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**Ecologia das interações entre plantas e pequenos mamíferos no Cerrado: avaliação de  
desenho amostral, efeitos da severidade do fogo e disponibilidade de recursos**

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**Ecologia das interações entre plantas e pequenos mamíferos no Cerrado: avaliação de desenho amostral, efeitos da severidade do fogo e disponibilidade de recursos**

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## Resumo

A distribuição das espécies e das suas interações ecológicas varia espacial e temporalmente. As comunidades biológicas e por consequência suas interações podem ser afetadas por distúrbios como os incêndios, que são capazes de alterar a estrutura dos habitats e a disponibilidade de recursos. Para entendermos os padrões de distribuição das espécies, assim como detectar alterações após perturbações, é necessário mensurar adequadamente a diversidade dos grupos estudados. Isso é um desafio, sobretudo para grupos altamente diversos, como os pequenos mamíferos voadores neotropicais e em ambientes compostos por diferentes fisionomias, como o Cerrado. Nesse estudo, avaliamos: 1) como o desenho amostral afeta as estimativas de diversidade de pequenos mamíferos no Cerrado; 2) os efeitos da severidade do fogo, da disponibilidade de recursos e da estrutura do habitat nas redes de interação planta-animal das quais participam os pequenos mamíferos no Cerrado; e 3) os efeitos da severidade do fogo sobre o potencial de dispersão de sementes por pequenos mamíferos no Cerrado. O desenho amostral utilizado na amostragem de comunidades de pequenos mamíferos no Cerrado afetou as estimativas de abundância e riqueza desse grupo. Amostragens que utilizaram em conjunto armadilhas tipo gaiola e as de interceptação e queda (*pitfalls*) e que consideraram as duas estações climáticas (i. e. seca e chuvosa) foram mais eficientes, especialmente nas formações abertas. A análise de DNA *metabarcoding* nos permitiu detectar uma riqueza de plantas consumidas por roedores e marsupiais muito acima do que é possível através de métodos tradicionais. No total, identificamos 211 espécies de plantas nas fezes desses animais, contrastando com as 28 espécies de sementes detectadas pela análise visual em estereoscópio. As interações planta-animal entre pequenos mamíferos e a flora do Cerrado foram afetadas pelo fogo. A severidade do fogo tornou as redes de interações mais aninhadas, e com menor grau de modularidade e especialização nas matas de galeria atingidas mais severamente pelo incêndio. Nessas áreas, a diversidade de interações foi maior, possivelmente em decorrência da invasão

de espécies típicas de habitats abertos, favorecidas pelas modificações na estrutura do habitat causadas pelo fogo. A disponibilidade de recursos (i. e. frutos) também afetou a estrutura das redes planta-animal, embora essa disponibilidade não tenha apresentado relação direta com a severidade do fogo. Já a estrutura do habitat não afetou diretamente a estrutura das redes planta-animal. No entanto, esse fator foi explicado em grande parte pela severidade do fogo. Portanto, é possível que seus efeitos sobre a estrutura das interações tenham sido indiretos. O fogo também afetou o papel dos pequenos mamíferos como potenciais dispersores de sementes. Houve uma redução no número de potenciais dispersores e na diversidade de plantas dispersas pelo grupo nas matas de galeria mais severamente atingidas pelo incêndio. Esses efeitos foram espécie-específicos, variando ao longo do gradiente de severidade do fogo. Os resultados apresentados no presente estudo indicam que incêndios severos modificam as comunidades de pequenos mamíferos que habitam as matas de galeria mesmo após três anos da ocorrência do incêndio. Essas modificações têm efeitos sobre as interações planta-animal assim como sobre o papel ecossistêmico que roedores e marsupiais desempenham como dispersores de sementes, potencialmente impactando o recrutamento vegetal em áreas sensíveis ao fogo. Diante disso, recomendamos que planos de manejo integrado do fogo considerem a proteção dos ambientes mais sensíveis, pois os efeitos negativos de incêndios severos nessas áreas podem ser prolongados.

**Palavras-chave:** estimativas de diversidade, incêndios florestais, redes de interação planta-animal, dispersão de sementes, roedores, marsupiais, savana neotropical.

## **Abstract**

The distribution of species and their ecological interactions varies spatially and temporally. Biological communities and consequently their interactions can be affected by disturbances such as fires, which are capable of altering the structure of habitats and the availability of resources. To understand species distribution patterns, as well as detect changes following disturbances, it is necessary to adequately measure the diversity of the groups studied. This is a challenge, especially for highly diverse groups, such as neotropical non-volant small mammals, and in environments composed of distinct plant physiognomies, such as the Cerrado (neotropical savanna). In this study, we evaluated: 1) how the sampling design affects estimates of small mammal diversity in the Cerrado; 2) the effects of fire severity, resource availability, and habitat structure on plant-animal interaction networks in which small mammals participate in the Cerrado; and 3) the effects of fire severity on the potential for seed dispersal by small mammals in the Cerrado. The kind of trapping protocol used to sample small mammal communities in the Cerrado affected the abundance and richness estimates of this group. Sampling designs using both cage traps and pitfalls and considering both climatic seasons (i.e., dry and rainy) were more efficient, especially in open formations. DNA metabarcoding analysis allowed us to detect a high number of plants consumed by rodents and marsupials far above what is possible using traditional methods. In total, we identified 211 species of plants in the fecal samples, contrasting with the 28 species of seeds detected by stereoscopic visual analysis. Plant-animal interactions between small mammals and Cerrado flora were affected by fire. The severity of fire made the interaction networks more nested, and with a lower degree of modularity and specialization in gallery forests more severely affected by fire. In these areas, the diversity of interactions was higher, possibly because of the invasion of species typical of open habitats, favored by changes in the habitat structure caused by fire. The availability of resources (i.e. fruits) also affected the structure of plant-animal networks, although this



availability was not directly related to the fire severity. Habitat structure did not directly affect the structure of plant-animal networks, but this factor was largely explained by fire severity. Therefore, it is possible that its effects on the structure of interactions were indirect. Fire also affected the role of small mammals as potential seed dispersers. There was a reduction in the number of potential dispersers and in the diversity of plants dispersed by the group in the gallery forests most severely affected by fire. These effects were species-specific, varying along the fire severity gradient. The results presented in the present study indicate that severe fires modify the communities of small mammals that inhabit gallery forests even three years after the fire occurrence. These modifications have effects on plant-animal interactions as well as on the ecosystem roles that rodents and marsupials play as seed dispersers, potentially impacting plant recruitment in fire-sensitive areas. Considering this, we recommend that integrated fire management plans consider the protection of the most sensitive environments, as the negative effects of severe fires in these areas can be perceived on a long-term basis.

**Keywords:** diversity estimates, wildfire, plant-animal interaction networks, seed dispersal, rodents, marsupials, neotropical savanna.

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## INTRODUÇÃO GERAL

A ocorrência de uma espécie em uma comunidade depende não somente de sua capacidade de dispersão e tolerância às condições ambientais ali presentes, mas também de interações com outras espécies (Belyea and Lancaster 1999). De forma geral, a relação entre duas espécies que interagem pode ser classificada como antagonista, quando uma delas se beneficia em detrimento da outra, ou mutualista, quando ambas se beneficiam da interação. Competição, parasitismo e predação são exemplos de antagonismos, enquanto polinização e dispersão de sementes representam mutualismos.

A frugivoria (que pode incluir a dispersão ou predação de sementes) está entre as interações planta-animal mais amplamente distribuídas ao redor do mundo, com implicações para a dinâmica e estabilidade de diversos ecossistemas terrestres (Levey et al. 2002, Estrada and Fleming 2012). Esse tópico tem sido investigado crescentemente na ecologia, impulsionado em grande parte pelos trabalhos de Barbara K. Snow e David W. Snow, pioneiros em relacionar o período de frutificação com a dieta de aves em florestas tropicais (Snow 1965, Snow and Snow 1971).

Os padrões das interações variam no tempo e no espaço (Alarcón et al. 2008, Dugger et al. 2019). Essas interações, contudo, podem sofrer mudanças que estão associadas à ocorrência de distúrbios e perturbações. A invasão de espécies exóticas, por exemplo, pode causar alterações na disponibilidade de recursos e levar ao rearranjo de interações entre plantas e abelhas (Hachuy-Filho et al. 2020). Já a redução do hábitat, por sua vez, pode afetar a estrutura das interações em teias alimentares. Nesse caso, apesar da pouca variação na riqueza de espécies detectada, há um declínio na distribuição da frequência das interações, que passam a concentrar o fluxo energético em uma ou poucas interações em ambientes intensamente manejados (Tylianakis et al. 2007). A perda de habitat também contribuiu diretamente para a perda de espécies em redes planta-polinizador e indiretamente para a

reorganização das interações em savanas do norte da Flórida (Spiesman and Inouye 2013). Perdas de espécies e interações em teias alimentares também foram reportadas para ecossistemas de água doce após eventos de seca extrema (Ledger et al. 2012). Além desses distúrbios já indicados, eventos de fogo também são capazes de alterar as comunidades biológicas e suas interações (Ballarin et al. 2023).

O fogo é um distúrbio natural que atua historicamente na estrutura e composição da vegetação em diversos ecossistemas (Daubenmire 1968, Simon et al. 2009). O homem, por sua vez, tem influenciado globalmente o regime do fogo. Essas mudanças têm sido causadas principalmente pelas ocorrências de queimas de origem antrópica em áreas sensíveis e supressão de incêndios naturais em áreas propensas ao fogo, assim como por modificações nas condições ambientais propícias a sua ocorrência (Bowman et al. 2011, Rogers et al. 2020). As condições climáticas, a carga de combustível disponível e a topografia são fatores que determinam o comportamento do fogo (Countryman 1972). Assim, os eventos de fogo podem apresentar intensidades e velocidades de propagação distintas e a vegetação pode sofrer diferentes impactos que podem ser classificados em níveis de severidade de acordo com os danos causados, por exemplo, à cobertura do dossel (White et al. 1996, Flores et al. 2021). No Cerrado, incêndios naturais e queimas antrópicas são comuns, e estima-se que o fogo ocorra nessa região há pelo menos 30 mil anos (Salgado-Labouriau et al. 1997). Entretanto, atualmente a ausência de uma política consistente para uso do fogo nesse bioma ameaça a manutenção da savana tropical mais biodiversa do mundo (Durigan and Ratter 2016).

Nas diferentes fitofisionomias do Cerrado, que vão de campos abertos e savanas até formações florestais (Eiten 1972), ocorrem pelo menos 251 espécies de mamíferos, sendo que marsupiais e roedores representam quase metade deste total (Paglia et al. 2012). Como o Cerrado é um ambiente propenso ao fogo, esses animais são frequentemente expostos aos incêndios e queimas. Em áreas queimadas, a disponibilidade de recursos e estrutura do habitat

estão entre os principais determinantes da recuperação de populações de pequenos mamíferos (Sutherland and Dickman 1999). Após um incêndio na Austrália, por exemplo, o gradiente de vegetação ao longo dos estágios sucessionais pós-fogo permitiu a substituição de espécies de roedores e marsupiais (Fox 1982). No Cerrado, esse mesmo processo foi observado para pequenos mamíferos em áreas de cerrado sentido restrito (Briani et al. 2004). Espécies de roedores que conseguem utilizar melhor os recursos disponíveis logo após o fogo (principalmente insetos) são favorecidos em áreas queimadas. Já as espécies que dependem mais de frutos e sementes só retornam ou aumentam o número de indivíduos em estágios mais avançados da sucessão (Vieira and Briani 2013).

A maioria dos pequenos mamíferos inclui em algum grau frutos e sementes em sua dieta, podendo atuar tanto como predadores de sementes (Vieira et al. 2003, DeMattia et al. 2004) quanto como dispersores (Charles-Dominique et al. 1981, Brewer and Rejmánek 1999, Cáceres and Lessa 2012, Sahley et al. 2016). Assim, uma vez que esses animais exercem papel importante no recrutamento de espécies vegetais (Bricker et al. 2010, Vaz Ferreira et al. 2011) e devido à importância de eventos de fogo em áreas de Cerrado (Miranda et al. 2002), torna-se altamente relevante entender a estrutura das interações planta-animal das quais esses animais fazem parte e como elas são alteradas pelo fogo no Cerrado.

Análises de redes de interações têm sido extensivamente utilizadas a fim de elucidar padrões de interação entre organismos, assim como os processos ecológicos e evolutivos envolvidos (Quintero et al. 2022). Sob tal perspectiva, as espécies podem ser representadas por nós e, as interações existentes entre elas, por ligações que conectam esses nós (Barabási 2016). Essas análises permitem a investigação dos padrões de interações e os efeitos de alterações ambientais, que muitas vezes não são detectados por descritores convencionais de comunidades que não metrificam interações (Tylianakis et al. 2007). Além disso, a estrutura das redes de interações sofre influência da diversidade de espécies envolvidas e do número de

interações entre elas (Thébault and Fontaine 2010). Para a avaliação adequada das interações entre pequenos mamíferos e plantas é essencial que a diversidade e composição de espécies desses animais em suas áreas de ocorrência seja bem conhecida.

A mensuração adequada da diversidade de espécies ainda é um desafio. Especialmente para o grupo dos pequenos mamíferos não voadores neotropicais, que apresenta elevada diversidade (Luza et al. 2019), com espécies respondendo diferentemente aos métodos de amostragem (Lambert et al. 2005, Caceres et al. 2011, Barros et al. 2015, Ardente et al. 2017, Bovendorp et al. 2017). Efeitos de amostragem sobre as estimativas de diversidade calculadas para comunidades de pequenos mamíferos neotropicais foram reportados para diferentes ambientes florestais (Vieira et al. 2014, Barros et al. 2015, Santos-Filho et al. 2015, Bovendorp et al. 2017, Palmeirim et al. 2019). No entanto, esses efeitos podem ser diferentes em ambientes predominantemente não-florestais, com sazonalidade climática acentuada (Eiten 1972) e composição de espécies distintas (Paglia et al. 2012), caso do Cerrado. Apesar disso, estudos abrangentes sobre questões metodológicas afetando as estimativas de riqueza e abundância de pequenos mamíferos não voadores nesse bioma são inexistentes. Sendo assim, é importante entender como o desenho amostral pode influenciar as estimativas de riqueza, abundância, composição e diversidade em comunidades de pequenos mamíferos no Cerrado.

O presente estudo está estruturado em três capítulos, todos relacionados aos pequenos mamíferos do Cerrado brasileiro, incluindo suas interações ecológicas com as plantas e o efeito do fogo sobre estas interações. No primeiro capítulo, avaliei os efeitos de diferentes desenhos amostrais sobre as estimativas de diversidade para o grupo dos pequenos mamíferos não voadores no Cerrado. Já no capítulo 2, objetivei descrever as redes de interações entre pequenos mamíferos e as plantas das quais consomem frutos e sementes no Cerrado, investigando os efeitos da severidade do fogo, da disponibilidade de recursos e estrutura do habitat sobre estas redes. Por último, no capítulo 3, investiguei o potencial de dispersão de

sementes que roedores e marsupiais apresentam no Cerrado, assim como os impactos da severidade do fogo sobre os serviços de dispersão potencialmente providos por esses animais.

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## **Capítulo 1: Sampling design affects small mammal diversity estimates in a Neotropical savanna**

### **Abstract**

1. To comprehend the mechanisms behind the observed patterns of species distributions, an accurate description of the biological community diversity is necessary. However, adequate measurement of species diversity may be challenging for organisms such as neotropical non-volant small mammals, which are a highly speciose group that responds differently to the available sampling methods.
2. We assessed an extensive literature on small mammal studies conducted in a neotropical savanna aiming to evaluate the effect of trapping protocols used on small mammal community parameters and to identify the most adequate sampling protocol for different macrohabitats (forest, savanna, and grassland).
3. We compiled data on small mammal abundance and richness in the Cerrado from diverse sources and extracted information on sampling methods used: trap type, trap arrangement, sampling period, and trapping effort.
4. Using cage and pitfall traps simultaneously generated higher abundance and species richness estimates in all macrohabitats, reflecting a complementary effect of these two types of traps. For richness estimates, sampling periods that covered both seasons were more relevant in environments subject to major seasonal variations (savanna and grassland). Trap type and body mass interacted so that larger individuals were more frequently captured in cage traps and smaller individuals in pitfall traps. Trap effectiveness depended on the macrohabitat, with small Sherman traps capturing more species in savanna, while pitfall traps had higher success in forest.
5. Sampling methods used in small mammal communities affect the abundance and richness estimates of this group. Thus, to maximise sampling efficiency for future

studies, we suggest the use of pitfall traps combined with cage traps and sampling periods that account for seasonal variation of the region. Lastly, we recommend that the trap arrangement be aligned with the study goals, and that the kind, size, and shape of the study area should be considered.

**Keywords:** Cerrado, sampling protocol, rodent, marsupials, trap type.

## **Introduction**

The explanations for the observed patterns of occurrence and abundance of organisms on Earth remain pivotal questions in ecology (Gaston 2000; Tittensor et al. 2010). Understanding the mechanisms that produce these patterns depends on the identification and description of biological communities and their component species. Moreover, biodiversity measurements are essential, considering that ecosystem functioning is strongly related to species diversity (Isbell et al. 2014; Tilman et al. 2018). Nonetheless, the adequate measurement of species diversity is still a challenge for ecologists (Gotelli & Colwell 2011), specifically for neotropical non-volant small mammals, as species belonging to this highly speciose group (at least 204 species, comprising about 38% of the world richness for this group; Luza et al. (2019)) respond differently to the available sampling methods. For these species, the use of specific kinds of traps, baits, and trapping protocols can markedly influence the inferred diversity of a region (Lambert et al. 2005; Cáceres et al. 2011; Barros et al. 2015; Ardente et al. 2017; Bovendorp et al. 2017). The evaluation of the effects of distinct capture methods and sampling protocols on their estimated diversity can contribute to the elucidation of the processes that determine the patterns of occurrence and distribution of this group.

Because of its high richness and local abundance, small mammals constitute a highly relevant faunal component of the Cerrado, the greatest predominantly non-forested region of the Neotropics (Veblen et al. 2007). In this neotropical savanna, at least 118 species of rodents and marsupials occur (Paglia et al. 2012; Mendonça et al. 2018). The Cerrado is characterised by its high plant diversity and endemism, with > 10,000 plant species (Myers et al. 2000) that are distributed along distinct phytophysiognomies. These phytophysiognomies include grasslands, typical savanna environments (e.g. cerrado *sensu stricto*), and forest formations (Eiten 1972). This vegetal heterogeneity results in high diversity in the Cerrado, which is considered to be the most diverse (Klink & Machado 2005) and is probably the most threatened tropical savanna in the world (Myers et al. 2000; Strassburg et al. 2017).

Several distinct sampling methods have been used in small mammal studies in various Cerrado phytophysiognomies. The most commonly used traps are live-traps (i.e. cages; mainly Sherman® traps, Tomahawk®, and other wire-mesh cage traps), in which the animals are attracted by baits, and pitfalls (buckets buried into the ground), in which the animals are passively caught, generally being directed by drift fences (Martins et al. 2006; Carmignotto et al. 2014; Camargo et al. 2018; Ribeiro et al. 2019). Traps are generally placed in the field and are equally spaced, forming linear transects or rectangular grids. Each of these configurations has its advantages and drawbacks, and the best choice for estimating abundance and diversity is still a source of debate, with studies that compared them providing conflicting results (Steele et al. 1984; Read et al. 1988; Bujalska 1989; Pearson & Ruggiero 2003).

The possible effects of trapping protocols (e.g. trap type, trap configuration) on community metrics of neotropical small mammals have already been investigated in forested environments, such as the Amazon (Santos-Filho et al. 2015; Palmeirim et al. 2019) and Atlantic forests (Barros et al. 2014; Vieira et al. 2015; Bovendorp et al. 2017). Nonetheless,



these effects cannot be assumed to be the same for non-forested neotropical formations, such as the Cerrado. This neotropical savanna, in comparison to forested biomes, presents striking differences in species composition (Paglia et al. 2012), prevalence of non-forested formations (i.e. grasslands and typical savanna formations), and also a higher climatic seasonality (Eiten 1972). All these factors may affect trap efficiency and interact with each other in their effects on small mammal assemblages. For example, high between-season variation in resource availability in open cerrado formations (Ferreira & Huete 2004) might cause seasonal changes in the attractivity and efficiency of baited cage traps but not in the efficiency of passive pitfall traps.

Despite the potential relevance of all these methodological issues (i.e. trap configuration, trap type, and sampling effort) on the assessment of small mammal richness and abundance in the Cerrado, comprehensive studies on such subjects are nonexistent. The few available studies are restricted to only one habitat type (Cáceres et al. 2011) or are limited because of the small size of pitfall traps used for comparison (i.e. 30-l buckets; (Lyra-Jorge & Pivello 2001; Santos-Filho et al. 2008)).

In the present study, we conducted an extensive literature survey on small mammal studies conducted in the Cerrado aiming to achieve the following objectives: (1) to evaluate the effect of trapping protocols used (i.e. trap configuration, seasonal sampling, trap type, sampling effort) on the estimates of small mammal richness and abundance, and (2) to identify the most adequate sampling protocol for each of the three main Cerrado phytophysiognomies. Considering that the use of linear transects might maximise the number of individuals' home range covered by traps and potentially allow the capture of more animals, we expected higher observed abundance and richness with this trapping configuration in comparison to rectangular grids (Pearson & Ruggiero 2003). In relation to season and cerrado physiognomies, considering that forested habitats are potentially less

affected by seasonal climatic variation (Ferreira & Huete 2004), we expected sampling in only one season to be more effective in forested than in non-forested environments (i.e. grasslands and typical savanna environments) in the Cerrado. In relation to trap types used because of the specific characteristics of cages and pitfalls, we expected that the combination of both types would generate higher estimates of richness than when using only one of them. Moreover, since only cages allow arboreal captures, we expected the combined use of both cages and pitfalls to be more important in forested habitats than in non-forested habitats. We also expected the differences between trap types in their capturability of small mammal species to be related to the size of the animals (Hice & Schmidly 2002; Nicolas & Colyn 2006; Hice & Velazco 2013; Santos-Filho et al. 2015).

## **Material and methods**

### Study sites

The Cerrado is a neotropical savanna that covers > 2 million square kilometres in South America, with most of its distribution located in Brazilian territory (Klink & Machado 2005) (Fig. 1). This phytogeographic domain is characterised by a mosaic of distinct plant formations. These formations include open areas, dominated by a grassy stratum with few or no shrubs and trees at all; typical savanna environments, characterised by a gramineous layer with sparse shrubs and trees; and forest environments, which are dominated by tree species forming a canopy layer (Ribeiro & Walter 1998). Notwithstanding its high species diversity and endemism rate (Myers et al. 2000), the conservation of the Cerrado is currently a great challenge. At present, approximately 46% of its original plant cover has already been destroyed (Strassburg et al. 2017), and <8% if its total remaining area is legally protected (Oliveira et al. 2017).

The climate of the Cerrado is classified as AW type (tropical savanna-wet summer) (Köppen 1948) with a mean annual temperature ranging from 20°C to 26°C (Eiten 1972). The mean annual rainfall ranges from 750 mm in the driest parts of the Cerrado to up to 2,000 mm in the wettest areas. There are two well-defined seasons, a dry season from May to September and a rainy season between October and April, when ~90% of the annual precipitation occurs (Eiten 1972).

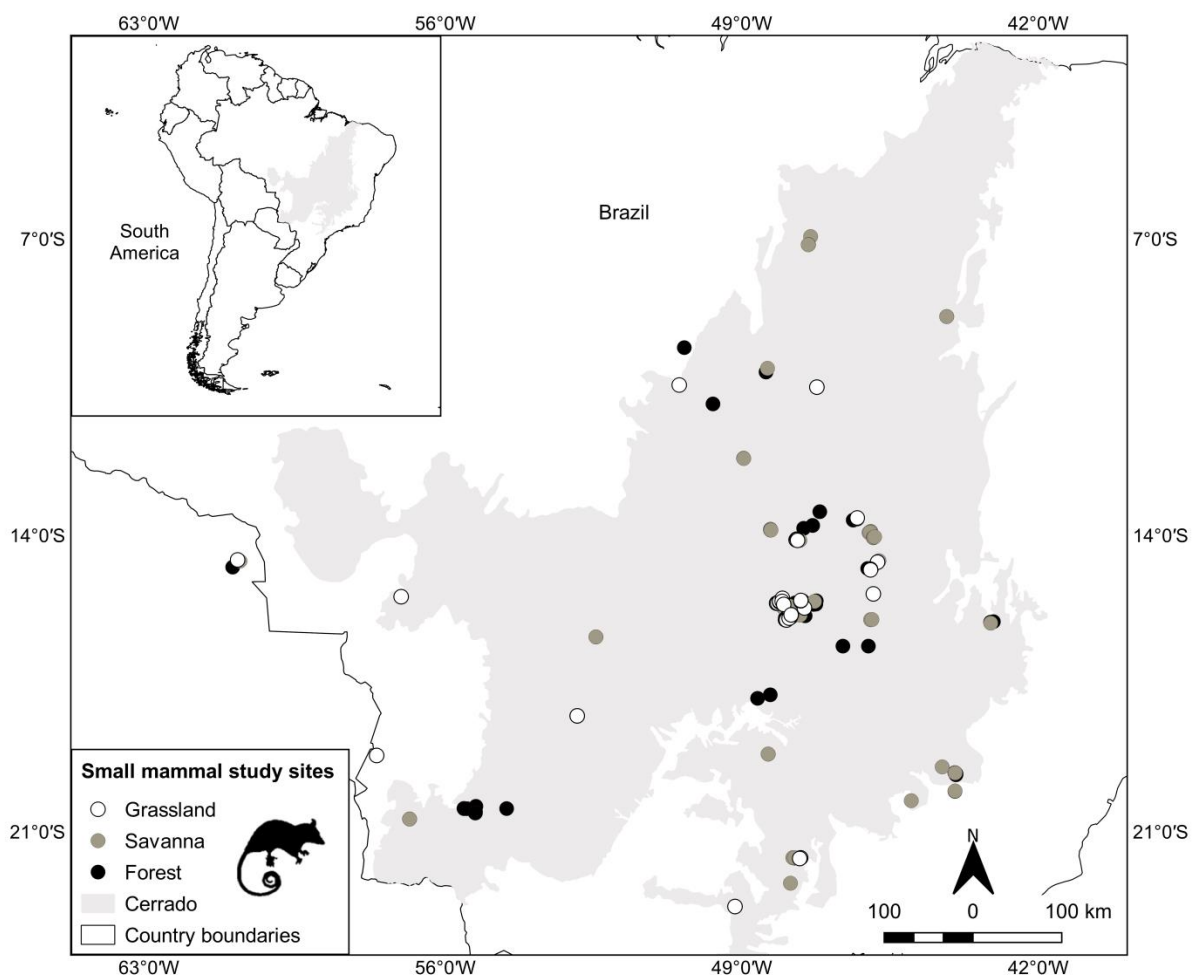


Figure 1. Study sites where small mammal communities were sampled in the three main macrohabitat types of the Cerrado.

## Dataset

For our analysis, we consulted a detailed dataset based on an intensive literature review of studies with rodents and marsupials in the Cerrado published by Mendonça et al. 2018. This is the largest available dataset on the distribution of small mammals in the Cerrado. It contains data on richness and abundance of small mammals from 96 studies (446 sites) conducted across the entire Cerrado region, including trapping methods used and vegetation types sampled. This dataset resulted in 24,283 individual records, including 29 marsupials and 87 rodents. This dataset was based on both published and unpublished material (i.e. dissertations, theses, and datasets provided by researchers). The search was performed in English, Portuguese, and Spanish with the following keywords: small mammal(s), rodents, marsupials, survey(s), inventory(ies), community(ies), assemblage(s), and Cerrado in online academic databases (e.g. ISI Web of Knowledge, Google Scholar, Scielo, Scopus, JStore), digital libraries of State and Federal Brazilian universities, references cited in literature, and email contacts with local experts. It contains data on richness and abundance of small mammals from 96 studies (446 sites) conducted across the entire Cerrado region, including trapping methods used and vegetation types sampled. This dataset resulted in 24,283 individual records, including 29 marsupials and 87 rodents.

From this dataset, we gathered data on small mammal richness and abundance obtained in 14 phytophysiognomic types of the Cerrado. We grouped these sites according to three main macrohabitat categories following Ribeiro and Walter (1998) (Fig. 1). Then, according to the dominant vegetational strata, we considered for this study: grasslands (wet grassland, open grassland, shrubby grassland, rocky grassland, 'murundu' [i.e., mound] fields), typical savanna vegetation (open savanna, rocky savanna, typical savanna, dense woodland), and forests (seasonal forest, semideciduous seasonal forest, gallery forest, riverine forest, savanna woodland forest). From these studies, we also extracted information on

location, sampling effort, trap type, trap design, and sampling period (climatic season) when available.

### Evaluation of Trapping Methods

To identify which methodology generates higher estimates of small mammal abundance and richness, we selected four methodological aspects (predictor variables) in studies conducted in the Cerrado: trap configuration (design), trap type (method), number of seasons covered by the study period (season), and sampling effort (Appendix S1). For analysis, we considered only the methodologies applied in at least 20 sites (i.e. methodologies used in 20 or more small mammal communities sampled independently). For the design variable, we considered the following categories: 1) grid, in which the traps were arranged in rectangular transects of  $n \times n$ , usually at equally spaced capture stations; and 2) linear, in which traps were arranged in linear transections, usually at equally spaced capture stations. We categorised the trap type used (method) as: 1) cage, which included sites where only cage traps such as Tomahawk®, Sherman®, and Young® were used and 2) cage and pitfall, which included sites sampled with both cage and pitfall traps. The category ‘pitfall traps’ was not considered in the analysis because of the low number of sites sampled exclusively with pitfall traps. For the predictor variable (season), we separated sites into 1) ‘one’, when sampling occurred during one climatic season (dry or wet) or 2) ‘both’, when the study covered both seasons (dry and wet). As it is expected that the number of species sampled will increase with the capture effort employed, for the analysis of richness, we considered a variable effort to control this factor. We calculated effort by multiplying the number of traps used in each sampling period by the number of days in which sampling occurred.

### Comparison between trap types

Comparisons between trap types in terms of trapping success and species capturability are generally hindered by between-studies differences in terms of local habitat structure and resource availability and also in specific environmental conditions during the trapping period (e.g. moon phase, rain occurrence). Specifically, for our dataset, the low number of studies with pitfall traps and the lack of detailed information regarding trapping success and species captured by different trap types was an additional issue. To avoid these drawbacks, we compared richness estimates provided by distinct trap types and their capture rates based on data obtained from a single large study included in our dataset. This study (hereafter referred to as the restricted dataset) was conducted in three distinct geographic areas and comprised 39 sampled sites (Ribeiro, 2016). These sites covered the main vegetation types occurring in the Cerrado: grasslands (dry and wet grasslands, 6 sites), typical savanna vegetation (cerrado *sensu stricto* and rocky cerrado, 21 sites), and forests (gallery forests, 12 sites). All these sites were sampled with the simultaneous use of pitfalls and cage traps. For all the comparisons between trap types using this restricted dataset, we considered all species combined because sample size was not adequate for analysing rodents and marsupials separately.

The study that was used for comparison of trap types (restricted dataset) was conducted by the same research laboratory as the present study, and we had obtained detailed information on trapping procedures for all sites. In each of these sites, a trapping plot composed of four types of traps was placed, covering an area of approximately 12 ha. These plots included two linear transects of eight pitfall traps each (60 L plastic buckets placed 5 m from each other with 50 cm tall plastic drift fence interconnecting them) and one linear transect with three kinds of cage traps: five wire mesh cages (wire-mesh traps;  $16 \times 16 \times 45$  cm with 1 cm gap between wires), 25 small Sherman® traps ( $9 \times 9.5 \times 23$  cm), and five large Sherman® traps ( $11 \times 12.5 \times 37$  cm). All cage traps were baited with a mixture of mashed banana, cod liver oil, corn meal, peanut butter, and vanilla essence. Each site was sampled for

two years (2012–2013), with one trapping session (each one consisting of 8 days of capture) in each season (wet and dry), resulting in four trapping sessions per site. In each trapping season, all trap types were set simultaneously. We considered each trapping plot to be independent, with the distance between transects within each area ranging from 300 to 1000 m. The details of this methodology are also discussed in another study (Ribeiro et al. 2019). The overall trapping effort was 54,008 trap-days, including 10,048 trap-days for pitfalls, 31,400 trap-days for small Shermans, 6,280 trap-days for large Shermans, and 6,280 trap-days for wire mesh cages.

### Data analysis

#### Overall dataset

To evaluate the effects of sampling design on small mammal captures across the entire dataset, we used the total abundance and species richness of each assemblage as dependent variables. We corrected the overall site abundance by dividing the total number of individuals captured by total trapping effort (i.e. number of traps  $\times$  number of sampling days), obtaining a measure of catch per unit effort (Lambert et al. 2005; Santos-Filho et al. 2015; Bovendorp et al. 2017). Our predictor variables were all related to the methods used for small mammal sampling in the Cerrado and included trap configuration (linear transect or rectangular grid), trap type (cage trap [of any kind] or cage trap + pitfall), number of seasons covered by the study period (one [wet or dry] or both seasons), and total trapping effort. We used  $z$ -transformed values of total trapping effort for dealing with differences in scale between trapping effort (up to 19,200 trap-days) and species richness (up to 18 species).

To evaluate the performance of different sampling protocols in distinct plant formations from the Cerrado, we assigned each phytophysiognomy to one of the three macrohabitat categories considered (grasslands, savannas, and forests). We excluded from the analysis data from human-disturbed areas or from under-represented phytophysiognomies (<

20 sites in the dataset). Considering that the effectiveness of sampling methods may vary according to the taxonomic group (Moura et al. 2008; Vieira et al. 2014), we created independent models for rodents and marsupials and also for both groups combined. For marsupials only, we did not create models for the 'grasslands' because their number of captures was insufficient. Thus, only rodents and rodents+marsupials were evaluated for this macrohabitat type. Therefore, for each of the two metrics considered (abundance/effort and species richness) we created eight models, three for 'forests' (rodents, marsupials, and rodents+marsupials), three for 'savannas' (rodents, marsupials, and rodents+marsupials), and two for 'grasslands' (rodents and rodents+marsupials). The models for abundance as the response variable included the three variables related to sampling protocols: design, method, and season. In addition to these three variables, we also included the variable 'total effort' for the response variable 'richness'.

To evaluate the effects of these sampling protocols on the community metrics of small mammals, we used generalised linear models (GLMs). These models were adjusted using a Poisson error structure (log link) for richness and gamma (inverse link) for abundance (corrected for effort). We considered the effect of the predictor variables as significant when the 95% confidence intervals of their estimated coefficients did not contain zero. Prior to the analysis, we verified our dataset for the occurrence of outliers, collinearity of the predictor variables, variance homogeneity, and spatial autocorrelation. We identified outliers in small mammal abundance data, which were excluded before analysis. This removal was possible because our dataset was robust and no relevant reduction in the number of samples was observed. We used the variance inflation factor (VIF) to verify the potential correlation between predictor variables, and considered values of  $VIF < 3$  as evidence of absence of collinearity (Zuur et al. 2010). All VIF values we found were below this limit; therefore, our predictor variables were assumed to be uncorrelated with each other. We also observed that



our data did not violate the assumption of homogeneity of variances. To verify the occurrence of spatial autocorrelation, we applied Moran's correlogram to the model residuals. For the models that showed evidence of spatial autocorrelation, we explicitly considered the spatial structure of the data, adding to the model spatial predictor variables generated by Moran's eigenvector maps (MEM) (Dray Stéphane et al. 2006; Legendre & Legendre 2012). No spatial autocorrelation was detected after the application of MEM. All overall dataset analyses were performed using R software (Team 2009). For modelling, we used the car package (Fox & Weisberg 2019) and for MEM analyses, we used adespatial v.0.3-7 (Dray et al. 2019) and spdep (Bivand et al. 2015) packages.

#### Restricted dataset

For a specific comparison of trap types across the 39 sites with simultaneous use of different trap types (restricted dataset), we compared overall richness estimates (rodents and marsupials combined) generated by distinct trap types. This comparison was performed by creating sampled-based rarefaction and extrapolation curves (Colwell et al., 2012). We generated these curves independently for each macrohabitat category, using the default options of EstimateS version 9.1.0 (Colwell 2013). We considered each trapping campaign as a sample and extrapolated richness estimates for each trap type up to two times the original sample size. We generated these curves for savannas and forests but not for grasslands because of the limited number of samples with at least one capture for this latter macrohabitat type (<20 samples; Gotelli and Colwell 2011). We considered curves with non-overlapping 95% confidence intervals to be significantly different (Colwell et al., 2012).

Using generalised linear mixed models (GLMM), we also tested the effect of plant formation (grasslands, savannas, and forests) and trap type (pitfall, small Sherman®, large Sherman®, and wire mesh cage) on capture success (i.e. total number of individuals captured

per total effort for each species), including species as a random factor. Considering that trap effectiveness is affected by individual body mass (Lyra-Jorge & Pivello 2001; Hice & Velazco 2013; Santos-Filho et al. 2015), we also considered the ln-transformed body mass as a factor (26 species, body mass range: 9 – 604 g; Appendix S2). We used mean values of body mass for each species based on individuals (both juveniles and adults) captured during the fieldwork of the source study. These analyses were performed using the R package nlme (Pinheiro et al. 2020).

## Results

### Overall dataset

Of the 96 studies (446 sites) compiled in our overall dataset, we did not include six studies in the analyses due to the presence of outliers, sampling effort not informed, or only human-disturbed sites sampled. Thus, our final dataset comprised information from 336 sites for small mammal richness (forest: 150; savanna: 115; grassland: 71) and 326 sites for abundance/effort (outliers removed) (forest: 149; savanna: 107; grassland: 70). In total, 113 small mammal species were recorded (29 marsupials and 84 rodents) belonging to 49 genera. Studies that used only cage traps employed a sampling mean effort of 1,950 trap-nights (range: 60 to 19,200), while studies that used cage and pitfall traps simultaneously employed a sampling mean effort of 1,581 trap-nights (range: 48 to 13,860).

The models that evaluated the effect of trap arrangement, trap type, and number of sampling seasons on abundance estimates indicated that small mammal estimates (rodents and marsupials combined) were higher when cage and pitfall traps were used simultaneously in comparison to the use of cage traps only (Fig. 2, Appendix S3). This pattern applied for the three macrohabitats and for the two groups of small mammals when analysed separately. Samples that covered both seasons generated significantly higher estimates in the grassland

and forest macrohabitats (but not in the savannah) for both small mammals combined and for rodents only. When marsupials were analysed separately, however, there was a significant effect of the number of sampling seasons only for the savannah macrohabitat. The evaluated macrohabitats, however, did not differ significantly in abundance estimates when considering distinct trap arrangements (Fig. 2, Appendix S3).

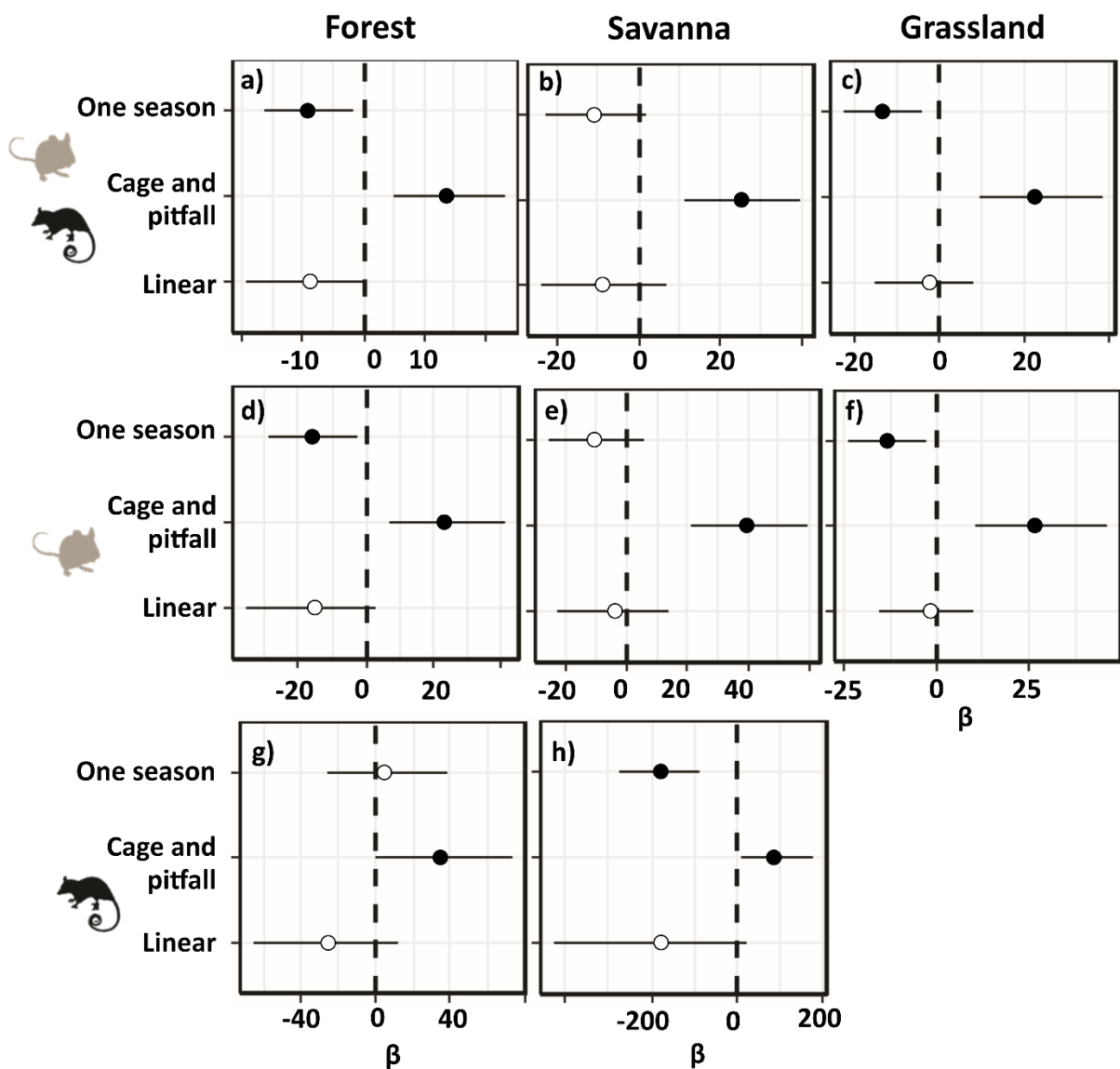


Figure 2. Estimates ( $\beta$ ) and confidence interval (95%) for the distinct methodologies used in small mammal sampling in the Cerrado for abundance corrected for effort. Results are presented for marsupials and rodents analysed together (a, b, and c), for rodents (d, e, and f),

and for marsupials (g and h) in the main vegetation types of the Cerrado (due to low number of marsupials sampled in grasslands, this vegetation was not included in the models for this group).  $\beta$  values represent the difference in estimates in relation to the intercept (see Table 2 for intercept values), which includes predictor variable levels not shown (i.e., both seasons, only cage, and grid arrangement). Confidence intervals that do not touch zero indicate a significant effect (closed circles), while confidence intervals that touch zero indicate no effect (open circles).

The evaluation of the potential effects of methodological factors on richness estimates indicated that the combined use of cage and pitfall traps positively affected small mammal richness in all the cerrado macrohabitats (Fig. 3, Appendix S4). For each group analysed separately, however, we did not detect any significant effect for rodents, and a positive effect of using both trap types on marsupial richness occurred only in forest environments. The richness estimates of both groups were significantly lower in the savanna macrohabitat when sampling occurred in only one season. For the other macrohabitats, however, no effect of the sampling period was detected. Moreover, we did not observe any effect of trap arrangement on species richness estimates in any of the macrohabitats. These estimates were significantly affected by sampling effort, with a positive effect on small mammals (both groups combined) in forest and savanna macrohabitats. When each group of small mammals was analysed separately, this effect was observed to have occurred only for forest environments (Fig. 3, Appendix S4).

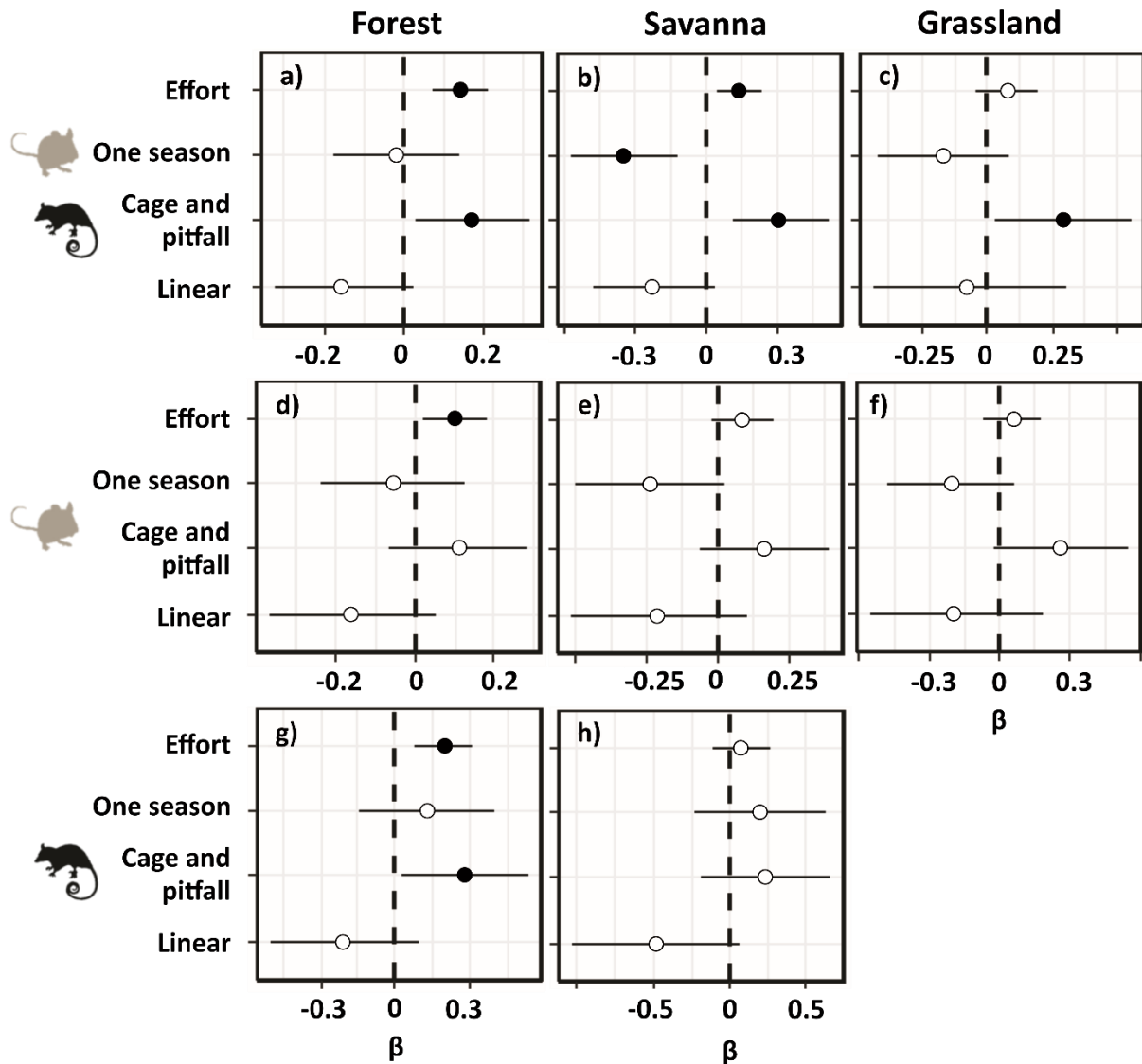


Figure 3. Estimates ( $\beta$ ) and confidence interval (95%) for the distinct methodologies used in small mammal sampling in the Cerrado for species richness. Results are presented for marsupials and rodents analysed together (a, b, and c), for rodents (d, e, and f), and for marsupials (g and h) in the main vegetation types of the Cerrado (due to low number of marsupials sampled in grasslands, this vegetation was not included in the models for this group).  $\beta$  values represent the difference in estimates in relation to the intercept (see Table 3 for intercept values), which includes predictor variable levels not shown (i.e., both seasons, only cage, and grid arrangement). Confidence intervals that do not touch zero indicate a

significant effect (closed circles), while confidence intervals that touch zero indicate no effect (open circles).

### Restricted dataset

We evaluated the effects of trap type, macrohabitat, and body mass on capture rates by using mixed models, and the results indicated that capture rates are affected by macrohabitat type and by the interaction between trap type and body mass (Appendix S5). Thus, the effectiveness of distinct trap types was affected by body size, with smaller species being more captured by pitfall traps, whereas larger species being better captured by large Shermans and wire mesh cages (Fig. 4).

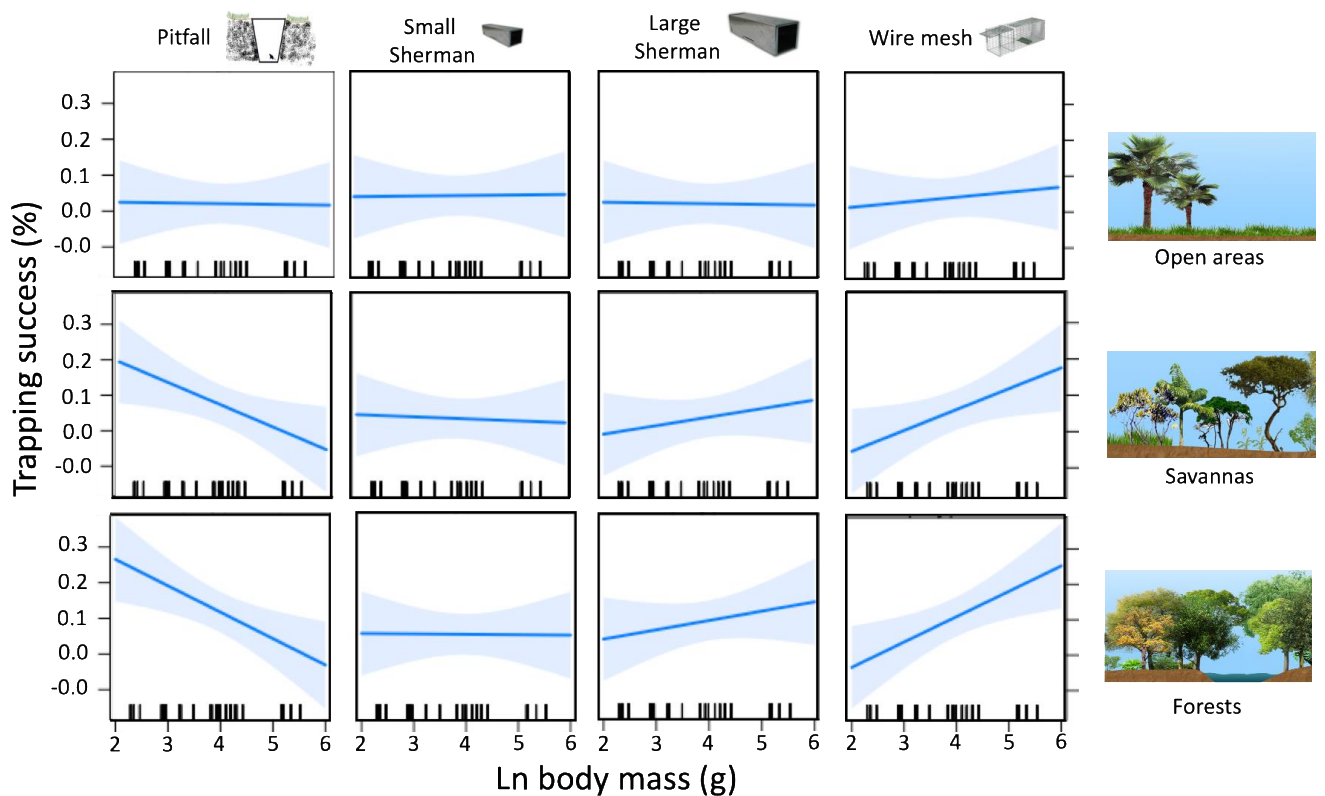


Figure 4. Relationships between small mammal body mass and trapping success (number of individuals captured per trap expressed as a percentage) in three macrohabitat types (top row: grasslands, middle row: savannas, and bottom row: forests) with four trap types (from left to

right columns: pitfall, small Sherman®, large Sherman®, and wire mesh cage). Small vertical bars on the x-axis indicate body mass of each species. See Appendix S2 for complete list of species and body mass values. Statistical results are indicated in Table 1.

To evaluate the effect of trap types on richness estimates in areas with simultaneous use of four types of traps, we generated species accumulation curves as a function of the number of samples (but plotted against number of individuals) for each trap type. We performed these analyses for the two macrohabitats with a sufficient sample size (i.e. savanna and forests), and contrasting patterns were detected. For the savannas, small Shermands provided significantly higher estimates than pitfall traps, whereas for the forests, the highest richness estimate was observed for pitfall traps, but with no significant differences among trap types (Fig. 5).

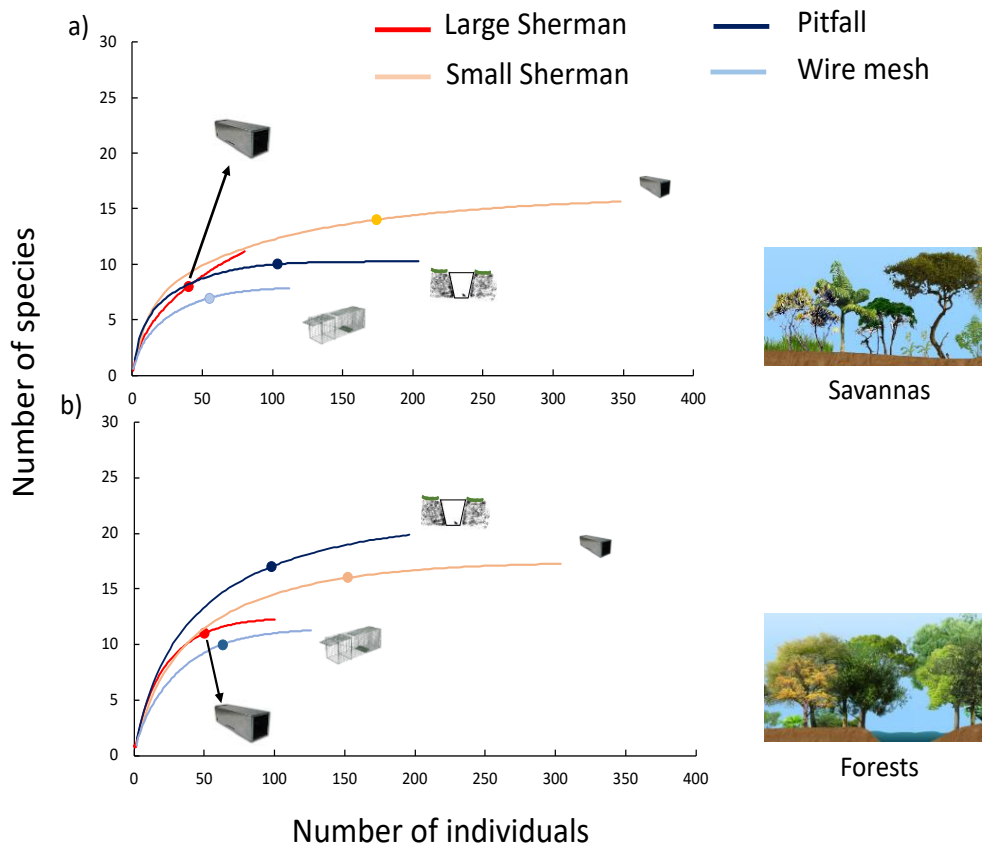


Figure 5. Patterns of species richness (sample-based rarefaction and extrapolation) for four trap types used simultaneously in 33 cerrado sites in two macrohabitat types: a) savannas and b) forests. Circles indicate the observed total number of species for each trap type. The x-axis was rescaled for number of individuals.

## **Discussion**

Our results indicated that the type of trap (but not its disposition in the field), the combination of different types of traps, and the number of seasons covered by the sampling period affect the measurements of diversity of small mammal communities. This effect differed among the main macrohabitats of the Cerrado (grasslands, savannas, and forests). We also observed that the capture success of small mammals was influenced by the macrohabitat type and by the interaction between trap type and individual body mass. Sherman traps potentially capture more species in savanna macrohabitats while no significant differences between cage traps (Sherman and wire mesh cages) and pitfall traps were observed in forest macrohabitats.

As expected, the use of different trap types performed better than the use of a single trap type. The highest estimates of abundance and species richness achieved when cage and pitfall traps were used simultaneously may reflect a complementarity effect resulting from different capture patterns associated with each trap type. First, traps can differ with respect to the size of the captured individuals. Our results for the restricted dataset reveal that the trapping success of larger individuals is greater with cage traps, while smaller individuals are captured more frequently in pitfall traps. This has also been observed in other studies in savanna and rainforest environments (Dizney et al. 2008; Cáceres et al. 2011; Santos-Filho et al. 2015). Second, cage traps are frequently installed in the undergrowth and canopy, allowing the capture of species with arboreal habits that would hardly ever be captured by pitfall traps



(but see Umetsu et al. 2006). Third, some species of small mammals avoid entering cage trap types (Hammond & Anthony 2006), so they are more likely to be captured in pitfall traps. Thus, it is not unusual for small mammal species to exhibit specificity for a particular type of trap, that is, they are captured exclusively in one trap type (Lambert et al. 2005; Nicolas & Colyn 2006; Umetsu et al. 2006; Ardente et al. 2017; Palmeirim et al. 2019).

Our results indicated that the arrangement of traps (grid or linear) does not affect the estimates of abundance and richness of small mammals in the Cerrado, regardless of the macrohabitat. Therefore, we suggest that the arrangement of the traps should be adjusted to the objective of each study. Grids can be a more interesting option when the aim of the study is to evaluate population aspects such as home range and population density, since these parameters depend on area measurements. On the other hand, linear transections can cross more microhabitats and the home range of more individuals (Pearson & Ruggiero 2003), enabling the capture of species associated with different microhabitats and more individuals, being more suitable for studies whose objective involves community diversity. Another factor that should be considered is the kind, size, and shape of the study area. In the Cerrado, one of the most common forested environments is the gallery forest, which is a naturally narrow forest strip (generally up to 80 m wide) that surrounds water courses (Ribeiro & Walter 1998). This kind of habitat configuration may not allow the establishment of a trapping grid with appropriate trap spacing and the size of the covered area. In such a case, a linear transect is probably the most viable option.

In relation to the sampling period, our analyses suggest that the estimated abundance is higher when trapping occurs in both seasons (i.e. dry and wet seasons). This pattern was observed for all macrohabitats. Small mammal populations may experience seasonal fluctuations, and it is common to observe population increases during the wet season (O'Connell, 1989; Bergallo H., 1994; Mares & Ernest, 1995; Carmignotto et al., 2014). In

general, this pattern is related to the greater availability of food resources (i.e. fruits and arthropods) that accompany the period of the year with the highest rainfall (Bergallo & Magnusson 1999; Gentile et al. 2012). However, some rodent and marsupial species can also show population peaks during drier months (O'Connell 1989). Therefore, it is reasonable to expect that small mammal community sampling carried out over very short periods and that do not include seasonal variation in the region of interest may generate underestimated abundance values.

For species richness, however, there was a tendency for the number of seasons sampled to be less important in forest environments when compared to savanna and grassland environments. In the Cerrado, forest environments tend to be more stable over the climatic seasons than open vegetation types (Ferreira & Huete 2004). Forest fruit production, for example, is more evenly distributed throughout the year, while savanna environments show peak production in the rainy months (Maruyama et al. 2019). Hence, small mammal species inhabiting forest environments may experience less variation in resources over the year, with communities being less affected by seasonality in this habitat type.

The smaller of the small mammals in the Cerrado are more often captured in pitfall traps, whereas larger species have a higher capture rate in Sherman and wire mesh cages. To capture animals, cage traps depend on a force being exerted on a platform for the trap to be triggered. Therefore, larger individuals are more often caught in this type of trap than very light individuals (e.g. young, very small species) (Umetsu et al. 2006), as they may not exert the force necessary to trigger the mechanism of these traps. Pitfall traps, on the other hand, are independent of this type of mechanism and are able to capture smaller individuals more frequently (Hice & Schmidly 2001; Lyra-Jorge & Pivello 2002). However, when it comes to larger individuals, the capture success may be reduced, since these animals are probably able to escape from the buckets used as pitfall traps (Hice & Schmidly 2002).

The results of the restricted dataset indicated that Sherman traps potentially capture more species than pitfall traps in savanna macrohabitats. This pattern had not been reported previously in neotropical environments and may be related to bait attractivity and also the relatively similar efficiency of the Sherman traps for capturing different-sized species in cerrado savannas. On the other hand, in forest macrohabitats, pitfall traps performed better (but not significantly) than cage traps. We detected that pitfall traps were also effective in capturing arboreal species in cerrado forests as reported for other forested areas (Umetsu et al. 2006; Palmeirim et al. 2019). Our results, however, are not in total agreement with those observed for small mammal sampling carried out in rainforests, which indicate higher richness for pitfalls in comparison to cage traps (Lima et al. 2010; Barros et al. 2015; Bovendorp et al. 2017).

## **Conclusion**

We present the first large study, in terms of spatial scale and volume of data, to assess the influence of methodology on the estimates of abundance and richness of small mammals, a highly speciose group, in a neotropical savanna. We were able not only to compare the efficiency of the different methodologies between each other, but also between the Cerrado macrohabitats and between different groups of small mammals. We demonstrate that the method used in small mammal community sampling affects the abundance and richness estimates of this group. For all Cerrado macrohabitats analysed, small mammal estimates were higher when cage and pitfall traps were used together, and sampling both climatic seasons was more efficient, especially in savanna and grassland formations. We detected a bias in the size of individuals caught by each trap type, with larger animals captured by pitfall traps and smaller animals by cage traps. We also observed that, in savanna

environments, regular Sherman traps are more efficient in capturing a greater number of species than pitfall traps.

Based on our findings, we propose a simple small mammal sampling protocol to be used as a guide for future studies to maximise sampling efficiency. Regarding the trap type utilised, we suggest the use of pitfall traps combined with cage traps such as Sherman and wire mesh cages for all macrohabitats. In this way, the best possible representation of the community is obtained, capturing larger and smaller species, young and adult individuals, and animals that avoid entering cage traps. We also recommend conducting sampling that accounts for seasonal variation of the region, especially in environments that experience marked changes throughout the year (e.g., open vegetation formations), which may affect the composition and structure of small mammal communities. Finally, we endorse that the arrangement of the traps should be aligned with the study goals and that the kind, size and shape of the study area should be considered. In open areas from Cerrado, for example, the use of pitfall traps is not always possible, because some grassland areas are associated to rocky soils or else subject to seasonal flooding (Oliveira-Filho & Ratter 2002). In relation to trap arrangement, in some situations a square grid may not be applicable, as in the narrow gallery forests. In such cases, arranging traps in linear transections may be the best option.

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## Supporting information

Appendix S1. Description of predictor and response variables used in the overall dataset analyses.

Variable	Variable type	Description
<b>Abundance/effort</b>	Response (quantitative)	Number of small mammal individuals captured for each species divided by the total sampling effort applied at the respective site.
<b>Richness</b>	Response (quantitative)	Number of small mammal species captured in each site.
<b>Method</b>	Predictor (qualitative)	Trap type used in the sampling: 1) cage (e.g. Tomahawk®, Sherman®, Young®) or 2) cage and pitfall (cage traps simultaneously used with pitfall traps)
<b>Design</b>	Predictor (qualitative)	Trap arrangement in the field during the sampling: 1) linear (traps are placed, usually equally spaced, forming linear transects) or 2) grid (traps are placed, usually equally spaced, in rectangular grids)
<b>Season</b>	Predictor (qualitative)	Number of seasons covered by the sampling period: 1) one season (small mammal sampling occurred only in one of the season, i.e. in the dry or in the wet season) or 2) both seasons (sampling occurred in dry and wet seasons).
<b>Effort</b>	Predictor (quantitative)	Number of traps used in each sampling multiplied by the number of days that sampling occurred.



<i>Carterodon sulcidens</i>	61.0	-	-	0.104	-	-	-	-	-	-	-	-	-	-
<i>Clyomys laticeps</i>	251.0	-	-	-	-	-	0.018	-	-	-	-	-	-	-
<i>Thrichomys apereoides</i>	237.0	-	0.042	-	0.208	-	0.113	0.566	0.982	-	0.041	0.153	0.153	-
<i>Thrichomys</i> sp	165.0	-	-	-	-	-	-	-	-	-	0.010	-	0.102	-

Appendix S3. Generalized linear models results for the effect of trap arrangement (linear transect or grid), trap type (cage only or cage + pitfall), and trapping period (only one or two [dry and rainy] seasons) on estimates of small mammal abundance (corrected by effort). Analysis were conducted for small mammals as a group and also for rodents and marsupials separately. The intercept of each model includes the predictor variables levels not showed (i.e., grid, cage only, and both seasons). Confidence interval in bold indicates a significant effect.

	Forest			Savannah			Grassland		
	$\beta$	SE	95% CI	$\beta$	SE	95% CI	$\beta$	SE	95% CI
Marsupials and Rodents									
Intercept	41.473	4.813	<b>32.684 to 51.575</b>	53.188	6.711	<b>40.911 to 67.265</b>	31.331	5.696	<b>21.349 to 43.806</b>
Linear	-8.868	5.113	-19.457 to 0.642	-8.414	7.803	-24.107 to 6.625	-2.386	5.931	-15.318 to 8.069
Cage and pitfall	13.855	4.710	<b>4.972 to 23.488</b>	25.116	7.331	<b>11.068 to 39.893</b>	22.762	7.442	<b>9.349 to 38.649</b>
One season	-9.130	3.777	<b>-16.471 to -1.612</b>	-10.814	6.303	-23.028 to 1.811	-13.259	4.715	<b>-22.821 to -4.245</b>
Rodents									
Intercept	60.785	9.240	<b>44.304 to 80.613</b>	52.970	7.282	<b>39.931 to 68.540</b>	31.819	6.040	<b>21.278 to 45.080</b>
Linear	-15.055	9.699	-35.595 to 2.599	-3.711	9.196	-22.410 to 13.812	-1.355	6.442	-15.349 to 10.043
Cage and pitfall	23.008	8.845	<b>6.593 to 41.424</b>	39.861	9.786	<b>21.172 to 59.672</b>	26.830	9.029	<b>10.709 to 46.277</b>
One season	-15.769	6.801	<b>-29.096 to -2.267</b>	-10.223	8.098	-25.730 to 6.170	-13.189	5.364	<b>-24.067 to -2.934</b>
Marsupials									
Intercept	106.129	17.608	<b>75.036 to 144.201</b>	407.64	102.81	<b>237.997 to 643.632</b>			
Linear	-24.606	19.784	-65.972 to 12.082	-178.47	112.34	-427.957 to 18.688			
Cage and pitfall	35.382	18.574	<b>0.504 to 73.728</b>	90.65	42.08	<b>11.216 to 179.541</b>			
One season	5.346	16.450	-26.079 to 38.828	-177.47	46.71	<b>-274.761 to -89.926</b>			

Appendix S4. Generalized linear models results for the effect of trap arrangement (linear transect or grid), trap type (cage only or cage + pitfall), trapping period (only one or two [dry and rainy] seasons), and total effort on estimates of small mammal richness. Analysis were conducted for small mammals as a group and also for rodents and marsupials separately. The intercept of each model includes the predictor variables levels not showed (i.e., grid, cage, and both seasons). Confidence interval in bold indicates a significant effect.

	Forest			Savannah			Grassland		
	$\beta$	SE	95% CI	$\beta$	SE	95% CI	$\beta$	SE	95% CI
Marsupials and Rodents									
Intercept	1.839	0.081	<b>1.678 to 1.996</b>	1.725	0.100	<b>1.523 to 1.919</b>	1.430	0.161	<b>1.098 to 1.733</b>
Linear	-0.152	0.088	-0.325 to 0.022	-0.220	0.131	-0.479 to 0.038	-0.077	0.190	-0.440 to 0.306
Cage and pitfall	0.173	0.074	<b>0.027 to 0.318</b>	0.311	0.104	<b>0.108 to 0.518</b>	0.294	0.133	<b>0.032 to 0.555</b>
One season	-0.018	0.080	-0.176 to 0.139	-0.345	0.113	<b>-0.571 to -0.125</b>	-0.167	0.128	-0.421 to 0.082
Effort	0.143	0.034	<b>0.074 to 0.209</b>	0.144	0.047	<b>0.048 to 0.235</b>	0.081	0.061	-0.043 to 0.196
Rodents									
Intercept	1.552	0.09	<b>1.363 to 1.734</b>	1.506	0.119	<b>1.266 to 1.735</b>	1.430	0.154	<b>1.113 to 1.721</b>
Linear	-0.158	0.106	-0.366 to 0.052	-0.209	0.158	-0.518 to 0.103	-0.193	0.188	-0.553 to 0.184
Cage and pitfall	0.111	0.088	-0.063 to 0.283	0.163	0.116	-0.062 to 0.394	0.265	0.145	-0.021 to 0.548
One season	-0.053	0.091	-0.234 to 0.125	-0.234	0.133	-0.501 to 0.023	-0.201	0.136	-0.471 to 0.065
Effort	0.102	0.041	<b>0.017 to 0.181</b>	0.088	0.056	-0.026 to 0.197	0.057	0.063	-0.072 to 0.175
Marsupials									
Intercept	0.779	0.134	<b>0.510 to 1.037</b>	0.796	0.201	<b>0.384 to 1.173</b>			
Linear	-0.208	0.151	-0.502 to 0.092	-0.481	0.279	-1.035 to 0.064			
Cage and pitfall	0.279	0.129	<b>0.023 to 0.532</b>	0.226	0.214	-0.182 to 0.659			
One season	0.126	0.137	-0.144 to 0.395	0.201	0.217	-0.236 to 0.617			
Effort	0.196	0.058	<b>0.077 to 0.306</b>	0.078	0.095	-0.118 to 0.258			



## Appendix S5

Results of a generalized linear mixed model for the overall effects of Cerrado macrohabitats (open area, savanna, and forest) and trap type (pitfall, small Sherman®, large Sherman®, and wire mesh cage) on small mammal trapping success, considering species as a random factor. Analysis were conducted using the restricted dataset (39 sampling sites were sampled simultaneously with the four trap types, see text for details). F- and p-values and associated degrees of freedom are indicated. Asterisks indicate significant values

Effects	Degrees of freedom	F Value	<i>P</i> Value
(Intercept)	1:264	15.474	0.0001*
Ln body mass	1:24	0.015	0.90
Trap type	3:264	1.434	0.23
Macrohabitat	2:264	4.916	0.008*
Body Mass : TrapType	3:364	10.324	<0.0001*
Body mass : Macrohabitat	2:264	0.203	0.82
Trap type : Macrohabitat	6:264	0.330	0.92
Body Mass : Trap type : Macrohabitat	6:264	0.963	0.45

## **Capítulo 2: Plant-animal interaction networks of Neotropical small mammals are affected by fire severity and resource availability but not by habitat structure**

### **Abstract**

Ecological interactions can determine the occurrence of species in communities with frugivory being among the most widely distributed plant-animal interactions worldwide. Different interaction patterns can be associated with changes that communities undergo because of disturbances such as natural and anthropogenic fires. However, the impacts of fire events may vary, with different parts of a landscape experiencing distinct levels of fire severity. Here, we investigated plant-animal interaction networks involving small mammals and plant species consumed by these animals in fire-sensitive Cerrado (neotropical savanna) forests 3 years after burning. We identified 728 interactions between 211 plant species and 11 small mammal species. Fire severity altered the structure of plant-animal networks. Networks in areas severely affected by fires tended to be more nested, with greater diversity of interactions, less specialized, and less modular. Also, resource availability impacted plant-animal networks, with forests with more available resources being less nested and diverse, but more specialized and modular. Lastly, we found that habitat structure was associated with the gradient of fire severity, though it did not directly influence the evaluated network metrics. We highlight that fire-sensitive areas could have their interaction networks compromised, as these plant-animal networks become structurally distinct from unburned or less severely burned ones.

**Keywords:** Cerrado, gallery forest, wildfire, metabarcoding

## **Introduction**

Ecological interactions can determine the occurrence of species in communities (Belyea and Lancaster 1999). One of the most widely distributed plant-animal interaction worldwide is frugivory, which influences the dynamics and stability of various terrestrial ecosystems (Levey et al. 2002, Estrada and Fleming 2012). Patterns of interactions between plants and animals are not static but vary both spatially and temporally (Alarcón et al. 2008, Dugger et al. 2019). This variation may be influenced by changes in both animal species composition and in plant resource availability. Both these factors are affected by disturbances, such as natural and anthropogenic fires (Sousa 1984). With climate change, fire events are anticipated to increase in both frequency and intensity. This projection is driven by the expected rise in extreme events, such as prolonged drought periods (Hoegh-Guldberg et al. 2019). Consequently, it is imperative for the conservation of natural systems the understanding of how fire affects plant-animal networks, especially in fire-prone ecosystems.

Fire regimes in terrestrial ecosystems are undergoing several changes in the last decades. Excessive suppression of natural fires in fire-prone environments, the deliberate ignition of fires in sensitive areas, and alterations in environmental conditions are the primary human activities that have contributed to changes in burning patterns (Bowman et al. 2011). While fire is a natural disturbance and an evolutionary factor in fire-prone ecosystems (Daubenmire 1968, Simon et al. 2009), alterations in its regime can have adverse effects on the biodiversity and functioning of these environments (Williams et al. 2009). One such fire-prone ecosystem is the Cerrado (Neotropical savanna), where fire events have occurred for at least 30,000 years (Salgado-Labouriau et al. 1997). However, this biome has experienced more intensified fire regimes in recent years (Schmidt and Eloy 2020), posing a particular threat to areas highly sensitive to this disturbance, such as gallery forests within extensive savanna and grassland landscapes (Dantas and Pausas 2013).

The distinct phytophysiognomies found in the Cerrado, including grassland, savanna, and forest formations, harbor a highly diverse flora, with estimates of around 10,000 plant species occurring (Ribeiro and Walter 1998, CEPF 2017, Sano et al. 2019). This diversity of habitats constitutes a heterogeneous landscape, promoting a high faunal diversity that includes at least 251 mammal species, of which 103 are rodents and marsupials (Paglia et al. 2012). Many of these animals incorporate fruits and seeds into their diets, resulting in complex plant-animal interaction networks in the Cerrado.

The network analysis approach has been one of the primary methods for describing interactions between plants and frugivores and for assessing changes in interaction patterns due to environmental changes (Quintero et al. 2022). Various metrics have been proposed to evaluate ecological interaction networks, with some of the most commonly used ones describing the degree of nestedness and modularity in interaction networks (Fortuna et al. 2010). Nested networks exhibit interactions involving specialist species as subsets of interactions involving more generalist species. This pattern is often observed in mutualistic interaction networks as well as host-parasite networks (Bascompte et al. 2003, Vázquez et al. 2005). In contrast, when a network displays a modular pattern, the species within it form subsets that interact more with each other than with species in other subgroups. Such modular structures are commonly reported in food webs (Krause et al. 2003), but have also been observed in mutualistic networks (Olesen et al. 2007). Further, a single network may exhibit a combination of these patterns, as is the case when modular networks have nestedness within the modules (Lewinsohn et al. 2006). In addition to nestedness and modularity, other metrics can provide further insights into the overall structure of networks, such as specialization, which describes the degree of specialization in species interactions (Blüthgen et al. 2006), and interaction diversity.

Our understanding of how ecological interactions are affected by fire in the Cerrado is still limited, constituting a relatively small portion of the studies concerning the impact of fire in this biome (Arruda et al. 2018). Most investigations into the responses of plant-animal interactions to fire events in this biome have primarily centered around plant-ant and plant-pollinator interactions (Ballarin et al. 2023). This highlights a gap in our knowledge regarding the effects of fire on frugivory and seed dispersal interactions.

Fire has direct effects (e.g., causing the death of individuals) and indirect effects (e.g., altering environmental conditions in affected areas) on both plants and animals (Michaletz and Johnson 2007, Tomas et al. 2021, Bergstrom et al. 2023). Specifically, in the case of small mammals, a species turnover can be observed during the post-fire period, with some species increasing their populations while others decline (Fox 1982, Vieira and Marinho-Filho 1998, Vieira 1999, Briani et al. 2004). The availability of resources and the habitat structure after a fire are among the key factors influencing the recovery of small mammal populations in burned areas (Sutherland and Dickman 1999). However, the impacts of fire events vary depending on the type of vegetation, as well as topography, weather conditions, and fuel load (Countryman 1972). Therefore, different parts of a landscape may experience varying levels of fire severity (White et al. 1996), leading to different responses from animal populations and, consequently, affecting the ecological interactions within the group.

In the present study, we investigated plant-animal interaction networks involving small mammals and the plant species consumed by these animals in the Cerrado, while also examining the impact of fire severity on these networks. Since it was not possible to distinguish the type of interaction observed, i.e., whether it was mutualistic or antagonistic, the interactions were assessed together. Our objectives encompassed: 1) to describe the patterns of these plant-animal interaction networks between small mammals and plant species, and 2) to evaluate the effects of fire severity, resource availability, and habitat structure on

these plant-animal interaction networks within gallery forests three years after a major fire event. Given that both resource availability and habitat structure can be influenced by fire, and that these factors drive the responses of small mammal species in burned areas (Sutherland and Dickman 1999), we anticipate that the plant-animal interaction networks will exhibit distinct structures along the fire severity gradient. Specifically, we expect to observe more generalized interactions in areas severely affected by fire, as well as in forest areas with lower resource availability and highly modified habitat structures.

## **Methods**

### Study sites

We conducted our study within two contiguous Conservation Units (UC) located in the Central Brazilian Cerrado: the Chapada dos Veadeiros National Park (PNCV) and the Fazenda Mata Funda Private Natural Heritage Reserve (RPPN Fazenda Mata Funda) (Figure 1). The PNCV encompasses approximately 240,000 hectares spread across five municipalities in the northeastern region of the state of Goiás. On the other hand, the RPPN Fazenda Mata Funda is situated in close proximity to the PNCV, covering 110 hectares within the municipality of Alto Paraíso de Goiás. This region experiences an equatorial climate with a dry winter period (Kottek et al. 2006) typically extending from May to September. Similar to much of the Cerrado, this area has historically faced recurring wildfires during the peak of the dry season (Silva et al. 2021). In fact, between 2008 and 2019, the cumulative fire scars in the PNCV reached an area equivalent to 225% of the current extent of this protected area (Matos et al. 2020). The most recent significant wildfire in this region occurred in 2017, a year marked by mega-fires on different continents (Fidelis et al. 2018). In the Chapada dos Veadeiros specifically, this event likely resulted from a combination of a prolonged dry

period and escalating land conflicts related to the expansion of the PNCV, which was declared in the same year.

Within our study area, we sampled seven gallery forests that had been affected by varying degrees of severity during the 2017 fire (Figure 1). Gallery forests are forested areas associated with watercourses, characterized by an average tree height ranging from 20 to 30 meters and canopy coverage ranging from 70% to 95% (Ribeiro and Walter 1998). These forest formations play a pivotal role in preserving the diversity of non-flying mammals in the Cerrado (Redford and Fonseca 1986) and are more susceptible to fire damage compared to open Cerrado formations. To ensure that we captured distinct small mammal communities, we selected gallery forests with at least a 1-kilometer separation between them.

#### Small mammal sampling and sample collection

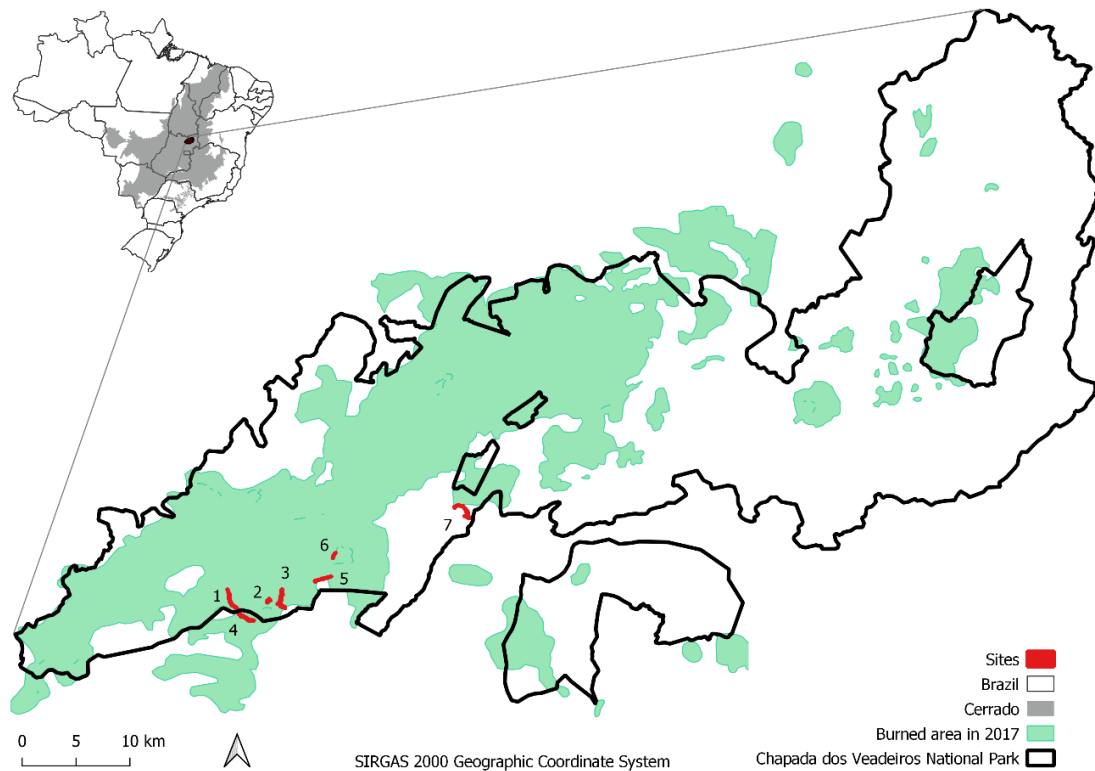
We conducted two sampling campaigns to study small mammals, one during the rainy season (February and March 2020) and the other in the dry season (September and October 2020). In the first campaign, we sampled five gallery forests (Estiva 1, Maytrea 1, Maytrea 2, Mulungu 1, and Mulungu 2), and in the second campaign, we revisited these areas and included two additional gallery forests (Estiva 2 and Pouso Alto), making a total of seven areas. To capture animals in these areas, we established two transects, each consisting of 30 equidistant sampling points spaced 15 meters apart. At each point, we placed two types of traps: Sherman traps (one small – 9 cm x 9.5 cm x 23 cm and one large – 11 cm x 12.5 cm x 37 cm) on the ground and in the understory alternately. Moreover, at five sampling points in each transect, we substituted the large Sherman traps with Tomahawk traps (45 cm x 16 cm x 16 cm). All traps remained open for five consecutive nights and were baited on the first day of sampling with a mixture of banana, cornmeal, sardines, peanut butter, and palm oil. We refreshed the bait every two days or as needed.

We identified the captured animals, recorded basic body measurements, determined their sex, and noted their reproductive status. After marking them with numbered ear tags, we released the individuals at the same capture location. To analyze the plant species consumed by the small mammals, we collected feces found in the traps where the animals were captured or obtained during their handling. Subsequently, we preserved the samples in 70% alcohol and stored them in a freezer. All animal handling procedures adhered to the guidelines of the American Society of Mammal Zoologists (Sikes et al. 2011) and the study received approval from the Animal Ethics Committee of the University of Brasília (CEUA) under protocol number 4783821.

#### Fruit availability

To assess fruit availability in the seven gallery forests, we conducted a count of fruiting individuals. To do this, we selected a starting point in each transect (in a non-systematic manner) and walked up to the tenth point, recording the number of fruiting individuals encountered. We considered specimens in all vertical strata located within 1.5 meters of the central trail and bearing fruits at any stage of ripeness. As in some cases fruit observations ceased at the ninth point in some transects, we utilized the values of the number of fruiting individuals divided by the total number of points covered for our analyses.





**Figure 1.** Map of the studied Cerrado (Neotropical savanna) region indicating the area burned in 2017 and the location of the study sites in the Chapada dos Veadeiros National Park, central Brazil. From left to right, images represent examples of gallery forest in the three classes of fire severity: unburned (Pouso), low (Mulungu 2) and moderate (Estiva 1).

### Habitat structure

To characterize the habitat structure in the sampled gallery forests, we measured six variables at all sampling points in each of the seven areas. For these measurements, we established a circle centered on each sampling point (with a radius of 1 meter), which was subsequently

divided into four quadrants. Within these quadrants, we collected data on: a) canopy coverage by assessing the proportion of greenery in photographic records taken from a height of approximately 2 meters, with the camera facing upward toward the sky, and later analyzed using Image J software (Rasband 2018); b) herbaceous coverage, following the same methodology as for canopy coverage estimation but with the camera positioned at approximately 50 cm in height and directed toward the ground; c) distance to the nearest tree with a circumference of at least 15 cm at breast height; d) circumference of the nearest tree; e) obstruction in the understory, determined using the intersection method in which we horizontally extended a 1.5-meter metal rod marked with 10 equidistant points and recorded how many of these points were intersected by vegetation; and f) the presence of fallen tree trunks with a circumference of at least 20 cm.

#### Metabarcoding analysis and bioinformatic

In order to assess the plant resources consumed by small mammals, we performed DNA extraction from the feces of the captured individuals. To do this, we first separated up to 0.22 milligrams from each fecal sample and followed the manufacturer's protocol for the QIAamp Fast DNA Stool Mini Kit (Qiagen) to carry out DNA extraction from 200 out of 228 distinct samples collected. Subsequently, genetic material from individuals of the same species captured at the same sampling site was homogenized to create a single sample. Next, the DNA concentration of each extraction was determined through fluorometry using the Qubit™ dsDNA HS Assay Kit (High Sensitivity - Thermo Fisher Scientific) and the Qubit® 3.0 fluorometer (Thermo Fisher Scientific), following the manufacturer's instructions.

Following that, the DNA was amplified in triplicate through the polymerase chain reaction (PCR) using the primer set ITS2-ITS3 (ITS2 F-ATGCGATACTTGGTGTGAAT; ITS3 R-GACGCTTCTCCAGACTACAAT). This primer set amplifies a region of up to 450

base pairs from the intergenic transcribed spacer (ITS) region, which is one of the most commonly used fragments in molecular systematics of plants due to its potentially high resolution of intraspecific relationships. This characteristic facilitated the description of dietary components for granivores, frugivores, and omnivores.

The PCR reactions were prepared for a final volume of 25  $\mu\text{L}$ , containing 5  $\mu\text{L}$  of Buffer (5x); 2  $\mu\text{L}$  of dNTPs (2 mM each); 2.4  $\mu\text{L}$  of  $\text{MgCl}_2$  (25 mM); 0.5  $\mu\text{L}$  of each oligonucleotide (10 pmol); an average of 5 ng of DNA; 1.25 U of GoTaq G2 Flexi DNA Polymerase (Promega); 2  $\mu\text{L}$  of DMSO; 5  $\mu\text{L}$  of TBT-PAR buffer (Samarakoon et al. 2013); and sterile, nuclease-free ultrapure water to reach the final reaction volume.

The amplification was carried out using a Veriti Thermal Cycler® (Applied Biosystems). The temperature profiles for amplification followed these steps: enzyme activation at 94 °C for 3 minutes, followed by 30 amplification cycles of 1 minute at 94 °C, 1 minute at 54 °C, 1 minute at 72 °C, and a final extension step at 72 °C for 7 minutes. After amplification, the amplicons were analyzed on a 1.2% agarose gel using 5  $\mu\text{L}$  of the PCR product to assess quality. Subsequently, we proceeded with library construction for sequencing on the Illumina platform, following the protocol provided by the manufacturer (Illumina 2013). The purified libraries were analyzed on a BioAnalyzer 2100 (Agilent Technologies) and combined into sequencing pools using equimolar ratios, with the addition of 10% PhiX. Finally, the libraries were sequenced on the Illumina MiSeq platform using the MiSeq High Output kit (600-cycles) (Illumina 2013).

The FastQ files containing the reads generated from sequencing were processed using the Pimba pipeline (Pipeline for MetaBarcoding Analysis), developed at Instituto Tecnológico Vale (ITV) (Oliveira et al. 2021). Reads shorter than 100 bp and reads with an average Phred quality score of < 20 were discarded. For taxonomic assignment of ASVs, we employed ASAP— Assemble Species by Automatic Partitioning (Puillandre et al. 2021). This method

constructs species partitions from single-locus sequence alignments. The implementation is based on a hierarchical clustering algorithm that utilizes pairwise genetic distances, and the scoring system used does not require any prior knowledge of intraspecific diversity. In our analyses, we selected the default settings (recursive splitting = 1%, showing the top 10 scores) and used only the ASAP partition with the best score and partitions with significant p-values.

## Data analysis

### *Network analysis*

To construct plant-animal interaction networks, we utilized the ASVs identified through DNA analysis of small mammal feces. In these networks, the nodes representing animals correspond to small mammal species, while the nodes representing plants correspond to the botanical families of the consumed plants. To assess the topological patterns in weighted networks, we assigned weights to the detected interactions, which reflected the number of ASVs (i.e., the richness of plants each small mammal species interacted with within each botanical family). These weighted bipartite networks were created for each of the assessed gallery forests.

Given the challenges in estimating the capture of resource diversity in our samples, we decided to analyze the topological patterns of the networks only for areas where we could analyze fecal samples from at least 15 individuals of small mammals within the community. Consequently, we examined four networks for areas sampled during the rainy season and five networks for areas sampled during the dry season. We opted for separate analyses for each season due to the pronounced seasonality observed in the Cerrado (Oliveira and Marquis 2002). This seasonality affects habitat conditions and resource availability, both of which can influence the structure of interaction networks.

To assess the topological pattern of plant-animal networks, we calculated the following metrics: nestedness, modularity, specialization, and Shannon interaction diversity. Nestedness describes the degree to which interactions in a network are organized such that specialist consumers interact with a subset of items consumed by more generalist species. For this metric, we used weighted NODF values, which range from 0 to 100 (Almeida-Neto and Ulrich 2011). Modularity, on the other hand, indicates the extent to which the network consists of subgroups of species that interact more with each other than with species in other subgroups within the network. For this metric, we employed the algorithm proposed by Beckett (2016), with values ranging from 0 to 1. Specialization, in turn, reflects the degree of exclusivity in interactions based on partner availability. For this metric, we used the H2' index, which ranges from 0 to 1 (Blüthgen et al. 2006). Finally, we obtained interaction diversity through the Shannon index, applied to count interactions instead of species abundance. This provided values that describe how much species are interacting and how evenly distributed these interactions are.

We opted for utilizing quantitative metrics because they are less susceptible to the effects of sample effort (Fründ et al. 2016, Vizentin-Bugoni et al. 2016). In a similar vein, we determined the significance of these metrics using null models. To achieve this, we employed the "vaznull" null model, which maintains the same observed connectivity while randomizing interactions between the two partitions of the network (Vázquez et al. 2007). We generated 1000 random networks from each of the observed networks and assessed the significance of the observed values using the Monte Carlo test to infer whether these values deviated from what would be expected by chance ( $\alpha = 5\%$ ).

For all network analyses, we utilized the "bipartite" package (Dormann et al. 2009) in the R software (R Core Team 2022). The basic script for randomizing networks and comparing observed values with those expected by chance was developed by Renata

Muylaert, Pavel Dodonov, and Marco Mello (available at <https://github.com/marmello77/network-significance>).

### *Fruit availability*

To determine if the observed values of network metrics could be accounted for by fruit availability, we conducted individual linear regressions for each of these metrics, with fruit availability serving as the independent variable. To satisfy the assumptions of the linear model, we took the square root of the values obtained for this availability.

### *Habitat structure*

We also explored potential effects of habitat structure on the calculated network metrics. For this purpose, we first summarized the six variables related to habitat structure using Principal Component Analysis (PCA). In this analysis, we employed the z-scores of the variables to standardize and remove scale effects among them (Zar 2009). Subsequently, we examined whether the average values of PCA axes 1 and 2 for each gallery forest could be explained by the average values of the dNBR – Differentiated Normalized Burn Ratio (which is the difference between pre- and post-fire values of the Normalized Burn Ratio (Escuin et al. 2008)) through linear regression. The dNBR values were obtained by satellite images and is closely tied to vegetation structure and commonly used for assessing the severity of fire impact on vegetation (Keeley 2009, Soverel et al. 2010). Additionally, we utilized linear regressions to determine if the observed values for network metrics could be accounted for by the values of PCA axes 1 and 2.

## **Results**

We identified 771 distinct genetic sequences representing plant species found in the feces of rodents and marsupials captured in seven gallery forests within the Cerrado region.

Using the ASAP, these sequences were categorized into 211 plant species spanning 56 families (see appendix S1). The families with the highest number of identified taxa were Myrtaceae (n = 37), Melastomataceae (n = 33), Fabaceae (n = 20), Onagraceae (n = 14), and Rubiaceae (n = 11), accounting for a total of 54% of the identifications.

We captured 11 species (or group of species, because we considered species of the same genus whose accurate identification was not possible in the field as only one 'species'), as following: *Cerradomys scotti* (n = 1), *Didelphis albiventris* (n = 8), *Gracilinanus agilis* (n = 21), *Hylaeamys megacephalus* (n = 14), *Necomys lasiurus* (n = 4), *Nectomys rattus* (n = 36), *Oecomys* spp. (included *O. gr. catherinae* and *O. cleberi*; n = 20), *Oligoryzomys* spp. (included *O. mato Grossoe* and *O. nigripes*, n = 10), *Oxymycterus delator* (n = 42), *Proechimys roberti* (n = 2), and *Rhipidomys macrurus* (n = 80). Among the assessed small mammals, *Oecomys* spp. was the species that interacted with the highest number of plants (n = 105), followed by *Hylaeamys megacephalus* (n = 103), *Nectomys rattus* (n = 96), and *Rhipidomys macrurus* (n = 80). Together, these four species accounted for 52.7% of the total 728 interactions detected. As for botanical families, those with the highest number of interactions were Melastomataceae (n = 110), Myrtaceae (n = 87), Fabaceae (n = 77), Onagraceae (n = 44), Asteraceae (n = 39), Poaceae (n = 38), and Rubiaceae (n = 38), totaling 59% of all interactions detected (see appendix S2 and S3).

#### Plant-animal networks and fire severity

The assessment of nestedness patterns in plant-animal interaction networks revealed a positive relation between the nestedness of networks during the dry season and the severity of fire. However, there was no such relation between nestedness in networks during the rainy season and fire severity. Additionally, regardless of the season, the observed nestedness values did not significantly differ from those expected by chance (Figure 2a).

Regarding modularity, a negative association was observed between this metric and fire severity for networks during the dry season, whereas no such relationship was found for modularity in networks during the rainy season. Furthermore, irrespective of seasonality, the observed modularity values tended to be lower than expected by chance, with six out of the nine assessed networks exhibiting a significant difference when compared to null models (Figure 2b).

We also noted a negative relation between fire severity and the degree of specialization within the networks (Figure 2c). This relation indicates that, as fire severity increased, the degree of specialization tended to be lower than expected by chance. Only the networks related to unburned areas displayed observed specialization values that did not differ significantly from those expected by chance. This effect was more pronounced in networks during the dry season but was also observed in networks during the rainy season (Figure 2c).

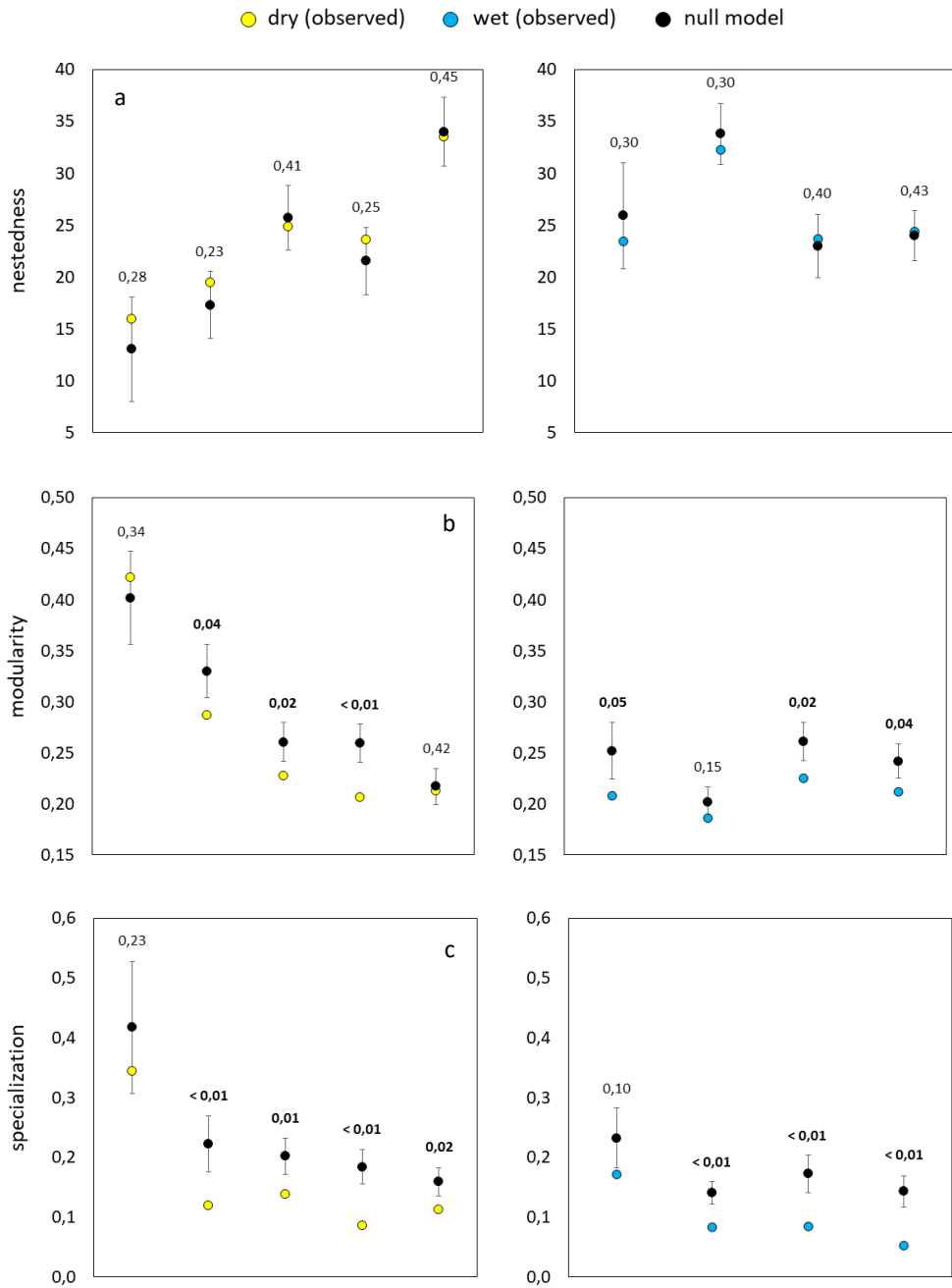
We identified a relationship between fire severity and the calculated interaction diversity values (Shannon index) of the networks (Figure 2d), with higher diversity values associated with areas more severely affected by fire. A comparison with randomized values indicated, in general, that the observed diversity values tended to be lower than expected by chance, both in networks during the dry season and those during the rainy season (Figure 2d).

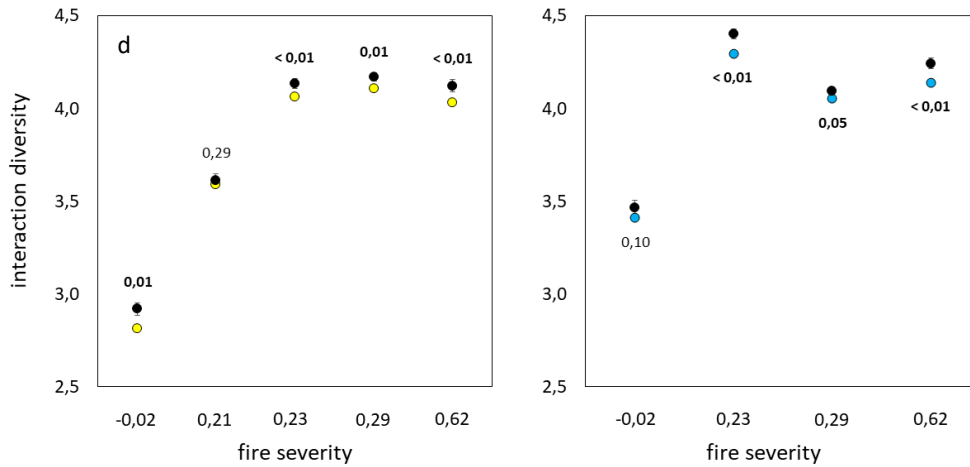
#### Plant-animal networks and fruit availability

We observed a significant negative relationship between fruiting and both nestedness ( $R^2 = 0.51$ ;  $p = 0.03$ ) and interaction diversity ( $R^2 = 0.57$ ;  $p = 0.02$ ). In other words, higher observed fruiting was associated with lower values of these metrics (Figure 3; a and d). The relationship between fruiting and network specialization also tended to be negative but was not statistically significant ( $R^2 = 0.37$ ;  $p = 0.08$ ; Figure 3c). Additionally, we detected a significant positive relationship between fruiting and network modularity ( $R^2 = 0.59$ ;  $p =$

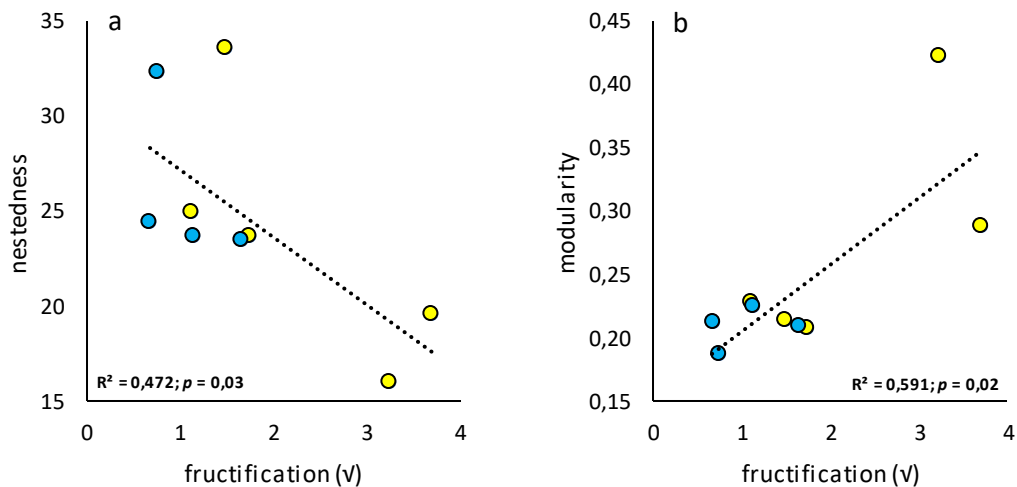


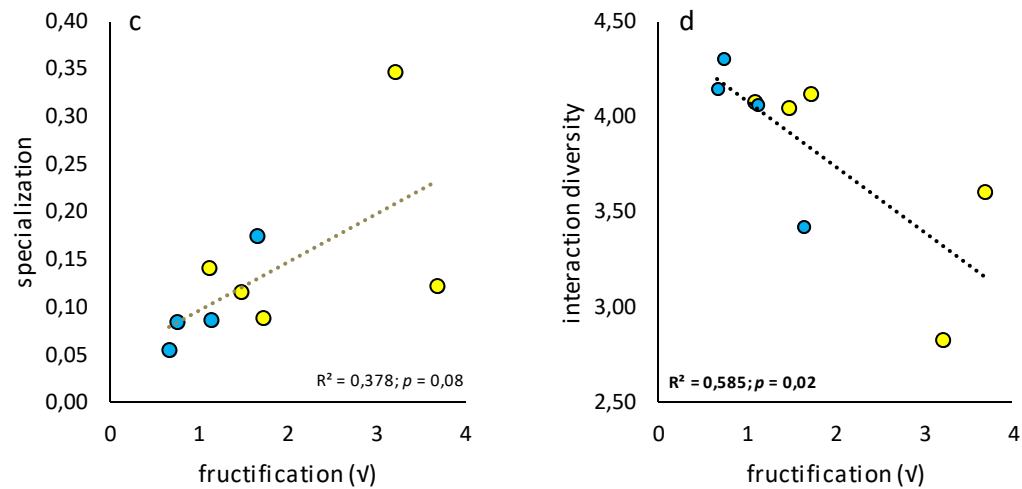
0.02; Figure 3b). On the other hand, the relation between fruiting and fire severity was not significant ( $R^2 = 0.233$ ;  $p = 0.17$ ).





**Figure 2.** Observed and expected values for a) nestedness, b) modularity, c) specialization, and d) interaction (Shannon) diversity obtained for plant-animal interaction networks in five gallery forests in the Cerrado. Black circles indicate the expected mean value based on 1000 randomizations of the networks, and vertical bars indicate the standard deviation around this mean. Numbers above the bars indicate the p-values obtained by randomization (bold numbers indicate that the observed value for the metric was different from what would be expected by chance).





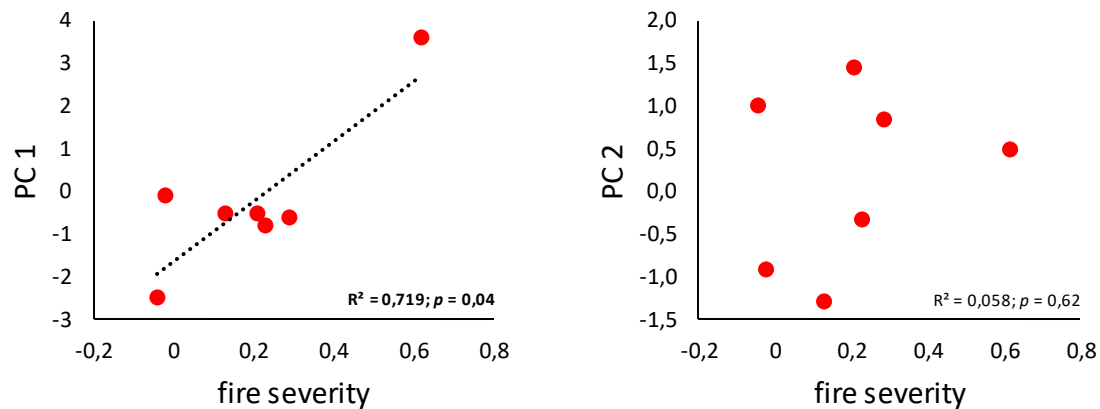
**Figure 3.** Relationship between fructification and a) nestedness, b) modularity, c) specialization, and d) interaction (Shannon) diversity of plant-animal interaction networks in five gallery forests in the Cerrado. Trend lines are shown for  $p < 0.1$  values (obtained through permutation; black lines indicate relationships with  $p < 0.05$ ). Blue circles represent interaction networks for the rainy season, and yellow circles represent interaction networks for the dry season.

#### Plant-animal networks and habitat structure

Considering the habitat structure, the first axis (PC 1) of the Principal Component Analysis (PCA) explained 55% of the observed variance, while the second axis (PC 2) accounted for 19%. The habitat variables most strongly correlated with PC 1 were: a) distance to the nearest tree (0.52); b) canopy coverage (-0.50); c) circumference of the nearest tree (0.48); and d) herbaceous cover (0.47). Consequently, areas with more negative values along PC 1 exhibit denser vegetation, whereas areas with more positive values feature more open vegetation. On the other hand, for PC 2, only the presence of fallen logs showed a high value (0.85), while the other variables had values below 0.40.

We observed a significant positive relationship between the values of PC 1 and fire severity ( $R^2 = 0.719$ ;  $p = 0.04$ ; Figure 4a). However, for the second axis, we did not identify

any relationship between the axis values and fire severity ( $R^2 = 0.058$ ;  $p = 0.62$ ; Figure 4b). Additionally, we found no association between PC 1 and PC 2 and any of the four network topological metrics evaluated (see appendix S4 and S5).



**Figure 4.** Relationship between fire severity (dNBR) and the first (PC 1 = 55%) and second (PC 2 = 19%) axes of the Principal Component Analysis (PCA) conducted with the six habitat variables (canopy cover, herbaceous cover, distance to the nearest tree, circumference of the nearest tree, understory obstruction, and quantity of fallen logs) measured in seven gallery forests in the Cerrado. Trend lines indicate relationships with  $p < 0.05$  (obtained by permutation).

## Discussion

We conducted this study to examine the impacts of fire severity, resource availability, and habitat structure on plant-animal interactions within the Cerrado ecosystem. This was the first study to employ *metabarcoding* analyses to identify dietary components (i.e., plants), allowing us to build interaction networks for small mammal communities affected by fires in the Cerrado. The use of this method enabled us to identify 728 interactions between 11 species (rodents and marsupials) and 211 plants, representing 56 different families. This level

of detail has never been documented in a single study before. For example, in the third chapter of this thesis, based on 395 fecal samples observed on stereoscope, we were only able to identify 28 plant species belonging to eight botanical families. Our findings indicate that the severity of fires altered the structure of plant-animal networks. It resulted in networks becoming more nested, exhibiting greater diversity of interactions, while also being less specialized and less modular in areas severely affected by fires. This effect was particularly pronounced during the dry season. Interestingly, we did not observe a correlation between resource availability (such as fruiting) and fire severity. However, higher resource availability did impact the structure of plant-animal networks, making them less nested and diverse, but more specialized and modular. Lastly, we found that habitat structure was associated with the gradient of fire severity, though it did not directly influence the evaluated network metrics.

#### Fire severity, resource availability, and habitat structure

Our findings did not reveal a significant correlation between fire severity and fruit availability, contrary to our initial expectations. In various ecosystems, there is an indication of a link between fire occurrences and a decrease in fruit production. For instance, in the Amazon rainforest, areas affected by a fire induced by an extended dry period caused by the El Niño had reduced fruit production (Barlow and Peres 2006). Decreases in fruit abundance in post-fire years have even been reported in fire-prone environments. In an Amazonian savanna, for example, Sanaiotti and Magnusson (1995) observed a reduction in fruiting for shrubs and herbaceous plants (though not for tree species) in areas subjected to two consecutive years of burning and again two years after fire cessation. Significant reductions of up to 99% in fruit abundance in areas burned with fire return intervals of 1 to 2 years were also reported for temperate forests dominated by *Pinus* trees in North Carolina, USA (Lashley et al. 2017). Nevertheless, apart from fire occurrence, our understanding of the impact of fire

severity on fruit abundance in affected vegetation remains limited. In some instances, the reduced availability of fruit reported in the studies mentioned was associated with increased fire frequency or shorter fire return intervals, conditions that differ from those we examined in the current study. Therefore, it is plausible that the absence of recent fire history in gallery forests, coupled with the time vegetation had to recover between the fire event and our samplings (a span of 3 years), may have provided plant species the opportunity to reproduce and yield fruit independently of fire severity. In our study, we were unable to assess whether fire severity affected other relevant aspects of fruit availability, such as richness and composition of fruiting species.

Conversely, fire severity had a significant impact on the habitat structure of the studied gallery forests, aligning with our expectations. This relationship indicated that more severely affected gallery forests displayed a more open structure, characterized by lower canopy cover, greater distances to the nearest tree, larger circumferences of the nearest tree, and greater herbaceous ground cover. Fire severity is gauged by assessing the damage inflicted on vegetation, a metric influenced by factors such as topography, weather conditions, and available fuel load (Countryman 1972, White et al. 1996). Thus, when evaluating a gradient of fire severity, it is expected that areas more severely impacted will experience greater alterations in habitat structure, as our study has shown. In fact, Flores et al. (2021) when examining gallery forests affected by the same fire in PNCV, identified varying levels of fire severity, with the most affected areas losing up to 80% of canopy cover.

#### Plant-animal networks and fire severity

Our results indicated a positive relationship between the nestedness of plant-animal networks and fire severity, as expected, during the dry season. The mechanisms governing the recovery of small mammal populations in burned areas largely involve species' responses to changes in

resource availability and habitat structure following fires (Sutherland and Dickman 1999). We anticipated that interaction networks in areas most affected by fire would exhibit higher levels of nestedness due to reduced fruit availability. However, fire severity showed no correlation with fruiting. Another possibility is that the increased nestedness of networks in heavily burned forests was an indirect result of changes in the composition of small mammal communities. The simplification of forest habitat (primarily through reduced canopy cover and increased herbaceous ground cover) likely favored the invasion of species typical of open habitats into the gallery forests affected by the fire. In fact, there was an increase in taxonomic diversity of small mammals along the fire severity gradient. This increase in species richness, however, was accompanied by a decrease in the abundance of forest specialist species (Souza 2023). In the southern Amazon basin, experimentally burned forest areas also exhibited increased diversity of ants typical of open formations, at the expense of a reduction in the diversity of forest specialist ants (Paolucci et al. 2017). Similarly, Puig-Gironès et al. (2022) observed a positive relationship between the richness of open-habitat specialist birds and fire severity in burned areas in Catalonia, a Mediterranean region. Since the studied mammals shared a less structured environment, spatial segregation (e.g., between distinct vertical strata) may have been reduced. In this scenario, rodents and marsupials likely expanded their dietary niches, adopting more generalist diets. This could explain the increased nestedness of networks in more severely burned areas, at least during the dry season, a time of year when the availability of these resources is generally lower (; but see Darosci et al. 2021).

Regarding the networks modularity, we observed that as fire severity increases, modularity decreases. While these topological patterns are not mutually exclusive (Pinheiro et al. 2019), there is often a negative relation between nestedness and modularity values in ecological networks (Thébault and Fontaine 2010). In areas most severely impacted by fire, rodents' and marsupials' diets exhibited a more generalist pattern, which would reduce the

occurrence of modules in plant-animal interaction networks. Furthermore, we also observed a negative relationship between fire severity and the degree of specialization in plant-animal interaction networks, indicating that higher severity levels may lead to the formation of more generalized interaction networks. Species are classified as specialists on a particular resource when they interact with a subset of the potentially available resources. In this context, when assessing interaction networks at the community level, we can expect that the networks predominantly composed of specialist species will exhibit higher specialization values than those primarily composed of generalist species (Blüthgen et al. 2006).

We found a positive relationship between fire severity and the calculated values of interaction diversity in the networks, supporting our expectations. The occurrence of fire may be positively associated with the richness of certain vertebrate groups, such as birds and mammals (Moritz et al. 2023). Specifically, for rodents and marsupials, a higher richness of this group in burned forests appears to be related to the influx of species from adjacent open formations, favored by changes in habitat structure caused by fire (Camargo et al. 2018). As discussed earlier, we detected a positive relationship between fire severity and the taxonomic diversity of these animals in our study area, a result of the invasion of species typical of open areas into the gallery forests affected by the fire (Souza 2023). Furthermore, as fire severity increased, we observed a decline in the degree of specialization of the networks. In other words, small mammal communities became more generalist in terms of fruit and seed consumption, interacting with a greater richness of plants. Therefore, both the increased species richness of small mammals and the lower degree of specialization in the networks along the fire severity gradient may have contributed to a higher diversity of interactions in more severely affected areas. However, an increase in interaction diversity is not necessarily positive. For instance, we did not assess the strength of these pairwise interactions.



### Plant-animal networks and fruit availability

As anticipated, our results indicated a negative relationship between resource availability (i.e., fruiting) and the nestedness of the networks. According to the optimal diet theory, in a scenario of increased food resource availability, individuals may adopt a more specialized dietary strategy (Svanbäck and Bolnick 2005). Similarly, if species within a community also adopt a more specialized diet when resources are abundant, there would be less overlap in the food items included in their diets. In interaction networks, this could result in lower nestedness, consistent with our observations. Similarly to our study, Hachuy-Filho et al. (2020) found more nested plant-bee networks with greater niche overlap during periods of lower availability of floral resources in *campo cerrado* areas. There are other studies, however, that have reported results contrary to ours, showing a positive relationship between food resource abundance and the nestedness of ecological networks. For instance, Cantor et al. (2013) observed a nested structure in interaction networks between *D. albiventris* and fruits consumed exclusively during the rainy season, a period with higher resource availability. When investigating plant-frugivore networks in seasonal ecosystems in Mexico, Ramos-Robles et al. (2016) found a positive correlation between nestedness and the abundance of fruits available to local bird species. Additionally, in a Cerrado-Atlantic Forest ecotone, plant-frugivore networks involving bats as consumers exhibited greater nestedness during the rainy season, a time when resources were more abundant (Laurindo et al. 2017). Thus, our results, along with the information available in the literature, suggest distinct patterns in the relationship between food resource abundance and the nestedness of plant-animal networks.

As expected, our findings indicated a positive relationship between resource availability (i.e., fruiting) and modularity. Applying the optimal diet theory, in a scenario with increased availability of food resources, species may adopt a more specialized dietary

strategy, leading to greater niche partitioning. Consequently, this could result in the formation of modules within plant-animal networks, where certain animal species interact more closely with specific groups of plants than with plants from other groups. Similar to our findings, Ballarin et al. (2019) observed a similar pattern in plant-ant interaction networks in the Atlantic Forest, with modularity positively associated with the availability of food resources (i.e., quality and quantity of nectar). In individual-resource networks, a positive relationship was found between fruit abundance in *cerradão* (woodland savanna) areas and network modularity for various populations of the Neotropical marsupial *Gracilinanus agilis* (Camargo et al. 2019). Similarly, there is evidence that plant-bee networks become more specialized and modular during periods of increased availability of floral resources in *campo cerrado* areas (Hachuy-Filho et al. 2020). Regarding specialization, our results suggest a positive correlation between this metric and fruiting, similar to what has been observed in other plant-animal interaction networks (Ballarin et al. 2019, Hachuy-Filho et al. 2020). This trend reinforces the hypothesis that plant-animal interactions may become more specialized and modular in environments with higher resource availability, as discussed earlier.

The negative relationship between fruiting and interaction diversity may have resulted from increased specialization in areas with higher resource availability. Furthermore, considering the optimal diet theory, species may adopt a more specialized dietary strategy when food resources are more abundant in the environment. Consequently, there would be a reduction in the richness of pairwise interactions, as each small mammal species would consume a subset of all fruits and seeds, ceasing to interact with the other available resources in the community. However, in other plant-animal interaction systems, a greater availability of resources has been associated with an increase in the diversity of observed interactions, as reported for plant-bee interactions in Cerrado savannas with sparse tree cover (i.e., 'campo cerrado'; Hachuy-Filho et al. 2020). At present, we cannot explain why these responses

diverge. These different patterns, however, may be related to the different types of interactions we investigated, as well as the animal groups involved and the distinct types of vegetation formations.

#### Plant-animal networks and habitat structure

Our results did not indicate a relationship between habitat structure and the topology of the studied networks, as might be expected. For instance, individual-resource interaction networks were more nested in *cerradão* areas where habitat structure featured more open vegetation with greater tree spacing (Camargo et al. 2019). We hypothesize that the effect of habitat structure (modified by fire) on network topology may have been indirect, determining the set of species that make up the small mammal community. This composition, in turn, would lead to modifications in the network metrics we assessed. For example, Zylinski et al. (2022), found indirect effects of fire, mediated by habitat changes, on the activity of mammals inhabiting eucalyptus forests in Australia.

#### **Conclusion**

Plant-animal interaction networks are affected by fires, and the impacts on network structure vary with fire severity. In general, more severely affected gallery forests exhibited more generalist interactions, resulting in networks with higher nestedness and reduced modularity and specialization. The diversity of interactions was also higher in areas that burned more severely. This pattern likely occurred in response to the increased richness of small mammals due to the invasion of species typical of open areas into these gallery forests.

Plant-animal interaction networks were also affected by resource availability (i.e., fruiting), although this availability did not show a direct relationship with fire severity. Gallery forests with higher fruit availability had less generalist interactions, resulting in

networks with higher modularity and specialization and reduced nestedness. The diversity of interactions was also lower in areas with higher resource availability. This likely occurred because in these gallery forests, each of the small mammal species interacted with a subset of all available fruits, reducing the total number of interactions in the networks. Regarding habitat structure, we did not observe direct effects of this factor on the structure of interaction networks, three years after the fire event. It is possible that habitat structure, altered in gallery forests by the fire, may have influenced changes in small mammal communities, affecting their composition and having indirect effects on the structure of interaction networks.

In this study, the increased detection of interactions through the use of DNA *metabarcoding* analyses may have contributed to the observed patterns, as it allowed for the identification of interactions previously unknown due to limitations of traditional methods. We emphasize that fire-sensitive areas, when severely impacted, may have the robustness of their interaction networks compromised, as these plant-animal networks become structurally less modular and more nested, diverging from areas unburned or affected by low severity fire.

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## Supporting information

**Appendix S1.** Plants detected in the feces of 11 species of rodents and marsupials captured in seven gallery forests affected by different levels of fire severity in the Chapada dos Veadeiros National Park and Fazenda Mata Funda Private Natural Heritage Reserve. The values indicate presence (1) or absence (0).

Species	<i>Cerradomys scotti</i>	<i>Didelphis albiventris</i>	<i>Gracilinanus agilis</i>	<i>Hylaeamys megacephalus</i>	<i>Necromys lasiurus</i>	<i>Nectomys rattus</i>	<i>Oecomys</i> spp.	<i>Oligoryzomys</i> spp.	<i>Oxymycterus delator</i>	<i>Proechimys roberti</i>	<i>Rhipidomys macrurus</i>	Total
Amaranthaceae												
Amaranthaceae sp.1	0	0	0	0	0	0	0	1	0	0	0	1
Anacardiaceae												
Anacardiaceae sp.1	0	0	0	0	0	0	0	0	0	0	1	1
Anacardiaceae sp.2	0	1	1	1	0	0	1	0	1	0	1	6
Apiaceae												
Apiaceae sp.1	0	0	0	1	0	0	1	0	0	0	0	2
Apiaceae sp.2	0	0	0	1	1	1	0	0	0	0	0	3
Araceae												
Araceae sp.1	0	1	0	0	0	0	0	0	0	0	0	1
Asteraceae												
Asteraceae sp.1	0	1	1	1	1	1	1	1	1	0	0	8
Asteraceae sp.2	0	1	1	0	1	1	1	1	1	0	1	8
Asteraceae sp.3	0	1	1	1	0	0	1	0	1	0	0	5
Asteraceae sp.4	0	0	0	1	0	0	0	0	1	0	0	2
Asteraceae sp.5	0	0	0	0	0	1	0	0	0	0	0	1
Asteraceae sp.6	0	0	0	1	0	1	1	1	1	0	1	6
Asteraceae sp.7	0	0	0	0	1	1	0	1	0	0	0	3
Asteraceae sp.8	0	1	1	1	0	1	0	1	0	0	1	6
Brassicaceae												
Brassicaceae sp.1	0	0	1	0	0	0	0	0	0	0	0	1
Brassicaceae sp.2	0	0	0	1	0	0	0	0	0	0	0	1
Bursaceae												
Bursaceae sp.1	0	1	0	1	0	0	1	1	0	0	0	4
Bursaceae sp.2	0	0	1	1	0	0	1	0	0	0	1	4
Calophyllaceae												
Calophyllaceae sp.1	0	0	1	0	0	0	0	0	0	0	0	1
Cannabaceae												

Cannabaceae sp.1	0	1	1	1	1	1	1	1	1	1	1	10
Celastraceae												
Celastraceae sp.1	0	1	1	1	0	1	1	0	0	1	1	7
Celastraceae sp.2	0	0	0	1	0	1	0	0	0	1	1	4
Celastraceae sp.3	0	0	0	0	0	0	0	0	0	0	1	1
Chloranthaceae												
Chloranthaceae sp.1	0	0	1	0	0	0	1	0	0	0	1	3
Chrysobalanaceae												
Chrysobalanaceae sp.1	0	0	0	1	0	0	1	1	0	1	1	5
Chrysobalanaceae sp.2	0	0	0	1	0	0	0	0	0	1	0	2
Clusiaceae												
Clusiaceae sp.1	0	0	0	1	0	0	0	0	0	0	1	2
Cucurbitaceae												
Cucurbitaceae sp.1	0	0	0	0	0	0	1	1	0	0	0	2
Cucurbitaceae sp.2	0	1	1	1	1	1	1	0	1	0	1	8
Cyperaceae												
Cyperaceae sp.1	0	0	0	0	0	0	0	0	1	0	0	1
Cyperaceae sp.2	0	0	0	0	0	1	0	0	0	0	0	1
Elaeocarpaceae												
Elaeocarpaceae sp.1	1	0	0	0	0	0	1	0	0	0	0	2
Erythroxylaceae												
Erythroxylaceae sp.1	0	1	0	0	0	0	0	0	0	0	0	1
Euphorbiaceae												
Euphorbiaceae sp.1	0	1	1	1	1	1	1	1	1	1	1	10
Euphorbiaceae sp.2	0	0	0	1	0	1	0	0	0	0	0	2
Euphorbiaceae sp.3	0	0	1	0	0	1	1	0	0	0	0	3
Euphorbiaceae sp.4	0	1	1	1	0	1	1	0	1	0	1	7
Euphorbiaceae sp.5	0	0	1	0	1	1	0	0	1	1	0	5
Fabaceae												
Fabaceae sp.1	0	1	1	0	0	1	0	0	0	0	0	3
Fabaceae sp.2	0	0	0	1	0	0	1	0	0	0	1	3
Fabaceae sp.5	0	1	0	1	0	1	0	0	1	0	0	4
Fabaceae sp.6	0	0	0	0	0	0	1	0	0	0	1	2
Fabaceae sp.7	0	0	0	1	0	0	0	0	0	0	0	1
Fabaceae sp.8	0	1	0	1	0	1	1	1	1	0	1	7
Fabaceae sp.9	0	1	0	1	0	0	1	1	0	1	0	5
Fabaceae sp.10	0	0	0	1	1	0	0	0	0	0	1	3
Fabaceae sp.11	0	1	0	1	0	1	0	0	0	0	0	3
Fabaceae sp.12	0	0	0	1	0	0	1	0	1	0	1	4
Fabaceae sp.13	0	1	0	1	0	0	1	0	0	0	1	4
Fabaceae sp.14	0	1	1	1	1	1	1	1	1	0	1	9
Fabaceae sp.15	0	0	0	1	0	0	0	1	0	0	0	2
Fabaceae sp.16	0	0	0	1	0	0	1	0	0	0	0	2
Fabaceae sp.17	0	1	1	1	0	1	1	0	1	0	1	7
Fabaceae sp.18	0	0	0	1	0	1	1	0	1	0	0	4
Fabaceae sp.19	0	0	0	0	0	1	0	1	0	0	0	2



Fabaceae sp.20	0	1	0	0	0	1	0	0	0	0	0	2
Fabaceae sp.21	0	1	0	1	0	1	1	1	1	1	1	8
Fabaceae sp.22	0	1	0	0	0	0	0	1	0	0	0	2
Gentianaceae												
Gentianaceae sp.1	0	1	1	1	1	1	1	0	1	0	1	8
Gesneriaceae												
Gesneriaceae sp.1	0	1	1	0	0	1	1	1	1	0	0	6
Heliconiaceae												
Heliconiaceae sp.1	0	0	0	0	0	0	1	0	0	0	0	1
Heliotropiaceae												
Heliotropiaceae sp.1	0	0	0	0	0	0	1	0	0	0	0	1
Juncaceae												
Juncaceae sp.1	0	0	0	0	0	0	0	1	0	0	0	1
Juncaceae sp.2	0	0	0	0	0	1	1	1	0	0	0	3
Lamiaceae												
Lamiaceae sp.1	0	0	1	0	0	1	1	1	0	0	0	4
Lythraceae												
Lythraceae sp.1	0	0	0	0	1	0	0	1	1	0	0	3
Lythraceae sp.2	0	0	0	0	0	0	1	0	0	0	0	1
Malpighiaceae												
Malpighiaceae sp.1	0	1	1	1	0	1	1	0	0	1	1	7
Malpighiaceae sp.2	0	1	1	1	1	1	1	0	1	0	1	8
Malpighiaceae sp.3	0	0	0	1	0	0	0	0	0	0	0	1
Malvaceae												
Malvaceae sp.1	0	0	0	0	1	0	0	0	0	0	0	1
Malvaceae sp.2	0	0	0	0	0	0	0	0	0	0	1	1
Marcgraviaceae												
Marcgraviaceae sp.1	0	1	1	1	1	1	1	1	1	1	1	10
Marcgraviaceae sp.2	0	0	0	1	1	0	0	0	0	0	0	2
Melastomataceae												
Melastomataceae sp.1	0	1	0	0	0	1	1	1	0	0	0	4
Melastomataceae sp.3	0	1	0	1	0	1	1	1	0	0	0	5
Melastomataceae sp.4	0	0	0	0	0	0	1	0	0	0	0	1
Melastomataceae sp.5	0	0	0	0	0	1	0	1	0	0	0	2
Melastomataceae sp.6	0	1	0	0	0	0	1	0	0	0	0	2
Melastomataceae sp.7	0	0	1	1	0	0	1	0	1	0	0	4
Melastomataceae sp.8	0	1	0	0	0	0	0	0	0	0	1	2
Melastomataceae sp.9	0	1	0	0	0	1	0	0	1	0	1	4
Melastomataceae sp.10	0	1	0	0	0	0	0	0	0	0	1	2
Melastomataceae sp.11	0	1	0	0	0	0	0	0	0	0	0	1
Melastomataceae sp.12	0	1	0	0	0	0	1	1	0	0	0	3
Melastomataceae sp.13	0	0	0	0	0	0	1	0	0	0	1	2
Melastomataceae sp.14	0	1	1	0	0	1	0	0	0	0	0	3
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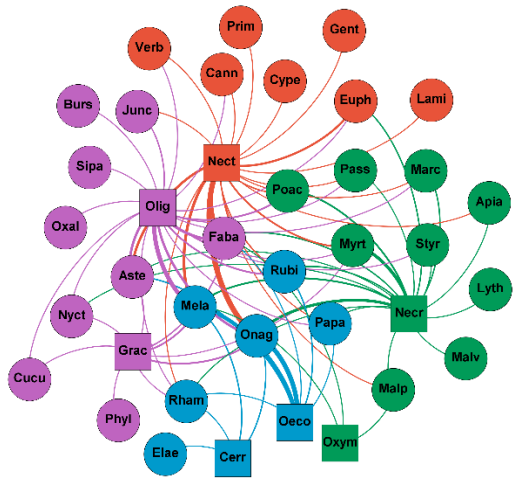
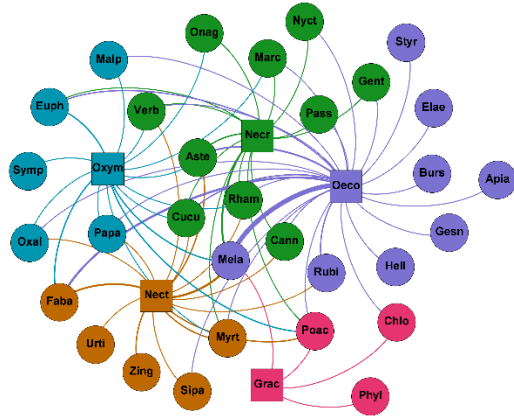
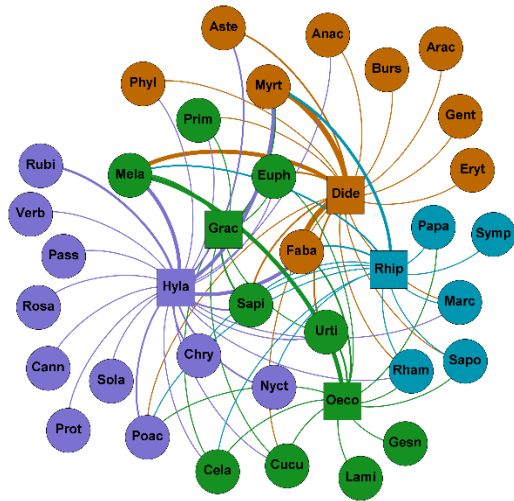
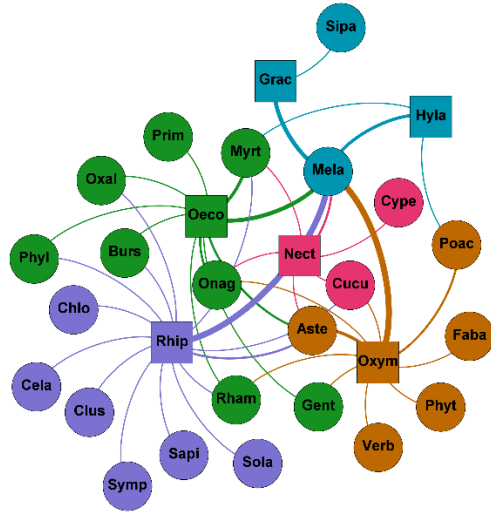
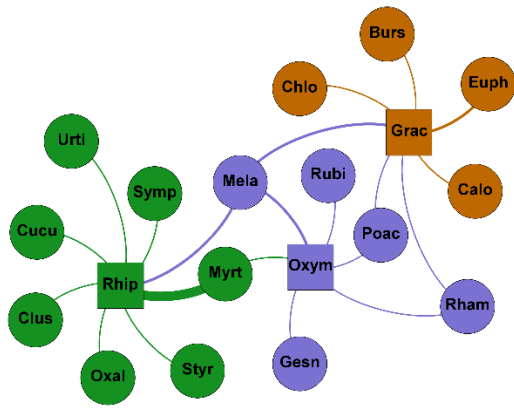
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Melastomataceae sp.31	0	0	0	0	0	0	1	0	0	0	0	1
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Melastomataceae sp.33	0	0	0	0	0	0	0	0	0	0	1	1
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Myrtaceae												
Myrtaceae sp.1	0	0	0	1	0	0	1	0	0	0	0	2
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Myrtaceae sp.5	0	0	0	0	1	0	0	0	0	0	0	1
Myrtaceae sp.6	0	0	0	0	1	0	0	0	0	0	0	1
Myrtaceae sp.7	0	0	0	0	1	0	0	0	0	0	0	1
Myrtaceae sp.8	0	0	0	0	1	0	0	0	0	0	0	1
Myrtaceae sp.9	0	0	0	0	1	0	0	0	0	0	0	1
Myrtaceae sp.10	0	0	0	1	0	0	1	0	0	0	0	2
Myrtaceae sp.11	0	0	0	0	1	0	0	0	0	0	0	1
Myrtaceae sp.12	0	0	1	1	0	0	1	0	0	0	1	4
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Myrtaceae sp.34	0	0	0	0	0	1	0	0	0	0	0	1
Myrtaceae sp.35	0	0	1	0	0	1	0	0	1	1	0	4
Myrtaceae sp.36	0	0	1	0	0	1	0	0	0	0	0	2
Myrtaceae sp.37	0	0	1	1	0	1	0	1	1	0	0	5
Nyctaginaceae												
Nyctaginaceae sp.1	0	1	1	1	1	1	1	1	1	1	1	10
Nyctaginaceae sp.2	0	0	1	0	0	0	0	0	0	0	1	2
Nyctaginaceae sp.3	0	0	0	1	0	0	1	0	0	0	0	2
Nyctaginaceae sp.4	0	0	1	0	0	0	0	0	0	1	1	3
Nyctaginaceae sp.5	0	0	0	0	0	0	0	0	0	1	1	2
Onagraceae												
Onagraceae sp.1	1	1	1	1	1	1	1	1	1	0	0	9
Onagraceae sp.2	1	0	1	0	1	1	1	1	1	0	0	7
Onagraceae sp.3	0	0	0	0	0	0	0	1	0	0	0	1
Onagraceae sp.4	0	0	0	0	1	1	0	0	0	0	0	2
Onagraceae sp.5	0	0	0	0	0	1	0	0	0	0	0	1
Onagraceae sp.6	0	0	0	0	1	1	1	0	0	0	0	3
Onagraceae sp.7	0	0	0	0	0	1	1	0	0	0	0	2
Onagraceae sp.8	0	0	1	0	0	1	1	0	0	0	0	3
Onagraceae sp.9	0	0	0	0	1	1	1	0	0	0	0	3
Onagraceae sp.10	0	0	0	0	0	1	1	0	0	0	0	2
Onagraceae sp.11	0	0	0	0	0	1	1	1	0	0	0	3
Onagraceae sp.12	0	0	0	0	0	1	1	1	0	0	0	3
Onagraceae sp.13	0	0	0	0	1	1	1	0	0	0	0	3
Onagraceae sp.14	0	0	0	0	0	1	1	0	0	0	0	2
Orchidaceae												
Orchidaceae sp.1	0	0	0	0	0	1	0	0	1	0	0	2
Oxalidaceae												
Oxalidaceae sp.1	0	0	0	0	0	1	1	1	1	0	1	5
Papaveraceae												
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Passifloraceae												
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Phyllanthaceae												
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Phyllanthaceae sp.2	0	1	1	0	0	0	1	0	0	0	1	4
Phytolaccaceae												
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Poaceae												
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Poaceae sp.3	0	1	1	1	1	1	1	1	1	1	1	10

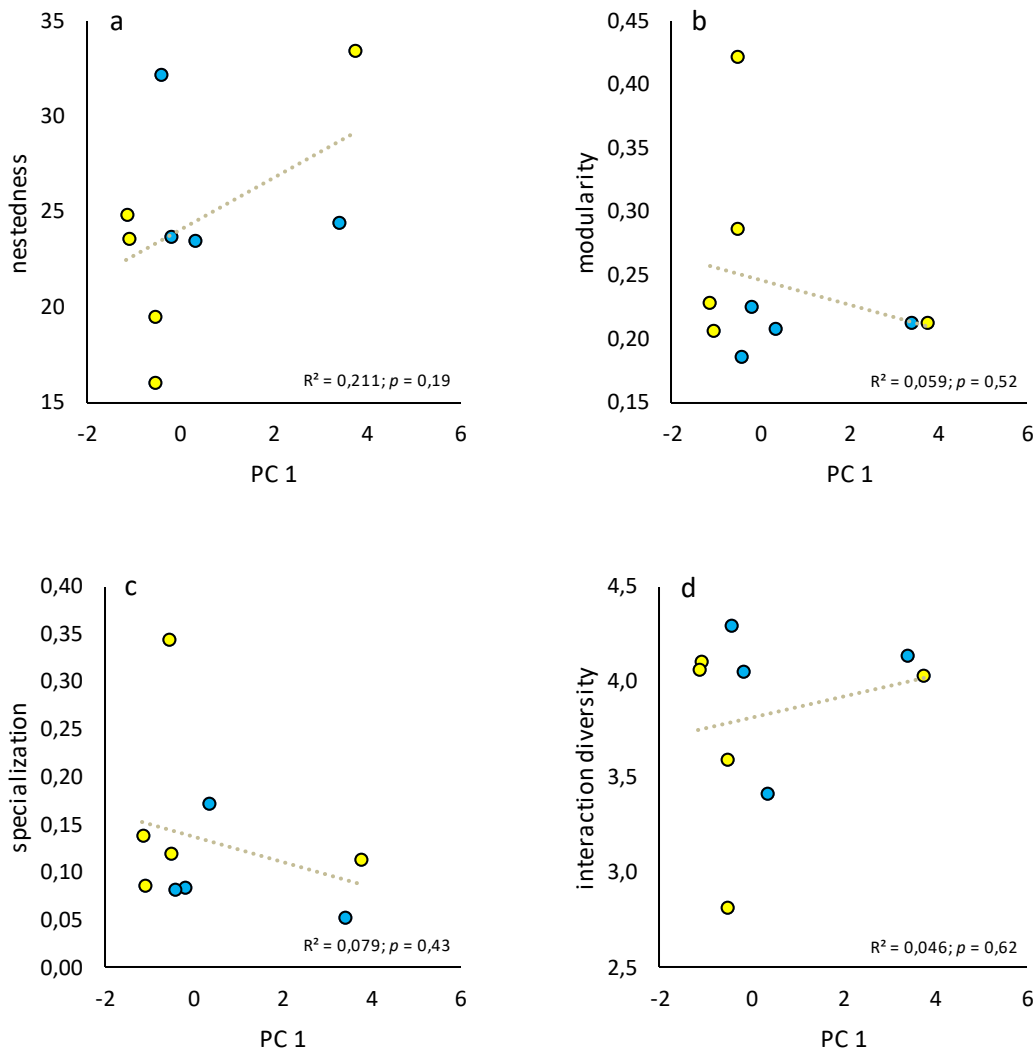
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Poaceae sp.7	0	0	0	0	0	0	0	0	1	0	0	1
Polygalaceae												
Polygalaceae sp.1	0	1	0	0	0	1	1	0	0	0	0	3
Primulaceae												
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Primulaceae sp.2	0	1	0	1	0	1	1	0	0	0	1	5
Primulaceae sp.3	0	0	0	1	0	0	0	0	0	0	0	1
Proteaceae												
Proteaceae sp.1	0	0	1	0	0	1	0	0	0	0	0	2
Proteaceae sp.2	0	0	0	1	0	0	0	0	0	0	0	1
Rhamnaceae												
Rhamnaceae sp.1	1	1	1	1	1	1	1	1	1	1	1	11
Rosaceae												
Rosaceae sp.1	0	0	0	1	0	0	0	0	0	0	0	1
Rubiaceae												
Rubiaceae sp.1	0	0	0	1	0	1	0	1	0	0	0	3
Rubiaceae sp.2	0	0	0	1	0	1	1	0	0	0	1	4
Rubiaceae sp.3	0	0	0	1	1	1	1	0	0	0	0	4
Rubiaceae sp.4	0	0	0	1	0	0	0	0	0	0	0	1
Rubiaceae sp.5	0	0	0	0	0	0	0	0	0	0	1	1
Rubiaceae sp.6	0	0	1	0	0	1	0	1	0	1	0	4
Rubiaceae sp.8	0	0	0	1	0	0	1	0	0	0	1	3
Rubiaceae sp.9	0	0	0	1	0	0	1	0	0	0	1	3
Rubiaceae sp.10	0	0	1	0	1	1	0	1	0	0	1	5
Rubiaceae sp.11	0	1	0	1	0	0	1	0	0	0	1	4
Rubiaceae sp.12	0	1	0	1	0	1	1	0	1	0	1	6
Rutaceae												
Rutaceae sp.1	0	0	1	0	0	0	0	1	0	0	0	2
Rutaceae sp.2	0	0	1	1	0	1	1	1	1	0	0	6
Sapindaceae												
Sapindaceae sp.1	0	1	1	1	0	0	0	1	0	0	0	4
Sapindaceae sp.2	0	1	1	1	0	0	0	0	0	0	1	4
Sapotaceae												
Sapotaceae sp.1	0	1	0	1	0	0	1	0	0	0	1	4
Siparunaceae												
Siparunaceae sp.1	0	0	1	0	0	1	1	1	0	0	0	4
Solanaceae												
Solanaceae sp.1	0	0	0	1	0	0	0	0	0	0	1	2
Styracaceae												
Styracaceae sp.1	0	0	0	0	0	0	1	0	0	0	1	2
Styracaceae sp.2	0	0	0	1	1	1	0	1	0	0	0	4
Symplocaceae												
Symplocaceae sp.1	0	1	1	1	0	0	0	0	0	0	1	4

Symplocaceae sp.2	0	0	0	0	0	1	0	0	1	0	1	3
Urticaceae												
Urticaceae sp.1	0	1	0	0	0	0	1	0	0	0	0	2
Urticaceae sp.2	0	1	1	1	0	1	1	0	0	0	1	6
Verbenaceae												
Verbenaceae sp.1	0	1	1	1	1	1	1	1	1	1	1	10
Zingiberaceae												
Zingiberaceae sp.1	0	0	0	0	0	1	0	0	0	0	0	1
Zingiberaceae sp.2	0	0	0	0	0	1	0	0	0	0	0	1
Total	6	77	73	103	44	96	105	61	56	27	80	728



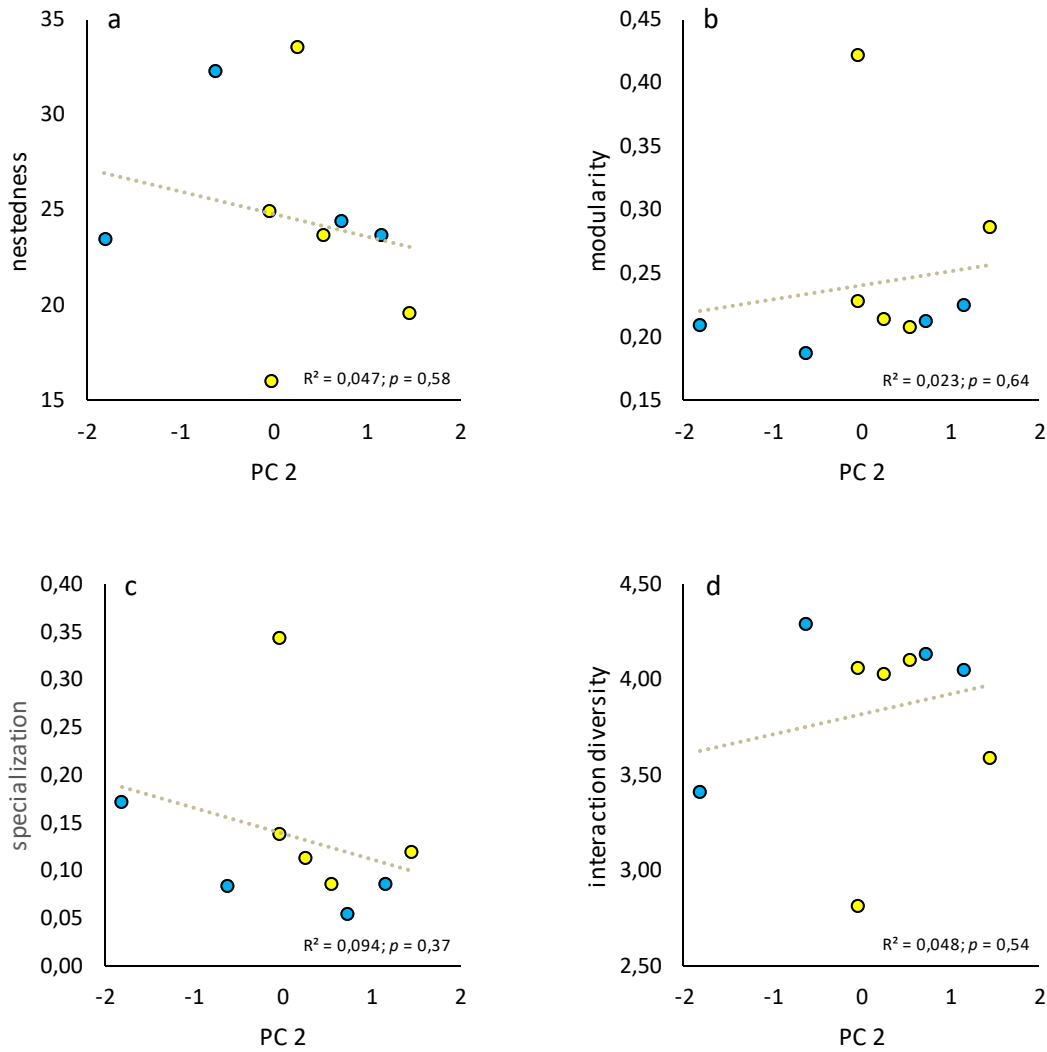


**Appendix S3.** Plant-animal interaction networks for dry season in five gallery forests in the Cerrado. Sites from left to right, from top to bottom: Mulungu 1 (unburned), Estiva 2 (low), Maytreia 2 (low), Maytreia 1 (moderate), and Estiva 1 (moderate).



**Appendix S4.** Relationship between the observed values for a) nestedness, b) modularity, c) specialization, and d) interaction diversity (Shannon) and the values of PC 1 axes from Principal Component Analysis (PCA) conducted with six habitat variables (canopy cover, herbaceous cover, distance to the nearest tree, circumference of the nearest tree, understory obstruction, and quantity of fallen logs) in five gallery forests in the Cerrado. Blue circles represent interaction networks for the rainy season, and yellow circles represent interaction networks for the dry season.





**Appendix S5.** Relationship between the observed values for a) nestedness, b) modularity, c) specialization, and d) interaction diversity (Shannon) and the values of PC 2 axes from Principal Component Analysis (PCA) conducted with six habitat variables (canopy cover, herbaceous cover, distance to the nearest tree, circumference of the nearest tree, understory obstruction, and quantity of fallen logs) in five gallery forests in the Cerrado. Blue circles represent interaction networks for the rainy season, and yellow circles represent interaction networks for the dry season.

### **Capítulo 3: Fire severity affects consumption and potential dispersal of seeds by small mammals in a Neotropical savanna**

#### **Abstract**

The seed dispersal process holds the potential to influence the recruitment of plant species, yielding profound consequences on vegetation structure, particularly in ecologically diverse habitats and environments undergoing succession. Nonetheless, disruptions in the phases of the dispersal cycle can be induced by environmental disturbances, such as fires, leading to varied impacts on the agents involved. We investigated the potential role of rodents and marsupials as seed dispersers in a neotropical savanna (Cerrado). We also evaluated the impact of fire severity on the seed dispersal services provided by these small mammals in gallery forests three years after a major fire event. For 13 small mammal species captured, we recorded a total of 11,688 seeds in fecal samples, encompassing 28 plant species from at least eight families. An NMDS analysis revealed differences among rodent and marsupial species in terms of potentially dispersed plants, with most seed species being consumed by a single species ( $n = 18$ ). Fire severity negatively affected richness of defecated seeds and changed the relative role of these animals as seed dispersers. Evaluation of fire-severity effects on seed richness indicated lower richness in areas burned with higher severity for each of the four most abundant small mammals. Furthermore, fire severity significantly affected the composition of seed species occurring in the fecal samples. Our results indicated that high-severity wildfires affect highly relevant ecological processes, such as seed dispersal by animals. These species-specific effects could impact the recruitment dynamics of plant species and, consequently, the vegetation recovery in fire-affected areas.

**Keywords:** Cerrado, Plant-animal interactions, gallery forest, wildfire, Rodentia, Didelphimorphia, endozoochory

## **Introduction**

Seed dispersal is a fundamental process within the plant life cycle (Wang & Smith 2002) whose intricate mechanism can be facilitated by a variety of animal groups. Animals may increase the likelihood that dispersed seeds will evade local competition and escape seed predators and pathogens (van der Pijl 1982, Howe & Miriti 2004). Nonetheless, disruptions in the different phases of the dispersal cycle can be induced by environmental disturbances, such as fire events. These events lead to varied impacts on the agents involved in the dispersion process (Parr et al. 2007, Markl et al. 2012, Cazetta & Vieira 2021). Understanding the ramifications of fire-induced alterations is imperative for comprehending how ecosystems will react to fire events of distinct magnitudes.

Fire events are a prevalent phenomenon in the Cerrado (Neotropical savanna), with a history of occurrence spanning over 30,000 years (Salgado-Labouriau et al. 1997). The Cerrado encompasses a diverse array of plant formations that range from grasslands and savannas to forested physiognomies (Sano et al. 2019). The open formations, including grasslands and savannas, have evolved to tolerate and even benefit from fire, while the forested areas are more vulnerable to such disturbances (Dantas & Pausas 2013). In recent years, the Cerrado has been suffering intensified fire regimes (Schmidt & Eloy 2020), mainly because of global climate changes, human land use, and the lack of a cohesive fire management policy (Durigan & Ratter 2016, Schmidt & Eloy 2020).

Natural or human-made burnings influence directly or indirectly the fauna inhabiting fire-prone ecosystems (Bergstrom et al. 2023). Particularly for small mammals, certain species thrive while others decline, resulting in a turnover of species over the post-burn period (Fox 1982, Vieira & Marinho-Filho 1998, Vieira 1999, Briani et al. 2004). In forested ecosystems that experience infrequent fires, the post-fire recovery of small mammal communities is slow, taking years for populations of some fire-sensitive species (mostly

arboreal or scansorial species) to reestablish themselves (Mendonça et al. 2015, Cazetta & Vieira 2021). This longer recovery period is probably a consequence of the lower resilience and more protracted post-fire regeneration of forest plant communities (Hoffmann et al. 2009, Armenteras et al. 2021, González et al. 2021).

The impacts of fire can also have indirect effects on ecological processes involving small mammals. These animals can function as both seed predators (Vieira et al. 2003, DeMattia et al. 2004) or dispersers (Charles-Dominique et al. 1981, Magnusson & Sanaiotti 1987, Brewer & Rejmánek 1999, Cáceres & Lessa 2012, Sahley et al. 2016). Dispersal services are provided mainly by consumption of fruits containing small seeds, which can remain viable after passing through the digestive tract (Magnusson & Sanaiotti 1987, Camargo et al. 2011, Lessa et al. 2019, Godó et al. 2022). The role of small mammals as seed predators or dispersers, however, can be influenced by several factors, such as seed/fruit physical, chemical, and phenological traits and the availability of fruits and other food resources in the environment (Rusch et al. 2014, Gong et al. 2015, Stuhler & Orrock 2016, Zeng et al. 2022). These factors can be abruptly and markedly affected by environmental changes such as fires, which ultimately also affects interactions between seeds and animals (Godó et al. 2022).

The impacts of fire on forest formations of the Cerrado depend on several factors, including weather conditions, available fuel load, and topography – all of which collectively determine the fire's behavior (Countryman 1972). As a consequence of all these factors, fire incidents can manifest different intensities and propagation rates, thereby causing divergent impacts on vegetation, which can be categorized according to levels of severity, including damage to canopy cover (Flores et al. 2021). Distinct levels of fire severity can cause diverse effects not only on small mammal species but also on their roles as seed predators and seed dispersers. Nonetheless, despite the Cerrado hosting at least 103 small mammals (rodents and

marsupials) that include fruits and seeds in their diets (Paglia et al. 2012), our understanding of the role of these species as seed dispersers is very scarce (but see Magnusson & Sanaiotti 1987, Camargo et al. 2011, Lessa et al. 2019). Even less known are the impacts caused by fire on seed dispersal processes facilitated by small mammals within the Cerrado (but see Cazetta & Vieira 2021).

We investigated the potential role of rodents and marsupials as seed dispersers in Cerrado areas and the impact of fire severity on dispersal services provided by these animals in gallery forests three years after the occurrence of a large wildfire. To achieve that, we assessed the groups of plants consumed and potentially dispersed by these animals and identified which small mammal species would play a relevant role in the endozoochoric dispersal process. Regarding the influence of fire, we investigated the effects of fire severity on potential seed dispersal services provided by small mammals in gallery forests of the Cerrado. We hypothesized that fire severity alters the dispersal potential of small mammal species, leading to changes in seed consumption patterns by these animals. This might result in a reduction of both quantity and richness of seeds consumed in the areas most affected by fire. Thus, we predicted that seed diversity would be higher in gallery forests that experienced less severe fire impact.

## **Methods**

### Study area

We conducted the study in the Chapada dos Veadeiros National Park (PNCV) and the Private Natural Heritage Reserve (RPPN) Fazenda Mata Funda, two contiguous Conservation Units (Cus) in the Cerrado of central Brazil (Appendix S1). The PNCV covers approximately 240,000 hectares in the northeast of the Goiás state while the contiguous RPPN Fazenda Mata Funda covers 110 hectares. The region has an equatorial climate with a marked dry season

(Kottek et al. 2006) from May to September. As in most of the Cerrado, this region has historically suffered from recurrent fires in the late dry season (Silva et al. 2021). The most recent major fire in this region occurred in 2017 and burned about 66,000 ha (>27% of the total area of the park, see Nunes et al. 2023 for details). In this area burned in 2017, we sampled for small mammals in gallery forests and adjacent grasslands. Gallery forests are associated with watercourses with an average height of 20-30 meters and canopy cover between 70 and 95% (Redford & Fonseca 1986). These forests are of great importance for maintaining the diversity of non-volant mammals in the Cerrado (Redford & Fonseca 1986) and are more sensitive to fire than the open formations (Hoffmann et al. 2009).

#### Small mammal sampling

We conducted small mammal sampling during the rainy (February and March 2020) and dry season (September and October 2020). In the rainy season, we sampled five gallery forests and five adjacent grasslands. These sites were sampled again in the dry season, together with two additional gallery forests and two adjacent grasslands, for a total of 14 study sites. These sites had at least 1 km of distance between them (Appendix S1). For trapping small mammals, we established two transects with 30 equidistant trapping stations spaced at 15-meter intervals. We placed live traps (Sherman® traps) of two sizes ('small': 9 cm x 9.5 cm x 23 cm; and 'large': 11 cm x 12.5 cm x 37 cm) alternately on the ground and in the understory at each station, except for five stations where we placed wire mesh cage traps (45 cm x 16 cm x 16 cm) instead of large Sherman traps. All traps were set for five consecutive nights and were baited with a homogeneous mixture of banana, cornmeal, sardines, peanut butter, and palm oil. We renewed the bait every two days or as needed.

For each captured animal we recorded species, sex, and reproductive status, releasing the individuals at their original capture point after ear-tagging. Our animal handling

procedures adhered to the guidelines of the American Society of Mammal Zoologists (Sikes et al. 2011), and the study received ethical approval from the University of Brasília's Animal Ethics Committee (CEUA), protocol number 4783821.

#### Fecal sampling and analysis

In order to assess the seeds potentially dispersed by small mammals, we collected the fecal samples from the traps where the animals were captured and those obtained during animal handling. In the laboratory, we washed the collected samples and examined them under a stereoscope, specifically looking for seeds that seemed to be undamaged. For the taxonomic identification of these seeds, we referred to pertinent literature sources (Kuhlmann & Darosci 2018, Kuhlmann & Fagg 2018) and sought the expertise of a botanical specialist in seeds of Cerrado flora (Dr. Marcelo Kuhlmann). Subsequently, we tested a subset of seeds for viability using the tetrazolium test. This is a commonly employed test which indicates whether the embryos present viable tissue (Bartuszevige & Gorchoy 2006, Genrich et al. 2017, França-Neto & Krzyzanowski 2019).

#### Data analysis

For evaluating the relation between small mammals and consumed plant species we run the NMDS (non-metric multidimensional scaling) ordination technique using R 4.2.1 software (R Core Team 2022), with the vegan package (Oksanen J 2022). We arranged the small mammal species based on the seed species found in their fecal samples, utilizing the Bray-Curtis index. For this analysis, we considered only rodent and marsupial species with a minimum of five fecal samples obtained from the 14 sampled areas.

We organized the small mammals according to their potential roles as seed dispersers, classifying the species (minimum of five captured individuals) based on the following attributes (considered to be relevant for their role as seed dispersers): (1) estimated seed

richness (considering 10 samples, calculated using EstimateS 9.1.0 software; Colwell 2013); (2) proportion of fecal samples containing seeds; (3) average number of seeds per sample; and (4) abundance of the species in the surveyed areas as indicated by number of individuals captured. Considering the variance in magnitudes across these variables, we used the sum of z-score values obtained for each attribute as an indicator of the relevance of each small mammal as seed disperser.

We evaluated the effect of fire severity on diversity and species composition of seeds potentially dispersed only in the forest sites sampled ( $n = 7$ ). For this, we used the Differentiated Normalized Burn Ratio (dNBR), which is the difference between pre- and post-fire values of the Normalized Burn Ratio (NBR) (Escuin et al. 2008) (see Appendix S2 for details). This index is closely tied to vegetation structure and is commonly used for assessing the severity of fire impact on vegetation (Keeley 2009, Soverel et al. 2010), being categorized as follows: 1) regeneration ( $< -0.1$ ); 2) unburned or similar (between  $-0.1$  and  $+0.1$ ); 3) low severity (between  $+0.1$  and  $+0.27$ ); 4) moderate severity (between  $+0.27$  and  $+0.66$ ); and 5) high severity ( $> 0.66$ ). For our studied sites, there was not any site in the 'high severity' class.

We compared the richness of visually undamaged seeds in fecal samples among distinct severity classes associated to the sampled forest sites (unburned, low, and moderate). For these comparisons, we constructed sample-based interpolation (rarefaction) and extrapolation curves using the software iNEXT online (Chao et al. 2014, Chao et al. 2016) with 999 randomization and 84% confidence intervals, used for between-curve comparisons because it mimics a statistical test with an  $\alpha$  level of 5% (null hypothesis rejection in case of non-overlapping intervals; MacGregor-Fors & Payton 2013). These comparisons were made for the entire small mammal community (fecal samples of all species considered together) and independently for each species with at least seven fecal samples in each fire-severity class.



We also compared the seed species composition among fire-severity classes performing a one-way permutation multivariate ANOVA analysis (PERMANOVA; Anderson 2001), grouping the fecal samples (all mammal species considered together) according to the three classes (unburned, low, and moderate) and using the Bray-Curtis dissimilarity. Prior to the analysis, we applied a Wisconsin transformation to the species matrices, for reducing the influence of highly abundant seed species (Legendre & Gallagher 2001). We run a principal coordinate analysis (PCoA) to illustrate differences in ‘community’ (i.e. group of seed species associated to each fire-severity class) composition between the fire-severity classes. We also performed a PERMDISP test on the same Bray–Curtis matrix to test for between-group differences in the multivariate dispersion. Moreover, we used a similarity percentage (SIMPER) analysis to determine the seed species that best explained the differences in the ‘community’ composition. We performed the PERMANOVA and SIMPER analyses in Past software (Hammer et al. 2001) and PERMDIST analysis in the R package vegan (Oksanen et al. 2022).

## Results

For a total effort of 14,400 trap nights, we captured 405 individuals of small mammals. We considered species of the same genus whose accurate identification was not possible in the field as only one ‘species’. The following species (or group of species) were captured: the rodents *Calomys* spp. (included *C. expulsus* and *C. tener*, n = 15 individuals), *Cerradomys scotti* (n = 5), *Hylaeamys megacephalus* (n = 14) *Necomys lasiurus* (n = 46), *Nectomys* spp. (includes *N. squamipes* and *N. rattus*, n = 41), *Oecomys* spp. (included *O. gr. catherinae* and *O. cleberi*; n = 21), *Oligoryzomys* spp. (included *O. mattogrossae* and *O. nigripes*, n = 10); *Oxymycterus delator* (n = 134), *Oxymycterus* sp. (n = 3), *Proechimys roberti* (n = 2),

*Rhipidomys macrurus* (n = 81), and *Thrichomys apereoides* (n = 4); and two marsupials (*Didelphis albiventris*, n = 8; and *Gracilinanus agilis*, n = 21).

We collected 395 fecal samples of which 139 (35.18%) contained at least one apparently undamaged seed. In total, we tallied 11,688 seeds encompassing 28 plant species belonging to eight families (Asteraceae, n = 2; Cucurbitaceae, n = 1; Melastomataceae, n = 9; Piperaceae, n = 2; Poaceae, n = 5; Rubiaceae, n = 1; Solanaceae, n = 1; and Urticaceae, n = 2; Appendix S3), with five morphotypes whose taxonomic identity could not be determined. The mean seed diameter was 1.35 mm (standard deviation = 0.63; median = 1 mm, range: 0.6-3.0 mm).

We detected seeds in at least one fecal sample for 13 out of the 14 species captured, with the exception of *P. roberti*. The evaluation of the relation between small mammals and seeds found intact in the fecal samples, conducted using NMDS, revealed distinct patterns among the animals in terms of the consumed plant species (Figure 1). Most of the seed species were consumed by only one small mammal species (n = 18). Some pioneer species (from the genera *Cecropia* and *Miconia*), however, were consumed by at least three mammal species (Appendix S3). For seeds belonging to the *Miconia* (Melastomataceae) genus, for which the tetrazolium test could be performed, 23% of 1456 seeds tested remained viable after passing through the digestive tract.

Our results indicated that fire severity affected the richness of potential small mammal dispersers. We captured seven small mammals in the low-severity sites with >6 fecal samples but only four in the moderate-severity sites (Figure 2). Fire severity also changed the relative potential role of small mammals as seed dispersers. The marsupial *D. albiventris* was the best-ranked potential seed disperser in the gallery forests with low severity but was apparently absent in the forests affected by moderate fire severity. In these forests, the best-ranked species was the rodent *O. delator* (Figure 2). For the unburned sites, however, only two

species had sufficient sample size, *R. macrurus* (49 individuals) and *Nectomys* spp (6 individuals), which precluded the ordination of the species. In these sites, *R. macrurus* was the main potential seed disperser (seeds occurred in 38% of 48 samples, estimated seed richness = 2.74, and mean seed number per sample = 4.85). Only one sample (16.7%) of *Nectomys* spp contained seeds (one seed).

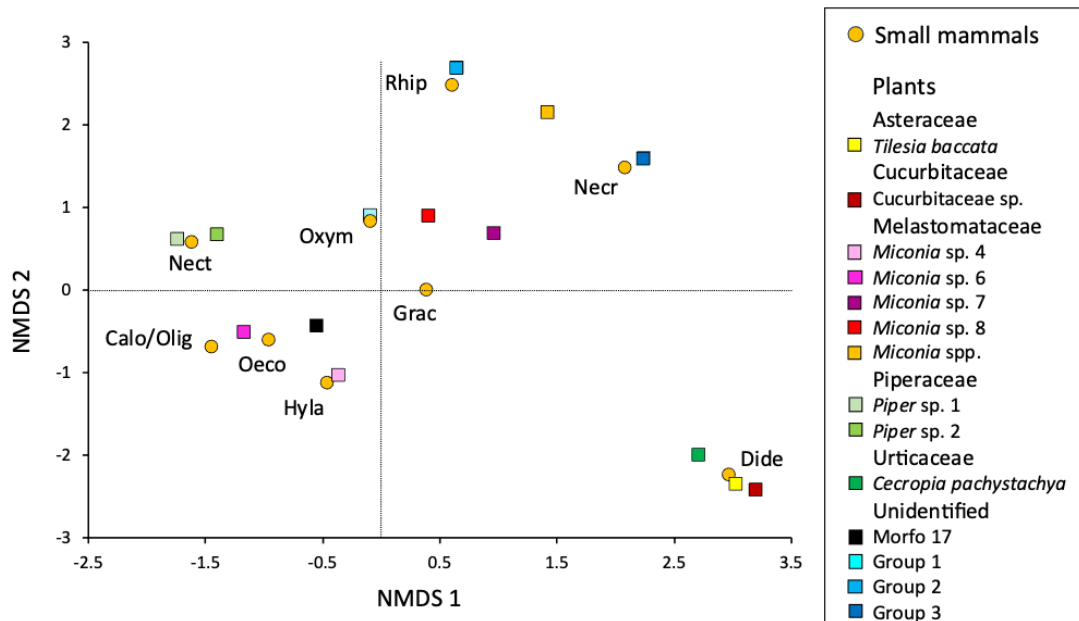


Figure 1. NMDS of seed species found in the feces of different small mammal species sampled in seven gallery forests and seven adjacent open areas in the Cerrado of central Brazil (stress = 0.062; Bray-Curtis similarity index). Abbreviations for small mammal species.: Calo = *Calomys* spp.; Dide = *Didelphis albiventris*; Grac = *Gracilinanus agilis*; Hyla = *Hylaeamys megacephalus*; Necr = *Necomys lasiurus*; Nect = *Nectomys* sp.; Oeco = *Oecomys* spp; Olig = *Oligoryzomys* spp.; Oxym = *Oxymycterus delator*; Rhip = *Rhipidomys macrurus*. Plant species with the same positions in NMDS two-dimensional space were represented by a single point, according to the following groups: Group 1: *Clibadium armani* (Asteraceae), morfo 12, morfo 18, morfo 24, and Poaceae sp.1; Group 2: *Miconia* sp. 2 (Melastomataceae), morfo 26, Poaceae sp. 5, and *Cecropia* sp.1 (Urticaceae); Group 3:

*Miconia* sp. 1 (Melastomataceae), *Miconia* sp. 3 (Melastomataceae), *Poaceae* sp. 2, *Poaceae* sp. 3, *Poaceae* sp. 4, *Sabicea brasiliensis* (Rubiaceae), and *Solanum* sp. (Solanaceae).

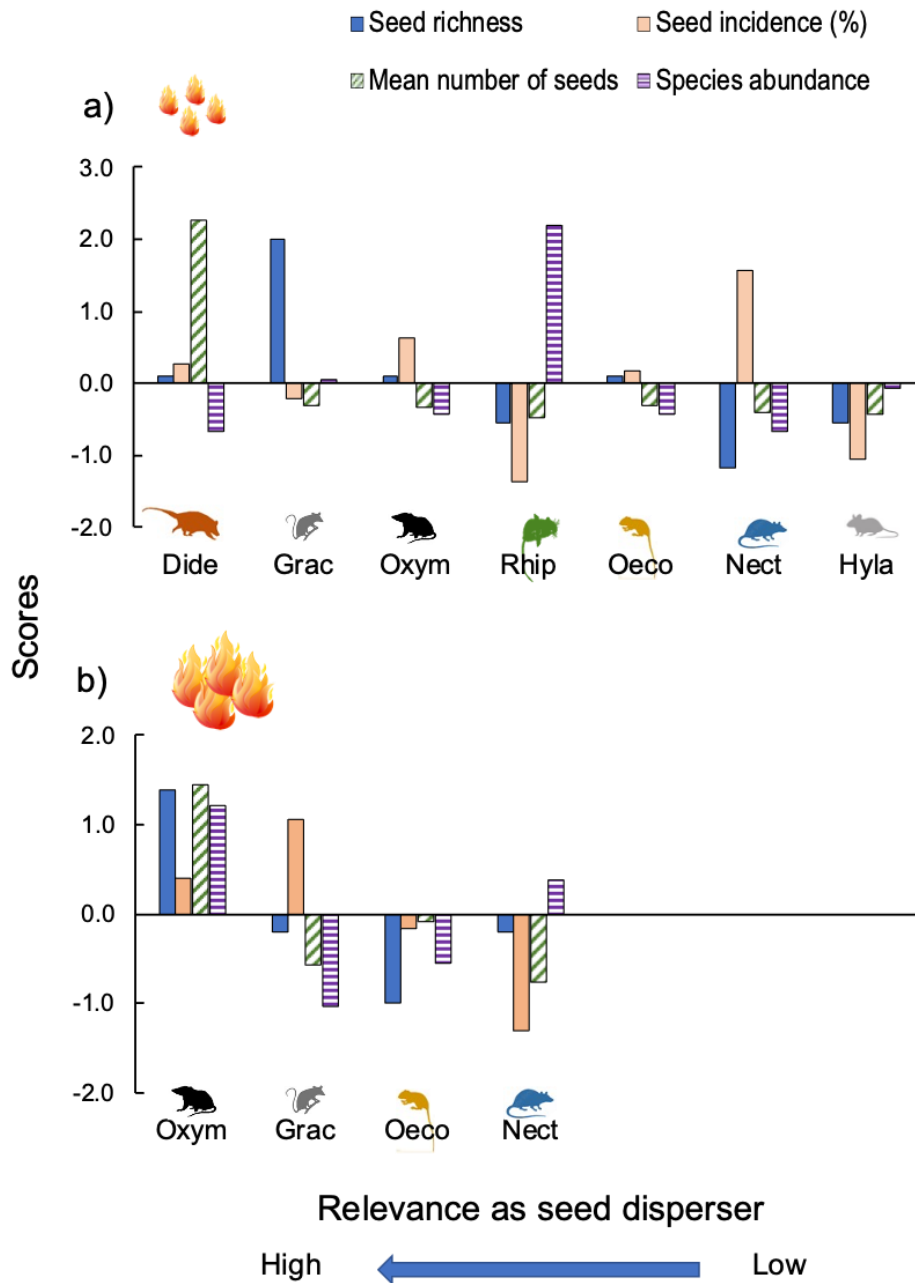


Figure 2. Effect of fire severity on the potential role of small mammals as seed dispersers in Cerrado gallery forests. The role of each species as seed disperser was determined considering four characteristics, as following: 1) estimated seed richness considering 10 fecal samples (see Figure 3), for between-species comparison, 2) percentage of samples containing seeds (seed incidence), 3) mean number of seeds per sample, and 4) species abundance (*i.e.* number

of captured individuals). For each characteristic, we used z-transformed values for enabling comparison among variables. We used the sum of these z-scores of these four variables for ranking small mammals in relation to their potential role as seed dispersers in forests within each class of fire intensity. Classes of fire severity with sufficient sample size for analyses were 'Low' (a) and 'Moderate' (b).

Fire severity affected seed dispersal services provided by small mammals. For each of the four most abundant species, the classes of higher fire severity presented lower richness than the classes with lower fire severity. Similarly, for the overall seed-species richness (gathering all fecal samples), the lowest richness was found for the sites in the highest fire severity class (*i.e.*, moderate), but with some overlapping between confidence intervals (Figure 3).

The evaluation of the effect of fire severity on the composition of plant species found intact in the feces indicated significant differences among the three severity classes (unburned, low, and moderate; PERMANOVA test:  $SS = 19.06$ ;  $d.f. = 2, 68$ ; Pseudo-F = 2.621;  $P = 0.013$ ; 9999 permutations; Figure 4). These differences were not caused by differences in dispersion between groups (PERMDIST test:  $SS = 0.909$ ;  $d.f. = 2, 68$ ;  $F = 2.175$ ,  $P = 0.12$ ; 999 permutations). *A posteriori* between-group comparisons indicated that the fire-severity class 'unburned' differed from both 'low' ( $P = 0.020$ ) and 'moderate' ( $P = 0.018$ ) but these two latter classes did not differ from each other ( $P = 0.236$ ). The SIMPER analyses for paired comparisons between the class 'unburned' with the two other classes indicated that the same three species were among the four most relevant seed species contributing to the dissimilarity between class pairs (~68% of the total dissimilarity for both comparisons; Table 1). These species were two *Miconia* species (sp6 and sp8) and *Tilesia baccata* (Asteraceae). The *Miconia* species presented much higher percentage of contribution

to the total dissimilarity (>56% for the two species combined in both paired comparisons) than any other one (all remaining species presented <4.5% of contribution for both paired comparisons). These two dominating *Miconia* species showed opposite patterns of dominance in relation to occurrence in the unburned class, whereas *T. baccata* occurred only in the fecal samples obtained in sites with low or moderate fire severity (Table 1).

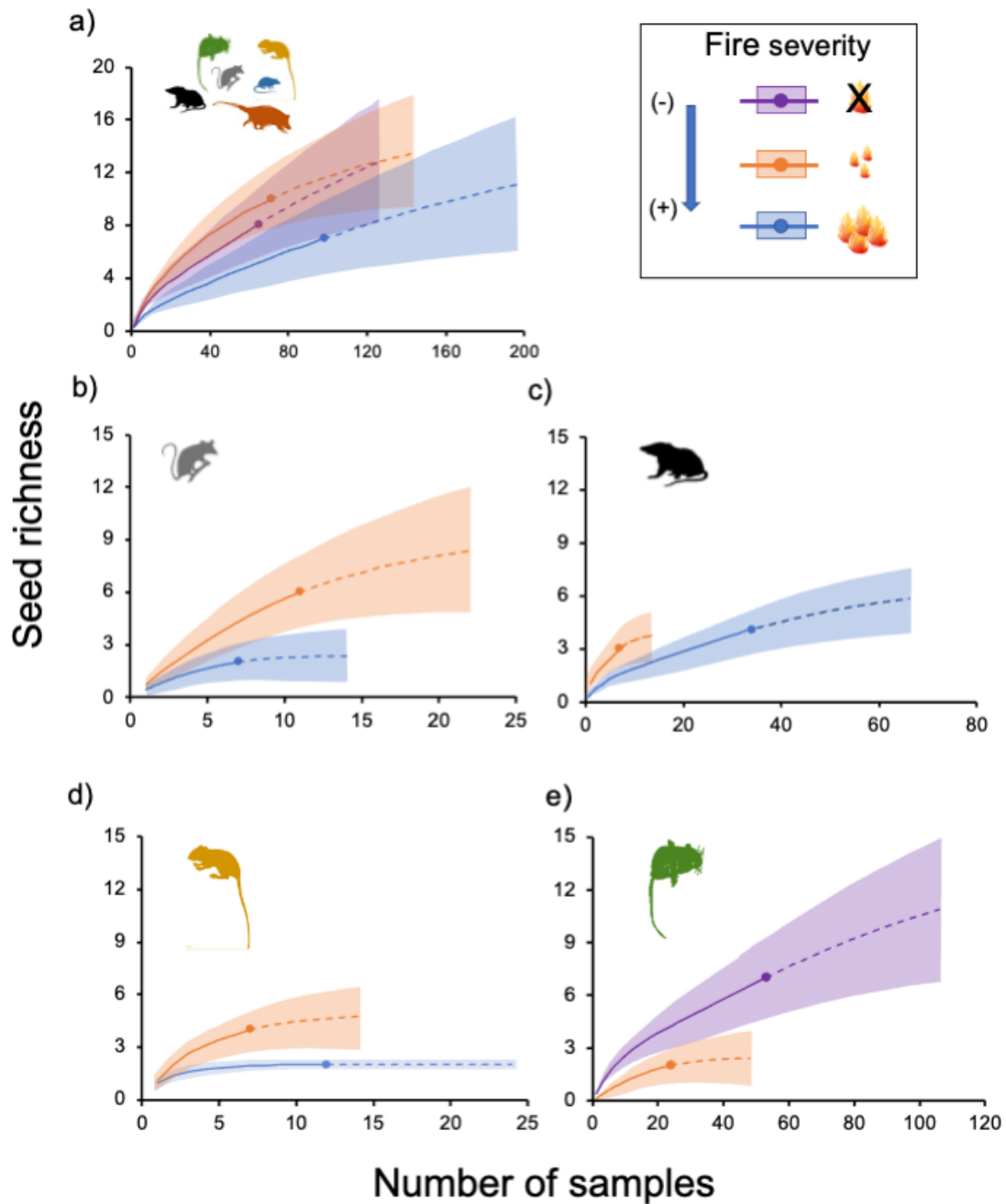


Figure 3. Rarefaction and extrapolation curves of species richness of seeds found in fecal samples of small mammals (rodents and marsupials) sampled in seven gallery forests in the Cerrado of central Brazil. These forests were grouped in three categories according to the severity of a large wildfire that occurred three years before sampling. These categories were: unburned areas, areas that suffered low severity fire, and areas that suffered moderate severity fire (severity inferred using the differenced normalized burn ratio - dNBR). The analyses were performed for all species considered together (11 species; a) and for the four species (or genus) with sufficient sample size for analysis ( $n \geq 7$  per fire severity class; b = *Gracilinanus agilis*, c = *Oxymycterus delator*, d = *Oecomys* spp, e = *Rhipidomys macrurus*). For within species comparisons, limited sample sizes precluded the evaluation among the three classes of fire severity.

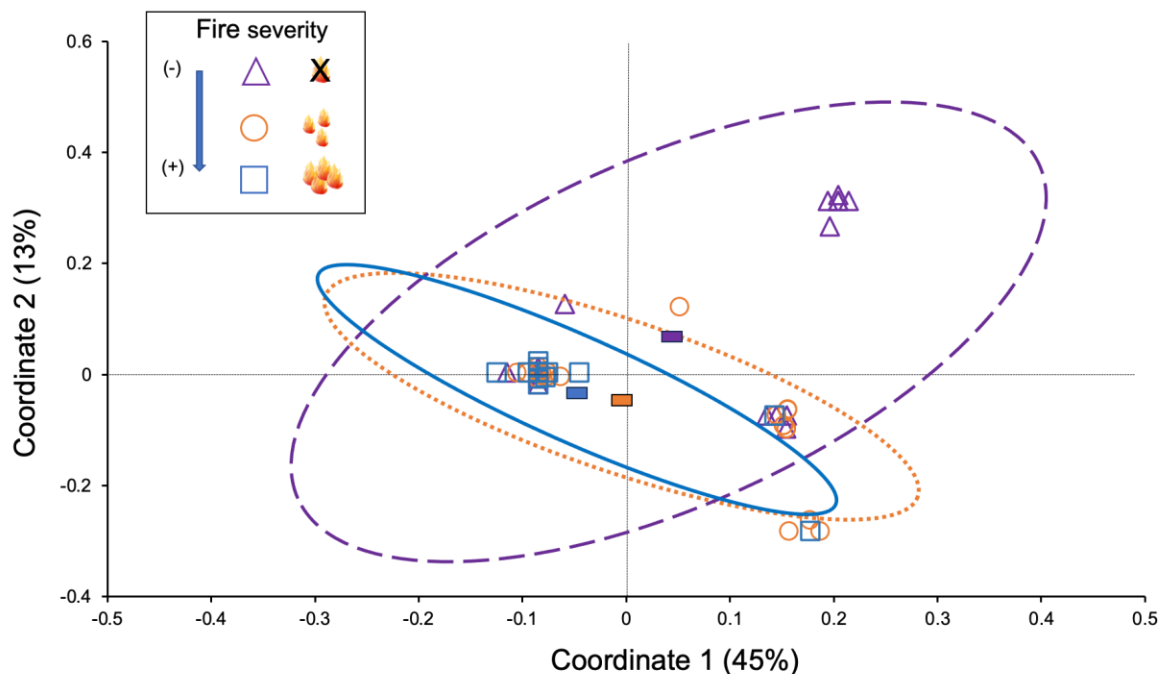


Figure 4. PCoA (principal coordinate analysis) plot of seed community dissimilarity (based on seeds found in small-mammal fecal samples) among forest sites belonging to 3 fire-severity classes (triangle = unburned, circle = low, square = moderate) sampled 3 years after the

occurrence of fire in gallery forests of the Brazilian Cerrado. Filled rectangles indicate the centroids of the 95% ellipses. Percentage of total variation explained by each axis is indicated between parentheses.

## **Discussion**

We investigated the potential role of small mammals as seed dispersers in the neotropical savanna (Cerrado) and the effects of a large wildfire on such role. We found apparently undamaged seeds of 28 plant species belonging to eight families (mainly Melastomataceae and Poaceae) in 35.18% of fecal samples belonging to 13 of 14 small mammals captured. The role of these animals as potential seed dispersers was inversely related with the level of fire severity three years after the fire occurrence. In gallery forests that suffered a low level of fire severity, we recorded seven small mammals dispersing seeds whereas in gallery forests with moderate level of fire severity this number dropped to four. Moreover, an increase in fire severity caused a reduction in the richness of plant species potentially dispersed by each of the four most common small mammal species.

The group of potentially dispersed plants was predominantly composed of species with small-seeded fruits (mean seed diameter = 1.35 mm), which is mainly determined by morphological limitations of these small animals. Similarly, Lessa *et al.* (2019) investigated fecal contents of small mammals in riparian forests of southeastern Brazil and reported that 92% of the seeds found in the feces of six small rodents had a diameter of < 1 mm. The prevalence of small seeds is a characteristic feature of pioneer species (Dalling & Hubbell 2002), which can potentially benefit from fire events to establish themselves within forested areas. Consequently, by specifically dispersing these small seeds, small mammals might play a significant role in facilitating the establishment of pioneer plant populations in regions affected by fires.



We detected that the family exhibiting the highest richness and quantity of seeds in the fecal samples was Melastomataceae (Appendix S3). Several plants of this highly speciose family (177 genera and ~5,750 species; Goldenberg *et al.* 2023) are categorized as pioneers due to their diminutive fruits and seeds, which are frequently consumed by small mammals (Lessa & da Costa 2010, Camargo *et al.* 2011, Camargo & Vieira 2022). This family includes *Miconia*, the most speciose genus occurring in the samples. Seeds of *Miconia* remain viable even after passing through the digestive tract of small mammals (as indicated by our viability testes; see also Magnusson & Sanaiotti 1987, Sahley *et al.* 2016), which reinforces the potential role of small mammals as dispersers of *Miconia* spp. Species from this genus are highly abundant in the Cerrado and exhibit massive fruiting, sometimes spanning several months (Messeder *et al.* 2020). These plants possibly serve as a relevant source of water and sugar in the diet of small mammals, particularly during periods of drought (Camargo *et al.* 2011), making them pivotal resources for Neotropical fauna (Messeder *et al.* 2020).

Our results indicated that the role of small mammals as seed dispersers through endozoochory is related to a restricted group of small-seeded plants. This potential service, however, must not be underestimated. Small mammals constitute nearly half of all mammal species, have a widespread global distribution, and make up a substantial portion of terrestrial mammal populations in diverse natural environments (Mittermeier & Wilson 2015, Lacher *et al.* 2016, Wilson *et al.* 2017). In the neotropical region, most small rodents and marsupials feed on fruits and seeds to some extent (Paglia *et al.* 2012). Seed viability after passing through the digestive tract may range from 23% (for *Miconia* seeds in the present study) to 30% (overall percentage for 7 neotropical small rodents; Sahley *et al.* 2016). While this proportion may be low, these animals generally occur in high densities and ingest high absolute numbers of seeds. Thus, it is likely that they deposit a substantial quantity of seeds in suitable germination sites, potentially contributing to the establishment of small-seeded plants

(Godó et al. 2022). Additional components of the seed dispersal cycle (*e.g.*, quality of deposition sites, germination rates, and seedling establishment; Wang & Smith 2002), however, must be understood for the evaluation of the actual small-rodent contributions to seedling recruitment.

The role of small rodents in facilitating seed dispersal, however, is not limited to endozoochory. In some cases, these animals remove and store fruits and seeds, which may eventually germinate (Jensen 1985, Nyiramana *et al.* 2011). Moreover, small rodents often consume only the pulp of fruits with large seeds, leaving several seeds unharmed (Vieira *et al.* 2003), in some cases far from the parent tree (Briani *et al.* 2001). This behavior can enhance seed germination in suitable locations for seedling establishment.

The role of small mammals in seed dispersal undergoes changes when fires alter vegetation structure and small mammal communities. This can result in reduced seed removal rates (Paglia *et al.* 1995, Cazetta & Vieira 2021; but see Zwolak *et al.* 2010). These changes might be caused by an increased perception of predation risk experienced by small mammals in more open environments, directly influencing their foraging choices (Boone *et al.* 2022, Merz *et al.* 2023). While our study did not specifically investigate the concept of a "landscape of fear", this phenomenon could be present in gallery forests that have been severely impacted by fires. In certain cases, canopy cover has been reduced to as low as 20% in our study areas (Flores *et al.* 2021), potentially creating conditions that affect the behavior of small mammals.

The differences among small mammals in terms of seed species consumed that we detected (Figure 1) likely reflect the interaction of various factors, including arboreal activity, nutritional requirements, body size, and skull morphology. In our study, the largest species captured (*D. albiventris*; ~0.5–2.0 kg) consumed exclusively two out of the three seed species found in its fecal samples, including the largest seeds found in any sample (Cucurbitaceae sp.; diameter = 3mm). This marsupial ranked first among potential seed dispersers in forests

classified with the lowest level of fire severity but was absent in sites more severely impacted by fire. This absence could potentially have a detrimental effect on seed dispersal processes, particularly for seeds that are not dispersed by other small mammals in the area. Marsupials of the *Didelphis* genus are known to be relevant seed dispersers in Neotropical forests (Medellin 1994, Cáceres *et al.* 1999, Cáceres 2002, Cantor *et al.* 2010). Their body mass facilitates the consumption of larger seeds in greater quantities, as well as the ability to travel longer distances (Cáceres & Lessa 2012). Consequently, the role of this marsupial as a disperser probably are not exerted by other small mammals in areas severely impacted by fires, at least for certain plant species.

Another marsupial species, though smaller (*Gracilinanus agilis*), was a relevant seed disperser in gallery forests affected by low or moderate fire severity. This result supports available data regarding the frugivory and seed dispersal role of *G. agilis* in other Cerrado regions, particularly for pioneer plants (Lessa & da Costa 2010, Camargo *et al.* 2011). Therefore, considering that the availability of dispersers is reduced in areas more severely affected by fire, the persistence of this species might be even more relevant for vegetation regeneration in these areas. This was also the case of the rodent *Oxymycterus delator*, one of the top three species in the ranking of seed dispersers in forests under low fire severity and ascending to the first position in forests under moderate fire severity. This finding was unexpected, since *Oxymycterus* spp are reported to consume mainly invertebrates (Suarez 1994, Talamoni *et al.* 2008, Ribeiro *et al.* 2019). Our results indicated, however, that *O. delator* may present a flexible diet, opportunistically exploiting fruits and seeds.

Except for *O. delator*, the best-ranked potential dispersers are recognized as basically frugivores, like arboreal rodents of the genus *Oecomys* and *Rhipidomys* (Paglia *et al.* 2012, Ribeiro *et al.* 2019, Camargo *et al.* 2021). Indeed, *R. macrurus* was the main potential seed disperser in ‘unburned’ sites. This rodent was among the species most negatively impacted by

fire severity, displaying an intermediate role as a potential disperser in low-severity areas and with very few records in areas more severely impacted by fire (only 2 samples). As an arboreal species, this rodent probably feeds mainly in the forest canopy (Camargo *et al.* 2018), possibly feeding on fruits of plants that do not thrive in areas severely affected by fire. Consequently, it becomes less abundant (and may even disappear) in these heavily impacted areas.

The small mammal communities showed relatively low redundancy regarding the seed species potentially dispersed (Figure 1). In systems with limited functional redundancy, species loss can result in more relevant impacts since the remaining species are unable to compensate for the same functions (Naeem 1998). In addition to the low functional redundancy observed, there was also a reduction in the diversity of forest-specialist species (*i.e.*, arboreal species) in areas more severely impacted by fire. A similar pattern was reported for arboreal marsupials in Australian forests, where some species had their populations reduced in patches affected by high-severity fires (Lindenmayer *et al.* 2013). In our study, the combination of low functional redundancy and the absence (or at least reduced abundance) of forest-specialist species in the most disturbed areas could lead to a decline in the seed dispersal function performed by small mammals. The persistence of these impacts could be long-lasting, as fire-affected animal populations might not revert to pre-fire conditions even after 10 years following high-severity fire events (Campbell-Jones *et al.* 2022).

The variation in composition and abundance of potentially dispersing small mammals across the severity gradient was likely associated with differences in vegetation structure, as suggested for other forested environments (González *et al.* 2021). The recovery of vegetation structure in severely burned areas might also be considerably slower than in less severely impacted ones due to greater tree mortality, loss of canopy coverage, and reduced understory connectivity. In our study area, there was a variation in the impacts suffered by gallery forests

during the 2017 fire, but with some areas experiencing up to 80% loss in canopy coverage (Flores *et al.* 2021). Moreover, the gallery forests cover a limited total area within the landscape, located relatively far from each other (from the perspective of a small animal) and immersed in a non-forested matrix (Appendix 1). This spatial configuration probably hinders the recolonization of forest-dwelling species (*e.g.*, *R. macrurus*, *Oecomys* spp.) in the more severely impacted sites and may have contributed to maintaining lower abundances of these species in these sites even three years after the fire event. This landscape effect on the recolonization of burned areas by small mammals has been suggested for other Cerrado forests (Mendonça *et al.* 2015). On the other hand, if population recovery relies on individuals that survived the fire event, as indicated for small mammals in diverse Australian ecosystems (Banks *et al.* 2017, Hale *et al.* 2022), population growth will be linked to the number of founding individuals as well as the availability of required resources for the species (*e.g.*, food and shelter).

The differences in the composition of consumed seeds by small mammals among the fire severity classes may reflect fire-induced changes in floristic composition in the studied forests. In fact, the impacts of fire on floristic diversity can be observed across various forest ecosystems. For instance, recurrent or more severe burns significantly reduced the diversity of plants in the understory of the Amazon Forest (Cochrane & Schulze 1999, Prestes *et al.* 2020). Moreover, forest patches that experienced more severe fire damage exhibited a prevalence of pioneer species (Cochrane & Schulze 1999), likely due to reduced canopy coverage and subsequent increased light penetration. Thus, the changes in flora within fire-affected forests can drive shifts in the diversity of fruits and seeds available for consumption by fauna, potentially impacting the role of animals as seed dispersers.

## **Conclusion**

We showed that high-severity wildfires may affect highly relevant ecological processes, such as seed dispersal by small mammals. These effects include a reduction in the number of potentially dispersing small mammal species and in the number of plant species dispersed by these animals. These effects on the dispersal role of small mammals were species-specific, being associated to the gradient of fire severity of the gallery forests burned three years before. Considering the low redundancy (in terms of dispersed plant species) among the rodents and marsupials that may serve as dispersers, the absence (or low abundance) of species in areas more severely impacted by fire can compromise the role of the small mammal group as seed dispersers. This reduction could impact the recruitment dynamics of plant species and, consequently, the vegetation recovery in fire-affected areas. However, this effect will depend on the relative importance of the small mammal species in the dispersal processes of each plant that interacts with these animals.

### **Author contributions**

AL: conceptualization, methodology, formal analysis, investigation, data curation, writing—original draft, visualization, project administration. CVS: conceptualization, methodology, investigation, project administration, reviewing and editing the manuscript. AFM: conceptualization, reviewing and editing the manuscript. PFL: data collection, laboratory work, reviewing and editing the manuscript. GGR: data collection, laboratory work, reviewing and editing the manuscript. RPM: data collection and preliminary analysis, laboratory work, reviewing and editing the manuscript. EMV: conceptualization, methodology, investigation, reviewing and editing the manuscript, supervision, funding acquisition, project administration.

### **Supporting information**

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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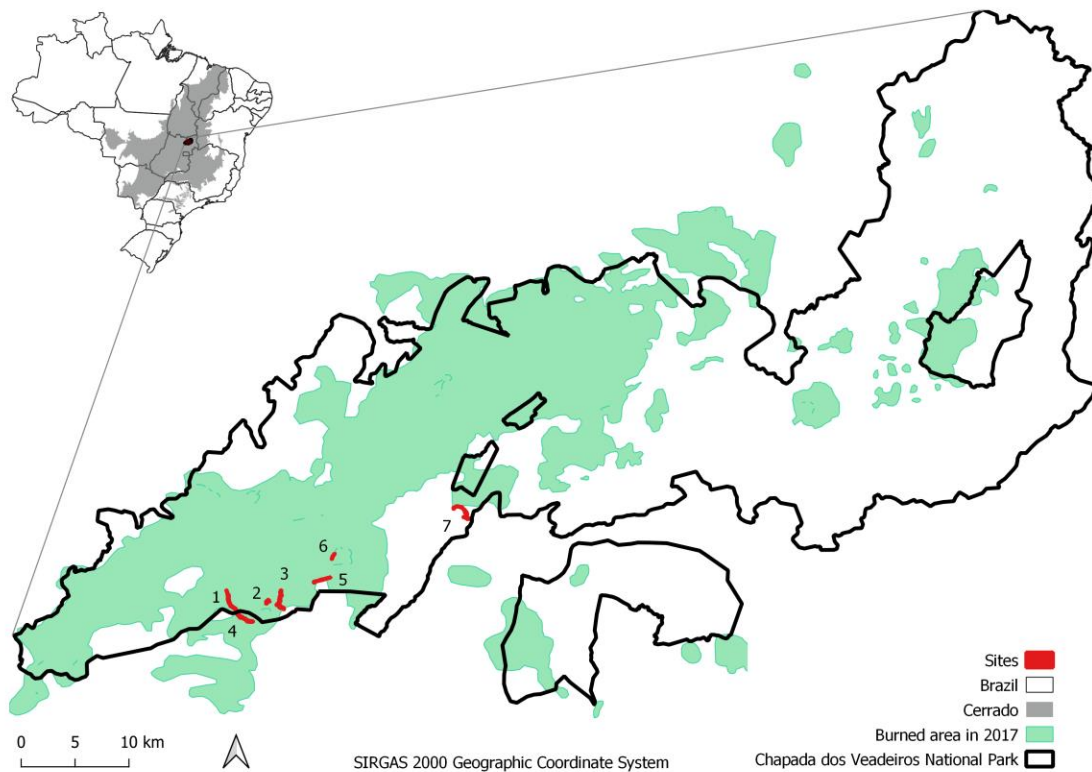
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## Supporting information

**Appendix S1.** Map of the studied Cerrado (Neotropical savanna) region indicating the area burned in 2017 and the location of the study sites in the Chapada dos Veadeiros National Park and the Fazenda Mata Funda Private Natural Heritage Reserve, central Brazil. Site names are (numbers were ranked according to dNBR index; see Appendix 2): 1 = Estiva1, 2 = Maytrea1, 3 = Maytrea2, 4 = Estiva2, 5 = Mulungu2, 6 = Mulungu1, 7 = and Pouso Alto. Sites 4 (located in the Fazenda Mata Funda Private Natural Heritage Reserve) and 7 were sampled only in the dry season.



**Appendix S2.** Classification of the seven sampled gallery forests in 2020 in the Chapada dos Veadeiros National Park and the Fazenda Mata Funda Private Natural Heritage Reserve according to fire severity estimated by the Differentiated Normalized Burn Ratio (dNBR). This index was used for evaluating the effect of fire severity on diversity and species composition of seeds potentially dispersed by the small mammals. For the calculation of the dNBR, we determined fire severity for each of the seven gallery forest sites sampled using images from the Sentinel 2A satellite obtained before and after the 2017 wildfire (available in <https://earthexplorer.usgs.gov>). After that, we computed for pre-fire and post-fire instances using the formula  $(B8 - B12) / (B8 + B12)$ , where B8 represents the near-infrared spectrum (with a resolution of 10m) and B12 corresponds to the shortwave infrared spectrum. The difference between pre- and post-fire values of the Normalized Burn Ratio (NBR) is the dNBR (Escuin *et al.* 2008). Also indicated is the total number of fecal samples obtained in each site (Samples).

Site	dNBR	Severity class	Samples
Estiva1	0.62	Moderate	53
Maytrea1	0.29	Moderate	45
Maytrea2	0.23	Low	46
Estiva2	0.21	Low	20
Mulungu2	0.13	Low	10
Mulungu1	-0.02	Unburned	52
Pouso Alto	-0.04	Unburned	7

**Appendix S3.** Identified seed species and their respective abundances found in the feces of small mammals sampled in the months of February and March (rainy season) and September and October (dry season) of 2020 in the central Brazilian Cerrado (Chapada dos Veadeiros National Park and Fazenda Mata Funda Private Natural Heritage Reserve). Species codes: Ca = *Calomys* spp., Cs = *Cerradomys scotti*, Da = *Didelphis albiventris*, Ga = *Gracilinanus agilis*, Hm = *Hylaeamys megacephalus*, Nl = *Necomys lasiurus*, Ne = *Nectomys rattus*., Oe = *Oecomys* spp., Ol = *Oligoryzomys* spp., Od = *Oxymycterus delator*, Ox = *Oxymycterus* sp., Rm = *Rhipidomys macrurus*, Ta = *Thrichomys apereoides*.

Species	Ca	Cs	Da	Ga	Hm	Nl	Ne	Oe	Ol	Od	Ox	Rm	Ta	Total
<b>Asteraceae</b>														
<i>Clibadium armanii</i>	0	0	0	0	0	0	0	0	0	1	0	0	0	1
<i>Tilesia baccata</i>	0	0	3698	0	0	0	0	5	0	0	0	0	0	3703
<b>Cucurbitaceae</b>														
<i>Cucurbitaceae</i> sp.	0	0	29	0	0	0	0	0	0	0	0	0	0	29
<b>Melastomataceae</b>														
<i>Miconia</i> sp. 1	0	0	0	0	0	197	0	0	0	0	0	0	0	197
<i>Miconia</i> sp. 2	0	0	0	0	0	0	0	0	0	0	0	2	0	2
<i>Miconia</i> sp. 3	0	0	0	0	0	29	0	0	0	0	0	0	0	29
<i>Miconia</i> sp. 4	0	0	0	54	100	0	0	0	0	1	0	0	0	155
<i>Miconia</i> sp. 5	0	0	0	0	0	0	0	0	0	0	1	0	0	1
<i>Miconia</i> sp. 6	2	95	0	456	54	246	285	516	6	5100	0	218	0	6978
<i>Miconia</i> sp. 7	0	0	0	1	0	5	0	0	0	2	0	0	0	8
<i>Miconia</i> sp. 8	0	0	0	8	0	0	0	0	0	11	0	13	0	32
<i>Miconia</i> spp.	0	0	0	0	0	9	0	0	0	0	0	6	1	16
<b>Piperaceae</b>														
<i>Piper</i> sp. 1	0	0	0	0	0	0	1	0	0	0	0	0	0	1
<i>Piper</i> sp. 2	0	0	0	0	0	0	6	0	0	13	0	0	0	19
<b>Poaceae</b>														
<i>Poaceae</i> sp. 1	0	0	0	0	0	0	0	0	0	1	0	0	0	1
<i>Poaceae</i> sp. 2	0	0	0	0	0	1	0	0	0	0	0	0	0	1
<i>Poaceae</i> sp. 3	0	0	0	0	0	1	0	0	0	0	0	0	0	1
<i>Poaceae</i> sp. 4	0	0	0	0	0	1	0	0	0	0	0	0	0	1
<i>Poaceae</i> sp. 5	0	0	0	0	0	0	0	0	0	0	0	1	0	1
<b>Rubiaceae</b>														
<i>Sabicea brasiliensis</i>	0	29	0	0	0	34	0	0	0	0	0	0	0	92
<b>Solanaceae</b>														
<i>Solanum</i> sp.	0	0	0	0	0	2	0	0	0	0	0	0	0	2
<b>Urticaceae</b>														
<i>Cecropia</i>	0	0	345	90	0	0	0	0	0	1	0	0	0	436
<i>Cecropia</i> sp. 1	0	0	0	0	0	0	0	0	0	0	0	3	0	3
<b>Unidentified</b>														
Morfo 12	0	0	0	0	0	0	0	0	0	1	0	0	0	1
Morfo 17	0	0	0	2	0	0	0	1	0	0	0	0	0	3

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Morfo 18	0	0	0	0	0	0	0	0	0	2	0	0	0	2
Morfo 24	0	0	0	0	0	0	0	0	0	1	0	0	0	1
Morfo 26	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Total	2	124	4072	611	154	525	292	522	6	5134	1	244	1	11688

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## CONSIDERAÇÕES FINAIS

O desenho amostral utilizado na amostragem de comunidades de pequenos mamíferos no Cerrado afetou as estimativas de abundância e riqueza desse grupo. Para todas as macroformações analisadas, as estimativas de diversidade foram maiores quando foram utilizadas em conjunto armadilhas tipo gaiola (i. e. *live-traps*) e as de interceptação e queda (i. e. *pitfalls*). Amostragem que consideraram as duas estações climáticas foram mais eficientes, especialmente nas formações abertas (i. e. campos e savanas). Detectamos um viés no tamanho dos indivíduos capturados por cada tipo de armadilha, com animais maiores sendo capturados por armadilhas de interceptação e queda e animais menores por armadilhas tipo gaiola. Também observamos que, em ambientes de savana, esse último tipo é mais eficiente na captura de um maior número de espécies.

Portanto, com base no presente estudo e na literatura disponível, sugerimos ambos tipos de armadilhas (i. e. tipo gaiola e de interceptação e queda), para amostragem em todas as macroformações. Dessa forma, obteremos a melhor representação possível da comunidade, capturando espécies maiores e menores, indivíduos jovens e adultos, e animais que evitam entrar em armadilhas tipo gaiola. Também recomendamos a realização de amostragem que leve em consideração a variação sazonal da região, bem como que a disposição das armadilhas esteja alinhada com os objetivos do estudo e que o tipo, tamanho e forma da área de estudo sejam considerados.

As interações planta-animal entre pequenos mamíferos e a flora do Cerrado são afetadas pelo fogo. A severidade do fogo modificou o padrão estrutural das redes, tornando-as mais aninhadas, e com menor grau de modularidade e especialização nas matas de galeria atingidas mais severamente por um incêndio. Esses resultados provavelmente estão relacionados com um consumo de frutos e sementes mais generalista por roedores e marsupiais presentes nas áreas que queimaram de forma mais severa. Nessas áreas, a

diversidade de interações foi maior, possivelmente em decorrência da invasão de espécies típicas de habitats abertos nessas matas de galeria que tiveram sua estrutura mais intensamente modificada pelo incêndio.

A disponibilidade de recursos (i. e. frutos) também afetou a estrutura das redes planta-animal, embora essa disponibilidade não tenha apresentado relação direta com a severidade do fogo. Interações mais generalistas levaram à formação de redes mais modulares e especializadas em áreas com maior disponibilidade de frutos, assim como a um grau de aninhamento menor. Nessas áreas, a diversidade de interações foi menor. Esse resultado possivelmente reflete uma maior partição de nicho entre as espécies, que passaram a consumir um subconjunto de frutos dentre todos aqueles disponíveis para a comunidade, levando à redução do número total de interações realizadas quando comparado ao número total de interações possíveis (i. e. todas espécies de animais interagindo com todas as espécies de plantas).

A estrutura do habitat não afetou diretamente a estrutura das redes planta-animal, embora tenha sido explicada em grande parte pela severidade do fogo. A variação na estrutura do habitat ao longo do gradiente de severidade do fogo pode ter determinado mudanças na composição das comunidades de pequenos mamíferos. Assim, é possível que seus efeitos sobre a estrutura das interações tenham sido indiretos.

Ao avaliarmos a dieta de roedores e marsupiais por meio da análise de DNA *metabarcoding*, pudemos detectar uma riqueza de plantas consumidas muito acima do que é possível através de métodos tradicionais. Por esse método, conseguimos identificar 211 espécies de plantas nas fezes desses animais, contrastando com as 28 espécies de sementes detectadas pela análise visual em estereoscópio.

O fogo também afetou o papel dos pequenos mamíferos como potenciais dispersores de sementes. Esses efeitos incluíram a redução no número de potenciais dispersores e na

diversidade de plantas potencialmente dispersas nas matas de galeria mais severamente atingidas pelo incêndio. Esses efeitos sobre o papel das espécies foram espécie-específicos, variando ao longo do gradiente de severidade do fogo. Considerando a baixa redundância (em termos de espécies de plantas dispersas) entre os roedores e marsupiais que podem atuar como dispersores, a ausência (ou baixa abundância) de espécies em áreas mais severamente impactadas pelo fogo pode comprometer o papel do grupo de pequenos mamíferos como dispersores de sementes. Essa redução pode afetar a dinâmica de recrutamento das espécies vegetais e, conseqüentemente, a recuperação da vegetação em áreas afetadas pelo fogo. No entanto, esse efeito vai depender da importância relativa das espécies de pequenos mamíferos nos processos de dispersão de cada planta que interage com esses animais.

Por fim, destacamos que a proteção de áreas de Cerrado sensíveis aos impactos do fogo (como as matas de galeria avaliadas) precisa ser considerada nos planos de manejo integrado do fogo aplicados nesse bioma. Os resultados apresentados no presente estudo indicam que incêndios severos modificam as comunidades de pequenos mamíferos que habitam as matas de galeria. Essas modificações têm efeitos sobre as interações planta-animal assim como sobre o papel ecossistêmico que roedores e marsupiais desempenham como dispersores de sementes, potencialmente impactando o recrutamento vegetal em matas de galeria queimadas de forma mais severa. Ademais, esses efeitos foram detectados três anos após o incêndio, indicando que os impactos sofridos pela vegetação e pela fauna podem ser prolongados. Desta forma, contribuindo para a alteração desses ambientes, a médio e longo prazo, em relação às características de matas de galeria que não tenham sido atingidas pelo fogo.