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

# Efeitos da pirodiversidade e severidade do fogo na diversidade taxonômica, funcional e no uso do espaço por mamíferos no Cerrado

Clarice Vieira de Souza

Brasília – DF
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Tese de Doutorado apresentada ao Programa de Pós-Graduação *stricto sensu* em Ecologia da Universidade de Brasília como parte dos requisitos para obtenção do título de Doutora em Ecologia.

Orientador: Professor Dr. Emerson Monteiro Vieira

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TERMO DE APROVAÇÃO

CLARICE VIEIRA DE SOUZA

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Tese de doutorado apresentada em 02 de março de 2023, junto ao Programa de Pós-Graduação em Ecologia do Instituto de Ciências Biológicas da Universidade de Brasília, sob orientação do Prof. Dr. Emerson Monteiro Vieira, com o apoio financeiro da Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES), como parte dos requisitos para obtenção do título de Doutora em Ecologia.

BANCA EXAMINADORA:

Prof. Dr. Emerson Monteiro Vieira
Presidente/Orientador
Universidade de Brasília (UnB)
Laboratório de Ecologia de Vertebrados – Ecovert

Prof. Dr. Guarino Rinaldi Colli
Membro titular interno vinculado ao PPG
Universidade de Brasília (UnB)
Coleção Herpetológica da Universidade de Brasília – CHUNB

Profª. Drª. Ana Paula Carmignotto
Membro titular externo
Universidade Federal de São Carlos (UFSCar)
Laboratório de Sistemática de Mamíferos - LASISMA

Prof. Dr. Ricardo Siqueira Bovendorp
Membro titular externo
Universidade Estadual de Santa Cruz (UESC)
Laboratório de Ecologia Aplicada à Conservação - LEAC

Prof. Dr. Murilo Sversut Dias
Membro suplente
Universidade de Brasília (UnB)
Laboratório de Macroecologia e Biogeografia Aquática – AMBio

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## RESUMO

Distúrbios como o fogo alteram a distribuição espacial e temporal dos recursos utilizados pela fauna e geram heterogeneidade ambiental. Consequentemente, animais podem modificar o uso do espaço em resposta às mudanças provocadas pelo fogo. Tais respostas aos efeitos do fogo podem depender das características funcionais das espécies, afetando as comunidades taxonômica e funcionalmente. Nós usamos regressões lineares para testar a hipótese da “pirodiversidade gera biodiversidade” para métricas taxonômicas e funcionais das comunidades de mamíferos. Nós também aplicamos modelos de ocupação para avaliar como a variação espaço-temporal no regime do fogo afeta o uso do espaço por médios e grandes mamíferos. Além disso, nós verificamos o efeito da severidade do fogo nas comunidades de pequenos mamíferos não voadores que habitam matas de galeria. Nossos resultados demonstraram que a riqueza taxonômica e funcional de mamíferos aumentou com a pirodiversidade, mas a diversidade taxonômica e a dispersão funcional de mamíferos foram maiores em valores intermediários de pirodiversidade. No nível populacional, nós observamos efeitos espécie-específicos do regime do fogo sobre o uso do espaço por mamíferos. *Chrysocyon brachyurus* usou mais intensivamente áreas pirodiversas e com maior proporção de área recém-queimada. Já *Tapirus terrestris* preferiu utilizar áreas com menor pirodiversidade. O uso do espaço por cervídeos não foi afetado pelo mosaico de fogo. Em matas de galeria, a severidade do fogo afetou positivamente a diversidade taxonômica e a dispersão funcional de pequenos mamíferos. No entanto, este efeito ocorreu à custa de forte redução nas espécies dependentes de habitats florestais em matas severamente queimadas. Este estudo contribui para reduzir as lacunas no conhecimento dos efeitos do fogo sobre pequenos, médios e grandes mamíferos neotropicais e reforça que o manejo do fogo deve ser feito considerando o contexto local e as respostas espécie-específicas da fauna. Além disso, nós enfatizamos a necessidade de proteger habitats sensíveis ao fogo, como as formações florestais, contra incêndios severos. Diante do aumento na frequência de eventos extremos de incêndios, existe o risco de perdemos componentes fundamentais da biodiversidade não adaptada ao fogo.

**Palavras-chave:** Fogo, savana Neotropical, herbívoros, carnívoros, marsupiais, roedores, ecologia de comunidade.

# ABSTRACT

Disturbances like fire alter the spatial and temporal distribution of resources for fauna and generate environmental heterogeneity. Consequently, animals may modify their use of the space in response to fire-induced changes. How animals respond to fire effects depends on the species' traits, affecting the communities taxonomically and functionally. We used linear regressions to test the hypothesis of “pyrodiversity begets biodiversity” for taxonomic and functional metrics of mammalian communities of a neotropical savanna. We also applied occupancy modeling to evaluate how spatiotemporal variation in fire regime affects the use of space by medium and large mammals. Also, we verified the effects of fire severity on non-volant small mammal communities of gallery forests. Our results demonstrated that mammal taxonomic and functional richness increased with pyrodiversity while taxonomic diversity and functional dispersion were higher at intermediate values of pyrodiversity. At the population level, we found species-specific effects of fire regime on the space used by mammals. *Chrysocyon brachyurus* used more intensively pyrodiverse areas and sites with a higher proportion of recently burned areas. In contrast, *Tapirus terrestris* preferred sites with lower pyrodiversity. Fire mosaic did not affect space use by deer. In gallery forests, fire severity positively affected taxonomic diversity and functional dispersion of small mammals. However, this effect occurred at the expense of a marked decrease in forest-dependent species in sites severely burned. This study contributes to reducing gaps in the knowledge concerning the fire effects on neotropical small, medium, and large mammals and reinforces that fire management strategies must consider the local context and species-specific faunal responses to fire. Furthermore, we highlight the urgency of protecting fire-sensitive habitats against severe wildfires. As extreme wildfire events become more frequent there is a risk of losing fundamental components of biodiversity not fire-adapted.

**Keywords:** Fire, Neotropical savanna, herbivores, carnivores, marsupials, rodents, community ecology.

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# SUMÁRIO

# INTRODUÇÃO GERAL

Ao longo do ciclo de vida, organismos devem ser capazes de desempenhar funções vitais como obter recursos suficientes para a sua sobrevivência, escapar de predadores e encontrar parceiros para reprodução. No entanto, as condições ambientais, os recursos e os próprios organismos não estão distribuídos igualmente no espaço (Scheiner & Willig 2008). Essa heterogeneidade afeta como os indivíduos usam o ambiente para realizar suas atividades, tendo implicações para as populações, comunidades e ecossistemas (Pickett & Cadenasso 1995). Dessa forma, entender os efeitos da heterogeneidade ambiental sobre os organismos em diferentes escalas é uma importante questão da Ecologia (Wiens 1989; Sutherlan et al. 2013). Parte da heterogeneidade ambiental resulta da ocorrência de distúrbios, sejam eles comuns ou não ao ambiente. Um distúrbio pode ser definido como qualquer evento capaz de alterar a estrutura da população, da comunidade ou do ecossistema, bem como a disponibilidade de recursos e as condições físicas do ambiente (Pickett & White 1985). Alterações comportamentais que envolvem mudanças no uso do habitat, na seleção de recursos e na mobilidade estão entre os vários tipos de resposta que as espécies apresentam após a ocorrência de um distúrbio (Sergio et al. 2018). O conhecimento dessas alterações comportamentais é essencial para o entendimento de como os distúrbios podem afetar as populações e comunidades animais.

O fogo é uma importante fonte de heterogeneidade, sendo um distúrbio que ocorre naturalmente em muitos ambientes e que influencia os padrões e processos de ecossistemas terrestres (Bond & Keeley 2005; Bowman et al. 2009). Entretanto, atividades humanas e mudanças climáticas têm alterado o regime natural do fogo (Alencar et al. 2015; Wang et al. 2015), reduzindo a resiliência dos ecossistemas aos incêndios (Stevens-Rumann et al. 2018) e expandindo temporal e espacialmente a ocorrência de queimadas (Balch et al. 2017). Áreas frequentemente submetidas ao fogo apresentam redução na complexidade estrutural da vegetação (Mistry 1998). Em ambientes florestais, incêndios diminuem a cobertura da copa e a densidade de troncos, reduzem a cobertura e profundidade da serrapilheira, simplificam a estrutura do sub-bosque e promovem o aumento da cobertura de herbáceas (Hoffmann 2002; Numata et al. 2017; Camargo et al. 2018). Também são esperadas alterações na abundância de recursos. No geral, a disponibilidade de frutos tende a diminuir em áreas atingidas por queimadas (Peres et al. 2003; Barlow & Peres 2006) e, embora apresente uma resposta menos intensa do que a produção de frutos, a abundância de invertebrados é reduzida após o fogo (Zwolak et al. 2011; Vieira & Briani 2013).

Em ecossistemas dependentes do fogo, o manejo do fogo por meio de queimas prescritas é constantemente utilizado para gerar manchas de habitat com diferentes regimes de fogo (Brockett et al. 2001; Watson et al. 2012; Schmidt et al. 2018). Essa heterogeneidade espacial resultante do mosaico de regimes de fogo permitiria a coexistência de espécies com afinidades distintas em relação ao fogo, gerando comunidades mais diversas. Tal ideia está baseada na hipótese de que "pirodiversidade gera biodiversidade" proposta por Martin and Sapsis (1992). Ou seja, em mosaicos formados por áreas em diferentes estágios sucessionais pós-fogo (pirodiversidade), cada estágio estaria associado a determinado conjunto de espécies, resultando em maior biodiversidade. A hipótese da "pirodiversidade gera biodiversidade" foi testada para vários ecossistemas e grupos taxonômicos, recebendo suporte variado (Jones & Tingley 2022). Entretanto, estudos conduzidos em savanas neotropicais ainda são escassos (Jones & Tingley 2022). Isto é particularmente relevante visto que o manejo do fogo foi recentemente implantado no Cerrado, mas pouco se sabe sobre os padrões de mosaicos de fogo que geram habitats adequados para a fauna (Schmidt et al. 2018).

A associação entre as espécies e as áreas com diferentes regimes de fogo está relacionada com os indivíduos usarem preferencialmente alguns tipos de habitat em detrimento de outros. Nesse processo, indivíduos selecionam determinadas características do ambiente em resposta ao balanço entre os custos e benefícios de utilizar determinado habitat (Rosenzweig 1981). A seleção de habitat é vista como um importante mecanismo ecológico não só por ter um papel na regulação populacional e na dinâmica predador-presa, mas também por permitir a coexistência entre as espécies por meio da seleção de habitat diferencial entre os indivíduos (Rosenzweig 1981). Apesar da sua relevância ecológica, estudos sobre a seleção de habitat frequentemente não consideram múltiplas escalas espaciais, negligenciando possíveis efeitos dependentes de escala (McGarigal et al. 2016). Johnson (1980) sugere que o processo de seleção de habitat ocorre de forma hierarquizada em relação à escala espacial. Na escala mais ampla (seleção de 1ª ordem), a seleção é definida pela distribuição geográfica da espécie. Dentro dessa área de distribuição, indivíduos selecionam sua área de vida (seleção de 2ª ordem), a qual contém os habitats utilizados pelos indivíduos (seleção de 3ª ordem). Por fim, mesmo dentro desses habitats, os indivíduos podem selecionar determinadas características do ambiente (seleção de 4ª ordem), configurando a seleção de micro-habitats.

Uma das áreas do mundo que apresenta alta heterogeneidade ambiental e que também é caracterizada por uma alta incidência de queimadas é o Cerrado brasileiro. Considerado uma das savanas mais diversas do mundo, essa ecorregião abriga espécies da flora e da fauna adaptadas ao fogo (Simon et al. 2009; Pausas 2018). De uma maneira geral, o Cerrado é caracterizado por um mosaico de fitofisionomias moldadas, pelo menos em parte, pelo fogo (Salgado-Labouriau et al. 1997). Essas fitofisionomias englobam desde campos abertos até áreas florestais (Ribeiro & Walter 1998; Lewis et al. 2022), as quais possuem diferentes suscetibilidades e tolerâncias ao fogo. Áreas abertas, como campos e savanas, apresentam maior frequência de incêndios, mas são mais tolerantes aos efeitos da passagem do fogo. Já áreas florestais, como matas de galeria, são menos susceptíveis à ocorrência de queimadas, entretanto, sofrem efeitos mais severos (Miranda 2010).

Mamíferos compõem importante parcela da fauna do Cerrado, desempenhando papéis ecológicos fundamentais como dispersores e predadores de sementes (Vieira et al. 2003; DeMattia et al. 2004; Cáceres & Monteiro-Filho 2007; Camargo et al. 2011), como componentes da dieta de muitas outras espécies, ou como mesopredadores ou predadores de topo (Jácomo et al. 2004; Foster et al. 2013), polinizadores (Amorim et al. 2020) e controladores de invertebrados (Camargo et al. 2022). Mamíferos são excelentes modelos para avaliar os impactos do fogo sobre a fauna. A diversidade de modos de locomoção, dieta, associação com a vegetação e tamanho corporal desse grupo (Paglia et al. 2012) permite verificar o efeito das queimadas sob diferentes aspectos funcionais das espécies. Dessa forma, também é possível entender possíveis efeitos do fogo sobre o funcionamento do ecossistema. Além disso, os estudos acerca dos efeitos do fogo sobre mamíferos do Cerrado ainda são poucos (Arruda et al. 2018) e raramente envolvem mais de uma escala espacial (porém, ver Camargo et al. 2018).

Embora mamíferos ocorram em vários tipos de vegetação do Cerrado, algumas espécies mostram associação a habitats específicos enquanto outras são generalistas (Juarez & Marinho-Filho 2002; Lima et al. 2009; Santos-Filho et al. 2012). A ocorrência do fogo, entretanto, pode afetar a dinâmica espacial dessas espécies. Conforme a estrutura da vegetação é modificada pelo fogo, a abundância relativa e a ocorrência das espécies de mamíferos são alteradas (Fox 1982; Fox et al. 2003). No geral, espécies generalistas ou associadas a áreas abertas são favorecidas pelos incêndios (Zwolak et al. 2011; Horn et al. 2012; Vieira & Briani 2013; Camargo et al. 2018), enquanto espécies dependentes de áreas florestais são afetadas negativamente (Banks et al. 2011; Mendonça et al. 2015; Flanagan-Moodie et al. 2018). Já espécies de predadores geralmente são atraídas para áreas recém-queimadas (Dees et al. 2001; Leahy et al. 2016; Hradsky et al. 2017), ao passo que presas podem evitar áreas abertas devido ao risco de predação por espécies visualmente orientadas

(Doherty et al. 2015; Fordyce et al. 2016). Por outro lado, áreas não queimadas fornecem uma vegetação mais densa. Essa vegetação favorece predadores que emboscam suas presas (Doherty et al. 2022), espécies que dependem de abrigos encontrados em árvores antigas (Flanagan-Moodie et al. 2018) e presas buscando proteção contra predadores cursoriais (Cherry et al. 2017).

Entender como a biota responde à variação no regime do fogo é primordial para elaborar estratégias de manejo do fogo que busquem proteger áreas sensíveis ao fogo e sua fauna associada. Ao mesmo tempo, as estratégias usadas devem buscar estabelecer mosaicos adequados para as espécies que habitam as áreas manejadas. Para o Cerrado, as políticas e ações voltadas para lidar com a ocorrência de incêndios ainda são recentes, restritas a poucas áreas e necessitam de informações para melhorar as estratégias existentes (Durigan & Ratter 2016; Schmidt et al. 2018). Diante do exposto, este estudo visa avaliar como diferentes regimes do fogo influenciam a comunidade de mamíferos do Cerrado em escalas distintas. Para isso, investigamos como médios e grandes mamíferos usam o habitat em função do regime do fogo e como este altera a diversidade taxonômica e funcional da comunidade de mamíferos. Além disso, verificamos como mudanças na estrutura da vegetação de áreas sensíveis ao fogo (matas de galeria) provocadas por um grande incêndio florestal afetam a composição e diversidade da comunidade de pequenos mamíferos não voadores. Esta tese está estruturada em três capítulos:

Capítulo 1 – Avaliação dos efeitos da pirodiversidade sobre a abundância, riqueza taxonômica, diversidade taxonômica, riqueza funcional e dispersão funcional de médios e grandes mamíferos. Este capítulo foi submetido e seguiu as normas da revista *Biodiversity and Conservation* (Qualis A2).

Capítulo 2 – Investigação dos efeitos da pirodiversidade, da proporção de área recém-queimada e da proporção de área com longo histórico sem fogo sobre o uso do espaço por cinco espécies de médios e grandes mamíferos. Este capítulo foi submetido e seguiu as normas da revista *Fire* (Qualis A2).

Capítulo 3 – Avaliação dos impactos da severidade do fogo na abundância, composição, riqueza e diversidade de pequenos mamíferos não voadores em matas de galeria sensíveis ao fogo.

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# Capítulo 1. Pyrodiversity begets taxonomic and functional richness of neotropical mammals

## Abstract

Understanding how species respond to the environmental heterogeneity created by fire (i.e., pyrodiversity) is essential to protect biodiversity in the face of current changes in the natural fire regime. Pyrodiversity is hypothesized to promote biodiversity, but this hypothesis has mixed support, and has never been tested for medium- and large-sized mammals in a neotropical savanna. Here, we investigated how mammalian communities respond to fire frequency, fire age, and spatiotemporal variations in these fire regime elements (pyrodiversity) at multiple spatial scales (from 0.8 to 78.5 ha). We sampled medium- and large-sized mammals using camera traps distributed on 30 sites in grassland and typical savanna formations during 15 months. We applied multiple regression analysis to describe the relationships between fire regime variables and mammal communities. Mammals responded to the fire regime (fire age and frequency) only when the spatiotemporal variation (diversity) was considered. Taxonomic and functional mammal richness increased with diversity in fire age, but mammal diversity and functional dispersion were greater at intermediate levels of pyrodiversity. Moreover, mammal abundance responded positively to diversity of fire frequency but negatively to fire age diversity. Our results indicate that pyrodiversity can lead to taxonomically and functionally rich communities, probably due to more forage, shelter, and movement opportunities for different species in heterogeneous environments. Nonetheless, its effect on abundance seems limited. We recommend focusing fire management in savanna landscapes on the diversity of fire age mosaics, at least for medium and large mammals. Moreover, management conducted on scales of 80 ha is sufficient to generate pyrodiversity that effectively affects mammal communities.

Key words: fire regime mosaics; environmental heterogeneity; savanna; biodiversity; fire management; mammalian community

## Introduction

In fire-prone ecosystems, the occurrence of fire can promote biodiversity (He et al. 2019), provide ecosystem services (Pausas and Keeley 2019), and generate environmental heterogeneity (Dantas et al. 2013). This heterogeneity affects how individuals use the environment and has implications for populations and communities (Pickett and Cadenasso 1995). However, climate change and human activities are altering the natural regime of fire. The trend is toward more extensive, frequent, and severe wildfires (Bowman et al. 2020; Iglesias et al. 2022). This altered fire regime can have adverse effects on biodiversity. Species can be affected directly through the immediate death of individuals (Tomas et al. 2021), as well as indirectly through landscape homogenization (Cassell et al. 2019), resource reduction (Barlow and Peres 2006; Peres et al. 2003; Vieira and Briani 2013), and habitat loss (Geary et al. 2022; Ward et al. 2020). In this scenario, understanding how species respond to fire regimes and to the spatial heterogeneity created by them is essential to plan actions that protect biodiversity and make biological communities more resilient in the face of changes in the fire regime.

The spatiotemporal heterogeneity created by the fire regime defines the pyrodiversity of an area (Martin and Sapsis 1992). This pyrodiversity is hypothesized to promote biodiversity through the presence of a mosaic of patches at different post-fire successional stages (Martin and Sapsis 1992). Each of these stages is associated with different species, providing greater biological diversity. This hypothesis is related to other ecological concepts, such as the intermediate disturbance hypothesis (Connell 1978), and has been a topic of increasing interest over the last decade and across several ecosystems. The world's ecosystems, however, are unequally represented by studies that have investigated the pyrodiversity–biodiversity hypothesis. For South America, for instance, only one study evaluating such a hypothesis is available (focused on ants; Maravalhas and Vasconcelos 2014). Research on under-represented ecosystems is essential to broaden our understanding of pyrodiversity and the pyrodiversity–biodiversity hypothesis (Jones and Tingley 2022).

The mechanisms behind the pyrodiversity–biodiversity relationship are associated with changes caused by fire in the composition and structure of vegetation and availability of resources, and with biota responses to these changes (He et al. 2019). For example, recently burned areas can provide better quality foraging for herbivores (Nieman et al. 2022), induce flowering of some species that attract pollinators (Fidelis and Zirondi 2021; Pilon et al. 2018; Ponisio et al. 2016), and provide a simplification of vegetation, attracting predators that use visual cues (Hradsky et al. 2017). On the other hand, unburned areas provide denser vegetation. This density may favor predators that use an ambush strategy to attack their prey (Doherty et al. 2022), provide shelter for species dependent on old trees (Flanagan-Moodie et al. 2018), and offer protection against cursorial predators (Cherry et al. 2017). Thus, it is expected that heterogeneous environments formed by a mosaic of fire regimes allow species coexistence and generate biological diversity (Chesson 2000).

Despite these mechanisms explaining the relationship between pyrodiversity and biodiversity, empirical studies show mixed support for this hypothesis (Jones and Tingley 2022). For terrestrial mammals, most studies either did not detect an effect of pyrodiversity (Kelly et al. 2012; Kelly et al. 2015; Lawes et al. 2015) or the response was species-dependent (Jorge et al. 2020; Senior et al. 2021). On the other hand, some studies suggest that great mammal abundance and richness occur in sites with the highest pyrodiversity (Beale et al. 2018; Bird et al. 2018; Radford et al. 2020). This positive effect, however, may be associated with intermediate levels of pyrodiversity (Davies et al. 2018; Furnas et al. 2022). This lack of consensus is part of the criticism of the hypothesis when applied for conservationist purposes without well-established guidelines and monitoring (Parr and Andersen 2006). Thus, for pyrodiversity to be considered a relevant factor in biodiversity-oriented fire management, there is an urgent need for more empirical evidence.

The responses of animal communities to the effects of fire can be evaluated both from taxonomic and functional perspectives (e.g. Moretti et al. 2010). These two distinct components of biodiversity do not always respond equally to landscape heterogeneity (Mouillot et al. 2013; Safi et al. 2011). Furthermore, the functional aspect of the community can be directly related to ecological processes and services (Cadotte et al. 2011). In general, functional attributes of mammals are based on the classification of species by diet, habit, period of activity, and body size (e.g., Gorczynski et al. 2021). Such characteristics represent different roles that species play within the community as well as the different uses they make of resources (food, space, and time). Mammal assemblages may present variation in their functional dispersion, which represents distinct breadths of functional roles across species (Cooke et al. 2019). This variation potentially affects the range of responses of these assemblages to environmental perturbations (Elmqvist et al. 2003; Meza-Joya et al. 2020).

In the present study, we investigated the possible effects of fire regime on communities of medium and large-sized mammals (> 1kg). We tested the pyrodiversity-biodiversity hypothesis in a highly diverse and fire-prone Neotropical savanna (Cerrado). In our study area (Chapada dos Veadeiros National Park - CVNP), the Integrated Fire Management (IFM) program has been implemented since 2017 to prevent large wildfires and protect areas of high sensitivity to fire (Fidelis et al. 2018; Schmidt et al. 2018). The IFM occurs through prescribed and controlled burning during the early dry season. This burning reduces the amount of dry fuel available and creates mosaics of patches with different fire regimes. Thus, the CVNP is formed by patches with different fire frequencies and in different post-fire successional stages. Such a pattern results from the combination of wildfire events and, more recently, controlled fires under the IFM. This makes our study area a highly relevant landscape to test the effect of pyrodiversity on fauna. In addition, there are still very few studies on the effects of prescribed burning on fauna, specifically, on mammals, in neotropical savannas (but see Durigan et al. 2020) in contrast to studies evaluating wildfire effects in other regions (Berlinck et al 2021).

To assess how the mammalian community responds to changes in fire regime, we considered variables related to this variation. As predictor variables, we used variables directly related to the fire regime in the areas (frequency of fire events and time since the last event – fire age) and also variables that explicitly indicate spatial and temporal heterogeneity of fire occurrence, reflecting the local pyrodiversity (diversity of fire frequency and of fire age). Specifically, we tested the effects of these predictor variables on several mammal community metrics, both taxonomic (richness, diversity, and total abundance) and functional (functional richness and functional dispersion). We verified these potential effects at three distinct spatial scales (0.8 ha, 19.6 ha, and 78.5 ha).

Following the “pyrodiversity begets biodiversity” hypothesis (Martin and Sapsis 1992), we expect a positive effect of the fire frequency and fire age diversity on mammal richness and diversity. This effect would be present in both taxonomic and functional aspects. However, we predict that the relationship would be stronger between pyrodiversity and taxonomic variables when compared to functional variables. This pattern would emerge because the number of species may be more sensitive to habitat changes than the number of functional characters in the community (Mouillot et al. 2013). Furthermore, we expect a positive relationship between mammal abundance and pyrodiversity. This relationship would result from the availability of different resources in a pyrodiverse mosaic and the possibility of complementarity in the use of these resources by species (Nimmo et al. 2019). We also predict little or no effect of fire frequency and fire age *per se* on the mammal community. This would occur due to the presence of species attracted to areas recently or frequently burned, compensating for the absence of species that use later post-fire stages or that avoid areas with a more frequent fire regime. On the other hand, in sites that do not burn for a longer time or experience few fire events, the presence of species typical of late stages or associated with areas having less fire frequency would counterbalance the lack of species typical of more intense regimes. Likewise, we expect little or no effect of fire frequency and fire age *per se* on mammal abundance.

## Materials and methods

### *Study area*

We conducted fieldwork in the Chapada dos Veadeiros National Park (CVNP) (~240,000 ha) located in the state of Goiás, Brazil (Fig. 1). The CVNP is a protected area preserving the Cerrado, a highly biodiverse neotropical savanna (Myers et al. 2000). The Cerrado vegetation is a combination of vegetation types that include both open formations (e.g., grasslands and savannas) and forest formations (e.g., gallery forests) (Ribeiro and Walter 1998). This heterogeneity can be explained, among other factors (e.g., soil characteristics and water availability), by fire dynamics in the region (Bueno et al. 2018).

This fire dynamics is more evident in grassland and savanna areas, which are more susceptible to fire occurrence (Miranda et al. 2009). These two vegetation types predominate in the CVNP (Lewis et al. 2022). We concentrated our sampling on four representative plant communities of these vegetation types: 1) campo limpo, characterized by low canopy cover (<5%) and strong presence of grasses; 2) campo rupestre, a rupestrian habitat formed by a herbaceous-shrub layer associated with rocky outcrops and drained soil; 3) cerrado rupestre, composed of tree-shrub vegetation with canopy cover between 5% and 20%, also associated with rocky outcrops; and 4) cerrado sensu stricto, characterized by tree-shrub vegetation, canopy coverage between 10% and 60%, and canopy height between 3 and 6 m (Lewis et al. 2022; Ribeiro and Walter 1998). Thus, we established all our sample units in open formations subjected to some level of fire regime.

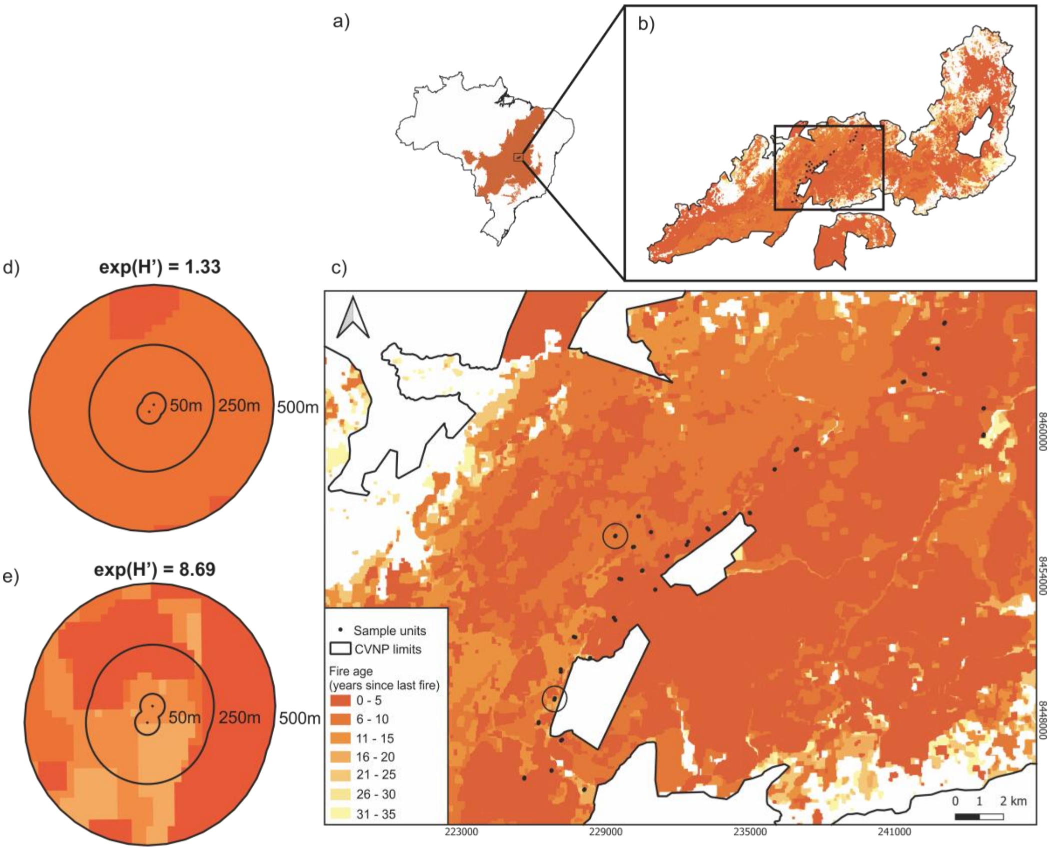

**Fig. 1** Location of the study area, the Chapada dos Veadeiros National Park (CVNP). a) Cerrado distribution in the Brazilian territory and location of the CVNP; b) sampled areas within the CVNP; c) fire history of the study area and location of sampling units; d) and e) fire history mosaic for the sampling units with the lowest and highest index of pyrodiversity, respectively, and the spatial scales used (circular buffers with radius of 50 m, 250 m, and 500 m). Exp(H') values based on the 500-m buffer

The fire regime in the CVNP region is characterized by the annual occurrence of wildfire, and a larger burned area is associated with the end of the dry season (September/October) (MapBiomas 2022). The major causes of fire in the CVNP include arson (41%), unknown origin fire (25%), pasture burning (15%), and lightning (12%) (Silva et al.

2021). A large wildfire of anthropic origin occurred in the CVNP in 2017, 2.5 years before the beginning of our sampling in 2020. This event was one of the most severe wildfires since the creation of the reserve, burning 80% of the CVNP area at the time (Flores et al. 2021). We installed part of our sample units within the area affected by the wildfire of 2017.

The climate of the region is tropical, with the dry season occurring in winter (Köppen-Geiger classification) (Beck et al. 2018). The average annual temperature is 23.4ºC, with October being the hottest month (monthly average temperature = 25.3ºC) and June and July being the coldest months (monthly average temperature = 20.8ºC) (Cardoso et al. 2014). The average rainfall is 1500mm/year (average 1989 - 1999), with rainfall concentrated between October and April (precipitation > 50mm/month) and the dry period occurring between May and September (precipitation < 50mm/month) (Cardoso et al. 2014).

### *Medium- and large-sized mammal sampling*

We sampled medium and large mammals using 60 Bushnell® model camera traps. Sampling occurred from February 2020 to April 2021 (15 months) and covered dry and rainy seasons. This allowed us to conduct a more effective sampling since community composition and capture success of medium and large mammals can vary between seasons (Ferreguetti et al. 2019; Nunes 2022). Using a systematic approach to allocate the camera traps (Meek et al. 2014), we established 30 sample units within the boundaries of the CVNP along a highway that cuts through it and secondary roads within the CVNP. We kept a minimum spacing of 1km between sampling points to ensure data independence. However, when necessary, some stations were at a distance below this value (the shortest distance between stations was 0.820km). The average minimum distance between stations was 1,258km. In addition, we set the sample units at least 300m from the nearest highway or secondary roads to reduce any possible effect of roads on mammalian responses.

We monitored all sampling units using two camera traps simultaneously but orientated at different points in the landscape. We looked for recent mammalian tracks, such as footprints, feces, trails, and horn marks, and placed the camera near these tracks. When possible, we also positioned the cameras toward water bodies to increase the chances of capturing mammals. Hence, the distance between the two traps of the same unit was not uniform, varying between 10  and 150 m (average distance: 51m). Furthermore, we installed the camera traps at a level of 30 cm above the ground and did not use any type of attractive bait.

From February 2020 to August 2020 and from December 2020 to April 2021, we set all cameras to take three pictures with each shot, with a 10-second interval between shots. Between September 2020 and November 2020, we configured all cameras to record 15-second videos with a one-second shooting interval. Regardless of the configuration (photo or video), all camera traps functioned to record 24 hours a day. We sampled all units simultaneously over the 15 months of collection. However, due to battery drain and memory cards filling up completely, some cameras stopped recording before maintenance (battery and memory card replacement). There was also an occurrence of loss of equipment due to fire. Consequently, the trapping effort was not identical for all the stations. We established a minimum interval of 30 minutes to consider records of the same species as independents.

### *Fire regime and pyrodiversity characterization*

The fire regime of a region is characterized by spatial, temporal, and behavioral parameters related to fire events (Krebs et al. 2010). For the present study, we used two temporal parameters and two spatiotemporal parameters to describe the fire regime in our study area: fire frequency, fire age, diversity of fire frequency, and diversity of fire age. We defined fire frequency as the number of fire events within a period of 36 years and fire age as the number of years since the last fire occurrence in the area. This last parameter is strongly related to the successional stage of the vegetation (Blanchard et al. 2021; López-Mársico et al. 2021; Pilon et al. 2021).

We described the fire regime of the study area using data from a 36-year interval (1985 – 2020) of fire scars provided by MapBiomas (MapBiomas 2022) with a resolution of 30m. From the fire scar data, we created a map for each evaluated fire regime parameter, in which we established the fire frequency and fire age for each pixel using the Quantum Gis software (QGIS 2021). We calculated the fire frequency and fire age associated with each sample unit at different spatial scales. To achieve this, we established buffers of 50-m, 250-m, and 500-m radius around each camera trap (Brennan et al. 2002). These buffers represent the spatial scales of 0.8 ha, 19.6 ha, and 78.5 ha, respectively. We used these scales based on studies that found fire-induced responses of medium and large mammals in spatial scales of 80 ha or finer (Bird et al. 2018; Delaney et al. 2021). Although mammals may also respond to fire on broader scales (Furnas et al. 2021; Radford et al. 2021), we limited our larger buffer to a 500-m radius to avoid overlapping the sampling unit buffers, which could compromise data independence. We superimposed the buffers around the cameras of the same sampling unit at the same spatial scale. This was necessary to obtain only one value per sample unit per scale. Then, we calculate the weighted average of the fire frequency for each buffer. We based this average on the percentage of area occupied by each fire frequency within the buffer. The same approach was applied to the fire age. In this case, we calculated the average based on the percentage of area occupied by each fire age.

Additionally, we estimated pyrodiversity using the same maps for fire frequency and fire age described above. From these maps, we estimated fire frequency and fire age diversity for each sampling unit and each scale evaluated (50m, 250m, and 500m buffers). Each buffer captured the spatiotemporal variation in fire frequency and fire age associated with each sampling unit. Such an approach allowed us to test the pyrodiversity–biodiversity hypothesis directly (*sensu* Jones and Tingley 2022).

### *Functional mammal traits*

For each mammal species recorded by our camera traps, we assigned functional traits based on Wilman et al. (2014), a large dataset containing the attributes of 9993 birds and 5400 mammals present in the literature. In this dataset, the diet of mammals represents the percentage of consumption of different food items (e.g., invertebrates, vertebrates, fruits). The habit defines the use of the vegetation strata (e.g., terrestrial, scansorial, arboreal). The period of activity of the species is a binary attribute, indicating the presence or absence of foraging activity by the species in a given period of the day (e.g., day, night, twilight). Finally, the body size describes the average body mass of adult individuals of each species. All the functional information gathered for the species that we registered in the CVNP is contained in Table S1 of Online Resource 1.

Identification at the species level was not possible for two pairs of similar species detected in the camera traps, two deer species (*Mazama americana* and *Subulo* [=*Mazama*] *gouazoubira*) and two small cats (*Leopardus emiliae* and *Leopardus wiedii*). These pairs of species are functionally very similar to each other (Table S1, Online Resource 1) and were considered together as ‘functional species’ (*Mazama* sp. and *Leopardus* sp.). We addressed minor differences in the diet and body mass of *M. americana* and S. *gouazoubira* by considering the dietary information for *S. gouazoubira* because the diet of the latter has one more item than the diet of *M. americana* (i.e., fruits). Thereby, we ensured that no functional information was lost. Likewise, *Leopardus emiliae* and *Leopardus wiedii* showed minor differences in diet and activity period, and we used information for the species with more diverse attributes. Body mass for *Mazama* sp. and *Leopardus* sp. was defined as the average mass between both species of each pair. There were no differences between species regarding habit.

*Statistical analyses*

Pyrodiversity represented spatial and temporal heterogeneity in the fire frequency and fire age (fire frequency diversity, and fire age diversity). We estimated fire frequency and fire age diversity for each sampling unit using the exponential of Shannon's entropy (exp H’). We obtained this index from the fire frequency and fire age values calculated for each pixel of our fire regime maps. We considered the area occupied by pixels of the same value for fire frequency/fire age as the “abundance” of that frequency/age in the sampling unit. We used this "abundance" to estimate Shannon's index of the fire frequency and fire age in the sampling units (pyrodiversity) (Delaney et al. 2021; Farnsworth et al. 2014; Nimmo et al. 2012). This index was obtained for each of the spatial scales analyzed (0.8 ha, 19.6 ha, and 78.5 ha). The exp H' gives the ‘true’ diversity or effective number of species, that is, the number of equally common species needed to obtain a specific value of Shannon's entropy (Jost 2006). Here, the exp H' represents the effective number of patches with different fire frequencies/ages.

We calculated the total abundance of mammals by summing the independent records of all medium and large-sized mammal species. For each sampling unit, we also estimated the taxonomic richness of mammals using the Chao2 index for incidence data, with 1000 randomizations and camera days as the number of samples (Gotelli and Colwell 2010). This analysis was conducted in the EstimateS program (Colwell 2013). We used the true Shannon's diversity index to estimate the taxonomic diversity of mammals. In this calculation, we used the number of independent records for each species as a proxy of species abundance.

We evaluated the functional aspect of the mammalian community using two response variables, functional richness and functional dispersion. The first variable is related to the size of the functional space and represents the sum of differences between species. On the other hand, functional dispersion measures how dispersed the functional space is, being related to the average difference between species (Mammola et al. 2021). We estimated the functional richness as the total length of the branches of the functional dendrogram (Petchey and Gaston 2006). Using the species attribute matrix (Table S1, Online Resource 1), we generated a distance matrix applying the Gower distance method. This method is suitable when quantitative and qualitative functional attributes are analyzed together (Podani and Schmera 2006). Then, we used the Unweighted Pair Group Method with Arithmetic Mean (UPGMA) to generate a dendrogram. This clustering method was determined by comparing the cophenetic correlation coefficient of several clustering methods (ward, UPGMA, single, complete, UPGMC, WPGMC, and WPGMA). The UPGMA method had the highest coefficient (0.65), indicating less loss of information contained in the original data matrix. Finally, we obtained the functional richness of each sampling unit by calculating the total length of the branches of the dendrogram containing the species recorded for the sampling unit. The advantage of using this method is that it allows the analysis of several functional characteristics simultaneously. Moreover, the functional dendrogram method is robust against the gain or loss of functionally redundant species (Petchey and Gaston 2006). We conducted this analysis in the “fundiv” package (Bartomeus 2013) for the R environment (R Core Team 2022). The resulting dendrogram is in Fig. S1 of Online Resource 1.

We calculated the functional dispersion as the average distance of species to the centroid of the functional space composed of all species in the sample unit (Laliberté and Legendre 2010). In this method, we balanced the average distance using the species abundance while shifting the centroid towards the most abundant species. The same attribute matrix used to generate the dendrogram was used in this analysis. We applied the Gower distance method due to the presence of quantitative and qualitative attributes. The calculation of functional dispersion requires at least two species records in the sampling unit. Thus, when only one species was present, the functional dispersion was zero. The use of the functional dispersion described by Laliberté and Legendre (2010) has two main advantages. Its calculation is not affected by the number of species in the sample and the relative abundance of the species is accounted for.

Before analyses, we checked for possible outliers in the taxonomic and functional richness data using visual tools. We detected one possible outlier for both variables, which was confirmed using the Grubbs test (functional richness: $G = 3.32$, $p < 0.05$; taxonomic richness: $G = 4.48$, $p < 0.05$), which was conducted in the R environment using the “outliers” package (Komsta 2022). These discrepant values for taxonomic and functional richness corresponded to the same sampling unit located inside a farm. Human presence and non-native animals, such as cattle and domestic dog records, were frequent at this site. To avoid the effect of outliers and minimize the influence of factors external to the fire regime, we excluded this sample unit and the records of non-native animals from the analysis.

For each response variable, we identified the adequate spatial scale for evaluating the potential effects of the predictor variables using a model selection approach based on the Akaike criterion with adjustment for small samples (AICc). For that, we created three models for all combinations of response variables and predictor variables. Each model represented a spatial scale in which the predictor variable was measured (0.8 ha, 19.6 ha, and 78.5 ha). The model selection consisted of comparing the three models representing the different spatial scales for the same response variable-predictor variable relationship. In each model, we added the effort as a covariate to deal with unbalanced sampling effort between units. We considered models with $\Delta \text{AICc} < 2$ to have good explanatory power (Burnham and Anderson 2002).

Thus, the spatial scales represented in these models corresponded to the ‘best’ spatial scale for the evaluation of the effect exerted by the predictor variable on the response variable. When more than one model had $\Delta$AICc < 2, we used all the spatial scales contained in these models in the multiple regression analyses. However, when the correlation between these spatial scales was > 0.5, we utilized only the spatial scale present in the model with $\Delta$AICc = 0 (Table S2, Online Resource 1). Thus, some regressions presented more than one spatial scale for the same predictor variable, while others presented only one spatial scale per predictor variable. We used the AICcmodavg package (Mazerolle 2020) in the R program to conduct the model selection analysis.

After finding the spatial scales representative of the relationship between predictor variables and response variables, we applied multiple linear regressions to identify the nature of these relationships. For this, we created a model containing the predictor variables related to the fire regime (fire frequency, fire age, fire frequency diversity, and fire age diversity) for each response variable (Table 1). We also included trapping effort as a covariate in the models to account for differences in the number of trap days between sampling units. All predictor variables and the effort covariate were standardized to have a mean equal to zero and a standard deviation equal to one. The spatial scales of the predictor variables that entered the models were determined according to the previously described model selection. We plotted each response variable against each predictor variable individually. These plots revealed potential quadratic relationships between taxonomic diversity and pyrodiversity and between functional dispersion and fire age diversity. To test whether the quadratic relationship had a better fit than the linear relationship, we compared the models for taxonomic diversity and functional dispersion with and without the quadratic relationship using the $\Delta$AICc and the adjusted $r^2$. This comparison showed that the quadratic relationship had a better fit (Table S3, Online Resource 1). We did not detect collinearity between predictor variables as all models showed variance inflation factor < 3 (Zuur et al. 2010). We inspected the residuals' distribution of the multiple regressions to verify the assumption of normality and compared the residuals with predicted values and predictor variables for validation. All models had residuals whose distribution was close to the normal distribution, and all models were validated.

Finally, we applied the Moran Index associated with a hypothesis test to verify the occurrence of spatial dependence for the community metrics used (total abundance, functional and taxonomic richness, taxonomic diversity, and functional dispersion). All tests returned p-values > 0.05, so we considered that there was no spatial autocorrelation in our data. We conducted this analysis using the "ape" package (Paradis et al. 2004) for the R environment.

**Table 1** Description of predictor variables used in multiple linear regression analyses. Cont. = continuous. All variables (except effort) were measured at the spatial scales of 0.8 ha, 19.6 ha, and 78.5 ha

| Predictor variable | Abbreviation | Type | Description |
|---|---|---|---|
| Fire frequency | freq | Cont. | Number of years with fire occurrence from 1985 to 2020. Multiple spatial scales |
| Fire age | age | Cont. | Number of years since the last fire occurrence. Multiple spatial scales |
| Fire frequency diversity | div-freq | Cont. | Fire frequency diversity calculated by the exponential of Shannon's Diversity Index (exp H'). Multiple spatial scales |
| Fire age diversity | div-age | Cont. | Fire age diversity calculated by the exponential of Shannon's Diversity Index (exp H'). Multiple spatial scales |
| Effort | effort | Cont. | Sampling effort in each sampling unit calculated as the number of trap days |

## Results

We set camera traps from February 2020 to April 2021, resulting in a sampling effort of 10112 trap days. We obtained 472 mammal records, from which 22 species were identified (94.5% of records identified) (Table S4, Online Resource 1). The most-recorded species were: pampas deer (*Ozotoceros bezoarticus*, 199 records), maned wolf (*Chrysocyon brachyurus*, 54), brocket deer (*Mazama* sp., 38), crab-eating fox (*Cerdocyon thous*, 32) and tapir (*Tapirus terrestris*, 27). In addition to the native species, we recorded two exotic mammals in the CVNP, the domestic dog (*Canis lupus familiaris*) and the cattle (*Bos taurus*). Most of these records occurred at a single sampling unit located close to a farm and were not included in the analyses.

The fire regime showed high variation in the study area. At the broader spatial scale (78.5 ha), average fire frequency ranged from 3.9 to 15.1 years with fire occurrence in the period of 36 years (1985 - 2020) (Online Resource 2). Most sample units had a fire frequency lower than 10 annual occurrences in the last 36 years. Regarding the average fire age, the sampled areas varied from 0.9 to 14.6 years since the last fire. Moreover, in more than half of the units, we registered fire occurrences within the previous five years. The pyrodiversity (exp H’) varied between 4.2 and 14.8 for fire frequency and between 1.3 and 8.6 for fire age at the 78.5-ha scale.

We detected a positive effect of the pyrodiversity on the taxonomic richness and diversity of medium and large-sized mammal, as indicated by multiple linear regression (Fig. 2; Table 2). This effect was significant considering the fire age diversity at the broadest spatial scale evaluated (78.5 ha). An increase of one unit in the effective number of fire ages (fire age diversity) represented an increase of 1.4 in the mean taxonomic richness. Fire frequency and fire age *per se*, however, did not significantly affect mammal richness. On the other hand, for taxonomic diversity, we detected significant quadratic relationships with pyrodiversity. At the broadest scale, mammal diversity was higher in intermediate values of fire age diversity whereas at the finest scale (0.8 ha) this diversity was higher in intermediate values of fire frequency diversity (Fig. 2; Table 2).

Pyrodiversity also had a significant effect on total mammal abundance. The total number of mammals was positively affected by fire frequency diversity at the broadest scale (78.5 ha; Fig. 2; Table 2). This means that if the effective number of patches with different fire frequencies increases by one unit, the average mammal abundance increases by 5.5 individuals. On the other hand, fire age diversity had the opposite effect on total mammal abundance at the finest spatial scale (0.8 ha). This effect indicates that increasing the effective number of patches with different fire ages by one unit reduces the average mammal abundance by 5.8 individuals.

The evaluation of the effect of pyrodiversity on funcional aspects of mammalian communities also indicated significant relationships for both funcional richness and dispersion at the broadest scale (Fig. 3; Table 2). For functional richness, there was a positive and linar relationship with fire age diversity. For this predictor variable, an increase of one unit induces an increase of 0.2 in the mean functional richness. The pyrodiversity effect was more intense, however, for taxonomic richness than for the functional richness, as indicated by the model coefficient values (Table 2). For funcional dispersion, we detected a quadratic relationship with pyrodiversity, with greater dispersion observed for intermediate values of fire age diversity (Fig. 3, Table 2).

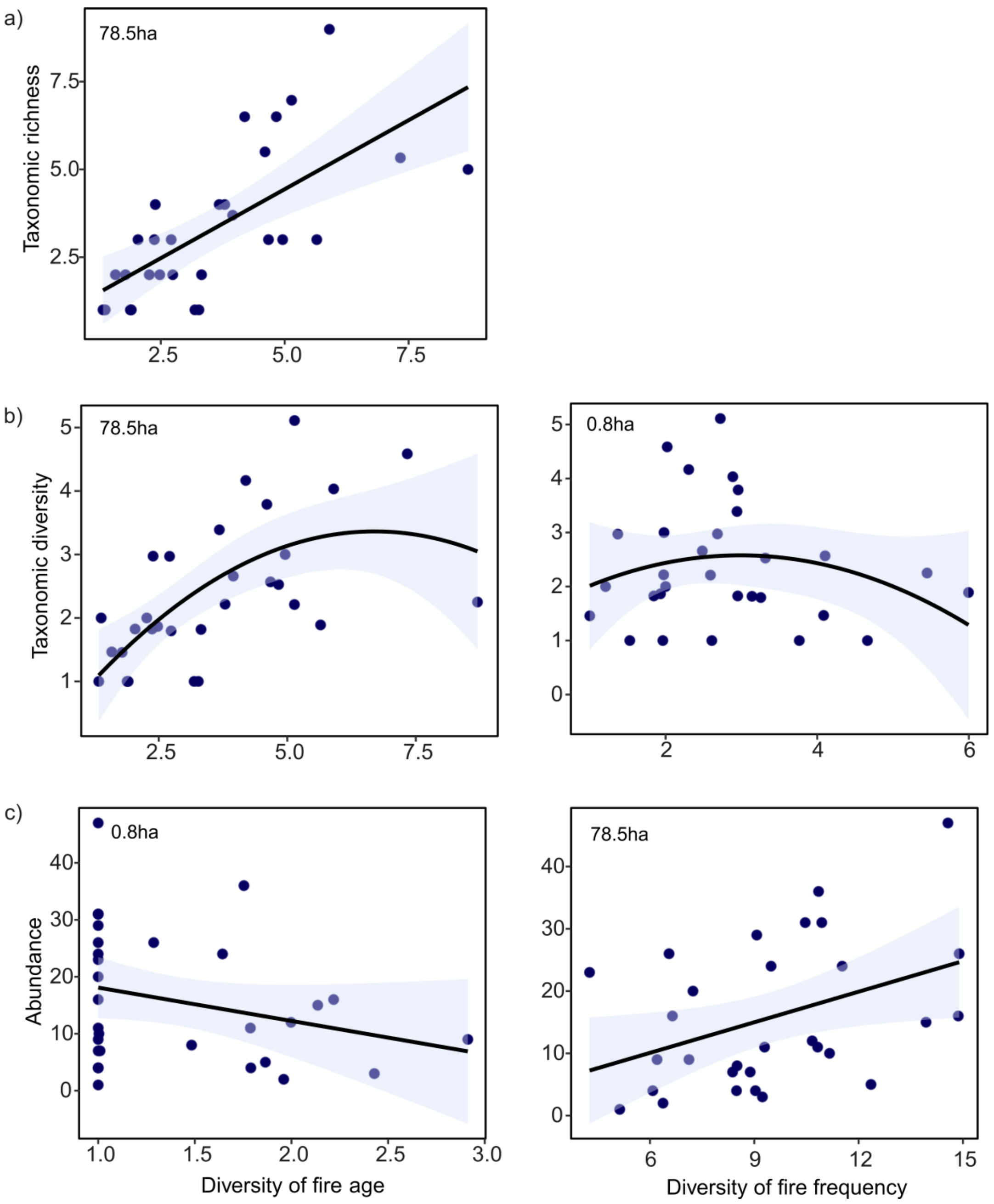

**Fig. 2** Relationship between the diversity of fire regimes (i.e., pyrodiversity, considering fire frequency in the previous 36 years – fire frequency [right column], and time since last fire – fire age [left column]) and several aspects of the community of medium and large-sized mammals from the Cerrado (Neotropical savanna). The mammalian community aspects considered were taxonomic richness (a), taxonomic diversity (exponential of Shannon entropy; b), and total abundance (c). Pyrodiversity was quantified using the exponential of Shannon entropy as the metric of variation of the fire characteristic evaluated (fire frequency and fire age). The spatial scale of fire-variable measurements in the models is indicated for each plot. The blue shade indicates the 95% confidence interval. See text for details.

**Table 2** Multiple regression analysis coefficients (β) and respective standard errors (SE), t-values (t), and p-values (p). Significant relationship ($p < 0.05$) between response variables (taxonomic richness, functional richness, taxonomic diversity, functional dispersion, and mammal abundance) and predictors variables are in bold. The numbers 50, 250, and 500 with the variable names indicate the radius (m) of the buffers used in the variables measurement. These buffers are related to the 0.8-ha, 16.9-ha, and 78.5-ha spatial scales, respectively.

| | **β** | **SE** | **t** | **p** |
|---|---|---|---|---|
| Taxonomic richness | | | | |
| **Intercept** | **3.381** | **0.309** | **10.934** | **0.000** |
| freq500 | 0.058 | 0.461 | 0.126 | 0.901 |
| age500 | 0.062 | 0.530 | 0.118 | 0.907 |
| div-freq500 | 0.298 | 0.408 | 0.730 | 0.473 |
| **div-age500** | **1.428** | **0.447** | **3.196** | **0.004** |
| effort | -0.207 | 0.365 | -0.567 | 0.576 |
| Taxonomic diversity | | | | |
| **Intercept** | **2.890** | **0.179** | **16.160** | **0.000** |
| freq50 | 0.322 | 0.183 | 1.761 | 0.093 |
| age50 | 0.288 | 0.186 | 1.546 | 0.137 |
| **div-freq50** | **-0.379** | **0.169** | **-2.237** | **0.036** |
| **(div-freq50)$^2$** | **-0.224** | **0.106** | **-2.106** | **0.047** |
| div-freq500 | 0.067 | 0.148 | 0.454 | 0.655 |
| **div-age500** | **0.901** | **0.182** | **4.950** | **0.000** |
| **(div-age500)$^2$** | **-0.304** | **0.115** | **-2.652** | **0.015** |
| **effort** | **0.470** | **0.162** | **2.901** | **0.009** |
| Mammal abundance | | | | |
| **Intercept** | **15.700** | **1.791** | **8.764** | **0.000** |
| freq50 | -1.240 | 2.422 | -0.512 | 0.613 |
| age500 | 0.389 | 2.421 | 0.161 | 0.874 |
| **div-freq500** | **5.564** | **2.058** | **2.704** | **0.012** |
| **div-age50** | **-5.845** | **2.042** | **-2.862** | **0.009** |
| **effort** | **3.935** | **1.961** | **2.007** | **0.056** |
| Functional richness | | | | |
| **Intercept** | **0.794** | **0.052** | **15.223** | **0.000** |
| freq50 | -0.023 | 0.072 | -0.319 | 0.753 |
| age50 | -0.181 | 0.109 | -1.659 | 0.111 |
| div-freq500 | -0.035 | 0.074 | -0.478 | 0.637 |
| **div-age500** | **0.267** | **0.078** | **3.432** | **0.002** |
| effort | 0.044 | 0.058 | 0.763 | 0.453 |
| Functional dispersion | | | | |
| **Intercept** | **0.128** | **0.011** | **11.393** | **0.000** |
| freq250 | 0.005 | 0.013 | 0.404 | 0.690 |
| age500 | -0.011 | 0.015 | -0.737 | 0.469 |
| div-freq50 | -0.018 | 0.010 | -1.826 | 0.081 |
| div-freq500 | -0.005 | 0.011 | -0.448 | 0.659 |
| **div-age500** | **0.054** | **0.014** | **3.897** | **0.001** |
| **(div-age500)$^2$** | **-0.022** | **0.008** | **-2.867** | **0.009** |
| **effort** | **0.025** | **0.012** | **2.187** | **0.040** |

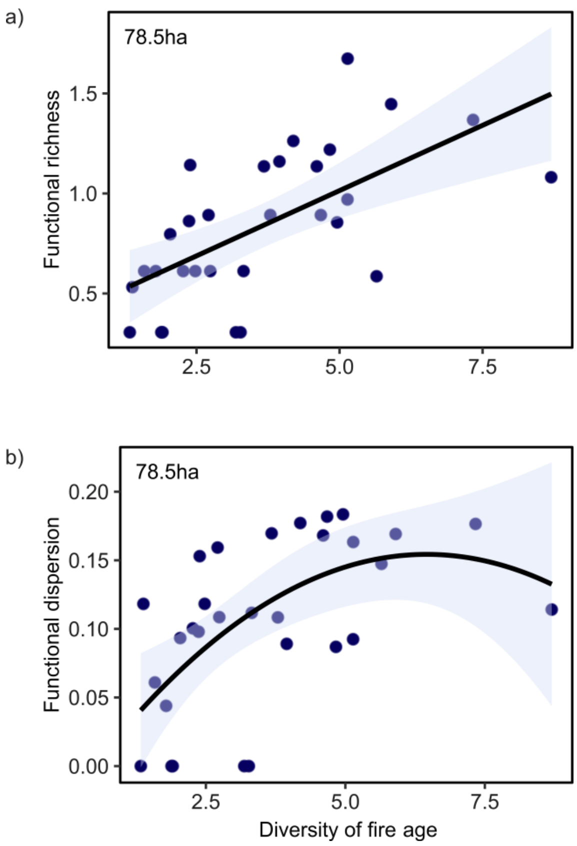

**Fig. 3** Relationship between the diversity of fire regimes (i.e., pyrodiversity; considering the number of fire events in the previous 36 years – fire frequency, and time since last fire – fire history) and functional metrics of medium and large-sized mammal communities from the Cerrado (Neotropical savanna). The functional aspects considered were functional richness (a) and functional dispersion (b). The spatial scale of fire variables used in the models is reported in parentheses. See text for details.

## Discussion

We evaluated the effect of fire frequency, fire age, and spatiotemporal variation related to both these parameters (i.e., pyrodiversity) on mammal communities from a tropical savanna. We found a positive relationship between pyrodiversity and both taxonomic and functional mammal richness. This effect was strongly associated with diversity of fire ages (i.e., time since last fire). We also detected that, for mammals, taxonomic richness is more sensitive to variations in fire age diversity than functional richness. Furthermore, we detected a non-linear relationship between pyrodiversity and two of the evaluated metrics - taxonomic diversity and functional dispersion of mammals. These two variables reached maximum values when pyrodiversity was intermediate. Moreover, distinct pyrodiversity aspects affected mammal abundance in opposite ways. Fire age diversity negatively affected total abundance, whereas fire frequency diversity positively affected this metric. In relation to the spatial scale of effect, mammals responded to pyrodiversity on more than one scale, but the effect of fire age diversity was more evident at the broadest spatial scale analyzed (78.5 ha). Diversity of fire frequency, however, had effects on the mammal communities both at the finest scale (0.8 ha) and at the broadest scale.

### *Pyrodiversity effects on mammal taxonomic richness and diversity*

Our prediction that higher spatiotemporal variation in fire age is associated with the higher taxonomic richness of medium and large-sized mammals was confirmed by our results. The positive relationship found between pyrodiversity and mammal taxonomic richness supports the hypothesis that 'pyrodiversity begets biodiversity' (Martin and Sapsis, 1992). This response is consistent with studies conducted for several taxonomic groups and ecosystems, including bats, terrestrial mammals, and birds in humid African savannas (Beale et al. 2018), birds in conifer forests (Jorge et al. 2022; Tingley et al. 2016), reptiles in Australian Mallee vegetation (Farnsworth et al. 2014), and invertebrates in a Neotropical savanna (Maravalhas and Vasconcelos 2014). On the other hand, there are also several studies that do not support the pyrodiversity–biodiversity hypothesis [e.g., vertebrates in general in Australia (Pastro et al. 2011); birds in Australian woodlands (Burgess andand Maron 2016; Wills et al. 2020) and in African savanna (Docherty et al. 2020); and grassland plants in Australia (Pastro et al. 2011)]. Such variation in empirical support for the pyrodiversity–biodiversity hypothesis may be driven by differences in the definition and measurement of pyrodiversity, the historical context of the region, and the temporal and spatial scale of the study (Jones and Tingley 2022). Our results suggest that, for medium and large-sized mammals, a high effective number of patches with different fire ages promotes more speciose communities in a tropical savanna.

We found that mammal taxonomic richness was affected by spatiotemporal variation in the fire age at the 78.5-ha spatial scale. Several biotic and abiotic factors can affect the richness patterns of mammal communities (Dorph et al. 2021; González-Maya et al. 2016; Rich et al. 2017; Sandom et al. 2013). For example, high environmental heterogeneity is related to increased mammal richness (Regolin et al. 2020; Sukma et al. 2019). Likewise, interspecific relationships such as predation and competition can influence mammal communities (Carreira et al. 2020; Fedriani et al. 2000). We suggest that the effect of pyrodiversity on the mammal community was exerted through both environmental heterogeneity and species interactions. The fire age diversity in our study area is associated with a mosaic of patches in different post-fire successional stages (Blanchard et al. 2021). These stages have specific vegetation structures that affect mammal activity (Zylinski et al. 2022). For example, recently burned areas can provide better foraging for herbivores (Cherry et al. 2018; Nieman et al. 2022) and favor predators with cursorial hunting mode (Hradsky et al. 2017). They may also facilitate individual movements because of the reduction of vegetation complexity after the fire (Nimmo et al. 2019). On the other hand, areas that have not burned for a long time can provide den sites for scansorial species (Flanagan-Moodie et al. 2018) and protection from predators (Cherry et al. 2017). Furthermore, mesopredators may avoid areas where fire favors the presence of top predators (Geary et al. 2018). Thus, pyrodiverse areas with high environmental heterogeneity offer opportunities for foraging, shelter, hunting, and movement for different species. This may result in high taxonomic richness in areas that experience high spatial variation in fire regime.

Our results for mammal taxonomic diversity partially corroborated our predictions related to the pyrodiversity-biodiversity hypothesis. At the broadest scale evaluated (78.5 ha), fire age diversity had a positive effect on taxonomic diversity up to intermediate values of variables. Mammal taxonomic diversity also increased up to intermediate values of fire frequency diversity, but this relationship occurred at the finer scale (0.8 ha). Beyond these values, mammal diversity did not continue to increase in response to pyrodiversity increase. Similar non-linear responses to pyrodiversity have already been reported for Carnivore mammals in fire-prone forests in the USA (Furnas et al. 2022) and small mammals in the Australian savanna (Davies et al. 2018). Several studies suggest that the extension of the area with a specific fire age or fire frequency is a better predictor for species response to fire than pyrodiversity (Chia et al. 2016; Docherty et al. 2020; Griffiths et al. 2015; Kelly et al. 2012; Nimmo et al. 2013). Indeed, negative effects of pyrodiversity may arise when species depend upon resources present only in patches with a specific fire age (Flanagan-Moodie et al. 2018) or a particular fire frequency (López-Baucells et al. 2021). If these patches are not available in sufficient amount (Berry et al. 2015) or are too far away to be detected by the animals (Nimmo et al., 2019), highly pyrodiverse environments may not be suitable. On the other hand, species that use patches with different fire regimes to complement their use of resources (Nimmo et al., 2019; Senior et al., 2021) can benefit from environments with a more diverse fire regime. These two contrasting pressures might result in high diversity at intermediate pyrodiversity levels.

As pointed out by some studies, few species use exclusively one fire age, but their abundances or occurrence may vary between patches in different post-fire successional stages (Chia et al. 2016; Driscoll and Henderson 2008; Nimmo et al. 2013). This pattern may be related to species using patches in distinct successional stages post-fire differently. Some species may occasionally use some fire ages when dispersing to patches with more suitable fire ages. Such movement type is not common and contrasts with the frequent use of certain fire ages (Nimmo et al. 2019). This variation in response between species that coexist within the same fire regime can lead to intermediate values of pyrodiversity being more suitable for the maintenance of individual species, leading to more diverse communities. This kind of variation is probably more evident when considering changes in abundance and not just the presence/absence of species.

### *Pyrodiversity effects on mammal abundance*

The influence of individual species responses on mammal diversity patterns in fire age mosaics seems to be corroborated by our results for mammal abundance observed at the 0.8-ha spatial scale. Contrary to our expectations, we found a negative effect of fire age diversity on the total number of mammal records. This may be due to the most common species in our study area presenting affinities with unburned (*Mazama* sp.) or recently burned areas (*O. bezoarticus* and *C. brachyurus*) (Nunes 2022). Thus, such species would not necessarily benefit from highly pyrodiverse mosaics. Herbivores such as *O. bezoarticus* may be attracted to recently burned areas due to the availability of food resources (Eby et al. 2014; Nieman et al. 2022). In turn, *C. thous* and *C. brachyurus*, which include small mammals in their diets (Giordano et al. 2018; Juarez and Marinho-Filho, 2002), may be attracted to newly burned areas in response to increased prey abundance (or their catchability) after a fire event (Briani et al. 2004). However, in our sampling units, the average proportion of areas burned up to two years before the start of sampling was twice as small as the area burned at a longer time (Online Resource 2). Thus, the fire age mosaic of the study area may not have been adequate for the requirements of these species.

Contrary to the pattern observed for fire age diversity, fire frequency diversity had a positive effect on mammal abundance. Such effect occurred at the broadest spatial scale evaluated (78.5 ha). This result was expected and may reflect the fire frequency associated with different types of vegetation that compose the Cerrado. Forested vegetation in Cerrado rarely burns (Miranda et al. 2009) and can serve as a refuge during frequent fires in grassland and savanna areas (Robinson et al. 2013), facilitating *in situ* survival of individuals after a fire (Hale et al. 2022; Leahy et al. 2016; Shaw et al. 2021). Thus, a mosaic of distinct vegetation with different fire frequencies, such as the mosaics formed by grasslands, savannas, and gallery forests, could allow for more abundant populations of mammals.

### *Pyrodiversity effects on functional metrics*

We found that the functional richness of mammals responded positively to fire age diversity at the 78.5-ha spatial scale. However, this response was less intense than the response observed for taxonomic richness. This means that an increase in the number of species promoted by pyrodiversity is not fully accompanied by additions of functional attributes to the community, leading to communities with higher functional equivalence between species. Such a pattern follows the global pattern for mammals in which taxonomically richer regions have high levels of functional redundancy (Oliveira et al. 2016). Ecological processes acting differently on distinct dimensions of diversity may have driven this pattern (Safi et al. 2011). For example, environmental filters can generate communities with high convergence of functional attributes (Farias and Jaksic 2011; Zhang et al. 2018) but not necessarily affect the number of species (Docherty et al. 2020). Pyrodiverse environments have the potential to act as environmental filters since mammals can be affected by fire according to their functional characteristics (Camargo et al. 2018; Culhane et al. 2022). Furthermore, as species inhabiting a fire-prone ecosystem, the mammals we recorded have attributes that represent adaptations to the fire dynamics of the region (Pausas and Parr 2018). Such attributes are related to the ability to explore environments modified by fire (Prada

2001; Prada and Marinho-Filho 2004). This ability is likely advantageous in pyrodiverse environments and may have led to the positive effect of fire age diversity on mammal functional richness that we found.

Functional dispersion of mammals increased with pyrodiversity up to intermediate values of fire age diversity at the broadest spatial scale analyzed (78.5-ha scale). These results are in line with studies that found an effect of disturbances such as habitat degradation (Fontúrbel et al. 2022), habitat fragmentation (Meza-Joya et al. 2020), fire frequency (Adams et al. 2022), and fire age (Sitters et al. 2016) on vertebrate functional dispersion. However, our results differ from the study by Docherty et al. (2020), which did not indicate an effect of pyrodiversity on the functional dispersal of birds. Unlike our study, which indicated marked effects of pyrodiversity for several community metrics, Docherty et al. (2020) observed that the proportion of recently burnt and long unburnt areas were more important variables than the pyrodiversity. Functional dispersion represents distinct breadths of functional roles across species (Cooke et al. 2019) and our results indicate that this breadth is higher when the mosaic is composed of approximately five to seven effective patches with different fire ages. More patches beyond these values are unlikely to increase the mammal functional dispersion. Considering that limited mammal functional dispersion occurs in regions with high functional redundancy (Cooke et al. 2019), the response we found for functional richness suggests that this is the case for our studied mammalian community. This pattern of high functional redundancy and low functional dispersion is found in ecoregions under constant disturbance, like fire-prone ecosystems, including Brazilian, African, and Australian savannas, and is probably driven by environmental filtering (Cooke et al. 2019).

We found that the pyrodiversity operated beyond the taxonomic dimension and influenced mammal communities functionally. The functional dimension is of great ecological importance since it is closely related to several aspects of ecosystem functioning, such as productivity and stability (Cadotte et al. 2011; Tilman 2001). Greater functional richness, functional dispersion, and functional redundancy may confer biological communities more resilience to disturbance (Biggs et al. 2020; Díaz and Cabido 2001). This is particularly relevant in fire-prone ecosystems, where the frequency of large wildfires tends to increase (Bowman et al. 2020). Our results suggest that more stable and resilient environments can be achieved by establishing patch mosaics with different fire ages. For medium and large mammals in Cerrado, these mosaics should ideally be composed of five to seven patches with similar areas in different post-fire successional stages. Such a configuration would be associated with higher functional richness and functional dispersion of mammals and, consequently, increase the functioning and robustness of the ecosystem (Biggs et al. 2020; Díaz and Cabido 2001). Our study joins several others in highlighting the importance of assessing ecological patterns from the perspective of different dimensions of biological diversity (Devictor et al. 2010; González-Maya et al. 2016; Martín-Regalado et al. 2019). Such dimensions not only reveal how distinct community aspects (e.g., taxonomic, functional, phylogenetic) respond to environmental variation but can also shed light on the historical and ecological processes behind the observed diversity patterns (Safi et al. 2011).

### *Spatial scale of the pyrodiversity effects*

We observed that the effect of pyrodiversity on the mammal community occurred at multiple spatial scales. Except for total abundance, however, fire age diversity affected all community variables mostly at the 78.5-ha scale. We detected that, for fire frequency effects, both 0.8-ha and 78.5-ha scales were relevant. These results agree with the studies by Bird et al. (2018) and Radford et al. (2021), who found that the effects of pyrodiversity on mammals occurred at spatial scales between 1 ha and 2800 ha. The response of mammals at distinct spatial scales is evidently related to their home range sizes. The broadest spatial scale that we considered (78.5 ha) is smaller than the average home range of 83% of the species of medium and large mammals analyzed (Grotta-Neto et al. 2020; Jácomo et al. 2004; Jones et al. 2009; Medici et al. 2022; Reis et al. 2006; Varela et al. 2010; Vila et al. 2008). Only *Conepatus semistriatus* (home range: 18 ha – 53 ha), *Sylvilagus minensis* (4 ha), and *Dasyprocta azarae* (3 ha) have a home range size between 0.8 and 78.5 ha. This suggests that, for species with large home ranges, pyrodiversity may affect how individuals select distinct fire patches within their home ranges (3rd order selection *sensu* Johnson 1980). A similar pattern was observed by Bird et al. (2018) for dingoes, a large carnivore that responded to spatial variation in fire at the 1-ha scale. For species with small home range sizes, mosaics of different fire regimes may compose the entire home range of individuals (mosaics at broader scales, 2nd order selection) or contain some habitats used by these animals (mosaics at finer scales, 3rd order selection).

We showed that different aspects of communities are affected at different scales depending on how pyrodiversity was measured. For example, mammal richness and diversity, considering both taxonomic and functional aspects, were affected by fire age diversity at the 78.5 ha scale. Fire frequency diversity, in turn, affected taxonomic diversity at the finest spatial scale evaluated (0.8ha). For mammal abundance, we observed the opposite pattern. Fire age diversity had effects on abundance at the 0.8-ha scale, whereas fire frequency diversity had effects at the 78.5-ha scale. These results reinforce the current idea that the effects of pyrodiversity should be investigated at multiple scales (Jones et al. 2022) while taking into account different aspects of the fire regime (Beale et al. 2018; Steel et al. 2021).

### *Pyrodiversity and fire management*

Based on our findings, we suggest that managing fire at relatively small spatial scales (e.g. site scale) (~ 80ha) is sufficient to create pyrodiverse mosaics that maintain biodiversity (Pons et al. 2003). We recommend that, at this spatial scale, prescribed burning should be used to establish mosaics composed of five to seven patches with similar area sizes but with different fire ages. These values are sufficient to increase mammal taxonomic and functional richness without negatively affecting mammal taxonomic diversity and functional dispersion. Furthermore, we recommend maintaining newly burned (< 2 years) and long-unburnt areas to address the needs of some species associated with specific fire ages. It is also relevant to consider mosaics with spatial variation in fire frequency. Overall, maintaining around 10 to 15 patches with different fire frequencies at the 80ha scale while maintaining less than five patches at the 0.8ha scale should retain more diverse communities without decreasing species abundance.

We reinforce that these results probably do not fit all groups and ecosystems as the response to pyrodiversity can be highly variable (Jones and Tingley 2022). This variation in biota response to pyrodiversity may lead to context-specific recommendations for fire management (Kelly et al. 2016). We argue that to use fire in favor of biodiversity, fire management must be based on a deep understanding of the dynamics between biological communities and the fire regime. This knowledge can only be achieved by integrating the information included in studies assessing the short, medium, and long-term impacts of fires and planned burnings on communities, considering the various aspects of the fire regime and the regional and local contexts (SThe negative effect of pyrodiversity that we observed for the total abundance of mammals indicates that probably not all species will benefit from a highly pyrodiverse environment. Thus, it is essential to evaluate species-specific responses of the distinct fire regimes (Jorge et al. 2020; Jorge et al. 2022; Steel et al. 2019). This can be challenging since different responses of populations that coexist in an area make it difficult to establish a mosaic of fire regimes capable of meeting the needs of all species (Verdon and Clarke 2022). In such a situation, fire management should be directed toward species that have more specific requirements regarding the spatiotemporal variation in the fire regime (Parr and Andersen 2006).

## Conclusions

To our knowledge, this is the first study to evaluate the direct effects of pyrodiversity (*sensu* Jones et al. 2021) on medium and large mammals in a Neotropical savanna. We showed that pyrodiversity effects go beyond the taxonomic dimension, also affecting communities functionally, which has important implications for ecosystem functioning. Our findings provide support to the hypothesis "pyrodiversity begets diversity" (Martin and Sapsis 1992), but not for all community metrics considered. We demonstrated consistent positive effects of pyrodiversity on mammalian taxonomic and functional richness at the 78.5-ha spatial scale. These effects probably result from more forage, shelter, and movement opportunities for different species in heterogeneous environments. Nonetheless, the variation in response between species that coexist within the same fire regime and species affinity for specific fire ages suggests that intermediate pyrodiversity is more suitable for maintaining high functional diversity, functional dispersion, and mammal abundance. We argue that, at least for medium and large neotropical mammals, management of savanna landscapes to increase pyrodiversity must be more focused on the diversity of fire ages (i.e., time since the last fire) than the diversity of fire frequencies. Moreover, we highlight that using fire management based on a deep understanding of the dynamics between biological communities and the fire regime should be a target.

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## Supplementary Material

Table S1. Matrix of functional attributes of medium and large sized mammals recorded in the CVNP. Invert = invertebrates; vert1 = mammals and birds; vert2 = reptiles, amphibians, and salamanders; vert3 = fish; carn = remains, carrion; strata use = animal use of vertical strata; scan = scansorial; terr = terrestrial; not = nocturnal; crepusc = crepuscular; diur = diurnal; weight = species average weight. Data from  Wilman et al. 2014.

| | invert | vert1 | vert2 | vert3 | carn | fruit | nectar | seed | plant | strata use | not | crepusc | diur | weight (kg) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Tapirus terrestris* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 100 | terr | 1 | 0 | 0 | 207.5 |
| *Cerdocyon thous* | 50 | 0 | 0 | 0 | 10 | 0 | 0 | 0 | 0 | terr | 1 | 0 | 0 | 5.2 |
| *Conepatus semistriatus* | 80 | 0 | 10 | 0 | 0 | 10 | 0 | 0 | 0 | terr | 1 | 0 | 0 | 1.2 |
| *Leopardus pardalis* | 0 | 70 | 20 | 10 | 0 | 0 | 0 | 0 | 0 | terr | 1 | 0 | 0 | 11.9 |
| *Chrysocyon brachyurus* | 10 | 50 | 20 | 0 | 0 | 10 | 0 | 0 | 10 | terr | 1 | 1 | 0 | 23.2 |
| *Puma concolor* | 0 | 100 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | terr | 1 | 1 | 1 | 51.6 |
| *Eira barbara* | 0 | 90 | 0 | 0 | 0 | 10 | 0 | 0 | 0 | terr | 1 | 1 | 1 | 3.9 |
| *Ozotoceros bezoarticus* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 100 | terr | 1 | 1 | 1 | 40 |
| *Euphractus sexcinctus* | 50 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 50 | terr | 1 | 1 | 1 | 4.8 |
| *Tamandua tetradactyla* | 100 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | scan | 1 | 1 | 1 | 5.5 |
| *Mazama sp.* | 0 | 0 | 0 | 0 | 0 | 30 | 0 | 20 | 50 | terr | 1 | 1 | 1 | 19.7 |
| *Herpailurus yagouaroundi* | 10 | 80 | 0 | 0 | 0 | 10 | 0 | 0 | 0 | terr | 0 | 1 | 1 | 6.9 |
| *Myrmecophaga tridactyla* | 100 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | terr | 1 | 1 | 1 | 22.3 |

|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Cabassous squamicaudis* | 100 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | terr | 1 | 1 | 0 | 4.8 |
| *Leopardus sp.* | 0 | 80 | 0 | 0 | 0 | 20 | 0 | 0 | 0 | scan | 1 | 1 | 0 | 2.7 |
| *Sylvilagus minensis* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 100 | terr | 1 | 1 | 0 | 0.9 |
| *Dasypus novemcinctus* | 100 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | terr | 1 | 0 | 0 | 4.2 |
| *Dasyprocta azarae* | 10 | 0 | 0 | 0 | 0 | 40 | 0 | 0 | 50 | terr | 0 | 1 | 1 | 2.3 |

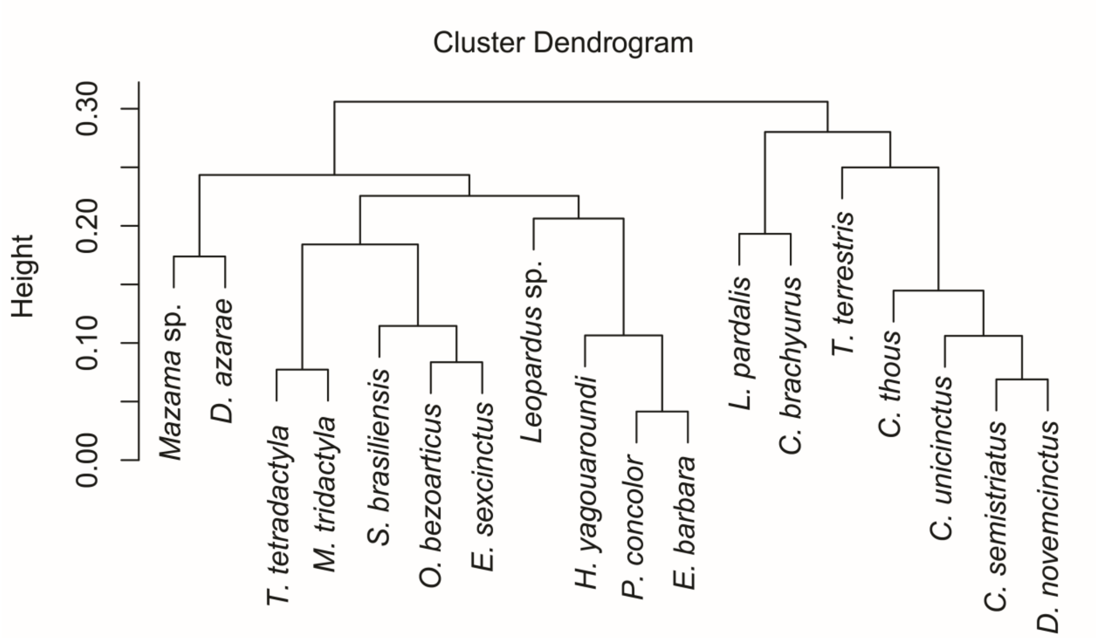

Fig. S1. Functional dendrogram of the medium and large-sized mammal community of the CVNP. Height = Gower distance, clustering method = UPGMA; cophenetic correlation coefficient = 0.65.

Table S2. Model selection comparing the fit of the spatial scales in which the predictor variables were measured (fire frequency, fire age, fire frequency diversity, and fire age diversity). 50, 250, and 500 represent the radius (m) of the buffers related to the spatial scales of 0.8 ha, 19.6 ha, and 78.5 ha, respectively.

|  | K | AICc | ΔAICc | AICcWt | Cum.Wt | LL |
|---|---|---|---|---|---|---|
| **Taxonomic richness** |  |  |  |  |  |  |
| tax.ric ~ freq500 + effort | 4 | 131.52 | 0 | 0.36 | 0.36 | -60.93 |
| tax.ric ~ freq50 + effort | 4 | 131.7 | 0.18 | 0.33 | 0.68 | -61.02 |
| tax.ric ~ freq250 + effort | 4 | 131.74 | 0.22 | 0.32 | 1 | -61.04 |
| tax.ric ~ age500 + effort | 4 | 130.34 | 0 | 0.41 | 0.41 | -60.34 |
| tax.ric ~ age250 + effort | 4 | 130.61 | 0.27 | 0.36 | 0.77 | -60.47 |
| tax.ric ~ age50 + effort | 4 | 131.49 | 1.15 | 0.23 | 1 | -60.91 |
| tax.ric ~ div-freq500 + effort | 4 | 129.54 | 0 | 0.55 | 0.55 | -59.94 |
| tax.ric ~ div-freq250 + effort | 4 | 130.96 | 1.41 | 0.27 | 0.82 | -60.65 |
| tax.ric ~ div-freq50 + effort | 4 | 131.78 | 2.24 | 0.18 | 1 | -61.06 |
| tax.ric ~ div-age500 + effort | 4 | 115.29 | 0 | 0.99 | 0.99 | -52.81 |
| tax.ric ~ div-age250 + effort | 4 | 123.99 | 8.71 | 0.01 | 1 | -57.16 |
| tax.ric ~ div-age50 + effort | 4 | 131.77 | 16.49 | 0 | 1 | -61.05 |

| | | | | | | |
|---|---|---|---|---|---|---|
| **Functional richness** | | | | | | |
| func.ric ~ freq50 + effort | 4 | 28.36 | 0 | 0.4 | 0.4 | -9.38 |
| func.ric ~ freq250 + effort | 4 | 28.9 | 0.55 | 0.3 | 0.7 | -9.65 |
| func.ric ~ freq500 + effort | 4 | 28.94 | 0.58 | 0.3 | 1 | -9.67 |
| func.ric ~ age50 + effort | 4 | 26.5 | 0 | 0.58 | 0.58 | -8.45 |
| func.ric ~ age250 + effort | 4 | 28.34 | 1.84 | 0.23 | 0.81 | -9.37 |
| func.ric ~ age500 + effort | 4 | 28.69 | 2.19 | 0.19 | 1 | -9.55 |
| func.ric ~ div-freq500 + effort | 4 | 25.25 | 0 | 0.59 | 0.59 | -7.83 |
| func.ric ~ div-freq250 + effort | 4 | 26.83 | 1.58 | 0.27 | 0.86 | -8.62 |
| func.ric ~ div-freq50 + effort | 4 | 28.13 | 2.88 | 0.14 | 1 | -9.26 |
| func.ric ~ div-age500 + effort | 4 | 18.49 | 0 | 0.51 | 0.51 | -4.45 |
| func.ric ~ div-age250 + effort | 4 | 18.55 | 0.06 | 0.49 | 1 | -4.48 |
| func.ric ~ div-age50 + effort | 4 | 28.77 | 10.28 | 0 | 1 | -9.58 |
| **Taxonomic diversity** | | | | | | |
| tax.div ~ freq50 + effort | 4 | 95.93 | 0 | 0.34 | 0.34 | -43.16 |
| tax.div ~ freq500 + effort | 4 | 95.96 | 0.03 | 0.34 | 0.68 | -43.18 |
| tax.div ~ freq250 + effort | 4 | 96.05 | 0.12 | 0.32 | 1 | -43.22 |
| tax.div ~ age50 + effort | 4 | 94.15 | 0 | 0.52 | 0.52 | -42.28 |
| tax.div ~ age250 + effort | 4 | 95.58 | 1.42 | 0.25 | 0.77 | -42.99 |
| tax.div ~ age500 + effort | 4 | 95.8 | 1.64 | 0.23 | 1 | -43.1 |
| tax.div ~ div-freq500 + effort | 4 | 93.49 | 0 | 0.48 | 0.48 | -41.95 |
| tax.div ~ div-freq50 + effort | 4 | 94.36 | 0.87 | 0.31 | 0.79 | -42.38 |
| tax.div ~ div-freq250 + effort | 4 | 95.09 | 1.6 | 0.21 | 1 | -42.75 |
| tax.div ~ div-age500 + effort | 4 | 87.63 | 0 | 0.5 | 0.5 | -39.01 |
| tax.div ~ div-age250 + effort | 4 | 87.72 | 0.09 | 0.48 | 0.98 | -39.06 |
| tax.div ~ div-age50 + effort | 4 | 94.42 | 6.79 | 0.02 | 1 | -42.41 |
| **Functional dispersion** | | | | | | |
| func.disp ~ freq250 + effort | 4 | -79.57 | 0 | 0.34 | 0.34 | 44.59 |
| func.disp ~ freq50 + effort | 4 | -79.57 | 0.01 | 0.34 | 0.68 | 44.58 |
| func.disp ~ freq500 + effort | 4 | -79.46 | 0.11 | 0.32 | 1 | 44.53 |
| func.disp ~ age500 + effort | 4 | -79.43 | 0 | 0.33 | 0.33 | 44.51 |
| func.disp ~ age250 + effort | 4 | -79.42 | 0 | 0.33 | 0.67 | 44.51 |
| func.disp ~ age50 + effort | 4 | -79.42 | 0.01 | 0.33 | 1 | 44.51 |
| func.disp ~ div-freq500 + effort | 4 | -80.59 | 0 | 0.42 | 0.42 | 45.1 |
| func.disp ~ div-freq50 + effort | 4 | -79.83 | 0.76 | 0.29 | 0.71 | 44.72 |
| func.disp ~ div-freq250 + effort | 4 | -79.81 | 0.78 | 0.29 | 1 | 44.71 |
| func.disp ~ div-age500 + effort | 4 | -84.74 | 0 | 0.79 | 0.79 | 47.17 |
| func.disp ~ div-age250 + effort | 4 | -81.41 | 3.33 | 0.15 | 0.94 | 45.51 |
| func.disp ~ div-age50 + effort | 4 | -79.7 | 5.05 | 0.06 | 1 | 44.6 |
| **Total abundance** | | | | | | |
| abund ~ freq50 + effort | 4 | 237.95 | 0 | 0.35 | 0.35 | -114.18 |
| abund ~ freq500 + effort | 4 | 238.07 | 0.12 | 0.33 | 0.68 | -114.24 |
| abund ~ freq250 + effort | 4 | 238.13 | 0.17 | 0.32 | 1 | -114.26 |
| abund ~ age500 + effort | 4 | 237.54 | 0 | 0.4 | 0.4 | -113.97 |
| abund ~ age250 + effort | 4 | 237.89 | 0.35 | 0.34 | 0.74 | -114.15 |
| abund ~ age50 + effort | 4 | 238.39 | 0.84 | 0.26 | 1 | -114.39 |
| abund ~ div-freq500 + effort | 4 | 233.93 | 0 | 0.62 | 0.62 | -112.16 |
| abund ~ div-freq250 + effort | 4 | 235.32 | 1.4 | 0.31 | 0.92 | -112.86 |
| abund ~ div-freq50 + effort | 4 | 238.1 | 4.18 | 0.08 | 1 | -114.25 |
| abund ~ div-age50 + effort | 4 | 233.44 | 0 | 0.86 | 0.86 | -111.92 |
| abund ~ div-age250 + effort | 4 | 238.39 | 4.95 | 0.07 | 0.93 | -114.39 |
| abund ~ div-age500 + effort | 4 | 238.46 | 5.03 | 0.07 | 1 | -114.43 |

Table S3. Models fit considering linear and quadratic relationships. K = number of parameters; LL = log likelihood.

| Models | K | AICc | ΔAICc | AICc weight | LL | Adj.R² |
|---|---|---|---|---|---|---|
| **Taxonomic diversity**<br>tax.div ~ freq50 + age50 + div-freq50 + div-freq50² + div-freq500 + div-age500 + div-age500² + effort | 10 | 79.56 | 0 | 0.97 | -23.99 | 0.66 |
| tax.div ~ freq50 + age50 + div-freq50 + div-freq500 + div-last500 + effort | 8 | 86.46 | 6.9 | 0.03 | -31.8 | 0.48 |
| **Functional dispersion**<br>func.disp ~ freq250 + age500 + div-freq50 + div-freq500 + div-age500 + div-age500² + effort | 9 | -82.25 | 0 | 0.94 | 54.63 | 0.43 |
| func.disp ~ freq250 + age500 + div-freq50 + div-freq500 + div-age500 + effort | 8 | -76.87 | 5.38 | 0.06 | 49.86 | 0.25 |

Table S4. List of mammal species recorded in the CVNP using camera traps from February 2020 to April 2021. Status according to IUCN: Near Threatened (NT), Least Concern (LC), Vulnerable (VU), and Endangered (EN). “*” indicates exotic species.

| **Species** | **Common name** | **Records** | **IUCN** |
|---|---|---|---|
| **Pilosa** | | | |
| *Myrmecophaga tridactyla* | Giant anteater | 4 | VU |
| *Tamandua tetradactyla* | Collared anteater | 1 | LC |
| **Cingulata** | | | |
| *Cabassous squamicaudis* | Southern naked-tailed armadillo | 2 | LC |
| *Euphractus sexcinctus* | Six-banded armadillo | 3 | LC |
| *Dasypus novemcinctus* | Nine-banded armadillo | 1 | LC |
| **Rodentia** | | | |
| *Galea flavidens* | Cavy | 1 | - |
| *Dasyprocta azarae* | Azara's agouti | 1 | DD |
| **Primates** | | | |
| *Callithrix penicillata* | Black-tufted marmoset | 1 | LC |
| **Artiodactyla** | | | |
| *Ozotoceros bezoarticus* | Pampas deer | 199 | NT |
| *Mazama* sp. | Gray brocket/Red brocket deer | 38 | LC/DD |
| *Bos taurus** | Cattle | 32 | |
| **Lagomorpha** | | | |
| *Sylvilagus minensis* | Common tapeti | 1 | EN |

|  |  |  |  |
|---|---|---|---|
| **Carnivora** |  |  |  |
| *Herpailurus yagouaroundi* | Jaguarundi | 10 | LC |
| *Puma concolor* | Cougar | 1 | LC |
| *Leopardus pardalis* | Ocelot | 2 | LC |
| *Leopardus* sp. | Oncilla/Margay | 1 | - |
| *Conepatus semistriatus* | Striped hog-nosed skunk | 5 | LC |
| *Eira barbara* | Tayra | 2 | LC |
| *Chrysocyon brachyurus* | Maned wolf | 54 | NT |
| *Cerdocyon thous* | Crab-eating fox | 32 | LC |
| *Canis lupus familiaris** | Domestic dog | 28 |  |
| **Perissodactyla** |  |  |  |
| *Tapirus terrestris* | Tapir | 27 | VU |
| **Not identified** | - | 26 | - |
| **Total** |  | 472 |  |
| **Total identified** |  | 446 |  |

# Capítulo 2. Species-specific responses of medium and large mammals to pyrodiversity and to the proportion of recently burned areas in a fire-prone neotropical savanna

## Abstract

Fire occurrence affects the distribution of key resources for fauna in natural ecosystems worldwide. For fire management strategies adequate for biodiversity conservation, the understanding of how species respond to fire-induced changes is essential. In this study, we investigated the role of fire regime on space use by medium and large mammals at multiple spatial scales (0.8 ha to 78.5 ha) in a fire-prone savanna ecosystem (Brazilian Cerrado). We sampled mammals using 60 camera traps distributed in 30 sampling units located in grassland and typical savanna formations. We applied single-species occupancy models and AIC-based model selection to access how mammals use the space in response to pyrodiversity (both diversity of fire frequencies and diversity of fire ages), proportion of recently burned area, and proportion of long-unburned area while accounting for detectability. Our results showed that fire regime variables affected differently the study species. Deer used the space regardless of mosaic pyrodiversity and proportion of specific fire ages. Fire-related variables, however, affected space use by tapirs and maned wolves. Tapirs preferred to use fire mosaics with lower diversity of fire frequencies whereas maned wolves used more intensively mosaics with high fire age diversity and proportion of recently burned areas. Based on our findings, we recommend that fire management should not focus on maximum pyrodiversity. Instead, we suggest a management strategy combining "patch mosaic burning" with the maintenance of specific fire-age patches suitable for different species requirements.

Keywords: fire regime mosaic, habitat use, herbivores, carnivores, neotropical savanna, fire management

## Introduction

Habitat use by animals is affected by several factors, including the distribution of food resources, occurrence of potential predators and competitors, and vegetation cover [1-7]. The distribution and effectivity of these factors, however, may be altered by disturbance events [8], affecting the space use by the animals [9]. In fire-prone ecosystems, fire is a common disturbance that modifies vegetation structure and resource availability [10-14]. Understanding how species respond to these fire-induced changes is fundamental, considering the increase in large severe wildfires worldwide [15-16]. Such knowledge may contribute to establish fire management strategies adequate for preventing large wildfires while creating fire mosaics more suitable for species conservation [17-19].

For fire management to be an efficient tool in protecting biodiversity, management strategy must create relevant fire mosaics so species can thrive in these areas [20]. Many fire management programs are based on the establishment of heterogeneous fire mosaics to promote community biodiversity ("patch-mosaic burning") [21-23]. Such strategy follows the "pyrodiversity begets biodiversity" hypothesis, which proposes a relationship between spatial variation in successional stages post-fire and more diverse communities [24]. At the population level, some species also seem to be positively affected by pyrodiversity [25-27]. However, the empirical support for these positive effects on community and populations are not consistent across ecosystems and taxa [27-30]. An alternative strategy is to keep large proportions of areas with specific fire ages [20]. Some studies report a positive effect on species when long unburned or recently burned areas are retained [31-33]. These studies indicated the extension of areas with specific fire ages as a better predictor for fire-induced faunal responses than pyrodiversity. Considering this variation in key fire-related factors affecting animals and context-specific faunal responses to distinct management strategies, the establishment of fire management actions must be based on the knowledge of local fire regime characteristics and how animal populations react to such characteristics.

In fire-prone ecosystems, terrestrial mammals are generally markedly affected by fire events [30, 33-35]. For predators, fire-induced responses are driven mainly by changes in prey availability, hunting success, and habitat cover [36]. Furthermore, responses to habitat cover change can be regulated by species hunting strategies. While ambush predators may prefer long-unburned areas with more structured vegetation [37-38], cursorial species may select open habitats found in recently burned areas [38-40]. Burning may also affect large herbivores. This group may use recently burned areas more intensively in searching for high-quality forage [41-42] or avoid them when predators [43] or competitors [44] are attracted to these areas. The effects of areas with different fire ages within the landscape (i.e. pyrodiversity) on mammal space use seem to be variable. In Australia, for instance, the presence of a large carnivore [dingo; 25], and large marsupials [45] was higher in pyrodiverse areas. On the other hand, in North America the abundance (an indicator of space use) of coyotes was lower in highly pyrodiverse areas [30]. Such negative effects of pyrodiversity may result from strong associations between species and specific fire regimes [46-47] whereas positive effects may arise when species use multiple patches of the fire mosaic landscape [48].

Mammals may respond to pyrodiversity or extension of fire age from site-scales [up to 1 ha; 25, 49] to landscape-scales [30, 50]. This suggests that fire mosaic configuration may affect mammal space use related to home range, habitat, and micro-habitat selection [2nd, 3rd, and 4th habitat selection orders, respectively; *sensu* 51]. This variation highlights the necessity of evaluating fire effects in multiple spatial scales.

In this study, we investigated fire and use of habitat by medium and large terrestrial mammals in the Cerrado (neotropical savanna). We evaluated the potential effects of pyrodiversity and the proportion of recently burned and long-unburned areas on space use by these animals. We conducted our study in the Chapada dos Veadeiros National Park. This Park is characterized by high fire frequency, with burning occurring mainly at the end of the dry season [52]. The local spatiotemporal configuration of the fire regime is caused by recurrent occurrence of wildfires and, more recently, by prescribed burning [53]. We verified the responses of medium/large mammal species to this spatiotemporal variation in fire regime. The species studied were: *Ozotoceros bezoarticus* (pampas deer), *Mazama* sp. (gray and red brocket deer species combined), *Tapirus terrestris* (lowland tapir), and *Chrysocyon brachyurus* (maned wolf). The first four species/groups are herbivores that show different preferences for vegetation types. Pampas deer (mean body mass = 30 kg, [54]) has affinities with grassland and savanna formations [55], brown and red brocket deer species (mean body mass = 20 kg and 30 kg, respectively, [56]) prefer forests and forest-open formation transition areas [57-59], and the lowland tapir (mean body mass = 200 kg, [60]) is associated with forest formations but frequently uses open habitats [61]. Lastly, the maned wolf is the largest canid in South America (mean body mass = 23 kg, Wilman, et al. [62]), having an omnivorous diet and preying mainly on small-sized mammals [63-64]. This canid has affinities with grassland and savanna formations [64]. Although all these species inhabit fire-prone regions, little is known about the effects of fire on habitat use by these animals [but see 65, 66].

Our objective was to identify the role of pyrodiversity (fire frequency diversity and fire age diversity), proportion of recently burned areas, and proportion of long-unburned areas in relation to the total available area on space use by mammals while accounting for detectability. If pyrodiversity is relevant for mammalian occurrence, we expect a positive effect of diversity of fire frequency and fire age on space use by large mammals. A pyrodiverse landscape would offer a greater variety of resources [67-68] and the opportunity for species to use these resources in a complementary way [69]. If the proportion of recently burned and long-unburned areas is important, we predict a positive effect of recently burned areas on the occurrence of mammals. These areas may offer better quality foraging for herbivores [42], adequate hunting habitats for cursorial predators [38], and facilitate the movement of cursorial species [69]. Considering that mammal responses to the predictor variables are potentially affected by the spatial scale considered [49], we tested these responses for three distinct spatial scales (from 0.8 ha to 78.5 ha).

## Materials and methods

### *Study area*

We conducted fieldwork in the Chapada dos Veadeiros National Park (CVNP), a protected area of 240,000 ha located in the state of Goiás, Brazil (Figure 1). This region has a tropical climate with the dry season occurring in winter according to the Köppen-Geiger classification [70]. The average annual temperature is 23.4ºC, with the highest average temperature recorded in October (monthly average = 25.3 ºC) and the lowest average temperatures observed in June and July (monthly average = 20.8 ºC) [71]. The average annual rainfall is 1500 mm. Its distribution throughout the year defines two climatic seasons: the dry season, with mean monthly precipitation of 23.2 mm (between May and September), and the wet season, with mean monthly precipitation of 197.6 mm (between October and April) [71].

The vegetation in CVNP is the Cerrado, a tropical savanna. Cerrado vegetation combines three major formations: grassland, typical savanna, and forest [72]. Grasslands include physiognomies dominated by grasses and herbaceous plants with some areas showing sparse shrubby vegetation cover but an overall canopy cover < 5%. Savanna formation consists of continual to sparse grass layers, with low-density tree cover (canopy cover 5-60%). This formation also includes palm swamps, a seasonally flooded physiognomy dominated by grasses and herbaceous plants with buriti palm (*Mauritia flexuosa* L. f.) stands. Lastly, forest formation comprises deciduous, semi-deciduous, and evergreen forests (canopy cover 60-95%), including riparian and gallery forests alongside watercourses [72-73]. In this study, we focused on habitat use by mammals in grassland and savanna formations. These vegetation types are more susceptible to fire [74] and dominate the landscape of the study region [73].

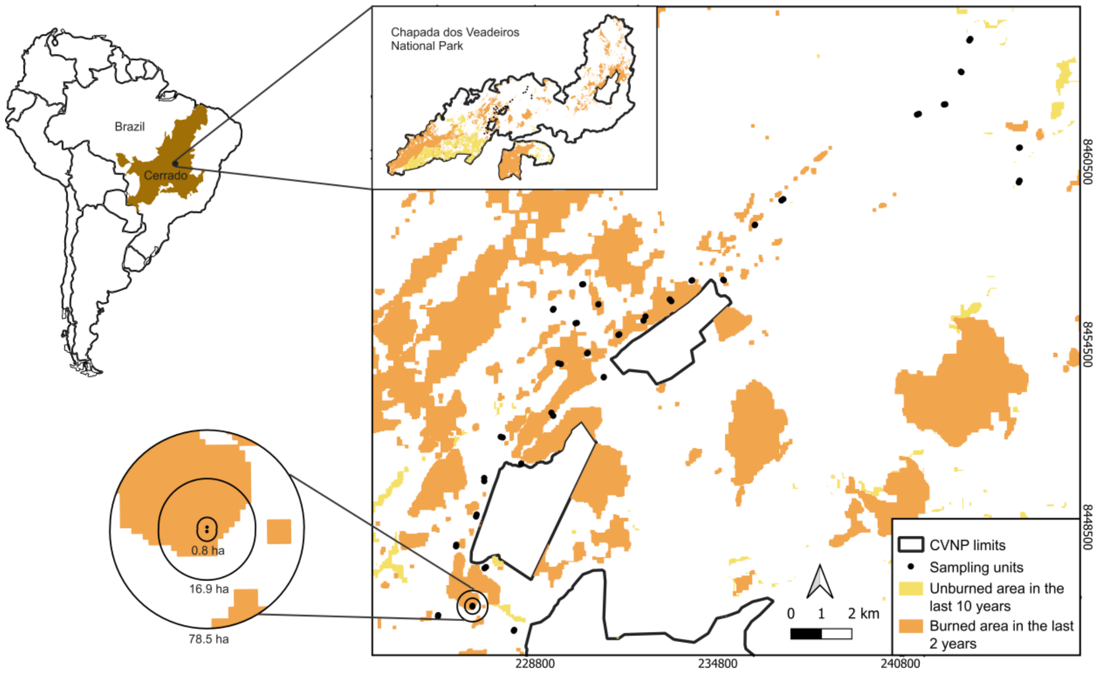

Figure 1. Mammal sampling units location and spatial distribution of areas recently burned (burned in the last two years before sampling) and long unburned (> 10 years without fire occurence) in the Chapada dos Veadeiros National Park. Spatial scales used were 0.8 ha, 16.9 ha, and 78.5 ha (circular buffers around sampling units with radius of 50 m, 250 m, and 500 m, respectively).

Until recently, the fire exclusion policy was dominant in Brazilian protected areas [75]. However, in 2014 the Integrated Fire Management program (IFM) started to be implemented in protected savanna areas [53]. In the CVNP, the implementation of the IFM started only in 2017, at fine spatial scales [17]. Based on patch-mosaic burning techniques to create pyrodiversity, the IFM performs prescribed and controlled burnings, establishing mosaics with heterogeneous fire regimes. These burnings reduce the amount of dry fuel available and help prevent the occurrence of large wildfires and protect fire-sensitive vegetation [53]. In fact, in the protected areas where the IFM has been carried out since 2014, there is a trend toward a decrease in the total area burned and the size of fire scars [17]. Nonetheless, identifying which burning patterns create suitable habitats for fauna is still an issue to be addressed [53].

*Sampling of medium and large mammals*

We conducted mammal sampling between February 2020 and April 2021, comprising both dry and wet seasons. We installed a pair of Bushnell® camera traps in 30 fixed sampling units in the CVPN, totaling 60 camera traps installed (Figure 1). All sampling units were located in areas of open vegetation, varying between grassland and savanna formations. We allocated the sampling units along a highway and secondary roads inside the CVNP using a systematic approach [76]. To minimize possible effects of roads on habitat use by mammals, the minimum distance between the camera traps and the road/secondary roads was 300 m. We also established a minimum spacing between sampling units of 1 km to avoid spatial dependence between data. However, some stations were at a distance below this value when necessary (shortest distance between adjacent stations = 0.82 km). The average minimum distance between adjacent stations was 1.26 km.

We directed the camera traps of the same sampling unit to different points in the landscape and adopted a minimum distance of 10 m and a maximum distance of 150 m between them (average distance = 51 m). This variation was necessary for allowing positioning the cameras towards water bodies, footprints, trails, feces, or any trace that indicated the passage of mammals. Furthermore, we positioned the camera traps 30 cm above the ground, attached to logs or stakes. The configuration for the cameras to take photos or videos varied throughout the study. From February 2020 to August 2020 and from December 2020 to April 2021, all cameras were set to take three pictures with each shot, with a 10-second interval between shots. Between September 2020 and November 2020, all cameras were set to record 15-second videos with a one-second shooting interval. All camera traps were active for 24 h, regardless of the configuration (photo or video). We did not use any bait to attract animals. In addition, all stations were sampled simultaneously over the 15 months.

### *Predictor variables*

We characterized the fire mosaic of the study area using information on fire scars from 1985 to 2020 (36 years) provided by MapBiomas [52]. The MapBiomas platform uses Landsat satellite images to map fire scars throughout Brazil with a resolution of 30m. From these fire scar data and using the Quantum Gis software [77], we extracted four variables associated with fire regime: fire frequency diversity, fire age diversity, proportion of recently burned area (burned in the last two years), and proportion of the long-unburned area (not burned in the last 10 years). First, we collected information on the years in which fire events occurred for each pixel and generated two maps containing the frequency and the year since the last fire event for each pixel. We defined fire frequency as the number of years in which a fire scar was present in a given pixel considering the time series from 1985 to 2020. This same time series was used for determining fire age, defined as the number of years since the last occurrence of fire. This occurrence was indicated by the presence of a fire scar in a given pixel.

We evaluated the fire mosaic at three distinct spatial scales, establishing buffers with radii of 50 m, 250 m, and 500 m around camera traps. These buffers represent the multiple spatial scales evaluated in this study (0.8 ha, 19.6 ha, and 78.5 ha, respectively) [78]. We overlapped the same scale buffers of the camera trap pair of the same sampling unit to obtain a final buffer per sampling unit. Finally, we estimated fire frequency and fire age diversity for each sampling unit and spatial scale using the exponential of Shannon H' entropy - exp (H'), which represents the effective number of equally abundant species needed to obtain a given index value [79]. In our estimation of pyrodiversity, instead of species, we estimated the effective number of patches with distinct fire frequencies and fire ages for each sampling unit. We considered the area within the buffers occupied by each fire frequency and fire age as the "abundance" of these fire regimes.

We established the proportion of recently burned area and long-unburned area in relation to the total buffer area based on the fire age map created. We considered the proportion of the area within the buffer that burned in 2019, 2020, or both as recently burned. For the proportion of long-unburned area, we considered areas not burned for more than 10 years within the buffer, that is, the last fire event occurred in 2009 or before. We calculated the proportion of recently burned area and long-unburned area for the same scales used for frequency and fire age diversity (0.8 ha, 19.6 ha, and 78.5 ha).

Considering that detectability of the animals may vary in relation to habitat cover, we evaluated possible effects of vegetation cover on species detection using the Normalized Difference Vegetation Index (NDVI). This index is related to vegetation characteristics such as canopy structure, biomass, and leaf area [80] and differentiates the Cerrado formations [81]. In general, higher NDVI values are associated with forest formations while lower values occur in savanna and grassland formations [81]. To obtain the NDVI, we used satellite images from Landsat 8 for the 02/09/2020 date with a resolution of 30 m. For each sampling unit and each spatial scale, we averaged the pixel values for the NDVI.

We also tested for possible seasonal effects on species detection. For that, we included in the analysis a categorical variable with two levels: dry season and wet season. This division followed the amount of monthly precipitation [71]. Additionally, we tested for any potential bias caused by distinct camera configurations (photographs or videos) including a methodological predictor variable. This method categorical variable consisted of two levels: photo, in the periods between February 2020 and August 2020 and between December 2020 and April 2021; and video, between September 2020 and November 2020.

### *Statistical analysis*

In our study, we established an interval of five consecutive days to consider records of the same species in the same sampling unit as independent. This approach is indicated for occupancy analysis when the studied species have a low population density, larger home range than the sampled sites, and high mobility, which is common for larger mammals [82-83]. For the analyses, we combined the records of two similar deer species *Mazama americana* and *Subulo* (=*Mazama*) *gouazoubira* in the group *Mazama* sp. By grouping the records, we avoided misidentification as these species are not easily differentiated using camera trap records.

We used single-species single-season occupancy models to estimate the probability of occupancy (ψ) of sampling units and the probability of detection (p) of large mammal species considering the effect of predictor variables. Occupancy models permit dealing with false absences, i.e., the species is present at the site but has not been detected [84]. Moreover, these models allow the incorporation of predictor variables that may explain the observed variations in the occupancy and detection probabilities of the species [83]. Although the occupancy model assumes that the occurrence of a species in an area does not change within a sampling period, this assumption can be relaxed and the presence/absence of the species is interpreted as use/non-use of a given site [85]. Thus, in our study, the occupancy probability should be interpreted as the “probability of use” of the site. We considered this probability of use as a proxy for the intensity of use of the space by the studied species. Such type of modeling has been widely applied in studies that aim to identify environmental factors affecting the use of different habitats by species, including the fire occurrence [86-89].

To investigate the effect of fire regime on occupancy and possible spatial and temporal variations in detectability (Table 1) of species while considering different spatial scales, we structured the occupancy models according to the results of two-step analyses. First, we identified the model structure that best described species detection. For this, we checked the spatial scale of the NDVI effect on detectability and whether the method (photo or video) and seasonality affect the detection of mammals. We created three models which estimated the influence of NDVI on the detection (p) of species at the three distinct spatial scales. We compared the performance of these models according to the Akaike Information Criterion adjusted for small samples (AICc) [90]. The spatial scales represented in the models with good support ($\Delta$AICc $< 2$) were used in the following analyses. When more than one spatial scale model presented $\Delta$AICc $< 2$ and the NDVI values measured at these scales were correlated (Pearson correlation $> 0.5$), we used the spatial scale of the model with the lowest $\Delta$AICc (Supplementary Materials Table S1).

After defining the appropriate spatial scales, we created models that included the NDVI (in the appropriate spatial scale), seasonality, and method to verify the effect of these variables on species detection (p). These variables were considered isolated or combined in the same model. We also established a model in which detection was constant over time. While we modeled the detection, we kept the occupancy ($\psi$) varying according to the fire regime variables. This approach avoids possible variations in occupancy from reflecting on detection probability if occupancy was kept constant [83]. To define the variables influencing the detection, we compared the models using the AICc. Variables contained in the models with $\Delta$AICc $< 2$ were considered to have high support and were used in the next step of the analyses.

In the second step, we defined the spatial scales for the fire regime variables and their role in occupancy ($\psi$). Similarly to the approach used for defining the appropriate spatial scale for the effect of the NDVI on detectability, we compared the spatial scales of fire regime variables using AICc-based model selection and selected the spatial scale contained in the model with the lowest $\Delta$AICc. After defining the spatial scale, we accessed the effect of fire frequency diversity, fire age diversity, proportion of recently burned area, and proportion of long-unburned area on ψ. For this, we built occupancy models with different combinations of these variables. We also established models considering the effect of the variables alone and constant ψ. While we modeled the effect of fire on ψ, the detection (p) was modeled according to the results of the first step.

Table 1. Predictor variables used in single-species single-season occupancy models evaluating the effects of vegetation cover, seasonality, and fire mosaic configuration on medium and large-sized mammals space use in Cerrado. We also modeled a potential bias related to different camera trap protocols (photo or video) during the sampling period.

| **Variable** | **Type** | **Multiple spatial scales** | **Description** |
|---|---|---|---|
| NDVI | Continuous | Yes | Normalized Difference Vegetation Index indicating the vegetation cover. |
| season | Categorical | No | Temporal variable representing the two seasons according with monthly precipitation: wet season and dry season. |
| method | Categorical | No | Variable representing the methods used during the sampling period: photo and video. |
| div-freq | Continuous | Yes | Fire frequency diversity estimated using the exponential of Shannon entropy. Div-freq values represent the number of effective patches with different fire frequency needed to obtain the diversity index value. |
| div-age | Continuous | Yes | Fire age diversity estimated using the exponential of Shannon diversity index. Div-age values represent the number of effective patches with different fire ages needed to obtain the diversity index value. |
| burned<2 | Continuous | Yes | Proportion of area burned in the two years before the mammal sampling. Proportion was calculated relative to total area of the buffer around the camera. |
| unburned>10 | Continuous | Yes | Proportion of area unburned in the previous 10 years before the mammal sampling. Proportion was calculated relative to total area of the buffer around the camera. |

We compared the distinct occupancy models generated using the AICc. When more than one model was supported by the data, we used model averaging to access the estimates (beta estimates) and their respective unconditional standard errors. We included only models with high or medium support ($\Delta$AICc < 4) in the model averaging [90]. Furthermore, we evaluated the relative importance of the predictor variables by summing the weights of the models in which the variable was present, including only models with $\Delta$AICc < 4. We excluded from the analyses models that did not converge [as in 87, 91].

All predictor variables were standardized (mean = 0; standard deviation = 1) and tested for collinearity using the Variance Inflation Index (VIF). Whenever a variable had VIF > 3 [92], we excluded it from models with other variables. We also checked whether our species records were spatially correlated. Using the Moran Index in the “ape” package [93] for R environment [94], we found no evidence of spatial autocorrelation for any of the variables considered (Supplementary Materials Table S2). Finally, we evaluated whether the data had more variation than assumed by the model with more variables (overdispersion). We use the ĉ-value from the goodness-of-fit analysis to determine the presence of overdispersion. All tested models presented ĉ-value < 1, therefore, our data did not show overdispersion. All occupancy models were implemented in the “unmarked” package [95] for R environment.

## Results

From February 2020 to April 2021, we carried out a sampling effort of 10,112 camera days, obtaining 123 records of pampas deer (*Ozotoceros bezoarticus*), 52 of maned wolf (*Chrysocyon brachyurus*), 29 of brown deer and red deer combined (*Mazama* sp.) and 23 of tapir (*Tapirus terrestris*). All species increased their occurrence when imperfect detection was considered (comparison between naïve occupancy and occupancy probability) (Supplementary Materials Table S3). The pampas deer, the most common species in the study area, occurred in 83% of the sampling units and had the highest occupancy probability. On the other hand, *Mazama* sp. showed the lowest occupancy among the species analyzed in the study area. Individuals in this group were present in 24% of the sample units.

In the study area, pyrodiversity varied between 4.26 and 14.89 for fire frequency diversity and between 1.33 and 8.69 for fire age diversity (78.5-ha scale). This means that the sampling units with the highest pyrodiversity had, in terms of effective number of patches, around 14 patches with different fire frequencies and eight patches with different fire ages. The sampling units with lower pyrodiversity have about four patches with different fire frequencies and one patch with a single fire age. The sampling units varied a lot in terms of the proportion of areas that burned in the last two years. For seven sampling units we did not record fire two years before the mammal sampling. The sampling unit with the highest proportion of recently burned area had 88% of its area affected by fire (scale of 78.5 ha). Of the three sampling units with more than 70% of their total area recently burned, two were subjected to prescribed burning two years before mammal sampling. All sampling units had some part of their area burned in the last 10 years at the 78.5 ha scale while, at the 0.8 ha scale, one unit had not burned in the last 10 years. The sample unit with the highest proportion of unburned area in ten years had 71% of its area unburned (scale of 78.5ha).

The NDVI (a proxy for vegetation cover) affected mammal detection probability (p). The model selection indicated an effect of the NDVI on the detection probability of all mammals analyzed. Models containing only the NDVI variable showed $\Delta$AICc < 2 for all species (Supplementary Materials Table S4). Seasonality (wet or dry seasons) and method (photo or video) did not affect species detectability. Although these variables integrated models with $\Delta$AICc < 2 (high support), this occurred only when the model also contained the NDVI. Models with the season and method variables alone had negligible support.

Table 2. Occupancy models evaluating the effect of fire regime variables on space use (ψ) by medium and large-sized mammals in Cerrado. Only models with ΔAICc < 4 are shown. K represents the number of parameters in the model, AICcWt and Cum.Wt indicate the relative weight of the model and the accumulated weight, respectively, and -2LL is the log-likelihood. The numbers 50, 250, and 500 with the variable names indicate the radius (m) of the buffers used in the variables measurement. These buffers are related to the 0.8-ha, 16.9-ha, and 78.5-ha spatial scales, respectively. The scales were used accordingly to the results of previous analyses (Supplementary Material Table S1).

| Modelos | K | AICc | ΔAICc | AICcWt | Cum.Wt | -2LL |
|---|---|---|---|---|---|---|
| ***O. bezoarticus*** | | | | | | |
| ψ(.), p(ndvi_50) | 3 | 800.75 | 0 | 0.22 | 0.22 | -396.91 |
| ψ(unburned>10_250), p(ndvi_50) | 4 | 801.62 | 0.87 | 0.14 | 0.36 | -396.01 |
| ψ(burned<2_250), p(ndvi_50) | 4 | 801.74 | 1.00 | 0.13 | 0.49 | -396.07 |
| ψ(div-age_50), p(ndvi_50) | 4 | 802.27 | 1.52 | 0.1 | 0.59 | -396.33 |
| ψ(div-age_50 + burned<2_250), p(ndvi_50) | 5 | 802.58 | 1.83 | 0.09 | 0.68 | -395.04 |
| ψ(div-freq_250), p(ndvi_50) | 4 | 803.38 | 2.63 | 0.06 | 0.74 | -396.89 |
| ψ(div-freq_250 + burned<2_250), p(ndvi_50) | 5 | 803.43 | 2.68 | 0.06 | 0.8 | -395.46 |
| ψ(burned<2_250 + unburned>10_250), p(ndvi_50) | 5 | 803.5 | 2.75 | 0.05 | 0.85 | -395.5 |
| ψ(div-freq_250 + unburned>10_250), p(ndvi_50) | 5 | 804.3 | 3.55 | 0.04 | 0.89 | -395.9 |
| ψ(div-age_50 + unburned>10_250), p(ndvi_50) | 5 | 804.42 | 3.67 | 0.03 | 0.92 | -395.96 |
| ***Mazama* sp.** | | | | | | |
| ψ(.), p(ndvi_50) | 3 | 206.76 | 0 | 0.21 | 0.21 | -99.92 |
| ψ(unburned>10_250), p(ndvi_50) | 4 | 207.03 | 0.27 | 0.18 | 0.39 | -98.72 |
| ψ(div-freq_500), p(ndvi_50) | 4 | 208.07 | 1.31 | 0.11 | 0.5 | -99.24 |
| ψ(div-age_250), p(ndvi_50) | 4 | 208.23 | 1.47 | 0.1 | 0.59 | -99.32 |
| ψ(div-freq_500 + unburned>10_250), p(ndvi_50) | 5 | 208.47 | 1.71 | 0.09 | 0.68 | -97.98 |
| ψ(burned<2_250), p(ndvi_50) | 4 | 208.85 | 2.09 | 0.07 | 0.76 | -99.62 |
| ψ(div-freq_500 + burned<2_250), p(ndvi_50) | 5 | 209.58 | 2.81 | 0.05 | 0.81 | -98.54 |
| ψ(div-age_250 + unburned>10_250), p(ndvi_50) | 5 | 209.68 | 2.92 | 0.05 | 0.85 | -98.59 |
| ψ(burned<2_250 + unburned>10_250), p(ndvi_50) | 5 | 209.9 | 3.13 | 0.04 | 0.9 | -98.7 |
| ψ(div-age_250 + burned<2_250), p(ndvi_50) | 5 | 210.49 | 3.73 | 0.03 | 0.93 | -99 |
| ***C. brachyurus*** | | | | | | |
| ψ(burned<2_250), p(ndvi_250) | 4 | 429.38 | 0 | 0.21 | 0.21 | -209.89 |
| ψ(div-age_500 + burned<2_250), p(ndvi_250) | 5 | 429.68 | 0.3 | 0.18 | 0.4 | -208.59 |
| ψ(div-age_500 + unburned>10_500), p(ndvi_250) | 5 | 430.24 | 0.86 | 0.14 | 0.54 | -208.87 |
| ψ(div-age_500 + burned<2_250 + unburned>10_500), p(ndvi_250) | 6 | 430.94 | 1.56 | 0.1 | 0.63 | -207.64 |
| ψ(div-freq_50 + burned<2_250), p(ndvi_250) | 5 | 431.27 | 1.89 | 0.08 | 0.72 | -209.39 |
| ψ(div-age_500), p(ndvi_250) | 4 | 431.47 | 2.09 | 0.08 | 0.79 | -210.93 |
| ψ(burned<2_250 + unburned>10_500), p(ndvi_250) | 5 | 432.25 | 2.87 | 0.05 | 0.84 | -209.87 |
| ψ(div-freq_50 + div-age_500 + burned<2_250), p(ndvi_250) | 6 | 432.78 | 3.4 | 0.04 | 0.88 | -208.56 |
| ψ(.), p(ndvi_250) | 3 | 432.97 | 3.59 | 0.04 | 0.92 | -213.02 |

|  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|
| ***T. terrestris*** |  |  |  |  |  |  |
| ψ(div-freq_250), p(ndvi_500) | 4 | 222.77 | 0 | 0.41 | 0.41 | -106.59 |
| ψ(div-freq_250 + div-age_250), p(ndvi_500) | 5 | 223.84 | 1.06 | 0.24 | 0.64 | -105.67 |
| ψ(div-freq_250 + unburned>10_500), p(ndvi_500) | 5 | 225 | 2.22 | 0.13 | 0.78 | -106.25 |
| ψ(div-freq_250 + burned<2_250), p(ndvi_500) | 5 | 225.61 | 2.84 | 0.1 | 0.88 | -106.56 |

Considering the spatial variation in fire regime, *O. bezoarticus* used the space uniformly with little effect of fire related variables (pyrodiversity and proportion of recently burned or long-unburned areas). Occupancy probability for this species was 90% when considering false absences. Furthermore, the model selection ranked the model with occupancy probability ($\psi$) constant as the best supported model (Table 2). This suggests that pampas deer used the space regardless the spatial configuration of the fire mosaic. Some models containing fire regime variables showed high and medium support ($\Delta$AICc < 4). However, the weight sum for fire regime variables suggests low relative importance of these variables on space use by *O. bezoarticus* (weight sum < 0.35 for all variables; Figure 2a).

The other two deer species, analyzed together (*Mazama* sp.), were those with the most restricted use of space in the study area. However, the model with constant $\psi$ presented the best rank in model selection (Table 2), suggesting no variation in habitat use across the areas related to spatial variation in fire regime. Although some models containing fire variables showed medium to high support ($\Delta$AICc < 4), in general, the relative importance of these variables in the use of space by *Mazama* sp. was low (weight sum < 0.40 for all variables; Figure 2b).

The spatial configuration of the fire mosaic seemed to influence habitat use by the maned wolf *C. brachyurus*. More than half of the sampling units were used by this predator ($\psi = 0.6$) and model selection results indicated several models with medium to high support ($\Delta$AICc < 4) for the species (Table 2). Fire age diversity and the proportion of area recently burned were the most frequent variables in the models with high support ($\Delta$AICc < 2). This result is in line with the considerable relative importance of these variables in the use of space by *C. brachyurus* (weight sum ≥ 0.60 for both fire age diversity and proportion of recently burned area; Figure 2c). Beta estimate values indicated that fire age diversity and the proportion of area recently burned positively affected maned wolf occupancy (Figure 3c). That is, maned wolves used areas where the fire mosaic had higher effective number of patches with different fire ages and more area of patches burned in the last two years then patches with older fire ages.

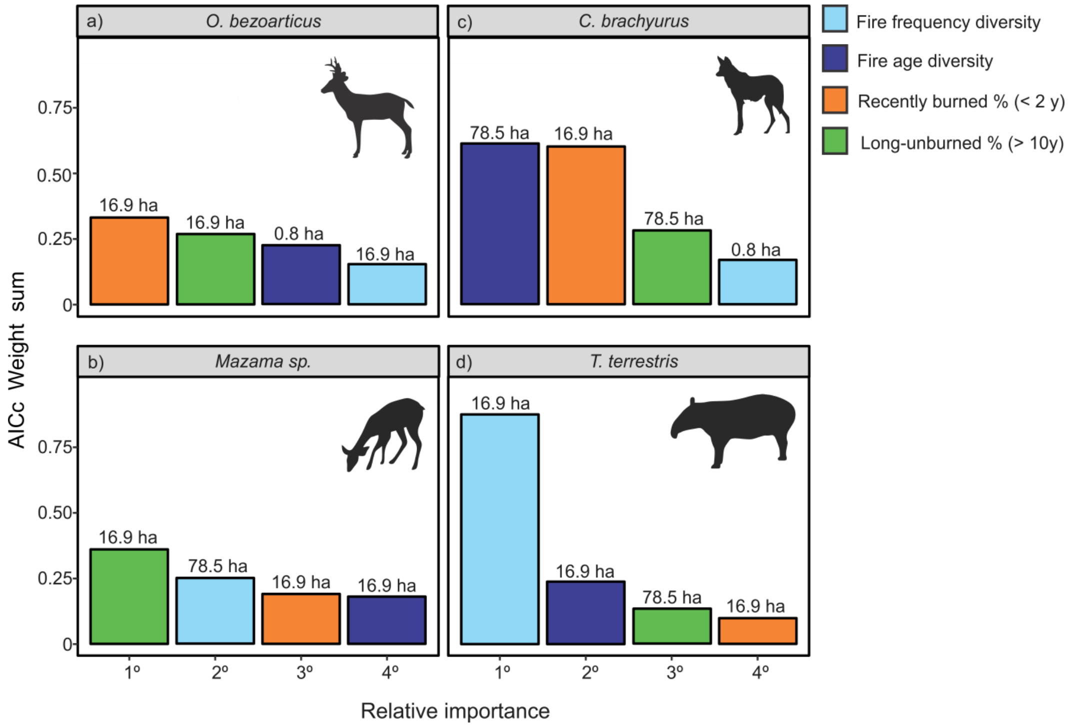

Figure 2. Relative importance of fire regime variables on occupancy probability (interpreted as a proxy for intensity of habitat use) of *O. bezoarticus* (a; pampas deer), *Mazama* sp. (b; brown brocket deer and red brocket deer combined), *C. brachyurus* (c; maned wolf), and *T. terrestris* (d; tapir) in the Cerrado. Variable value of importance was calculated as the sum of model weights with ΔAICc < 4 that included the variable. Fire frequency and fire age diversity were estimated using the exponential of Shannon entropy. Percentage of recently burned area represents the proportion of area burned up to two years before the sampling period and percentage of long-unburned area represents the proportion of area not burned in the last 10 years before the sampling period. For each species, fire variables are ranked in descending order of importance according to their sum of ΔAICc weights. Spatial scales in which fire variables were analyzed are indicated above the bars. The scales were used accordingly to the results of previous analyses (Supplementary Material Table S1).

The results obtained for the tapir *T. terrestris* indicated that habitat use by this large herbivore was influenced by the spatial configuration of fire mosaic. This species used half of the sampling units ($\psi = 0.53$) and model selection resulted in four models with medium to high support ($\Delta$AICc < 4) for occupancy data (Table 2). All of these models included fire frequency diversity. This variable showed high relative importance in the use of space by this species (weight sum = 0.87; Figure 2d). According to beta estimate values, tapir responded negatively to fire frequency diversity (Figure 3d). This result suggests avoidance of pyrodiverse mosaics by tapir. The other variables showed low relative importance and were present in supported models only when accompanied by fire frequency diversity. Models containing these variables alone had no support.

In general, the spatial scales measured for the same predictor variable were correlated. This pattern was clearer for NDVI, diversity of fire age, proportion of recently burned areas, and proportion of long-unburned areas. For these variables, all spatial scales showed a correlation > 0.5. Thus, to avoid inflating our models, we used only one scale per variable. The NDVI measured at the finest spatial scale (0.8 ha) showed a better fit for the detection data of *O. bezoarticus* and *Mazama* sp. when compared to the NDVI on the broader scales (Supplementary Materials Table S1). Conversely, the broadest spatial scale (78.5 ha) had a better fit describing the relationship between *T. terrestris* detection and NDVI. For *C. brachyurus*, the different spatial scales at which the NDVI was measured had similar support. Except for fire age diversity (*C. brachyurus*, 78.5 ha) and fire frequency diversity (*T. terrestris*, 19.6 ha), the spatial scales had similar support for explaining the effect of fire regime variables on space used by mammals.

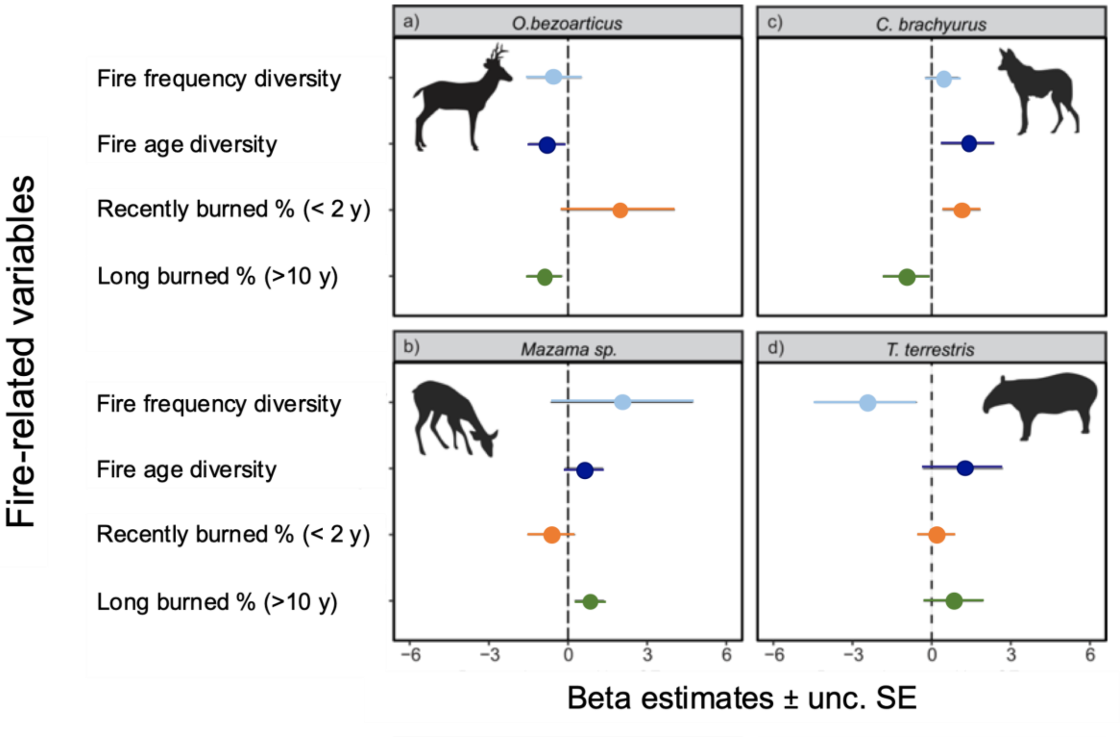

Figure 3. Mean coefficient estimates (β) and unconditional standard errors (unc. SE) for the effect of fire regime variables on occupancy probability (interpreted as intensity of use) of pampas deer - *O. bezoarticus* (a), brown brocket deer and red brocket deer combined - *Mazama* sp. (b), maned wolf - *C. brachyurus* (c), and tapir - *T. terrestris* (d) in the Cerrado. Fire frequency and fire age diversity were estimated using the exponential of Shannon entropy. Percentage of recently burned area represents the proportion of area burned up to two years before the mammal sampling. Percentage of long-unburned area represents the proportion of area not burned in the last 10 years before the sampling period. β and unc. SE were based on model averaging of models with ΔAICc < 4. The spatial scale used for each relationship between fire variable and species occupancy were the same of Table 1 and Figure 2.

## Discussion

Medium and large mammals showed species-specific responses to fire-related variables. The pyrodiversity and the proportion of recently burned areas had different roles in the space used (occupancy) by the species. For deer species (*O. bezoarticus* and *Mazama* sp.), these variables had low relative importance on their space use. On the other hand, for *C. brachyurus* occupancy, fire age diversity and the proportion of recently burned areas were important variables affecting maned wolves positively. For *T. terrestris* occupancy, fire frequency diversity was the most important variable, having a negative effect on tapir habitat use. We observed that vegetation cover affected the detectability of the study species. With few exceptions, different spatial scales had similar support for explaining the effect of fire regime on mammal occupancy..

### *Fire regime and mammal occupancy*

Fire regime variables had distinct effects on mammal occupancy when corrected for differences in detectability. In relation to space use by the deer species, neither *O. bezoarticus* nor *Mazama* sp. were markedly affected by pyrodiversity, proportion of recently burned, or proportion of long-unburned areas. On the other hand, fire-related variables affected space use by *T. terrestris* and *C. brachyurus*. For deer, the results showed a generalized use of the space, but with a more restricted use by *Mazama* sp. than by *O. bezoarticus*. These results are compatible with the study by [65] in the Cerrado, which found that *O. bezoarticus* used recently burned and unburned areas with the same intensity. However, our findings for deer disagree with a comprehensive literature indicating herbivore species preferences for recently burned patches related to better forage quality in these areas [41-42, 66, 96]. This variation in herbivore responses to fire suggests a context-specific influence of fire regime on habitat use. For example, large herbivores in the African savanna [43] and mule deer in conifer forests [38, 97] regulate the use of recently burned areas in response to predator activity. Reid et al. [44], in turn, suggested that cattle foraging in recently burned areas may displace native herbivores (via competition) to long-unburned patches. In our study area, records of cattle and potential predators like *Puma concolor* and *Panthera onca* [98-100] were rare during our sampling [only one record of *P. concolor*, but see 66]. Thus, it seems unlikely that competition and predation are strongly regulating the use of space by deers in response to fire in our study area. The results obtained for *O. bezoarticus* and *Mazama* sp. may be related to their feeding habits, since these deer species are browsers, especially in open formations [59, 101-103]. Browsing herbivores seem to be less attracted to recently burned patches than grazers [104-105]. This may have driven the generalist response to fire observed for deer species in our study area.

Unlike the other studied herbivore species, *T. terrestris* was strongly affected by the fire regime at the intermediate spatial scale (16.9 ha). Based on the weight sum of the variables, our results suggest a high relative importance of fire frequency diversity in the habitat use by this species. Differently from the expected pattern, this effect was negative, which indicate less use of areas with higher pyrodiversity. Negative effects of pyrodiversity on the abundance and occupancy of mammal species have already been reported [30, 106] but not for large herbivores. For this group, available studies indicate that pyrodiverse areas provide advantages for herbivores by offering more foraging opportunities [34-35]. For tapir populations, the indirect effects of fire are poorly known, and the scarce available information is based on single fire events [65].

The negative effect of fire frequency diversity on *T. terrestris* suggests that this species may be strongly associated with areas with a given fire frequency regime. Areas that burn frequently experience reduced vegetation complexity [10], facilitating movement between habitat patches [69]. This can be particularly advantageous for *T. terrestris* which travels long distances and has large home ranges [61, 107]. For example, it was verified that habitat use by *T. terrestris* is associated with the presence of water bodies [108] and the distribution of food resources [109]. In our study area, gallery forests and palm swamps are important sources of water and fruits present in the diet of tapirs [109-111], but these habitat types occur in low proportion when compared to other Cerrado formations [73]. *T. terrestris* may prefer to use the structurally simplified vegetation of frequently burned areas to move between gallery forests and palm swamps and access such resources. Such areas simplified by fire may be underrepresented in highly pyrodiverse mosaics, leading to negative effects of pyrodiversity [29]. The intense use of areas burned up to one year before in the CVNP reported by Nunes [66] provides support for this suggested preference for specific fire regimes by tapirs (but see Prada [65]).

Less structured vegetation is also found in recently burned areas [112-113] and may attract cursorial predators due to better displacement in the simplified vegetation after fire [38]. This may explain the important and positive effect of proportion of recently burned areas on the space used by *C. brachyurus* in our study. Such effect was stronger at the intermediate spatial scale (16.9 ha). Our results confirm previous studies that found an association between recently burned areas and predator species, including manned wolf [40, 66, 114-115]. *C. brachyurus* can be considered a cursorial predator [116] that preys mainly on small mammals in open areas [63, 117-118]. This type of prey may show increases in abundance [119] or be more exposed to predation after fire [120]. We suggest that the type of hunting strategy of *C. brachyurus* associated with higher predation success in recently burned areas may have led this species to use more intensively areas that burned two years ago or less.

In addition to the proportion of recently burned areas, space use by maned wolves was affected by pyrodiversity. As we expected, fire age diversity positively affected maned wolf occupancy. However, different from the proportion of recently burned area, the effect of fire age diversity was stronger at the broadest spatial scale evaluated (78.5 ha). Our results for *C. brachyurus* corroborate previous studies that evaluated the influence of fire age diversity on mammals and other vertebrates in different fire-prone ecosystems [25, 27, 30, 121]. However, there is also evidence for these groups responding negatively or showing no response to pyrodiversity [49, 122-125]. Pyrodiversity may be advantageous for species when individuals use the resources offered by the different patches of the fire mosaic in a complementary way

[25, 27, 69, 126]. This is potentially important for *C. brachyurus*, which has large average home ranges (between 3300 ha and 6700 ha) [127-128] and a generalist diet [117, 129]. Furthermore, this species tends to hunt in open vegetation and rest under a dense layer of tall grasses [130-131]. More open and sparse vegetation can be found in recently burned areas while the presence of denser and taller vegetation is associated with later post-fire successional stages [132-133]. Thus, areas formed by a diversified mosaic of patches at different ages since the last burning can provide favorable environments for the multiple activities of *C. brachyurus*.

### *Spatial scales*

Predictor variables influenced mammal space use at different spatial scales. Radford, et al. [49] observed multiple spatial scales associated with the effects of fire on mammal abundance in a savanna. The authors found that the proportion of recently burned areas was relevant at local and landscape scales (0.25 ha to 31400 ha) but with more evident effects of pyrodiversity detected at the local scale (2800 ha). Our results reinforce the importance of fire influence on local ecological processes that regulate the mammalian population and community dynamics in fire-prone ecosystems [12, 25, 33, 134-135]. In our study area, the proportion of recently burned areas and the diversity of fire ages influenced the habitat use by mammals at the scales of 16.9 ha and 78.5 ha. Such pattern indicates that these fire regime attributes affect microhabitat use by medium large mammals [51, 136] for foraging, hunting, movement between habitat patches, and resting.

For most predictor variables here analyzed, we identified multiple spatial scales with similar importance (evaluated by AICc comparison). The exceptions were the 78.5-ha scale for the relationship between fire age diversity and *C. brachyurus* occupancy and the 19.6-ha scale for the relationship between fire frequency diversity and *T. terrestris* occupancy. Holland and Yang [137] argue that the lack of a marked scale of effect may result from relationships that are not biologically important or because relationships occur at multiple spatial scales. The first case seems to have occurred in our study. We identified the scale of effect of the variables that were important in explaining the effects of fire on the two species (*C. brachyurus* and *T. terrestris*). We did not find a clear scale of effect, however, when fire regime variables were not important to explain space use by species.

We limited the spatial scale of our study (maximum = 78.5 ha) to avoid spatial dependence between sampling units. Jackson and Fahrig [138] recommend the evaluation of spatial scales ranging from areas smaller than the home range of the species to nine times its average dispersal distance. In fact, the effect of fire on mammals was observed for finer scales (≤ 1 ha) and much larger than the home range of the analyzed species (> 31400 ha) [25, 49]. For the species that we studied, the mean home range varies between 120 ha (*Mazama* sp.) and 6700 ha (*C. brachyurus*) [55, 57, 61, 127] and the dispersion distance is expected to be much larger [139]. If the fire variables analyzed in our study affect the home range of species, for example, such an effect may not emerge at finer spatial scales. Thus, we cannot discard the possibility that some responses were not detected because the spatial scale associated with them was larger than the spatial scales we analyzed. Yet, we detected relevant effects of fire regime on space used by mammals within the spatial scale range that we considered (0.8 to 78.5 ha).

### *Implications for fire management*

In fire-prone ecosystems, the idea that heterogeneous fire mosaics are associated with higher biodiversity has encouraged the establishment of pyrodiverse landscapes through prescribed burning [17, 21, 23, 53, 140]. However, this approach is subject to criticism due to the mixed support for the hypothesis “pyrodiversity begets biodiversity” [22, 28, 141]. Complex mosaics with maximum pyrodiversity are not always necessary to enable biodiversity [124, 142]. Area extent with a specific fire age may be more relevant for animal populations and communities than highly pyrodiverse mosaics [20, 31, 49, 143]. Here, we demonstrate that both pyrodiversity and the proportion of recently burned areas are important predictors of space use by some medium and large mammals. We suggest that fire management should aim to create heterogeneous mosaics that balance the proportion of recently burned, middle-aged burned, and long-unburned areas, without focusing only on a maximum pyrodiversity value. This approach may be more viable from a logistical and biological point of view. Logistic because it eliminates the complexity of planning and executing prescribed burns aiming highly pyrodiverse mosaics. Biological because it can be suitable for a higher number of species and avoid the negative effects that a high pyrodiversity can have on some species.

Our results demonstrated that the relationship between fauna and fire regime depends on the species studied [27, 30], the spatial scale analyzed [123, 144] and how the fire regime is characterized [145]. These findings are particularly relevant because they contribute to reducing gaps related to species-specific responses to fire, multi-scale fire effects, and the importance of evaluating multiple fire metrics (Jones et al. 2022). On the other hand, the proportion of long-unburned areas had negligible influence on mammals. Specifically, our results indicated that maned wolves more frequently use fire mosaics composed of multiple fire ages at the 78.5-ha scale. Moreover, at the 19.6-ha scale, this species made intense use of areas burned up to two years ago. For *T. terrestris*, our findings pointed out that fire mosaics at this same scale (19.6 ha) combining patches with a few different fire frequencies are more frequently used. In contrast, habitat use by deer species seemed to be less affected by variation in fire regime, probably because of their feeding habits. We recommend that establishment of fire mosaics for conservation purposes should be context-specific [19] and species-specific. In addition, fire management strategies that combine “patch mosaic burning” with the maintenance of specific fire-age habitat patches may be a better approach to deal with distinct species requirements. Finally, we highlight that even when conducted at fine spatial scales, fire management may influence the habitat used by medium and large-sized species.

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## Supplementary material

Table S1. Model selection evaluating the effect of spatial scale on medium and large-sized mammal detection (p) and occupancy (ψ) in Cerrado. K represents the number of parameters in the model, AICcWt and Cum.Wt indicate the relative weight of the model and the accumulated weight, respectively, and -2LL is the log-likelihood. Numbers 50, 250, and 500 represent the spatial scales in which the variables were measured. Spatial scales used in the analysis are in bold. Occupancy (Ψ) was fitted using the fire regime variables at 250-m scale (div-freq + div-age + burned<2 + unburned>10, indicated as “fire regime”) for the NDVI spatial scale analysis. To compare the spatial scales of fire-related variables for ψ, we fitted detection (p) using NDVI at the spatial scale previously selected.

| | K | AICc | ΔAICc | AICcWt | Cum.Wt | -2LL |
|---|---|---|---|---|---|---|
| ***O. bezoarticus*** | | | | | | |
| NDVI | | | | | | |
| **ψ(fire regime), p(NDVI50)** | **7** | **809.05** | **0** | **0.99** | **0.99** | **-394.98** |
| ψ(fire regime), p(NDVI250) | 7 | 818.25 | 9.2 | 0.01 | 1 | -399.58 |
| ψ(fire regime), p(NDVI500) | 7 | 821.43 | 12.37 | 0 | 1 | -401.17 |
| DIV. FIRE FREQUENCY | | | | | | |
| **ψ(DIV-FREQ250), p(NDVI50)** | **5** | **804.55** | **0** | **0.5** | **0.5** | **-396.02** |
| ψ(DIV-FREQ500), p(NDVI50) | 5 | 804.58 | 0.04 | 0.5 | 1 | -396.04 |
| ψ(DIV-FREQ50), p(NDVI50) | | | Did not converge | | | |
| DIV. FIRE AGE | | | | | | |
| **ψ(DIV-AGE50), p(NDVI50)** | **5** | **801.95** | **0** | **0.53** | **0.53** | **-394.72** |
| ψ(DIV-AGE500), p(NDVI50) | 5 | 803.45 | 1.5 | 0.25 | 0.78 | -395.48 |
| ψ(DIV-AGE250), p(NDVI50) | 5 | 803.72 | 1.78 | 0.22 | 1 | -395.61 |
| AREA BURNT <2 YRS | | | | | | |
| **ψ(BURNED<2Y250), p(NDVI50)** | 5 | 802.9 | 0 | 0.63 | 0.63 | -395.2 |
| ψ(BURNED<2Y500), p(NDVI50) | 5 | 803.99 | 1.09 | 0.37 | 1 | -395.75 |
| ψ(BURNED<2Y50), p(NDVI50) | | | Did not converge | | | |
| AREA NOT BURNT >10 YRS | | | | | | |
| **ψ(UNBURNED>10Y250), p(NDVI50)** | **5** | **802.69** | **0** | **0.36** | **0.36** | **-395.09** |
| ψ(UNBURNED>10Y500), p(NDVI50) | 5 | 802.87 | 0.18 | 0.33 | 0.7 | -395.18 |
| ψ(UNBURNED>10Y50), p(NDVI50) | 5 | 803.05 | 0.37 | 0.3 | 1 | -395.28 |
| ***Mazama* sp.** | | | | | | |
| NDVI | | | | | | |
| **ψ(fire regime), p(NDVI50)** | **7** | **214.81** | **0** | **0.96** | **0.96** | **-97.86** |
| ψ(fire regime), p(NDVI250) | 7 | 221.64 | 6.84 | 0.03 | 0.99 | -101.28 |
| ψ(fire regime), p(NDVI500) | 7 | 224.41 | 9.6 | 0.01 | 1 | -102.66 |
| DIV. FIRE FREQUENCY | | | | | | |
| **ψ(DIV-FREQ500), p(NDVI50)** | **5** | **804.55** | **0** | **0.5** | **0.5** | **-396.02** |
| ψ(DIV-FREQ50), p(NDVI50) | 5 | 804.58 | 0.04 | 0.5 | 1 | -396.04 |
| ψ(DIV-FREQ250), p(NDVI50) | | | Did not converge | | | |
| DIV. FIRE AGE | | | | | | |
| **ψ(DIV-AGE250), p(NDVI50)** | **4** | **208.23** | **0** | **0.46** | **0.46** | **-99.32** |

| | | | | | | |
|---|---|---|---|---|---|---|
| ψ(DIV-AGE500), p(NDVI50) | 4 | 209.26 | 1.03 | 0.27 | 0.73 | -99.83 |
| ψ(DIV-AGE50), p(NDVI50) | 4 | 209.29 | 1.06 | 0.27 | 1 | -99.85 |
| AREA BURNT <2 YRS | | | | | | |
| **ψ(BURNED<2Y250), p(NDVI50)** | **4** | **208.85** | **0** | **0.35** | **0.35** | **-99.62** |
| ψ(BURNED<2Y500), p(NDVI50) | 4 | 208.88 | 0.03 | 0.35 | 0.7 | -99.64 |
| ψ(BURNED<2Y50), p(NDVI50) | 4 | 209.2 | 0.36 | 0.3 | 1 | -99.8 |
| AREA NOT BURNT >10 YRS | | | | | | |
| **ψ(UNBURNED>10Y250), p(NDVI50)** | **4** | **207.03** | **0** | **0.39** | **0.39** | **-98.72** |
| ψ(UNBURNED>10Y500), p(NDVI50) | 4 | 207.4 | 0.37 | 0.33 | 0.72 | -98.9 |
| ψ(UNBURNED>10Y50), p(NDVI50) | 4 | 207.74 | 0.71 | 0.28 | 1 | -99.07 |
| ***C. brachyurus*** | | | | | | |
| NDVI | | | | | | |
| **ψ(fire regime), p(NDVI250)** | **7** | **430.9** | **0** | **0.53** | **0.53** | **-205.9** |
| ψ(fire regime), p(NDVI500) | 7 | 432.5 | 1.61 | 0.24 | 0.77 | -206.71 |
| ψ(fire regime), p(NDVI50) | 7 | 432.54 | 1.64 | 0.23 | 1 | -206.72 |
| DIV. FIRE FREQUENCY | | | | | | |
| **ψ(DIV-FREQ50), p(NDVI250)** | **4** | **430.79** | **0** | **0.53** | **0.53** | **-210.6** |
| ψ(DIV-FREQ250), p(NDVI250) | 4 | 432.37 | 1.58 | 0.24 | 0.77 | -211.38 |
| ψ(DIV-FREQ500), p(NDVI250) | 4 | 432.45 | 1.65 | 0.23 | 1 | -211.42 |
| DIV. FIRE AGE | | | | | | |
| **ψ(DIV-AGE500), p(NDVI250)** | **4** | **428** | **0** | **0.69** | **0.69** | **-209.2** |
| ψ(DIV-AGE250), p(NDVI250) | 4 | 430.18 | 2.18 | 0.23 | 0.93 | -210.29 |
| ψ(DIV-AGE50), p(NDVI250) | 4 | 432.48 | 4.48 | 0.07 | 1 | -211.44 |
| AREA BURNT <2 YRS | | | | | | |
| **ψ(BURNED<2Y250), p(NDVI250)** | **4** | **427.21** | **0** | **0.62** | **0.62** | **-208.81** |
| ψ(BURNED<2Y500), p(NDVI250) | 4 | 428.72 | 1.51 | 0.29 | 0.91 | -209.56 |
| ψ(BURNED<2Y50), p(NDVI250) | 4 | 430.96 | 3.74 | 0.09 | 1 | -210.68 |
| AREA NOT BURNT >10 YRS | | | | | | |
| **ψ(UNBURNED>10Y500), p(NDVI250)** | **4** | **432.36** | **0** | **0.35** | **0.35** | **-211.38** |
| ψ(UNBURNED>10Y50), p(NDVI250) | 4 | 432.49 | 0.13 | 0.33 | 0.68 | -211.45 |
| ψ(UNBURNED>10Y250), p(NDVI250) | 4 | 432.52 | 0.17 | 0.32 | 1 | -211.46 |
| ***T. terrestris*** | | | | | | |
| NDVI | | | | | | |
| **ψ(fire regime), p(NDVI500)** | **7** | **231.12** | **0** | **0.74** | **0.74** | **-106.02** |
| ψ(fire regime), p(NDVI250) | 7 | 234.37 | 3.25 | 0.15 | 0.89 | -107.64 |
| ψ(fire regime), p(NDVI50) | 7 | 234.95 | 3.83 | 0.11 | 1 | -107.93 |
| DIV. FIRE FREQUENCY | | | | | | |
| **ψ(DIV-FREQ250), p(NDVI500)** | **4** | **222.77** | **0** | **0.82** | **0.82** | **-106.59** |
| ψ(DIV-FREQ500), p(NDVI500) | 4 | 226.13 | 3.36 | 0.15 | 0.97 | -108.26 |
| ψ(DIV-FREQ50), p(NDVI500) | 4 | 229.27 | 6.5 | 0.03 | 1 | -109.84 |
| DIV. FIRE AGE | | | | | | |
| **ψ(DIV-AGE250), p(NDVI500)** | **4** | **231.51** | **0** | **0.35** | **0.35** | **-110.95** |
| ψ(DIV-AGE50), p(NDVI500) | 4 | 231.64 | 0.13 | 0.33 | 0.68 | -111.02 |
| ψ(DIV-AGE500), p(NDVI500) | 4 | 231.7 | 0.19 | 0.32 | 1 | -111.05 |
| AREA BURNT <2 YRS | | | | | | |
| **ψ(BURNED<2Y250), p(NDVI500)** | **4** | **231.29** | **0** | **0.37** | **0.37** | **-110.84** |

| | | | | | | |
|---|---|---|---|---|---|---|
| ψ(BURNED<2Y50), p(NDVI500) | 4 | 231.61 | 0.32 | 0.32 | 0.69 | -111.01 |
| ψ(BURNED<2Y500), p(NDVI500) | 4 | 231.61 | 0.32 | 0.31 | 1 | -111.01 |
| AREA NOT BURNT >10 YRS | | | | | | |
| **ψ(UNBURNED>10Y500), p(NDVI500)** | **4** | **230.9** | **0** | **0.39** | **0.39** | **-110.65** |
| ψ(UNBURNED>10Y250), p(NDVI500) | 4 | 231.18 | 0.28 | 0.34 | 0.74 | -110.79 |
| ψ(UNBURNED>10Y50), p(NDVI500) | 4 | 231.71 | 0.81 | 0.26 | 1 | -111.05 |

Table S2. Results for the spatial autocorrelation test using Moran’s Index (I). Iobs and Iexp represent observed and expected Moran´s Index, respectively. If p-value is > 0.05, the null hypothesis of no correlation between sampling units is accepted.

| Species | Iobs | Iexp | Standard deviation | p-value |
|---|---|---|---|---|
| *O. bezoarticus* | 0.02 | -0.03 | 0.05 | 0.23 |
| *Mazama* sp. | -0.06 | -0.03 | 0.04 | 0.59 |
| *C. brachyurus* | -0.08 | -0.03 | 0.05 | 0.29 |
| *T. terrestris* | 0.04 | -0.03 | 0.05 | 0.1 |

Table S3. Number of records (detections), number of sampling sites with detections, naïve occupancy, estimated detection probability (p), estimated occupancy probability (ψ), and relative abundance of large sized mammals of a Neotropical savanna. Detection and occupancy probability and standard deviation estimated by model averaging of models with ΔAICc < 4.

| Species | Detections | Sites with detection | Naïve occupancy | Detection probability (p) ± SD | Occupancy probability (ψ) ± SD |
|---|---|---|---|---|---|
| *O. bezoarticus* | 123 | 25 | 0.83 | 0.09±0.04 | 0.90±0.06 |
| *C. brachyurus* | 52 | 16 | 0.53 | 0.05±0.01 | 0.60±0.20 |
| *Mazama* sp | 29 | 7 | 0.24 | 0.04±0.06 | 0.38±0.10 |
| *T. terrestris* | 23 | 11 | 0.37 | 0.03±0.02 | 0.53±0.34 |

Table S4. Model selection used to evaluate the effect of NDVI, season (wet or dry), and method (photo or video) on medium and large-sized mammals detection (p) in Cerrado. K represents the number of parameters in the model, AICcWt and Cum.Wt indicate the relative weight of the model and the accumulated weight, respectively, and -2LL is the log-likelihood. Occupancy (Ψ) was fitted using the fire regime variables (div-freq + div-age + burned<2 + unburned>10).

| | K | AICc | ΔAICc | AICcWt | Cum.Wt | -2LL |
|---|---|---|---|---|---|---|
| ***O.bezoarticus*** | | | | | | |
| ψ(fire regime), p(NDVI) | 7 | 809.05 | 0 | 0.63 | 0.63 | -394.98 |
| ψ(fire regime), p(NDVI + season) | 8 | 810.97 | 1.91 | 0.24 | 0.87 | -394.05 |
| ψ(fire regime), p(NDVI + method) | 8 | 812.75 | 3.69 | 0.1 | 0.97 | -394.94 |
| ψ(fire regime), p(NDVI + season + method) | 9 | 814.96 | 5.91 | 0.03 | 1 | -393.98 |
| ψ(fire regime), p(.) | 6 | 826.79 | 17.73 | 0 | 1 | -405.57 |
| ψ(fire regime), p(season) | 7 | 828.3 | 19.24 | 0 | 1 | -404.6 |
| ψ(fire regime), p(method) | 7 | 830.2 | 21.14 | 0 | 1 | -405.55 |
| ψ(fire regime), p(season + method) | 8 | 831.97 | 22.92 | 0 | 1 | -404.56 |
| ***Mazama* sp.** | | | | | | |
| ψ(fire regime), p(NDVI) | 7 | 214.81 | 0 | 0.56 | 0.56 | -97.86 |
| ψ(fire regime), p(NDVI + method) | 8 | 216.46 | 1.66 | 0.24 | 0.8 | -96.8 |
| ψ(fire regime), p(NDVI + season) | 8 | 217.9 | 3.09 | 0.12 | 0.92 | -97.52 |
| ψ(fire regime), p(NDVI + season + method) | 9 | 220 | 5.19 | 0.04 | 0.96 | -96.5 |
| ψ(fire regime), p(.) | 6 | 221.43 | 6.62 | 0.02 | 0.98 | -102.89 |
| ψ(fire regime), p(season) | 7 | 222.89 | 8.08 | 0.01 | 0.99 | -101.9 |
| ψ(fire regime), p(method) | 7 | 224.08 | 9.27 | 0.01 | 1 | -102.49 |
| ψ(fire regime), p(season + method) | 8 | 225.91 | 11.1 | 0 | 1 | -101.52 |
| ***C. brachyurus*** | | | | | | |
| ψ(fire regime), p(.) | 6 | 430.13 | 0 | 0.39 | 0.39 | -207.24 |
| ψ(fire regime), p(NDVI) | 7 | 430.9 | 0.77 | 0.26 | 0.65 | -205.9 |
| ψ(fire regime), p(method) | 7 | 432.85 | 2.72 | 0.1 | 0.75 | -206.88 |
| ψ(fire regime), p(season) | 7 | 432.87 | 2.74 | 0.1 | 0.85 | -206.89 |
| ψ(fire regime), p(NDVI + season + method) | 8 | 433.79 | 3.66 | 0.06 | 0.91 | -205.47 |
| ψ(fire regime), p(NDVI + season) | 8 | 434.06 | 3.94 | 0.05 | 0.96 | -205.6 |
| ψ(fire regime), p(season + method) | 8 | 435.72 | 5.59 | 0.02 | 0.99 | -206.43 |
| ψ(fire regime), p(NDVI + method) | 9 | 437.16 | 7.03 | 0.01 | 1 | -205.08 |
| ***T.terrestris*** | | | | | | |
| ψ(fire regime), p(NDVI) | 7 | 231.12 | 0 | 0.44 | 0.44 | -106.02 |
| ψ(fire regime), p(.) | 6 | 232.15 | 1.03 | 0.27 | 0.71 | -108.25 |
| ψ(fire regime), p(NDVI + season) | 8 | 234.39 | 3.27 | 0.09 | 0.8 | -105.77 |
| ψ(fire regime), p(NDVI + season + method) | 8 | 234.88 | 3.75 | 0.07 | 0.86 | -106.01 |
| ψ(fire regime), p(season) | 7 | 234.91 | 3.79 | 0.07 | 0.93 | -107.91 |
| ψ(fire regime), p(method) | 7 | 235.58 | 4.45 | 0.05 | 0.98 | -108.24 |
| ψ(fire regime), p(NDVI + method) | 9 | 238.53 | 7.41 | 0.01 | 0.99 | -105.77 |
| ψ(fire regime), p(season + method) | 8 | 238.68 | 7.55 | 0.01 | 1 | -107.91 |

# Capítulo 3. Losers and winners after a large wildfire: small mammal mixed responses to fire severity

## Abstract

Large wildfires are becoming more frequent in natural ecosystems affecting plants and animals worldwide. Understanding their impacts on the biota is crucial for the conservation of fire-sensitive habitats and their associated species. Here, we investigated small mammal community responses to fire severity after a large wildfire in a Neotropical savanna (Cerrado). We sampled small mammals in seven gallery forests (and their adjacent open habitats) affected by the wildfire, representing a gradient of fire severity. We accessed changes in taxonomic and functional community metrics related to fire severity using linear regressions and multivariate analysis. We captured 407 individuals (238 individuals in forest sites and 169 in open sites) belonging to 13 rodents and two marsupial species. Fire severity classes ranged from unburned to moderate-high severity. Our results indicated mixed effects of fire severity on small mammal communities. Firstly, taxonomic diversity and functional dispersion increased with fire severity. In contrast, the representativeness of forest specialist species decreased with increasing fire severity. These patterns were mainly driven by the presence of generalists and open-habitats species and a low proportion of forest specialists in more severely burned forests. Such a shift in community composition probably resulted from fire-induced changes in vegetation structure affecting species according to their habitat affinities. Furthermore, our findings suggest a potential biotic homogenization effect of large severe wildfires as severely burned forests become taxonomic similar to open habitats. Our study reinforces the valuable information for biodiversity conservation of fire-sensitive habitats provided by natural unplanned wildfires experiments and for fire management of tropical savannas.

Keywords: gallery forests, rodents, marsupials, fire-sensitive habitat, Neotropical savanna

## Introduction

Extreme wildfire events result from the interaction between human, physical, and ecological processes and conditions (e.g. land conversion to crops, weather, and vegetation cover) (Tedim et al. 2018). The recent occurrence of such events worldwide (e.g. Australia, Portugal, Brazil, USA) exemplifies the increasing commonness of severe wildfires and their direct and indirect effects on biodiversity (Fidelis et al. 2018, Tran et al. 2020, Ward et al. 2020, Baranowski et al. 2021, Tomas et al. 2021, Iglesias et al. 2022). Measuring the impacts of wildfires is crucial to promote mitigation actions. However, quantifying the effects of wildfires on biota is challenging given the unpredictability of extreme wildfire events, which limits comparisons between pre- and post-fire community conditions. Studies based on prescribed burning permit such comparisons (Sitters et al. 2015, Kuchinke et al. 2020) and are fundamental tools for fire management and species conservation (Brockett et al. 2001, Fidelis et al. 2018, Santos et al. 2021). Nonetheless, extrapolations of their results to large wildfire impacts should be seen with caution. Prescribed burning rarely reproduces the severity and spatial scales observed in large severe wildfires (Arkle and Pilliod 2010). Therefore, such studies may underestimate fire impacts on biota, mainly in Southern Hemisphere (Pastro et al. 2014, González et al. 2022). Conversely, opportunistic studies evaluating post-wildfire effects on biota offer unique contributions to understanding the impacts on population and communities following large wildfires. For instance, studies conducted after large severe wildfires revealed direct effects of these events on animals (e.g., burn injuries) (Barros et al. 2022) and indirect impacts, affecting habitat selection, animal movement, and community species structure (Berry et al. 2016, González et al. 2021, Culhane et al. 2022).

In fire-prone ecosystems, flora and fauna may be less impacted by wildfire effects. Species that evolved in such ecosystems may exhibit physiological, morphological, and behavioral adaptations permitting their survival and persistency during and after wildfires (Simon et al. 2009, Pausas 2018). Examples of these adaptations for plants include thick bark and resprouting. For animals, some adaptations to fire are hiding in shelters during fire events and the capacity to use burned areas. However, fire-sensitive vegetation inserted in fire-prone regions may be strongly affected by wildfires due to lack of such adaptations. These fire-sensitive habitats rarely burn compared with fire-adapted habitats (e.g. grasslands) (Miranda et al. 2009) but may suffer severe impacts after large wildfires (Mendonça et al. 2015, Camargo et al. 2018, Flores et al. 2021). Thus, it is expected animals associated with fire-sensitive vegetation to be more vulnerable to the direct and indirect effects of wildfires (Nimmo et al. 2021).

Direct mortality of animals during wildfires is generally zero or low but may increase with fire severity and extension (Banks et al. 2011, Tomas et al. 2021, Hale et al. 2022, Jolly et al. 2022). Even in the absence of immediate mortality, post-fire effects on environmental conditions can affect individual survival. After fire, individuals may face higher predation risk (Leahy et al. 2016, Hradsky et al. 2017), reduced food resources (Barlow and Peres 2006, Vieira and Briani 2013), reduced habitat (Ward et al. 2020), and loss of shelter sites (Banks et al. 2011, Flanagan-Moodie et al. 2018). The novel conditions after fire generally occur through changes in vegetation structure. Forested habitats, for example, exhibit canopy cover loss, decrease in vertical connectivity, reduction in litter depth and tree density, and increase in ground layer cover (Hoffmann 2002, Numata et al. 2017, Camargo et al. 2018, Flores et al. 2021). The recovery time from these changes are longer for upper strata (> 1 m), being more than two years (Huerta et al. 2022). Moreover, areas affected by higher fire severity experience more drastic changes in plant species composition and vegetation structure than areas less affected by fire (Poulos et al. 2021).

Animal responses to fire-induced changes may depend on traits intrinsic to the species (Plavsic 2014, Bowman et al. 2017, González et al. 2021, Culhane et al. 2022). Such traits are associated with the functional role of the species in the ecosystem. Small mammals are a highly trait-diverse group (Paglia et al. 2012). Their variable diet (e.g. frugivore, insectivore, nectarivore), for example, makes this group important agents of ecological processes like seed predation and dispersion (Vieira et al. 2003, DeMattia et al. 2004, Cáceres and Monteiro-

Filho 2007), invertebrate control (Camargo et al. 2022), and pollination (Amorim et al. 2020). Thus, understanding the impacts of wildfires under a functional-trait perspective can contribute to elucidate fire effects on ecological processes and ecosystem functioning (Cadotte et al. 2011). Usually, forest-dependent species (e.g. arboreal foraging, tree-nesting species) are negatively affected by tree loss and reduced canopy cover and vertical connectivity after fire (Mendonça et al. 2015, Camargo et al. 2018, Law et al. 2022). In contrast, generalist species (e.g. omnivorous diet) may be less affected by fire-induced changes in vegetation and food resources (Vieira and Briani 2013, Santos et al. 2014) or show higher foraging success in burned than in unburned areas (Zwolak et al. 2011). Furthermore, the increase in herbaceous cover in forests affected by fire may facilitate the entrance of species typical of open vegetation in forest habitats (Camargo et al. 2018). Such a shift in species composition may lead to a biotic homogenization process as the similarity between areas severely affected by wildfires increases (Steel et al. 2019).

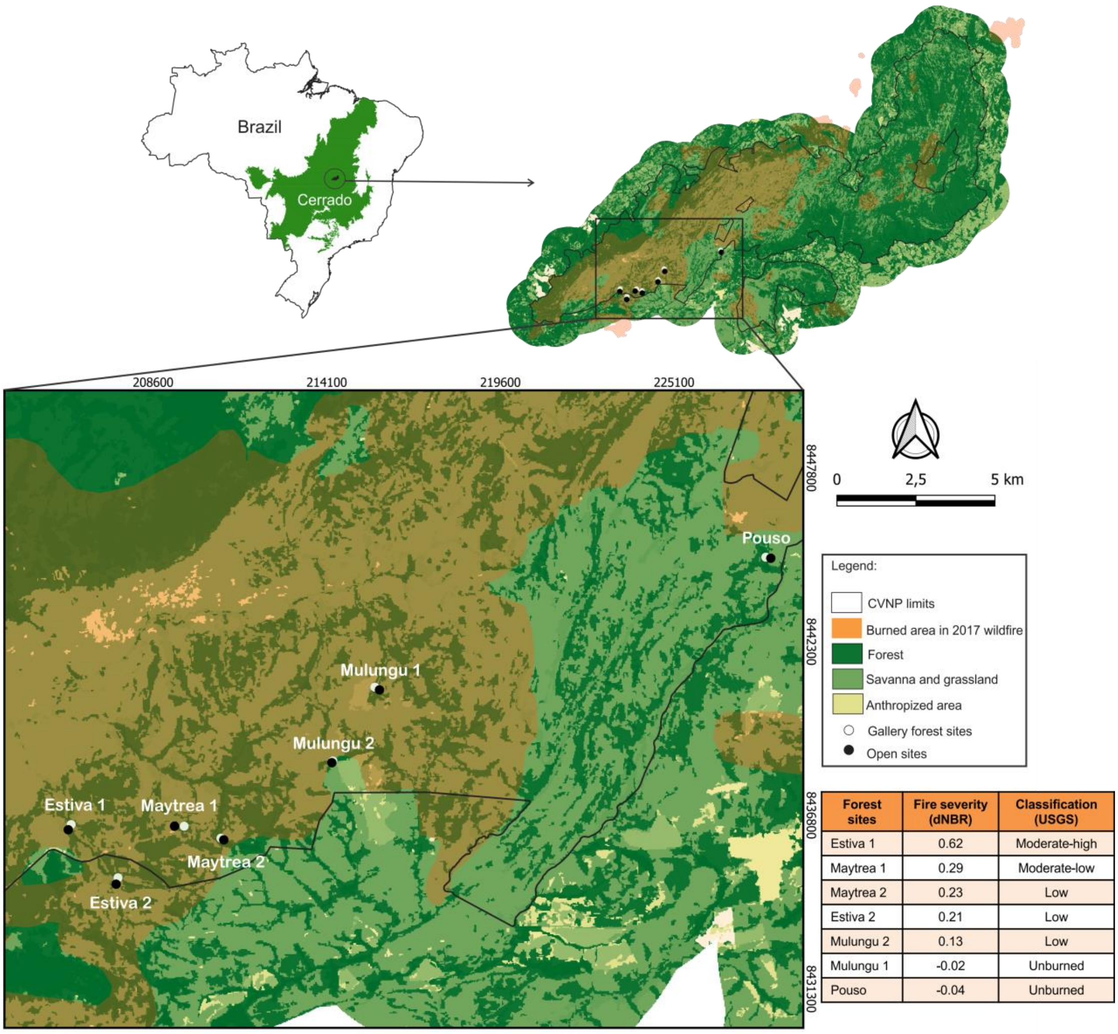
In this study, we evaluated the effects of fire severity on small mammal communities in two protected areas (Chapada dos Veadeiros National Park and Mata Funda Private Natural Heritage Reserve) in a Neotropical savanna. Our investigation focused on small mammal communities inhabiting gallery forests, a fire-sensitive formation. Three years before the sampling, the gallery forests of our study area experienced variate fire severity following a large wildfire in 2017. Specifically, our aims were: 1) to evaluate the effects of fire severity on small mammal richness (taxonomic and functional), taxonomic diversity, total abundance; and functional dispersion; 2) to test if small mammals restrict to forest habitats are affected by fire severity; and 3) to investigate how species composition of small mammal communities change in response to variation in fire severity. We hypothesize negative responses of mammal community metrics related to species richness, taxonomic diversity, functional dispersion, and total abundance to fire severity. This pattern would result from changes in forest vegetation structure and loss of critical resources essential to species in more severe fires (Mendonça et al. 2015, Flores et al. 2021, Culhane et al. 2022). We expect a decrease in the proportion of forest-specialist species as fire severity increases. Gallery forests experiencing more severe fire show canopy cover reduction, herbaceous layer increase, and high tree mortality (Flores et al. 2021, Poulos et al. 2021). Such changes can be adverse for forest-specialists. Finally, we expected small mammal communities in forests experiencing higher fire severity to be more similar to open formations. This homogenization would result from the reduction of forest-specialists species and the presence of generalists and species typical of open formations in burned forests (Camargo et al. 2018).

## Material and Methods

### *Study area*

We conducted this study in the Chapada dos Veadeiros National Park (CVNP) and Private Natural Heritage Reserve Mata Funda (PNHR Mata Funda). The CVNP is an integral protected reserve with approximately 240,000 ha. The RPPN is a reserve of sustainable use, adjacent to the CVNP, with 110 ha. Both reserves are located in the state of Goiás, Brazil. According to the Köppen-Geiger classification (Beck et al. 2018), the climate of the region is tropical with a dry winter season. The average annual temperature is 23.4ºC, with October registering the highest average temperature (monthly average = 25.3ºC) and June and July presenting the lowest temperatures of the year (monthly average = 20.8ºC). The average annual rainfall is 1500mm (mean from 1989 to 1999) and precipitation is not well distributed throughout the year (Cardoso et al. 2014). Thus, two seasons are defined according to the amount of monthly rainfall: the dry season, which occurs between May and September (mean monthly precipitation = 23.2mm), and the rainy season, which occurs between October and April (mean monthly precipitation = 197.6 mm) (Cardoso et al. 2014).

The vegetation of the region comprises a mosaic of grassland, savanna, and forest formations (Ribeiro and Walter 1998). Such pattern results, in part, from the occurrence of fire (Bueno et al. 2018) and the different susceptibilities and tolerances to fire shown by these distinct formations. Open areas, such as grasslands and savannas, have higher fire frequency but are more tolerant to the effects of this disturbance. In contrast, forest formations, such as gallery forests, are less susceptible to fire occurrence but suffer more severe impacts when affected by wildfires (Miranda et al. 2009). Although they occupy only 11% of the CVNP area (MapBiomas 2022), gallery forests are fundamental habitats for maintaining local diversity, supporting a large number of mammalian species (Bonvicino et al. 2005, Ribeiro et al. 2019).



| Forest sites | Fire severity (dNBR) | Classification (USGS) |
|---|---|---|
| Estiva 1 | 0.62 | Moderate-high |
| Maytrea 1 | 0.29 | Moderate-low |
| Maytrea 2 | 0.23 | Low |
| Estiva 2 | 0.21 | Low |
| Mulungu 2 | 0.13 | Low |
| Mulungu 1 | -0.02 | Unburned |
| Pouso | -0.04 | Unburned |

Figure 1. Location of gallery forests and open vegetation sites sampled in CVNP and PNHR Mata Funda within the area affected by the 2017 wildfire. Fire severity for each forest sampled is given by dNBR index with the corresponding classification.

To assess the effects of fire on the small mammal community in sensitive formations, we sampled seven gallery forests affected by different fire severity due to a large wildfire in October 2017 (Figure 1). Burning about 80% of the total area of the CVNP and reaching areas sensitive to fire, this wildfire is considered the most severe and the second most extensive since the creation of the CVNP (Flores et al. 2021). The impacts caused by the 2017 wildfire in gallery forests included canopy cover reduction, tree density decrease, and herbaceous cover increase (Flores et al. 2021). To compare small mammal communities between fire-sensitive and fire-dependent formations, we also sampled the open formations adjacent to gallery forests affected by the fire.

*Fire severity*

Fire severity is used to characterize fire effects on vegetation and belowground organic matter. In field, severity is measured by tree crown canopy scorch, crown volume kill, and tree mortality (Keeley 2009). Remotely, fire severity can be quantified comparing satellite images pre and post-fire to generate an index of severity (Escuin et al. 2008). Here, we used the Differentiated Burning Index by Normalized Ratio (dNBR) to estimate fire severity in selected gallery forests. This severity index is given by the difference between the NBR (Burning Index by Normalized Ratio) of the area before and after the fire. To obtain the NBR, we used Sentinel 2A satellite images of the study area before and after the 2017 wildfire. After processing and correcting the images, we applied the formula (B8 – B12) / (B8 + B12) to the spectral bands, in which B8 represents near infrared (10 m resolution) and B12 represents shortwave infrared (20m resolution). The difference between the NBR values (dNBR) informs about the severity of the fire. This index is widely applied to categorize the severity of fires, being related to measures of vegetation structure (Keeley 2009, Soverel et al. 2010). According to United States Geological Survey (USGS) (Lutes et al. 2006), fire severity can be categorized based on the dNBR values. This classification includes the following categories: high severity (dNBR > 0.66), moderate-high severity (0.44 to 0.65), moderate-low severity (0.27 to 0.43), low severity (0.1 to 0.26), unburned (-0.1 to 0.09), and enhance regrowth (< -0.1).

### *Small mammal sampling*

We conducted non-flying small mammal captures during two sampling campaigns, one in the wet season (February/2020 and March/2020) and one in the dry season (September/2020 and October/2020). In the first campaign, we sampled five gallery forests (Estiva1, Maytrea1, Maytrea2, Mulungu1, and Mulungu2). In the second campaign, we sampled seven gallery forests (Estiva1, Estiva2, Maytrea1, Maytrea2, Mulungu1, Mulungu2, and Pouso). All forests were partially or completely included in the 2017 wildfire area (Figure 1). To compare the community composition between gallery forests and open habitats, we also sampled small mammals in open-vegetation sites adjacent to each gallery forest. Forest site and the adjacent open site were sampled simultaneously. In each forest site, we established two linear transects with 30 permanent stations each. These transects were located in opposite sides of the water course present in gallery forests. Due to differences in forest and water courses width, distance between transects varied from 20 m to 55 m (average distance = 34.6 m). We maintained a distance of 15 m between the stations distributed along the transects. We placed two Sherman® traps with different sizes per station (small and large traps), one on the ground and the other in the understory (1.5 m high from the ground). We alternated the position (ground or understory) of the small and large traps between stations. In each site, we placed Tomahawk traps instead of large Sherman traps in five stations.

Similarly to gallery forest sampling, in the open sites we positioned two linear transects with 30 stations 15 m apart. We kept a minimum distance of 20 m and a maximum distance of 50 m from the edge of the forest sites to install the transects in the open sites. These transects were positioned parallel to the gallery forest, except for the Maytrea1 site. Due to the configuration of the Maytrea1 forest, we were not able to install transects in the open site parallel to the forest site. In this case, the transects in the open site were positioned perpendicular to the gallery forest. We sampled only the ground strata (but maintained two traps per station) in the open sites due to less structured vegetation in these areas.

In each site, the sampling period lasted for five nights. During this period, we visited the traps daily in search of captured mammals. All traps received a mixture of mashed banana, peanuts, sardine, and palm oil as bait. In addition, we put a slice of sweet potato inside the traps. This was necessary to avoid the complete depletion of bait inside the traps when ants removed the bait mixture. Moreover, we renewed the bait after two nights of sampling or when we observed the complete bait depletion inside the traps. In total, our sampling effort was 6,000 trap nights in the first campaign and 8,400 trap nights in the second campaign, totaling 14,400 trap nights. We identified all captured individuals at the species level (with few exceptions). Furthermore, we recorded body measurements, sex, age, and reproductive condition of all captured mammals. The individuals handling followed the guidelines established by the American Society of Mammal Zoologists (Sikes et al. 2011) and was approved by the Committee on Ethics in Animal Use of University of Brasília (CEUA, protocol code 134/2019). After handling, we returned the animals to the same station where they were captured.

### *Functional traits*

We extracted small mammal trait data from a large compilation of ecological attributes for 9993 and 5400 extant bird and mammal species (Wilman et al. 2014). From this compilation, we used information related to the species diet, use of strata, activity time, and body size. The diet information indicates the percentage of consumption of different food items (invertebrates, vertebrates, carrion, fruits, nectar, seeds, and other plant parts). The use of vertical strata categorizes the species in arboreal, scansorial or ground-dwelling according to their use of distinct vegetation strata. The activity period informs the presence or absence of foraging activity in three periods of the day: day, night, and twilight. Lastly, the body size describes the average body mass of adult individuals of each species.

Differentiation between pairs of species was not possible for two genera with similar species captured, *Calomys expulsus/Calomys tener* and *Oligoryzomys nigripes/Oligoryzomys mattogrossae*. According to Wilman et al. (2014), the species within the same genera presented the same traits for diet, strata use, and activity time. Besides, the species also have similar body masses which we averaged for each genus. Thus, we treated these pairs of species within the same genera as unique functional species, *Calomys* spp and *Oligoryzomys* spp, in our functional analysis. Identification at the species level for *Oecomys sp.*1, *Oecomys sp*.2, and *Oxymycterus* sp.2 was also not possible. Again, diet, strata use, and activity time were the same for species belonging to the same genus (Wilman et al. 2014). We deal with the minor variation in body size reported between species by using the mean weight of the individuals captured in our study. In general, it is unlikely that the incomplete identification of some species affected our analysis once the species within the same genera have similar ecological traits. Trait information for the species captured is in Supplementary Material S1.

*Statistical analyses*

We analyzed the effects of fire severity on small mammals by modeling several community metrics related to taxonomic and functional dimensions. For each forest site, we calculated the following taxonomic metrics: taxonomic richness, taxonomic diversity, total abundance, and proportion of forest-specialists. We estimated taxonomic richness and diversity in iNEXT (Chao et al. 2014, Chao et al. 2016) using the Hill numbers for $q = 0$ (richness) and $q = 1$ (Shannon-Wiener diversity). For comparison across sites, we standardized rarefied values for all sites considering the site with less captures (Pouso, $n = 7$). For total abundance, we used the number of individuals captured for 100 trap nights as a proxy for the abundance of small mammals. The proportion of forest specialist was calculated as the relative abundance of forest-specialist individuals (number of forest-individuals captured divided by all individuals captured).

Moreover, we calculated two functional metrics, functional richness and functional dispersion. Functional richness was estimated by the total length of the branches of the functional dendrogram (Petchey and Gaston 2006). To generate this dendrogram, we used the functional trait matrix for small mammals (Supplementary Material S1) to create a distance matrix applying the Gower distance method. Such a method is appropriate when analyzing qualitative and quantitative attributes together (Podani and Schmera 2006). Next, we utilized the distance matrix to generate several dendrograms based on different clustering methods (ward, UPGMA, single, complete, UPGMC, WPGMC, and WPGMA). Then, we selected the clustering method with less loss of information contained in the original matrix by comparing the cophenetic correlation coefficient of these methods. The Unweighted Pair Group Method with Arithmetic Mean (UPGMA) presented a higher coefficient (0.91) and was the clustering method applied in the dendrogram used for functional richness calculation (Supplementary Material S2). We weighted functional richness by abundance of each species (individuals/100 traps). We conducted this analysis in the “fundiv” package (Bartomeus 2013) for R environment (R Core Team 2022).

We also estimated the functional dispersion of the studied communities. This metric represents the average distance of species to the centroid of the functional space composed of all species in the sample unit (Laliberté and Legendre 2010). In this method, the average distance is balanced by the species relative abundance while the centroid is orientated towards the most abundant species. For the calculation of functional dispersion, we generated a trait-based dendrogram using Gower distance while accounting for the relative abundance of species. Whereas functional richness is related to the size of the functional space and represents the sum of differences between species, functional dispersion measures how dispersed the functional space is, being related to the average difference between species (Mammola et al. 2021).

We investigated the effect of fire severity on the multiple community metrics separately. Thus, we fitted a linear regression of fire severity (dNBR index) against each response variable (community metrics). Residual distribution was close to normal distribution for all regressions (quantile-quantile plot visualization). Because of that, we assumed a normal distribution for all modeling analyses. For model validation, we compared the residuals with predicted values and the predictor variables. We did not detect any pattern in the plotted distribution of points. Therefore, all regressions were validated. Finally, we applied the Moran Index associated with a hypothesis test to identify possible spatial autocorrelation in our data. For each response variable, we used residuals of the regressions in the analysis. The results indicated that none of the response variables presented significant spatial autocorrelation. We established a significance level (α) of 0.05 to test the effect of fire severity on our response variables. We fitted linear regressions and conducted the analysis of spatial autocorrelation in the “stats” and “ape” (Paradis et al. 2004) packages for R environmental (R Core Team 2022), respectively.

We evaluated the species composition patterns across fire severity and habitat types (gallery forest and open vegetation) using a nonmetric multidimensional scaling (NMDS) ordination. To verify if variation in species composition could be explained by fire severity, we applied linear regressions with fire severity as the predictor variable and the first and second axis from NMDS as response variables. NMDS and regression analysis were conducted in “vegan” (Oksanen et al. 2013) and “stats” package for R environmental (R Core Team 2022).

## Results

We captured 407 individuals (238 individuals in forest sites and 169 in open-vegetation sites), resulting in trapping success of 3.38%. We recorded 13 rodent species and two marsupial species (Supplementary Material S3). The most common species was *Oxymycterus delator*. This rodent occurred mainly in open sites. In forest sites, the rodent *Rhipidomys macrurus* was the most common species. Fire severity index, dNBR, ranged from -0.04 (Pouso) to 0.62 (Estiva1) (Figure 1). According to dNBR values, forests were affected by four fire severity classes: 1) unburned, this class included Mulungu1 and Pouso forests; 2) low severity, included Maytrea2, Estiva2, and Mulungu2; 3) low-moderate severity, included Maytrea1; and 4) moderate-high severity, this class included Estiva1 forest and was the highest severity class observed.

Linear regression analysis indicated mixed effects of fire severity on small mammal community metrics (Table 1). We found a positive effect of dNBR index, our measure for fire severity, on small mammal taxonomic diversity (Figure 2a). In contrast, dNBR index strongly reduced the proportion of forest-specialist species captured in gallery forests (Figure 2b).

Although taxonomic richness and total abundance of small mammals did not respond to fire severity variation.

Fire severity influenced small mammal communities functionally (Table 1). Linear regression results indicated a positive effect of dNBR index on functional dispersion (Figure 2c). Functional richness seems to respond positively to dNBR but fire severity effect was not significant ($p = 0.06$; Table 1).

Table 1. Linear regression analysis coefficients (β) and respective standard errors (SE), t-values, and p-values. Significant relationship ($p < 0.05$) between response variables (taxonomic richness, taxonomic diversity, total abundance, proportion of forest specialists, functional richness, and functional dispersion) and fire severity are indicated by "*". The models adjustment are given by $R^2$.

| | β | SE | t-value | p-value | $R^2$ |
|---|---|---|---|---|---|
| **Taxonomic richness** | | | | | |
| Intercept | 2.499 | 0.499 | 5.007 | 0.004 | 0.43 |
| Fire severity | 3.367 | 1.714 | 1.965 | 0.107 | |
| **Taxonomic diversity** | | | | | |
| Intercept | 1.978 | 0.395 | 5.005 | 0.004 | 0.57 |
| Fire severity | 3.530 | 1.357 | 2.602 | 0.048***** | |
| **Total abundance** | | | | | |
| Intercept | 2.465 | 0.773 | 3.188 | 0.024 | 0.24 |
| Fire severity | 3.383 | 2.655 | 1.274 | 0.259 | |
| **Proportion of forest specialists** | | | | | |
| Intercept | 0.918 | 0.026 | 35.589 | < 0.0001 | 0.96 |
| Fire severity | -1.067 | 0.089 | -12.048 | < 0.0001***** | |
| **Functional richness** | | | | | |
| Intercept | 0.481 | 0.077 | 6.274 | 0.002 | 0.53 |
| Fire severity | 0.626 | 0.263 | 2.377 | 0.063 | |
| **Functional dispersion** | | | | | |
| Intercept | 0.105 | 0.022 | 4.713 | 0.005 | 0.65 |
| Fire severity | 0.236 | 0.076 | 3.100 | 0.027***** | |

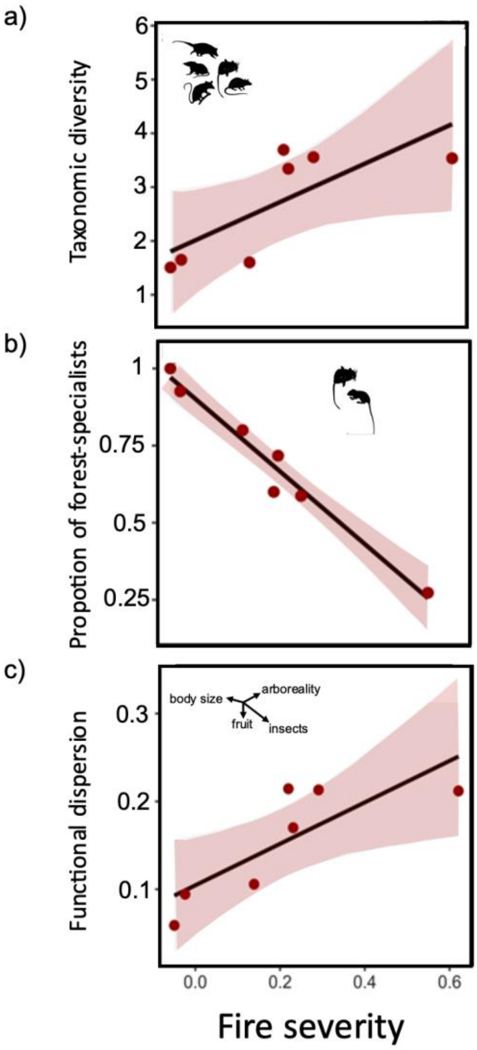


Figure 2. Small mammal community responses to fire severity index (dNBR) in gallery forest in the Cerrado. Taxonomic metrics presented are taxonomic diversity (exponential of Shannon entropy; a), proportion of forest specialists in the communities (b) and functional dispersion of communities (c). Complete statistical results for all community metrics evaluated are presented in Table 1.

Small mammal species were not equally captured across the different classes of fire severity, suggesting an effect of fire severity on species composition. *C. scotti* and *Oligoryzomys* spp rodents were present only in the forest affected by moderate-high fire severity (the highest fire severity category in our study area) (Figure 3). Similarly, *Necromys lasiurus*, *Oxymycterus delator*, *Nectomys rattus*, *Oecomys* sp1, and *Oecomys* sp.2 were captured more frequently in the forests that experienced moderate-high or low-moderate fire severity. Except for *Nectomys rattus* and *Oecomys* sp1, all forest-specialist species were absent from the forest in the highest fire severity class. These results are in line with the significant and negative effect of fire severity on forest-specialists' relative abundance (Figure 2).

Variation in species composition was also revealed by the NMDS analysis (Figure 4a). In the NMDS ordination, the proximity between objects corresponds to their similarity. Thus, our results showed that the 1st NMDS axis markedly discriminated the community composition of forest and open sites (Figure 4b). Moreover, the two forests that had the highest classification of fire severity (Maytrea1 and Estiva1) were closer to their adjacent open sites along the 1st NMDS axis than those unburned or within the low severity class (Estiva2 seems to be an exception). This pattern suggests higher composition similarity between forests and open sites where fire was severer.

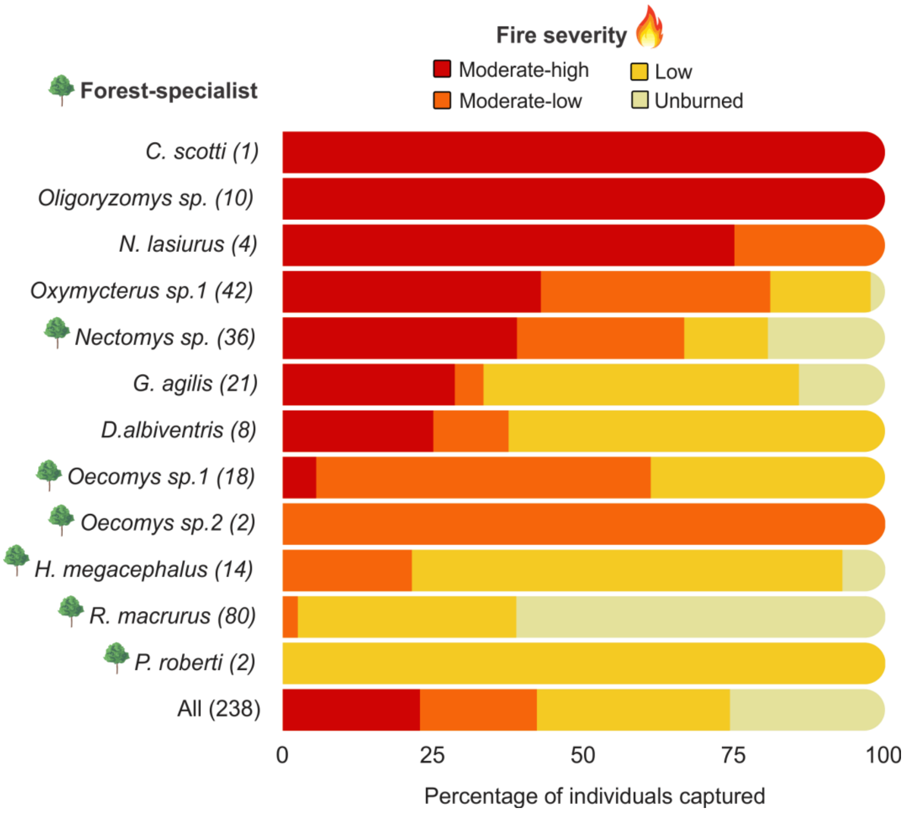


Figure 3. Pattern of small mammal captures in gallery forests Cerrado across different classes of fire severity. Forest-specialist species are indicated with a tree symbol. Other species were considered generalists or typical of open habitats. Fire severity classes follow USGS categorization for dNBR fire severity index (Lutes et al. 2006). Absolute numbers for captures are in parenthesis.

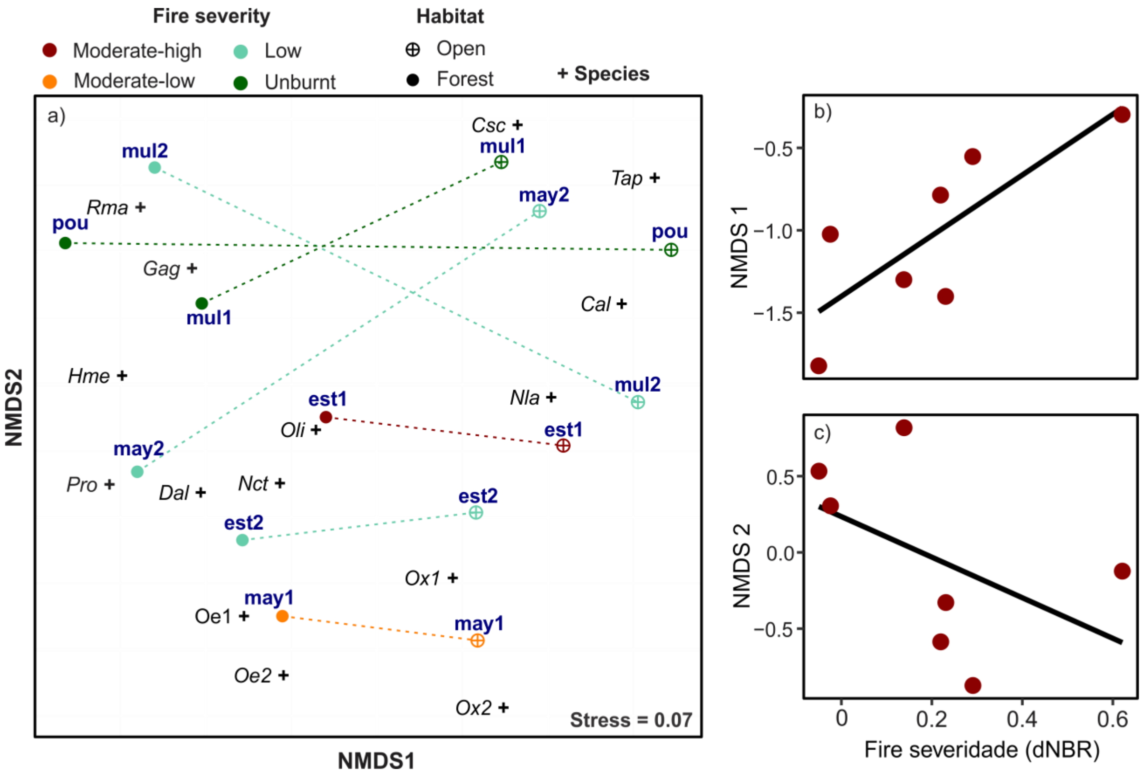


Figure 4. Small mammal community composition across habitat types and fire severity classes for gallery forests and open-vegetation habitats in Cerrado as showed by a) Nonmetric multidimensional scaling analysis (NMDS) and relationship between b) first and c) second NMDS axis with fire severity. Fire severity classes follow USGS categorization for dNBR fire severity index. Broken lines link forest sites with their respective adjacent open-area sites. Abbreviations for forest and adjacent open sites are defined as follows: est1 = Estiva 1, est2 = Estiva 2, mul1= Mulungu 1, mul 2 = Mulungu 2, may1 = Maytrea 1, may2 = Maytrea 2, and pou = Pouso. Abbreviations for small mammal species are defined as follows: Dal = *Didelphis albiventris*, Gag = *Gracilinanus agilis*, Cal = *Calomys* spp, Oe1 = *Oecomys* sp1, Oe2 = *Oecomys* sp2, Oli = *Oligoryzomys* spp, Nct = *Nectomys rattus*, Hme = *Hylaeamys megacephalus*, Ox1 = *Oxymycterus delator*, Ox2 = *Oxymycterus* sp2, Nla = *Necromys lasiurus*, Rma = *Rhipidomys macrurus*, Pro = *Proechimys roberti*, Csc = *Cerradomys scotti*, and Tap = *Thrichomys apereoides*. Regression results for the relationship between NMDS axis and fire severity were b) NMDS1: β-estimate = 1.84, $r^2 = 0.61$, $p = 0.03$, and c) NMDS2: β-estimate = 1.33, $r^2 = 0.23$, $p = 0.26$.

## Discussion

We investigated the effects of fire severity on small mammal communities in fire-sensitive forests affected by a large wildfire. Our results indicated mixed effects of fire severity on community metrics. Small mammal diversity increased with fire severity. This increase, however, seems to occur at the cost of forest-specialist species. The proportion of species associated with forest habitats was markedly lower in sites affected by higher fire severity. Most forest-specialist species were absent from the forest that experienced the highest fire severity. We also observed that fire severity affects small mammal communities in the functional dimension, since the functional dispersion of communities was higher in forests impacted by more severe fires. Moreover, fire-induced changes in species composition of forest habitats are probably increasing the similarity between forests and open sites.

We found a positive effect of fire severity on small mammal diversity. Animal responses to fire are often driven by changes in vegetation structure and post-disturbance resource availability (Roberts et al. 2008, Diffendorfer et al. 2012, Camargo et al. 2018, Palm et al. 2022, Zylinski et al. 2022). The intensity of such changes is greater in forests impacted by more severe wildfires (Poulos et al. 2021). Thus, it is expected for fire-induced changes to reduce the density or exclude sensitive species (Mendonça et al. 2015) and amplify the abundance of a few tolerant species (Zwolak 2009, Culhane et al. 2022). Rather, our findings suggest that forests severely burned had more species with similar abundances than forests less impacted by fire. Diffendorfer et al. (2012) found a similar result when evaluating the community structure of small mammals in Chaparral after disturbance. In the first two years after a wildfire, they observed more even abundance of species in burned than in unburned areas which were dominated by one rodent species. In our study, forests with the lowest severity index presented few species and high dominance of *R. macrurus*, a forest-specialist rodent. This dominance determined the low diversity in these sites. This pattern follows the intermediate disturbance hypothesis that states lower diversity in little or no disturbed areas when compared to areas subject to some disturbance (Connell 1978). However, we reinforce that this increase in diversity was related to the “invasion” of open-habitat species into forest habitats and the reduction of forest-specialist species.

Positive response of communities to fire severity may arise when changes in vegetation structure favor the presence of disturbed-dependent species (Greenberg et al. 2023). Small mammal communities of forested habitats (dry woodlands) affected by fire in the Cerrado may show an increase in the presence of open-habitat species in response to fire-induced changes in vegetation (Camargo et al. 2018). Furthermore, fire may have minor effects on generalist species (Vieira and Briani 2013, Santos et al. 2014, Dickman and Happold 2022, Rossi and Leiner 2023) preventing species loss. Indeed, in our study area open-habitat and generalist small mammals (*C. scotti*, *Oligoryzomys* spp, *N. lasiurus*, and *Oxymycterus delator*) were more frequent in forests affected by higher levels of fire severity. This probably contributed to the greater diversity associated with severe fire.

Another factor that could have influenced the positive response of small mammal diversity to fire severity is the presence of unburned patches within the wildfire extension (Leonard et al. 2014). These patches may represent refuges for fauna allowing individuals to survive during wildfires and persist in post-fire environments (Watson et al. 2012, Robinson et al. 2013, Fordyce et al. 2016). For example, Mazzella and Koprowski (2020) observed that flying squirrel use of severely burned sites was possible due to canopy cover presence and low tree mortality within the burned area. Likewise, site occupancy of an arboreal mammal was positively influenced by the proportion of unburned and unlogged areas in the landscape (Lefoe et al. 2022). In our study area, even the gallery forest that experienced the highest level of fire severity (Estiva1) showed some canopy cover and understory structure (CVS, personal observation). Also, mammal sampling occurred three years after the 2017 wildfire. This period could have allowed post-fire colonization and re-colonization as succession progressed (Fox 1982, Fisher and Wilkinson 2005). Together, these factors may have enabled the presence of scansorial-generalist species like *G. agilis* and *D. albiventris* and the forest-specialist water rat *Nectomys rattus*. in severely burned sites. The occurrence of such species combined with the presence of open-habitat species probably increased the local diversity.

In contrast to community diversity, we observed a marked decline in forest-specialist mammals as fire severity increased, with fire severity explaining almost all variation in the proportion of forest-specialist species across sampling sites ($R^2 = 0.96$). This result corroborates previous studies observing adverse fire effects on forest-dependent species (Mendonça et al. 2015, Camargo et al. 2018, Flanagan-Moodie et al. 2018, Cazetta and Vieira 2021, Jones et al. 2021, Campbell-Jones et al. 2022). Four of six forest-specialist species were absent from Estiva1, the most severely burned forest, but these species dominated communities less affected by fire. *Rhipidomys macrurus*, the most common species in less impacted forests, shows strong negative responses to fire occurrence, being absent from burned Cerrado forests during the year following fire disturbance (Mendonça et al. 2015, Camargo et al. 2018). Our findings indicated that this absence may last for at least three years after moderate-high severe wildfires. Such intense responses observed for *R. macrurus* and other forest-specialist species suggest high mortality during wildfire events or, surviving the fire, individuals were unable to deal with the fire-altered environment. This pattern is expected for species inhabiting fire-sensitive habitats that rarely burn such as gallery forests. In these areas, animals may lack adaptive responses to fire since this disturbance does not represent a selective force (Nimmo et al. 2021).

Taxonomic responses to fire were accompanied by functional variation in small mammal communities submitted to different levels of fire severity. Results from linear regression demonstrated increasing in functional dispersion as fire severity increases. There was also a positive but non-significant relationship ($r^2 = 0.53$, $p = 0.06$) between functional richness and fire severity. Functional richness represents the size of the trait space whereas functional dispersion is related to the average differences between species in the trait space (Mammola et al. 2021). Our findings suggest that fire severity had less impact on trait space size, which may be due to more trait homogeneous communities not exhibiting functional responses to disturbances (Hu et al. 2016). Small mammal communities in Cerrado forests may present minor variations in body mass (> 70% of species have less than 100g), period of activity, and few species restrict their diets to specific food types (Wilman et al. 2014). Thus, weak fire severity effect on functional richness could be associated with minor differences in the space trait size of the communities. Such redundancy in small mammal functional traits is particularly important in habitats affected by fire since functional redundancy may promote community stability and resilience to disturbances (Biggs et al. 2020).

In contrast, fire severity seems to affect the distribution of observations in trait space, leading to more functionally dispersed communities. Higher functional dispersion can arise in more heterogeneous environments due to effective resource partitioning between species with different traits (Stein et al. 2014, Sukma et al. 2019). Non-uniform burning pattern in forests may create a heterogeneous habitat that permits the coexistence of species with variable requirements. In our study, the presence of open-habitat species in forests affected by severe fires probably contributed to higher functional dispersion in these areas. For example, forests less impacted by fire were dominated by species that rely mainly on fruits and other plant parts (Wilman et al. 2014, Ribeiro et al. 2019). Conversely, forests affected by more severe fires counted with species showing variable feeding habits (e.g. invertebrates, vertebrates, fruits) and more balanced abundance between species. These forests also presented species with a more diverse use of strata (ground, scansorial, and arboreal) than forests less affected by fire (ground and arboreal). Even with severe-affected forests showing more functional dispersion, ecological processes associated with species traits may be compromised if key species are negatively affected by disturbances (Rodriguez-Cabal et al. 2007, Pires and Galetti 2023). For instance, the absence of predominantly frugivorous species such as *R. macrurus* and *H. megacephalus* from sites with higher fire severity may reduce seed dispersion, possibly limiting forest regeneration after fire.

The fire-induced changes in community composition that we observed in more impacted forests may explain the higher similarity between these sites and open habitats. The NMDS plots placed forest sites experiencing severe fires closer to open habitats than forest sites affected by low-severe fires or unburned. This suggests higher similarity in species composition between forest and open habitats where fire was more severe. Usually, large severe wildfires create homogenous landscapes (Cassell et al. 2019). In gallery forests, the reduction in canopy cover and the proliferation of herbaceous layer (Flores et al. 2021) generate habitat conditions with similarities to those found in adjacent open habitats (e.g. grasslands). In the Cerrado, forested habitats occur along water courses (e.g. gallery forests, palm swamps) in a matrix of native open vegetation (Lewis et al. 2022). Such configuration probably facilitated the entrance of open-habitat mammal species into forests after fire-induced changes in vegetation. Although fire may promote α-diversity by generating local habitat heterogeneity, at broader scales, severe fires could decrease β-diversity by reducing differences between habitats. Accordingly, Steel et al. (2019) found higher similarity in bat community composition between forests affected by highly severe fires. These findings highlight the potential for biota homogenization as large severe wildfires become more frequent.

The results presented here contribute to the knowledge of how wildfire severity affects small mammal communities in a fire-sensitive habitat. Such knowledge is crucial considering the increasing frequency of severe wildfires and their impacts on ecosystems (Tomas et al. 2021, Iglesias et al. 2022). Nevertheless, the opportunistic character of our study implies a conservative interpretation of the results. Natural experiments like ours may be limited by the number of independent sampling sites, treatment levels, and lack of pre-fire data (Driscoll et al. 2010). For example, we could not address potential pre-fire differences in mammal communities between sampling sites as we had no data from the period before the 2017 wildfire. Yet, our findings had robust support from analysis and are consistent with other studies evaluating fire effects on fauna communities (Diffendorfer et al. 2012, Camargo et al. 2018, Culhane et al. 2022). Moreover, even with few sampling sites ($n = 7$), we were able to find clear relationships with a considerable level of explanation ($r^2$ range: 0.57 to 0.96). Thus, our study reinforces the valuable information offered by opportunistic studies for biodiversity conservation of fire-sensitive habitats.

## Conclusions

We evaluated the effects of fire severity on small mammal communities after a large wildfire in a fire-sensitive habitat. We demonstrated that small mammal taxonomic diversity and functional dispersion responded positively to fire severity in gallery forests. These responses are probably due to fire-induced changes in vegetation structure and heterogeneous burning patterns favoring the occurrence of generalists and open-habitat species in more severely burned forests. Despite this general positive response to fire severity, our results revealed that forest-specialists are strongly and negatively affected by increasing fire severity. Such impact may compromise ecosystem processes crucial to forest regeneration following disturbances. Finally, the changes in species composition that we observed could lead to a biotic homogenization as communities from severely burned forest become more similar to open-habitat communities. Our results highlight the relevance of opportunistic studies to unveil patterns of community response to large severe wildfires.

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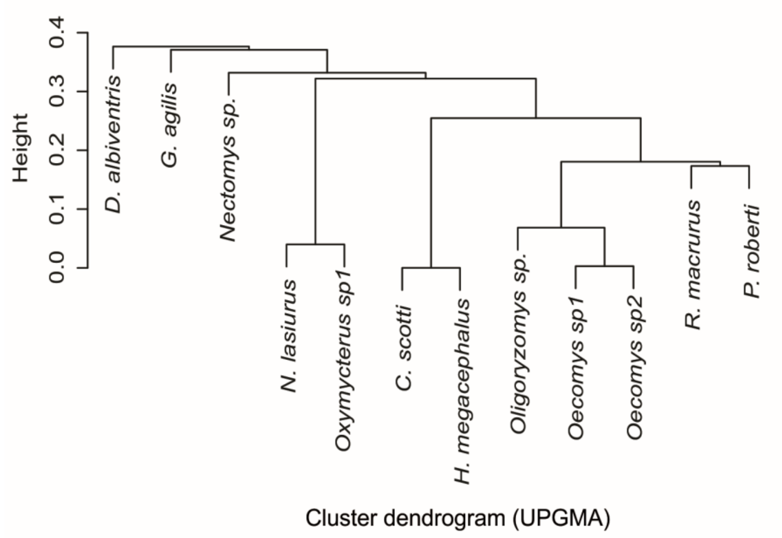
## Supplementary material

S1. Matrix of functional attributes of small mammals captured in gallery forest and open habitats in CVNP and PNHR Mata Funda. Invert = invertebrates; vert1 = mammals and birds; vert2 = reptiles, amphibians, and salamanders; vert3 = fish; scav = remains, carrion; S = scansorial; G = ground; A = arboreal; not = nocturnal; crepusc = crepuscular; diur = diurnal. Data from Wilman et al. 2014.

| **Species** | **invert** | **vert1** | **vert2** | **vert3** | **scav** | **fruit** | **nect** | **seed** | **plant** | **strata use** | **not** | **crepusc** | **diur** | **weight (kg)** |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Calomys* spp | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 100 | G | 1 | 1 | 0 | 0.054 |
| *Cerradomys scotti* | 20 | 0 | 0 | 0 | 0 | 20 | 0 | 20 | 40 | G | 1 | 1 | 1 | 0.058 |
| *Didelphis albiventris* | 20 | 0 | 0 | 0 | 30 | 0 | 0 | 0 | 20 | S | 1 | 0 | 0 | 0.904 |
| *Gracilinanus agilis* | 50 | 0 | 0 | 0 | 0 | 30 | 20 | 0 | 0 | S | 1 | 1 | 0 | 0.022 |
| *Hylaeamys megacephalus* | 20 | 0 | 0 | 0 | 0 | 20 | 0 | 20 | 40 | G | 1 | 1 | 1 | 0.057 |
| *Necromys lasiurus* | 70 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 30 | G | 0 | 0 | 1 | 0.040 |
| *Nectomys rattus* | 30 | 0 | 20 | 20 | 0 | 0 | 0 | 0 | 30 | G | 1 | 0 | 0 | 0.191 |
| *Oecomys* sp1 | 0 | 0 | 0 | 0 | 0 | 50 | 0 | 50 | 0 | G | 1 | 0 | 0 | 0.063 |
| *Oecomys* sp2 | 0 | 0 | 0 | 0 | 0 | 50 | 0 | 50 | 0 | G | 1 | 0 | 0 | 0.026 |
| *Oligoryzomys* spp | 30 | 0 | 0 | 0 | 0 | 30 | 0 | 40 | 0 | G | 1 | 0 | 0 | 0.022 |
| *Oxymycterus delator* | 90 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 10 | G | 0 | 0 | 1 | 0.085 |
| *Oxymycterus* sp2 | 90 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 10 | G | 0 | 0 | 1 | 0.083 |
| *Proechimys roberti* | 0 | 0 | 0 | 0 | 0 | 20 | 0 | 10 | 70 | G | 1 | 0 | 0 | 0.285 |
| *Rhipidomys macrurus* | 20 | 0 | 0 | 0 | 0 | 20 | 0 | 30 | 30 | A | 1 | 0 | 0 | 0.080 |
| *Thrichomys sp.* | 0 | 0 | 0 | 0 | 0 | 60 | 0 | 40 | 0 | G | 1 | 0 | 0 | 0.339 |



S2. Functional dendrogram of small mammal community of the Chapada dos Veadeiros National Park and Private Natural Heritage Reserve Mata Funda in Cerrado. Height = Gower distance, clustering method = UPGMA; cophenetic correlation coefficient = 0.92.

S3. Number of captures of small mammal species recorded in Chapada dos Veadeiros National Park and Private Natural Heritage Reserve Mata Funda in Cerrado.

| **Species** | **Gallery forest** | **Open habitat** | **Order** | **Habitat affinity** |
|---|---|---|---|---|
| *Calomys* spp | 0 | 15 | Rodentia | Open |
| *Cerradomys scotti* | 1 | 4 | Rodentia | Open |
| *Didelphis albiventris* | 8 | 0 | Didelphimorphia | Generalist |
| *Gracilinanus agilis* | 21 | 0 | Didelphimorphia | Generalist |
| *Hylaeamys megacephalus* | 14 | 0 | Rodentia | Forest |
| *Necromys lasiurus* | 4 | 44 | Rodentia | Open |
| *Nectomys rattus* | 36 | 5 | Rodentia | Forest |
| *Oecomys* sp1 | 18 | 1 | Rodentia | Forest |
| *Oecomys* sp2 | 2 | 0 | Rodentia | Forest |
| *Oligoryzomys* spp | 10 | 0 | Rodentia | Generalist |
| *Oxymycterus delator* | 42 | 94 | Rodentia | Open |
| *Oxymycterus* sp2 | 0 | 1 | Rodentia | Open |
| *Proechimys roberti* | 2 | 0 | Rodentia | Forest |
| *Rhipidomys macrurus* | 80 | 1 | Rodentia | Forest |
| *Thrichomys apereoides* | 0 | 4 | Rodentia | Open |

# CONSIDERAÇÕES FINAIS

A variação temporal e espacial do regime do fogo afetou populações e comunidades de pequenos, médios e grandes mamíferos do Cerrado brasileiro. Esse resultado evidencia o papel fundamental do fogo em moldar os padrões de diversidade e uso do habitat em ecossistemas frequentemente afetados por esse distúrbio. A variação espacial na frequência, no tempo decorrido desde a última ocorrência de fogo (histórico) e severidade do fogo cria ambientes heterogêneos, provavelmente afetando a distribuição de recursos, competidores e predadores. Tais mudanças provocadas pelo fogo parecem ter efeitos distintos sobre a biodiversidade. Nossos resultados indicaram que a ocorrência de efeitos positivos, negativos ou a ausência de efeito do fogo depende da métrica avaliada e de características intrínsecas às espécies. Além disso, nós constatamos que esses efeitos podem ocorrer em escalas espaciais diferentes e que mesmo variações no regime do fogo em escalas pequenas afetam médios e grandes mamíferos.

A pirodiversidade, isto é, a heterogeneidade temporal e espacial criada pelo regime de fogo foi um fator determinante para a riqueza, diversidade e abundância de médios e grandes mamíferos do Cerrado. Nossos resultados sugerem que áreas mais pirodiversas, em termos de histórico do fogo, podem sustentar comunidades mais ricas taxonômica e funcionalmente. Esse resultado reforça a importância de ambientes heterogêneos em permitir a coexistência de espécies com diferentes requerimentos e funções no ecossistema. Porém, ressalta-se que o efeito da pirodiversidade sobre a diversidade e abundância de mamíferos é limitado. Tal limitação pode estar associada às respostas individuais das espécies ao fogo. De fato, nós observamos que o uso do mosaico de fogo diferiu entre as espécies estudadas. Nós sugerimos que estudos abordando concomitantemente os efeitos do fogo sobre as populações e comunidades fornecem um entendimento mais holístico dos mecanismos por trás dos padrões ecológicos observados.

Apesar do suporte variado que recebe de estudos empíricos em diferentes ecossistemas e taxa, a hipótese de que “pirodiversidade gera biodiversidade” inspira as estratégias de manejo do fogo com fins conservativos. Baseados nessa informação e nos nossos resultados, nós propomos que, para proteger a biodiversidade, o manejo do fogo deve ser baseado no contexto local e considerar as respostas distintas das espécies ao regime do fogo. Como pode ser desafiador atender às necessidades de todas as espécies, o manejo do fogo pode focar em espécies com respostas mais fortes ao fogo enquanto a comunidade como um todo é monitorada. É importante destacar que este é o primeiro estudo a testar a hipótese de pirodiversidade-biodiversidade para médios e grandes mamíferos em uma savana neotropical (Cerrado). Dessa forma, nós recomendamos que mais estudos sejam conduzidos a fim de testar essa hipótese. Isso é particularmente relevante diante das mudanças no regime natural do fogo e da recente implantação de programas de queimas prescritas em áreas protegidas no Brasil.

A redução de grandes incêndios é um dos principais objetivos de programas de manejo do fogo atualmente coordenados no Cerrado. Os eventos extremos de fogo geram impactos negativos sobre a biodiversidade, principalmente em habitats sensíveis a esse distúrbio. Nas matas de galeria, pequenos mamíferos dependentes de ambientes florestais mostraram-se altamente vulneráveis à severidade do fogo. Visto que essas espécies são potenciais dispersoras de sementes, esse efeito da severidade pode representar o comprometimento de processos ecológicos fundamentais para a regeneração dessas matas após o fogo. Além disso, nossos resultados indicam que o aumento da frequência de incêndios severos pode levar à homogeneização das comunidades biológicas. Incêndios mais severos modificam a estrutura da vegetação das matas, favorecendo a ocorrência de espécies típicas de habitats abertos. Em conjunto, a redução de espécies típicas de habitats florestais e a “invasão” de espécies de áreas abertas nas matas de galeria diminuem a diversidade biológica da paisagem.