Diannelidis, B.E., & Delivopoulos, S. 2008. Water content and reserve allocation patterns within the bulb of the perennial geophyte red squill (*Liliaceae*) in relation to the Mediterranean climate. *Botany* 86: 291–299.
- Alvares, C.A., Stape, J.L., Sentelhas, P.C., De Moraes Gonçalves, J.L., & Sparovek, G. 2013. Köppen's climate classification map for Brazil. *Meteorologische Zeitschrift* 22: 711–728.
- Appezato-da-Glória, A.B., Curry, G., Kasue, M., Soares, M., Hayashi, A.H., Appezato-de-glória, B., The, S., Society, B., Feb, N.J., Appezato-da-gl, B., Cury, G., Kasue, M., Soares, M., & Hayashi, A.H. 2008. Underground Systems of Asteraceae Species from the Brazilian Cerrado. 135: 103–113.
- Archibald, S., Hempson, G.P., & Lehmann, C. 2019. A unified framework for plant life-history strategies shaped by fire and herbivory. *New Phytologist* 224: 1490–1503.
- Assis, G.B., Pilon, N.A.L., Siqueira, M.F., & Durigan, G. 2021. Effectiveness and costs of invasive species control using different techniques to restore cerrado grasslands. *Restoration Ecology* 29:.
- Bai, Y., & Cotrufo, M.F. 2022. Grassland soil carbon sequestration: Current understanding, challenges, and solutions. 608: 603–608.
- Baldocchi, D. 2008. “Breathing” of the terrestrial biosphere: lessons learned from a global network of carbon dioxide flux measurement systems. *Australian Journal of Botany* 56: 1.
- Bardgett, R.D., Bullock, J.M., Lavorel, S., Manning, P., Schaffner, U., Ostle, N., Chomel, M., Durigan, G., L. Fry, E., Johnson, D., Lavallee, J.M., Le Provost, G., Luo, S., Png, K., Sankaran, M., Hou, X., Zhou, H., Ma, L., Ren, W., Li, X., Ding, Y., Li, Y., & Shi, H. 2021. Combatting global grassland degradation. *Nature Reviews Earth & Environment* 2: 720–735.
- Bastin, J.-F.F., Finegold, Y., Garcia, C., Mollicone, D., Rezende, M., Routh, D., Zohner, C.M., & Crowther, T.W. 2019. The global tree restoration potential. *Science* 365: 76–79.
- Beringer, J., Hutley, L.B., Abramson, D., Arndt, S.K., Briggs, P., Bristow, M., Canadell, J.G., Cernusak, L.A., Eamus, D., Edwards, A.C., Evans, B.J., Fest, B., Goergen, K., Grover, S.P., Hacker, J., Haverd, V., Kanniah, K., Livesley, S.J., Lynch, A., Maier, S., Moore, C., Raupach, M., Russell-Smith, J., Scheiter, S., Tapper, N.J., & Uotila, P. 2015. Fire in Australian savannas: From leaf to landscape. *Global Change Biology* 21: 62–81.
- BFG, T.B.F.G. 2015. Growing knowledge: an overview of Seed Plant diversity in Brazil. *Rodriguésia* 66: 1085–1113.
- Bombo, A.B., Appezato-da-Glória, B., & Fidelis, A. 2022. Fire exclusion changes belowground bud bank and bud-bearing organ composition jeopardizing open savanna resilience. *Oecologia* 199: 153–164.

- Bombo, A., Siebert, F., & Fidelis, A. 2021. Fire and herbivory shape belowground bud banks in a semi-arid African savanna. *African Journal of Range & Forage Science*. doi: 10.2989/10220119.2021.1982004
- Bonanomi, J., Tortato, F.R., Gomes, R. de S.R., Penha, J.M., Bueno, A.S., & Peres, C.A. 2019. Protecting forests at the expense of native grasslands: Land-use policy encourages open-habitat loss in the Brazilian cerrado biome. *Perspectives in Ecology and Conservation* 17: 26–31.
- Bond, W.J. 2022. Out of the shadows: ecology of open ecosystems. *Plant Ecology & Diversity* 14: 205–222.
- Bond, W.J., & Keeley, J.E. 2005. Fire as a global “herbivore”: The ecology and evolution of flammable ecosystems. *Trends in Ecology and Evolution* 20: 387–394.
- Bond, W.J., & Parr, C.L. 2010. Beyond the forest edge: Ecology, diversity and conservation of the grassy biomes. *Biological Conservation* 143: 2395–2404.
- Bond, W.J., Woodward, F.I., & Midgley, G.F. 2005. The global distribution of ecosystems in a world without fire. *New Phytologist* 165: 525–538.
- Bowman, D.M.J.S., Kolden, C.A., Abatzoglou, J.T., Johnston, F.H., van der Werf, G.R., & Flannigan, M. 2020. Vegetation fires in the Anthropocene. *Nature Reviews Earth & Environment*. doi: 10.1038/s43017-020-0085-3
- Bueno, M.L., Pennington, R.T., Dexter, K.G., Kamino, L.H.Y., Pontara, V., Neves, D.M., Ratter, J.A., & de Oliveira-Filho, A.T. 2017. Effects of Quaternary climatic fluctuations on the distribution of Neotropical savanna tree species. *Ecography* 40: 403–414.
- Buisson, E., Archibald, S., Fidelis, A., & Suding, K.N. 2022. Ancient grasslands guide ambitious goals in grassland restoration. *Science* 377: 594–598.
- Buisson, E., Le Stradic, S., Silveira, F.A.O., Durigan, G., Overbeck, G.E., Fidelis, A., Fernandes, G.W., Bond, W.J., Hermann, J.-M., Mahy, G., Alvarado, S.T., Zaloumis, N.P., & Veldman, J.W. 2019. Resilience and restoration of tropical and subtropical grasslands, savannas, and grassy woodlands. *Biological Reviews*. doi: 10.1111/brv.12470
- Carmona, C.P., Bueno, C.G., Toussaint, A., Träger, S., Díaz, S., Moora, M., Munson, A.D., Pärtel, M., Zobel, M., & Tamme, R. 2021. Fine-root traits in the global spectrum of plant form and function. *Nature* 597: 683–687.
- Case, M.F., Nippert, J.B., Holdo, R.M., & Staver, A.C. 2020. Root-niche separation between savanna trees and grasses is greater on sandier soils. *Journal of Ecology* 108: 2298–2308.
- Cavaleri, M.A., & Sack, L. 2010. Comparative water use of native and invasive plants at multiple scales: a global meta-analysis. *Ecology* 91: 2705–2715.
- Chapin, F.S., Matson, P.A., Vitousek, P.M., Chapin, F.S., Matson, P.A., & Vitousek, P.M. 2011a. Carbon Inputs to Ecosystems. In *Principles of Terrestrial Ecosystem Ecology*, pp. 123–156. Springer New York.

- Chapin, F.S., Matson, P.A., Vitousek, P.M., Chapin, F.S., Matson, P.A., & Vitousek, P.M. 2011b. Plant Carbon Budgets. In *Principles of Terrestrial Ecosystem Ecology*, pp. 157–181. Springer New York.
- Chen, S., Wang, W., Xu, W., Wang, Y., Wan, H., Chen, D., Tang, Z., Tang, X., Zhou, G., Xie, Z., Zhou, D., Shangguan, Z., Huang, J., He, J.S., Wang, Y., Sheng, J., Tang, L., Li, X., Dong, M., Wu, Y., Wang, Q., Wang, Z., Wu, J., Stuart Chapin, F., & Bai, Y. 2018. Plant diversity enhances productivity and soil carbon storage. *Proceedings of the National Academy of Sciences of the United States of America* 115: 4027–4032.
- Chong, K.Y., Corlett, R.T., Nuñez, M.A., Chiu, J.H., Courchamp, F., Dawson, W., Kuebbing, S., Liebhold, A.M., Padmanaba, M., Souza, L., Andersen, K.M., Fei, S., Lee, B.P.Y.-H., Lum, S., Luskin, M.S., Ngo, K.M., & Wardle, D.A. 2021. Are Terrestrial Biological Invasions Different in the Tropics? *Annual Review of Ecology, Evolution, and Systematics* 52: 291–314.
- Clarke, P.J., Lawes, M.J., Midgley, J.J., Lamont, B.B., Ojeda, F., Burrows, G.E., Enright, N.J., & Knox, K.J.E. 2013. Resprouting as a key functional trait: how buds, protection and resources drive persistence after fire. *New Phytologist* 197: 19–35.
- Conant, R.T., Cerri, C.E.P., Osborne, B.B., & Paustian, K. 2017. Grassland management impacts on soil carbon stocks: A new synthesis: A. *Ecological Applications* 27: 662–668.
- Coutinho, L.M. 1990. Fire in the Ecology of the Brazilian Cerrado. In *Fire in the Tropical Biota*, pp. 82–105. Springer, Berlin, Heidelberg, Freiburg.
- Cowling, R.M. 1987. Fire and its role in coexistence and speciation in Gondwanan. *South African Journal of Science* 83:.
- 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: 3621–3629.
- De Castro, E.A., & 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.
- De Deyn, G.B., Cornelissen, J.H.C., & Bardgett, R.D. 2008. Plant functional traits and soil carbon sequestration in contrasting biomes. *Ecology Letters* 11: 516–531.
- De Deyn, G.B., Shiel, R.S., Ostle, N.J., Mcnamara, N.P., Oakley, S., Young, I., Freeman, C., Fenner, N., Quirk, H., & Bardgett, R.D. 2011. Additional carbon sequestration benefits of grassland diversity restoration. *Journal of Applied Ecology* 48: 600–608.
- de Moraes, M.G., de Carvalho, M.A.M., Franco, A.C., Pollock, C.J., & Figueiredo-Ribeiro, R. de C.L. 2016. Fire and Drought: Soluble Carbohydrate Storage and Survival Mechanisms in Herbaceous Plants from the Cerrado. *BioScience* 66: 107–117.
- Dhakal, S., Minx, J.C., Toth, F., Abdel-Aziz, A., Figueroa Meza, M.J., Hubacek, K., Jonckheere, I.G.C., Kim, Y.-G., Nemet, G.F., Pachauri, S., Tan, X.C., & Wiedmann, T. 2022. Emissions Trends and Drivers. In *IPCC, 2022: Climate Change 2022: Mitigation of Climate Change. Contribution of Working Group III to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*, p. 127. Cambridge University Press, Cambridge, UK and New York, NY, USA.

- Dixon, A.P., Faber-Langendoen, D., Josse, C., Morrison, J., & Loucks, C.J. 2014. Distribution mapping of world grassland types. *Journal of Biogeography* 41: 2003–2019.
- Díaz, S., & Cabido, M. 2001. Vive la différence: plant functional diversity matters to ecosystem processes. *Trends in Ecology & Evolution* 16: 646–655.
- Dudley, N., Eufemia, L., Fleckenstein, M., Periago, M.E., Petersen, I., & Timmers, J.F. 2020. Grasslands and savannahs in the UN Decade on Ecosystem Restoration. *Restoration Ecology* 28: 1313–1317.
- Durigan, G. 2020. Zero-fire: Not possible nor desirable in the Cerrado of Brazil. *Flora: Morphology, Distribution, Functional Ecology of Plants* 268: 151612.
- Durigan, G., De Siqueira, M.F., & Franco, G.A.D.C. 2007. Threats to the Cerrado remnants of the State of São Paulo, Brazil. *Scientia Agricola* 64: 355–363.
- Durigan, G., & Ratter, J.A. 2016. The need for a consistent fire policy for Cerrado conservation. *Journal of Applied Ecology* 53: 11–15.
- Ehrenfeld, J.G. 2010. Ecosystem consequences of biological invasions. *Annual Review of Ecology, Evolution, and Systematics* 41: 59–80.
- Eiten, G. 1978. Delimitation of the cerrado concept. *Vegetatio* 36: 169–178.
- Eiten, G. 1972. The cerrado vegetation of Brazil. *The Botanical Review* 38: 201–341.
- Enright, N.J., Fontaine, J.B., Lamont, B.B., Miller, B.P., & Westcott, V.C. 2014. Resistance and resilience to changing climate and fire regime depend on plant functional traits. *Journal of Ecology* 102: 1572–1581.
- Ens, E., Hutley, L.B., Rossiter-Rachor, N.A., Douglas, M.M., & Setterfield, S.A. 2015. Resource-use efficiency explains grassy weed invasion in a low-resource savanna in north Australia. *Frontiers in Plant Science* 6: 1–10.
- February, E., Pausch, J., & Higgins, S.I. 2020. Major contribution of grass roots to soil carbon pools and CO<sub>2</sub> fluxes in a mesic savanna. *Plant and Soil* 454: 207–215.
- Fei, S., Phillips, J., & Shouse, M. 2014. Biogeomorphic Impacts of Invasive Species. *Annual Review of Ecology, Evolution, and Systematics* 45: 69–87.
- Fidelis, A., Alvarado, S.T., Barradas, A., & Pivello, V. 2018. The Year 2017: Megafires and Management in the Cerrado. *Fire* 1: 49.
- Fidelis, A., Appezzato-da-Glória, B., Pillar, V.D., & Pfadenhauer, J. 2014. Does disturbance affect bud bank size and belowground structures diversity in Brazilian subtropical grasslands? *Flora: Morphology, Distribution, Functional Ecology of Plants* 209: 110–116.
- Fidelis, A., Lyra, M.F. di S., & Pivello, V.R. 2013. Above- and below-ground biomass and carbon dynamics in Brazilian Cerrado wet grasslands (O. Wildi, Ed.). *Journal of Vegetation Science* 24: 356–364.
- Freschet, G.T., Roumet, C., Comas, L.H., Weemstra, M., Bengough, A.G., Rewald, B., Bardgett, R.D., De Deyn, G.B., Johnson, D., Klimešová, J., Lukac, M., McCormack, M.L., Meier, I.C., Pagès, L., Poorter, H., Prieto, I., Wurzbürger, N., Zadworny, M., Bagniewska-Zadworna, A., Blancaflor, E.B.,



- Brunner, I., Gessler, A., Hobbie, S.E., Iversen, C.M., Mommer, L., Picon-Cochard, C., Postma, J.A., Rose, L., Ryser, P., Scherer-Lorezen, M., Soudzilovskaia, N.A., Sun, T., Valverde-Barrantes, O.J., Weigelt, A., York, L.M., & Stokes, A. 2021. Root traits as drivers of plant and ecosystem functioning: current understanding, pitfalls and future research needs. *New Phytologist*. doi: 10.1111/nph.17072
- Freschet, G.T., Violle, C., Bourget, M.Y., Scherer-Lorezen, M., & Fort, F. 2018. Allocation, morphology, physiology, architecture: the multiple facets of plant above- and below-ground responses to resource stress. *New Phytologist* 219: 1338–1352.
- Friedlingstein, P., Jones, M.W., O’Sullivan, M., Andrew, R.M., Bakker, D.C.E., Hauck, J., Le Quéré, C., Peters, G.P., Peters, W., Pongratz, J., Sitch, S., Canadell, J.G., Ciais, P., Jackson, R.B., Alin, S.R., Anthoni, P., Bates, N.R., Becker, M., Bellouin, N., Bopp, L., Chau, T.T.T., Chevallier, F., Chini, L.P., Cronin, M., Currie, K.I., Decharme, B., Djeutchouang, L.M., Dou, X., Evans, W., Feely, R.A., Feng, L., Gasser, T., Gilfillan, D., Gkritzalis, T., Grassi, G., Gregor, L., Gruber, N., Gürses, Ö., Harris, I., Houghton, R.A., Hurtt, G.C., Iida, Y., Ilyina, T., Luijkx, I.T., Jain, A., Jones, S.D., Kato, E., Kennedy, D., Klein Goldewijk, K., Knauer, J., Korsbakken, J.I., Körtzinger, A., Landschützer, P., Lauvset, S.K., Lefèvre, N., Lienert, S., Liu, J., Marland, G., McGuire, P.C., Melton, J.R., Munro, D.R., Nabel, J.E.M.S., Nakaoka, S.-I., Niwa, Y., Ono, T., Pierrot, D., Poulter, B., Rehder, G., Resplandy, L., Robertson, E., Rödenbeck, C., Rosan, T.M., Schwinger, J., Schwingshackl, C., Séférian, R., Sutton, A.J., Sweeney, C., Tanhua, T., Tans, P.P., Tian, H., Tilbrook, B., Tubiello, F., van der Werf, G.R., Vuichard, N., Wada, C., Wanninkhof, R., Watson, A.J., Willis, D., Wiltshire, A.J., Yuan, W., Yue, C., Yue, X., Zaehle, S., & Zeng, J. 2022. Global Carbon Budget 2021. *Earth System Science Data* 14: 1917–2005.
- Funk, J.L., Cleland, E.E., Suding, K.N., & Zavaleta, E.S. 2008. Restoration through reassembly: plant traits and invasion resistance. *Trends in Ecology and Evolution* 23: 695–703.
- Funk, J.L., & Vitousek, P.M. 2007. Resource-use efficiency and plant invasion in low-resource systems. *Nature* 446: 1079–1081.
- Garcia, D.B., Xavier, R.O., Camargo, P.B., Vieira, S.A., & Pivello, V.R. 2022. Can an invasive African grass affect carbon and nitrogen stocks in open habitats of the Brazilian Cerrado? *Flora: Morphology, Distribution, Functional Ecology of Plants* 286: 151968.
- Garnier, E., Navas, M.-L., & Grigulis, K. 2016. *Plant Functional Diversity*.
- Giambelluca, T.W., Scholz, F.G., Bucci, S.J., Meinzer, F.C., Goldstein, G., Hoffmann, W.A., Franco, A.C., & Buchert, M.P. 2009. Evapotranspiration and energy balance of Brazilian savannas with contrasting tree density. *Agricultural and Forest Meteorology* 149: 1365–1376.
- Gill, R.A., & Jackson, R.B. 2000. Global patterns of root turnover for terrestrial ecosystems. *New Phytologist* 147: 13–31.
- Gomes, L., Miranda, H.S., Silvério, D.V., & Bustamante, M.M.C. 2020. Effects and behaviour of experimental fires in grasslands, savannas, and forests of the Brazilian Cerrado. *Forest Ecology and Management* 458:.
- 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: 423–431.

- Grace, J., José, J.S., Meir, P., Miranda, H.S., & Montes, R.A. 2006. Productivity and carbon fluxes of tropical savannas. In *Journal of Biogeography*, pp. 387–400.
- Griscom, B.W., Adams, J., Ellis, P.W., Houghton, R.A., Lomax, G., Miteva, D.A., Schlesinger, W.H., Shoch, D., Siikamäki, J.V., Smith, P., Woodbury, P., Zganjar, C., Blackman, A., Campari, J., Conant, R.T., Delgado, C., Elias, P., Gopalakrishna, T., Hamsik, M.R., Herrero, M., Kiesecker, J., Landis, E., Laestadius, L., Leavitt, S.M., Minnemeyer, S., Polasky, S., Potapov, P., Putz, F.E., Sanderman, J., Silvius, M., Wollenberg, E., & Fargione, J. 2017. Natural climate solutions. *Proceedings of the National Academy of Sciences* 114: 11645–11650.
- He, T., Lamont, B.B., & Downes, K.S. 2011. Banksia born to burn. *New Phytologist* 191: 184–196.
- He, T., Lamont, B.B., & Manning, J. 2016. A Cretaceous origin for fire adaptations in the Cape flora. *Scientific Reports* 6: 34880.
- He, T., Lamont, B.B., & Pausas, J.G. 2019. Fire as a key driver of Earth’s biodiversity. *Biological Reviews*. doi: 10.1111/brv.12544
- Hodge, A. 2004. The plastic plant: root responses to heterogeneous supplies of nutrients. *New Phytologist* 162: 9–24.
- Hoffmann, W.A., Geiger, E.L., Gotsch, S.G., Rossatto, D.R., Silva, L.C.R., Lau, O.L., Haridasan, M., & 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: 759–768.
- Honda, E.A., & Durigan, G. 2016. Woody encroachment and its consequences on hydrological processes in the savannah. *Philosophical Transactions of the Royal Society B: Biological Sciences* 371:.
- IPBES. 2019. Global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (E. S. Brondizio, J. Settele, S. Díaz, & H. T. Ngo, Eds.). IPBES secretariat, Bonn, Germany.
- IPCC. 2022. Climate Change 2022: Mitigation of Climate Change. Contribution of Working Group III to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change (P. R. Shukla, J. Skea, R. Slade, A. A. Khourdajie, R. van Diemen, M. D. McCollum, S. Pathak, P. Some, R. Vyas, M. Fradera, A. Belkacemi, G. Hasija, S. Lisboa, & J. M. Luz, Eds.). Cambridge University Press, Cambridge, UK and New York, NY, USA.
- Jackson, R.B., Lajtha, K., Crow, S.E., Hugelius, G., Kramer, M.G., & Piñeiro, G. 2017. The Ecology of Soil Carbon: Pools, Vulnerabilities, and Biotic and Abiotic Controls. *Annual Review of Ecology, Evolution, and Systematics* 48: 419–445.
- Jackson, A.R.B., Mooney, H.A., & Schulze, E. 2016. A Global Budget for Fine Root Biomass , Surface Area , and Nutrient Contents Published by : National Academy of Sciences Stable URL : <http://www.jstor.org/stable/42683> A global budget for fine root biomass , surface area , and nutrient contents. 94: 7362–7366.
- Jobbagy, E.G., & Jackson, R.B. 2000. The Vertical Distribution of Soil Organic Carbon and Its Relation to Climate and Vegetation. *Ecological Applications* 10: 423.

- Jones, M.W., Santín, C., van der Werf, G.R., & Doerr, S.H. 2019. Global fire emissions buffered by the production of pyrogenic carbon. *Nature Geoscience* 12: 742–747.
- Jørgensen, D. 2015. Ecological restoration as objective, target, and tool in international biodiversity policy. *Ecology and Society* 20:.
- Keeley, J.E., & Pausas, J.G. 2019. Distinguishing disturbance from perturbations in fire-prone ecosystems. *International Journal of Wildland Fire* 28: 282–287.
- 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: 406–411.
- Klimešová, J., Martínková, J., & Ottaviani, G. 2018. Belowground plant functional ecology: Towards an integrated perspective (K. Field, Ed.). *Functional Ecology* 32: 2115–2126.
- Klimešová, J., Martínková, J., Pausas, J.G., de Moraes, M.G., Herben, T., Yu, F.-H., Puntieri, J., Vesk, P.A., de Bello, F., Janeček, Š., Altman, J., Appezzato-da-Glória, B., Bartušková, A., Crivellaro, A., Doležal, J., Ott, J.P., Paula, S., Schnablová, R., Schweingruber, F.H., & Ottaviani, G. 2019. Handbook of standardized protocols for collecting plant modularity traits. *Perspectives in Plant Ecology, Evolution and Systematics* 40: 125485.
- Kornelius, E., Saueressig, M.G., & Goedert, W.J. 1979. Pastures establishment and management in the cerrado of Brazil. In *Pasture production in acid soil of the tropics*, pp. 147–166. O3EG-5. CIAT, Cali, Colombia.
- Kramer-Walter, K.R., Bellingham, P.J., Millar, T.R., Smissen, R.D., Richardson, S.J., & Laughlin, D.C. 2016. Root traits are multidimensional: specific root length is independent from root tissue density and the plant economic spectrum. *Journal of Ecology* 104: 1299–1310.
- Lamont, B.B., & Downes, K.S. 2011. Fire-stimulated flowering among resprouters and geophytes in Australia and South Africa. *Plant Ecology* 212: 2111–2125.
- Lamont, B.B., He, T., & Downes, K.S. 2013. Adaptive responses to directional trait selection in the Miocene enabled Cape proteas to colonize the savanna grasslands. *Evolutionary Ecology* 27: 1099–1115.
- Lamont, B.B., He, T., & Yan, Z. 2019. Evolutionary history of fire-stimulated resprouting, flowering, seed release and germination. *Biological Reviews* 94: 903–928.
- Lange, M., Eisenhauer, N., Sierra, C.A., Bessler, H., Engels, C., Griffiths, R.I., Mellado-Vázquez, P.G., Malik, A.A., Roy, J., Scheu, S., Steinbeiss, S., Thomson, B.C., Trumbore, S.E., & Gleixner, G. 2015. Plant diversity increases soil microbial activity and soil carbon storage. *Nature Communications* 6:.
- Laughlin, D.C., Mommer, L., Sabatini, F.M., Bruelheide, H., Kuyper, T.W., McCormack, M.L., Bergmann, J., Freschet, G.T., Guerrero-Ramírez, N.R., Iversen, C.M., Kattge, J., Meier, I.C., Poorter, H., Roumet, C., Semchenko, M., Sweeney, C.J., Valverde-Barrantes, O.J., van der Plas, F., van Ruijven, J., York, L.M., Aubin, I., Burge, O.R., Byun, C., Čuštrevska, R., Dengler, J., Forey, E., Guerin, G.R., Hérault, B., Jackson, R.B., Karger, D.N., Lenoir, J., Lysenko, T., Meir, P., Niinemets, Ü., Ozinga, W.A., Peñuelas, J., Reich, P.B., Schmidt, M., Schrod, F., Velázquez, E., & Weigelt,

- A. 2021. Root traits explain plant species distributions along climatic gradients yet challenge the nature of ecological trade-offs. *Nature Ecology & Evolution*. doi: 10.1038/s41559-021-01471-7
- Law, B. 2005. Carbon dynamics in response to climate and disturbance: Recent progress from multi-scale measurements and modeling in AmeriFlux. In *Plant Responses to Air Pollution and Global Change*, pp. 205–213. Springer Japan, Tokyo.
- 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: 4143–4157.
- Lecocq, F., Winkler, H., Daka, J.P., Fu, S., Gerber, J.S., Kartha, S., Krey, V., Lofgren, H., Masui, T., Marthur, R., Portugal-Pereira, J., Sovacool, B.K., Vilarino, M.V., & Zhou, N. 2022. Mitigation and development pathways in the near- to mid-term. In IPCC, 2022: *Climate Change 2022: Mitigation of Climate Change*. Contribution of Working Group III to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change, p. 156. Cambridge University Press, Cambridge, UK and New York, NY, USA.
- Linder, H.P., Lehmann, C.E.R., Archibald, S., Osborne, C.P., & Richardson, D.M. 2018. Global grass (Poaceae) success underpinned by traits facilitating colonization, persistence and habitat transformation. *Biological Reviews* 93: 1125–1144.
- Lloyd, J., Bird, M.I., Vellen, L., Miranda, A.C., Veenendaal, E.M., Djangbletey, G., Miranda, H.S., Cook, G., & Farquhar, G.D. 2008. Contributions of woody and herbaceous vegetation to tropical savanna ecosystem productivity: A quasi-global estimate. *Tree Physiology* 28: 451–468.
- Loreau, M. 2000. Biodiversity and ecosystem functioning: Recent theoretical advances. *Oikos* 91: 3–17.
- MapBiomass. 2022. MapBiomass Collection 7 (1985–2021).
- McCormack, M.L., Dickie, I.A., Eissenstat, D.M., Fahey, T.J., Fernandez, C.W., Guo, D., Helmisaari, H.S., Hobbie, E.A., Iversen, C.M., Jackson, R.B., Leppälammi-Kujansuu, J., Norby, R.J., Phillips, R.P., Pregitzer, K.S., Pritchard, S.G., Rewald, B., Zadworny, M., Leppälammi-Kujansuu, J., Norby, R.J., Phillips, R.P., Pregitzer, K.S., Pritchard, S.G., Rewald, B., & Zadworny, M. 2015. Redefining fine roots improves understanding of below-ground contributions to terrestrial biosphere processes. *New Phytologist* 207: 505–518.
- McLauchlan, K.K., Higuera, P.E., Miesel, J., Rogers, B.M., Schweitzer, J., Shuman, J.K., Tepley, A.J., Varner, J.M., Veblen, T.T., Adalsteinsson, S.A., Balch, J.K., Baker, P., Batllori, E., Bigio, E., Brando, P., Cattau, M., Chipman, M.L., Coen, J., Crandall, R., Daniels, L., Enright, N., Gross, W.S., Harvey, B.J., Hatten, J.A., Hermann, S., Hewitt, R.E., Kobziar, L.N., Landesmann, J.B., Loranty, M.M., Maezumi, S.Y., Mearns, L., Moritz, M., Myers, J.A., Pausas, J.G., Pellegrini, A.F.A., Platt, W.J., Roozeboom, J., Safford, H., Santos, F., Scheller, R.M., Sherriff, R.L., Smith, K.G., Smith, M.D., & Watts, A.C. 2020. Fire as a fundamental ecological process: Research advances and frontiers. *Journal of Ecology* 108: 2047–2069.
- Medeiros, M.B., & Miranda, H.S. 2008. Post-Fire Resprouting and Mortality in Cerrado Woody Plant Species Over a Three-Year Period. *Edinburgh Journal of Botany* 65:.
- Mendonça, R.C., Felfili, J.M., Walter, B.M.T., Silva-Júnior, M.C., Rezendo, A.V., Filgueiras, T.S., Nogueira, P.E., & Fagg, C.W. 2008. Flora vascular do bioma Cerrado: checklist com 12356

- hr data-bbox="111 60 886 65"/>
- especies. In *Cerrado: Ecologia e Flora*, Embrapa Cerrados/ Embrapa Informações Tecnológica, Brasília, DF.
- Miranda, A.C., Miranda, H.S., Lloyd, J., Grace, J., Francey, R.J., McIntyre, J.A., Meir, P., Riggan, P., Lockwood, R., & Brass, J. 1997. Fluxes of carbon, water and energy over Brazilian cerrado: An analysis using eddy covariance and stable isotopes. *Plant, Cell and Environment* 20: 315–328.
- Mokany, K., Raison, R.J., & Prokushkin, A.S. 2006. Critical analysis of root: Shoot ratios in terrestrial biomes. *Global Change Biology* 12: 84–96.
- Musso, C., Fontenele, H.G.V., Pinto, G., Oliveira, R., Correia, C., Moutinho-Pereira, J.M., Soares, A.M.V.M., & Loureiro, S. 2021. Effects of water and nutrient availability on morphological, physiological, and biochemical traits of one invasive and one native grass of a Neotropical savanna. *Environmental and Experimental Botany* 182:.
- Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B., & Kent, J. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403: 853–858.
- Norby, R.J., & Jackson, R.B. 2000. Root dynamics and global change: seeking an ecosystem perspective: REVIEW Root dynamics and global change. *New Phytologist* 147: 3–12.
- Oliveira, R.S., Bezerra, L., Davidson, E.A., Pinto, F., Klink, C.A., Nepstad, D.C., & Moreira, A. 2005. Deep root function in soil water dynamics in cerrado savannas of central Brazil. *Functional Ecology* 19: 574–581.
- Oliveira-Filho, A.T., & Ratter, J.A. 2002. Vegetation physiognomies and woody flora of the Cerrado Biome. In Oliveira, P.S. & Marquis, R.J. (eds.), *The Cerrados of Brazil: Ecology and Natural History of a Neotropical Savanna*, pp. 91–120. Columbia University Press, New York.
- 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: 368–380.
- Ottaviani, G., Martínková, J., Herben, T., Pausas, J.G., & Klimešová, J. 2017. On Plant Modularity Traits: Functions and Challenges. *Trends in Plant Science* 22: 648–651.
- Ottaviani, G., Molina-Venegas, R., Charles-Dominique, T., Chelli, S., Campetella, G., Canullo, R., & Klimešová, J. 2020. The Neglected Belowground Dimension of Plant Dominance. *Trends in Ecology and Evolution* 35: 763–766.
- Overbeck, G.E., Vélez-martin, E., Menezes, S., Anand, M., Baeza, S., Carlucci, M.B., Michele, S., Durigan, G., Fidelis, A., Guido, A., Moro, M.F., Munhoz, B.R., Reginato, M., Rodrigues, R.S., Fermina, M., Sampaio, A.B., Barbosa, H., Fernando, A.O., Sosinski, Ê.E., Staude, I.R., Temperton, V.M., Turchetto, C., Veldman, W., Viana, P.L., & Zappi, D.C. 2022. Placing Brazil's grasslands and savannas on the map of science and conservation. *Perspectives in Plant Ecology, Evolution and Systematics*. doi: 10.1016/j.ppees.2022.125687
- Parr, C.L., Lehmann, C.E.R., Bond, W.J., Hoffmann, W.A., & Andersen, A.N. 2014. Tropical grassy biomes: Misunderstood, neglected, and under threat. *Trends in Ecology and Evolution* 29: 205–213.

- Pausas, J.G., & Bond, W.J. 2020a. Alternative Biome States in Terrestrial Ecosystems. *Trends in Plant Science* 25: 250–263.
- Pausas, J.G., & Bond, W.J. 2019. Humboldt and the reinvention of nature. *Journal of Ecology* 107: 1031–1037.
- Pausas, J.G., & Bond, W.J. 2020b. On the Three Major Recycling Pathways in Terrestrial Ecosystems. *Trends in Ecology and Evolution* 35: 767–775.
- 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: 1435–1448.
- Pausas, J.G., & Paula, S. 2020. Grasses and fire: the importance of hiding buds: A response to Moore et al. (2019) ‘Effects of drought and fire on resprouting capacity of 52 temperate Australian perennial native grasses.’ *New Phytologist* 226: 957–959.
- Pellegrini, A.F.A., Ahlström, A., Hobbie, S.E., Reich, P.B., Nieradzik, L.P., Staver, A.C., Scharenbroch, B.C., Jumpponen, A., Anderegg, W.R.L., Randerson, J.T., & Jackson, R.B. 2018. Fire frequency drives decadal changes in soil carbon and nitrogen and ecosystem productivity. *Nature* 553: 194–198.
- Pellegrini, A.F.A., Caprio, A.C., Georgiou, K., Finnegan, C., Hobbie, S.E., Hatten, J.A., & Jackson, R.B. 2021. Low-intensity frequent fires in coniferous forests transform soil organic matter in ways that may offset ecosystem carbon losses. *Global Change Biology* 27: 3810–3823.
- Pellegrini, A.F.A., McLauchlan, K.K., Hobbie, S.E., Mack, M.C., Marcotte, A.L., Nelson, D.M., Perakis, S.S., Reich, P.B., & Whittinghill, K. 2020. Frequent burning causes large losses of carbon from deep soil layers in a temperate savanna. *Journal of Ecology* 108: 1426–1441.
- Petchey, O.L., & Gaston, K.J. 2006. Functional diversity: Back to basics and looking forward. *Ecology Letters* 9: 741–758.
- Petchey, O.L., & Gaston, K.J. 2002. Functional diversity (FD), species richness and community composition. *Ecology Letters* 5: 402–411.
- Pilon, N.A.L., Cava, M.G.B., Hoffmann, W.A., Abreu, R.C.R., Fidelis, A., & Durigan, G. 2021. The diversity of post-fire regeneration strategies in the cerrado ground layer. *Journal of Ecology*. doi: 10.1111/1365-2745.13456
- 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., 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: 111–123.
- Pivello, V.R., Shida, C.N., & Meirelles, S.T. 1999. Alien grasses in Brazilian savannas: A threat to the biodiversity. *Biodiversity and Conservation* 8: 1281–1294.
- Poorter, H., Niklas, K.J., Reich, P.B., Oleksyn, J., Poot, P., & Mommer, L. 2012. Biomass allocation to leaves, stems and roots: Meta-analyses of interspecific variation and environmental control. *New Phytologist* 193: 30–50.



- Prommer, J., Walker, T.W.N., Wanek, W., Braun, J., Zezula, D., Hu, Y., Hofhansl, F., & Richter, A. 2020. Increased microbial growth, biomass, and turnover drive soil organic carbon accumulation at higher plant diversity. *Global Change Biology* 26: 669–681.
- Pyšek, P., & Richardson, D.M. 2007. Traits Associated with Invasiveness in Alien Plants: Where Do we Stand? *Biological Invasions* 193: 97–125.
- 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: 33–41.
- Ribeiro, J.F., & Walter, B.M.T. 2008. As principais fitofisionomias do bioma Cerrado. In Sano, S.M., De Almeida, S.P., & Ribeiro, J.F. (eds.), *Cerrado: Ecologia e flora*, pp. 152–212. Embrapa Cerrados/Embrapa Informações Tecnológica.
- Ricciardi, A., Iacarella, J.C., Aldridge, D.C., Blackburn, T.M., Carlton, J.T., Catford, J.A., Dick, J.T.A., Hulme, P.E., Jeschke, J.M., Liebhold, A.M., Lockwood, J.L., MacIsaac, H.J., Meyerson, L.A., Pyšek, P., Richardson, D.M., Ruiz, G.M., Simberloff, D., Vilà, M., & Wardle, D.A. 2021. Four priority areas to advance invasion science in the face of rapid environmental change. *Environmental Reviews* 29: 119–141.
- 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: 427–433.
- Rodrigues, A.C., & Estelita, M.E.M. 2009. Morphoanatomy of the stem in Cyperaceae. *Acta Botanica Brasilica* 23: 889–901.
- 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.
- Santos, F.L.M., Nogueira, J., Souza, R.A.F. de, Falleiro, R.M., Schmidt, I.B., & Libonati, R. 2021. Prescribed Burning Reduces Large, High-Intensity Wildfires and Emissions in the Brazilian Savanna. *Fire* 4: 56.
- Santos, A.J.B., Silva, G.T.D.A., Miranda, H.S., Miranda, A.C., & Lloyd, J. 2003. Effects of fire on surface carbon, energy and water vapour fluxes over campo sujo savanna in central Brazil. *Functional Ecology* 17: 711–719.
- Schenk, H.J., & Jackson, R.B. 2002. The global biogeography of roots. *Ecological Monographs* 72: 18.
- Schmidt, I.B., & Eloy, L. 2020. Fire regime in the Brazilian Savanna: Recent changes, policy and management. *Flora: Morphology, Distribution, Functional Ecology of Plants* 268: 151613.
- Schmidt, I.B., Moura, L.C., Ferreira, M.C., Eloy, L., Sampaio, A.B., Dias, P.A., & Berlinck, C.N. 2018. Fire management in the Brazilian savanna: First steps and the way forward (R. Zenni, Ed.). *Journal of Applied Ecology* 55: 2094–2101.
- Scholze, M., Knorr, W., Arnell, N.W., & Prentice, I.C. 2006. A climate-change risk analysis for world ecosystems. *Proceedings of the National Academy of Sciences of the United States of America* 103: 13116–13120.

- Schreiner-McGraw, A.P., Vivoni, E.R., Ajami, H., Sala, O.E., Throop, H.L., & Peters, D.P.C. 2020. Woody Plant Encroachment has a Larger Impact than Climate Change on Dryland Water Budgets. *Scientific Reports* 10: 1–9.
- Scott, R.L., Huxman, T.E., Barron-Gafford, G.A., Darrel Jenerette, G., Young, J.M., & Hamerlynck, E.P. 2014. When vegetation change alters ecosystem water availability. *Global Change Biology* 20: 2198–2210.
- Silveira, F.A.O., Negreiros, D., Barbosa, N.P.U., Buisson, E., Carmo, F.F., Carstensen, D.W., Conceição, A.A., Cornelissen, T.G., Echternacht, L., Fernandes, G.W., Garcia, Q.S., Guerra, T.J., Jacobi, C.M., Lemos-Filho, J.P., Le Stradic, S., Morellato, L.P.C., Neves, F.S., Oliveira, R.S., Schaefer, C.E., Viana, P.L., & Lambers, H. 2016. Ecology and evolution of plant diversity in the endangered campo rupestre: a neglected conservation priority. *Plant and Soil* 403: 129–152.
- Simberloff, D., Martin, J.L., Genovesi, P., Maris, V., Wardle, D.A., Aronson, J., Courchamp, F., Galil, B., García-Berthou, E., Pascal, M., Pyšek, P., Sousa, R., Tabacchi, E., & Vilà, M. 2013. Impacts of biological invasions: What's what and the way forward. *Trends in Ecology and Evolution* 28: 58–66.
- 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.
- Simpson, K.J., Bennett, C., Atkinson, R.R.L., Mockford, E.J., McKenzie, S., Freckleton, R.P., Thompson, K., Rees, M., & Osborne, C.P. 2020. Photosynthesis and the economic spectra of leaf and root traits independently influence growth rates in grasses (Y. Le Bagousse-Pinguet, Ed.). *Journal of Ecology* 108: 1899–1909.
- Simpson, K.J., Jardine, E.C., Archibald, S., Forrestel, E.J., Lehmann, C.E.R., Thomas, G.H., & Osborne, C.P. 2021. Resprouting grasses are associated with less frequent fire than seeders. *New Phytologist* 230: 832–844.
- Simpson, K.J., Olofsson, J.K., Ripley, B.S., & Osborne, C.P. 2019. Frequent fires prime plant developmental responses to burning. *Proceedings of the Royal Society B: Biological Sciences* 286:.
- Souza, C.M., Shimbo, J.Z., Rosa, M.R., Parente, L.L., Alencar, A.A., Rudorff, B.F.T., Hasenack, H., Matsumoto, M., Ferreira, L.G., Souza-Filho, P.W.M., de Oliveira, S.W., Rocha, W.F., Fonseca, A.V., Marques, C.B., Diniz, C.G., Costa, D., Monteiro, D., Rosa, E.R., Vélez-Martin, E., Weber, E.J., Lenti, F.E.B., Paternost, F.F., Pareyn, F.G.C., Siqueira, J.V., Viera, J.L., Neto, L.C.F., Saraiva, M.M., Sales, M.H., Salgado, M.P.G., Vasconcelos, R., Galano, S., Mesquita, V.V., & Azevedo, T. 2020. Reconstructing three decades of land use and land cover changes in brazilian biomes with landsat archive and earth engine. *Remote Sensing* 12:.
- Spawn, S.A., Sullivan, C.C., Lark, T.J., & Gibbs, H.K. 2020. Harmonized global maps of above and belowground biomass carbon density in the year 2010. *Scientific Data* 7: 112.
- Staver, A.C., Archibald, S., & Levin, S.A. 2011. The global extent and determinants of savanna and forest as alternative biome states. *Science* 334: 230–232.
- Stevens, N., Bond, W., Feurdean, A., & Lehmann, C.E.R. 2022. Grassy Ecosystems in the Anthropocene. *Annual Review of Environment and Resources* 47: annurev-environ-112420-015211.

- Strömberg, C.A.E., & Staver, A.C. 2022. The history and challenge of grassy biomes. *Science* 377: 592–593.
- Tilman, D. 2001. Functional Diversity. In Levin, S.A. (ed.), *Encyclopedia of Biodiversity*, pp. 109–120. Academic Press, New York.
- Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M., & Siemann, E. 1997. The influence of functional diversity and composition on ecosystem processes. *Science* 277: 1300–1302.
- Tobin, B., Čermák, J., Chiatante, D., Danjon, F., Di Iorio, A., Dupuy, L., Eshel, A., Jourdan, C., Kalliokoski, T., Laiho, R., Nadezhdina, N., Nicoll, B., Pagès, L., Silva, J., & Spanos, I. 2007. Towards developmental modelling of tree root systems. *Plant Biosystems - An International Journal Dealing with all Aspects of Plant Biology* 141: 481–501.
- Tomlinson, K.W., Sterck, F.J., Bongers, F., da Silva, D.A., Barbosa, E.R.M., Ward, D., Bakker, F.T., van Kaauwen, M., Prins, H.H.T., de Bie, S., & van Langevelde, F. 2012. Biomass partitioning and root morphology of savanna trees across a water gradient. *Journal of Ecology* 100: 1113–1121.
- Tubiello, F.N., Lin, G., Druitt, J.W., & Marino, B.D.V. 1999. Ecosystem-level evapotranspiration and water-use efficiency in the desert biome of Biosphere 2. *Ecological Engineering* 13: 263–271.
- UNFCCC, U.N.F.C. on C.C. 2015. Adoption of the Paris Agreement. In United Nations, Paris, France.
- UNFCCC, U.N.F.C. on C.C. 2021. Glasgow Climate Pact, Decision -/CP.26, advance unedited version'. In Glasgow, UK.
- Van Der Werf, G.R., Randerson, J.T., Giglio, L., Van Leeuwen, T.T., Chen, Y., Rogers, B.M., Mu, M., Van Marle, M.J.E., Morton, D.C., Collatz, G.J., Yokelson, R.J., & Kasibhatla, P.S. 2017. Global fire emissions estimates during 1997–2016. *Earth System Science Data* 9: 697–720.
- Veldman, J.W., Buisson, E., Durigan, G., Fernandes, G.W., Le Stradic, S., Mahy, G., Negreiros, D., Overbeck, G.E., Veldman, R.G., Zaloumis, N.P., Putz, F.E., & Bond, W.J. 2015. Toward an old-growth concept for grasslands, savannas, and woodlands. *Frontiers in Ecology and the Environment* 13: 154–162.
- Veldman, J.W., Overbeck, G.E., Negreiros, D., Mahy, G., Le Stradic, S., Fernandes, G.W., Durigan, G., Buisson, E., Putz, F.E., & Bond, W.J. 2015. Tyranny of trees in grassy biomes. *Science* 347: 484–485.
- Veldman, J.W., Silveira, F.A.O., Fleischman, F.D., Ascarrunz, N.L., & Durigan, G. 2017. Grassy biomes: An inconvenient reality for large-scale forest restoration? A comment on the essay by Chazdon and Laestadius. *American Journal of Botany* 104: 649–651.
- Vila, M., Espinar, J.L., Hejda, M., Hulme, P.E., Jarosik, V., Maron, J.L., Pergl, J., Schaffner, U., Sun, Y., & Pysek, P. 2011. Ecological impacts of invasive alien plants: A meta-analysis of their effects on species, communities and ecosystems. *Ecology Letters* 14: 702–708.
- Villalobos-Vega, R., Salazar, A., Miralles-Wilhelm, F., Haridasan, M., Franco, A.C., & Goldstein, G. 2014. Do groundwater dynamics drive spatial patterns of tree density and diversity in Neotropical savannas? (K. Wesche, Ed.). *Journal of Vegetation Science* 25: 1465–1473.

- Wang, J., Sun, J., Yu, Z., Li, Y., Tian, D., Wang, B., Li, Z., & Niu, S. 2019. Vegetation type controls root turnover in global grasslands (B. Enquist, Ed.). *Global Ecology and Biogeography* 28: 442–455.
- Weemstra, M., Kiorapostolou, N., van Ruijven, J., Mommer, L., de Vries, J., & Sterck, F. 2020. The role of fine-root mass, specific root length and life span in tree performance: A whole-tree exploration. *Functional Ecology* 34: 575–585.
- Weng, E., Luo, Y., Wang, W., Wang, H., Hayes, D.J., McGuire, A.D., Hastings, A., & Schimel, D.S. 2012. Ecosystem carbon storage capacity as affected by Disturbance regimes: A general theoretical model. *Journal of Geophysical Research: Biogeosciences* 117: 1–15.
- Wigley, B.J., Augustine, D.J., Coetsee, C., Ratnam, J., & Sankaran, M. 2020. Grasses continue to trump trees at soil carbon sequestration following herbivore exclusion in a semiarid African savanna. *Ecology* 101: 1–10.
- Wigley, B.J., Staver, A.C., Zytowski, R., Jagodzinski, A.M., & Wigley-Coetsee, C. 2019. Root trait variation in African savannas. *Plant and Soil* 441: 555–565.
- Williams, D.G., & Baruch, Z. 2000. African grass invasion in the Americas: Ecosystem consequences and the role of ecophysiology. *Biological Invasions* 2: 123–140.
- Yang, Y., Tilman, D., Furey, G., & Lehman, C. 2019. Soil carbon sequestration accelerated by restoration of grassland biodiversity. *Nature Communications* 10: 718.
- Zhou, Y., Singh, J., Butnor, J.R., Coetsee, C., Boucher, P.B., Case, M.F., Hockridge, E.G., Davies, A.B., & Staver, A.C. 2022. Limited increases in savanna carbon stocks over decades of fire suppression. *Nature*.
- Zhou, Y., Wigley, B.J., Case, M.F., Coetsee, C., & Staver, A.C. 2020. Rooting depth as a key woody functional trait in savannas. *New Phytologist* 227: 1350–1361.
- Zou, J., Ziegler, A.D., Chen, D., McNicol, G., Ciais, P., Jiang, X., Zheng, C., Wu, J., Wu, J., Lin, Z., He, X., Brown, L.E., Holden, J., Zhang, Z., Ramchunder, S.J., Chen, A., & Zeng, Z. 2022. Rewetting global wetlands effectively reduces major greenhouse gas emissions. *Nature Geoscience* 15: 627–632.
- 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:.

# Fire promotes functional plant diversity and modifies soil carbon dynamics in tropical savanna

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**Abstract:** Fire is an evolutionary environmental filter in tropical savanna ecosystems altering functional diversity and associated C pools in the biosphere and fluxes between the atmosphere and biosphere. Therefore, alterations in fire regimes (e.g. fire exclusion) will strongly influence ecosystem processes and associated dynamics. In those ecosystems C dynamics and functions are underestimated by the fire-induced offset between C output and input. To determine how fire shapes ecosystem C pools and fluxes in an open savanna across recently burned and fire excluded areas, we measured the following metrics: (I) plant diversity including taxonomic (i.e. richness, evenness) and plant functional diversity (i.e. functional diversity, functional richness, functional dispersion and community weighted means); (II) structure (i.e. above- and below-ground biomass, litter accumulation); and (III) functions related to C balance (i.e. net ecosystem carbon dioxide (CO<sub>2</sub>) exchange (NEE), ecosystem transpiration (ET), soil respiration (soil CO<sub>2</sub> efflux), ecosystem water use efficiency (eWUE) and total soil organic C (SOC). We found that fire promoted aboveground live and belowground biomass, including belowground organs, coarse and fine root biomass and contributed to higher biomass allocation belowground. Fire also increased both functional diversity and dispersion. NEE and total SOC were higher in burned plots compared to fire-excluded plots whereas soil respiration recorded lower values in burned areas. Both ET and eWUE were not affected by fire. Fire strongly favored functional diversity, fine root and belowground organ biomass in piecewise SEM models but the role of both functional diversity and ecosystem structure to mediate the effect of fire on ecosystem functions remain unclear. Fire regime will impact C balance, and fire exclusion may lead to lower C input in open savanna ecosystems.

**keywords:** carbon dynamics, functional diversity, above and belowground interactions, fire-prone ecosystems, neotropical savanna, resilience.

## **INTRODUCTION**

Disturbances (e.g., fire) can alter carbon (C) dynamics and overall C balance by shifting the amount of C input and output from ecosystems consequently altering stocks in the biosphere and fluxes between the atmosphere and biosphere (Goetz et al., 2007). Fire is fundamental for the maintenance of C balance and ecosystem function at fire prone-ecosystems, such as open tropical savannas (McLauchlan et al., 2020). However, currently fire regimes of many fire-prone systems have been deeply changed across the globe (Archibald, 2016; Rogers et al., 2020) potentially altering C dynamics in fire-dependent ecosystems. Some studies already suggested that fire suppression in savannas will lead to changes of C dynamic equilibrium, decreasing the ecosystem C sink capacity (Beringer et al., 2015; Yin et al., 2020). Even so, the indirect and direct impacts of changes in fire regimes on C dynamics remain still poorly understood and are not explicitly analyzed addressing interfaces of fluxes between the atmosphere and biosphere alongside with C stocks to capture overall C dynamics (Pausas and Bond, 2020; Yin et al., 2020).

Changes in tropical savanna fire regimes (i.e., increase or decrease of fire frequencies) will lead to changes in vegetation structure or soil composition for example, causing plant-soil feedback that might modify the global C dynamics (Da Silva and Batalha, 2008; Grace et al., 2006; Pellegrini et al., 2020). Those plant-soil feedback alterations may occur due to differential responses of vegetation regrowth after fire (C input) (Archibald et al., 2018), soil respiration modification (C release), variations on soil organic carbon (SOC, C input), and changes in microbial activities (C fixing, Chapin et al., 2011; Dove et al., 2021; Pressler et al., 2019). Fire exclusion may increase aboveground biomass, decreasing grasses fuel load, affecting thus fire intensity (Fidelis et al., 2018, 2013). Thus, due to changes in fuel load and vegetation structure by the replacement of grassy by woody vegetation, C input after fire as a result of regrowing



vegetation may be compromised. First, because fire exclusion can negatively impact the herbaceous layer, since some species may disappear after some time without fire (Pilon et al., 2021b). Secondly, in fire-excluded areas, as a consequence to increasing woody cover, the release of C to the atmosphere will contribute more in case of fire, compromising C balance (Richards et al., 2011; Simpson et al., 2021). In addition, woody encroachment caused by fire exclusion may lead to changes in SOC pool, i.e. SOC losses and decrease in soil respiration which are fundamental properties of interconnections between the biosphere and the atmosphere (Abreu and Durigan, 2011; Chen et al., 2003; February et al., 2020; Jackson et al., 2002). On the other hand, SOC may increase after fire exclusion due to the stabilization of soil organic matter (Pellegrini et al., 2021) and thus, further studies about the effects of changes in fire regimes are needed to elucidate carbon dynamics in different fire-prone ecosystems.

Moreover, changes in fire frequency will lead to changes in biomass allocation and belowground traits, both greatly influencing soil C pools and fluxes balance (Jackson et al., 2000). Indeed, higher C investment in belowground biomass in tropical grassy biomes is partly in response to fire (De Castro and Kauffman, 1998; Fidelis et al., 2013), where plants shift their strategy by allocating resources from above to belowground (Archibald et al., 2019, 2018). The belowground biomass investment represents the major component of C input in grassy biomes (De Castro and Kauffman, 1998; Ottaviani et al., 2020). Belowground traits, especially root traits, are key functional traits that shape several ecosystem processes (Freschet et al., 2021) and are subject to be affected by fire and changes in vegetation structure (Loiola et al., 2015). For example, root traits from grasses such as higher specific root length and dense root system in the superficial soil layer promote efficiency of water and nutrients use (Case et al., 2020; Freschet et al., 2018; Linder et al., 2018) being related to ecosystem C input mainly at shallow soil layer (Jobbagy and Jackson,

2000). Root traits (e.g. rooting depth) from trees and shrubs are more correlated with tree growth and water uptake at deeper soil promoting efficiency of water use (Case et al., 2020; Zhou et al., 2020), and ecosystems C input at deep soil layer (Pellegrini et al., 2021, 2020). In addition, root traits (e.g. specific root length, root length density) also are related to ecosystem C loss due to plant-soil respiratory processes (Bardgett et al., 2014; De Deyn et al., 2008). Further, any changes in root functional traits can have consequences on C flux balance by altering root depth, root respiration, microbial communities or nutrient uptake for example (Bardgett et al., 2014; De Deyn et al., 2008; Freschet and Roumet, 2017).

Fire modifies C flux balance by affecting both taxonomic (Abreu et al., 2017; Finn et al., 2013) and functional diversity (De Deyn et al., 2008; Hoffmann et al., 2012; Keeley et al., 2011). Fire maintains species richness and fitness in tropical savanna ecosystems (Lamont et al., 2018; Pilon et al., 2021a). Thus, fire can influence ecosystem function (Petchey and Gaston, 2006) by filtering species with functional traits that are key to ensure higher plant fitness and are related to C cycling in such ecosystems (Bardgett et al., 2014; De Deyn et al., 2008). Fire should therefore promote functional diversity through functional dispersion (Silva et al., 2013) and, by selecting plant-soil response and further positively impacting C dynamics flux balance (Freschet and Roumet, 2017; Hanif et al., 2019).

Our study aimed to integrate total environment responses -atmospheric and biosphere dynamics- by understanding whether fire impacts (I) ecosystem C and water dynamics (i.e., total SOC, net ecosystem carbon dioxide (CO<sub>2</sub>) and water exchange, ecosystem water use efficiency and soil respiration), ecosystem diversity (i.e. plant taxonomic and functional diversity) and ecosystem structure (i.e. above and belowground biomass) on open Cerrado (Brazilian savanna) physiognomy; and (II) how changes in ecosystem diversity and/or structure in response to fire will

affect ecosystem C dynamics. We hypothesized that: (a) fire occurrence modifies the overall balance between C release and input, increasing C input while reducing C output through changes in both functional diversity and biomass allocation; (b) fire increases C input in the system, by increasing biomass allocation in the belowground compartment; and (c) fire will promote higher taxonomic and functional diversity in Cerrado open physiognomy compared to areas excluded from fire.

## MATERIAL AND METHODS

### *Study site*

We conducted our study at the *Reserva Natural Serra do Tombador* (RNST hereafter; 13° 35-38' S and 47° 45'-51' W, 8900ha, 560–1118m a.s.l., Figure S1), a protected area of Cerrado (Fundação Grupo Boticário, 2011). RNST exhibits a mosaic of fire history, with a fire-interval in open savannas of ca. 2-4 years (Daldegan et al., 2014) and a prevalence of open savannas (Fundação Grupo Boticário, 2011). Our study site at the RNST is classified as open savannas (*campo sujo*), a species-rich open savanna mainly composed of C4 grasses mixed with forbs and scattered dwarf trees and shrubs, representing overall low tree cover (< 5%) and basal area (Coutinho, 1978; Ribeiro and Walter, 2008). The climate is marked by two seasons: dry (May to October) and wet (November to April) (Fundação Grupo Boticário, 2011). The region of the study site has year-round average temperatures of ~23°C, and annual precipitation of ~1778mm, of which 82% is concentrated between the months of November and April (Fick and Hijmans, 2017). We performed all measurements during the rainy season (January-February 2019) at the peak of vegetation productivity (Cornelissen et al., 2003; Díaz et al., 2016; Pérez-Harguindeguy et al., 2013).

We selected one area (~3600 m<sup>2</sup>) subjected to long-term fire experiment established in the area since 2013 (for more details, see Rissi et al., 2017), and one area with long-term fire exclusion (~0.36 ha). Before the establishment of the fire experiments, the area was subjected to high fire frequency (i.e. 2-3 year fire interval, Daldegan et al., 2014). Both areas presented two contrasting fire frequencies: the first area was experimentally burned every two years (fire hereafter) in the middle of the dry season (July since 2013) and mimic *campo sujo* historical fire interval (Pivello, 2011). Fire intensity in the area is 1850 - 2700 kW.m<sup>-1</sup>, being characterized by a surface fire with high combustion efficiency (>90%, Rissi et al., 2017; Rodrigues et al., 2021). The second area was excluded from fire for 16 years (one fire event in the last 20 years, referred as fire exclusion hereafter) (Figure S1). Within each area, we randomly selected 12 1m<sup>2</sup> plots (12 plots × 2 treatments = 24 plots), with a minimum distance of 2 m between plots. All measurements for both fire frequencies were carried within those 1m<sup>2</sup> plots, 18 months after fire experiments in the burned plots.

## Method

### *Net Ecosystem C fluxes and Soil C pools*

We determined fire effects on interconnected fluxes between the atmosphere and the biosphere by measuring net ecosystem exchange by assessing CO<sub>2</sub> and water (H<sub>2</sub>O) vapor exchange between the biosphere and the atmosphere by tracking the net ecosystem C exchange (NEE; μmols CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup>) and water exchange (ET; ecosystem evapotranspiration; μmols H<sub>2</sub>O m<sup>-2</sup> s<sup>-1</sup>). We estimated NEE at each plot in both fire frequencies before biomass sampling, during the rainy season (March 2019) by recording the flux of CO<sub>2</sub> and H<sub>2</sub>O vapor on three separate sunny days (March 23<sup>rd</sup>, 25<sup>th</sup>, and 26<sup>th</sup> 2019) between 11a.m. and 2p.m. to ensure maximum ecosystem-

level photosynthetic activity. NEE and ET from each plot was measured using the LiCOR 7500 infrared gas analyzer (Li-Cor Inc.,) mounted on a tripod and two 15cm diameter electric fans to mix the air within a chamber ( $0.49\text{m}^2$  total area and  $0.37\text{m}^3$  volume) covered with woven rip-stop polyethylene that reduced PAR by 25% while maintaining temperatures constant (e.g., temperature increasing during measurement period did not exceed  $<1^\circ\text{C}$ ). The chamber was placed in each plot for 120 seconds where  $\text{CO}_2$  was recorded overtime for 90 seconds- the first 30 seconds we allowed for the air to mix and stabilize (Arnone and Obrist, 2003; Huxman et al., 2004; Potts et al., 2006a). Linear declines in  $\text{CO}_2$  and increases in  $\text{H}_2\text{O}$  vapor concentrations during the measurement periods demonstrate the alterations in water vapor were not significant to alter stomatal conductance, canopy photosynthesis or soil respiration (Huxman et al., 2004). NEE of  $\text{CO}_2$  and  $\text{H}_2\text{O}$  vapor were analyzed using Jasoni et al. (2005) approach to estimate fluxes at the system level. As the NEE integrated both  $\text{CO}_2$  uptake by the vegetation via plant photosynthesis and  $\text{CO}_2$  release by soil respiration (roots and microorganism respiration, respectively), to clearly measure soil  $\text{CO}_2$  release, alone we measured soil respiration which is soil average efflux ( $\mu\text{mol CO}_2\text{m}^{-2}\text{s}^{-1}$ ) with a LI-6400 gas analyzer (Li-Cor Inc., Lincoln, NE, USA). Finally, ecosystem water use efficiency (eWUE,  $\mu\text{mol CO}_2 / \mu\text{mol H}_2\text{O m}^{-2}\text{s}^{-1}$ ) was determined by calculating the ratio of NEE per amount of ET.

#### *Plant and Soil C Stocks*

Within each  $1\text{m}^2$  plot, we harvested all the aboveground biomass in one subplot of  $0.5\text{m} \times 0.5\text{m}$  and we sampled the belowground biomass in one subplot of  $0.25\text{m} \times 0.25\text{m}$  with  $0.2\text{m}$  depth. to quantify biomass of coarse roots (roots  $> 2\text{mm}$ ) and belowground organs (i.e., rhizomes, bulbs, xylopodia). Within each subplot used for the belowground biomass, fine roots (roots  $< 2\text{mm}$ ) were

quantified based on a soil core sample using an auger of 5 cm diameter and 20 cm depth since 50% of root biomass is found in the top 20cm of the soil (De Castro and Kauffman, 1998; Delitti et al., 2001; Loiola et al., 2015).

We sorted all aboveground biomass into litter, live and dead biomass, and then dried the samples at 80°C for 48h. The sum of live and dead biomass represented the total aboveground biomass. We washed the belowground biomass to remove soil particles and separate coarse root biomass from belowground organs. Fine root (< 2mm) samples were sieved at 2mm, 1.40mm and 850 µm before being washed. For assessing fine root biomass, we considered all fine roots (roots < 2 mm) as a result of the sum of acquisitive and transport roots (McCormack et al., 2015). The total belowground biomass was the sum of belowground organs, coarse and fine roots.

We used total aboveground biomass, live and dead biomass, litter, total belowground biomass, belowground organs biomass, coarse and fine root biomass measurements to characterize the system structure metrics. To evaluate biomass allocation, we considered the ratio of total aboveground: total belowground biomass and live aboveground: fine root biomass to evaluate biomass allocation for each plot.

We determined total SOC through total soil organic matter (SOM) of sieved soil samples taken in each plot (remaining soil from fine root samples sieve at 850 µm). SOM was determined by the Soil Lab from the Universidade de São Paulo– ESALQ, Brazil, through organic matter titration of dichromate solution added to soil samples (Camargo et al., 2009). We used the WB method (Walkley and Black, 1934) to determine total SOC using the following formula:  $\text{SOM (g.kg}^{-1}\text{)} = \text{SOC (g.kg}^{-1}\text{)} \times 1.724$ .

### *Plant diversity*

In the 24 1m<sup>2</sup> plots, we determined overall plant community species richness and percentage cover of each plant species (see Table S4) using a modified Braun-Blanquet scale (Wikum and Shanholtzer, 1978, using intervals of 10%). Species richness, Simpson's index and evenness index were used as the system taxonomic diversity metrics. The taxonomic diversity metrics were obtained by using the R package *vegan* (Oksanen et al., 2019).

We measured three above and three belowground plant functional traits on the dominant species from each fire and fire exclusion plots (30m x 30m) to determine functional diversity, richness, evenness, community weight means (CWM) and dispersion. We measured (i) aboveground functional traits: growth-form, specific leaf area (SLA), individual height; and (ii) belowground traits: root specific length (SRL), root dry matter content (RDMC) and root tissue density (RTD). Plant functional traits selected are associated with C dynamics (e.g. C stock) because they reflect individual ecophysiological adaptations and trade-off mainly related to resources allocations and acquisition (Bardgett et al., 2014; De Deyn et al., 2008; Pérez-Harguindeguy et al., 2013).

We considered as dominant plant species, those plants which represented 80% of vegetation cover at community level from each fire frequency. For fire plots, 25 species represented 80% of total cover, and 12 species accounted for 80% of total cover in the fire exclusion area (see Table S5). Aboveground functional traits have been assessed in 10 different individuals for each species and belowground in 5 different individuals for each species (Cornelissen et al., 2003). Since in savannas several plants may have clonal growth (Lamont et al., 2011; Pausas et al., 2018), each individual was sampled at least three meters from the nearest neighbor of the same species to avoid measuring the same genet.



To measure the roots functional traits, roots were first washed under water and then fine roots (<2mm) were classified in acquisitive (first three root order) and transport roots (McCormack et al., 2015). To measure the root morphological traits (i.e., SRL, RDMC and RTD), a sub-sample of acquisitive roots was used. Each sub-sample was weighed (fresh roots), digitized using a scanner EPSON Perfection V800 (Copyright© 2015 Epson America, Inc.) at resolution of 1200dpi. Root volume, diameter, and length was assessed with the software WinRHIZO™ 2013e (Copyright© 1996-2019 Régent Instruments Inc., Canada) (Bouma et al., 2000; Rose and Lobet, 2019) using digitized images. After image analysis, each sub-sample was dried 72h at 50°C in an oven and weighed to determine dry biomass. Specific root length (SRL, m g<sup>-1</sup>) was measured as the ratio between root length and root dry mass, root dry matter content (RDMC, mg g<sup>-1</sup>) was measured as the ratio between fresh wet (in mg) and dry weight (in g), and root tissue density (RTD, g cm<sup>-3</sup>) was assessed as the ratio between root dry mass and root volume

System functional diversity metrics were represented by functional richness (FRich) (Villéger et al., 2008), functional evenness (FEve), functional dispersion (FDis) (Laliberté and Legendre, 2010), functional diversity (FDp) (Petchey and Gaston, 2006, 2002) and the CWM index which is the abundance-weighted mean trait value for a community (Kleyer et al., 2012). FRich, FEve, FDis and CWM index were obtained by using the R package *FD* (Laliberté et al., 2014) and FDp using package *picante* (Kembel et al., 2010).

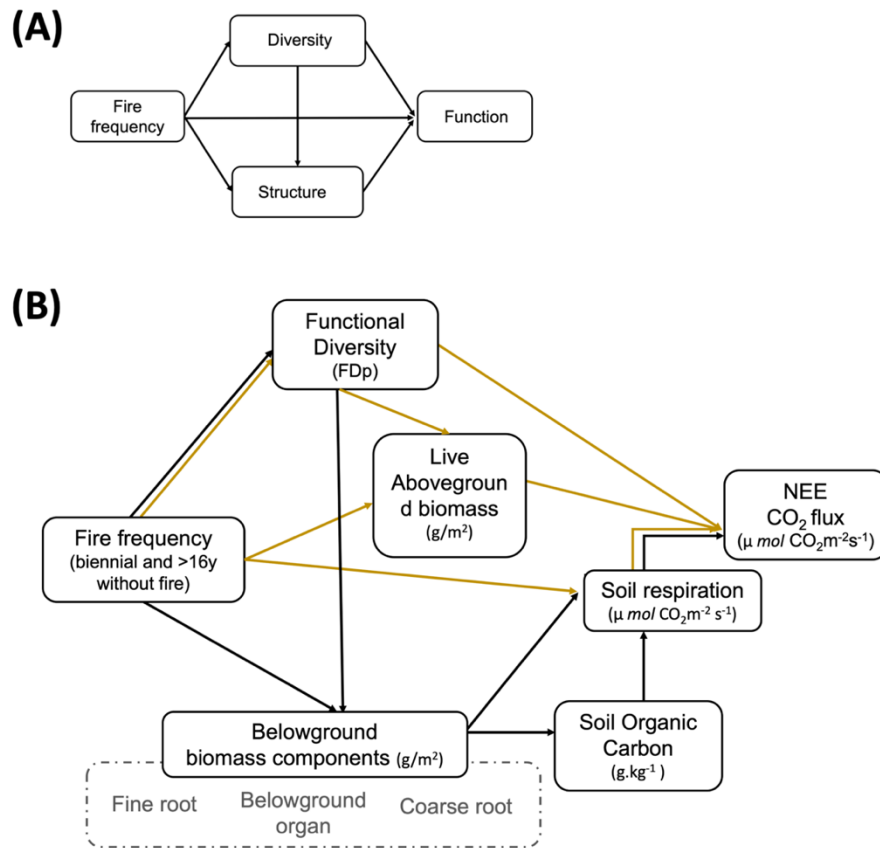
### *Data analysis*

To quantify the direct effect of fire frequencies on system diversity, structure, and ecosystem C balance, we performed the Effect-size test using Cohen's D index (Cohen, 1988). We calculated the standardized effect size (d) by assessing the standardized mean difference between

the fire plots ( $m_t$ ) and fire exclusion plots (control,  $m_c$ ) of the value of a given system metric, using the pooled standard deviation of the same component in the treatment ( $sd_t$ ) and control ( $sd_c$ ) plots, with a correlation of the two samples (fire exclusion and fire) to make it less biased (McGrath and Meyer, 2006), as the following formula:

$$d = \frac{(m_t - m_c)}{\sqrt{\frac{sd_t^2 + sd_c^2}{2}}} \quad (1)$$

A positive value of Cohen's D index for a given system metric means that fire increases the ecosystem metric in relation to fire exclusion. A value of Cohen's D index near zero means that fire has no effect on the given system metric. All NEE values were multiple by -1 to simplify results interpretation. To examine how changes in diversity and structure promoted by fire will lead to direct and indirect changes on ecosystem C balance we used a piecewise structural equation model (piecewiseSEM; Lefcheck, 2016). Piecewise SEM's has a non-significant p-value ( $p > 0.05$ ) as an indicative of a well-fit model, similarly to the lower AIC value (Lefcheck, 2016). We built four different piecewise SEM models based on our hypothesis from the results of our effect-size analyses, using variables that have shown significant effect according to fire and supporting our theoretical hypothesis (Figure 1, hypothesis one is in brown, hypothesis two is in black). Also, to ensure good explanatory power at each of our piecewiseSEM models, we respected the general rule of the ratio of the total number of observations to the number of variables as  $d=5$  (Grace et al., 2015). Based on this, each of the four piecewise SEM model, representing our hypothesis, considered only one system structure metric at a time respectively the live aboveground biomass (first piecewise SEM and first hypothesis), fine root (second), coarse root (third), and belowground organ (forth) representing our second hypothesis.



**Figure 1.** Conceptual model based on our hypothesis examined within our piecewise SEM models. (A) Hypothetical model regarding the general pathways of the effect of fire presence on system diversity, structure and thus system function to carbon balance. (B) Detail of our hypothetical model, considering the metrics we used in our piecewiseSEM models. Hypotheses one and two are represented by the brown and black arrows, respectively. To ensure good explanatory power at our piecewiseSEM models, belowground biomass components from our second hypothesis, were separately analyzed in our piecewiseSEM models.

Each SEM model was built from five linear mixed effect models (*lme*) (see supplementary material, Table S3). The first *lme* aims to explain total SOC as the response variable according to system structure (i.e., fine roots biomass, belowground organ biomass, coarse roots biomass, live aboveground biomass) and fire frequencies as predictor variables. The second *lme* aims to explain system structure (i.e., live aboveground biomass, fine roots biomass, belowground organ biomass, coarse roots biomass) as the response variable according to fire frequencies and functional

diversity (FDp index). The third *lme* used NEE as the response variable, and the functional diversity, soil respiration, total SOC, fire frequencies and system structure (i.e., aboveground biomass, fine root biomass, belowground organ biomass, coarse root biomass) as explanatory variables. The fourth *lme* aims to explain soil respiration according to system structure, fire frequencies and NEE as predictor variables. Finally, the fifth *lme* examined functional diversity as a response to fire frequencies. We log-transformed all response and predictor variables to achieve normality assumptions. We kept fire frequency as a categorical variable, and to check the contribution of each category in the model (fire and fire exclusion), we performed an estimated marginal mean analysis for each significant model (Lefcheck, 2019). We used Fisher's C to assess the completeness of our model. We included plot as a random variable in all model regressions and we did not remove non-significant links in our final SEM.

All analyses were conducted using the R version 3.6.3 environment (R Development Core Team, 2020) and package *piecewiseSEM* (Lefcheck, 2016), *nlme* (Pinheiro et al., 2020) and package *effsize* (Torchiano, 2017).

## RESULTS

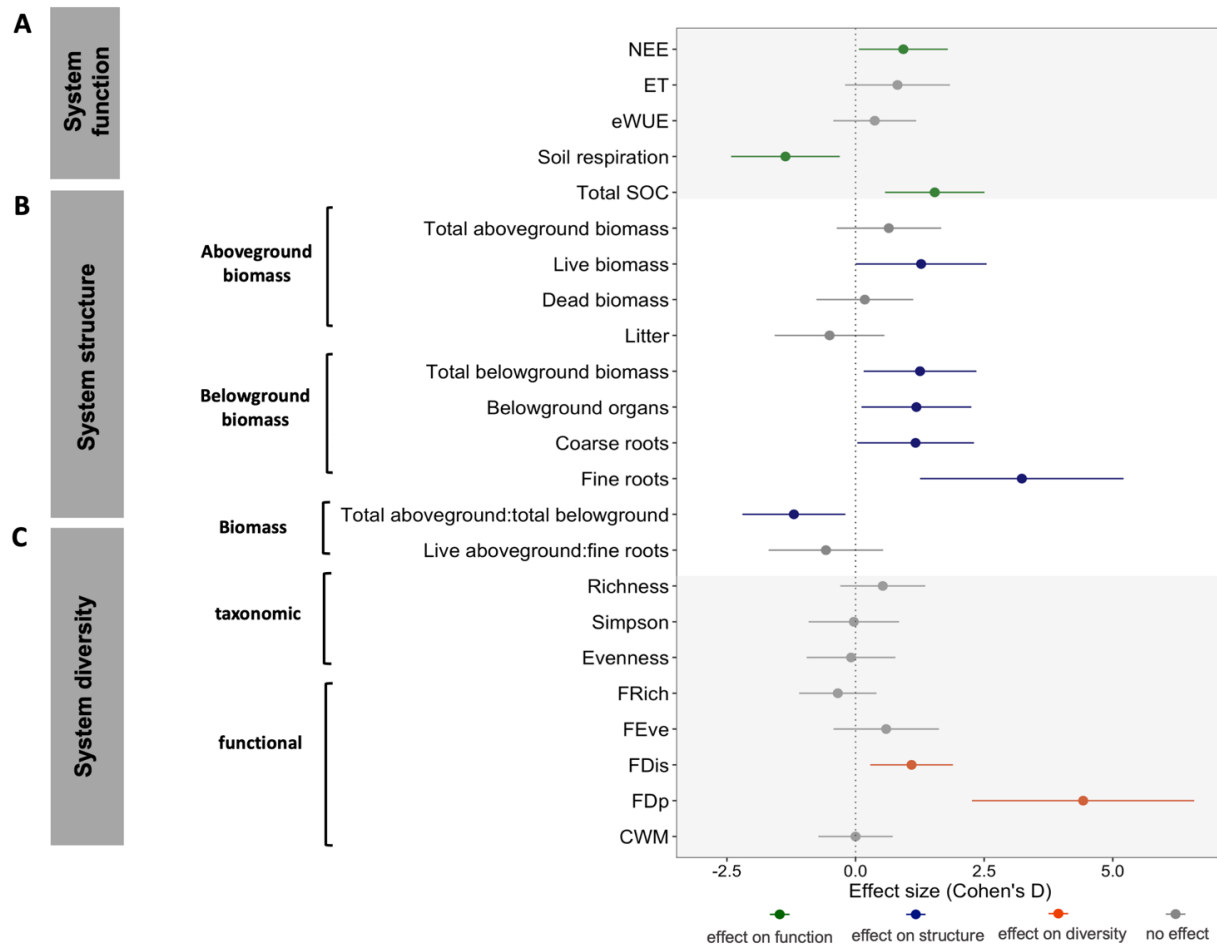
### *Direct effect of fire on ecosystem diversity, structure & function*

Fire impacted all three system components: system diversity, structure, and system function (Figure 2). Fire has a positive effect on diversity by promoting functional diversity and functional dispersion. However, fire did not impact taxonomic diversity metrics (Figure 2, Table S1-S2).

Fire promoted live biomass and all belowground biomass components including belowground organs, coarse and fine roots biomass (Figure 2). The ratio between above- and belowground biomass responded negatively to fire, indicating a higher biomass allocation to

belowground with fire (Figure 2). Fire had no effect on dead biomass and litter, as well as on the ratio between live aboveground biomass and fine roots.

Finally, fire impacted system function, positively affecting NEE and total SOC while negatively impacting soil respiration. Fire had no effect on ET and eWUE.



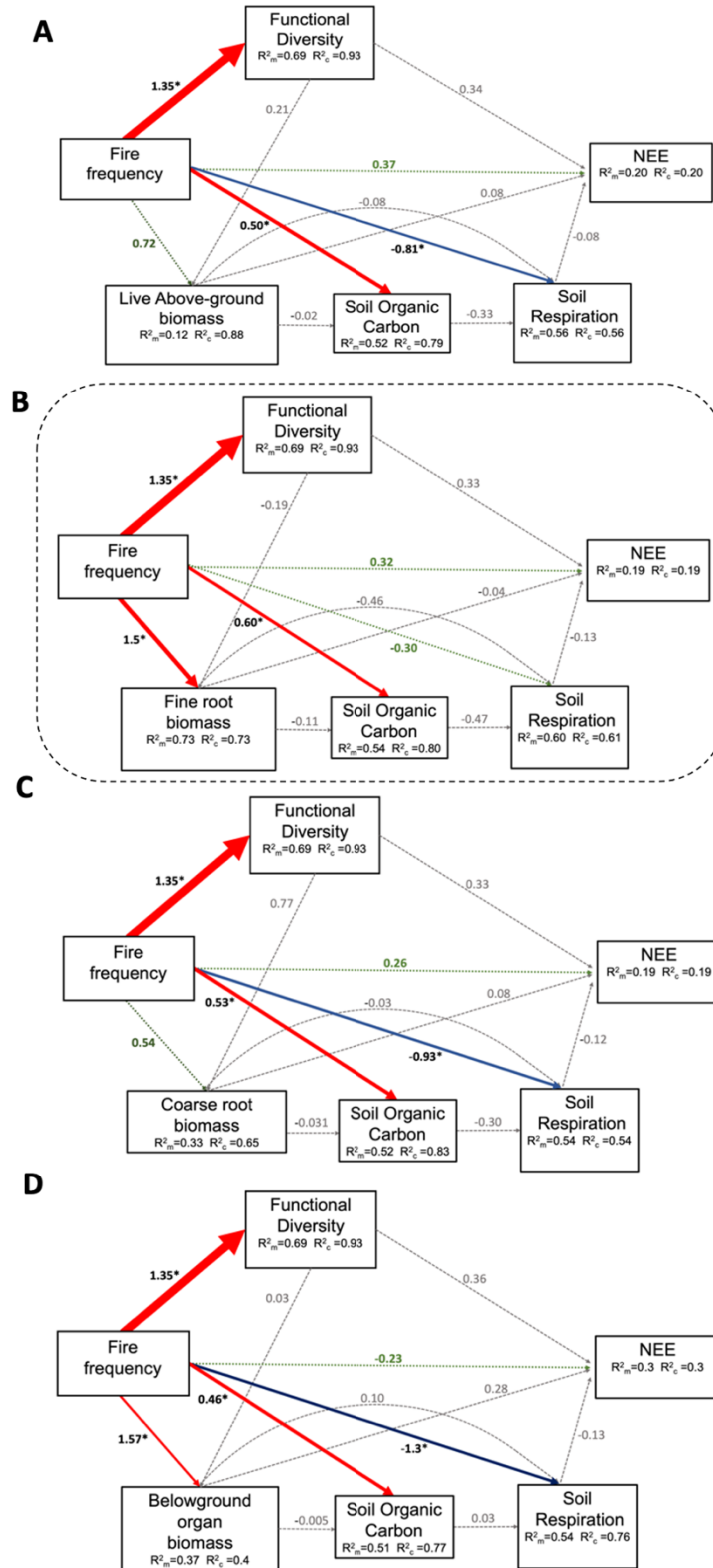
**Figure 2.** Effect of fire on (A) system function to carbon balance considering total soil carbon content (SOC), rates of net ecosystem exchange (NEE), ecosystem evapotranspiration (ET), ecosystem water use efficiency (eWUE) and soil respiration, (B) system structure considering total aboveground biomass as well as live and dead biomass, and total belowground biomass in addition to fine root, coarse root and belowground organs biomass, total aboveground biomass:belowground biomass ratio and live aboveground biomass:live fine root biomass, and litter biomass; and (C) system diversity considering plant community taxonomic diversity (i.e. richness, Simpson, and evenness index) and functional diversity: functional richness (FRich), functional evenness (FEve), functional dispersion (FDis); functional diversity plot-based

dendrogram (FDp), community weighted means (CWM). (C) Positive values mean that fire promotes the system variable while negative values indicate that fire negatively affects the system variable. Values near zero indicate that fire did not have a significant effect. The values were based on Cohen's D index ( $\alpha=95\%$ ), obtained from plots located in burned and fire excluded areas.

### *Fire impacts on ecosystem C dynamics through shifts in structure & diversity*

Models consistently indicated a fire-induced increase on SOC (Figure 3, Table S3) and a decline in soil respiration (Figure 3C). All piecewise SEM models showed strong positive and direct relation between fire and plant functional diversity (Figure 3, Table S3). The models also showed that fire induced greater belowground biomass input, especially fine root and belowground organ biomass (Figure 3B and D) whereas coarse roots biomass was minimally affected by fire (Figure 3C). NEE in most models (except Figure 3D) was positively, besides marginally, affected by fire (Figure 3).

Overall, the model that included fine root biomass was the best model to explain how fire impacted ecosystem C stocks and fluxes (Fisher's  $C=2.194$ ,  $AIC=58.194$ ,  $p\text{-value}=0.7$ , Figure 3B). In that model, fire marginally reduced soil respiration while promoting NEE, leading towards higher ecosystem C flux input. Further, fire affected positively and directly both functional diversity and fine root biomass (Figure 3B). Although our models showed a marginal positive relationship between fire and NEE, they did not allow us to establish a direct relationship between fire and NEE, or a clear indirect relation mediated by functional diversity, belowground biomass, soil respiration or SOC.



**Figure 3.** Piecewise structural equation model (SEM) depicting the direct and indirect effects of fire frequency on system diversity, structure and system function associated with carbon balance. (A) Piecewise

SEM based on our first hypothesis that considers live-aboveground biomass as a system structure metric. The model presented the lower goodness of fit for our data: Fisher's  $C = 3.266$ ,  $AIC=59.266$ ,  $p\text{-value}=0.514$ . The following piecewiseSEM models were based on our second hypothesis that considered separately the different belowground biomass components: (B) fine roots biomass, (C) coarse roots biomass and (D) below organs biomass. (B) The model considering the fine root biomass presented the best good fit for our data: Fisher's  $C = 2.194$ ,  $AIC=58.194$ ,  $p\text{-value}=0.7$ . (C) The model with coarse roots biomass, also presented a good fit for our data: Fisher's  $C=6.757$ ,  $AIC= 62.757$ ,  $p\text{-value}=0.149$ . (D) The last model considered below organs biomass and has a good fit for our data: Fisher's  $C = 5.364$ ,  $AIC=59.266$ ,  $p\text{-value}=0.252$ . Partial  $R^2$  values are under each predicted variable, and standardized path estimates are provided next to each path with line thickness scaled based on the magnitude of the estimated variable. Red and dark blue arrows indicate positive and negative relationships, respectively. Grey dashed arrows represent non-significant paths ( $p>0.05$ ), and the green represents the marginally significant paths. Asterisks (\*) indicate significance ( $p < 0.05$ ). Black dashed block indicates the model with the best fit for our data.

## DISCUSSION

In Cerrado open savanna, fire is promoting C input in the system through increases in live above- and belowground biomass as well as a higher biomass allocation belowground, ultimately promoting the input of C into soils. Our results also showed a higher NEE and total SOC with fire whereas soil respiration declined i.e., soil C efflux (C output), corroborating the higher C input in burned compared to unburned areas. While fire enhanced functional diversity, our results did not support positive fire effects on taxonomic diversity as found in other studies (Abreu et al., 2017; Gomes et al., 2020; Pilon et al., 2021a). Although our results support direct effects of fire in ecosystem functions associated with C dynamics (i.e., NEE, total SOC or soil respiration), how ecosystem structure and diversity mediated these relationships remain less straightforward.

Our results highlighted that fire modifies C balance with higher NEE in burned plots, illustrating a higher C input and lower C release. C flux is very cyclic in the Cerrado (Santos et al., 2003; Vourlitis and da Rocha, 2010) and compared to unburned savanna areas, frequently burned



savannas rapidly become a stronger sink for CO<sub>2</sub> (Santos et al., 2003). However, after 12 months, the negative impact of fire (i.e. C release, biomass lost) on the open savannas is eliminated, indicating the potential of the system to compensate for C losses due to combustion (Potts et al., 2006; Potts et al., 2012). The increase of photosynthetic activities promoted by the newly produced leaves from the vegetation regrowth compensates the C loss, providing the whole system C uptake (e.g., greater NEE in burned than unburned plots) (Baldocchi, 2008; Huxman et al., 2004; Potts et al., 2012).

Fast regeneration in open savanna is primarily ensured by the quick regeneration of grass species that produce newly photosynthetic leaves (Pilon et al., 2021a), since grasses are the most resilient growth form to fire in savannas (Bond, 2004). Graminoids morphological architecture that protects buds and meristems ensures fast recovery (Linder et al., 2018; Pilon et al., 2021a; Wigley et al., 2020), being also the most flammable element of the fuel load (Simpson et al., 2016). Also, high annual productivity of grasses can be related to the energetic cost investment of resprouting, that is focused on the production of photosynthetically active tissue (Linder et al., 2018; Simpson et al., 2021). Frequent fires will promote mainly grasses live aboveground biomass as shown in our results. In savannas, fire occurrence is closely related with grass abundance (De Castro and Kauffman, 1998), favoring grass species over woody species (Bond et al., 2005; Bond and Keeley, 2005).

C input in burned plots is also shown through the increase in belowground biomass. Our results showed that fire enhanced total belowground biomass, especially fine root and belowground organ biomass and promoted biomass allocation in the belowground compartment, corroborating with our hypothesis. In open tropical savannas, plants allocate a large proportion of biomass in belowground compartments (Fidelis et al., 2013; Jobbagy and Jackson, 2000; Poorter et al., 2011).

Fire is indeed expected to lead towards plant investment to belowground organs, for bud protection, resource storage and resource acquisition, allowing plants to survive and quickly resprout after fire (Clarke et al., 2013; Enright et al., 2014; Lawes and Clarke, 2011). Further, fire stimulates fine root biomass production at the shallow soil layer (0-20cm depth) to improve the nutrient acquisition (Jackson et al., 2002; Le Stradic et al., 2021; Oliveras et al., 2013; Pellegrini et al., 2020). However, at deeper soil (> 30cm-100cm), Cerrado open savannas areas with different fire histories and frequencies did not show differences on fine root biomass (Le Stradic et al., 2021).

Higher total SOC in burned areas illustrates the overall increase in C input in tropical open savannas. Grassy ecosystems can boost SOC at the shallow soil layer because of the higher grass root biomass in the upper 20 cm of the soil (Berhongaray et al., 2019; February et al., 2020, 2013; Le Stradic et al., 2021). Indeed, the increase of total SOC may be related to higher grass fine root decomposition which represents the great deal of organic matter input in the soil (De Deyn et al., 2011). However, in burned sites we also observed a reduction of soil respiration which suggests a reduced microbial activity. Fire can enhance plant microbiome diversity and composition (Dove et al., 2021) that might affect C input into soil through modification in microbial activities and increase in microbial by-product (Rossi et al., 2020). In addition, increases in belowground organ and fine roots at the shallow soil layer due to fire, can overtime contribute towards greater soil C through slow decomposition and mycorrhizal association (Freschet et al., 2013; Godbold et al., 2006). Although the belowground communities seem to play an important role in the soil respiration and for soil C input, further studies are needed to understand how they may affect C flux and storage in a fire-prone environment (Pressler et al., 2019).

In Cerrado open savannas, litter deposition and decomposition is relatively slow (Carvalho et al., 2012; Kauffman et al., 1994; Valenti et al., 2008), especially due to recalcitrant compounds of C4 grasses that decompose more slowly relative to C3 plants (Martin et al., 1990). Indeed, most of the dead grass material remains attached in the tussocks (Wragg et al., 2018) which slows down substrate quantity deposition and may decrease soil respiration (Chapin et al., 2011). In addition, in case of recurrent and frequent fires like in Cerrado, litter accumulation is limited and removed frequently by fire, which may reduce microbial activity related to litter decomposition. Cerrado soils are relatively nutrient poor with acidic pH (Pivello et al., 2010), which may also limit soil microbial activities, lowering therefore soil respiration, and thus C loss from microbial activities (Fierer and Jackson, 2006; Funakawa et al., 2014; Rousk et al., 2010). Finally, microbial activity associated with soil respiration may also be limited in post-fire environments since fire may have burned superficial microbial communities.

Overtime, fire promoted functional diversity in plant communities with greater trait variability across species (Dantas et al., 2013). Post-fire conditions promote new opportunities for plant colonization (Fidelis et al., 2012; Pausas et al., 2003), due to higher environmental heterogeneity and higher resource availability (He et al., 2019; Krawchuk and Moritz, 2011; Pivello et al., 2010), and increasing niche availability generating species coexistence and greater diversity. High diversity of post-fire strategies is associated with higher trait diversity, dispersion and consequently trait divergence (Lhotsky et al., 2016; Mason et al., 2013) as highlighted by our results. In addition, functional diversity can be stimulated by fire because over time species could complement each other in the resource use by capturing resources with different strategies (Garnier et al., 2016). Functional diversity associated with functional divergence may influences plant-soil feedback responses, such as plant and soil respiration, and efficiency on water and nutrients use,

and thus impacting the ecosystem function of C balance (De Deyn et al., 2008; Jackson et al., 2000; Petchey and Gaston, 2006), besides our results did not allow to conclude about that. However, we may hypothesize belowground communities seem to play an important role in the processes of plant-soil feedback responses and C balance. Further studies are needed to understand how belowground community dynamics affect C flux and storage in a fire-prone environment (Pressler et al., 2019).

Finally, in a context of climate changes and modification of fire regimes, it seems essential to better understand mechanisms between fire and the ecosystem C cycle which are complex in different fire-prone ecosystems. Quantifying tropical open savannas potential C pools and fluxes is not trivial and identifying system pathways trajectories and mediation will provide a way to assess and describe fluctuations in ecosystem function in response to modification in fire regime under climate change. Furthermore, our findings also should help ecosystem base restoration and fire management plans in savanna open ecosystems to maintain system structure, diversity, and function. We acknowledge that our results dealt with the C pool at the shallow soil layer of an open savanna, and we did not account for C in the deeper soil layers, which may have a higher contribution of trees and shrubs. Whereas our results showed that fire promoted SOC at the soil surface, fire may decrease SOC in deeper soil layer, as shown by other study in a temperate savanna (Pellegrini et al., 2020). In addition, in savannas where the woody cover has a higher importance, the presence of trees and shrubs is expected to differently affect C balance. In woody tropical savannas, fire may decrease C stock in soil and plant biomass due to a reduction on nutrient mineralization rates, and nitrogen viability, that decreases tree net primary production and consequently soil and plant C input (Cook et al., 2005; Richards et al., 2011; Williams et al., 2004).

## **CONCLUSIONS**

Our study showed that high fire frequency in Cerrado open savannas lead overall to C input into the system by increasing soil C, plant belowground biomass and by declining C fluxes from the biosphere back to the atmosphere. However, we need to acknowledge that the relationship and the underlined mechanisms between functional diversity, changes in biomass allocation and changes in ecosystem functions remained unclear. In addition, our findings also highlight the importance of fire to promote functional diversity on Cerrado open ecosystems. Once fire is excluded, functional diversity was reduced, so potentially the diversity of response to disturbances and environmental changes. Functional diversity losses could be an issue in terms of regeneration possibility after a fire, should limit system resilience in areas excluded from fire for long-time, limiting vegetation regeneration and jeopardizing the ability of the natural system to compensate for the C lost during combustion altering biosphere and atmosphere dynamics.

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## REFERENCES

- Abreu, R.C.R. de, Durigan, G., 2011. Changes in the plant community of a brazilian grassland savannah after 22 years of invasion by *pinus elliottii* engelm. *Plant Ecol. Divers.* 4, 269–278. <https://doi.org/10.1080/17550874.2011.594101>
- Abreu, R.C.R., Hoffmann, W.A., Vasconcelos, H.L., Pilon, N.A., Rossatto, D.R., Durigan, G., 2017. The biodiversity cost of carbon sequestration in tropical savanna. *Sci. Adv.* 3, 1–8. <https://doi.org/10.1126/sciadv.1701284>
- Archibald, S., 2016. Managing the human component of fire regimes: Lessons from Africa. *Philos. Trans. R. Soc. B Biol. Sci.* 371. <https://doi.org/10.1098/rstb.2015.0346>
- Archibald, S., Hempson, G.P., Lehmann, C., 2019. A unified framework for plant life-history strategies shaped by fire and herbivory. *New Phytol.* 224, 1490–1503. <https://doi.org/10.1111/nph.15986>
- Archibald, S., Lehmann, C.E.R., Belcher, C.M., Bond, W.J., Bradstock, R.A., Daniau, A.L., Dexter, K.G., Forrester, E.J., Greve, M., He, T., Higgins, S.I., Hoffmann, W.A., Lamont, B.B., McGlenn, D.J., Moncrieff, G.R., Osborne, C.P., Pausas, J.G., Price, O., Ripley, B.S., Rogers, B.M., Schwilk, D.W., Simon, M.F., Turetsky, M.R., Van Der Werf, G.R., Zanne, A.E., 2018. Biological and geophysical feedbacks with fire in the Earth system. *Environ. Res. Lett.* 13. <https://doi.org/10.1088/1748-9326/aa9ead>
- Arnone, J.A., Obrist, D., 2003. A large daylight geodesic dome for quantification of whole-ecosystem CO<sub>2</sub> and water vapour fluxes in arid shrublands. *J. Arid Environ.* 55, 629–643. [https://doi.org/10.1016/S0140-1963\(02\)00291-4](https://doi.org/10.1016/S0140-1963(02)00291-4)
- Baldocchi, D., 2008. TURNER REVIEW No. 15. “Breathing” of the terrestrial biosphere: Lessons learned from a global network of carbon dioxide flux measurement systems. *Aust. J. Bot.* 56, 1–26. <https://doi.org/10.1071/BT07151>
- Bardgett, R.D., Mommer, L., De Vries, F.T., 2014. Going underground: Root traits as drivers of ecosystem processes. *Trends Ecol. Evol.* 29, 692–699. <https://doi.org/10.1016/j.tree.2014.10.006>
- Berhongaray, G., Cotrufo, F.M., Janssens, I.A., Ceulemans, R., 2019. Below-ground carbon inputs contribute more than above-ground inputs to soil carbon accrual in a bioenergy poplar plantation. *Plant Soil* 434, 363–378. <https://doi.org/10.1007/s11104-018-3850-z>
- Beringer, J., Hutley, L.B., Abramson, D., Arndt, S.K., Briggs, P., Bristow, M., Canadell, J.G.,

- Cernusak, L.A., Eamus, D., Edwards, A.C., Evans, B.J., Fest, B., Goergen, K., Grover, S.P., Hacker, J., Haverd, V., Kanniah, K., Livesley, S.J., Lynch, A., Maier, S., Moore, C., Raupach, M., Russell-Smith, J., Scheiter, S., Tapper, N.J., Uotila, P., 2015. Fire in Australian savannas: From leaf to landscape. *Glob. Chang. Biol.* 21, 62–81. <https://doi.org/10.1111/gcb.12686>
- Bond, W.J., 2004. Fire, in: Cowling, R.M., Richardson, D.M., Pierce, S.M. (Eds.), *Vegetation of Southern Africa*. Cambridge University Press, pp. 421–446.
- Bond, W.J., Keeley, J.E., 2005. Fire as a global “herbivore”: The ecology and evolution of flammable ecosystems. *Trends Ecol. Evol.* 20, 387–394. <https://doi.org/10.1016/j.tree.2005.04.025>
- Bond, W.J., Woodward, F.I., Midgley, G.F., 2005. The global distribution of ecosystems in a world without fire. *New Phytol.* 165, 525–538. <https://doi.org/10.1111/j.1469-8137.2004.01252.x>
- Bouma, T.J., Nielsen, K.L., Koutstaal, B., 2000. Sample preparation and scanning protocol for computerised analysis of root length and diameter. *Plant Soil* 218/2, 185–196. <https://doi.org/10.1023/A:1014905104017>
- Camargo, O.A., Moniz, A.C., Jorge, J.A., Valadares, J.M.A. da S., 2009. Métodos de Análise Química, Mineralógica e Física de Solos do Instituto Agronômico de Campinas.
- Carvalho, I. de M., Fernandes, M.F., Chaer, G.M., Junior, F.B. dos R., 2012. Biological functioning of Brazilian Cerrado soils under different vegetation types. *Plant Soil* 359, 183–195. <https://doi.org/10.1007/s11104-012-1195-6>
- Case, M.F., Nippert, J.B., Holdo, R.M., Staver, A.C., 2020. Root-niche separation between savanna trees and grasses is greater on sandier soils. *J. Ecol.* 108, 2298–2308. <https://doi.org/10.1111/1365-2745.13475>
- Chapin, F.S., Matson, P.A., Vitousek, P.M., Chapin, F.S., Matson, P.A., Vitousek, P.M., 2011. Plant Carbon Budgets, in: *Principles of Terrestrial Ecosystem Ecology*. Springer New York, pp. 157–181. [https://doi.org/10.1007/978-1-4419-9504-9\\_6](https://doi.org/10.1007/978-1-4419-9504-9_6)
- Chen, X., Hutley, L.B., Eamus, D., 2003. Carbon balance of a tropical savanna of northern Australia. *Oecologia* 137, 405–416. <https://doi.org/10.1007/s00442-003-1358-5>
- Clarke, P.J., Lawes, M.J., Midgley, J.J., Lamont, B.B., Ojeda, F., Burrows, G.E., Enright, N.J., Knox, K.J.E., 2013. Resprouting as a key functional trait: how buds, protection and resources drive persistence after fire. *New Phytol.* 197, 19–35. <https://doi.org/10.1111/nph.12001>
- Cook, G.D., Liedloff, A.C., Eager, R.W., Chen, X., Williams, R.J., O’Grady, A.P., Hutley, L.B.,



2005. The estimation of carbon budgets of frequently burnt tree stands in savannas of northern Australia, using allometric analysis and isotopic discrimination. *Aust. J. Bot.* 53, 621–630. <https://doi.org/10.1071/BT04150>
- Cornelissen, J.H.C., Lavorel, S., Garnier, E., Díaz, S., Buchmann, N., Gurvich, D.E., Reich, P.B., Steege, H. ter, Morgan, H.D., Heijden, M.G.A. van der, Pausas, J.G., Poorter, H., 2003. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Aust. J. Bot.* 51, 335. <https://doi.org/10.1071/BT02124>
- Coutinho, L.M., 1978. O Conceito de Cerrado. *Revs. Bras. Bot.* 1, 17–23.
- Da Silva, D.M., Batalha, M.A., 2008. Soil-vegetation relationships in cerrados under different fire frequencies. *Plant Soil* 311, 87–96. <https://doi.org/10.1007/s11104-008-9660-y>
- Daldegan, G.A., de Carvalho Júnior, O.A., Guimarães, R.F., Gomes, R.A.T., Ribeiro, F. de 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 Sens.* 6, 9873–9894. <https://doi.org/10.3390/rs6109873>
- Dantas, V. de L., Pausas, J.G., Batalha, M.A., de Paula Loiola, P., Cianciaruso, M.V., 2013. The role of fire in structuring trait variability in Neotropical savannas. *Oecologia* 171, 487–494. <https://doi.org/10.1007/s00442-012-2431-8>
- De Castro, E.A., Kauffman, J.B., 1998. Ecosystem structure in the Brazilian Cerrado: A vegetation gradient of aboveground biomass, root mass and consumption by fire. *J. Trop. Ecol.* 14, 263–283. <https://doi.org/10.1017/S0266467498000212>
- De Deyn, G.B., Cornelissen, J.H.C., Bardgett, R.D., 2008. Plant functional traits and soil carbon sequestration in contrasting biomes. *Ecol. Lett.* 11, 516–531. <https://doi.org/10.1111/j.1461-0248.2008.01164.x>
- De Deyn, G.B., Shiel, R.S., Ostle, N.J., Mcnamara, N.P., Oakley, S., Young, I., Freeman, C., Fenner, N., Quirk, H., Bardgett, R.D., 2011. Additional carbon sequestration benefits of grassland diversity restoration. *J. Appl. Ecol.* 48, 600–608. <https://doi.org/10.1111/j.1365-2664.2010.01925.x>
- Delitti, W.B.C., Pausas, J.G., Burger, D.M., 2001. Belowground biomass seasonal variation in two neotropical savannas (Brazilian Cerrados) with different fire histories. *Ann. For. Sci.* 58, 713–721.
- Díaz, S., Kattge, J., Cornelissen, J.H.C., Wright, I.J., Lavorel, S., Dray, S., Reu, B., Kleyer, M.,

- Wirth, C., Colin Prentice, I., Garnier, E., Bönisch, G., Westoby, M., Poorter, H., Reich, P.B., Moles, A.T., Dickie, J., Gillison, A.N., Zanne, A.E., Chave, J., Joseph Wright, S., Sheremet Ev, S.N., Jactel, H., Baraloto, C., Cerabolini, B., Pierce, S., Shipley, B., Kirkup, D., Casanoves, F., Joswig, J.S., Günther, A., Falczuk, V., Rüger, N., Mahecha, M.D., Gorné, L.D., 2016. The global spectrum of plant form and function. *Nature* 529, 167–171. <https://doi.org/10.1038/nature16489>
- Dove, N.C., Klingeman, D.M., Carrell, A.A., Cregger, M.A., Schadt, C.W., 2021. Fire alters plant microbiome assembly patterns: integrating the plant and soil microbial response to disturbance. *New Phytol.* <https://doi.org/10.1111/nph.17248>
- Enright, N.J., Fontaine, J.B., Lamont, B.B., Miller, B.P., Westcott, V.C., 2014. Resistance and resilience to changing climate and fire regime depend on plant functional traits. *J. Ecol.* 102, 1572–1581. <https://doi.org/10.1111/1365-2745.12306>
- February, E., Pausch, J., Higgins, S.I., 2020. Major contribution of grass roots to soil carbon pools and CO<sub>2</sub> fluxes in a mesic savanna. *Plant Soil* 454, 207–215. <https://doi.org/10.1007/s11104-020-04649-3>
- February, E.C., Cook, G.D., Richards, A.E., 2013. Root dynamics influence tree-grass coexistence in an Australian savanna. *Austral Ecol.* 38, 66–75. <https://doi.org/10.1111/j.1442-9993.2012.02376.x>
- Fick, S.E., Hijmans, R.J., 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *Int. J. Climatol.* 37, 4302–4315. <https://doi.org/10.1002/joc.5086>
- Fidelis, A., Alvarado, S.T., Barradas, A., Pivello, V., 2018. The Year 2017: Megafires and Management in the Cerrado. *Fire* 1, 49. <https://doi.org/10.3390/fire1030049>
- 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. *J. Veg. Sci.* 23, 552–562. <https://doi.org/10.1111/j.1654-1103.2011.01364.x>
- Fidelis, A., Lyra, M.F. di S., Pivello, V.R., 2013. Above- and below-ground biomass and carbon dynamics in Brazilian Cerrado wet grasslands. *J. Veg. Sci.* 24, 356–364. <https://doi.org/10.1111/j.1654-1103.2012.01465.x>
- Fierer, N., Jackson, R.B., 2006. The diversity and biogeography of soil bacterial communities. *Proc. Natl. Acad. Sci. U. S. A.* 103, 626–631. <https://doi.org/10.1073/pnas.0507535103>
- Finn, J.A., Kirwan, L., Connolly, J., Sebastià, M.T., Helgadottir, A., Baadshaug, O.H., Bélanger,

- G., Black, A., Brophy, C., Collins, R.P., Čop, J., Dalmannsdóttir, S., Delgado, I., Elgersma, A., Fothergill, M., Frankow-Lindberg, B.E., Ghesquiere, A., Golinska, B., Golinski, P., Grieu, P., Gustavsson, A.M., Höglind, M., Huguenin-Elie, O., Jørgensen, M., Kadziulienė, Z., Kurki, P., Llurba, R., Lunnan, T., Porqueddu, C., Suter, M., Thumm, U., Lüscher, A., 2013. Ecosystem function enhanced by combining four functional types of plant species in intensively managed grassland mixtures: A 3-year continental-scale field experiment. *J. Appl. Ecol.* 50, 365–375. <https://doi.org/10.1111/1365-2664.12041>
- Freschet, G.T., Cornwell, W.K., Wardle, D.A., Elumeeva, T.G., Liu, W., Jackson, B.G., Onipchenko, V.G., Soudzilovskaia, N.A., Tao, J., Cornelissen, J.H.C., 2013. Linking litter decomposition of above- and below-ground organs to plant-soil feedbacks worldwide. *J. Ecol.* 101, 943–952. <https://doi.org/10.1111/1365-2745.12092>
- Freschet, G.T., Roumet, C., 2017. Sampling roots to capture plant and soil functions. *Funct. Ecol.* 31, 1506–1518. <https://doi.org/10.1111/1365-2435.12883>
- Freschet, G.T., Roumet, C., Comas, L.H., Weemstra, M., Bengough, A.G., Rewald, B., Bardgett, R.D., De Deyn, G.B., Johnson, D., Klimešová, J., Lukac, M., McCormack, M.L., Meier, I.C., Pagès, L., Poorter, H., Prieto, I., Wurzbürger, N., Zadworny, M., Bagniewska-Zadworna, A., Blancaflor, E.B., Brunner, I., Gessler, A., Hobbie, S.E., Iversen, C.M., Mommer, L., Picon-Cochard, C., Postma, J.A., Rose, L., Ryser, P., Scherer-Lorenzen, M., Soudzilovskaia, N.A., Sun, T., Valverde-Barrantes, O.J., Weigelt, A., York, L.M., Stokes, A., 2021. Root traits as drivers of plant and ecosystem functioning: current understanding, pitfalls and future research needs. *New Phytol.* nph.17072. <https://doi.org/10.1111/nph.17072>
- Freschet, G.T., Violle, C., Bourget, M.Y., Scherer-Lorenzen, M., Fort, F., 2018. Allocation, morphology, physiology, architecture: the multiple facets of plant above- and below-ground responses to resource stress. *New Phytol.* 219, 1338–1352. <https://doi.org/10.1111/nph.15225>
- Funakawa, S., Fujii, K., Kadono, A., Watanabe, T., Kosaki, T., 2014. Could Soil Acidity Enhance Sequestration of Organic Carbon in Soils?, in: *Soil Carbon*. Springer International Publishing, pp. 209–216. [https://doi.org/10.1007/978-3-319-04084-4\\_22](https://doi.org/10.1007/978-3-319-04084-4_22)
- Fundação Grupo Boticário, 2011. Plano de Manejo da Reserva Natural Serra do Tombador, Cavalcante – GO. Plano Manejo da Reserv. Nat. Serra do Tombador, Cavalcante – GO, Vol. 1.
- Garnier, E., Navas, M.-L., Grigulis, K., 2016. Plant Functional Diversity, Plant Functional

- Diversity. <https://doi.org/10.1093/acprof:oso/9780198757368.001.0001>
- Godbold, D.L., Hoosbeek, M.R., Lukac, M., Cotrufo, M.F., Janssens, I.A., Ceulemans, R., Polle, A., Velthorst, E.J., Scarascia-Mugnozza, G., De Angelis, P., Miglietta, F., Peressotti, A., 2006. Mycorrhizal hyphal turnover as a dominant process for carbon input into soil organic matter. *Plant Soil* 281, 15–24. <https://doi.org/10.1007/s11104-005-3701-6>
- Goetz, S.J., MacK, M.C., Gurney, K.R., Randerson, J.T., Houghton, R.A., 2007. Ecosystem responses to recent climate change and fire disturbance at northern high latitudes: Observations and model results contrasting northern Eurasia and North America. *Environ. Res. Lett.* 2. <https://doi.org/10.1088/1748-9326/2/4/045031>
- Gomes, L., Miranda, H.S., Soares-Filho, B., Rodrigues, L., Oliveira, U., Bustamante, M.M.C., 2020. Responses of Plant Biomass in the Brazilian Savanna to Frequent Fires. *Front. For. Glob. Chang.* 3, 1–11. <https://doi.org/10.3389/ffgc.2020.507710>
- Grace, J., José, J.S., Meir, P., Miranda, H.S., Montes, R.A., 2006. Productivity and carbon fluxes of tropical savannas, in: *Journal of Biogeography*. pp. 387–400. <https://doi.org/10.1111/j.1365-2699.2005.01448.x>
- Grace, J.B., Scheiner, S.M., Schoolmaster, D.R.J., 2015. Structural equation modeling: building and evaluating causal models, in: Fox, G.A., Negrete-Yankelevich, S., Sosa, V.J. (Eds.), *Ecological Statistics: Contemporary Theory and Application*. Oxford University Press, New York, NY, pp. 168–199.
- Hanif, M.A., Yu, Q., Rao, X., Shen, W., 2019. Disentangling the contributions of plant taxonomic and functional diversities in shaping aboveground biomass of a restored forest landscape in Southern China. *Plants* 8. <https://doi.org/10.3390/plants8120612>
- He, T., Lamont, B.B., Pausas, J.G., 2019. Fire as a key driver of Earth's biodiversity. *Biol. Rev.* <https://doi.org/10.1111/brev.12544>
- Hoffmann, W.A., Geiger, E.L., Gotsch, S.G., Rossatto, D.R., Silva, L.C.R., Lau, O.L., Haridasan, M., Franco, A.C., 2012. Ecological thresholds at the savanna-forest boundary: How plant traits, resources and fire govern the distribution of tropical biomes. *Ecol. Lett.* 15, 759–768. <https://doi.org/10.1111/j.1461-0248.2012.01789.x>
- Huxman, T.E., Cable, J.M., Ignace, D.D., Eilts, J.A., English, N.B., Weltzin, J., Williams, D.G., 2004. Response of net ecosystem gas exchange to a simulated precipitation pulse in a semi-arid grassland: The role of native versus non-native grasses and soil texture. *Oecologia* 141,

- 295–305. <https://doi.org/10.1007/s00442-003-1389-y>
- Jackson, A.R.B., Schenk, H.J., Jobbagy, E.G., Canadell, J., Colello, G.D., Field, C.B., Friedlingstein, P., Heimann, M., Hibbard, K., Kicklighter, D.W., Neilson, R.P., Parton, W.J., Sala, O.E., Sykes, M.T., 2000. Belowground Consequences of Vegetation Change and Their Treatment in Models. *Ecol. Appl.* 10, 470–483.
- Jackson, R.B., Banner, J.L., Jobbaágy, E.G., Pockman, W.T., Wall, D.H., 2002. Ecosystem carbon loss with woody plant invasion of grasslands. *Nature* 418, 623–626. <https://doi.org/10.1038/nature00910>
- Jasoni, R.L., Smith, S.D., Arnone, J.A., 2005. Net ecosystem CO<sub>2</sub> exchange in Mojave Desert shrublands during the eighth year of exposure to elevated CO<sub>2</sub>. *Glob. Chang. Biol.* 11, 749–756. <https://doi.org/10.1111/j.1365-2486.2005.00948.x>
- Jobbagy, E.G., Jackson, R.B., 2000. The Vertical Distribution of Soil Organic Carbon and Its Relation to Climate and Vegetation. *Ecol. Appl.* 10, 423. <https://doi.org/10.2307/2641104>
- Kauffman, J.B., Cummings, D.L., Ward, D.E., 1994. Relationships of Fire , Biomass and Nutrient Dynamics along a Vegetation Gradient in the Brazilian Cerrado. *Br. Ecol. Soc.* 82, 519–531.
- 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 Plant Sci.* 16, 406–411. <https://doi.org/10.1016/j.tplants.2011.04.002>
- Kembel, S., Cowan, P., Helmus, M., Cornwell, W., Morlon, H., Ackerly, D., Blomberg, S., Webb, C., 2010. Picante: R tools for integrating phylogenies and ecology. *Bioinformatics* 26, 1463–1464.
- Kleyer, M., Dray, S., Bello, F., Lepš, J., Pakeman, R.J., Strauss, B., Thuiller, W., Lavorel, S., 2012. Assessing species and community functional responses to environmental gradients: Which multivariate methods? *J. Veg. Sci.* 23, 805–821. <https://doi.org/10.1111/j.1654-1103.2012.01402.x>
- Krawchuk, M.A., Moritz, M.A., 2011. Constraints on global fire activity vary across a resource gradient. *Ecology* 92, 121–132. <https://doi.org/10.1890/09-1843.1>
- Laliberté, A.E., Shipley, B., Laliberté, M.E., 2014. Package ‘ FD .’
- Laliberté, E., Legendre, P., 2010. A distance-based framework for measuring functional diversity from multiple traits, *Ecology*. <https://doi.org/10.1890/08-2244.1>
- Lamont, B.B., Enright, N.J., He, T., 2011. Fitness and evolution of resprouters in relation to fire.

- Plant Ecol. 212, 1945–1957. <https://doi.org/10.1007/s11258-011-9982-3>
- Lamont, B.B., He, T., Yan, Z., 2018. Evolutionary history of fire-stimulated resprouting, flowering, seed release and germination. *Biol. Rev.* <https://doi.org/10.1111/brv.12483>
- Lawes, M.J., Clarke, P.J., 2011. Ecology of plant resprouting: populations to community responses in fire-prone ecosystems. *Plant Ecol.* 212, 1937–1943. <https://doi.org/10.1007/s11258-011-9994-z>
- 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. *J. Ecol.* 1–15. <https://doi.org/10.1111/1365-2745.13786>
- Lefcheck, J., 2019. Structural Equation Modeling in R for Ecology and Evolution.
- Lefcheck, J.S., 2016. piecewiseSEM: Piecewise structural equation modelling in r for ecology, evolution, and systematics. *Methods Ecol. Evol.* 7, 573–579. <https://doi.org/10.1111/2041-210X.12512>
- Lhotsky, B., Kovács, B., Ónodi, G., Csecserits, A., Rédei, T., Lengyel, A., Kertész, M., Botta-Dukát, Z., 2016. Changes in assembly rules along a stress gradient from open dry grasslands to wetlands. *J. Ecol.* 104, 507–517. <https://doi.org/10.1111/1365-2745.12532>
- Linder, H.P., Lehmann, C.E.R., Archibald, S., Osborne, C.P., Richardson, D.M., 2018. Global grass (Poaceae) success underpinned by traits facilitating colonization, persistence and habitat transformation. *Biol. Rev.* 93, 1125–1144. <https://doi.org/10.1111/brv.12388>
- Loiola, P. de P., Cianciaruso, M.V., Silva, I.A., Batalha, M.A., 2010. Functional diversity of herbaceous species under different fire frequencies in Brazilian savannas. *Flora Morphol. Distrib. Funct. Ecol. Plants* 205, 674–681. <https://doi.org/10.1016/j.flora.2010.04.006>
- Loiola, P. de P., Scherer-Lorenzen, M., Batalha, M.A., 2015. The role of environmental filters and functional traits in predicting the root biomass and productivity in savannas and tropical seasonal forests. *For. Ecol. Manage.* 342, 49–55. <https://doi.org/10.1016/j.foreco.2015.01.014>
- Martin, A., Mariotti, A., Balesdent, J., Lavelle, P., Vuattoux, R., 1990. Estimate of organic matter turnover rate in a savanna soil by <sup>13</sup>C natural abundance measurements. *Soil Biol. Biochem.* 22, 517–523. [https://doi.org/10.1016/0038-0717\(90\)90188-6](https://doi.org/10.1016/0038-0717(90)90188-6)
- Mason, N.W.H., De Bello, F., Mouillot, D., Pavoine, S., Dray, S., 2013. A guide for using functional diversity indices to reveal changes in assembly processes along ecological

- gradients. *J. Veg. Sci.* 24, 794–806. <https://doi.org/10.1111/jvs.12013>
- McCormack, M.L., Dickie, I.A., Eissenstat, D.M., Fahey, T.J., Fernandez, C.W., Guo, D., Helmisaari, H.S., Hobbie, E.A., Iversen, C.M., Jackson, R.B., Leppälammi-Kujansuu, J., Norby, R.J., Phillips, R.P., Pregitzer, K.S., Pritchard, S.G., Rewald, B., Zadworny, M., 2015. Redefining fine roots improves understanding of below-ground contributions to terrestrial biosphere processes. *New Phytol.* 207, 505–518. <https://doi.org/10.1111/nph.13363>
- McGrath, R.E., Meyer, G.J., 2006. When effect sizes disagree: The case of *r* and *d*. *Psychol. Methods* 11, 386–401. <https://doi.org/10.1037/1082-989X.11.4.386>
- McLauchlan, K.K., Higuera, P.E., Miesel, J., Rogers, B.M., Schweitzer, J., Shuman, J.K., Tepley, A.J., Varner, J.M., Veblen, T.T., Adalsteinsson, S.A., Balch, J.K., Baker, P., Batllori, E., Bigio, E., Brando, P., Cattau, M., Chipman, M.L., Coen, J., Crandall, R., Daniels, L., Enright, N., Gross, W.S., Harvey, B.J., Hatten, J.A., Hermann, S., Hewitt, R.E., Kobziar, L.N., Landesmann, J.B., Loranty, M.M., Maezumi, S.Y., Mearns, L., Moritz, M., Myers, J.A., Pausas, J.G., Pellegrini, A.F.A., Platt, W.J., Roozeboom, J., Safford, H., Santos, F., Scheller, R.M., Sherriff, R.L., Smith, K.G., Smith, M.D., Watts, A.C., 2020. Fire as a fundamental ecological process: Research advances and frontiers. *J. Ecol.* 108, 2047–2069. <https://doi.org/10.1111/1365-2745.13403>
- 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.H., Szoecs, E., Wagner, H., 2019. *vegan: Community Ecology Package*. R package version 2.4-2. *Community Ecol. Packag.* 2.5-6, 1–296.
- 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. *Int. J. Wildl. Fire* 22, 368–380. <https://doi.org/10.1071/WF10136>
- Ottaviani, G., Molina-venegas, R., Charles-dominique, T., Chelli, S., Campetella, G., Canullo, R., Klime, J., 2020. Forum The Neglected Belowground Dimension of Plant Dominance xx, 1–4. <https://doi.org/10.1016/j.tree.2020.06.006>
- Pausas, J.G., Bond, W.J., 2020. On the Three Major Recycling Pathways in Terrestrial Ecosystems. *Trends Ecol. Evol.* 35, 767–775. <https://doi.org/10.1016/j.tree.2020.04.004>
- Pausas, J.G., Lamont, B.B., Paula, S., Appezzato-da-Glória, B., Fidelis, A., 2018. Unearthing belowground bud banks in fire-prone ecosystems. *New Phytol.* 217, 1435–1448.

- <https://doi.org/10.1111/nph.14982>
- Pausas, J.G., Ouadah, N., Ferran, A., Gimeno, T., Vallejo, R., 2003. Fire severity and seedling establishment in *Pinus halepensis* woodlands, eastern Iberian Peninsula. *Plant Ecol.* 169, 205–213. <https://doi.org/10.1023/A:1026019528443>
- Pellegrini, A.F.A., Caprio, A.C., Georgiou, K., Finnegan, C., Hobbie, S.E., Hatten, J.A., Jackson, R.B., 2021. Low-intensity frequent fires in coniferous forests transform soil organic matter in ways that may offset ecosystem carbon losses. *Glob. Chang. Biol.* 27, 3810–3823. <https://doi.org/10.1111/gcb.15648>
- Pellegrini, A.F.A., McLauchlan, K.K., Hobbie, S.E., Mack, M.C., Marcotte, A.L., Nelson, D.M., Perakis, S.S., Reich, P.B., Whittinghill, K., 2020. Frequent burning causes large losses of carbon from deep soil layers in a temperate savanna. *J. Ecol.* 108, 1426–1441. <https://doi.org/10.1111/1365-2745.13351>
- Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., Bret-Harte, M.S., Cornwell, W.K., Craine, J.M., Gurvich, D.E., Urcelay, C., Veneklaas, E.J., Reich, P.B., Poorter, L., Wright, I.J., Ray, P., Enrico, L., Pausas, J.G., De Vos, A.C., Buchmann, N., Funes, G., Quétier, F., Hodgson, J.G., Thompson, K., Morgan, H.D., Ter Steege, H., Van Der Heijden, M.G.A., Sack, L., Blonder, B., Poschlod, P., Vaieretti, M. V., Conti, G., Staver, A.C., Aquino, S., Cornelissen, J.H.C., 2013. New handbook for standardised measurement of plant functional traits worldwide. *Aust. J. Bot.* 61, 167–234. <https://doi.org/10.1071/BT12225>
- Petchey, O.L., Gaston, K.J., 2006. Functional diversity: Back to basics and looking forward. *Ecol. Lett.* 9, 741–758. <https://doi.org/10.1111/j.1461-0248.2006.00924.x>
- Pilon, N.A.L., Cava, M.G.B., Hoffmann, W.A., Abreu, R.C.R., Fidelis, A., Durigan, G., 2021a. The diversity of post-fire regeneration strategies in the cerrado ground layer. *J. Ecol.* 0–2. <https://doi.org/10.1111/1365-2745.13456>
- Pilon, N.A.L., Durigan, G., Rickenback, J., Pennington, R.T., Dexter, K.G., Hoffmann, W.A., Abreu, R.C.R., Lehmann, C.E.R., 2021b. Shade alters savanna grass layer structure and function along a gradient of canopy cover. *J. Veg. Sci.* 32, 1–11. <https://doi.org/10.1111/jvs.12959>
- Pinheiro, J., Bates, D., DebRoy, S., Deepayan, S., EISPACk, authors; Heisterkamp, S., Willigen, B. Van, R-core, team, 2020. Package “nlme.”



- Pivello, V.R., 2011. The use of fire in the cerrado and Amazonian rainforests of Brazil: Past and present. *Fire Ecol.* 7, 24–39. <https://doi.org/10.4996/fireecology.0701024>
- 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 Soil* 337, 111–123. <https://doi.org/10.1007/s11104-010-0508-x>
- Poorter, H., Niklas, K.J., Reich, P.B., Oleksyn, J., Poot, P., Mommer, L., 2011. Biomass allocation to leaves, stems and roots: meta-analysis of interspecific variation and environmental control. *New Phytol.* 193, 30–50. <https://doi.org/10.1111/j.1469-8137.2011.03952.x>
- Potts, D.L., Huxman, T.E., Cable, J.M., English, N.B., Ignace, D.D., Eilts, J.A., Mason, M.J., Weltzin, J.F., Williams, D.G., 2006a. Antecedent moisture and seasonal precipitation influence the response of canopy-scale carbon and water exchange to rainfall pulses in a semi-arid grassland. *New Phytol.* 170, 849–860. <https://doi.org/10.1111/j.1469-8137.2006.01732.x>
- Potts, D.L., Huxman, T.E., Scott, R.L., Williams, D.G., Goodrich, D.C., 2006b. The sensitivity of ecosystem carbon exchange to seasonal precipitation and woody plant encroachment. *Oecologia* 150, 453–463. <https://doi.org/10.1007/s00442-006-0532-y>
- Potts, D.L., Suding, K.N., Winston, G.C., Rocha, A.V., Goulden, M.L., 2012. Ecological effects of experimental drought and prescribed fire in a southern California coastal grassland. *J. Arid Environ.* 81, 59–66. <https://doi.org/10.1016/j.jaridenv.2012.01.007>
- Pressler, Y., Moore, J.C., Cotrufo, M.F., 2019. Belowground community responses to fire: meta-analysis reveals contrasting responses of soil microorganisms and mesofauna. *Oikos* 128, 309–327. <https://doi.org/10.1111/oik.05738>
- R Development Core Team, 2020. R: a language and environment for statistical computing. <https://doi.org/ISBN 3-900051-07-0>
- Ribeiro, J.F., Walter, B.M.T., 2008. As principais fitofisionomias do bioma Cerrado, in: Sano, S.M., De Almeida, S.P., Ribeiro, J.F. (Eds.), *Cerrado: Ecologia e Flora*. Embrapa Cerrados/Embrapa Informações Tecnológica, pp. 152–212.
- Richards, A.E., Cook, G.D., Lynch, B.T., 2011. Optimal Fire Regimes for Soil Carbon Storage in Tropical Savannas of Northern Australia. *Ecosystems* 14, 503–518. <https://doi.org/10.1007/s10021-011-9428-8>
- Rissi, M.N., Baeza, M.J., Gorgone-Barbosa, E., Zupo, T., Fidelis, A., 2017. Does season affect

- fire behaviour in the Cerrado? *Int. J. Wildl. Fire* 26, 427–433. <https://doi.org/10.1071/WF14210>
- Rodrigues, C.A., Zironi, H.L., Fidelis, A., 2021. Fire frequency affects fire behavior in open savannas of the Cerrado. *For. Ecol. Manage.* 482, 118850. <https://doi.org/10.1016/j.foreco.2020.118850>
- Rogers, B.M., Balch, J.K., Goetz, S.J., Lehmann, C.E.R., Turetsky, M., 2020. Focus on changing fire regimes: interactions with climate, ecosystems, and society. *Environ. Res. Lett.* 15. <https://doi.org/10.1088/1748-9326/ab6d3a>
- Rose, L., Lobet, G., 2019. Accuracy of image analysis tools for functional root traits: A comment on Delory et al. (2017). *Methods Ecol. Evol.* 10, 702–711. <https://doi.org/10.1111/2041-210X.13156>
- Rossi, L.M.W., Mao, Z., Merino-Martín, L., Roumet, C., Fort, F., Taugourdeau, O., Boukcim, H., Fourtier, S., Del Rey-Granado, M., Chevallier, T., Cardinael, R., Fromin, N., Stokes, A., 2020. Pathways to persistence: plant root traits alter carbon accumulation in different soil carbon pools. *Plant Soil* 452, 457–478. <https://doi.org/10.1007/s11104-020-04469-5>
- Rousk, J., Bååth, E., Brookes, P.C., Lauber, C.L., Lozupone, C., Caporaso, J.G., Knight, R., Fierer, N., 2010. Soil bacterial and fungal communities across a pH gradient in an arable soil. *ISME J.* 4, 1340–1351. <https://doi.org/10.1038/ismej.2010.58>
- Santos, A.J.B., Silva, G.T.D.A., Miranda, H.S., Miranda, A.C., Lloyd, J., 2003. Effects of fire on surface carbon, energy and water vapour fluxes over campo sujo savanna in central Brazil. *Funct. Ecol.* 17, 711–719. <https://doi.org/10.1111/j.1365-2435.2003.00790.x>
- Silva, D.M., Batalha, M.A., Cianciaruso, M.V., 2013. Influence of fire history and soil properties on plant species richness and functional diversity in a neotropical savanna. *Acta Bot. Brasilica* 27, 490–497. <https://doi.org/10.1590/S0102-33062013000300005>
- Simpson, K.J., Jardine, E.C., Archibald, S., Forrestel, E.J., Lehmann, C.E.R., Thomas, G.H., Osborne, C.P., 2021. Resprouting grasses are associated with less frequent fire than seeders. *New Phytol.* 230, 832–844. <https://doi.org/10.1111/nph.17069>
- Simpson, K.J., Ripley, B.S., Christin, P.A., Belcher, C.M., Lehmann, C.E.R., Thomas, G.H., Osborne, C.P., 2016. Determinants of flammability in savanna grass species. *J. Ecol.* 104, 138–148. <https://doi.org/10.1111/1365-2745.12503>
- Torchiano, M., 2017. Package “effsize” Title Efficient Effect Size Computation.

- Valenti, M.W., Cianciaruso, M. V., Batalha, M.A., 2008. Seasonality of litterfall and leaf decomposition in a cerrado site. *Brazilian J. Biol.* 68, 459–465. <https://doi.org/10.1590/S1519-69842008000300002>
- Villéger, S., Mason, N.W.H., Mouillot, D., 2008. New Multidimensional Functional Diversity indices for a multifaceted framework in Functional Ecology. *Ecology* 89, 2290–2301. <https://doi.org/10.1890/07-1206.1>
- Vourlitis, G.L., da Rocha, H.R., 2010. Flux Dynamics in the Cerrado and Cerrado–Forest Transition of Brazil, in: Hill, M.J., Hanan, N.P. (Eds.), *Ecosystem Function in Savannas*. CRC Press. <https://doi.org/10.1201/b10275>
- Walkley, A., Black, I.A., 1934. An examination of the degtjareff method for determining soil organic matter, and a proposed modification of the chromic acid titration method. *Soil Sci.* 37, 29–38. <https://doi.org/10.1097/00010694-193401000-00003>
- Wigley, B.J., Augustine, D.J., Coetsee, C., Ratnam, J., Sankaran, M., 2020. Grasses continue to trump trees at soil carbon sequestration following herbivore exclusion in a semiarid African savanna. *Ecology* 101, 1–10. <https://doi.org/10.1002/ecy.3008>
- Wikum, D.A., Shanholtzer, G.F., 1978. Application of the Braun-Blanquet cover-abundance scale for vegetation analysis in land development studies. *Environ. Manage.* 2, 323–329. <https://doi.org/10.1007/BF01866672>
- Williams, R.J., Hutley, L.B., Cook, G.D., Russell-Smith, J., Edwards, A., Chen, X., 2004. Assessing the carbon sequestration potential of mesic savannas in the Northern Territory, Australia: Approaches, uncertainties and potential impacts of fire. *Funct. Plant Biol.* 31, 415–422. <https://doi.org/10.1071/FP03215>
- Wragg, P.D., Mielke, T., Tilman, D., 2018. Forbs, grasses, and grassland fire behaviour. *J. Ecol.* 106, 1983–2001. <https://doi.org/10.1111/1365-2745.12980>
- Yin, Y., Bloom, A.A., Worden, J., Saatchi, S., Yang, Y., Williams, M., Liu, J., Jiang, Z., Worden, H., Bowman, K., Frankenberg, C., Schimel, D., 2020. Fire decline in dry tropical ecosystems enhances decadal land carbon sink. *Nat. Commun.* 11, 1–7. <https://doi.org/10.1038/s41467-020-15852-2>
- Zhou, Y., Wigley, B.J., Case, M.F., Coetsee, C., Staver, A.C., 2020. Rooting depth as a key woody functional trait in savannas. *New Phytol.* 227, 1350–1361. <https://doi.org/10.1111/nph.16613>

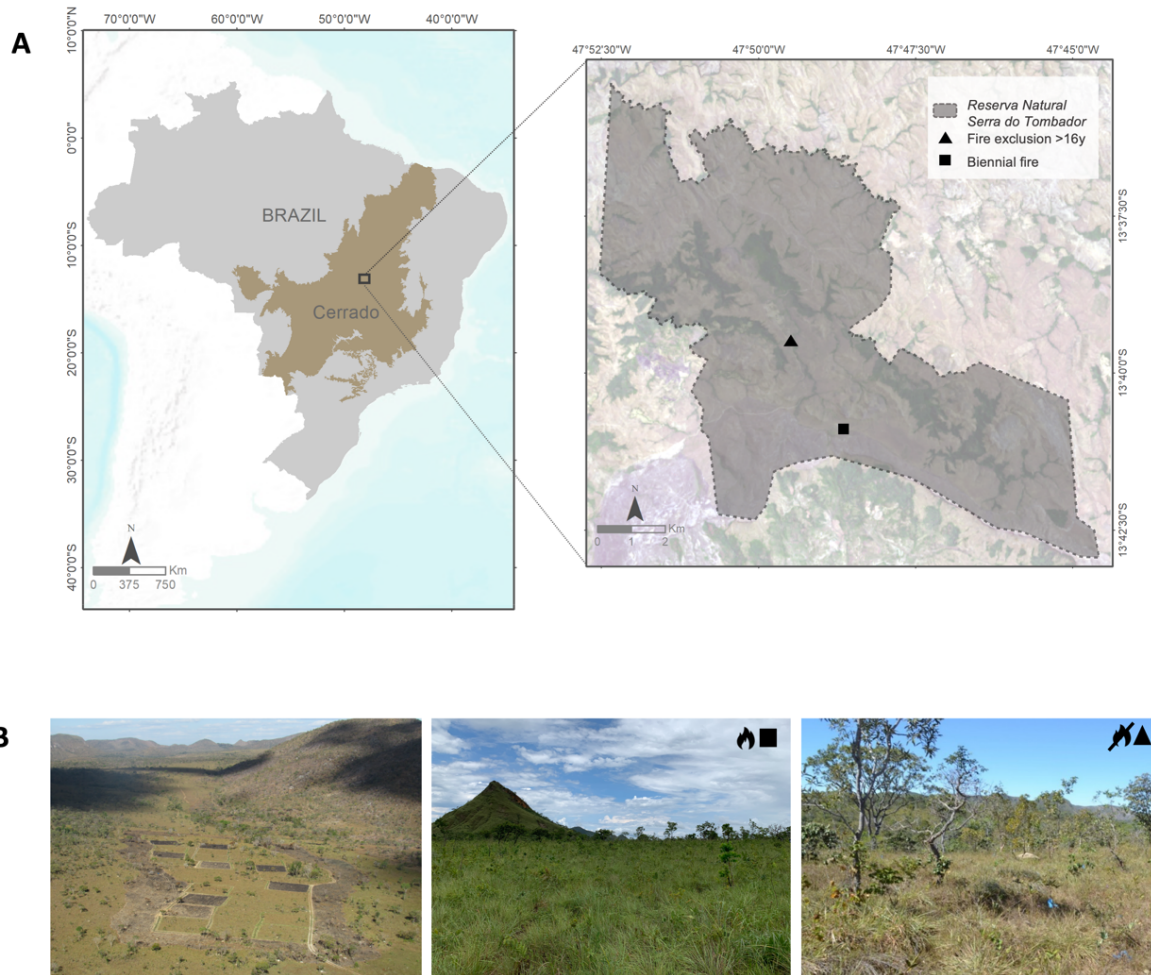
## **Material Suplementar**

Os seguintes materiais suplementares para este capítulo estão disponíveis em

<https://doi.org/10.1016/j.scitotenv.2021.152317>.

Todos os dados que suportam os achados desse estudo estão disponíveis no repositório Zenodo

(<https://doi.org/10.5281/zenodo.5796239>).



**Figure S1.** Location of the study area at (A) *Reserva Natural Serra do Tombador* (RNST; 13° 35-38' S and 47° 45'-51' W, 8900ha, 560–1118m a.s.l), a protected area of Cerrado with a mosaic of fire history. The black points represent the two fire frequencies areas studied (referred as fire treatments in this study). (B) Detail of the study area from left to right: overview of long-term fire experiment (see Rissi et al., 2007), area of the biennial fire interval treatment, and area where fire has been excluded for 16 years (fire exclusion). Background images: ©Esri, NOA and USGS.

**Table S1.** System diversity, structure and function variables (mean $\pm$ SE) measured in fire treatment and fire exclusion treatment (<16 years without fire) in open savannas, Central Brazil. FRich (functional richness); FEve (functional evenness); FDis (functional dispersion); FDp (functional diversity); CWM (community weight means).

|                                           | variables                                                                                       | Fire treatment (biennial fire) |       |        | Fire exclusion (>16y without fire) |       |       |
|-------------------------------------------|-------------------------------------------------------------------------------------------------|--------------------------------|-------|--------|------------------------------------|-------|-------|
| <b>System Diversity</b>                   | Richness                                                                                        | 16.58                          | $\pm$ | 1.09   | 13.75                              | $\pm$ | 0.93  |
|                                           | Evenness                                                                                        | 0.29                           | $\pm$ | 0.02   | 0.3                                | $\pm$ | 0.02  |
|                                           | Simpson                                                                                         | 0.78                           | $\pm$ | 0.06   | 0.77                               | $\pm$ | 0.05  |
|                                           | FRich                                                                                           | 4.29                           | $\pm$ | 1.68   | 119.42                             | $\pm$ | 1.79  |
|                                           | FEve                                                                                            | 0.74                           | $\pm$ | 0.02   | 98.30                              | $\pm$ | 0.03  |
|                                           | FDis                                                                                            | 3.09                           | $\pm$ | 0.06   | 512.94                             | $\pm$ | 0.15  |
|                                           | FDp                                                                                             | 118.54                         | $\pm$ | 4.48   | 272.51                             | $\pm$ | 2.60  |
|                                           | CWM                                                                                             | -8.12E-18                      | $\pm$ | 0.13   | 12.06                              | $\pm$ | 0.16  |
| <b>System Structure (g.m<sup>2</sup>)</b> | Aboveground biomass                                                                             | 693.91                         | $\pm$ | 50.63  | 225.15                             | $\pm$ | 55.40 |
|                                           | Live aboveground biomass                                                                        | 267.12                         | $\pm$ | 26.38  | 43.57                              | $\pm$ | 17.23 |
|                                           | Dead aboveground biomass                                                                        | 106.70                         | $\pm$ | 7.23   | 2.81                               | $\pm$ | 10.43 |
|                                           | Belowground biomass                                                                             | 1540.73                        | $\pm$ | 268.76 | 10.67                              | $\pm$ | 68.01 |
|                                           | Beloworgans biomass                                                                             | 1328.58                        | $\pm$ | 247.04 | 112.63                             | $\pm$ | 65.02 |
|                                           | Coarse roots biomass                                                                            | 200.26                         | $\pm$ | 36.79  | -2.92                              | $\pm$ | 9.39  |
|                                           | Fine roots biomass                                                                              | 37.92                          | $\pm$ | 1.80   | 14.74                              | $\pm$ | 1.18  |
|                                           | Aboveground: belowground biomass                                                                | 1.04                           | $\pm$ | 0.22   | 6.11                               | $\pm$ | 0.33  |
|                                           | Live aboveground: fine roots biomass                                                            | 7.10                           | $\pm$ | 0.63   | 0.58                               | $\pm$ | 1.69  |
|                                           | Litter                                                                                          | 82.81                          | $\pm$ | 7.24   | 6.67                               | $\pm$ | 14.84 |
| <b>System Function</b>                    | total SOC (g.kg <sup>-1</sup> )                                                                 | 9.57                           | $\pm$ | 0.40   | 7.45                               | $\pm$ | 0.31  |
|                                           | NEE ( $\mu$ mol CO <sub>2</sub> m <sup>-2</sup> s <sup>-1</sup> )                               | -6.38                          | $\pm$ | 0.85   | 0.67                               | $\pm$ | 0.49  |
|                                           | ET ( $\mu$ mol H <sub>2</sub> O m <sup>-2</sup> s <sup>-1</sup> )                               | 0.86                           | $\pm$ | 1.03   | 2.41                               | $\pm$ | 0.89  |
|                                           | eWUE ( $\mu$ mol CO <sub>2</sub> / $\mu$ mol H <sub>2</sub> O m <sup>-2</sup> s <sup>-1</sup> ) | 8.00                           | $\pm$ | 0.09   | 30.85                              | $\pm$ | 0.03  |
|                                           | Soil respiration ( $\mu$ mol CO <sub>2</sub> m <sup>-2</sup> s <sup>-1</sup> )                  | 4.84                           | $\pm$ | 0.38   | 1.33E-17                           | $\pm$ | 1.87  |

**Table S2.** Effect size results based on Cohen's D index to quantify the effect of fire treatment on system diversity, structure and function in an open savanna, in Central Brazil.

| variables                            | Cohen's D  | CI lower   | CI upper   | SD         |
|--------------------------------------|------------|------------|------------|------------|
| Richness                             | 0.5293555  | -0.2978205 | 1.3565315  | 1.654352   |
| Evenness                             | -0.087777  | -0.9510305 | 0.7754765  | 1.726507   |
| Simpson                              | 0.03319599 | -0.9131489 | 0.846757   | 1.7599059  |
| Frich                                | -0.3460599 | -1.098266  | 0.406146   | 1.504412   |
| Feve                                 | 0.5953125  | -0.430584  | 1.621209   | 2.051793   |
| Fdisp                                | 1.089364   | 0.2848826  | 1.8938444  | 1.6089618  |
| FDp                                  | 4.42356    | 2.262681   | 6.584439   | 4.321758   |
| CWM                                  | -2.79E-17  | -0.7230904 | 0.7230904  | 1.4461808  |
| Aboveground biomass                  | 0.6478866  | -0.3679516 | 1.6637248  | 2.0316764  |
| Live aboveground biomass             | 1.275474   | 0.00279674 | 2.54815114 | 2.54535441 |
| Dead aboveground biomass             | 0.1794174  | -0.7625196 | 1.1213544  | 1.883874   |
| Belowground biomass                  | 1.254199   | 0.1581665  | 2.3502319  | 2.1920654  |
| Below organs                         | 1.18302    | 0.1147422  | 2.2512978  | 2.1365556  |
| Coarse roots                         | 1.166974   | 0.03329725 | 2.30065085 | 2.2673536  |
| Fine roots                           | 3.231905   | 1.254677   | 5.209132   | 3.954455   |
| Aboveground: Belowground biomass     | -1.199825  | -2.2005595 | -0.1990907 | 2.0014688  |
| Live aboveground: fine roots biomass | -0.5766852 | -1.6909549 | 0.5375845  | 2.2285394  |
| Litter biomass                       | -0.5062618 | -1.5736228 | 0.5610992  | 2.134722   |
| Total SOC                            | 1.53999    | 0.57441    | 2.50557    | 1.93116    |
| NEE                                  | 0.9297844  | 0.06505173 | 1.794517   | 1.72946527 |
| ET                                   | 0.81601    | -0.20452   | 1.83654    | 2.04106    |
| eWUE                                 | 0.37232    | -0.43385   | 1.17848    | 1.61233    |
| Soil respiration                     | -1.36367   | -2.41888   | -0.30847   | 2.11041    |

**Table S3.** Piecewise structural equation models (SEM) coefficients results.

| model              | Response              | Predictor                            | Estimate | Std.Error | DF | Crit.Value | p-value      |   | Std.Estimate | estimate<br>emmeans | t-value<br>(means<br>std.estimate) | p-value<br>emmeans |
|--------------------|-----------------------|--------------------------------------|----------|-----------|----|------------|--------------|---|--------------|---------------------|------------------------------------|--------------------|
| Fine-roots biomass | SOC                   | fine roots                           | -0.1175  | 0.0968    | 9  | -1.214     | 0.2556       |   | -0.2986      |                     |                                    |                    |
|                    | SOC                   | treatment                            | -        | -         | 1  | 18.0617    | 0 ***        | - |              | <b>0.609</b>        | 4.25                               | 0.0021***          |
|                    | SOC                   | treatment = fire<br>treatment = excl | 2.3898   | 0.0993    | 9  | 24.0652    | 0.00E+00 *** | - |              | 2.37                |                                    |                    |
|                    | SOC                   | fire                                 | 1.7811   | 0.0871    | 9  | 20.4455    | 0 ***        | - |              | 1.79                |                                    |                    |
|                    | fine roots<br>biomass | FDp                                  | -0.1945  | 0.2142    | 9  | -0.9083    | 0.3874       |   | -0.2195      |                     |                                    |                    |
|                    | fine roots<br>biomass | treatment                            | -        | -         | 1  | 19.1254    | 0 ***        | - |              | <b>1.5</b>          | 4.373                              | 0.0018***          |
|                    | fine roots<br>biomass | treatment = fire<br>treatment = excl | 3.7483   | 0.1877    | 9  | 19.9659    | 0 ***        | - |              | 3.75                |                                    |                    |
|                    | fine roots<br>biomass | fire                                 | 2.2512   | 0.1877    | 9  | 11.991     | 0 ***        | - |              | 2.75                |                                    |                    |
|                    | NEE                   | fine roots                           | -0.0443  | 0.5081    | 6  | -0.0871    | 0.9334       |   | -0.0394      |                     |                                    |                    |
|                    | NEE                   | FDp                                  | 0.3351   | 0.4744    | 6  | 0.7064     | 0.5065       |   | 0.3365       |                     |                                    |                    |
|                    | NEE                   | SOC                                  | -0.5046  | 0.8437    | 6  | -0.5981    | 0.5716       |   | -0.1767      |                     |                                    |                    |
|                    | NEE                   | soil respiration                     | -0.1336  | 0.3901    | 6  | -0.3425    | 0.7437       |   | -0.1166      |                     |                                    |                    |
|                    | NEE                   | treatment                            | -        | -         | 1  | 0.0935     | 0.7597       | - |              | 0.326               | 0.306                              | 0.7717             |
|                    | NEE                   | treatment = fire<br>treatment = excl | 1.4377   | 0.5571    | 6  | 2.5808     | 0.0417 *     | - |              |                     |                                    |                    |
|                    | NEE                   | fire                                 | 1.1122   | 0.5571    | 6  | 1.9965     | 0.0929       | - |              |                     |                                    |                    |
|                    | soil respiration      | fine roots                           | -0.4675  | 0.2685    | 8  | -1.741     | 0.1199       |   | -0.4766      |                     |                                    |                    |
|                    | soil respiration      | SOC                                  | -0.4735  | 0.4675    | 8  | -1.0127    | 0.3408       |   | -0.1899      |                     |                                    |                    |
|                    | soil respiration      | treatment                            | -        | -         | 1  | 0.4562     | 0.4994       | - |              | -0.301              | -0.675                             | 0.5184             |
|                    | soil respiration      | treatment = fire<br>treatment = excl | 1.8765   | 0.244     | 8  | 7.6915     | 1.00E-04 *** | - |              | 1.88                |                                    |                    |
|                    | soil respiration      | fire                                 | 2.1779   | 0.2422    | 8  | 8.9917     | 0 ***        | - |              | 2.18                |                                    |                    |



Continue Table S3...

| model                    | Response                       | Predictor                   | Estimate | Std.Error | DF | Crit.Value | p-value      | Std.Estimate | estimate<br>emmeans | t-value<br>(means<br>std.estimate) | p-value<br>emmeans |
|--------------------------|--------------------------------|-----------------------------|----------|-----------|----|------------|--------------|--------------|---------------------|------------------------------------|--------------------|
| Fine roots<br>biomass    | FDp                            | treatment                   | -        | -         | 1  | 102.67     | 0 ***        | -            | <b>1.35</b>         | 10.13                              | <0.0001***         |
|                          | FDp                            | treatment = fire            | 4.6808   | 0.1558    | 12 | 30.0446    | 0 ***        | -            | 4.68                |                                    |                    |
|                          | FDp                            | treatment = excl<br>fire    | 3.3326   | 0.1288    | 10 | 25.8817    | 0 ***        | -            | 3.33                |                                    |                    |
| Live aboveground biomass | SOC                            | liveabove                   | -0.0234  | 0.0425    | 9  | -0.5518    | 0.5945       | -0.1006      |                     |                                    |                    |
|                          | SOC                            | treatment                   | -        | -         | 1  | 26.5304    | 0 ***        | -            | <b>0.492</b>        | 5.151                              | 0.0062***          |
|                          | SOC                            | treatment = fire            | 2.3314   | 0.0854    | 9  | 27.3032    | 0.00E+00 *** | -            | 2.33                |                                    |                    |
|                          | SOC                            | treatment = excl<br>fire    | 1.8396   | 0.07      | 9  | 26.2815    | 0 ***        | -            | 1.84                |                                    |                    |
|                          | live<br>aboveground<br>biomass | FD.branch                   | 0.217    | 0.5776    | 9  | 0.3756     | 0.7159       | 0.1448       |                     |                                    |                    |
|                          | live<br>aboveground<br>biomass | treatment                   | -        | -         | 1  | 0.7424     | 0.3889       | -            | 0.722               | 0.862                              | 0.4112             |
|                          | live<br>aboveground<br>biomass | treatment = fire            | 5.2066   | 0.5816    | 9  | 8.9516     | 0 ***        | -            | 5.21                |                                    |                    |
|                          | live<br>aboveground<br>biomass | treatment = excl<br>fire    | 4.4848   | 0.5732    | 9  | 7.8242     | 0 ***        | -            | 4.48                |                                    |                    |
|                          | live aboveground<br>biomass    | live aboveground<br>biomass | 0.0876   | 0.1597    | 6  | 0.5483     | 0.6033       | 0.1317       |                     |                                    |                    |
|                          | NEE                            | FDp                         | 0.3437   | 0.4668    | 6  | 0.7363     | 0.4893       | 0.3451       |                     |                                    |                    |
|                          | NEE                            | SOC                         | -0.4485  | 0.8104    | 6  | -0.5535    | 0.6          | -0.1571      |                     |                                    |                    |
|                          | NEE                            | soil respiration            | -0.0802  | 0.3701    | 6  | -0.2167    | 0.8356       | -0.07        |                     |                                    |                    |
|                          | NEE                            | treatment                   | -        | -         | 1  | 0.0513     | 0.8208       | -            | 0.372               | 0.514                              | 0.6256             |
|                          | NEE                            | treatment = fire            | 1.3715   | 0.4564    | 6  | 3.0053     | 0.0238 *     | -            |                     |                                    |                    |
|                          | NEE                            | treatment = excl<br>fire    | 1.1785   | 0.4564    | 6  | 2.5823     | 0.0416 *     | -            |                     |                                    |                    |

Continue Table S3...

| model                    | Response            | Predictor                | Estimate | Std.Error | DF | Crit.Value | p-value  |     | Std.Estimate | estimate<br>emmeans | t-value<br>(means<br>std.estimate) | p-value<br>emmeans |
|--------------------------|---------------------|--------------------------|----------|-----------|----|------------|----------|-----|--------------|---------------------|------------------------------------|--------------------|
| Live aboveground biomass | soil respiration    | live aboveground biomass | -0.0894  | 0.0948    | 8  | -0.9435    | 0.373    |     | -0.1542      |                     |                                    |                    |
|                          | soil respiration    | SOC                      | -0.3342  | 0.4737    | 8  | -0.7055    | 0.5005   |     | -0.1341      |                     |                                    |                    |
|                          | soil respiration    | treatment                | -        | -         | 1  | 7.9917     | 0.0047   | **  | -            | <b>-0.819</b>       | -2.827                             | 0.0223***          |
|                          | soil respiration    | treatment = fire         | 1.6186   | 0.1755    | 8  | 9.2233     | 0        | *** | -            | 1.56                |                                    |                    |
|                          | soil respiration    | treatment = excl         | 2.4372   | 0.1755    | 8  | 13.8879    | 0.00E+00 | *** | -            | 2.5                 |                                    |                    |
|                          | soil respiration    | fire                     |          |           |    |            |          |     |              |                     |                                    |                    |
|                          | FDp                 | treatment                | -        | -         | 1  | 102.67     | 0        | *** | -            | <b>1.35</b>         | 10.13                              | <0.0001***         |
|                          | FDp                 | treatment = fire         | 4.6808   | 0.1558    | 12 | 30.0446    | 0        | *** | -            | 4.68                |                                    |                    |
|                          | FDp                 | treatment = excl         |          |           |    |            |          |     |              |                     |                                    |                    |
|                          | FDp                 | fire                     | 3.3326   | 0.1288    | 10 | 25.8817    | 0        | *** | -            | 3.33                |                                    |                    |
| Belowground biomass      | SOC                 | beloworgans biomass      | -0.0058  | 0.0384    | 9  | -0.1508    | 0.8835   |     | -0.0266      |                     |                                    |                    |
|                          | SOC                 | treatment                | -        | -         | 1  | 18.6644    | 0        | *** | -            | <b>0.469</b>        | 4.32                               | 0.0019***          |
|                          | SOC                 | treatment = fire         | 2.318    | 0.089     | 9  | 26.049     | 0.00E+00 | *** | -            | 2.32                |                                    |                    |
|                          | SOC                 | treatment = excl         |          |           |    |            |          |     |              |                     |                                    |                    |
|                          | SOC                 | fire                     | 1.8493   | 0.0727    | 9  | 25.4198    | 0        | *** | -            | 1.85                |                                    |                    |
|                          | beloworgans biomass | FDp                      | 0.0321   | 0.6042    | 9  | 0.0532     | 0.9588   |     | 0.0201       |                     |                                    |                    |
|                          | beloworgans biomass | treatment                | -        | -         | 1  | 2.6299     | 0.1049   |     | -            | <b>1.57</b>         | 1.622                              | 0.013***           |
|                          | beloworgans biomass | treatment = fire         | 6.603    | 0.5347    | 9  | 12.3498    | 0        | *** | -            | 6.6                 |                                    |                    |
|                          | beloworgans biomass | treatment = excl         |          |           |    |            |          |     |              |                     |                                    |                    |
|                          | beloworgans biomass | fire                     | 5.0377   | 0.5303    | 9  | 9.5003     | 0        | *** | -            | 5.04                |                                    |                    |

Continue Table S3...

| model                | Response                | Predictor                | Estimate | Std.Error | DF | Crit.Value | p-value      |   | Std.Estimate | estimate<br>emmeans | t-value<br>(means<br>std.estimate) | p-value<br>emmeans |
|----------------------|-------------------------|--------------------------|----------|-----------|----|------------|--------------|---|--------------|---------------------|------------------------------------|--------------------|
| Coarse roots biomass | SOC                     | treatment = excl<br>fire | 1.822    | 0.0759    | 9  | 24.0036    | 0 ***        | - |              | 1.82                |                                    |                    |
|                      | coarse roots<br>biomass | FDp                      | 0.7753   | 0.6767    | 9  | 1.1456     | 0.2815       |   | 0.429        |                     |                                    |                    |
|                      | coarse roots<br>biomass | treatment                | -        | -         | 1  | 0.2628     | 0.6082       | - |              | 0.54                | 0.513                              | 0.6205             |
|                      | coarse roots<br>biomass | treatment = fire         | 4.2033   | 0.6402    | 9  | 6.566      | 0.0001 ***   | - |              | 6.6                 |                                    |                    |
|                      | coarse roots<br>biomass | treatment = excl<br>fire | 3.663    | 0.604     | 9  | 6.0647     | 0.0002 ***   | - |              | 5.04                |                                    |                    |
|                      | NEE                     | coarse roots             | 0.008    | 0.1466    | 6  | 0.0549     | 0.958        |   | 0.0146       |                     |                                    |                    |
|                      | NEE                     | FDp                      | 0.3342   | 0.4838    | 6  | 0.6907     | 0.5155       |   | 0.3356       |                     |                                    |                    |
|                      | NEE                     | SOC                      | -0.4892  | 0.8173    | 6  | -0.5986    | 0.5714       |   | -0.1713      |                     |                                    |                    |
|                      | NEE                     | soil respiration         | -0.1212  | 0.3654    | 6  | -0.3316    | 0.7514       |   | -0.1058      |                     |                                    |                    |
|                      | NEE                     | treatment                | -        | -         | 1  | 0.0984     | 0.7538       | - |              | 0.266               | 0.314                              | 0.7644             |
|                      | NEE                     | treatment = fire         | 1.4082   | 0.4555    | 6  | 3.0913     | 0.0214 *     | - |              |                     |                                    |                    |
|                      | NEE                     | treatment = excl<br>fire | 1.1418   | 0.4555    | 6  | 2.5064     | 0.0461 *     | - |              |                     |                                    |                    |
|                      | soil<br>respiration     | coarse roots<br>biomass  | -0.0003  | 0.0877    | 8  | -0.0038    | 0.9971       |   | -0.0007      |                     |                                    |                    |
|                      | soil<br>respiration     | SOC                      | -0.3081  | 0.4881    | 8  | -0.6313    | 0.5454       |   | -0.1236      |                     |                                    |                    |
|                      | soil<br>respiration     | treatment                | -        | -         | 1  | 9.8532     | 0.0017 **    | - |              | <b>-0.931</b>       | -3.139                             | 0.0138***          |
|                      | soil<br>respiration     | treatment = fire         | 1.5623   | 0.1797    | 8  | 8.6964     | 0.00E+00 *** | - |              | 1.56                |                                    |                    |
|                      | soil<br>respiration     | treatment = excl<br>fire | 2.4935   | 0.1797    | 8  | 13.8798    | 0 ***        | - |              | 2.49                |                                    |                    |
|                      | FDp                     | treatment                | -        | -         | 1  | 102.67     | 0 ***        | - |              | <b>1.35</b>         | 10.13                              | <0.0001***         |
|                      | FDp                     | treatment = fire         | 4.6808   | 0.1558    | 12 | 30.0446    | 0 ***        | - |              | 4.68                |                                    |                    |
|                      | FDp                     | treatment = excl<br>fire | 3.3326   | 0.1288    | 10 | 25.8817    | 0 ***        | - |              | 3.33                |                                    |                    |

**Table S4.** Species list sampled in this study in both fire treatment areas (fire and fire exclusion) at the *Reserva Natural Serra do Tombador* (RNST).

| Site                          | Cerrado<br>phytophysognomy | Family         | Species                                                    |
|-------------------------------|----------------------------|----------------|------------------------------------------------------------|
| Serra do Tombador (GO,Brazil) | Campo sujo                 | Acanthaceae    | <i>Justicia lanstykii</i> Rizzini                          |
| Serra do Tombador (GO,Brazil) | Campo sujo                 | Acanthaceae    | <i>Ruellia angustifolia</i> (Nees) Lindau                  |
| Serra do Tombador (GO,Brazil) | Campo sujo                 | Acanthaceae    | <i>Ruellia nitens</i> (Nees) Wassh.                        |
| Serra do Tombador (GO,Brazil) | Campo sujo                 | Annonaceae     | <i>Annona tomentosa</i> R.E.Fr.                            |
| Serra do Tombador (GO,Brazil) | Campo sujo                 | Apocynaceae    | <i>Aspidosperma</i> sp1.                                   |
| Serra do Tombador (GO,Brazil) | Campo sujo                 | Apocynaceae    | <i>Hemipogon acerosus</i> Decne.                           |
| Serra do Tombador (GO,Brazil) | Campo sujo                 | Arecaceae      | <i>Syagrus</i> sp.                                         |
| Serra do Tombador (GO,Brazil) | Campo sujo                 | Asteraceae     | <i>Aldama grandiflora</i> (Gardner) E.E. Schill & Panero   |
| Serra do Tombador (GO,Brazil) | Campo sujo                 | Asteraceae     | <i>Ayapana amygdalina</i> (Lam.) R.M.King & H.Rob.         |
| Serra do Tombador (GO,Brazil) | Campo sujo                 | Asteraceae     | <i>Ichthyothere hirsuta</i> Gardner                        |
| Serra do Tombador (GO,Brazil) | Campo sujo                 | Bignoniaceae   | <i>Anemopaegma arvense</i> (Vell.) Stellfeld ex de Souza   |
| Serra do Tombador (GO,Brazil) | Campo sujo                 | Calophyllaceae | <i>Kielmeyera</i> sp.                                      |
| Serra do Tombador (GO,Brazil) | Campo sujo                 | Calophyllaceae | <i>Kielmeyera abdita</i> Saddi                             |
| Serra do Tombador (GO,Brazil) | Campo sujo                 | Calophyllaceae | <i>Kielmeyera rubriflora</i> Cambess var. major            |
| Serra do Tombador (GO,Brazil) | Campo sujo                 | Connaraceae    | <i>Connarus suberosus</i> Planch.                          |
| Serra do Tombador (GO,Brazil) | Campo sujo                 | Convolvulaceae | <i>Ipomoea echicoides</i> Choisy                           |
| Serra do Tombador (GO,Brazil) | Campo sujo                 | Cyperaceae     | <i>Bulbostylis</i> sp.                                     |
| Serra do Tombador (GO,Brazil) | Campo sujo                 | Cyperaceae     | <i>Bulbostylis paradoxa</i> (Spreng.) Lindm.               |
| Serra do Tombador (GO,Brazil) | Campo sujo                 | Cyperaceae     | Morfotype 2                                                |
| Serra do Tombador (GO,Brazil) | Campo sujo                 | Cyperaceae     | <i>Rhynchospora consanguinea</i> (Kunth) Boeckeler         |
| Serra do Tombador (GO,Brazil) | Campo sujo                 | Cyperaceae     | <i>Rhynchospora globosa</i> (Kunth) Roem. & Schult.        |
| Serra do Tombador (GO,Brazil) | Campo sujo                 | Cyperaceae     | <i>Rhynchospora hirta</i> (Nees) Boeckeler                 |
| Serra do Tombador (GO,Brazil) | Campo sujo                 | Euphorbiaceae  | <i>Bernardia hirsutissima</i> (Baill.) Müll.Arg.           |
| Serra do Tombador (GO,Brazil) | Campo sujo                 | Euphorbiaceae  | <i>Croton antisyphiliticus</i> Mart.                       |
| Serra do Tombador (GO,Brazil) | Campo sujo                 | Euphorbiaceae  | <i>Croton gracilescens</i> Müll.Arg.                       |
| Serra do Tombador (GO,Brazil) | Campo sujo                 | Euphorbiaceae  | <i>Euphorbia potentilloides</i> Boiss.                     |
| Serra do Tombador (GO,Brazil) | Campo sujo                 | Euphorbiaceae  | <i>Euphorbia</i> sp.                                       |
| Serra do Tombador (GO,Brazil) | Campo sujo                 | Euphorbiaceae  | <i>Manihot kalungae</i> M.J. Silva & R.C. Sodrê            |
| Serra do Tombador (GO,Brazil) | Campo sujo                 | Fabaceae       | <i>Bauhinia dumosa</i> Benth.                              |
| Serra do Tombador (GO,Brazil) | Campo sujo                 | Fabaceae       | <i>Chamaecrista clausenii</i> (Benth.) H.S.Irwin & Barneby |
| Serra do Tombador (GO,Brazil) | Campo sujo                 | Fabaceae       | <i>Mimosa pteridifolia</i> Benth.                          |
| Serra do Tombador (GO,Brazil) | Campo sujo                 | Fabaceae       | <i>Aeschynomene</i> sp.                                    |
| Serra do Tombador (GO,Brazil) | Campo sujo                 | Fabaceae       | <i>Calliandra dysantha</i> Benth.                          |
| Serra do Tombador (GO,Brazil) | Campo sujo                 | Fabaceae       | <i>Chamaecrista isidorea</i> (Benth.) H.S.Irwin & Barneby  |
| Serra do Tombador (GO,Brazil) | Campo sujo                 | Fabaceae       | <i>Chamaecrista ochrosperma</i> (H.S.Irwin & Barneby)      |
| Serra do Tombador (GO,Brazil) | Campo sujo                 | Fabaceae       | H.S.Irwin & Barneby                                        |
| Serra do Tombador (GO,Brazil) | Campo sujo                 | Fabaceae       | <i>Eriosema congestum</i> Benth.                           |
| Serra do Tombador (GO,Brazil) | Campo sujo                 | Fabaceae       | <i>Galactia</i> sp.                                        |
| Serra do Tombador (GO,Brazil) | Campo sujo                 | Fabaceae       | <i>Harpalyce brasiliiana</i> Benth.                        |
| Serra do Tombador (GO,Brazil) | Campo sujo                 | Fabaceae       | <i>Mimosa flavocaesia</i> Barneby                          |
| Serra do Tombador (GO,Brazil) | Campo sujo                 | Fabaceae       | <i>Mimosa gracilis</i> Benth.                              |

Continue Table S4...

| Site                          | Cerrado<br>phytophysiognomy | Family          | Species                                                                      |
|-------------------------------|-----------------------------|-----------------|------------------------------------------------------------------------------|
| Serra do Tombador (GO,Brazil) | Campo sujo                  | Fabaceae        | <i>Mimosa leioccephala</i> Benth.                                            |
| Serra do Tombador (GO,Brazil) | Campo sujo                  | Fabaceae        | <i>Senna corifolia</i> (Benth.) H.S.Irwin & Barneby var.<br><i>corifolia</i> |
| Serra do Tombador (GO,Brazil) | Campo sujo                  | Fabaceae        | <i>Stylosanthes</i> sp.                                                      |
| Serra do Tombador (GO,Brazil) | Campo sujo                  | Gentianaceae    | <i>Calolisianthus</i> sp.                                                    |
| Serra do Tombador (GO,Brazil) | Campo sujo                  | Iridaceae       | <i>Trymezia</i> sp.                                                          |
| Serra do Tombador (GO,Brazil) | Campo sujo                  | Iridaceae       | <i>Trimezia juncifolia</i> (Klatt) Benth. & Hook.f                           |
| Serra do Tombador (GO,Brazil) | Campo sujo                  | Iridaceae       | <i>Cipura xanthomelas</i> Klatt                                              |
| Serra do Tombador (GO,Brazil) | Campo sujo                  | Lamiaceae       | <i>Eriope glandulosa</i> (Harley) Harley                                     |
| Serra do Tombador (GO,Brazil) | Campo sujo                  | Lamiaceae       | <i>Medusantha mollissima</i> (Benth.) Harley & J.F.B.Pastore                 |
| Serra do Tombador (GO,Brazil) | Campo sujo                  | Lamiaceae       | <i>Gymneia chapadensis</i> Harley                                            |
| Serra do Tombador (GO,Brazil) | Campo sujo                  | Lamiaceae       | <i>Hypenia</i> sp.                                                           |
| Serra do Tombador (GO,Brazil) | Campo sujo                  | Lamiaceae       | <i>Hyptis remota</i> Pohl ex Benth.                                          |
| Serra do Tombador (GO,Brazil) | Campo sujo                  | Lamiaceae       | <i>Hyptis</i> sp.                                                            |
| Serra do Tombador (GO,Brazil) | Campo sujo                  | Lythraceae      | <i>Cuphea ericoides</i> Cham. & Schltdl.                                     |
| Serra do Tombador (GO,Brazil) | Campo sujo                  | Lythraceae      | <i>Diplusodon punctatus</i> Pohl                                             |
| Serra do Tombador (GO,Brazil) | Campo sujo                  | Malpighiaceae   | <i>Banisteriopsis pannosa</i> Griseb.                                        |
| Serra do Tombador (GO,Brazil) | Campo sujo                  | Malpighiaceae   | <i>Heteropterys campestris</i> A. Juss.                                      |
| Serra do Tombador (GO,Brazil) | Campo sujo                  | Malvaceae       | <i>Byttneria jaculifolia</i> Pohl                                            |
| Serra do Tombador (GO,Brazil) | Campo sujo                  | Malvaceae       | <i>Pavonia grandiflora</i> A.St.-Hil.                                        |
| Serra do Tombador (GO,Brazil) | Campo sujo                  | Melastomataceae | <i>Tibouchina</i> sp.                                                        |
| Serra do Tombador (GO,Brazil) | Campo sujo                  | Melastomataceae | <i>Miconia albicans</i> (Sw.) Triana                                         |
| Serra do Tombador (GO,Brazil) | Campo sujo                  | Melastomataceae | <i>Miconia</i> sp                                                            |
| Serra do Tombador (GO,Brazil) | Campo sujo                  | Melastomataceae | <i>Tibouchina melastomoides</i> (Naudin) Cogn.                               |
| Serra do Tombador (GO,Brazil) | Campo sujo                  | Moraceae        | <i>Brosimum gaudichaudii</i> Trécul                                          |
| Serra do Tombador (GO,Brazil) | Campo sujo                  | Morfotype       | Morfotype 4.                                                                 |
| Serra do Tombador (GO,Brazil) | Campo sujo                  | Myrtaceae       | <i>Eugenia paracatuana</i> O.Berg                                            |
| Serra do Tombador (GO,Brazil) | Campo sujo                  | Myrtaceae       | <i>Myrcia lauruoteana</i> Cabess.                                            |
| Serra do Tombador (GO,Brazil) | Campo sujo                  | Myrtaceae       | <i>Myrcia</i> sp1                                                            |
| Serra do Tombador (GO,Brazil) | Campo sujo                  | Myrtaceae       | <i>Myrcia</i> sp2                                                            |
| Serra do Tombador (GO,Brazil) | Campo sujo                  | Ochnaceae       | <i>Ouratea lanceolata</i> (Pohl) Engl.                                       |
| Serra do Tombador (GO,Brazil) | Campo sujo                  | Oxalidaceae     | <i>Oxalis goyazensis</i> Turcz.                                              |
| Serra do Tombador (GO,Brazil) | Campo sujo                  | Poacea          | <i>Oncorachis ramosa</i> (Zuloaga & Soderstr.) Morrone &<br><i>Zuloaga</i>   |
| Serra do Tombador (GO,Brazil) | Campo sujo                  | Poacea          | Morfotype 5                                                                  |
| Serra do Tombador (GO,Brazil) | Campo sujo                  | Poacea          | <i>Schizachyrium consaguineum</i> Stapf                                      |
| Serra do Tombador (GO,Brazil) | Campo sujo                  | Poaceae         | <i>Anthaenantia lanata</i> (Kunth) Benth.                                    |
| Serra do Tombador (GO,Brazil) | Campo sujo                  | Poaceae         | <i>Aristida</i> sp.                                                          |
| Serra do Tombador (GO,Brazil) | Campo sujo                  | Poaceae         | <i>Aristida setifolia</i> Kunth                                              |
| Serra do Tombador (GO,Brazil) | Campo sujo                  | Poaceae         | <i>Axonopus aureus</i> P. Beauv.                                             |
| Serra do Tombador (GO,Brazil) | Campo sujo                  | Poaceae         | <i>Axonopus</i> sp1.                                                         |
| Serra do Tombador (GO,Brazil) | Campo sujo                  | Poaceae         | <i>Elionurus muticus</i> (Spreng.) Kuntze                                    |
| Serra do Tombador (GO,Brazil) | Campo sujo                  | Poaceae         | <i>Trichantecium</i> sp.                                                     |
| Serra do Tombador (GO,Brazil) | Campo sujo                  | Poaceae         | Morfotype 3                                                                  |
| Serra do Tombador (GO,Brazil) | Campo sujo                  | Poaceae         | <i>Andropogon villosus</i> (nees) Ekman                                      |

Continue Table S4...

| Site                          | Cerrado<br>phytophysiognomy | Family        | Species                                                          |
|-------------------------------|-----------------------------|---------------|------------------------------------------------------------------|
| Serra do Tombador (GO,Brazil) | Campo sujo                  | Poaceae       | <i>Trichantheum cyanescens</i> (Nees ex Trin.) Zuloaga & Morrone |
| Serra do Tombador (GO,Brazil) | Campo sujo                  | Poaceae       | <i>Mesosetum ferrugineum</i> (Trin.) Chase                       |
| Serra do Tombador (GO,Brazil) | Campo sujo                  | Poaceae       | <i>Paspalum pectinatum</i> Nees ex Trin.                         |
| Serra do Tombador (GO,Brazil) | Campo sujo                  | Poaceae       | <i>Trachypogon spicatus</i> (L.f.) Kuntze                        |
| Serra do Tombador (GO,Brazil) | Campo sujo                  | (Trin.) Chase | <i>Mesosetum loliforme</i>                                       |
| Serra do Tombador (GO,Brazil) | Campo sujo                  | Rhamnaceae    | <i>Crumenaria choretroides</i> Mart. ex Reissek                  |
| Serra do Tombador (GO,Brazil) | Campo sujo                  | Rubiaceae     | Morfotype 1                                                      |
| Serra do Tombador (GO,Brazil) | Campo sujo                  | Rubiaceae     | <i>Borreria poaya</i> (A.St.-Hil.) DC.                           |
| Serra do Tombador (GO,Brazil) | Campo sujo                  | Rubiaceae     | <i>Spermacoce tenella</i> Kunth                                  |
| Serra do Tombador (GO,Brazil) | Campo sujo                  | Rubiaceae     | <i>Declieuxia lancifolia</i> J.H.Kirkbr.                         |
| Serra do Tombador (GO,Brazil) | Campo sujo                  | Salicaceae    | <i>Casearia sylvestris</i> Sw.                                   |
| Serra do Tombador (GO,Brazil) | Campo sujo                  | Turnecaceae   | <i>Turnera incana</i> Cambess.                                   |
| Serra do Tombador (GO,Brazil) | Campo sujo                  | Velloziaceae  | <i>Vellozia squamata</i> Pohl                                    |
| Serra do Tombador (GO,Brazil) | Campo sujo                  | Verbenaceae   | <i>Lippia grandiflora</i> Mart. & Schauer                        |
| Serra do Tombador (GO,Brazil) | Campo sujo                  | Vivianiaceae  | <i>Caesaria</i> sp.                                              |

**Table S5.** Average of individual traits measurements at species representing 80% of cover dominance from fire biennial treatment (25 species total) and fire exclusion treatment (12 species total). We measured (i) aboveground functional traits: growth-form, specific leaf area (SLA), individual height in 10 different individuals; and (ii) belowground traits: root specific length (SRL), root dry matter content (RDMC) and root tissue density (RTD) have been assessed in 5 different individual species, classifying separately fine roots (<2mm) in acquisitive and transport roots (see McCormack et al., 2015).

| Family         | Specie                                                                  | hight (cm) | Grow form | Leaf Area (m2) | Specif leaf area (m2.kg) | Specif Fine Root LenghtSRL (m.g) | Specicif Transport Root Length (m.g) | Fine Root Tissue Density (g.cm3) | Transport Root Tissue Density (g.cm3) | Fine Root Dry Matter Content (mg.g) | Trans Root Dry Matter Content (mg.g) | Fine Root Length (cm) | Transport Root Length (cm) |
|----------------|-------------------------------------------------------------------------|------------|-----------|----------------|--------------------------|----------------------------------|--------------------------------------|----------------------------------|---------------------------------------|-------------------------------------|--------------------------------------|-----------------------|----------------------------|
| Poaceae        | <i>Axonopus aureus</i> P. Beauv.                                        | 29.3       | graminoid | 0.000619       | 1.3737933                | 28.71071                         | 4.721936                             | 0.423                            | 0.418039                              | 296.092                             | 350.7509                             | 39.797                | 77.66323                   |
| Asteracea      | <i>Aldama grandiflora</i> (Gardner) E.E. Schill & Panero                | 47.64      | forb      | 0.003822       | 0.9355817                | 52.04142                         | 3.924013                             | 0.26822                          | 0.682762                              | 269.906                             | 409.3571                             | 82.399                | 62.81503                   |
| Poaceae        | <i>Anthaenantia lanata</i> (Kunth) Benth.                               | 64.55      | graminoid | 0.002416       | 0.444897                 | 30.91914                         | 3.783789                             | 0.79385                          | 0.317016                              | 260.684                             | 297.1891                             | 77.824                | 69.79996                   |
| Poaceae        | <i>Aristida</i> sp.                                                     | 37.5       | graminoid | 0.000335       | 0.4591023                | 5.876396                         | 9.479524                             | 3.25361                          | 0.730298                              | 293.797                             | 333.5237                             | 12.099                | 122.3323                   |
| Fabaceae       | <i>Bauhinia dumosa</i> Benth.                                           | 61.3       | shurb     | 0.006564       | 0.7951964                | 60.25946                         | 12.12688                             | 3.70952                          | 0.530955                              | 260.421                             | 321.3526                             | 21.424                | 19.85133                   |
| Cyperaceae     | <i>Bulbostylis paradoxa</i> (Spreng.) Lindm.                            | 15.55      | graminoid | 9.83E-05       | 0.8847903                | 244.7888                         | 5.557447                             | 0.15953                          | 0.51286                               | 308.695                             | 343.6416                             | 31.19                 | 75.56825                   |
| Malpighiaceae  | <i>Banisteriopsis pamosa</i> Griseb.                                    | 39.3       | shrub     | 0.00277        | 0.5648358                | 43.48189                         | 10.65626                             | 0.85733                          | 0.626356                              | 329.853                             | 429.7175                             | 26.698                | 36.0483                    |
| Fabaceae       | <i>Chamaecrista clausenii</i> (Benth.) H.S.Irwin & Bameby               | 42.5       | shrub     | 0.013046       | 0.4563282                | 12.70148                         | 4.761847                             | 3.81405                          | 0.52978                               | 319.708                             | 367.594                              | 24.159                | 53.21576                   |
| Euphorbiaceae  | <i>Croton gracilienscens</i> Müll.Arg.                                  | 40.09      | forb      | 0.001209       | 1.1928283                | 105.5476                         | 4.601879                             | 0.3205                           | 0.490165                              | 211.83                              | 365.0376                             | 31.622                | 16.23638                   |
| Euphorbiaceae  | <i>Bernardia hirsutissima</i> (Baill.) Müll.Arg.                        | 28.3       | forb      | 0.000737       | 0.7638524                | 43.81513                         | 3.50815                              | 0.602                            | 0.653758                              | 339.417                             | 517.8173                             | 31.986                | 19.78133                   |
| Fabaceae       | <i>Chamaecrista ochrosperma</i> (H.S.Irwin & Bameby) H.S.Irwin & Bameby | 39.9       | shrub     | 0.004272       | 0.4086964                | 559.271                          | 7.751941                             | 0.19187                          | 0.554301                              | 1234.74                             | 378.3887                             | 86.696                | 36.20198                   |
| Poaceae        | <i>Elionurus muticus</i> (Spreng.) Kuntze                               | 59.5       | graminoid | 0.000905       | 0.5431616                | 19.71492                         | 3.170698                             | 1.46396                          | 0.500316                              | 300.567                             | 296.6947                             | 52.225                | 115.8335                   |
| Lamiaceae      | <i>Gymnea chapadensis</i> Harley                                        | 16.8       | forb      | 0.001228       | 1.3157773                | 470.1123                         | 13.52594                             | 0.23263                          | 0.469696                              | 268.269                             | 331.0577                             | 94.52                 | 18.0741                    |
| Lamiaceae      | <i>Hyptis remota</i> Pohl ex Benth.                                     | 33.6       | forb      | 0.001228       | 1.3157773                | 199.8637                         | 5.104528                             | 0.28898                          | 0.501286                              | 256.954                             | 353.9357                             | 49.444                | 28.89688                   |
| Asteraceae     | <i>Ichthyothere hirsuta</i> Gardner                                     | 29.9       | forb      | 0.001285       | 1.2140723                | 157.2222                         | 5.597652                             | 0.075                            | 0.426791                              | 258.993                             | 273.6833                             | 56.603                | 6.90175                    |
| Calophyllaceae | <i>Kielmeyera rubriflora</i> Cambess.                                   | 68         | shrub     | 0.00066        | 1.074261                 | 46.22671                         | 18.28556                             | 0.38274                          | 0.473873                              | 288.626                             | 298.0372                             | 49.705                | 47.42286                   |
| Poaceae        | <i>Mesosetum ferrugineum</i> (Trin.) Chase                              | 42.6       | graminoid | 0.002333       | 0.891921                 | 34.15161                         | 3.83137                              | 0.37579                          | 0.532407                              | 287.672                             | 377.1171                             | 114.22                | 88.81068                   |
| Poaceae        | <i>Mesosetum loliforme</i> (Hochst.) Chase                              | 33.82      | graminoid | 0.000409       | 1.1048283                | 12.59268                         | 10.6171                              | 10.6274                          | 0.456996                              | 328.576                             | 237.2173                             | 28.32                 | 126.2704                   |
| Lamiaceae      | <i>Medusantha mollissima</i> (Benth.) Harley & J.F.B.Pastore            | 34.3       | shrub     | 0.000108       | 1.2417387                | 8.613411                         | 3.941463                             | 6.20532                          | 0.580696                              | 315.145                             | 381.3268                             | 28.132                | 17.6728                    |

Continue Table S5...

| Family         | Specie                                                                                                  | hight (cm) | Grow form | Leaf Area (m2) | Specif leaf area (m2.kg) | Specif Fine Root LenghtSRL (m.g) | Specicif Transport Root Length (m.g) | Fine Root Tissue Density (g.cm3) | Transport Root Tissue Density (g.cm3) | Fine Root Dry Matter Content (mg.g) | Trans Root Dry Matter Content (mg.g) | Fine Root Length (cm) | Transport Root Length (cm) |
|----------------|---------------------------------------------------------------------------------------------------------|------------|-----------|----------------|--------------------------|----------------------------------|--------------------------------------|----------------------------------|---------------------------------------|-------------------------------------|--------------------------------------|-----------------------|----------------------------|
| Poaceae        | <i>Oncorachis ramosa</i> (Zuloaga & Soderstr.) Morrone & Zuloaga                                        | 49.5       | graminoid | 0.00237        | 0.4995795                | 23.66875                         | 2.476937                             | 1.40773                          | 0.704069                              | 340.377                             | 394.6327                             | 21.345                | 91.65118                   |
| Oxalidaceae    | <i>Oxalis goyazensis</i> Turcz.                                                                         | 76.2       | forb      | 0.000484       | 0.9796463                | 83.98628                         | 3.973031                             | 5.18783                          | 0.693292                              | 220.186                             | 414.6153                             | 44.408                | 25.03473                   |
| Acanthaceae    | <i>Ruellia nitens</i> (Nees) Wassh.<br><i>Trichantheum cyanescens</i> (Nees ex Trin.) Zuloaga & Morrone | 47.1       | shrub     | 0.00058        | 1.370531                 | 27.12807                         | 3.889196                             | 2.2541                           | 0.528749<br>0.517715                  | 308.29                              | 353.8041                             | 64.107                | 129.3298                   |
| Poaceae        | <i>Trachypogon spicatus</i> (L.f.) Kuntze                                                               | 39.8       | graminoid | 0.000283       | 0.8791774                | 38.78395                         | 18.2757                              | 1.97831                          | 0.523389                              | 270.628                             | 292.5229                             | 91.496                | 115.325                    |
| Poaceae        | <i>Calliandra dysantha</i> Benth.                                                                       | 44.36      | graminoid | 0.000664       | 0.5047911                | 46.21647                         | 7.292151                             | 0.42963                          | 0.511916                              | 230.284                             | 386.7429                             | 143.88                | 61.70794                   |
| Fabaceae       | <i>Declieuxia lancifolia</i> J.H.Kirkbr.                                                                | 45.7       | shrub     | 0.017342       | 0.7940074                | 156.4809                         | 8.634975                             | 0.17701                          | 0.470729                              | 367.227                             | 385.2002                             | 17.12                 | 10.75423                   |
| Rubiaceae      | <i>Eriope glandulosa</i> (Harley) Harley                                                                | 32.8       | forb      | 6.22E-05       | 1.7764579                | 50.93603                         | 5.015386                             | 0.50762                          | 0.659104                              | 286.783                             | 325.4285                             | 77.27                 | 62.9945                    |
| Lamiaceae      | <i>Euphorbia potentilloides</i> Boiss.                                                                  | 23.5       | forb      | 0.000265       | 1.0710841                | 101.1258                         | 4.9225                               | 0.21006                          | 0.432108                              | 469.895                             | 439.906                              | 81.925                | 17.76223                   |
| Euphorbiaceae  | <i>Hemipogon acerosus</i> Decne.                                                                        | 45.1       | forb      | 9.77E-05       | 1.2100529                | 2267.127                         | 16.54771                             | 0.12014                          | 0.40332                               | 146.587                             | 352.246                              | 57.876                | 12.7858                    |
| Apocynaceae    | <i>Ipomoea fiebrigii</i> Hassl. ex O'Donell                                                             | 32         | forb      | 2.09E-05       | 1.0554135                | 164.2897                         | 15.84616                             | 0.16452                          | 0.360351                              | 365.272                             | 286.8153                             | 141.77                | 9.7018                     |
| Convolvulaceae | <i>Mimosa gracilis</i> Benth.                                                                           | 28.7       | forb      | 0.000136       | 0.8658345                | 335.9935                         | 13.40525                             | 0.04252                          | 0.469707                              | 380.495                             | 288.1378                             | 65.518                | 6.565367                   |
| Fabaceae       | <i>Mimosa pteridifolia</i> Benth.                                                                       | 62.5       | forb      | 0.000207       | 0.7138188                | 328.3611                         | 1.882803                             | 0.0392                           | 0.657897                              | 345.485                             | 290.9147                             | 62.934                | 54.94905                   |
| Fabaceae       | Morphotype 2                                                                                            | 44         | shrub     | 0.006304       | 1.7714955                | 4.824609                         | 2.095421                             | 8.12276                          | 0.542938                              | 361.424                             | 433.5357                             | 28.814                | 38.58648                   |
| Cyperaceae     | <i>Croton gracilienscens</i> Müll.Arg.                                                                  | 29.13      | graminoid | 5.11E-05       | 3.3451778                | 43.60218                         | 13.90974                             | 0.41766                          | 0.421354                              | 359.051                             | 368.6699                             | 359.05                | 152.7087                   |
| Euphorbiaceae  | <i>Eugenia paracatuana</i> O.Berg                                                                       | 29.4       | forb      | 0.001013       | 7.5324537                | 30.14163                         | 8.483292                             | 0.38214                          | 0.460606                              | 323.644                             | 275.3691                             | 323.64                | 50.41875                   |
| Myrtaceae      | <i>Gymmeia chapadensis</i> Harley                                                                       | 28.6       | shrub     | 0.001384       | 7.2192197                | 233.3333                         | 9.684211                             | 0.15                             | 0.380519                              | 115.385                             | 393.7824                             | 115.38                | 14.7184                    |
| Lamiaceae      | <i>Mesosetum ferrugineum</i> (Trin.) Chase                                                              | 14.1       | forb      | 0.001485       | 0.7485573                | 74.64443                         | 21.60924                             | 0.61682                          | 0.456996                              | 278.085                             | 286.1228                             | 278.08                | 32.6059                    |
| Poaceae        | <i>Mesosetum loliiforme</i> (Hochst.) Chase                                                             | 43.9       | graminoid | 0.001452       | 7.5728065                | 44.64302                         | 6.369115                             | 0.32433                          | 0.477207                              | 225.933                             | 325.2403                             | 225.93                | 120.5131                   |
| Poaceae        | <i>Rhynchospora consanguinea</i> (Kunth) Boeckeler                                                      | 25         | graminoid | 0.000326       | 11.727298                | 63.31953                         | 11.79294                             | 0.36363                          | 0.443044                              | 267.31                              | 344.5924                             | 267.31                | 138.6641                   |
| Cyperaceae     | <i>Turnera incana</i> Cambess.                                                                          | 28.1       | graminoid | 0.000268       | 6.6946274                | 38.07652                         | 11.07917                             | 0.4181                           | 0.546875                              | 267.214                             | 350.9652                             | 267.21                | 125.2638                   |
| Tumecaceae     | <i>Trichantheum cf. cyanescens</i> (Nees ex Trin.) Zuloaga & Morrone                                    | 34.2       | shrub     | 0.000423       | 5.8744732                | 54.07794                         | 5.008571                             | 0.32198                          | 0.549379                              | 270.628                             | 358.9744                             | 214.91                | 35.0647                    |
| Poaceae        | <i>Trachypogon spicatus</i> (L.f.) Kuntze                                                               | 56         | graminoid | 0.000288       | 5.9489092                | 43.96764                         | 10.75101                             | 0.36064                          | 0.477951                              | 287.487                             | 253.7011                             | 287.49                | 67.94198                   |
| Poaceae        | <i>Heteropterys campestris</i> A.Juss.                                                                  | 32.4       | graminoid | 0.000764       | 6.3803886                | 54.57939                         | 7.049027                             | 0.33751                          | 0.528655                              | 287.48                              | 373.7853                             | 287.48                | 87.21522                   |
| Malpighiaceae  | <i>Calliandra dysantha</i> Benth.                                                                       | 52.5       | shrub     | 0.002528       | 7.3243044                | 59.76318                         | 4.665591                             | 0.31196                          | 0.514901                              | 246.665                             | 368.6408                             | 246.67                | 33.83523                   |
| Fabaceae       |                                                                                                         | 43.8       | shrub     | 0.013133       | 0.8993042                | 43.56155                         | 5.890337                             | 0.34135                          |                                       | 226.919                             | 339.765                              | 30.971                | 12.14267                   |



Does fire affect belowground biomass  
allocation and composition in tropical grassland  
and savannas?

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**Abstract**

**Aims:** Belowground biomass, i.e. roots and belowground organs, plays a significant role in open fire-prone ecosystems although the relationship between fire and the belowground compartment is undervalued. We analyzed the fire effect on belowground biomass by testing i) if fire promotes belowground allocation and ii) if fire affects belowground organ composition, in five tropical open ecosystems (open savanna and grassland) under distinct fire regime.

**Locations:** Five open savannas of the Cerrado in central Brazil (*campo sujo*; Brasília National Park Brasília [PNB], Reserva Natural Serra do Tombador [RNST], Chapada dos Guimarães National Park [PNCG]), Southwest Brazil (*campo rupestre*; Serra do Cipó National Park [PNSC]), and in an open savanna enclave in Brazilian Amazon (*campos amazônicos*; Campos Amazônicos National Park [PNCA]).

**Methods:** In each site, we assessed plant biomass in twenty 0.25 m × 0.25 m plots for belowground biomass and twenty 1 m × 1 m plots for aboveground biomass according to two distinct fire regimes: burnt and fire-excluded areas. Biomass was sorted as: live aboveground, belowground organs, coarse (>2 mm) and fine roots (< 2 mm). We also estimated belowground biomass allocation by quantifying the ratio of belowground dry biomass and live aboveground biomass. Belowground organs were classified into bud-bearing organ types according to functional categories (e.g., xylopodia, woody rhizome, fleshy rhizome).

**Results:** Fire promoted total belowground biomass as well as belowground allocation in Cerrado open savannas, primarily by increasing root biomass. We did not observe variation in belowground organ biomass with fire. Fire also drove change in belowground organ composition through the increase in the proportion of Xylopodia with fire, a bud-bearing organ associated with fire presence. Without fire most structures were related to lateral spread.

**Conclusions:** Fire primarily affect root biomass and drove variation in the importance of belowground organs composition, increasing the proportion of organs without clonal ability. Keeping species with diverse regeneration strategies are crucial for the biodiversity conservation of fire-prone ecosystems.

**Keywords:** open savannas, belowground allocation, belowground organs, biomass, fire, Cerrado.

## **INTRODUCTION**

High allocation belowground in open ecosystems reflects plant adaptation and community structure in response to the evolutive environmental factors such as fire (Veldman et al. 2015; Buisson et al. 2019; Ottaviani et al. 2020; Buisson et al. 2022). Indeed, greater biomass allocation belowground and the presence of different belowground structures such as bud-bearing organs and roots are a major plant strategy to survive and persist during fire especially in open ecosystems (Fidelis et al. 2013; Fidelis et al. 2014; Jackson et al. 2016; Pausas et al. 2018; Le Stradic et al. 2021). Resprouting from belowground structures is the dominant persistence strategy in fire-prone open ecosystems, ensured by the well-protected and insulated buds from fire (Clarke et al. 2013; Pausas et al. 2018). However, biomass allocation belowground is not straightforward and may vary according to fire regime and other environmental factors (i.e., soil, nutrient content, precipitation) (Le Stradic et al. 2021). We then need to understand whether fire may modify belowground biomass allocation independently of different environmental factors. Despite the importance of the belowground components in fire-prone open ecosystems, the relationship between fire and belowground biomass distribution remains undervalued, especially when considering the different belowground structures (but see Fidelis et al. 2014; Bombo et al. 2021; Le Stradic et al. 2021; Bombo et al. 2022). To estimate this relationship will contribute to the overall understanding of the impact of fire on the regeneration capacity of open ecosystems (Pilon et al. 2021; Zupo et al. 2021) and the potential belowground carbon contribution from open ecosystem on global carbon stocks (De Castro & Kauffman 1998; Silva et al. 2006; Bai & Cotrufo 2022; Zhou et al. 2022).

In fire-prone ecosystems, how biomass is allocated belowground (i.e., root and belowground organ types) will strongly determine plant responses to fire, due to anatomical (i.e.,

meristems reserve, type of storage component), morphological (i.e., number and location of dormant buds, root diameter) and functional differences (i.e., persistence, resprouting, lateral spread) (Pausas et al. 2018; Klimešová et al. 2019; Pilon et al. 2021). For example, 80% of the biomass invested belowground in those ecosystems correspond to the root production in the upper soil layer (< 30 cm) (De Castro & Kauffman 1998; Oliveira et al. 2005). Plant allocation towards root biomass allows rapid resource acquisition by plant species, necessary to the post-fire regeneration, and to reach reproductive maturity during favorable environmental conditions (Kramer-Walter et al. 2016; Simpson et al. 2019). Fine roots (< 2mm) are primarily related to the acquisition and uptake of soil resources (McCormack et al. 2015). Coarse roots (> 2mm) instead, support the fine roots network and plant structures, the transport of nutrients and water to shoots, and are more associated with woody vegetation (Oliveras et al. 2013; Le Stradic et al. 2021). In tropical open systems, fire stimulates fine root production mainly from graminoids species at the upper soil layer (Oliveras et al. 2013; Le Stradic et al. 2021). These fine roots allow plants to use resources in post-fire environments (resprouting and persistence); as fire leads to a short nutrient input due to ash deposition (Pivello et al. 2010).

The belowground biomass investment in tropical open ecosystems is also related to the belowground bud-bearing organs (Clarke et al. 2013; Fidelis et al. 2013; Pausas et al. 2018). Some belowground organs concede several functions to plants like to colonize new areas and to help the post-fire resprouting due to their nutrient storage capacity (e.g. both fleshy and woody rhizomes, gemiferous roots) (Ottaviani et al. 2017; Pausas et al. 2018). Other organs allow plants to resprout after fire (e.g., xylopodia, root crown), guarantee important bud bank, but do not have clonal ability (Apezzato-da-Glória et al. 2008; Pausas et al. 2018). Bulbs and corms, on the other hand, do not have a large bud bank, but they provide great bud protection and great storage capacity ensuring

quick post fire regeneration (Apezatto-da-Glória 2015; Almeida et al. 2015; Ottaviani et al. 2017). In addition, the diversity and composition of bud-bearing organs in fire-prone ecosystems might be influenced by fire frequency. Some studies showed greater diversity in belowground organs at more frequently burned areas when compared to unfrequently ones (Fidelis et al. 2014; Bombo et al. 2021; Bombo et al. 2022). Structures such as xylopodia and root crown are mainly related to areas under high fire frequency (Fidelis et al. 2014; Pausas et al. 2018; Bombo et al. 2022). Under fire exclusion, those structures might disappear or drastically decrease in total numbers (Fidelis et al. 2014; Bombo et al. 2022). Also, bulbs and corms can be related to areas with low fire frequency or fire exclusion, as founded in South African savanna (Bombo et al. 2021). Therefore, any variation in fire frequency leading to changes in composition of belowground organs might then impact post-fire regeneration strategies (Keeley et al. 2016; Pilon et al. 2021; Simpson et al. 2021).

Our study aimed to investigate how fire affects belowground biomass allocation in tropical open ecosystems analyzing i) the biomass allocation between the different belowground compartments, i.e., roots and belowground organs, and ii) the biomass distribution of belowground organs, between areas frequently burned and areas excluded from fire (i.e., last 12 years excluded from fire). We used as a model five different sites of fire-prone open ecosystems in Cerrado, to test if the relationship between fire and belowground was similar. Those systems present great belowground allocation, both in fine roots and belowground organs (Abdala et al. 1998; De Castro & Kauffman 1998; Fidelis et al. 2013). First, we tested the effect of fire on belowground root biomass (i.e., fine roots and coarse roots) and on belowground organs biomass. Secondly, we tested whether fire is changing the biomass composition in belowground organs compared to unburned sites. We expected that burnt plant communities would have higher investment in belowground biomass both in roots and in belowground organs, compared to plant communities excluded from

fire. We expected that the high belowground investment in burnt areas will be mainly driven by the occurrence of greater biomass from belowground organs such as xylopodia as they are associated with rapid resprouting in fire-prone ecosystems. Plant communities frequently burnt will also present an increase of fine root biomass due to the need to increase soil resources acquisition as a response to post-fire nutrient input.

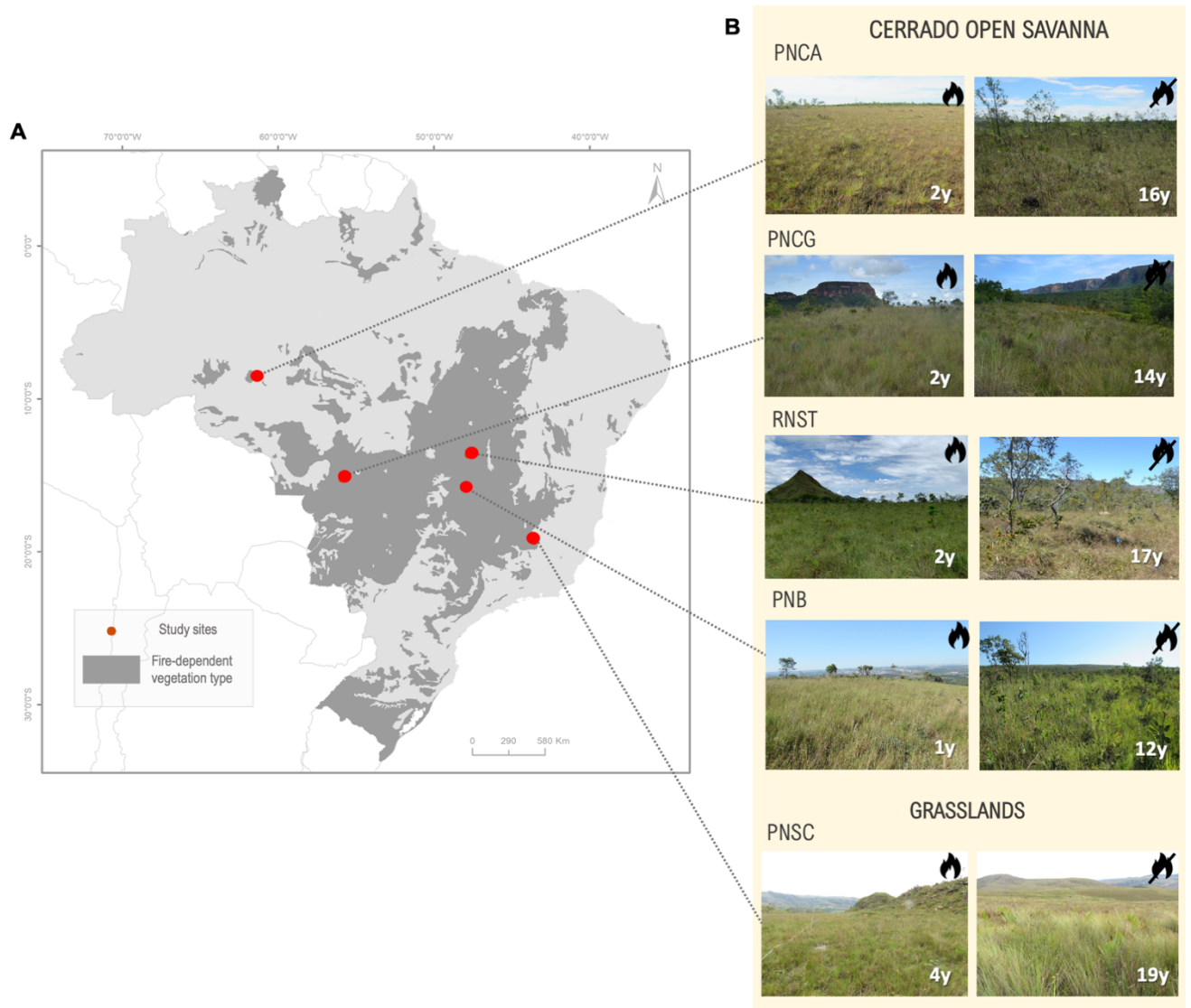
## METHODS

We chose five sites of open ecosystems spread over Brazil from northern limit of Cerrado in Amazonian forest (latitude 8°22'53.71"S) to southeast limit (Minas Gerais, latitude 19°20'58.61"S, Figure 1), to take into account the diversity of Cerrado open savannas and grasslands (Coutinho 1990; Overbeck et al. 2022). All grassland sites are characterized by a ground layer dominated by C4 grasses, and open savannas have a graminoid layer scattered with small palms, shrubs and trees representing < 5% of total cover (Ribeiro & Walter 2008). All sites are subject to two marked seasons, a dry and a rainy season, with >70% of the total amount of annual precipitation occurring in the rainy season (Eiten 1972). Length of the dry season varies between 5 to 7 months (Oliveira & Marquis 2002), with July and August as the driest months (Eiten 1972). In each site we selected one area frequently burned (between 5 to 16 fires in the last 35 years, Table 1), and where the last fire occurred at least 4 years before sampling (fire hereafter). We also selected one area per site that burnt between 1 to 7 fires in the last 35 years, and was excluded from fire for at least 12 years before sampling (exclusion hereafter, Table 1).

The first site location is in the Serra do Cipó National Park, located at the southeast of Brazil (PNSC hereafter, -19°20'34.20" S and -43°37'5.99" W). Sampling was carried out in sandy grasslands of *campo rupestre*. Vegetation is composed by species-rich herbaceous layers with

some subshrubs and almost no shrub occurring on shallow and acidic soils developed from nutrient poor-rocks (Le Stradic et al. 2015; Silveira et al. 2016). The other three sites' location are in the Cerrado open savannas in Central Brazil, as followed: Brasília National Park (PNB hereafter, -15° 44' 10.19" S and -47° 55' 21.59" W), Chapada dos Guimarães National Park (PNCG hereafter, -20° 14' 60.00" S and -46° 29' 59.99" W), and Reserva Natural Serra do Tombador (RNST hereafter, 13° 35'-38' S and 47° 45'-51' W). Vegetation is dominated by C4 grasses and forbs, with scattered shrubs and dwarf trees (Oliveira-Filho & Ratter 2002), occurring on acidic nutrient-poor soils, eventually with small rocky outcrops (Ribeiro & Walter 2008). The last site is the Campos Amazônicos National Park (PNCA hereafter, 8° 22' 4" S and 61° 15' 50" W), an open ecosystem enclave located in southern Brazilian Amazon (ICMBio 2016; Alves & Pérez-Cabello 2017) called *campos amazônicos*. *Campos amazônicos* are tropical open savanna dominated by grasses and sedges with scattered shrubs and small trees, occurring on sites with a short period of dry season, and on sandy or stony soils with high soil exposures amplifying the dry season water deficit (ICMBio 2016).





**Figure 1.** Geographic location of the five selected study sites of fire-prone ecosystems in Brazil (A). Study sites encompass the diversity of Cerrado open ecosystems (B). Two types of areas were selected: burnt (Fire) and unburnt (exclusion) areas (Table 1). Numbers (bottom right corner) represent the time since last fire (in years). For more detail about the fire regime see Table 1. The map was modified from Pivello et al. (2021). The icons were modified from the original version designed by Yadi RS (fire, A-B) from thenounproject.com. Abbreviations means: RNST- Reserva Natural Serra do Tombador; PNB- Brasilia National Park; PNCG: Chapada dos Guimarães National Park; PNSC- Serra do Cipó National Park ; PNCA- Campos Amazônicos National Park.

**Table 1.** Fire and general information about the different sampling areas of open ecosystems including geographical coordinates, temperature, rainfall, altitude, fire regime (i.e., fire and exclusion), time since last fire in relation to the sampling period (in years), number of fires (between 1985 and 2019) and year of the last fire. Year-round average temperatures and rainfall were obtained through WordClim2 data set (Fick & Hijmans 2017). Abbreviation means: RNST- Reserva Natural Serra do Tombador; PNB- Brasília National Park; PNCG- Chapada dos Guimarães National Park; PNSC- Serra do Cipó National Park; PNCA- Campos Amazônicos National Park.

| Sites | Open ecosystem type | coordinates                       | Temperature (min. - max. year-round average) | Rainfall (annual) | Altitude (a.s.l.) | Fire      | Time since last fire | Number of fires (last 35 years) | Year of the last fire |
|-------|---------------------|-----------------------------------|----------------------------------------------|-------------------|-------------------|-----------|----------------------|---------------------------------|-----------------------|
| PNSC  | grassland           | -19°17'11.09"S;<br>-43°35'43.34"W | 15°C - 27°C                                  | 1550 mm           | 1180m             | Fire      | 4                    | 5                               | 2014                  |
|       |                     | -19°14'50.37"S;<br>-43°30'48.81"W |                                              |                   | 1290m             | Exclusion | 19                   | 1                               | 1999                  |
| PNB   | savanna             | -15°40'31.61"S;<br>-47°53'1.77"W  | 16°C - 27°C                                  | 1573 mm           | 1249m             | Fire      | 1                    | 6                               | 2018                  |
|       |                     | -15°40'30.82"S;<br>-47°53'2.49"W  |                                              |                   | 1115m             | Exclusion | 12                   | 4                               | 2007                  |
| PNCA  | savanna             | 8°28'35"S;<br>61°38'48"W          | 20°C - 31°C                                  | 2414 mm           | 224m              | Fire      | 2                    | 8                               | 2017                  |
|       |                     | 8°25'59"S;<br>61°38'49"W          |                                              |                   | 220m              | Exclusion | 16                   | 5                               | 2003                  |
| PNCG  | savanna             | 15°26'6.88"S;<br>55°51'37.59"W    | 17°C - 29°C                                  | 1542 mm           | 634m              | Fire      | 2                    | 16                              | 2017                  |
|       |                     | 15°21'1.44"S;<br>55°49'50.33"W    |                                              |                   | 329m              | Exclusion | 14                   | 6                               | 2005                  |
| RNST  | savanna             | 13°40'53.50"S;<br>47°48'37.26"W   | 18.5°C - 29°C                                | 1778 mm           | 831m              | Fire      | 2                    | 19                              | 2017                  |
|       |                     | 13°39'30.15"S;<br>47°49'27.75"W   |                                              |                   | 770m              | Exclusion | 17                   | 7                               | 2002                  |

*Sampling design and plant biomass measurements*

At each sampling area, at the peak of the vegetation growth (rainy season, January-April 2019), we randomly established three transects of 30 m x 1 m, at least 10 m apart from each other. At each transect, every 3 m, we established 1 plot of 0.25 m<sup>2</sup> (0.5 x 0.5 m) to harvest all aboveground biomass totaling 30 plots at each area (fire and exclusion). At the laboratory, aboveground biomass was sorted into live and dead biomass (i.e., standing dead biomass) and then dried at 80°C for 48 h before being weighed. We considered total biomass the sum of live and dead biomass.

Within each plot we established one subplot of 0.25 x 0.25 m with 0.2 m depth, for soil sampling to quantify biomass of coarse roots (roots >2 mm diameter) and belowground organs (see below for more details). More than half of the total belowground organ and root biomass is found in the top 20 cm of the soil (De Castro & Kauffman 1998; Delitti et al. 2001; Le Stradic et al. 2021). All soil samples were water-washed to remove soil particles and to separate belowground organs from coarse roots. Belowground organs were classified into bud-bearing organ types according to functional categories (i.e., woody rhizome, fleshy rhizome, bulb/corm, xylopodia, root crown and gemiferous roots) based on an adapted version of Bombo et al. (2021), Pausas et al. (2018) (see Table S1 at supporting information). All samples were dried at 80°C for 48h before being weighed. We considered total belowground organ biomass the weight of all bud-bearing organs.

To assess fine root biomass (roots  $\leq$  2 mm diameter), we sampled soil cores using an auger of 5 cm diameter and up to 20 cm depth within each plot. Soil samples were sieved at 2 mm, 1.40 mm and 850  $\mu$ m before being washed with water to remove soil, stones, and vegetal debris from fine roots. Roots were dried at 60°C for 72h before being weighed. In total, we had 450 samples (5 sites x 2 fire frequencies x 15 plots/fire frequency/site=150 samples for each/aboveground

biomass, belowground biomass and fine roots biomass). We considered total root biomass the sum of coarse and fine root biomass (all values were standardized by  $\text{g/m}^2$  before the sum). The total belowground biomass was the sum of belowground organs and root biomass.

To estimate belowground allocation, we calculated root:shoot ratio and organs:shoot ratio respectively as the ratio of total root biomass to the total live aboveground biomass, and as the ratio of total belowground organ biomass to the total live aboveground biomass. Total belowground allocation (B:A ratio) was calculated as the ratio between total belowground biomass and live aboveground biomass.

### *Data Analyses*

Generalized linear mixed effect models (GLMM) were performed to test if fire increased belowground allocation (i.e., B:A ratio, organs:shoot and root:shoot ratio), and the different belowground biomass (i.e., belowground organs, coarse and fine root biomass). Fire (fire and exclusion) was the fixed factor, and the different sites were considered as the random factor. Log transformation was performed for belowground allocation, belowground organ biomass, fine root biomass, root:shoot and organs:shoot data to fulfill normality and variance homogeneity requirements of gaussian family models (Zuur et al. 2009). All GLMM were also performed for each site individually to understand the fire effect within sites.

To understand how fire could affect the composition of belowground organ types we performed a permutational multivariate analyses of variance (Anderson 2001) considering the biomass of the different belowground organs as the response variable and fire as the explanatory variable. The statistical significance of the multivariate variance components, and dispersion was tested using 999 unrestricted permutations of the raw data ( $p < 0.05$ , bootstrap 999) (Anderson

2001; Anderson & Braak 2003), and pairwise comparisons. We adjusted p-value results by Bonferroni's correction to avoid the risk of a type I error as we are making multiple statistical tests (Cabin & Mitchell 2000; Legendre & Legendre 2012). We use Bray-Curtis as the dissimilarity distance, after square root transformation of raw data to achieve a metric dissimilarity index, down-weighting dominant organ types and bringing out the signal of non-dominant types (Legendre & Gallagher 2001; Legendre & Legendre 2012; Anderson & Walsh 2013).

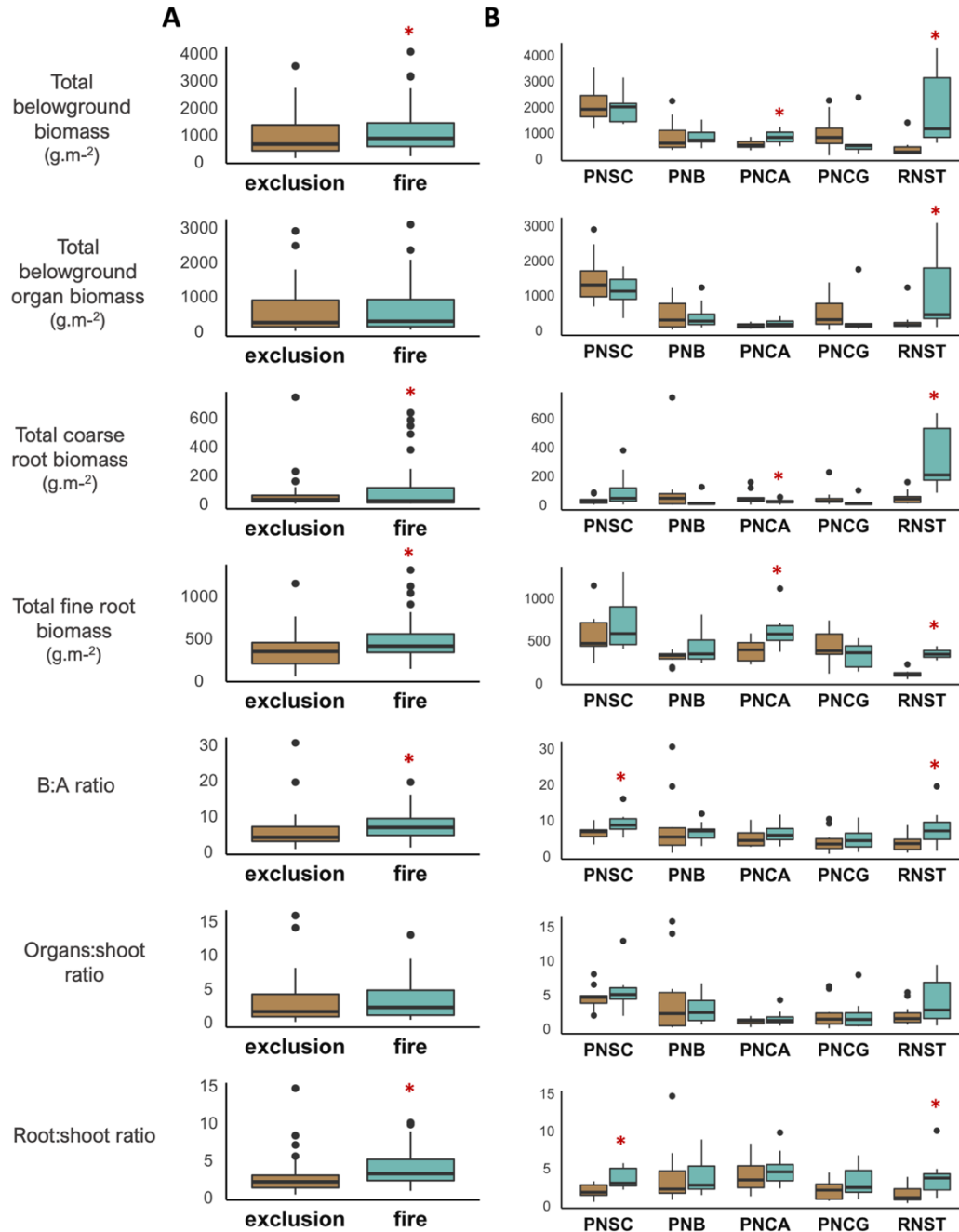
All analyses were performed at R environment version R.4.1.1. (R Core Team 2021), using *glmmMTB* (Bolker 2019), *psych* (Revelle 2021), *DHARMA* (Hartig & Lohse 2021), *performance* (Lüdtke et al. 2021), *randomForest* (Liaw & Wiener 2002), and *vegan* (Oksanen et al. 2020) packages. We used package *ggplot2* (Wickham et al. 2020) for data visualization.

## RESULTS

### *Biomass allocation and belowground biomass*

Burned open savannas and grasslands had belowground biomass, mostly due to the higher amount of root biomass (both fine and coarse roots) (Figure 2A, Table S4). All analyzed variables were significantly higher in burned and excluded areas, except total belowground organs biomass and organs:shoot ratio that were not significantly different (Figure 2A). Further, when fire and exclusion areas were analyzed within each site, we noticed great variability in belowground biomass responses (Figure 2B). However, except for PNCG, it is possible to observe that the total belowground and fine root biomass followed the general trend to increase at fire areas, although no significant difference was always observed. The overall trend was also observed for B:A and root:shoot ratio (Figure 2B), with high biomass allocated belowground in fire areas. We may observe deviation from the general trend for total belowground organ biomass and coarse root

biomass when looking at the different sites. At PNSC, PNB and PNCG the tendency highlights greater belowground organ biomass at exclusion area, and at PNB, PNCA and PNCG higher coarse root biomass at exclusion area compared to fire area (Figure 2B).

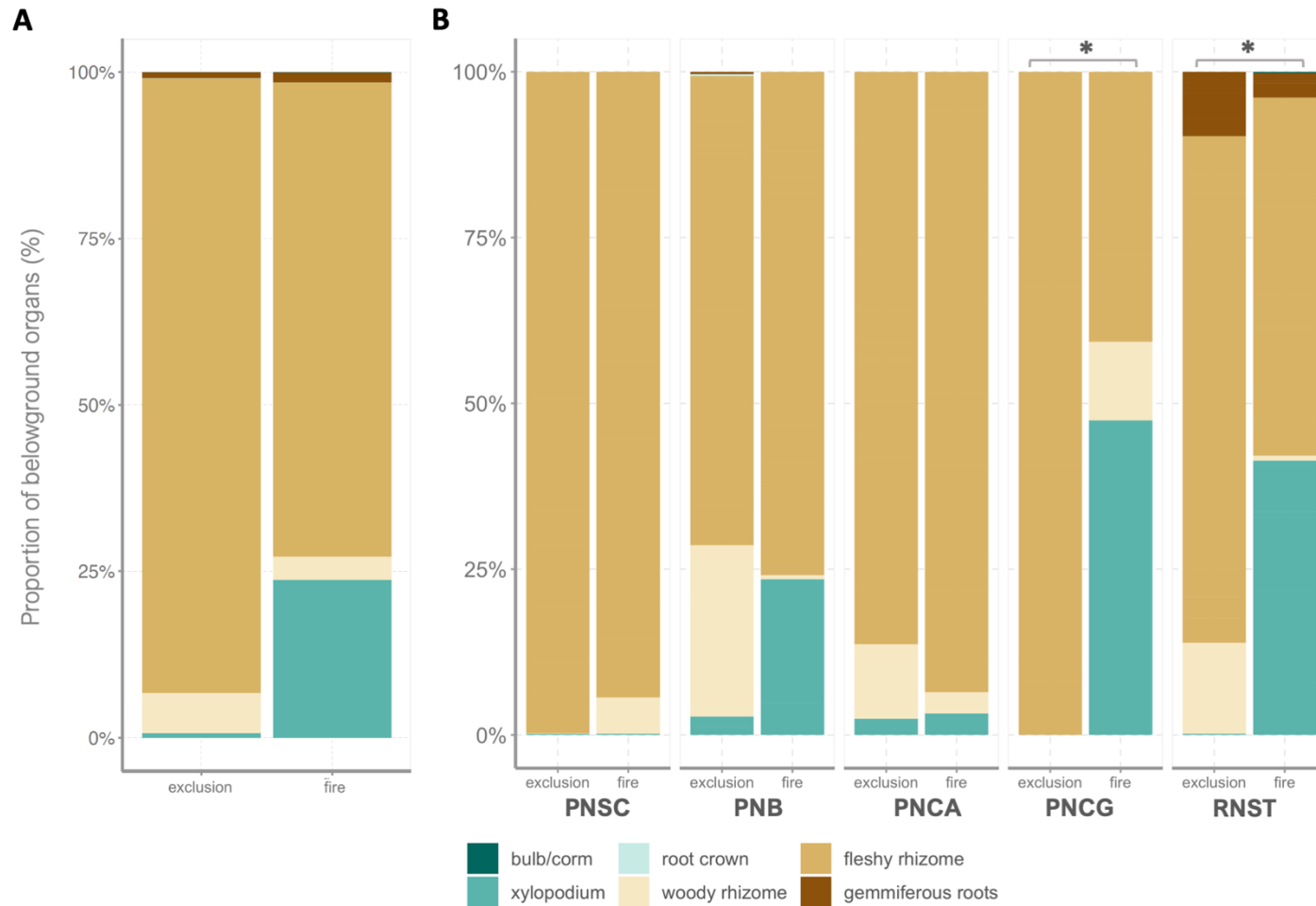


**Figure 2.** Belowground biomass (g.m<sup>-2</sup>) comprising total belowground, belowground organs, coarse and fine root biomass, and belowground allocation comprising belowground: aboveground (B:A ratio), root:shoot and organs: shoot ratio, between burnt (fire in blue) and fire-excluded areas (exclusion in brown) considering all sites (A) and within each site (B). Significant effects were distinguished by red

asterisk ( $p < 0.05$ ) resulting from generalized linear mixed models (Table S4 and S6). Abbreviations means: RNST- Reserva Natural Serra do Tombador; PNB- Brasília National Park; PNCG- Chapada dos Guimarães National Park; PNSC- Serra do Cipó National Park; PNCA- Campos Amazônicos National Park. PNSC is a grassland. RNST, PNB, PCG, PNCA are open savannas.

### *Belowground organ composition*

We found differences in the proportion of belowground organ types between fire and exclusion areas (Figure 3A). Overall, although no significant differences were found, fire areas had a higher proportion of xylopodium compared to exclusion areas (Figure 3A). Rhizomes were the most common belowground organs in both fire and exclusion areas, but the proportion of rhizomes tended to decrease in fire areas. The composition of belowground organs varied with fire at PNCG and RNST ( $p < 0.05$ ), with higher proportion of xylopodium in burnt areas (Figure 3B, Table S5). At RNST, xylopodia just occurred in fire areas (Figure 3B). The same trend was observed for PNB, with an increasing proportion of xylopodium with fire (Figure 3B). The other belowground organs, i.e. bulbs, corms and root crowns, had the lowest proportion. These organs were present only at RNST fire areas and PNB exclusion areas (Figure 3B, Table S5). Woody rhizomes did not show any patterns, but the proportion of woody rhizomes was higher in excluded areas for PNB, PNCA and RNST, compared to fire areas whereas it was the contrary in PNSC and PNCG. At RNST we found a slight decrease of gemiferous root proportion in fire area (Figure 3B).



**Figure 3.** Proportion (%) of each type of belowground organ considering (A) all sites and (B) within each site between burnt (fire) and fire-excluded areas (exclusion). Significant effects were distinguished by gray asterisk ( $p < 0.05$ ) resulting from permutational multivariate analysis of variance (PERMANOVA) with  $p$ -values adjusted by Bonferroni correction. Abbreviation means: RNST- Reserva Natural Serra do Tombador; PNB- Brasília National Park; PNCG- Chapada dos Guimarães National Park; PNCA- Campos Amazônicos National Park. PNCA is a grassland. RNST, PNB, PCG, PNCA are open savannas.



## **DISCUSSION**

Our study showed that belowground biomass was higher at fire compared to exclusion areas, primarily due to the greater root biomass investment. This finding indicates that root biomass is one of the first variables to respond to fire in tropical open ecosystems. Higher root biomass allows the increase of nutrient uptake (Qi et al. 2019), mainly by the investment in absorptive fine roots (Le Stradic et al. 2021). Great biomass investment in the root system might be an adaptation of plants from nutrient-poor environments, as Cerrado grasslands and savannas, to effectively increase the nutrient uptake, especially from the nutrients released from ash after fire at soil surface (Pivello et al. 2010; Oliveras et al. 2013). The increase of nutrient uptake promotes plant shoot regrowth as part of the plant regenerative strategy in those ecosystems (Le Stradic et al. 2021). Coarse root biomass was greater at fire areas than in exclusion areas, but we also observed variations between sites: at RNST and PNSC, coarse root biomass was higher at fire areas, in the other sites coarse biomass was higher in exclusion areas. In all those cases the increase of coarse root biomass might just mirror the increase in fine roots in fire area, once the main function of coarse root is to support fine roots network (Oliveira et al. 2005; Tobin et al. 2007).

The important biomass investment in roots in fire area led to higher biomass allocation belowground in relation to aboveground biomass. Fire removed aboveground biomass and then increase the demand for belowground resources to promote shoot regrowth (Mokany et al. 2006; Le Stradic et al. 2021). We expected greater belowground organ investment compared to live aboveground biomass at fire areas compared to exclusion areas, because at fire-prone ecosystems the allocation of biomass belowground is primarily through belowground organs (Pausas et al. 2016; Ottaviani et al. 2020). However, we did not find any differences in our study, which might reflect the absence of differences found for belowground organ biomass between fire and exclusion

areas. Fire is expected to enhance biomass allocation in belowground organs as a strategy to enhance vegetation ability to persist in fire-prone ecosystem through resprouting (Lamont & Wiens 2003; Simon & Pennington 2012; Pilon et al. 2021; Zupo et al. 2021). Areas with long intervals without fire can show a lower amount of belowground organs in some open ecosystems, such as tropical wet grasslands (Fidelis et al. 2014) and opens savannas (Bombo et al. 2022). However, belowground organs are long-lived structures and can remain in the system for many years (Pausas et al. 2018; Ott et al. 2019). The absence of differences found in the total belowground organ biomass in our study may be related to the great capacity of belowground organs to remain in the system, even after 12 years of fire exclusion, or sometimes more (e.g. 19 year of fire exclusion at PNSC). However, at RNST, 17 year of fire exclusion decreased drastically belowground organs biomass, indicating that fire exclusion might impact the belowground organ biomass.

Fire also drove variation in belowground organ composition. As we hypothesized, fire areas had a higher proportion of xylopodia. Xylopodia is a bud-bearing organ commonly found in Cerrado plants, mostly related to areas under high fire frequency (Appezato-da-Glória et al. 2008; Bombo et al. 2022). Xylopodia are usually associated with storage structures (i.e., stems or tuberous roots) that have non-structural carbohydrate, and a protected bud bank under soil surface (Rizzini & Heringer 1961; Appezato-da-Glória et al. 2008; Pausas et al. 2018). These traits guarantee rapid production of new aboveground shoots after fire, promoting plant resprouting and persistence after fire (Clarke et al. 2013; Pausas & Keeley 2014). Fleshy rhizomes decreased at fire areas, but they remain as the dominant belowground organ. Fleshy rhizomes are structures related to grasses that increase their ability to survive after aboveground biomass removal (Pausas

et al. 2018; Pausas & Paula 2020), indicating the greater resilience capacity of graminoids species (Edwards et al. 2010).

At exclusion areas we observed a change in the importance of belowground organs related with strategies of persistence in burnt systems, to belowground organs more related to strategy of exploration of new locals thought lateral spread. Exclusion areas had a lower proportion of xylopodia. Xylopodia is highly related to areas under frequent fires (Pausas et al. 2018), once fire is excluded, this is the first structure to be affected, since it decreases in proportion (Fidelis et al. 2014; Bombo et al. 2022). We also observed in exclusion areas a high proportion of woody and fleshy rhizomes, indicating the important presence of lateral spread. Woody rhizomes are long-lived structures that grow horizontally, accumulating dormant buds and producing new aerial stems using its own carbohydrate storage (Tiedemann et al. 1987; Alves et al. 2013; Pausas et al. 2018). Fleshy rhizomes are more associated with more diverse types of carbohydrate (e.g., starch or oligosaccharides), mineral nutrient and water storage in grasses (Almeida et al. 2015; de Moraes et al. 2016) rather than accumulation of buds, leading to rapid clonal growth and the formation of large networks of interconnect ramets (Herben et al. 2016; Herben & Klimešová 2020). The carbohydrate storage from those belowground organs ensure great efficiency for plants to occupy available niche (Keeley & Rundel 2005; de Moraes et al. 2016; Ottaviani et al. 2017; Vesik & Yen 2019).

Looking at each site, we observed variation of belowground allocation and biomass in response to fire. The differences in time since last fire, fire frequencies, vegetation composition or edaphic factors such as differences in water soil holding capacity, physical and chemical soil composition could also play a role in belowground allocation, explaining the great variability found among sites. For example, sites that historically registered contrasting fire regimes as in

RNST, showed clear biomass allocation belowground with fire. Areas that recorded a more recent increase of number of fire as PNB, did not show any significant differences between fire and exclusion areas. In such case, the recent increase of fire might be not enough to promote significant differences between fire and exclusion areas. Also, some areas sharing the same time since the last fire, presented marked difference between fire and exclusion areas (e.g., RNST, PNCA), whereas others did not (PNCG). In addition, for some sites such as PNSC and PNCA, edaphic factors such as soil nutrients or water soil holding capacity might be more relevant to explain biomass allocation and belowground biomass than fire.

## **CONCLUSION**

Fire primarily increased root biomass: a prompt response to increase resource uptake provided by post-fire environment, and to ensure vegetation recovery. Our findings also highlighted that even after long period of fire exclusion (>12 years) belowground organs were still present in both fire- and fire-excluded areas. However, fire exclusion also led to differences in belowground allocation, changing the importance of organs related to strategy of persistence in disturbed/burnt systems, to organs related to strategy of exploration of new locals through lateral spread. Those changes might influence system regeneration, because the species with belowground organs with clonal capacity can quickly colonized new sites, whereas, for the species without clonal capacity, the colonization of new sites can be slow or not even possible. This is an important information for fire-prone open ecosystem management and restoration actions, that should focus on conservation of belowground plants structures to guarantee the recovery of plant richness and functions (Nerlekar & Veldman 2020; Buisson et al. 2022). Those goals could be achieved through the reestablishment of feedbacks among fire and vegetation to stimulate the increase of

belowground bud bank (Bombo et al. 2021; Buisson et al. 2022). Furthermore, the biomass allocation belowground in fire-prone open ecosystems considering the distinct belowground structures and the heterogeneity of those ecosystems should be more investigated.

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**REFERENCES**

- Abdala, G.C., Caldas, L.S., Haridasan, M., & Eiten, G. 1998. Above and belowground organic matter and root:shoot ratio in a cerrado in central Brazil. *Brazilian Journal of Ecology* 23.
- Almeida, V.O., Carneiro, R.V., Carvalho, M.A.M., Figueiredo-Ribeiro, R.C.L., & Moraes, M.G. 2015. Diversity of non-structural carbohydrates in the belowground organs of five Iridaceae species from the Cerrado (Brazil). *South African Journal of Botany* 96: 105–111.
- Alves, D.B., & Pérez-Cabello, F. 2017. Multiple remote sensing data sources to assess spatio-temporal patterns of fire incidence over Campos Amazônicos Savanna Vegetation Enclave (Brazilian Amazon). *Science of the Total Environment* 601–602: 142–158.
- Alves, R.J.V., Silva, N.G.D., Fernandes Junior, Alu.J., & Guimaraes, A.R. 2013. Longevity of the Brazilian belowground tree *Jacaranda decurrens* Cham. *Anais da Academia Brasileira de Ciências* 85: 671–678.
- Anderson, M.J. 2001. A new method for non parametric multivariate analysis of variance. *Austral ecology* 26: 32–46.
- Anderson, M., & Braak, C.T. 2003. Permutation tests for multi-factorial analysis of variance. *Journal of Statistical Computation and Simulation* 73: 85–113.
- Anderson, M.J., & Walsh, D.C.I. 2013. PERMANOVA , ANOSIM , and the Mantel test in the face of heterogeneous dispersions : What null hypothesis are you testing ? Author ( s ): Marti J . Anderson and Daniel C . I . Walsh Published by: Wiley Stable URL : <http://www.jstor.org/stable/23596913> REF. *Ecological Monographs* 83: 557–574.
- Apazzato-da-Glória, B. 2015. Morphology of plant belowground systems. 3i Editora, Belo Horizonte.
- Apazzato-da-Glória, A.B., Curry, G., Kasue, M., Soares, M., Hayashi, A.H., Apazzato-da-Glória, B., The, S., Society, B., Feb, N.J., Apazzato-da-gl, B., Cury, G., Kasue, M., Soares, M., & Hayashi, A.H. 2008. Belowground Systems of Asteraceae Species from the Brazilian Cerrado. 135: 103–113.
- Bai, Y., & Cotrufo, M.F. 2022. Grassland soil carbon sequestration: Current understanding, challenges, and solutions. 608: 603–608.
- Bolker, B. 2019. Getting started with the glmmTMB package. Cran.R-Project Vignette 9.
- Bombo, A.B., Apazzato-da-Glória, B., & Fidelis, A. 2022. Fire exclusion changes belowground bud bank and bud-bearing organ composition jeopardizing open savanna resilience.

- Oecologia 199: 153–164.
- Bombo, A., Siebert, F., & Fidelis, A. 2021. Fire and herbivory shape belowground bud banks in a semi-arid African savanna. *African Journal of Range & Forage Science*. doi: 10.2989/10220119.2021.1982004
- Buisson, E., Archibald, S., Fidelis, A., & Suding, K.N. 2022. Ancient grasslands guide ambitious goals in grassland restoration. *Science* 377: 594–598.
- Buisson, E., Le Stradic, S., Silveira, F.A.O., Durigan, G., Overbeck, G.E., Fidelis, A., Fernandes, G.W., Bond, W.J., Hermann, J.-M., Mahy, G., Alvarado, S.T., Zaloumis, N.P., & Veldman, J.W. 2019. Resilience and restoration of tropical and subtropical grasslands, savannas, and grassy woodlands. *Biological Reviews*. doi: 10.1111/brv.12470
- Cabin, R.J., & Mitchell, R.J. 2000. To Bonferroni or Not to Bonferroni : When and How Are the Questions. *America* 81: 246–248.
- Clarke, P.J., Lawes, M.J., Midgley, J.J., Lamont, B.B., Ojeda, F., Burrows, G.E., Enright, N.J., & Knox, K.J.E. 2013. Resprouting as a key functional trait: how buds, protection and resources drive persistence after fire. *New Phytologist* 197: 19–35.
- Coutinho, L.M. 1990. Fire in the Ecology of the Brazilian Cerrado. In *Fire in the Tropical Biota*, pp. 82–105. Springer, Berlin, Heidelberg, Freiburg.
- De Castro, E.A., & 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.
- Delitti, W.B.C., Pausas, J.G., & Burger, D.M. 2001. Belowground biomass seasonal variation in two neotropical savannas (Brazilian Cerrados) with different fire histories. *Annals of Forest Science* 58: 713–721.
- de Moraes, M.G., de Carvalho, M.A.M., Franco, A.C., Pollock, C.J., & Figueiredo-Ribeiro, R. de C.L. 2016. Fire and Drought: Soluble Carbohydrate Storage and Survival Mechanisms in Herbaceous Plants from the Cerrado. *BioScience* 66: 107–117.
- Edwards, E.J., Osborne, C.P., Strömberg, C.A.E., Smith, S.A., Bond, W.J., Christin, P.A., Cousins, A.B., Duvall, M.R., Fox, D.L., Freckleton, R.P., Ghannoum, O., Hartwell, J., Huang, Y., Janis, C.M., Keeley, J.E., Kellogg, E.A., Knapp, A.K., Leakey, A.D.B., Nelson, D.M., Saarela, J.M., Sage, R.F., Sala, O.E., Salamin, N., Still, C.J., & Tipple, B. 2010. The origins of C4 Grasslands: Integrating evolutionary and ecosystem science. *Science* 328: 587–591.



- Eiten, G. 1972. The cerrado vegetation of Brazil. *The Botanical Review* 38: 201–341.
- Fick, S.E., & Hijmans, R.J. 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology* 37: 4302–4315.
- Fidelis, A., Appezzato-da-Glória, B., Pillar, V.D., & Pfadenhauer, J. 2014. Does disturbance affect bud bank size and belowground structures diversity in Brazilian subtropical grasslands? *Flora: Morphology, Distribution, Functional Ecology of Plants* 209: 110–116.
- Fidelis, A., Lyra, M.F. di S., & Pivello, V.R. 2013. Above- and below-ground biomass and carbon dynamics in Brazilian Cerrado wet grasslands (O. Wildi, Ed.). *Journal of Vegetation Science* 24: 356–364.
- Hartig, F., & Lohse, L. 2021. Package “DHARMA” - Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models. 1–61.
- Herben, T., & Klimešová, J. 2020. Evolution of clonal growth forms in angiosperms. *New Phytologist* 225: 999–1010.
- Herben, T., Tackenberg, O., & Klimešová, J. 2016. Reproduction by seed and clonality in plants: correlated syndromes or independent strategies? (M. Rees, Ed.). *Journal of Ecology* 104: 1696–1706.
- ICMBio, C.M.I. for B.C. 2016. Plano de Manejo: Parque Nacional dos Campos Amazônicos.
- Jackson, A.R.B., Mooney, H.A., & Schulze, E. 2016. A Global Budget for Fine Root Biomass , Surface Area , and Nutrient Contents Published by : National Academy of Sciences Stable URL : <http://www.jstor.org/stable/42683> A global budget for fine root biomass , surface area , and nutrient contents. 94: 7362–7366.
- Keeley, J.E., & Rundel, P.W. 2005. Fire and the Miocene expansion of C4 grasslands. *Ecology Letters* 8: 683–690.
- Keeley, J.E., Thomas Parker, V., & Vasey, M.C. 2016. Resprouting and seeding hypotheses: a test of the gap-dependent model using resprouting and obligate seeding subspecies of *Arctostaphylos*. *Plant Ecology* 217: 743–750.
- Klimešová, J., Martínková, J., Pausas, J.G., de Moraes, M.G., Herben, T., Yu, F.-H., Puntieri, J., Vesek, P.A., de Bello, F., Janeček, Š., Altman, J., Appezzato-da-Glória, B., Bartušková, A., Crivellaro, A., Doležal, J., Ott, J.P., Paula, S., Schnablová, R., Schweingruber, F.H., & Ottaviani, G. 2019. Handbook of standardized protocols for collecting plant modularity traits. *Perspectives in Plant Ecology, Evolution and Systematics* 40: 125485.

- Kramer-Walter, K.R., Bellingham, P.J., Millar, T.R., Smissen, R.D., Richardson, S.J., & Laughlin, D.C. 2016. Root traits are multidimensional: specific root length is independent from root tissue density and the plant economic spectrum. *Journal of Ecology* 104: 1299–1310.
- Lamont, B.B., & Wiens, D.L. 2003. Is seed set always low among species that resprout after fire, and why? a meta analysis. *Evolutionary Ecology* 17: 277–292.
- Le Stradic, S., Buisson, E., & Fernandes, G.W. 2015. Vegetation composition and structure of some Neotropical mountain grasslands in Brazil. *Journal of Mountain Science* 12: 864–877.
- 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: 4143–4157.
- Legendre, P., & Gallagher, E.D. 2001. Ecologically meaningful transformations for ordination of species data. *Oecologia* 129: 271–280.
- Legendre, P., & Legendre, Louis. 2012. *Numerical ecology*. Elsevier.
- Liaw, A., & Wiener, M. 2002. Classification and Regression by randomForest. *R News* 2: 18–22.
- Lüdecke, D., Ben-Shachar, M., Patil, I., Waggoner, P., & Makowski, D. 2021. performance: An R Package for Assessment, Comparison and Testing of Statistical Models. *Journal of Open Source Software* 6: 3139.
- McCormack, M.L., Dickie, I.A., Eissenstat, D.M., Fahey, T.J., Fernandez, C.W., Guo, D., Helmisaari, H.S., Hobbie, E.A., Iversen, C.M., Jackson, R.B., Leppälammi-Kujansuu, J., Norby, R.J., Phillips, R.P., Pregitzer, K.S., Pritchard, S.G., Rewald, B., Zadworny, M., Leppälammi-Kujansuu, J., Norby, R.J., Phillips, R.P., Pregitzer, K.S., Pritchard, S.G., Rewald, B., & Zadworny, M. 2015. Redefining fine roots improves understanding of below-ground contributions to terrestrial biosphere processes. *New Phytologist* 207: 505–518.
- Mokany, K., Raison, R.J., & Prokushkin, A.S. 2006. Critical analysis of root: Shoot ratios in terrestrial biomes. *Global Change Biology* 12: 84–96.
- Nerlekar, A.N., & Veldman, J.W. 2020. High plant diversity and slow assembly of old-growth grasslands. *Proceedings of the National Academy of Sciences of the United States of America* 117: 18550–18556.
- 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., Henry, M., Stevens, H., Szoecs, E., & Maintainer, H.W. 2020. Package “vegan” Title Community Ecology Package Version 2.5-7.

- Oliveira, R.S., Bezerra, L., Davidson, E.A., Pinto, F., Klink, C.A., Nepstad, D.C., & Moreira, A. 2005. Deep root function in soil water dynamics in cerrado savannas of central Brazil. *Functional Ecology* 19: 574–581.
- Oliveira, P.S., & Marquis, R.J. (Eds.). 2002. The cerrados of Brazil: ecology and natural history of a neotropical savanna. Columbia University Press, New York.
- Oliveira-Filho, A.T., & Ratter, J.A. 2002. Vegetation physiognomies and woody flora of the Cerrado Biome. In Oliveira, P.S. & Marquis, R.J. (eds.), *The Cerrados of Brazil: Ecology and Natural History of a Neotropical Savanna*, pp. 91–120. Columbia University Press, New York.
- 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: 368–380.
- Ott, J.P., Klimešová, J., & Hartnett, D.C. 2019. The ecology and significance of below-ground bud banks in plants. *Annals of Botany* 123: 1099–1118.
- Ottaviani, G., Martínková, J., Herben, T., Pausas, J.G., & Klimešová, J. 2017. On Plant Modularity Traits: Functions and Challenges. *Trends in Plant Science* 22: 648–651.
- Ottaviani, G., Molina-Venegas, R., Charles-Dominique, T., Chelli, S., Campetella, G., Canullo, R., & Klimešová, J. 2020. The Neglected Belowground Dimension of Plant Dominance. *Trends in Ecology and Evolution* 35: 763–766.
- Overbeck, G.E., Vélez-martin, E., Menezes, S., Anand, M., Baeza, S., Carlucci, M.B., Michele, S., Durigan, G., Fidelis, A., Guido, A., Moro, M.F., Munhoz, B.R., Reginato, M., Rodrigues, R.S., Fermina, M., Sampaio, A.B., Barbosa, H., Fernando, A.O., Sosinski, Ê.E., Staude, I.R., Temperton, V.M., Turchetto, C., Veldman, W., Viana, P.L., & Zappi, D.C. 2022. Placing Brazil's grasslands and savannas on the map of science and conservation. *Perspectives in Plant Ecology, Evolution and Systematics*. doi: 10.1016/j.ppees.2022.125687
- Pausas, J.G., & Keeley, J.E. 2014. Evolutionary ecology of resprouting and seeding in fire-prone ecosystems. *New Phytologist* 204: 55–65.
- 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: 1435–1448.
- Pausas, J.G., & Paula, S. 2020. Grasses and fire: the importance of hiding buds: A response to Moore et al. (2019) 'Effects of drought and fire on resprouting capacity of 52 temperate

- Australian perennial native grasses.' *New Phytologist* 226: 957–959.
- Pausas, J.G., Pratt, R.B., Keeley, J.E., Jacobsen, A.L., Ramirez, A.R., Vilagrosa, A., Paula, S., Kaneakua-Pia, I.N., & Davis, S.D. 2016. Towards understanding resprouting at the global scale. *New Phytologist* 209: 945–954.
- Pilon, N.A.L., Cava, M.G.B., Hoffmann, W.A., Abreu, R.C.R., Fidelis, A., & Durigan, G. 2021. The diversity of post-fire regeneration strategies in the cerrado ground layer. *Journal of Ecology*. doi: 10.1111/1365-2745.13456
- 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: 111–123.
- Pivello, V.R., Vieira, I., Christianini, A.V., Ribeiro, D.B., da Silva Menezes, L., Berlinck, C.N., Melo, F.P.L., Marengo, J.A., Tornquist, C.G., Tomas, W.M., & Overbeck, G.E. 2021. Understanding Brazil's catastrophic fires: Causes, consequences and policy needed to prevent future tragedies. *Perspectives in Ecology and Conservation* 19: 233–255.
- Qi, Y., Wei, W., Chen, C., & Chen, L. 2019. Plant root-shoot biomass allocation over diverse biomes: A global synthesis. *Global Ecology and Conservation* 18: e00606.
- R Core Team. 2021. R: a language and environment for statistical computing.
- Revelle, W. 2021. psych: Procedures for Psychological, Psychometric, and Personality Research. 1–457.
- Ribeiro, J.F., & Walter, B.M.T. 2008. As principais fitofisionomias do bioma Cerrado. In Sano, S.M., De Almeida, S.P., & Ribeiro, J.F. (eds.), *Cerrado: Ecologia e flora*, pp. 152–212. Embrapa Cerrados/ Embrapa Informações Tecnológica.
- Rizzini, C.T., & Heringer, E.P. 1961. Belowground organs of plants from some southern Brazilian savannas, with special reference to the xylopodium. *Phyton* 17: 105–124.
- Silva, J.F., Farinas, M.R., Felfili, J.M., & Klink, C.A. 2006. Spatial heterogeneity, land use and conservation in the cerrado region of Brazil. *Journal of Biogeography* 33: 536–548.
- Silveira, F.A.O., Negreiros, D., Barbosa, N.P.U., Buisson, E., Carmo, F.F., Carstensen, D.W., Conceição, A.A., Cornelissen, T.G., Echternacht, L., Fernandes, G.W., Garcia, Q.S., Guerra, T.J., Jacobi, C.M., Lemos-Filho, J.P., Le Stradic, S., Morellato, L.P.C., Neves, F.S., Oliveira, R.S., Schaefer, C.E., Viana, P.L., & Lambers, H. 2016. Ecology and evolution of plant diversity in the endangered campo rupestre: a neglected conservation priority. *Plant and Soil*

403: 129–152.

- Simon, M.F., & Pennington, T. 2012. Evidence for adaptation to fire regimes in the tropical savannas of the Brazilian Cerrado. *International Journal of Plant Sciences* 173: 711–723.
- Simpson, K.J., Jardine, E.C., Archibald, S., Forrestel, E.J., Lehmann, C.E.R., Thomas, G.H., & Osborne, C.P. 2021. Resprouting grasses are associated with less frequent fire than seeders. *New Phytologist* 230: 832–844.
- Simpson, K.J., Olofsson, J.K., Ripley, B.S., & Osborne, C.P. 2019. Frequent fires prime plant developmental responses to burning. *Proceedings of the Royal Society B: Biological Sciences* 286:.
- Tiedemann, A., R., Clary, W., P., & Barbour, R., J. 1987. Belowground Systems of Gambel Oak (*Quercus gambelii*) in Central Utah. *American Journal of Botany* 74: 1065–1071.
- Tobin, B., Čermák, J., Chiatante, D., Danjon, F., Di Iorio, A., Dupuy, L., Eshel, A., Jourdan, C., Kalliokoski, T., Laiho, R., Nadezhdina, N., Nicoll, B., Pagès, L., Silva, J., & Spanos, I. 2007. Towards developmental modelling of tree root systems. *Plant Biosystems - An International Journal Dealing with all Aspects of Plant Biology* 141: 481–501.
- Veldman, J.W., Buisson, E., Durigan, G., Fernandes, G.W., Le Stradic, S., Mahy, G., Negreiros, D., Overbeck, G.E., Veldman, R.G., Zaloumis, N.P., Putz, F.E., & Bond, W.J. 2015. Toward an old-growth concept for grasslands, savannas, and woodlands. *Frontiers in Ecology and the Environment* 13: 154–162.
- Vesk, P.A., & Yen, J.D.L. 2019. Plant resprouting: How many sprouts and how deep? Flexible modelling of multi-species experimental disturbances. *Perspectives in Plant Ecology, Evolution and Systematics* 41:.
- Wickham, H., Chang, W., Henry, L., Pedersen, T.L., Takahashi, K., Woo, C., Kara, W., Yutani, H., Dunnington, D., & RStudio. 2020. Package “ggplot2” Title Create Elegant Data Visualisations Using the Grammar of Graphics.
- Zhou, M., Guo, Y., Sheng, J., Yuan, Y., Zhang, W.H., & Bai, W. 2022. Using anatomical traits to understand root functions across root orders of herbaceous species in a temperate steppe. *New Phytologist*. doi: 10.1111/nph.17978
- 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:.
- Zuur, A.F., Ieno, E.N., Walker, N., Saveliev, A.A., & Smith, G.M. 2009. Mixed effects models

and extensions in ecology with R. Springer New York, New York, NY.

## **Material Suplementar**

Até o momento da publicação desse manuscrito, todos os dados que suportam os achados desse estudo estarão disponíveis no repositório Zenodo.

**Table S1.** Belowground organ classification according to bud-bearing functions based on Bombo et al. (2021) and Pausas et al. (2018).

| Underground organ type | General description                                                                                                                                                                                                                                                          | Function                                                             |
|------------------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|----------------------------------------------------------------------|
| Bulb/corm              | Swollen underground structures with one or few buds (i.e. bulb, corm).                                                                                                                                                                                                       | persistence and resprouting.                                         |
| xylopodium             | Woody basal burls with buds located at the upper part of the structure and associated with roots.                                                                                                                                                                            | persistence and resprouting (if associated with storage structures). |
| root crown             | Buds located at the root shoot transition zone with no basal burls.                                                                                                                                                                                                          | <i>in situ</i> persistence and resprouting.                          |
| woody rhizome          | Woody burls with buds located at the knots or rhizome associated with stems growing horizontally.                                                                                                                                                                            | persistence, resprouting and lateral spreading.                      |
| rhizome                | The sum of herbaceous subterranean axis stems with buds that grow horizontally or semi vertically from a parent plant without a defined limit (i.e., fleshy rhizomes) and stems that grow downwards with buds deeply buried and that give rise to roots (i.e., rhizophores). | persistence, resprout, and lateral spreading.                        |
| gemiferous roots       | Roots with buds that produced vertical suckers, or one or few stems (i.e., taproot tuber, bud bearing root, adventitious roots tuber).                                                                                                                                       | persistence, resprouting and lateral spreading.                      |
| others                 | Non identify fragment of bud-bearing organs that could not fitted in the categories pervious described.                                                                                                                                                                      | -                                                                    |

## Reference

- Bombo, A., Siebert, F., & Fidelis, A. 2021. Fire and herbivory shape belowground bud banks in a semi-arid African savanna. *African Journal of Range & Forage Science*. doi: 10.2989/10220119.2021.1982004
- 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: 1435–1448.



**Table S2.** Belowground allocation variables (mean  $\pm$  SE) measured in tropical open ecosystems comparing areas frequently burn (i.e., the last 35 years burned 5-19 times, fire hereafter) to areas excluded from fire in the last 12 years (i.e., the last 35 years burned 1-7 times, exclusion hereafter).

|                  |             | Total<br>belowground<br>biomass (gm <sup>-2</sup> ) | Total<br>belowground<br>organ biomass<br>(gm <sup>-2</sup> ) | Total coarse<br>root biomass<br>(gm <sup>-2</sup> ) | Total fine root<br>biomass (gm <sup>-2</sup> ) | B:A<br>allocation | Organs:shoot<br>ratio | Root:shoot<br>ratio |
|------------------|-------------|-----------------------------------------------------|--------------------------------------------------------------|-----------------------------------------------------|------------------------------------------------|-------------------|-----------------------|---------------------|
| <b>Exclusion</b> | <i>All</i>  | 966.27 $\pm$ 110.37                                 | 558.60 $\pm$ 91.37                                           | 56.35 $\pm$ 15.14                                   | 351.31 $\pm$ 30.68                             | 5.53 $\pm$ 0.69   | 2.82 $\pm$ 0.45       | 2.71 $\pm$ 0.35     |
|                  | <i>PNC</i>  | 2057.43 $\pm$ 227.40                                | 1470.26 $\pm$ 228.70                                         | 30.35 $\pm$ 9.17                                    | 556.83 $\pm$ 85.18                             | 6.44 $\pm$ 0.62   | 4.52 $\pm$ 0.57       | 1.93 $\pm$ 0.30     |
|                  | <i>PNB</i>  | 889.62 $\pm$ 200.73                                 | 475.86 $\pm$ 145.60                                          | 109.31 $\pm$ 71.35                                  | 304.45 $\pm$ 23.07                             | 8.45 $\pm$ 2.95   | 4.53 $\pm$ 1.83       | 3.93 $\pm$ 1.34     |
|                  | <i>PNCA</i> | 550.39 $\pm$ 55.25                                  | 122.56 $\pm$ 22.17                                           | 47.74 $\pm$ 15.80                                   | 380.09 $\pm$ 39.77                             | 5.23 $\pm$ 0.90   | 1.05 $\pm$ 0.15       | 4.18 $\pm$ 0.80     |
|                  | <i>PNCG</i> | 984.40 $\pm$ 213.78                                 | 504.98 $\pm$ 155.85                                          | 47.71 $\pm$ 20.48                                   | 431.71 $\pm$ 63.95                             | 4.13 $\pm$ 1.03   | 2.09 $\pm$ 0.70       | 2.05 $\pm$ 0.39     |
|                  | <i>RNST</i> | 405.56 $\pm$ 106.22                                 | 250.20 $\pm$ 99.32                                           | 47.54 $\pm$ 13.89                                   | 107.83 $\pm$ 13.51                             | 3.60 $\pm$ 0.72   | 2.00 $\pm$ 0.50       | 1.60 $\pm$ 0.33     |
| <b>Fire</b>      | <i>All</i>  | 1246.35 $\pm$ 135.89                                | 621.88 $\pm$ 99.62                                           | 155.73 $\pm$ 48.27                                  | 468.74 $\pm$ 32.97                             | 6.99 $\pm$ 0.51   | 3.13 $\pm$ 0.39       | 3.86 $\pm$ 0.30     |
|                  | <i>PNC</i>  | 1935.70 $\pm$ 186.98                                | 1141.73 $\pm$ 160.85                                         | 99.86 $\pm$ 42.67                                   | 694.11 $\pm$ 104.97                            | 9.28 $\pm$ 1.02   | 5.55 $\pm$ 1.04       | 3.73 $\pm$ 0.46     |
|                  | <i>PNB</i>  | 816.00 $\pm$ 110.73                                 | 391.10 $\pm$ 117.38                                          | 19.20 $\pm$ 11.58                                   | 405.71 $\pm$ 57.46                             | 6.70 $\pm$ 0.87   | 2.89 $\pm$ 0.68       | 3.80 $\pm$ 0.78     |
|                  | <i>PNCA</i> | 831.96 $\pm$ 77.69                                  | 194.69 $\pm$ 34.97                                           | 23.57 $\pm$ 5.33                                    | 613.71 $\pm$ 65.06                             | 6.40 $\pm$ 0.92   | 1.52 $\pm$ 0.35       | 4.89 $\pm$ 0.72     |
|                  | <i>PNCG</i> | 628.65 $\pm$ 197.57                                 | 282.00 $\pm$ 163.44                                          | 15.07 $\pm$ 9.44                                    | 331.58 $\pm$ 46.28                             | 5.11 $\pm$ 1.02   | 1.97 $\pm$ 0.73       | 3.14 $\pm$ 0.63     |
|                  | <i>RNST</i> | 1948.05 $\pm$ 406.76                                | 1063.56 $\pm$ 293.93                                         | 538.74 $\pm$ 161.44                                 | 345.76 $\pm$ 15.48                             | 7.57 $\pm$ 1.38   | 3.83 $\pm$ 0.91       | 3.74 $\pm$ 0.67     |

Abbreviations: B:A, belowground :aboveground.

**Table S3.** Belowground organ types (mean  $\pm$  SE) measured in tropical open ecosystems comparing areas frequently burn (i.e., the last 35 years burned 5-19 times, fire hereafter) to areas excluded from fire in the last 12 years (i.e., the last 35 years burned 1-7 times, exclusion hereafter).

|           |      | Bulb/corm<br>(gm <sup>-2</sup> ) | Xylopodium<br>(gm <sup>-2</sup> ) | Root<br>Crown (gm <sup>-2</sup> ) | Woody rhizome<br>(gm <sup>-2</sup> ) | Rhizome (gm <sup>-2</sup> ) | Gemiferous<br>roots (gm <sup>-2</sup> ) | others<br>(gm <sup>-2</sup> ) |
|-----------|------|----------------------------------|-----------------------------------|-----------------------------------|--------------------------------------|-----------------------------|-----------------------------------------|-------------------------------|
| Exclusion | All  | 0.00 $\pm$ 0.00                  | 3.78 $\pm$ 1.82                   | 0.25 $\pm$ 0.25                   | 33.13 $\pm$ 17.93                    | 509.69 $\pm$ 91.25          | 5.31 $\pm$ 2.56                         | 6.45 $\pm$ 3.39               |
|           | PNC  | 0.00 $\pm$ 0.00                  | 3.04 $\pm$ 2.23                   | 0.00 $\pm$ 0.00                   | 0.98 $\pm$ 0.98                      | 1465.18 $\pm$ 228.62        | 0.00 $\pm$ 0.00                         | 1.06 $\pm$ 0.89               |
|           | PNB  | 0.00 $\pm$ 0.00                  | 12.80 $\pm$ 8.49                  | 1.28 $\pm$ 1.28                   | 118.27 $\pm$ 83.50                   | 324.13 $\pm$ 94.83          | 1.63 $\pm$ 1.22                         | 17.74 $\pm$ 13.63             |
|           | PNCA | 0.00 $\pm$ 0.00                  | 2.98 $\pm$ 2.04                   | 0.00 $\pm$ 0.00                   | 13.60 $\pm$ 13.60                    | 104.50 $\pm$ 22.19          | 0.00 $\pm$ 0.00                         | 1.49 $\pm$ 1.08               |
|           | PNCG | 0.00 $\pm$ 0.00                  | 0.00 $\pm$ 0.00                   | 0.00 $\pm$ 0.00                   | 0.00 $\pm$ 0.00                      | 504.98 $\pm$ 155.85         | 0.00 $\pm$ 0.00                         | 0.00 $\pm$ 0.00               |
|           | RNST | 0.00 $\pm$ 0.00                  | 0.41 $\pm$ 0.41                   | 0.00 $\pm$ 0.00                   | 32.82 $\pm$ 26.68                    | 182.37 $\pm$ 104.18         | 23.15 $\pm$ 10.48                       | 11.45 $\pm$ 9.48              |
| Fire      | All  | 0.49 $\pm$ 0.49                  | 143.31 $\pm$ 54.45                | 0.00 $\pm$ 0.00                   | 20.89 $\pm$ 12.67                    | 431.16 $\pm$ 66.92          | 8.90 $\pm$ 4.65                         | 17.14 $\pm$ 9.17              |
|           | PNC  | 0.00 $\pm$ 0.00                  | 1.99 $\pm$ 1.99                   | 0.00 $\pm$ 0.00                   | 62.47 $\pm$ 62.47                    | 1073.75 $\pm$ 174.57        | 0.11 $\pm$ 0.11                         | 3.41 $\pm$ 2.77               |
|           | PNB  | 0.00 $\pm$ 0.00                  | 86.34 $\pm$ 68.93                 | 0.00 $\pm$ 0.00                   | 2.29 $\pm$ 1.73                      | 278.97 $\pm$ 112.73         | 0.00 $\pm$ 0.00                         | 23.50 $\pm$ 13.98             |
|           | PNCA | 0.00 $\pm$ 0.00                  | 6.32 $\pm$ 6.32                   | 0.00 $\pm$ 0.00                   | 6.24 $\pm$ 6.24                      | 182.13 $\pm$ 28.49          | 0.00 $\pm$ 0.00                         | 0.00 $\pm$ 0.00               |
|           | PNCG | 0.00 $\pm$ 0.00                  | 130.66 $\pm$ 130.66               | 0.00 $\pm$ 0.00                   | 32.72 $\pm$ 32.72                    | 112.02 $\pm$ 18.75          | 0.00 $\pm$ 0.00                         | 6.61 $\pm$ 6.608              |
|           | RNST | 2.08 $\pm$ 2.08                  | 421.47 $\pm$ 179.72               | 0.00 $\pm$ 0.00                   | 7.56 $\pm$ 4.93                      | 549.53 $\pm$ 129.74         | 37.73 $\pm$ 17.86                       | 45.19 $\pm$ 36.61             |

**Table S4.** Statistical models to analyze belowground allocation (biomasses in g.m<sup>-2</sup>) variables relative to areas frequently burn (i.e., the last 35 years burned 5-19 times, fire hereafter) and to areas excluded from fire in the last 12 years (i.e., the last 35 years burned 1-7 times, exclusion hereafter) in Cerrado open ecosystems. Estimates of predictive variables are informed together with confidence intervals (inside the parenthesis). The model intercepts are also presented. More details on the statistical analyses are available in the main text.

|                                                         | Belowground                          | Belowground<br>organs           | Coarse root                | Fine root                             | B:A allocation                      | Root:shoot ratio                   | Organs:shoot<br>ratio        |
|---------------------------------------------------------|--------------------------------------|---------------------------------|----------------------------|---------------------------------------|-------------------------------------|------------------------------------|------------------------------|
| (Intercept)                                             | <b>6.56***</b><br>(6.17 – 6.95)      | <b>5.58***</b><br>(4.90 – 6.26) | 53.32<br>(-48.78 – 155.42) | <b>5.66 ***</b><br>(5.32 – 6.00)      | <b>1.43***</b><br>(1.18 – 1.68)     | <b>2.72***</b><br>(1.92 – 3.52)    | 0.42<br>(-0.10 – 0.94)       |
| Fire- Exclusion                                         | <b>0.34**</b> (log)<br>(0.08 – 0.59) | 0.33 (log)<br>(-0.11 – 0.76)    | 95.82*<br>(4.52 – 187.13)  | <b>0.41***</b> (log)<br>(0.23 – 0.59) | <b>0.38*</b> (log)<br>(0.13 – 0.63) | <b>1.15**</b> (log)<br>0.28 – 2.01 | 0.32 (log)<br>(-0.09 – 0.73) |
| N <sub>local</sub>                                      | 5                                    | 5                               | 5                          | 5                                     | 5                                   | 5                                  | 5                            |
| Marginal R <sup>2</sup> /<br>Conditional R <sup>2</sup> | 0.047 / 0.303                        | 0.015 / 0.283                   | 0.035 / 0.159              | 0.109 / 0.441                         | 0.073 / 0.153                       | 0.059 / 0.120                      | 0.019 / 0.190                |

Abbreviations: B:A, belowground :aboveground. Bold text indicates significance (\*\*\*)  $p < 0.001$ ; \*\*  $p < 0.01$ ; \*  $p < 0.05$ ). (log) refers to log transformation.

**Table S5.** Permutational multivariate analysis of variance (PERMANOVA) for the dissimilarities (999 bootstrap,  $p < 0.05$ ) of the underground organ types between areas comparing areas frequently burn (i.e., the last 35 years burned 5-19 times, fire hereafter) to areas excluded from fire in the last 12 years (i.e., the last 35 years burned 1-7 times, exclusion hereafter) in Cerrado open ecosystems. Adjusted p-values were obtained though Bonferroni correction. Bold text indicates significance ( $p < 0.05$ ).

|                   |      | F-model | R <sup>2</sup> | p-value       | p-value adjusted |
|-------------------|------|---------|----------------|---------------|------------------|
| Fire vs Exclusion | All  | 1.416   | 0.014          | 0.274         | 0.234            |
|                   | PNC  | 0.700   | 0.040          | 0.652         | 0.323            |
|                   | PNB  | 0.998   | 0.053          | 0.427         | 0.426            |
|                   | PNCA | 1.551   | 0.079          | 0.161         | 0.088            |
|                   | PNCG | 3.250   | 0.153          | <b>0.004*</b> | <b>0.007*</b>    |
|                   | RNST | 4.002   | 0.160          | <b>0.003*</b> | <b>0.001*</b>    |

**Table S6.** Statistical models to analyze belowground allocation and biomass ( $\text{g.m}^{-2}$ ) variables relative to areas frequently burn (i.e., the last 35 years burned 5-19 times, fire hereafter) and areas excluded from fire in the last 12 years (i.e., the last 35 years burned 1-7 times, exclusion hereafter), in each one of the Cerrado open ecosystem sampled. Estimates of predictive variables are informed together with confidence intervals (inside the parenthesis). The model intercepts are also presented. More details on the statistical analyses are available in the main text.

|      |                          | Belowground          | Belowground<br>organs | Coarse roots           | Fine roots           | B:A ratio           | Root:shoot<br>ratio  | Organs:shoot<br>ratio |
|------|--------------------------|----------------------|-----------------------|------------------------|----------------------|---------------------|----------------------|-----------------------|
| PNC  | (Intercept)              | <b>2057.43***</b>    | <b>1470.26***</b>     | 30.35                  | <b>6.22***</b>       | <b>1.73***</b>      | <b>1.68***</b>       | <b>4.52***</b>        |
|      |                          | (1676.66 – 2438.20)  | (1105.79 – 1834.72)   | (-22.59 – 83.30)       | (5.96 – 6.49)        | (1.64 – 1.83)       | (1.46 – 1.94)        | (3.05 – 5.98)         |
|      | Fire- Exclusion          | -121.74              | -328.52               | 69.51(*)               | 0.24(log)            | <b>0.91*</b> (log)  | <b>0.78**</b> (log)  | 1.03                  |
|      |                          | (-674.98 – 431.51)   | (-858.08 – 201.03)    | (-7.42 – 146.43)       | (-0.15 – 0.62)       | (0.85 – 0.98)       | (0.66 – 0.91)        | (-1.10 – 3.16)        |
| PNB  | (Intercept)              | <b>6.64***</b>       | <b>5.44***</b>        | <b>7.36***</b>         | <b>5.69***</b>       | <b>1.64***</b>      | <b>0.98*</b>         | 0.49                  |
|      |                          | (6.21 – 7.08)        | 4.69 – 6.19           | (3.89 – 10.83)         | (5.48 – 5.89)        | 1.16 – 2.12         | (0.54 – 1.42)        | (-0.30 – 1.28)        |
|      | Fire- Exclusion          | -0.44(log)           | 0.16 (log)            | -3.94(sqrt)            | 0.24(log)            | 0.17 (log)          | 0.19 (log)           | 0.3 (log)             |
|      |                          | (-1.06 – 0.17)       | -0.90 – 1.22          | -8.84 – 0.97           | (-0.05 – 0.53)       | -0.51 – 0.85        | (-0.44 – 0.81)       | (-0.82 – 1.41)        |
| PNCA | (Intercept)              | <b>6.26***</b>       | <b>122.56***</b>      | <b>5.8***</b>          | <b>5.89***</b>       | <b>1.92***</b>      | <b>1.26***</b>       | -0.09                 |
|      |                          | (6.08 – 6.45)        | (68.12 – 177.00)      | (3.95 – 7.66)          | (5.69 – 6.08)        | (1.71 – 2.16)       | (0.94 – 1.58)        | (-0.47 – 0.29)        |
|      | Fire- Exclusion          | <b>0.42**</b>        | 72.13(*)              | -1.36(sqrt)            | <b>0.49***</b> (log) | 0.92 (log)          | 0.24 (log)           | 0.3                   |
|      |                          | (0.15 – 0.68)        | (-4.87 – 149.12)      | (-3.98 – 1.26)         | (0.21 – 0.76)        | (0.79 – 1.07)       | (-0.21 – 0.69)       | (-0.24 – 0.84)        |
| PNCG | (Intercept)              | <b>6.64***</b>       | 5.39                  | <b>6.02***</b>         | <b>5.94***</b>       | <b>1.11***</b>      | <b>0.52***</b>       | -0.14                 |
|      |                          | (6.21 – 7.08)        | (4.42 – 6.35)         | (4.10 – 7.94)          | (5.62 – 6.27)        | (0.65 – 1.58)       | (0.12 – 0.92)        | (-1.10 – 0.81)        |
|      | Fire- Exclusion<br>(log) | -0.44                | -0.45(log)            | <b>-3.3*</b> (sqrt)    | -0.26                | 0.32 (log)          | 0.44 (log)           | 0.31                  |
|      |                          | (-1.06 – 0.17)       | (-1.82 – 0.91)        | (-6.02 – -0.59)        | (-0.72 – 0.20)       | -0.34 – 0.98        | (-0.12 – 1.01)       | (-1.04 – 1.66)        |
| RNST | (Intercept)              | <b>5.79***</b>       | <b>5.13***</b>        | 47.54                  | <b>4.61***</b>       | <b>1.08***</b>      | 0.24                 | <b>2**</b>            |
|      |                          | (5.40 – 6.18)        | 4.57 – 5.70           | (-181.72 – 276.80)     | (4.45 – 4.77)        | (0.70 – 1.46)       | (-0.14 – 0.61)       | (0.56 – 3.45)         |
|      | Fire- Exclusion          | <b>1.52***</b> (log) | <b>1.3**</b> (log)    | <b>491.21**</b> (sqrt) | <b>1.22***</b> (log) | <b>0.76**</b> (log) | <b>0.93***</b> (log) | 1.82(*)               |
|      |                          | (0.98 – 2.07)        | 0.52 – 2.09           | (173.81 – 808.60)      | (1.00 – 1.45)        | (0.23 – 1.29)       | (0.41 – 1.45)        | (-0.18 – 3.83)        |

Abbreviations: B:A, belowground :aboveground allocation. Bold text indicates significance (\*\*\*  $p < 0.001$ ; \*\*  $p < 0.01$ ; \*  $p < 0.05$  and (\*) marginal significant  $p < 0.08$ ). (log) and (sqrt) refers to log and square root transformation.

Ecosystem dynamics in response to fire  
frequency and biological invasion in the  
Cerrado

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**Abstract:** Changes in fire frequencies and the occurrence of biological invasion are current threats to the functioning of terrestrial ecosystems. In tropical savannas, it is not clear how these global changes might alter ecosystem processes including carbon and water fluxes. Using a tropical savanna as model and considering the seasonal variation of the system (i.e. rainy and dry season), we aimed to understand how net ecosystem and carbon exchange (NEE), water (ET, evapotranspiration) and the ecosystem water use efficiency (eWUE) were responding to different fire frequencies, i.e., high frequency (annual and biennial fires treatment) and decrease of fire frequency (4-5 years without fire, fire exclusion treatment); and biological invasion (invaded by African grass vs. uninvaded areas). At high fire frequencies NEE rates decreased after fire but recovered quickly during the first rainy season after fire, up to values similar to unburnt areas. ET rates were low after fire but increased during rainy season for biennial fires but important interannual variation were also observed. Biennial fires increased eWUE after fire, whereas for annual and fire exclusion eWUE did not show variation. While NEE varies in the non-invaded areas between rainy and dry season, it did not vary in invaded areas. We concluded that the effect of high fire frequency on NEE was quickly reestablished in the first rainy season after fire, and that the effect of biological invasion was primarily to buffer the seasonal variation observed in uninvaded system.

**Keywords:** fire regime, biological invasion, carbon flux, water flux, open ecosystems, tropical savanna, Cerrado

## **INTRODUCTION**

Changes in fire regimes (e.g. fire frequency) and biological invasions are major threats to tropical savanna conservation worldwide (Keeley and Pausas 2019; Bowman and others 2020; Bond 2022; Stevens and others 2022). Changes in fire regime alter vegetation structure and biodiversity as well the ecosystem functions of natural ecosystems (Scheffer and others 2001; Scheffer and Carpenter 2003; Ratajczak and others 2018; Stevens and others 2022). Biological invasions (Pyšek and others 2020) can also modify the structure of tropical savannas, by increasing dead biomass accumulation, decreasing the cover of native species, and generating biodiversity loss. These modifications affect tropical savanna functioning, including carbon fluxes (Damasceno and others 2018; Linders and others 2019; Pyšek and others 2020). Then, both changes in fire regime and biological invasion, may modify both carbon (C) and water dynamics (Scholze and others 2006; Rogers and others 2020) and then the balance of atmospheric gases, and the biogeochemical cycles.

Contrasting fire frequencies, levels of biological invasion, and vegetation types strongly determine C and water fluxes in tropical savannas (Miranda and others 1997; Grace and others 2006; Catford and others 2012; Teixeira and others 2022). Alterations in C and water dynamics affect ecosystems C sink and source, and water use efficiency, because it acts on ecosystem C balance, budget, and water stability (Le Quéré and others 2009; Scott and others 2014). However, which variation in fire frequency and which cover of invasive species are required to effectively impact processes like C and water dynamics, remain poorly evaluated in tropical open savannas (but see Garcia and others 2022). In addition, the interaction between these factors and the seasonal climate is an additional difficulty to evaluate how ecosystem functioning will be affected by variations in fire frequency and biological invasion.



Tropical savannas under current fire regime (i.e., low intensity fires, with fire frequency of two to six years for open ecosystems in Brazil) (Eiten 1972; Mistry 1998; Pivello 2011; Fidelis and others 2018) quickly compensate carbon loss due to emission from fire by the prompt regeneration of the vegetation (Santos and others 2003; Bowman and others 2020; McLauchlan and others 2020). However, the increase of fire frequencies (i.e., fire intervals <1-2 years), promotes a decrease of vegetation cover (grasses and woody), fuel load and an increase of bare soil (Pivello and Coutinho 1996; Govender and others 2006; Pivello 2011; Rodrigues and others 2021). These changes in vegetation structure may compromise general C uptake by decreasing soil evapotranspiration and net ecosystem carbon exchange (NEE) (Miranda and others 2002; Quesada and others 2004; Gomes and others 2020). On the other hand, fire suppression might result in a shift from a dominant herbaceous layer to woody and forest vegetation (Abreu and others 2017), increasing ecosystem evapotranspiration (ET) (Honda and Durigan 2016; Schreiner-McGraw and others 2020) and decreasing ecosystem water use efficiency (eWUE) (Scott and others 2014), or even showing no effect on ET and eWUE (Teixeira and others 2020). Once encroached, the increase of carbon storage capacity in such systems can be limited due the lower belowground C stock capacity of encroached system (Zhou and others 2022), although a greater C investment on aboveground biomass (Abreu and others 2017).

Biological invasion by exotic grasses may not lead to strong modification of water and C fluxes in tropical savannas (Ens and others 2015), as grasses are still the dominant growth form in the community. Indeed, when the invasive species is functionally similar to the dominant native species (Strauss and others 2006; Funk and others 2008); we may expect that the ecosystem processes remained similar or only slightly altered (Garcia and others 2022). However, African grasses invading the Cerrado produce higher biomass than native grasses (Damasceno and others

2018). We then may expect an increase of water fluxes since photosynthetic rates are higher in invaded than in non-invaded systems and ET might also increase (Williams and Baruch 2000; Van Kleunen and others 2010). Besides, in nutrient-poor savannas like Cerrado, invasive species have higher eWUE compared to native ones (Funk and Vitousek 2007; Musso and others 2021), further increasing biomass productivity and promoting the persistence of the invasive species (Damasceno and others 2018).

Seasonality also strongly drives both C and water fluxes in tropical open savannas (Grace and others 2006; Kutsch and others 2008). At the beginning of the rainy season, ecosystem carbon and water fluxes increase due to the high leaf area from growth of live biomass necessary for ensuring high photosynthetic rates (Miranda and others 1997; Giambelluca and others 2009). These fluxes then decrease during the dry season with the transformation of live to dead biomass (Miranda and others 1997; Santos and others 2003; Oliveras and others 2013). Changes in fire regime in combination with seasonality can even more strongly alter carbon and water fluxes balance (Bowman and others 2020; Miller and others 2021). Fire exclusion might boost C release from vegetation during the rainy season by the reduction of eWUE (Santos and others 2003). The system then switches from being a sink of atmospheric CO<sub>2</sub> to becoming a source of atmospheric CO<sub>2</sub> (Huxman and others 2004; Scott and others 2014). In the same manner, the interaction between biological invasion and seasonality may also disrupt water and C fluxes, as a consequence of modification in phenology, biomass production and alteration of microclimate by the invasive species (D'Antonio and Vitousek 1992; Setterfield and others 2008; Vila and others 2011). In open savannas, due to greater biomass production by the invasive species (Litton and Giardina 2008; Lannes and others 2012), alterations in ecosystem processes may happen by increasing ET and eWUE during the dry season (Levine and others 2003).

Our study focused on these two factors: fire frequency and biological invasion, which might alter carbon and water fluxes of open savannas of the Cerrado. We investigated how net ecosystem C and water fluxes (i.e., NEE, ET and eWUE) in tropical open savannas will vary according to contrasting fire frequencies (i.e., high fire frequency – both annual and biennial, and decrease of fire frequency – 4-5 years without fire – fire exclusion, fire frequency hereafter), and biological invasion by *Urochloa brizantha* (Hochst. ex A. Rich.) R.D. Webster, an African grass species presenting functional similarity with the native Cerrado grasses (i.e. invaded and non-invaded, biological invasion hereafter). We also assessed how the effect of fire and biological invasion on C and water fluxes was modulated by the seasonal variations. We expected (i) higher ET but lower eWUE and NEE at the fire exclusion in comparison with high fire frequencies; and (ii) higher NEE, ET and eWUE during the rainy season and lower NEE, ET and eWUE during the dry season in high fire frequency areas contrary to fire exclusion areas. During the dry season, we predicted low eWUE at fire exclusion (high ET and no changes in NEE). We expected (iii) higher eWUE, NEE and ET at invaded areas compared to non-invaded areas and (iv) higher eWUE during dry season at invaded systems (high NEE and low ET) due to the high efficiency of the invasive species.

## MATERIAL AND METHODS

### *Study site*

The study was conducted at the Reserva Natural Serra do Tombador (hereafter RNST; 1313° 35-38' S and 47° 45'-51' W, 8900ha, 560–1118m a.s.l.) in Central Brazil during the rainy season of 2015, and rainy and dry season of 2016. The RNST is characterized by high fire frequency (3-year intervals) (Daldegan and others 2014) and the occurrence of patches dominated by invasive African grasses *Urochloa brizantha* and *Melinis minutiflora* P. Beauv. (Gorgone-Barbosa 2016).

The climate of the region is tropical and markedly seasonal with wet summer between November and April (i.e. total precipitation > 1000mm), and dry winter between May and October (i.e. total precipitation <100mm) (Zanzarini and others 2022). The mean annual temperature is 24°C and the mean annual precipitation is 1300-1500mm (Fundação Grupo Boticário 2011). The RNST has a mosaic of Cerrado vegetation types with the prevalence of open savannas (campo sujo, Fundação Grupo Boticário 2011). They are composed by a C4 grass layer, rich in forb species with scattered trees and small shrubs, presenting overall low tree cover (Coutinho 1978). We used for this study two distinct areas in RNST: one area with native vegetation, where a long-term fire experiment was set up (the area burned every 2-3 years before the establishment of the experiment in 2013, Daldegan and others 2014) to evaluate fire frequency effects. To assess the effects of biological invasions, we selected an area with patches invaded by *Urochloa brizantha*. This area has been excluded from fire since 2006 (Gorgone-Barbosa 2016). Both areas were excluded from grazing since 2006.

#### *Treatments of fire frequencies*

In 2013, a long-term fire experiment was set up in an area of open savanna (see Rissi and others 2017; Rodrigues and others 2021). The fire experiment presents different treatments of fire frequency including annual and biennial burnings and fire exclusion (since 2011, 4-5 years without fire during the time the measurements for this study were taken). Annual and biennial fire frequency treatment represent high fire frequency and fire exclusion treatment represent the decrease of fire frequency. Each treatment was independently applied in four plots of 30 × 30m. For our study, we randomly selected three plots of each fire treatment (3 plots x 3 treatments = 9 plots, Table 1). The measurements of ecosystems processes (i.e. NEE, ET and eWUE, see below

for more details) were performed in October 2015 (end of the dry season), January 2016 (rainy season) and October 2016 (end of the dry season). Fires were set in July 2015 (annual and biennial plots) and July 2016 (annual plots). Hereafter, we used the name of each one of the fire frequency treatments to distinguish high fire frequency and decreased of fire frequency.

**Table 1.** General information about the different treatments of fire frequencies (i.e. annual, biennial and fire exclusion) at the Reserva Natural Serra do Tombador (RNST) including number of fires (between 2011 and 2016), years and months of fire and time since the last fire (in months (m) or in years (y) ) regarding the date when measurements were taken (i.e., dry season of 2015 and 2016 and rain season of 2016).

| Treatments of fire frequencies | Years of fires                     | Time since last fire |                   |                 |
|--------------------------------|------------------------------------|----------------------|-------------------|-----------------|
|                                |                                    | 2015 dry season      | 2016 rainy season | 2016 dry season |
| Annual                         | 2011, 2012, 2013, 2014, 2015, 2016 | 3m                   | 6m                | 3 m             |
| Biennial                       | 2011, 2013, 2015                   | 3m                   | 6 m               | 15m             |
| Fire exclusion                 | 2011                               | 4 y                  | 4.5 y             | 5 y             |

### *Biological invasion*

In the invaded area, we selected four invaded patches with at least 50% cover of *Urochloa brizantha* and four non-invaded patches. All patches sized at least 20 × 15 m (Gorgone-Barbosa 2016). The measurements (i.e. NEE, ET and eWUE) were carried out in 2015 at the end of the dry season (October) and in 2016 at the peak of the rainy season (January).

### *C and Water measurements*

We measured net ecosystem exchange of carbon and water (NEE and ET) and ecosystem water use efficiency (eWUE) to assess both C and water fluxes in the ecosystem. The measurements were done in 3 randomly distributed 1m<sup>2</sup> subplots within each of our selected plots. For the fire treatment we then totalized 81 measurements (i.e. 3 subplots × 3 plots × 3 seasons × 3 fire frequencies) and for biological invasion we totalized 48 measurements (i.e. 3 subplots × 4 patches × 2 season × 2 invaded and non-invaded areas). We measured net ecosystem exchange by tracking both the net ecosystem C exchange (NEE;  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ) and water exchange (ET; ecosystem evapotranspiration;  $\mu\text{mol H}_2\text{O m}^{-2} \text{ s}^{-1}$ ) between the biosphere and the atmosphere using the LiCOR 7500 infrared gas analyzer (Li-Cor Inc.) inside a chamber (0.49m<sup>2</sup> total area and 0.37m<sup>3</sup> volume) covered with woven rip-stop polyethylene. The CO<sub>2</sub> was recorded over time during 120 seconds at each subplot covered previously by the chamber (Arnone and Obrist 2003; Huxman and others 2004; Potts and others 2006). Then, ecosystem water use efficiency (eWUE,  $\mu \text{ mol CO}_2 / \mu \text{ mol H}_2\text{O m}^{-2} \text{ s}^{-1}$ ) was determined by calculating the ratio of NEE per the amount of its water lost, i.e. ecosystem evapotranspiration (ET). Negative NEE values mean ecosystem carbon uptake (higher carbon exchange), and positive values means ecosystem carbon release (lower carbon exchange). Due to technical problems during field sampling, we used only 71 observations for the fire treatment.

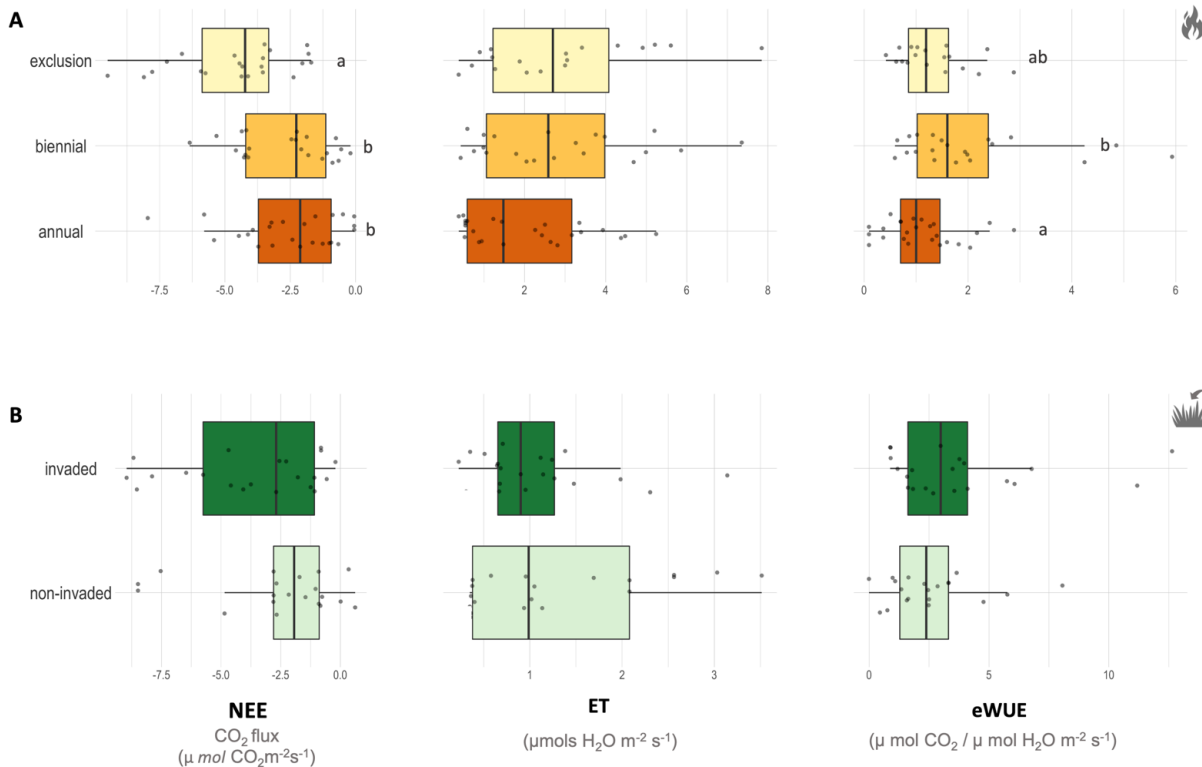
### *Data Analyses*

To quantify the variation of C and water fluxes in response to variation in fire frequency treatments and to biological invasion, we performed linear mixed effect models for each response variable (i.e. NEE, ET and eWUE) (Zuur and others 2009). We first considered as fixed factors each one of the treatments (i.e. the different fire frequencies or biological invasion) to assess their

individual effect on C and water fluxes. To evaluate C and water flux variation including the seasonal variation, we performed a second model considering the interaction of season and treatment as a fixed factor. When the interaction between season and treatment was not significant, we operated model simplification by removing the interaction from the model and considering season and treatment separately as fixed factors. To incorporate the variation of the post-fire condition, the measurements made during the two dry seasons (i.e., October 2015 and October 2016) were not embedded. For all models, we considered the 1 m<sup>2</sup> subplots nested within the treatment plot as a random effect. When the fixed effect was significant, we performed pairwise comparisons using 95% of the confidence interval. We also performed an ANOVA-like to check the random effect significance at each model. All analyses were performed at R environment version 4.1.1 (R Core Team 2021) using *nlme4* (Bates and others 2020) and *emmeans* packages (Lenth and others 2022). We used package *ggplot2* (Wickham and others 2020) for data visualization.

## RESULTS

Fire and biological invasion differed in their effects on the selected ecosystem processes of open savannas. NEE mean value is 19% higher in fire exclusion than in both annual and biennial fire frequencies (Figure 1A, Table S1). The effects of annual and biennial fires on NEE were similar to each other. Biennial fires led to higher values of eWUE compared to annual fires but did not differ with fire exclusion (Figure 1A, Table S3). ET values were similar across all fire frequencies. The presence of the invasive species did not significantly impact NEE, ET and eWUE ( $p>0.05$ , Figure 1B, Table S5).



**Figure 1.** CO<sub>2</sub> net ecosystem exchange (NEE; μmol CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup>), Ecosystem evapotranspiration (ET; μmol H<sub>2</sub>O m<sup>-2</sup> s<sup>-1</sup>) and water use efficiency (eWUE; μmol CO<sub>2</sub> / μmol H<sub>2</sub>O m<sup>-2</sup> s<sup>-1</sup>) at open savannas located in Central Brazil, according to: (A) different treatments of fire frequencies (annual and biennial fires and fire exclusion - 4-5 years without fire); and (B) invasion by an African grass *Urochloa brizantha* (invaded x non-invaded areas). Negative values for NEE means carbon uptake and positive values means carbon release. The letters represent significant comparisons results (p<0.005) from linear mixed effect models. Boxplots are represented in addition to raw data points. The icons were modified from the original version designed by Aisyah (fire, a), Milinda Courey (grass, b), from *thenounproject.com*.

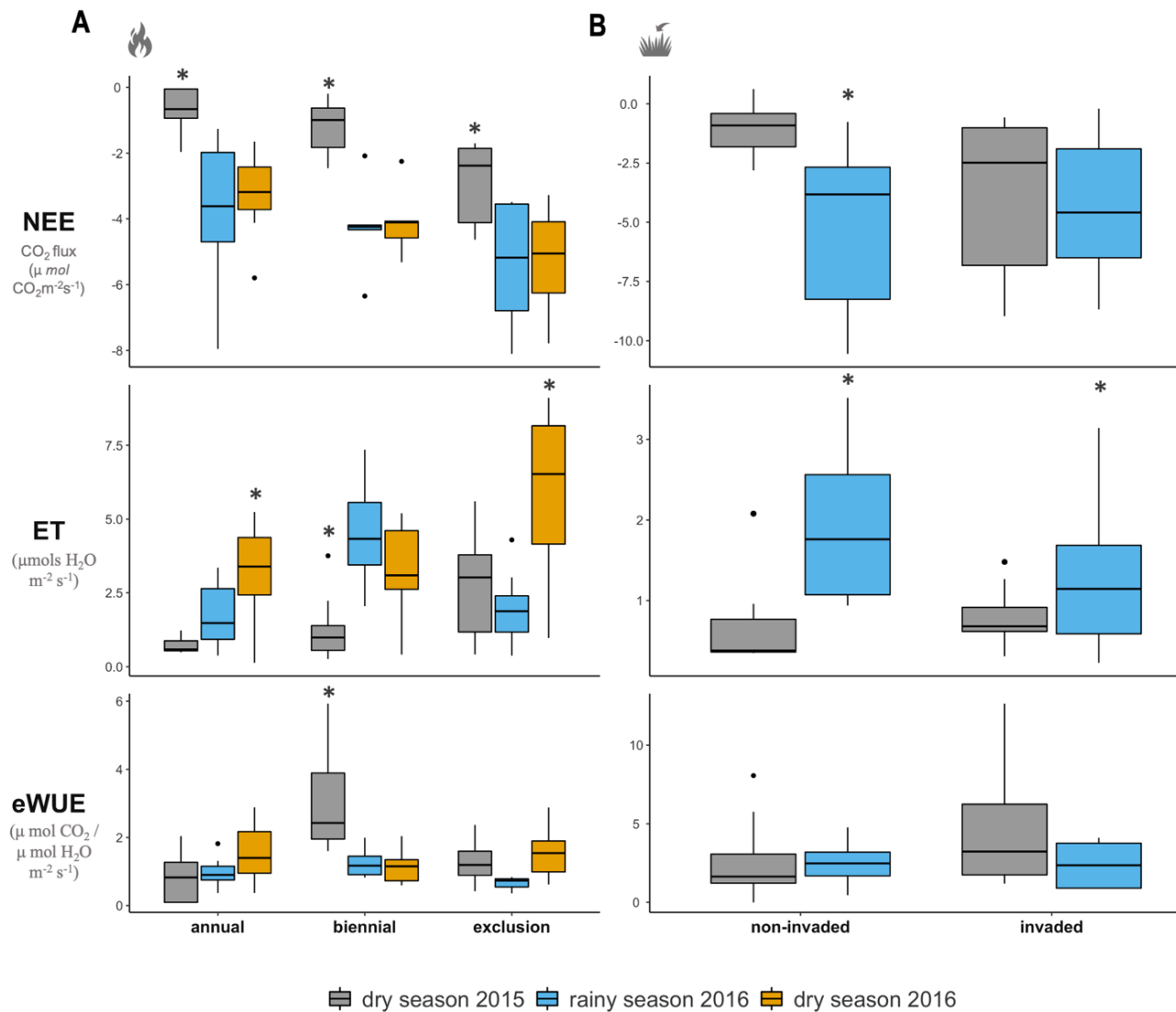
We clearly saw seasonal variations in NEE, ET and eWUE in both cases i.e., fire frequencies and biological invasion (Figure 2). NEE was on average 37% lower (i.e. values close to 0) in the dry season 2015 for all fire frequencies compared to the subsequent rainy and dry seasons of 2016 (Figure 2A, Table S2). Annual and biennial fires caused an average reduction of 80% and 50% in NEE respectively (i.e. values close to 0), compared to fire exclusion, during the first dry season (2015). However, in both annual and biennial fires treatment, NEE values quickly increased with time to reach values similar to fire exclusion treatment areas during the following rainy and dry



season (2016) ( $p>0.05$ , Figure 2A, Table S4). The non-invaded areas registered a reduction of NEE (i.e. values closed to 0) during the dry season of 2015 and an increase of NEE during the rainy season of 2016 (Figure 2B, Table S6). Within the invaded plots, NEE did not vary between dry and rainy seasons (Figure 2B).

ET average increased by ca. 23% from the dry season 2015 to the dry season 2016 for all fire frequencies (Figure 2A, Table S2). In biennial fires, ET increased significantly from the dry (2015) to rainy season of 2016 (Table S4). On the other hand, ET in annual fire and fire exclusion exhibited a lagged response and increased significantly only during the dry season of 2016 (Figure 2A). ET average also increased by ca. 31% and 44% from the dry season 2015 to the rainy season of 2016 in both invaded and non-invaded plots respectively (Figure 2B, Table S3).

eWUE was higher by 35% in average at biennial fire frequency during the dry season of 2015 in comparison to rainy season of 2016 (Figure 2A), while eWUE did not differ between seasons for annual fire frequency and fire exclusion treatments (Figure 2A). eWUE did not differ between dry or rainy season in both invaded and non-invaded patches, although invaded plots tended to present higher eWUE rates during the dry season (Figure 2B, Table S6).



**Figure 2.**  $\text{CO}_2$  net ecosystem exchange (NEE;  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ), Ecosystem evapotranspiration (ET;  $\mu\text{mol H}_2\text{O m}^{-2} \text{ s}^{-1}$ ) and water use efficiency (eWUE,  $\mu\text{mol CO}_2 / \mu\text{mol H}_2\text{O m}^{-2} \text{ s}^{-1}$ ) considering seasonality according to (A) treatments of fire frequencies: annual and biennial fire and fire exclusion treatment (4-5 years without fire); and (B) invasion by an African grass *Urochloa brizantha*. Asterisk represents significant results ( $p < 0.005$ ) from linear mixed effect models. The comparisons were made individually for each treatment (i.e., fire frequencies, invaded and non-invaded) between seasons. For statistical details of the models see supplementary material (Table S3 to S6). Boxplots are represented. Part A and B are represented at a different scale. The icons were modified from the original version designed by Aisyah (fire, a), Milinda Courey (grass, b), from *thenounproject.com*.

## **DISCUSSION**

Our results showed that both fire and biological invasion impacted C and water fluxes, while seasonal variations also played a role in flux variations. We show that all fire frequencies promoted carbon uptake (i.e. NEE negative values) and that C and water fluxes are quickly reestablished in the first rainy season in both annual and biennial fires. Biennial fires presented high values in water use efficiency, especially during the dry season 2015 after fire. Then, we also showed that biological invasion buffered the seasonal dynamic of C fluxes compared to uninvaded plots.

### *Effects of fire frequencies on ecosystem processes: NEE, ET and eWUE*

Fire exclusion treatment had greater carbon input (i.e., lower NEE) compared to burned areas (annual and biennial fires) whereas exchange of water (ET) and water use efficiency (eWUE) did not differ, contrary to what we hypothesized. When seasonal variation was considered, we observed the decrease of the CO<sub>2</sub> uptake (i.e. NEE values close to 0) after fire during the dry season during at annual and biennial fires. This decrease in NEE values is directly related to the recent removal of biomass by fire, once measurements were taken three months after fire. On the other hand, during the same dry season, in fire exclusion, NEE also decreased (i.e. more negative values) but to a lesser extent to what we observed in burnt areas. This result illustrated higher CO<sub>2</sub> uptake and carbon gain by the unburnt vegetation compared to burnt areas: the vegetation was not removed by fire leading to higher biomass, and low bare soil (Rodrigues 2019; Starns and others 2020). Biomass removal may impact carbon fluxes by modifying microbial activities that will even promote the rates of NEE (Pinto and others 2002; Pellegrini and others 2018; Pressler and others 2019). In both annual and biennial fires, ecosystem CO<sub>2</sub> uptake increased i.e. rapid increases in NEE rates, in the subsequent rainy season, demonstrating ecosystem resilience after fire (Pinto and

others 2002; Oliveras and others 2013). The input of nutrients in the post-fire conditions (Pivello and others 2010) coupled with the increase in water availability during the rainy season, ensured the quick vegetation recovery (Osborne and Beerling 2006; Ripley and others 2015), and consequently increased plant productivity (Grace and others 2006). Indeed, plant investment in belowground structure (e.g. bud banks) and reserves (belowground organs) allow the quick vegetation regrowth in these savannas (Pilon and others 2021; Zupo and others 2021; Bombo and others 2022). The plant productivity during the first post-fire rainy season guarantees important CO<sub>2</sub> uptake and may lead to rate values similar to unburnt areas in 12 months after fire (Santos and others 2003).

ET increased during the rainy season in biennial plots whereas it increased only during the dry season 2016 in both the annual fire and exclusion areas. During the dry season 2015, fire at annual and biennial areas just happened juts 3 months ago, leading to an absence of vegetation, i.e. biomass removal by fire, and resulting in more bare soil surface. More bare soil increases surface soil temperature and decreases soil moisture (Quesada and others 2004; Makhado and Scholes 2011), leading the system to water conservation (having low ET relative to NEE) (Giambelluca and others 2009; Christoffersen and others 2014). ET increased during the rainy season 2016 in biennial areas, potentially because vegetation recovery (6 months after the fire), and the biomass accumulation may lead to lower bare soil (Rodrigues and others 2021) and greater soil water availability. The presence of vegetation might generate higher water loss in biennial fire areas during the dry season 2016 (Geissler and others 2019; Deng and others 2021). Annual show a tendency to increased but was not significant. ET in annual fire areas showed a tendency to increase but was not significant. However, ET increased both in annual and exclusion fire during the dry season which indicate loss of water from the system. For both annual and exclusion, we

expected to observe similar ET rates for the dry seasons of 2015 and 2016. Indeed, in annual fires measurements were taken 3 months after fire both in 2015 and 2016. In fire exclusion treatment, measurements were also taken at the same period and without fire. We might expect an increase of dead biomass accumulation through time at exclusion areas (Fidelis and others 2013; Rodrigues 2019), leading to low bare soil and more soil moisture and mitigating the stress of the dry season. However, it is unlikely that the accumulation of dead biomass during only one year lead to such significant differences between both dry seasons (Rodrigues 2019). We therefore suggested that inter-annual variation of climatic conditions, might explain the strong difference in ET rates between both dry seasons observed at fire exclusion and annual plots.

Annual fires and fire exclusion showed reduced water use efficiency (Emmerich 2007; Scott and others 2014), that did not differ between seasons, whereas biennial fires presented high eWUE rates right after fire. This result is due to the concomitant low ET and NEE values close to 0 which increased the ratio of carbon uptake in relation to water release and thus eWUE. Usually, the post-fire condition of open savannas is marked by an increase in physiological activity that contributes to higher carbon assimilation (Beer and others 2009; Brunsell and others 2014) and results in positive eWUE. However, annual fires may affect plant communities by repetitive resprout events due to recurrent fires and decrease plant productivity due to the decrease of live biomass (Rodrigues and others 2021). Thus, annual fires, by decreasing plant productivity and consequently physiological activities (Quesada and others 2004; Potts and others 2012), lead to lower rates of eWUE after fire compared to biennial fires.

*Effect of biological invasion on ecosystem processes*

The presence of *Urochloa brizantha* did not lead to strong modification in C and water fluxes compared to uninvaded areas when seasonal variation was not considered, which may be due to the functional similarity between native and invasive grass species (Funk and others 2008). When seasonal variations were considered, ET rates were greater during the rainy season both in invaded and non-invaded areas, illustrating the constraint that dry season generates on the water flux. African invasive grasses, likewise Cerrado native grasses, accumulate dry biomass during periods of water limitation, decreasing plant transpiration thus affecting systems evapotranspiration due to the reduction of live biomass (Oliveira and others 2005). Besides that, we observed that NEE values did not differ with season in invaded plots. Probably because invasive species are more efficient in nutrient and water assimilation (Lannes and others 2012), show extended growing season, and the maintenance of green biomass longer (Williams and Baruch 2000; Lannes and others 2012; Gorgone-Barbosa and others 2015; Reeb and others 2020), when compared to native Cerrado species. The differences between invaded and non-invaded areas on carbon and water fluxes were also illustrated by a trend of higher eWUE values during the dry season in invaded patches, in opposition to constant eWUE values in non-invaded patches. The better efficiency of invasive grasses in using limited resources especially during the restrictive period (Funk and Vitousek 2007; Musso and others 2021) favor them over native species and enhance their invasiveness (Pyšek and Richardson 2007; Reeb and others 2020; Xavier and others 2021).

Our study highlighted that *Urochloa brizantha* can alter the seasonal C ecosystem fluxes by buffering the effects of seasonality, a crucial environmental filter for tropical open savannas (Furley and others 2010; Huntley and Walker, 1984). Invasive species have bottom-up impacts (Vila and others 2011), which means that effects on ecosystem functions will be noticed on other

levels, such as at the individual and community level (Damasceno 2022). Beyond direct impacts on energy and matter fluxes, plant invasions can promote legacy effects in the system, e.g. through changes in soil properties (Elgersma and others 2011) even years after removal of the invasive species (Zenni and others 2020), ultimately affecting ecosystem processes such as C and water fluxes (Bauer 2012).

## **CONCLUSIONS**

Our findings highlighted how different fire frequencies and the presence of invasive grasses can alter open savanna's carbon and water exchange. We showed a quick reestablishment of NEE, associated with C uptake, and water flux in areas under high fire frequencies during the first rainy season right after fire. The presence of invasive grasses buffered seasonal variations of C uptake, showing the better performance of the invader in using resources even during the dry season. Finally, additional factors potentially influencing C and water fluxes, like climatic inter-annual variation, different scales (i.e., individual, community or ecosystems), longer time scale and intensity of changes (i.e., lower, or higher fire frequency intervals and increase of biological invasion), should be further evaluated. Whereas we still do not know how large-scale changes on fire regime will impact carbon and water cycling (Brunsell and others 2014; Deng and others 2021), our study brings new data to better measure the effects of different fire frequencies and biological invasion further helping with open ecosystem conservation and restoration.

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## REFERENCES

- Abreu RCR, Hoffmann WA, Vasconcelos HL, Pilon NA, Rossatto DR, Durigan G. 2017. The biodiversity cost of carbon sequestration in tropical savanna. *Science Advances* 3:1–8.
- Arnone JA, Obrist D. 2003. A large daylight geodesic dome for quantification of whole-ecosystem CO<sub>2</sub> and water vapour fluxes in arid shrublands. *Journal of Arid Environments* 55:629–43.
- Bates D, Maechler M, Bolker B, Walker S, Christensen RHB, Singmann H, Dai B, Scheipl F, Grothendieck G, Green P, Fox J, Bauer A, Krivitsky PN. 2020. Package ‘lme4’.
- Bauer JT. 2012. Invasive species: ‘back-seat drivers’ of ecosystem change? *Biological Invasions* 14:1295–304.
- Beer C, Ciais P, Reichstein M, Baldocchi D, Law BE, Papale D, Soussana JF, Ammann C, Buchmann N, Frank D, Gianelle D, Janssens IA, Knohl A, Köstner B, Moors E, Rouspard O, Verbeeck H, Vesala T, Williams CA, Wohlfahrt G. 2009. Temporal and among-site variability of inherent water use efficiency at the ecosystem level. *Global Biogeochemical Cycles* 23:1–13.
- Bombo AB, Appezzato-da-Glória B, Fidelis A. 2022. Fire exclusion changes belowground bud bank and bud-bearing organ composition jeopardizing open savanna resilience. *Oecologia* 199:153–64.
- Bond WJ. 2022. Out of the shadows: ecology of open ecosystems. *Plant Ecology & Diversity* 14:205–22.
- Bowman DMJS, Kolden CA, Abatzoglou JT, Johnston FH, van der Werf GR, Flannigan M. 2020. Vegetation fires in the Anthropocene. *Nature Reviews Earth & Environment*. <http://dx.doi.org/10.1038/s43017-020-0085-3>
- Brunsell NA, Nippert JB, Buck TL. 2014. Impacts of seasonality and surface heterogeneity on water-use efficiency in mesic grasslands. *Ecohydrology* 7:1223–33.
- Catford JA, Vesk PA, Richardson DM, Pyšek P. 2012. Quantifying levels of biological invasion: Towards the objective classification of invaded and invadable ecosystems. *Global Change Biology* 18:44–62.
- Christoffersen BO, Restrepo-Coupe N, Arain MA, Baker IT, Cestaro BP, Ciais P, Fisher JB, Galbraith D, Guan X, Gulden L, van den Hurk B, Ichii K, Imbuzeiro H, Jain A, Levine N, Miguez-Macho G, Poulter B, Roberti DR, Sakaguchi K, Sahoo A, Schaefer K, Shi M, Verbeeck H, Yang ZL, Araújo AC, Kruijt B, Manzi AO, da Rocha HR, von Randow C, Muza MN, Borak J, Costa MH, Gonçalves de Gonçalves LG, Zeng X, Saleska SR. 2014. Mechanisms of water supply and vegetation demand govern the seasonality and magnitude of evapotranspiration in Amazonia and Cerrado. *Agricultural and Forest Meteorology* 191:33–50.

- Coutinho LM. 1978. O Conceito de Cerrado. *Revsa brasil Bot* 1:17–23.
- Daldegan GA, de Carvalho Júnior OA, Guimarães RF, Gomes RAT, Ribeiro F de 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* 6:9873–94.
- Damasceno G. 2022. Invasion by African grasses and restoration of open Cerrado formations: an approach by state-and-transition models. <https://repositorio.unesp.br/handle/11449/234806>
- Damasceno G, Souza L, Pivello VR, Gorgone-Barbosa E, Girollo PZ, Fidelis A. 2018. Impact of invasive grasses on Cerrado under natural regeneration. *Biological Invasions* 20:3621–9.
- D’Antonio CM, Vitousek PM. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Review of Ecology and Systematics* 23:63–87.
- Deng Y, Li X, Shi F, Hu X. 2021. Woody plant encroachment enhanced global vegetation greening and ecosystem water-use efficiency. *Global Ecology and Biogeography*:1–17.
- Eiten G. 1972. The cerrado vegetation of Brazil. *The Botanical Review* 38:201–341.
- Elgersma KJ, Ehrenfeld JG, Yu S, Vor T. 2011. Legacy effects overwhelm the short-term effects of exotic plant invasion and restoration on soil microbial community structure, enzyme activities, and nitrogen cycling. *Oecologia* 167:733–45.
- Emmerich WE. 2007. Ecosystem water use efficiency in a semiarid shrubland and grassland community. *Rangeland Ecology and Management* 60:464–70.
- Ens E, Hutley LB, Rossiter-Rachor NA, Douglas MM, Setterfield SA. 2015. Resource-use efficiency explains grassy weed invasion in a low-resource savanna in north Australia. *Frontiers in Plant Science* 6:1–10.
- Fidelis A, Alvarado ST, Barradas A, Pivello V. 2018. The Year 2017: Megafires and Management in the Cerrado. *Fire* 1:49.
- Fidelis A, Lyra MF di S, Pivello VR. 2013. Above- and below-ground biomass and carbon dynamics in Brazilian Cerrado wet grasslands. Wildi O, editor. *Journal of Vegetation Science* 24:356–64.
- Fundação Grupo Boticário. 2011. Plano de Manejo da Reserva Natural Serra do Tombador, Cavalcante – GO. Plano de Manejo da Reserva Natural Serra do Tombador, Cavalcante – GO, volume 1:217. <http://www.fundacaogrupoboticario.org.br/pt/o-que-fazemos/reservas-naturais/pages/reserva-natural-serra-tombador-projetos.aspx>
- Funk JL, Cleland EE, Suding KN, Zavaleta ES. 2008. Restoration through reassembly: plant traits and invasion resistance. *Trends in Ecology and Evolution* 23:695–703.

- Funk JL, Vitousek PM. 2007. Resource-use efficiency and plant invasion in low-resource systems. *Nature* 446:1079–81.
- Garcia DB, Xavier RO, Camargo PB, Vieira SA, Pivello VR. 2022. Can an invasive African grass affect carbon and nitrogen stocks in open habitats of the Brazilian Cerrado? *Flora: Morphology, Distribution, Functional Ecology of Plants* 286:151968.
- Giambelluca TW, Scholz FG, Bucci SJ, Meinzer FC, Goldstein G, Hoffmann WA, Franco AC, Buchert MP. 2009. Evapotranspiration and energy balance of Brazilian savannas with contrasting tree density. *Agricultural and Forest Meteorology* 149:1365–76.
- Gomes L, Miranda HS, Silvério DV, Bustamante MMC. 2020. Effects and behaviour of experimental fires in grasslands, savannas, and forests of the Brazilian Cerrado. *Forest Ecology and Management* 458.
- Gorgone-Barbosa E. 2016. A relação entre fogo e uma gramínea invasora no Cerrado: O fogo pode ser utilizado como uma estratégia de controle? <https://repositorio.unesp.br/handle/11449/138106>
- Gorgone-Barbosa E, Pivello VR, Bautista S, Zupo T, Rissi MN, Fidelis A. 2015. How can an invasive grass affect fire behavior in a tropical savanna? A community and individual plant level approach. *Biological Invasions* 17:423–31.
- Govender N, Trollope WSW, Van Wilgen BW. 2006. The effect of fire season, fire frequency, rainfall and management on fire intensity in savanna vegetation in South Africa. *Journal of Applied Ecology* 43:748–58.
- Grace J, José JS, Meir P, Miranda HS, Montes RA. 2006. Productivity and carbon fluxes of tropical savannas. In: *Journal of Biogeography*. Vol. 33. pp 387–400.
- Honda EA, Durigan G. 2016. Woody encroachment and its consequences on hydrological processes in the savannah. *Philosophical Transactions of the Royal Society B: Biological Sciences* 371.
- Huxman TE, Snyder KA, Tissue D, Leffler AJ, Ogle K, Pockman WT, Sandquist DR, Potts DL, Schwinning S. 2004. Precipitation pulses and carbon fluxes in semiarid and arid ecosystems. *Oecologia* 141:254–68.
- Keeley JE, Pausas JG. 2019. Distinguishing disturbance from perturbations in fire-prone ecosystems. *International Journal of Wildland Fire* 28:282–7.
- Kutsch WL, Hanan N, Scholes B, McHugh I, Kubheka W, Eckhardt H, Williams C. 2008. Response of carbon fluxes to water relations in a savanna ecosystem in South Africa. *Biogeosciences* 5:1797–808.
- Lannes LS, Bustamante MMC, Edwards PJ, Venterink HO. 2012. Alien and endangered plants in the Brazilian Cerrado exhibit contrasting relationships with vegetation biomass and N : P stoichiometry. *New Phytologist* 196:816–23.

- Le Quéré C, Raupach MR, Canadell JG, Marland G, Bopp L, Ciais P, Conway TJ, Doney SC, Feely RA, Foster P, Friedlingstein P, Gurney K, Houghton RA, House JI, Huntingford C, Levy PE, Lomas MR, Majkut J, Metzl N, Ometto JP, Peters GP, Prentice IC, Randerson JT, Running SW, Sarmiento JL, Schuster U, Sitch S, Takahashi T, Viovy N, Van Der Werf GR, Woodward FI. 2009. Trends in the sources and sinks of carbon dioxide. *Nature Geoscience* 2:831–6.
- Lenth RV, Buerkner P, Herve M, Love J, Miguez F, Riebl H, Singmann H. 2022. emmeans: Estimated Marginal Means, aka Least-Squares Means.
- Levine JM, Vilà M, D’Antonio CM, Dukes JS, Grigulis K, Lavorel S. 2003. Mechanisms underlying the impacts of exotic plant invasions. *Proceedings of the Royal Society B: Biological Sciences* 270:775–81.
- Linders TEW, Schaffner U, Eschen R, Abebe A, Choge SK, Nigatu L, Mbaabu PR, Shiferaw H, Allan E. 2019. Direct and indirect effects of invasive species: Biodiversity loss is a major mechanism by which an invasive tree affects ecosystem functioning. Alpert P, editor. *J Ecol* 107:2660–72.
- Litton CM, Giardina CP. 2008. Below-ground carbon flux and partitioning: Global patterns and response to temperature. *Functional Ecology* 22:941–54.
- Makhado RA, Scholes RJ. 2011. Determinants of soil respiration in a semi-arid savanna ecosystem, Kruger National Park, South Africa. *Koedoe* 53:1–8.
- McLauchlan KK, Higuera PE, Miesel J, Rogers BM, Schweitzer J, Shuman JK, Tepley AJ, Varner JM, Veblen TT, Adalsteinsson SA, Balch JK, Baker P, Batllori E, Bigio E, Brando P, Cattau M, Chipman ML, Coen J, Crandall R, Daniels L, Enright N, Gross WS, Harvey BJ, Hatten JA, Hermann S, Hewitt RE, Kobziar LN, Landesmann JB, Loranty MM, Maezumi SY, Mearns L, Moritz M, Myers JA, Pausas JG, Pellegrini AFA, Platt WJ, Roozeboom J, Safford H, Santos F, Scheller RM, Sherriff RL, Smith KG, Smith MD, Watts AC. 2020. Fire as a fundamental ecological process: Research advances and frontiers. *Journal of Ecology* 108:2047–69.
- Miller AD, Inamine H, Buckling A, Roxburgh SH, Shea K. 2021. How disturbance history alters invasion success: biotic legacies and regime change. Seabloom E, editor. *Ecology Letters*:ele.13685.
- Miranda AC, Miranda HS, Lloyd J, Grace J, Francey RJ, McIntyre JA, Meir P, Riggan P, Lockwood R, Brass J. 1997. Fluxes of carbon, water and energy over Brazilian cerrado: An analysis using eddy covariance and stable isotopes. *Plant, Cell and Environment* 20:315–28.
- Miranda HS, Bustamante MMC, Miranda AC. 2002. The Fire Factor. In: Oliveira P aulo S, Marquis RJ, editors. *The Cerrados of Brazil: Ecology and Natural History of a Neotropical Savanna*. New York, NY: Columbia University Press. pp 51–68.

- Mistry J. 1998. Fire in the cerrado (savannas) of Brazil: an ecological review. *Progress in Physical Geography: Earth and Environment* 22:425–48.
- Musso C, Fontenele HGV, Pinto G, Oliveira R, Correia C, Moutinho-Pereira JM, Soares AMVM, Loureiro S. 2021. Effects of water and nutrient availability on morphological, physiological, and biochemical traits of one invasive and one native grass of a Neotropical savanna. *Environmental and Experimental Botany* 182.
- Oliveira RS, Bezerra L, Davidson EA, Pinto F, Klink CA, Nepstad DC, Moreira A. 2005. Deep root function in soil water dynamics in cerrado savannas of central Brazil. *Functional Ecology* 19:574–81.
- Oliveras I, Meirelles ST, Hirakuri VL, Freitas CR, Miranda HS, Pivello VR. 2013. Effects of fire regimes on herbaceous biomass and nutrient dynamics in the Brazilian savanna. *International Journal of Wildland Fire* 22:368–80.
- Osborne CP, Beerling DJ. 2006. Nature's green revolution: The remarkable evolutionary rise of C<sub>4</sub> plants. *Philosophical Transactions of the Royal Society B: Biological Sciences* 361:173–94.
- Pellegrini AFA, Ahlström A, Hobbie SE, Reich PB, Nieradzik LP, Staver AC, Scharenbroch BC, Jumpponen A, Anderegg WRL, Randerson JT, Jackson RB. 2018. Fire frequency drives decadal changes in soil carbon and nitrogen and ecosystem productivity. *Nature* 553:194–8.
- Pilon NAL, Durigan G, Rickenback J, Pennington RT, Dexter KG, Hoffmann WA, Abreu RCR, Lehmann CER. 2021. Shade alters savanna grass layer structure and function along a gradient of canopy cover. *Journal of Vegetation Science* 32:1–11.
- Pinto A de S, Bustamante MM da C, Kiselle K, Burke R, Zepp R, Viana LT, Varella RF, Molina M. 2002. Soil emissions of N<sub>2</sub>O, NO, and CO<sub>2</sub> in Brazilian Savannas: Effects of vegetation type, seasonality, and prescribed fires. *Journal of Geophysical Research* 107:8089.
- Pivello VR. 2011. The use of fire in the cerrado and Amazonian rainforests of Brazil: Past and present. *Fire Ecology* 7:24–39.
- Pivello VR, Coutinho LM. 1996. A qualitative successional model to assist in the management of Brazilian cerrados. *Forest Ecology and Management* 87:127–38.
- Pivello VR, Oliveras I, Miranda HS, Haridasan M, Sato MN, Meirelles ST. 2010. Effect of fires on soil nutrient availability in an open savanna in Central Brazil. *Plant and Soil* 337:111–23.
- Potts DL, Huxman TE, Cable JM, English NB, Ignace DD, Eilts JA, Mason MJ, Weltzin JF, Williams DG. 2006. Antecedent moisture and seasonal precipitation influence the response of canopy-scale carbon and water exchange to rainfall pulses in a semi-arid grassland. *New Phytologist* 170:849–60.

- Potts DL, Suding KN, Winston GC, Rocha AV, Goulden ML. 2012. Ecological effects of experimental drought and prescribed fire in a southern California coastal grassland. *Journal of Arid Environments* 81:59–66.
- Pressler Y, Moore JC, Cotrufo MF. 2019. Belowground community responses to fire: meta-analysis reveals contrasting responses of soil microorganisms and mesofauna. *Oikos* 128:309–27.
- Pyšek P, Hulme PE, Simberloff D, Bacher S, Blackburn TM, Carlton JT, Dawson W, Essl F, Foxcroft LC, Genovesi P, Jeschke JM, Kühn I, Liebhold AM, Mandrak NE, Meyerson LA, Pauchard A, Pergl J, Roy HE, Seebens H, Kleunen M, Vilà M, Wingfield MJ, Richardson DM. 2020. Scientists’ warning on invasive alien species. *Biol Rev* 95:1511–34.
- Pyšek P, Richardson DM. 2007. Traits Associated with Invasiveness in Alien Plants: Where Do we Stand? *Biological Invasions* 193:97–125.
- Quesada CA, Miranda AC, Hodnett MG, Santos AJB, Miranda HS, Breyer LM. 2004. Seasonal and depth variation of soil moisture in a burned open savanna (campo sujo) in central Brazil. *Ecological Applications* 14:33–41.
- R Core Team. 2021. R: a language and environment for statistical computing. <https://www.r-project.org>
- Ratajczak Z, Carpenter SR, Ives AR, Kucharik CJ, Ramiadantsoa T, Stegner MA, Williams JW, Zhang J, Turner MG. 2018. Abrupt Change in Ecological Systems: Inference and Diagnosis. *Trends in Ecology and Evolution* 33:513–26.
- Reeb RA, Acevedo I, Heberling JM, Isaac B, Kuebbing SE. 2020. Nonnative old-field species inhabit early season phenological niches and exhibit unique sensitivity to climate. *Ecosphere* 11.
- Ripley B, Visser V, Christin P, Archibald S, Ripley B, Visser V, Christin P, Archibald S, Martin T, Osborne C. 2015. Fire ecology of C 3 and C 4 grasses depends on evolutionary history and frequency of burning but not photosynthetic type Martin and Colin Osborne Published by: Wiley on behalf of the Ecological Society of America Stable URL : <http://www.jstor.org/stable/>. *Ecological Society of America* 96:2679–91.
- Rissi MN, Baeza MJ, Gorgone-Barbosa E, Zupo T, Fidelis A. 2017. Does season affect fire behaviour in the Cerrado? *International Journal of Wildland Fire* 26:427–33.
- Rodrigues CA, Zironi HL, Fidelis A. 2021. Fire frequency affects fire behavior in open savannas of the Cerrado. *Forest Ecology and Management* 482:118850.
- Rodrigues CAS. 2019. Quantas vezes devemos queimar o Cerrado? Efeitos da frequência de fogo em comunidades de campo sujo de Cerrado.

- Rogers BM, Balch JK, Goetz SJ, Lehmann CER, Turetsky M. 2020. Focus on changing fire regimes: interactions with climate, ecosystems, and society. *Environmental Research Letters* 15.
- Santos AJB, Silva GTDA, Miranda HS, Miranda AC, Lloyd J. 2003. Effects of fire on surface carbon, energy and water vapour fluxes over campo sujo savanna in central Brazil. *Functional Ecology* 17:711–9.
- Scheffer M, Carpenter S, Foley JA, Folke C, Walker B. 2001. Catastrophic shifts in ecosystems. *Nature* 413:591–6.
- Scheffer M, Carpenter SR. 2003. Catastrophic regime shifts in ecosystems: Linking theory to observation. *Trends in Ecology and Evolution* 18:648–56.
- Scholze M, Knorr W, Arnell NW, Prentice IC. 2006. A climate-change risk analysis for world ecosystems. *Proceedings of the National Academy of Sciences of the United States of America* 103:13116–20.
- Schreiner-McGraw AP, Vivoni ER, Ajami H, Sala OE, Throop HL, Peters DPC. 2020. Woody Plant Encroachment has a Larger Impact than Climate Change on Dryland Water Budgets. *Scientific Reports* 10:1–9.
- Scott RL, Huxman TE, Barron-Gafford GA, Darrel Jenerette G, Young JM, Hamerlynck EP. 2014. When vegetation change alters ecosystem water availability. *Global Change Biology* 20:2198–210.
- Setterfield S, Douglas M, Hutley L, Ferdinands K, Ens E, Brooks K, Rossiter N. 2008. Ecosystem impacts of an exotic grass in northern Australia : effects on structure and carbon stocks. *Proceedings of the Royal Society of London*:2008–2008.
- Starns HD, Taylor CA, Garza NE, Tolleson DR. 2020. Effects of Fire Exclusion on Previously Fire-Managed Semiarid Savanna Ecosystem. *Rangeland Ecology and Management* 73:93–6.
- Stevens N, Bond W, Feurdean A, Lehmann CER. 2022. Grassy Ecosystems in the Anthropocene. *Annu Rev Environ Resour* 47:annurev-environ-112420-015211.
- Strauss SY, Webb CO, Salamin N. 2006. Exotic taxa less related to native species are more invasive. *Proceedings of the National Academy of Sciences of the United States of America* 103:5841–5.
- Teixeira AMC, Curran TJ, Jameson PE, Meurk CD, Norton DA. 2020. Post-Fire Resprouting in New Zealand Woody Vegetation: Implications for Restoration. *Forests* 11:269.
- 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.

- Van Kleunen M, Weber E, Fischer M. 2010. A meta-analysis of trait differences between invasive and non-invasive plant species. *Ecology Letters* 13:235–45.
- Vila M, Espinar JL, Hejda M, Hulme PE, Jarosik V, Maron JL, Pergl J, Schaffner U, Sun Y, Pysek P. 2011. Ecological impacts of invasive alien plants: A meta-analysis of their effects on species, communities and ecosystems. *Ecology Letters* 14:702–8.
- Wickham H, Chang W, Henry L, Pedersen TL, Takahashi K, Woo C, Kara W, Yutani H, Dunnington D, RStudio. 2020. Package ‘ggplot2’ Title Create Elegant Data Visualisations Using the Grammar of Graphics.
- Williams DG, Baruch Z. 2000. African grass invasion in the Americas: Ecosystem consequences and the role of ecophysiology. *Biological Invasions* 2:123–40.
- Xavier RO, Christianini AV, Pegler G, Leite MB, Silva-Matos DM. 2021. Distinctive seed dispersal and seed bank patterns of invasive African grasses favour their invasion in a neotropical savanna. *Oecologia* 196:155–69.
- Zanzarini V, Andersen AN, Fidelis A. 2022. Flammability in tropical savannas: Variation among growth forms and seasons in Cerrado. *Biotropica* 54:979–87.
- Zenni RD, da Cunha WL, Musso C, de Souza JV, Nardoto GB, Miranda HS. 2020. Synergistic impacts of co-occurring invasive grasses cause persistent effects in the soil-plant system after selective removal. *Functional Ecology* 34:1102–12.
- Zhou Y, Singh J, Butnor JR, Coetsee C, Boucher PB, Case MF, Hockridge EG, Davies AB, Staver AC. 2022. Limited increases in savanna carbon stocks over decades of fire suppression. *Nature*.
- Zupo T, Daibes LF, Pausas JG, Fidelis A. 2021. Post-fire regeneration strategies in a frequently burned Cerrado community. *Journal of Vegetation Science* 32.
- Zuur AF, Ieno EN, Walker N, Saveliev AA, Smith GM. 2009. Mixed effects models and extensions in ecology with R. New York, NY: Springer New York <http://link.springer.com/10.1007/978-0-387-87458-6>. Last accessed 11/11/2020



## **Material Suplementar**

Até o momento da publicação desse manuscrito, todos os dados que suportam os achados desse estudo estarão disponíveis no repositório Zenodo.

**Table S1.** Carbon and water flux variables (mean  $\pm$  SE), i.e. Carbon net ecosystem exchange (NEE), water ecosystem exchange (evapotranspiration, ET), and ecosystem water use efficiency (eWUE), according to treatments of fire frequencies and biological invasion in Cerrado open savanna.

|          |             | <b>NEE</b><br>( $\mu \text{ mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ) | <b>ET</b><br>( $\mu \text{ mol H}_2\text{O m}^{-2} \text{ s}^{-1}$ ) | <b>eWUE</b><br>( $\mu \text{ mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ / $\mu \text{ mol H}_2\text{O m}^{-2} \text{ s}^{-1}$ ) |
|----------|-------------|------------------------------------------------------------------------|----------------------------------------------------------------------|-------------------------------------------------------------------------------------------------------------------------------|
| Fire     | annual      | -2.52 $\pm$ 0.40                                                       | 2.03 $\pm$ 0.30                                                      | 1.12 $\pm$ 0.14                                                                                                               |
|          | biennial    | -2.803 $\pm$ 0.38                                                      | 2.85 $\pm$ 0.42                                                      | 2.02 $\pm$ 0.30                                                                                                               |
|          | exclusion   | -4.58 $\pm$ 0.51                                                       | 2.90 $\pm$ 0.47                                                      | 1.34 $\pm$ 0.15                                                                                                               |
| Invasion | non-invaded | -2.59 $\pm$ 0.61                                                       | 1.29 $\pm$ 0.22                                                      | 2.54 $\pm$ 0.43                                                                                                               |
|          | invaded     | -3.730 $\pm$ 0.64                                                      | 1.06 $\pm$ 0.15                                                      | 3.81 $\pm$ 0.69                                                                                                               |

**Table S2.** Carbon and water flux variables (mean  $\pm$  SE), i.e. Carbon net ecosystem exchange (NEE), water ecosystem exchange (evapotranspiration, ET), and ecosystem water use efficiency (eWUE), according to treatments of fire frequencies and biological invasion and including seasonal variation in Cerrado open savanna.

|          |             | NEE ( $\mu \text{ mol CO}_2\text{m}^{-2}\text{s}^{-1}$ ) |                   |                  | ET ( $\mu \text{ mol H}_2\text{Om}^{-2}\text{s}^{-1}$ ) |                   |                 | eWUE ( $\mu \text{ mol CO}_2\text{m}^{-2}\text{s}^{-1} / \mu \text{ mol H}_2\text{Om}^{-2}\text{s}^{-1}$ ) |                   |                 |
|----------|-------------|----------------------------------------------------------|-------------------|------------------|---------------------------------------------------------|-------------------|-----------------|------------------------------------------------------------------------------------------------------------|-------------------|-----------------|
|          |             | 2015 dry season                                          | 2016 rainy season | 2016 dry season  | 2015 dry season                                         | 2016 rainy season | 2016 dry season | 2015 dry season                                                                                            | 2016 rainy season | 2016 dry season |
| Fire     | annual      | -0.67 $\pm$ 0.20                                         | -3.74 $\pm$ 0.78  | -3.36 $\pm$ 0.44 | 0.72 $\pm$ 0.08                                         | 1.89 $\pm$ 0.38   | 3.66 $\pm$ 0.36 | 0.85 $\pm$ 0.23                                                                                            | 1.56 $\pm$ 0.31   | 0.98 $\pm$ 0.15 |
|          | biennial    | -1.29 $\pm$ 0.24                                         | -4.24 $\pm$ 0.55  | -4.06 $\pm$ 0.50 | 1.38 $\pm$ 0.31                                         | 4.53 $\pm$ 0.77   | 3.79 $\pm$ 0.55 | 3.00 $\pm$ 0.46                                                                                            | 1.15 $\pm$ 0.22   | 1.10 $\pm$ 0.13 |
|          | exclusion   | -2.85 $\pm$ 0.42                                         | -5.82 $\pm$ 0.73  | -5.05 $\pm$ 0.69 | 3.16 $\pm$ 0.65                                         | 1.90 $\pm$ 0.40   | 6.52 $\pm$ 1.31 | 1.32 $\pm$ 0.23                                                                                            | 1.48 $\pm$ 0.25   | 0.78 $\pm$ 0.05 |
| Invasion | non-invaded | -1.08 $\pm$ 0.35                                         | -4.44 $\pm$ 1.00  |                  | 0.75 $\pm$ 0.20                                         | 1.94 $\pm$ 0.32   |                 | 2.62 $\pm$ 0.71                                                                                            | 2.44 $\pm$ 0.44   |                 |
|          | invaded     | -3.80 $\pm$ 0.93                                         | -3.65 $\pm$ 0.89  |                  | 0.76 $\pm$ 0.09                                         | 1.46 $\pm$ 0.29   |                 | 4.81 $\pm$ 1.10                                                                                            | 2.47 $\pm$ 0.46   |                 |

**Table S3.** Statistical results of models testing the variation of net ecosystem CO<sub>2</sub> exchange (NEE;  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ), Ecosystem evapotranspiration (ET;  $\mu\text{mol H}_2\text{O m}^{-2} \text{ s}^{-1}$ ) and water use efficiency (eWUE,  $\mu \text{ mol CO}_2 / \mu \text{ mol H}_2\text{O m}^{-2} \text{ s}^{-1}$ ) in relation to treatments of fire frequencies in Cerrado open savanna. Estimates of predictive variables are informed together with confidence intervals (inside the parenthesis). The model intercepts and the pairwise comparisons (95% of the confidence interval) are also presented. Bold text indicates significance (\*\*\*  $p < 0.001$ ; \*\*  $p < 0.01$ ; \*  $p < 0.05$ ).

|                             | NEE                                 | ET                             | eWUE                                |
|-----------------------------|-------------------------------------|--------------------------------|-------------------------------------|
| (Intercept)                 | <b>-2.52</b> ***<br>(-3.30 – -1.73) | <b>2.04</b> *<br>(1.31 – 2.76) | <b>1.13</b> ***<br>(0.73 – 1.52)    |
| annual-biennial             | -0.28<br>(-1.44 – 0.89)             | 0.82<br>(-0.25 – 1.89)         | <b>0.9</b> **<br>(0.31 – 1.49)      |
| annual-exclusion            | <b>-2.07</b> **<br>(-3.19 – -0.82)  | 0.87<br>-0.25 – 1.99           | 0.22<br>(-0.39 – 0.84)              |
| <i>Pairwise comparisons</i> |                                     |                                |                                     |
| annual-biennial             | 0.279<br>( -1.221 – 1.78)           | -0.821<br>(-2.18 – 0.534)      | <b>-0.897</b> *<br>(1.647 – -0.147) |
| annual-exclusion            | <b>2.004</b> **<br>(0.500 – 3.63)   | -0.87<br>(-2.29 – 0.547)       | -0.224<br>(-1.007 – 0.560)          |
| biennial-exclusion          | <b>1.788</b> *<br>(0.190 – 3.39)    | -0.049<br>(-1.50 – 1.400)      | 0.674<br>(-0.128 – 1.475)           |
| Observations                | 64                                  | 64                             | 64                                  |
| Marginal R <sup>2</sup>     | 0.165                               | 0.05                           | 0.133                               |

**Table S4.** Statistical results of models testing the variation in net ecosystem CO<sub>2</sub> exchange (NEE;  $\mu\text{mols CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ), and Ecosystem evapotranspiration water (ET; ecosystem evapotranspiration;  $\mu\text{mols H}_2\text{O m}^{-2} \text{ s}^{-1}$ ) exchange, and ecosystem water use efficiency (eWUE,  $\mu \text{ mol CO}_2 / \mu \text{ mol H}_2\text{O m}^{-2} \text{ s}^{-1}$ ) in relation to seasonality and treatments of fire frequencies and the interaction between these two variables in Cerrado open savanna. Estimates of predictive variables are informed together with confidence intervals (inside the parenthesis). The model intercepts and the pairwise comparisons (95% of the confidence interval) are also presented. Bold text indicates significance (\*\*\*)  $p < 0.001$ ; \*\*  $p < 0.01$ ; \*  $p < 0.05$ ).

|                                     | NEE                                 |  | ET                                     |  | eWUE                                |
|-------------------------------------|-------------------------------------|--|----------------------------------------|--|-------------------------------------|
| (Intercept)                         | -0.71<br>(-1.45 – 0.03)             |  | 0.71<br>(-0.11 – 1.53)                 |  | <b>0.86</b> *                       |
| dry season 2015 - rainy season 2016 | <b>-3.01</b> ***<br>(-3.82 – -2.21) |  | <b>1.17</b> *<br>(0.02 – 2.32)         |  | 0.7<br>(-0.07 – 1.47)               |
| dry season 2015 - dry season 2016   | <b>-2.63</b> ***<br>(-3.55 – -1.72) |  | <b>2.95</b> ***<br>(1.78 – 4.11)       |  | 0.21<br>(-0.58 – 1.00)              |
| annual - biennial                   | -0.59<br>(-1.45 – 0.26)             |  | 0.67<br>(-0.46 – 1.80)                 |  | <b>2.14</b> ***<br>(1.36 – 2.92)    |
| annual - exclusion                  | <b>-2.06</b> ***<br>(-2.97 – -1.15) |  | <b>2.45</b> ***<br>(1.22 – 3.69)       |  | 0.45<br>(-0.40 – 1.30)              |
| rainy season 2016* biennial         | -                                   |  | <b>1.96</b> *<br>(0.27 – 3.65)         |  | <b>-2.52</b> ***<br>(-3.66 – -1.38) |
| dry season 2016 * biennial          | -                                   |  | -0.52<br>(-2.27 – 1.24)                |  | <b>-2.09</b> **<br>(-3.28 – -0.90)  |
| rainy season 2016 * exclusion       | -                                   |  | <b>-2.43</b> **<br>(-4.09 – -0.77)     |  | -0.52<br>(-1.63 – 0.60)             |
| dry season 2016 * exclusion         | -                                   |  | 0.44<br>(-1.82 – 2.69)                 |  | -0.72<br>(-2.25 – 0.81)             |
| Pairwise comparisons                |                                     |  |                                        |  |                                     |
| <i>Annual</i>                       |                                     |  |                                        |  |                                     |
| dry season 2015 - rainy season 2016 | <b>3.012</b> ***<br>(2.03 – 3.996)  |  | -1.168<br>(-2.581 – 0.246)             |  | -0.7002<br>(-1.652 – 0.252)         |
| dry season 2015 - dry season 2016   | <b>2.633</b> ***<br>(1.51 – 3.759)  |  | <b>-2.948</b> ***<br>(-4.383 – -1.512) |  | -0.2065<br>(-1.180 – 0.767)         |
| rainy season 2016 - dry season 2016 | -0.379<br>(-1.55 – 0.791)           |  | <b>-1.78</b> *<br>(-3.254 – -0.305)    |  | 0.4937<br>(-0.505 – 1.492)          |

Continue Table S4...

|                                                      | NEE              |  | ET                |  | eWUE              |
|------------------------------------------------------|------------------|--|-------------------|--|-------------------|
| <i>Biennial</i>                                      |                  |  |                   |  |                   |
| dry season 2015 - rainy season 2016                  | <b>3.012</b> *** |  | <b>-3.127</b> *** |  | <b>1.8186</b> *** |
|                                                      | (2.03 – 3.996)   |  | (-4.646 – -1.608) |  | (0.789 – 2.849)   |
| dry season 2015 - dry season 2016                    | <b>2.633</b> *** |  | <b>-2.432</b> **  |  | <b>1.8861</b> *** |
|                                                      | (1.51 – 3.759)   |  | (-4.046 – -0.819) |  | (0.794 – 2.978)   |
| rainy season 2016 - dry season 2016                  | -0.379           |  | 0.695             |  | 0.0676            |
|                                                      | (-1.55 – 0.791)  |  | (-1.113 – 2.502)  |  | (-1.164 – 1.299)  |
| <i>Exclusion</i>                                     |                  |  |                   |  |                   |
| dry season 2015 - rainy season 2016                  | <b>3.012</b> *** |  | 1.26              |  | -0.1837           |
|                                                      | (2.03 – 3.996)   |  | (-0.209 – 2.728)  |  | (-1.174–0.807)    |
| dry season 2015 - dry season 2016                    | <b>2.633</b> *** |  | <b>-3.383</b> **  |  | 0.5101            |
|                                                      | (1.51 – 3.759)   |  | (-5.785 – -0.981) |  | (-1.119 – 2.139)  |
| rainy season 2016 - dry season 2016                  | -0.379           |  | <b>-4.642</b> *** |  | 0.6938            |
|                                                      | (-1.55 – 0.791)  |  | (-6.994 – -2.291) |  | (-0.904 – 2.291)  |
| Observations                                         | 64               |  | 64                |  | 64                |
| Marginal R <sup>2</sup> / Conditional R <sup>2</sup> | 0.585 / 0.596    |  | 0.572 / 0.605     |  | 0.402 / 0.475     |

**Table S5.** Statistical results of the models aiming to assess net ecosystem CO<sub>2</sub> exchange (NEE;  $\mu\text{mols CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ), Ecosystem evapotranspiration water (ET; ecosystem evapotranspiration;  $\mu\text{mols H}_2\text{O m}^{-2} \text{ s}^{-1}$ ) exchange, and ecosystem water use efficiency (eWUE,  $\mu \text{ mol CO}_2 / \mu \text{ mol H}_2\text{O m}^{-2} \text{ s}^{-1}$ ) in relation to biological invasion i.e., non-invaded and invaded, in Cerrado open savanna. Estimates of predictive variables are informed together with confidence intervals (inside the parenthesis). The model intercepts are also presented. Bold text indicates significance (\*\* $p < 0.001$ ; \*\*  $p < 0.01$ ; \*  $p < 0.05$ ).

|                         | NEE                                | ET                               | eWUE                            |
|-------------------------|------------------------------------|----------------------------------|---------------------------------|
| (Intercept)             | <b>-2.6 ***</b><br>(-3.88 – -1.31) | <b>1.29 ***</b><br>(0.89 – 1.68) | <b>2.55 **</b><br>(1.12 – 3.98) |
| invaded-non-invaded     | -1.14<br>(-2.94 – 0.66)            | -0.22<br>(-0.78 – 0.33)          | 1.43<br>(-0.53 – 3.39)          |
| Observations            | 41                                 | 41                               | 41                              |
| Marginal R <sup>2</sup> | 0.04                               | 0.017                            | 0.065                           |

**Table S6.** Statistical results of models assessing net ecosystem CO<sub>2</sub> exchange (NEE;  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ), Ecosystem evapotranspiration water (ET; ecosystem evapotranspiration;  $\mu\text{mol H}_2\text{O m}^{-2} \text{ s}^{-1}$ ) exchange, and ecosystem water use efficiency (eWUE,  $\mu \text{ mol CO}_2 / \mu \text{ mol H}_2\text{O m}^{-2} \text{ s}^{-1}$ ) in relation to seasonality, biological invasion and the interaction between both variables in Cerrado open savanna. Estimates of predictive variables are informed together with confidence intervals (inside the parenthesis). The model intercepts and pairwise comparisons (95% of the confidence interval) are also presented. Bold text indicates significance (\*\*\*  $p < 0.001$ ; \*\*  $p < 0.01$ ; \*  $p < 0.05$ ).

|                                                      | NEE                               | ET                                    | eWUE                      |
|------------------------------------------------------|-----------------------------------|---------------------------------------|---------------------------|
| (Intercept)                                          | -1.09<br>(-2.71 – 0.54)           | <b>0.86</b> ***<br>(0.45 – 1.26)      | 3.12 ***<br>(1.72 – 4.52) |
| dry season 2015 - rainy season 2016                  | <b>-3.36</b> **<br>-5.77 – -0.94  | <b>0.94</b> ***<br>(0.50 – 1.39)      | -1.28<br>(-2.95 – 0.39)   |
| non-invaded - invaded                                | <b>-2.63</b> *<br>(-3.55 – -1.72) | -0.21<br>(-0.70 – 0.28)               | 1.23<br>(-0.42 – 2.89)    |
| rainy season 2016 * invaded                          | <b>-2.72</b> *<br>(-4.96 – -0.47) |                                       |                           |
| Pairwise comparisons                                 |                                   |                                       |                           |
| <i>Non-invaded</i>                                   |                                   |                                       |                           |
| dry season 2015 - rainy season 2016                  | <b>3.36</b> *<br>(0.839 – 5.88)   | <b>-0.944</b> ***<br>(-2.581 – 0.246) | 1.28<br>(-0.448 – 3.01)   |
| <i>Invaded</i>                                       |                                   |                                       |                           |
| dry season 2015 - rainy season 2016                  | -0.15<br>(-2.605 – 2.30)          | <b>-0.944</b> ***<br>(-1.4 – 0.485)   | 1.28<br>(-0.448 – 3.01)   |
| Observations                                         | 41                                | 41                                    | 41                        |
| Marginal R <sup>2</sup> / Conditional R <sup>2</sup> | 0.198                             | 0.305 / 0.409                         | 0.108                     |



## CONSIDERAÇÕES FINAIS

O principal objetivo desta tese foi investigar como o fogo e a invasão biológica podem afetar a dinâmica do carbono em ecossistemas neotropicais campestres e savânicos, utilizando como modelo de estudo o Cerrado. No capítulo 1, nós mostramos que o fogo promoveu a entrada de carbono no ecossistema (NEE), favoreceu a diversidade funcional e a biomassa subterrânea, além de promover o carbono no solo (SOC) (Figura 1). Estes resultados demonstram que quando o fogo é excluído do sistema, a diversidade funcional diminui. A longo prazo, a diminuição da diversidade funcional pode afetar a resiliência do sistema em áreas onde o fogo foi excluído, por afetar a rápida e diversa resposta pós-fogo (Pilon et al. 2021; Zupo et al. 2021; Le Stradic et al. 2021).

Por se tratar de ambientes naturalmente inflamáveis, estes ecossistemas queimam, naturalmente ou até mesmo por meio do estabelecimento do manejo integrado de fogo e (ver Schmidt et al. 2018; Schmidt & Eloy 2020). Os eventos de fogo globalmente estão mais frequentes (Chergui et al. 2018), intensos (Singleton et al. 2019) e extensos (Collins et al. 2021). Áreas excluídas do fogo por muito tempo geram usualmente incêndios de maiores proporções e severidade, devido ao maior acúmulo do material combustível (Fidelis et al. 2018). Estes fatores levam ao aumento da emissão de gases atmosféricos (Bowman et al. 2020), desaceleração do ciclo de nutrientes (Archibald et al. 2018), e a perda de espécies típicas de savanas (Durigan & Ratter 2016; Abreu et al. 2017). Assim, com a perda de espécies típicas de savanas, e a diminuição da diversidade funcional observada em nosso estudo, as estratégias de resposta ao fogo (e.g., rápido rebrote, eficiência no uso de recurso pós-fogo) podem ser perdidas. Com isso, a habilidade natural destes ecossistemas em compensar a perda de carbono provinda da combustão de biomassa, através do rebrote, também pode ser comprometida, alterando então, a dinâmica do carbono.

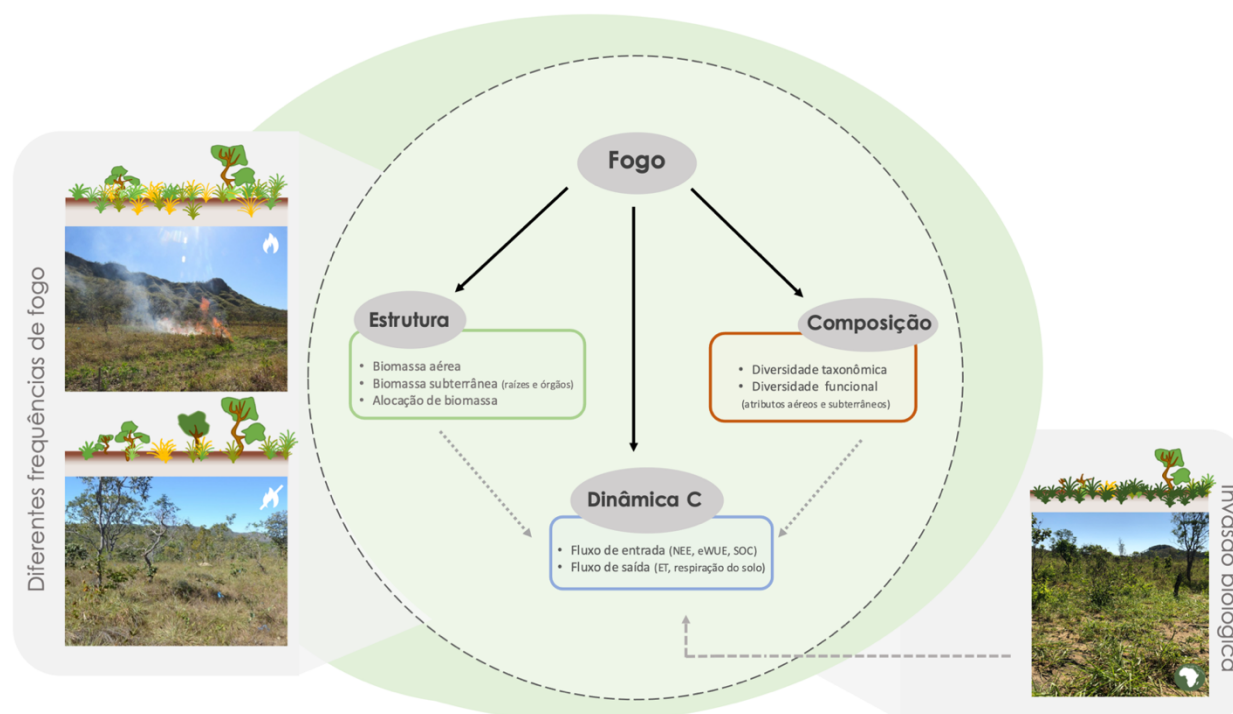
A relação entre as modificações dos processos ligados ao fluxo de entrada de carbono (SOC e NEE) e a diversidade funcional não foi evidenciada em nosso estudo. Outros estudos evidenciaram que a entrada de carbono em ecossistemas está fortemente associada aos atributos de raízes, porém ela é fortemente mediada por atividades microbianas (Rossi et al. 2020; Bai & Cotrufo 2022). A dinâmica do microbioma das plantas tem um papel muito importante nas respostas solo-plantas que afetam a entrada e a saída de carbono em ambientes inflamáveis (Pressler et al. 2019; Vermeire et al. 2021). Estudos recentes também indicam que atributos relacionados com a interação raízes-

atividades microbianas (i.e., quantidade e composição de exsudatos de raízes), podem trazer mais precisão ao entendimento da relação entre os atributos funcionais de plantas e a dinâmica de carbono (Freschet et al. 2020; Freschet et al. 2021). Especialmente, em ecossistemas complexos, como os ecossistemas campestres e savânicos, acreditamos que futuros estudos relacionados à avaliação do componente subterrâneo das comunidades vegetais e o papel que ele oferece no ciclo de carbono poderia ajudar no entendimento da relação entre a diversidade funcional e o fluxo de entrada de carbono nestes sistemas. Assim, este estudo abre precedentes para a inclusão da dinâmica do microbioma das plantas para o completo entendimento das relações que permeiam a dinâmica de carbono de um ambiente inflamável.

No capítulo 2, quando olhamos para a biomassa subterrânea e a sua alocação, a presença do fogo gerou maior alocação de biomassa na parte subterrânea devido a um investimento importante no sistema radicular, incluindo-se tanto as raízes finas (<2mm) como grossas (> 2mm) (Figura 1). Também demonstramos que mais de 12 anos de exclusão de fogo ainda não foram suficientes para modificar a biomassa total de órgãos subterrâneos. Porém, este tempo foi suficiente para alterar a composição desta biomassa de órgãos subterrâneos. Com a exclusão de fogo, a maior biomassa é proveniente de órgãos relacionados ao crescimento clonal (rizomas) e o desaparecimento de órgãos que são exclusivamente relacionados ao rebrote e a presença de fogo como os xilopódios. Contrariamente, demonstramos que nas aéreas que queimam há maior biomassa de xilopódios, indicando a sua importância para a persistência de plantas adaptadas ao fogo. Essas mudanças, por sua vez, podem influenciar a capacidade de regeneração do sistema. Espécies com órgãos subterrâneos com capacidade clonal podem rapidamente colonizar novas áreas, enquanto espécies com órgãos sem a capacidade clonal, a colonização de novas áreas pode ser lenta, ou até mesmo não ocorrer (Bombo et al. 2022). Estes resultados são de grande importância para ações relacionadas ao manejo de fogo e à restauração de ecossistemas campestres e savânicos do Cerrado. Indicamos que estas ações devem priorizar a manutenção dos feedbacks entre a vegetação o fogo, para garantir a conservação do banco de gemas e, principalmente, a diversidade dos órgãos subterrâneos destes ecossistemas.

No capítulo 3, olhamos os fluxos de entrada e saída de carbono em resposta a distintas frequências de fogo e à invasão biológica. Nossos resultados demonstraram que: (i) a alta frequência de fogo diminui os fluxos de carbono logo após o evento de fogo. Porém os sistemas demonstram rápido restabelecimento de seus fluxos, logo na primeira estação chuvosa; (ii) a

exclusão do fogo apresenta maiores valores para a entrada de carbono (NEE); e (ii) que a invasão biológica apesar de não promover alterações nos fluxos, neutraliza o efeito da variação sazonal destes processos, diferentemente do que acontece nos ambientes não invadidos, que respondem a variação sazonal (Figura 1). A partir de nossos resultados, sugerimos que sejam feitos novos estudos que estimem o efeito de longo prazo nas mudanças do regime de fogo e do estabelecimento dos processos de invasão biológica nestes ecossistemas.



**Figura 1.** Resumo esquemático dos achados gerais desta tese com base nos pontos de investigação realizados em savanas abertas do Cerrado. As setas representam os efeitos e interações estudadas neste trabalho. As setas pretas representam as relações evidenciadas, e as setas tracejadas as evidências não encontradas.

Mudanças de longo-prazo nas frequências de fogo e no estabelecimento dos processos de invasão biológica podem modificar processos ecossistêmicos através da modificação da composição e de estrutura das comunidades vegetais (Damasceno et al. 2018; Buisson et al. 2019; Pausas & Bond 2020). Além da perda de biodiversidade, gramíneas africanas invasoras podem promover modificações no comportamento do fogo, por exemplo, através do aumento da altura das chamas e da temperatura (Gorgone-Barbosa et al. 2015; Williamson et al. 2020). Isso acontece,

porque gramíneas invasoras tem maior acúmulo de material combustível (Damasceno & Fidelis 2020). Assim, mudanças do comportamento do fogo, em especial o aumento da temperatura, podem acarretar a mortalidade da microbiota presente na superfície no solo (Dove et al. 2021), levando a possíveis alterações nos fluxos de carbono do sistema. Por sua vez, a abundância de espécies invasoras, como as gramíneas africanas, também é dependente do regime de fogo (Damasceno and Fidelis 2020). Estudos que abordem os diferentes regimes de fogo em conjunto com a invasão biológica, em diferentes escalas espaciais (i.e. populações, comunidades, ecossistemas) e temporais (médio e longo prazo), são fundamentais para a completa compreensão da intensidade e magnitude dos efeitos da frequência do fogo e invasões biológicas na dinâmica do carbono dos ecossistemas campestres e savânicos neotropicais (Damasceno 2022).

Por fim, as evidências encontradas neste trabalho ressaltam a importância da manutenção dos distúrbios naturais como o fogo para a conservação e provisão das funções e serviços ecossistêmicos em ecossistemas campestres e savânicos (He et al. 2019; Zhao et al. 2020), em especial os do Cerrado. Ressaltamos que o fogo é parte estratégica para a manutenção da dinâmica do carbono (Bai & Cotrufo 2022; Zhou et al. 2022), um ciclo biogeoquímico de suma importância para a humanidade. Desta maneira, qualquer alteração nestes distúrbios, assim como o aumento da intensidade dos processos de invasões biológicas, pode levar à alterações da dinâmica do carbono, e potencialmente à perda de um dos importantes serviços ecossistêmicos oferecidos por estes ecossistemas: o estoque de carbono (Fidelis et al. 2013; Wigley et al. 2020; Bardgett et al. 2021; Zhou et al. 2022).

Recentemente, o Painel Intergovernamental para a Mudança do Clima (IPCC) reconheceu que apesar do grande volume de emissões da queima de áreas naturais, as formações abertas têm alto potencial para o sequestrar uma quantidade de carbono aproximadamente equivalente à biomassa consumida (Jia et al. 2021). Porém, os modelos elaborados pelo IPCC não olham para o fluxo de carbono destas formações como gerador de subprodutos de carbono que podem ser armazenados por longos períodos de tempos com magnitudes superiores às emissões atmosféricas (Jones et al. 2019). Esta tese pode ajudar a subsidiar tais modelos, destacando a importância não só das formações abertas, mas do componente subterrâneo como um todo destas formações e da relação planta-solo, responsáveis pela provisão e manutenção de serviços ecossistêmicos que auxiliam no controle das mudanças climáticas.

## REFERÊNCIAS

- Abreu, R.C.R., 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: 1–8.
- Archibald, S., Lehmann, C.E.R., Belcher, C.M., Bond, W.J., Bradstock, R.A., Daniau, A.L., Dexter, K.G., Forrester, E.J., Greve, M., He, T., Higgins, S.I., Hoffmann, W.A., Lamont, B.B., McGlinn, D.J., Moncrieff, G.R., Osborne, C.P., Pausas, J.G., Price, O., Ripley, B.S., Rogers, B.M., Schwill, D.W., Simon, M.F., Turetsky, M.R., Van Der Werf, G.R., & Zanne, A.E. 2018. Biological and geophysical feedbacks with fire in the Earth system. *Environmental Research Letters* 13:.
- Bai, Y., & Cotrufo, M.F. 2022. Grassland soil carbon sequestration: Current understanding, challenges, and solutions. *608*: 603–608.
- Bardgett, R.D., Bullock, J.M., Lavorel, S., Manning, P., Schaffner, U., Ostle, N., Chomel, M., Durigan, G., L. Fry, E., Johnson, D., Lavalley, J.M., Le Provost, G., Luo, S., Png, K., Sankaran, M., Hou, X., Zhou, H., Ma, L., Ren, W., Li, X., Ding, Y., Li, Y., & Shi, H. 2021. Combatting global grassland degradation. *Nature Reviews Earth & Environment* 2: 720–735.
- 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: 153–164.
- Bowman, D.M.J.S., Kolden, C.A., Abatzoglou, J.T., Johnston, F.H., van der Werf, G.R., & Flannigan, M. 2020. Vegetation fires in the Anthropocene. *Nature Reviews Earth & Environment*. doi: 10.1038/s43017-020-0085-3
- Buisson, E., Le Stradic, S., Silveira, F.A.O., Durigan, G., Overbeck, G.E., Fidelis, A., Fernandes, G.W., Bond, W.J., Hermann, J.-M., Mahy, G., Alvarado, S.T., Zaloumis, N.P., & Veldman, J.W. 2019. Resilience and restoration of tropical and subtropical grasslands, savannas, and grassy woodlands. *Biological Reviews*. doi: 10.1111/brv.12470
- Chergui, B., Fahd, S., Santos, X., & Pausas, J.G. 2018. Socioeconomic Factors Drive Fire-Regime Variability in the Mediterranean Basin. *Ecosystems* 21: 619–628.
- Collins, L., Bradstock, R.A., Clarke, H., Clarke, M.F., Nolan, R.H., & Penman, T.D. 2021. The 2019/2020 mega-fires exposed Australian ecosystems to an unprecedented extent of high-severity fire. *Environmental Research Letters* 16: 044029.
- Damasceno, G. 2022. Invasion by African grasses and restoration of open Cerrado formations: an approach by state-and-transition models.
- Damasceno, G., & Fidelis, A. 2020. Abundance of invasive grasses is dependent on fire regime and climatic conditions in tropical savannas. *Journal of Environmental Management* 271: 111016.
- 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: 3621–3629.
- Dove, N.C., Klingeman, D.M., Carrell, A.A., Cregger, M.A., & Schadt, C.W. 2021. Fire alters plant microbiome assembly patterns: integrating the plant and soil microbial response to disturbance. *New Phytologist*.

- Durigan, G., & Ratter, J.A. 2016. The need for a consistent fire policy for Cerrado conservation. *Journal of Applied Ecology* 53: 11–15.
- Fidelis, A., Alvarado, S.T., Barradas, A., & Pivello, V. 2018. The Year 2017: Megafires and Management in the Cerrado. *Fire* 1: 49.
- Fidelis, A., Lyra, M.F. di S., & Pivello, V.R. 2013. Above- and below-ground biomass and carbon dynamics in Brazilian Cerrado wet grasslands (O. Wildi, Ed.). *Journal of Vegetation Science* 24: 356–364.
- Freschet, G., Pagès, L., Iversen, C., Comas, L., Rewald, B., Roumet, C., Klimešová, J., Zadworny, M., Poorter, H., Postma, J., Freschet, G., Pagès, L., Iversen, C., Comas, L., & Rewald, B. 2020. A starting guide to root ecology: strengthening ecological concepts and standardizing root classification, sampling, processing and trait measurements To cite this version: HAL Id: hal-02918834.
- Freschet, G.T., Roumet, C., Comas, L.H., Weemstra, M., Bengough, A.G., Rewald, B., Bardgett, R.D., De Deyn, G.B., Johnson, D., Klimešová, J., Lukac, M., McCormack, M.L., Meier, I.C., Pagès, L., Poorter, H., Prieto, I., Wurzbürger, N., Zadworny, M., Bagniewska-Zadworna, A., Blancaflor, E.B., Brunner, I., Gessler, A., Hobbie, S.E., Iversen, C.M., Mommer, L., Picon-Cochard, C., Postma, J.A., Rose, L., Ryser, P., Scherer-Lorenzen, M., Soudzilovskaia, N.A., Sun, T., Valverde-Barrantes, O.J., Weigelt, A., York, L.M., & Stokes, A. 2021. Root traits as drivers of plant and ecosystem functioning: current understanding, pitfalls and future research needs. *New Phytologist*. doi: 10.1111/nph.17072
- He, T., Lamont, B.B., & Pausas, J.G. 2019. Fire as a key driver of Earth's biodiversity. *Biological Reviews*. doi: 10.1111/brv.12544
- Jia, G., Shevliakova, E., Artaxo, P., Noblet-Ducoudré, N.D., Houghton, R., House, J., Kitajima, K., Lennard, C., Popp, A., Sirin, A., Sukumar, R., & Verchot, L. 2021. 2019: Land–climate interactions. In Shukla, P.R., Skea, J., Buendía, E.C., Masson-Delmotte, V., Pörtner, H.-O., Roberts, D.C., Zhai, P., Slade, R., Connors, S., Diemen, R. van, Ferrat, M., Haughey, E., Luz, S., Neogi, S., Pathak, M., Petzold, J., Portugal, J., Pereira, P., Vyas, E., Huntley, K., Kissick, M., & Belkacemi, J.M. (eds.), *Climate Change and Land: an IPCC special report on climate change, desertification, land degradation, sustainable land management, food security, and greenhouse gas fluxes in terrestrial ecosystems*,
- Jones, M.W., Santín, C., van der Werf, G.R., & Doerr, S.H. 2019. Global fire emissions buffered by the production of pyrogenic carbon. *Nature Geoscience* 12: 742–747.
- 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: 4143–4157.
- Pausas, J.G., & Bond, W.J. 2020. On the Three Major Recycling Pathways in Terrestrial Ecosystems. *Trends in Ecology and Evolution* 35: 767–775.
- Pilon, N.A.L., Cava, M.G.B., Hoffmann, W.A., Abreu, R.C.R., Fidelis, A., & Durigan, G. 2021. The diversity of post-fire regeneration strategies in the cerrado ground layer. *Journal of Ecology*. doi: 10.1111/1365-2745.13456

- Pressler, Y., Moore, J.C., & Cotrufo, M.F. 2019. Belowground community responses to fire: meta-analysis reveals contrasting responses of soil microorganisms and mesofauna. *Oikos* 128: 309–327.
- Rossi, L.M.W., Mao, Z., Merino-Martín, L., Roumet, C., Fort, F., Taugourdeau, O., Boukcim, H., Fourtier, S., Del Rey-Granado, M., Chevallier, T., Cardinael, R., Fromin, N., & Stokes, A. 2020. Pathways to persistence: plant root traits alter carbon accumulation in different soil carbon pools. *Plant and Soil* 452: 457–478.
- Schmidt, I.B., & Eloy, L. 2020. Fire regime in the Brazilian Savanna: Recent changes, policy and management. *Flora: Morphology, Distribution, Functional Ecology of Plants* 268: 151613.
- Schmidt, I.B., Moura, L.C., Ferreira, M.C., Eloy, L., Sampaio, A.B., Dias, P.A., & Berlinck, C.N. 2018. Fire management in the Brazilian savanna: First steps and the way forward (R. Zenni, Ed.). *Journal of Applied Ecology* 55: 2094–2101.
- Singleton, M.P., Thode, A.E., Sánchez Meador, A.J., & Iniguez, J.M. 2019. Increasing trends in high-severity fire in the southwestern USA from 1984 to 2015. *Forest Ecology and Management* 433: 709–719.
- Vermeire, M.-L., Thoresen, J., Lennard, K., Vikram, S., Kirkman, K., Swemmer, A.M., Te Beest, M., Siebert, F., Gordijn, P., Venter, Z., Brunel, C., Wolfaard, G., Krumins, J.A., Cramer, M.D., & Hawkins, H.-J. 2021. Fire and herbivory drive fungal and bacterial communities through distinct above- and belowground mechanisms. *Science of The Total Environment* 785: 147189.
- Wigley, B.J., Augustine, D.J., Coetsee, C., Ratnam, J., & Sankaran, M. 2020. Grasses continue to trump trees at soil carbon sequestration following herbivore exclusion in a semiarid African savanna. *Ecology* 101: 1–10.
- Zhao, Y., Liu, Z., & Wu, J. 2020. Grassland ecosystem services: a systematic review of research advances and future directions. *Landscape Ecology* 35: 793–814.
- Zhou, Y., Singh, J., Butnor, J.R., Coetsee, C., Boucher, P.B., Case, M.F., Hockridge, E.G., Davies, A.B., & Staver, A.C. 2022. Limited increases in savanna carbon stocks over decades of fire suppression. *Nature*.
- 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:.



