UNIVERSIDADE FEDERAL DE LAVRAS

NAYARA LETÍCIA REIS

DUNG BEETLES (COLEOPTERA: SCARABAEINAE): TRENDS AND GAPS IN KNOWLEDGE, SPECIES ASSOCIATIONS AND FIRE IMPACTS IN TROPICAL SAVANNAS

LAVRAS - MG
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Prof. Dr. Júlio Neil Cassa Louzada
Orientador

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BESOUROS ESCARABEÍNEOS (COLEOPTERA: SCARABAEINAE): TENDÊNCIAS E LACUNAS NO CONHECIMENTO, ASSOCIAÇÕES DE ESPÉCIES E IMPACTOS DO FOGO EM SAVANAS TROPICAIS

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Dr (ª). Marina Regina Frizzas-UnB
Dr (ª). Raquel Luiza de Carvalho-USP
Dr (ª). Vanesca Korasaki-UEMG
Dr (º). Antônio Cesar Medeiros de Queiroz-UFLA

Dr. Júlio Neil Cassa Louzada
Orientador

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RESUMO

Os padrões de co-ocorrência são cruciais para compreender a estrutura das comunidades e a coexistência das espécies, além de prever os efeitos das perturbações sobre o funcionamento dos ecossistemas. Os escarabeíneos (Coleoptera: Scarabaeinae) são excelentes organismos para testar hipóteses ecológicas e mecanismos de coexistência em ecossistemas tropicais. A coexistência dos escarabeíneos pode ser mediada por fatores como estrutura do habitat, diversidade de nichos e recursos disponíveis e interações bióticas. Em florestas tropicais, a coexistência de várias espécies de escarabeíneos é favorecida pela elevada diversidade de nichos e recursos disponíveis. Enquanto nas savanas tropicais, distúrbios frequentes (ex. fogo) e variações microclimáticas do ambiente podem limitar a coexistência. Apesar dos avanços no conhecimento dos padrões de co-ocorrência de escarabeíneos em ecossistemas tropicais, a compreensão dos efeitos de distúrbios como o fogo no Cerrado, ainda é limitada. Dada a resistência e resiliência dos escarabeíneos ao fogo no Cerrado, e seu papel crucial nesse ecossistema a compreensão dos mecanismos que promovem a coexistência dessas espécies e a recuperação pós-fogo dessas comunidades, pode ser crucial para o desenvolvimento de estratégias de manejo e conservação. Essa tese busca ampliar a nossa compreensão sobre a ecologia e os processos que moldam as comunidades de besouros escarabeíneos em ecossistemas tropicais, com foco nas savanas. A tese está dividida em três partes: A primeira aborda em um contexto global, o conhecimento da ecologia dos besouros escarabeíneos nas savanas tropicais. Neste capítulo, nós realizamos uma revisão sistemática da literatura sobre “besouros escarabeíneos em savanas tropicais”. Esta revisão, nos permitiu identificar as principais tendências e lacunas no conhecimento acerca do tema, fornecendo insights e direcionamentos para pesquisas futuras. A segunda parte da tese, aborda num contexto regional, os fatores que determinam a coexistência das espécies de escarabeíneos em ecossistemas tropicais. Neste segundo capítulo, nós testamos a influência de fatores como tipo de habitat, recursos alimentares e tempo de amostragem sobre os padrões de co-ocorrência das espécies em um mosaico de ecossistemas, incluindo savanas. Nós vimos que habitat e recurso alimentar explicam a coexistência das espécies de escarabeíneos. Além disso, descobrimos que a coexistência das espécies na comunidade é moldada principalmente por processos estocásticos. Estes resultados nos permitiram entender a dinâmica dessas comunidades em ambientes tropicais, e reforçaram a importância de se conservar um mosaico com fisionomias compostas por florestas e savanas, uma vez que esses ambientes são responsáveis por moldar a diversidade de escarabeíneos. A terceira parte, abrange num contexto local, a resposta das comunidades de besouros escarabeíneos ao fogo em ambientes savânicos. Neste terceiro capítulo, nós investigamos a resposta pós-fogo das comunidades de besouros escarabeíneos em áreas abertas de Cerrado. Nós descobrimos que o fogo teve um impacto mínimo na comunidade e na co-ocorrência das espécies. Nós observamos também que tanto processos estocásticos quanto determinísticos moldam a comunidade. Estes resultados nos permitiram contribuir com uma melhor compreensão dos processos ecológicos envolvidos na recuperação de paisagens queimadas no Cerrado, além de fornecer insights para o desenvolvimento de estratégias de manejo e conservação nesse ambiente.

Palavras-chave: Savanas Tropicais. Padrões de Co-ocorrência. Besouros Rola-bosta. Efeitos do Fogo.

ABSTRACT

Patterns of co-occurrence are crucial for understanding community structure and species coexistence, as well as predicting the effects of disturbances on ecosystem functioning. Scarab beetles (Coleoptera: Scarabaeinae) are excellent organisms for testing ecological hypotheses and mechanisms of coexistence in tropical ecosystems. The coexistence of scarab beetles may be mediated by factors such as habitat structure, niche diversity, available resources, and biotic interactions. In tropical forests, the coexistence of various scarab beetle species is favored by the high diversity of niches and available resources. In tropical savannas, frequent disturbances (e.g., fire) and microclimatic variations may limit coexistence. Despite advances in understanding scarab beetle co-occurrence patterns in tropical ecosystems, the understanding of the effects of disturbances such as fire in the Cerrado is still limited. Given the resistance and resilience of scarab beetles to fire in the Cerrado and their crucial role in this ecosystem, understanding the mechanisms that promote the coexistence of these species and post-fire recovery of these communities may be crucial for the development of management and conservation strategies. This thesis seeks to broaden our understanding of the ecology and processes shaping scarab beetle communities in tropical ecosystems, with a focus on savannas. The thesis is divided into three parts: The first part addresses the global context of scarab beetle ecology in tropical savannas. In this chapter, we conduct a systematic review of the literature on "scarab beetles in tropical savannas." This review allows us to identify key trends and gaps in knowledge on the subject, providing insights and directions for future research. The second part of the thesis examines, in a regional context, the factors determining the coexistence of scarab beetle species in tropical ecosystems. In this second chapter, we test the influence of factors such as habitat type, food resources, and sampling time on species co-occurrence patterns in a mosaic of ecosystems, including savannas. We find that habitat and food resources explain the coexistence of scarab beetle species, with the community dynamics primarily shaped by stochastic processes. These results help us understand the dynamics of these communities in tropical environments and emphasize the importance of conserving a mosaic of landscapes composed of both forests and savannas, as these environments shape scarab beetle diversity. The third part covers, in a local context, the response of scarab beetle communities to fire in savanna environments. In this third chapter, we investigate the post-fire response of scarab beetle communities in open Cerrado areas. We find that fire had minimal impact on the community and species co-occurrence. We also observe that both stochastic and deterministic processes shape the community. These results contribute to a better understanding of ecological processes involved in the recovery of burned landscapes in the Cerrado, providing insights for the development of management and conservation strategies in this environment.

Keywords: Tropical Savannas. Co-occurrence Patterns. Dung Beetles. Fire Effects.

SUMÁRIO

PRIMEIRA PARTE

INTRODUÇÃO GERAL

A compreensão dos processos que estruturam as comunidades tem sido um tópico central na ecologia e é fundamental para a realização de pesquisas aplicadas (DIAMOND, 1975). Tradicionalmente, os padrões de co-ocorrência são utilizados para se obter informações sobre as regras de montagem nas comunidades, a coexistência das espécies e a diversidade nos ecossistemas (DIAMOND, 1975; GOTELLI; MCCABE, 2002). Além disso, esses padrões podem auxiliar na previsão dos efeitos das perturbações sobre a dinâmica e o funcionamento dos ecossistemas (ELO *et al.*, 2021; TAVELLA; CAGNOLO, 2018; RIVERA *et al.*, 2021).

Os padrões de co-ocorrência são determinados por processos determinísticos (interações bióticas ou filtros ambientais) e/ou estocásticos (deriva ecológica, nascimentos e mortes) (CHESSON, 2000; CHAVE, 2004; VELEND, 2010; CHASE; MYERS, 2011). Neste contexto, as ocorrências positivas podem ser o resultado de interações entre espécies (ex. mutualismo, comensalismo) ou de requisitos de habitats semelhantes (SIH, 1984; ARAÚJO; ROZENFELD, 2014). Similarmente, as ocorrências negativas podem ser o resultado de relações antagônicas (ex. competição, predação) ou de requisitos de habitats e nichos diferentes (DIAMOND, 1975; ARAÚJO; ROZENFELD, 2014). E por fim, as ocorrências aleatórias, podem ser o resultado de eventos de dispersão, imigração e emigração de espécies (HUBBELL, 2001; CHAVE, 2004).

As informações sobre os mecanismos que determinam a distribuição e os padrões de co-ocorrência das espécies nas comunidades, são a base para o planejamento e a definição de prioridades de conservação (MARGULES; PRESSEY, 2000; WILSON, 2000). Além disso, o conhecimento detalhado e prévio da distribuição das espécies no ambiente é fundamental para que os esforços de conservação sejam eficazes (WILSON, 2000; JETZ *et al.*, 2011).

Os insetos são um grupo altamente diversificado e abundante na região tropical (STORK, 2018; EGGLETON, 2020). Contudo, nos últimos anos tem sido observado um declínio contínuo tanto na abundância quanto na diversidade de insetos nessa região (HALLMANN *et al.*, 2017; RAVEN; WAGNER, 2021; OUTHWAITE *et al.*, 2022). Tais perdas têm sido impulsionadas principalmente pelas mudanças climáticas e pelas alterações nos habitats naturais (HALSCH *et al.*, 2020; WILSON; FOX, 2020; OUTHWAITE *et al.*, 2022). Dada a gravidade documentada, torna-se crucial realizar estudos sobre a ecologia e a distribuição das espécies de insetos, sobretudo em grupos chave que apresentam uma elevada diversidade e, ao mesmo tempo, uma notável vulnerabilidade. Além disso, é importante ressaltar que na região tropical, os esforços de conservação são urgentes (SANKARAN, 2009; DUFFUS *et al.*, 2023).

Os escarabeíneos (Coleoptera: Scarabaeinae) são um grupo de insetos útil para se testar hipóteses ecológicas e mecanismos de coexistência, sobretudo na região tropical (BEIROZ *et al.*, 2019; EDWARDS, 2021; RIVERA *et al.*, 2021; RIBEIRO *et al.*, 2022). Esses organismos, se alimentam de material orgânico em decomposição, principalmente fezes, e a maioria das espécies possuem o hábito de enterrar os recursos no solo, para alimentação e reprodução (HALFFTER; MATTHEWS, 1966; HALFFTER; EDMONDS, 1982; LOUZADA, 2008).

A maior diversidade e abundância de escarabeíneos é principalmente encontrada em ambientes de floresta tropical e savanas (DAVIS *et al.*, 2002; HANSKI; CAMBEFORT, 1991; MILHOMEM *et al.*, 2003; CUNHA; FRIZZAS, 2020). A coexistência das espécies de escarabeíneos nesses ambientes pode ser mediada por uma série de fatores, tais como, estrutura do habitat, diversidade de nichos e recursos disponíveis e interações bióticas (ex. competição, predação, mutualismo) (GILLER; DOUBE, 1994; NICHOLS *et al.*, 2009; CULOT *et al.*, 2013; RIBEIRO *et al.*, 2022). Nas florestas tropicais, a coexistência de muitas espécies de escarabeíneos pode ser principalmente impulsionada pela elevada diversidade de nichos e recursos (ESTRADA *et al.*, 1998; ESTRADA *et al.*, 1999; FEER; HINGRAT, 2005). Em contrapartida, em habitats degradados e sujeitos a distúrbios, como as savanas tropicais, a intensa competição e as variações microclimáticas podem ser as principais causas sobre a composição e a coexistência das espécies (GILLER; DOUBE, 1994; RIBEIRO *et al.*, 2022).

O fogo é um distúrbio natural, recorrente e essencial ao funcionamento dos ecossistemas savânicos ao redor do mundo (BOND *et al.*, 2005; MURPHY; BOWMAN, 2012). Na América do Sul, o Cerrado, por exemplo, possui uma antiga relação histórico-evolutiva com o fogo, e muitos dos processos ecossistêmicos desse ambiente dependem da ação das queimadas para a sua manutenção (COUTINHO, 1990; LEDRU, 2002; DURIGAN; RATTER, 2016). Embora tenha havido um avanço no conhecimento sobre os padrões de co-ocorrência de besouros escarabeíneos em diversos ecossistemas tropicais, incluindo o Cerrado (GILLER; DOUBE, 1994; BEIROZ *et al.*, 2019; EDWARDS *et al.*, 2021; RIBEIRO *et al.*, 2022). A compreensão dos efeitos do fogo sobre a coexistência das espécies de escarabeíneos nas savanas, ainda é escassa. Sendo os diferentes mecanismos subjacentes à reestruturação pós-fogo das comunidades ainda pouco avaliados experimentalmente (NUNES *et al.*, 2019; GONÇALVES *et al.*, 2022).

Os escarabeíneos demonstram grande resistência e resiliência às queimadas no Cerrado (LOUZADA *et al.*, 2010; NUNES *et al.*, 2019; GONÇALVES *et al.*, 2022; REIS *et al.*, 2023). No entanto, a resposta e o grau de sensibilidade às perturbações provocadas pelo fogo são específicos da espécie (LOUZADA, 2010). Esses organismos desempenham uma série de funções e serviços essenciais ao funcionamento, manutenção e restauração de ambientes queimados no Cerrado (NICHOLS *et al.*, 2008; SLADE *et al.*, 2016; DOUBE, 2018; GONÇALVES *et al.*, 2022). Portanto, a compreensão dos mecanismos que impulsionam a coexistência dos escarabeíneos, bem como a recuperação dessas comunidades após a ocorrência do fogo, pode ser útil para o desenvolvimento e o estabelecimento de estratégias de manejo para a conservação da biodiversidade do Cerrado.

Essa tese teve como objetivo geral, ampliar a nossa compreensão sobre a ecologia e os processos que moldam as comunidades de besouros escarabeíneos em ecossistemas tropicais, com foco nas savanas tropicais. A tese está dividida em três capítulos, escritos no formato de artigos científicos. A primeira parte é composta pelo *Capítulo I* e abrange, num contexto global, o conhecimento da ecologia dos besouros escarabeíneos em savanas tropicais. Neste capítulo, realizamos uma revisão sistemática da literatura para identificar o atual estado de conhecimento sobre o tema “besouros escarabeíneos em savanas tropicais", visando identificar as principais tendências e lacunas acerca do tema e fornecendo diretrizes para pesquisas futuras. Nossas principais perguntas foram: i) Como tem sido o avanço nas pesquisas sobre escarabeíneos em savanas tropicais ao longo dos anos? ii) Em qual região está concentrado o maior número de estudos envolvendo besouros escarabeíneos: savanas da América do Sul, savanas afrotropicais ou nas savanas australasianas? iii) Quais os tópicos mais comumente abordados nos estudos? iv) Em quais tipos de ambientes de savana e outros habitats os estudos se concentraram? e, v) Quais as métricas comumente avaliadas pelos pesquisadores nos artigos? Este artigo foi submetido aos *Annals of the Entomological Society of America* (edição especial) e se encontra formatado de acordo com as normas da revista.

A segunda parte é composta pelo C*apítulo II* e abrange num contexto regional, os fatores que determinam a coexistência das espécies de besouros escarabeíneos em um mosaico de ecossistemas, utilizando como proxy as florestas tropicais. Neste capítulo, nós avaliamos como o tipo de habitat, os recursos alimentares e o período de amostragem influenciam os padrões de co-ocorrência das espécies de besouros escarabeíneos. Nós hipotetizamos que, os fatores tipo de habitat, recursos alimentares e tempo de amostragem, poderiam potencialmente determinar a co-ocorrência das espécies observadas. Este artigo foi aceito para publicação na revista *Acta Oecologica* e encontra-se formatado de acordo com as normas da revista.

A terceira parte é composta pelo *Capítulo III* e abrange, em um contexto local, a resposta das comunidades de besouros escarabeíneos ao fogo em ambientes savânicos. Neste terceiro capítulo, nós avaliamos a resposta pós-fogo das comunidades de besouros escarabeíneos em áreas abertas de Cerrado, com foco na riqueza, composição e padrões de co-ocorrência das espécies. Nós hipotetizamos que o fogo teria um efeito mínimo e de curto prazo sobre a riqueza e composição das espécies. E que os padrões de co-ocorrência seriam similares entre áreas queimadas e não queimadas. Além disso, nós hipotetizamos que haveria uma recuperação conjunta entre a comunidade de escarabeíneos e a cobertura da vegetação do solo após o fogo. Este artigo encontra-se formatado de acordo com as normas da revista científica *Acta Oecologica*.

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Trends and knowledge gaps in the ecology of dung beetles (Coleoptera: Scarabaeidae) in tropical savannas

REIS N. L [1*], PABLO A. LÓPEZ-BEDOYA [1,2,], LOUZADA J [1].

[1] Laboratório de Ecologia e Conservação de Invertebrados (LECIN), Departamento de Ecologia e Conservação, Instituto de Ciências Naturais, Universidade Federal de Lavras, CEP 37.203-202, Lavras (MG), Brasil.

[2] Programa de Pós-graduação em Entomologia, Departamento de Entomologia (DEN), Universidade Federal de Lavras, CEP 37.203-202, Lavras (MG), Brasil.

*Autor Correspondence: Nayara Letícia Reis, Departamento de Ecologia e Conservação, Universidade Federal de Lavras (UFLA), PO Box 3037, CEP 37202-203, Lavras, MG, Brasil. e-mail: nayara.reis015@gmail.com; nayara.reis@estudante.ufla.br

Abstract

Tropical savannas among the world's most biodiverse ecosystems, face threats like land-use change, and climate change impacting fire regimes. These threats, coupled with knowledge gaps in biodiversity, hamper conservation efforts in these regions. Dung beetles, vital for understanding land-use impact on savannas, lack comprehensive studies. We conducted a systematic review of the current state of knowledge regarding dung beetles in tropical savannas, encompassing the geographical distribution, research topics, investigated habitats, and key metrics assessed in the studies. Our systematic review reveals a focus on Neotropical regions, particularly Brazil, leaving a significant dung beetle ecology knowledge deficit in Afro-tropical regions and Australian savannas. Most articles focused on savanna grasslands, savanna woodlands, and anthropic habitats such as introduced pastures. Most research has assessed community patterns, habitat replacement, and degradation, emphasizing metrics such as abundance, richness, and species composition. However, dung beetle behavior, reproductive biology, and physiological aspects across all zoogeographical regions remain poorly understood. This knowledge gap poses a barrier to effective management and conservation strategies in tropical savannas. Given the high diversity and ecological importance of dung beetles in savannas, urgent research efforts are essential for these environments. Emphasizing the need for comprehensive metrics, including biomass, morphometrics, and ecological functions of dung beetles, is crucial to enhancing understanding of dung beetles' significance and roles within ecosystems. In conclusion, addressing these knowledge gaps is crucial for the development of substantiated conservation strategies in the face of the growing threats to tropical savannas.

Keywords: Tropical Savannah, Scarabaeinae, Systematic review, Biodiversity conservation.

Resumo

As savanas tropicais, entre os ecossistemas mais biodiversos do mundo, enfrentam ameaças como alterações no uso da terra e mudanças climáticas que impactam os regimes de incêndios. Essas ameaças, aliadas a lacunas no conhecimento sobre biodiversidade, prejudicam os esforços de conservação nessas regiões. Os besouros rola-bosta, cruciais para entender o impacto do uso da terra nas savanas, carecem de estudos abrangentes. Realizamos uma revisão sistemática do estado atual do conhecimento sobre besouros rola-bosta em savanas tropicais, abrangendo a distribuição geográfica, temas de pesquisa, habitats investigados, e principais métricas avaliadas nos estudos. Nossa revisão sistemática revela um foco nas regiões Neotropicais, especialmente no Brasil, deixando uma significativa lacuna no conhecimento da ecologia dos besouros rola-bosta nas regiões Afro-tropicais e nas savanas australianas. A maioria dos artigos se concentrou em pastagens de savana, florestas de savana e em habitats antropizados, como as pastagens introduzidas. A maior parte das pesquisas avaliou padrões de comunidade, substituição e degradação de habitats, enfatizando métricas como abundância, riqueza e composição de espécies. No entanto, o comportamento, a biologia reprodutiva e os aspectos fisiológicos dos besouros rola-bosta em todas as regiões zoogeográficas permanecem pouco compreendidos. Essa lacuna de conhecimento representa uma barreira para estratégias eficazes de gestão e conservação nas savanas tropicais. Dada a alta diversidade e importância ecológica dos besouros rola-bosta nas savanas, esforços de pesquisa urgentes são essenciais para esses ambientes. Destacamos a necessidade do uso de métricas, incluindo biomassa, morfometria e funções ecológicas dos besouros rola-bosta, para aprimorar a compreensão de sua importância e papéis nos ecossistemas savânicos. Em conclusão, abordar estas lacunas de conhecimento é crucial para o desenvolvimento de estratégias de conservação fundamentadas face às ameaças crescentes às savanas tropicais.

Palavras-chave: Savanas Tropicais, Scarabaeinae, Revisão sistemática, Conservação da biodiversidade.

1. Introduction

Tropical savannas are recognized as one of the most biodiverse ecosystems, globally, characterized primarily by the presence of endemic species (Ratter 1997, Myers et al. 2000, Andresen et al. 2015, Murphy et al. 2016). These savannas, with their rich biodiversity, offer various benefits to humanity, including food production, water supply, and carbon storage and regulation (Greiner et al. 2009, Marchant 2010, Williams et al. 2022).

Despite their significant biodiversity value, tropical savannas are among the most threatened natural systems on a global scale (Myers et al. 2000, Murphy et al. 2016). Rapid land-use expansion, and climate change, both contribute to alterations in fire frequency have been identified as the primary threats (Beerling and Osborne 2006, Hoffman and Vogel 2008, Andersen et al. 2012, Williams et al. 2022). Over the last two decades, savannas in South America such as the Cerrado, have already lost approximately 50% of their original area to crops like soy, sugarcane, corn, and pasture for livestock (Klink and Machado 2005, Gomes et al. 2019, Aragão et al. 2022, Tovar et al. 2023).

It is well-established that the conversion of natural savanna landscapes into anthropogenic environments leads to adverse impacts on biodiversity, ecosystem functioning, and consequently, human well-being (Fischer and Lindenmayer 2007, Watson et al. 2016, López-Bedoya et al. 2022). Hence, conservation efforts in savannas of utmost importance (Overbeck et al. 2022, Williams et al. 2022), given that the quantity of areas designated for conservation remains disproportionately low (Watson et al. 2016, Lewis et al. 2022), with only 19.7% of tropical savannas currently protected (Williams et al. 2022).

Despite the availability of global maps on species richness of important taxonomic groups and notable advances in biodiversity knowledge, there are still significant gaps regarding the global distribution of biodiversity and its conservation importance (Jenkins et al. 2013, Kier et al. 2005, Murphy et al. 2016). When it comes to tropical savannas, we observe a neglected and overshadowed knowledge of the biodiversity of these ecosystems (Parr et al. 2014, Murphy et al. 2016). In many instances, conservation endeavours have been less effective on tropical savannas, mainly due to the dearth of biological information or the fragmentation of knowledge concerning biodiversity (Sankaran 2009, Hortal et al. 2015, López-Bedoya et al. 2023). In this context, it is imperative to evaluate the current state of knowledge regarding biodiversity in savannas, particularly in taxonomic groups exhibiting high diversity and extreme vulnerability to habitat loss, which also play pivotal ecological roles in these ecosystems.

Dung beetles (Coleoptera: Scarabaeinae) represent a widely distributed insect group with a significant presence in tropical savannas (Hanski and Cambefort 1991). These organisms constitute the soil macrobiota of savannas, with the majority of adults primarily utilizing mammal dung as their food source and reproductive medium (Halffter and Matthews 1966, Halffter and Edmonds 1982). They play a fundamental role in the natural management of organic matter by significantly contributing to the removal, burial, and decomposition of substantial quantities of dung (Hanski and Cambefort 1991, Anduaga 2004, Nervo et al. 2014). Furthermore, through their dung resource management activities, dung beetles perform a series of essential functions and services crucial for the maintenance and functioning of the savanna ecosystem. These services include nutrient cycling and soil aeration (Nichols et al. 2008, Doube 2018), parasite control (Ridsdill-Smith et al. 2009), secondary seed dispersal (Kunz and Krell 2011), and the mitigation of greenhouse gas emissions (specifically, methane and nitrous oxide) originating from dung (Slade et al. 2016).

We conducted a systematic literature review to assess the current state of knowledge regarding "Dung Beetles in Tropical Savannas." Through an examination of research trends and gaps in this field, our objective was to enhance our comprehension of the interplay between dung beetles and savanna environments, elucidating their significance and roles therein, and providing guidance for future investigations. Specifically, we sought answers to the following inquiries: i) How has research evolved over time? ii) In which regions are most studies concentrated: South American savannas, Afrotropical savannas, or Australian savannas? iii) What are the prevailing subjects of inquiry in studies on dung beetles in tropical savannas? iv) Which types of savanna environments and other habitats were the studies focused on? and v) What are the commonly assessed metrics in the literature?

2. Material and Methods

2.1 Selection of tropical savannas ecosystems

To delineate the classification and the geographical positioning of tropical savannas, we adopted the framework proposed by Jung et al. (2020) and Davis et al. (2002) respectively. Jung et al. (2020) employed the International Union for Conservation of Nature (IUCN) habitat classification scheme to categorize savanna habitats, while Davis et al. (2002) utilized species distribution of dung beetles to delineate zoogeographical zones. Consequently, we focused exclusively on savannas located between 30° north and south latitudes, encompassing both tropical and subtropical regions, characterized by the highest abundance of dung beetle species.

According to Jung et al. (2020), savannas represent a native and transitional environment between grasslands and forests, characterized by a grass-dominated layer with scattered tree and shrub cover. Within this definition, we employed two classifications: *savanna woodlands* for areas with a closed canopy; and *savanna grasslands* for areas with an open canopy, akin to the campos limpos found in the Brazilian savannahs.

2.2 Data Search

We conducted the bibliographic search in the Web of Science, Scopus, and Scielo databases, following the PRISMA methodology (Moher et al. 2009) (see Figure S1). We defined a minimum time limit for article selection, including in this review only those published after the year 1991, as this is the year when the book containing the chapter on dung beetles and savannas was published (see Hanski and Cambefort 1991). Additionally, we chose to include articles published up until March 2023 as our maximum time frame. We looked for articles that included at least one of the keywords mentioned in the following equation in their titles, abstracts, and/or full texts: ("dung beetle*" OR scarabaei* OR scarab* OR "scarab beetle*" OR "coprophagous beetle*" OR "necrophagous beetle*") AND (savanna* OR "tropical grassland" OR "native grassland*" OR grassland* OR "native pasture" OR "dry forest" OR "rupestrian field*") in three languages: English, Portuguese, and Spanish (see supplementary material). These terms were selected as they are the most used in the scientific articles to refer to the taxonomic group and biomes of our interest.

2.3 Literature inclusion and exclusion criteria

We included in the database only articles that met the following criteria: i) papers published in indexed journals. By selecting indexed articles, we improved the review's information quality. That's because, these articles have undergone rigorous peer review, ensuring clear and replicable method descriptions, along with accurate and reliable results; ii) papers that address at least one native savanna area (i.e., woodlands or grassland savannas) in their methodology, which may also include comparisons with other natural and/or anthropogenic systems (i.e., non-savanna environments, pasturelands etc.). This ensures a more comprehensive and contextualized analysis of the relationship between dung beetles and the savanna environment; iii) papers whose study area is located within the pre-defined tropical and subtropical zone (according to Davis et al. 2002 and Jung et al. 2020). This geographical restriction is essential to ensure that the studies are focused on regions with specific savanna-like climate and vegetation characteristics, allowing the results obtained to be consistent and applicable to these regions.

We initially identified a total of 1.056 articles in the accessed databases (Figure S1, supplementary material). As an exclusion criterion, we removed the grey literature, such as thesis, monographs, unpublished dissertations, as well as review articles, book chapters, and conference abstracts. Subsequently, we eliminated 467 duplicates, i.e., documents that appeared more than once in different databases (Figure S1, supp.). We then evaluated the abstracts of 589 papers, of which 354 did not meet the proposed criteria and were consequently excluded. Finally, we thoroughly reviewed the full text of 235 papers, ultimately excluding 61 papers that do not align with the study's objectives. After Following this rigorous process, our final database consisted of 174 papers (please refer to Figure S1 and Table S1 supp. for further details).

2.4 Data extraction

For each paper, we extracted the following variables: i) year of publication; ii) geographical information (country and zoogeographical region and geographical coordinates); iii) study topic; iv) type of sampled habitat (i.e., savanna grasslands, introduced pastures, agricultural areas), categorized to according as follows: *pasturelands*: encompassing secondary and permanent grasslands, sometimes subjected to treatments like fertilization or re-seeding (e.g., introduced pastures); *agricultural areas*: encompassing large-scale cultivation of crops, including tree and shrub plantations (e.g., Eucalyptus), as well as the cultivation of crops such as coffee, soybeans, corn, and sugarcane; *urban areas*: defined as metropolitan and commercial areas predominated by asphalt, concrete, and rooftops, including houses, buildings, parks, and the like; *unidentified habitats*: covering areas that were either not identified by the authors or lacked clear information about the specific habitat characteristics. And finally: v) assessed metrics (i.e., richness, abundance, species composition, biomass). Study topics were categorized after analyzing the papers into three main categories: *Ecosystem, Community,* and *Population.* Within the *Ecosystem* category, we have: i) "Habitat replacement" for papers that assess the effects generated by the disturbance of natural areas by human actions, where there are changes in land use and replacement of natural area by an anthropized environment; and ii)

"Habitat degradation" for papers that assess the effects generated by the disturbance of natural areas by human actions or natural events. Here, natural habitats are still maintained, with no change in land use, but with impacts leading to degradation (e.g., deforestation, exotic species etc.). Within the *Community* category, we have: i) "Community patterns" for papers that assess the effects of biotic and/or abiotic factors on different parameters of the dung beetle community; ii) "Species distributions" for papers that address the geographic distribution of dung beetles; and iii) "Inventories" for studies whose objective is to characterize the dung beetle fauna of a specific location. Within the *Population* category, we have: i) "Behavior" for papers that assess patterns of behavior and activity of dung beetles; ii) "Reproductive biology" for papers that describe aspects related to the reproductive biology of species; iii) "Physiology" for papers that assess aspects related to the physiology of dung beetles; and iv) "Bait attractivity" for papers that address the selection and consumption of food resources by dung beetles.

Each paper may address more than one topic at the same time, and these topics may be nested within one or more categories. For example, papers that address both "Community patterns" and "Habitat replacement" (see Jankielsohn et al. 2001, Tovar et al. 2023, Table S1 supp.). Additionally, a paper may have been conducted in more than one different habitat, for example, papers that evaluate dung beetles in "Natural Pastures" and "Forest plantation" (see Chaves et al. 2017, Davis et al. 2005, Gebert et al. 2019, Table S1 supp.). Finally, papers may evaluate various metrics.

3. Results

3.1 General Trends

We found 174 papers on dung beetles in tropical savannas (Table S1, supplementary material). These papers were conducted between the years 1991 to 2023 (see Figure 1). The number of papers varied over years (Figure 1). Most studies were conducted in the Neotropical region (125 articles), followed by the Afrotropical region (49), and Australasia region (2 articles) (Figure 2). The studies were distributed across 21 countries, with 12 countries in the African continent, eight in the Neotropical region (corresponding to Central and South America), and one in Australasia region (Figure 2). Brazil had the highest number of publications (81 articles), accounting for approximately 46% of the total recorded (see Figure S2, supplementary material). Following Brazil, we had Colombia and South Africa, both with 28 articles each, representing around 16% of the total (Figure S2, supp.). Among the less represented countries were Australia (about 1%), Ecuador, Nicaragua, and Uganda (each less than 1%) (Figure S2, supp.).

3.2 Study topics, habitat types, and evaluated metrics

The major proportion of papers evaluated "Community patterns" (84%), followed by studies assessing the effects of "Habitat replacement" (33%), "Bait Attractivity" (23%), and "Habitat degradation" (17%) on dung beetles (Figure 3). The topics "Species distributions" (11.5%), "Inventories" (8.6%), "Behavior" (8.6%), "Reproductive Biology" (2%), and "Physiology" (1.7%) were less common in the articles (Figure 3).

When we reviewed the type of habitat, we found many studies conducted in savanna grasslands and savanna woodlands (both at 64%) (Figure 4), followed by studies in Pasturelands (about 30%). Agricultural areas were represented in 23% of the studies (Figure 4). Urban areas were studied in a smaller percentage of studies (about 1%), while approximately 2% of the studies either lacked sufficient data or the information about the study area was absent.

We observed that abundance was the most evaluated metric in nearly all studies (about 98%), followed by Richness (90%), Species Composition (59%), Diversity Index (58.6%), and Functional Diversity (41%) (Figure 5). The least evaluated metrics were, respectively, Biomass and Morphometry, both represented in 19% of the studies, followed by Ecological Functions (11%). Studies assessing "Descriptive Observations" of species were less common (about 7%) (Figure 5).

4. Discussion

We highlight notable trends and knowledge gaps about dung beetles in tropical savannas, offer recommendations for future research, and discuss the implications of these findings for conserving these environments. However, the understanding of the ecology and diversity of dung beetles in savannas is still quite limited, especially in Afrotropical and Australasian regions. Most articles have focused on native savanna grasslands and forests, as well as introduced pastures, primarily assessing the effects of habitat substitution and degradation on community patterns. We noted a limited knowledge regarding issues related to behavior, reproductive biology, and physiology of dung species across all zoogeographic regions. Finally, we found that the main metrics used were abundance, richness, and species composition, and the complementary metrics such as biomass, morphometrics, and ecological functions were less used.

Neotropical, Afrotropical, and Australasian Savannas

The majority of studies were conducted in the Neotropical region, and a considerable portion was concentrated in Brazil. This pattern is interesting, especially because Brazil is home to two important savannah ecosystems. The Cerrado is considered the largest savanna in South America and the most biodiverse in the world (Klink and Machado 2005, Mendonça et al. 2008). The Pantanal harbors a great diversity of fauna and flora distributed across extensive flooded savannah fields (Junk et al. 2006).

It is important to emphasize that we have identified a knowledge gap in the ecology and diversity of dung beetles in other regions of South America, indicated primarily by the low number of articles recorded in Colombia, Mexico, Argentina, and Bolivia. These information gaps have been similarly identified in other Neotropical countries with savanna ecosystems (Noriega et al. 2015), as well as in other biomes with high biodiversity and vulnerability of natural ecosystems (Lopez-Bedoya et al. 2023).

We did not find any records of articles in the savannas of Venezuela. Venezuela and Colombia are home to the second largest region dominated by savannas in South America, known as the Llanos (Medina and Silva 1990, Boval et al. 2016). Over decades, the Llanos have been impacted by the expansion of agriculture and livestock farming, estimated that approximately 15.5% of these ecosystems have already been replaced (Huertas 2014, Eufêmia et al. 2019).

We recorded a few studies in the Afrotropical region, and these records were mainly concentrated in South Africa. Although the taxonomy of dung beetles is relatively well-known in African savannas, the number of ecological studies in these regions is still low (Hanski and Cambefort 1991, Giller and Doube 1994). Additionally, we observed that little articles has been conducted on the use of these organisms as indicators of habitat quality, especially in South African grasslands (McGeoch et al. 2002, Tocco et al. 2018). This pattern is intriguing, as there is a growing invasion of commercial agriculture and livestock farming in these regions, where a significant portion of savannas has already had their vegetation modified for crop cultivation and establishment of livestock (Davis 2002, Davis et al. 2012, Lascaleia et al. 2018).

Finally, we observed that the ecology of dung beetle communities, especially in the grasslands of the Australian savanna, remains poorly understood (Doube and MacQueen 1991, Carvalho et al. 2020). These data are relevant, considering that Australian savannas cover about 25% of the country's total land area and host many native dung beetle species, with over 500 species already identified (Faleiro and Neto 2009).

Dung beetles' knowledge and Tropical Savannas Conservation

Dung beetles are commonly found in the neotropical region, where there are high levels of diversity (Davis et al. 2002). Consequently, many ecological studies are focused on this region (Doube 1991, Hanski and Cambefort 1991). However, more studies on dung beetles are needed in other regions such as the Afrotropical and Australian, and in some under-sampled locations in South America. This is because such studies help improve our understanding of species composition and conservation needs in these regions.

Furthermore, it is known that for any conservation strategy to be effective, it is essential to have prior understanding of how diversity is structured within the area of interest (McNaughton 1994, Sankaran 2009). Therefore, gaps in the knowledge of dung beetle ecology and diversity can present an obstacle to the implementation of management and conservation plans, as well as hinder the identification of priority areas for savanna conservation.

Finally, we believe that the lack of information about dung beetles, particularly in Latin American countries such as Colombia, Venezuela, and Bolivia, for example, can be attributed to various factors, including logistical constraints related to accessibility to study sites, as well as a lack of financial investment and adequate research infrastructure (Ciocca and Delgado 2017, Barlow et al. 2018, Carvalho et al. 2023).

Trends and gaps in Study topics

The most evaluated topics in the articles were community patterns, followed by studies testing the effects of habitat replacement and degradation on dung beetles. Tropical regions face the highest rates of land use change and degradation (Barlow et al. 2018), with agriculture and livestock farming being the primary drivers of transformation in tropical savannas (Overbeck et al. 2022, Tovar et al. 2023). Therefore, it is expected that researchers have directed their studies towards understanding the impacts of habitat conversion on dung beetle communities. Additionally, it is common for many researchers to use dung beetles for comparisons between native and anthropogenic environments, as these organisms have been considered excellent bioindicators, providing an efficient way to assess the impacts of land use changes on biodiversity and ecosystem integrity (McGeoch et al. 2002, Spector 2006, Gardner et al. 2008, Carvalho et al. 2020).

Our review identified a lack of knowledge regarding the behavior, reproductive biology, and physiology of dung beetle species in tropical savannas. Pioneering works conducted by Halffter and Matthews (1966) and Halffter and Edmonds (1982) on the natural history and nesting behaviors of these species were instrumental in advancing our understanding of the underlying mechanisms of individual species' responses to their environment. We emphasize the importance of conducting further studies in this regard, particularly because this foundational information, coupled with research examining the responses of dung beetle communities to changes in land use, can form an integrated system, enabling a deeper understanding of both the persistence and loss of biodiversity in for example, savannas modified by human activity.

Habitats type

Most of the articles has been conducted in savanna grasslands and savanna woodlands, followed by anthropogenic environments such as introduced pastures, agricultural areas (e.g., Eucalyptus plantation, corn, coffee, soybean crops, among others), and lastly urban areas. These results are expected given that natural tropical savanna grasslands and woodlands cover an extensive area across the Earth's surface (Boval et al. 2016, Hutley and Setterfield 2019). Additionally, upon analysing the articles, we observed that the majority of authors made comparisons of dung beetle diversity between native savanna areas (grasses and woodlands) and anthropogenic environments (introduced pastures and eucalyptus plantations). Livestock farming is the most widely distributed land use sector, and pastures cover about 30% of the planet's surface (Bruinsma 2017).

In Brazil, for example, most studies focused on both native and exotic pastures in the Cerrado and Pantanal regions (Almeida et al. 2011, Correa et al. 2016, Correa et al. 2019, Macedo et al. 2020). Besides, the conversion of native pastures into exotic pastures for cattle breeding and feeding is predominant, especially in the Pantanal region, which currently supports the second largest cattle herd in Brazil (5.8 million individuals). In addition to livestock farming, intensive agriculture has been growing in Brazil, and the Brazilian Cerrado has become an important source of crops like soybeans, corn, cotton, and sugarcane over the past 30-50 years (Klink et al. 2020), along with livestock and forest monoculture activities (Lahsen et al. 2016, Velazco et al. 2019). Therefore, understanding the impacts of substitution and degradation on dung beetle communities in these two important South American savannas is fundamental, as such research can provide a foundation for conservation and management policies to protect biodiversity in these environments.

We identified a lack of studies assessing the effect of urbanization on dung beetle communities. In this context, more efforts should be directed in this regard, as significant savanna ecosystems like the Cerrado, for example, have been facing high rates of urbanization (Duarte and Leite 2020). Especially since important agricultural centers are located near the areas of Cerrado in Brazil, such as the central-western region (Goiás state) (Chaveiro 2010, Duarte and Leite 2020). It has been reported that the expansion of urban center can have a strong influence on the structure of dung beetle communities, primarily leading to species loss (Korasaki et al. 2012, Frizzas et al. 2020). Therefore, dung beetles can serve as important key components for monitoring biodiversity response to urbanization, and consequently contribute to the success of conservation efforts.

Evaluated Metrics

Abundance and species richness were the most commonly assessed metrics in the studies, followed by species composition, diversity index, and functional diversity. Taxonomic metrics such as abundance, richness, and species composition are traditionally used because they are relatively easy to understand and can be obtained through passive sampling without additional manipulations, measurements, or data acquisition (Saint-Germain et al. 2007, López-Bedoya et al. 2023). Furthermore, these metrics have been employed to assess the impacts of various anthropogenic disturbances on dung beetle communities. However, it is important to salient these metrics, as they provide limited information and may not be good predictors of species' importance in ecosystems (Hooper et al. 2005, Magurran 2016).

Complementary metrics related to functional attributes and species characteristics (e.g., biomass) can be more informative and allow for the investigation of, for example, the relationship and contribution of different dung beetle species to ecosystem functioning (Noriega et al. 2018, Castro-Arrazola et al. 2022). Although there has been an increase in the use of biomass in dung beetle studies in recent decades (Gillett and Barr 2018, Correa et al. 2019, Nependa et al. 2021), This was one of the least assessed metrics in the studies, followed by Morphometry. Cultid-Medina and Escobar (2016) suggest that biomass can provide complementary information when the objective is to assess, for example, the impacts of land use on dung beetle community structure, as well as to describe the functional role of dung beetles in ecosystems. Additionally, biomass is considered a key variable for understanding energy flow, productivity, and food chain dynamics (Brown et al. 2004, Saint-Germain et al. 2007).

Although the research evaluating dung beetles from a functional perspective is growing. Functional diversity was assessed in just under half of the articles recorded in this review. The dung beetles have been considered a good functional model and exhibit high plasticity in response to environmental conditions and resource availability (Audino et al. 2014). However, in most of the articles with dung beetles they still many limitations in functional diversity knowledge, linked to the number of functional traits assessed, obtaining categorical traits, and the absence of measurements, as well as the non-inclusion of physiological information about the species (Silva and Hernandez 2015, Griffiths et al. 2016).

Finally, few studies have assessed the ecological functions of dung beetles in the environment, which indicates that knowledge and use of this type of metric are still quite limited. Arellano et al. (2023) observed similar data, recording only 18 articles that evaluated at least one function of beetles in pastures. Additionally, most of the available information relies on indirect measurements or the use of proxies to correlate diversity with ecosystem functioning, rather than being performed experiments (Noriega et al. 2018). These data are concerning, as quantifying and understanding the ecological functions performed by dung beetles form the basis for measuring ecosystem functioning and comprehending the impacts of land use changes on the biodiversity (Nichols et al. 2008, Braga et al. 2013).

Directions for Future Research

In view of the trends and gaps observed regarding the ecology of dung beetles in tropical savannas, our review emphasizes the importance of prioritizing studies in less explored regions such as some countries in South America, as well as the Afrotropical and Australasian regions. The lack of information in these locations may hinder the generalization of research results and impede the direction of data in the application of conservation strategies. In this context, we also recommend that more studies be conducted in critically threatened savanna locations, particularly concerning the assessment of dung beetle biodiversity in savannas affected by urban and agricultural expansion. Understanding the impacts of these activities on dung beetles may be essential in clarifying the response of dung beetles to degradation and providing insights into guiding conservation strategies in these areas.

We also suggest that researchers should expand the knowledge on the behavior, reproductive biology, and physiology of dung beetle species in savannas, as well as make use of complementary metrics such as biomass, ecological functions, and functional diversity. These aspects are crucial for understanding the individual responses of dung beetles to the environment, and of their contributing to the functioning of savanna ecosystems.

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Author Contribution

NLR: Conceptualization; Data curation; Investigation; Methodology; Formal analysis; Validation; Visualization; Project administration; Writing - original draft; Writing - review & editing. PAB: Conceptualization; Data curation; Investigation; Methodology; Validation; Project administration; Visualization; Writing – original draft; Writing- review & editing. JL: Conceptualization; Funding acquisition; Investigation; Methodology; Project administration; Resources; Supervision; Validation; Writing - original draft; Writing - review & editing.

Conflict of Interest

The authors declare they did not have a financial or commercial relationship could be construed as a potential conflict of interest in this research.

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FIGURE LEGENDS

Figure 1. Temporal trend in the number of published articles with dung beetles in tropical savannas over the years. The y-axis indicates the number of articles recorded over the years. The x-axis represents the time scale for data collected between 1991 and 2023.

Figure 2. Map of the geographic distribution of articles on dung beetles in tropical savannas. The red point on the map represents each recorded paper, totalling 174 points and some locations include more than one paper.

Figure 3. Distribution of registered studies by study topic. The y-axis indicates the list of recorded topics. The colours of the circles separate the topics according to each category (pink for Ecosystem, blue for Community, and red for Population). The x-axis represents the percentage of studies per studied topic. The size of the circles varies according to the percentage of reference (20% to 80%) indicated to the right of the graph.

Figure 4. Percentage and number of articles by type of habitat studied. The y-axis represents the types of habitats. The x-axis indicates the percentage of studies calculated in relation to the total number of studies (n=174) for each habitat. The number of studies per habitat is indicated next to the bars.

Figure 5. Distribution and number of studies by evaluated metric. The y-axis indicates the types of metrics evaluated in the studies. The x-axis indicates the percentage of studies recorded for each metric, calculated in relation to the total number of studies (n=174). The values of the number of studies per metric are indicated next to the bars.

FIGURES

Figure 1

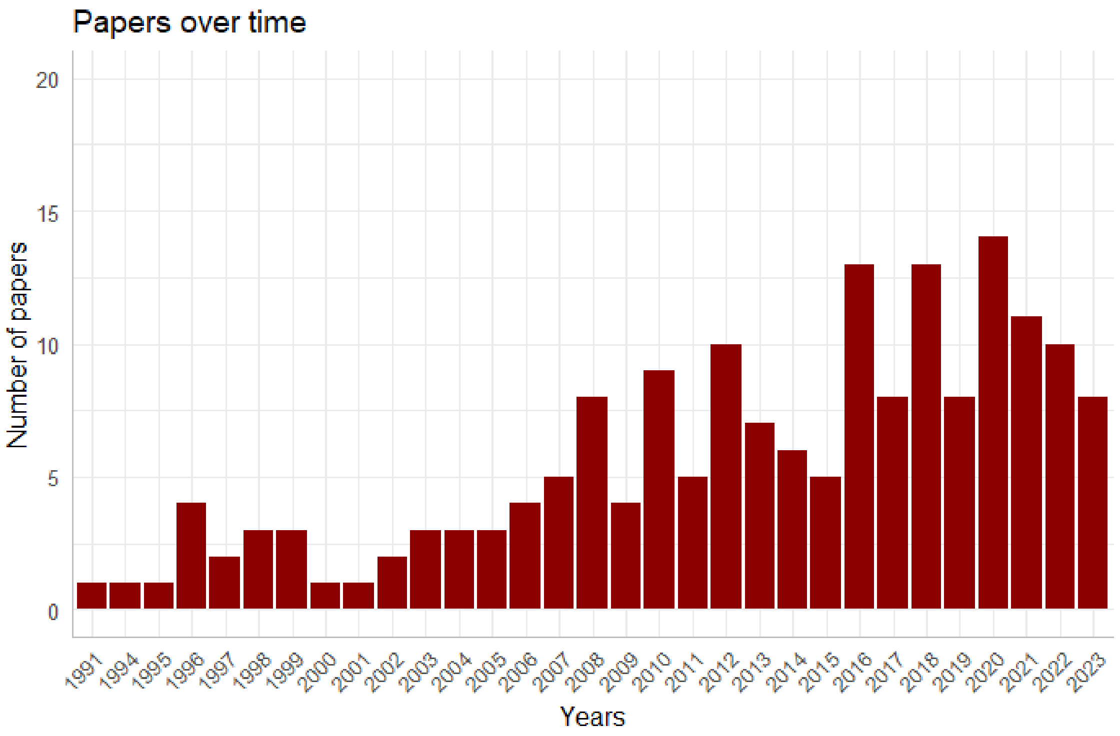
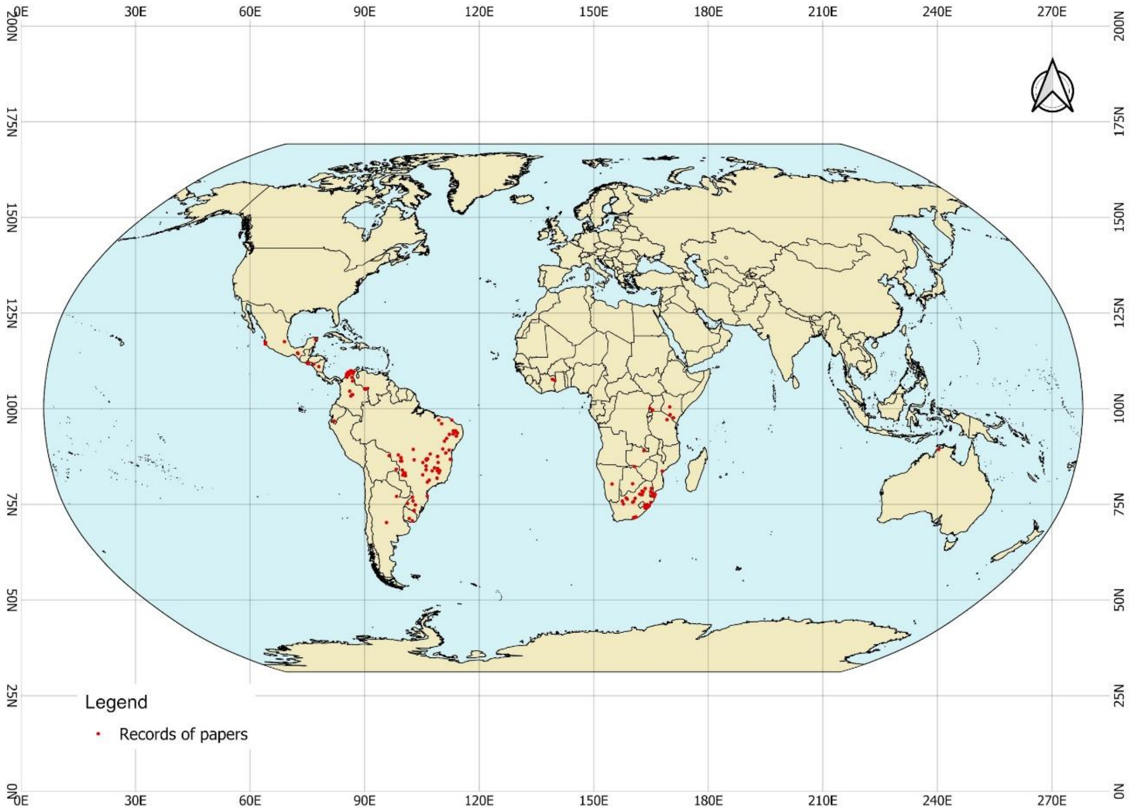


Figure 2


0E
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60E
90E
120E
150E
180E
210E
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50N
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Legend
Records of papers

Figure 3

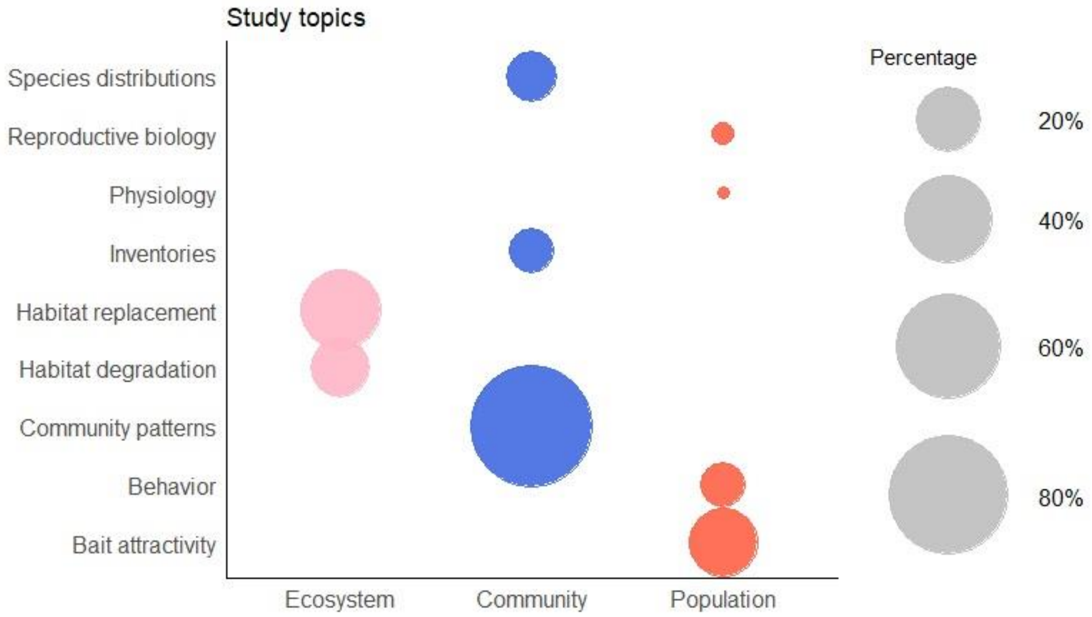

Study topics
Species distributions
Reproductive biology
Physiology
Inventories
Habitat replacement
Habitat degradation
Community patterns
Behavior
Bait attractivity
Ecosystem
Community
Population
Percentage
20%
40%
60%
80%

Figure 4

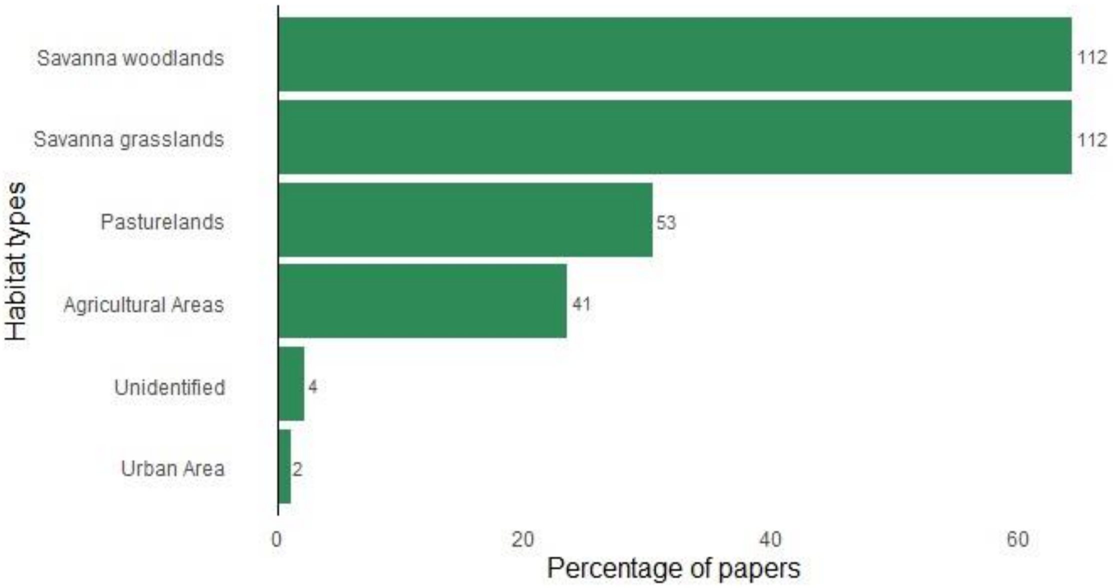
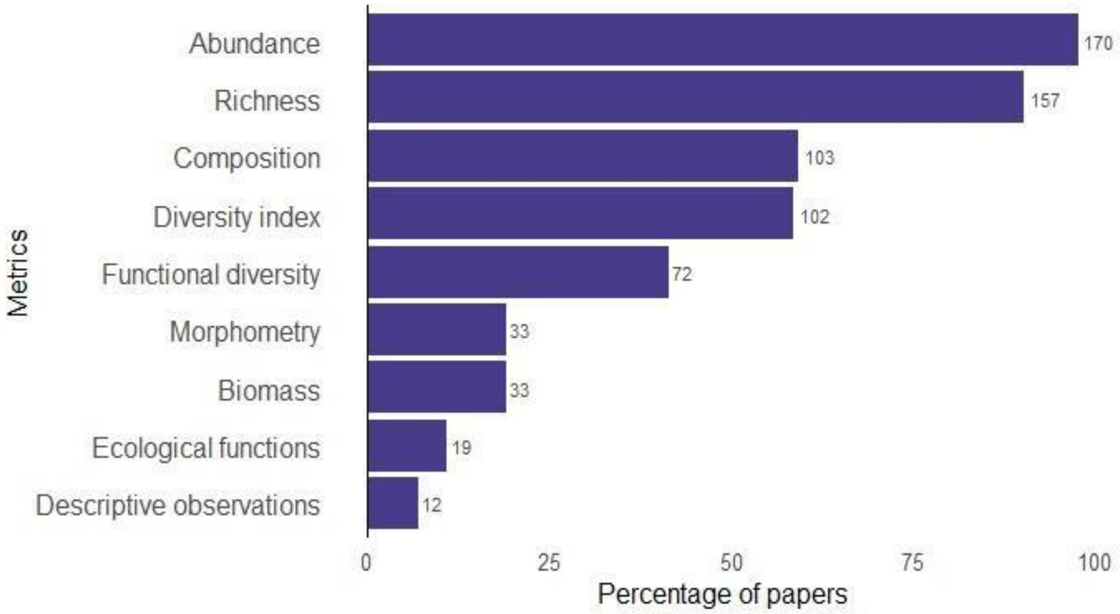

Habitat types
Savanna woodlands
Savanna grasslands
Pasturelands
Agricultural Areas
Unidentified
Urban Area
112
112
53
41
4
2
0
20
40
60
Percentage of papers

Figure 5


Abundance
Richness
Composition
Diversity index
Functional diversity
Morphometry
Biomass
Ecological functions
Descriptive observations
Metrics
170
157
103
102
72
33
33
19
12
0
25
50
75
100
Percentage of papers

Supplementary material

Trends and knowledge gaps in the ecology of dung beetles (Coleoptera: Scarabaeidae) in tropical savannas

REIS N. L [1*], PABLO A. LÓPEZ-BEDOYA [2, 3], LOUZADA J [1].

[1] Laboratório de Ecologia e Conservação de Invertebrados (LECIN), Departamento de Ecologia e Conservação, Instituto de Ciências Naturais, Universidade Federal de Lavras, CEP 37.203-202, Lavras (MG), Brasil.

[2] Programa de Pós-graduação em Entomologia, Departamento de Entomologia (DEN), Universidade Federal de Lavras, CEP 37.203-202, Lavras (MG), Brasil.

[3] Grupo de Ecología y Diversidad de Anfibios y Reptiles, Facultad de Ciencias Exactas y Naturales, Universidad de Caldas, Manizales, Colombia.

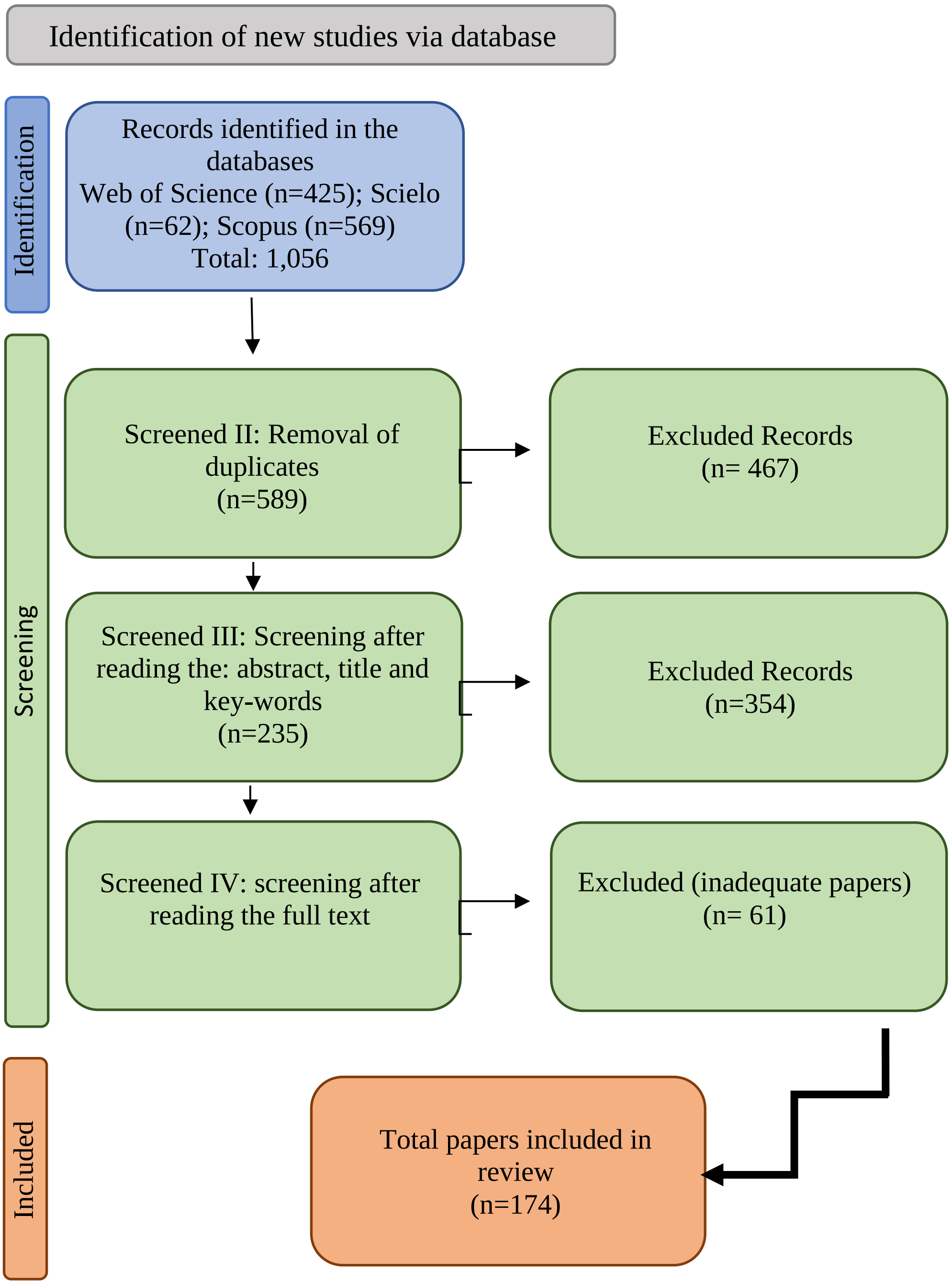


Figure S1- Diagram adapted from the PRISMA methodology (Moher et al., 2009).

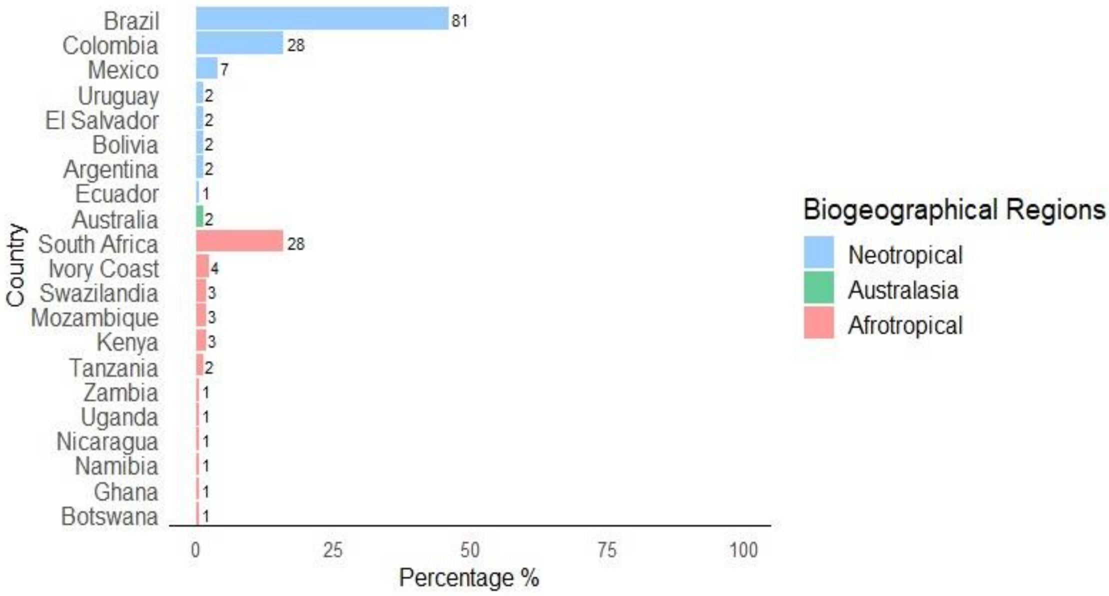


Figure S2 - Graphic of the distribution of papers by country and by biogeographic region (Neotropical, Afrotropical, and Australasia). The y-axis indicates the list of countries where the papers were recorded. The values of the number of registered papers for each country are shown next to the bars. The x-axis represents the percentage of papers per country, calculated in relation to the total number (n=174).

Table S1- Summary of the studies used in this systematic review, where publication year, country, zoogeographic region, study topic, covers and evaluated metrics are detailed. Study topics: (A) Community patterns, (B) Habitat degradation, (C) Species distribution, (D) Behavior, (E) Physiology, (F) Habitat replacement, (G) Bait attractivity, (H) Reproductive biology, and (I) Inventories; Habitats type: NF (Native Forest), NP (Native Pastures), IP (Introduced Pastures), FP (Forest Plantations), AA (Agricultural Areas); UA (Urban Areas), U (Unidentified Habitats). Metrics evaluated: R (Richness), Ab (Abundance), C (composition), B (Biomass), Di (Diversity index), Do (Descriptive observations), Ef (Ecological functions), Fd (Functional diversity) and M (Morphometry).

ID	Ref.	Year	Country	Region	Study topic	Covers	Metrics
Doube & MacQueen 1991	1	1991	Australia	Australasia	A, B, C	NF, NP, IP	R, Ab,C,M
Giller & Doube 1994	2	1994	South Africa	Afrotropical	A, D	NP	R, Ab,C,M,Fd
Chown et al. 1995	3	1995	South Africa	Afrotropical	C, E	NF	B, Fd
Chown & Steenkamp 1996	4	1996	South Africa	Afrotropical	A	NP	R, Ab, B, Fd
Davis 1996a	5	1996	South Africa	Afrotropical	A, D	NP	R,Ab,B,M,Fd
Davis 1996b	6	1996	South Africa	Afrotropical	A, D	NP	R,Ab,B,Fd,Ef
Steenkamp & Chown 1996	7	1996	South Africa	Afrotropical	A, F	NP, FP	R,Ab,Di, B,M,Fd
Krell et al. 1997	8	1997	Ivory Coast	Afrotropical	G	NF	R,Ab
Sato 1997	9	1997	Kenya	Afrotropical	D, H	NP	Ab, Do
Hertel & Colli, 1998	10	1998	Brazil	Neotropical	D, H	NP	Ab, Do,Ef
Sato 1998	11	1998	Kenya	Afrotropical	D, H	NP	Ab, Do, M
Vaz de Mello et al. 1998	12	1998	Brazil	Neotropical	D	U	R, Ab
Davis et al. 1999	13	1999	South Africa	Afrotropical	C, F	NP	R,Ab,Di,C
Amézquita et al. 1999	14	1999	Colombia	Neotropical	A, B	NF	R,Ab,Di,C,B
Van Rensburg et al. 1999	15	1999	South Africa	Afrotropical	A	NF,NP	R,Ab,Di,C
Van Rensburg et al. 2000	16	2000	South Africa	Afrotropical	A, C	NF,NP	R,Ab
Jankielsohn et al. 2001	17	2001	South Africa	Afrotropical	A, F	NP, IP	R,Ab,Di,B,Fd
Gutiérrez & Rumiz 2002	18	2002	Bolivia	Neotropical	I	NF,NP	R,Ab,Di,C
McGeoch et al. 2002	19	2002	South Africa	Afrotropical	A, B	NF	R,Ab,Di,
Krell et al. 2003	20	2003	Ivory Coast	Afrotropical	A, D	NF,NP	Ab,Fd
Milhomem et al. 2003	21	2003	Brazil	Neotropical	A, G	NF,NP	R,Ab,Di,
Spector & Ayzama 2003	22	2003	Bolivia	Neotropical	A	NP	R,Ab,Di,C,B
Krell 2004	23	2004	Kenya	Afrotropical	G	NP	Do
Krell-Westerwalbesloh et al. 2004	24	2004	Ivory Coast	Afrotropical	A, D, G	NF	Ab,Fd
Davis & Scholtz 2004	25	2004	South Africa	Afrotropical	A, C	NP	R,Ab,Di,C,Ef
Davis et al. 2005	26	2005	South Africa	Afrotropical	A, F	NF,NP,IP,FP	R,Ab,Di,C
Durães et al. 2005	27	2005	Brazil	Neotropical	A	NF	R,Ab,Di,C
Andresen 2005	28	2005	México	Neotropical	A	NF	R,Ab,Di,M,Fd

ID	Ref.	Year	Country	Region	Study topic	Covers	Metrics
Botes et al. 2006	29	2006	Mozambique	Afrotropical	A, B	NF	R,Ab,C,
Magagula 2006	30	2006	Swaziland	Afrotropical	A, F	NF,NP,FP	R,Ab,Di,C
Silveira et al. 2006	31	2006	Brazil	Neotropical	G	U	Ab, Do,M,Ef
Kriger et al. 2006	32	2006	South Africa	Afrotropical	D, H	NF,NP,IP	Ab,Do
Coetzee et al. 2007	33	2007	South Africa	Afrotropical	A, F	NP,IP	R,Ab,Di,M
Noriega et al. 2007	34	2007	Colombia	Neotropical	A, B	NF,NP	R,Ab,Di,
Horgan 2007	35	2007	El Salvador	Neotropical	A, F, G	NF,NP,IP,FP	R,Ab,C
Horgan 2007	35	2007	Nicarágua	Neotropical	A, F, G	NF,NP,IP,FP	R,Ab,C
Verdú et al. 2007	36	2007	México	Neotropical	A, B	NF,NP	R,Ab,Di,C
Davis et al. 2008	37	2008	South Africa	Afrotropical	A, C	NF,NP	R,Ab,Di
Da Silva et al. 2008	38	2008	Brazil	Neotropical	A, I	NF,NP	R,Ab,Di,Fd
Orozco & Pérez 2008	39	2008	Colombia	Neotropical	A, F	NF,NP,AA	R,Ab
Jiménez-Ferbans et al. 2008	40	2008	Colombia	Neotropical	I	NF	R,Ab
Tshikae et al. 2008	41	2008	Botswana	Afrotropical	G	NF,NP	R,Ab,Di,C
Horgan 2008	42	2008	El Salvador	Neotropical	A, C, F, G	NF,IP	R,Ab,C,B,Fd,Ef
Arellano et al. 2008	43	2008	México	Neotropical	A, F	NF,IP	R,Ab,Di,C,
Andresen 2008	44	2008	México	Neotropical	A, F	NF,IP	R,Ab,Di,C,
Almeida & Louzada 2009	45	2009	Brazil	Neotropical	A	NF,NP	R,Ab,Di,C,Fd
Da Silva et al. 2009	46	2009	Brazil	Neotropical	A, I	NP	R,Ab,M,Fd
Martínez et al. 2009	47	2009	Colombia	Neotropical	A	NF	R,Ab,Di,C,
Bohórquez & Montoya Lerma 2009	48	2009	Colombia	Neotropical	F, G	NF,NP	Ab
Carpaneto et al. 2010	49	2010	Uganda	Afrotropical	A, G	NP	R,Ab,Di,B,Fd
Da Silva et al. 2010a	50	2010	Brazil	Neotropical	A	NF,NP	R,Ab,C
Barraza et al. 2010	51	2010	Colombia	Neotropical	A, F	NF,IP	R,Ab,Di,C,Fd
Martinez-H et al. 2010a	52	2010	Colombia	Neotropical	A, B	NF	R,Ab,Di,C,Fd
Neves et al. 2010	53	2010	Brazil	Neotropical	A, B	NF,NP	R,Ab,C
Jacobs et al. 2010	54	2010	Mozambique	Afrotropical	A, F	NF,NP,IP,FP	R,Ab,Di,C
Martínez-H et al. 2010b	55	2010	Colombia	Neotropical	A	NF	R,Ab,Di,C,Fd
Da Silva et al. 2010b	56	2010	Brazil	Neotropical	A, G	NP	R,Ab,C
Rodrigues et al. 2010	57	2010	Brazil	Neotropical	A	NF,NP	R,Ab,Fd
Almeida et al. 2011	58	2011	Brazil	Neotropical	A, F	NP,IP	R,Ab,Di,C,B
Kunz & Krell 2011	59	2011	Ivory Coast	Afrotropical	A	NF,NP	R,Ab,B,Fd,Ef
Liberal et al. 2011	60	2011	Brazil	Neotropical	A, F	NF,IP,AA	R,Ab,Di,C
De Andrade et al. 2011	61	2011	Brazil	Neotropical	A, B	NF	R, Ab, C
Rosa et al. 2011	62	2011	Brazil	Neotropical	A, G	NP	R,Ab
Davis & Scholtz 2012	63	2012	South Africa	Afrotropical	A, B	NF,NP,IP	R,Ab,Di,C,B
Resende 2012	64	2012	Brazil	Neotropical	A, F	NF,IP,AA	R,Ab,C
González-Vainer et al. 2012	65	2012	Uruguay	Neotropical	A, F	NP	R,Ab,Di,C
Gries et al. 2012	66	2012	Brazil	Neotropical	A, F	NF,NP,FP	R,Ab,Di,C
Martínez-Hernandez et al. 2012	67	2012	Colombia	Neotropical	A, G	NF	R,Ab,C,Fd
Da Silva et al. 2012	68	2012	Brazil	Neotropical	I, G	NP	R,Ab,Fd

ID	Ref.	Year	Country	Region	Study topic	Covers	Metrics
Nunes et al. 2012	69	2012	Brazil	Neotropical	I, G	NP	R,Ab
Rangel-Acosta et al. 2012	70	2012	Colombia	Neotropical	A, G	NF	R,Ab,Di,C,Fd
Midgley et al. 2012	71	2012	South Africa	Afrotropical	C, G	U	Ab,Do, Ef
Vieira & Silva 2012	72	2012	Brazil	Neotropical	A, I	NF	R,Ab
Iannuzzi et al. 2013	73	2013	Brazil	Neotropical	D	NF,NP	Ab,Do
Mayer & Vasconcelos 2013	74	2013	Brazil	Neotropical	G	NF	R,Ab,Fd
Pryke et al. 2013	75	2013	South Africa	Afrotropical	A, F	NF,IP,FP	R,Ab,Di,C
Puker et al. 2013	76	2013	Brazil	Neotropical	A, F, G	NF,NP,IP	R,Ab,C,Fd
Lima et al. 2013	77	2013	Brazil	Neotropical	A, I	NF	R,Ab,Di
Tshikae et al. 2013a	78	2013	South Africa	Afrotropical	A, C, G	NF,NP	R,Ab,Di,C,B
Tshikae et al. 2013b	79	2013	South Africa	Afrotropical	A, C, G	NF,NP	R,Ab,Di
Daniel et al. 2014	80	2014	Brazil	Neotropical	A	NF,NP	R,Ab,C,Fd
Medina & Lopes 2014a	81	2014	Brazil	Neotropical	A	NF	R,Ab,C
Medina & Lopes 2014b	82	2014	Brazil	Neotropical	A, G	NF	R,Ab,C,M
Puker et al. 2014	83	2014	Brazil	Neotropical	A, F, G	NF,IP	R,Ab,M
Caballero & León-Cortés 2014	84	2014	México	Neotropical	A, G	NF,IP	R,Ab,Di,C,Fd, Ef
Costa-Silva et al. 2014	85	2014	Brazil	Neotropical	A, B	NF,NP	R,Ab,Di
Domínguez et al. 2015	86	2015	Ecuador	Neotropical	A, I	NF	R,Ab,Di, Fd
Lima et al. 2015	87	2015	Brazil	Neotropical	A, F, G	NF,NP,IP	R,Ab,Di,Fd
Gilroy et al. 2015	88	2015	Colombia	Neotropical	A, F	NP	R,Ab,Di,C
Damborsky et al. 2015	89	2015	Argentina	Neotropical	A, F, G	NF,NP,IP	R,Ab,Di,C
Tissiani et al. 2015	90	2015	Brazil	Neotropical	A, I	NF,NP,IP	R,Ab,C,Fd
Correa et al. 2016a	91	2016	Brazil	Neotropical	A, F	NP,IP	R,Ab,C,Fd
Correa et al. 2016b	92	2016	Brazil	Neotropical	A, F	NP,IP	R,Ab,Di,C,M,Fd
Martello et al. 2016	93	2016	Brazil	Neotropical	A, F	NF,IP,FP,AA	R,Ab,C,Fd
Marques et al. 2016	94	2016	Brazil	Neotropical	A, F	NF,NP,IP	R,Ab,Di,C,Fd
Noriega et al. 2016	95	2016	Colombia	Neotropical	A	NF	R,Ab
Novais et al. 2016	96	2016	Brazil	Neotropical	A	NF	R,Ab,Di
Nunes et al. 2016	97	2016	Brazil	Neotropical	A	NF, NP	R,Ab,Di,C,B,Fd
Pryke et al. 2016	98	2016	South Africa	Afrotropical	A, F	NP, FP	R,Ab,Di,C
Montoya-Molina et al. 2016	99	2016	Colombia	Neotropical	A, F	NF, IP	R, Ab, Di
Rangel-Acosta et al. 2016b	100	2016	Colombia	Neotropical	A, F	NF, IP	R,Ab,Di,C,Fd
Rangel-Acosta et al. 2016a	101	2016	Colombia	Neotropical	A	NF, IP	R,Ab,Di,C,Fd
Tovar et al. 2016	102	2016	Colombia	Neotropical	A, B	NP	R,Ab,Fd
Davis et al. 2016	103	2016	South Africa	Afrotropical	A, C	NP	R,Ab,Di,C,B,Fd
Chaves et al. 2017	104	2017	Brazil	Neotropical	A, F	NP, IP, FP, AA	R,Ab,Di,Fd
Correa et al. 2017	105	2017	Brazil	Neotropical	A, G	NP, IP	R,Ab,M,Fd
Pessôa et al. 2017	106	2017	Brazil	Neotropical	A, B	NF, NP	R,Ab,Di,M,Fd
Rangel-Acosta & Martínez-Hernández 2017	107	2017	Colombia	Neotropical	A, F	NF, IP	R,Ab,Di,C

ID	Ref.	Year	Country	Region	Study topic	Covers	Metrics
Salomão & Iannuzzi 2017	108	2017	Brazil	Neotropical	A, B, G	NF	R,Ab,Di,C
Roque et al. 2017	109	2017	Brazil	Neotropical	A, B	NF, NP, IP, AA	R,Ab,C
Vieira et al. 2017	110	2017	Brazil	Neotropical	A, B	NF	R,Ab,Di,C
Alvarado et al. 2017	111	2017	México	Neotropical	A, F	NF, IP	R,Ab,Di,C,B
Lascaleia et al. 2018	112	2018	Suazilandia	Afrotropical	A, F	NP, AA	R,Ab,Di,
Da Silva 2018	113	2018	Brazil	Neotropical	A	NF, NP	R,Ab,Di,C
Ernesto et al. 2018	114	2018	Brazil	Neotropical	I	NF	R,Ab
Nunes et al. 2018	115	2018	Brazil	Neotropical	A	NP	R,Ab,B,Fd,Ef
Rangel-Acosta et al. 2018	116	2018	Colombia	Neotropical	A, B	NF	R,Ab,Di,C
Martínez–Revelo et al. 2018	117	2018	Colombia	Neotropical	I	NF,NP,FP	R,Ab
Gillett & Barr 2018	118	2018	Zambia	Afrotropical	C, I	NF, NP	R,Ab
Gillett & Barr 2018	118	2018	Swaziland	Afrotropical	C, I	NF, NP	R, Ab
Aquino et al. 2018	119	2018	Brazil	Neotropical	G	U	Do,Ef
Tocco et al. 2018	120	2018	South Africa	Afrotropical	A, G	NP	R,Ab,Di,Fd
Salomão et al. 2018	121	2018	Brazil	Neotropical	A, G	NF	R,Ab,C
Veldhuis et al. 2018	122	2018	South Africa	Afrotropical	A	NF, NP	R,Ab,Ef
Ocampo-Castillo & Andresen 2018	123	2018	México	Neotropical	A	NF	Ef
Correa et al. 2019a	124	2019	Brazil	Neotropical	A, B	NP	R,Ab, Di, C,B,M,Fd, Ef
Correa et al. 2019b	125	2019	Brazil	Neotropical	A, F	NF, IP	R,Ab,Di,C,Fd
Gebert et al. 2019	126	2019	Tanzania	Afrotropical	A, C, F	NP, IP, FP	R,Ab,C,Fd
Amell-Caez et al. 2019	127	2019	Colombia	Neotropical	A, C, F	NF, NP, IP	R, Ab, Di, C, Fd
Da Silva & Cassenote 2019	128	2019	Brazil	Neotropical	A, C	NF, NP	R, Ab, C, M, Fd
Nunes et al. 2019	129	2019	Brazil	Neotropical	A, B	NP	R, Ab, Di, C, B
Ortega-Echeverría et al. 2019	130	2019	Colombia	Neotropical	A, I	NF	R, Ab, Di, C, M, Fd
Salomão et al. 2019	131	2019	Brazil	Neotropical	A	NF, NP	R, Ab
Barreto et al. 2020	132	2020	Brazil	Neotropical	A	NF, NP	R, Ab, Di, C, M, Fd
Macedo et al. 2020	133	2020	Brazil	Neotropical	F, G	NP, IP	R, Ab, C
Carvalho et al. 2020	134	2020	Australia	Australasia	A, B, G	NF	R, Ab, Di, C
Guerra-Alonso et al. 2020	135	2020	Argentina	Neotropical	A, B, C	NF, IP	R, Ab, Di, C
Bernardes et al. 2020	136	2020	Brazil	Neotropical	A, F	NP, FP	R, Ab, Di, C
Correa et al. 2020	137	2020	Brazil	Neotropical	A, B	NP	R,Ab,C,B,Fd
Cunha & Frizzas 2020	138	2020	Brazil	Neotropical	A	NP	R, Ab, Di, C, Fd
Frizzas et al. 2020	139	2020	Brazil	Neotropical	A, B, G	NP	R, Ab, Di
Khaldy et al. 2020	140	2020	South Africa	Afrotropical	D, E	NF, NP	Ab, Do, M
Da Silva et al. 2020	141	2020	Brazil	Neotropical	A	NF, NP	R, Ab, Di, C. Fd
Correa et al. 2020b	142	2020	Brazil	Neotropical	A, F	NP,IP	R,Ab,Di,C,Fd
Filho et al. 2020	143	2020	Brazil	Neotropical	A, F	NP, FP	Ab
Rangel-Acosta et al. 2020	144	2020	Colombia	Neotropical	A, F	NF, IP	R, Ab, Di, C, B
Noriega et al. 2020	145	2020	Colombia	Neotropical	A, B	NF	R, Ab, Di
Escobar et al. 2021	146	2021	Mozambique	Afrotropical	A, B	NF, NP	R, Ab, Di, C

ID	Ref.	Year	Country	Region	Study topic	Covers	Metrics
Khaldy et al. 2021	147	2021	South Africa	Afrotropical	D, E	NF, NP	Ab, Do, M
Neves et al. 2021	148	2021	Brazil	Neotropical	A	NP	R, Ab, Di
Correa et al. 2021a	149	2021	Brazil	Neotropical	A, F	NP,IP	R,Ab,Di,C,M,Fd
Oliveira et al. 2021	150	2021	Brazil	Neotropical	A, F	NP, IP	R, Ab, Di, C, B, M, Fd, Ef
Stanbrook et al. 2021	151	2021	Tanzania	Afrotropical	A, F	NP, AA	R, Ab, Di, C
Nependa et al. 2021	152	2021	Namíbia	Afrotropical	A, F, G	NP, IP	R, Ab, Di, C, B, M, Fd
Correa et al. 2021b	153	2021	Brazil	Neotropical	A, F	NP, UA	R, Ab, Di, C, M, Fd
Correa et al. 2021c	154	2021	Brazil	Neotropical	A, F	NP, UA	R,Ab,Di,C,M,Fd
Rodríguez-García et al. 2021	155	2021	Colombia	Neotropical	A, B	NF	R, Ab, Di, CM, Fd
Davies et al. 2021	156	2021	Colombia	Neotropical	A, F	NF, IP, PF	R, Ab, C, M, Fd, Ef
Gonçalves et al. 2022	157	2022	Brazil	Neotropical	A, B	NP	R, Ab, Di, C, B, Fd
Canziani & González-Vainer 2022	158	2022	Uruguay	Neotropical	A, F, G	NP, FP	R, Ab, Di, C, B, Fd
Oliveira et al. 2022	159	2022	Brazil	Neotropical	A	NF, NP	R, Ab, Di, C, Fd
Lira & Frizzas 2022	160	2022	Brazil	Neotropical	D, G	NP	Do, M, Ef
Martínez-Hernández et al. 2022	161	2022	Colombia	Neotropical	A	NF	R, Ab, Di, C, B, M, Fd
Salomão et al. 2022	162	2022	Brazil	Neotropical	A, I	NF	R, Ab, Di
Carvalho et al. 2022	163	2022	Brazil	Neotropical	A, F	NP, IP, FP	R, Ab, Di, C, B, M, Fd
Da Silva et al. 2022	164	2022	Brazil	Neotropical	A, C	NF	R, Ab, Di
Estupiñan-Mojica et al. 2022	165	2022	Brazil	Neotropical	A, F	NF, NP, IP	R, Ab, Di, C
Magagula 2022	166	2022	South Africa	Afrotropical	A, C	NF, NP	R, Ab, Di, C, Fd
Tovar et al. 2023	167	2023	Colombia	Neotropical	A, B	NP	R, Ab, Di, B, Fd
Reis et al. 2023	168	2023	Brazil	Neotropical	B, D, G	NP, IP	B, Ef
Maciel et al. 2023	169	2023	Brazil	Neotropical	A, F	NP, IP	R, Ab, C, B, M, Fd, Ef
Pêssoa et al. 2023	170	2023	Brazil	Neotropical	A, F	NF, IP	R, Ab, Di, C, Fd
Korasaki et al. 2023	171	2023	Brazil	Neotropical	A, C, F	NP, IP	R, Ab, C, B
Franco et al. 2023	172	2023	Brazil	Neotropical	A, F	NP,IP,FP	R, Ab, B, M, Ef
Philips et al. 2023	173	2023	Ghana	Afrotropical	A, C, G	NP	R, Ab, Di,C,
Gigliotti et al. 2023	174	2023	Brazil	Neotropical	A, G	NP	R, Ab, Di, C

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ARTIGO II

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Habitat and Food Resource Type, Rather than Sampling Date, Drive Co-occurrence of Dung Beetle Species in a Tropical Ecosystem Mosaic

REIS, N. L.[a*]; SANTOS, K. A.[b]; VIEIRA, L.[c]; LOUZADA, J.[d]

[a,d] Universidade Federal de Lavras, Laboratório de Ecologia e Conservação de Invertebrados (LECIN), Departamento de Ecologia e Conservação, Instituto de Ciências Naturais, CEP 37.203-202, Lavras, MG, Brasil.

[b.] Universidade Federal de Lavras, Laboratório de Manejo de Pragas Florestais, Departamento de Entomologia, CEP 37.203-202, Lavras, MG, Brasil.

[c.] Universidade Federal de Lavras, Laboratório de Ecologia Florestal, Departamento de Ciências Florestais e Programa de Pós-Graduação em Entomologia, Departamento de Entomologia, CEP 37.203-202, Lavras, MG, Brasil.

* Corresponding author: Nayara Letícia Reis, Universidade Federal de Lavras (UFLA), Departamento de Ecologia e Conservação, PO Box 3037, CEP 37.203-202, Lavras, MG, Brasil. E-mail: nayara.reis015@gmail.com; nayara.reis@estudante.ufla.br

Abstract

The species’ coexistence and distribution patterns are fundamental in community ecology research. Niche partitioning is used to evaluate co-occurrence patterns resulting from species interactions. Dung beetle communities are ideal models for understanding ecological patterns and processes. However, their co-occurrence patterns remain poorly understood. We tested if habitat type, sampling date, and food resources could explain the co-occurrence patterns of dung beetles. We expected that habitat would have the most impact on species co-occurrence, followed by food resource and sampling date. We conducted our study during the rainy season of 2012, using baited pitfall traps in a mosaic of four habitats including montane semideciduous forest, cerrado, rupestrian field, and introduced pasture, resulting in 16 sites. We used the Cooccur R package to analyze species co-occurrence probabilities and tested the effects of niche partitioning on species co-occurrence via DistLM analysis. We collected 2.743 individuals, representing 86 dung beetle species. In most co-occurring pairs, species exhibited random associations. Our results supported the hypothesis that habitat and food resources explained dung beetle co-occurrence. Habitat explains 13% of the total variance in co-occurrence patterns, food resources (7%), and sampling date (6%). Overall, our model explained 31% of the variance correspond to the sum of each variable isolated with the values shared between them. Our results suggested that dung beetle species' co-occurrence was stochastic. I.e., non-biotic external factors can also potentially explain the coexistence of species with similar requirements. Food resources were important in co-occurrence. This is consistent with the lottery competition since colonization by species on ephemeral resources is random and by chance. Niche partitioning had little explanatory power for co-occurrence patterns, however, tropical forests have the potential to maintain many positive species associations. Here, the sampling date did not influence the species' co-occurrence, possibly due to stable temperatures and consistent precipitation during the season.

Keywords: Assembly rules; Coexistence; Community structure; Insect ecology; Niche partitioning; Scarabaeinae.

1. Introduction

Understanding how species are distributed and which processes shape their distribution patterns is a central goal of community ecology (McCreadie and Bedwell, 2012; Sutherland et al., 2013; Vellend, 2017). Species co-occurrence patterns, on the other hand, provide insights into community structure, species coexistence, and the biological diversity that an ecosystem can support (Tilman, 1982; Williams et al., 2014; Camarota et al., 2016). Knowledge of the mechanisms that underlie the structure of biotic communities is essential and can provide valuable information for designing and planning integrated conservation efforts (Hung et al., 2019; Edwards et al., 2021).

Species co-occurrence patterns can also reflect niche partitioning resulting from biotic interactions within communities (Weiher et al., 2011). Therefore, changes in the habitat conditions or the loss of interactions can alter co-occurrence patterns (Edwards et al., 2021; Xue et al., 2022). Additionally, species interactions and niche partitioning can be affected by factors such as the historical context of the landscape, species dispersal ability, and physiological constraints (MacArthur and Levins, 1967; Camarota et al., 2016).

The analysis of co-occurrence patterns in insect communities has ranged from simple pairwise comparisons between all community members to direct hypothesis testing that addresses different taxonomic levels (McCreadie and Bedwell, 2012; Griffith et al., 2016; Elo et al., 2021). However, co-occurrence patterns are rarely studied across multiple ecosystems within the same study (King, 2007; Pitzalis et al., 2017).

Dung beetles are highly diversified in most terrestrial tropical ecosystems, and they feed on ephemeral resources, subjecting them to intense competition (Hanski and Cambefort, 1991; Spector, 2006; Gardner et al., 2008; Nichols and Gardner, 2011; Beiroz et al., 2019). The Neotropical Forest and savanna ecosystems are home to greater diversity and abundance of dung beetles than other environments (Hanski and Cambefort 1991; Milhomem et al., 2003; Almeida and Louzada, 2009; Bitencourt et al., 2019; Cunha and Frizzas, 2020; Silva et al., 2021). The coexistence of numerous dung beetle species in forest ecosystems may be attributed to the high diversity of resources and niches available (Estrada et al., 1998; Estrada et al., 1999; Feer and Hingrat, 2005). Besides, dung beetle communities are strongly influenced by habitat structure and microclimate, which can lead to significant changes in species composition. In degraded ecosystems, alterations in biotic and abiotic factors can have even more pronounced effects on species. This is particularly true because habitat degradation results in increased temperature and luminosity, as well as reduced soil moisture, making the microclimate an unfavourable environment for certain dung beetle species (Andresen and Laurance, 2007; Vieira et al., 2008; Gries et al., 2011; Martello et al., 2016; Gómez-Cifuentes et al., 2017; Vieira et al., 2022). In addition, local food resources availability local plays a crucial role in shaping dung beetle communities. (Nichols et al., 2009; Louzada et al., 2009; Macedo et al., 2020), with a positive correlation between the dung beetle richness and abundance and the quantity and variability of food resources (Estrada et al., 1998; Bogoni et al., 2016; Pessôa et al., 2020).

The dung beetles are a valuable model for testing ecological hypotheses and coexistence mechanisms, as they are a cost-effective sampling group (Spector, 2006; Gardner et al., 2008; Beiroz et al., 2019), and are taxonomically and ecologically well-studied (Spector, 2006). There is a significant knowledge gap regarding the co-occurrence patterns of dung beetles in tropical ecosystems and the factors influencing them (Giller and Doube, 1994; Beiroz et al., 2019; Edwards et al., 2021). A comprehensive understanding of the mechanisms that drive species coexistence in biological communities is critical for the development of effective management and conservation strategies, particularly for dung beetles. These insects are of great ecological importance in tropical ecosystems, providing essential ecosystem services (Gardner et al., 2008; Nichols et al., 2008; Nichols and Gardner 2011).

We assessed that the species co-occurrence patterns in dung beetle communities are influenced by factors like habitat type, food sources, and sampling dates in tropical ecosystems. We hypothesize that factors, such as habitat type, food resources, and sampling date, could potentially determine the observed co-occurrence of dung beetles. To assess the influence of the interaction between these factors on co-occurrence patterns, we employed the variance partitioning approach. We expect the habitat would be the main driver of species co-occurrence patterns due to the physiological constraints imposed on specialized dung beetle species associated with canopy cover and spatial heterogeneity. Therefore, we predicted that forests would support a greater number of positive associations among dung beetle species due to the availability of diverse niches and food resources, which are more abundant compared to other habitats. Conversely, the harsh environmental conditions in Savannas and Rupestrian fields, including frequent fire disturbances, higher temperature, and humidity amplitude, were likely to result in fewer positive co-occurrence associations and predominance of random associations. We also speculated that the low diversity of food resources, mainly cattle dung, at Introduced pastures could lead to generalist species dominance and a higher number of negative associations. We also hypothesized that distinct food sources could influence interspecific competition pressures. Finally, we expected that the sampling date would have a weaker effect on the dung beetle co-occurrence patterns due to the relatively mild climatic changes observed during the summer season (Fabrant, 2000).

2. Material and Methods

2.1 Study area

Our survey was conducted within the protected areas of Serra São José that cover approximately 4758.0 ha, located in the Minas Gerais State, Brazil (21°4′29.02″S; 44°8′19.12″W) (Fig. 1). This region encompasses the Serra de São José mountains, which serve as home to two key conservation units -the Environmental Protected Area of the Serra São José (APA Serra São José) and the Wildlife Refuge "Libélulas of the Serra São José". These protected areas play a crucial role in safeguarding the regional and preserving endangered species. Notably, the Serra São José Mountain range has been identified as a Priority Conservation Area for Invertebrates in Minas Gerais, with a particular focus on the conservation of dragonflies.

The regional climate is characterized by rainy summers (October-March) and dry winters (April-September) (Silva et al., 2004; Alves and Kolbek, 2009). The annual mean precipitation is approximately 1.500 mm, and the temperature is approximately 19 °C, with a maximum of 21-22 °C in the summer and a minimum of 15-17 °C during the winter (Fabrant, 2000). The altitude is approximately 900-1.943 m (Cirino and Lima, 2008).

2.2 Dung beetles sampling

We sampled dung beetles once a month during the region's rainy season: January, February, and March of 2012. Dung beetle activity and local diversity are well observed and sampled during the rainy season (Halffter and Matthews, 1966; Hanski and Cambefort, 1991). We established four sampling sites with a minimum of 1 ha each, distanced from each other by at least 500 m in the four main ecosystems of the Serra São José mountains, namely Semideciduous Forest, Cerrado (Brazilian savannah), Rupestrian field, and Introduced pasture, totaling 16 sampling sites.

The selected forest habitats on Serra São José consist of semi-deciduous Atlantic Forest remnants. These areas are rich in biodiversity and form essential ecological pockets within the region. At the summit, hills are located the rupestrian fields of Serra São José with high-altitude plants dispersed in a mosaic of rocky outcrops made up of quartzitic soil types and sandy textured álico cambissol (Oliveira-Filho and Machado, 1993). Additionally in these fields, an herbaceous-shrub stratum with less than 5% tree cover makes up the predominant grassland phytophysiognomy (Pereira and Fernandes, 2022). The Cerrado selected belongs to the *sensu stricto* type, characterized by low, gnarled trees, shrubs, grasses, and various herbaceous plants. And a portion of the study areas was composed of *Brachiaria spp.* based introduced pastures.

To collect dung beetles, we used baited pitfall traps. Each trap consisted of a plastic jar measuring 12 cm in diameter and 9 cm high (see Figure A4, supplementary material). We buried the plastic jars until their top was at soil level. We then placed a smaller plastic cup containing 50 g of the baits: 1) omnivorous dung (40 g of human feces mixed with 10 g of pig dung); 2) herbivorous dung (cattle dung); or 3) carrion (rotten spleen) (Figure A4, supplementary material). We filled the plastic jars with a solution of 250 ml of water, detergent, and salt and covered the trap with a plastic lid supported by wood stickers. The traps were left in the field for 48 hours.

We placed three sets of three pitfalls in each site, resulting in a total of nine pitfalls per site (Figure A4, supplementary material). To assess the effectiveness of different bait types, we used different baits in each set of traps, resulting in three types of bait that were replicated three times at each sample site. The traps were spaced 20 m apart within a set, while the sets of pitfall traps were installed 50 m apart from each other at a site (Figure A4, supplementary material).

We identified the dung beetles to a species level and the species identity were confirmed by Dr. Fernando A. B. Silva and Dr. Fernando Z. Vaz-de-Mello. Voucher specimens were stored at the Entomological Collection of Federal University of Mato Grosso, Brazil (CEMT-UFMT) collection and the Entomological Collection of Federal University of Lavras at the Center of Biodiversity and Genetic Resources (CEUFLA-UFLA).

We obtained the functional and trophic attributes of the dung beetles through a comprehensive literature search. Two specific attributes were considered: (1) resource allocation strategy and (2) diet. Regarding the resource allocation strategy, the species were classified into three groups: dwellers, rollers, and tunnellers, based on their respective behaviors. In terms of diet, we classified the dung beetles into three categories: coprophages, scavengers, and generalists, based on their feeding preferences and habits.

2.3 Statistical analysis

In this study, we analyzed co-occurrence patterns for 31 species, each observed with a minimum of 16 individuals. We established this criterion based on the maximum number of collection sites (16 sites). By requiring at least 16 individuals per species, we ensured that each species occurred at least once at every collection site. We built a presence/absence matrix for each sample, and these matrices were subjected to Cooccur analysis (Probabilistic Species Co-

Occurrence Analysis) using the "cooccur ()" function in the "cooccur" R package, R 4.2.2 (R Core Team 2022). The cooccur function performs pair-to-pair matches for each species in the matrix, generating occurrence probabilities for each pair. The probabilistic model of species co-occurrence measures occurrence based on the number of sites where two species occur. The comparison between observed and expected co-occurrence is obtained by multiplying the occurrence probabilities of species pairs by the number of sampling sites. These probabilities were then used to identify whether species co-occur at higher or lower frequencies than expected co-occurrence. The Cooccur analysis considers the individual distributions of species. Therefore, species pairs with an expected occurrence of less than 1 were excluded from the analysis. The results were subsequently presented as co-occurrence combination and co-occurrence species probability tables. The associations between species pairs were classified as positive, negative, or random based on values of the probabilities the species co-occur greater or less than what is observed in our data. Co-occurrence analyse are a distribution-free method, and the results may be interpreted as p values, where p values < 0.05 are significant and indicate positive or negative associations between species (Griffith et al., 2016).

We tested the influence of local variables (habitat type, food resource, and sampling date) on dung beetle species co-occurrence by performing a distance-based linear model (DistLM). This multivariate analysis tests the relationship between categorical or continuous predictors and the distance-based matrix (the response variable) through variance partitioning based on single or multiple regression models. The distance-based matrix represents the distances or dissimilarities between a pair of observations, and it was constructed by calculating the Euclidean distance between samples based on their characteristics or attributes. The model provides the following values: SS (trace) stands for Sum of Squares and measures the variability explained by each predictor variable (habitat type, food resource, and sampling date) about the response variable (species co-occurrence); Pseudo-F measures the ratio of variability among the predictor variables and the variability within the group of predictor variables, indicating the strength of each variable's ‘effect on the species co-occurrence; Prop., which represents the proportion of variance of the response variable that can be explained by each predictor variable, and a p-value that indicates the significant effect ($p < 0.05$) a predictor variable has on the response variable (rejecting the null hypothesis). We first created a triangular matrix using the co-occurrence probabilities among species pairs as the distance index. Then we create a matrix for each variable (habitat type, food resource, and sampling date), using the number of species occurrence (presence/absence). Next, we tested the influence of these three dimensions (habitat type, food resource, and sampling date) on the species co-occurrence, via conditional and partial tests.

3. Results

We collected 2.743 individuals from 86 species of dung beetles. The most abundant species were *Onthophagus catharinensis* (n=616), *Canthon histrio* (n=229), *Canthon* aff. *modestus* (n=178), *Canthidium* aff. *aterrimum* (n=143), *Deltochilum* (*Deltohyboma*) sp. 1 (n=141), and *Oxysternon palaemon* (n=101).

According to the literature, most of the captured beetles are generalists (34 species); they feed on many resources (e.g., carcasses, feces, and decomposing fruits). Among the generalist species were *Canthon histrio*, *Canthon* aff. *modestus*, *Deltochilum* (*Deltohyboma*) sp.1, *Canthon* aff. *pilluliformes*, *Eurysternus hirtellus*, *Onthophagus catharinensis,* and *Canthidium* aff. *aterrimum* We also found 22 species considered coprophages (feeding on feces), among which were *Oxysternon palaemon*, *Dichotomius nisus*, and *Onthophagus hirculus*, and nine species that are considered scavengers (feeding on carcass), including *Coprophanaeus spitzi*, *Dichotomius crinicollis*, and *Canthon conformis*. The remaining 21 species could not be classified due to a lack of information in the literature.

Regarding feeding behaviour, the majority of the species were tunneller (41 species); followed by rollers (20 species) and dwellers (6 species). However, 19 species could not be classified due to insufficient information in the literature.

The Cooccur analysis resulted in 465 pairs of species. Eighty-four pairs (18.06% of the total) were excluded from the analysis as their expected co-occurrence was less than 1. Thus, 381 pairs were analyzed, resulting in 246 random associations, 96 positives, and 39 negatives (Fig. 2) (Table A2, supplementary material).

In all the habitat types, the co-occurrence patterns of dung beetles were dominated by random associations. The Semideciduous Montane Forest showed the highest number of positive associations (n = 21 positives), with *Deltochilum brasiliense* displaying six positive associations and *Deltochilum fucatum* having five positive associations (Fig. A1-a, supplementary material). Only one negative association was observed between *Canthidium* aff. *abreviatum* and *Paracanthon* sp.1 in the forest habitat.

In the Cerrado habitat, 231 pairs were analyzed, and a large number of positive associations (n = 10) were also observed. *Deltochilum* (Deltohyboma) sp.1 displayed five positive associations and *Canthon histrio* had two positive associations (Fig. A1-b, supplementary material).

We found no negative associations among species in the Cerrado, Introduced pasture, and Rupestrian field habitats (Fig. A1 b-d, supplementary material). A total of 120 pairs were analyzed in Introduced pasture, and *Deltochillum* (Deltohyboma) sp. 1 exhibited two positive associations, with the species *E. hirsutum* and *E. hirtellus* (Fig. A1-c, supplementary material). In the Rupestrian field 78 pairs were analyzed, and only two species, *Dichotomius nisus,* and *Oxysternon palaenon,* showed positive associations (Fig. A1-d, supplementary material).

Across all food resource types, the dominant patterns were random co-occurrence. A total of 435 species pairs were identified for feces and carrion baits. The fecal resource showed more random associations (Fig. A2 -a, supplementary material), whereas the carrion baits showed more positive associations (Fig. A2 -c, supplementary material). For herbivorous dung baits, 325 pairs were analyzed, and there were 317 random associations, eight positive associations, and no negative associations (Fig. A2 -b, supplementary material).

The results indicate a dominant pattern of random associations across all sampling months (Fig. A3 a-c, supplementary material). A total of 465 species pairs were analyzed in January, February, and March, with January showing more negative associations (n = 8) (Fig. A3 -a, supplementary material) and March showing more positive associations (n = 67) (Fig. A3 -c, supplementary material).

Species abundance in different habitats was the most critical variable in explaining species co-occurrence patterns. The direct effect of habitat type on the co-occurrence matrix was 13%, while the combined effect of food resource and sampling date explained 31% of the variation in habitat type. The food resource variable (bait) explained only 7% (Table 1, Fig. 3) of the variance in the co-occurrence matrix, and the combined effect of habitat and sampling date accounted for 11.0% of the variation in food resources. The sampling date variable explained 6% of the variance in the co-occurrence matrix and did not contribute to the species co-occurrence patterns (Table 2, Fig. 3).

4. Discussion

This study provided evidence that environmental factors and ecological interactions play a critical role in mediating the co-occurrence of dung beetle species in tropical ecosystems. Habitat and food resource type, but not sampling date, were identified as key factors structuring the co-occurrence patterns of dung beetles in a mosaic of open habitats and forested systems in Southern Brazil.

Most of the interactions between the pairs of species were found to be random at the habitat level, suggesting that stochastic processes strongly shape the dung beetle community.

This suggests that external (non-biotic) factors also play a significant role in structuring the dung beetle community, potentially explaining the coexistence of species with high similarity in food and habitat requirements. Random co-occurrence patterns are commonly observed in biotic communities and have been reported for insects in various ecosystems (Sanders et al., 2007; Pitta et al., 2012; Magura et al., 2018; Ortega-Martinez et al., 2020; Elo et al., 2021).

Seasonality is known to have a significant impact on the structure of dung beetle communities, particularly regarding species richness (Hanski and Cambefort, 1991; Pêssoa et al., 2020). Besides that, when contrasting the dry season with the rainy season, it is possible to see frequent changes in the dung beetle community, and this is mostly because of rainfall occurrence (Andresen, 2005; Nyeko, 2009; Araujo et al., 2022). Here, the species co-occurrence patterns of dung beetles were not significantly impacted by the sampling date. We believe that this lack of influence may be related to the fact that we sampled in a single season in which temperatures are relatively stable, without major extremes of heat or cold, and precipitation is generally consistent and regular.

We observed that the habitat type plays a significant role in facilitating associations among species. Specifically, we found that the percentage of the total variance in both positive and negative associations can be explained by the type of habitat. This is consistent with the widely accepted notion that vegetation structure, particularly in tropical landscapes, can have a strong influence on dung beetle communities. This influence can impact several factors, including species richness, abundance, species, and guilds composition (Larsen et al., 2008; Alvarado et al., 2020; Macedo et al., 2020). We suppose that the quality, type, ephemerality, and availability of resources should affect the dung beetle’s survival and abundance, and consequently, the species coexistence. Recent research by Macedo et al. (2020) has supported this hypothesis by demonstrating that the type of food resource, such as human or bovine excrement, can shape the dung beetle community in tropical savannas.

Dung and carcass are characterized by their ephemeral nature and irregular distribution (Hanski and Cambefort, 1991; Davis, 2000; Dormont et al., 2004; Pessôa et al., 2020). Dung beetles are known to quickly colonize these resource patches upon odor detection, which can provide a competitive advantage for those individuals that first reach the resource (Herrera et al. 2002; Jacobs et al. 2008). This behaviour is consistent with the lottery competition model, which posits that species colonization in ephemerous patches is random and determined by chance. The lottery competition model has been documented in numerous studies, including Sale (1978), Busing and Brokaw (2002), Munday (2004), and Verster and Borenstein (2018).

All habitats showed a co-occurrence pattern dominated by random associations between species and there were no proportionally observed differences in non-random associations (positive and negative) between them. Previous researches suggested that the dung beetle communities, in tropical forests, are modelled by niche-based processes, especially by environmental filters (Audino et al., 2017; Ortega-Martinez et al., 2020). While we observed numerous positive and a few negative associations between dung beetle species in the forest habitats, the dominant patterns appeared to be random associations. This suggests that biotic interactions and/or environmental filters have a limited effect on the co-occurrence of species. However, as deterministic, and stochastic mechanisms are not mutually exclusive, possibly both affected the assembly of these communities, as suggested by Carbonell et al., (2017). The number of random associations observed can be influenced by generalist dung beetles. Although specialization is typically expected to promote coexistence and species diversity in forests (Becerra, 2015; Andresen et al., 2018). In this case, the trophic generality combined with randomness facilitated the coexistence of the dung beetle species.

We have found evidence that supports the hypothesis that most associations between dung beetle species in the Cerrado and Rupestrian fields are random and influenced by generalist dung beetles. The ephemerality and sporadic occurrence of food resources in open savannah environments, combined with variable climatic conditions, may favour species with generalist habits, as well as fast colonization and the random use of resources (Halffter, 1991; Correa et al., 2016; Barretto et al., 2020). However, we also observed some positive associations between species, indicating that deterministic processes such as environmental filtering or competition may also be acting on the co-occurrence patterns in these environments.

Although strong environmental filters often act in modified environments (Chase 2007, 2010), we refuted our hypothesis that there would be a higher number of negative associations between the species in the Introduced pastures. The dung beetle co-occurrence patterns in Introduced pastures was dominated by random associations due to the low variability in environmental conditions. Similar patterns were observed for dung beetles in introduced pastures in Mexico and for ground beetles in managed pastures (Ortega-Martínez et al., 2020; Elo et al., 2021). We found few positive associations between species. In particular, it has been shown that disturbed habitats tend to have fewer positive co-occurrences (Kay et al. 2018). Furthermore, we believe that environmental filtering may explain the positive associations, as species that co-occur in the pasture have similar habitat and resource requirements (Elo et al., 2021) (see Table 1 and Table 2, supplementary material).

By providing evidence that patterns of dung beetle co-occurrence are shaped by the type of habitat and the availability of resources, we highlight the importance of conserving the unique vegetation physiognomies found in regional ecological mosaics and food-producing vertebrate fauna (Culot et al., 2013; Bogoni et al., 2016). We argue that the regional landscape mosaic, composed of forests and savannas of the Brazilian Cerrado, is a critical factor shaping the diversity of dung beetles in Brazil. Furthermore, we believe that additional measures are necessary to safeguard this diversity, considering the intricate matrix of habitat types and the species that co-occur in each of these ecosystems (Almeida and Louzada, 2009).

Author contributions

The manuscript idea and hypothesis were collaboratively developed by all authors (NLR, KAS, LV, and JL), LV was responsible for designing the fieldwork, and NLR and LV were responsible for sampling the dung beetle species. All authors contributed to the statistical analysis, and NLR wrote the manuscript in its entirety, with significant input from co-authors KAS, LV, and JL.

Conflict of Interest Statement

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as potential conflicts of interest. All authors participated in all phases of the study.

License permits

The sampling work was conducted using the sampling permit number SISBIO 28097-1.

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TABLES

Table 1

MARGINAL TESTS				
Group	SS (trace)	Pseudo-F	P	Prop.
Habitat	2.116	1.4966	0.001*	0.14258
Food	1.081	1.0998	0.043*	7.28E-02
Sampling date	1.046	1.0622	0.091	7.05E-02

Table 2

SEQUENTIAL TESTS						
Group	Adj R^2	SS (trace)	Pseudo-F	P	Prop.	Cumul.
Habitat	0.04731	2.116	1.4966	0.001*	0.14258	0.14258
Food	0.05712	1.064	1.1405	0.003*	7.17E-02	0.21427
Sampling date	0.06305	1.0004	1.0791	0.192	6.74E-02	0.28168

FIGURE and TABLE LEGENDS

Figure 1 - Geographic localization of the study area (Apa São José, Minas Gerais, Brazil). The sample points are highlighted in yellow and correspond to the 16 sites sampled selected (4 Cerrado *sensu strictu*, 4 Semideciduous Montane Forest, 4 Rupestrian fields, and 4 Introduced pasture).

Figure 2 – Co-occurrence matrix of the dung beetle species (n =31). Yellow squares represent negative associations between species pairs (39), blue squares represent positive associations between species pairs (96), and gray squares represent random associations between species pairs (246).

Figure 3 - Venn diagram illustrating the proportion of variance explained by habitat type (habitat), food resource (food), and sampling date (time) in the species co-occurrence patterns.

Table 1- Distance-based linear model (DistLM) marginal tests result of variation in co-occurrence patterns explained by three variables: habitat (Semideciduous Montane Forest, Cerrado, Rupestrian field, or Pasture); food resource (carrion, herbivorous dung, or omnivorous dung), and sampling date (January, February, or March).

Table 2- Distance-based linear model (DistLM) sequential tests result of variation in co-occurrence patterns. Variables: habitat, food resource, and sampling date.

FIGURES

Figure 1

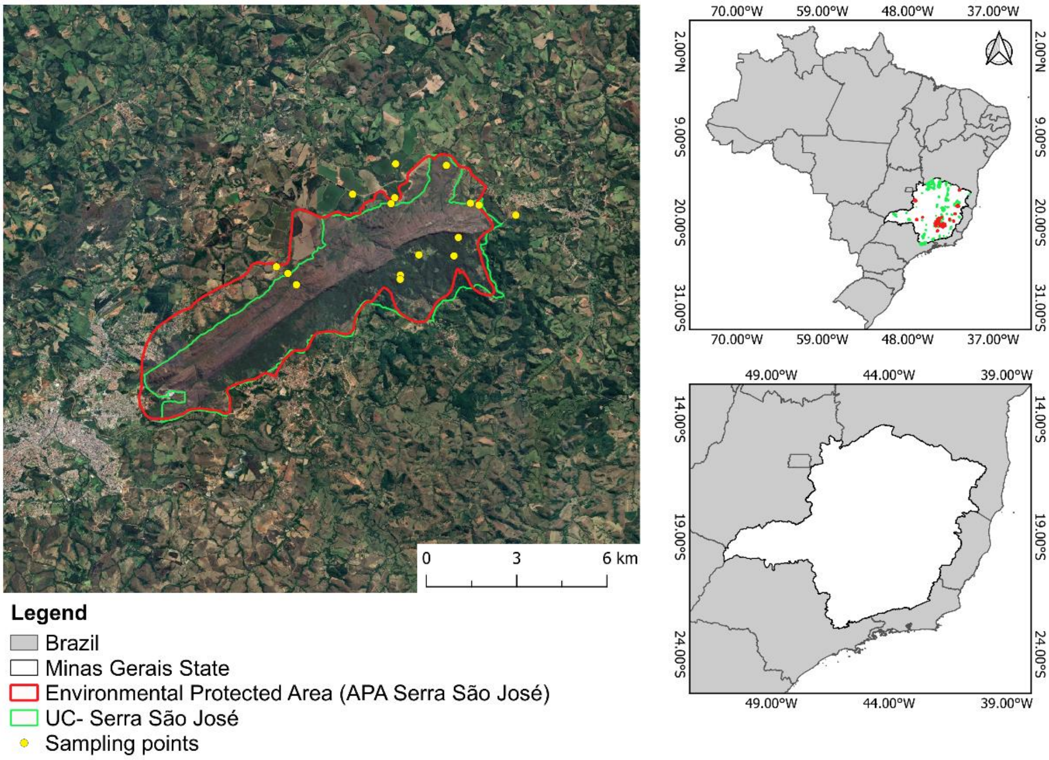


Figure 2

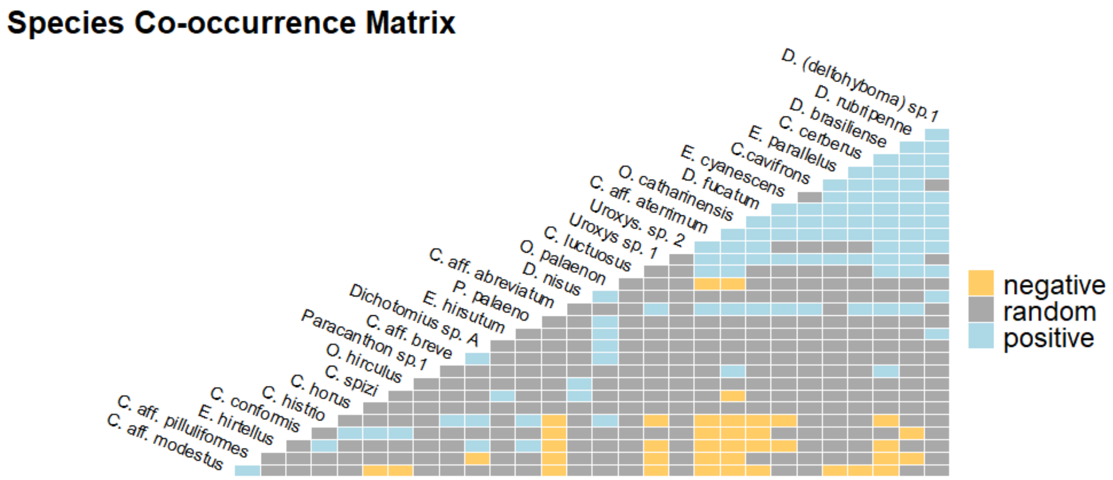
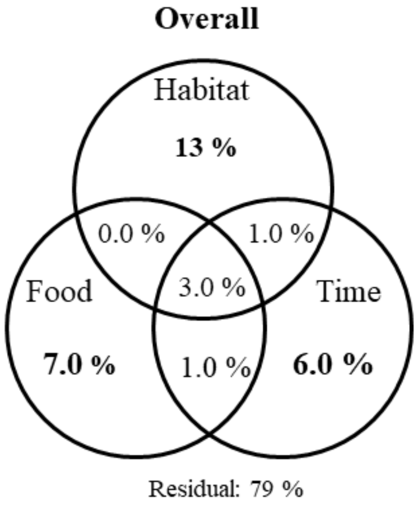

Species Co-occurrence Matrix
D. (deltohyboma) sp.1
D. rubripenne
D. brasiliense
C. cerberus
E. parallelus
C.cavifrons
E. cyanescens
D. fucatum
O. catharinensis
C. aff. aterrimum
Uroxys. sp. 2
Uroxys sp. 1
C. luctuosus
O. palaenon
D. nisus
C. aff. abreviatum
P. palaeno
E. hirsutum
Dichotomius sp. A
C. aff. breve
Paracanthon sp.1
O. hirculus
C. spizi
C. horus
C. histrio
C. conformis
E. hirtellus
C. aff. pilluliformes
C. aff. modestus
negative
random
positive

Figure 3



Supplementary material

Habitat and Food Resource Type, Rather than Sampling Date, Drive Co-occurrence of Dung Beetle Species in a Tropical Ecosystem Mosaic

REIS, N. L.[a*]; SANTOS, K. A.[b] ; VIEIRA, L. [c] ; LOUZADA, J.[d]

[a,d] Universidade Federal de Lavras, Laboratório de Ecologia e Conservação de Invertebrados (LECIN), Departamento de Ecologia e Conservação, Instituto de Ciências Naturais, CEP 37.203-202, Lavras, MG, Brazil.

[b.] Universidade Federal de Lavras, Laboratório de Manejo de Pragas Florestais, Departamento de Entomologia, CEP 37.203-202, Lavras, MG, Brazil.

[c.] Universidade Federal de Lavras, Laboratório de Ecologia Florestal, Departamento de Ciências Florestais e Programa de Pós-Graduação em Entomologia, Departamento de Entomologia, CEP 37.203-202, Lavras, MG, Brazil.

*Corresponding author: Nayara Letícia Reis
E-mail: nayara.reis@estudante.ufla.br

Table A1- List of data on the presence/absence, and richness of species of dung beetles in four habitat types (semideciduous forest, Cerrado *sensu stricto*, rupestrian field, and introduced pasture) and in three food resources type (cattle dung, rotten spleen, and omnivorous dung).

	Brazilian savannah			Semideciduous Forest			Introduced pasture			Rupestrian field			
	rotten spleen	cattle dung	omnivorous dung	rotten spleen	cattle dung	omnivorous dung	rotten spleen	cattle dung	omnivorous dung	rotten spleen	cattle dung	omnivorous dung	total richnes
Canthidium aff. *abreviatum*	0	0	0	1	1	1	0	0	0	0	0	0	17
Canthidium aff. *aterrimum*	0	0	0	1	1	1	0	0	0	0	0	0	23
Canthidium aff. *breve*	1	1	1	1	1	1	0	1	1	1	1	1	33
Canthidium cavifrons	0	0	0	1	1	1	0	0	0	0	0	0	10
Canthidium refulgens	1	1	1	0	0	0	1	1	1	0	0	0	12
Canthon conformis	1	0	1	0	0	0	1	1	1	1	0	0	22
Canthon aff. *modestus*	0	0	1	0	0	0	0	0	0	1	1	1	26
Canthon aff. *pilluliformes*	1	1	1	1	0	0	1	1	1	1	1	1	28
Canthon histrio	1	1	1	0	0	0	1	0	1	1	1	1	33
Canthon luctuosus	0	0	0	1	1	1	0	0	0	0	0	0	7
Coprophanaeus cerberus	1	0	0	1	1	1	0	0	0	0	0	0	14
Coprophanaeus horus	1	0	0	0	0	0	1	1	0	0	0	0	8
Coprophanaeus spizi	1	0	0	0	0	0	1	0	1	0	0	0	14
Deltochilum (Deltohyboma) sp.1	1	0	1	1	1	1	1	0	1	1	0	1	44
Deltochilum brasiliense	1	0	1	1	1	1	0	0	0	0	0	0	24

Deltochilum fucatum	0	0	0	1	0	1	0	0	0	0	0	0	18
Deltochilum rubripenne	1	0	0	1	1	1	0	0	0	0	0	1	21
Dichotomius bos	0	1	1	0	0	0	0	1	1	0	0	1	9
Dichotomius nisus	1	0	1	1	0	0	1	0	1	0	0	1	19
Dichotomius sp. A	1	1	1	1	0	0	0	1	0	0	0	0	13
Eurysternus cyanescens	0	0	0	1	0	1	0	0	0	0	0	0	11
Eurysternus parallelus	1	1	1	1	0	1	1	0	1	0	0	0	20
Eurysternus hirtellus	1	1	1	0	0	0	1	0	1	1	1	1	32
Eutrichillum hirsutum	1	0	1	1	0	0	1	0	0	0	0	0	11
Onthophagus catharinensis	0	0	0	1	1	1	1	0	0	0	0	0	26
Onthophagus hirculus	1	0	1	0	1	1	1	1	1	0	0	1	24
Oxysternon palaenon	1	1	1	0	0	0	0	0	0	0	0	1	18
Phanaeus palaeno	1	1	1	0	0	0	0	0	0	0	0	1	9
Paracanthon sp.1	0	0	0	1	1	1	0	0	0	0	0	0	6
Uroxys sp.1	0	0	0	1	1	1	0	0	0	0	0	0	15
Uroxys sp.2	0	1	1	1	1	1	0	0	0	0	0	0	8

Table A2 - List of positive and negative associations between dung beetle species based on Cooccur analysis.

Species	**Negative associations**	**Positive associations**	**Negatively associated species**	**Positively associated species**
Canthon aff. *modestus*	10	1	*Coprophanaeus spizi, Onthophagus hirculus, Canthidium abreviatum, Uroxys* sp. 1, *Canthidium* aff. *aterrimum, Onthophagus catharinensis, Deltochilum fucatum, Eurysternus parallelus, Coprophanaeus cerberus, Deltochilum brasiliense*	*Canthon* aff. *pilluliformes*
Canthon aff. *pilluliformes*	7	1	*Dichotomius* sp. A, *Canthidium* aff. *abreviatum, Uroxys* sp. 1, *Canthidium* aff. *aterrimum, Onthophagus catharinensis, Deltochilum brasiliense, Deltochilum rubripenne*	*Canthon* aff. *modestus*
Eurysternus hirtellus	7	3	*Canthidium* aff. *breve, Uroxys* sp. 1, *Canthidium* aff. *aterrimum, Onthophagus catharinensis, Deltochilum fucatum, Eurysternus cyanescens, Deltochilum brasiliense*	*Canthon histrio, Dichotomius* sp. A, *Phanaeus palaeno*

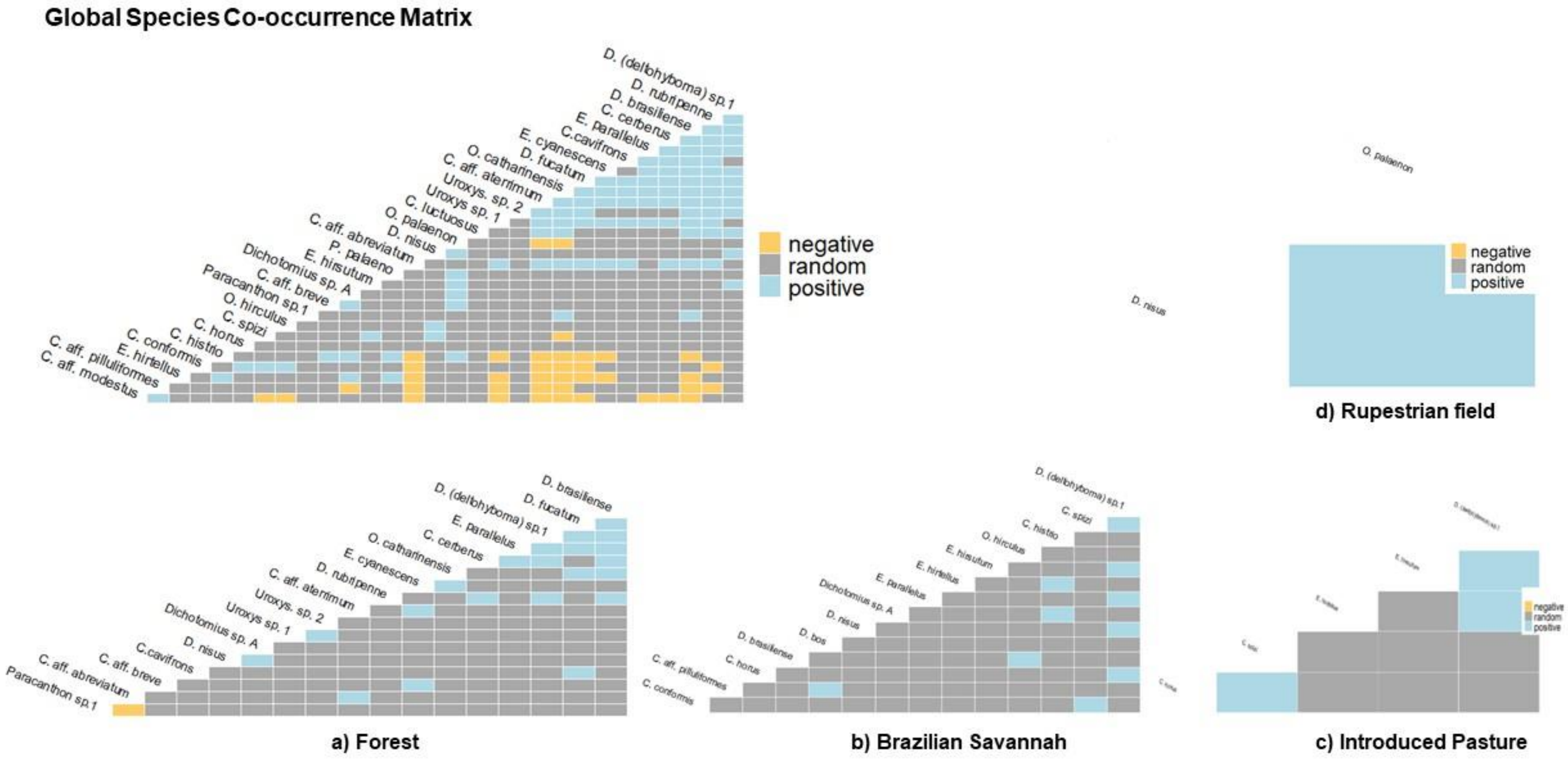
Canthon conformis	5	3	*Canthidium* aff. *abreviatum, Canthidium* aff. *aterrimum, Onthophagus catharinensis, Deltochilum fucatum, Deltochilum rubripenne*	*Coprophanaeus horus, Coprophanaeus spizi, Onthophagus hirculus*
Canthon histrio	7	5	*Canthidium* aff. *abreviatum, Uroxys* sp. 1*, Canthidium* aff. *aterrimum, Onthophagus catharinensis, Deltochilum fucatum, Eurysternus cyanescens, Deltochilum brasiliense*	*Eurysternus hirtellus, Canthidium* aff. *breve, Dichotomius* sp. A*, Phanaeus palaeno, Oxysternon palaenon*
Coprophanaeus horus	0	1	-	*Canthon conformis*
Coprophanaeus spizi	2	3	*Canthon* aff. *modestus, Onthophagus catharinensis*	*Canthon conformis, Dichotomius nisus, Eutrichillum hirsutum*
Onthophagus hirculus	1	2	*Canthon* aff. *modestus*	*Dichotomius nisus, Canthon conformis*
Paracanthon sp.1	0	2	-	*Onthophagus catharinensis* and *Deltochilum brasiliense*
Canthidium aff. *breve*	0	3	-	*Canthon histrio, Dichotomius* sp. A*, Oxysternon palaenon*
Dichotomius sp. A	1	4	*Canthon* aff. *pilluliformes*	*Canthidium* aff. *breve, Canthon histrio, Eurysternus hirtellus, Oxysternon palaenon*
Eutrichillum hirsutum	0	3	-	*Coprophanaeus spizi, Deltochilum* (Deltohyboma) sp. 1*, Oxysternon palaenon*

Phanaeus palaeno	0	3	-	*Canthon histrio, Oxysternon palaenon, Eurysternus hirtellus*
Canthidium aff. *abreviatum*	5	9	*Canthon* aff. *modestus, Canthon* aff. *pilluliformes, Eurysternus hirtellus, Canthon conformis, Canthon histrio*	*Uroxys* sp. 1, *Canthidium* aff. *aterrimum, Onthophagus catharinensis, Deltochilum fucatum, Eurysternus cyanescens, Canthidium cavifrons, Deltochilum brasiliense, Coprophanaeus cerberus, Deltochilum rubripenne*
Dichotomius nisus	0	4	-	*Deltochilum* (Deltohyboma) sp. 1, *Oxysternon palaenon, Onthophagus hirculus, Coprophanaeus spizi*
Oxysternon palaenon	2	6	*Canthidium* aff. *aterrimum, Onthophagus catharinensis*	*Dichotomius nisus, Phanaeus palaeno, Eutrichillum hirsutum, Dichotomius* sp. A, *Canthidium* aff. *breve, Canthon histrio*
Canthon luctuosus	0	5	-	*Deltochilum* (Deltohyboma) sp. 1, *Deltochilum rubripenne, Deltochilum brasiliense, Onthophagus catharinensis, Canthidium* aff. *aterrimum*
Uroxys sp.1	4	10	*Canthon histrio, Eurysternus hirtellus, Canthon aff. pilluliformes, Canthon* aff. *modestus*	*Canthidium* aff. *abreviatum, Canthidium* aff. *aterrimum, Onthophagus catharinensis, Deltochilum fucatum, Eurysternus cyanescens, Canthidium cavifrons, Eurysternus parallelus, Coprophanaeys cerberus, Deltochilum brasiliense, Deltochilum rubripenne*
Uroxys sp.2	0	6	-	*Canthidium* aff. *aterrimum, Onthophagus catharinensis, Deltochilum fucatum, Deltochilum brasiliense, Deltochilum rubripenne, Deltochilum* (Deltohyboma) sp. 1

Canthidium aff. *aterrimum*	6	13	*Oxysternon palaenon*, *Canthon* aff. *modestus*, *Canthon* aff. *pilluliformes*, *Eurysternus hirtellus*, *Canthon histrio*, *Canthon conformis*	*Onthophagus catharinensis*, *Deltochilum fucatum*, *Eurysternus cyanescens*, *Canthidium cavifrons*, *Eurysternus parallelus*, *Coprophanaeus cerberus*, *Deltochilum brasiliense*, *Deltochilum rubripenne*, *Deltochilum* (Deltohyboma) sp. 1, *Uroxys* sp. 2, *Uroxys* sp. 1, *Canthon luctuosus*, *Canthidium* aff. *abreviatum*
Onthophagus catharinensis	7	14	*Oxysternon palaenon*, *Coprophanaeus spizi*, *Canthon histrio*, *Canthon* aff. *modestus*, *Eurysternus hirtellus*, *Canthon* aff. *pilluliformes*, *Canthon conformis*	*Deltochilum fucatum*, *Eurysternus cyanescens*, *Canthidium cavifrons*, *Eurysternus parallelus*, *Coprophanaeus cerberus*, *Deltochilum brasiliense*, *Deltochilum rubripenne*, *Deltochilum* (Deltohyboma) sp. 1, *Canthidium* aff. *aterrimum*, *Uroxys* sp. 2, *Uroxys* sp. 1, *Canthon luctuosus*, *Canthidium* aff. *abreviatum*, *Paracanthon* sp. 1
Deltochilum fucatum	4	12	*Canthon histrio*, *Canthon conformis*, *Eurysternus hirtellus*, *Canthon* aff. *modestus*	*Eurysternus cyanescens*, *Canthidium cavifrons*, *Eurysternus parallelus*, *Coprophanaeus cerberus*, *Deltochilum brasiliense*, *Deltochilum rubripenne*, *Deltochilum* (Deltohyboma) sp. 1, *Onthophagus catharinensis*, *Canthidium* aff. *aterrimum*, *Uroxys* sp. 2, *Uroxys* sp. 1, *Canthidium* aff. *breve*
Eurysternus cyanescens	2	10	*Eurysternus hirtellus*, *Canthon histrio*	*Eurysternus parallelus*, *Coprophanaeus cerberus*, *Deltochilum brasiliense*, *Deltochilum rubripenne*, *Deltochilum* (Deltohyboma) sp. 1, *Deltochilum fucatum*, *Onthophagus catharinensis*, *Canthidium* aff. *aterrimum*, *Uroxys* sp. 1, *Canthidium* aff. *abreviatum*

Canthidium cavifrons	0	9	-	*Eurysternus parallelus, Coprophanaeus cerberus, Deltochilum brasiliense, Deltochilum rubripenne, Deltochilum fucatum, Onthophagus catharinensis, Canthidium* aff. *aterrimum, Uroxys* sp. 1, *Canthidium* aff. *abreviatum*
Eurysternus parallelus	1	10	*Canthon* aff. *modestus*	*Coprophanaeus cerberus, Deltochilum brasiliense, Deltochilum rubripenne, Deltochilum* (Deltohyboma) sp. 1*, Canthidium cavifrons, Eurysternus cyanescens, Deltochilum fucatum, Onthophagus catharinensis, Canthidium* aff. *aterrimum, Uroxys* sp. 1
Coprophanaeus cerberus	1	11	*Canthon* aff. *modestus*	*Deltochilum brasiliense, Deltochilum rubripenne, Deltochilum* (Deltohyboma) sp. 1*, Eurysternus parallelus, Canthidium cavifrons, Eurysternus cyanescens, Deltochilum fucatum, Onthophagus catharinensis, Canthidium* aff. *aterrimum, Uroxys* sp. 1*, Canthidium* aff. *abreviatum*
Deltochilum brasiliense	4	14	*Canthon* aff. *modestus, Canthon* aff. *pilluliformes, Eurysternus hirtellus, Canthon histrio*	*Deltochilum rubripenne, Deltochilum* (Deltohyboma) sp. 1*, Coprophanaeus cerberus, Eurysternus parallelus, Canthidium cavifrons, Eurysternus cyanescens, Deltochilum fucatum, Onthophagus catharinensis, Canthidium* aff. *aterrimum, Uroxys* sp. 2*, Uroxys* sp. 1, *Canthon luctuosus, Canthidium* aff. *abreviatum, Paracanthon* sp.1
Deltochilum rubripenne	2	13	*Canthon* aff. *pilluliformes, Canthon conformis*	*Deltochilum* (Deltohyboma) sp. 1*, Deltochilum brasiliense, Coprophanaeus cerberus, Eurysternus parallelus, Canthidium cavifrons, Eurysternus cyanescens, Deltochilum fucatum, Onthophagus catharinensis, Canthidium* aff. *aterrimum, Uroxys* sp.

				1, *Uroxys* sp. 2, *Canthon luctuosus*, *Canthidium* aff. *abreviatum*
Deltochilum (Deltohyboma) sp. 1	0	12	-	*Deltochilum rubripenne*, *Deltochilum brasiliense*, *Coprophanaeus cerberus*, *Eurysternus parallelus*, *Eurysternus cyanescens*, *Deltochilum fucatum*, *Onthophagus catharinensis*, *Canthidium* aff. *aterrimum*, *Uroxys* sp. 2, *Canthon luctuosus*, *Dichotomius nisus*, *Eutrichillum hirsutum*



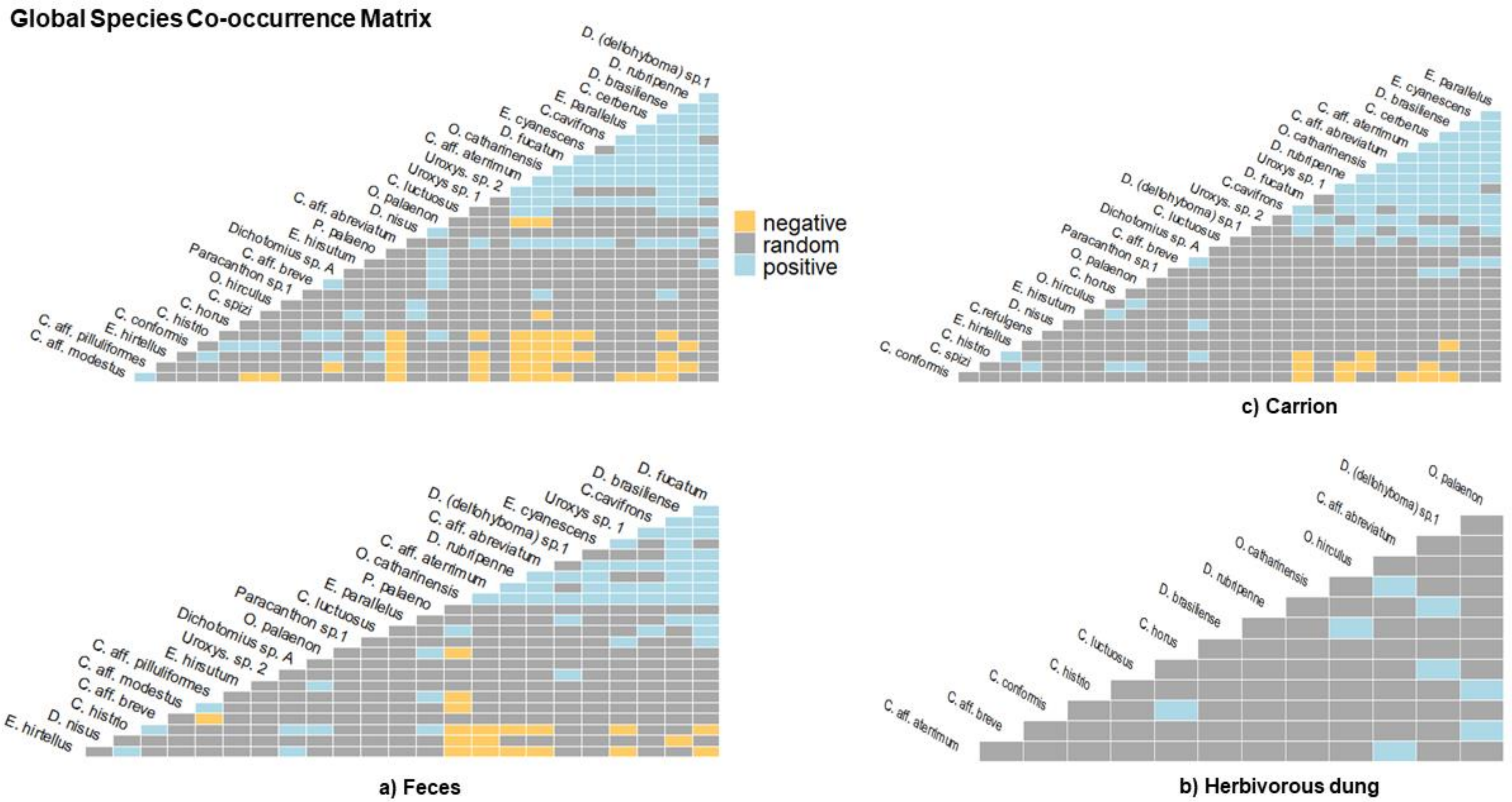
d) Rupestrian field

a) Forest

b) Brazilian Savannah

c) Introduced Pasture

Figure A1 – Global Co-occurrence Matrix for all the dung beetle community (including all variables) and Species Co-occurrence Matrix for each habitat type: a) Forest; b) Brazilian savannah (*stricto sensu*)*;* c) Introduced pasture and d) Rupestrian field. Yellow squares represent negative associations between species pairs, blue squares represent positive associations between species pairs, and gray squares represent random associations.

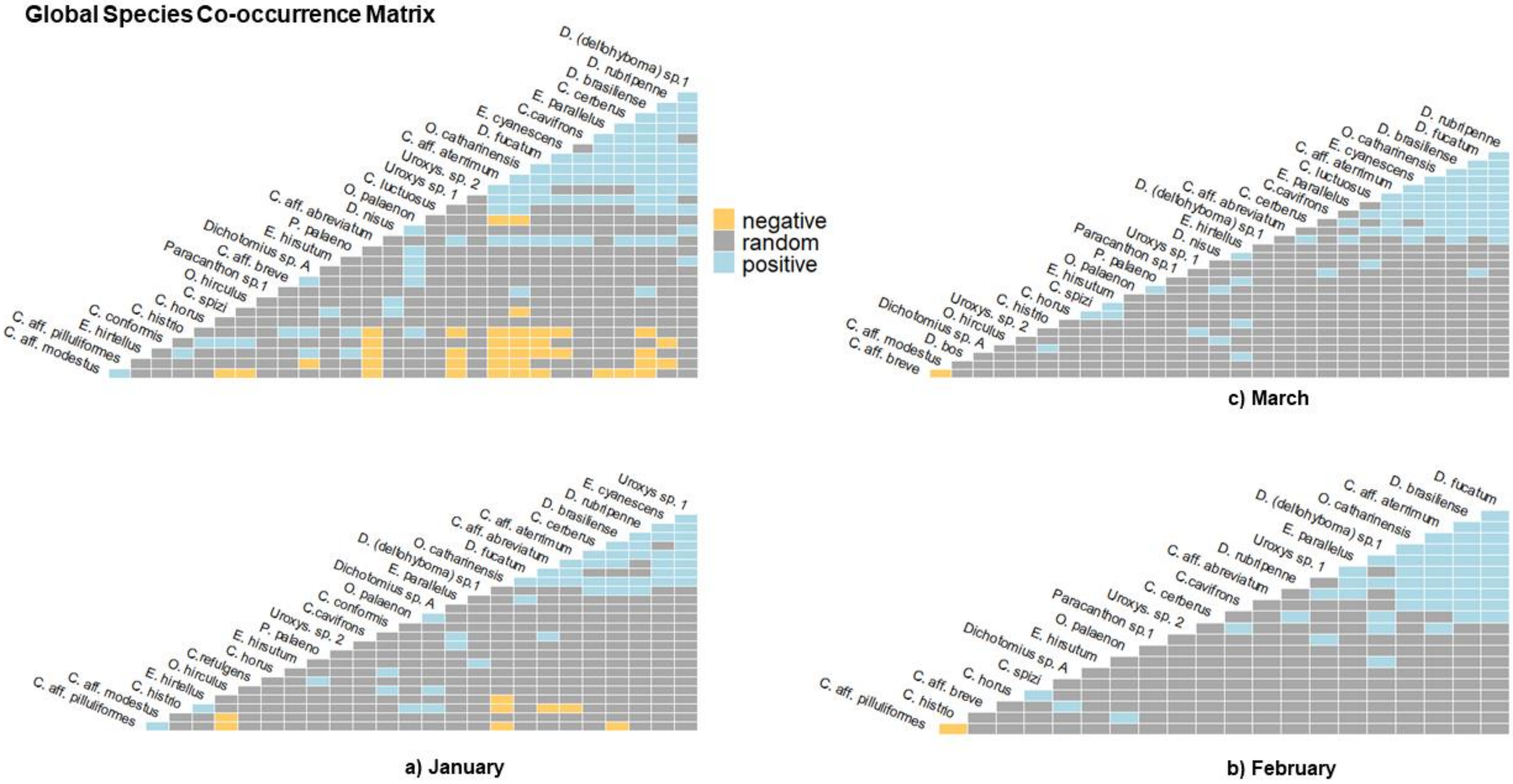


c) Carrion

a) Feces

b) Herbivorous dung

Figure A2 – Global Co-occurrence Matrix of the dung beetle species (all variables) and Species Co-occurrence Matrix for each food resource type: a) feces (omnivorous dung); b) herbivorous dung and c) carrion. Yellow squares represent negative associations between species pairs, blue squares represent positive associations and gray squares are random associations.



c) March

a) January

b) February

Figure A3 – Global Co-occurrence Matrix of the dung beetle species and Species Co-occurrence Matrix of each sampling date: a) January; b) February and c) March. Yellow squares are negative associations between species pairs, blue squares indicate positive associations and gray squares represent random associations between species pairs.

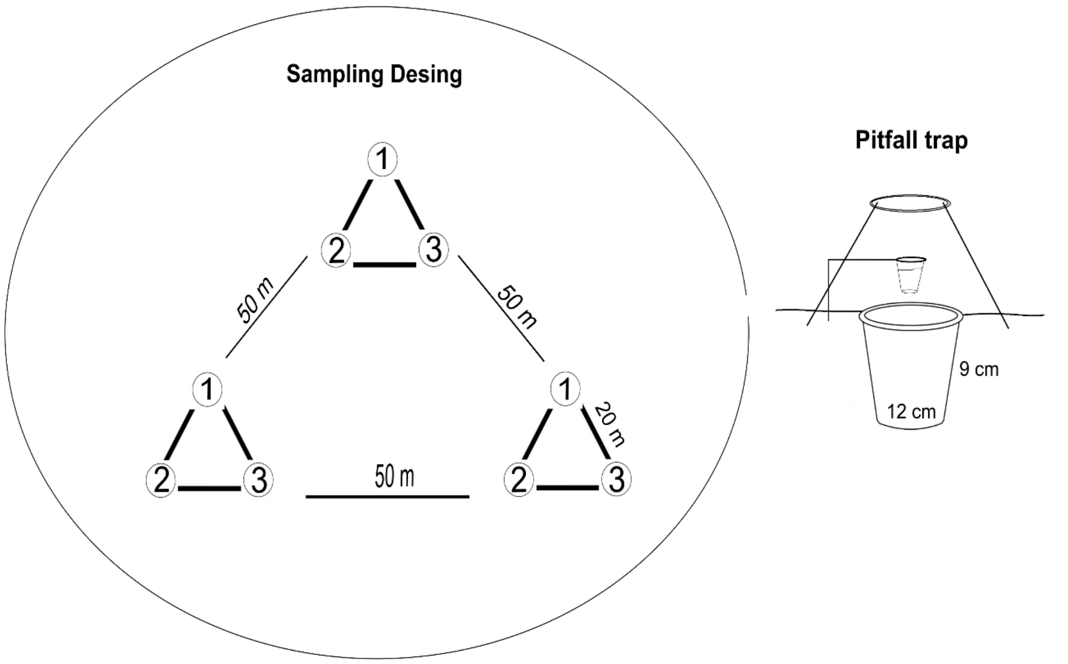


Figure A4- Experimental design for the capture of dung beetles' community. The circles on the diagram represent the pitfall traps, and the numbers inside each circle indicate the type of bait used in the corresponding trap. The number 1 corresponds to the bait of human feces + pig feces, number 2 indicates carrion bait and number 3 corresponds to the herbivorous dung bait. The traps were arranged in a triangle format within each habitat, comprising three sets of traps each (resulting in a total of nine pitfalls per habitat). Each pitfall was placed 20 meters away from the others in the same set, and the sets of traps were positioned 50 meters from one another.

ARTIGO III

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Dung beetles in burned Neotropical savannas: Resilience to Fire and temporal-vegetation dynamics after fire shaping community structure

REIS, N. L.[a]; SANTOS, K. A.[b]; CORTEZ L.[c]; LOUZADA, J.[d]

[a,c,d] Universidade Federal de Lavras, Laboratório de Ecologia e Conservação de Invertebrados (LECIN), Departamento de Ecologia e Conservação, Instituto de Ciências Naturais, CEP 37.203-202, Lavras, MG, Brasil.

[b.] Universidade Federal de Lavras, Laboratório de Manejo de Pragas Florestais, Departamento de Entomologia, CEP 37.203-202, Lavras, MG, Brasil.

* Corresponding author: Nayara Letícia Reis, Universidade Federal de Lavras (UFLA), Departamento de Ecologia e Conservação, PO Box 3037, CEP 37.203-202, Lavras, MG, Brasil. e-mail: nayara.reis015@gmail.com; nayara.reis@estudante.ufla.br

Abstract

Fire is a common natural disturbance in the Cerrado ecosystem, influencing its structure and diversity. Dung beetles are crucial for Cerrado's functioning. While many dung beetles exhibit high resilience to Cerrado fire, some species can be sensitive to disturbance. Co-occurrence of species is a parameter providing valuable insights into dung beetles disturbance responses. We tested the post-fire response of the dung beetle community in an open Savannah, focusing on species richness, composition, and co-occurrence patterns. We predicted minimal and short-term fire effects on species richness and composition, with co-occurrence patterns similar between unburned and burned areas. We anticipated swift and parallel recovery of both the dung beetle community and vegetation cover. The study occurred in open Brazilian savannas, during the rainy season, from October 2020 to March 2021. We sampled dung beetles using baited pitfall traps in four control and four burned areas. We used generalized mixed linear model (GLMM) to assess relationships between fire (unburned and burned areas), time since fire, and vegetation cover with species richness. We used distance-based linear model construction (DistLM) to understand the contribution of fire, time since fire, and vegetation cover to species composition variance. We conducted a probabilistic species co-occurrence analysis to evaluate fire´s influence on species co-occurrence. We collected 2.701 dung beetles of 46 species. Fire did not affect species richness. However, richness pattern varied over time since fire and across vegetation cover. Composition was influenced by all factors, with time since fire explaining 32.8%, fire 10%, and vegetation cover 4.6% of the variance. Co-occurrence patterns were similar between areas, and species interactions were mainly random. We conclude that the dung beetle community displayed high resistance and resilience to fire. Yet some species responded differently to disturbance, and community composition changed over time. We suggest that factors like seasonality and vegetation regeneration may have structured the post-fire community. Both stochastic and deterministic processes influenced the community. Understanding the processes shaping dung beetle communities post-fire aid in development fire management strategies for Cerrado biodiversity conservation.

Keywords: Fire; Cerrado; Community Resilience; Coexistence; Scarab Beetles.

1. Introduction

The Brazilian Cerrado is considered the largest savanna in South America and boasts the title of the world’s biodiverse savanna (Klink and Machado, 2005; Pivello, 2011; Durigan and Ratter, 2016). This ecosystem encompasses a wide array of phytophysiognomies, ranging from grass-dominated savannas to forested habitats like *cerradão* and riparian forests (Ribeiro and Walter, 1998; Ribeiro and Walter, 2008). Fire serves as frequent and natural disturbance in the Cerrado (Coutinho, 1990; Miranda et al., 2002), emerging as the principal force responsible for shaping vegetation structure and composition and the ecosystem biodiversity (Miranda et al., 2002; Parr et al., 2014; Durigan and Ratter, 2016; Fidelis et al., 2019). In this context, the physiognomies of open savannas are particularly susceptible to recurrent fire events (Ramos Neto and Pivello, 2000; Walter and Ribeiro, 2010; Schmidt and Eloy, 2020).

Fire exerts various impacts on the biotic and abiotic components of the savannah environment, with its effects on vegetation being reasonably well-documented (Frizzo et al., 2011). Plants, having coevolved with fire, exhibit numerous morphological and physiological adaptations. Furthermore, the vegetation demonstrates substantial resilience, with most species regenerating shortly after a fire event (Coutinho, 1990; Pivello, 2011; Fidelis and Zirondi, 2021). Post-fire, a successional process commences, characterized by rapid vegetation recovery fuelled by a substantial influx of nutrients from ash and increased light availability (Coutinho, 1976; Soares et al., 2006; Fidelis and Zirondi, 2021). While modifying vegetation composition and structure, fire can also alter biotic interactions among species, impacting the resources available to fauna, including shelter, food, and microhabitats (Coutinho, 1990; Frizzo et al., 2011; Almeida et al., 2014). Nonetheless, despite these effects, the typical Cerrado fauna has demonstrated a high level of adaptation to fire (Durigan et al., 2020; Arrua et al., 2023; Coelho et al., 2023; Deus et al., 2023; Fernandes et al., 2023; Reis et al., 2023).

Dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae) exhibit a greater diversity of species in open savannahs (Silva et al., 2010). These beetles primarily feed on decomposing organic material, particularly vertebrate dung (Halffter, 1991; Halffter and Matthews, 1966; Louzada, 2008), while performing ecological functions such as nutrient cycling, secondary seed dispersal, increase in soil porosity, and consequently enhancement of plant growth (Nichols et al., 2008; Huerta et al., 2013; Doube, 2018). These organisms play an indispensable role in the maintenance and functioning of savanna ecosystems (Correa et al., 2021; Oliveira et al., 2021) and can contribute significantly to post-fire environmental recovery (Doube, 2018; Nunes et al., 2019; Gonçalves et al., 2022).

Although some studies have revealed the remarkable resilience of dung beetles to fire in the Cerrado (Louzada et al., 2010; Nunes et al., 2019; Gonçalves et al., 2022; Reis et al., 2023), it is essential to acknowledge that certain species may exhibit varying degrees of sensitivity to fire, resulting in changes in community composition due to species substitutions (Louzada et al., 2010). This sensitivity arises from their high responsiveness to habitat alterations, particularly regarding vegetation structure (Halffter, 1991; Andresen, 2005; Gardner et al., 2008; Louzada et al., 2010). Vegetation cover plays a fundamental role in dung beetle communities by regulating microclimatic conditions and the availability of habitat resources (Hanski and Cambefort, 1991; Halffter, 1991; Correa et al., 2022).

Understanding the processes that shape communities in the aftermath of disturbances holds paramount importance for applied research, such as species conservation and habitat restoration (Keddy, 1999; Temperton, 2004; Audino et al., 2017; Wearn et al., 2018). Analysing co-occurrence patterns has proven to be an invaluable tool for comprehending the distribution of various species within a given environment and predicting the impact of disturbances on organisms and ecosystem dynamics and functioning (Veech, 2013; Griffith et al., 2016; Carbonell et al., 2017; Elo et al., 2021). Despite this, limited attention has been devoted to investigating the effects of disturbances on co-occurrence patterns in dung beetles (Audino et al., 2017; Ortega-Martínez et al., 2020; Edwards et al., 2021), and no studies have delved into the evaluation of fire's effects while probing the diverse mechanisms behind the restructuring of these communities’ post-fire in open Brazilian savannas.

Our study was primarily focused on examining the post-fire response of the dung beetle community in an open Savannah, with a specific emphasis on species richness, composition, and the intricate co-occurrence patterns of among species. Dung beetles have garnered recognition as exemplary organisms for assessing coexistence mechanisms and post-fire impacts on the community (Nichols and Gardner, 2011; Beiroz; Vieira and Louzada, 2019; Nunes et al., 2019). Consequently, unravelling co-occurrence patterns in dung beetles and elucidating short-term community responses to fire disturbances can furnish vital insights into the ecological processes underpinning the recolonization and rehabilitation of burnt landscapes in the Cerrado. Additionally, these insights can inform the development of fire management strategies aimed at conserving Cerrado biodiversity.

To this end, we posed two central questions: i) What is the impact of fire on the richness, composition, and co-occurrence patterns within the dung beetle community in the short term? ii) If differences exist in the dung beetle community structure, do they correspond with the process of post-fire vegetation recovery? We advanced several hypotheses: H1) Fire will exert minimal, transient, and short-term effects on species richness, composition, and co-occurrence. Should fire minimally influence the dung beetle community, we anticipate that discrepancies in species richness and composition between unburned areas and recently burnt ones will diminish over time, eventually disappearing in the short term. H2) Co-occurrence patterns between unburned and recently burned areas will not exhibit differences. Should this hold true, both areas are expected to display a similar pattern, characterized predominantly by random associations among species. H3) The dung beetle community and soil vegetation cover will undergo a swift and parallel post-fire recovery process, aligning over time. If recuperation of dung beetle species richness and composition parallels the percentage increase in vegetation cover, it would signify congruence between these two variables.

2. Material and Methods

2.1 Study area

Our study was conducted in the Campo Limpo region, situated within the Brazilian savannas approximately 8.2 kilometers from the municipality of Itumirim, Minas Gerais State, Brazil (21°20'43.9"S 44°47'56.4"W) (Fig. 1). The local vegetation encompasses fragments of the Atlantic Forest and Cerrado *stricto sensu*, interspersed with agricultural crops and introduced pastures (Loschi et al., 2013; Carvalho, 1992).

In accordance with the Köppen classification, the region boasts a Cwa climate, characterized by dry winters and rainy summers. The average annual temperature stands at 19.4°C, with a minimum of 15.8°C recorded during the cooler month of July, and a maximum temperature exceeding 22°C in the hotter month of February. Annual precipitation averages 1,530 mm, with a mere 23 mm during the dry season in July and a substantial 296 mm in December, a period of heavy rainfall. The local altitude is approximately 850 meters above sea level (Brasil, 1992; Alvares et al., 2014).

In our experiment within the Campo Limpo sites, we deliberately selected four unburned control areas (Figure A1, supplementary material) and an additional four areas that had been freshly subjected to fire (with a one-week post-fire interval) (see Figure A1, supplementary material). These areas each encompassed a minimum of one hectare and were positioned at least 100 meters apart from one another. The choice of these specific area sizes and the careful selection of a contiguous mosaic of habitats aimed to mitigate the influence of point factors (sample dependence) and geographic factors (e.g., mountainous terrain, climatic variables, and soil types) that could potentially confound the results.

2.2 Dung beetle sampling

We conducted dung beetles sampling during the rainy season, spanning from October 2020 to March 2021. This particular period in the neotropical region is renowned for heightened diversity and activity of dung beetles (Halffter and Matthews, 1966; Hanski and Cambefort, 1991).

To capture dung beetles, we employed baited pitfall traps. Within each area, we strategically placed four traps along a transect, ensuring a 50 meters separation between each trap. Each trap consisted of a 12 cm diameter and 9 cm height, plastic container, positioned at ground level. The containers were filled with approximately 250 ml of a preservative liquid (comprising a water and salt mixture) placed at the base. The was then covered with a plastic lid of identical dimensions, supported by wooden sticks to shield against rain. The pitfall traps were baited with a mixture consisting of approximately 50g of human feces combined with homogenized pig dung at a ratio of 2:8. Following 48 hours of field exposure, we retrieved the captured beetles, and subsequently, a fresh collection initiated. Over the course of six months, we conducted two samplings per month in each area, resulting in a total of 192 sampling traps (8 sites x 4 pitfalls per site x 2 samplings per month / 6 months of sampling).

We proceeded to identify the dung beetles at the species level through the use of a dichotomous key (Vaz de Mello et al., 2011) and by cross-referencing them with reference materials housed in the Entomological Collection of the Center for Biodiversity and Genetic Resources at the Federal University of Lavras (CEUFLA). For species confirmation, the task was entrusted to the specialized taxonomist, Fernando Zaguri Vaz-de-Mello (UFMT).

2.3 Vegetation Cover

To comprehensively assess the ground vegetation coverage at across sampling point, encompassing both control areas (unburned) and recently burned areas, we conducted meticulous quantification. Within each area, specifically beside each installed pitfall, we executed measurements at four distinct points, culminating in a cumulative total of 32 points examined monthly throughout a continuous span of 6 months.

The methodology adopted for measurement acquisition involved capturing photographs of the ground vegetation at each designated point, all taken at a standardized height of 1.20 meters. These photographic endeavours were conducted within a wooden quadrant measuring 50 x 50 cm, as elucidated in Figure A2 (supplementary material). Subsequently, each photograph underwent meticulous processing within the ImageJ software, facilitating the quantification of both white (corresponding to vegetation cover) and black pixels (corresponding to exposed bare ground).

The determination of ground vegetation coverage percentage within the quadrant was achieved by applying the following formula: white pixels / (white pixels + black pixels). This rigorous methodology ensured a robust assessment of ground vegetation coverage across the designated areas.

2.4 Statistical Analysis

To investigate the intricate relationship between dung beetle species richness and a suite of crucial variables, including fire (in both unburned and burned areas), time elapsed since fire (spanning from zero to six months), and the percentage of vegetation cover, we conducted an in-depth analysis utilizing a generalized mixed linear model (GLMM). Within this analysis, the mean dung beetle species richness was designated as the response variable, while treatments (unburned and burned), vegetation cover percentage, and time since fire were categorized as explanatory variables. Notably, time since fire owing to its capacity to introduce natural fluctuations within a given location, was deemed a random effect, whereas treatments and vegetation cover were classified as fixed effects during model formulation. Employing a stepwise approach, we progressively streamlined the model, retaining only those variables that exhibited statistical significance. To derive parameter estimates and dissect variances, we adopted the restricted maximum likelihood method (REML). The model was fittingly framed using the "Poisson" family, and the analyses were conducted with the assistance of the statistical packages "lme4" (Bates et al., 2009). Additionally, to bolster our analysis, we subjected the model to a pairwise contrast examination, harnessing the “lsmeans" package (Lenth, 2016) within the R 4.4.2 software (R Core Team, 2022).

To access the individual and partitioned effects of the variables (fire, time since fire, and vegetation cover) on dung beetle composition, we used a distance-based linear model (DistLM). The DistLM framework facilitates the modelling of the relationship between multivariate data and categorical and continuous variables via multiple regression models. The composition data, factoring in presence and absence of species, were transformed, and combinate into an individual matrix by using the Jaccard similarity index. We adopted the adjusted R2 selection criterion for analysis, commencing with the Marginal test to identify variables, considering their mutual independence, and that exerted a significant influence on dung beetle composition. Subsequently, we employed the Sequential test to progressively eliminate the effect of the initial variable while successively incorporating the remaining variables to elucidate the variance within the dataset. This allowed us to disentangle and distribute the total variability across the dimensions of area, time since fire, and vegetation cover. Consequently, we were able to assess the variance explained by these variables after removing the area effect.

Finally, to assess the co-occurrence patterns of dung beetle species between unburned and burned areas, we constructed presence/absence matrices for each area and conducted a Cooccur analysis (Probabilistic Species Co-Occurrence Analysis). Leveraging the "cooccur" package within the R 4.2.2 software (R Core Team 2022), this analysis scrutinized species co-occurrence at the sampling point level, with each pitfall serving as an autonomous sampling unit. To ensure the independence of samples we meticulously positioned each point at a minimum distance of 50 meters from one another (Larsen and Forsyth, 2005; Silva and Hernandez, 2015).

The Cooccur analysis evaluates the direct co-occurrence of species by contrasting the observed co-occurrence against the expected co-occurrence (Veech, 2013; Griffith et al., 2016). Expected co-occurrence is computed as the product of the probabilistic occurrences of two species, multiplied by the total number of sampling sites. Subsequently, the analysis employs a combinatory approach to ascertain whether the observed frequency of co-occurrence significantly deviates from the expected frequency. The results are interpretable based on the relationship between observed frequency (OF) and expected frequency (EF): when OF significantly surpasses EF, it signifies positive associations between species; conversely, if OF is notably less than EF, negative associations are inferred. In the absence of a significant difference or when OF aligns with EF, random associations between species are indicated (Veech, 2013; Griffith et al., 2016). However, it is essential to acknowledge that the Cooccur analysis's sensitivity to the volume of sampling data, precluded the evaluation of co-occurrence patterns on a month-to-month basis.

3. Results

In our data collection efforts, we amassed a total of 2.701 dung beetles, representing 46 distinct species and spanning across 20 genera (refer to Table 1S in the supplementary material for details). The most prevalent species in our study included *Dichotomius glaucus* (741 individuals), *Phanaeus* aff. *palaeno* (299 individuals), *Canthon corpulentos* (219 individuals), and *Canthon* aff. *pilluliformis* (199 individuals) (see Table 1S). In unburned areas, we recorded 40 species comprising 1.667 individuals, with *Dichotomius glaucus* (457 individuals) and *Canthon* aff. *pilluliformis* (197 individuals) emerging as the dominant species (as per Table 1S in the supplementary material). In contrast, in burned areas, our observations encompassed 38 species and 1.034 individuals, with *Dichotomius glaucus* (284 individuals) assuming dominance, followed closely by *Phanaeus* aff. *palaeno* (152 individuals) (refer to Table A1 in the supplementary material).

When it comes to assessing the average dung beetle species richness, we uncovered no significant disparity between unburned and burned areas (F value = 1.36, p =0.5761) (as depicted in Fig. 2). Remarkably, the temporal patterns of richness mirrored one another across these areas (Fig. 2). Richness exhibited temporal variations independently of the area (F value = 6.60, p < 0.0003), characterized by modest mean values in October, followed by notable increases in November, December, and January (Fig. 2). Noteworthy distinctions in mean species richness emerged between October and subsequent sampled months: November (p = 0.0003), December, January, February, and March (p < 0.0001) (Fig. 2). In addition, differences in species richness were noted between the months of January and February (p = 0.0064) and January and March (p = 0.0465). However, no significant discrepancies surfaced in species richness between November and the months of December (p = 0.5056), January (p = 0.1763), February (p = 0.8723), and March (p = 0.9887), or between December and the months of January (p = 0.9915), February (p = 0.0863), and March (p = 0.2982). Furthermore, no significant differences were detected between February and March (p = 0.9861) (Fig. 2).

We further delved into the influence of different vegetation cover percentages on species richness (F value = 17.55, p < 0.00002), identifying an interaction between the months and vegetation cover variables (F value = 4.20, p = 0.0005). This interaction suggests temporal fluctuations in vegetation cover (see Fig. 3), particularly notable between October and January (p = 0.0484), December and March (p = 0.0203), and January and March (p = 0.0048) (Fig. 3).

In the endeavour to decode the intricate dynamics governing dung beetle species composition, we introduced fire (unburned and burned areas), time since fire, and vegetation cover as key variables. Intriguingly, time since fire emerged as a potent explanatory factor, singly elucidating approximately 32.8% of the composition variance in our dataset. In contrast, fire in isolation accounted for 10% of the variance, and vegetation cover, when analyzed independently, explained approximately 4.6% (refer to Table 1). Subsequent partitioning of these variables unveiled that fire independently elucidated 4% of the data's variance, and the removal of fire's influence, encompassing both unburned and burned areas, eliminated all the explanatory power attributed to the vegetation cover variable. This left time since fire to account for roughly 25% of the data's variance. Notably, no shared effect was observed between fire and time since fire variables on vegetation cover, yet fire and vegetation cover jointly contributed to explaining 7% of the variance (see Fig. 4, Table 2). In totality, our comprehensive model illuminated 35.5% of the data's variance, encompassing the cumulative influence of each isolated variable within the sequential test alongside their shared contributions (see Fig. 4, Table 2).

Moreover, the proportionality of co-occurrence patterns between species in unburned and burned areas, indicated that the occurrence of fire did not exert any discernible influence on species co-occurrence (refer to Fig. 5a-b). Our Cooccur analysis yielded 780 pairs of species combinations for the unburned sites, with 337 pairs (43.21%) being excluded due to their expected co-occurrence being less than 1. Consequently, 443 pairs were subjected to analysis, resulting in 424 random associations, (refer to Fig. 5a). Of these, two exhibited positive associations, while four displayed negative species associations within unburned areas (refer to Fig. 5a). In the context of burned sites, our Cooccur analysis generated 703 pairs of species combinations, with 371 pairs (52.77%) removed from the analysis. Thus, 332 pairs were analyzed, culminating in 321 random associations (refer to Fig. 5b). This analysis also uncovered five positive species associations and two negative species associations within burned areas (refer to Fig. 5b).

4. Discussion

Our study yields compelling evidence suggesting that fire exerts a minimal and transient impact on the dung beetle community in open neotropical savannahs. Intriguingly, this impact does not extend to the species co-occurrence pattern, and the community remaining predominantly characterized by random associations. Furthermore, our observations reveal a swift recuperation of the dung beetle community, a phenomenon that is likely driven by seasonality and the post-fire regeneration of vegetation.

The observed pattern of species richness variation between unburned and burned areas strikingly resembles one another statistically, effectively signifying the absence of any fire-induced effects on richness. This result harmonizes with previous findings, particularly in the context of the Cerrado biome, where evidence underscores the remarkable resistance and resilience of dung beetles to fire (Nunes et al., 2019; Gonçalves et al., 2022). In parallel with the findings of Nunes et al. (2019) within rupestrian fields, our study postulate that the hypothesis of individual movement rooted in metacommunity dynamics (Leibold et al., 2004) may offer a plausible explanation for our observations. Given the dung beetle's notable capacity for dispersal and colonization (Silva and Hernández, 2015), it's conceivable that rapid species recolonization within burned areas transpired through the movement of individuals from neighbouring unburned zones (Brotons et al., 2005).

Irrespective of fire occurrence, our study unveils that species richness undergoes fluctuations in response to both time since fire and vegetation cover. The study unveiled diminished average species richness in October, subsequently followed by a marked increase in November, December, and January. Dung beetles are renowned for their pronounced seasonality (Andresen, 2005; Andrade et al., 2011), with their activities and species prevalence tightly tethered to the onset of rainfall (Hanski and Cambefort, 1991; Milhomem et al., 2003; Andrade et al., 2011; Frizzas et al., 2020; Corrêa et al., 2021). Within the Cerrado, the advent of rain typically commences in October, progressively intensifying throughout the season, culminating in abundance during November and December (Abot et al., 2012; Milhomem et al., 2003; Frizzas et al., 2020). Consequently, the surge in species richness from November onwards can be attributed to the increased incidence of rainfall during this period. Furthermore, an augmented species richness correlates with a heightened vegetation cover percentage, substantiating the hypothesis that vegetation structure wields significant influence over dung beetle communities (Louzada et al., 2010; Martello et al., 2016; Macedo et al., 2020). It's conceivable that both direct and indirect impacts of vegetation, encompassing environmental microclimate regulation and shifts in fecal resource availability, are instrumental in elucidating this richness pattern (Menendez and Gutierrez, 2004; Macedo et al., 2020; Pessôa et al., 2021).

Each facet, including fire, time since fire, and vegetation cover, plays a pivotal role in shaping the variation within the composition of dung beetle species. Notably, time since fire emerges as an independent explanatory factor, delineating approximately 32.8% of the composition variance in isolation. In stark contrast, fire alone elucidates 10% of the variance, and when considered independently, vegetation cover contributes to the explanation of approximately 4.6% (as documented in Table 1). Upon dissecting these variables, it comes to light that fire independently clarifies 4% of the data variance, with the removal of fire's influence on both unburned and burned areas subsequently nullifying all explanatory power ascribed to the vegetation cover variable. This leaves time since fire to account for roughly 25% of the data's variance. Of particular interest is the absence of a shared effect between fire and time since fire variables on vegetation cover, with fire and vegetation cover, collaboratively contributing to 7% of the explained variance (refer to Fig. 4, Table 2). Collectively, our comprehensive model demystifies 35.5% of the data's variance, encompassing the cumulative influence of each isolated variable within the sequential test alongside their shared contributions (refer to Fig. 4, Table 2).

Furthermore, our study underscores that fire does not exert any discernible influence on the co-occurrence pattern of species, within the dung beetle community, which persists in being predominantly characterized by random associations. This stochasticity was an anticipated outcome, aligning with several extant studies highlighting the prevalence of this pattern across diverse taxa (Pitta et al., 2012; Willians et al., 2014; Lyons et al., 2016; Fanfarillo et al., 2020), including beetles (Magura and Lövei, 2019; Ortega-Martínez et al., 2020; Elo et al., 2021). Our central hypothesis positing that fire does not function as an environmental filter sufficiently potent to induce discernible variations in species co-occurrence patterns receives validation from these findings. Indeed, stochastic processes unrelated to fire are proposed as the principal driving mechanisms behind the occurrences of dung beetle species. Furthermore, these stochastic processes may be construed as a composite of dispersion and colonization events within randomly scattered habitats and resource patches by various dung beetle species. In a parallel study, Ortega-Martínez et al. (2020), while assessing dung beetles within impacted landscapes, reported a predominant prevalence of random species patterns and affirmed that stochastic processes wielded the primary force governing these communities. In a complementary example, Cadena-Zamudio et al. (2022), demonstrated that stochastic processes primarily underpinned the recovery of soil arthropod communities following forest fires in Mexico.

Within our observations, both positive and negative associations surfaced among dung beetle species in both unburned and burned areas. Notably, species such as *Canthidium decoratum* and *Canthon histrio* exhibited positive associations within unburned areas, implying shared habitat requirements or behaviors conducive to coexistence. Conversely, we identified instances of negative associations, especially within unburned areas such as *Dichotomius crinicollis* displaying a negative association with *Canthon virens*. Such occurrences potentially signify competitive exclusion or divergent habitat requirements between these species (Diamond, 1975). Our findings thus affirm that deterministic processes, encompassing biotic factors such as species interactions and abiotic factors like environmental filters, play a substantial role in the structuring of dung beetle communities (Ellwood et al., 2009). It's imperative to acknowledge that the observed positive and negative associations may not necessarily be indicative of direct species interactions but rather reflect disparities in habitat requirements among them (Blanchet; Cazelles and Gravel, 2020).

In summary, our study elucidates that the dung beetle community in open Cerrado areas exhibits a notable degree of resilience to fire, with species diversity and co-occurrence patterns remaining largely unaltered by this disturbance. However, it is crucial to underscore that dung beetles' responses to fire perturbation can be variable, potentially leading to species turnover and shifts in community composition over time, particularly in response to frequent non-natural fire events. Furthermore, our research posits that in addition to fire, factors such as seasonality and soil vegetation regeneration may significantly contribute to the structuring of community dynamics post-fire.

While stochastic processes predominantly influence dung beetle community dynamics, the presence of both positive and negative associations suggests that deterministic influences wield significance as well. We advocate for the utilization of species occurrence patterns as a potent tool for predicting the consequences and responses of dung beetle communities to disturbances, with a particular emphasis on fire. Furthermore, we recommend that future research endeavours explore the intrinsic characteristics of dung beetle species in conjunction with occurrence patterns, as this combined information can yield a clearer understanding of the assembly rules governing dung beetle communities, offering insights into whether stochastic mechanisms, environmental filters, or biotic interactions predominate. Additionally, an invaluable approach involves the examination of species co-occurrence networks, providing a comprehensive understanding of species interactions, with each co-occurrence contextually situated relative to all other co-occurrences within the network.

Ultimately, our study serves a pivotal role in unravelling the underlying processes that shape dung beetle communities following fires in savanna ecosystems. Moreover, our findings hold practical significance in applied research, offering valuable insights for the formulation of fire management strategies aimed at conserving the rich biodiversity of the Cerrado biome.

Author contributions

All authors (NLR, KAS, LC and JL) worked together to develop the idea and hypothesis for the manuscript. NLR, LC and JL were responsible of planning the fieldwork, and NLR and LC conducted the collecting samples of the dung beetles. The statistical analysis was contributed to by all authors, and NLR author produced the entire text with help from co-authors KAS and JL.

Conflict of Interest Statement

The authors declare the absence of any commercial or financial relationships that could be potential conflicts of interest. And the authors participated in all the process of this study.

License permits

We utilized the sampling permission number SISBIO 28097-1, for the sampling of data.

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FIGURE and TABLE LEGEND

Figure 1. Geographical map indicating the location of the collection sites (Brazilian savannah), Itumirim, Minas Gerais State, Brazil. Sampling points are highlighted in unburned sites (yellow balls) and burned sites (red balls).

Figure 2. Richness Dung beetle species in unburned areas and burned areas (Brazilian Savannas) throughout the six months of sampling (October to March). The X-axis indicates the time of sampling (months), and the Y-axis indicates the richness average of species. The vertical lines indicate the variance of data for each month and each site, the blue lines represent the unburned areas, and the red lines represent burned areas.

Figure 3. Vegetation cover percentage throughout the six months of sampling (October to March). The X-axis indicates the time (months), and the Y-axis indicates the vegetation cover average. The vertical lines indicate the variance of data for each month.

Figure 4. Venn Diagram illustrates the proportion of variance of composition explained by fire (unburned and burned area), time since fire (months), and vegetation cover percentage. Within each circle, is the individual proportion of variance explained by variables (fire, time since fire, and vegetation cover), while the overlapping regions of the circles depict the proportion of variance shared among variables.

Figure 5. Co-occurrences matrix of the dung beetle species (n =31). a) unburned sites: yellow squares represent negative associations between species pairs (4), blue squares represent positive associations between species pairs (2), and gray squares represent random associations between species pairs (n total = 424); b) burned sites: yellow squares represent negative associations between species pairs (2), blue squares represent positive associations between species pairs (5), and gray squares represent random associations between species pairs (321).

Table 1. Distance-based linear model (DistLM) marginal tests result from variation in composition of Dung beetle species explained by variables: areas (unburned and burned), time since fire (months), and vegetation cover percentage.

Table 2. Distance-based linear model (DistLM) sequential tests result from variation in composition of Dung beetle species. Variables: areas (unburned and burned), time since fire (months), and vegetation cover percentage.

TABLES

Table 1

MARGINAL TESTS				
Variables	SS (trace)	Pseudo-F	P	Prop.
Area	14035	2.4912	0.0001*	0.0997
Time since fire	46307	3.349	0.0001*	0.3289
Vegetation cover	6466.8	2.2146	0.004*	0.0459

Table 2

SEQUENTIAL TESTS						
Variables	Adj R^2	SS (trace)	Pseudo-F	P	Prop.	Cumul.
Area	5.97E-02	14035	2.4912	0.0001*	0.0997	0.0997
Time since fire	0.24301	36052	3.1797	0.0001*	0.25607	0.35575
Vegetation cover	0.24301	5.22E-11	0	1	3.71E-16	0.35575

FIGURES

Figure 1

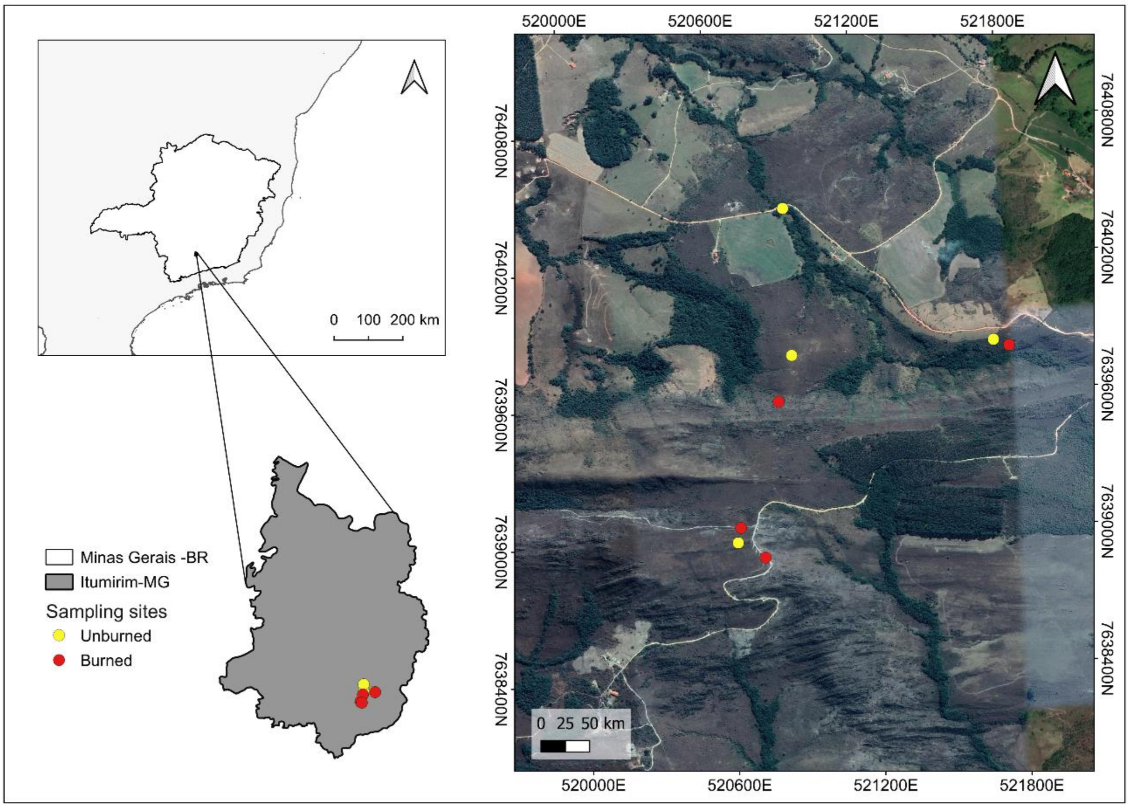
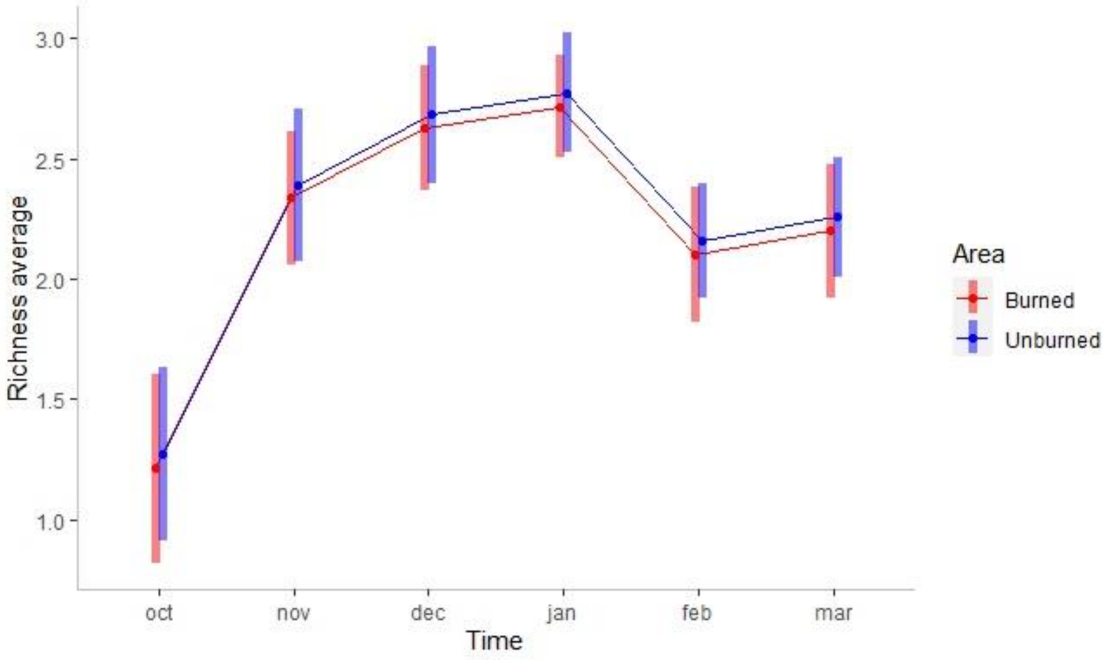


Figure 2


Richness average
3.0
2.5
2.0
1.5
1.0
oct
nov
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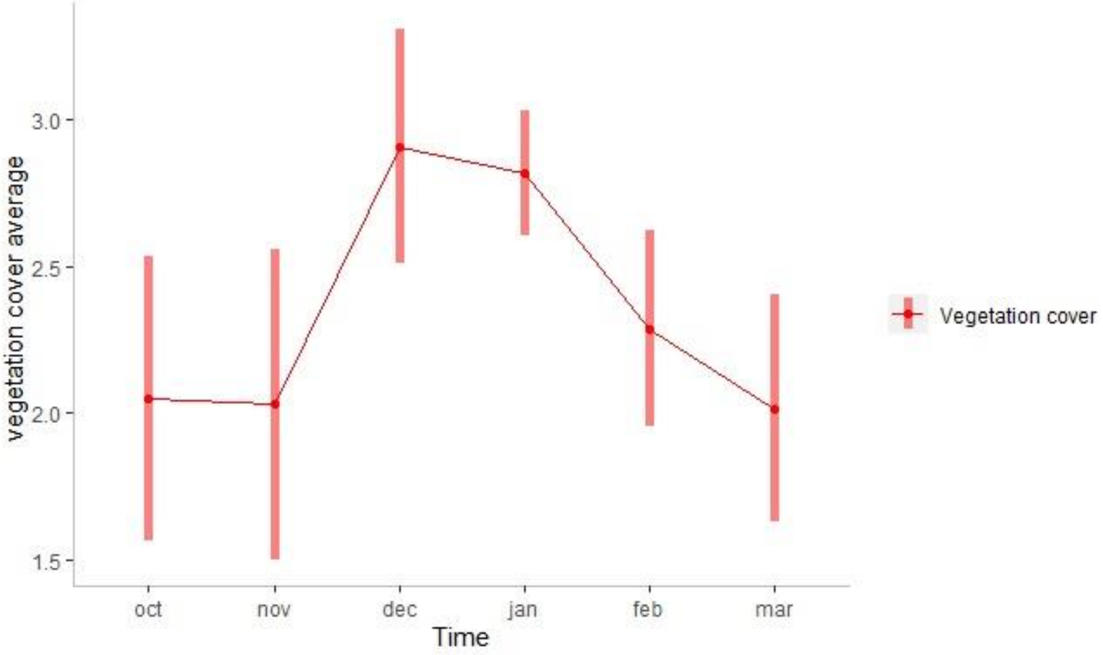
jan
feb
mar
Time
Area
Burned
Unburned

Figure 3


3.0
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vegetation cover average
oct
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dec
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feb
mar
Time
Vegetation cover

Figure 4

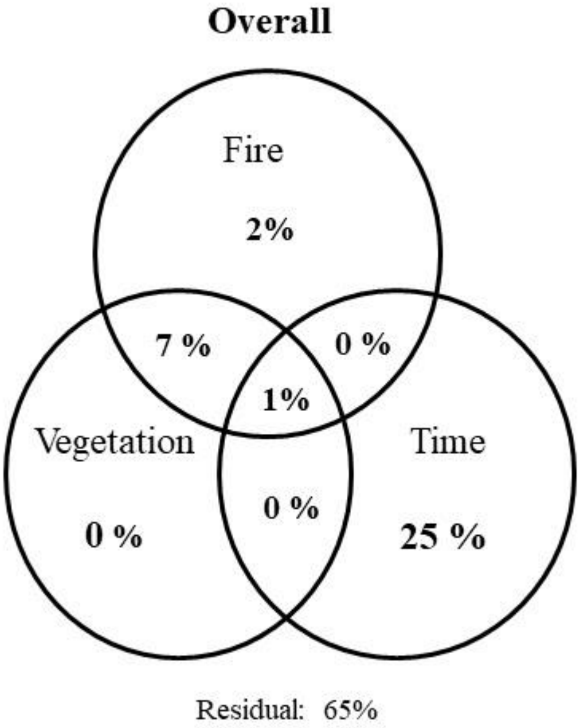
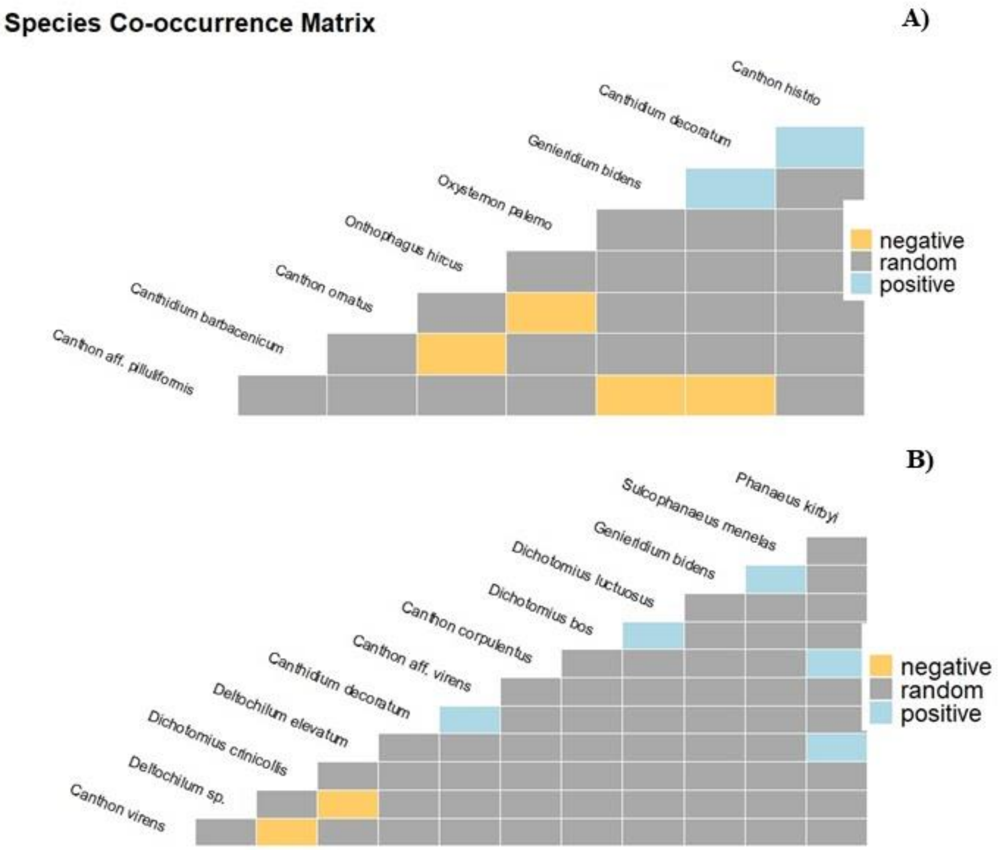


Figure 5


Species Co-occurrence Matrix
A)
Canthon histrio
Canthidium decoratum
Genieridium bidens
Oxysternon palemo
Onthophagus hircus
Canthon ornatus
Canthidium barbacenicum
Canthon aff. pilluliformis
negative
random
positive
B)
Phanaeus kirbyi
Sulcophanaeus menelas
Genieridium bidens
Dichotomius luctuosus
Dichotomius bos
Canthon corpulentus
Canthon aff. virens
Canthidium decoratum
Deltochilum elevatum
Dichotomius crinicollis
Deltochilum sp.
Canthon virens
negative
random
positive

Supplementary material

Dung beetles in burned Neotropical savannas: Resilience to Fire and temporal-vegetation dynamics after fire shaping community structure

REIS, N. L.[a]; SANTOS, K. A.[b]; CORTEZ L.[c]; LOUZADA, J.[d]

[a,c,d] Universidade Federal de Lavras, Laboratório de Ecologia e Conservação de Invertebrados (LECIN), Departamento de Ecologia e Conservação, Instituto de Ciências Naturais, CEP 37.200-900, Lavras, MG, Brasil.

[b.] Universidade Federal de Lavras, Laboratório de Manejo de Pragas Florestais, Departamento de Entomologia, CEP 37.200-900, Lavras, MG, Brasil.

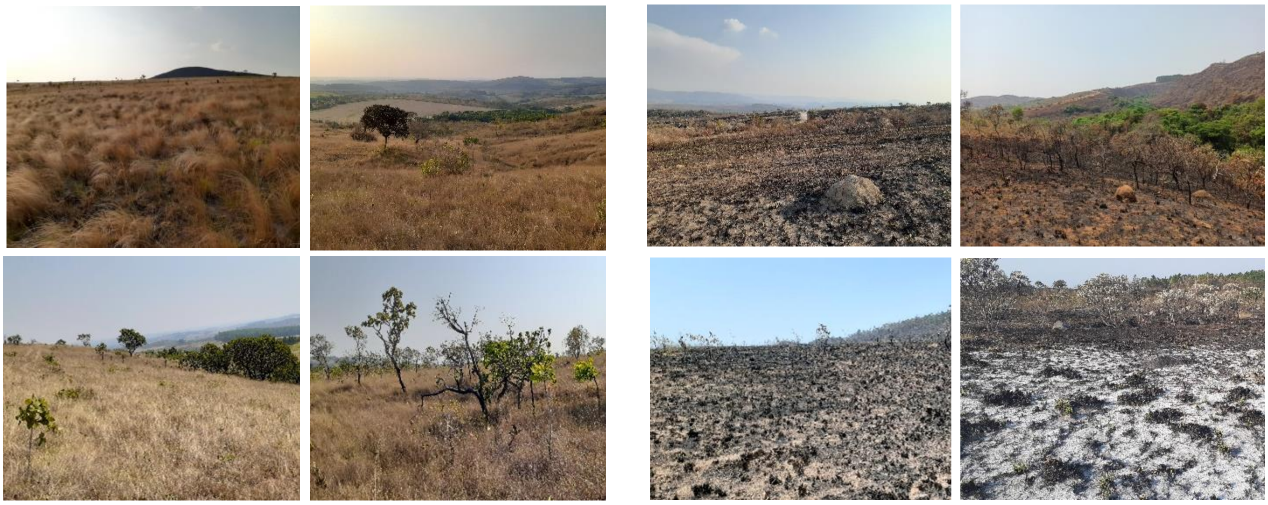


Figure A1 - Illustration of Cerrado Campo Limpo locations: Unburned (control) and burned areas.

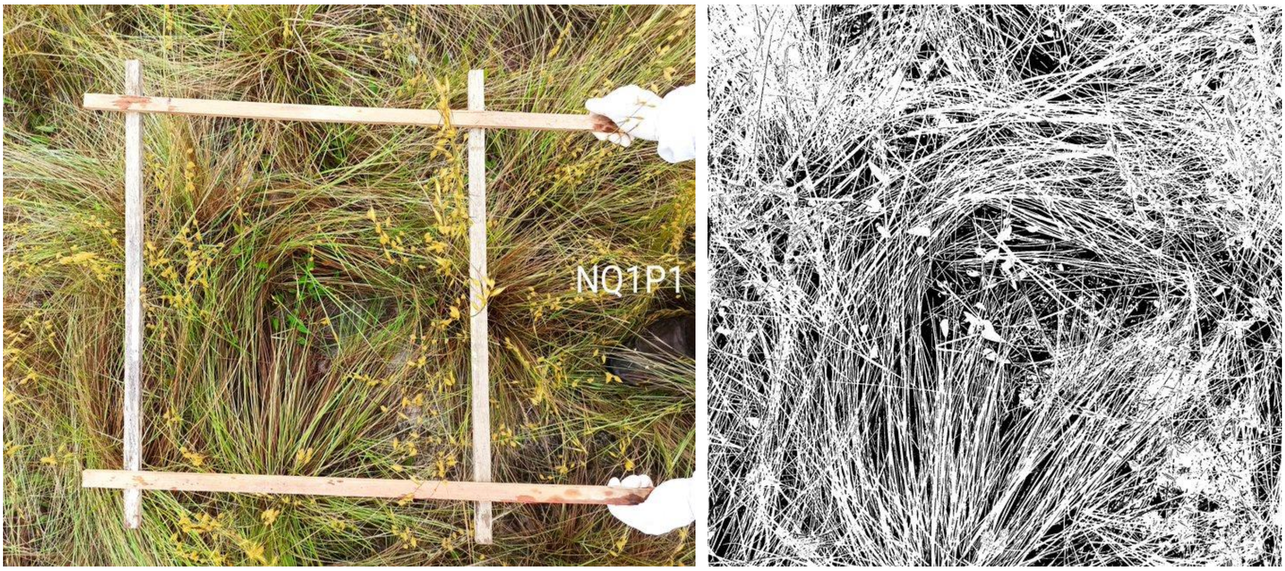


Figure A2 Illustration of the methodology adopted for measurement of the vegetation cover and photographic image j processing.

Table A1- List of dung beetle species sampled in unburned and burned areas in open savannahs, Itumirim, Minas Gerais State.

Dung beetle species	**Unburned area**	**Burned area**	**Total**
Agamopus unguicularis	7	0	7
Agamopus viridis	4	0	4
Anisocanthon sp.	0	4	4
Ateuchus aff. *puncticollis*	0	1	1
Ateuchus striatulus	8	5	13
Ateuchus vividus	6	4	10
Canthidium aff. *hyla*	0	4	4
Canthidium barbacenicum	9	0	9
Canthidium breve	0	1	1
Canthidium decoratum	26	18	44
Canthidium marseuli	2	3	5
Canthidium sp. 1	0	1	1
Canthon aff. *pilluliformis*	197	2	199
Canthon aff. *virens*	2	9	11
Canthon corpulentus	146	73	219
Canthon dives	1	0	1
Canthon histrio	16	30	46
Canthon ornatus	7	2	9
Canthon unicolor	1	0	1
Canthon virens	49	88	137
Coprophanaeus aff. *horus*	10	6	16
Coprophanaeus spitzi	5	2	7
Deltochilum elevatum	3	5	8
Deltochilum sp.	149	39	188
Dendropaemon viridipenne	1	0	1

Dichotomius aff. *lycas*	1	0	1
Dichotomius bos	65	27	92
Dichotomius crinicollis	8	5	13
Dichotomius glaucus	457	284	741
Dichotomius luctuosus	7	8	15
Dichotomius nisus	76	39	115
Dichotomius semiaeneus	3	4	7
Eurysternus parallelus	1	1	2
Eutrichillum sp.	2	0	2
Genieridium bidens	51	28	79
Isocopris inhiatus	3	1	4
Ontherus ulcopygus	1	1	2
Onthophagus bucculus	6	4	10
Onthophagus hircus	19	58	77
Oxysternon palemo	66	81	147
Phanaeus aff. *palaeno*	147	152	299
Phanaeus kirbyi	54	21	75
Sulcophanaeus menelas	33	15	48
Trichillum adjunctum	6	3	9
Trichillum externepunctatum	12	4	16
Uroxys sp.	0	1	1
Total of individuals	**1667**	**1034**	**2701**
Species richness	**40**	**38**	**46**

CONSIDERAÇÕES FINAIS

Essa tese ofereceu uma visão abrangente sobre a ecologia e a dinâmica das comunidades de besouros escarabeíneos em ecossistemas tropicais, com foco nas savanas. Ao revisarmos o estado atual de conhecimento sobre os besouros escarabeíneos nas savanas tropicais, nós observamos que apesar da conhecida diversidade de espécies nesses ambientes, há ainda importantes lacunas sobre a ecologia do grupo. Nós observamos uma distribuição não homogênea das pesquisas ao longo dos trópicos, ou seja, houve uma maior concentração de estudos em regiões específicas (ex. Neotrópicos), com destaque para o Brasil, e consideráveis lacunas nas regiões Afro-tropical e Australasia. Além disso, nós notamos uma predominância de pesquisas em pastagens, florestas de savana nativa e ambientes antropizados com foco em métricas tradicionais, como abundância e riqueza e composição de espécies. Recomendamos que futuras pesquisas ampliem seu escopo para incluir métricas adicionais, como biomassa e funções ecológicas, a fim de obter uma compreensão mais completa do papel desses besouros nos ecossistemas, além disso, nós recomendamos a expansão de estudos em áreas menos exploradas e sujeitas a degradação.

Ao investigarmos os padrões de coocorrência das espécies de besouros escarabeíneos em diferentes habitats savânicos, tomando como proxy as florestas tropicais. Nós observamos que fatores como o tipo de habitat desempenharam um papel crucial sobre a coexistência das espécies. Além disso, vimos que embora haja uma tendência nas associações aleatórias entre as espécies na comunidade, a presença de associações negativas e positivas indicam a importância de se considerar tantos processos determinísticos e estocásticos na estruturação das comunidades. Como o tipo de habitat foi um fator importante na coexistência das espécies na comunidade, ressaltamos a importância de se preservar um mosaico com diferentes fitofisionomias, uma vez que esses ambientes são responsáveis por manter a diversidade de escarabeíneos.

No contexto da resposta das comunidades de escarabeíneos ao fogo do Cerrado, nós observamos uma notável resiliência da comunidade, o que é crucial para a manutenção e para o funcionamento do ecossistema do Cerrado. No entanto, também identificamos que a variabilidade na resposta das espécies ao fogo pode levar a mudanças na composição e na diversidade da comunidade ao longo do tempo. Isso ressalta a importância de considerar não apenas o fogo, mas outros fatores, como a sazonalidade e a regeneração da vegetação do solo. Além disso, reforçamos que a compreensão dos processos que moldam as comunidades de escarabeíneos após incêndios, pode ser útil para o desenvolvimento de estratégias eficazes de manejo do fogo no Cerrado.

Em síntese, essa tese oferece uma visão abrangente além de fornecer insights valiosos sobre a ecologia e a resposta das comunidades de besouros escarabeíneos nas savanas tropicais. Esses achados podem ter implicações significativas para o manejo e a conservação das savanas tropicais.