University of São Paulo
"Luiz de Queiroz" College of Agriculture
Center of Nuclear Energy in Agriculture

Effects of woody encroachment and prescribed fire on a small mammal community from a Cerrado fragment: subsidies for the improvement of an integrated management

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Dissertation presented to obtain the degree of Master in Science. Area: Applied Ecology

Piracicaba
2022

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Bachelor of Science in Biology

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versão revisada de acordo com a Resolução CoPGr 6018 de 2011

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Dados Internacionais de Catalogação na Publicação
DIVISÃO DE BIBLIOTECA – DIBD/ESALQ/USP

Furtado, Luciana de Oliveira

Effects of woody encroachment and prescribed fire on a small mammal community from a Cerrado fragment: subsidies for the improvement of an integrated management / Luciana de Oliveira Furtado. - - versão revisada de acordo com a Resolução CoPGr 6018 de 2011. - - Piracicaba, 2022.

99 p.

Dissertação (Mestrado) - - USP / Escola Superior de Agricultura “Luiz de Queiroz”. Centro de Energia Nuclear na Agricultura.

1. Rodentia 2. Didelphimorphia 3. Conservação 4. Microhabitat 5. Uso do habitat 6. Supressão do fogo 7. Savana I. Título

DEDICATÓRIA

Dedico a minha dissertação de mestrado à minha mãe, que por anos lutou para que eu pudesse viver os meus sonhos e fazer o que eu amo, e ao meu pai (in memoriam) que foi um exemplo de vida e amor.

Dedico também ao Brasil, um país incrível e rico em uma (bio)diversidade que precisa ser protegida.

AGRADECIMENTOS

A ciência é uma escolha de todos os dias, por amor. Amor ao mundo de perguntas, de descobertas, de conclusões e de mais perguntas! Escolher fazer e ser ciência é um processo complicado. Ainda mais em um período onde a desinformação toma conta do mundo, e ocorrem cortes e mais cortes de recursos para a ciência. É um balanço tênue ter o privilégio de escolher e poder fazer ciência em uma sociedade tão desigual onde nem todos (na verdade, poucos) têm acesso à educação de qualidade. Eu tive esse privilégio. Graças a pessoas incríveis que sempre acreditaram (e trabalharam MUITO) por mim, como a minha mãe. O fato de eu ter tido acesso a uma boa educação foi algo de total mérito dela. Ainda estou no início desse processo, de um dia, talvez, me tornar cientista. O mestrado foi um período incrível, parte desse processo, de total aprendizado e crescimento. Um crescimento não somente acadêmico, mas um crescimento pessoal. Gostaria de destacar e agradecer a algumas pessoas que foram importantes durante esse período:

À minha mãe, quero agradecer imensamente ser a primeira pessoa que acreditou sempre em meu potencial, e sempre apoiou minhas escolhas acadêmicas. Muito obrigada por lutar para eu ter o melhor dentro das nossas possibilidades. Foi você que me trouxe até aqui, seja passando horas em uma fila e insistindo para o diretor da “melhor” escola pública que conhecia me matricular, ou para que eu ficasse de olho na chamada do vestibular, ou torcendo para minha aprovação no processo seletivo do mestrado. Obrigada pelo apoio, amor e por toda uma vida de incentivo. Eu te amo.

Agradeço ao meu companheiro, Yohann Freddi, que sempre me motivou a crescer e buscar os meus objetivos. Obrigada por sempre me apoiar durante todos os momentos, mesmo aqueles que eu estive ausente em alguma viagem de campo. Obrigada por ser o primeiro a ouvir sobre minhas ideias de pesquisa e principais achados durante esses últimos anos, e vibrar junto comigo. E sem dúvida, obrigada pelo “apoio técnico” com softwares e programações, e também pelo suporte emocional. Você foi essencial. Eu sempre serei grata por poder compartilhar meus medos, conquistas e sonhos com você.

Agradeço ao meu cunhado Riziery Freddi e aos sogros, Saulo e Jocélia Freddi, por todo apoio e carinho durante esses anos. Obrigada por sempre se preocuparem e se disponibilizarem a me ajudar quando eu precisei. Rizi, muito obrigada pelas caronas para Piracicaba, foram divertidas e importantes para mim.

Agradeço muito aos meus queridos amigos que acompanharam de perto essa jornada. Eliany Santana e Maicon Biondo, vocês foram um suporte essencial. Agradeço especialmente

ao Henrique Frama, pela amizade e presença. Obrigada pelo apoio logístico durante minhas (breves) estadias em São Paulo, e principalmente por sempre se preocupar, me ajudar a manter o foco, e pelo imenso entusiasmo em cada novidade e conquista do meu mestrado. Você é um ótimo amigo.

Agradeço aos meus orientadores por me acolherem e confiarem em mim. Considero-me com muita sorte por ter tido orientadores tão competentes, profissionais e amigos. Especialmente à minha orientadora, Profa. Dra. Ana Paula Carmignotto, obrigada por me apresentar a esse mundo incrível da mastozoologia e trabalhos em campo, onde me encontrei. Agradeço por todo o suporte, conhecimento, conselhos, experiências, acolhimento e amizade que você me proporcionou. Você é uma inspiração, e uma professora e pesquisadora incrível. Ao meu orientador, Prof. Dr. Marcio Martins, sou muito grata e feliz por você aceitar entrar nessa jornada conosco, obrigada por todas as trocas, todo o apoio, sugestões e aprendizado nesse período.

Agradeço aos meus colegas de laboratórios (e campo) por todas as trocas, ajudas, discussões, risadas e amparos que só nós entendemos. Às pesquisadoras incríveis do LaSisMa, muitas que já conheço desde a graduação, obrigada pela amizade, ajuda, conselhos e amparo. Especialmente a minha parceira de campo, Giovana Felício, que esteve presente na maioria das viagens, muito obrigada por todos esses anos de amizade, apoio e perrengues durante nossos vários dias pelo Cerrado. Aos queridos "girinos" do LabVert, obrigada por me acolherem, por toda ajuda e amparo, aprendi muito com todos vocês. Agradeço imensamente a todos que passaram pela "equipe alpha", especialmente João Paulo Vieira-Alencar (JP), Juan Camilo Díaz e Filipe Serrano, que compartilharam muitos momentos e mútuas ajudas durante nossos dias em campo. Juan, agradeço muito pela sua ajuda e apoio especial durante o início do meu mestrado, seus conselhos e apoio durante o processo seletivo foram muito importantes. JP, agradeço muito também pela troca e toda a ajuda durante o desenvolvimento desta dissertação, e pela parceria acadêmica fruto de uma interação despretensiosa no Cerrado, que gerou um trabalho que adorei participar e onde aprendi muito. Agradeço também a Carolina Schlosser, pela ajuda e parceria desbravando metodologias, obrigada pelas conversas e apoio.

Agradeço aos funcionários incríveis da Estação Ecológica de Santa Bárbara, por todo apoio durante as nossas viagens de campo. Obrigada principalmente ao Marcos Pestana, querido "Marcão", por sempre nos receber (e socorrer!) com tanta alegria e simpatia, e por todo apoio logístico que foi essencial para o desenvolvimento deste estudo.

Agradeço aos membros do meu Comitê de Acompanhamento, Profa. Dra. Katia Ferraz e Prof. Dr. Alexander Christianini, pelas importantes sugestões ao longo do desenvolvimento desta dissertação. Especialmente ao Prof. Dr. Alexander, pela ótima parceria e colaboração que resultou no primeiro capítulo desta dissertação, seu trabalho, sugestões e ajuda foram essenciais, e eu aprendi muito com todas elas.

Agradeço aos membros da banca da minha qualificação, Profa. Dra. Giselda Durigan e Prof. Dr. Alexandre Percequillo, pelas importantes colocações e discussões que com certeza melhoraram esta dissertação.

Agradeço aos membros da comissão julgadora desta dissertação, Profa. Dra. Vânia Pivello, Prof. Dr. Emerson Vieira, e Prof. Dr. Thomas Püttker por toda a colabração na minha avaliação e formação, bem como pelas ótimas sugestões a este trabalho.

Agradeço ao Programa de Pós-Graduação Interunidades em Ecologia Aplicada da Universidade de São Paulo e a todos os seus funcionários e docentes, que acreditaram e proporcionaram o desenvolvimento desse estudo. De forma especial, muito obrigada a Antônia Mara Casarin, secretária do PPGI-EA, por toda a ajuda, paciência e preocupação durante o meu mestrado. Você foi muito importante para muitas etapas e com certeza a conclusão do meu mestrado é em grande parte graças a todo o seu apoio.

Agradeço à Coodenação de Aperfeiçoamento de Pessoal de Nível Superior – Brasil (CAPES), pelo financiamento que permitiu a minha dedicação a este estudo (Código de Financiamento 001), e à Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP), pelo financiamento dos projetos temáticos ao qual esta dissertação é fruto (Processos #2015/21259-8, #2018/14091-1, #2020/12658-4).

Por fim, agradeço a todos que de alguma forma contribuíram para o desenvolvimento desse estudo, e que me auxiliaram no caminho até aqui.

EPÍGRAFE

Roedor do Cerrado - *Arte de Thaís Ferreira, tatuadora e amiga da autora*

"O campo rico em flores mais bonito que eu já vi na minha vida
foi aquele que queimou em outubro"

Eugene Warming

"A natureza é sempre mais sutil, mais complexa e mais elegante
do que aquilo que somos capazes de imaginar"

Carl Sagan

SUMÁRIO

RESUMO

Efeitos do adensamento lenhoso e de queimadas prescritas sobre a comunidade de pequenos mamíferos de um fragmento de Cerrado: subsídios para o aprimoramento do manejo integrado do fogo

O adensamento lenhoso é um fenômeno que promove o aumento da densidade lenhosa em ambientes savânicos, e vem sendo responsável pela descaracterização dos habitats abertos de savanas pelo mundo todo. Ao contrário dos ecossistemas sensíveis ao fogo, as savanas coevoluiram com queimadas naturais, que contribuem para a manutenção das áreas abertas compostas por espécies adaptadas ao regime de fogo local. Alterações nesse regime histórico de fogo podem ter efeitos negativos na biodiversidade desses ecossistemas. Como resultado de anos de supressão ativa do fogo, as áreas de Cerrado vem enfrentando as consequências do aumento na densidade lenhosa, que já afetou quase um terço da maior savana da América do Sul. As principais consequências da supressão do fogo e do adensamento lenhoso são o risco de incêndios descontrolados, e a perda de biodiversidade especialista de áreas abertas, respectivamente. O manejo do fogo é considerado uma estratégia de conservação e manutenção das fisionomias abertas de savana, e atua controlando o adensamento lenhoso e promovendo a biodiversidade local. Os pequenos mamíferos não voadores são bons indicadores de alterações ambientais, devido à especificidade no uso do habitat e baixa capacidade de dispersão. Até o momento, não existiam estudos sobre os impactos do adensamento lenhoso na fauna de pequenos mamíferos do Cerrado, e em relação ao impacto de queimadas, as pesquisas se concentram na região central do bioma. O objetivo deste estudo, dividido em dois capítulos, foi avaliar pela primeira vez o impacto do adensamento lenhoso e do uso do fogo prescrito em uma comunidade de pequenos mamíferos no sudeste do Cerrado brasileiro. No primeiro capítulo, foram comparados dados coletados em 2003 e 2018, afim de avaliar os efeitos de 15 anos de adensamento lenhoso sobre a diversidade taxonômica (riqueza, abundância e composição) dos pequenos mamíferos. Além disso, a comunidade foi caracterizada quanto ao uso do habitat em duas escalas: macro e microhabitat. Os resultados deste capítulo demonstram uma estruturação clara da comunidade de pequenos mamíferos quanto ao uso do habitat nas duas escalas. Apesar de não influenciar a riqueza de espécies, o adensamento lenhoso vem alterando a fauna de pequenos mamíferos, favorecendo espécies associadas a ambientes florestais, enquanto afeta negativamente espécies relacionadas a fisionomias abertas. O segundo capítulo abordou os efeitos de um evento de fogo prescrito em fisionomias campestres de Cerrado através de dois experimentos: 1. temporal (antes e depois do fogo em uma área de campo sujo) e 2. espacial (campo cerrado queimado e não queimado). O fogo afetou a comunidade de maneira diferente nos dois experimentos. No primeiro experimento, espécies de roedores especialistas de habitats abertos e vulneráveis ao adensamento lenhoso foram beneficiadas pelo fogo, enquanto marsupiais tiveram sua riqueza e abundância negativamente afetadas. Já no experimento espacial, não houveram mudanças significativas nos parâmetros de diversidade. O manejo do fogo se mostrou uma estratégia eficiente no controle dos efeitos do adensamento lenhoso para a comunidade de pequenos mamíferos. A manutenção de um mosaico de habitats queimados e não queimados pode ser essencial para garantir a conservação de espécies especialistas de habitats abertos em ambientes savânicos.

Palavras-chave: Rodentia, Didelphimorphia, Conservação, Microhabitat, Uso do habitat, Supressão do fogo, Savana

ABSTRACT

Effects of woody encroachment and prescribed fire on a small mammal community from a Cerrado fragment: subsidies for the improvement of an integrated management

The woody encroachment is a phenomenon that has been responsible for open habitat shifts in savannas around the world, through the increase in woody density. Unlike fire-sensitive ecosystems, savannas evolved with natural burns that act shaping open habitats richness in these fire-prone ecosystems where species are adapted to the local fire regime. Changes in these fire regimes can lead to negative outcomes in the local biodiversity. As a result of years of fire suppression, almost one-third of the largest South American savanna, the Cerrado, has been suffering from woody encroachment. The main consequences of fire suppression and woody encroachment are the increase in wildfires and the loss of open-area specialist biodiversity. The fire management is considered an important conservation tool for open habitats maintenance, controlling the woody encroachment and promoting the local biodiversity. The non-flying small mammals are good environmental indicators, due to their high habitat specificity and low dispersion capacity. Until the moment, no study addressing the woody encroachment impacts in Cerrado small mammal fauna was published, and regarding fire management influence, researches are concentrated in the Cerrado core region. Here, we evaluated for the first time - along two chapters - the impacts of woody encroachment and a prescribed fire event in a small mammal community in the southeast of Brazilian Cerrado. In the first chapter we compared data from 2003 and 2018, in order to assess the effects of 15 years of woody encroachment in the taxonomic diversity (richness, abundance and composition) of small mammals. We also evaluated the habitat use by the small mammal community considering two distinct scales (macro and microhabitat). Our results showed that small mammals are structured regarding habitat use across both scales. Although not affecting species richness, the woody encroachment is changing the local small mammal fauna, favoring forest-dwellers at the cost of open-area specialists. In the second chapter, we assess the impacts of a prescribed fire event in Cerrado grassland formations based on two experiments: 1. Temporal (before and after the fire in a '*campo sujo*' patch), and 2. Spatial (unburned and burned '*campo cerrado*' patches). The fire affected the small mammal community in different ways in the two experiments. In the Temporal experiment, open-area specialist rodents that were also vulnerable to woody encroachment were favored by the fire, while the richness and abundance of marsupials were negatively impacted. On the other hand, in the Spatial experiment, there were no major changes in the diversity parameters due to fire. The fire management seems to be an efficient strategy for woody encroachment impact control in the small mammal community. The maintenance of a mosaic composed of burned and unburned habitats can be essential to the conservation of open-area specialist species in savanna environments.

Keywords: Rodentia, Didelphimorphia, Conservation, Microhabitat, Habitat use; Fire suppression, Savanna

1. INTRODUÇÃO GERAL

O Cerrado é o principal representante das savanas tropicais na América do Sul, sendo considerado um dos hotspots mundiais da biodiversidade, com elevada riqueza de espécies e grau de ameaça (Myers et al., 2000; Mittermeier et al., 2005). Por ser uma ecorregião que evoluiu em conjunto com queimadas ao longo de milhares de anos, o fogo exerce um papel importante na conservação da sua biodiversidade, contribuindo para a manutenção do mosaico de habitats abertos e florestais (Miranda & Sato, 2005; Parr et al., 2014). O combate excessivo das queimadas nesses ambientes tem consequências negativas para o Cerado, como o acúmulo de biomassa que pode causar incêndios descontrolados e graves, levando à perda de biodiversidade (Bond & Keeley, 2005; Durigan & Ratter, 2016). Além disso, a supressão do fogo é a principal causa do adensamento lenhoso no Cerrado brasileiro, fenômeno caracterizado pelo aumento na densidade lenhosa em habitats abertos (campestres e savânicos) em savanas ao redor do mundo (Sano et al., 2010; Rosan et al., 2019). O adensamento lenhoso leva à substituição de fisionomias abertas nativas por formações com maior densidade arbórea. Associado a isso, a biodiversidade especialista de habitats abertos também é perdida (Van Auken, 2009; Abreu et al., 2017; Archer et al., 2017). No estado de São Paulo, as formações campestres de Cerrado são escassas e sua preservação é essencial para garantir a conservação das espécies que ocorrem apenas, ou principalmente, nestes ambientes (Melo & Durigan, 2011; Honda & Durigan, 2016; Durigan et al., 2020). O manejo controlado do fogo é apontado como uma alternativa para preservar estas fisionomias, que estão desaparecendo no Cerrado paulista, e para controlar o adensamento lenhoso (Durigan & Ratter, 2016; Abreu et al., 2017).

Compreender como a fauna e a flora de cada região do Cerrado responde a fatores como o adensamento lenhoso e o uso do fogo contribui para o aprimoramento do manejo adequado e preservação desses remanescentes. A mastofauna do Cerrado é uma das mais ricas do mundo e segue vulnerável devido à perda de habitat crescente (Abreu et al., 2021). Dada a elevada seletividade de habitats e baixa capacidade de dispersão, os pequenos mamíferos não voadores (marsupiais e pequenos roedores) são considerados bons indicadores para a investigação do efeito de alterações ambientais (Bonvicino et al., 2002; Griffiths & Brook, 2014; Carmignotto, 2019). Neste sentido, o objetivo geral deste estudo é avaliar o efeito do adensamento lenhoso e do uso do fogo prescrito sobre a diversidade de pequenos mamíferos, em uma das poucas unidades de conservação que ainda preservam fisionomias abertas no Cerrado paulista. A Estação Ecológica de Santa Bárbara (EESB) conta majoritariamente com vegetação nativa de Cerrado expressa em um gradiente de fisionomias (campestres a florestais), as quais estão sob adensamento lenhoso devido à política de supressão do fogo por 30 anos (Melo & Durigan, 2011; Abreu et al., 2017). Além disso, a EESB abriga espécies de pequenos mamíferos endêmicos e ameaçados de extinção como o roedor *Clyomys laticeps* (Percequillo & Kierulff, 2009; de Vivo et al., 2011; Abreu et al., 2017; São Paulo, 2018). Essa região faz parte do distrito biogeográfico do Sul (S), segundo Françoso et al. (2019), que abriga 12% das espécies endêmicas do Cerrado. Não existem estudos prévios dos efeitos do adensamento e do fogo na comunidade de pequenos mamíferos para o Cerrado do sudeste meridional, onde essa pesquisa foi desenvolvida.

Este estudo está dividido em dois capítulos, que foram produzidos em formato de artigos em inglês para a publicação em periódicos indexados, seguindo as normas das respectivas revistas científicas a qual foram/serão submetidos:

O **Capítulo I** tem enfoque no efeito do adensamento lenhoso na comunidade de pequenos mamíferos e no uso do habitat pelas espécies em fisionomias nativas de Cerrado. O objetivo principal deste capítulo foi avaliar o impacto de 15 anos do adensamento lenhoso na Estação Ecológica de Santa Bárbara na abundância, riqueza e composição de espécies da comunidade de pequenos mamíferos não voadores, a partir da comparação de dados coletados em 2003 e em 2018. O índice de vegetação avançado (EVI) foi utilizado para quantificar o adensamento lenhoso na EESB nesse período de tempo, e relacionamos a alteração nos valores desse índice com os indicadores de diversidade anteriormente citados. Nós também avaliamos a utilização do habitat pelos pequenos mamíferos a partir de duas escalas: macro, utilizando a distinção entre habitats campestres (com vegetação mais aberta), savânicos, e florestais; e micro, através de variáveis indicativas da estrutura vegetal, como a cobertura herbácea, arbustiva e arbórea. Nós esperávamos que o adensamento lenhoso estivesse alterando a comunidade, favorecendo espécies associadas a habitats mais densos (como as fisionomias florestais), e impactando negativamente espécies relacionadas a habitats abertos (como os campos). A partir dessas análises, nós corroboramos essa hipótese, e identificamos espécies que se beneficiam e espécies vulneráveis ao adensamento lenhoso, e relacionamos esses resultados com o uso do habitat identificado para cada uma delas. Esse capítulo foi publicado no tópico de pesquisa "*Drivers of Small-Mammal Community Structure in Tropical Savannas*" do periódico *Frontiers in Ecology and Evolution*, em dezembro de 2021 (Furtado et al., 2021).

O **Capítulo II** teve como objetivo avaliar o efeito de um evento de fogo prescrito experimental nas fisionomias campestres sobre a comunidade de pequenos mamíferos através de dois experimentos: 1- experimento temporal: comparação entre os períodos anterior e posterior ao fogo prescrito na mesma área amostrada de campo sujo; e 2- experimento espacial:

comparação entre áreas de campo cerrado espacialmente adjacentes, queimadas e não queimadas, no mesmo intervalo de tempo. As alterações no microhabitat (estrutura da vegetação) após o fogo foram caracterizadas para ambos os experimentos, em quatro períodos de tempo, e relacionadas aos indicadores de diversidade dos pequenos mamíferos. Nós esperávamos que a diversidade de pequenos mamíferos decaísse logo após o fogo, mas com rápido aumento nos parâmetros após poucos meses, não resultando em perda de diversidade em ambos os experimentos. Nossos resultados demonstraram que o fogo de fato afeta a comunidade de pequenos mamíferos, entretanto de diferentes formas, como demonstrado pelas diferenças nos resultados dos dois experimentos, apresentados neste capítulo. Esse capítulo será submetido para publicação após o depósito dessa dissertação e apreciação pela Comissão Julgadora, que com certeza contribuirá com sugestões e discussões melhorando a qualidade deste trabalho. Os resultados deste estudo fornecem subsídios para o aprimoramento do manejo integrado do fogo na porção meridional do Cerrado, a partir da perspectiva da fauna de pequenos mamíferos não voadores.

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2. REVISÃO BIBLIOGRÁFICA

2.1. Cerrado: uma savana ameaçada

Savanas são ecologicamente definidas como comunidades compostas por uma cobertura contínua de gramíneas e por um estrato disperso de árvores lenhosas tolerantes a perturbações causadas pelo fogo, variando de 0-80% de cobertura arbórea (Goedert et al., 2008; Parr et al., 2014; Pennington et al., 2018). Na América do Sul, o Cerrado é o principal representante das savanas tropicais devido à sua larga extensão, de cerca de 2,2 milhões de km^2 (Alencar et al., 2020). Além de ocupar cerca de 25% do território brasileiro, o Cerrado apresenta grande variedade de fisionomias, desde campos densos de gramíneas até áreas com cobertura florestal quase total (Ribeiro & Walter, 2008; Simon et al., 2009; Batalha, 2011; Parr et al., 2014; Durigan & Ratter, 2016). O Cerrado é considerado o único *hotspot* mundial da biodiversidade de ambiente savânico, devido à elevada riqueza, alto endemismo e perda de habitats (Myers et al., 2000; Mittermeier et al., 2005). Apesar disso, o enfoque da conservação no país e no mundo é voltado para as florestas tropicais úmidas, como a Mata Atlântica e a Amazônia, levando à desvalorização dessa ecorregião (Pennington & Hughes, 2014; Pennington et al., 2018).

O Cerrado já perdeu metade de sua área original devido à pecuária extensiva, monoculturas (especialmente soja) e ocupação humana. A taxa de conversão de vegetação nativa no Cerrado é quase duas vezes mais alta do que na Amazônia (Lehmann & Parr, 2016; Pennington et al., 2018; Alencar et al., 2020). O estado de São Paulo, conta com a menor porcentagem de remanescentes de Cerrado naturais no Brasil, atualmente reduzidas em mais de 90%, representando menos de 3% da área do estado (Durigan, et al., 2003; Sano et al., 2010; Instituto Florestal, 2020). Além disso, uma parcela pequena dessas áreas remanescentes de Cerrado está protegida por lei em Unidades de Conservação (UC), resultado da negligência em relação a esta ecorregião. Estima-se que o Cerrado tem apenas 8% da sua extensão protegida em UCs, sendo que apenas cerca de um terço estão na categoria de Proteção Integral (CNUC, 2021). Além disso, o tamanho, a distribuição e a conectividade destas áreas podem não ser suficientes para manter populações viáveis da maioria das espécies ameaçadas do Cerrado (Nalon et al., 2005; Percequillo & Kierulff, 2009).

2.2. Dinâmica do fogo e o adensamento lenhoso no Cerrado

Responsáveis por 85% da área mundial queimada anualmente, as savanas constituem a maior área global com queimadas (Parr et al., 2014). A dinâmica ecológica que se estende a partir das queimadas naturais leva a um equilíbrio tênue e necessário para a existência desses ambientes (Silva & Batalha, 2010; Walter & Ribeiro, 2010; He et al., 2019). O fogo exerceu e ainda exerce uma pressão evolutiva sobre as espécies, promovendo a diversificação dos organismos, heterogeneidade de habitats, alterando a estrutura do ecossistema, sua composição e o ciclo dos nutrientes (Kauffman et al., 1994; Simon et al., 2009; He et al., 2019). Registros de queimadas nas savanas tropicais apontam que estes eventos eram raros até o final do Mioceno (~5 milhões de anos atrás), e para o Cerrado se tornaram mais presentes no final do Pleistoceno (~32 mil anos atrás) (Salgado-Labouriau & Ferraz-Vicentini, 1994; Miranda & Sato, 2005). As queimadas controlam a quantidade de biomassa gerada pelo ecossistema, queimando a matéria seca da camada herbácea e matando caules de árvores jovens, influenciando, assim, na sobrevivência de árvores, enquanto promove o crescimento de gramíneas. Dessa forma, o fogo limita a densidade das árvores e da cobertura lenhosa, e favorece o estabelecimento de fisionomias abertas, como as savânicas e campestres, propiciando a manutenção do mosaico de habitats típicos do Cerrado (Parr et al., 2014; Durigan et al., 2020). As queimadas são mais propícias na estação seca, devido às condições climáticas favoráveis, onde a elevada biomassa de gramíneas (grupo mais inflamável do Cerrado) gerada nos meses mais chuvosos se torna matéria seca morta, favorecendo a ocorrência de incêndios, que podem ter causas naturais (como por raios) ou antrópicas (Bond & Keeley, 2005; Pivello, 2011; Zanzarini et al., 2022).

O combate excessivo e supressão ativa do fogo em áreas preservadas de Cerrado podem levar a uma descaracterização das fisionomias locais, além do acúmulo excessivo de biomassa, que pode causar incêndios intensos e descontrolados, com graves emissões de poluentes na atmosfera e perda de biodiversidade (Bond & Keeley, 2005; Durigan & Ratter, 2016; Durigan, 2020). A supressão do fogo já facilitou a invasão por lenhosas e gramíneas exóticas em áreas da Ásia, África e no Brasil, levando à maior vulnerabilidade destes ambientes (D’Antonio & Vitousek, 1992; Klink & Machado, 2005; Lehmann & Parr, 2016). No Cerrado, a principal consequência da supressão do fogo é o aumento rápido da biomassa lenhosa em formações abertas nativas, fenômeno conhecido como adensamento lenhoso, que vem afetando savanas no mundo todo (Stevens et al., 2016; Rosan et al., 2019). O Cerrado é a savana com maior taxa de aumento na densidade lenhosa (7% por década), e estima-se que cerca de 19%

das áreas remanescentes estejam sob adensamento lenhoso (Stevens et al., 2016; Rosan et al., 2019). No Cerrado paulista, fisionomias campestres vêm sendo substituídas pelas savânicas e florestais, alterando significativamente o regime hidrológico e causando perdas na diversidade especialista de áreas abertas (Honda & Durigan, 2016; Abreu et al., 2017).

O manejo controlado do fogo tem sido sugerido como uma ferramenta para preservar as fisionomias campestres e a diversidade associada a essas formações, que estão desaparecendo no estado de São Paulo devido ao adensamento lenhoso (Durigan & Ratter, 2016; Durigan et al., 2020). Apesar dessa prática vir sendo utilizada recentemente de forma experimental em UCs do Cerrado (Silva et al. 2011; Fidelis et al. 2018), ainda há resistência por parte da comunidade científica em relação a este tipo de manejo (Driscoll et al., 2010; Pivello, 2017; Durigan, 2020). Estudos sobre o efeito de queimadas controladas em áreas protegidas são necessários para responder questões ainda em aberto, aprimorando as estratégias de manejo do fogo considerando os aspectos históricos e ecológicos locais (Miranda & Sato, 2005; Walter & Ribeiro, 2010; Fidelis & Pivello, 2011; He et al., 2019).

Este estudo foi desenvolvido na Estação Ecológica de Santa Bárbara, com predominância de vegetação nativa de Cerrado, especialmente de fisionomias campestres (Melo & Durigan, 2011). A EESB é um contraponto ao que se observa para o resto do Cerrado brasileiro, que apresenta a maioria das suas áreas remanescentes formadas por fisionomias savânicas (Alencar et al., 2020). No geral, o estado de São Paulo conta com a maior parte de suas áreas nativas de Cerrado constituídas de formações florestais (cerradão) e savânicas (cerrado sensu stricto; Melo & Durigan, 2011). A EESB está sob adensamento lenhoso devido a cerca de 30 anos de supressão de queimadas, e o uso do fogo prescrito vem sendo utilizado experimentalmente nos últimos anos (Abreu et al., 2017; Durigan et al., 2020).

2.3. Os pequenos mamíferos do Cerrado

O Brasil apresenta uma das mastofaunas neotropicais mais ricas, com 770 espécies pertencentes a 11 ordens (Abreu et al., 2021). Os pequenos mamíferos englobam representantes das ordens Chiroptera (morcegos), Didelphimorphia (marsupiais) e Rodentia (roedores), que constituem o grupo mais diversificado de mamíferos dos biomas neotropicais (Burgin et al., 2018). Uma parte significativa desta diversidade encontra-se no Cerrado brasileiro, atualmente considerada a savana mais rica em espécies de mamíferos do mundo, com 227 espécies (11% endêmicas) representando 10 ordens, sendo os morcegos (Chiroptera) e roedores (Rodentia) os grupos mais diversos (Carmignotto et al., 2012). Essa biodiversidade, entretanto, é impactada pelas diversas ameaças que o Cerrado enfrenta, com cerca de 26% de sua mastofauna classificada em algum nível de risco de extinção (Percequillo & Kierulff, 2009; Paglia et al., 2012). No caso dos pequenos mamíferos não voadores (marsupiais e pequenos roedores), além da elevada riqueza no Cerrado (113 espécies), cerca de 20% são endêmicas (Carmignotto et al., 2012; Gutiérrez & Marinho-Filho, 2017), tornando estas espécies alvo para conservação (ICMBio, 2018). Além disso, este grupo de mamíferos apresenta uma distribuição heterogênea ao longo do Cerrado e estreitamente relacionada ao mosaico de habitats (Carmignotto et al., 2022). O alto nível de endemismo, especificidade no uso do habitat, além da baixa capacidade de dispersão, tornam os pequenos mamíferos sensíveis às alterações no ambiente (Bezerra et al., 2009; Pardini et al., 2010; Carmignotto, 2019). Estas características, consequentemente, os tornam bons bioindicadores de alterações ambientais, sendo utilizados como grupo alvo em vários estudos, incluindo aqueles voltados a investigar o efeito do fogo nestas espécies (e.g., Monasmith et al., 2010; Griffiths & Brooks, 2014; Roberts et al., 2015; Namukonde et al., 2017).

As mudanças nas características do habitat causadas por eventos de fogo, como a redução da cobertura vegetal lenhosa, podem favorecer a presença e o aumento da fauna associada às áreas abertas e levar a uma redução na abundância e riqueza de espécies associadas às formações arbustivas e/ou arbóreas (Killgore et al., 2009; Mendonça et al., 2015). No Brasil, já foi observado que o fogo altera significativamente a composição e estrutura da comunidade de pequenos mamíferos no Cerrado (e.g., Vieira & Marinho-Filho, 1998; Vieira, 1999; Henriques et al., 2000; Briani et al., 2004; Layme et al., 2004; Henriques et al., 2006; Mendes-Oliveira et al., 2012; Mendonça et al., 2015; Camargo et al., 2018). Entretanto, estes registros se concentram na porção central dessa ecorregião, com raros estudos desenvolvidos em outras regiões do Cerrado, como em um ecótono de Cerrado e Floresta Amazônica no Mato Grosso (Mendes-Oliveira et al., 2012) e na região de Savana Amazônica no Pará (Layme et al., 2004). O trabalho de Durigan et al. (2020) apresenta resultados preliminares aos obtidos neste estudo, e é atualmente o único que aborda os efeitos de queimadas prescritas sobre a comunidade de pequenos mamíferos no Cerrado paulista.

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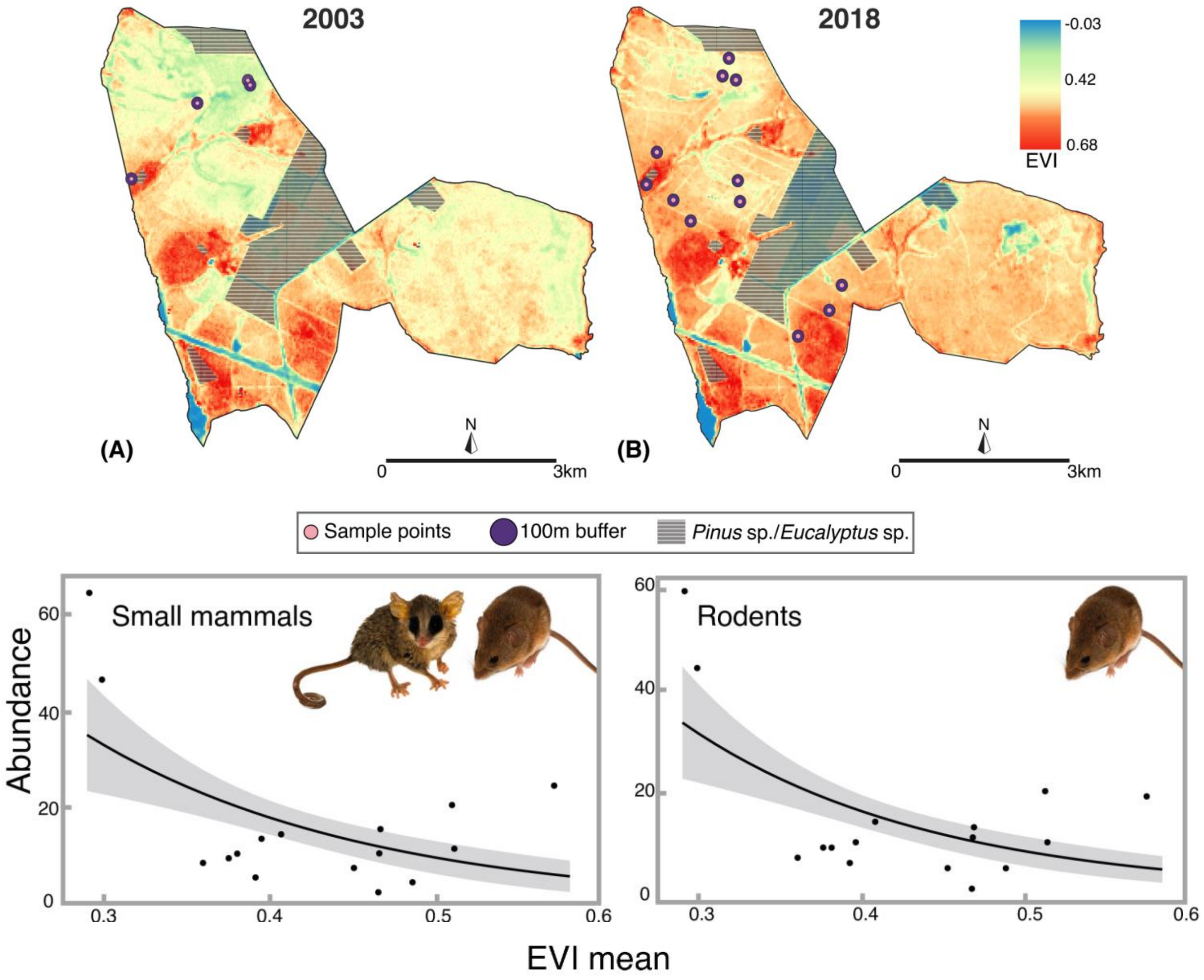
3. CAPÍTULO I - WINNERS AND LOSERS: HOW WOODY ENCROACHMENT IS CHANGING THE SMALL MAMMAL COMMUNITY STRUCTURE IN A NEOTROPICAL SAVANNA



Furtado, L. O., Felicio, G. R., Lemos, P. R., Christianini, A. V., Martins, M., & Carmignotto, A. P. (2021). Winners and Losers: How Woody Encroachment is Changing the Small Mammal Community Structure in a Neotropical Savanna. *Frontiers in Ecology and Evolution*, *9* (December). https://doi.org/10.3389/fevo.2021.774744

– CAPÍTULO I –

Winners and losers: how woody encroachment is changing the small mammal community structure in a Neotropical savanna

Abstract

Years of fire suppression, decreases in herbivores and global climate change have led to shifts in savannas worldwide. Natural open vegetation such as grasslands and shrublands are increasing in wood density, but the effects for small mammals are not well understood. While most of the mammal studies from the Brazilian Cerrado is concentrated in the core area of this large Neotropical savanna, its southern portions are suffering from biome shifting through woody encroachment. Herein, we surveyed a small mammal community from the southeastern boundary of Cerrado (Santa Bárbara Ecological Station) and evaluated the micro and macro environmental variables shaping community structure in order to investigate how the woody encroachment in the last 15 years may have influenced this assemblage. We recorded 17 species of marsupials and rodents along five distinct habitats in a gradient from grasslands to woodlands. Although richness was not affected by microhabitat variables, total and relative abundance varied according to habitat type and in relation to herbaceous, shrub and tree density. Rodents such as *Calomys tener* and *Clyomys laticeps* were positively affected by increasing herb cover, *Cerradomys scotti* and *Oligoryzomys nigripes* by shrub cover, while the marsupial *Didelphis albiventris* had higher association with increasing tree cover. We detected an increase of 27.4% in vegetation density (EVI) between 2003 and 2018 in our study site, and this woody encroachment negatively affected the abundance of some small mammals. The open-area specialists *Cryptonanus chacoensis* and *C. scotti* had a decrease in abundance, while *D. albiventris* and *O. nigripes* were favored by woody encroachment. Our data suggest that woody encroachment is shifting community composition: small mammals often associated with grasslands and open savannas are likely to be negatively affected by woody encroachment; while species that rely on tree covered habitats are likely to benefit from an increasing woody landscape. Therefore, forest-dwellers are gradually replacing open-vegetation inhabitants. Active management of open formations (e.g., with prescribed burning) may be needed to maintain Cerrado biodiversity, especially considering the open-area endemics.

Keywords: Cerrado, Didelphimorphia, EVI, Microhabitat selectivity, Habitat use, Rodentia, Fire suppression, Grasslands.

3.1. Introduction

Savannas worldwide have faced an increase of woody plant cover in the last century (Stevens et al., 2016a; Archer et al., 2017; García Criado et al., 2020). Changes in savannas natural landscapes due to tree encroachment have been described in Africa (e.g., Mitchard and Flintrop, 2013; Blaser et al., 2014; Stevens et al., 2016b), Australia (e.g., Fensham et al., 2005; Prince and Morgan, 2008), North America (e.g., Archer, 1994; Van Auken, 2009; Ratajczak et al., 2012) and South America (e.g., Honda and Durigan, 2016; Passos et al., 2018; Rosan et al., 2019). The fast increase in woody biomass, stem density, woody cover, and/or woody density in an ecosystem defines woody encroachment, which leads to the conversion of natural open habitats into woodlands (Stevens et al., 2016a; Rosan et al., 2019; Eldridge and Ding, 2021). This increase in forest formations across savanna landscapes often leads to a decrease in herbaceous cover and changes in associated biodiversity, primarily at the expense of savanna specialists (Van Auken, 2009; Abreu et al., 2017; Archer et al., 2017). The main causes of woody encroachment vary regionally as different and complex mechanisms act across savanna ecoregions, differing in ecological, climatic, evolutionary, and social aspects (Archer, 1994; Archer et al., 2017). Changes in natural fire regime, herbivory, climate (temperature and precipitation), land use and higher atmospheric CO_2 are suggested as the main causes for this phenomenon and are often associated with human disturbance in these ecosystems (Bond and Midgley, 2000; Stevens et al., 2016a; García Criado et al., 2020).

South American savannas showed the highest mean of woody cover increase (7.4% per decade) across tropical savannas (Stevens et al., 2016a). Moreover, 19% of the remaining Brazilian Cerrado areas are under woody encroachment, probably induced by fire suppression and agricultural land abandonment, intensified by the increase in atmospheric CO_2 (Moreira, 2000; Roitman et al., 2008; Passos et al., 2018; Rosan et al., 2019). Fire is a determinant driver for savanna dynamics, which has a historical evolution modeled by fire and herbivory processes, along with other fire-prone ecosystems (Bond and Keeley, 2005; Parr et al., 2014; Fidelis, 2020). The Cerrado high biodiversity is a result of these processes, with a rich mosaic of habitats (from open grasslands to woodland savannas) and endemic species adapted and often dependent on frequent fire events to maintain their populations (Simon et al., 2009; Fidelis and Blanco, 2014; Pilon et al., 2018, 2020). Brazilian Cerrado already lost about half of its natural vegetation due to extensive agriculture, especially soybean monoculture, and human occupation, leading to a high level of fragmentation (Motta et al., 2002; Sano et al. 2010). Changes in the natural balance of the local fire regime (such as frequency and intensity) can lead to declines in local populations or even local extinction, particularly for savanna specialists (Bowman et al., 2020). For instance, the Santa Bárbara Ecological Station (SBES), located in southeastern Brazil, has been under almost complete fire suppression for about 30 years, and recently (since 2015) fire management was introduced (Durigan et al., 2020). Over three decades (1985 to 2015), this remnant of Cerrado experienced woody encroachment and decreases in plant (especially herbs and shrubs) and ant species typical of open habitats (Abreu et al., 2017, 2021).

Most studies on the consequences of woody encroachment are focused on plants and biogeochemical cycles (e.g., Moreira, 2000; Huxman et al., 2005; Price and Morgan, 2008; Van Auken, 2009; Ratajczak et al., 2012; Blaser et al., 2014; Honda and Durigan, 2016; García Criado et al., 2020) with few dedicated to the responses of animal communities (e.g., Eldridge et al., 2011; Abreu et al. 2017; Stanton et al., 2017; Andersen and Steidl, 2019). Stanton et al. (2017) highlight a minor research effort about shrub encroachment impacts on vertebrates in all continents, with a higher number of studies on bird communities (almost twice those on mammals and herpetofauna, individually). For mammals, studies show a decrease in diversity and abundance with shrub encroachment in Africa (Stanton et al., 2017). Thus, it is urgent to study the possible impacts of woody encroachment on mammals from Cerrado, the richest savanna for mammal species, most of which composed of small mammals (Paglia et al., 2012; Mendonça et al., 2018). About 20% of the Cerrado non-flying small mammals (rodents and marsupials) are endemic and present high habitat selectivity and low dispersal capacity, what makes them highly vulnerable to changes in their habitat remnants (Pardini et al., 2010; Gutiérrez and Marinho-Filho, 2017; Carmignotto et al., 2012; 2019).

Habitat structure modifications unleashed by the increase in tree density include a decrease in the area covered by the herbaceous layer due to competition for resources such as soil moisture, nutrients and light, and intolerance to high canopy shading (Archer, 1994; Van Auken, 2009; Parr et al., 2014). This modified ecosystem will probably impact animal communities of savanna specialists, for instance through changes in macro and microhabitat variables, such as the amount of sunlight that reaches the soil, microclimate, water, food and refuge availability, and vegetation structure (Abreu et al., 2017; Loggins et al., 2019). As small mammals exhibit high habitat selectivity, and have a heterogeneous distribution associated with the mosaic of habitats in the Cerrado, these changes in habitat structure can lead to a shift in the composition of local small mammal communities (Carmignotto et al., 2012, 2014). Although the microhabitat perspective has been explored by small mammal ecologists since the 60s (e.g., Morris, 1987; Stancampiano and Schnell, 2004; Melo et al., 2013; Corrêa et al., 2017), the definition and clarity of which variables and scale define it varies among studies (see review by Jorgensen, 2004). There are few studies evaluating microhabitat effects on the density of Cerrado small mammals (e.g., Vieira, 2003; Rocha et al., 2011), a topic that is broadly explored for the neighbor Atlantic Forest (e.g., Püttker et al., 2008; Melo et al., 2013). In this study, we evaluated habitat selectivity from both the macro and microhabitat perspectives, aiming to contribute to the understanding of which factors, at different scales, shape a small mammal community at the southeastern Cerrado boundary. We also aimed to evaluate how the woody encroachment in the last 15 years may have influenced community structure. We expect a notable change in the small mammal community of Cerrado sites under woody encroachment, with forest-dwellers gradually replacing open-vegetation inhabitants, partially due to differential habitat and microhabitat preferences.

3.2. Materials and Methods

3.2.1. Study Area

Our study was conducted in the Santa Bárbara Ecological Station (hereafter SBES; 22°46′-22°51′S/49°10′-49°16′ W, 600-680 m above sea level, Águas de Santa Bárbara municipality, São Paulo, Brazil), one of the few protected areas that preserves open savannas in the southern Brazilian Cerrado (Durigan et al., 2020). SBES is characterized by a mosaic of savannas and Atlantic Forest patches (Melo and Durigan, 2011), comprising 2,715 ha. Currently, SBES vegetation is mostly represented by native Cerrado formations, from grasslands (‘*campo sujo*’ and ‘*campo cerrado*’) and savannas (‘*cerrado sensu stricto*’) to woodlands (‘*cerradão*’) (Oliveira-Filho and Ratter, 2002; Araujo et al., 2010; Melo and Durigan, 2011). The SBES was under a fire suppression policy for 30 years (1985 - 2015; Abreu et al., 2017; Durigan et al., 2020). The grasslands that we studied here are among the few ones that had some accidental fire events more recently. The 2003 ‘*campo limpo*’ (‘*campo sujo*’ in the 2017-2018 survey) patch had at least four fire events before 2008, when the last one was registered. One ‘*campo cerrado*’ patch had only one fire event recorded in the last 30 years, in 2001, and the other patch in 2011, and both have been under fire suppression since then. The other plots that were sampled, burned for the last time before 1985 (Melo and Durigan, 2011; Conciani et al., 2021). Although these sparse fire events contributed to the grasslands maintenance in the area, SBES have been suffering under woody encroachment across this period (Melo and Durigan, 2011; Abreu et al., 2017; 2021). The study site also holds stands of exotic timber plantations, including *Eucalyptus* sp. and *Pinus* sp. Dry/cold (April to September) and wet/warm (October to March) seasons are strongly marked. The climate is classified as Köppen Cfa-type, with annual rainfall between 1010-2051 mm and an average of 1454 mm (Alvares et al., 2013; CIIAGRO, 2016). The mean temperature of the coldest months is 17°C and for the hottest months, 24°C, with a maximum of 35.2°C and a minimum of 3.4°C. These data correspond to the period from 1995-2014 and come from the weather station in the municipality of Manduri, São Paulo, Brazil, 20 km from our study area (CIIAGRO, 2016). SBES soils are characterized as deep oxisols with low nutrient and high sand content, high saturation of aluminum and low capacity of holding water (Melo and Durigan, 2011).

3.2.2. Data Sampling

3.2.2.1. Small Mammal Surveys

To characterize the habitat and microhabitat preferences in order to investigate the role of woody encroachment in the small mammal community (rodents and marsupials), we used data from two temporally spaced surveys: (1) the 2003 survey carried out during January and February 2003, in four Cerrado habitats of SBES including open grasslands (‘*campo limpo*’, and ‘*campo sujo*’), savanna (‘*cerrado sensu stricto*’), and woodland (‘*cerradão*’), comprising a 10-day field-trip and a capture effort of 1,365 live trap nights and 1,680 pitfall trap nights (more details about the sampling design of the 2003 survey can be found in Carmignotto, 2005); and (2) the 2017-2018 survey, from August 2017 to July 2018, with 12 monthly 10-day field trips, also in four Cerrado habitats, from grassland to woodland (‘*campo sujo*’, ‘*campo cerrado*’, ‘*cerrado sensu stricto*’ and ‘*cerradão*’), comprising 2,880 live trap nights and 2,880 pitfall trap nights in each habitat surveyed (three sampling points by habitat), totaling 11,520 live trap nights and 11,520 pitfall trap nights across the 12 sampling points. Each sampling point had eight live traps: four Sherman traps (25 x 8 x 9 cm - Sherman^{TM}) and four wire mesh traps (two of 30 x 16 x 18 cm and two of 32 x 20 x 20 cm, Metal Miranda), alternated and 15 m apart. Traps were distributed in two arrays (A and B, each with two Shermans and two wire mesh traps) 60 m apart. In the beginning of each field trip, the live traps were set on the ground and baited with a mix of peanut butter, cornmeal and canned sardines. This bait was fixed on pieces of sweet potatoes in the wire mesh traps. Each sampling point was also composed of two lines of pitfall traps, 60 m apart, each with four 100-L buckets, 10 m apart, connected by a 60-70 cm high and ~10 cm buried plastic drift fence. The pitfall trap arrays were 60 m apart from the live trap lines, and the buckets were opened and closed at the beginning and ending of each field trip.

The individuals captured were identified at species level (Voss and Jansa, 2009, and Fegies et al., 2021, for marsupials; and Patton et al., 2015, for rodents), weighted and sexed. Other information about age (juvenile, subadult, and adult), behavior, and reproduction was taken when possible. We collected tissue samples from the ear of all individuals for taxonomic identification through molecular analysis. This small cut also served as recapture recognition for individuals weighing less than 30 g (although not allowing recognition at the individual level). We used numbered ear tags (ZT 900 by Zootech) for individual identification of animals weighing over 30 g. Some individuals were collected for morphological taxonomic identity and subjected to taxidermy or fixed with 10% formaldehyde solution and preserved in 70% alcohol

(SISBIO 50658-3 collection permit). These vouchers will be deposited in the mammal collection of the Museu de Zoologia da Universidade de São Paulo (MZUSP), São Paulo, Brazil. All procedures of capture and collection were made following the ASM guidelines for the use of wild mammals in research (Sikes et al., 2016) and were approved by the Animal Ethical Committee (#CEUA-IB-USP 241/2016).

3.2.2.2. Habitat and Microhabitat Use

In order to assess the habitat use by the SBES small mammals, we used the number of individuals captured in the 2017-2018 survey along the four habitat types sampled. These habitats were chosen in the field and represent a gradient of natural increasing woody cover, typical of Cerrado mosaics. The '*campo sujo*' and '*campo cerrado*' are both open formations with a predominance of herbaceous layer, but '*campo sujo*' is a grassland characterized by scattered shrubs and small trees, and '*campo cerrado*' by sparse trees and higher shrub cover, but still with a large proportion of herbs; '*cerrado sensu stricto*' is also known as 'typical cerrado', and is a savanna formation dominated by shrubs and trees up to 3-8 m tall often covering 30% of the crown canopy, but still with a high herb cover; and '*cerradão*' is a forest formation, a woodland savanna with often 50-90% of canopy coverage composed of higher trees 8-12 m tall (see Oliveira-Filho and Ratter, 2002). The field classification was later confirmed by the enhanced vegetation index (EVI) obtained at each habitat surveyed.

To evaluate the potential role of microhabitat features in structuring small mammal communities, we measured seven variables at each live trap station during the 2017-2018 survey: (1) percentage of canopy cover; (2) number of trees with diameter at breast height (DBH) > 10 cm; (3) percentage of herbaceous soil cover; (4) percentage of soil covered by the invasive grass, *Urochloa* sp.; (5) number of stems of shrubs that branch up to 1 m in height; and understory density, through (6) the number of touches up to 0.5 m height, and (7) between 0.5-1 m in height on a stick held vertically in different directions (S, N, L, O). Variables 1-3 were visually estimated within a radius of 5 m from each live trap, and variables 4-7 were measured within a radius of 2 m from the live traps. These variables were selected based on their use in previous microhabitat small mammal studies (e.g., Freitas et al., 2002; Vieira et al., 2005; Rocha et al., 2011), and due to their close relationship with vegetation cover (herb, shrub, and trees) and canopy openness, differentiating well the distinct Cerrado habitats analyzed. We did not measure the microhabitat variables for pitfall stations since the area near each trap was cleared for the installation of pitfall traps. Therefore, the capture data used for microhabitat analysis were restricted to live trap stations. To increase independence of records, we did not consider recaptures of the same individual in the same live trap and month. Recaptures in different field trips and live trap lines were kept, as they could indicate the suitability of microhabitats for that species.

3.2.2.3. Woody Encroachment

We used the enhanced vegetation index (EVI) to quantify the vegetation change over the 15 years between both surveys (2003 and 2017-2018) across the sampled habitats. We calculated the mean EVI values for each sampling point based on surface reflectance images from Landsat 7 for 2003, and from Landsat 8 for 2018, obtained from the United States Geological Survey satellite products (USGS, https://espa.cr.usgs.gov/). Furthermore, we used the available images from the survey periods, or as near as possible to the date, that presented conditions with minimum cloud cover. The satellite image manipulation and EVI values calculation were performed in the software QGis version 3.4.14 (QGIS, 2021). Abreu et al. (2017) showed that the EVI index is highly correlated with tree basal area, and Chaves et al. (2013) also argue that the EVI index is more sensitive to canopy changes, mainly in places with a higher concentration of biomass when compared with the NDVI index. Thereby, we consider the EVI index a suitable proxy to quantify woody encroachment in our study site.

3.2.3. Data Analysis

We used different datasets for each analysis performed here, according to its scale and goals. The datasets are derived from the total data we collected in both surveys (2003 and 2017-2018) and are described in Table 1 and at each analysis item below.

Statistical analyzes were performed in R (version 4.1.0; R Core Team, 2021). The model selection for all linear models described below were made through hypothesis testing approach ($\alpha = 0.05$), comparing nested models through *anova* function using the variance partition from the F-statistic for linear models and the residual deviance and chi-square tests for generalized linear models (Zuur et al., 2009). The diagnoses of the fitted models were made with the ‘DHARMa’ package, we tested the model fitness for over and underdispersion, uniformity, outliers (along with Cook’s distance plot), and zero-inflation (Harting, 2021, Supplementary Table 3). The prediction graphics of the models were made with the package ‘ggiraphExtra’, function *ggPredict* (Lüdecke et al., 2021).

Table 1. Description of each dataset used in this study.

Dataset	Definition	Topic addressed
1	Total number of individuals captured from both surveys (2003 and 2017/2018) in live and pitfall trap lines, excluding all recaptures.	Small mammal community structure
2	Total number of individuals captured in the 2017/2018 survey, in both live and pitfall trap lines, excluding all recaptures.	Habitat selection
3	Number of individuals captured in the 2017/2018 survey, only in the live traps, excluding recaptures of the same individual in the same live trap and month. Recaptures in different field trips and trap lines were kept.	Microhabitat selection
4	Number of individuals captured in Jan/Feb 2003 and Jan/Feb 2018, in live and pitfall trap lines, excluding all recaptures.	Woody encroachment

3.2.3.1. Small Mammal Community Structure

To characterize the community structure and compare patterns of small mammals between the two distinct surveys, we considered all data (dataset 1, Table 1) from pitfalls and live traps (except for recaptures, which were removed) from both the 2003 and 2017-2018 surveys. Community structure was characterized by its alpha taxonomic diversity with the CHAO1 estimator, which allows estimating the absolute number of species in a community based on the number of rare species in the sample (Whittaker, 1972; Dias, 2004). We also estimated species richness through rarefaction/extrapolation species curves (Colwell et al., 2012; Chao et al., 2014). To evaluate the adequacy of sampling effort, the abundance data were used to calculate the coverage estimator which represents the proportion of the total number of individuals in an assemblage belonging to a species represented in the sample, estimated in percentage, as a measure of completeness. These analyses were made using the ‘iNEXT’ R package (Hsieh et al., 2016). Confidence intervals (95%) were used as thresholds in comparisons (Chao and Chiu, 2016). Abundance was defined as the total number of individuals captured per species, and to determine the dominance and identify rare species in the communities we used the Abundance-based Coverage Estimator (ACE) with the *ChaoSpecies* function from the ‘SpadeR’ package (Moreno, 2001; Chao and Chiu, 2016).

3.2.3.2. Habitat and Microhabitat Use

In order to investigate the habitat use by the SBES small mammals, we performed a Non-Metric Multidimensional Scaling (NMDS) ordination with the ‘vegan’ R package (Oksanen et al., 2020), function *metaMDS*, based on the number of individuals captured in the four habitats surveyed (‘*campo sujo*’, ‘*campo cerrado*’, ‘*cerrado sensu stricto*’ and ‘*cerradão*’). For the NMDS we used dataset 2 (Table 1), which consisted of the total number of individuals captured in pitfalls and live traps (except for recaptures, which were removed) in the 2017-2018 survey. In order to not obscure the patterns found, we considered only species with n > 5 individuals. We also performed the Shepard plot (or stress plot), in order to observe the goodness of fit of the data into the NMDS analysis, using the *stressplot* R function.

The microhabitat analyzes were performed only for the 2017-2018 survey, considering only the live trap data (dataset 3, Table 1), as explained above. First, we reduced the dimensionality of the seven microhabitat variables through a Principal Components Analysis (PCA) with a correlation matrix using the ‘stats’ package and retained the principal components with eigenvalues >1. Then we fitted generalized linear mixed models (GLMM) with the package ‘lme4’ (*glmer* function, family = poisson, link = log; Bates et al., 2021) for the abundance (number of captures per species) and richness of the small mammals as a function of the two principal components extracted from the PCA. The random effect considered for these GLMM was the 12 sampling points (three for each habitat), since for the microhabitat analyzes we treated each trap station as our sampling unit and considered it as non-independent within the 12 sampling points analyzed. For species with n > 10 individuals, we also built GLMM for the number of captures of each species in relation to the principal components selected.

3.2.3.3. Woody Encroachment

In order to investigate the effect of woody encroachment across time on small mammals, we used the dataset 4 (Table 1), which included the total number of individuals captured in both pitfall and live traps (except the recaptures), of the 2003 survey (3,045 trap-nights). For the 2017-2018 survey, we restricted our data to those obtained in January-February (3,840 trap-nights), in order to standardize the capture effort between the two surveys analyzed. The same approach was employed for the analysis of satellite images, as explained in the data sampling item above.

To quantify the increase in tree cover between the two surveys, we fitted linear models (‘stats’ R package, *lm* function) using the mean EVI values for each sampling point as a function of the sampling period (2003 x 2018) and habitat (‘*campo limpo*’, ‘*campo sujo*’, ‘*campo cerrado*’, ‘*cerrado sensu stricto*’ and ‘*cerradão*’). To test the woody encroachment impact on the small mammal community, we fitted generalized linear models (GLM) for total richness and abundance of small mammals, and per order (rodents and marsupials), as a function of the EVI mean values for each sampling unit for the 2003 and 2018 surveys. A dissimilarity analysis based on the number of individuals captured between the two surveys was made by estimating beta diversity using the function *beta* from the ‘BAT’ package (Carvalho et al., 2012; Cardoso et al., 2015) in order to detect changes in species composition across time between the two assemblages analyzed.

3.3. Results

3.3.1. Small Mammal Community Structure

We captured 1,112 individuals of 17 native species of marsupials and rodents, in the gradient from grasslands to woodland savanna, considering both surveys (2003 and 2017-2018). Rodents and marsupials represented 67% and 33% of the total richness, respectively (Table 2).

The 2003 survey recorded 10 species of small mammals (60% of total SBES richness), of which 70% were rodents and 30% marsupials, with a total of 124 individuals captured. In the 2017-2018 survey, 987 individuals were captured belonging to 17 species (100% of SBES total richness), of which 65% were rodents and 35% marsupials. Comparing both surveys, for 2003 we did not record the rodents *Hylaeamys megacephalus*, *Nectomys* cf. *squamipes*, *Oxymycterus delator* and *Rhipidomys* cf. *macrurus*, and the marsupials *Didelphis albiventris*, *Gracilinanus agilis* and *Gracilinanus microtarsus* in the habitats analyzed.

The species richness observed for the complete 2003 survey and for ‘*campo sujo*’ and ‘*cerradão*’ habitats were relatively close to the richness estimated by the Chao1 estimator (Table 3), indicating that the sampling effort was appropriate to survey this community, as was shown also by the coverage estimate (98%, 97% and 83%, respectively). On the other hand, for the *‘campo limpo’* and ‘*cerrado sensu stricto’*, the observed richness was only half of the estimated richness, which is clear through the low coverage value for ‘*cerrado sensu stricto’* (55%), but not for *‘campo limpo’* (92%), indicating that a more extensive sampling in the ‘*cerrado sensu stricto’* would be necessary (Table 3). Despite the extremely low species richness value obtained for ‘*cerradão*’, the rarefaction-extrapolation curves for the 2003 assemblage indicate no differences in the species richness among the habitats sampled, with values estimated for extrapolated data, corroborating the results of the Chao1 richness estimator (Figure 1A).

For the 2017-2018 survey, all the observed and estimated species richness were also similar, with high coverage values (99% for total data and habitats), evidencing that the sampling effort was sufficient to estimate the community richness (Table 3). This result corroborates those obtained by the rarefaction/extrapolation curves, which also indicates that only the *‘campo cerrado*’ differed in relation to the other habitats surveyed, showing comparatively lower richness (Figure 1B).

The species with the highest abundance for the 2003 survey was *Necromys lasiurus*, representing 71% of the assemblage (Figure 2A), followed by other rodents such as *Cerradomys scotti* (6.5%) and *Oligoryzomys mattogrossae* (4.8%). Furthermore, the less abundant species were the rodents *Akodon* cf. *montensis* and *Calomys tener,* with only one individual captured each, representing, together, 1.6% of total abundance (Figure 2A). This pattern became clear in the Abundance-based Coverage Estimator (ACE) analysis, which considered only *N. lasiurus* as an abundant species, and the nine remaining species as rare (k < 10). For the 2017-2018 survey, the species of *Oligoryzomys* were the most abundant, with *O. nigripes* comprising 25.4% of the assemblage and *O. mattogrossae* 18.6%. Other abundant species in this assemblage were the rodents *Calomys tener* (14.8%) and *Cerradomys scotti* (11.2%). The rarest species were the rodents *Nectomys* cf. *squamipes* (1 individual) and *Oxymycterus delator* (2 individuals), representing, together, less than 0.4% of total abundance (Figure 2B). For 2017-2018, the ACE analysis indicates 12 abundant species (k > 10), and five rare species.

3.3.2. Habitat and Microhabitat Use

For patterns of habitat use, the non-metric multidimensional scaling for the 2017-2018 survey (Figure 3; stress= 0.09, Supplementary Figure 1) showed distinct species groups, one composed by *Calomys tener*, *Cerradomys scotti*, *Oligoryzomys mattogrossae* and *Cryptonanus chacoensis* that seemed more related to ‘*campo cerrado*’, a grassland formation; and another formed by *Didelphis albiventris*, *Gracilinanus agilis* and *Hylaeamys megacephalus* that were located closer to ‘*cerradão*’, a forested habitat. Also related with ‘*cerradão*’ are *Gracilinanus microtarsus* and *Rhipidomys* cf. *macrurus*, but more dispersed than the previous species.

Akodon cf. *montensis* and *Oligoryzomys nigripes* were located in between ‘*cerrado sensu stricto*’ (savanna) and ‘*cerradão*’ (forest). The species *Cryptonanus* aff. *chacoensis* and *Clyomys laticeps* were a bit more dispersed, but relatively close to the ‘*campo sujo*’, the most open habitat at SBES. *Monodelphis kunsi* was located in a transition between ‘*cerradão*’, ‘*cerrado sensu stricto*’ and ‘*campo sujo*’, and *Necromys lasiurus* between ‘*cerrado sensu stricto*’, ’*campo cerrado*’ and ‘*campo sujo*’.

Table 2. Relative abundance (%) of small mammals in the Santa Bárbara Ecological Station, São Paulo, Brazil, in the 2003 and 2017-2018 surveys. Habitats are ordered by increasing woody cover: CL= '*campo limpo*', CS = '*campo sujo*', CC = '*campo cerrado*', CE = '*cerrado sensu stricto*', CD = '*cerradão*'. The habitat use is expressed by G for grasslands (here including CS = '*campo sujo*', and CC = '*campo cerrado*'), S for savannas (CE = '*cerrado sensu stricto*') and F for forest habitats (CD = '*cerradão*') according to the NMDS analysis performed for the 2017-2018 data (see Figure 3).

Species	**Habitat use**	**2003**					**2017-2018**				
		CL	CS	CE	CD		CS	CC	CE	CD	
Didelphimorphia											
Didelphidae											
Cryptonanus chacoensis	G	0.8	3.2	0.8	-		1.2	1.4	0.6	-	
Cryptonanus aff. *chacoensis**	G	1.6	1.6	0.8	-		0.6	-	-	-	
Didelphis albiventris	F	-	-	-	-		0.2	0.3	1.2	4.1	
Gracilinanus agilis	F	-	-	-	-		-	0.4	1.6	2.3	
Gracilinanus microtarsus	F	-	-	-	-		0.3	-	0.4	3.4	
Monodelphis kunsi	G/S/F	-	-	-	1.6		-	0.2	0.2	0.4	
Rodentia											
Cricetidae											
Akodon cf. *montensis*	S/F	0.8	-	-	-		0.2	0.2	0.7	1.6	
Calomys tener	G	-	0.8	-	-		8.8	2.6	2.6	0.8	
Cerradomys scotti	G	0.8	4.8	0.8	-		3.0	6.4	2.1	0.2	
Hylaeamys megacephalus	F	-	-	-	-		0.2	-	0.1	2.4	
Necromys lasiurus	G/S	30.6	39.5	0.8	-		0.6	0.3	0.4	0.4	
Nectomys cf. *squamipes*	-	-	-	-	-		0.1	-	0.1	-	
Oligoryzomys mattogrossae	G	-	0.8	4.0	-		5.5	8.4	3.7	1.0	
Oligoryzomys nigripes	S/F	0.8	1.6	-	0.8		0.8	1.3	7.6	15.7	
Oxymycterus delator	-	-	-	-	-		0.1	-	-	-	
Rhipidomys cf. *macrurus*	F	-	-	-	-		-	-	0.2	0.8	
Echimyidae											
Clyomys laticeps	G	2.4	-	-	-		1.8	-	-	-	
	TOTAL	37.9	52.4	7.3	2.4	**100**	23.5	21.6	21.7	33.3	**100**
	N species	**7**	7	5	2	**10**	14	10	14	12	**17**
	Survey effort (trap-nights)	790	790	715	750	**3,045**	5,760	5,760	5,760	5,760	**23,040**

* This taxon refers to *Cryptonanus chacoensis* lineage B of Fegies et al. (2021). The name *C. chacoensis* (Tate, 1932) was applied for *C. chacoensis* lineage A.

Table 3. Observed and estimated species richness, with standard errors and sample coverage, of small mammals for the 2003 and 2017-2018 surveys in distinct habitats surveyed at SBES. The habitats are: CL: *'campo limpo'*; CS: '*campo sujo*'; CC: '*campo cerrado*'; CE: '*cerrado sensu stricto'*; and CD: '*cerradão*'.

Assemblages	**Richness observed**	**Richness estimated Chao1**	**Standard error**	**Sample coverage**
2003	10	12.0	3.7	98%
CL	7	14.8	11.4	92%
CS	7	8.0	1.8	97%
CE	5	10.3	6.3	55%
CD	2	2.3	0.9	83%
2017-2018	17	17.5	1.3	99%
CS	14	14.7	1.3	99%
CC	10	10.0	0.6	100%
CE	14	15.0	1.9	99%
CD	12	12.0	0.4	100%

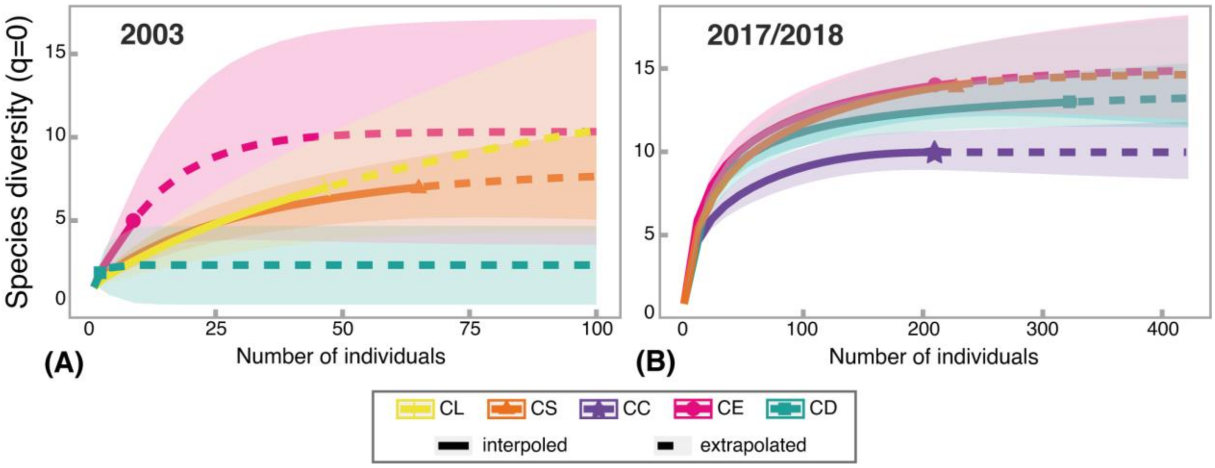


Figure 1. Rarefaction/Extrapolation curves for **(A)** the 2003 survey generated with 1000 bootstraps and 100 individuals as endpoint and for **(B)** the 2017-2018 survey generated with 1000 bootstraps and 420 individuals as endpoint. The shadow surface represents the 95% confidence interval for each curve. The habitats are: CL: '*campo limpo*'; CS: '*campo sujo*'; CC: '*campo cerrado*'; CE: '*cerrado sensu stricto'*; and CD: '*cerradão*'.

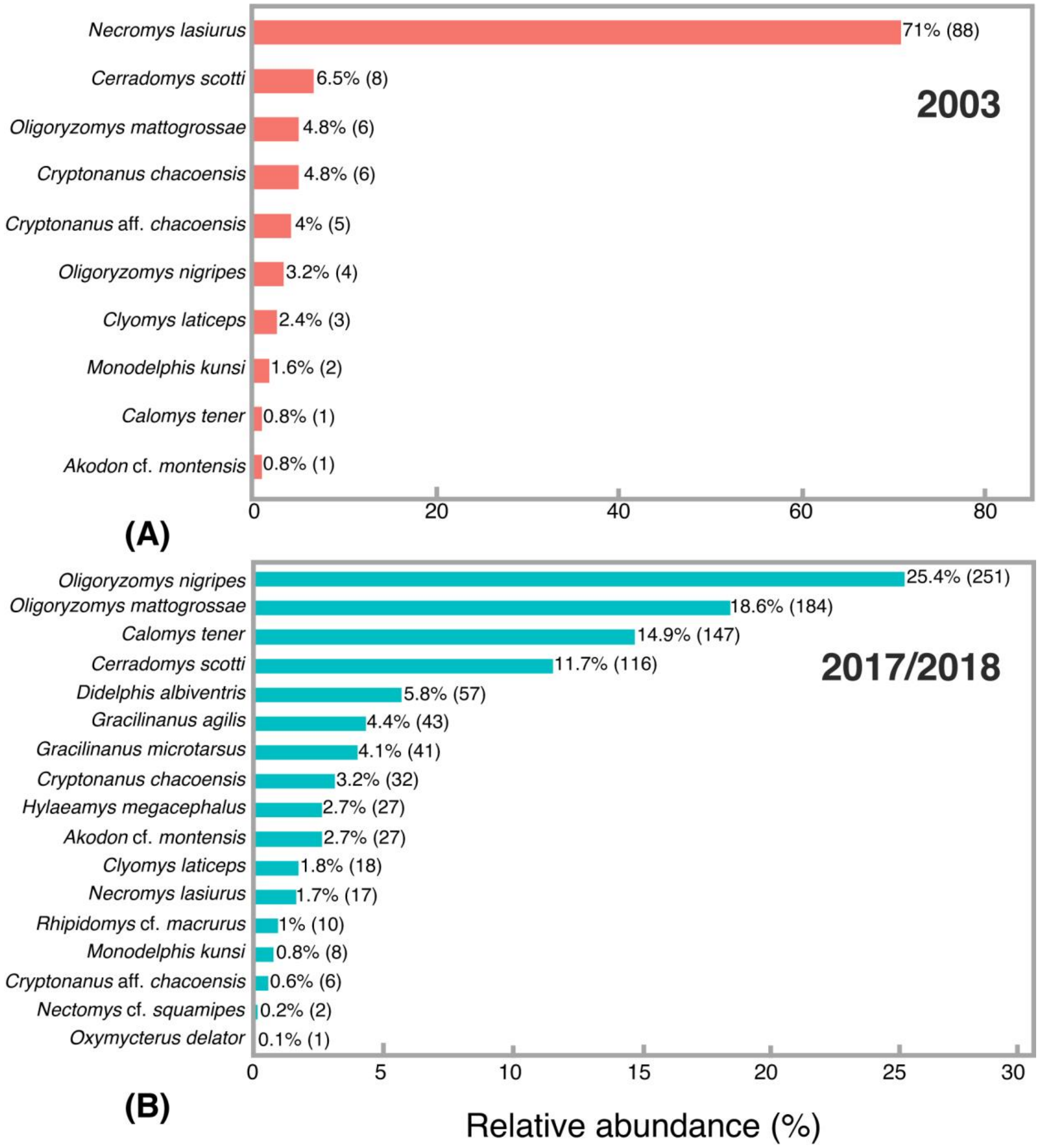


Figure 2. Relative abundances and number of individuals (in parentheses) of small mammals from SBES captured in **(A)** 2003 survey (3,045 trap-nights) and **(B**) 2017-2018 survey (23,040 trap-nights).

The seven microhabitat variables were reduced to two principal components with eigenvalues > 1 (3.12 and 1.58, respectively, Supplementary Table 1) that represented about two thirds of the total variance in our dataset (67.2%, Supplementary Table 1 and Supplementary Figure 2). The first principal component (hereafter PC1 variable) represented 44.6% of the total variance and is an indicator of high herb cover and low tree cover. The second principal component retained (hereafter PC2 variable) is an indicator of high shrub cover and low herb cover and represented 22.6% of the total variance (Supplementary Table 2). The gradient in relation to vegetation cover and canopy openness is visible in the PCA graph and is evidently related with the PC1 and PC2 variables (Supplementary Figure 2). There was no difference in richness considering the PC1 and PC2 variables (null model: $p = 0.50$), i.e., richness did not differ across the habitat gradient. Despite that, total abundance was positively affected by shrub cover and negatively by herb cover (PC2), with an average increase of 18% in abundance per unit of PC2 ($p < 0.001$).

For the relative abundance (for species with $n > 10$ captures), the rodents *Calomys tener* ($p < 0.001$) and *Clyomys laticeps* ($p = 0.01$) were positively associated with herb cover. The estimated average increase in the relative abundance of *Calomys tener* in areas with high herb cover was 80.7% per PC1 unit ($p < 0.001$). On the other hand, *Clyomys laticeps* showed an average decrease of 74% per unit of PC2 ($p = 0.004$), which indicates a high positive relation with herb cover and a negative relation with shrub cover. *Cerradomys scotti* ($p = 0.015$) and *Oligoryzomys nigripes* ($p = 0.02$) were the species positively associated with shrub cover, with an average increase of 45% and 51.8% ($p = 0.02$) in their relative abundance per unit of PC2, respectively. *Oligoryzomys mattogrossae* was associated with both herb and shrub habitats ($p < 0.001$), with an estimated average increase of 53% ($p = 0.04$) in herbaceous areas and 58% in shrub units ($p < 0.001$). The marsupial *Didelphis albiventris* was positively related with tree and shrub cover ($p < 0.001$), with an average increase of 67.3% in its abundance in forest areas, and 18% for shrublands. The marsupial *Gracilinanus agilis* and the rodent *Hylaeamys megacephalus* were not influenced by PC1 and PC2 in their relative abundances ($p = 0.14$ and 0.58, respectively).

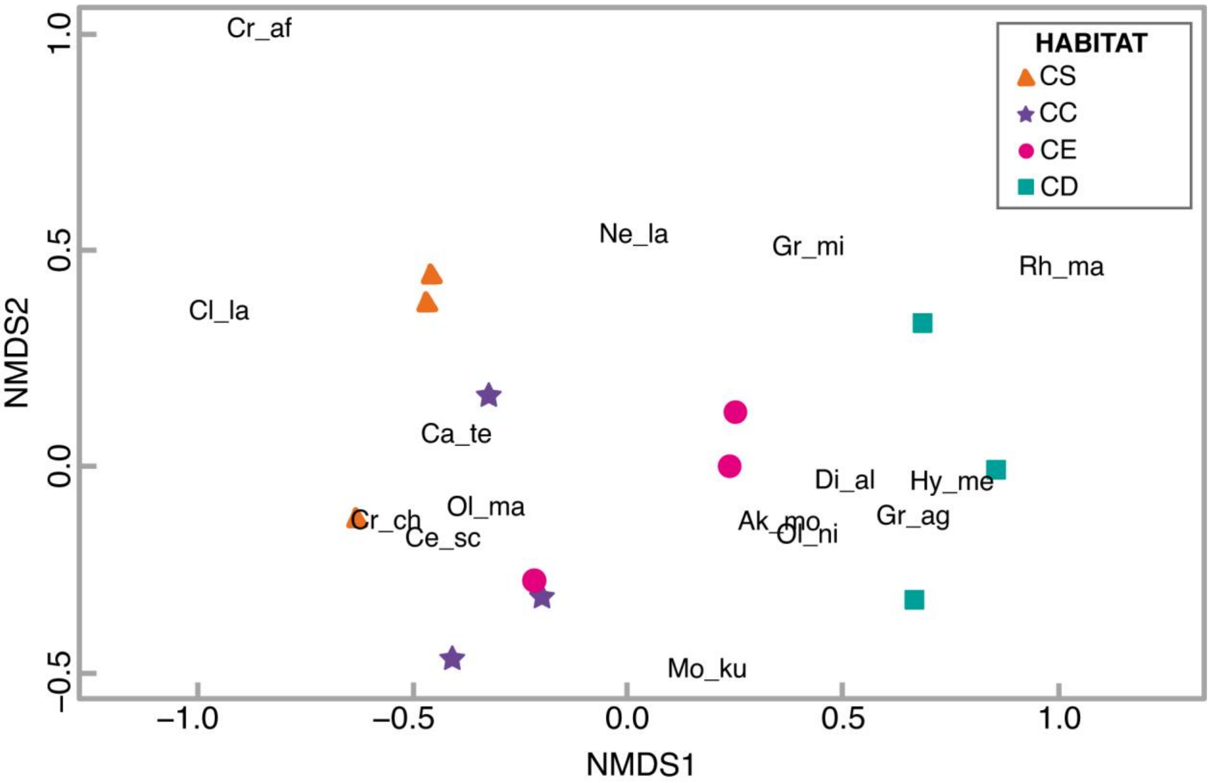


Figure 3. Non-metric multidimensional scaling (NMDS) for small mammal abundances during the 2017-2018 survey. Small mammal species are: Ak_mo: *Akodon* cf. *montensis*; Ca_te: *Calomys tener*; Ce_sc: *Cerradomys scotti*; Cl_la: *Clyomys laticeps*, Cr_ch: *Cryptonanus chacoensis*; Cr_af: *Cryptonanus* aff. *chacoensis*; Di_al: *Didelphis albiventris*; Gr_ag: *Gracilinanus agilis*; Gr_mi: *Gracilinanus microtarsus*; Hy_me: *Hylaeamys megacephalus*; Mo_ku: *Monodelphis kunsi*; Ne_la: *Necromys lasiurus*; Ol_ma: *Oligoryzomys mattogrossae*; Ol_ni: *Oligoryzomys nigripes*; Rh_ma: *Rhipidomys* cf. *macrurus*. The habitats are: CS: '*campo sujo*'; CC: '*campo cerrado*'; CE: '*cerrado sensu stricto'*; and CD: '*cerradão*'.

3.3.3. Woody Encroachment

Our linear model showed an increase of 0.1 on the EVI mean between the 2003 and 2018 survey (R^2 adj. = 0.26, $F_{1,14} = 6.38$, p = 0.02). This result indicates an increase in vegetation density of 27.4% in 15 years, affecting primarily the open areas (Figures 4 and 5A). The linear model for EVI regarding the habitat types demonstrated a clear difference in its EVI mean values (R^2 adj. = 0.62, $F_{4,11} = 7.1$, p = 0.004, Figure 5B), with the open habitats ('*campo limpo*', '*campo sujo*' and '*campo cerrado*') not different considering their EVI mean values, despite following a gradual increase on averages (0.30, 0.36 and 0.41, respectively). However, for the intermediate habitat, '*cerrado sensu stricto'*, we estimate an increase of 46.6% on the EVI mean value compared to the more open habitat ('*campo limpo*'), with an EVI mean value of 0.44. For the forest formation, '*cerradão*', the model estimated a difference in the EVI mean value of 70% higher in relation to the '*campo limpo'* area, reaching the highest EVI mean value, 0.51 (Figure 5B).

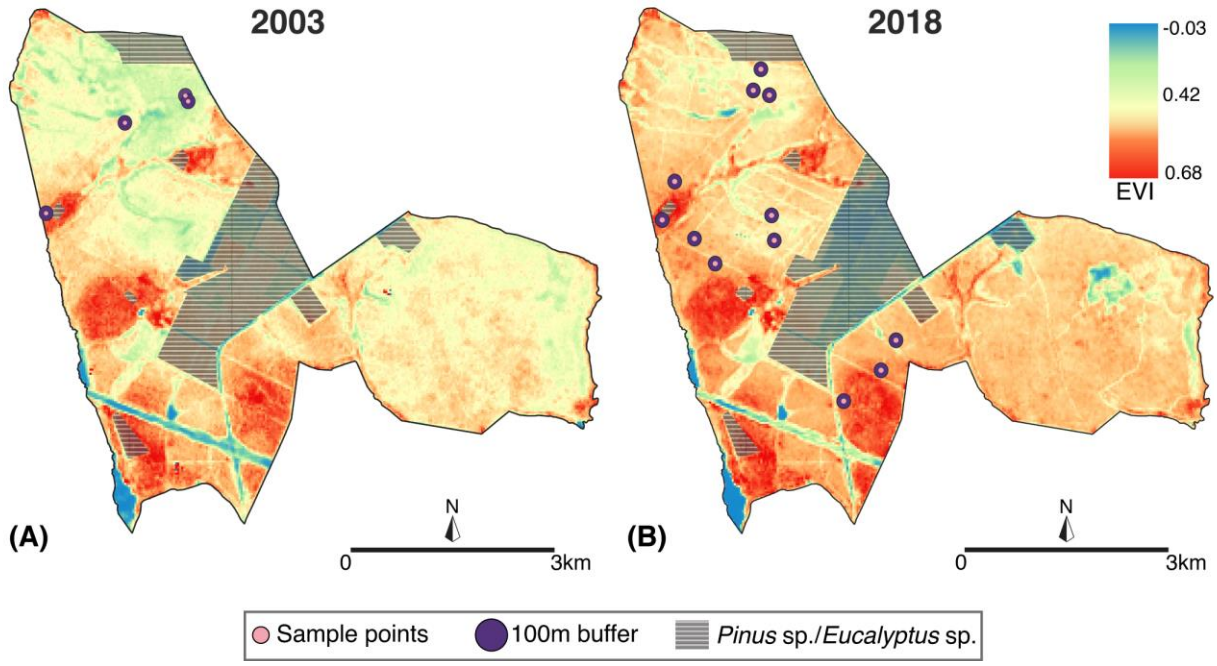


Figure 4. Variation in the enhanced vegetation index (EVI) between the sampling periods of **(A)** 2003 and **(B)** 2018 for the study area, Santa Barbara Ecological Station (SBES), São Paulo, Brazil. Dots indicate the location of sampling units.

The richness of small mammals was not affected by the increase in wood density (p = 0.39). We also tested the richness per mammal order, and obtained the same results, with no difference in richness as a function of EVI mean (Rodents: p = 0.27; Marsupials: p = 0.90). The total abundance of small mammals, on the other hand, was negatively affected by an increase in wood density (p = 0.02, Figure 6A), and for the rodents alone a similar result was obtained (p = 0.01, Figure 6B). However, the total abundance of marsupials was not affected by changes in mean EVI (p = 0.61). We also fitted models excluding captures of *Necromys lasiurus* (due to its dominance in the 2003 survey), and the null models were selected for total and rodent abundances (Total community: p = 0.17; Rodents: p = 0.06).

Among the species with at least 10 individuals captured, the rodents *Calomys tener*, and *Oligoryzomys mattogrossae* seemed to be unaffected by the increase in EVI mean values (p = 0.44 and 0.20, respectively). The marsupial *Cryptonanus chacoensis* and the rodents *Cerradomys scotti* and *Necromys lasiurus* were negatively affected by the local woody encroachment, with a decrease in their abundances related to higher mean EVI (p = 0.001, < 0.001 and 0.01, respectively, Figures 6C, 6E and 6G). The marsupial *Didelphis albiventris* and the rodent *Oligoryzomys nigripes* were positively affected by increases in EVI mean (p = 0.001 and p < 0.001, respectively, Figure 6D and 6F).

The Beta diversity analysis showed high dissimilarity between the 2003 and 2018 surveys (β_{total}= 0.84), which is explained by the replacement of species (β_{repl}= 0.84 and β_{rich}= 0). The composition in the 2018 survey presented an increase of four species compared to the 2003 survey, *Didelphis albiventris*, *Gracilinanus agilis*, *Hylaeamys megacephalus* and *Rhipidomys* cf. *macrurus*, most of them associated with the '*cerradão*', a forest formation (Figure 3).

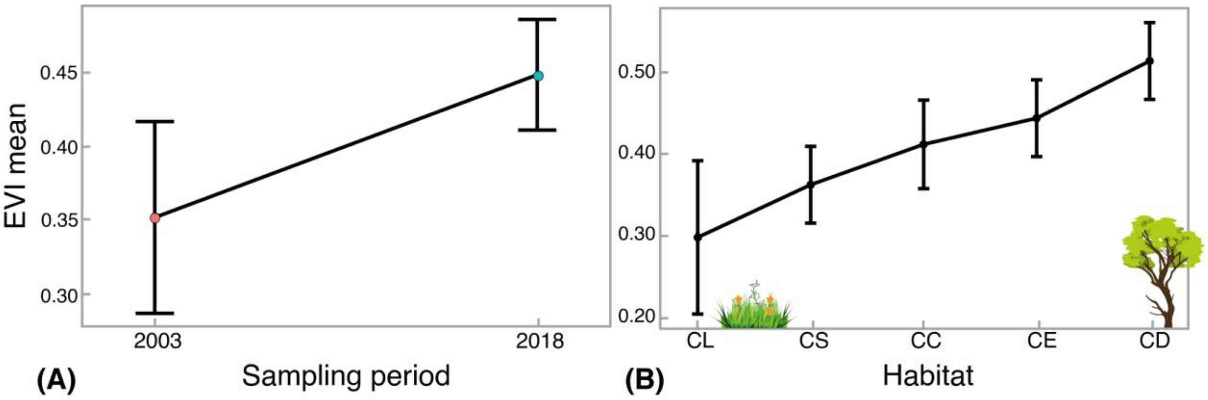


Figure 5. Means of enhanced vegetation index (EVI) and standard deviation estimated by linear models for **(A)** sampling periods and **(B)** Cerrado habitats. The habitats are: CL: '*campo limpo*'; CS: '*campo sujo*'; CC: '*campo cerrado*'; CE: '*cerrado sensu stricto'*; and CD: '*cerradão*'.

3.4. Discussion

We found that SBES small mammal community is structured by the main microhabitat characteristics associated with the different habitats, including herb and canopy cover, and shrub and tree density. This community is responding to the advancing woody encroachment in the area through time. Our models indicated that such changes are predictable, with species typical of open-vegetation habitats (such as *Cryptonanus chacoensis* and *Cerradomys scotti*) showing declines while forest-dwellers (such as *Didelphis albiventris* and *Oligoryzomys nigripes*) are increasing in abundance. Therefore, woody encroachment is changing this community structure in predictive ways and creating "winners and losers", which turn on an alert about the future of open-area specialists in face of the Cerrado encroachment.

3.4.1. Small Mammal Community Structure

A high diversity of small mammals was found in our study area. We recorded at SBES 15% of the 113 native small mammal species from Cerrado (Mendonça et al., 2018; Fegies et al., 2021). The total richness observed (17 species) is high, given that only about 8% of the Cerrado small mammal communities are composed of more than 10 species (Mendonça et al., 2018), evidencing the completeness of the surveys in SBES. Rodents were the richest order, a recurrent pattern (Quintela et al., 2020; Abreu et al., 2021), with five sigmodontine rodents representing 74% of the total abundance in the SBES assemblage (*Oligoryzomys nigripes*, *O. mattogrossae*, *Calomys tener*, *Cerradomys scotti* and *Necromys lasiurus*). The general abundance pattern recorded for SBES is also in accordance with previous Cerrado studies (see Mendonça et al., 2018 review), with *Necromys lasiurus* being the dominant species in the 2003 survey, and *O. nigripes* in the 2017-2018 survey.

Although based on different sampling design and effort, the two temporally spaced surveys showed high values of sampling coverage, both for the total assemblages, and for each similar habitat surveyed, allowing general comparisons between the community structure patterns found. While the 2003 survey were characterized by lower species richness, the habitats with higher observed and estimated richness were the grasslands (‘*campo limpo*’ and ‘*campo sujo*’) and the savanna (‘*cerrado sensu stricto*’), with the forest ‘*cerradão*’ being the poorest habitat. On the other hand, the higher species richness found in the 2017-2018 survey was evenly distributed among grasslands (‘*campo sujo*’), savannas (‘*cerrado sensu stricto*’) and ‘*cerradão*’, but with ‘*campo cerrado*’, a grassland habitat, showing lower species richness. Moreover, the seven additional species recorded in the 2017-2018 survey are mostly associated with denser covered habitats, such as savannas and forests, as is the case of *Didelphis albiventris*, *Gracilinanus agilis*, *Hylaeamys megacephalus*, and *Rhipidomys* cf. *macrurus* (e.g., Santos-Filho et al., 2012; Carmignotto et al., 2014; 2019; this study). Indeed, two species typical of Atlantic Forest (*G. microtarsus* and *Nectomys* cf. *squamipes*), which also occur in southern and eastern Cerrado, especially using gallery forests, seasonal forests and ‘*cerradão’* patches (Costa, 2003; Carmignotto et al., 2012), were only represented in the 2017-2018 survey.

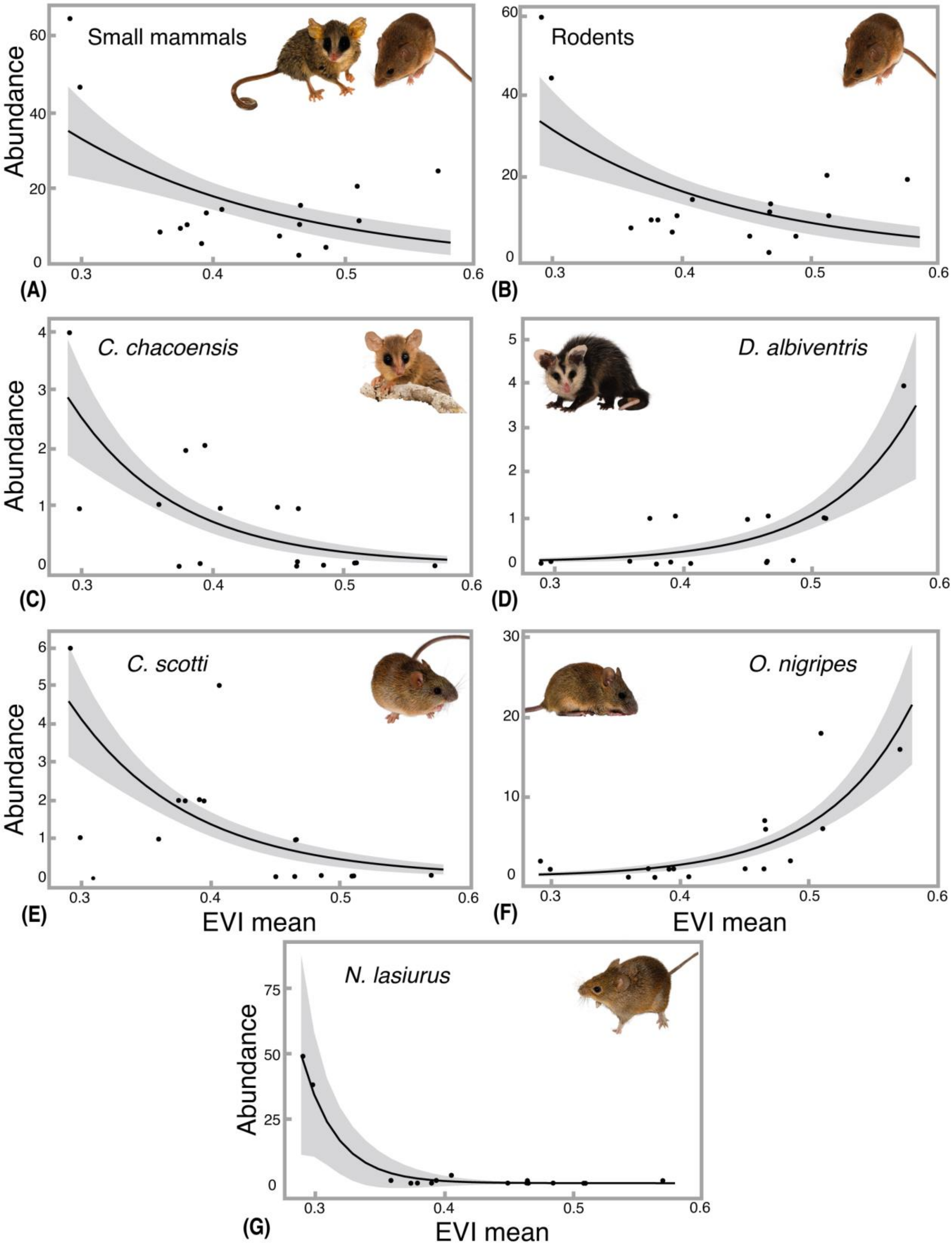


Figure 6. Predicted effect of mean EVI on the **(A)** total abundance of small mammals, **(B)** abundance of rodents, and abundance of different species: **(C)** *Cryptonanus chacoensis*, **(D)** *Didelphis albiventris*, **(E)** *Cerradomys scotti*, **(F)** *Oligoryzomys nigripes*, and **(G)** *Necromys lasiurus* estimated by generalized linear models for the sampling units in SBES. The shadows represent the 95% confidence intervals. All photos by Bruno Ferreto Fiorillo.

Regarding species abundances, we observed that in the 2003 survey, the most abundant species were also represented by grassland and savanna species. Although *Necromys lasiurus* is considered a habitat generalist (Vieira et al., 2005; Ribeiro et al., 2019), in Cerrado it prefers open habitats, represented by grasslands and savannas (Becker et al., 2007; Carmignotto et al., 2019). A similar pattern was found for *C. scotti* and *O. mattogrossae* (Henriques et al., 1997; Vieira et al., 2005; Weksler and Bonvicino, 2015). In the 2017-2018 survey, in turn, the most abundant species, the rodent *O. nigripes*, is more associated with savanna and forests (Weksler and Bonvicino, 2005; 2015). Moreover, some species that were more abundant in the 2003 survey, became rare in 2017-2018, such as the grassland specialist *Cryptonanus* aff. *chacoensis* (Fegies et al., 2021). Vegetation shifts may trigger shifts in small mammal abundance (Loggins et al. 2019), but other factors, such as resource availability, reproductive activity, presence of competitors (Verberk, 2011), may also play a role. Since several of our comparisons were made between 2003 and 2017-2018 surveys controlling for the period of sampling (January-February), we believe we were able to reduce the influence of some of these confounding factors in our results.

3.4.2. Habitat and Microhabitat Use

Cerrado small mammals present high habitat association, contributing with the well-known pattern of open (grasslands and savannas) versus forest specialists found across this ecoregion (e.g., Alho, 2005; Carmignotto et al., 2012). The SBES assemblage also fits into this pattern, showing open and forest specialists as well as generalists (occupying both open and forest habitats). Considering habitat use, the 2003 survey was mostly represented by open-habitat species, with few generalists. In the 2017-2018 survey, we observed an increase in generalists and forest specialists. Despite the maintenance of grassland specialists between surveys, two species (*Cryptonanus* aff. *chacoensis* and *Clyomys laticeps*) were restricted to the most open habitat currently present at SBES (‘*campo sujo*’), indicating a strong association with open grasslands (Carmignotto et al., 2014; Bezerra and Bonvicino, 2015; Bezerra et al., 2016; Fegies et al., 2021).

The microhabitat preference of species corroborates the results found at a larger, habitat scale in our study. For instance, *Calomys tener* and *Clyomys laticeps* show a higher association with high herbaceous cover (Carmignotto and Aires, 2011; Rocha et al., 2011; Bezerra et al., 2016). For *Clyomys laticeps*, however, our models indicate a negative relationship with high shrub cover, highlighting the dependence of this species on open grasslands (Vieira, 2003; Bezerra and Bonvicino, 2015). Other rodents (*Cerradomys scotti*, *Oligoryzomys nigripes* and *O. mattogrossae*) were positively affected by shrub density. *Cerradomys scotti* and *O. mattogrossae* are open-habitat species, exhibiting a preference for grassland areas with higher shrub cover (Vieira et al., 2005). *Oligoryzomys nigripes*, however, is known to be associated with forest habitats, such as gallery forest in the Cerrado (Weksler and Bonvicino, 2005). Our findings are in accordance with these results since most captures were recorded in the '*cerradão*'. Püttker et al. (2008) also reported a higher association of this species with areas with low canopy and dense understory in the Atlantic Forest. *Didelphis albiventris*, on the other hand, seems to benefit from increasing canopy cover and tree density, agreeing with previous studies where its presence was related to fallen logs and shrub (*Piper* sp.) density (Melo et al., 2013). *Gracilinanus agilis* and *Hylaeamys megacephalus* showed no clear response to the microhabitat variables tested, and their presence should be due to other factors not considered in our study, such as resource abundance or disturbances (Verberk, 2011; Loggins et al., 2019). These results highlight the importance of evaluating habitat use at different scales to better understand the potential reasons behind differential occurrence of small mammal species across the Cerrado, and to reinforce why some species would be favored or disfavored in a woody encroachment scenario.

3.4.3. Woody Encroachment

We observed an increase in vegetation density in SBES throughout the 15 years between the two surveys analyzed (from 2003 to 2018), corroborating that woody encroachment may be a common phenomenon in the Cerrado (e.g., Moreira, 2000; Roitman et al., 2008; Pinheiro and Durigan, 2009; Abreu et al. 2017; 2021). The 27% increase in the mean EVI affected primarily the grasslands. Indeed, the '*campo sujo'* surveyed in 2018 were located at the same areas previously classified as '*campo limpo*' in the 2003 survey, clearly showing a shift in vegetation with the increase in density of shrubs and small trees (see also Melo and Durigan, 2011). Overall, the small mammal species richness was not affected by the woody encroachment observed in the study area, but the total abundance was negatively related to the increase in mean EVI, as observed for other plant and invertebrate groups studied at SBES (Abreu et al., 2017). Indeed, our results show a clear negative effect of woody encroachment on the density of rodents, but not for marsupials. This is expected since most marsupials are associated with savannas or forest habitats due to their scansorial and arboreal habits (Astúa, 2015). Rodents have shown a two-way relationship with vegetation thickening in other open regions. On one hand, they can contribute to seed removal and consequently decrease woody density at habitats in the initial phase of encroachment, as recorded for open habitats of Africa, Argentina, and Australia (Busch et al., 2012; Bergstrom, 2013; Teman et al., 2021). On the other hand, they can be negatively affected by the encroachment, which impacts their ecological features, such as reducing predator detection, habitat use and local persistence (Loggins et al., 2019), similar to what our results have indicated here. Our results for total and rodent abundance may have been influenced by the high number of *Necromys lasiurus* individuals in the 2003 survey. When we excluded this species from the analyses, no influence of woody encroachment for small mammals and rodent abundance was detected. Thus, these results should be carefully interpreted due to this outlier influence and low sample size, and additional sampling should be made to confirm our interpretations.

Regarding the seven most abundant species, two open-habitat specialists (*C. tener* and *O. mattogrossae*) were not affected by woody encroachment. These species can occupy a wide range of open habitats, from grasslands to savannas in the Cerrado (Carmignotto et al., 2014; Salazar-Bravo, 2015; Weksler et al., 2017; Bezerra et al., 2020). This pattern indicates plasticity in their habitat use. On the other hand, the open-habitat specialists *Cryptonanus chacoensis, Cerradomys scotti* and *Necromys lasiurus* were negatively affected by woody encroachment, indicating a dependence on grasslands formations at SBES. The negative impacts of woody encroachment on species of the genus *Cryptonanus* are expected, since its diversification is highly associated with the open habitats of the Cerrado (Fegies et al., 2021). In fact, SBES shelters a sympatric species, *Cryptonanus* aff. *chacoensis,* considered rare and endemic of Brazilian Cerrado, which may face even more severe impacts by the woody encroachment (Fegies et al., 2021). *Cerradomys scotti* showed a slight preference for shrubby habitats in our microhabitat analyzes, which is in accordance with the negative response to the tree encroachment found here, a pattern previously observed by Vieira et al. (2005), where this species was related to grass height but not to arboreal cover. In fact, there seems to be a tenuous line for species that may benefit from shrub cover due to protection against predation, and also may be negatively affected by a decrease in food resources, since several species uses herbaceous sources for feeding (Vieira et al., 2005; Ribeiro et al., 2019), which, in turn, decrease with shrub encroachment, as shown for small mammals in African shrub-invaded grasslands (Loggins, et al., 2019).

The rodent *Necromys lasiurus* also showed a decrease in abundance between 2003 and 2017-2018 potentially due to woody encroachment, since it is associated with open and grassy areas (Vieira et al., 2005; Becker et al., 2007; Rocha et al., 2011). This species was the most abundant in open areas in 2003 but among the rarest ones in 2018, extending its distribution to savanna habitats, its preferred habitat in other studies (Henriques and Alho, 1991), indicating its habitat plasticity within open formations. Our results show that *Cryptonanus chacoensis* and *Cerradomys scotti* may not persist in areas with woody encroachment if grasslands disappear. Meanwhile, forest-specialists and opportunistic species seem to benefit from woody encroachment at the SBES. *Didelphis albiventris*, although considered a habitat generalist (Cáceres et al., 2012), was not captured in the 2003 survey, but in 2018 became the most abundant marsupial in the assemblage. This didelphid was also the only species that was positively associated with microhabitats with higher tree density, which corroborates its fostering by woody encroachment. The rodent *Oligoryzomys nigripes* was also favored by the encroachment, and its higher association with forest habitats may allow its spread in habitats with higher woody density (Weksler and Bonvicino, 2015). Mammals across savannas worldwide are differently influenced by vegetation encroachment (Stevens et al., 2016a), but they seem to be more sensitive than other vertebrates, such as birds, due to their specialized habitat preferences and foraging strategies. Turnover in species composition following woody encroachment is also recorded in African savannas, with browser mammals replacing grazers (Smit and Prins, 2015), pointing to woody encroachment as a general concern across savannas.

Our models indicate shifts in species abundance across time, with such changes being predictable to some extent. Species typical of grasslands show declines, while forest-dwellers are increasing in abundance. In the case of forest-savanna ecotone regions, climate, and land-use change, especially fire and deforestation, are leading to an invasion of savanna species into disturbed forests, shifting the forest fauna assemblages towards a “savannization” (Sales et al., 2020). Similarly, the woody encroachment is changing southern Cerrado assemblages towards a “forestization”, with the invasion of species from adjacent forest biomes and the loss of savanna specialists (Abreu et al., 2017; 2021). Our findings highlight the importance of the maintenance of the mosaic of open formations in Cerrado remnants in order to shelter a high diversity of small mammal grassland specialists. Species that showed a clear decline and high association with open vegetation structure in fact can become locally extinct, consequently altering species range, since these areas are mainly located at Cerrado boundaries. This may be particularly true for Cerrado endemics and regionally vulnerable species such as *Clyomys laticeps* and *Cerradomys scotti* (Percequillo et al., 2008; São Paulo, 2018), besides a rare and still undescribed species (*Cryptonanus* aff. *chacoensis*; Fegies et al., 2021). In fact, the SBES was created with the goal to protect the open formations of the southern Cerrado, but 30 years of fire suppression are probably the main cause of the local woody encroachment and the resulting changes in biodiversity (Abreu et al., 2017; 2021). Fire management is considered a key tool to maintain open savannas and its associated diversity, and the current fire experiments at SBES so far demonstrate no loss in small mammal diversity with prescribed fire (Durigan et al., 2020). Without active management of the landscape to keep open habitats, the long-term maintenance of the open-habitat specialists (with special attention to the rarest ones) will give place to an increasing replacement by forest specialists and habitat generalists in the SBES small mammal community and in other remnants in the southern portion of the Cerrado. Woody encroachment needs to be treated as a global scale problem to natural open ecosystems (Stevens et al., 2016a), and its impacts on biodiversity at local scales should continue to be investigated in order to guarantee the conservation of savanna and grassland biodiversity.

Author Contributions

APC, AVC, and MM conceived this study and designed the methodology. APC, PRL, GRF, and LOF collected the data. LOF performed the statistical analysis and led the manuscript writing. APC, AVC, LOF and MM interpreted results and contributed to the writing and reviews. All authors gave final approval for submission.

Funding

AVC was funded by Neotropical Grassland Conservancy, MM and APC was funded by FAPESP grants #2015/21259-8, #2018/14091-1 and #2020/12658-4, APC was also funded by FAPESP grants #98/05075-7 and #00/06642-4, and LOF was funded by CAPES - Finance Code 001.

Acknowledgments

We are grateful to the Santa Barbara Ecological Station management team, especially Marcos Pestana, and Instituto Florestal for all the support during the field campaigns. We are also thankful for Bárbara Armando Godinho, Bruna de França Gomes, Bruno Ferreto Fiorillo, Carolina Farhat, Carolina Henkes Inamassu, Evelin de Campos da Costa, Giordano Novak Rossi, Guilherme Zamarian Rezende, Jairo Roldan, Jorge Henry Maciel, Julia dos Santos Gutierres, Karine Yumi Tominaga, and Mirela Alcolea assistance in data collection; for Bruno Ferreto Fiorillo kindly providing the small mammal photos; for João Paulo dos Santos Vieira-Alencar and Carolina Freitas Schlosser help with the EVI values extraction; and for Yohann Freddi assistance with the software programs. We also thank Giselda Durigan and Alexandre Reis Percequillo for valuable suggestions to this study. The illustrations from Figure 5 were modified from vectors designed by Freepik. The collection permit was issued by Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio) #50658-1. The authors have no conflict of interest to disclose.

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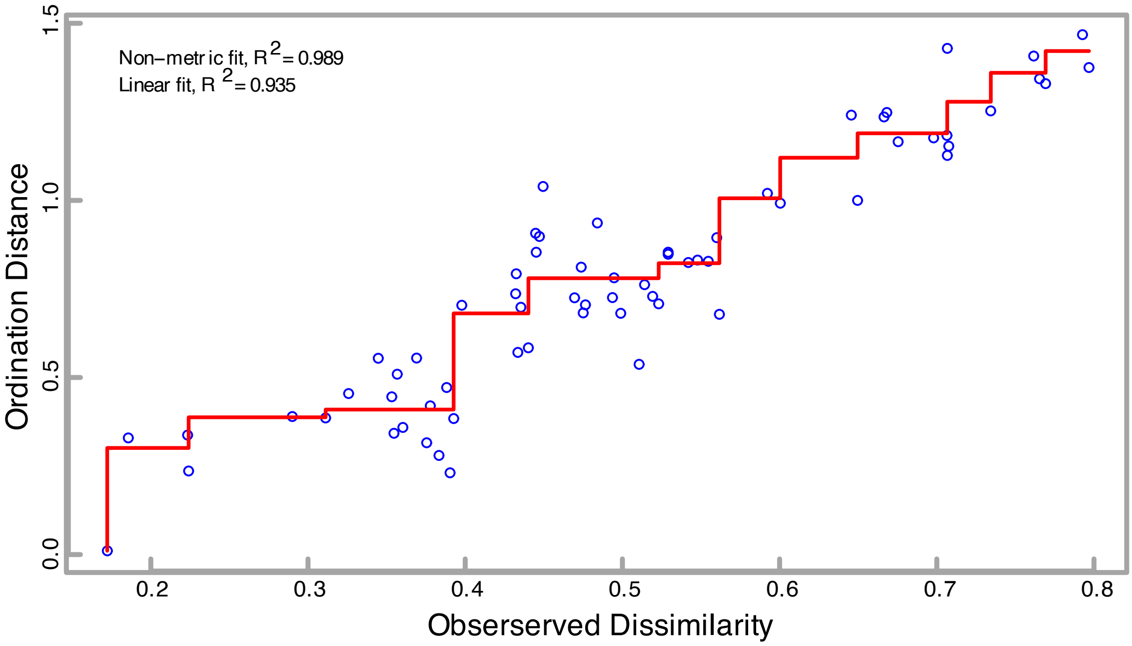
Supplementary Material

Habitat and Microhabitat use

NMDS Analysis



Supplementary Figure 1. Shepard plot (stress plot) for the NMDS analyses based on the 2017-2018 small mammal abundances at each habitat surveyed at SBES. This plot was obtained using the *stressplot* R function.

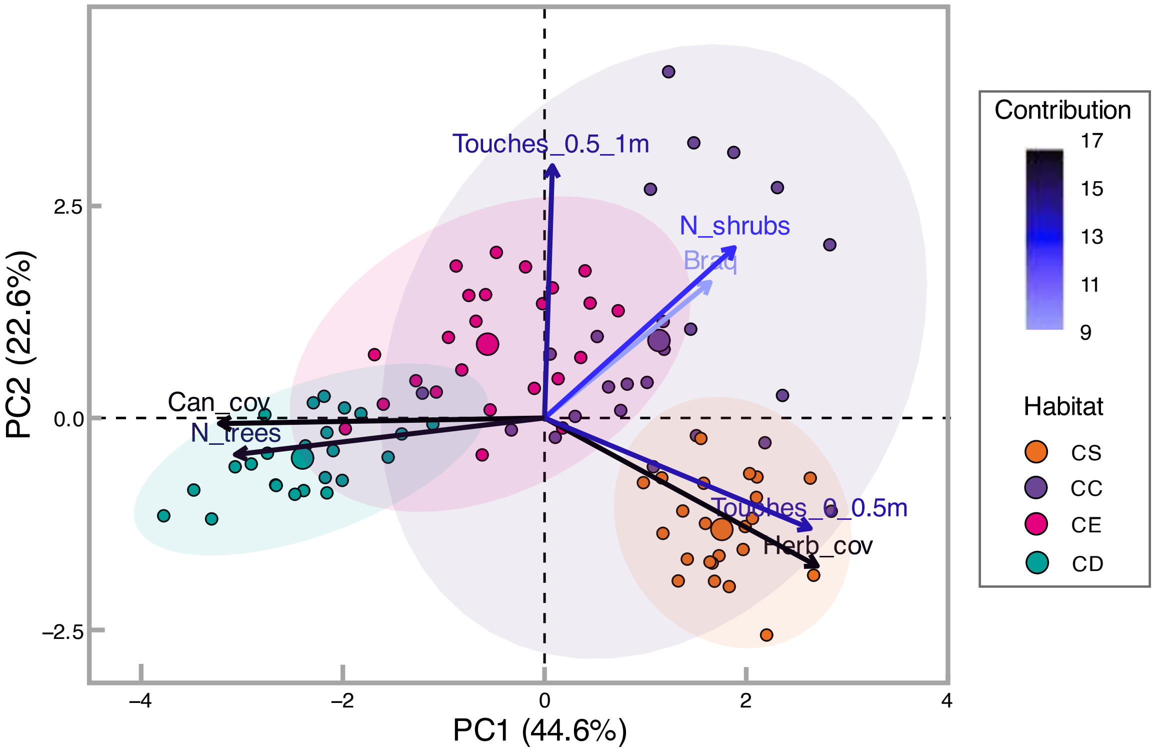
PCA Analysis

Supplementary Table 1. Eigenvalues and variance percentage for each eigenvector from the Principal Component Analysis.

Eigenvectors	Eigenvalues	Variance (%)
PC1	3.12	44.6
PC2	1.58	22.6
PC3	0.84	12
PC4	0.55	7.9
PC5	0.37	5.4
PC6	0.31	4.4
PC7	0.22	3.1

Supplementary Table 2. Microhabitat variables loadings for each eigenvector from the Principal Component Analysis. The highest positive and negative loadings for the first and second principal components are highlighted.

Microhabitat variables	Eigenvectors						
	PC1	**PC2**	**PC3**	**PC4**	**PC5**	**PC6**	**PC7**
N touches_0-0.5 m	**0.42**	**-0.29**	0.32	-0.32	0.56	0.47	0.02
N touches_0.5-1 m	0.01	**0.66**	0.16	-0.71	-0.03	-0.16	-0.06
Canopy cover	**-0.51**	-0.01	0.19	0.05	0.16	0.18	-0.80
Herb cover	**0.43**	**-0.39**	0.03	-0.15	-0.03	-0.69	-0.42
Urochloa sp. cover	0.26	**0.35**	0.72	0.52	-0.01	-0.12	0.00
N shrubs	**0.30**	**0.44**	-0.54	0.30	0.54	-0.05	-0.21
N trees	**-0.48**	-0.09	0.16	-0.01	0.61	-0.48	0.36

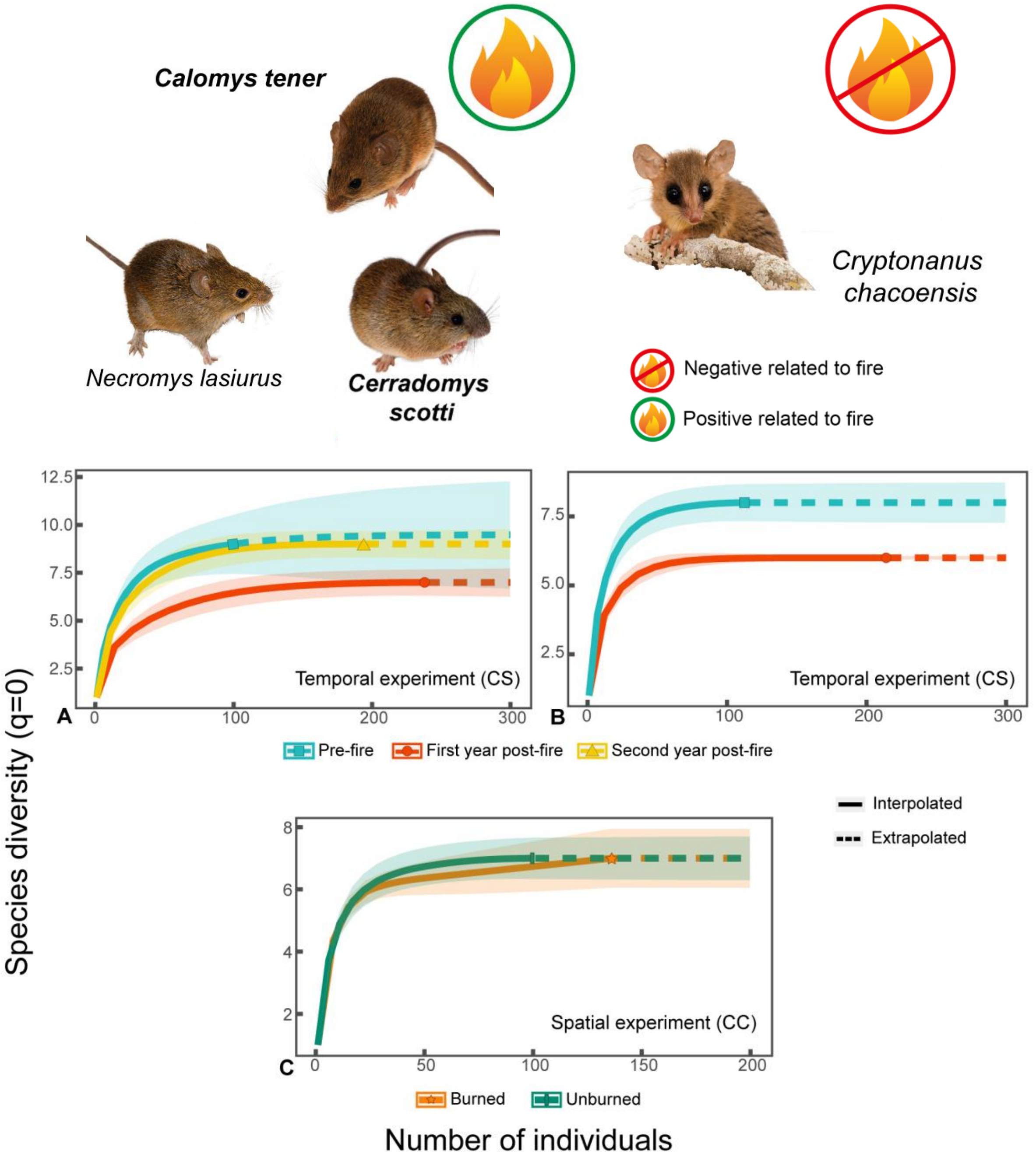


Supplementary Figure 2. Contribution of the microhabitat variables in the PC1 and PC2 axis, with the grouping of sampling units (dots) for the Cerrado habitats sampled during the 2017-2018 survey at SBES. The microhabitat variables are expressed as: Can_cov: percentage of canopy cover; N_trees: number of trees with diameter at breast height (DBH) > 10 cm; Herb_cov: percentage of herbaceous soil cover; Braq: percentage of soil cover by the invasive grass, *Urochloa* sp.; N_shrubs: number of stems of shrubs that branch up to 1 m in height; Touches_0_0.5m: number of touches on a stick up to 0.5 m; and Touches_0.5_1m: number of touches on a stick within 0.5 to 1 m. The habitats are: CS: '*campo sujo*'; CC: '*campo cerrado*'; CE: '*cerrado sensu stricto'*; and CD: '*cerradão*'.

Datasets and diagnoses of linear models

Supplementary Table 3. Datasheet with all the datasets used for this study (tabs 1-3). The sampling points coordinates are presented in tab 5. The results of the diagnoses tests for the linear models are presented in the last tab.

4. CAPÍTULO II – PRESCRIBED FIRES IN A NEOTROPICAL SAVANNA: RESPONSES OF A SMALL MAMMAL COMMUNITY



Furtado, L. O., Martins, M., & Carmignotto, A. P. (to be submitted). Prescribed fires in a Neotropical Savanna: responses of a small mammal community.

– CAPÍTULO II –

Prescribed fires in a Neotropical savanna: responses of a small mammal community

Abstract

Fire management is considered a valuable tool to conserve biodiversity in fire-prone ecosystems. Small mammals are sensitive to habitat alteration and are good bioindicators of environmental changes. Herein, we surveyed a small mammal community at the southeastern boundary of Cerrado (Santa Bárbara Ecological Station) from 2017 to 2020. We investigated the effects of a low intensity prescribed fire event on species diversity (richness and relative abundance) in two experiments - Temporal, i. e., before and after the fire, and Spatial, i. e., control and burned area - at grassland formations using pitfall and live traps to capture small mammals. We expected major differences in community structure right after the fire, with a decrease in the diversity parameters, but a rapid recovery and no loss in diversity after a few months post-fire. We assessed the effects of fire on small mammal communities through generalized linear models. We also evaluated the importance of microhabitat variables related to herbaceous, shrub, tree and *Urochloa* sp. cover regarding the vegetation recovery after the fire for small mammal diversity. The Temporal experiment showed a significant decrease in marsupial species richness and an increase in rodent abundance, mostly for open-area inhabitants (e.g., *Calomys tener*, *Cerradomys scotti* and *Necromys lasiurus*), after the fire. On the other hand, the Spatial experiment provided no major differences in community structure between burned and unburned areas. Despite that, in both experiments marsupials were negatively affected (e.g., *Cryptonanus* species). Fire also altered the microhabitat preferences of some rodents, such as *C. tener* and *Clyomys laticeps*. We found that prescribed fires can affect the small mammal community in a heterogeneous way, depending on species-level features, such as a relationship with vegetation structure. A strategy towards maintaining a mosaic of unburned and burned patches seems to lead to no significant losses of small mammal communities in fire-prone grasslands and may promote local diversity. Prescribed burning of open formations may be needed to maintain open-area species diversity in the Cerrado.

Keywords: Rodentia; Didelphimorphia; Cerrado; Grasslands; Fire management.

4.1. Introduction

Fire-prone ecosystems such as tropical savannas have evolved for millions of years with frequent burns that shaped part of its ecological dynamics and acted as an important driver for their biodiversity (Bond and Keeley, 2005; Simon et al., 2009; He et al., 2019). Fire acts by controlling the system biomass, promoting herbaceous growth and reproduction, and killing stalks of young trees (Parr et al., 2014; Pilon et al., 2018). Burn characteristics such as intensity, frequency, and extent, and the resilience of the local species can determine the benefits and costs of a fire event (Bond and Keeley, 2005; Bowman et al., 2016). Unfortunately, the historical fire regimes established in these ecosystems are being changed by humans (Archibald, 2016; Bowman et al., 2016). Even in fire-prone adapted ecosystems, large and intense fires can destroy and disrupt the system, leading to biodiversity loss (Fidelis et al., 2018; 2020). On the other hand, open formations, such as grasslands and savannas, are being replaced by forests due to fire suppression (Stevens et al., 2016; Archer et al., 2017; García Criado et al., 2020). Prescribed fires are considered an important management tool to restore and maintain the ecological balance of open areas in these ecosystems (Kelly and Brotons, 2017; Durigan et al. 2020).

The use of prescribed fire for the conservation of open formations in protected areas is slowly being accepted by local managers as evidence of benefits of its use have been frequently provided by ecologists (Durigan and Ratter, 2016; Pivello, 2017). In Brazil, for example, policies of fire exclusion are implemented regardless of the specific requirements of the Cerrado ecoregion, the largest savanna and fire-prone ecosystem in South America (Durigan, 2020; Fidelis, 2020; Conciani et al., 2021). This is a result of a series of disasters associated to intense wildfires (related to deforestation and land cleaning) that have been occurring in all Brazilian ecoregions and leading to negative impacts, specially to the fire-sensitive ones such as the Amazon Forest (Fidelis et al., 2018; Pivello et al., 2021). In the case of fire-prone ecosystems, the active management with prescribed fires can mitigate the negative impacts of fire suppression by controlling woody encroachment, promoting the diversity of open specialist plant and animal species, and preventing flammable biomass accumulation that can lead to large wildfires (Durigan et al., 2020). In order to succeed, prescribed fire programs need to be grounded by local studies that evaluate the better fire regime to be used, considering all the historical and ecological specificities from each system (Kelly and Brotons, 2017; He et al., 2019).

To determine which fire regime is desirable for an ecosystem is challenging. The same fire regime applied to different places can result in different outcomes even in the same ecoregion (Kelly et al., 2016). The responses of animal communities to fire in savannas are variable and often associated with species-specific traits (Griffiths and Brook, 2014; Kelly et al., 2016; Pausas, 2019). Non-flying small mammals (rodents and marsupials) exhibit high habitat selectivity, showing a heterogeneous distribution associated with the mosaic of habitats, specially linked to vegetation structure (Carmignotto et al., 2014; Ribeiro et al., 2019; González et al., 2021). Changes in habitat structure caused by fire can lead to a shift in the composition of the local small mammal community. The responses of small mammals to fire also differ among continents, and are mostly related to habitat requirements, body size and fire features (Griffiths and Brook, 2014; Griffiths et al., 2015).

In this study, we evaluate the impacts of a prescribed fire event on small mammal community structure in grasslands in southeastern Brazilian Cerrado. We also assess the microhabitat requirements related to vegetation structure over the post fire period. We expect major differences in community structure right after the fire, with a decrease in the diversity parameters (richness and abundance), but a rapid recovery and no loss in diversity after a few months post-fire (Durigan et al., 2020). Open-area specialist species must be favored or tolerant to fire and associated with microhabitat variables such as herbaceous cover (Furtado et al., 2021). Fire-sensitive species may thus show a decrease in all diversity parameters and even disappear from burned patches, even months after the fire (Griffiths and Brook, 2014).

4.2. Material and Methods

4.2.1. Study area

The Santa Bárbara Ecological Station (SBES; 22º46′-22º51′S, 49º10′-49º16′ W, 600-680 m above sea level; Águas de Santa Bárbara municipality, state of São Paulo, Brazil, Figure 1) is located on the southern border of the largest South American savanna ecoregion, the Cerrado. SBES has a marked seasonal climate, Köppen Cfa-type, with a dry/cold season from April to September (mean annual rainfall of 429 mm and temperature of 17º C), and a wet/warm season from October to March (mean annual rainfall of 1028 mm and temperature of 24º C, Alvares et al., 2013; CIIAGRO, 2022). Overall, the maximum temperature is 35.2° C, and the minimum is 3.4° C, with an annual rainfall around 1010-2051 mm, based on data from 1993-2021 recorded by a weather station 20 km away from our study area, located in Manduri, state of São Paulo, Brazil (CIIAGRO, 2022). The SBES is among the few protected areas that preserve open savannas in the southeastern Brazilian Cerrado. Its 2,715 ha are composed primarily of native Cerrado vegetation in a gradient from open grasslands to woodland savannas, with a few Atlantic Forest patches (Melo and Durigan, 2011; Durigan et al., 2020). Soils are deep oxisols with low nutrient and elevated sand content, high aluminum saturation, and low holding water capacity (Melo and Durigan, 2011).

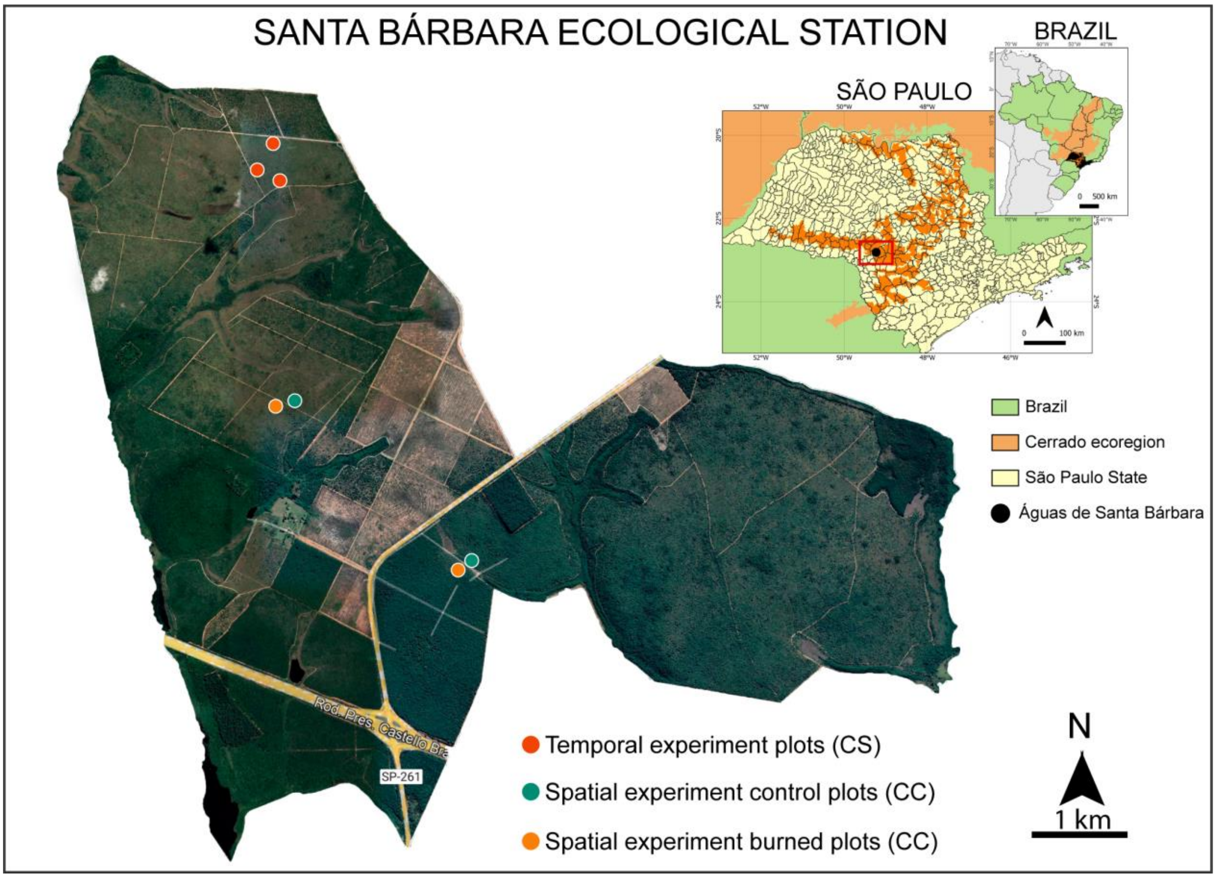


Figure 1. Santa Bárbara Ecological Station, located in the southeastern Cerrado ecoregion, in São Paulo state, Brazil. The sampling plots are indicated with color circles. The grassland formations are: CS: ‘*campo sujo*’, and CC: ‘*campo cerrado*’.

4.2.2. Fire history

The SBES is facing a local woody encroachment, associated with fire suppression policies applied in the past 30 years, with an increase of woodland formations and consequently losses of open grasslands and savannas and its specialist biota (Abreu et al., 2017; Furtado et al., 2021). Different areas of the SBES vary in the frequency of burning events across these decades, and our study comprises only grassland formations that are among the few plots that burned more recently (Durigan et al., 2020). The most open grassland formation patches (herein called ‘*campo sujo*’, a grassland with a low density of shrubs and small trees) are located on a single block that burned for the last time in 2008, with at least four fire events before that. As for the other grassland formation studied, ‘*campo cerrado*’ (grasslands with a higher density of shrubs and trees), one patch burned only once in the last 30 years, in 2011, and the second patch burned for the last time in 1964 (Melo and Durigan, 2011; Conciani et al., 2021). In these patches, we used two plots as control treatments and two as burned treatments. The burned patches have been under fire management since 2015, with two prescribed fire events before that we assessed in this study (2015 and 2016, Figure 1). More details about the historical fires in the SBES and its surrounding region, and on the application of prescribed fires can be found in Durigan et al. (2020).

4.2.3. Data sampling

4.2.3.1. Fire experiments

To assess the prescribed fire impacts on the SBES small mammals, we conducted two experiments: the Temporal experiment, i. e., before and after the fire, and the Spatial experiment, i. e., unburned and burned area. In both experiments, the grassland areas sampled were submitted to a prescribed fire event of low intensity in July 2018, promoted and managed by an Instituto Florestal research team (Figure 2C; Durigan et al., 2020).

For the Temporal experiment, we sampled the small mammal community in three sampling points of '*campo sujo*' (Figures 1 and 2A). The control data (pre-fire treatment) was collected during 12 monthly five-days field trips before the prescribed fire, between August 2017 and July 2018 (12 months), comprising an effort of 1,152 live trap-nights and 1,152 pitfall trap-nights. After the prescribed fire, in July 2018 (Figures 2C and 2D), the same areas were sampled for 20 consecutive months, from August 2018 to March 2020 (post-fire treatments), with an effort of 1,920 live trap-nights and 1,920 pitfall trap-nights. These data were separated in three treatment categories for the analysis: pre-fire, first year post-fire and second year post-fire. The comparisons were made between: (1) First year pre and post-fire treatments; and (2) The first eight months (August-March) of each treatment (pre-fire, first year post-fire and second year post-fire), to equal the sampling efforts to 1,536 trap-nights per treatment, and infer about the post fire total effects.

The Spatial experiment was performed in two sampling points of '*campo cerrado*' (Figure 2B), each comprising an unburned area (unburned treatment), and an adjacent area submitted to the prescribed fire in July 2018 (burned treatment, Figures 1 and 2E). The sampling occurred simultaneously in the two treatments (unburned and burned), from August 2018 to October 2019 (15 months), totaling 1,280 live trap-nights and 1,280 pitfall trap-nights in each treatment.

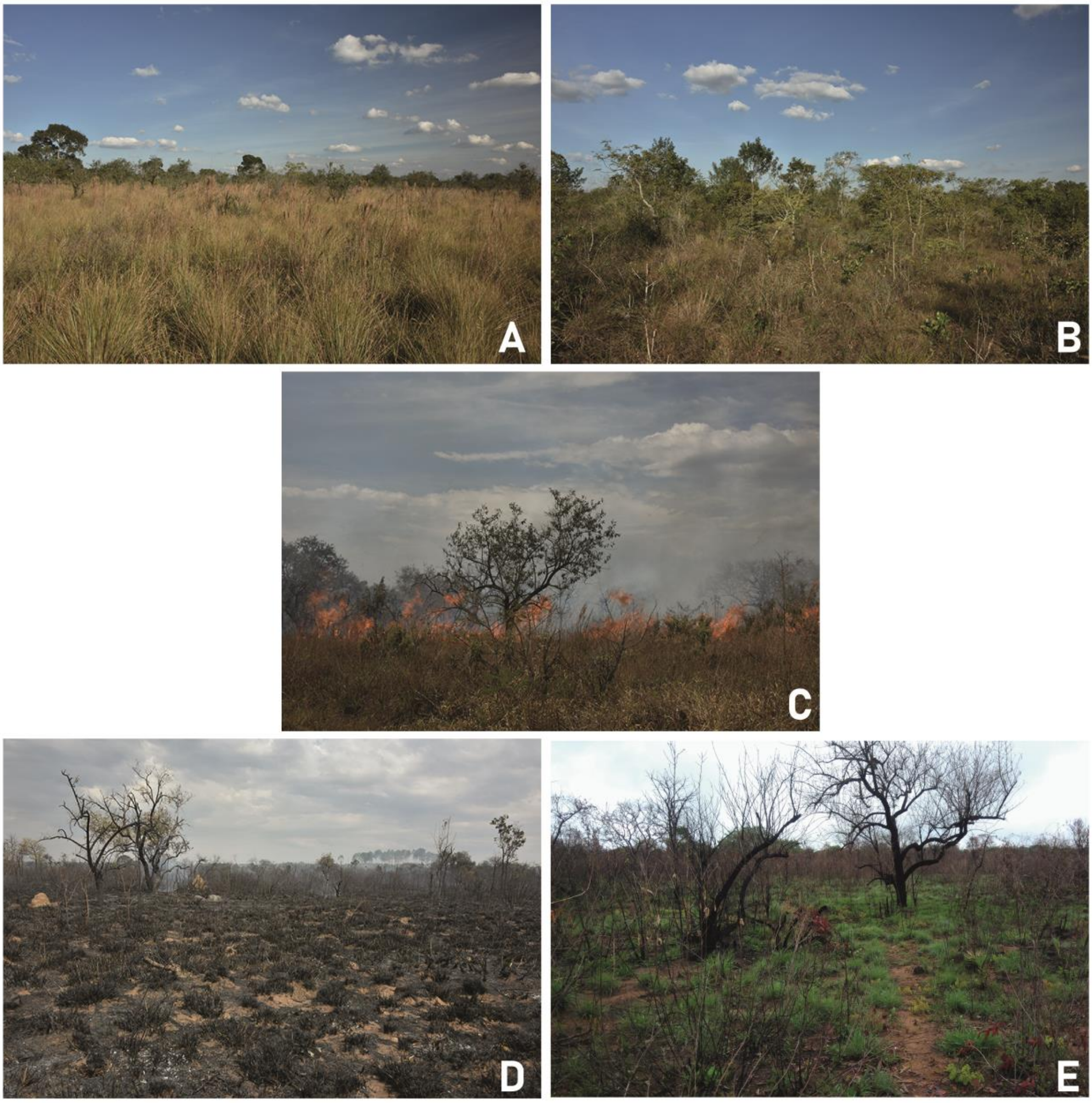


Figure 2. Grassland areas sampled in Santa Bárbara Ecological Station (SBES), Águas de Santa Bárbara, São Paulo, Brazil. **(A)** '*campo sujo'* area before the prescribed fire event (pre-fire treatment); **(B)** '*campo cerrado*' unburned area; **(C)** '*campo sujo*' plot during the prescribed fire event; **(D)** '*campo sujo*' area after the prescribed fire (post-fire treatment); and **(E)** '*campo cerrado*' burned area, one month after the prescribed fire. Photos A-D: Marcio Martins. Photo E: Luciana Furtado.

4.2.3.2. Small mammal survey

To investigate the role of the prescribed fire in the small mammal community (rodents and marsupials), we used a complementary sampling approach using live and pitfall traps (Bovendorp et al., 2017). For each sampling point, we installed one live trap and one pitfall trap transect. The live trap transect was composed of four Shermans (25 x 8 x 9 cm - ShermanTM) and four wire mesh traps (30 x 16 x 18 cm - Metal Miranda, and 32 x 20 x 20 cm, respectively), 15 m apart, distributed in two arrays 60 m apart (Figure 3). The live traps were baited with a mix of peanut butter, cornmeal, and canned sardines and set on the ground at the beginning of the survey. The pitfall transect was set 60 m apart from the live trap transect, divided in two arrays, each with four 100-L buckets connected by a 60-70 cm high and ~10 cm buried plastic drift fence, 10 m apart. The buckets were opened and closed at the beginning and end of each field trip (Figure 3).

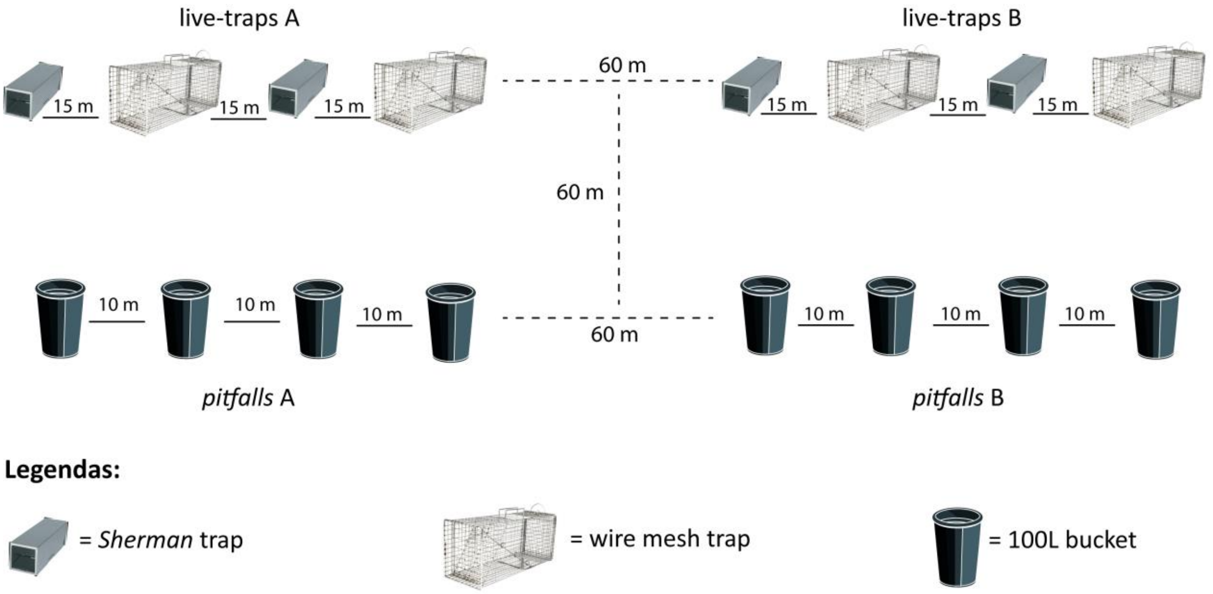


Figure 3. Distribution of trap transects and stations at each sampling point.

We identified the captured individuals at species level, when possible (Voss and Jansa, 2009, and Fegies et al., 2021, for marsupials; and Patton et al., 2015, for rodents), and collected data on weight, sex, age (juvenile, subadult, and adult), behavior, and reproduction. The individuals weighing >30 g were marked with numbered ear tags (ZT 900 by Zootech) to identify recaptures, and those weighing <30 g were marked with a small cut in the left ear (Furtado et al., 2021). The ear tissue samples were preserved and will be used in future molecular analyses. Vouchers were collected for morphological taxonomic identity and will be deposited in the mammal collection of the Museu de Zoologia da Universidade de São Paulo (MZUSP, São Paulo, Brazil, SISBIO 50658-3 collection permit). All procedures of capture and collection were made following the American Society of Mammalogists guidelines for the use of wild mammals in research (Sikes et al., 2016) and were approved by the Animal Ethical Committee (#CEUA-IB-USP 241/2016).

4.2.3.3. Microhabitat

We used seven variables related to the herbaceous, shrub, tree, and *Urochloa* sp. cover to characterize the microhabitat (see details in Furtado et al., 2021). We measured the microhabitat variables in four periods within a five-month interval: September 2018 (T1), two months after the prescribed fire and at the end of the dry season; February 2019 (T2), seven months after the fire, and at the end of the wet season; July 2019 (T3), one year after the fire event and at the beginning of the dry season; and December 2019 (T4), seventeen months post-fire, and at the middle of the wet season. We did not measure those variables for pitfall trap stations since we cleared the area near each trap for the installation of pitfall traps. Therefore, we restricted the microhabitat analysis to the live trap stations. We paired each period of microhabitat measuring (T1, T2, T3, and T4) with a four-month period of small mammal survey, to equal sampling effort. We did consider recaptures in different field trips and live trap sampling points, as they could indicate the suitability of microhabitats for the species. The other recapture data were excluded in order to guarantee the independence of records.

4.2.4. Data analysis

We conducted all the statistical analyses in R (version 4.1.0; R Core Team, 2021), using the hypothesis testing approach ($\alpha = 0.05$) for model selection, through the comparison of nested models (*anova* function) with variance partition from the F-statistic for linear models, and the residual deviance and chi-square tests for generalized linear models (Zuur et al., 2009). Prediction graphics of the selected models were also made using the *ggPredict* function from the ‘ggiraphExtra’ package (Moon, 2020). We used ‘DHARMa’ and ‘performance’ packages for the diagnosis of the fitted models regarding over dispersion, zero-inflation, uniformity, and outliers (Harting, 2021; Lüdecke et al., 2021).

We performed a Principal Components Analysis (PCA) based on a correlation matrix of the microhabitat variables (‘stats’ package and *prcomp* function, R Core Team, 2021) and retained only the principal components with eigenvalues >1. In order to characterize the changes in the vegetation structure after the fire, we fitted linear models (LM) using the microhabitat PCA scores selected previously, as a function of time (related to the period in which the variables were measured, as described above) and grassland formation (post-fire ‘*campo sujo*’ and burned ‘*campo cerrado*’) using the *lm* function from ‘stats’ package. We fitted generalized linear models (GLMM) for rodent richness and abundance, and total abundance of species with n > 10 individuals as a function of the PCA variables, using the sampling points as a random effect (package ‘glmmTMB’, *glmmTMB* function, family = poisson or negative binomial, link = log; Brooks et al., 2022). We only made these analyses considering rodent species because, in the reduced data used (four months for each period), no marsupial species was recorded.

To investigate the effect of the prescribed fire on small mammals taxonomic diversity, we generated GLMM models for total species richness and abundance of small mammals, by order (rodents and marsupials), and considering the relative abundance of species with n >10 individuals captured, as a function of the fire treatments. Richness was characterized as the number of species recorded for each plot, and abundance as the number of individuals captured (excluding recaptures). The community structure was characterized and compared within treatments by its richness through rarefaction/extrapolation curves built with ‘iNEXT’ R package (Whittaker, 1972; Colwell et al., 2012; Chao et al., 2014). The sampling effort completeness was evaluated by a coverage estimator percentage based on abundance data (‘iNEXT’ R package, Hsieh et al., 2016). All comparisons within analyses were conducted with 95% confidence intervals as thresholds (Chao and Chiu, 2016).

4.3. Results

4.3.1. Temporal experiment

We observed a total richness of eight small mammal species in the ‘*campo-sujo*’ pre-fire survey: two marsupials (13 individuals) and six rodents (100 individuals), totaling 113 individuals captured (Table 1). For the first 12 months post-fire, we recorded the same six rodent species, totaling 214 individuals and no marsupial. In the second-year post-fire, we captured 91 individuals from those six rodent species, and six individuals from the two marsupial species, totaling 97 small mammal individuals. Two species with less than three individuals captured were excluded from our analyses (*Gracilinanus microtarsus* and *Hylaeamys megacephalus*) as they could inflate the rare species estimates (Verbeck, 2011, Supplementary Table 1). The sample coverage indicated that our survey effort was efficient in recording the diversity estimated for all treatments (100%). The total richness was not affected by fire, considering the first eight months of data for each treatment (p = 0.21, Figure 4A). Despite that, when the total data from 12 months were compared, the first-year post-fire treatment had lower richness than the pre-fire, as indicated by the rarefaction-extrapolation curves ($p < 0.001$, Figure 4B), with no marsupial species recorded for 12 months after the prescribed fire (Figure 5B).

The total mean abundance increased significantly after the fire ($p < 0.001$), especially in the first year, with an average increase of 136% in the first eight months post-fire, as demonstrated by our linear models results ($p < 0.001$). The abundance was still higher in the second-year post-fire when compared to the pre-fire treatment, but to a lower degree, with 95% of average increase ($p < 0.001$). Rodents were the main responsible for this increase in total abundance. For the first-year post-fire (eight months), we estimated that rodents increased 19-fold in average abundance per sampling unit, compared with pre-fire levels ($p < 0.001$). For the second year, this increase was 14-fold ($p < 0.001$). The abundance of the rodents *Calomys tener*, *Cerradomys scotti*, and *Necromys lasiurus* were positively affected by the fire, mainly in the first-year post-fire (Figures 4A e 4B). *Calomys tener* was the dominant species in all treatments (Figure 5A), and its abundance increased in ~4-fold in the first eight months post-fire, and 2.4-fold in the second year, compared with pre-fire abundance ($p < 0.001$ and 0.005, respectively). *Cerradomys scotti* had an average increase of 2-fold in abundance for the first-year post-fire and 1.5-fold for the second year ($p = 0.008$ and 0.03, respectively). *Necromys lasiurus* was the least abundant species in the pre-fire treatment and had an increase of 5-fold in abundance for the first year and of 13-fold for the second-year post-fire, becoming the third most abundant species after the fire ($p < 0.001$ and 0.01, respectively, Figure 4A). The rodents *Oligoryzomys mattogrossae*, *Oligoryzomys nigripes* and *Clyomys laticeps* were not affected by the fire, with no significant changes in their abundances ($p = 0.06$, 0.65, and 0.5, respectively). Regarding marsupials, although the two species recorded in the pre-fire treatment were recorded only in the second-year post-fire, its abundance did not differ from the control treatment ($p =0.9$).

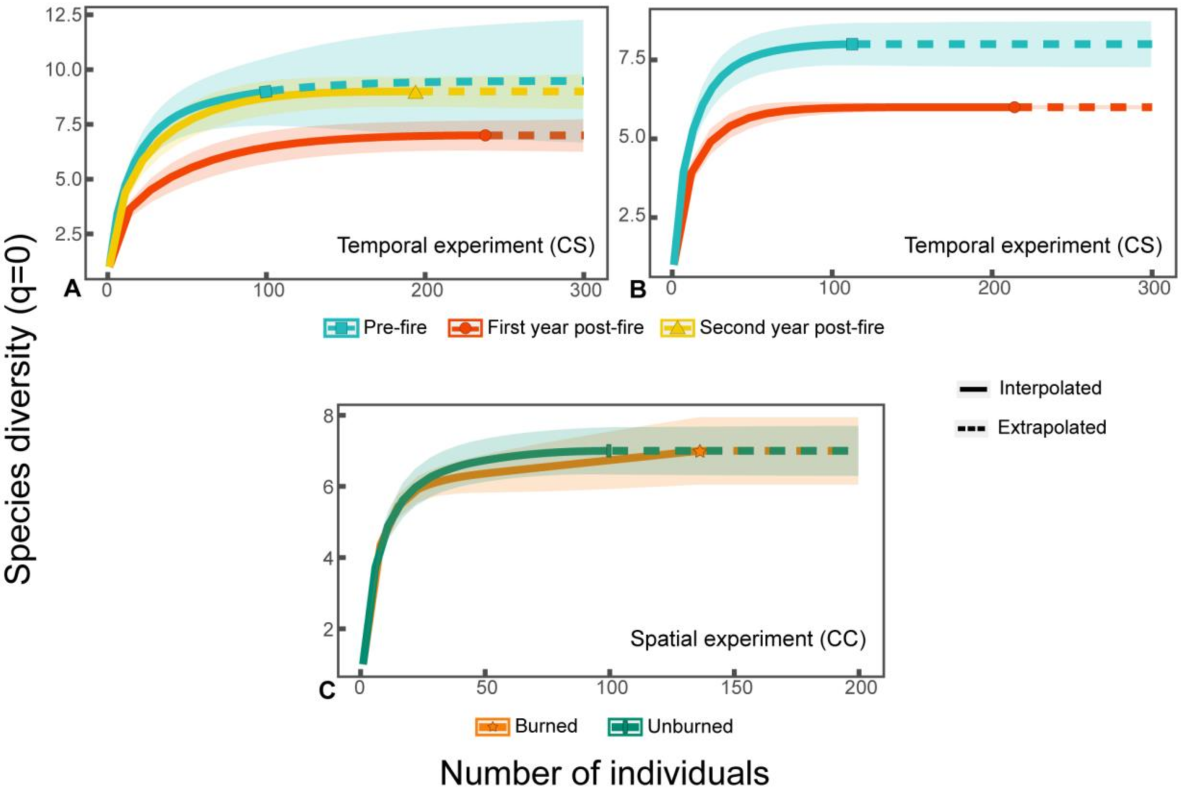


Figure 4. Rarefaction/extrapolation curves based on abundance data for the **(A)** whole Temporal experiment (8 months per treatment) and **(B)** Temporal experiment considering first year post-fire versus pre-fire treatment (12 months each), generated with 1,000 bootstraps and 300 individuals as an endpoint; and **(C)** Spatial experiment curve generated with 1,000 bootstraps and 200 individuals as an endpoint. The shadows represent the 95% confidence interval for each curve. The grassland formations are CS: '*campo sujo*', and CC: '*campo cerrado*'.

Table 1. Richness and abundance of small mammals for the Temporal and Spatial experiments in the Santa Bárbara Ecological Station, Águas de Santa Bárbara, São Paulo, Brazil.

Small mammal species	**Temporal Experiment**					**Spatial Experiment**	
	Individuals captured in ‘*campo sujo*’					Individuals captured in ‘*campo cerrado*’	
	Pre-fire		**Post-fire**			**Unburned**	**Burned**
			First-year		Second-year		
	*Partial data**	*Total*	*Partial data**	*Total*	*Total**		
Didelphimorphia							
Didelphidae							
Cryptonanus chacoensis	4	7	-	-	3	6	1
Cryptonanus aff. *chacoensis***	2	5	-	-	3	-	-
Rodentia							
Cricetidae							
Akodon cf. *montensis*	-	-	-	-	-	8	12
Calomys tener	17	47	80	112	41	10	26
Cerradomys scotti	7	14	22	54	18	19	24
Necromys lasiurus	1	2	6	12	14	2	12
Oligoryzomys mattogrossae	9	23	5	20	7	34	45
Oligoryzomys nigripes	5	6	4	10	7	21	16
Echimyidae							
Clyomys laticeps	5	9	2	6	4	-	-
Total	50	**113**	119	**214**	**97**	**100**	**136**
N species	8	**8**	6	**6**	**8**	**7**	**7**
Survey effort (traps/night)	1,536	2,304	1,536	2,304	1,536	2,560	2,560

*The partial data for pre-fire and first-year post-fire treatments are related to data collected from August to March of the respective survey years, to equal the survey effort with the second-year post-fire data (1,536 trap nights). ** This taxon refers to *Cryptonanus chacoensis* lineage B of Fegies et al. (2021). The name *C. chacoensis* (Tate, 1932) was applied for *C. chacoensis* lineage A of Fegies et al. (2021).

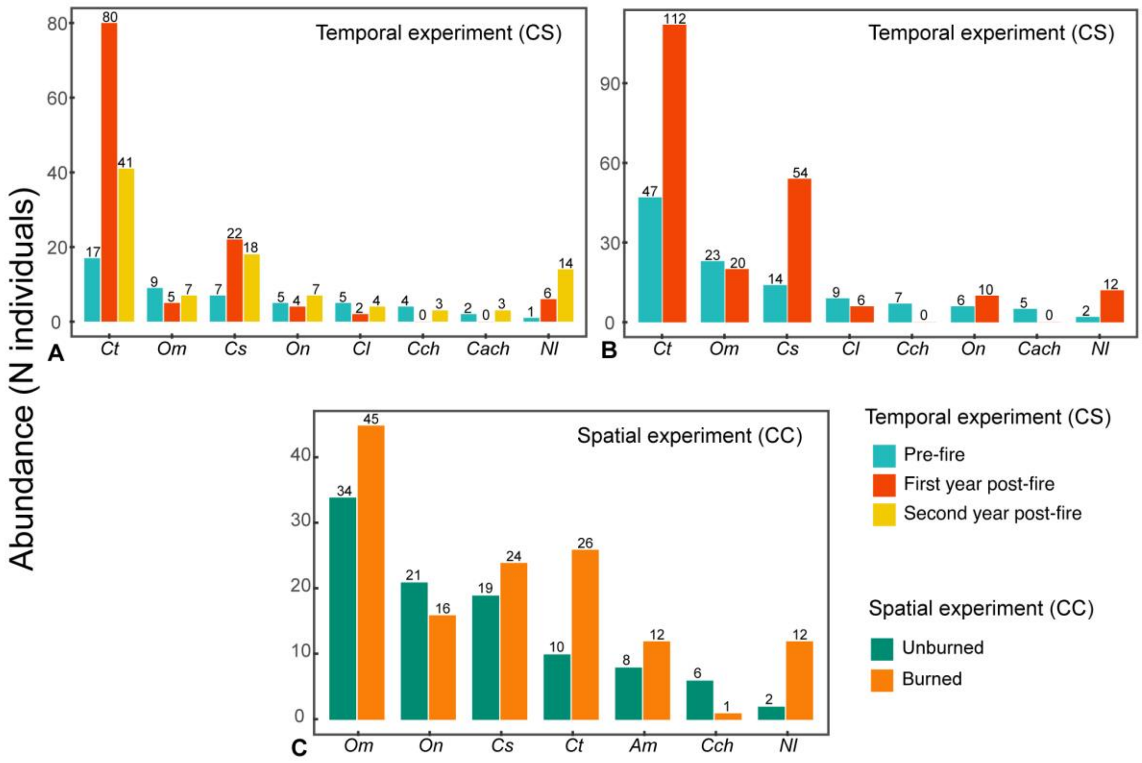


Figure 5. Abundance of small mammals expressed by the total number of individuals captured for the **(A)** whole Temporal experiment (8 months per treatment), **(B)** complete pre-fire versus first-year post-fire (12 months); and **(C)** Spatial experiment. The grassland formations are CS: '*campo sujo*', and CC: '*campo cerrado*'. Small mammal species are: Am: *Akodon* cf. *montensis*, Ct: *Calomys tener*, Cs: *Cerradomys scotti*, Cl: *Clyomys laticeps*, Cach: *Cryptonanus* aff. *chacoensis*, Cch: *Cryptonanus chacoensis*, Nl: *Necromys lasiurus*, Om: *Oligoryzomys mattogrossae*, and On: *Oligoryzomys nigripes*.

4.3.2. Spatial experiment

We recorded seven small mammal species in '*campo cerrado*' unburned plots, one marsupial (six individuals), and six rodents (94 individuals), among 100 individuals captured. For the burned plots, we found the same small mammal species, among 136 individuals captured, of which only one individual was a marsupial (Table 1). The marsupials *Gracilinanus agilis* and *Didelphis albiventris*, and the rodents *Rhipidomys* cf. *macrurus* and *Clyomys laticeps* were not considered for these analyses because they represented singletons (Supplementary Table 1). We observed no differences in species richness among the treatments, as indicated by the rarefaction-extrapolation curves (p = 0.57, Figure 4C). The total abundance of small mammals was not affected by the fire (p = 0.4, Figure 5C). The rodent *Necromys lasiurus* were the only species that had a significant increase in its abundance in this experiment, with an average increase of 5-fold in the burned plots, compared with the unburned ones (p = 0.01, Figure 5C). The rodents *Calomys tener*, *Cerradomys scotti*, *Oligoryzomys nigripes*, *Oligoryzomys mattogrossae*, and *Akodon* cf. *montensis* were not affected by the fire ($p = 0.15$, 0.42, 0.53, 0.52, and 0.96, respectively). The abundance of *Cryptonanus chacoensis* had an average decrease of 83.3% in the burned plots ($p = 0.05$; Figure 5C).

4.3.3. Microhabitat

The seven microhabitat variables were reduced to three principal components through a PCA analysis. These principal components accounted for 73.5% of the explained variance in the data (Supplementary Figure 1). The first axis, principal component one (PC1), indicates high herbaceous and shrub cover, and represents 38.3% of the total variance (Supplementary Figure 2A). The second principal component (PC2) represents low canopy cover and accounts for 17.9% of the total variance (Supplementary Figure 2B). The third principal component (PC3) is related primarily to high cover by the invasive grass *Urochloa* sp. and represents 17.3% of the total variance (Supplementary Figure 2C).

The '*campo cerrado*' and '*campo sujo*' burned plots had a significant increase in herbaceous and shrub cover after seven months post-fire (T2), evidenced by the increase in PC1 values (Figure 6A, R^2 adj. = 0.76, $F_{7,144} = 68.11$, $p < 0.001$). This effect was slightly more pronounced in '*campo-sujo*', with an average increase of 3.11 units of PC1 between T1 and T2 (Figure 6A, $p < 0.001$). The '*campo-sujo*' herbaceous and shrub cover continued to increase across time, but in a more tenuous way, reaching the highest values of PC1 one year and a half after the fire (T4, $p < 0.001$). On the other hand, for the '*campo cerrado*', the herb and shrub cover decreased after one year (T3) compared to the previous period (T2), and increased again towards T4, but with lower herbaceous and shrub cover compared to '*campo-sujo*' through both periods analyzed (Figure 6A, $p < 0.001$ for both).

Regarding tree cover, the variation through time was similar in both burned formations, but with '*campo cerrado*' presenting lower canopy cover than '*campo sujo*' in general, in an average increase of 0.8 units of PC2 (Figure 6B, R^2 adj. = 0.25, $F_{4,147} = 13.63$, $p < 0.001$). The tree cover significantly increased after seven months post-fire (T2), with an average increase of 1.17 PC2 units, compared to two months after the fire (T1, $p < 0.001$). Despite that, in 17 months post-fire, the tree cover decreased to similar values compared to T1, right after the fire, with no differences between these two periods (Figure 6B, $p = 0.21$).

The *Urochloa* sp. cover varied in different ways between the two types of burned grasslands (Figure 6C, R^2 adj. = 0.26, $F_{7,144} = 8.64$, $p < 0.001$). The '*campo cerrado*' burned plots had an increase in *Urochloa* sp. cover of 1.17 in PC3 average values after seven months of the burn (p = 0.001), although in the last period evaluated (T4), the values returned to T1 values, with no significant changes (Figure 6A, p = 0.08). The ‘*campo sujo*’ plots had no significant changes in *Urochloa* sp. cover through the first years after fire (T2 and T3, p = 0.42 and 0.09, respectively) but had a decrease after seventeen months post-fire of 0.7 in PC3 average, compared to two months after the fire (Figure 6C, p = 0.01).

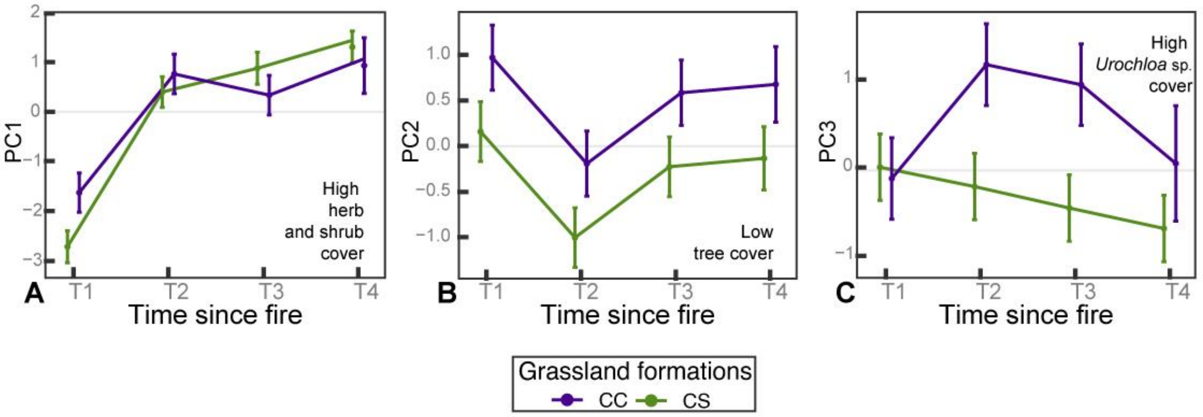


Figure 6. Predicted mean changes and standard deviation estimated by linear models regarding microhabitat dynamics throughout time post-fire for **(A)** herbaceous and shrub cover (PC1), **(B)** tree cover (PC2), and **(C)** *Urochloa* sp. cover (PC3). The grassland formations are expressed as: CS: ‘*campo sujo*’ post-fire, and CC: ‘*campo cerrado*’ burned. Times are: T1 = September 2018, two months after the prescribed fire and at the end of the dry season; T2 = February 2019, seven months after the fire, and at the end of the wet season; T3 = July 2019, one year after the fire event and at the beginning of the dry season; and T4 = December 2019, seventeen months post-fire, and at the middle of the wet season.

Rodent richness was not affected by the reduced microhabitat variables (p = 0.91). On the other hand, in ‘*campo cerrado*’ burned plots, their abundance was negatively influenced by the decrease in tree cover (PC2, Figure 7A, p = 0.004) and increase in *Urochloa* sp. cover (PC3, Figure 7B, p = 0.05), with an average decrease of 39% and 34% in the abundance, respectively. The rodent *Calomys tener* had its abundance negatively affected by low tree cover only in ‘*campo cerrado*’ burned plots, with an average decrease of 51% (Figure 7C, p = 0.04). The association was positive in the ‘*campo sujo*’, with an increase of 111% in abundance for plots with low tree cover (Figure 7C, p = 0.007). Furthermore, *C. tener* abundance decreased by 39% with the increase of herbaceous and shrub cover (Figure 7D, p < 0.001). *Clyomys laticeps* had an estimated decrease of 50% in its abundance related to low tree cover in both grassland formations (Figure 7E, p = 0.02). For the analyzed species, *Cerradomys scotti* was the only that was not affected by any microhabitat variable post-fire (p = 0.07).

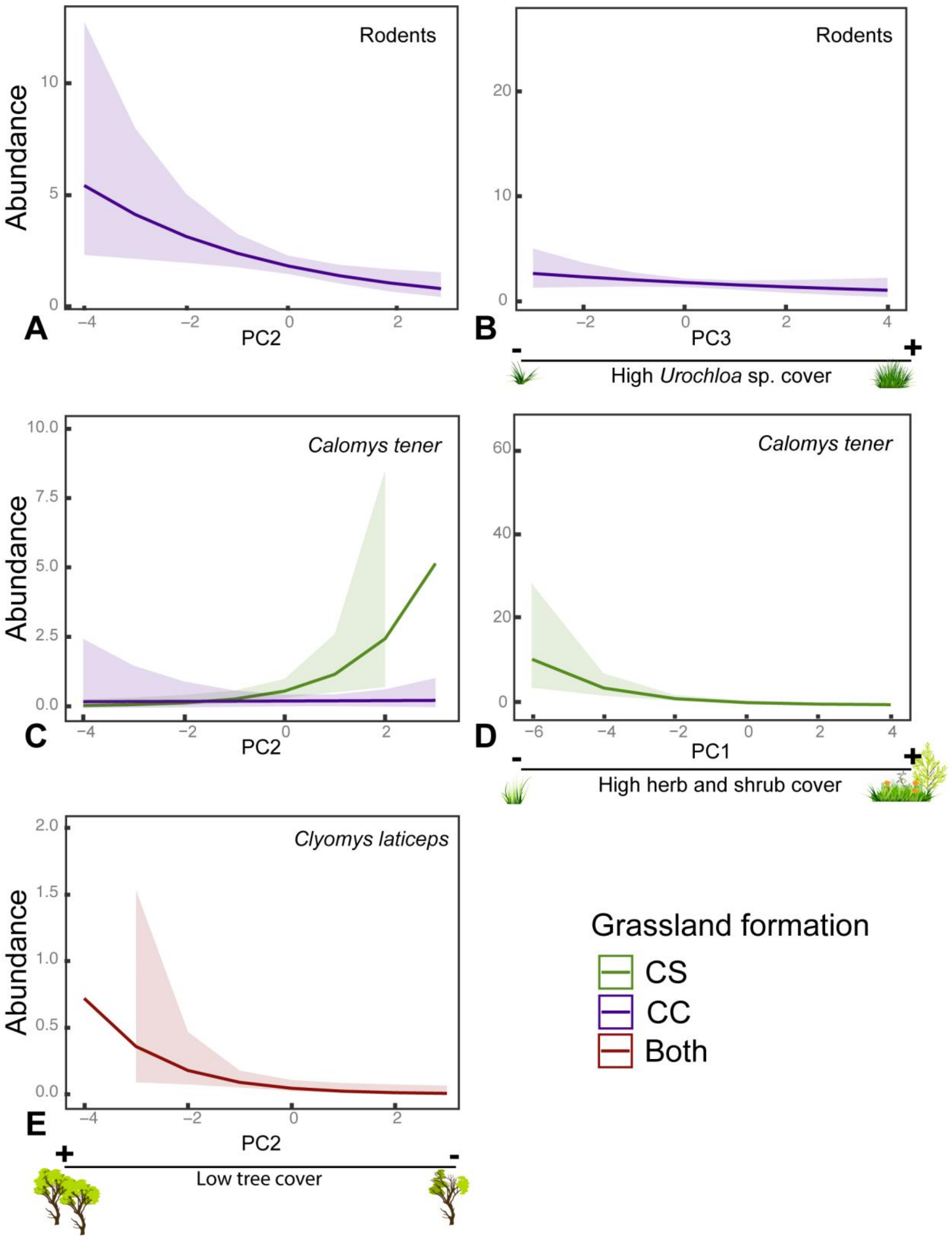


Figure 7. Predicted effects of microhabitat on **(A)** rodents' abundance by PC2, **(B)** rodents' abundance by PC3, **(C)** *Calomys tener* abundance by PC2, **(D)** *Calomys tener* abundance by PC3, and **(E)** *Clyomys laticeps* by PC2. The predicted values were based on generalized linear models estimates. The shadows represent the 95% confidence intervals. The grassland formations are expressed as CS: '*campo sujo*' post-fire, and CC: '*campo cerrado*' burned. The principal components are PC1: high herbaceous and shrub cover, PC2: low tree cover, and PC3: high *Urochloa* sp. cover; all principal components are derived from the PCA analysis based on the microhabitat variables.

4.4. Discussion

We assessed the effects of a low-intensity prescribed fire on the taxonomic diversity of the small mammal community from two grassland formations in the southeastern Brazilian Cerrado. Our results indicated that the prescribed fire changed the small mammal community structure in different ways in this fire-prone ecosystem. We obtained distinct results for the two experiments we assessed, with no changes in small mammals' total richness and abundance due to fire in the Spatial experiment at '*campo cerrado*' formations. On the other hand, at the Temporal experiment in open grasslands, rodents seem to be positively affected by fire, as demonstrated by the increase in abundance of the open-area specialists. Otherwise, marsupials were negatively affected in both experiments. Both grassland formations showed changes in microhabitat features after the fire (e.g., increase in herbaceous and shrub cover, changes in *Urochloa* sp. cover). Rodent abundances were negatively affected by *Urochloa* sp. density, with some species altering (or expanded) their microhabitats associations, such as *Calomys tener* that was favored by the low tree cover in '*campo sujo*' burned plots but was negatively affected in '*campo cerrado*' due to the increase in *Urochloa* sp. cover.

The difference between the experiments' responses regarding small mammal abundances was not expected, although our hypothesis of no net loss in diversity and the promotion of open-area specialists was consistent with our results so far. The Spatial experiment showed no changes in richness or total abundance for the community, although minor alterations related to two species were observed (e.g., *Necromys lasiurus* and *Cryptonanus chacoensis*). This pattern was identified in other studies of fire effect in small mammals (see review by Griffiths and Brook, 2014), and no changes in species richness, composition and abundance were previously recorded for plants, ants, frogs, and lizards in the burned grasslands of our study area (Durigan et al., 2020). The Temporal experiment led to major changes in the community after the prescribed burn. The earlier introduction of fire management in the '*campo cerrado*' burned plots (since 2015) may have been responsible for the resilience to fire found at the local community, compared with the '*campo sujo*' assemblage, which has been free of fire for at least 10 years (Durigan et al., 2020). Therefore, '*campo sujo*' plots probably had more accumulated fuel, which may lead to a more intense burn and resulted in greater structural changes in the habitat compared to the '*campo cerrado*'. Besides that, the '*campo cerrado*' unburned and burned plots were closer to each other, and the unburned plot may have functioned as a source of refuge and promoted individuals' displacement to the burned plots right after the fire, although we did not observe an increase in the control plots (Kelly et al., 2012). This dynamic may have homogenized the two communities, leading to minor differences between the treatments. Promoting a mosaic of burned and unburned plots in the same landscape seems to be efficient in guaranteeing open-habitat diversity (Durigan et al. 2020). The differences in responses among experiments may also be due to methodological influences, since in the Temporal experiment we did not have a spatial control simultaneously, and other factors, such as climate and seasonal fluctuation may have influenced population changes in abundance (Vieira and Briani, 2013).

Rodents seem to benefit from fire, as indicated primarily by our Temporal experiment. The increase in abundance was much more evident in the first-year post-fire. Several rodent species that were recorded in SBES community are omnivorous that feed heavily on C3 and C4 plants (Ribeiro et al., 2019). They may benefit from the increase in these resources associated with the rapid regrowth of vegetation after fire, as indicated by the microhabitat changes after the fire event that we recorded here, which included a considerable increase in herbaceous and shrub layers. This increase in herbaceous and shrub cover associated with fire is well established since fire promotes a rapid regeneration through resprouting and induces flowering, which has been recorded in other South American savannas (Pilon et al., 2018; Durigan et al., 2020; Fidelis and Zirondi, 2021; González et al., 2021). Contrary to our expectations, their abundance did not drastically fall right after the prescribed burn, but in fact, had a variable growth until reaching the maximum values exactly one year after the fire, with a decreasing trend after this period in both experiments. Other studies in South America have shown that small mammals show a decrease in diversity parameters right after the fire, but quickly return to numbers recorded before the fire, sometimes reaching higher diversity (e.g., Henriques et al., 2000, 2006; Briani et al., 2004). The main survival strategy known used by rodents to remain in burning habitats is using burrows made by fossorial species as refuge and termic isolation during fire events (Coutinho, 1990; Vieira and Marinho-Filho, 1998).

Marsupials were negatively affected in both experiments in similar ways, disappearing from the community for at least 12 months. The two marsupial species were not recorded in the first-year post-fire in ‘*campo sujo*’, but returned in the second year, in similar abundances. Although in ‘*campo cerrado*’ analyses their richness were not affected, the abundance decreased significantly, and the only individual recorded was also captured only after one year of the burn. The marsupial assemblage is basically represented by two sympatric *Cryptonanus* species. Although the genus *Cryptonanus* diversified in association with grassland formations (Fegies et al., 2021, Carmignotto et al., 2022), its species may not be able to find refuge locally during and right after the fire as recorded for rodents (Coutinho, 1990; Vieira and Marinho-

Filho, 1998), and must be forced to disperse to nearby habitats, returning only after a considerable amount of time after the fire as evidenced by our results. The negative response of marsupials to fire was also recorded in a gallery forest nearby savanna patches after an accidental fire by González et al. (2021).

Among species-level responses, three sigmodontines were clearly favored by the fire: *Calomys tener*, *Cerradomys scotti*, and *Necromys lasiurus* (Figure 5). Their abundances have been commonly related as fire-induced in the Cerrado ecoregion (Vieira and Marinho-Filho, 1998; Vieira and Briani, 2013; Griffiths and Brook, 2014). These species are known to have large feeding plasticity and may benefit from an increase in invertebrate and seed resources after the fire (Ribeiro et al., 2019; Pilon et al., 2020). *Calomys tener* was the dominant species in '*campo sujo*' plots before and after the fire and became the second most abundant in the burned '*campo cerrado*'. Its dominance in grasslands and savanna habitats has been recorded for other Cerrado areas (Carmignotto et al., 2022). Our results corroborate the suggestion that *C. tener* has an early post-fire increase in Cerrado, reaching high values of abundance a few months after the burn, and its opportunistic habits may be responsible for the increase in abundance after habitat disturbances (Briani et al., 2004; Vieira and Briani, 2013). *Necromys lasiurus* showed the same pattern of post-fire increase in both grassland formations and was the only rodent that continued to increase in abundance after one-year post-fire (Figure 5A). This result is in accordance with responses observed in a Cerrado core area, where *N. lasiurus* showed an abundance peak three years after fire (Briani et al., 2004). Despite not being the dominant species in the grassland communities here assessed, it had the higher proportional effect on abundance, moving from the less abundant to the third more abundant species in the '*campo sujo*' community. *Necromys lasiurus* is frequently the most abundant species in small mammal communities throughout the Cerrado and has been shown to be negatively affected by woody encroachment (Becker et al., 2007; Mendonça et al., 2018; Furtado et al., 2021).

Calomys tener and *Cerradomys scotti* were previously suggested to be associated with higher herbaceous and shrub cover in unburned grasslands (Furtado et al., 2021). However, *C. tener* seems to have expanded its association to other microhabitat variables after the burn in '*campo sujo*', being negatively associated with herb and shrub cover (Figure 6D). This may be related to drastic local changes in microhabitat features right after fire, such as a reduced cover in all vegetation variables due to fuel consumption. Considering that the abundance of *C. tener* in the first months post fire was high, due to its opportunistic behavior, the association with low vegetation structure may be influenced by the abundance increase right-after fire. In fact, the peak of *C. tener* abundance was four months post-fire (November 2019), during the middle of two periods of microhabitat evaluation, where there was a rapid increase in herb and shrub cover. We suggest that *C. tener* presents high habitat plasticity and may expand their niche after habitat disturbances such as fire, but maintain more restricted preferences in fully recovered grasslands, acting as an open-area specialist (Briani et al., 2004; Furtado et al., 2021). Furthermore, *C. tener* also showed a divergent response to tree cover, being negatively associated with tree cover in '*campo sujo*' (as expected), but positively affected by tree cover in '*campo cerrado*' (Figure 6C). The same effect occurred for *Clyomys laticeps*, an open-area specialist that has been related to the herbaceous layer in unburned grasslands (Furtado et al., 2021), and that showed to be positively influenced by tree cover after the fire. The *Urochloa* sp. negative influence in '*campo cerrado*' plots are more evident, as demonstrated by our results for rodent abundance in general (Figure 6B), as more plots are under a major invasion by this alien grass. Considering the higher tree density in '*campo cerrado*' formation, this may have influenced the negative relationship of these two species. Fire may control *Urochloa* sp. in early invasion stages, as our results indicate for '*campo sujo*' plots, which had no more than 25% of *Urochloa* sp. cover before the fire and had a considerable decrease after the fire (Figure 6C).

Fire impacts on small mammals are extensively recognized but controversial among different communities and regions, and seem to be related to local conditions, such as vegetation structure, habitat requirements, and taxonomic features (Griffiths and Brook, 2014). In Australian savannas, several losses in small mammal diversity are related to high intensity and frequent fires, such as an increase in predation rates and invasive species (Woinarski et al., 2010; Lawes et al., 2015). Australian small mammals are considered more fire-sensitive than those from other regions, while South American small mammals seem to be more tolerant to fire than those from the other continents in fire-prone ecosystems (Andersen et al., 2012; Griffiths and Brook, 2014). In fact, this tolerance was clear in our study, as we obtained higher abundance in burned treatments, primarily for rodents and species associated with open-habitat requirements, the opposite of the overall pattern identified for other continents (except Asia; Griffiths and Brook, 2014). This study assesses a unique prescribed fire event, and posterior patterns related to fire regime must be investigated to determine the most accurate fire management from a small mammal perspective (Griffiths et al., 2015).

Our results highlight that prescribed fire can affect the small mammal community in a heterogeneous way, depending on species-level features such as their association with vegetation structure. Species tolerant to fire seems to be associated with open microhabitat variables such as higher herbaceous cover, and fire-sensitive species to forest-related microhabitats such as canopy cover, although this dynamic can change due to other factors, such as habitat plasticity and the presence of invasive grasses (Furtado et al., 2021). Promoting fire management in order to maintain a mosaic of unburned and burned patches in a heterogeneous landscape must increase local small mammal diversity (Durigan et al., 2020; Carmignotto et al., 2022). To achieve that, future studies about prescribed fire should address the impacts of more than one fire event and differences in fire regime (intensity, frequency, and extent) in the local communities from additional perspectives, such as functional and phylogenetic diversity (Griffiths and Brook, 2014). This may be a key point to preserve open-specialist and threatened species (e.g., the rodents, *Cerradomys scotti* and *Clyomys laticeps*; São Paulo, 2018) from grasslands suffering from woody encroachment, such as most protected areas in the southeastern Brazilian Cerrado (Abreu et al., 2017; Furtado et al., 2021).

Author Contributions

APC and MM conceived this study and designed the methodology. APC, and LOF collected the data. LOF performed the statistical analysis and led the manuscript writing. All authors interpreted results, contributed to the writing and reviews, and gave final approval for submission.

Funding

This study was funded by FAPESP grants #2015/21259-8, #2018/14091-1, #2020/12658-4, and #00/00. LOF received a fellowship from CAPES - Finance Code 001.

Acknowledgments

We are grateful to the Santa Bárbara Ecological Station management team, especially Marcos Pestana, and Instituto Florestal for all the support during fieldwork. We are also thankful for Bárbara Armando Godinho, Bruna de França Gomes, Bruno Ferreto Fiorillo, Carolina Farhat, Carolina Henkes Inamassu, Carolina Freitas Schlosser, Evelin de Campos da Costa, Filipe Serrano, Giovana Felício, Giordano Novak Rossi, Guilherme Zamarian Rezende, Jairo Roldan, João Paulo dos Santos Vieira-Alencar, Jorge Henry Maciel, Juan Camilo Díaz, Julia dos Santos Gutierres, Karine Yumi Tominaga, Mirela Alcolea and Paula Rocha for assistance in data collection; and for Yohann Freddi for assistance with the softwares. We also thank Alexander Christianini and Katia Ferraz for valuable suggestions to this study. The collection permit was issued by Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio) #50658-1. The authors have no conflict of interest to disclose.

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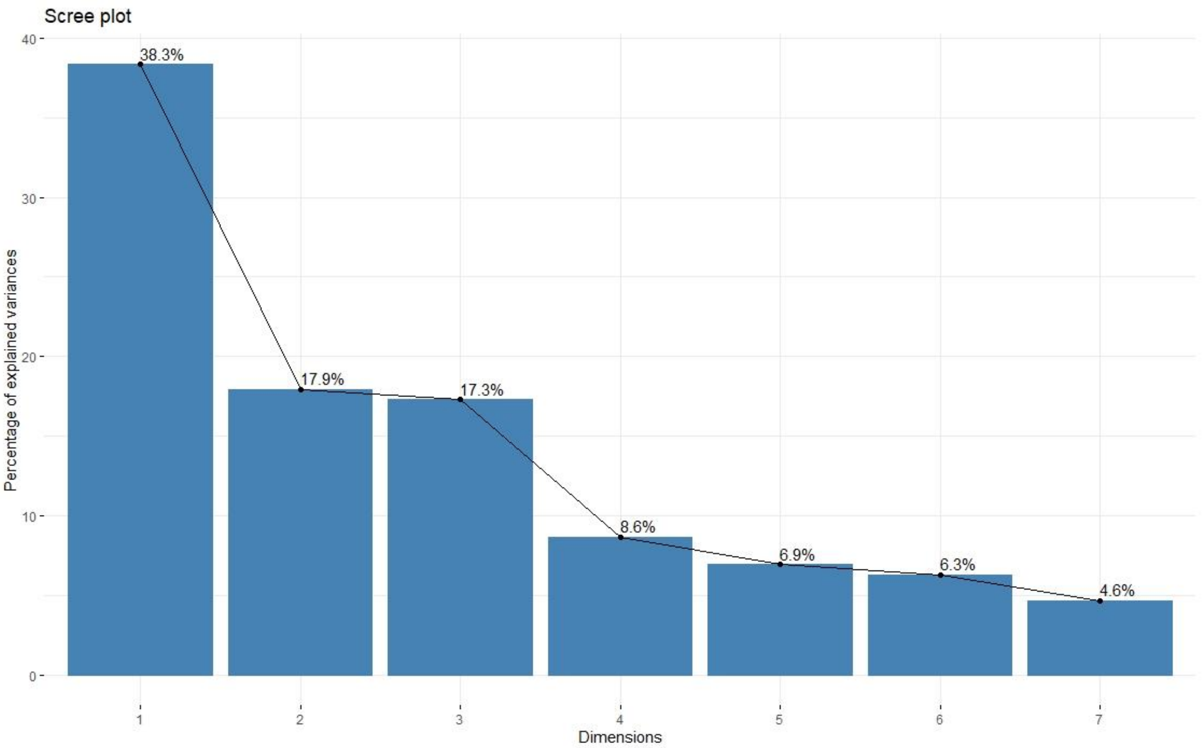
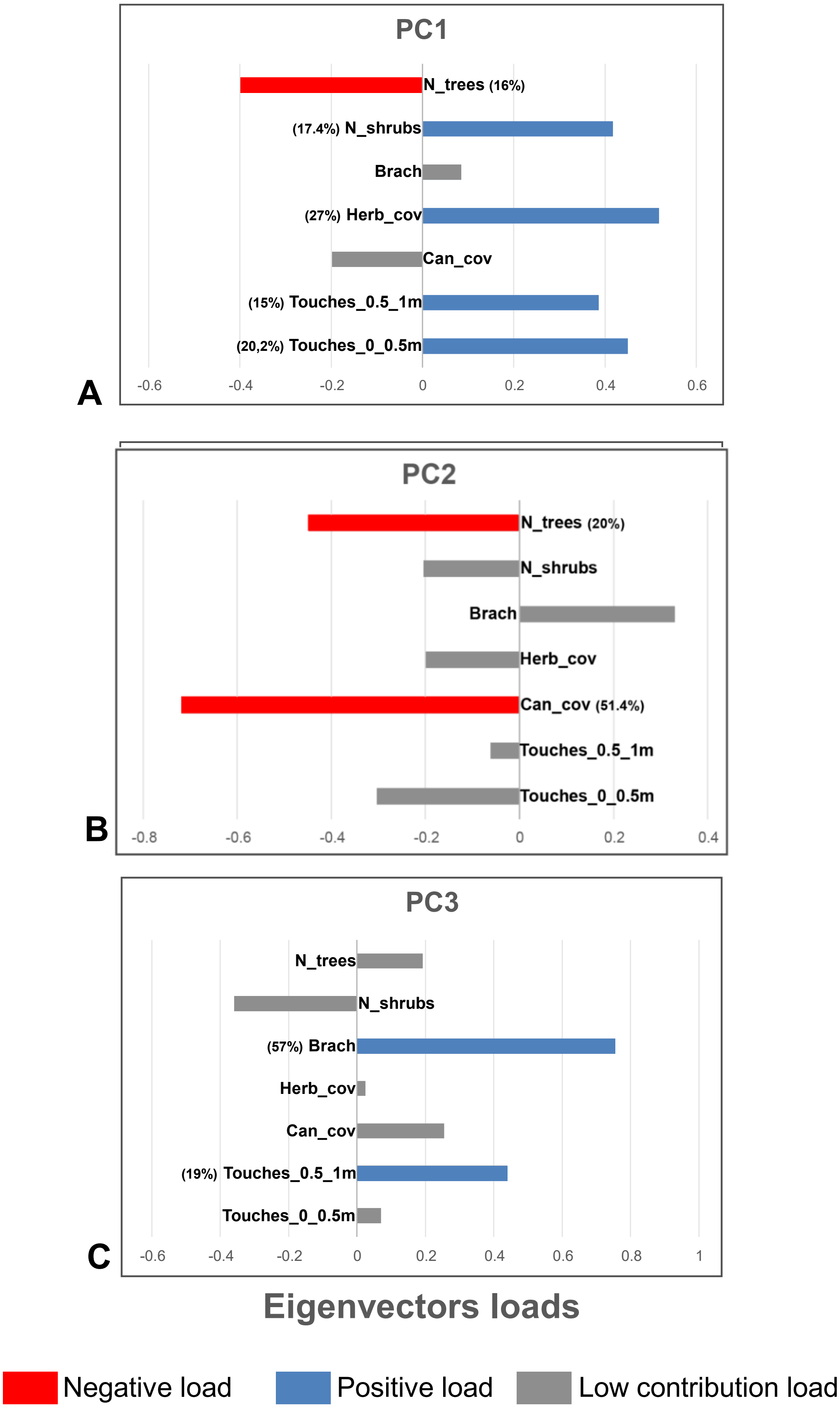
Supplementary Material

Supplementary Table 1. Abundance (number of individuals captured) of rare small mammal species excluded from the analyses.

Excluded especies	**Temporal Experiment** Individuals captured in '*campo sujo*'		**Spatial Experiment** Individuals captured in '*campo cerrado*'	
	Pre-fire	**Post-fire**	**Unburned**	**Burned**
Didelphimorphia				
Didelphidae				
Didelphis albiventris	-	-	1	1
Gracilinanus agilis	-	-	1	-
Gracilinanus microtarsus	3	-	-	-
Rodentia				
Cricetidae				
Hylaeamys megacephalus	1	-	-	-
Rhipidomys cf. *macrurus*	-	-	1	-
Echimyidae				
Clyomys laticeps	-	-	-	1
Total	**4**	**0**	**3**	**2**



Supplementary Figure 1. Percentage of explained variance by the dimensions from PCA analysis based on microhabitat data. The tree first dimension are the principal components retained and represents 73.5% of total variance in data.



Supplementary Figure 2. Eigenvector loads for the tree principal components retained through PCA analysis. **(A)** PC1, **(B)** PC2, and **(C)** PC3. The contribution of the significant microhabitat variables for each eigenvector is showed in parentheses.

5. SISTEMATIZAÇÃO DOS PRINCIPAIS RESULTADOS E DISCUSSÃO

O adensamento lenhoso vem afetando a comunidade de pequenos mamíferos no Cerrado paulista, e o manejo do fogo prescrito parece ser uma estratégia importante para garantir a manutenção de populações de espécies vulneráveis a esse fator. Os roedores foram o grupo mais afetado negativamente pelo adensamento lenhoso, e o mais favorecido pela utilização do fogo prescrito nas fisionomias campestres. A comunidade de pequenos mamíferos demonstrou uma estruturação em relação ao uso do habitat nas duas escalas analisadas. As espécies associadas a habitats mais abertos (campestres e savânicos) foram negativamente afetadas pelo adensamento lenhoso, como por exemplo os roedores *Cerradomys scotti* e *Necromys lasiurus*, e o marsupial *Cryptonanus chacoensis* (Figura 1). Por outro lado, espécies relacionadas a variáveis de maior cobertura vegetal, como o marsupial *Didelphis albiventris* e o roedor *Oligoryzomys nigripes*, parecem ter sido beneficiadas pelo adensamento (Figura 1). Fatores relacionados ao regime do fogo prescrito podem afetar a resposta da comunidade de pequenos mamíferos (Griffiths et al., 2015). No experimento temporal, onde a mesma localidade de campo sujo foi amostrada antes e após o fogo, as diferenças na abundância de algumas espécies foram mais evidentes. Já no experimento espacial, onde áreas adjacentes queimadas e não queimadas de campo cerrado foram amostradas o fogo praticamente não afetou os parâmetros de diversidade analisados (veja também Durigan et al., 2020). Isso pode ser um indício da importância de se manter áreas não queimadas próximas aos quadrantes queimados, pois elas podem atuar como um refúgio e fonte de recursos para as espécies mais vulneráveis ao fogo, como os marsupiais (Kelly et al., 2012; Durigan et al., 2020).

Nossos resultados corroboram o aumento da densidade vegetal para a localidade de estudo (EESB), como já havia sido demonstrado por Abreu et al. (2017). Devido a isso, as fisionomias nativas de Cerrado vêm apresentando alterações em suas características estruturais (Rosan et al., 2019; este estudo), e isso foi visível inclusive durante as amostragens em campo. Formações campestres são as mais afetadas, como o quadrante de campo sujo no qual trabalhamos em 2018, que em 2003 se enquadrava na classificação fisionômica de campo limpo, uma fisionomia campestre bastante aberta e dominada por herbáceas. O uso do fogo prescrito nas fisionomias campestres favoreceu o aumento na cobertura herbácea e arbustiva, relação já bem conhecida para o Cerrado (Pilon et al., 2018; Durigan et al., 2020; Fidelis & Zirondi, 2021; este estudo). O aumento na densidade lenhosa, evidenciado pelos valores mais altos do índice de vegetação avançado (EVI) afetou a comunidade de pequenos mamíferos da EESB de maneiras diferentes. A riqueza de espécies parece não ter sido influenciada pelo aumento na densidade lenhosa, porém a abundância de roedores diminuiu em função do adensamento.

Espécies associadas ao uso de habitats mais abertos parecem estar sendo negativamente afetadas pelo adensamento lenhoso, como os roedores *Cerradomys scotti* e *Necromys lasiurus*. Essas espécies tiveram um aumento significativo na abundância após o uso do fogo prescrito nas fisionomias campestres, indicando que o fogo favoreceu essas populações (Figura 1). *Necromys lasiurus* é comumente a espécie mais abundante em comunidades do Cerrado (Mendonça et al., 2018), e em EESB foi a espécie dominante na amostragem de 2003. Porém, em 2018, sua abundância foi reduzida consideravelmente, voltando a aumentar após o uso do fogo prescrito, principalmente após um ano, nas duas fisionomias analisadas. O roedor *Cerradomys scotti* se mostrou associado a ambientes mais arbustivos, e apresentou uma associação negativa ao aumento de cobertura lenhosa (Figura 1). Essa espécie se tornou a segunda mais abundante nas áreas de campo sujo após o fogo. Outra espécie favorecida pelo fogo prescrito foi o roedor *Calomys tener*, espécie dominante na comunidade do campo sujo antes e depois do fogo. *C. tener* parece apresentar hábito oportunista após a queimada experimental, como já discutido na literatura (ver Briani et al., 2004; Vieira & Briani, 2013), alterando o uso do microhabitat, e demonstrando maior resiliência ao adensamento lenhoso. Apesar disso, em áreas não queimadas, *C. tener* parece apresentar um uso de habitat mais restrito, sendo positivamente associada a alta cobertura herbácea, característica das fisionomias campestres do Cerrado (Figura 1). A relação positiva desses roedores com o uso do fogo prescrito está de acordo com o observado em outras regiões do Cerrado (Vieira & Marinho-Filho, 1998; Vieira & Briani, 2013; Griffiths & Brook, 2014), porém, nossos resultados indicam que o adensamento lenhoso pode ser uma ameaça para alguma delas, como *C. scotti* e *N. lasiurus*. Algumas espécies abundantes na comunidade não foram influenciadas pelo adensamento lenhoso ou pelo fogo prescrito, como *Oligoryzomys mattogrossae* e *Akodon* cf. *montensis* (Figura 1). Já a espécie *Oligoryzomys nigripes*, apesar de não ter sido afetada pelo fogo prescrito, parece ser favorecida pelo adensamento lenhoso.

Os marsupiais, por outro lado, parecem ser mais sensíveis ao uso do fogo prescrito, apresentando uma diminuição na abundância e riqueza principalmente no primeiro ano após o fogo. Mesmo as duas espécies do gênero *Cryptonanus*, mais associadas às formações campestres e savânicas, foram negativamente afetadas pelo fogo. Apesar disso, ao final dos experimentos, ambas as espécies retornaram às comunidades, e não houve perda de riqueza. A espécie *Cryptonanus chacoensis* também se demonstrou sensível ao adensamento lenhoso (Figura 1). A existência de locais não queimados próximos ao habitat manejado pode ser importante para a permanência dessas espécies mais sensíveis ao fogo, como demonstrado pelo experimento espacial em áreas de campo cerrado (Durigan et al., 2020). Essas áreas servem de refúgio onde os indivíduos podem procurar abrigo e recursos durante e logo após o fogo, e dispersar novamente para as áreas queimadas quando possível (Vieira & Marinho-Filho, 1998; Kelly et al., 2012).

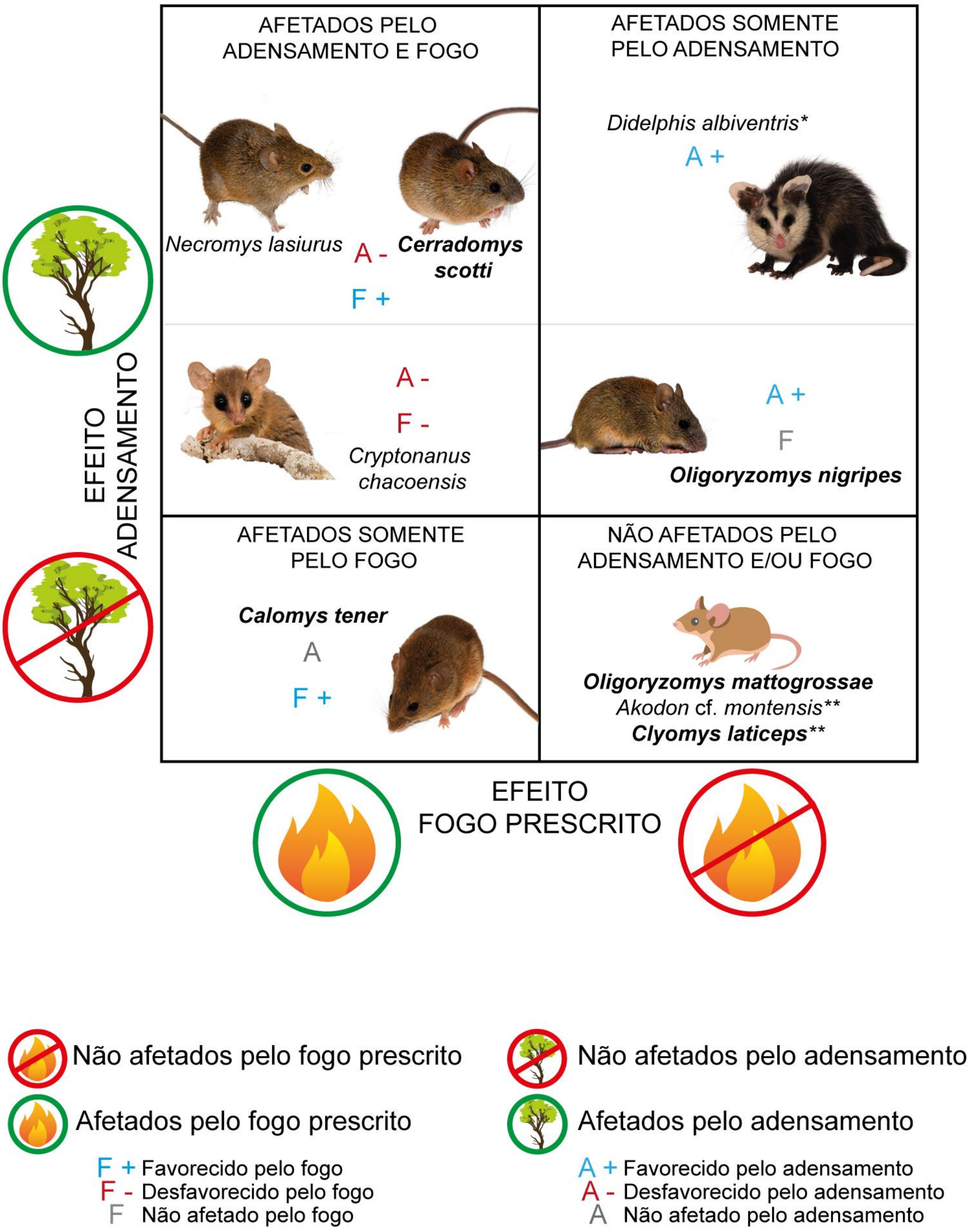


Figura 1. Resumo dos efeitos do adensamento lenhoso e do fogo prescrito sobre as espécies de pequenos mamíferos da Estação Ecológica de Santa Bárbara. Um asterisco indica espécies que não foram avaliadas quanto ao efeito do fogo. Dois asteriscos indicam espécies que não foram avaliadas quanto ao efeito do adensamento lenhoso. Espécies destacadas em negrito foram associadas a alta cobertura herbácea e/ou arbustiva nas análises de microhabitat. As ilustrações foram produzidas com vetores desenvolvidos por Freepik.com. Fotos: Bruno Ferreto Fiorillo.

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6. CONCLUSÃO E SUGESTÕES PARA TRABALHOS FUTUROS

Os resultados deste estudo indicam que o uso do fogo prescrito pode ser uma estratégia importante para garantir a permanência e manutenção da fauna especialista de áreas abertas, ameaçada pelo adensamento lenhoso que vem descaracterizando as fisionomias campestres e savânicas do Cerrado. Isso é particularmente relevante considerando as espécies ameaçadas de extinção para o Cerrado paulista, como os roedores *Clyomys laticeps* e *Cerradomys scotti*. Apesar de não terem sido analisadas neste estudo, as espécies raras associadas a fisionomias campestres, como o marsupial *Cryptonanus* aff. *chacoensis*, podem ser ainda mais vulneráveis aos efeitos do adensamento lenhoso. O manejo do fogo prescrito deve ser realizado de forma a manter parcelas de habitats não queimados próximos, criando um mosaico heterogêneo na paisagem que promova a diversidade local de pequenos mamíferos.

Este estudo abordou os efeitos de um único evento de fogo prescrito, e pesquisas futuras sobre a influência do regime de fogo (intensidade, frequência) são necessárias para compreender melhor o efeito desse tipo de manejo na diversidade de pequenos mamíferos não voadores. Além disso, ressalta-se a importância do desenvolvimento de estudos em diferentes regiões do Cerrado, visto que a fauna de pequenos mamíferos apresenta grande heterogeneidade na sua distribuição associada à elevada especificidade no uso do habitat. Nosso trabalho abordou a influência do adensamento e do uso do fogo apenas na diversidade taxonômica da comunidade, e recomendamos que os estudos futuros investiguem os impactos desses fatores em outros aspectos da diversidade de pequenos mamíferos, a partir da perspectiva funcional e filogenética.