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Influências da estrutura das paisagens do Cerrado sobre a diversidade biológica de besouros rola-bosta

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INFLUÊNCIAS DA ESTRUTURA DAS PAISAGENS DO CERRADO SOBRE A DIVERSIDADE BIOLÓGICA DE BESOUROS ROLA-BOSTA

Resumo: As savanas globais representam os ecossistemas mais ameaçados do mundo, em decorrência da expansão das atividades agropecuárias. Dentre essas savanas, está o Cerrado brasileiro, considerado um dos hotspots globais para a conservação. No Cerrado, as atividades agropecuárias tornaram as suas paisagens uma mesclagem entre ecossistemas antrópicos e nativos, com a predominância da primeira classe, incrementando fatores como grau de isolamento e fragmentação dos habitats. Assim, a diversidade biológica acaba sendo ameaçada em detrimento desses fatores, contexto que considera a necessidade de se avaliar essa característica das paisagens nos estudos envolvendo diversidade. A presente tese foi construída em dois capítulos, sendo o primeiro capítulo delineado para se avaliar a influência da configuração e da composição das paisagens sobre a diversidade biológica e o segundo capítulo para que seja possível compreender como está organizada a diversidade biológica desde o nível dos remanescentes de vegetação nativa até o nível das classes de paisagens dominantes no bioma (paisagens urbanas, de agricultura, de pecuária e nativas). Como resultados mais importantes, tem-se que o comportamento da diversidade à composição e configuração das paisagens depende da métrica analisada. Por exemplo, a diversidade beta envolvendo a riqueza de espécies aumentou no sentido dos remanescentes de vegetação para as classes de paisagens. O contrário ocorreu quando se analisa a diversidade de shannon. Além disso, quando se analisa a diversidade nas formações savânicas, foi encontrado um incremento da diversidade na medida em que há aumento de diversas coberturas antrópicas. Ambos os resultados são indícios de homogeneização da diversidade nas paisagens do Cerrado, indicando que as espécies generalistas, adaptadas aos ecossistemas antrópicos, podem estar aumentando a sua dominância, deslocando as espécies nativas. Assim, as atividades antrópicas no Cerrado precisam incluir o remodelamento dos componentes das paisagens, de modo a permitir que essa homogeneização seja interrompida, impedindo-se, assim, a perda de diversidade genética e biológica.

Abstract: Global savannas represent the most threatened ecosystems in the world due to the expansion of agricultural and livestock activities. Among these savannas is the Brazilian Cerrado, considered one of the global hotspots for conservation. In the Cerrado, agricultural and livestock activities have turned its landscapes into a mix of anthropogenic and native ecosystems, with the former predominating. This shift increases factors such as habitat isolation and fragmentation. As a result, biological diversity becomes threatened due to these factors, highlighting the need to assess landscape characteristics in studies involving biodiversity. This thesis is structured in two chapters. The first chapter is designed to evaluate the influence of landscape configuration and composition on biological diversity. The second chapter aims to understand how biological diversity is organized, from the level of native vegetation remnants to the dominant landscape classes in the biome (urban, agricultural, livestock, and native landscapes). Among the most important results, it was found that the response of diversity to landscape composition and configuration depends on the metric analyzed. For example, beta diversity related to species richness increased from vegetation remnants to landscape classes. The opposite was observed when analyzing Shannon diversity. Additionally, when analyzing diversity within savanna formations, there was an increase in diversity as various anthropogenic land covers increased. Both results suggest a homogenization of biodiversity in Cerrado landscapes, indicating that generalist species adapted to anthropogenic ecosystems may be increasing in dominance, displacing native species. Therefore, anthropogenic activities in the Cerrado must include the reshaping of landscape components in a way that interrupts this homogenization, thereby preventing the loss of genetic and biological diversity.

Palavras-chave: ecologia de paisagens, besouros rola-bosta, Cerrado, partição da diversidade.

INTRODUÇÃO GERAL

1. Caracterização do Cerrado

O Cerrado cobre pouco mais de dois milhões de quilômetros quadrados do território brasileiro (Silva et al. 2006, ICMBio 2024) e é caracterizado por duas estações climáticas bem definidas: uma estação chuvosa de outubro a março, e uma estação seca de abril a setembro (Silva et al. 2008). Os solos são antigos, profundos, altamente intemperizados, porosos, com baixas concentrações de nutrientes e matéria orgânica, apresentando elevado teor de alumínio e condições ácidas (Ribeiro e Walter 1998, Borghetti et al. 2019).

Embora comumente caracterizado como uma savana, o Cerrado é um mosaico de vegetação composto por campos, savanas e formações florestais com origens distintas (Ribeiro e Walter 2008). O surgimento das formações de savana (e campos) tem sido alvo de diversas teorias envolvendo fatores climáticos, bióticos e pedológicos. No entanto, atualmente há um consenso geral de que essas formações resultam da interação desses fatores, com o clima atuando como um fator temporal responsável pelo intemperismo dos solos e pela redução das concentrações de nutrientes essenciais — definindo os solos típicos dessas formações (Ribeiro e Walter 2008, Borghetti et al. 2019). Em contraste, a origem das formações florestais é discutida à luz da expansão e contração das florestas sul-americanas durante os principais ciclos climáticos, especialmente no Quaternário (Daniel e Vaz-de-Mello 2016, Borghetti et al. 2019). Esses ciclos climáticos permitiram que as formações florestais persistissem em locais com condições hidrográficas, topográficas e edáficas favoráveis, levando ao desenvolvimento de dois principais tipos de floresta: formações associadas a cursos d'água e florestas localizadas em zonas interfluviais (Ribeiro e Walter 2008).

As formações de savana do Cerrado são comumente encontradas em terrenos planos ou suavemente inclinados e apresentam alta heterogeneidade estrutural. Essa heterogeneidade resulta de variações em fatores locais, como tipo de solo, topografia, profundidade do lençol freático e frequência de queimadas (Borghetti et al. 2019). Por exemplo, a supressão de queimadas—uma das principais perturbações no Cerrado, com origens tanto antrópicas quanto naturais (Santos et al. 2021)—pode levar ao aumento da densidade de árvores, alterando a estrutura original das formações de savana no bioma (Gonçalves et al. 2021, Pinheiro et al. 2021). Devido à influência desses fatores locais, as formações de savana—também chamadas de cerrado sensu stricto—são tipicamente caracterizadas por árvores pequenas, inclinadas e retorcidas, com casca espessa, frequentemente marcada por cicatrizes de fogo e estriada. Os solos dessas formações são geralmente Latosolos (de cor avermelhada), altamente ou moderadamente ácidos, com baixos níveis de nutrientes essenciais e ricos em alumínio. Diversos subtipos de cerrado sensu stricto ocorrem dependendo dos fatores locais (como a estrutura da vegetação), sendo os principais: cerrado denso, cerrado típico, cerrado ralo e cerrado rupestre (Ribeiro e Walter 2008).

Em contraste, as formações florestais do Cerrado são proporcionalmente mais isoladas e ocorrem em áreas menores, mas também apresentam considerável heterogeneidade estrutural devido a variações em fatores ambientais locais (Flake et al. 2021; Martins et al. 2021). Essas formações são caracterizadas por uma estrutura de vegetação dominada por espécies arbóreas e pela presença de dossel. Fatores ambientais como a presença de cursos d'água (e a profundidade do lençol freático), a topografia, o teor de nutrientes do solo e a profundidade do solo determinam os tipos de formações florestais, que podem ser classificadas como floresta ripária e floresta de galeria (Ribeiro e Walter 2008). Ambas estão associadas a cursos d'água, mas as florestas ripárias são tipicamente encontradas em terrenos acidentados ao longo de canais de rios médios a grandes, sem formar um dossel fechado sobre o rio, e frequentemente apresentam graus variados de decidualidade durante a estação seca. As árvores das florestas ripárias são eretas, com altura variando de 20 a 25 metros, e a cobertura do dossel varia de cerca de 50% na estação seca até 90% na estação chuvosa. As florestas de galeria, por outro lado, são encontradas em fundos de vale ou nascentes, seguindo pequenos cursos d'água e formando um dossel fechado (galeria) sobre eles. Elas são dominadas por espécies perenes e apresentam uma camada de serapilheira mais espessa do que as florestas ripárias. A altura das árvores varia entre 20 e 30 metros, com cobertura do dossel entre 70% e 95%. Devido à ausência de decidualidade, as florestas de galeria mantêm condições microclimáticas mais estáveis em comparação com outros tipos de vegetação do Cerrado (Ribeiro e Walter 2008; Hoffmann et al. 2012). Diferentemente das florestas de galeria e das florestas ripárias, as florestas secas e o cerradão também são formações florestais, mas não estão associadas a cursos d'água; ocorrem em áreas interfluviais (Ribeiro e Walter 2008). Segundo a classificação de Ribeiro e Walter (2008), as florestas secas ocorrem geralmente em solos mais ricos em nutrientes e podem apresentar diferentes níveis de decidualidade durante a estação seca. As árvores são geralmente eretas, com altura entre 15 e 25 metros, formando uma cobertura do dossel entre 70% e 95%, embora essa cobertura possa cair para menos de 50% na estação seca, especialmente em florestas secas deciduais. Por fim, o cerradão é uma formação florestal com características esclerófilas. Ele ocorre tipicamente em áreas com solos profundos, de fertilidade média ou baixa, e pode ser dividido em dois subtipos fitofisionômicos: cerradão distrófico e cerradão mesotrófico. Essa formação é composta principalmente por espécies semidecíduas comumente encontradas no cerrado sensu stricto, em florestas secas semidecíduas e em florestas de galeria. A altura das árvores varia de 8 a 15 metros, com cobertura do dossel variando de 50% a 90%, dependendo da estação.

2. A importância do Cerrado

O Cerrado é o segundo maior bioma do Brasil em termos de extensão territorial e é considerado um dos hotspots globais de conservação da biodiversidade devido ao seu alto grau de ameaça antrópica e à sua diversidade biológica (Myers et al. 2000). Além disso, é um bioma com grande heterogeneidade ambiental de ecossistemas nativos, variando desde formações campestres até áreas florestadas (Ribeiro e Walter 1998). Consequentemente, é uma região com alto endemismo de espécies, com pouco menos de 50% de sua flora sendo endêmica do bioma, o que o torna a savana mais diversa do mundo (Klink e Machado 2005). Para além de sua heterogeneidade ambiental, o bioma desempenha um papel importante no ciclo hidrológico da América do Sul, com as áreas nativas contribuindo para o aumento das taxas de evapotranspiração (Anache et al. 2019; Bispo et al. 2023).

2.1. Aspectos Legais e Políticos Relacionados à Preservação do Cerrado

Apesar da importância ambiental e até mesmo econômica do Cerrado, o bioma continua sendo negligenciado em termos de proteção e, consequentemente, de conservação da biodiversidade. Por exemplo, o Código Florestal brasileiro, incorporado pela Lei nº 12.651 de 2012, estabelece a exigência de Reserva Legal de 35% para imóveis rurais localizados em áreas de Cerrado dentro da Amazônia Legal, enquanto esse percentual cai para 20% nas regiões fora da Amazônia Legal (Brasil, 2012). Em outras palavras, em cenários onde não existam Áreas de Preservação Permanente (APPs) em uma propriedade rural, até 80% da vegetação nativa em áreas de Cerrado fora da Amazônia Legal pode, legalmente, ser desmatada. Em contraste, nas áreas de floresta da Amazônia Legal, 80% da vegetação nativa em propriedades rurais deve ser mantida como Reserva Legal (Brasil, 2012). Além da baixa proteção legal para o Cerrado, algumas políticas governamentais nacionais e internacionais agravam essa insuficiência. Um exemplo é a Moratória da Soja, um esforço voltado para a agricultura sustentável que envolveu diversos setores da sociedade, incluindo produtores e o governo, com o objetivo de reduzir o desmatamento para produção de soja na Amazônia. As empresas comprometeram-se a não comprar soja de áreas desmatadas após 22 de julho de 2008, priorizando áreas abertas antes dessa data. O programa se mostrou eficaz ao combinar a redução do desmatamento com o aumento da produção de soja na região (Gibbs et al. 2015; Vibian et al. 2021). No entanto, sua aplicação é limitada à região amazônica, excluindo o

Cerrado — mesmo este sendo uma das maiores regiões produtoras de grãos do mundo e a principal região produtora de grãos do Brasil (Strassburg et al. 2017). Além disso, entre as influências internacionais, destaca-se a definição de "floresta" adotada pela Comissão Europeia em legislações sobre a importação de produtos oriundos de áreas não desmatadas: "floresta significa uma área de terra com mais de 0,5 hectare, com árvores superiores a 5 metros de altura e cobertura de copa superior a 10%, ou árvores capazes de atingir esses critérios no local, excluindo plantações agrícolas e terras predominantemente utilizadas para fins agrícolas ou urbanos". Essa definição torna 74% do Cerrado elegível para o desenvolvimento agrícola (Comissão Europeia 2021; Chaves et al. 2023).

Além disso, o Cerrado possui poucas áreas legalmente protegidas, apesar de sua alta diversidade biológica e das significativas ameaças antrópicas. De acordo com o Painel das Unidades de Conservação do Ministério do Meio Ambiente e Mudança do Clima, apenas 2,84% do bioma está legalmente protegido por unidades de conservação de proteção integral, totalizando 193 unidades — 106 estaduais, 64 municipais e 23 federais. Quando se consideram tanto as unidades de uso sustentável quanto as de proteção integral, esse percentual de proteção sobe para 9,36% do território do bioma, somando 600 unidades de conservação, sendo as principais as Reservas Particulares do Patrimônio Natural (239 unidades), os Parques Nacionais (128 unidades) e as Áreas de Proteção Ambiental (122 unidades). Em comparação, o bioma Amazônia possui 18,64% de seu território protegido por unidades de conservação de proteção integral, totalizando 275 unidades — 147 federais, 112 estaduais e 16 municipais. Esse percentual sobe para 28,98% quando se consideram tanto as unidades de proteção integral quanto as de uso sustentável (190 federais, 157 estaduais e 41 municipais). Nesse sentido, fica evidente que o Cerrado recebe menor atenção governamental em comparação a biomas como a Amazônia.

3. Ameaças intrínsecas ao Cerrado

Além dos aspectos legais e políticos que ameaçam o Cerrado — considerado uma das maiores fronteiras agrícolas do mundo (Dionizio et al. 2020; Chaves et al. 2023) — outros fatores também representam riscos. A expansão agrícola tem sido uma das principais causas da perda de habitat e do declínio da biodiversidade, além de contribuir para a intensificação das mudanças climáticas na região (Santos 2021; Rodrigues et al. 2022). Além disso, a disseminação de espécies exóticas invasoras, especialmente gramíneas africanas, e o manejo inadequado do fogo também constituem ameaças significativas ao bioma (Klink e Machado 2005).

A perda de habitat tem sido considerada um dos principais motores do declínio da biodiversidade em todo o mundo (Segan et al. 2016). De acordo com o MapBiomas, quase metade do Cerrado já foi convertida para uso antrópico, especialmente para a pecuária e a agricultura (Projeto MapBiomas 2024). Associado a isso, os índices de desmatamento na região permanecem elevados, indicando a continuidade dessa tendência. Por exemplo, em 2023 o desmatamento no Cerrado aumentou 67,7%, ultrapassando a Amazônia, tendo o agronegócio como principal vetor de pressão, responsável por 97% da perda de vegetação (RAD 2023).

As conversões do uso da terra para agricultura e pecuária estão impulsionando as mudanças climáticas na região. Em áreas antrópicas utilizadas para atividades agrícolas, já são perceptíveis reduções nas taxas de precipitação (Anache et al. 2019; Bispo et al. 2023). De fato, as taxas de precipitação no Cerrado como um todo já diminuíram mais de 50% ao se comparar o período entre 1960 e 2021, devido à conversão da vegetação nativa em pastagens e áreas agrícolas (Hofmann et al. 2023). Essa redução comprometerá a própria produtividade agrícola da região, podendo causar crises econômicas regionais (Chaves et al. 2023).

Além disso, a disseminação de espécies exóticas invasoras, frequentemente agravada pelo manejo inadequado do fogo, também tem sido um mecanismo severo de perda de habitat e biodiversidade no Cerrado. Aproximadamente metade das paisagens do bioma está vulnerável a invasões biológicas por espécies exóticas, e cerca de 60% das áreas protegidas apresentam algum grau de invasão por essas espécies (Silva et al. 2020). Entre essas espécies, destaca-se o grupo conhecido na literatura científica como gramíneas africanas, composto por espécies introduzidas intencionalmente no bioma para a formação de pastagens (Zenni 2014). As gramíneas africanas são conhecidas por seus efeitos negativos sobre a diversidade de espécies nativas, causando extinções locais, alterando os regimes de fogo (aumentando a frequência e a intensidade desses eventos), modificando microclimas e mudando as interações biológicas, comprometendo, em última instância, a estabilidade do ecossistema (Williams e Baruch 2020; Zenni et al. 2020). Além disso, essas espécies respondem positivamente ao fogo em comparação com as gramíneas nativas. Por exemplo, devido à ocorrência de fogo, frequentemente apresentam altas taxas de rebrote, crescem rapidamente e, ao final da estação seca, sua alta biomassa torna-se combustível, aumentando a intensidade do fogo e criando um ciclo de retroalimentação positiva que beneficia as populações invasoras em detrimento das populações nativas (Williams e Baruch 2020).

4. Configuração e Composição das Paisagens do Cerrado

Como consequência das pressões antrópicas sobre o Cerrado, os processos de perda e fragmentação de habitat continuam em ritmo acelerado, alterando a configuração e a composição das paisagens (Haddad et al. 2015). Mais especificamente, a fragmentação modifica a configuração da paisagem à medida que as áreas contínuas de vegetação nativa se tornam cada vez mais divididas, aumentando a relevância de atributos como densidade e tamanho das bordas, tamanho e número dos fragmentos, e o grau de isolamento entre eles (Oliveira et al. 2017; Silva et al. 2019). À medida que a fragmentação se intensifica, a conversão de áreas nativas em usos antrópicos da terra também avança, afetando diretamente a composição da paisagem. Dessa forma, a composição da paisagem pode ser descrita, por exemplo, pelas classes de uso da terra presentes, considerando tanto o número de classes quanto a extensão de cada classe dentro da paisagem (Silva et al. 2019).

De acordo com a Plataforma MapBiomas, as formações savânicas ocupam 56,11% das áreas nativas do bioma, enquanto as formações florestais cobrem 28,44%, e as formações campestres correspondem a 6,04% dessas áreas nativas. Em relação às áreas antrópicas, as pastagens, áreas agrícolas e áreas urbanas ocupam, respectivamente, 53,94%, 46,60% e 0,97% da classe antrópica (Projeto MapBiomas 2024). No Planalto Central do Brasil, as formações florestais estão distribuídas principalmente ao longo dos cursos d’água como áreas de preservação permanente, enquanto as formações savânicas abrangem maiores extensões territoriais e estão mais amplamente distribuídas em comparação com as formações florestais (Projeto MapBiomas 2024; Ribeiro e Walter 1998). Nesse contexto, as paisagens do Cerrado podem atualmente ser consideradas um mosaico de ecossistemas nativos e antrópicos.

4.1. Contribuição das paisagens para a Organização da Diversidade

A sensibilidade das espécies à estrutura da paisagem (composição e configuração) depende de várias características. Por exemplo, a amplitude dietária ou a preferência de habitat de uma espécie pode fazer com que ela seja negativamente ou positivamente afetada por mudanças estruturais na paisagem, sendo que espécies mais especializadas geralmente são impactadas negativamente, enquanto espécies generalistas são beneficiadas ou não apresentam resposta (Kellner et al. 2019; Souza et al. 2020). A mobilidade e, consequentemente, a capacidade de dispersão também são características importantes, com espécies que possuem maior capacidade de dispersão sendo menos afetadas do que aquelas com menor capacidade dispersiva (Moir et al. 2021).

Nesse contexto, estudos sobre diversidade precisam ser realizados considerando múltiplas escalas espaciais para abarcar os aspectos emergentes das paisagens. Isso é necessário porque alguns fatores ecológicos locais, como a capacidade de dispersão, o uso do habitat e as interações biológicas inter e intraespecíficas, predominam no nível local, mas em níveis superiores outros fatores (como barreiras à dispersão e diferenças climáticas) tornam-se mais importantes (Cunha e Frizzas 2020; Salgueiro et al. 2021). Atualmente, na região, os estudos focam na diversidade associada a tipos específicos de uso da terra, contexto no qual a detecção dos efeitos sobre a diversidade se limita aos inerentes ao tipo específico de uso da terra (por exemplo, Oliveira et al. 2021; Oliveira et al. 2022), deixando de fora os efeitos que emergem à medida que a escala espacial da análise se amplia.

5. Besouros rola-bostas

Um dos grupos taxonômicos mais importantes para compreender as influências da composição e configuração atuais das paisagens do Cerrado é o grupo formado pelos besouros do esterco. Com 799 espécies válidas e 62 endêmicas no Brasil (Vaz-de-Mello e Bordin 2025), a diversidade desses besouros está concentrada nos ecossistemas savânicos e florestais, apesar de ser um grupo cosmopolita (Hanski e Cambefort 1991). Eles pertencem à subfamília Scarabaeinae (Coleoptera: Scarabaeidae), caracterizada pela predominância de besouros que se alimentam e se reproduzem principalmente em fezes de mamíferos, estando, portanto, associados à presença da mastofauna (Bogoni et al. 2019). Como consequência do seu comportamento coprofágico, que exige o manejo das fezes no solo, os besouros do esterco mediam importantes serviços ecossistêmicos, como o ciclo de nutrientes, a bioturbação do solo, a dispersão secundária de sementes e o controle natural de parasitas (Nichols et al. 2008). Além disso, várias espécies são especialistas em habitat (Bitencourt et al. 2019; Silva et al. 2019; Fuzessy et al. 2021) e sensíveis às alterações ambientais, sendo assim consideradas um grupo bioindicador importante (Nichols e Gardner 2011; Noriega et al. 2020). Consequentemente, os besouros do esterco são comumente usados em ecossistemas florestais como organismos-modelo para descrever as interações da biodiversidade com distúrbios antrópicos, como mudanças no uso da terra e fragmentação (Nichols et al. 2007; Rös et al. 2012; Noriega et al. 2021; Williamson et al. 2021).

6. Lacunas do Conhecimento

Na região Neotropical, a maioria dos estudos sobre a diversidade de besouros do esterco está focada em ecossistemas florestais e considera principalmente a avaliação dos efeitos das mudanças no uso e cobertura do solo sobre a diversidade. Nesse contexto, destacam-se estudos que avaliaram as respostas desses besouros a gradientes ambientais formados pela sucessão ecológica causada por eventos antrópicos (Hernández et al. 2014; Bitencourt e Silva, 2016; Davies et al. 2020), assim como respostas a distúrbios como extração madeireira (França et al. 2017; Moura et al. 2021) e mudanças na cobertura do solo para formação de pastagens e monoculturas (Braga et al. 2013; Davies et al. 2021; Paladines et al. 2021; Oliveira et al. 2021). Em geral, os besouros do esterco são negativamente afetados por esses distúrbios, apresentando reduções em parâmetros como riqueza e abundância de espécies, o que leva a uma diminuição das funções ecossistêmicas proporcionadas por esses besouros (Braga et al. 2013; França et al. 2017; Moura et al. 2021; Noriega et al. 2021), embora existam algumas circunstâncias em que a diversidade aumenta em áreas com maior intensidade de uso do solo (Paladines et al. 2021). No Cerrado, um bioma caracterizado principalmente por ecossistemas não florestais (Ribeiro e Walter 2008), os estudos também estão focados nos efeitos das mudanças no uso e cobertura do solo sobre a diversidade de besouros do esterco, porém com uma variação relativamente maior nas respostas de diversidade. Por exemplo, alguns estudos não mostram diferenças significativas na diversidade entre remanescentes de vegetação e áreas convertidas para uso antrópico (Correa et al. 2019; Oliveira et al. 2021), enquanto outros demonstram influências negativas dessa conversão (Almeida et al. 2011; Martello et al. 2016; Correa et al. 2020; Macedo et al. 2020).

Um componente importante em escala regional que pode ajudar a explicar as variações nas respostas da diversidade de besouros do esterco às mudanças no uso e na cobertura do solo é a estrutura da paisagem. Por exemplo, em regiões neotropicais dominadas por ecossistemas florestais (onde a maioria dos estudos está situada), componentes relacionados à composição da paisagem têm sido considerados os principais contribuintes para a organização da diversidade de besouros do esterco nessa escala espacial (Sánchez-de-Jesús et al. 2016, Alvarado et al. 2018), mas outros estudos sugerem que componentes configuracionais são mais importantes nessa organização (Rivera et al. 2020, Souza et al. 2020). A maioria desses estudos mostra uma importância relativamente maior da composição da paisagem sobre a diversidade de besouros do esterco, especialmente devido ao efeito positivo da cobertura vegetal na diversidade (Sánchez-de-Jesús et al. 2016, Alvarado et al. 2018). Por outro lado, estudos que encontraram a configuração da paisagem como mais importante atribuem isso ao efeito de atributos como a densidade de bordas, que são responsáveis por declínios significativos na diversidade de besouros do esterco (Rivera et al. 2020, Souza et al. 2020). Assim, as respostas à configuração e composição da paisagem podem variar entre os agrupamentos porque dependem, por exemplo, da sensibilidade ambiental e das características morfofuncionais das espécies que compõem cada agrupamento (Silva et al. 2019, Souza et al. 2020).

7. Justificativas e Objetivos

O Cerrado é um hotspot de biodiversidade, considerado a savana mais biodiversa do mundo, e abriga diversos endemismos (Myers et al. 2000). Apesar disso, o bioma está passando por um processo crescente de fragmentação devido à intensificação de atividades como pecuária, agricultura, silvicultura e também como consequência da expansão urbana. Essas atividades já levaram à perda de quase metade da extensão original do bioma (Klink e Machado 2005, Projeto Mapbiomas 2024). Como resultado da fragmentação acelerada, as paisagens do bioma tornaram-se uma mistura de remanescentes de vegetação e ecossistemas antrópicos, especialmente monoculturas e pastagens (Klink e Machado 2005, Rada 2013). Portanto, além de entender como a diversidade está organizada localmente nos remanescentes de vegetação do Cerrado, é crucial que os estudos ecológicos levem em conta os efeitos emergentes das paisagens nas análises da diversidade, visando identificar os mecanismos reais por trás da organização da diversidade biológica no Cerrado.

Os besouros rola-bosta têm sido usados como objeto de estudo porque formam um grupo que inclui várias espécies sensíveis a mudanças ambientais (Louzada et al. 2010, Bogoni et al. 2019, Cunha e Frizzas 2020), são indicadores de biodiversidade (Bogoni et al. 2019) e intermediários de diversos serviços ecossistêmicos (Nichols et al. 2008). Apesar do significativo corpo de conhecimento científico sobre a diversidade dos besouros rola-bosta neotropicais, ainda existem lacunas: 1) a maioria dos estudos foca em paisagens florestais, ou tem como objetivo comparar diretamente os efeitos de ações antrópicas na diversidade (por exemplo, os efeitos das mudanças no uso da terra e do manejo florestal [França et al. 2017, Paladines et al. 2021, Oliveira et al. 2021, Maciel et al. 2023, Carvalho et al. 2023]); 2) somente recentemente os estudos começaram a considerar, conjuntamente, o efeito dos aspectos estruturais das paisagens na diversidade dos besouros rola-bosta (anteriormente, os estudos consideravam os aspectos estruturais isoladamente; por exemplo, o efeito do tamanho dos fragmentos na diversidade [Klein 1989, Andresen 2003]); 3) além disso, somente recentemente os estudos começaram a considerar os efeitos emergentes das paisagens na organização da diversidade no Cerrado (por exemplo, Cunha e Frizzas 2020). Compreender as relações entre a diversidade dos besouros rola-bosta e as paisagens do Cerrado tem implicações diretas para o entendimento dos impactos das modificações antrópicas das paisagens do Cerrado na biodiversidade.

À luz do exposto, o objetivo desta tese é descrever a diversidade taxonômica dos besouros rola-bosta no Cerrado, levando em consideração as influências das paisagens do bioma sobre essa diversidade. Para isso, foram estruturados dois capítulos. O primeiro capítulo foi planejado para avaliar as contribuições dos componentes da paisagem (configuração e composição) para a organização da diversidade taxonômica dos besouros rola-bosta. O segundo capítulo foi elaborado para avaliar as escalas das influências da paisagem na diversidade dos besouros rola-bosta. Isso é relevante porque a avaliação da diversidade em uma determinada escala espacial pode apresentar resultados diferentes daqueles encontrados em escalas maiores ou menores. Considerar uma abordagem multinível abrange as diversas respostas possíveis da diversidade às paisagens.

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CHAPTER I

Esse capítulo está formatado de acordo com o manual de publicação da revista “Biodiversity and Conservation”

Landscape composition is the main factor affecting diversity of dung beetles in the savannas of Central Brazil

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Abstract: One of the main factors responsible for shaping biological diversity is landscape structure. Landscape structure can be described by its composition and spatial configuration —attributes that influence ecological and biogeographical processes depending on the life history of species. In this context, it is important to understand how landscape structure affects biodiversity, especially in Neotropical savannas, where anthropogenic influences, mainly from agriculture and livestock, have drastically altered landscape patterns. In the Cerrado, the most biodiverse savanna in the world, landscapes already consist of a mosaic of anthropogenic and native ecosystems, with savanna and forest ecosystems standing out among the latter. Thus, the objective of this study was to evaluate the influence of structural landscape attributes of the Cerrado on biological diversity. To this end, dung beetles were used as the study organisms, and various metrics of landscape composition and configuration were obtained from rasterized maps from MapBiomas. These metrics were included in generalized linear models to assess the contribution of each structural metric to the organization of biological diversity. As results, we found that dung beetle diversity in savanna formations is primarily influenced by landscape composition, though not exclusively. Furthermore, native vegetation cover had a negative influence on species abundance and richness, while anthropogenic cover positively influenced diversity, contrary to previous studies. On the other hand, diversity in forest formations was exclusively affected by landscape composition, specifically by forest cover. Additionally, diversity responded positively to increases in forest cover. These results are associated with the observed distributions of species abundance and richness in the study, linked to the emergence of an apparent dominance of generalist species capable of displacing native species from savanna ecosystems. Given this, studies of biological diversity, especially in Neotropical savannas, need to include both species context and landscape structure to identify the true drivers directly impacting biodiversity organization.

Keywords: landscapes configuration, landscapes composition, dung beetle, landscape ecology.

INTRODUCTION

Landscape structure is one of the important factors organizing organism diversity. Among the structural factors of landscapes, composition and spatial configuration stand out. These attributes can influence ecological processes related to population dispersal and persistence (Carvalho et al. 2009, Souza et al. 2020), affecting diversity and potentially causing losses of sensitive species (Martin et al. 2016, Grab et al. 2019). However, biodiversity responses to landscape structure and the intensity of these responses may depend on various factors such as ecosystem type and species' tolerance to different habitats within the landscape (Martin et al. 2016, Silva et al. 2019).

Landscape composition has proven to be more important than configuration for maintaining biodiversity, especially due to the effects of vegetation cover. Regarding the composition of landscapes located in forested regions fragmented by anthropogenic activities, most studies indicate that forest cover at the landscape level is the main determinant of biodiversity, with positive effects on it (Arroyo-Rodríguez et al. 2016, Sánchez-de-Jesús et al. 2016, Rocha et al. 2017, Hannibal et al. 2018, Morante-Filho et al. 2020, Ramírez-Mejía et al. 2020). For savanna regions fragmented by anthropogenic activities, there are proportionally fewer studies than in fragmented forest regions, but some evidence also suggests that the amount of remaining cover (savanna, in this case) in the landscape is also a primary attribute for biodiversity, positively affecting it (e.g., Moreira et al. 2017, LaScaleia et al. 2018). The relevance of forest or savanna cover in the landscape for maintaining biodiversity is associated with the amount of habitat and connectivity in the landscape, which can affect taxa depending on characteristics such as the degree of specialization to these types of vegetation cover (Ke et al. 2018, Morante-Filho et al. 2020), diet (Arroyo-Rodríguez et al. 2016), mobility, and gregarious behaviors (Gonçalves et al. 2020). Because of these characteristics, some species may show attenuated responses to vegetation cover (Silva et al. 2019) or even positive responses to vegetation loss or fragmentation intensification (Carrara et al. 2015). Thus, the responses (as well as their directions and intensities) of biodiversity to landscape attributes depend on the characteristics of the taxa, and landscape composition is usually the attribute that most influences biodiversity.

The Cerrado is a biome characterized by a vegetation mosaic composed mainly of savannas and forests. According to Ribeiro and Walter (2008), savanna formations—also known as cerrado sensu stricto—are primarily characterized by the coexistence of shrub-subshrub and herbaceous layers with a low-stature arboreal layer (5 to 8 meters tall). This arboreal layer typically has trees with irregular, twisted branches, thick, cracked or grooved bark, and often shows burn scars. Forest formations also occur within the biome, but their distribution and subtypes depend on specific local factors such as hydrography, topography, soil conditions, and microclimate (Ribeiro and Walter 2008). For example, gallery forests and riparian forests are associated with watercourses and, as a result, tend to be more isolated in the landscape, more extensive than wide, and, compared to savanna formations, are less representative within landscapes (Ribeiro and Walter 2008, MapBiomas Project 2024). In contrast, savanna fragments are typically distributed over large areas and are less isolated from one another. Nevertheless, despite their differences, the landscapes where these vegetation types occur are being increasingly affected by activities such as livestock farming and agriculture (Carvalho et al. 2009). These activities put pressure on natural ecosystems—especially savanna formations (Klink and Machado 2005, Pinheiro and Durigan 2009)—and spread across vast areas, turning the biome's landscapes into a mix of natural and anthropogenic ecosystems (Klink and Machado 2005, Rada 2013). In this context, the Cerrado can be described as a biome threatened by the expansion of human activities, while at the same time being extremely important for conservation due to its endangered environmental heterogeneity and its role as a key biodiversity component among global savannas (Myers et al. 2000). Furthermore, the biome is considered the "cradle of waters" influencing even continental-scale rainfall regimes (Chagas et al. 2022). Therefore, biodiversity patterns must also be evaluated at the landscape scale in order to identify the impacts of anthropogenic pressures at this level.

Dung beetles form a group composed of approximately 799 species in Brazil (Vaz-de-Mello and Bordin 2025), with many species that are sensitive to environmental conditions (Louzada et al. 2010, Bogoni et al. 2019, Cunha and Frizzas 2020) and that exhibit preferences for specific ecosystems, such as savannas and forests, where the group's highest diversity is found (Hanski and Cambefort 1991, Daniel and Vaz-de-Mello 2016). These beetles feed primarily on mammal feces and also use this resource for nesting (Hanski and Cambefort 1991).

For dung beetles, certain patterns in biodiversity responses to landscape attributes are maintained, but knowledge gaps still exist. In the Neotropical region, this is related to the fact that species exhibit varying degrees of matrix tolerance and preferences for forest ecosystems. That is, some groups are forest specialists due to the milder environmental conditions (Silva et al. 2019), while some species have large home ranges and high daily dispersal rates—dynamics that are less constrained by fragmentation, making these species habitat generalists (Silva and Hernández 2015, Cunha and Frizzas 2020). However, in general, studies assessing the influence of landscape attributes on biodiversity (not only dung beetles) are mostly concentrated in forested regions, resulting in a knowledge gap concerning savanna regions.

The objective of this chapter is to describe the influence of landscape attributes (composition and configuration) of the Cerrado on the diversity of dung beetles in the savanna and forest formations of the biome. In this context, the following hypotheses will be tested: due to the spatial characteristics of forest formations in the biome (e.g., more isolated and less represented in the landscape) and the sensitivity of several Neotropical species to forest ecosystems, dung beetle diversity in these vegetative formations is expected to be primarily influenced by landscape configuration rather than composition. Conversely, dung beetle diversity in savanna formations is expected to be mainly influenced by landscape composition, rather than configuration.

MATERIALS AND METHODS

Study area

The study area encompasses the Federal District and municipalities of the State of Goiás (surrounding the Federal District), a region of the brazilian Cerrado, in Central Brazil. Sixteen landscapes were selected, within which the four main land-cover types of the Brazilian savannas are represented: native vegetation, agriculture, pasture, and urban areas (Fig. 1). In each landscape, a savanna fragment and a forest fragment were selected, with an average distance between fragments of approximately 1.79 km (minimum distance: 0.779 km; maximum distance: 3.95 km). These landscapes and their respective vegetation fragments were chosen based on logistical access considerations, such as the presence of nearby highways or trails. According to Köppen’s classification, the region's climate is of the Aw type, with the highest precipitation occurring between November and January, and the lowest precipitation between June and August (CODEPLAN 2017). The soils are predominantly latosols and cambisols, with occurrences of argisols, neosols, gleysols, and plinthosols (CODEPLAN 2017).

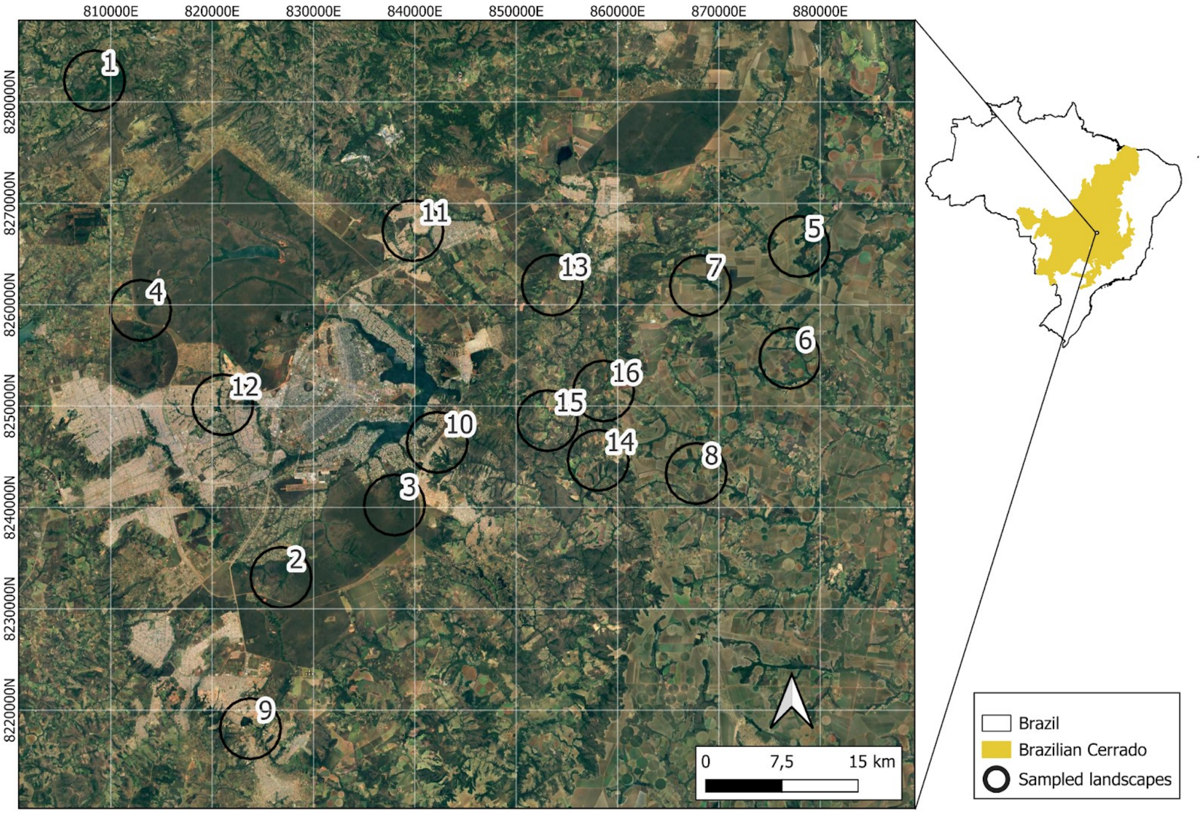


Fig. 1 Study area, located in the Central Plateau of Brazil. The landscapes are shown within a 3 km radius, which is the largest sampling radius in this study.

Community sampling

Sampling was conducted between November and December 2021, a period that corresponds to the rainy season in the brazilian Cerrado, which is considered the optimal time for dung beetle collection (Oliveira et al. 2011). In each of the 16 forest fragments and 16 savanna fragments, two transects were established, each containing five traps, with a minimum distance of 25 meters between traps. Furthermore, this was the distance at which it was possible to place the pitfalls closer to the center of the vegetation fragments, thereby more accurately sampling the actual diversity within the vegetation formations and minimizing the influence of occasional individuals coming from the surrounding matrix.

The traps used were of the pitfall type and consisted of two containers: the first container, with a 1-liter capacity, was filled with water and detergent to break the water's surface tension; the second container, with a 50-milliliter capacity, was suspended with wire above the first container and filled with 25 grams of bait. The bait consisted of human feces, considered the most attractive bait for dung beetles (Milhomem et al. 2003). A rain protection was placed above the two containers to prevent flooding.

The traps were removed after 48 hours of sampling, and the collected specimens were transferred to containers with 70% alcohol, properly labeled. In the laboratory, the specimens were identified using dichotomous keys and with the help of specialists. The vouchers were deposited in the Entomological Collection of the Department of Zoology at the University of Brasília (DZUB).

The research authorizations related to the sampling of the dung beetle community are SISBIO/ICMBio No. 80499-1 and the Research Authorization No. 16/2021 from the Department of the Environment and Water Resources (Botanical Garden).

Landscape Mapping and Metrics

To obtain the landscape metrics, raster files filtered for the Brazilian Cerrado were used, provided by the MapBiomas platform (MapBiomas Project 2024). These files are land cover and land use maps generated from Landsat satellite imagery and processed using machine learning algorithms on Google Earth Engine. The maps have a spatial resolution of 30 x 30 meters and an overall accuracy of 74.8% at the most detailed legend level (MapBiomas Project 2024). The land use and land cover classes considered from these maps are: savanna vegetation remnants, forest vegetation remnants, pasture, agriculture (combining temporary and perennial crops into a single class), and urban infrastructure. These classes were determined based on the predominance of a specific land cover type in the landscape, using a 70% threshold. For example, if 70% of the land cover in the landscape is native vegetation, the landscape is classified as a native landscape (Table 1).

Table 1 Classification of landscapes based on land cover percentages for each buffer size (1 km, 2 km, and 3 km). A 70% threshold was used to categorize the landscapes, meaning that if a landscape contains at least 70% of a given land cover type, it is classified according to that cover.

		Soil cover in landscape (%)				
Landscape size	Ladscape	Native	Agriculture	Urban	Pasture	Landscape Classes

(radius)						
1 km	1	71,30	1,56	0,00	27,14	Native
	2	100,00	0,00	0,00	0,00	Native
	3	99,91	0,00	0,00	0,09	Native
	4	85,46	3,99	1,17	9,38	Native
	5	16,77	72,30	0,00	10,93	Agriculture
	6	11,35	86,20	0,00	2,45	Agriculture
	7	18,67	70,45	0,00	10,88	Agriculture
	8	7,42	85,97	0,00	6,61	Agriculture
	9	9,55	1,40	79,00	10,05	Urban
	10	20,45	0,41	78,35	0,79	Urban
	11	10,28	0,00	78,50	11,22	Urban
	12	16,93	0,00	80,94	2,13	Urban
	13	18,34	3,33	0,00	78,33	Pasture
	14	28,46	0,33	0,00	71,21	Pasture
	15	23,53	0,04	0,00	76,43	Pasture
	16	15,80	12,15	0,70	71,35	Pasture
2 km	1	91,25	0,47	0,00	8,28	Native
	2	96,99	0,38	0,13	2,50	Native
	3	99,31	0,00	0,62	0,07	Native
	4	82,72	5,06	0,80	11,42	Native
	5	23,49	71,89	0,30	4,32	Agriculture
	6	14,74	80,75	0,69	3,82	Agriculture
	7	18,61	72,36	0,00	9,03	Agriculture
	8	12,38	82,78	0,06	4,78	Agriculture
	9	10,86	0,33	76,35	12,46	Urban
	10	23,56	0,08	75,32	1,04	Urban
	11	11,24	0,01	79,33	9,42	Urban
	12	14,38	2,34	82,42	0,86	Urban
	13	24,09	4,56	0,00	71,35	Pasture
	14	28,84	0,57	0,00	70,59	Pasture
	15	28,87	0,01	0,00	71,12	Pasture
	16	25,40	2,45	1,83	70,32	Pasture
3 km	1	88,65	0,78	0,00	10,57	Native
	2	85,50	0,92	8,58	5,00	Native
	3	87,27	0,02	11,31	1,40	Native
	4	82,53	6,18	1,27	10,02	Native
	5	27,12	70,11	0,01	2,76	Agriculture

	6	22,26	73,14	0,31	4,29	Agriculture
	7	20,28	73,64	0,05	6,03	Agriculture
	8	20,35	70,67	0,14	8,84	Agriculture
	9	25,99	0,18	71,16	2,67	Urban
	10	28,08	0,04	70,65	1,23	Urban
	11	18,24	2,22	71,49	8,05	Urban
	12	18,42	0,11	80,06	1,41	Urban
	13	26,39	2,47	0,00	71,14	Pasture
	14	26,33	3,22	0,00	70,45	Pasture
	15	28,34	0,50	0,13	71,03	Pasture
	16	26,05	3,29	0,23	70,43	Pasture

Landscape metrics were measured around each of the 30 fragments at three different spatial scales, defined by buffers with radii of 1, 2, and 3 km (with the community sampling site being the approximate centroid of each buffer). These radii were selected to best capture the wide range of buffer sizes found in previous studies (e.g., Sánchez-de-Jesús et al. 2016, Alvarado et al. 2018, Souza et al. 2020) and to account for potential scale-dependent effects on response variables. The spatial selection of fragments was conducted to prevent overlap between buffers of the same fragment class, while allowing overlap between buffers of different fragment classes (savanna and forest). This design enabled the assessment of the relative influence of specific landscape configuration and composition on biodiversity within each fragment type.

Landscape composition and configuration metrics were calculated using the landscapemetrics package (Hesselbarth et al. 2019). Composition was summarized by the total area of each land use class, as well as the remaining area of savanna and forest vegetation in each landscape. Configuration was represented by the following metrics: largest patch index (percentage of the landscape occupied by the largest fragment), edge density (total edge length in meters relative to landscape area in square meters), number of patches, and mean Euclidean nearest-neighbor distance (a measure of patch isolation). These metrics were calculated separately for forest and savanna fragments (e.g., largest patch index for forest and for savanna; edge density for each vegetation type, etc.). They were selected for their relevance to community organization in fragmented landscapes and for being commonly used in previous studies on dung beetle diversity (Sánchez-de-Jesús et al. 2016, Alvarado et al. 2018, Silva et al. 2019, Souza et al. 2020). All metrics were measured at each of the three buffer scales.

DATA ANALYSIS

Sample size sufficiency

To assess the sufficiency of the sampling effort, species accumulation curves based on individuals were used (Gotelli and Colwell 2001), through the iNEXT package version 2.0.20 (Hsieh et al. 2020). The total species richness estimate was calculated using the ACE estimator (Gotelli and Colwell 2011), through the fossil package version 0.3.7 (Vavrek 2012). All analyses were performed in R software version 3.5.3 (R Core Team 2024).

Generalized Linear Models

To assess the influence of landscape metrics on the richness and abundance of dung beetles, generalized linear models were developed. The models were fitted using the negative binomial distribution, as it is suitable for data with overdispersion (Hilbe 2011). The model selection method was based on the AICc criterion (corrected Akaike Information Criterion), with a cutoff point at ΔAICc < 4 (Burnham and Anderson 2002). Tests were performed involving the relationship between predictors and response variables for all landscape sizes (landscapes with radii of 1 km, 2 km, and 3 km), aiming to detect possible effects merely due to landscape sizes. All analyses were conducted using the MASS package version 7.3-65 (Ripley et al. 2002) in the R software (R Core Team 2024).

RESULTS

Sample size sufficiency

A total of 10,092 individuals were collected, distributed across 81 species (Table 2). The most abundant species were *Dichotomius opacus*, *Canthidium* sp. 3, *Canthidium barbacenicum*, *Oxyternon palemo*, and *Dichotomius lycas*, with 3163, 1141, 748, 575, and 353 individuals, respectively. Disregarding the singletons (14 species) and doubletons (7 species), the least abundant species were *Ateuchus* aff. *ovalis*, *Canthidium* sp. 9, *Canthidium viride*, *Pseudocanthon xanthurus*, and *Canthidium* aff. *refulgens*, with the first four species having 3 individuals each, and the last two species with 4 individuals each.

Table 2 Abundance of dung beetle species sampled, separated by vegetation formation and by landscape class (native, agriculture, urban and pasture classes). The data related to the "Vegetation Formations" group encompass the samples collected in savannas and forests within each of the four landscape classes.

	Vegetation Formations		**Landscapes Classes**			
Species	**Savanna**	**Forest**	**Native**	**Agriculture**	**Urban**	**Pasture**
Agamopus unguicularis	19	34	34	10	1	8
Ateuchus aff. *ovalis*	0	3	0	0	0	3
Ateuchus aff. *vigilans*	1	0	0	1	0	0
Ateuchus puncticollis	1	0	0	0	0	1
Ateuchus striatulus	4	3	3	2	0	2
Atheuchus vividus	0	1	1	0	0	0
Besourenga sp. 1	17	0	1	0	15	1
Besourenga sp. 2	2	0	0	0	0	2
Canthidium aff. *refulgens*	4	0	1	3	0	0
Canthidium aff. *hyla*	11	0	5	0	2	4
Canthidium aff. *lucidum*	0	1	0	0	0	1
Canthidium barbacenicum	747	1	1	56	571	120
Canthidium decoratum	6	1	1	0	5	1
Canthidium sp. 1	1	1	0	1	1	0
Canthidium sp. 2	2	6	6	1	0	1
Canthidium sp. 3	4	1137	12	232	417	480
Canthidium sp. 4	0	1	0	1	0	0
Canthidium sp. 5	13	0	5	0	0	8
Canthidium sp. 6	1	0	0	0	1	0
Canthidium sp. 7	42	0	1	41	0	0
Canthidium sp. 8	1	0	1	0	0	0
Canthidium sp. 9	3	0	0	0	3	0
Canthidium viride	3	0	0	0	3	0
Canthon aff. *paraguayanum*	1	0	0	0	0	1
Canthon aff. *virens*	2	0	1	0	0	1
Canthon aff. *pilluliformis*	244	0	85	21	4	134

Canthon conformis	9	15	15	1	2	6
Canthon histrio	26	0	26	0	0	0
Canthon lituratus	52	0	0	3	6	43
Canthon luctuosus	0	1	1	0	0	0
Canthon sp. 1	19	1	3	5	0	12
Canthon unicolor	2	0	0	0	0	2
Canthon virens	105	5	15	0	63	32
Canthonella sp. 1	0	6	0	6	0	0
Canthonella sp. 2	1	0	0	0	1	0
Chalcocopris inexpectatus	1	0	0	1	0	0
Coprophanaeus cyanescens	12	31	7	10	8	18
Coprophanaeus dardanus	1	42	41	1	0	1
Coprophanaeus ensifer	47	2	5	3	18	23
Coprophanaeus spitzi	24	2	9	5	7	5
Deltochilum pseudoicarus	2	0	0	2	0	0
Deltochilum sp. 1	1	82	58	3	3	19
Deltochilum sp. 2	0	42	36	2	0	4
Deltochilum sp. 3	28	0	11	3	1	13
Deltochilum sp. 4	28	256	54	1	36	193
Diabroctis mirabilis	30	0	4	0	25	1
Dichotomius angeloi	8	223	89	58	66	18
Dichotomius bicuspis	7	16	6	13	0	4
Dichotomius bos	39	9	4	18	0	26
Dichotomius carbonarius	82	3081	1570	379	824	390
Dichotomius cuprinus	23	34	38	4	5	10
Dichotomius lycas	337	16	117	5	120	111
Dichotomius nisus	22	6	6	6	3	13
Dichotomius reichei	8	111	29	17	4	69
Dichotomius zikani	5	89	25	6	0	63
Eurysternus caribaeus	15	268	174	67	7	35
Eurysternus nigrovirens	73	3	24	50	0	2
Eutrichillum hirsutum	89	63	14	45	41	52
Genieridium cryptops	318	4	80	125	46	71
Malagoniella sp. 1	44	0	0	0	44	0

Onoreidium sp. 1	0	1	0	1	0	0
Ontherus appendiculatus	35	15	5	22	20	3
Ontherus ulcopygus	47	12	35	11	13	0
Onthophagus aff. *haematopus*	0	118	106	0	12	0
Onthophagus buculus	64	0	0	22	42	0
Onthophagus hircus	3	29	29	0	3	0
Onthophagus ptox	11	0	0	8	0	3
Oxysternon palermo	565	10	91	180	294	10
Oxysternon silenus	0	2	2	0	0	0
Phanaeus kirbyi	2	0	0	0	1	1
Phanaeus palaemo	4	0	0	0	4	0
Phanaeus splendidulus	0	117	50	0	67	0
Pseudocanthon xanthurus	3	0	0	1	1	1
Tetramereia sp. 1	0	1	1	0	0	0
Trichillum adjunctum	108	0	10	22	51	25
Trichillum externenpuctatum	109	4	0	83	4	26
Trichillum heydeni	76	4	3	5	2	70
Uroxys aff. *corporaali*	1	0	0	1	0	0
Uroxys aff. *thoracalis*	188	0	146	0	42	0
Uroxys sp. 1	0	309	0	123	35	151
Uroxys sp. 2	35	35	8	12	14	36

The species accumulation curve shows an asymptotic trend for both the savanna and the forest (Fig. 2). Based on the ACE richness estimator, the sampling effort was sufficient to sample 82.7993% of the total species present in the study area. Regarding the vegetation formations, the sampling effort covered 87.5590% of the total species in the savannas and 83.2898% of the species in forests.

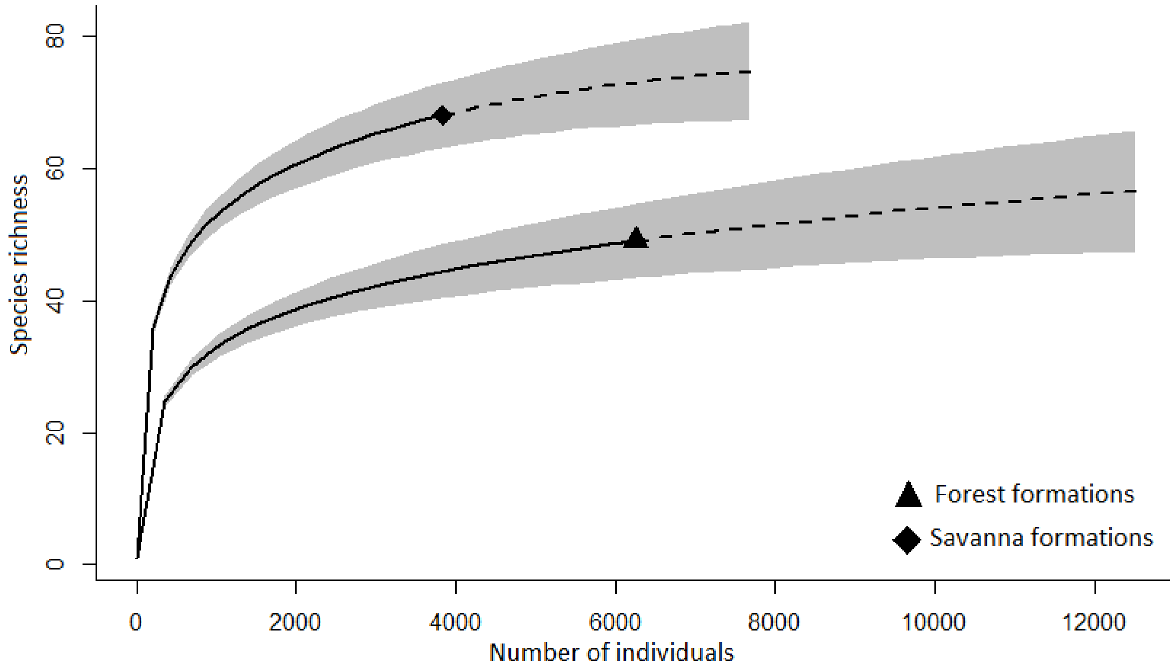


Fig 2 Species accumulation curve based on individuals involving the vegetation formations separately. The continuous line represents rarefaction, and the dashed line represents extrapolation.

Diversity in savanna formations

The Generalized Linear Models relating dung beetle diversity in savanna formations to landscape composition and configuration predictors showed distinct patterns, depending on the predictor, the response variable, and the landscape scale, defined by buffer sizes (Table 3).

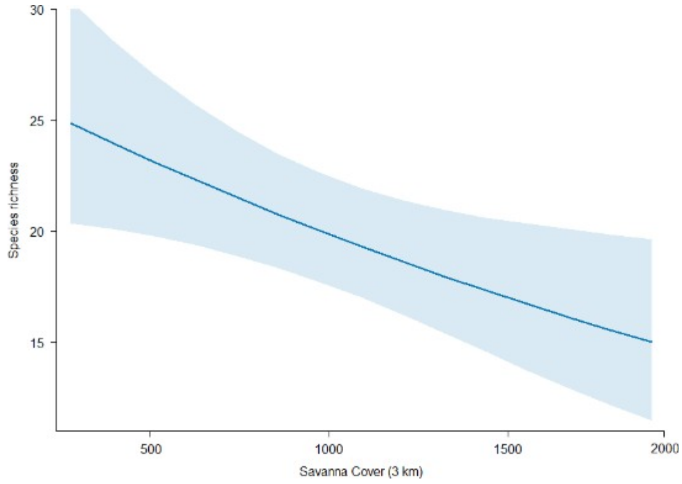
Table 3 Generalized linear models for dung beetle richness and abundance in relation to landscape metrics at each landscape size (1 km, 2 km, and 3 km buffers) for diversity in savanna formations. Models were selected using the AICc (corrected Akaike Information Criterion), with a cutoff point at ΔAICc < 4 (Burnham and Anderson 2002). Significance levels: *0.01; **0.001; *0; ns not significant.

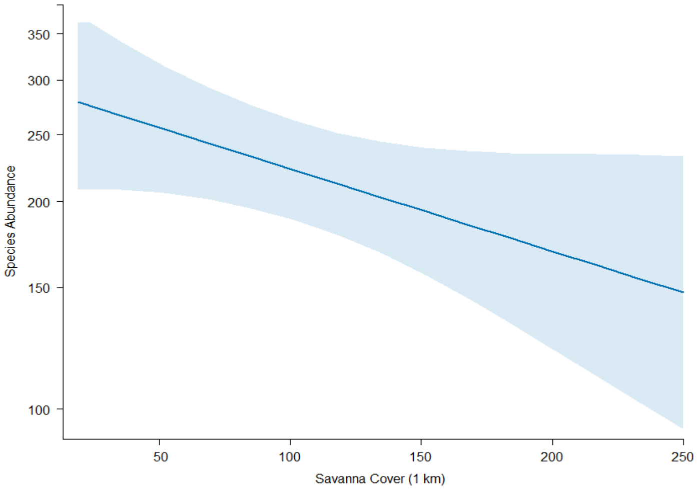
		Richness			**Abundance**		
Landscape Buffer	**Metrics**	**Estimate**	**Z value**	p value	**Estimate**	**Z value**	p value
1 km	Largest patch index				0,0174	4073	***
	Forest cover	-0,0043	-2,297	*			

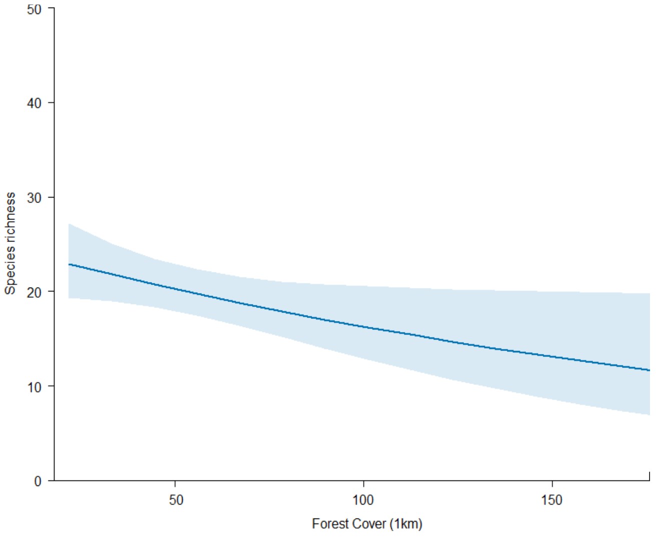
	Savanna cover	-0,0017	-1,907	*	-0,0027	-2,077	*
	Urban cover				0,0024	1,963	*
2 km	Number of patches				0,0333	2616	**
	Forest cover	-0,00093	-1,476	*			
	Savanna cover	-0,00053	-2,354	*			
	Pasture cover	0,00082	1,858	*			
3 km	Number of patches				0,0226	4,024	***
	Savanna cover	-0,00031	-2,731	*			
	Pasture cover	0,00077	2,6	*			

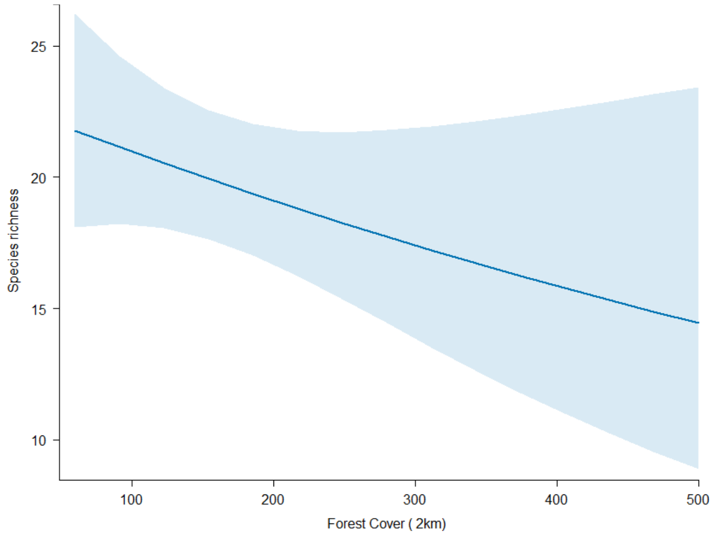
Regarding savanna cover, there was a significant reduction in species richness with increasing savanna cover across all three landscape scales. For species abundance, this pattern was observed only in landscapes defined by the 1 km buffer (Fig. 3). The same pattern was also found for species richness in relation to forest cover in landscapes defined by the 1 km and 2 km buffers (Fig. 3). In contrast, there was a significant increase in species abundance with increasing urban cover in landscapes defined by the 1 km buffer, and a significant increase in species richness with increasing pasture cover in landscapes defined by the 2 km and 3 km buffers (Fig. 3).

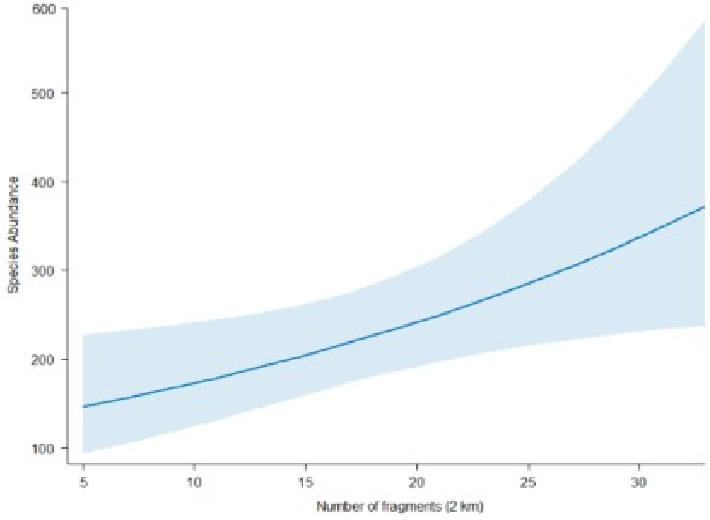
Regarding the predictors associated with landscape configuration, there was a significant increase in species abundance with increasing largest patch index (in landscapes defined by the 1 km buffer) and number of fragments (in landscapes defined by the 2 km and 3 km buffers) (Fig. 3).

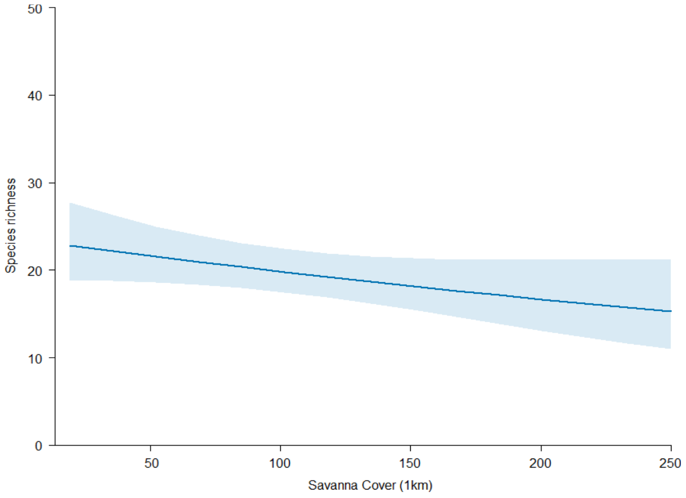


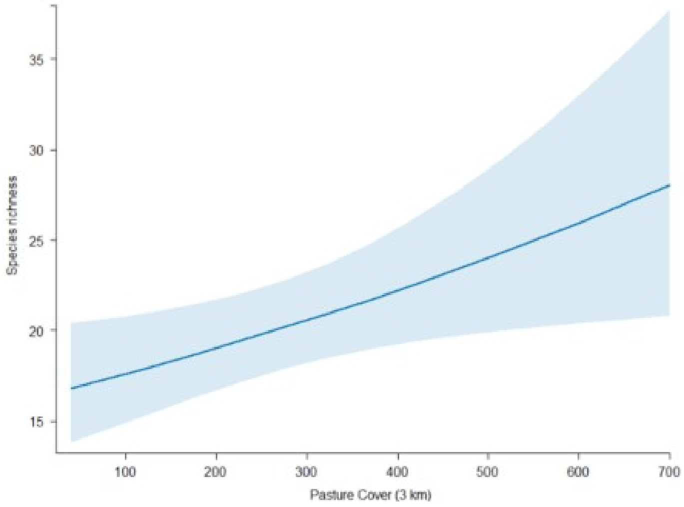


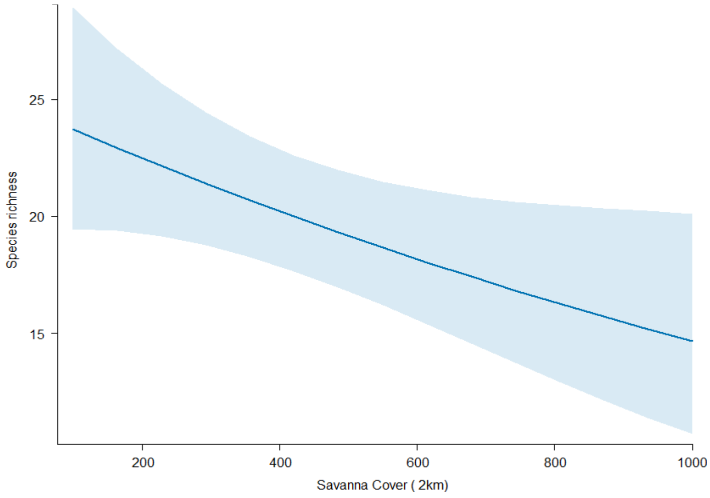

Species richness
50
40
30
20
10
0
50
100
150
Forest Cover (1km)


Species richness
25
20
15
10
100
200
300
400
500
Forest Cover (2km)


Species Abundance
600
500
400
300
200
100
5
10
15
20
25
30
Number of fragments (2 km)


Species richness
50
40
30
20
10
0
50
100
150
200
250
Savanna Cover (1km)


Species richness
35
30
25
20
15
100
200
300
400
500
600
700
Pasture Cover (3 km)


Species richness
25
20
15
200
400
600
800
1000
Savanna Cover (2km)

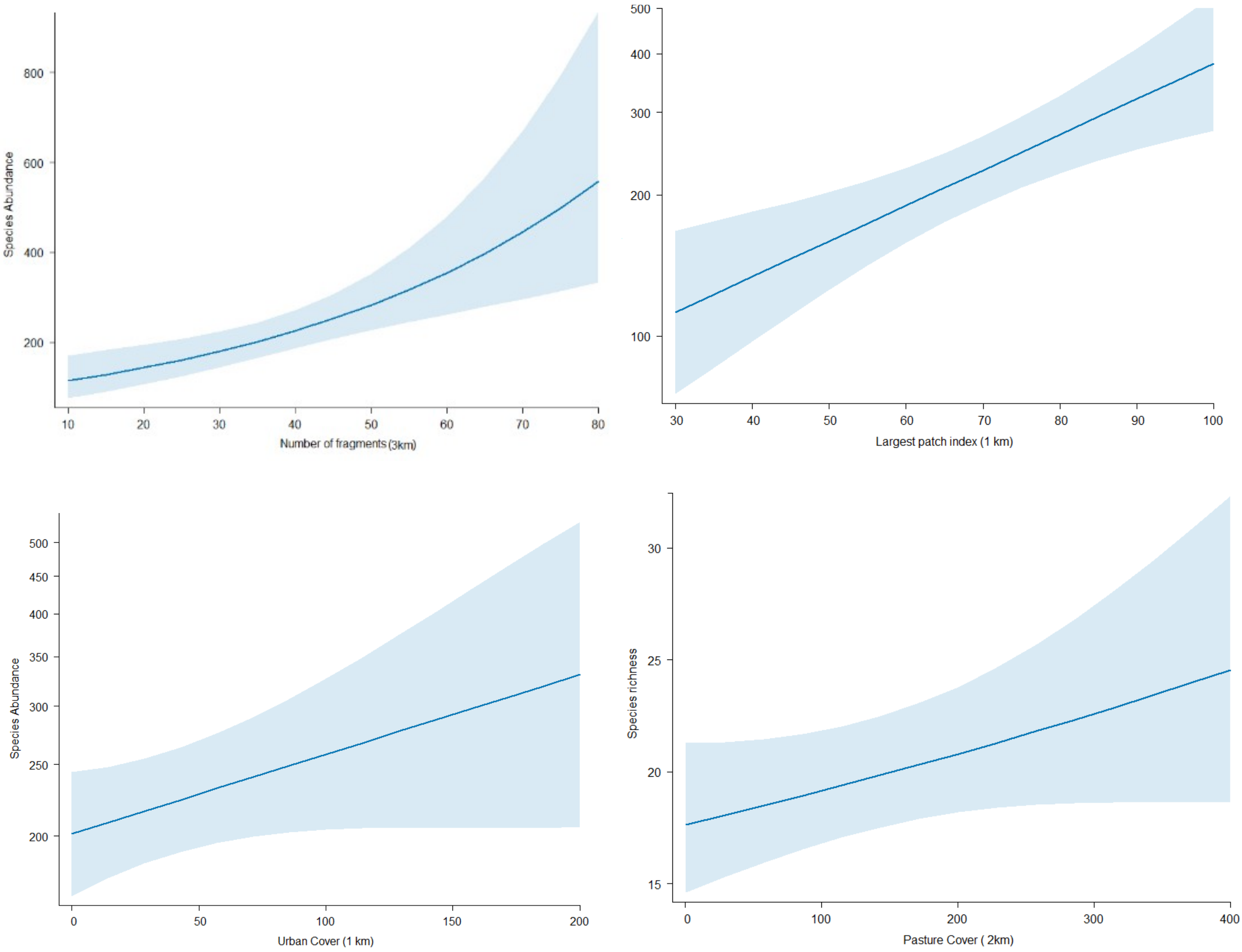


Fig. 3 Generalized linear models relating the response variables obtained in savanna formations (richness and abundance of dung beetles) to landscape configuration and composition predictors, across three distinct buffer radii, representing three different landscape size classes.

Diversity in forest formations

The generalized linear models involving dung beetle diversity in forest formations showed a pattern opposite to that observed for diversity in savanna formations: the only metric that had a significant effect in relation to landscape properties was forest cover, with a significant increase in diversity as forest cover increased (Fig. 4, Table 4). No metric related to landscape configuration had a significant effect on dung beetle diversity (Fig. 4, Table 4).

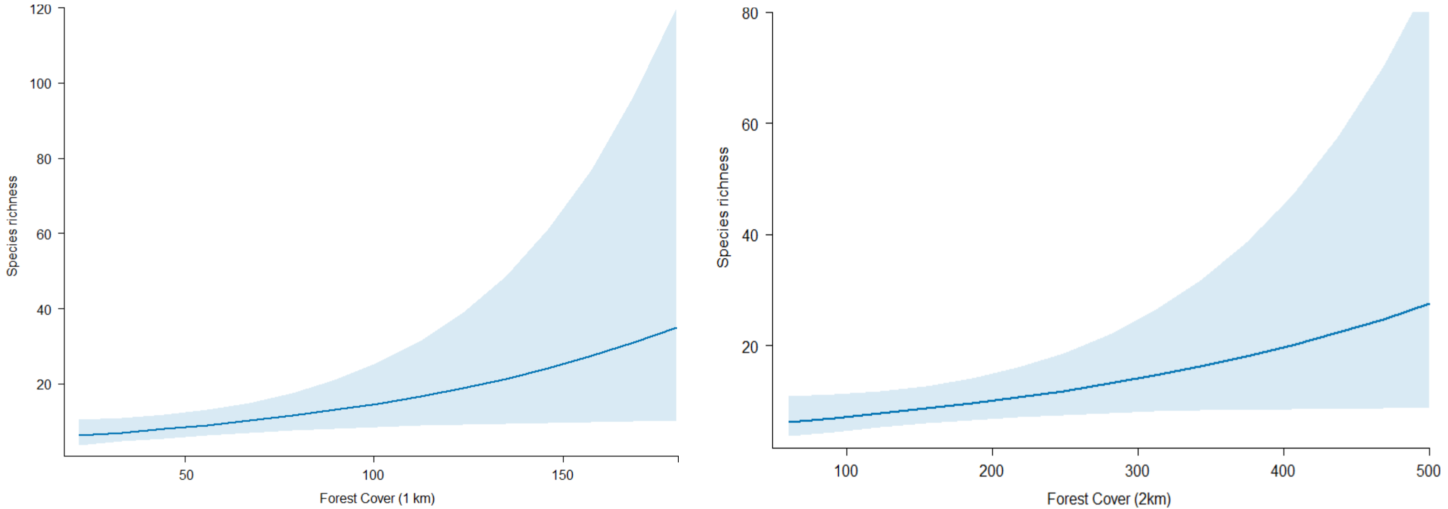


Fig. 4 Generalized linear models relating the response variables obtained in forest formations (richness and abundance of dung beetles) to landscape configuration and composition predictors, across three distinct buffer radii, representing three different landscape size classes.

Table 4 Generalized linear models for dung beetle richness and abundance in relation to landscape metrics at each landscape size (1 km, 2 km, and 3 km buffers) for diversity in forest formations. Models were selected using the AICc (corrected Akaike Information Criterion), with a cutoff point at ΔAICc < 4 (Burnham and Anderson 2002). Significance levels: *0.01; **0.001; *0; ns not significant.

		Richness			**Abundance**		
Landscape buffer	**Metrics**	**Estimate**	**Z value**	p	**Estimate**	**Z value**	p value
1 km	Largest patch index				-3,6379	-2,164	ns
	Forest cover	0,0109	2,416	*	0,0568	3,102	ns
	Agriculture cover				0,0162	2,742	ns
2 km	Largest patch index				-5,1924	-2,154	ns
	Forest cover	0,0033	2,171	*	13,8256	3,179	ns
	Pasture cover				-0,0054	-1,718	ns
3 km	Largest patch index				1,4563	0,433	ns
	Edge density	-0,0301	-0,936	ns	-0,2701	-1,594	ns
	Number of patches				0,1191	1,348	ns
	Forest cover	0,0027	1,716	ns	0,0106	2,033	ns
	Urban cover	-0,00034	-1,297	ns			

Scales of landscape influence on diversity

The landscape sizes (defined by the 1 km, 2 km, and 3 km buffers) did not affect the diversity patterns in relation to landscape composition and configuration attributes.

DISCUSSION

Sampling sufficiency

The species accumulation curve indicates that the sampling effort was sufficient to representatively capture the savanna and forest formations, as there are signs of an asymptotic trend. Regarding the total species richness estimates, the savanna formations exhibited higher richness compared to forest formations, corroborating other studies on dung beetles in the Cerrado (Silva et al. 2020, Oliveira et al. 2022). This is a common pattern in the Cerrado and can be attributed, for instance, to the high diversity of certain tribes that are more common in savanna formations, such as the Phanaeini and Ateuchini tribes (Cunha and Frizzas 2020, Oliveira et al. 2022). Additionally, this pattern may also be explained by the fact that savannas cover a much larger territorial extent within the Cerrado compared to forest formations (MapBiomas Project 2024), allowing for the co-occurrence of a greater number of species in these ecosystems.

Diversity in savanna formations

Dung beetle diversity in savanna formations was mainly influenced by landscape composition rather than configuration. On the other hand, forest formations were affected exclusively by landscape composition, specifically forest cover.

The only landscape configuration metrics that influenced dung beetle diversity in savanna formations were the number of fragments and the largest patch index. Although these are configuration metrics, they are intrinsically related to the amount of savanna habitat in the landscape, since a higher number of fragments and a larger largest patch index indicate more available habitat in the landscape, which corresponds to an increase in native vegetation cover in the landscape (Hesselbarth et al. 2019). In this context, it is possible to infer that landscape composition is the main landscape attribute affecting dung beetle diversity in savanna formations.

In the Cerrado, savanna formations represent approximately 66.31% of the biome, according to the Mapbiomas Project (2024). Furthermore, this vegetation type is relatively well distributed throughout the biome, unlike forest formations, which are mainly represented by gallery forests concentrated along watercourses. Consequently, compared to forest remnants, savanna remnants are primarily influenced by edge effects and natural and anthropogenic disturbances, such as fire. For example, savanna areas bordering agricultural lands are often impacted by pollutants from pesticide use in agriculture, which can negatively affect sensitive species, potentially causing local extinctions in these edge areas (Palharini et al. 2020). Specifically for dung beetles, some guilds are more or less affected than others, and certain diversity parameters, such as the abundance of roller beetles, tend to be higher in some classes of anthropogenic landscapes, such as pastures (Martello et al. 2016, Oliveira et al. 2021), a context in which edge effects are reduced on these species in savanna formations. Regarding fire, this disturbance frequently occurs anthropogenically during the dry months in the biome, often resulting in large wildfires (Arruda et al. 2024). These fires usually drastically alter vegetation structure, making it more open and therefore increasing solar incidence on the soil surface (Pivello et al. 2021), which can impact the fecal resources used by dung beetles (for example, by increasing desiccation rates).

On the other hand, it would be expected that dung beetle diversity would be negatively affected by other types of land cover (anthropogenic covers), due to factors associated with physical conditions that favor the desiccation of fecal resources used for feeding and nesting (Martello et al. 2016). However, this was not the pattern found in the present study for dung beetle diversity in savanna formations. In other words, dung beetle diversity in savanna formations declined as savanna and forest cover increased in the landscapes, with an increase in diversity as urban and pasture cover increased in the landscapes. This unexpected result may be related to the fact that the highest abundances recorded are of species able to persist in anthropogenic ecosystems, such as *Dichotomius opacus*, *Dichotomius lycas*, and species of the genus *Canthidium*. Furthermore, the total estimated species richness for the native landscape class is the third lowest among the different landscape classes. In this sense, it is possible that there is a dominance of generalist species that are able to establish themselves in anthropogenic matrices, especially in pasture areas, where species richness is highest, potentially leading to displacement of sensitive species in adjacent savanna ecosystems. Other studies in the same region have also found higher diversity parameters in anthropogenic areas, including pastures, compared to native areas. For example, Oliveira et al. (2021) found higher species abundances in pastures and soybean fields, with no significant difference in species richness among land use systems and without affecting ecosystem services. In that study, the authors argue that the high resource availability associated with its homogeneity in these anthropogenic areas is one explanation for this pattern. They also argue that biotic homogenization is occurring, where generalist species replace specialist and endemic species. Considering that the present study was conducted in the same region, this may be the same explanation for the pattern found here.

Diversity in forest formations

In contrast, dung beetle diversity in forest remnants responded solely to the increase in forest cover in the landscape, a variable related to landscape composition. Several studies have shown that the dung beetle group comprises many species that are sensitive and exclusive to forest ecosystems (e.g., Silva et al. 2019, Silva et al. 2020, Oliveira et al. 2022). One explanation for this spatial segregation of diversity between open and forest formations is niche partitioning as a way to reduce intra- and interspecific competition for fecal resources used for feeding and nesting (Oliveira et al. 2022). Besides spatial segregation to reduce competition for fecal resources, these resources tend to undergo less desiccation in forest ecosystems (Silva et al. 2017), thus remaining viable for longer periods. Moreover, species sensitive to forest ecosystems tend to exhibit lower tolerance to the surrounding matrix, leading to reduced colonization of these species in adjacent anthropogenic ecosystems (Silva et al. 2017, Salomão et al. 2023). Additionally, anthropogenic consequences such as edge effects are more noticeable in forest ecosystems, causing specialized species in these environments to experience greater population declines than species tolerant of open ecosystems (Silva et al. 2017, Pessoa et al. 2023). Thus, ecological processes related to forest cover in the landscape prevail over landscape configuration attributes, leading to an increase in dung beetle diversity in the study region.

Landscape sizes (defined by the 1 km, 2 km, and 3 km buffers) did not affect the diversity patterns in relation to landscape composition and configuration attributes, indicating that the scale of effect does not extend beyond these buffers. This possibly indicates that the home ranges of the populations sampled in the present study extend beyond these buffer sizes, and thus, larger buffers might cause differences in these results.

CONCLUSION

The hypotheses were partially supported. Dung beetle diversity in savanna formations was mainly affected by landscape composition, but there was also an influence of landscape configuration. On the other hand, contrary to the hypothesis, dung beetle diversity in forest formations was affected exclusively by composition, with no significant contribution from landscape configuration.

Despite the above, dung beetle diversity in savanna formations was positively affected by the availability of anthropogenic ecosystems in the landscape (mainly pastures), and negatively affected by the availability of native ecosystems. The interpretation of this result requires caution, especially regarding its use for the conservation of the group within the biome's landscapes. One explanation for this pattern is the dominance or biotic homogenization caused by generalist species that may be adapting to anthropogenic matrices and displacing the diversity of specialist species in savanna formations.

In the case of the increase in dung beetle diversity in forest formations as forest cover in the landscape increases, it is evident that the availability of forest habitat is more important than any landscape configuration variable evaluated. This may be due to the fact that, in forest formations, fecal resources used for nesting and feeding remain viable for longer periods because of more stable microclimatic conditions (Ribeiro and Walter 2008). Since fecal resources are ephemeral, their longer viability is an important factor in reducing inter- and intraspecific competition. Conversely, in savanna formations, which are composed of more open vegetation, fecal resources tend to dry out more quickly (Hanski and Cambefort 1991), a situation to which species occupying these formations are already adapted (Costa et al. 2013, Salomão et al. 2019). Being adapted, these species may also find it easier to colonize anthropogenic matrices, such as pastures, characterized by open vegetation and abundant, homogeneous fecal resources over large areas.

Conflict of interest: The authors declare no conflict of interest.

Data availability: Data supporting the results and conclusions of this study are available upon request from the corresponding author.

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CHAPTER II

Esse capítulo foi submetido e está formatado de acordo com as normas da revista
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The components of taxonomic diversity of dung beetles respond in opposite ways to the landscape features of savannas in Central Brazil

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Abstract: Global savanna regions have been facing major anthropogenic threats resulting from habitat fragmentation, land-use conversion for the implementation of monocultures, and the establishment of exotic pastures. Among these regions, the Brazilian Cerrado stands out as the most biodiverse savanna in the world and is also one of the global conservation *hotspots*. Considered a biome, the region has already lost nearly half of its original territory, mainly due to the expansion of agricultural and livestock areas. Today, its landscapes are characterized by a mixture of native and anthropogenic ecosystems. In this context, the aim of this study is to understand the organization of biological diversity from the level of vegetation fragments to the level of landscapes, which include, in addition to the fragments themselves, anthropogenic ecosystems such as agricultural and urban areas. To achieve this, we applied the additive partitioning method of diversity (using species richness and Shannon diversity metrics), which allows diversity to be broken down into various nested components of alpha and beta diversity, facilitating an understanding of the most relevant spatial levels in the organization of biodiversity. For this study, we used dung beetles as a model group due to their sensitivity to environmental variation, their specialization in habitat use, and their role as important providers of ecosystem services. We found contrasting results depending on the diversity metric used. For example, when partitioning species richness, we observed a gradient of increasing beta diversity, which was lowest at the level of vegetation formations and highest at the landscape level. In contrast, partitioning based on Shannon diversity revealed the opposite pattern, with a gradient of increasing beta diversity as spatial scale decreased—that is, from the landscape level to the vegetation formation level. This highlights the importance of evaluating multiple diversity metrics, even when addressing the same biological question. Furthermore, the results carry important implications for conservation. For example, while the savanna formations tend to have greater environmental heterogeneity due to structural differences between savanna and forest formations, and landscapes level tend to be more environmentally homogeneous due to the dominance of anthropogenic classes at that level, beta diversity in terms of species richness was higher at this level. This suggests that environmental heterogeneity is not the only factor shaping beta diversity; spatial factors such as biogeographic isolation, impermeable matrices, and other barriers that isolate populations also play a key role by increasing beta diversity. On the other hand, the pattern observed in Shannon diversity partitioning may be influenced by an important factor:

abundance evenness. In this study, we observed that various species were concentrated only in forests or in savannas—for example, *Dichotomius opacus* in forests. As a result, beta diversity increases at the level of vegetation formations. Thus, one important implication for conservation is the need to consider studies that include multiple diversity metrics prior to decision-making. Additionally, conservation strategies should take into account not only the degree of environmental heterogeneity but also the spatial organization of the remaining vegetation fragments. This approach can help ensure the continuity of gene flow between populations and, therefore, the maintenance of biodiversity in the face of ongoing anthropogenic pressures.

Keywords: additive partitioning, brazilian cerrado, biodiversity patterns, dung beetles

INTRODUCTION

Tropical savannas cover between 15 and 24.6 million square kilometers across South America, Asia, and Africa, yet they remain overlooked compared to exclusively forested ecoregions (Myers et al. 2000, Silva and Bates 2002). Among these savannas, the Cerrado stands out as one of the largest in geographic extent and the most threatened, in addition to having high biological diversity and species endemism (Myers et al. 2000). This brazilian biome is the second-largest biome in Brazil in terms of territorial extent, boasting a high richness of endemic species and being considered one of the world's conservation *hotspots* (Klink and Machado 2005). The typical composition of Cerrado landscapes directly impacts species, leading to changes in diversity. These impacts can be either positive or negative, depending on how species interact with their environment. For example, species with a broader diet and greater dispersal abilities are less affected by structural landscape changes compared to species with more specialized diets and limited dispersal capacities (Souza et al. 2020, Moir et al. 2021, Franco et al. 2023). Furthermore, even species with generalist traits (such as a wider dietary range and greater dispersal ability) that, in theory, would allow better adaptation to structural landscape changes, exhibit varied responses to these changes. This demonstrates that such structural modifications have heterogeneous effects, even on generalist species (Franco et al. 2023). As a result, diversity reflects the phenotypic responses of species to structural landscape changes. Therefore, it is essential to study diversity from a landscape perspective, especially in biomes like the Cerrado, which consists of various anthropogenic ecosystems adjacent to natural ecosystems.

Considering the landscapes of the Cerrado, which comprise both anthropogenic and natural ecosystems, and the fact that species respond differently to these compositions, ecological studies in this biome must account for the emergent characteristics of landscapes (Cunha and Frizzas 2020). In other words, a multilevel spatial approach is necessary for ecological studies in the biome. This need arises because different organizational processes of diversity operate across spatial scales (Cunha and Frizzas 2020, Salgueiro et al. 2021). For example, at the local scale, ecological processes are predominant and include factors such as structural and historical habitat differences caused by disturbances (e.g., fire), microclimate, and biotic interactions. At the regional scale, geographical processes play a dominant role and include factors such as dispersal barriers, climatic variations, and edaphic differences (Cunha and Frizzas 2020). In this context, studies focusing on taxonomic groups that encompass species with distinct morphofunctional traits must consider these spatial levels when analyzing diversity.

One of the largest taxonomic groups, which includes numerous morphofunctionally distinct species that perceive landscapes differently from one another, is the group of dung beetles. This group exhibits high diversity in both savannas and forests (Hanski and Cambefort 1991), is highly sensitive to environmental variations (Raine et al. 2018, Franco et al. 2023), serves as a biodiversity indicator for other sensitive taxonomic groups, particularly mammals (Raine and Slade 2019), provides various ecosystem services (Nichols et al. 2008), and includes species specialized in both open ecosystems, such as grasslands and savannas, and closed ecosystems, such as forests (Ribeiro et al. 2022). This last characteristic of dung beetles is particularly important in the Cerrado, where native vegetation remnants are predominantly composed of savanna and grassland ecosystems bordering patches of forest ecosystems (Ribeiro and Walter 2008). In this context, species that specialize in a particular habitat tend to have greater restrictions in terms of dispersal ability and dietary range compared to generalist species. Consequently, they perceive the landscape at a more local spatial scale, where community assembly rules are primarily driven by ecological processes, such as microclimate determined by vegetation structure, resource availability, and biotic interactions (Cunha and Frizzas 2020, Mattos et al. 2021, Ribeiro et al. 2022). On the other hand, habitat-generalist species, which can disperse across larger regions and have broader dietary ranges, tend to perceive the landscape at a more regional spatial scale. In this case, community assembly rules are mainly influenced by biogeographic factors such as dispersal barriers, topography, and edaphic differences (Cunha and Frizzas 2020, Mattos et al. 2021). This further reinforces the need to consider different spatial scales in diversity studies, particularly in the Cerrado, where vegetation formations exhibit high environmental heterogeneity and spatiotemporal co-occurrence.

Considering that Cerrado landscapes are composed of native vegetation remnants adjacent to anthropogenic ecosystems, this study aims to assess dung beetle diversity from a multilevel spatial perspective, incorporating the emergent landscape characteristics of the biome into diversity evaluations. This approach seeks to understand how diversity is structured, from the level of native vegetation remnants to the broader landscape scale, which includes not only these remnants but also the main anthropogenic ecosystems present in the biome, particularly those associated with agriculture, pasturelands, and urbanization. In this context, the following hypotheses will be tested: at the level of vegetation remnants, community differentiation (increase in beta diversity) is expected to be highest, as this spatial scale encompasses the greatest environmental heterogeneity (savanna and forest). Conversely, differentiation (decrease in beta diversity) is expected to be lowest at the landscape class scale (urban, native, pasture, and agricultural landscapes), due to the predominance of anthropogenic landscapes and the widespread distribution of abundant species adapted to these ecosystems. Additionally, hierarchically partitioned null models of diversity will be developed to test the hypothesis that, due to the relative environmental homogeneity at broader spatial scales, local/ecological processes play a more deterministic and predominant role in structuring diversity compared to regional processes.

MATERIALS AND METHODS

Biome characterization

The Cerrado biome can be divided into three classes of vegetation formations: grassland, savanna, and forest, with the latter two formations accounting for approximately 84% of the biome's remaining vegetation (Ribeiro and Walter 2008, Mapbiomas Project 2024). Despite this, 47% of the native vegetation areas have already been converted for agricultural and livestock activities (Mapbiomas Project 2024). In addition, the remaining native vegetation is affected by various degradation factors resulting from agricultural conversion, such as biological invasions by exotic grasses, monocultures, and soil erosion due to improper land management (Klink and Machado 2005). These degradation factors arise from the fact that most of the biome's vegetation remnants are surrounded by extensive areas under different land-use regimes, including agriculture, livestock farming, and urban expansion (Klink and Machado 2005, Strassburg et al. 2017). Beyond these pressures, approximately 40% of the remaining native vegetation is located within private properties dedicated to agriculture and livestock, making them legally subject to deforestation under the Brazilian Forest Code (Brasil 2012, Strassburg et al. 2017). As a result, about 77% of deforestation alerts in the Cerrado are concentrated within private lands (RAD 2023). Conversely, only 8.21% of the biome's territory is legally protected as Conservation Units (ICMBio 2024). In this context, the current landscapes of the Cerrado are characterized by a mosaic of native vegetation remnants and anthropogenic ecosystems, a distinctive feature of the biome observed only at the landscape level.

Study area

The study area encompasses the Federal District and municipalities of the State of Goiás (surrounding the Federal District), a region of the brazilian Cerrado, in Central Brazil. In this region, 16 landscapes were selected, with 4 landscapes from each land-cover class: native, agricultural, urban, and pasture (Fig. 1). These classes were defined based on the proportions of land cover within the landscape (for example, if at least 70% of the land cover in a given landscape is native vegetation, the landscape is classified as native). In each landscape, a savanna fragment and a forest fragment were selected, with an average distance between fragments of approximately 1.79 km (minimum distance: 0.779 km; maximum distance: 3.95 km). These landscapes and their respective vegetation fragments were chosen based on logistical access considerations, such as the presence of nearby highways or trails. According to Köppen’s classification, the region's climate is of the Aw type, with the highest precipitation occurring between November and January, and the lowest precipitation between June and August (CODEPLAN 2017). The soils are predominantly latosols and cambisols, with occurrences of argisols, neosols, gleysols, and plinthosols (CODEPLAN 2017).

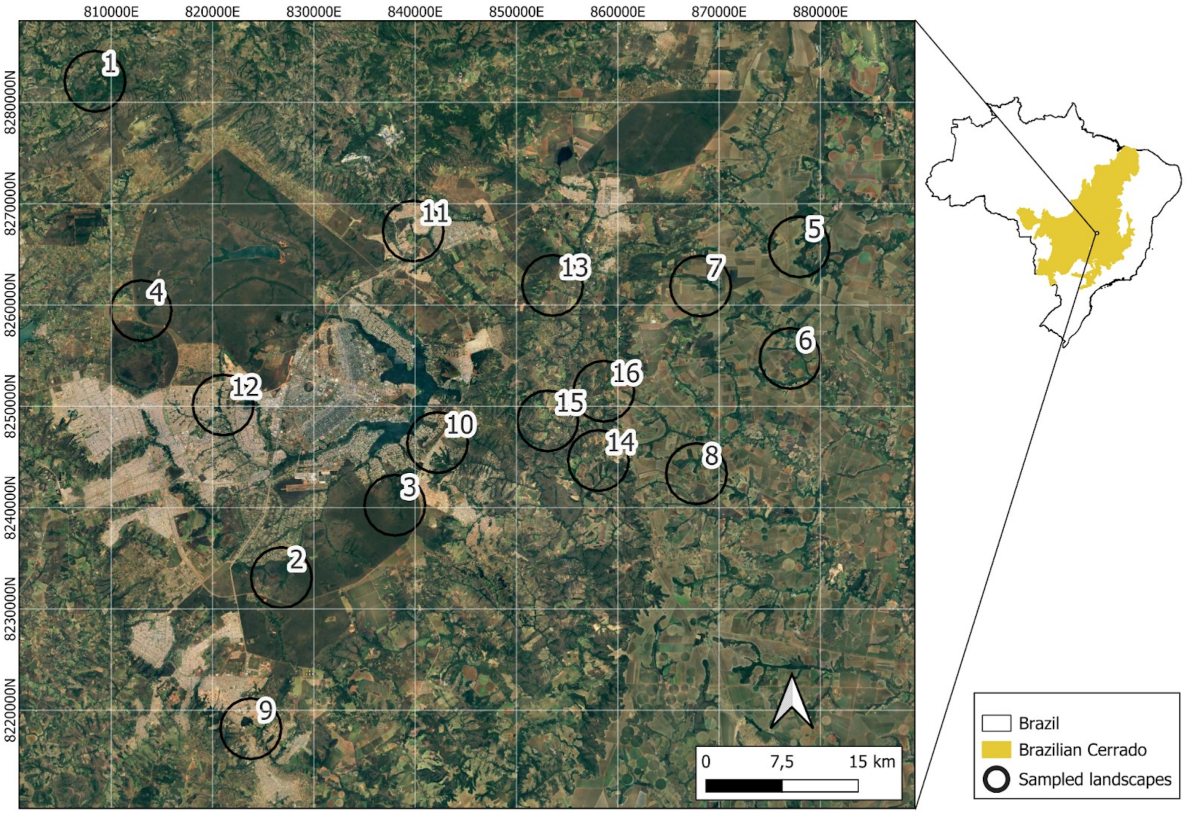


Fig. 1 Study area, located in the Central Plateau of Brazil. The sampled landscapes are organized into the following intervals: 1-4: native landscapes; 5-8: agricultural landscapes; 9-12: urban landscapes; 13-16: exotic pasture landscapes.

Community sampling

Sampling was conducted between November and December 2021, a period that corresponds to the rainy season in the brazilian Cerrado, which is considered the optimal time for dung beetle collection (Oliveira et al. 2011). In each of the 16 forest fragments and 16 savanna fragments, two transects were established, each containing five traps, with a minimum distance of 25 meters between traps. Furthermore, this was the distance at which it was possible to place the pitfalls closer to the center of the vegetation fragments, thereby more accurately sampling the actual diversity within the vegetation formations and minimizing the influence of occasional individuals coming from the surrounding matrix.

The traps used were of the pitfall type and consisted of two containers: the first container, with a 1-liter capacity, was filled with water and detergent to break the water's surface tension; the second container, with a 50-milliliter capacity, was suspended with wire above the first container and filled with 25 grams of bait. The bait consisted of human feces, considered the most attractive bait for dung beetles (Milhomem et al. 2003). A rain protection was placed above the two containers to prevent flooding.

The traps were removed after 48 hours of sampling, and the collected specimens were transferred to containers with 70% alcohol, properly labeled. In the laboratory, the specimens were identified using dichotomous keys and with the help of specialists. The vouchers were deposited in the Entomological Collection of the Department of Zoology at the University of Brasília (DZUB).

The research authorizations related to the sampling of the dung beetle community are SISBIO/ICMBio No. 80499-1 and the Research Authorization No. 16/2021 from the Department of the Environment and Water Resources (Botanical Garden).

DATA ANALYSIS

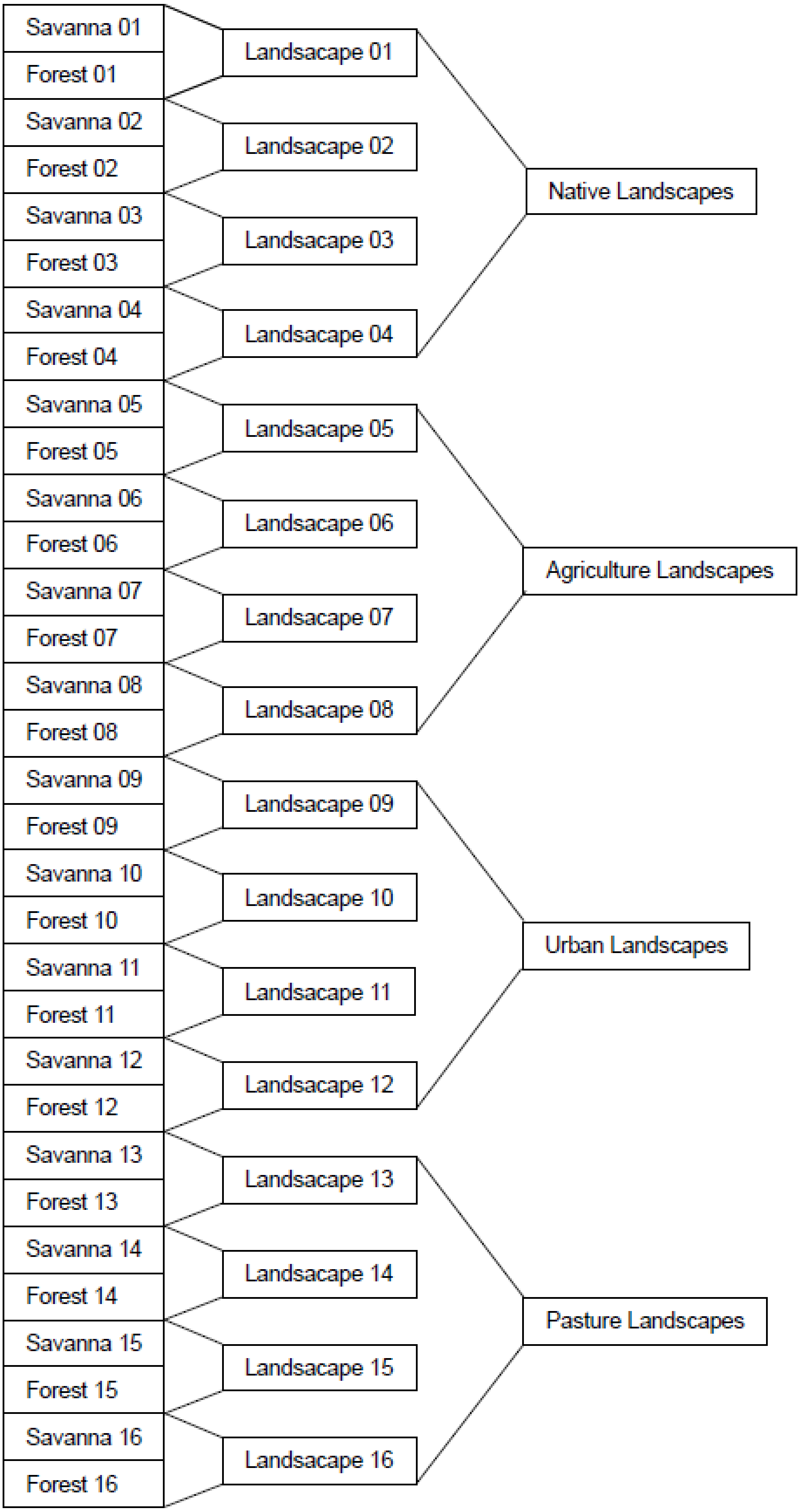
Sample size sufficiency

To assess the sufficiency of the sampling effort, species accumulation curves based on individuals were used (Gotelli and Colwell 2001), through the iNEXT package version 2.0.20 (Hsieh et al. 2020). The total species richness estimate was calculated using the ACE estimator (Gotelli and Colwell 2011), through the fossil package version 0.3.7 (Vavrek 2012). All analyses were performed in R software version 3.5.3 (R Core Team 2024).

Additive Partitioning of Diversity

To evaluate diversity across spatial levels (from remnants to landscape classes), diversity was partitioned using the additive partitioning method, as it allows assessing the contribution of diversity components to total diversity. Furthermore, it enables the identification of species richness that is exclusive to a particular spatial level, facilitating the understanding of beta diversity behavior from a multi-spatial perspective (Lande 1996, Veech et al. 2002, Gering et al. 2003).

The partitions encompass the components of diversity α and β, which were spatially partitioned into three levels: $\alpha 1$ = average diversity within vegetation remnants, $\beta 1$ = diversity between types of vegetation remnants, $\beta 2$ = diversity between landscapes, and $\beta 3$ = diversity between landscape classes (Fig. 2). Thus, regional diversity is given by $\gamma = \alpha 1 + \beta 1 + \beta 2 + \beta 3$.


Savanna 01
Forest 01
Savanna 02
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Landsacape 13
Landsacape 14
Landsacape 15
Landsacape 16
Native Landscapes
Agriculture Landscapes
Urban Landscapes
Pasture Landscapes

Fig. 2 Diagram of the experimental design used for the additive partitioning of diversity. In each landscape (landscapes 01 to 16), one savanna (savanna 01 to 16) and one forest (forest 01 to 16) were sampled. Depending on the dominant land use type in each landscape, they were grouped into four landscape classes: native (dominated by savanna and forest formations), agricultural (dominated by croplands, especially soybean and corn), urban (composed of cities), or pasture (entirely used for cattle ranching). Thus, the highest spatial level (landscape classes) is a nesting of the lower levels (landscapes and vegetation formations). The α1 component is the average diversity within vegetation formations (savannas and forests); β1 is the diversity between types of vegetation formations (savannas and forests); β2 is the diversity between landscapes; and β3 is the diversity between landscape classes.

To assess the preponderance of local and regional processes on the organization of diversity, additive partitions based on null models of the respective diversity components were created. To do so, species richness and abundance at a higher spatial level are determined by randomizing species and individuals from the lower hierarchical levels (Crist et al. 2003). Each diversity component generated in this additive partition represents a diversity value reflecting the hypothesis that this value is given at random, meaning there are no influences of processes acting on the structuring of diversity. Thus, by comparing these null values with the observed values in the specific case, it is possible to measure the size and direction of the influences of deterministic processes acting at each spatial level on the organization of diversity (Cunha and Frizzas 2020).

The statistical significance in the comparison between the observed and null diversity components represents the probability of obtaining, by chance, an α1, β1, β2, or β3 component with values higher (or lower) than those observed for the respective components. Mathematically, this significance is given by the proportion of null values generated that are higher (or lower) than the observed values (Crist et al. 2003).

The partitions were performed using species richness and diversity metrics (Shannon diversity). To construct the additive partition based on null models of diversity, randomizations based on individuals were created with 10,000 repetitions. After the partitions, specifically for Shannon diversity, the values of the components α1, β1, β2, and β3 were transformed through their respective exponentials, as this transformation makes these values additive (Jost et al. 2007). The partitions were performed using the vegan package version 2.5-2 (Oksanen et al. 2018) in R software version 3.5.3 (R Core Team 2024).

RESULTS

Sampling Sufficiency

A total of 10,092 individuals were collected, distributed across 81 species (Table 2). The most abundant species were *Dichotomius opacus*, *Canthidium* sp. 3, *Canthidium barbacenicum*, *Oxyternon palemo*, and *Dichotomius lycas*, with 3163, 1141, 748, 575, and 353 individuals, respectively. Disregarding the singletons (14 species) and doubletons (7 species), the least abundant species were *Ateuchus* aff. *ovalis*, *Canthidium* sp. 9, *Canthidium viride*, *Pseudocanthon xanthurus*, and *Canthidium* aff. *refulgens*, with the first four species having 3 individuals each, and the last two species with 4 individuals each.

Table 2 Abundance of dung beetle species sampled, separated by vegetation formation and by landscape class (native, agriculture, urban and pasture classes). The data related to the "Vegetation Formations" group encompass the samples collected in savannas and forests within each of the four landscape classes.

	Vegetation Formations		**Landscapes Classes**			
Species	**Savanna**	**Forest**	**Native**	**Agriculture**	**Urban**	**Pasture**
Agamopus unguicularis	19	34	34	10	1	8
Ateuchus aff. *ovalis*	0	3	0	0	0	3
Ateuchus aff. *vigilans*	1	0	0	1	0	0
Ateuchus puncticollis	1	0	0	0	0	1
Ateuchus striatulus	4	3	3	2	0	2
Atheuchus vividus	0	1	1	0	0	0
Besourenga sp. 1	17	0	1	0	15	1
Besourenga sp. 2	2	0	0	0	0	2
Canthidium aff. *refulgens*	4	0	1	3	0	0
Canthidium aff. *hyla*	11	0	5	0	2	4
Canthidium aff. *lucidum*	0	1	0	0	0	1
Canthidium barbacenicum	747	1	1	56	571	120
Canthidium	6	1	1	0	5	1

decoratum						
Canthidium sp. 1	1	1	0	1	1	0
Canthidium sp. 2	2	6	6	1	0	1
Canthidium sp. 3	4	1137	12	232	417	480
Canthidium sp. 4	0	1	0	1	0	0
Canthidium sp. 5	13	0	5	0	0	8
Canthidium sp. 6	1	0	0	0	1	0
Canthidium sp. 7	42	0	1	41	0	0
Canthidium sp. 8	1	0	1	0	0	0
Canthidium sp. 9	3	0	0	0	3	0
Canthidium viride	3	0	0	0	3	0
Canthon aff. *paraguayanum*	1	0	0	0	0	1
Canthon aff. *virens*	2	0	1	0	0	1
Canthon aff. *pilluliformis*	244	0	85	21	4	134
Canthon conformis	9	15	15	1	2	6
Canthon histrio	26	0	26	0	0	0
Canthon lituratus	52	0	0	3	6	43
Canthon luctuosus	0	1	1	0	0	0
Canthon sp. 1	19	1	3	5	0	12
Canthon unicolor	2	0	0	0	0	2
Canthon virens	105	5	15	0	63	32
Canthonella sp. 1	0	6	0	6	0	0
Canthonella sp. 2	1	0	0	0	1	0
Chalcocopris inexpectatus	1	0	0	1	0	0
Coprophanaeus cyanescens	12	31	7	10	8	18
Coprophanaeus dardanus	1	42	41	1	0	1
Coprophanaeus ensifer	47	2	5	3	18	23
Coprophanaeus spitzi	24	2	9	5	7	5
Deltochilum pseudoicarus	2	0	0	2	0	0
Deltochilum sp. 1	1	82	58	3	3	19
Deltochilum sp. 2	0	42	36	2	0	4
Deltochilum sp. 3	28	0	11	3	1	13
Deltochilum sp. 4	28	256	54	1	36	193
Diabroctis mirabilis	30	0	4	0	25	1
Dichotomius angeloi	8	223	89	58	66	18

Dichotomius bicuspis	7	16	6	13	0	4
Dichotomius bos	39	9	4	18	0	26
Dichotomius carbonarius	82	3081	1570	379	824	390
Dichotomius cuprinus	23	34	38	4	5	10
Dichotomius lycas	337	16	117	5	120	111
Dichotomius nisus	22	6	6	6	3	13
Dichotomius reichei	8	111	29	17	4	69
Dichotomius zikani	5	89	25	6	0	63
Eurysternus caribaeus	15	268	174	67	7	35
Eurysternus nigrovirens	73	3	24	50	0	2
Eutrichillum hirsutum	89	63	14	45	41	52
Genieridium cryptops	318	4	80	125	46	71
Malagoniella sp. 1	44	0	0	0	44	0
Onoreidium sp. 1	0	1	0	1	0	0
Ontherus appendiculatus	35	15	5	22	20	3
Ontherus ulcopygus	47	12	35	11	13	0
Onthophagus aff. *Haematopus*	0	118	106	0	12	0
Onthophagus buculus	64	0	0	22	42	0
Onthophagus hircus	3	29	29	0	3	0
Onthophagus ptox	11	0	0	8	0	3
Oxysternon palermo	565	10	91	180	294	10
Oxysternon silenus	0	2	2	0	0	0
Phanaeus kirbyi	2	0	0	0	1	1
Phanaeus palaemo	4	0	0	0	4	0
Phanaeus splendidulus	0	117	50	0	67	0
Pseudocanthon xanthurus	3	0	0	1	1	1
Tetramereia sp. 1	0	1	1	0	0	0
Trichillum adjunctum	108	0	10	22	51	25
Trichillum externenpuctatum	109	4	0	83	4	26
Trichillum heydeni	76	4	3	5	2	70
Uroxys aff. *corporaali*	1	0	0	1	0	0
Uroxys aff. *thoracalis*	188	0	146	0	42	0
Uroxys sp. 1	0	309	0	123	35	151

Uroxys sp. 2	35	35	8	12	14	36

The vegetation formation with the highest abundance was the forest formation, with 6,254 individuals (the savanna formation had 3,838 individuals) (Fig. 3A). Furthermore, the landscape class with the highest abundance was the native landscapes, with 3,105 individuals, followed by the urban landscapes, pastures, and finally, agricultural landscapes, with 2,958, 2,330, and 1,699 individuals, respectively (Fig. 3B).

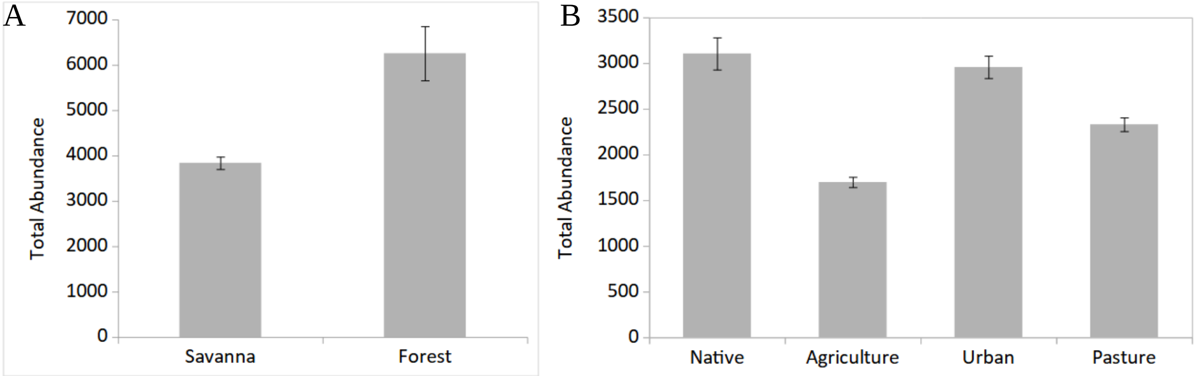

Fig. 3 Total abundance of dung beetles between forest and savanna formations (A) and among the landscape classes: native, agricultural, urban, and pasture (B).

In general, the sampling effort was sufficient to adequately represent the dung beetle community across the different vegetation formations (Fig. 4). On the other hand, no clear asymptote was observed in agricultural and pasture landscapes (Fig. 5).

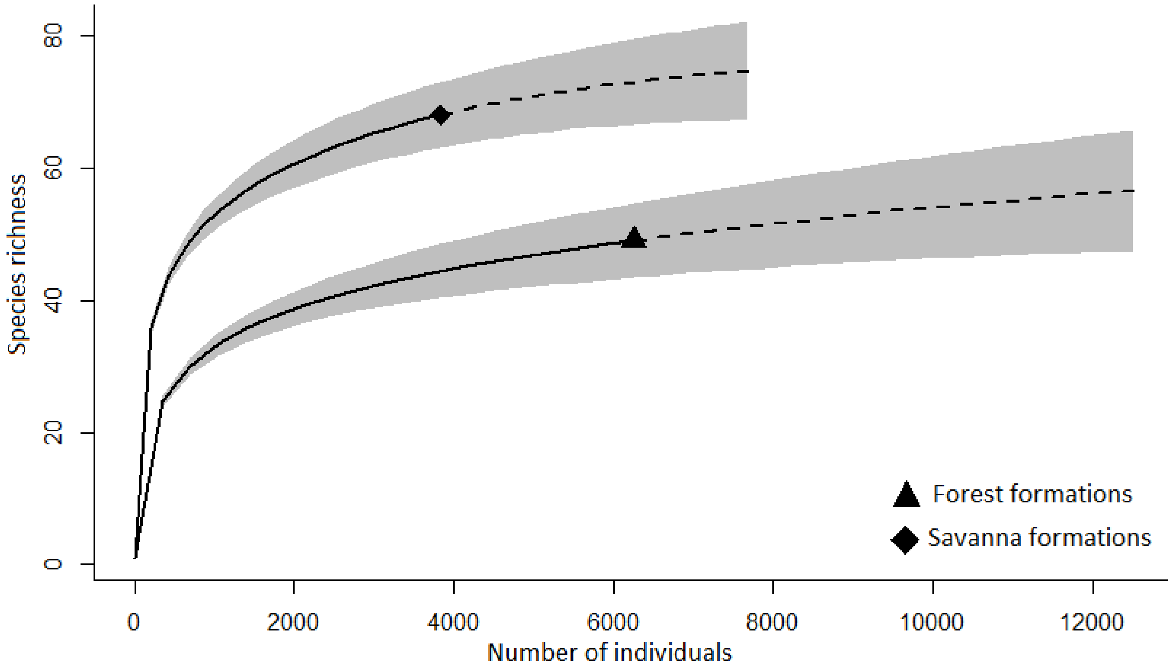

Fig 4 Species accumulation curve based on individuals involving the vegetation formations separately. The continuous line represents rarefaction, and the dashed line represents extrapolation.

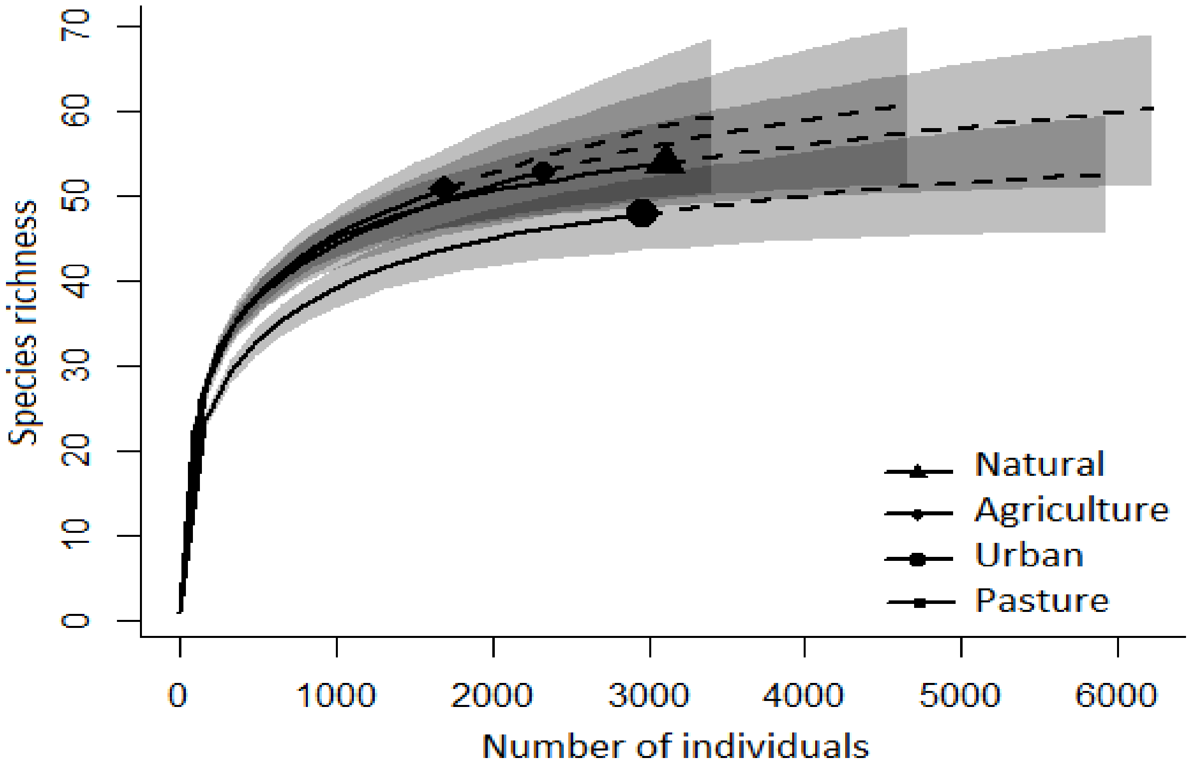

Fig 5 Species accumulation curve based on individuals involving the landscape classes separately. The continuous line represents rarefaction, and the dashed line represents extrapolation.

Based on the ACE richness estimator, the sampling effort was sufficient to sample 82.7993% of the total species present in the study area (Fig. 6). Regarding the vegetation formations, the sampling effort covered 87.5590% of the total species in the savannas and 83.2898% of the species in forests (Fig. 6). Finally, concerning the landscape classes, the current sampling effort was sufficient to sample 92.4150% of the species in urban landscapes, 91.6380% of the species in native landscapes, 84.2031% of the species in agricultural landscapes, and 81.1254% of the species in pasture landscapes (Fig. 6).

The total estimated richness in the savanna formations is higher than in the forest formations (Fig. 6). At the landscape level, the total estimated richness for pasture landscapes was the highest, followed by agricultural, native, and lastly urban landscapes, with the lowest total estimated richness (Fig. 6).

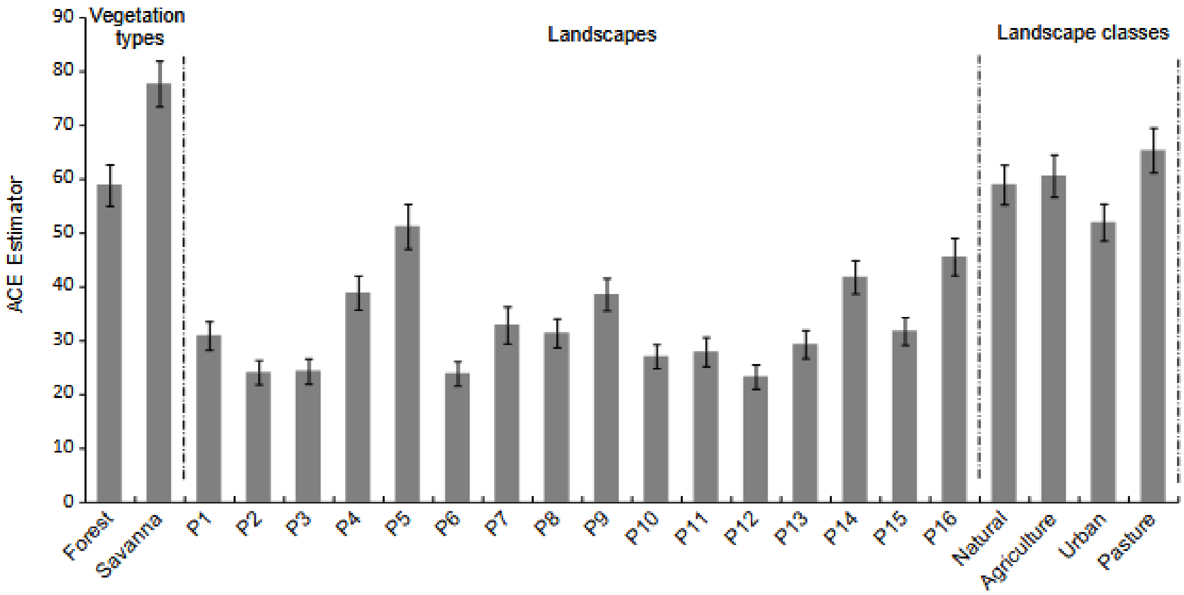

Fig 6 Total estimated richness based on the ACE (Abundance-Coverage Estimator) estimator for the entire community, between forest formations (forests and savannas), and between landscape classes (native, agricultural, urban, and pasture). P1 to P4: native landscapes; P5 to P8: agricultural landscapes; P9 to P12: urban landscapes; P13 to P16: pasture landscapes.

Additive Partitioning of Diversity

For the additive partition based on species richness, the higher the spatial level, the greater the contribution of beta diversity to total diversity (γ) (Fig. 7a). In other words, the highest observed beta diversity (β) was at the landscape class level (native, agricultural, urban, and pasture). The second highest beta diversity was at the landscape level, followed by the vegetation formations level.

For the additive partition based on Shannon diversity, the observed pattern was the opposite of that observed for the partition based on species richness (Fig. 7b). Thus, the higher the spatial level, the smaller the contribution of beta diversity (β) to total diversity (γ). In summary, the highest observed beta diversity (β) was at the vegetation formations level, followed by the landscape level, and finally, the landscape class level, where the lowest beta diversity (β) was found.

Regarding the α diversity component, in the additive partition based on Shannon diversity, it had the greatest contribution to total diversity (γ). Moreover, it was more than twice as large as the corresponding component in the partition based on species richness (Fig. 7a, 7b).

In the additive partitions based on null diversity models, some common patterns were also observed between the partitions based on species richness and Shannon diversity. For example, in both cases, the observed α component was significantly lower than expected by chance (Fig. 7a, 7b). Additionally, the observed β2 and β3 diversity components were significantly higher than expected by chance in both partitions (Fig. 7a, 7b). The exception to this pattern was the β1 component in the partition based on species richness, meaning it was the only observed β component that was lower than expected by chance (Fig. 7a).

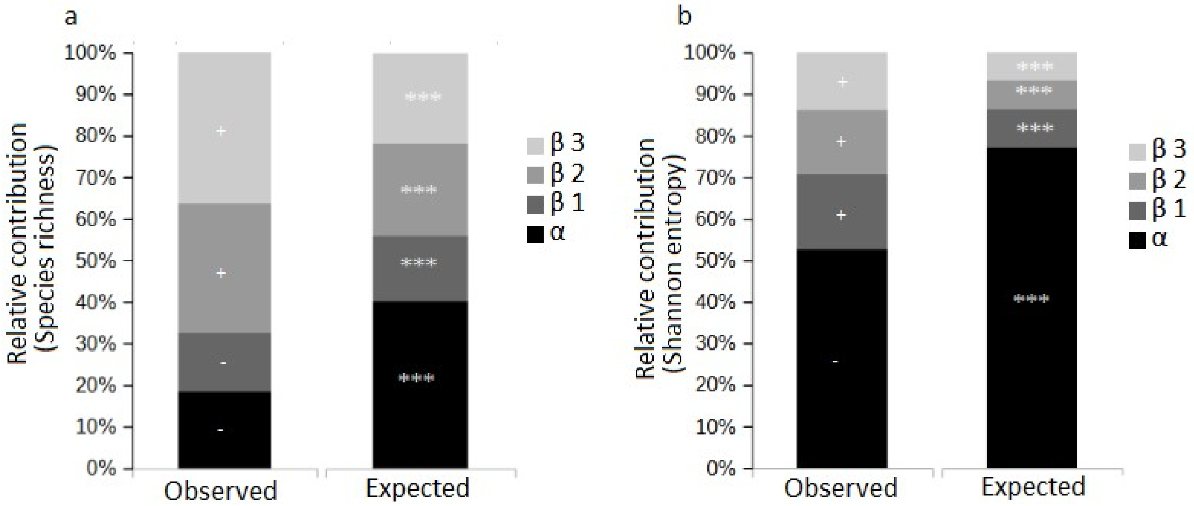

Fig 7 Additive partitioning based on observed and randomly expected species richness (a) and additive partitioning of observed and randomly expected Shannon diversity (b). The positive (+) and negative (-) signs indicate diversity values higher or lower than expected by chance, respectively. *** represents a p-value less than 0.0001, calculated using 10,000 randomizations.

DISCUSSION

Sampling sufficiency

The forest formation exhibited an abundance more than twice as high as that found in the savanna formation. However, this was due to the high dominance of *Dichotomius opacus* in forest formations. This pattern has also been observed in other studies in the Cerrado (e.g., Oliveira et al. 2022) and is linked to various factors, such as habitat structure and microclimate (Correa et al. 2019). Habitat structure, particularly vegetation complexity, is a key factor influencing dung beetle communities, even within open vegetation formations (Reis et al. 2023). The more structurally complex the habitat, the greater the niche heterogeneity and the variety of food resources (e.g., animal excrement, carcasses, and decomposing fruits), allowing for higher species abundances in these environments (Silva et al. 2024). Additionally, higher moisture levels in forest ecosystems enhance the reproductive success of dung beetle larvae compared to more open vegetation formations, as fecal desiccation is reduced in these environments (Durães et al. 2005). However, even in structurally complex ecosystems, anthropogenic factors related to soil conditions, for example, can become predominant, leading to a decline in dung beetle diversity (Silva and Hernández 2016, Silva et al. 2024). Thus, considering the intrinsic characteristics of forest formations, the high abundance of *D. opacus* in this formation may be attributed to factors such as soil moisture, which is one of the elements that extends the viability period of fecal resources in the soil, thereby facilitating reproductive processes (Dinghi 2013).

Native landscapes exhibited the highest abundance, which is attributed to the high dominance of *D. opacus* in one of the native landscapes, with 1570 individuals, accounting for 50.56% of the total abundance in this landscape class. On the other hand, the landscape class with the lowest abundance was agricultural landscapes. Even in this case, the most abundant species was also *D. opacus*, representing 22.31% of the total abundance in this landscape class. In other words, *D. opacus* was the most abundant species in all landscapes, except in pasture landscapes, where it was the second most abundant. This indicates that *D. opacus* is a species well adapted to these environments, at least within the study region. Like other species of the *Dichotomius* genus, it exhibits high dominance in anthropized Cerrado areas as well as in native areas. Moreover, it occurs in both forest and savanna ecosystems, employing mechanisms such as spatiotemporal segregation to mitigate intraspecific competition and sustain high abundances (Oliveira et al. 2022).

It is important to highlight that abundance patterns, at least for dung beetles, are variable and depend on local conditions and landscape configuration. For example, in the same study region but involving different landscapes, the highest dung beetle abundances were observed in anthropized areas (Oliveira et al. 2021), which contrasts with the results of the present study. This discrepancy can be explained by the presence of certain species that benefit from the available resources, which in these environments tend to be abundant and homogeneous over large areas (e.g., cattle dung in pastures and decomposing leaf litter in soybean monocultures). In this context, when species can take advantage of the available resources, they thrive simply due to the high resource availability and homogeneity across vast areas, reducing competition and increasing their abundances.

Regarding the total species richness estimates, the savanna formations exhibited higher richness compared to forest formations, corroborating other studies on dung beetles in the Cerrado (Silva et al. 2020, Oliveira et al. 2022). This is a common pattern in the Cerrado and can be attributed, for instance, to the high diversity of certain tribes that are more common in savanna formations, such as the Phanaeini and Ateuchini tribes (Cunha and Frizzas 2020, Oliveira et al. 2022). Additionally, this pattern may also be explained by the fact that savannas cover a much larger territorial extent within the Cerrado compared to forest formations (MapBiomas Project 2024), allowing for the co-occurrence of a greater number of species in these ecosystems.

At the landscape level, those composed predominantly of pastures exhibited the highest estimated total richness. This result is unexpected, as species richness tends to be higher in native landscapes compared to anthropogenic landscapes (Macedo et al. 2020, Maciel et al. 2023). However, this finding can be explained by several factors. First, the fact that estimated total richness was higher in pasture landscapes, combined with the fact that this landscape class had the second-lowest abundance, may indicate that species present in this matrix use it as a transitional area for dispersal rather than for colonization (Correa et al. 2019). Second, although the general rule states that Cerrado landscapes are a mosaic of native vegetation remnants immersed in anthropogenic ecosystems (Klink and Machado 2005), the study region itself presents high landscape heterogeneity, with nearly half of the area still in its native form (MapBiomas Project 2024). In addition, pastures have the highest availability of fecal resources among all landscape classes due to the presence of cattle. Third, species may have developed traits that allow them to adapt to the disturbances occurring in the Cerrado (Correa et al. 2019). In this context, these factors together may explain why the highest estimated total richness was found in pasture landscapes (Oliveira et al. 2021). Acting synergistically or independently, these three scenarios reinforce the importance of natural ecosystems embedded within agricultural landscapes, particularly regarding ecosystem services related to the degradation of fecal resources exposed on pasture soils (Nichols et al. 2008).

The asymptotic patterns of species accumulation curves begin to disappear as the spatial sampling scale is refined (Fig. 4, Fig. 5). This result is consistent with other studies conducted in the Neotropical region and is related to the number of individuals sampled at each spatial scale (Louzada et al. 2010).

Additive Partitioning of Diversity

1. Beta diversity in the partition based on species richness

In the partition based on species richness, the observed β-diversity components contribute more to γ-diversity as the spatial scale increases, with the landscape class level showing the highest contribution of β-diversity and the fragment level showing the lowest contribution.

At the landscape class level, the first explanation for this pattern is that dung beetles exhibit different levels of habitat specialization, with some species being exclusive to forest ecosystems (Silva et al. 2019, Oliveira et al. 2022) and others being characteristic of anthropogenic ecosystems (Silva et al. 2019, Oliveira et al. 2021). These factors may increase β-diversity at the landscape class level. Additionally, species dispersal may not be limited at smaller spatial scales and the opposite is true, reducing β-diversity at lower scales while increasing it at higher scales (Muller and Goßner 2010).

In addition, the life traits of species, especially diet (Macedo et al. 2020), are important local filters that, in the context of the present study, may be acting at the regional level. For example, in landscapes formed by pastures or plant biomass (agriculture), certain dung beetle groups are able to persist in these environments. That is, coprophagous species are relatively more adapted to pastures (where there is an abundance of cattle feces), while saprophagous species are more adapted to agricultural areas (where there is an abundance of dead biomass) (Oliveira et al. 2021). The importance of this, combined with the significance of native landscapes, where high diversity predominates due to environmental heterogeneity (Ribeiro and Walter 1998, Silva et al. 2019, Cunha and Frizzas 2020, Oliveira et al. 2022), may be one of the factors that increased β-diversity at the landscape class level.

Additionally, habitat use at the local scale and the surrounding landscape structure can synergistically affect diversity at higher spatial levels (Alvarado et al. 2017, Silva et al. 2019). For example, Carvalho et al. (2023) sampled dung beetle assemblages in five different land-use types (savanna, forest, eucalyptus, cattle pasture, and soybean) and recorded evidence that, depending on the matrix, species are able to colonize even anthropogenic ecosystems within the landscape (in a source-sink metapopulation model). More specifically, the amount of forest cover in the landscape made silvicultural areas favorable for dung beetle populations, showing that agricultural landscapes with some forest cover are beneficial to populations, compared to landscapes exclusively dominated by agriculture. This suggests that, if species are not tolerant to the matrices, they may become isolated within landscapes, without inter-landscape migration, increasing β-diversity through the species nesting mechanism, at the expense of species turnover (Baselga 2010). Considering that Cerrado landscapes are a mix of anthropogenic and native ecosystems and that the study area experiences anthropogenic pressures even in the adjacent native landscapes, this last explanation may be the most plausible for the observed increase in β-diversity in the partition based on species richness as the spatial scale increases.

At the landscape level, the contribution of β-diversity to γ-diversity may be a consequence of the effects of landscape configuration and composition on dung beetle diversity. The degree of fragmentation, the amount of forest cover, and land-use types are examples of landscape configuration and composition attributes that directly affect dung beetle diversity at the landscape scale (Silva et al. 2019, Arellano et al. 2024, Teixeira et al. 2024). More specifically, the increase in edge density, the loss of fragments, and the reduction of vegetation cover due to land-use conversion for anthropogenic activities are commonly the main drivers of population declines and species loss in dung beetles (Oliveira et al. 2021, Arellano 2024, Correa et al. 2024). On the other hand, nearly half of the study area still remains with native vegetation. However, this remaining vegetation is immersed in anthropogenic landscapes with different compositions and configurations, making the region highly heterogeneous from a landscape configuration and composition perspective. That is, there is a predominance of urban, agricultural, and native areas that interlace with each other in different configurations, making each landscape unique compared to the others (MapBiomas Project 2024). As a consequence, and considering that dung beetle species may exhibit morphological and behavioral traits that reflect adaptations to specific environments

(Oliveira et al. 2022) and that species have different dispersal abilities (Silva and Hernández 2015), it is common to observe an increase in β-diversity at this level, whether due to turnover effects or species nesting/loss.

At the level of native vegetation remnants, the contribution of β-diversity to γ-diversity at the level of vegetation types may have occurred due to the structural differences between savanna and forest formations, which result in the differentiation of dung beetle assemblages through the species turnover mechanism. In the present study, the two types of vegetation remnants sampled were savanna and forest, particularly gallery forests. These two vegetation types are mainly distinguished by the denser vegetation cover in forests, making these phytophysiognomies more humid and with milder temperatures compared to savanna formations (Ribeiro and Walter 1998). Consequently, several studies have shown that forest formations have a species composition distinct from that of open formations (e.g., Silva et al. 2019, Oliveira et al. 2022, Silva et al. 2024). This distinction in species composition is caused by characteristics related to vegetation structure, which determine the occurrence of certain species (Cunha and Frizzas 2020). For example, the moisture content in forest formations allows fecal resources, an organic material sensitive to desiccation, to remain viable for a longer time (Oliveira et al. 2022). Furthermore, gallery forests have the highest availability of fecal resources, as they host the greatest diversity of mammals in the Cerrado, and are considered a faunal corridor between the Amazon and the Atlantic Forest (Johnson et al. 1999). Despite this, food and nesting resources remain scarce not only in open formations but also in forest formations. The turnover of species occurs between vegetation types due to the spatial segregation of assemblages, a phenomenon where closely related species are spatially segregated to reduce competition for fecal resources (Oliveira et al. 2022). Thus, in savanna formations, it is expected that species adapted to the use of ephemeral and relatively more desiccated fecal resources will be more frequent, while in forest formations, species specialized in utilizing resources with higher humidity levels and lower desiccation rates are expected to occur.

2. βeta diversity in the partition based on Shannon diversity

In contrast to the previous explanation, the components of β-diversity in the partition based on Shannon diversity showed the opposite behavior, meaning that the contribution of the β-components to γ-diversity decreases as the spatial level increases. Since Shannon diversity is a metric that considers the weight of species abundance in its calculation, in the present study, this pattern may be related to the dominance caused by certain species at specific spatial levels. For example, at the level of native vegetation remnants, *D. opacus* exhibited an abundance variation ranging from 1 individual to 1570 individuals in forest formations, while this variation was smaller in savanna formations, ranging from 1 to 24 individuals. Other examples include *D. lycas* (where only one forest landscape recorded this species, with 16 individuals, whereas in savanna formations its abundance ranged from 1 to 97 individuals) and *Oxysternon palemo* (with high abundance in savanna formations and only 10 individuals in forest formations). Considering that the partition of γ-diversity into α and β components involves the nesting of lower hierarchical level assemblages into higher hierarchical level assemblages, the β-diversity resulting from this disparity in abundances at the lower hierarchical levels ends up being diluted when these levels are nested into higher hierarchical levels. In this context, it is expected that when considering the weight of species abundance, there would be higher β-diversity at the scales where the largest variations in abundance occur, that is, at the lower hierarchical levels.

3. Alpha diversity

Alpha diversity in the partition based on species richness was almost three times lower compared to alpha diversity in the partition based on Shannon diversity, which can be explained by species dominance and rarity patterns, as well as by the intrinsic characteristics of species richness metrics and Shannon diversity (Crist et al. 2003, Cunha and Frizzas 2020). In the partition based on species richness, the diversity components are calculated based on species occurrence data, where abundance values are converted into binary values indicating presence or absence. In this context, rare species, which are distributed in isolated locations, reduce alpha diversity values and increase beta diversity values. On the other hand, in the case of abundant species, when their abundance values are converted into presence and absence, this group increases alpha diversity compared to beta diversity, as most locations will have occurrences of abundant species. Therefore, when the weight of species abundance is considered in the partition of diversity, as it is in the partition based on Shannon diversity, alpha diversity values tend to surpass beta diversity values.

4. Null distribution of alpha and beta diversity components

The alpha diversity components from both partitions and β1 from the partition based on species richness were lower than expected by chance. The other components were higher than expected by chance.

The first case suggests that local ecological processes limit abundance and species turnover at those levels. Predation, competition, dispersal, micro-disturbances (such as fire and anthropization), and vegetation structure are examples of local ecological processes that can act as limits to the homogeneous distribution of abundances and may also restrict species turnover (Ricklefs 1987). In the case of dung beetles, for example, vegetation structure, microclimate, and competition for resources are local ecological processes that commonly distinguish the assemblages occurring between forest and savanna formations, which would lead beta diversity to be higher than expected by chance at this spatial level (Silva et al. 2019, Oliveira et al. 2022). However, in the present context, this did not occur, meaning that beta diversity was lower than expected by chance, probably due to anthropization adjacent to vegetation fragments, which attenuated the functioning of ecological filters intrinsic to these vegetation types, responsible for species turnover. On the other hand, the fact that the β1 component of the partition based on Shannon diversity was higher than expected by chance could be attributed to species that, despite being dominant, were primarily recorded in only one of the vegetation formations, such as *D. opacus* in forest formations and *O. palemo* in savanna formations.

In the second case, there is evidence that emergent ecological processes, dispersal limitations, and dominance patterns are factors that make the beta diversity components larger than expected by chance. For the partition based on species richness, dispersal limitations and emergent ecological processes at the landscape level, such as biogeographic isolation, could be the main factors contributing to the increase in beta diversity. The study area consists of landscapes where vegetation remnants are isolated by large matrices dedicated to agriculture, livestock, and urbanization (MapBiomas Project 2024), which may be limiting the dispersal of dung beetles, increasing beta diversity through species nesting. Furthermore, since dung beetles are intrinsically dependent on the diversity of mammals (as they use their fecal resources for feeding and nesting), and considering that mammal diversity depends on a larger habitat extent in the landscape (Bogoni et al. 2016), the anthropogenic nature of Cerrado landscapes may be acting as a mechanism that concentrates mammal diversity, and consequently dung beetle diversity, in certain areas with larger vegetation remnants. In the case of the partition based on Shannon diversity, the higher-than-expected beta diversity across spatial levels is associated with the aggregation of abundances at specific hierarchical levels, as seen with *D. opacus* in forest formations and *O. palermo* in savanna formations.

CONCLUSION

The hypotheses were partially supported. For the partition based on species richness, beta diversity was higher as the spatial level increased, i.e., it was lower at the scale of the vegetation formations and higher at the scale of the landscape classes. The opposite occurred for the partition based on Shannon diversity. This result is a consequence of several associated factors, such as the species' dispersal capacity, the degree of specialization, and the equitability of abundances across the samples. Moreover, the study region harbors a high heterogeneity of ecosystems that co-occur in space, which is one of the most plausible explanations for the observed patterns. In this sense, it is essential to consider spatial heterogeneity at the landscape level when conducting studies or surveys related to the diversity of organisms that have certain limitations in dispersal and diet, aiming to identify the true behaviors of diversity in response to land-use changes, especially in ecosystems as threatened as the Brazilian Cerrado.

Conflict of interest: The authors declare no conflict of interest.

Data availability: Data supporting the results and conclusions of this study are available upon request from the corresponding author.

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CONSIDERAÇÕES FINAIS

O Cerrado, reconhecido como a savana mais diversa do mundo, tem enfrentado um aumento acelerado nas atividades agropecuárias, além da fragmentação de seus habitats. Neste cenário, é fundamental entender de que forma a diversidade biológica é impactada pela estrutura das paisagens e por diferentes escalas espaciais, o que se torna uma necessidade nos estudos biológicos desse bioma. Dessa forma, esta tese foi desenvolvida em dois capítulos com a intenção de abordar essa questão, tendo como foco os besouros rola-bostas.

O primeiro capítulo abordou como a diversidade de rola-bostas é afetada pelos componentes estruturais das paisagens. Mais especificamente, foram analisados os efeitos da composição e da configuração das paisagens na diversidade de rola-bostas. Os resultados mais relevantes sugerem que a composição das paisagens é o conjunto de métricas que desempenha o papel mais primordial na estruturação da diversidade de rola-bostas, quando comparado às métricas de configuração. Contudo, nas formações savânicas, a diversidade de rola-bostas foi favorecida pela presença de ecossistemas antrópicos na paisagem, particularmente pastagens, e prejudicada pela presença de ecossistemas nativos. No entanto, essa interpretação deve ser feita com cautela, principalmente quando se trata de decisões relacionadas à conservação da biodiversidade no bioma. Uma possível explicação para esse resultado é a dominância ou homogeneização biótica provocada por espécies generalistas, capazes de se adaptar às matrizes antrópicas e deslocar espécies especialistas e sensíveis nas formações savânicas. Em contrapartida, em paisagens com predominância de cobertura florestal nativa, as comunidades se mostraram mais ricas e diversas, destacando o papel da vegetação remanescente como abrigo para espécies sensíveis. Em suma, esses resultados sugerem que a quantidade de cobertura florestal remanescente deve ser preservada, uma vez que é o fator mais crucial para a manutenção da diversidade. Ademais, é necessário investigar em pesquisas futuras se a predominância de espécies generalistas nos ecossistemas savânicos, que reagiram de forma positiva ao aumento das coberturas antrópicas, apresenta redundância ou complementariedade funcional. Isso é importante para proteger os serviços ecossistêmicos fornecidos pelos rola-bostas.

No segundo capítulo, a utilização da partição aditiva da diversidade demonstrou que as diversas métricas de diversidade reagem de forma oposta aos níveis espaciais das paisagens. Por exemplo, a diversidade beta fundamentada na riqueza de espécies foi mais elevada em escalas espaciais superiores, especialmente no nível das classes de paisagens. Em contrapartida, a diversidade beta baseada na diversidade de Shannon revelou-se mais relevante em escalas mais locais, particularmente no nível das formações florestais. Isso indica que diversos elementos da diversidade são afetados por diferentes processos ecológicos: a riqueza responde de forma mais intensa a filtros regionais e barreiras geográficas, enquanto a diversidade de Shannon é controlada principalmente por condições locais, como microclima, estrutura da vegetação e disponibilidade de recursos. Ademais, o capítulo 2 mostra que a organização da diversidade não pode ser compreendida a partir de uma única escala de análise. A presença simultânea de espécies especialistas e generalistas em biomas como o Cerrado destaca a importância de abordagens multiníveis nos estudos ecológicos nessa região. Portanto, em regiões altamente fragmentadas, como o Cerrado, os estudos ecológicos necessitam dessa abordagem multinível para determinar a contribuição de cada escala espacial para a preservação da diversidade.

Esses resultados destacam a necessidade de implementar políticas públicas que considerem as matrizes antrópicas na estruturação das paisagens, com o objetivo de promover e/ou melhorar a restauração ecológica, a criação de corredores ecológicos e o manejo sustentável do uso do solo. Finalmente, os resultados sugerem que os efeitos espaciais na diversidade são multiníveis e contextuais. Para evitar o aumento da perda de biodiversidade no Cerrado, é preciso adotar abordagens integradoras que combinem conhecimento técnico, políticas públicas e manejo de paisagens.