Universidade de Brasília

Instituto de Ciências Biológicas

Programa de Pós-Graduação em Ecologia

Efeitos a curto prazo de queimas prescritas na abundância e remoção de sementes por pequenos mamíferos e invertebrados em áreas de campo sujo do Cerrado

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Dissertação de Mestrado apresentada ao Programa de Pós-Graduação em Ecologia, do Instituto de Ciências Biológicas da Universidade de Brasília, como requisito para obtenção do grau de Mestre em Ecologia.

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“Se toda coincidência
Tende a que se entenda
E toda lenda
Quer chegar aqui
A ciência não se aprende
A ciência apreende
A ciência em si

Se toda estrela cadente
Cai pra fazer sentido
E todo mito
Quer ter carne aqui

A ciência não se ensina
A ciência insemina
A ciência em si

Se o que se pode ver, ouvir, pegar, medir, pesar
Do avião a jato ao jaboti
Desperta o que ainda não, não se pôde pensar
Do sono eterno ao eterno devir
Como a órbita da terra abraça o vácuo devagar
Para alcançar o que já estava aqui
Se a crença quer se materializar
Tanto quanto a experiência quer se abstrair

A ciência não avança
A ciência alcança
A ciência em si”

Gilberto Gil e Arnaldo Antunes

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Resumo

As queimadas prescritas são uma importante ferramenta para a gestão e conservação de áreas protegidas no Cerrado e o conhecimento científico é essencial para garantir sua eficácia. Apesar disso, poucos estudos avaliam seus impactos indiretos em processos ecológicos relevantes em savanas tropicais. No presente estudo, investigamos os efeitos de curto prazo de queimadas prescritas na remoção de sementes por pequenos mamíferos e invertebrados em áreas de campo sujo do Cerrado, a savana mais diversa do mundo. As queimas prescritas nas áreas amostradas foram realizadas em manchas entre 15 a 20 ha e consumiram grande parte da camada herbácea. Houve um efeito de curto prazo (até 3 meses) das queimadas prescritas na abundância de pequenos mamíferos e na composição de espécies deste grupo, mas não na abundância de invertebrados. O fogo não afetou de maneira marcante a taxa geral de remoção de sementes ou o papel relativo de pequenos mamíferos e invertebrados neste processo. No entanto, os invertebrados encontraram as estações de sementes com mais frequência quando consideradas as características do habitat (cobertura vegetal do solo e altura da vegetação), a ocorrência de queimadas e agente de remoção (pequenos mamíferos ou invertebrados). Também encontramos efeitos opostos da altura da vegetação na remoção de sementes. Pequenos mamíferos removeram sementes com maior frequência em alturas maiores, enquanto a remoção por invertebrados foi negativamente relacionada a essa variável, em concordância com o modelo de percepção de risco de predação ("cenário do medo") para pequenos mamíferos. Nossos resultados fornecem suporte para a hipótese de que incêndios prescritos realizados de forma controlada e no início da estação seca não afetam significativamente os processos naturais de predação e remoção de sementes por animais em áreas campestres de Cerrado. Mas pode promover mudanças a curto prazo na abundância e composição de pequenos mamíferos. Além de ser uma ferramenta importante para a prevenção de incêndios em grande escala, as queimas prescritas também podem promover maior diversidade de pequenos mamíferos em escala de paisagem.

Palavras-Chave: Predação de sementes; Roedores; Formigas; Savana; Manejo do Fogo Integrado

Abstract

Prescribed burns are an important tool for the management and conservation of protected areas and understanding their effects on the ecosystem is essential to ensure the effectiveness of these burns. Despite that, few studies assess the indirect impacts of prescribed fires on relevant ecological processes in tropical savannahs. In the present study, we investigated short-term effects of prescribed burns on seed removal by small mammals and invertebrates in grassland areas of the Cerrado, the most diverse savannah of the world. These prescribed burns were carried out in patches between 15 and 20 ha and consumed most of the herbaceous layer. There was a short-term effect (up to 3 months) of the prescribed burns on small mammal abundance and on species composition of this group, but not on invertebrate abundance. The fire did not markedly affect the overall seed removal rate or the relative role of small mammals and invertebrates in this process. However, invertebrates found seed depots more frequently when considering habitat characteristics (ground plant cover and vegetation height), the occurrence of burning, and removal agent (small mammals or invertebrates). We also found opposite effects of vegetation height on seed removal. Small mammals removed seeds more frequently at higher heights whereas removal by invertebrates was negatively related to this variable, in agreement with a ‘landscape of fear’ scenario for small mammals. Our results provided support for the assumption that prescribed fires carried out in a controlled manner and at the beginning of the dry season do not significantly affect the natural processes of predation and seed removal by animals in areas of Cerrado grasslands. These fires promote, however, short-term changes in abundance and composition of small mammals. Besides being an important tool for preventing large-scale fires, prescribed fires also promote greater small-mammal diversity at a landscape scale.

Key words: Seed predation; Rodents; Ants; Savanna; Fire management

Prólogo

A remoção de sementes pós-dispersão pode levar ao seu consumo por diversos grupos de animais, bem como, pode também representar mais uma etapa em um processo de dispersão (Vander Wall, Kuhn and Beck, 2005). A predação de sementes é definida como o consumo de sementes, total ou parcial, que leva a sua inviabilidade (Janzen, 1971). Este consumo pode diminuir a abundância de espécies vegetais e limitar seu recrutamento, afetando o estabelecimento de populações (Howe and Smallwood, 1982; Hulme and Hunt, 1999; Bricker, Pearson and Maron, 2010; Vaz Ferreira, Bruna and Vasconcelos, 2011). A dispersão é definida como o deslocamento de um diásporo (fruto ou semente) de sua planta parental, tendo importante papel na colonização de espécies (Howe and Smallwood, 1982; Levin *et al.*, 2003). Assim, a predação e dispersão de sementes por animais podem desempenhar papel fundamental no recrutamento de plantas e na estruturação da vegetação nos ecossistemas (Howe and Smallwood, 1982; Hulme, 1998; Levin *et al.*, 2003; Vaz Ferreira, Bruna and Vasconcelos, 2011). Diversos fatores podem influenciar essas interações, como viabilidade de sementes, predadores, condições de habitat e eventos de perturbação que modificam as características ambientais (Howe and Smallwood, 1982; Wang and Smith, 2002; McEuen and Curran, 2004; Cazetta and Vieira, 2021).

Uma dessas fontes de perturbação que afeta diretamente as condições do habitat e as interações entre plantas e animais é o fogo (Auld and Denham, 2001; Parr *et al.*, 2007; Zwolak *et al.*, 2010). Os eventos de fogo podem afetar a remoção de sementes não apenas modificando a estrutura do ambiente, mas também alterando a abundância de potenciais removedores de sementes (Auld and Denham, 2001; Reed, Kaufman and Kaufman, 2004; Pausas, 2019). Os principais removedores sementes pós-dispersas são invertebrados (principalmente formigas), pequenos mamíferos e aves. A predação por esses grupos distintos, no entanto, não afeta as populações de plantas da mesma forma (Hulme, 1998; Christianini and Galetti, 2007). Algumas espécies são eficientes em encontrar e consumir sementes, por outro lado, outros grupos podem não somente não danificá-las, como também promover seu deslocamento para locais que favoreçam o estabelecimento de mudas (Howe and Smallwood, 1982; Vander Wall, Kuhn and Beck, 2005). Assim, o comportamento de forrageamento de diferentes grupos pode fornecer diferentes destinos para as sementes, influenciando na demografia, distribuição espacial e colonização das plantas (Christianini and Galetti, 2007; Bricker, Pearson and Maron, 2010; Vaz Ferreira, Bruna and Vasconcelos, 2011). Os padrões de remoção de sementes pós-dispersas também variam de acordo com diferentes aspectos do habitat, como estrutura da vegetação e cobertura do solo, com os principais grupos de dispersores atuando de forma diferente em habitats distintos (Hulme, 1998; Manson *et al.*, 1998; Christianini and Galetti, 2007). Assim, entender a variação dos padrões de predação de sementes pós-dispersão causados por diferentes grupos faunísticos é necessário para avaliar o real impacto dessa predação nas populações de plantas (Hulme, 1998; Vander Wall, Kuhn and Beck, 2005).

Entre os grupos importantes de removedores naturais de sementes, estão os pequenos mamíferos, principalmente roedores (Whelan *et al.*, 1991; Hulme, 1998; Vieira, Pizo and Izar, 2003; Bricker, Pearson and Maron, 2010). Esses animais são frequentemente reconhecidos como predadores, podendo limitar a abundância e recrutamento de espécies vegetais (Auld and Denham, 2001; Bricker, Pearson and Maron, 2010). Porém, espécies de roedores também podem atuar como dispersores efetivos de sementes, através do transporte de sementes viáveis para locais adequados para germinação e estabelecimento ou pela passagem de pequenas sementes intactas pelo trato digestivo (Brewer and Rejmánek, 1999; Loayza *et al.*, 2014; Sahley *et al.*, 2016). O papel de pequenos mamíferos como dispersores e predadores de sementes apresenta variações entre diferentes condições do hábitat. As espécies desse grupo possuem preferências por distintos componentes do ambiente e níveis de cobertura vegetal (Henriques and Alho, 1991; Monamy and Fox, 2000; Briani *et al.*, 2004). Assim como, a complexidade ambiental e a diversidade de itens alimentares disponíveis podem influenciar suas preferencias alimentares (Vieira and Briani, 2013).

As queimadas são uma importante fonte de distúrbio que pode afetar a heterogeneidade ambiental (Miranda, Bustamante and Miranda, 2002; He, Lamont and Pausas, 2019). As modificações na estrutura da vegetação e os requerimentos de habitat das espécies são apontados como os principais fatores que conduzem as respostas de pequenos mamíferos após o fogo (Monamy and Fox, 2000; Culhane *et al.*, 2022; Zwolak, 2009; González *et al.*, 2021). Esses animais respondem principalmente alterando sua abundância relativa e hábitos alimentares e o fogo pode promover ou restringir a ocorrência de diferentes espécies (González *et al.*, 2021; Demarais *et al.*, 2010; Vieira and Briani, 2013; Legge *et al.*, 2008). Algumas são conhecidas por se beneficiar da ocorrência de distúrbios, aumentando sua abundância, enquanto outras podem se tornar raras ou ausentes em áreas recém-queimadas (Briani *et al.*, 2004; Henriques *et al.*, 2006; Owen, 2013; González *et al.*, 2021). A substituição de espécies é resultante de um "trade-off" entre o uso dos recursos e as condições do habitat pós-fogo (González *et al.*, 2021; Monamy and Fox, 2000; Vieira and Briani, 2013; Culhane *et al.*, 2022).

As alterações ambientais pós fogo também podem influenciar fortemente na remoção de sementes por pequenos mamíferos e na comunidade de plantas com as quais interagem (Hulme, 1998; Auld and Denham, 2001; Reed, Kaufman and Kaufman, 2004; Zwolak *et al.*, 2010). Em muitos locais, roedores são conhecidos como principais removedores de sementes de áreas recém-queimadas, podendo ser a maior fonte de perda de sementes após o fogo (Auld and Denham, 2001; Reed, Kaufman and Kaufman, 2004; Zwolak *et al.*, 2010; Suazo *et al.*, 2013). Por outro lado, outros estudos reportam uma redução na remoção de sementes e importância relativa desses animais comparado a outros removedores em áreas queimadas (Greenler *et al.*, 2019; Alcolea, Durigan and Christianini, 2022; Anderegg *et al.*, 2022).

Os efeitos do fogo na remoção de sementes por pequenos mamíferos podem estar relacionados não somente a abundância das populações, mas também a modificações no uso do habitat pelos animais. O conceito do "cenário do medo" descreve a variação espacial na percepção do risco de predação, que pode variar no espaço e no tempo em múltiplas escalas e entre presas (Gaynor *et al.*, 2019). Para roedores, a cobertura vegetal tem importante influência na percepção do risco de predação e esses animais evitam locais com menor cobertura vegetal, reduzindo assim sua vulnerabilidade a predadores (Bueno and Motta-Junior, 2015; Abom and Schwarzkopf, 2016; Loggins *et al.*, 2019; Carreira *et al.*, 2020). A redução imediata da vegetação após a passagem do fogo pode promover esse cenário e levar a alterações na remoção de sementes por esses animais em ambientes recém-queimados.

As formigas são importantes agentes removedores de sementes em ambientes recém-queimados e as modificações do habitat também estão diretamente relacionadas a esse processo (Andersen, 1988; Parr *et al.*, 2007; Alcolea, Durigan and Christianini, 2022; Barbosa *et al.*, 2022). O fogo pode criar um habitat temporariamente rico em recursos para comunidades de formigas, além de promover a simplificação do habitat, o que pode aumentar a riqueza de espécies e a eficiência de forrageamento (Parr *et al.*, 2007; Tasker *et al.*, 2011; Barbosa *et al.*, 2022). Isso pode levar a alterações na abundância e comportamento de diferentes espécies de formigas, afetando a frequência e destino das sementes removidas no ambiente pós queima (Parr *et al.*, 2007; Tasker *et al.*, 2011; Beaumont, Mackay and Whalen, 2013). A ocorrência de queimadas pode afetar a abundância de grupos específicos de formigas bem como promover uma maior atividade e distância de dispersão das sementes (Parr *et al.*, 2007; Tasker *et al.*, 2011; Beaumont, Mackay and Whalen, 2013).

O fogo possui uma forte relação evolutiva com o Cerrado, sendo considerado um fator ecológico crucial para a manutenção da estrutura, biodiversidade e funcionamento dos ecossistemas deste bioma (Coutinho, 1990; Miranda *et al.*, 2009; Durigan and Ratter, 2016). O Cerrado é um dos ambientes de savana mais diversos do planeta, considerado um *hotspot* mundial de biodiversidade (Myers, 2003; Colli, Vieira and Dianese, 2020). Tem uma extensão de cerca de 2 milhões de km² e é composto por um mosaico de diferentes comunidades vegetais, desde campos até formações florestais (Coutinho, 1990; Simon and Pennington, 2012; WWF-Brasil, 2015).

Embora o fogo seja considerado um importante componente, a rápida ocupação antrópica da região e a expansão da agricultura modificaram o regime natural das queimadas (Pivello *et al.*¸2021; Durigan and Ratter, 2016). Os incêndios naturais no Cerrado, como na maioria das savanas sazonais, acontecem no início da estação chuvosa, ocasionados por raios. Esses incêndios são caracterizados por queima superficial da camada herbácea e seguidos por chuva, sendo naturalmente controlados e geralmente não alcançando grandes extensões (França, Neto and Setzer, 2007; Frizzo *et al.*, 2011; Miranda *et al.*, 2009). Por outro lado, queimadas por ações antrópicas ocorrem com frequência na estação seca, período em que as condições de propagação do fogo são mais favoráveis, ocasionando incêndios incontroláveis de grandes proporções (França, Neto and Setzer, 2007; Schmidt and Eloy, 2020; Miranda *et al*., 2009). Tais incêndios são beneficiados com condições climáticas de altas temperaturas e baixa umidade do ar, além de grandes quantidades de combustível seco acumulado, podendo atingir áreas de mais de 50.000 hectares (Schmidt and Eloy, 2020). Esses incêndios frequentes e de grandes extensões podem ter consequências diretas e indiretas sobre a biota, modificando a paisagem e afetando consideravelmente as funções ecológicas das comunidades vegetais e animais (Coutinho, 1990; Pivello *et al.*¸2021; Durigan and Ratter, 2016).

Apesar dos impactos dos incêndios, as extinções locais causadas por queimadas naturais ou prescritas são raras e muitas espécies possuem mecanismos que conferem sua resiliência ao fogo, permitindo a rápida recuperação após queimadas (Durigan et al, 2020; Simon and Pennington, 2012; Pausas and Parr, 2018). Além disso, a supressão do fogo também pode ter consequências negativas, podendo causar a redução no número de espécies e o aumento do risco de grandes incêndios (Durigan and Ratter, 2016, Schmidt and Eloy, 2020; Abreu *et al.*, 2017). A "Política do Fogo Zero", implementada no Brasil por várias décadas, também contribuiu para a intensificação dos regimes de fogo no Cerrado (Durigan and Ratter, 2016). Com o intuito de evitar qualquer tipo de incêndio, a total exclusão do fogo nesse ecossistema levou ao acúmulo de combustível, aumentando o risco de grandes incêndios florestais (Durigan and Ratter, 2016; Schmidt and Eloy, 2020).

Buscando reverter os impactos da supressão do fogo, foi iniciado em 2014 o programa de Manejo Integrado do Fogo (MIF) em Unidades de Conservação e Territórios Indígenas do Brasil (Schmidt *et al.*, 2018). O uso de queimadas prescritas como parte das ações propostas pelo programa é uma ferramenta utilizada para diversos fins, entre eles, reduzir a carga de combustível e prevenir a ocorrência de grandes incêndios na estação seca (Christensen, 2005; Pillai and Vallabhan, 2009; Pivello, 2011; Schmidt *et al.*, 2018). Essa abordagem vem sendo implementada em diversos países, sendo apontada como uma importante ferramenta para a conservação dos ecossistemas (Christensen, 2005; Hardesty, Myers and Fulks, 2005; Sande Silva *et al.*, 2010; Schmidt *et al.*, 2018). As queimas prescritas geralmente são realizadas nos períodos de estiagem na estação chuvosa ou início da estação seca e tendem a ser de baixa intensidade. Assim, criam mosaicos de paisagem com diferentes históricos de queima e podem reduzir a frequência de incêndios em vegetações sensíveis ao fogo, como matas ciliares (Schmidt *et al.,* 2018). Porém, os benefícios dessa prática dependem de regimes adequados e devem ser baseados em evidências científicas que avaliem seus efeitos nos ecossistemas, garantindo sua eficácia na conservação da biodiversidade (Driscoll *et al.*, 2010; Pivello, 2011; Gomes, Miranda and Bustamante, 2018).

Apesar da importância do conhecimento científico para subsidiar o manejo do fogo em áreas protegidas do Cerrado (Driscoll *et al.*, 2010; Pivello, 2011), poucos estudos avaliam seus impactos indiretos em processos ecológicos relevantes, como a predação de sementes por animais. Estudos comparativos avaliando os efeitos de incêndios prescritos são necessários para fornecer evidências dos impactos e benefícios do fogo para a biodiversidade, processos ecológicos e serviços ecossistêmicos no Cerrado (Durigan and

Ratter, 2016; Gomes, Miranda and Bustamante, 2018). Além disso, estudos acerca desse tema são importantes para subsidiar o planejamento e implementação de queimadas prescritas em Unidades de Conservação no Brasil.

Considerando que as taxas de predação de sementes podem influenciar diretamente nas populações de plantas e na regeneração da vegetação e que os incêndios podem afetar profundamente esses processos, no presente estudo buscamos investigar os efeitos de curto prazo das queimadas prescritas na remoção de sementes e a abundância de seus principais removedores – pequenos mamíferos e invertebrados. Avaliamos a abundância de pequenos mamíferos e invertebrados em áreas naturais antes e depois dessas queimadas, buscando responder às seguintes questões: (1) Como a abundância de pequenos mamíferos e invertebrados se modifica nos primeiros meses após as queimadas; (2) Se existe efeito da queima prescrita na remoção de sementes por pequenos mamíferos e invertebrados ao longo dos meses após a queima; (3) Como as variáveis de micro-habitat afetam a remoção de sementes por pequenos mamíferos e invertebrados após a queima.

A abundância de pequenos mamíferos tende a estar positivamente associada à cobertura vegetal (Hulme, 1998; Monamy and Fox, 2000), e algumas espécies evitam áreas recém-queimadas (Vieira, 1999; Briani *et al.*, 2004). Por outro lado, alguns grupos de invertebrados, principalmente formigas, podem aumentar sua abundância após a ocorrência do fogo (Andersen, 1988; Parr *et al.*, 2007; Barbosa *et al.*, 2022). As queimadas prescritas tendem a ter características baixa intensidade, permitindo a rápida recuperação da vegetação alguns meses após a queima (Munhoz and Amaral, 2010; Gomes, Miranda and Bustamante, 2018; Schmidt *et al.*, 2018). As mudanças pós-queima nas condições de micro-habitat e disponibilidade de recursos são descritas como as principais causas de mudanças no uso de habitat por pequenos mamíferos e invertebrados (Vieira, 1999; Monamy and Fox, 2000; Vieira and Briani, 2013; Diniz and Morais, 2016; Barbosa *et al.*, 2022), bem como, na remoção de sementes por esses animais (Parr *et al.*, 2007; Zwolak *et al.*, 2010; Tasker *et al.*, 2011; Barbosa *et al.*, 2022).

Considerando tais aspectos, esperamos: (a) uma redução imediata na abundância de pequenos mamíferos e um aumento na abundância de invertebrados após a queima, como consequência de mudanças nas condições ambientais, com posterior retorno aos níveis pré-queima proporcionados pela a rápida recuperação da vegetação; (b) uma baixa remoção de sementes por pequenos mamíferos no primeiro mês após a queima devido à redução na abundância relativa do grupo (com um subsequente aumento na remoção após 2 a 3 meses devido à recuperação da população), enquanto para invertebrados tais reduções serão menos evidentes ou inexistentes; (c) um efeito significativo da altura e da cobertura vegetal na remoção de sementes ao longo dos meses após a queima.

Amostramos áreas submetidas a queimas prescritas no Parque Nacional da Chapada dos Veadeiros (PNCV) nos meses de março e abril de 2021. Também amostramos áreas não queimadas que foram consideradas como controle. As queimas prescritas nas áreas amostradas foram realizadas em manchas entre 15 a 20 ha e consumiram grande parte da camada herbácea e folhas e frutos de arbustos. Um mês após os incêndios, encontramos redução e descontinuidade da vegetação e muitos pontos de solo exposto. Por outro lado, muitas plantas apresentavam rebrota. Não encontramos sementes no solo e raros frutos secos não queimados. As amostragens foram realizadas antes e em diferentes períodos pós queima (um, três e seis meses). Para captura de pequenos mamíferos utilizamos armadilhas do tipo *Sherman*® (esforço de 8.803 armadilhas/noite) e para invertebrados tipo *pitfall* (400 armadilhas/noite) dispostas em transecções lineares. Para avaliar a remoção de sementes, ofertamos sementes de girassol (*Helianthus annuus*) sob gaiolas de exclusão com tratamentos que restringiam o acesso a invertebrados ou pequenos mamíferos. Para avaliar possíveis efeitos de variáveis de micro-habitat na remoção de sementes, estimamos a altura e cobertura da vegetação nas áreas queimadas e não queimadas durante as campanhas de amostragem.

Encontramos mudanças na abundância e composição de espécies de pequenos mamíferos nos primeiros meses após as queimas prescritas. Um mês após a queima, as áreas queimadas apresentaram redução marcante no sucesso de captura, enquanto houve aumento da captura em áreas não queimadas no mesmo período. As diferenças de abundância entre áreas queimadas e não queimadas foram menos pronunciadas após três meses de queima. Após o sexto mês, as áreas queimadas apresentaram maior abundância de pequenos mamíferos, indicando uma rápida recuperação da comunidade após queimas prescritas. O eixo principal (52,7% da variação total) da Análise de Correspondência (CA) indicou um agrupamento incluindo as áreas amostradas antes da queima e ás áreas não queimadas. Este grupo estava relacionado principalmente ao roedor *Necromys lasiurus,* espécie dominante nestas áreas. Nos períodos um e três meses após a queima, o padrão mais evidente foi a ausência de *N. lasiurus* e a presença das espécies *Calomys tener* e *Thylamys velutinus*. Esse padrão se modificou após seis meses de queima controlada, quando as áreas queimadas e não queimadas tornaram-se mais semelhantes na abundância e composição das espécies. Neste período também houve o retorno da abundância de *N. lasiurus* nas áreas amostradas.

Os invertebrados não apresentaram diferenças marcantes na abundância após um mês das queimas prescritas, o que pode ter contribuído para manter a remoção de sementes em áreas queimadas apesar da abundância reduzida de pequenos mamíferos. Após três meses, as áreas queimadas apresentaram um aumento na biomassa de invertebrados em relação ao período anterior, enquanto nas áreas não queimadas houve uma redução no mesmo período. A família Formicidae contribuiu para quase metade da biomassa total do grupo nesse período e apresentou um aumento de 239% em sua biomassa comparada ao primeiro mês após a queima. Após seis meses, as formigas apresentaram uma redução acentuada na biomassa nas áreas queimadas enquanto os invertebrados permaneceram com aumento de sua biomassa neste período.

Os resultados do modelo avaliando os efeitos da queima prescrita e agente removedor indicaram que as queimadas prescritas não alteram o número de sementes removidas. No entanto, as áreas amostradas apresentaram diferenças antes mesmo dos incêndios ocorrerem. Nas áreas queimadas, a passagem do fogo aparentemente impediu um aumento mais acentuado na remoção de sementes no primeiro mês após o incêndio. A comparação do número de sementes removidas entre os diferentes agentes removedores (invertebrados ou pequenos mamíferos) não indicou diferenças significativas entre esses dois grupos. Além disso, não encontramos efeitos da interação entre o agente removedor (exclusão) e a ocorrência de fogo, indicando que a queima não alterou o papel relativo de pequenos mamíferos e invertebrados nas taxas de remoção de sementes. Todavia, o modelo utilizando as variáveis de micro-habitat e a presença e ausência de remoção (variável resposta binária), os invertebrados removeram sementes com maior frequência quando comparado a pequenos mamíferos. Essa aparente inconsistência dos resultados pode estar relacionada aos diferentes tamanhos amostrais dos modelos, bem como ao uso de diferentes variáveis resposta. Embora o modelo não tenha indicado uma interação significativa entre os tratamentos fogo e exclusão, as formigas removeram três vezes mais sementes do que os pequenos mamíferos nas áreas queimadas, principalmente após três meses do fogo.

Não encontramos efeitos da cobertura do solo na remoção de sementes, que pode estar relacionada a rápida rebrota da vegetação após o fogo, minimizando os efeitos dessa variável. Por outro lado, encontramos uma interação significativa entre a altura da vegetação e o agente removedor com efeitos opostos nos diferentes grupos. Pequenos mamíferos removeram sementes com mais frequência em estações experimentais com vegetação mais alta, enquanto a remoção por invertebrados foi negativamente relacionada a essa variável.

Nossos achados contribuem para elucidar como as queimadas prescritas podem afetar a remoção de sementes e a abundância de seus principais removedores durante os primeiros meses após o fogo em áreas de campo sujo do Cerrado. Nossos resultados indicam que, em geral, queimadas prescritas realizadas de forma controlada e no início da estação seca não afetam significativamente os processos naturais de predação e remoção de sementes por animais. Por outro lado, podem contribuir para mudanças na abundância e composição de espécies de pequenos mamíferos. Isso reforça a importância de queimas prescritas não só para prevenção de grandes incêndios, como também para promover maior diversidade de espécies em uma escala de paisagem. Estudos em larga escala que combinem múltiplos fatores em diferentes escalas temporais são necessários para o avanço no conhecimento acerca dos efeitos de queimadas prescritas a longo prazo nos processos de remoção de sementes. Reforçamos também a importância de considerar os períodos de reprodução da vegetação, principalmente de frutos zoocóricos, no planejamento de queimadas prescritas, pois podem ser decisivos para garantir a disponibilidade e uso de recursos pela fauna após o incêndio.

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Short-term effects of prescribed fires on abundance and seed removal by small mammals and invertebrates in Cerrado grasslands

Bárbara de Araújo Gonçalves[1,2]*; Emerson Monteiro Vieira[1]

1-Laboratório de Ecologia de Vertebrados, Departamento de Ecologia, Instituto de Ciências Biológicas, Universidade de Brasília (UnB), Brasília, Brazil. *Corresponding author

2-Programa de Pós-graduação em Ecologia, Instituto de Ciências Biológicas, Universidade de Brasília, Brasília, Brazil

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Introduction

Seed predation and dispersal plays a fundamental role in plant recruitment and vegetation structuring in ecosystems (Howe and Smallwood, 1982; Vaz Ferreira, Bruna and Vasconcelos, 2011). Seed predation can decrease the abundance of species and limit their recruitment, affecting the establishment of populations (Howe and Smallwood, 1982; Hulme and Hunt, 1999; Bricker, Pearson and Maron, 2010; Vaz Ferreira, Bruna and Vasconcelos, 2011). Several factors can influence this process, such as seed viability, predator behaviour, habitat conditions, and disturbance events that modify environmental characteristics (Howe and Smallwood, 1982; Wang and Smith, 2002; McEuen and Curran, 2004; Cazetta and Vieira, 2021). One of these sources of disturbance that directly affects habitat conditions and interactions between plants and animals are fire events (Auld and Denham, 2001; Parr *et al.*, 2007; Zwolak *et al.*, 2010). Fires are common in tropical savannahs and considered to be a key factor controlling their composition and structure (He, Lamont and Pausas, 2019) Thus, the evaluation of the effects of this disturbance on seed predation by distinct animal groups is fundamental for understanding how fire shapes the ecological processes and for the establishment of adequate fire-management strategies in tropical savannahs.

Fire events may affect seed predation not only changing the microhabitat structure but also altering the abundance of seed dispersers (Auld and Denham, 2001; Reed, Kaufman and Kaufman, 2004; Pausas, 2019). The main post-seed dispersal predators are invertebrates (mainly ants), small mammals, and birds. Predation by these distinct groups, however, does not affect plant populations in the same way (Hulme, 1998; Christianini and Galetti, 2007). The foraging behaviour of different groups can provide different seed fates, influencing the demographics, spatial distribution and colonization of plants (Christianini and Galetti, 2007; Bricker, Pearson and Maron, 2010; Vaz Ferreira, Bruna and Vasconcelos, 2011). The patterns of removal of post-dispersed seeds also vary according to different aspects of the habitat, such as vegetation structure and soil cover, with the main groups of dispersers acting differently in distinct habitats (Hulme, 1998; Manson *et al.*, 1998; Christianini and Galetti, 2007).

Small mammals, mainly rodents, are often recognized as seed predators and may limit the abundance and recruitment of plant species (Hulme, 1998; Auld and Denham, 2001; Bricker, Pearson and Maron, 2010). These animals have preferences for distinct components of the habitat and levels of vegetation cover (Hulme, 1998; Monamy and Fox, 2000; Briani *et al.*, 2004), which potentially affects their role as dispersers and seed predators. Environmental heterogeneity and different stages of vegetation regeneration can strongly influence seed removal by small mammals and the plant community with which they interact (Hulme, 1998; Zwolak *et al.*, 2010).

Environmental heterogeneity can be affected by disturbance events, such as fires (He, Lamont and Pausas, 2019; Miranda *et al.*, 2009). Fire events can affect not only vegetation cover but also seed availability, leading to changes in abundance, composition and behaviour of predator species (Zwolak *et al.*, 2010; Vieira and Briani, 2013; Alcolea, Durigan and Christianini, 2022; Barbosa *et al.*, 2022). Both factors considerably affect seed predation and impacts of fire events on ecosystems are closely related to the frequency and severity of fire (Manson *et al.*, 1998; Reed, Kaufman and Kaufman, 2005; Tasker *et al.*, 2011; Barbosa *et al.*, 2022).

Fire occurrence is a crucial ecological factor for maintaining the structure, biodiversity and functioning of Cerrado ecosystems (neotropical savannah), which are known for their evolutionary relationship with fire (Coutinho, 1990; Miranda *et al.*, 2009;

Durigan and Ratter, 2016; Simon *et al.*, 2009). The Cerrado is one of the most diverse savannah environments on the planet, considered a world biodiversity hotspot (Myers, 2003; Colli, Vieira and Dianese, 2020). It has an extension of about 2 million km² and is composed of a mosaic of different plant communities, ranging from grasslands to forest formations (Coutinho, 1990; Simon and Pennington, 2012; WWF-Brasil, 2015).

Although fire is considered one of the determinants of the Cerrado, the rapid anthropic occupation of the region and expansion of agriculture modified the natural regime of fires. The natural fires in the Cerrado, as in most seasonal savannahs, occur at the beginning of the rainy season, caused by lightning. These fires are characterized by surface burning of the herbaceous layer and followed by rain, being controlled soon after its beginning, and generally do not reach large extents (França, Ramos Neto and Setzer, 2007). On the other hand, anthropic fires occur frequently in the dry season, a period in which the conditions of fire propagation are better, causing uncontrollable fires of great proportions (França, Ramos Neto and Setzer, 2007; Schmidt and Eloy, 2020). This frequent fires and large extents can have direct and indirect consequences on the biota, modifying the landscape and considerably affecting the ecological functions of plant and animal communities (Coutinho, 1990; Pivello *et al.*¸2021; Durigan and Ratter, 2016).

Despite the impacts of fires, local extinctions caused by natural and prescribed fires are rare and many species have specific adaptations that confer their resilience, allowing their survival and rapid recover after fire (Durigan et al, 2020; Simon and Pennington, 2012; Pausas and Parr, 2018). In this fire-prone ecosystems, the fire suppression can also have negative consequences, causing a species loss and increase the risk of large fires due to fuel accumulation (Durigan and Ratter, 2016, Schmidt and Eloy, 2020; Abreu *et al.*, 2017). This highlights the important role of fire in maintaining biodiversity in tropical savannas and the and the need for its adequate management for the conservation of biodiversity (Abreu *et al.*, 2017; Durigan and Ratter, 2016).

The use of prescribed fires as part of the management of protected areas has been implemented in several countries, being pointed out as an important tool for the conservation of ecosystems (Christensen, 2005; Hardesty, Myers and Fulks, 2005; Sande Silva *et al.*, 2010; Schmidt *et al.*, 2018). The benefits of this practice depend on adequate regimes and should be based on scientific evidence that evaluates its effects on ecosystems, ensuring its effectiveness in the conservation of savannah biodiversity (Driscoll *et al.*, 2010; Pivello, 2011; Gomes, Miranda and Bustamante, 2018). Few studies, however, assess fire impacts on relevant ecological processes, such as seed predation by animals. Studies evaluating the effects of prescribed fires are needed to provide evidence of impacts and benefits of fire for biodiversity, ecological processes, and ecosystem services in the Cerrado (Durigan and Ratter, 2016; Gomes, Miranda and Bustamante, 2018).

Considering that seed predation rates can directly influence plant populations and vegetation regeneration and that fires can profoundly affect these processes, we investigated short-term effects of prescribed burns on seed removal and on the abundance of their main removal agents – small mammals and invertebrates. Small mammal abundance tends to be positively associated with vegetative cover (Hulme, 1998; Monamy and Fox, 2000), and some species avoid newly burned areas (Vieira, 1999; Briani *et al.*, 2004). On the other hand, some invertebrates groups, especially ants, may increase their abundance and activity after the occurrence of fire (Andersen, 1988; Parr *et al.*, 2007; Barbosa *et al.*, 2022). Prescribed burns tend to have characteristics of low levels of plant damage, allowing the rapid recovery of vegetation a few months after burning (Munhoz and Amaral, 2010; Schmidt *et al.*, 2016; Gomes, Miranda and Bustamante, 2018; Alcolea, Durigan and Christianini, 2022). Post-burning changes in microhabitat conditions and availability of resources are the main causes of changes in habitat use by small mammals and invertebrates (Culhane *et al*, 2022*;* Monamy and Fox, 2000; Vieira and Briani, 2013; Diniz and Morais, 2016; Barbosa *et al.*, 2022), as well as, in the removal of seeds by these animals (Parr *et al.*, 2007; Zwolak *et al.*, 2010; Tasker *et al.*, 2011; Barbosa *et al.*, 2022).

We evaluated abundance of small mammals and invertebrates in natural areas before and after these fires, seeking to answer the following questions: (1) How the abundance of small mammals and invertebrates change over the first few months after burning; (2) Is there an effect of the prescribed burning on the removal of seeds by small mammals and invertebrates over the months after burning; (3) How microhabitat variables affect seed removal by small mammals and invertebrates after burning. Considering these questions, we hypothesized that: (a) there is an immediate reduction in abundance of small mammals and an increase in abundance of invertebrates after burning, as a consequence of changes in environmental conditions, with subsequent return to pre-burning levels provided by the rapid recovery of the vegetation; (b) there is a low seed removal by small mammals in the first month after burning due to the reduction in the relative abundance of small mammals (with a subsequent increase in removal after 2 to 3 months due to population recovery) whereas for invertebrates such reduction is less evident or inexistent; and (c) there is a significant effect of height and vegetation cover on seed removal over the months after burning.

Methods

Study area

We conducted the study in the Chapada dos Veadeiros National Park (CVNP), a Conservation Unit located, in the state of Goiás, central Brazil (14°05'05.32" S, 47°42'18.67" W) (Figure 1). This park is covered by a mosaic of phytophysiognomies of the Cerrado biome, with approximately 74% of its area of ~240,000 ha composed of savannah vegetation and 16% of grassland formations (Rosa and Tolentino, 2009). The climate of the region is defined as tropical Aw, according to the Köppen-Geiger classification, characterized by a rainy season, from November to March, and dry season, from May to September. The average annual temperature is 23.4ºC and the average rainfall is 1500 mm (Cardoso, Marcuzzo and Barros, 2014).

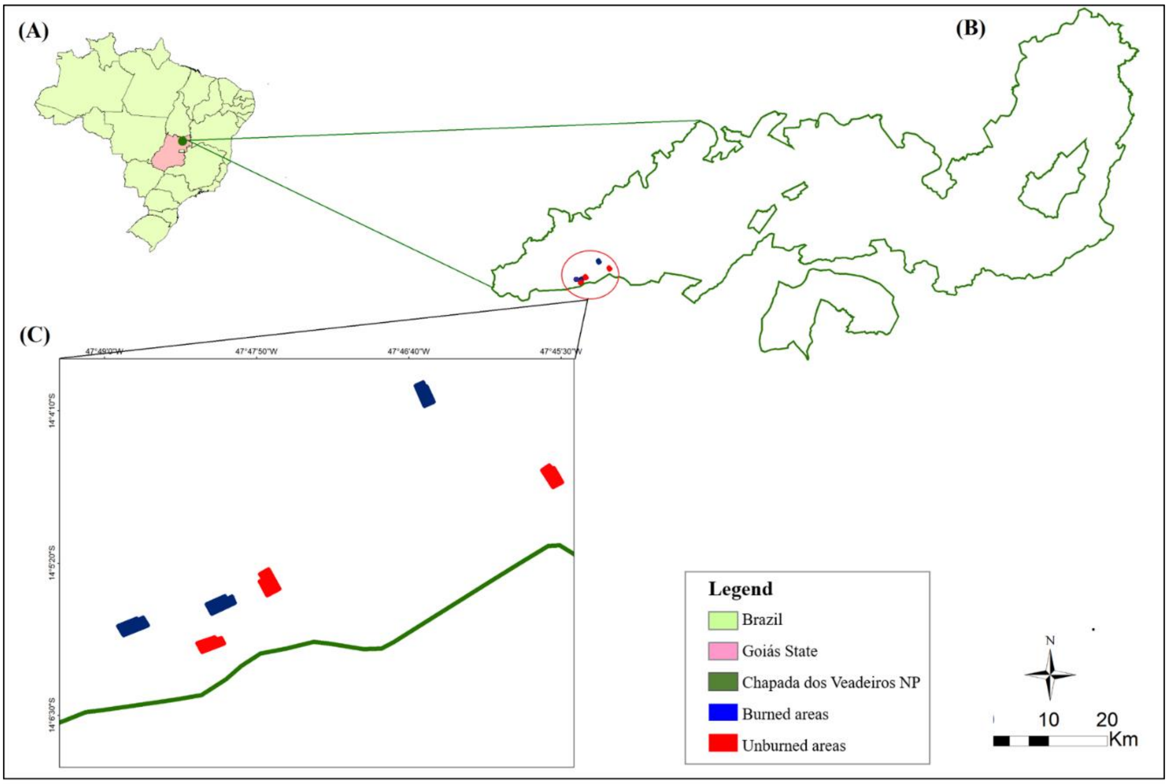

Figure 1. (A) Location of the study area in the Chapada dos Veadeiros National Park (dark green) in the state of Goiás (light pink) and Brazilian territory (light green). (B) Location of sampling areas within the boundaries of the CVNP. (C) Spatial arrangement of the sampled areas subjected to prescribed fires (red) and unburned (blue) in the CVNP.

As part of a Program for Integrated Fire Management (IFM), carried out in Brazil since 2014, fire management actions have been implemented by Federal Conservation Units (CU's) to reduce fuel plant material and prevent large wildfires (Schmidt *et al.*, 2018). The program's actions aim to carry out early burning (at the beginning of the dry season), creating landscape mosaics with different historic fire sites to protect fire-sensitive areas, such as riparian forests and woodland formations (Schmidt *et al.*, 2018).

Experimental design

The prescribed burns were carried out in the CVNP from January to April 2021 in different areas of the Cerrado grassland formation, totalling 5,817.42 ha of burned area. The sampled areas were burned in March and April of the same year in patches of ~ 15 to 20 ha. We conducted sampling campaigns in the areas submitted to burning, in addition to areas not burned for at least two years, considered as control. The prescribed burning consumed most of the herbaceous layer and shrubs. One month after the fires, we found reduction and discontinuity of vegetation and many exposed soil points. On the other hand, many remaining plants were sprouting, showing new leaves. We found no seeds in the soil and scarce unburned dry fruits (personal observation). In one of the burned areas, the fire did not completely consume the herbaceous vegetation and in some points, part of the dry cover still remained. Part of this area had a rocky soil and a discontinuity of vegetation before the fire, which may have favoured a less homogeneous fire. All the sampled sites were entirely burned and the closest unburned areas were at least one kilometer away from the sampled sites.

The areas were sampled before fire (February and March) and in distinct post-fire periods: one month (April and May), three months (June and July), and six months (September and October) after fire. In the field campaigns before and one month after burning, we sampled three burned (treatment) areas and one unburned (control) area. We sampled only one control area in these campaigns due to difficulties to find suitable areas in the CVNP compatible with our logistics. Three and six months after fire we sampled three burned areas and three control areas. In each area, we established parallel transects for the sampling of small mammals and seed removal experiments.

Sampling of small mammals

To capture small mammals, we established trapping grids (one in each sampled site) composed of 100 (4 × 25) capture stations placed in 4 parallel transects (20 m apart). We placed 50 small (9 cm x 18 cm x 24 cm) and 50 large (11 cm x 12.5 cm x 37 cm) *Sherman*® traps (H.B. Sherman Traps, Tallahassee, Florida) on the ground, arranged alternately at 15-m intervals, totalling 100 traps per site. In each campaign, we sampled the areas for four consecutive nights, for a total sampling effort of 8,803 trap nights at the end of the study. We used a mixture of peanut butter, corn flour, mashed bananas, palm oil and canned sardines as bait. Traps were checked daily early in the morning and captured animals were identified, weighed, sexed, ear-tagged (model 1005-1; National Band and Tag, Newport, Kentucky), and released at the point of capture.

Abundance of invertebrates

To estimate the abundance of invertebrates in burned and unburned areas over the period of the study, we installed five *pitfall* traps in a central linear transects placed in each sampled site. These *pitfalls* consisted of 500-ml plastic cups buried with the opening flush to the ground surface and filled with water (95%), salt (5%) and a few drops of detergent to break the water tension. These traps remained active on the field for four consecutive nights. The collected material was sifted and sorted in the laboratory and the captured invertebrates were identified at the family level for the most frequent groups (Coleoptera, Hemiptera, Hymenoptera and Orthoptera) and at the level of order for the others. Samples were dried in an oven (60°C) for three nights and we used this dry biomass for evaluating the abundance of invertebrates in the burned and unburned areas for each sampling campaign.

Seed removal experiment

To evaluate the effect of prescribed burning on seed removal by small mammals and invertebrates, we established two parallel transects distant 30 meters from each other, in the same sites of small mammal and invertebrate sampling. At each transect, we placed 15 experimental stations 20 m apart from each other, totalling 30 experimental stations per area. In each of these stations, we placed a petri dish (9 cm x 15 cm) on the soil containing 10 sunflower seeds (*Helianthus annuus*). We used sunflower seeds as a model for removal because they are attractive seeds consumed by the two groups investigated (small mammals and invertebrates) and are commonly used in seed removal studies (e.g., Manson *et al.*, 1998; Lindgren, Lindborg and Cousins, 2018; Alcolea, Durigan and Christianini, 2022; Widick *et al.*, 2022)

We covered the dishes with semipermeable exclosures using wire-mesh cages staked to the ground. For these exclosures, we used cages with two different sizes (24 cm x 24 cm wide and 10 cm high, mesh = 1.5 cm, side opening with 12 cm wide and 5 cm high; 40 cm x 40 cm wide and 13 cm high, mesh = 2.5 cm, side opening 12 cm wide and 8 cm high) available at the Laboratory of Vertebrate Ecology of the University of

Brasília. These cages allowed the access of small mammals (<400 g) but not of larger vertebrates.

Seed trial in each experimental station was submitted to one of the two following treatments. (1) Access of invertebrates, where we blocked the side entrances of the cages preventing access to small mammals. (2) Access of small mammals, where we cover the outer border of the petri dishes with Tanglefoot® glue (insect barrier), to prevent the access of non-flying insects to the seeds. With this methodology, access to other animals such as birds and vertebrates of medium and large size was prevented in both treatments. The cages of each treatment were arranged alternately in each transect, ensuring the same number of stations for each seed-remover group. The seed removal experiments lasted four consecutive nights and at the end, we verified the quantity of remaining seeds in the petri dishes. We considered as removed the difference between the number of seeds placed (10) and the remaining intact seeds. Seeds consumed, partially or totally, found in the petri dishes or nearby, were also considered as 'removed'.

Microhabitat variables

We evaluated the possible effects of microhabitat variables on seed removal in burned and unburned areas. For that, we assystematically established 6 points spaced at least 40 m from each other along the experimental station transects (first 3 odd stations and last 3 odd stations) for measuring the vegetation height and ground plant cover. For each point, we estimated the soil cover from photographs of the soil, taken vertically, framed with the aid of a square frame ($0.5m^2$) made of PVC pipe, and positioned perpendicularly to approximately 1 m of ground height. We analysed the photographs in the ImageJ program®, obtaining the percentage of ground cover in the area delimited by the frame. All vegetation (living or dead) present within the frame was considered as vegetation cover. We determinate the vegetation height using a measuring tape positioned at ground level and stretched to the maximum point where the vegetation touches the tape. We considered the mean of the values measured for the variables in four points located 2 m from the focal point in the four cardinal directions.

Statistical analyses

We evaluated potential differences in small-mammal community composition according to the occurrence of prescribed fire by performing a Correspondence Analysis (CA) on the site-by-species matrix, grouping the sites sampled in the same period in relation to the fire occurrence. This approach enabled comparison of burned and unburned sites before and after prescribed fires (with similar small-mammal communities appearing close to each other). This analysis was performed with the Past software (Hammer, Harper and Ryan, 2001). Considering the low number of individuals captured during the study (see Results section) we opted for not performing statistical testing for evaluating possible fire-related changes in abundance of small mammals in the sampled sites.

To evaluate the effect of fire over time on seed removal rate by small mammals and invertebrates, we used a Mixed Generalized Model (GLMM). The variables treatment (fire and control), exclusion (small mammals and invertebrates) and time (before, one, three and six months after fire) we considered fixed factors, and the sampled areas as a random factor. The number of seed removed from each dish was used as a response variable and, due to the high dispersion of the data, we used a GLMM with a negative binomial family to minimize this effect. We used 650 observations in this analysis.

To evaluate the effect of environmental variables on seed removal, we performed a GLMM with a binomial family, considering the variables treatment, exclusion, soil cover and vegetation height as fixed factors and areas as a random factor. For this analysis, we used only the removal points where the environmental variables were measured. The environmental variables were standardized by transformation z (Zar, 1999). For a better model fit, we considered the presence or absence of removal in each dish as a response variable (binary response). Moreover, due to similarities in vegetation cover and height of the areas before the occurrence of burning (Appendix S1), we disregarded this period. Thus, we used 107 observations in this analysis. We performed these analyses in the R program (R Core Team, 2022, version 4.2.1).

Results

Small mammals and invertebrates

The sampling of small mammals resulted in a total of 109 captured individuals, belonging to seven rodent species and one marsupial species (Table 1). The number of species ranged from 3 to 5 in the burned areas and from 1 to 5 species in the unburned areas. For both treatments the richness peak was attained in the period of three months after burning. The total trap success was 1.14%, being 1.05% (59 individuals of six species) for the burned areas and 1.56% for the unburned areas (50 individuals of six species). The rodent *Necromys lasiurus* was the most abundant species, with 54 captures (62% in unburned areas), followed by *rodent Calomys tener* with 20 captures (95% in burned areas).

Table 1. Number of individuals of the small mammals species captured one month before and up to six months after early prescribed fires in sites of *campo sujo* vegetation (grasslands with scattered shrubs) during the dry season in a neotropical savanna (Cerrado). Post-fire sampling occurred 1, 3, and 6 months after burning. We also present total abundance (number of individuals), richness (number of species) and trap success (individuals caught/100 trap nights) in each period sampled.

Specie	**Time in relation to fire** (days)								**Total**	
	Before		30 days		60 days		90 days			
	Unb	Unb	Bur	Unb	Bur	Unb	Bur	Unb	Bur	Unb
Didelphimorphia										
Thylamys velutinus	0	0	1	0	5	0	0	0	6	0
Rodentia										
Clyomys laticeps	0	0	0	2	6	1	1	7	7	10
Carterodon sulcidens	0	0	0	1	0	1	0	1	0	3
Calomys tener	0	0	1	0	7	0	11	1	19	1
Necromys lasiurus	8	2	0	7	1	20	11	5	20	34
Oxymycterus sp1	1	0	0	0	0	0	0	0	1	0
Oxymycterus sp2	0	0	0	0	0	1	0	0	0	1
Thrichomys apereoides	1	0	1	0	3	1	1	0	6	1
Abundace	10	2	3	10	22	24	24	14	59	50
Richness	3	1	3	3	5	5	4	4	6	6
Trap sucess (%)	0.83	0.5	0.25	2.5	1.1	2	2	1.16	0.94	1.56

The burned and unburned areas showed different patterns of variation in the abundance of individuals in the post-fire sampling period. Before burning, the abundances were similar between these areas. After one month of controlled burning, the burned areas showed a 70% reduction in trap success compared to pre-fire sampling, whereas in the unburned area there was a 400% increase in the same period. This difference between treatment and control areas was less pronounced 3 months after the fire and was inverted in the sampling 6 months after the fire. In this sampling, the burned areas showed a greater abundance of small mammals than the unburned areas, indicating a fast recovery time of the small mammal community (Figure 2a).

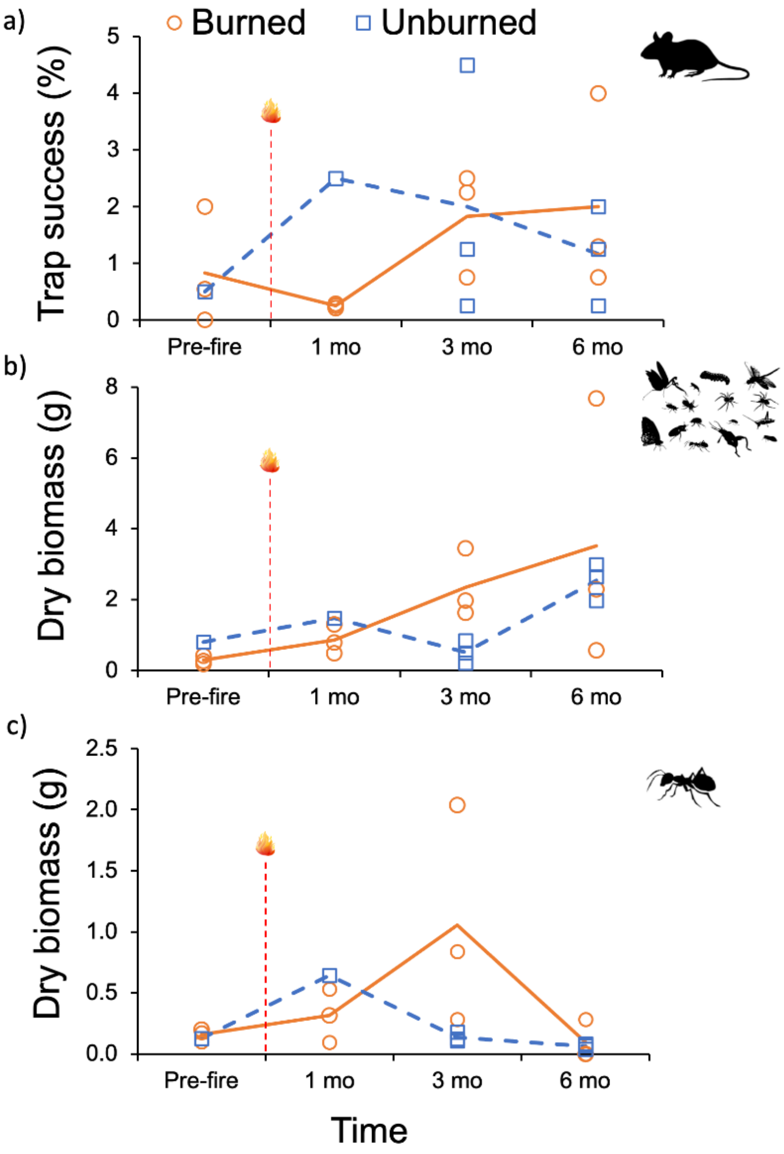

Figure 2. Abundance of small mammals (a), all invertebrates (b), and formicids (c) one month before and up to six months after early prescribed fires in sites of *campo sujo* vegetation (grasslands with scattered shrubs) during the dry season in a neotropical savanna (Cerrado). Post-fire sampling occurred 1, 3, and 6 months after burning. Small mammal abundance was estimated using individuals caught/100 trap nights and invertebrate abundance was estimated considering overall dry biomass obtained with pitfall traps (plastic cups). Three sites were sampled in each period and treatment (burned or unburned), except for pre-burning and 1st-month sampling periods in control (unburned) sites, for which there was only 1 site sampled. Lines indicate mean values for each treatment/period (burned = continuous orange lines, unburned = blue broken lines).

We did not detect a marked variation in richness that could be attributed to fire but there were changes in community composition as a function of the occurrence of prescribed burning. This variation was evident mainly along the first axis of Correspondence Analysis (CA). In this axis (51.7% of the total variation), there was a group that included the treatment areas sampled in the pre-fire period and the areas that did not burn (control). This group was mainly related to the rodent *Necromys lasiurus*, the dominant species in these areas. In contrast, one and three months after burning, the most evident pattern was the absence of *N. lasiurus* and the presence of the species *Calomys tener* and *Thylamys velutinus* (Figure 3, Table 1). This pattern modified after six months of controlled burning, when the burned (treatment) and non-burned areas became more similar (located close to the origin of the 1st axis). In this last sampling period, *N. lasiurus* again became the most abundant species in the sampled areas (Table 1).

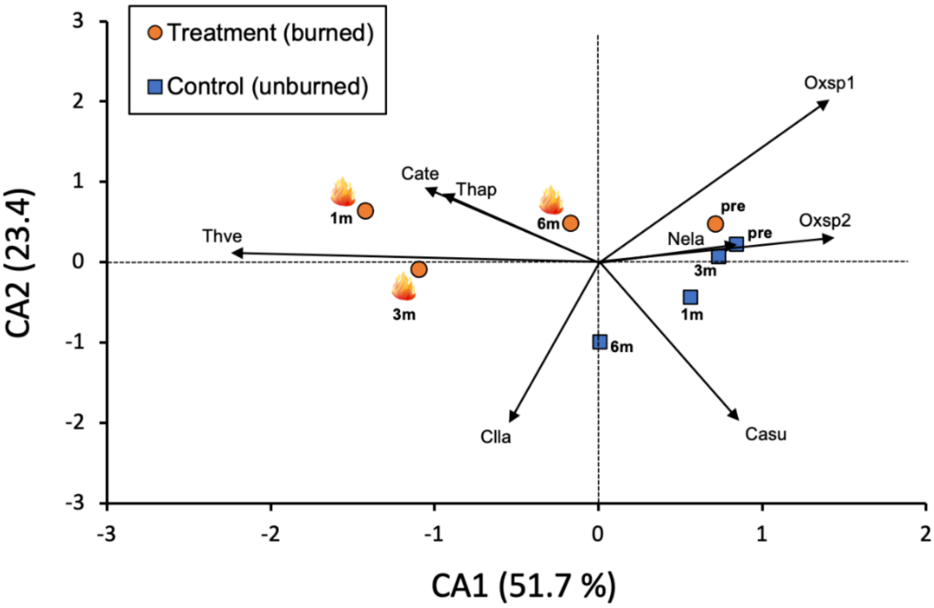

Figure 3. Correspondence analysis (CA) biplot of species compositions in the treatment (burned) and control (unburned) areas sample before and after prescribed fires. Time after fire is indicated in bold for each sampling period (pre = pre-fire sampling [up to 1 month before fire], 1m = 1 month after fire, 3m = 3 months after fire, and 6m = 6 months after fire). Arrows indicate the position of small mammal species. Species codes: Thve = *Thylamys velutinus*, Clla = *Clyomys laticeps*, Casu = *Carterodon sulcidens*, Cate = *Calomys tener*, Nela = *Necromys lasiurus*, Oxsp1 = *Oxymycterus sp1*, Oxsp2 = *Oxymycterus sp2*, Thap = *Thrichomys apereoides*. Variance explained by each axis is indicated between parentheses.

The sampling of invertebrates indicated no marked differences in total biomass between burned and unburned areas one month after the prescribed burns (Figure 2b). After three months, however, the burned areas showed a 176% increase in invertebrate biomass compared to the previous period, while in the unburned areas there was a 64% reduction at the same time. This pattern was more pronounced considering the biomass of the Formicidae family, which comprises almost half of the total biomass of invertebrates in this period (Figure 2c). Although the burned areas had a slightly lower invertebrate biomass compared to the unburned areas in the first month after burning, the ants showed a 239% increase in their biomass after three months, while there was a 78% reduction in the unburned areas in the same period. After six months of burning, the group showed a marked reduction of 90% in biomass in the burned areas compared to the previous sampling, while invertebrates remained with an increase in their biomass in this period (Figure 2).

Fire and seed removal by invertebrates and small mammals

The modeling of the effects of prescribed fires and removal agent (small mammals or invertebrates) on number of removed seeds over time indicated significant differences between treatment and control sites but, these differences were not caused by prescribed fires (Table 2; Figure 4). Although the post-fire removal (T1) in the control areas (no burning) increased much more in relation to pre-fire values (10.7 times increase in the estimated value) in relation to the increase in the burned area (1.4 times increase; Figure 4), there was no significant interaction between time and treatment (p = 0.089). The interaction between fire treatment and post-burn time was significant only for the sixth month after burning, indicating a reduction in seed removal in the burned areas compared to the control (Table 2, Figure 4). We did not find significant effects of the removal agent (invertebrates or rodents, exclusion treatment) and its interaction with other factors in seed removal. Although there was no significant interaction between time and exclusion treatment, three months after fire invertebrates removed more seeds compared to small mammals, both in unburned areas (7 times more) and in burned areas (3.5 times more) in this period (Table 2, Figure 4).

Table 2. GLMM results evaluating the effect of the treatment variables (fire - burned areas and control - unburned areas), exclusion (cages with exclusive access to small mammals or invertebrates) and time (different months sampled after burning).

	Estimate	**Std. Error**	***z* value**	**Pr(>|z|)**
Intercept	-0.02005	0.38138	-0.053	0.9581
Treatment (Unburned)	-2.00274	0.97343	-2.057	0.0396 *
Exclusion (Small mammals)	-0.78215	0.54609	-1.432	0.1521
Time (T1)	0.35788	0.50409	0.71	0.4777
Time (T3)	0.32247	0.46697	0.691	0.4898
Time (T6)	-0.35433	0.51901	-0.683	0.4948
Treatment*Exclusion	1.18816	1.30771	0.909	0.3636
Treatment*Time (T1)	1.99641	1.17495	1.699	0.0893
Treatment*Time(T3)	2.02515	1.06134	1.908	0.0564
Treatment*Time (T6)	2.21814	1.09333	2.029	0.0425 *
Exclusion*Time(T1)	-0.11491	0.73835	-0.156	0.8763
Exclusion*Time(T3)	-0.52508	0.68277	-0.769	0.4419
Exclusion*Time(T6)	1.14033	0.74071	1.54	0.1237
Treatment*Exclusion*Time (T1)	-0.07737	1.61967	-0.048	0.9619
Treatment *Exclusion*Time (T3)	-1.94318	1.48764	-1.306	0.1915
Treatment *Exclusion*Time (T6)	-2.64301	1.50226	-1.759	0.0785

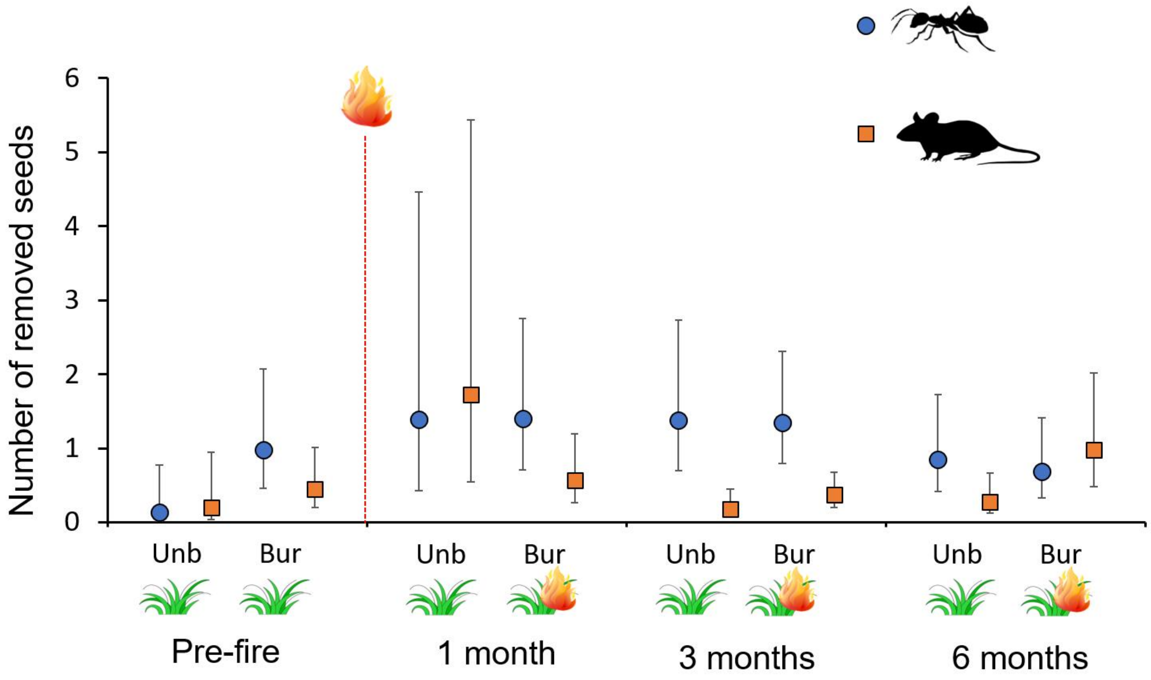

Figure 4. Estimated number of seeds removed by small mammals (orange square) and invertebrates (blue circle) in the treatment (burned = Bur) and control (unburned = Unb) sampled areas. The seed removal values were estimated by the GLMM model with negative binomial family. The treatment (burned or unburned), exclusion (partial exclusion cages with exclusive access by small mammals or invertebrates) and time were considered fixed factors, and the sampled areas were considered random factor. The time after fire is indicated below the x axis for each sampling period (pre-fire sampling [up to 1 month before fire], 1mo = 1 month after fire, 3mo = 3 months after fire, and 6mo = 6 months after fire).

Seed removal and micro-habitat variables

The evaluation of the effect of microhabitat variables, removal agent and fire treatment on seed removal indicated a significant effect of exclusion treatment on seed removal ocurrence (Table 3). This removal was higher for invertebrates when compared to small mammals. There was also a significant interaction between both factors (removal agent and vegetation height). This interaction indicated opposite seed-encounter responses by invertebrates and small mammals concerning vegetation height. Occurrence of seed removal by rodents was directly related to vegetation height whereas for invertebrates the response was reverse (Figure 5).

Table 3. GLMM results evaluating the effect of treatment variables (fire-burned areas and control-unburned areas), exclusion (cages with exclusive access for small mammals or invertebrates), soil cover and vegetation height on seed removal occurrence.

	Estimate	**Std. Error**	**z value**	**Pr(>|z|)**
Intercept	0.09163	0.65515	0.14	0.8888
Treatment (Burned)	-1.69867	0.91897	-1.848	0.0645
Exclusion (Small mammals)	-1.70808	0.82399	-2.073	0.0382 *
Soil cover	-0.48112	0.59689	-0.806	0.4202
Vegetation heigh	-0.23123	0.74939	-0.309	0.7577
Treatment*Exclusion	1.43199	1.23742	1.157	0.2472
Treatment:Soil cover	-0.04348	0.66973	-0.065	0.9482
Exclusion:Soil cover	1.09498	0.66461	1.648	0.0994 .
Treatment:Vegetation heigh	-0.24839	0.79069	-0.314	0.7534
Exclusion:Vegetation heigh	1.39369	0.62673	2.224	0.0262 *

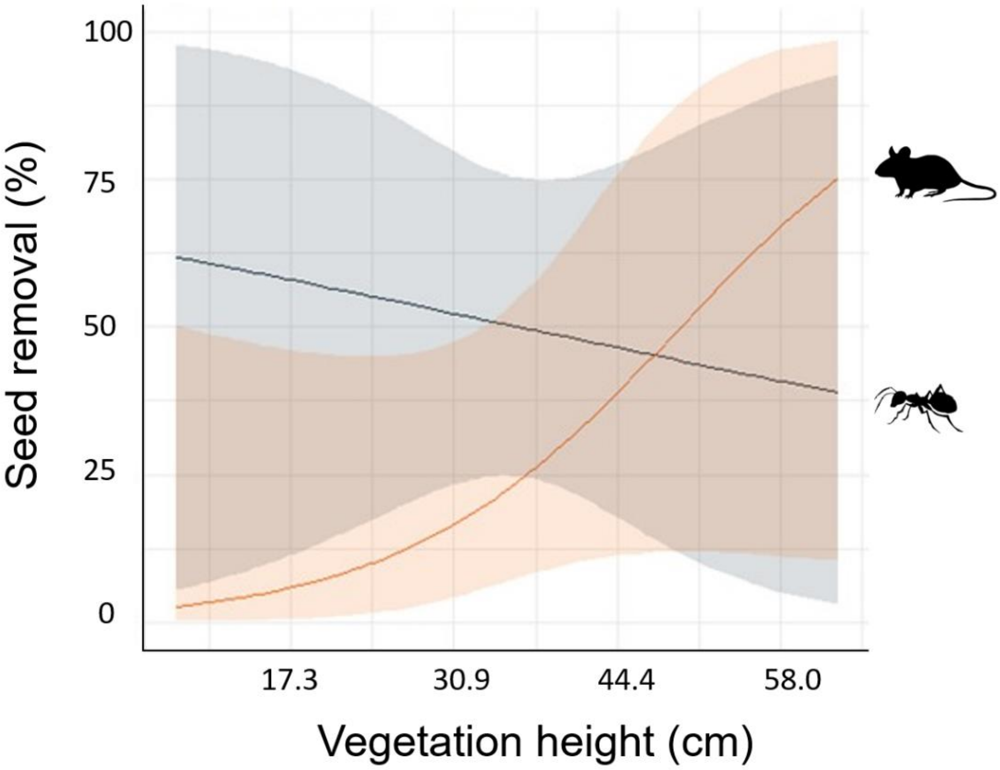

Figure 5. Estimated occurrence of seed removal by small mammals (orange line) and invertebrates (blue line) in relation to vegetation height (cm) occurring in the experimental stations. Seed removal values were predicted by the GLMM model with binomial family, considering the variables treatment (burned and unburned), exclusion (partial exclusion cages with exclusive access by small mammals or invertebrates), soil cover, and vegetation height as fixed factors and area as a random factor.

Discussion

We investigated how prescribed fires can affect the abundance and composition of potential seed removers in the Cerrado (small mammals and invertebrates). We also evaluated seed removal patterns over the first few months after burning in areas of *campo sujo* (grassland with sparse cover of shrubs) in a neotropical savannah. Apparently, there was a short-term effect (up to 3 months) of the prescribed burns on the abundance of small mammals and on the species composition of this group. The fire did not markedly affect the overall seed removal rate or the relative role of small mammals and invertebrates in this process. However, invertebrates found seed depots more frequently when considering habitat characteristics (ground plant cover and vegetation height), the occurrence of burning, and removal agent (small mammals or invertebrates). We also found opposite effects of vegetation height, with small mammals removing seeds more frequently at higher heights whereas removal by invertebrates was negatively related to this variable.

We detected fire-induced changes in the abundance of small mammal species, with an immediate reduction in individuals captured within one month after fire. Despite this reduction, the abundance of small mammals showed a fast recovery in the burned areas. Small mammal communities generally respond to the impacts of fires, mainly altering the relative abundance and feeding habits, with distinct species responding differently to this disturbance (Culhane *et al.*, 2022; González *et al.*, 2021;; Monamy and Fox, 2000; Briani *et al.*, 2004; Legge *et al.*, 2008; Vieira and Briani, 2013). Changes in abundance are possibly related by the extension of the burned area. In a large area (~7,000 ha) destroyed by fire in the Australian savannah, there were much more striking differences between burned and unburned sites (4-fold difference in abundance between sites; Legge *et al.* 2008).

Species of the genus *Calomys* and the marsupial *T. velutinus* generally colonize recently burned areas, increasing their population density a few months after the fire (Vieira, 1999; Briani *et al.*, 2004; Henriques *et al.*, 2006; Vieira and Briani, 2013). Our results are in agreement with these patterns, with both species occurring almost exclusively in burned areas, with a peak in their abundance three months after the fire. We also recorded a significant reduction in the abundance of *N. lasiurus* after burning in compared to unburned areas, where this species was dominant throughout the study. Studies carried out in areas of typical savannah (cerrado *sensu stricto*) in the Cerrado also show a reduction in the population density of the species after the occurrence of fires (Henriques *et al.*, 2006; Owen, 2013; Vieira and Briani, 2013). Thus, our results indicate that this pattern is also maintained in areas of *campo sujo* in the Cerrado.

The immediate reduction of vegetation cover after fire may hinder the permanence of species with specific requirements, modifying the structure and composition of communities (González *et al.*, 2021; Monamy and Fox, 2000; Culhane *et al.*, 2022). Small and essentially nocturnal species, such as *C. tener* and *T. velutinus* (Vieira and Baumgarten, 1995) are potentially favored in the initial periods of succession. These species might be able to take refuge more easily, whereas others need greater vegetation cover and, therefore, being potentially more strongly affected by post-fire changes in the environment (Briani *et al.*, 2004; Henriques *et al.*, 2006; Manyonyi *et al.*, 2020). The rapid return of vegetation in subsequent months allows for an increase in the abundance of other species, creating a pattern of successional changes over the post-fire time (Vieira, 1999; Briani *et al.*, 2004; Owen, 2013), as we found for *N. lasiurus*.

Changes in the availability of resources in the environment after the occurrence of burning may also contribute to the fire-induced variation in small mammal abundance that we found. In areas of cerrado *sensu stricto* (typical savannah vegetation), there is a reduction in the availability of fruits and seeds, compared to invertebrates, immediately after prescribed burning (Vieira and Briani, 2013). The generalist feeding habits of species such as *C. tener* and their ability to feed more on invertebrates after fire events (Vieira and Briani, 2013), may favor their survival in these environments. Species that are more dependent on fruits and seeds, such as *N. lasiurus*, are apparently more impacted by the shortage of these resources soon after burning. Thus, even if they also feed on invertebrates, this apparent greater dependence on resources of plant origin affects their permanence in these environments (Briani *et al.*, 2004; Vieira and Briani, 2013). The insectivorous habits of *T. velutinus* possibly also allow the presence of this species in recently burned areas (Vieira and Briani, 2013; Palma and Vieira, 2016), as we found in the present study.

Our results indicated that prescribed burns do not markedly alter the number of seeds removed. The sampled sites showed differences even before the fires occurred. After these fires, in the burned areas, the passage of the fire apparently prevented a more accentuated increase in seed removal in the first month after the fire. This increase occurred, in the same period, in the unburned control areas. Published studies indicate different patterns in seed removal, mostly with an increase in removal after the occurrence of fires (Andersen, 1988; Reed, Kaufman and Kaufman, 2005; Parr *et al.*, 2007; Zwolak *et al.*, 2010; Barbosa *et al.*, 2022). However, as in our case, fires sometimes do not affect the number of seeds removed (Broncano, Rodrigo and Retana, 2008; Alcolea, Durigan and Christianini, 2022) or may even contribute to reducing seed predation in management experiments for controlling of granivory in restoration areas (Greenler *et al.*, 2019; Anderegg *et al.*, 2022). These differences in post-fire removal patterns may be related to several factors, including type and season of burning, vegetation characteristics, as well as the abundance of different seed-removing species present after burning.

The comparison of number of removed seeds between distinct removal agents (invertebrates or small mammals) did not indicate significant differences between these two groups. In addition, we did not find effects of the interaction between the removing agent and the occurrence of fire, indicating that the burning did not alter the relative role of small mammals and invertebrates in the rates of seed removal. However, in evaluating the effect of micro-habitat variables (model with binary response), invertebrates removed seeds from more experimental stations when compared to small mammals. This apparent inconsistency may have been caused by the different sample sizes (we evaluated the microhabitat in about 20% of the total number of experimental stations used in the general analysis) or the different types of response variables used in each analysis. For the analysis related to the micro-habitat, we used data on the presence and absence of removal, which provides information on the probability of finding the seed, without considering the number of seeds removed. On the other hand, in the general analysis, we used number of seeds removed. This could explain the differences found between the removal agents (exclusion treatment) in this analysis. In recently burned areas, invertebrates apparently are more active, having found the experimental stations more frequently. However, when we consider the number of seeds removed (general analysis), there was no significant difference between invertebrates and small mammals. These patterns indicate that invertebrates could be more efficient in detecting seeds. This greater efficiency, however, would not lead to a greater number of seeds removed when they were grouped together.

We observed that ants removed three times more seeds than small mammals in the burned areas, especially three months after the fire. The model using number of removed seeds, however, did not indicate a significant interaction between fire treatment and exclusion. An increase in the importance of invertebrates in seed removal after prescribed burning, when compared to vertebrates, was also reported by Alcolea, Durigan and Christianini, (2022).However, in this study, conducted in areas of *campo cerrado* (with a greater contribution of the tree component compared to our study area), the response variable was the number of seeds removed. This pattern of a significant increase in the importance of invertebrates in post-burn removal has also been described in grasslands of southern Brazil (Barbosa *et al.*, 2022) and savannahs and *Eucalyptus* forests in Australia (Andersen, 1988; Parr *et al.*, 2007; Beaumont, Mackay and Whalen, 2013). On the other hand, several studies indicate that rodents may be the main removing agents in burned areas, and may even affect the regeneration of certain species after fire (Auld and Denham, 2001; Reed, Kaufman and Kaufman, 2004; Tasker *et al.*, 2011; Suazo *et al.*, 2013).

Despite the return of the abundance of small mammals three months after the burning, there was no significant increase in removal in this period. This may be related to food preferences and changes in the diet of the dominant species in the recent burned areas (Vieira and Briani, 2013; Palma and Vieira, 2016). Furthermore, a greater abundance of these animals could be counterbalanced by a greater availability of resources in general (probably mainly invertebrates) in the same post-fire period (Vieira and Briani, 2013). This high availability could reduce the relative value of the experimentally offered seeds (reducing their economic value or value-of-exchange, *sensu* Jansen, Bongers and Hemerik, 2004). Consequently, these seeds would become less attractive and seed predation would not increase despite the increase in abundance of seed predators. This kind of predation threshold might enhance seed survival in the first months after prescribed fires.

We detected a significant reduction in seed removal six months after prescribed fires. This reduction is also probably related to resource recovery in the study areas, which might decrease consumption of experimental seeds by the animals. In the Cerrado grasslands, after a post-burn immediate reduction of available plant resources, there is a rapid production of flowers and diaspores of herbaceous species. Some species may even disperse their seeds within the dry season (Munhoz and Felfili, 2005; Pilon *et al.*, 2018; Fidelis *et al.*, 2019; L. Zirondi, Ooi and Fidelis, 2021). This pattern of seed production after burning, however, may vary according to the dispersion syndrome of the plant species and zoochoric fruits have their fruiting peak at the beginning of the rainy season (Batalha and Mantovani, 2000; Munhoz and Felfili, 2005)..

Invertebrate abundance was not markedly affected by prescribed burning. This group of seed predators/removers may have contributed to keeping seed removal in burned areas at similar levels to unburned areas despite the reduced small mammal abundance. Ants generally are the main invertebrates responsible for an increase in seed removal after fire. These insects generally still occur even in recently burned areas, where both an increase in their abundance and in their foraging behavior may occur (Andersen, 1988; Parr *et al.*, 2007; Beaumont, Mackay and Whalen, 2013; Barbosa *et al.*, 2022). Fire occurrence may promote an increase in the abundance and richness of ants, mainly generalist species (Andersen, 1988;; Parr *et al.*, 2007; Barbosa *et al.*, 2022). The passage of fire promotes a simplification of the habitat at ground level, which favors displacement, reducing ant energy costs and increasing the finding of the resource and the efficiency of its foraging (Andersen, 1988; Parr *et al.*, 2007; Diniz and Morais, 2016; Barbosa *et al.*, 2022). Fire can act in this process by promoting not only an increase in the abundance of specific groups of ants, but also favoring an increase in seed removal distance through habitat simplification (Parr *et al.*, 2007; Tasker *et al.*, 2011; Barbosa *et al.*, 2022). In fact, we found a higher frequency of seed removal by invertebrates in seed depots with lower vegetation, indicating that the reduction of vegetation after prescribed burns may favor the presence and removal of seeds by invertebrates in burned areas.

We did not find effects of soil cover on seed removal, unlike was reported by Manson and Stiles (1998). This may be related to the rapid vegetation recovery after prescribed fires (Munhoz and Amaral, 2010; Alcolea, Durigan and Christianini, 2022). This regrowth allows a rapid ground cover, and may have minimized the effects of lack of cover over the first months after fire. On the other hand, when evaluated the vegetation height, we found a significant interaction between this microhabitat variable and the removal agent, with small mammals showing a higher frequency of removal in stations with higher vegetation. For these animals, the lack of cover and the reduction in vegetation height in recently burned areas provides greater exposure to the animals when visiting the experimental stations.

The ability to perceive predation risk can lead to changes in prey behavior, modifying their habitat use and activity schedules, to avoid encountering their predators. (Brown, Laundré and Gurung, 1999; Abom and Schwarzkopf, 2016; Gaynor *et al.*, 2019). The concept of the "landscape of fear" describes the spatial variation in the perception of predation risk, which can vary in space and time at multiple scales and between prey. (Gaynor *et al.*, 2019). For rodents, vegetation cover has an important influence on the perception of predation risk and these animals avoid places with less vegetation cover, thus reducing their vulnerability to predators (Bueno and Motta-Junior, 2015; Abom and Schwarzkopf, 2016; Loggins *et al.*, 2019; Carreira *et al.*, 2020). This concept may explain the positive correlation between seed removal by small mammals and vegetation height found in this study.

Our results suggest that small mammals and invertebrates may show distinct short-term responses after burning. Seed predation by different groups can differentially affect the recruitment of plant species in the first months, and can have a great importance in the post-fire regeneration process (Auld and Denham, 2001; Parr *et al.*, 2007; Tasker *et al.*, 2011; Suazo *et al.*, 2013). Fire behavior in early prescribed burns tends to be of low intensity, with incomplete fuel consumption and moderate damage on vegetation (Schmidt *et al.*, 2016; Gomes, Miranda and Bustamante, 2018). This may allow the permanence of some resources, such as fruits and seeds, undamaged by fire, as well as a rapid vegetation regrowth and production of flowers and fruits (Munhoz and Felfili, 2005; Pilon *et al.*, 2018; Fidelis *et al.*, 2019; L. Zirondi, Ooi and Fidelis, 2021). This creates a microhabitat mosaic with different vegetation cover and resources that are used by animals in different ways. Understanding the mechanisms that affect seed removal and the presence and behavior of seed removers can elucidate what role they play in vegetation regeneration after prescribed fires.

Our results indicated an immediate reduction in the abundance of small mammals in the first month after burning, with a subsequent return after three months. This corroborates with our first expectation presented, and is in a agreement with previous results reported for areas of cerrado *sensu stricto* (Henriques *et al.*, 2006; Vieira and Briani, 2013). We also found variations in species composition in the burned and unburned areas, with a dominance of species adapted to post-fire environments soon after the fire. In this period right after the fire, the abundance of invertebrates remained similar to pre-fire patterns, with no evident differences between treatment and control areas. In the third month after the fire, however, the burned areas (treatment fire) showed an increase in abundance that did not occur in the unburned areas, especially the Formicidae family. These post-fire response patterns contributed to maintaining seed removal in burned areas, even with the reduction of small mammals. Several studies also reported an increase in abundance and importance of ants in seed removal after fires (Andersen, 1988; Parr *et al.*, 2007; Beaumont, Mackay and Whalen, 2013; Diniz and Morais, 2016; Alcolea, Durigan and Christianini, 2022; Barbosa *et al.*, 2022)

We did not detect marked effects of burning on the total number of seeds removed by small mammals and invertebrates, which did not support our second expectation. This same pattern was found in other post-burn seed removal studies (Broncano, Rodrigo and Retana, 2008; Alcolea, Durigan and Christianini, 2022). However, the fire may have contributed to hinder an increase in removal in recently burned areas, which we detected in the control areas. Our third hypothesis was partially corroborated, as we found a positive relationship between vegetation height and seed removal by small mammals. The opposite occurred for invertebrates, showing a higher frequency of removal in lower vegetation. The abrupt and short-time reduction in vegetation height promoted by fire may have hampered seed removal by small mammals, because of the perception of predation risk (Gaynor *et al.*, 2019), as well as favoring the presence and efficiency of seed removal by ants (Parr *et al.*, 2007; Tasker *et al.*, 2011).

Conclusions

Prescribed burns are an important tool for the management and conservation of protected areas and their benefits depend on adequate planning to ensure their effectiveness (Driscoll *et al.*, 2010; Fidelis and Pivello, 2011; Pilon *et al.*, 2018). Our study provides important evidence that can contribute to the implementation and improvement of this practice. The prescribed burns carried out in the PNCV did not affect the total number of seeds removed but contributed to changes in the abundance of certain species of small mammals. These changes increase the small mammal diversity in the landscape (Larsen, Adams and Haughland, 2007). This reinforces the importance of prescribed burning as a tool to not only prevent large-scale fires, but also to promote greater species diversity on a landscape scale (Gomes, Miranda and Bustamante, 2018; Santos *et al.*, 2021; Roberts *et al.*, 2015).

Our results indicated that prescribed fires carried out in a controlled manner and at the beginning of the dry season do not significantly affect the natural processes of seed removal by animals in Cerrado grasslands. The impacts of fire on the system, however, depend on multiple factors and can vary according to the regime, severity, and season of fire (Govender, Trollope and Van Wilgen, 2006; Miranda *et al.*, 2009; Gomes, Miranda and Bustamante, 2018). Distinct spatial and temporal scales must also be considered in the evaluation of such impacts (Gomes, Miranda and Bustamante, 2018). Large-scale studies that combine multiple drivers at different time scales are still needed for advancing the understanding of fire ecology (Gomes, Miranda and Bustamante, 2018) and can elucidate effects of prescribed burns on long-term seed removal processes. We also reinforce the importance of considering the periods of production of diaspores and zoochoric fruits of the vegetation in the planning of prescribed burns, since they can be decisive to ensure the availability and use of resources by the fauna after the fire.

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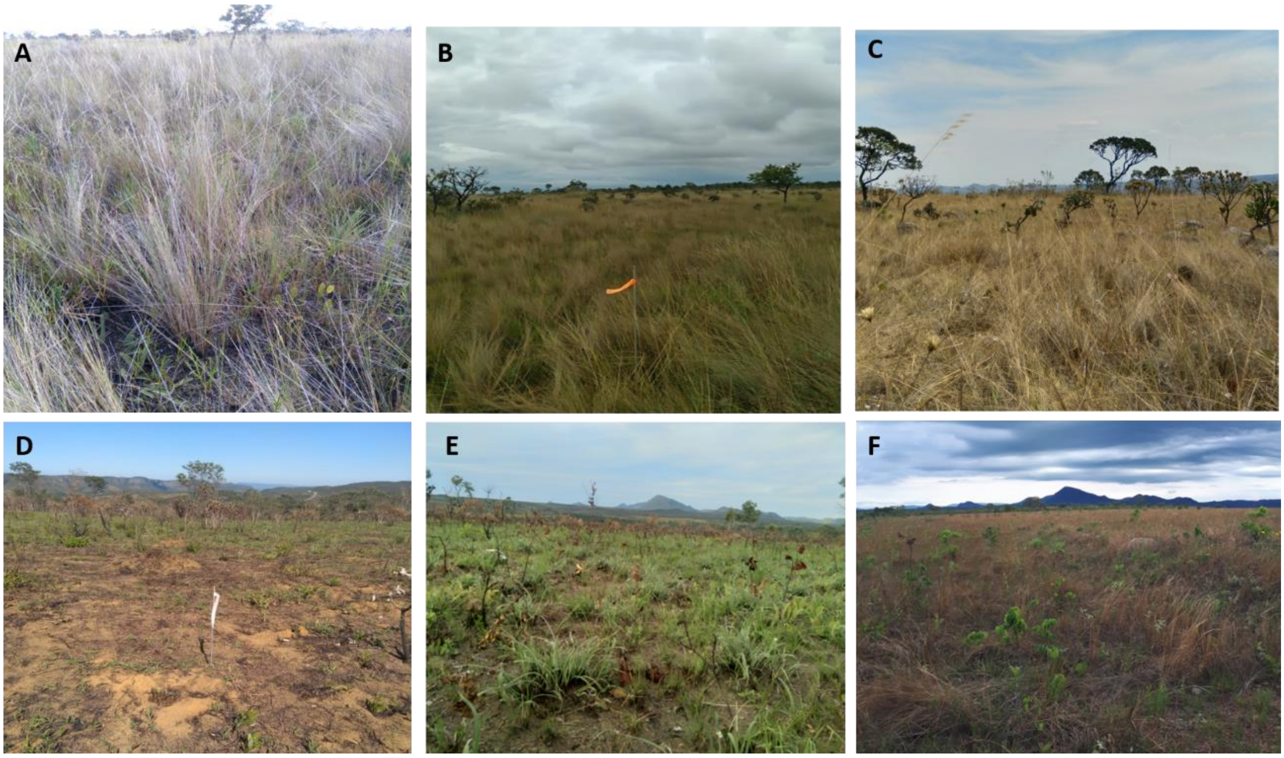
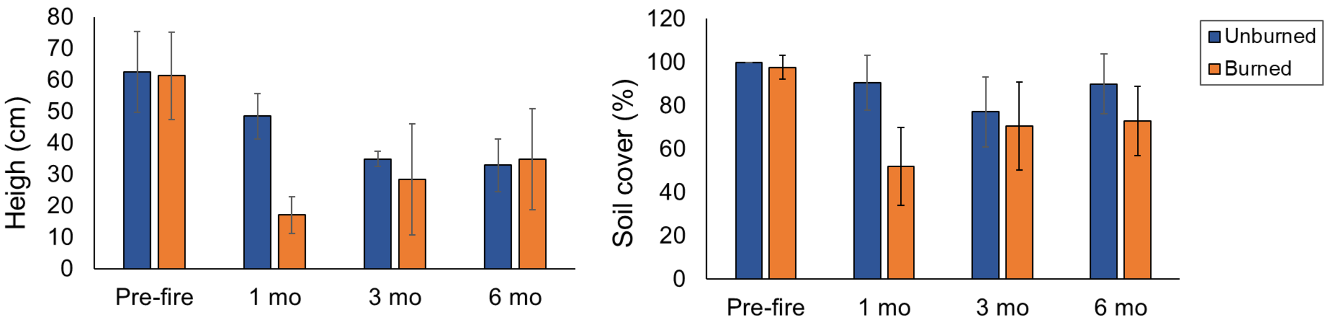
Anexos



Apêncie 1. Áreas amostradas no Parque Nacional da Chapada dos Veadeiros no ano de 2021 antes da queima (A e B) e área controle não queimada (C). Abaixo estão áreas amostradas em diferentes meses após a queima: um mês (D), três meses (E) e seis meses (F).



Appendix S1. Mean and standart deviation of vegetation height and soil cover in in sites of *campo sujo* vegetation (grasslands with scattered shrubs) submitted a prescribed burn and control before and in different months after burning.

Appendix S2. Incidence Rate Ratios, interval with 95% confiance and p value of GLMM evaluating the effect of the treatment variables (fire - burned areas and control - unburned areas), exclusion (cages with exclusive access to small mammals or invertebrates) and time (different months sampled after burning).

	Incidence Rate Ratios	**95% Confiance Interval**	***p***
Intercept	0.98	0.46 – 2.07	0.958
Fire (Unburned)	0.13	0.02 – 0.91	0.04*
Exclusion (Small mammals)	0.46	0.16 – 1.33	0.152
Time (T1)	1.43	0.53 – 3.84	0.478
Time (T3)	1.38	0.55 – 3.45	0.49
Time (T6)	0.7	0.25 – 1.94	0.495
Fire*Exclusion	3.28	0.25 – 42.57	0.364
Fire*Time (T1)	7.36	0.74 – 73.65	0.089
Fire*Time(T3)	7.58	0.95 – 60.66	0.056
Fire*Time (T6)	9.19	1.08 – 78.34	0.042*
Exclusion*Time(T1)	0.89	0.21 – 3.79	0.876
Exclusion*Time(T3)	0.59	0.16 – 2.25	0.442
Exclusion*Time(T6)	3.13	0.73 – 13.36	0.124
Fire*Exclusion*Time (T1)	0.93	0.04 – 22.13	0.962
Fire*Exclusion*Time (T3)	0.14	0.01 – 2.64	0.191
Fire*Exclusion*Time (T6)	0.07	0.00 – 1.35	0.079
Random Effects			
σ^2	1.89		
$\tau_{00\ \text{Area}}$	0.02		
ICC	0.01		
N_{Area}	8		
Observations	650		
Marginal R^2 / Conditional R^2	0.211 / 0.218		

Appendix S3. Odds Ratios, interval with 95% confiance and p value of GLMM evaluating the effect of the treatment variables (fire - burned areas and control - unburned areas), exclusion (cages with exclusive access to small mammals or invertebrates) soil cover and vegetation height on seed removal.

	Odds ratio	**95% Confiance interval**	***p***
Intercept	1.1	0.30 – 3.96	0.889
Fire (Burned)	0.18	0.03 – 1.11	0.065
Exclusion (Small mammals)	0	0.04 – 0.91	0.038
Soil cover	0.62	0.19 – 1.99	0.42
Vegetation heigh	0.79	0.18 – 3.45	0.758
Fire*Exclusion	4.19	0.37 – 47.34	0.247
Fire:Soil cover	0.96	0.26 – 3.56	0.948
Exclusion:Soil cover	2.99	0.81 – 11.00	0.099
Fire:Vegetation heigh	0.78	0.17 – 3.67	0.753
Exclusion:Vegetation heigh	4.03	1.18 – 13.76	0.026
Random Effects	3.29		
σ^2	0		
$\tau_{00\ \text{Area}}$	7		
N_{Area}	107		
Observations	0.314 / NA		
Marginal R^2 / Conditional R^2			