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Universidade Estadual de Santa Cruz

JOSÉ CLEMENSOU DOS REIS JÚNIOR

Estudos ecológicos sobre as assembleias de rola-bosta (Coleoptera: Scarabaeinae) em áreas de pastoreio e de preservação da Caatinga da região do Raso da Catarina

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Tese apresentada ao programa de Pós-graduação em Ecologia e Conservação da Biodiversidade da Universidade estadual de Santa Cruz, para obtenção do título de Doutor em Ecologia e Conservação.

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Co-orientador: Dr. Federico Escobar Sarria

ILHÉUS - BAHIA
2025

FICHA CATALOGRÁFICA

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AGRADECIMENTOS

Meus sinceros agradecimentos à universidade Estadual de Santa Cruz (UESC) em especial a PROPP pelo apoio financeiro. À Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) – pela concessão da minha bolsa de doutorado. A fundação Rufford pelo apoio financeiro ao projeto (36296-1), em especial Jane Raymond, pelo apoio. Ao programa de pós-graduação em Ecologia e Conservação da Biodiversidade, ao corpo docente, coordenadores e à equipe, em especial a Amábile e a Mayra, por toda atenção, disponibilidade e ajuda ao longo do curso. Ao laboratório MirmecoLab, Centro de Pesquisas do Cacau - CEPEC/CEPLAC pelo local de trabalho e pelas experiencias em grupo.

Ao professor doutor Jacques Delabie: agradeço pela incrível orientação ao longo desses anos, pelo incentivo, conselhos, pela paciência durante minha caminhada, linda amizade, e por ter me acolhido com tanto carinho, como um maravilhoso pai adotivo-acadêmico! Sempre disponível para resolver, discutir ou apenas escutar meus problemas acadêmicos e pessoais. Meu mais sincero muito obrigado! Estendo meus agradecimentos à sua linda família, Cléa e Laura!

Ao meu segundo papai acadêmico, professor doutor Federico Escobar: agradeço a incrível orientação, incentivo, amizade, e por ter primeiramente acreditado em mim para que eu pudesse pleitear uma vaga nesse doutorado, quando eu já me encontrava descrente dessa vida acadêmica. Obrigado também pelo apoio durante meu sanduiche no INECOL (Xalapa, México) e por ter me acolhido com tanto cuidado e carinho junto a sua família. Meu mais sincero muito obrigado! Estendo minha gratidão à sua querida esposa, Martha, e à sua filha, Isabel!

A minha querida amiga e mãezona do coração, Lourdinha, que me acolheu com tanto amor e carinho, fazendo dos meus dias no CEPEC menos difíceis. Meu imenso agradecimento e abraço!

Ao amigo "Formigão", grande Dr. Elmo Kock, pela amizade, incentivo, colaborações e estadias em seu apartamento, onde tantas vezes serviu como ponto de apoio em minhas viagens Caatinga <> Mata atlântica. Muito obrigado pela parceria e amizade!

Ao meu grande e querido amigo Fabiano, que sempre me recebeu de portas abertas em sua casa me abrigando sempre que precisei utilizar como entreposto entre a Mata atlântica e a Caatinga. Obrigado pelo imenso carinho e atenção de sempre (já somam bons anos desde a graduação)! Estendo meus agradecimentos ao seu querido Pai e meu amigo, o grande Juracy! Muito obrigado por sempre me receberem com tamanha alegria!

Aos amigos, Matheus e Eric que me acolheram com tanto carinho em minha primeira estadia em Cuiabá! Lhes agradeço de coração!

Ao Dr. Fernando Z. Vaz-de-Mello por ter me recebido de portas abertas em seu laboratório e em sua belíssima coleção entomológica. Por me dar acesso a toda sua biblioteca, bichos, pelos ensinamentos sobre os escaravelhos, parcerias e amizade. Estendo meus agradecimentos ao pessoal de seu Laboratório de Scarabaeoidea da UFMT, em especial a Duda Maldaner, Paulo Duarte, Bruna Bordin, Thamara, Victor, Edrielly e todos do lab., muito obrigado por me acolherem, pelos momentos de aprendizado, café e descontração!

Ao querido amigo colombiano, Jorge Arias-Buritica que me recebeu com tanto carinho em Cuiabá numa 2ª estadia na coleção da UFMT, pelos ensinamentos passados sobre taxonomia de *Dichotomius* spp. e pelas cervejas também!

Aos amigos, companheiros e colegas que fiz durante minha estadia no INECOL, México, meu muito obrigado! Em especial a Sofi, Marilú, Grillo, Sara, Larissa, Roger, Victória, Daniel, Fernanda, Alex, Kevin, David, Ricardo, Lucrecia, Viridiana e tantos outros que neste momento temo estar esquecendo. Muito obrigado pela recepção, momentos de descontração e acolhida!

Aos meus queridos pais Sônia e Clemensou pai (Aka Betor) por todo apoio ao longo da minha vida, por terem sido os pais maravilhoso que são, desde pequeno me apoiando e incentivando-me sempre, obrigado por serem essa fortaleza na minha vida!

A minha irmã Mª Betina e minha linda sobrinha Laura , amo vocês!

Aos meus queridos tios, tia Ninha, tio Branco e também meus primos, João Victor e Kaylaine Reis por sempre terem me recebido com tanto carinho em minhas idas à São Paulo, para resolver questões de pesquisas ou não.

Aos meus queridos amigos, Dani (minha prima) e Dilmo, por sempre terem me acolhido com todo carinho e atenção em minhas idas a Salvador.

Ao querido primo e amigo “Bodinho” Lomanto por sempre ter me apoiado e acreditado em minha carreira científico-acadêmica.

Ao meu compadre, primo e irmão, Netinho (Aka. Krukenoide), bem como minha comadre e minha afilhada, por terem sempre me acolhido e apoiado quando precisei.

A minha família, tios, tias e anexos que sempre estiveram de prontidão com uma palavra de apoio, mensagem. Em especial aos meus avós maternos – Dona Lourdes e meu saudoso avô “Seu Zé de Santo”, que faleceu antes que eu pudesse terminar minha tese e poder me perguntar “pra que serve isso agora?” hahaha.... aos meus saudosos avós paternos – Neca de Tibúrcio e Dona Laide que sempre foram apoiadores de meu crescimento e certamente estariam festejando comigo.

Agradeço a minha companheira, parceira de vida, apoiadora, meu amor, Nadir Yohana por todo amor e cuidado, paciência e compreensão durante não só este período de tese, mas toda essa caminhada acadêmica. Te amo!

Alfim, agradeço a todos e todas que de alguma forma me ajudaram direta ou indiretamente no desenvolvimento desta tese e que de alguma maneira meu cérebro falhou em lhes dar o devido crédito/agradecimento nominalmente, sintam-se, portanto, agradecidos!

SUMÁRIO

RESUMO

A pressão humana sobre as florestas tropicais tem transformado esses ambientes naturais em habitats modificados, resultando, quase sempre, no declínio da biodiversidade e na perda de serviços ecossistêmicos. Esta tese investigou os efeitos da pecuária sobre a biodiversidade de besouros coprófagos (Scarabaeinae) em diferentes escalas, combinando uma meta-análise continental com estudos de campo no bioma Caatinga, semiárido do Brasil. Os resultados mostram que a conversão de ecossistemas naturais em pastagens reduz de forma consistente a riqueza, abundância e diversidade funcional desses insetos, com maior severidade em florestas primárias e pastagens abertas. Fragmentos florestais de Caatinga ainda funcionam como refúgios de diversidade, mas as assembleias de organismos em pastagens são fortemente influenciadas pelo contexto da paisagem, mais do que por práticas locais de manejo. O uso de ivermectina e a dominância da espécie exótica de origem africana *Digitonthophagus gazella* podem contribuir para uma homogeneização biótica e uma erosão funcional, sobretudo devido à perda de paracoprídeos de tamanho grande, ameaçando a resiliência dos ecossistemas. Por outro lado, sistemas silvipastoris, árvores remanescentes e mosaicos de vegetação nativa podem mitigar parte dos impactos negativos da pecuária. Conclui-se que, embora essencial socioeconomicamente, a pecuária no semiárido impõe desafios ecológicos significativos, sendo necessária a implementação de estratégias sustentáveis de manejo para garantir a conservação da biodiversidade e a manutenção dos serviços ecossistêmicos na Caatinga.

Palavras-chave: Caatinga; Scarabaeinae; biodiversidade; pecuária; serviços ecossistêmicos; ecologia de paisagem.

ABSTRACT

Human pressure on tropical forests has transformed these natural environments into modified habitats, resulting in biodiversity decline and the loss of ecosystem services worldwide. This doctoral thesis investigated the effects of livestock farming on dung beetle (Scarabaeinae) diversity at different scales, combining a continental meta-analysis with field studies in the Caatinga biome, Brazil's semiarid region. Results indicate that the conversion of natural ecosystems into pastures consistently reduces species richness, abundance, and functional diversity, with the most severe impacts occurring in primary forests and open pastures. Caatinga forest fragments still act as important biodiversity refuges, but dung beetle assemblages in pastures are shaped primarily by landscape context rather than by local management practices. Ivermectin use and the dominance of the exotic African species *Digitonthophagus gazella* intensify biotic homogenization and functional erosion, particularly through the loss of large-bodied paracoprid beetles, thus compromising ecosystem resilience. Conversely, silvopastoral systems, remnant trees, and vegetation mosaics at landscape scale can mitigate part of the negative impacts of livestock. In conclusion, although livestock farming is socioeconomically vital in this region, it poses significant ecological challenges in semiarid regions, requiring the adoption of sustainable management strategies to reconcile biodiversity conservation with the maintenance of ecosystem services in the Caatinga.

Keywords: Caatinga; Scarabaeinae; biodiversity; livestock; ecosystem services; landscape ecology.

INTRODUÇÃO GERAL

Por que investigar os efeitos da pecuária sobre a biodiversidade?

O crescimento desenfreado da humanidade tem levado a modificação dos ambientes naturais de forma acelerada dada crescente necessidade de recursos naturais, por exemplo, alimentação (UN DESA, 2022; Jaureguiberry et al., 2022). Essas transformações têm gerado pressões antrópicas nos ambientes naturais, o que tem levado ao declínio de espécies e de seus serviços ecossistêmicos (Jaureguiberry et al., 2022). Essas transformações de uso da terra são consideradas uma das principais ameaças à biodiversidade e ao funcionamento das redes tróficas (Laurance et al., 2014; Zabel et al. 2019; Raven & Wagner, 2021; Jaureguiberry et al., 2022). Na Região Neotropical, a expansão da pecuária é um dos principais motivos de alteração e perda de áreas de vegetação nativa, em particular, florestas (Wassenaar et al., 2007; Caballero et al., 2023). Desta forma, a conversão em pastos desencadeia diversos efeitos sobre a biodiversidade (Fahrig, 2013; Haddad et al., 2015), dentre eles, a composição da matriz numa paisagem pode atuar como filtro que afeta o fluxo de espécies entre fragmentos. Essa matriz pode ser relativamente homogênea e dicotômica (Floresta-Pasto), ou heterogênea (Floresta-Pasto-Cultivos-Urbano), incluindo um mosaico de diferentes tipos de florestas (e.g., primária e secundária) e pastos (e.g. abertos e silvipastoril). Portanto, a pecuária pode afetar a biodiversidade em pelo menos duas escalas: ao nível da paisagem e ao nível local.

Os efeitos da pecuária a nível de paisagem

Em paisagens altamente modificadas pelo homem, a mudança do uso do solo, o estabelecimento de pastagens para pecuária se traduz pela perda direta de cobertura florestal, fragmentação e isolamento de fragmentos, resultando frequentemente em matrizes dissonantes e pouco favoráveis à manutenção da biodiversidade (Estrada-Carmona et al., 2020). Tais mudanças podem promover (i) uma maior heterogeneidade da biota (β diversity) – onde cada fragmento da paisagem abriga uma assembleia distinta do fragmento vizinho (Arroyo-Rodríguez et al., 2013; Dambros et al., 2024); ou (ii) uma homogeneização biótica, quando as extinções locais reduzem o conjunto regional de espécies, tornando as assembleias mais redundantes e semelhantes entre si (Lôbo et al., 2011; Siqueira et al., 2015; Arce-Peña et al., 2022). Entretanto, outros processos ecológicos podem atuar em paralelo ou sinergicamente, ajudando a (re)moldar as assembleias e provocando cenários de homogeneização ou heterogeneização da biota (McKinney & Lockwood, 1999; Tscharntke et al., 2012; Socolar et al., 2016).

Entretanto, nem todas as matrizes ou habitats antropogênicos que compõem uma paisagem modificada pelo homem para agropecuária têm impactos apenas negativos sobre a biodiversidade. Em alguns casos, a ocorrência de árvores remanescentes ou a adoção de sistemas silvipastoris, bem como a manutenção de matas de galerias e cercas vivas, na escala de paisagem, pode favorecer a manutenção da biodiversidade e de seus serviços ecossistêmicos (León & Harvey, 2006; Arellano et al., 2008, 2013, 2015; Francesconi et al., 2011; Ríos-Díaz et al., 2021).

Os efeitos da pecuária a nível local

Ao nível local, os efeitos da pecuária estão associados principalmente às práticas de manejo adotadas pelos produtores. Entre elas, destacam-se: a intensidade e a duração do pastoreio, a renovação das pastagens por meios mecanizados, queima, o uso de insumos agrícolas (por exemplo, fertilizantes, herbicidas, pesticidas) e o emprego de antiparasitários, tais como a ivermectina, para o controle de parasitas em bovinos. Tais práticas podem eliminar a capacidade de regeneração da vegetação nativa (gerando grandes porções de pastos abertos e dominados por gramíneas africanas), modificar as propriedades do solo (promovendo alta compactação ou solos desnudos, o que os torna propensos a processos de desertificação), e favorecer a propagação de espécies exóticas (Holmgren, 2002; Root et al., 2020). Além disso, o uso de produtos químicos pode gerar consequências ainda mais severas direta ou indiretamente nos organismos que vivem/utilizam as pastagens; por exemplo, os resíduos de ivermectinas metabolizados e secretados no esterco bovino apresentam efeitos negativos bem documentados sobre insetos coprófagos (Lumaret et al., 2012).

O pastoreio intenso a longo prazo pode favorecer espécies exóticas de besouros coprófagos com o passar do tempo (Morales-Trejo et al., 2024). O pastoreio mal planejado afeta drasticamente a biodiversidade, diminuindo riqueza e abundância das espécies e seus efeitos podem prevalecer por anos, mesmo após a exclusão do gado (Filazzola et al., 2020). Há também de se notar que o pastoreio, quando sob alta densidade de rebanhos e tempo prolongado, é fonte direta da compactação do solo nas pastagens, podendo superar a compactação provocada pelo maquinário agrícola (Bilotta et al., 2007). Entretanto, os efeitos do pastoreio não são universalmente negativos. Em ambientes secos (como as florestas secas tropicais sazonais ou

Seasonally Dry Tropical Forest, SDTFs em inglês), o pastoreio pode promover maior diversidade de besouros coprófagos, resultando até numa riqueza de espécies maior em áreas de pastagem do que em áreas de vegetação nativa, dependendo do bioma e das condições ambientais, como ocorre em áreas áridas do México (Verdú et al., 2007; Barragán et al., 2014). Esse contraste evidencia a dependência do contexto nos efeitos da pecuária, que variam conforme clima, tipo de vegetação e atributos funcionais das espécies. Não obstante, destaca-se a importância em investigar os mecanismos por trás da prevalência e da hiper abundância desses insetos em contextos de paisagem, em regiões de florestas secas tropicais sazonais.

O que sabemos sobre os besouros rola-bosta em pastagens?

O número acumulado de espécies de escaravelhos coprófagos numa determinada região e seus respectivos pastos, pode variar dependendo de fatores topológicos, processos em escala de paisagem, aspectos do manejo local, fatores biogeográficos e climáticos, entre outros (Halffter & Matthews, 1966; Escobar et al., 2005; Daniel et al., 2022; González-Gómez et al., 2023). No Brasil, cerca de 20 gêneros e 76 espécies de Scarabaeinae podem utilizar as pastagens com espécies pequenas >5 mm e grandes >20 mm (Tissiani et al., 2017). De modo geral, espera-se uma perda na diversidade quando se transforma ambientes naturais em pastos exóticos para pecuária (Nichols et al., 2007; ver Capítulo I). Entretanto, em alguns casos, há maior riqueza e abundância de besouros encontrados nos pastos do que nos seus respectivos habitats naturais (Verdú et al., 2007; Barragán et al., 2014). No entanto, uma hiper abundância de poucas espécies de besouros de corpo pequeno é esperado (Nichols et al., 2007; Basto-Estrella et al., 2012; Rivera et al., 2021), além do favorecimento de espécies exóticas (Morales-Trejo et al., 2024). O efeito das transformações dos ambientes naturais em pastagens e o pastoreio sobre as assembleias de rola-bosta tem sido estudado ao redor do mundo (Davis et al., 2012; Barragán et al., 2014; Buse et al., 2015; Kenyon et al., 2016; Frank et al., 2017; González-Gómez et al., 2023), com ênfase na Região Neotropical (Arellano et al., 2023), talvez por abrigar o maior rebanho de gado do mundo (FAO, 2023). As respostas das assembleias desses insetos variam, podendo ser positivas, como observado na Europa (Buse et al., 2015) ou, como em algumas regiões da Américas (Verdú et al., 2007; Barragán et al., 2014), negativas, com efeitos deletérios sobre a diversidade e seus serviços ecossistêmicos (Bourg et al., 2016; Cajaiba et al., 2017; Silva et al., 2017b; Alvarado et al., 2019; Guerra-Alonso et al., 2020).

Um dos mais impactantes efeitos de amplo espectro é o uso de insumos químicos em práticas de manejo local de uma pastagem, sobretudo os do grupo das Ivermectinas (Strong, 1992;

Lumaret et al., 2012; Jacobs & Scholtz, 2015). As ivermectinas possuem numerosos efeitos negativos sobre diversos organismos terrestres associados ao solo e às fezes, incluindo isópodes, nematódeos, minhocas e besouros coprófagos (Lumaret et al., 2012; Jacobs & Scholtz, 2015; Jochmann & Blanckenhorn, 2016; Junco et al., 2021). Nos rola-bosta coprófagos (Scarabaeinae), tais impactos já foram documentados em detalhe, abrangendo desde alterações das condições fisiológicas que comprometem sua capacidade funcional (Verdú et al. 2015), até efeitos reprodutivos (González-Tokman et al., 2017; Martínez et al., 2017). As ivermectinas podem ainda ser bioacumuladas (Verdú et al., 2020), levando à redução de abundância e até o declínio de espécies (Verdú et al., 2018), com impactos nos grupos funcionais (paracoprídeos e telecoprídeos) e biomassa de espécies grandes (Tonelli et al., 2020), o que pode gerar efeitos diretos nas taxas de serviços ecossistêmicos providos pelos rola-bosta.

Por outro lado, problemas com pragas e a baixa taxa de ciclagem do esterco em pastagens levaram à adoção de programas de introdução de espécies de besouros coprófagos em diferentes países (Pokhrel et al., 2021). O caso mais emblemático ocorreu na Austrália, onde, na década de 1960, a falência do sistema de produção pecuária motivou a criação de órgãos governamentais e programas de pesquisa para selecionar e introduzir espécies capazes de lidar com o esterco bovino (Edwards, 2009). Isso porque a fauna local de rola-bosta havia evoluído associada às fezes de marsupiais, sendo pouco eficiente no processamento do esterco de gado (Edwards, 2009), influenciando a introdução de espécies em outros países, como Brasil (Nascimento et al., 1990). *Digitonthophagus gazella* (Fabricius, 1787) é um exemplo emblemático de espécie amplamente distribuída em escala global devido a introduções destinadas a incrementar serviços ecossistêmicos providos por rola-bosta na pecuária. De origem africana, caracteriza-se por hábitos generalistas, ciclo reprodutivo rápido e elevada plasticidade ambiental (Noriega et al., 2017, 2020). Entretanto, diferentemente dos casos da Austrália e Nova Zelândia, o Brasil ou outros países da Região Neotropical provavelmente não necessitavam da introdução, pois há muitas espécies nativas que habitam os pastos e são capazes de utilizar o esterco bovino como alimento (Tissiani et al., 2017; Maldaner et al., 2024). As introduções de rola-bostas exóticos em pastagens podem afetar a diversidade, composição e a integridade dos serviços ecossistêmicos providos pelos escarabeídeos (Filho et al., 2018; Garcia et al., 2022; Queiroz et al., 2023; ver Capítulo IV).

Nichols e colaboradores (2007) sintetizaram parte do conhecimento sobre as respostas dos besouros rola-bosta às ações antrópicas, incluindo a conversão de ambientes naturais em pastagens; no entanto, os mecanismos subjacentes a essas respostas em uma escala mais fina não foram explorados (ver Capítulo I). Mas por que a mudança do uso da terra, de ambientes naturais para pastagens, implica em efeitos negativos sobre a fauna, pelo menos nas Américas? Essa questão é aprofundada no Capítulo I. Esclarecendo brevemente essa indagação, a conversão para pastagens implica numa alteração direta na complexidade do habitat, devido à redução dos níveis de complexidade da estrutura vertical da vegetação. Como consequência, aspectos microclimáticos são diretamente modificados, há uma acentuada perda de dimensões de nicho e, sobretudo, ocorre uma drástica redução na diversidade de mamíferos.

Devido à sua história evolutiva, os escaravelhos coprófagos (Scarabaeinae) neotropicais são, em sua maioria, caracterizados por serem estenotópicos – isto é, apresentam alta afinidade com ambientes sombreados e ombrófilos, possuindo, portanto, baixa tolerância a ambientes alterados e a mudanças microclimáticas (Halffter & Matthews, 1966). Além disso, esses insetos apresentam forte afinidade e coevolução com os mamíferos (Halffter & Matthews, 1966; Raine & Slade, 2019), sendo altamente dependentes de sua presença como fonte primária de alimento e reprodução. Assim, reduções na fauna de mamíferos podem levar a processos de coextinção local em populações de besouros coprófagos (Nichols et al., 2009; Raine et al., 2018; Bogoni et al., 2019).

Por que utilizar os besouros rola-bosta como grupo-alvo?

Os escaravelhos coprófagos das subfamílias Scarabaeinae e Aphodiinae são taxonomicamente diversos, sendo compostos por ~ 7.000 e 3.600 espécies, respectivamente (Schoolmeesters, 2025). No Brasil, o "Catálogo Taxonômico da Fauna Brasileira" (CTFB) reconhece 801 espécies válidas e 59 subespécies, em 71 gêneros, sendo 222 táxons endêmicos (Vaz-de-Mello & Bordin, 2025). São notáveis a diversidade biológica e a adaptação a diversos nichos dessas subfamílias, porquanto, é possível encontrar estes insetos em praticamente todos os habitats terrestres, ou mesmo como inquilinos em ninhos de cupins ou formigas (Vaz-de-Mello et al., 1998; Philips 2016; Gillett & Toussaint 2020), agarrados nos pelos de mamíferos, tais como o bicho preguiça (Arrow, 1933). Apesar de serem primariamente coprófagos, alguns podem exibir hábitos necrófagos ou saprófagos (Halffter & Matthews, 1966; Halffter & Edmonds 1982; Marinoni et al., 2001); por sua vez, outros apresentam hábitos frugívoros (Halffter & Halffter, 2009). O grupo biológico é especialmente importante por desempenhar variadas funções e serviços ecossistêmicos (Nichols et al., 2008; deCastro-Arrazola et al., 2023; Figura 1). Desta forma, esses insetos são conhecidos como provedores de serviços ecossistêmicos relacionados ao “Suporte”, “Cultural”, “Provisão” e “Regulação” de acordo com o Millennium Ecosystem Assessment (2005).

Os besouros rola-bosta, especialmente os coprófagos das subfamílias Scarabaeinae e Aphodiinae, desempenham um papel fundamental nos ecossistemas, sendo mediadores-chave da decomposição de matéria orgânica, aerificação ou bioturbação do solo, controle de parasitas, e redutor de emissões de metano em sistemas naturais e agropecuários (Nichols et al., 2008; Slade et al., 2016). Suas populações e comportamentos são fortemente influenciados pela complexidade ambiental (Halffter & Matthews, 1966; Reis et al., 2023), gradientes de elevação (Lobo & Halffter, 2000; Escobar et al., 2005, 2006, 2007), pela disponibilidade de recursos das diferentes fitofisionomias de um dado bioma (Halffter & Matthews, 1966), diversidade de mamíferos (Bogoni et al., 2019), características da paisagem (Rös et al., 2012; Sánchez-de-Jesús et al., 2016; Alvarado et al., 2018; González-Gómez et al., 2023), usos da terra (Escobar, 2004; Barragán et al., 2011; Reis et al., 2023), e no manejo local de determinado uso do solo (González-Gómez et al., 2023; ver Capítulo III). Isso evidencia a importância de diversificar os estudos sobre esses organismos, considerando sua relevância funcional em ambientes naturais e de uso agropecuário.

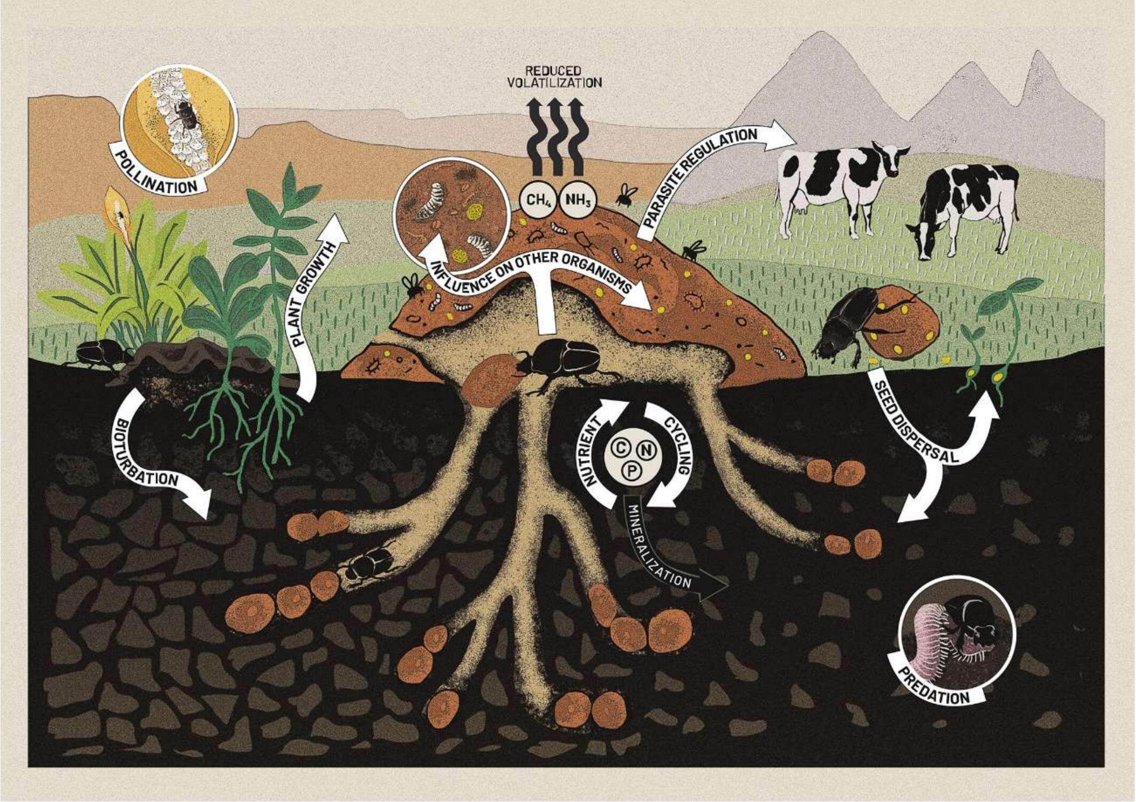


Figura 1. Serviços ou funções ecossistêmicas performadas pelos escaravelhos. Fonte: deCastro-Arrazola et al., 2023.

Caatinga: Um Bioma Singular e Desafiador

A Caatinga, ou mata (*ka'a*) branca (*tinga*), na língua indígena Tupi (Navarro, 2013), é o único bioma exclusivamente brasileiro, cobrindo aproximadamente 10% do território nacional, e se destaca por sua vegetação adaptada às condições extremas de semiárido, com baixa pluviosidade e temperaturas elevadas (Ab'Sáber, 1974; Bernardes, 1999; Silva et al., 2017a). Devido à sua proximidade com o Equador geográfico, as médias térmicas anuais na região variam entre 26 e 28 °C (Nimer, 1972). Aproximadamente 50 % da área da Caatinga recebe menos de 750 mm de precipitação anual, com algumas regiões apresentando índices inferiores a 500 mm, sendo raramente ultrapassados 1.000 mm anuais (Prado, 2003). Em relação aos meses secos, as chuvas se distribuem normalmente num período de seis e nove meses, embora existam exceções que vão de um mínimo de dois a três meses em brejos úmidos até extremos de 10 a 11 meses ao longo do ano (Nimer, 1972). Apesar das condições climáticas desafiadoras, como a irregularidade das chuvas e a ocorrência de períodos de secas severas (Ab'Sáber, 1974; Prado, 2003), a Caatinga é reconhecida como a região semiárida mais povoada do mundo e ao mesmo tempo mais biodiversa (Ab'Sáber, 1999; Silva et al., 2017a).

Apesar desses elementos climáticos que parecem ser desfavoráveis, a Caatinga abriga uma rica diversidade biológica, incluindo numerosas espécies endêmicas de flora e fauna que desempenham papéis ecológicos essenciais (Leal et al., 2005). No entanto, o bioma ainda carece de estudos científicos (Santos et al., 2011; Silva et al., 2017; Lessa et al., 2019) especialmente no que diz respeito à entomofauna (Santos et al., 2011), um grupo fundamental para a manutenção dos processos ecológicos, tais como polinização, decomposição, ciclagem dos nutrientes e controle biológico das pragas da agropecuária regional (Ramos et al., 2020).

A flora da Caatinga apresenta uma impressionante capacidade de adaptação às condições extremas do semiárido (Sampaio, 1995; Prado, 2003). Muitas espécies possuem mecanismos específicos de resistência à seca, como raízes profundas que alcançam o lençol freático (e.g., *Sarcomphalus joazeiro* (Mart.) Hauenschild; que se mantem verde ao longo do ano), folhas pequenas (microfilia) ou transformadas em espinhos para reduzir a evapotranspiração, tecidos suculentos que armazenam água em troncos, caules e raízes; ou raízes que mantêm reservas energéticas (e.g., *Spondias tuberosa* Arruda; “Batata de umbuzeiro”) (Sampaio, 1995; Prado, 2003; Andrade et al., 2017; Queiroz et al., 2017). A vegetação da Caatinga também pode ser marcada pela abundância de cactáceas, como *Cereus jamacaru* DC. (mandacaru) e *Xiquexique gounellei* (F.A.C.Weber ex K.Schum.) Lavor & Calvente (xique-xique), e bromélias, como *Encholirium spectabile* Mart. ex Schult. & Schult.f. (Macambira) e *Hohenbergia catingae* Ule. Essa complexa rede de adaptações fisiológicas e morfológicas não só permitem a sobrevivência das plantas, mas também sustenta uma vasta gama de organismos, incluindo insetos, aves e mamíferos, que dependem direta ou indiretamente dessas plantas para sua alimentação, abrigo e reprodução (Leal et al., 2005; Jorge et al., 2024).

Fitofisionomias e Ecorregiões da Caatinga: Diversidade e Interações Ecológicas

A Caatinga apresenta uma notável diversidade de fitofisionomias, que variam desde florestas secas e cerradões até campos abertos e áreas de vegetação arbustiva, que podem ser densas ou esparsas. Essas formações vegetais alternam entre a predominância de cactáceas e a dominação de leguminosas e euforbiáceas, sendo moldadas por fatores ambientais tais como clima, solo e topografia (Velloso et al., 2002; Prado, 2003). Do ponto de vista de estrutura e arranjo vegetal, quatro grandes grupos de Caatingas podem ser definidos, segundo o IBGE. As categorias são: (1) Savana-estépica florestada; (2) Savana-estépica arborizada; (3) Savana-estépica parque; e (4) Savana-estépica gramíneo-lenhosa (**Figura 2**) (IBGE, 2012). Prado (2003), por sua vez, propõe sete grandes unidades de vegetação e tipos de comunidades da Caatinga em um nível mais detalhado, com treze fitofisionomias relacionadas ao tipo de espécies vegetais predominante e tipo de solo (para mais detalhes, ver Tabela 1 em Prado, 2003).

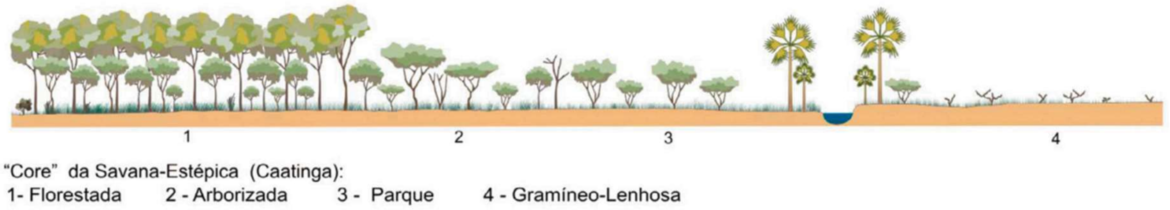


Figura 2. Perfis esquemáticos da Savana-Estépica (Caatinga). Fonte: IGBE (2012) adaptado de Veloso et al. (1991).

Quanto à estrutura vertical, a vegetação pode apresentar quatro estratos vegetais típicos diferentes : (i) arbóreo-alto (>12 metros; variando entre 15-20 metros), caracterizado por florestas altas e secas (Prado, 2003); (ii) arbóreo (8-12 metros), representado principalmente pela fitofisionomia 'Florestada'; (iii) arbustivo (2-5 metros), evidenciado pelas fitofisionomias 'Arborizada' e 'Parque'; e (iv) herbáceo (abaixo de 2 metros), representado pela formação 'Gramíneo-Lenhosa' (adaptado de Alves et al., 2009). Alguns representantes comuns de estrato arbóreo são: "Pau-pereiro" (*Aspidosperma pyrifolium* Mart.) com 9,5m de altura máxima, 'Catingueira' *Cenostigma pyramidale* (Tul.) Gagnon & G.P.Lewis com exemplares de 7 metros (Amorim et al., 2005). Não obstante, é possível encontrar árvores de porte ainda maiores na Caatinga, que facilmente superam os 10 metros, como "Braúna" (*Schinopsis brasiliensis* Engl.) e "Orelha-de-nego" (*Enterolobium contortisiliquum* (Vell.) Morong), entre outras (Observação pessoal; Prado, 2003).

A Caatinga e os besouros

Apesar de representarem a maior diversidade de organismos do planeta, correspondendo a 72% das formas de vida conhecidas (Chapman, 2009) e constituírem a maior parte da biomassa do reino Animalia, especificamente no filo Arthropoda (Bar-On et al., 2018), os insetos (entomofauna) estão entre os grupos de animais proporcionalmente menos estudados no mundo (Klink et al., 2024). Na Caatinga, essa lacuna de conhecimento é ainda mais evidente, com estudos limitados a algumas regiões, principalmente aquelas próximas a centros de pesquisa e universidades (Brandão et al., 2000; Santos et al., 2011; Lessa et al., 2019).

Dentre os invertebrados menos estudados desse bioma estão os coleópteros (Hexapoda, Coleoptera) (Brandão et al., 2000; Brandão & Yamamoto, 2004), um dos grupos mais diversos do Planeta (Chapman, 2009). A falta de conhecimento sobre formas, variações intraespecíficas e a necessidade de descrição de novas espécies torna o levantamento e o estudo abrangente desse grupo um grande desafio. Isso é especialmente relevante, considerando que os coleópteros representam 74% das espécies de invertebrados conhecidas no mundo (Chapman, 2009). Essa diversidade extraordinária, aliada à lacuna de informações, evidencia a necessidade de mais esforços para compreender e catalogar a entomofauna da Caatinga, um bioma rico e ainda incipientemente explorado.

Dentre os poucos estudos realizados sobre coleópteros na Caatinga, a maioria concentrou-se em grupos ou famílias específicas de interesse agronômicos, econômico ou cultural, tais como os besouros das famílias Scarabaeidae (Salomão et al., 2017; da Silva-Queiroz et al., 2023), Cerambycidae (Bezerra-Gusmão et al., 2022; Salomão et al., 2024), Buprestidae (Iannuzzi et al., 2006), ou Chrysomelidae (Salomão et al., 2024). No entanto, há diversas exceções quando uma variedade maior de grupos de insetos foi estudada num único estudo (por exemplo, Iannuzzi et al., 2003; Rafael et al., 2017; Guedes et al., 2019). Esses estudos utilizaram frequentemente armadilhas do tipo *pitfall* (iscadas ou não); ou de Malaise (Iannuzzi et al., 2021). A diversificação dos métodos de coleta num único estudo pode auxiliar a detectar espécies abundantes ou comuns, bem como espécies mais raras e vagantes (Iannuzzi et al., 2021).

A Caatinga e os escaravelhos

Apesar da indiscutível importância dos escaravelhos coprófagos na pecuária, pouco se sabe sobre o atual cenário das espécies presentes nos pastos da Caatinga, ou quaisquer fatores ecológicos que moldem suas assembleias, embora importantes estudos tenham tentado elucidar parte dessa problemática, como Tissiani et al. (2017) e mais recentemente Maldaner et al. (2024). Entretanto, Tissiani et al. (2017) apresentam uma lista de ocorrências ao nível do estado da Bahia para as espécies de Scarabaeinae, assim como uma chave dicotômica confiável para identificação das espécies. Porém, em razão da escassez de estudos basais para alimentar as bases de dados, essas informações tornam-se limitadas, apesar de contemplarem espécies que têm ampla distribuição no Nordeste. Por outro lado, Maldaner e colaboradores (2024) apresentaram dados para as espécies de Scarabaeinae que ocorrem em pastos da América do Sul. Neste estudo, os autores trazem um robusto banco de dados com ocorrências de diversas espécies nativas de Scarabaeinae, o qual foi constituído a partir de inventários e coleções entomológicas em pastagens. Apesar de incluir boa parte dos estados no Brasil, esses dados não são tão representativos para a Caatinga. Isso evidencia a lacuna de conhecimento sobre esta região e reforça a fragilidade do conhecimento em termos de levantamentos de Scarabaeinae (ver **Figura 3**).

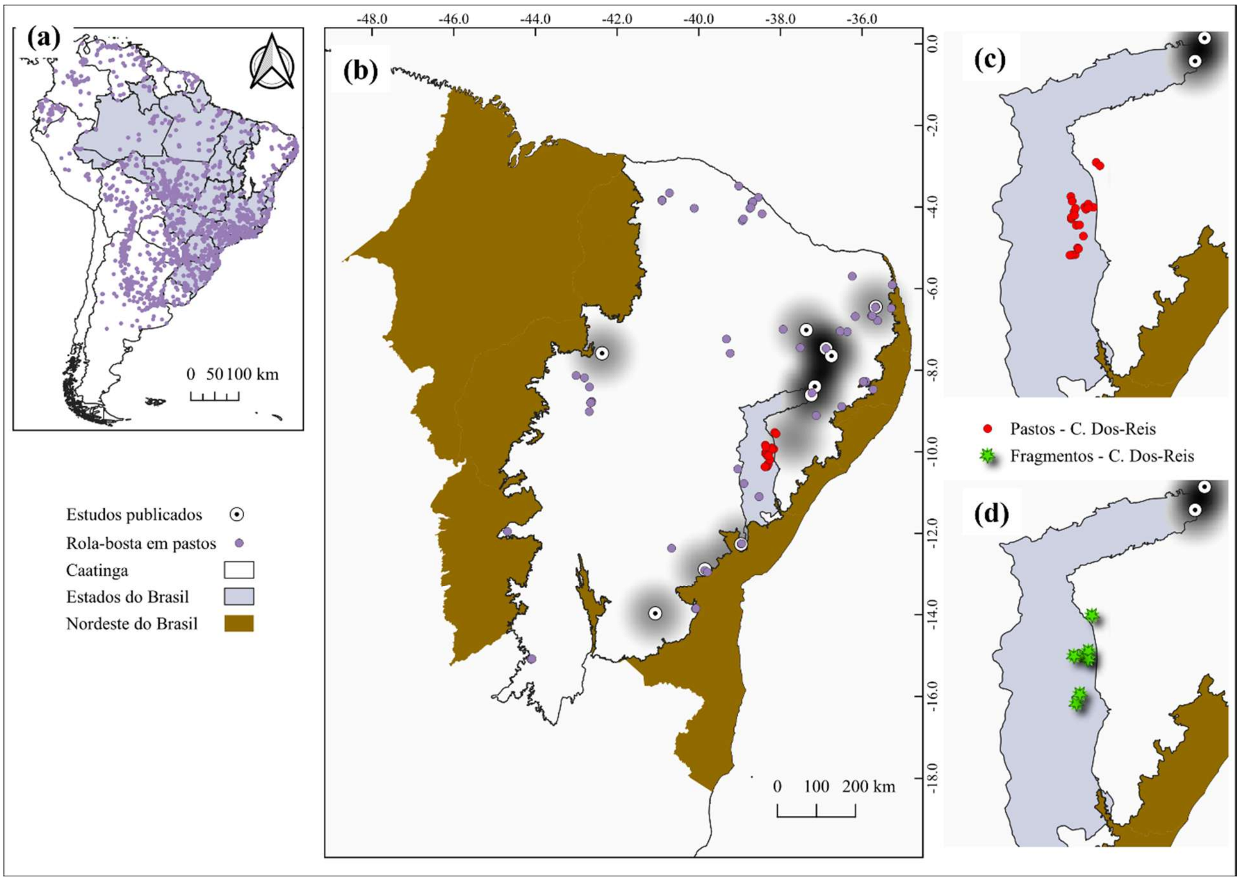
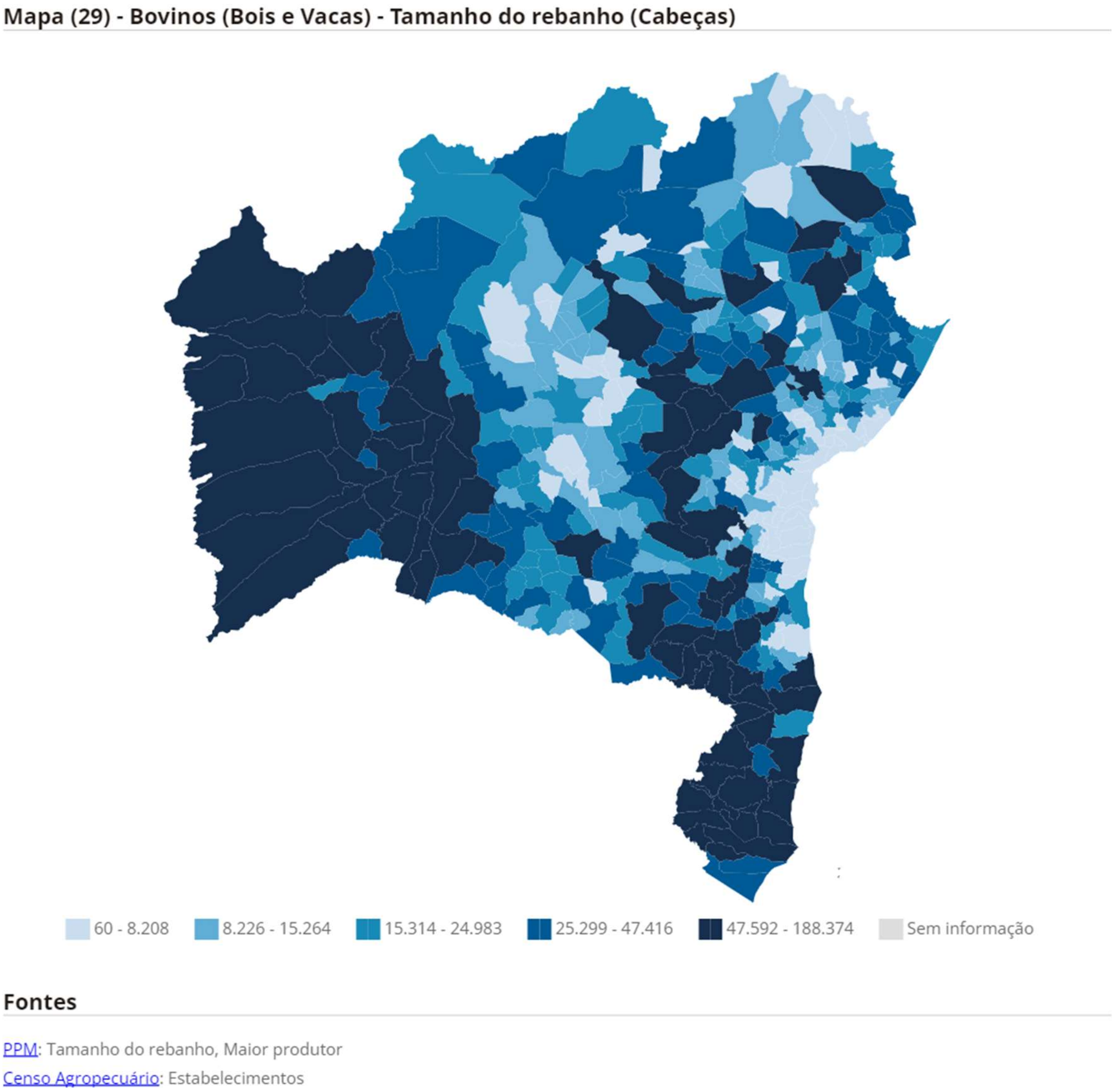


Figura 3. Registro de besouros rola-bosta (Scarabaeinae) em pastos da América do Sul (a) (dados de ocorrência extraídos de Maldaner et al., 2024). É importante frisar que os registros apresentados não são unicamente oriundos de inventários locais de Scarabaeidae; mas podem ser dados aproveitados de séries de coletas. (b) Ênfase na Caatinga, registros de pastos e inventários conduzidos na região. (c-d) locais de coleta dessa tese. Mancha de calor em escala de preto mostra a concentração dos trabalhos. Elaboração: C. Dos–Reis.

Panorama da pecuária na Bahia

A pecuária é uma das atividades econômicas mais antigas no Brasil Colônia, oriunda do tempo das capitanias hereditárias (Prado Junior, 1994). Atualmente, o Brasil possui um rebanho bovino de 238.626.442 cabeças (IBGE, 2023). Dentre os estados com o maior número de cabeças de gado, o rebanho bovino da Bahia ocupa a sétima colocação no país, com um total de 13.290.719 cabeças (IBGE, 2023). Praticamente todos os municípios da Bahia abrigam alguma atividade agropecuária (**Figura 4**). Contudo, essa atividade é distribuída irregularmente no estado. Na Região Nordeste, a pecuária remonta a meados do século XVII (Prado Junior, 1994).

Assim, a pecuária representa um componente central da economia e da paisagem da Caatinga. Compreender como essa atividade molda a diversidade de besouros coprófagos e afeta os serviços ecossistêmicos que eles fornecem é fundamental para conciliar produção pecuária e conservação da biodiversidade no semiárido brasileiro.



Mapa (29) - Bovinos (Bois e Vacas) - Tamanho do rebanho (Cabeças)

Fontes

PPM: Tamanho do rebanho, Maior produtor

Censo Agropecuário: Estabelecimentos

Figura 4. Importância do rebanho bovino (número de cabeças) por município no estado da Bahia, segundo IBGE (2023).

Objetivo geral

O objetivo geral desta tese é investigar como as pressões relacionadas à pecuária, em diferentes escalas: tanto em nível de paisagem quanto no manejo local, dos pastos e seus rebanhos afetam a diversidade e funções ecológicas dos besouros coprófagos (rola-bosta) na Caatinga, com ênfase em sua contribuição para os serviços ecossistêmicos em sistemas naturais e pastagens. Minha hipótese central é que as características da paisagem e as práticas locais de manejo afetam a diversidade, composição, estrutura e grupos funcionais desses besouros, afetando, em consequência, os serviços ecossistêmicos por eles prestados nos pastos. A conservação de árvores nativas e de outros elementos naturais, bem como a manutenção de cobertura florestal e de fragmentos, deve favorecer as assembleias de besouros mais diversas. O presente estudo procura integrar abordagens taxonômicas, ecológicas e aplicadas, visando promover o manejo pecuário sustentável e a conservação da biodiversidade no bioma Caatinga. Esta tese de doutorado está alinhada ao Objetivo de Desenvolvimento Sustentável 15 da Agenda 2030 das Nações Unidas (ONU, 2025).

Organização da tese

No **capítulo I**, sintetizo, por meio de uma meta-análise, os efeitos da conversão de ecossistemas naturais em pastagens sobre as assembleias de besouros coprófagos nas Américas, identificando quais componentes dessas assembleias são mais impactados e como eles variam conforme diferentes contextos biogeográficos, zonas climáticas, estrutura vegetal, gradiente latitudinal. Por fim, discuto o porquê as espécies não são capazes de persistir e proponho alternativas de conservação para garantia de diversidade nos pastos. No **capítulo II**, descrevo a diversidade de besouros coprófagos em fragmentos de Caatinga na região do Raso da Catarina, que são expostos ao pastoreio bovino, documentando a composição das espécies, grupos funcionais e como as espécies nativas utilizam o esterco bovino nesse habitat. No **capítulo III**, avalio o efeito de métricas de paisagem e práticas de manejo local sobre as assembleias de besouros coprófagos na ecorregião do Raso da Catarina, identificando se os fatores em escala de paisagem ou de manejo local são mais importantes para a estruturação das comunidades. Por fim, no **capítulo IV**, investigo o efeito da espécie africana *Digitonthophagus gazella*, que foi introduzida com finalidades de manejo e controle de parasitas nas fezes bovina e que se tornou invasora, sobre assembleias nativas e grupos funcionais, discutindo as implicações ecológicas de sua dominância para os serviços ecossistêmicos prestados por espécies nativas paracoprídeas e a relevância disso na pecuária da região. Alfim, apresento as lacunas científicas não resolvidas por esta tese, bem como principais achados e conclusões gerais.

THESIS ORGANIZATION

Chapter I

- **Dung beetles in a changing world: a comparative meta-analysis of effects on assemblages due to transformation from natural ecosystems to pasturelands in the Americas**

Chapter II

- **Dung beetle (Coleoptera: Scarabaeinae) assemblages' composition and structure of Caatinga of the Raso da Catarina ecoregion**

Chapter III

- **Landscape context is a better predictor of dung beetle diversity than local management in pastures of semi-arid Brazil**

Chapter IV

- **Dominance of the exotic African dung beetle *Digitonthophagus gazella* (Fabricius, 1787) in pastures suppresses native dung beetles from the threatened Caatinga biome**

Conclusões finais

- Principais resultados, lacunas preenchidas e remanescentes, sugestões de novas pesquisas e conclusões gerais.

CAPÍTULO I

DUNG BEETLES IN A CHANGING WORLD: A COMPARATIVE META-ANALYSIS OF EFFECTS ON ASSEMBLAGES DUE TO TRANSFORMATION FROM NATURAL ECOSYSTEMS TO PASTURELANDS IN THE AMERICAS

Dung beetles in a changing world: a comparative meta-analysis of effects on assemblages due to transformation from natural ecosystems to pasturelands in the Americas

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Abstract

The continuing conversion of natural ecosystems into pastures and croplands by human activity represents a significant threat to global biodiversity since agricultural land now constitutes approximately half of the habitable land on Earth. Consequently, it is imperative to conduct a thorough evaluation of the repercussions of agricultural land expansion. Dung beetles serve as a reliable bioindicator of biodiversity and for assessing a wide range of ecological services that are essential for supporting livestock production in many agricultural landscapes. In this study, we present the first comprehensive assessment of the impacts of livestock production on dung beetle assemblages across the Americas based on a meta–analysis. The analysis examines variation across biogeographical and climatic regions, latitude and elevation and develops an index of relative structural change to dung beetle assemblages and their functional groups according to the former natural vegetation and the type of replacement pastureland. We found a pervasive adverse impact on American dung beetle assemblages resulting from the conversion of natural ecosystems into exotic pastures, thereby potentially jeopardizing the ecosystem services they provide and threatening the stability and resilience of the ecosystem as a whole. Both dung beetle species richness and number of individuals reveal a consistent negative response to native ecosystem conversion. Although no effects were detected for biomass, dung beetle functional groups did respond negatively to habitat conversion into pastures, particularly paracoprids and large-bodied species. Magnitudes of dung beetle response differed between pasturelands suggesting that they are dependent on the magnitude of habitat change and land use intensity. More complex woody natural habitats tended to experience more severe significant effects on dung beetle assemblages after conversion into open pastures. However, limited changes in habitat complexity between natural woody habitats and silvopastoral livestock pastures resulted in non-significant differences between dung beetle assemblages. Thus, the adoption of silvopastoral systems over open pastures is recommended as an effective strategy for the conservation of biodiversity at both local and landscape scales.

Keywords: Anthropocene, Biodiversity, Land–use change, Scarabaeidae, Functional groups, Body size, Meta–analysis.

Introduction

Human pressure on natural resources is recognized as a major threat to global biodiversity and ecosystem functioning (Laurance et al. 2014; Zabel et al. 2019; Raven & Wagner, 2021). This pressure is expected to intensify as the human population is projected to reach 11 billion by 2100 (UN DESA, 2022), thus accelerating the transformation of natural ecosystems into human–modified landscapes to meet food production demands. Livestock expansion is a central component of this process: the conversion of native vegetation to pasture accounts for approximately 50% of global deforestation (Ritchie & Roser, 2019; FAO, 2022) and as much as 80% in the Neotropical region (Wassenaar et al., 2007).

Reconciling agricultural and pastoral production with biodiversity conservation is therefore essential for maintaining ecosystem services (Kehoe et al., 2017; Williams et al., 2020) and for balancing human well-being and economic activities with the stability and resilience of ecosystems (Wallace, 2007; Brussaard et al., 2010; Slade et al., 2014; Coutts & Hahn, 2015; Olander et al., 2018). It has been proposed that the impact of human activities on ecosystems can be reliably assessed using taxa capable of indicating land–use effects on both biodiversity and ecosystem functioning (Holt & Miller, 2011). Among the diverse and increasingly threatened insect groups, dung beetles have proven especially valuable for detecting land-use impacts, particularly those associated with livestock expansion and pasture management (Nichols & Gardner, 2011; Nunes et al., 2018; Carvalho et al., 2020; Reis et al., 2023). This is because dung beetles respond sensitively to variation in landscape heterogeneity, soil type, vegetation structure, and the spatial and temporal availability of dung resources (Halffter & Matthews, 1966; Lumaret et al., 1992; Ratoni et al., 2023; Reis et al., 2023). Dung beetles have a long evolutionary history associated with the dung of terrestrial vertebrates, especially mammals (Halffter & Matthews, 1966; Halffter & Edmonds, 1982; Culot et al., 2013; Bogoni et al., 2019; Raine & Slade, 2019). The three main subfamilies— Scarabaeinae (~7000 spp.), Aphodiinae (~3600 spp.), and Geotrupinae (~150 spp.)—display extensive taxonomic and functional diversity (Schoolmeesters, 2025), largely linked to food and nesting behaviors (e.g. kleptocoprids, endocoprids, paracoprids, and telecoprids) as well as variation in body size (from 0.5 to 50 mm). These functional differences influence the spatial and temporal segregation of species, their differing ecological roles, and their contributions to ecosystem functioning (Halffter & Edmonds, 1982; Hanski & Cambefort, 1991; Milotić et al., 2017; Tonelli, 2021). Through dung removal, dung beetles provide a range of key ecosystem services, including nutrient redistribution, soil aeration and water infiltration, enhanced plant–growth, secondary seed dispersal, fly control, parasite suppression, and reductions in greenhouse-gas emissions (Nichols et al., 2008; Ridsdill–Smith & Edwards, 2011; Doube, 2018 deCastro–Arrazola et al., 2023). These ecological services are highly relevant for pasture health and are of considerable economic importance to the livestock industry (Nichols et al., 2008; Nervo et al., 2014; Slade et al., 2016; deCastro–Arrazola et al., 2023).

We are interested in this study in understanding how dung beetle assemblages are affected by the conversion of native forest into pasturelands in tropical America. Assessing dung beetle responses to such habitat simplification requires consideration of the biogeographic origins of the dung beetle species currently found in open biomes. Unlike the Palaearctic, Neotropical open biomes harbor fewer dung beetle species but support distinctive, species–rich forest assemblages (Gill, 1991; Arellano et al., 2023), including many species with non-coprophagous diets such as necrophagy and saprophagy (Halffter & Matthews, 1966). Several historical processes may explain this contrast between these two biogeographic regions (Davis et al., 2002): (i) the extinction of large herbivores during Cenozoic climatic fluctuations (Dantas & Pausas, 2022; Buffan et al., 2025), (ii) the Great American Biotic Interchange following South America's prolonged geological isolation (Carrillo et al., 2020), and (iii) the historically limited extent of open biomes in the region (Bakker et al., 2016). Additionally, the introduction of cattle into the Americas in the sixteenth century (Fuzessy et al., 2021) has likely contributed to the relatively low richness of dung beetle assemblages in Neotropical pastures and to the increasing presence of alien species (Lobo, 2000). The global expansion of cattle farming has created a growing need for effective dung–removal strategies, including programmes that introduce exotic dung beetle species into regions lacking efficient native fauna (Fincher et al., 1983; Ridsdill–Smith & Edwards, 2011; Noriega et al., 2017; Doube, 2018; Noriega et al., 2020; deCastro–Arrazola et al., 2023; Vieira et al., 2024). Species of Afrotropical origin, such as *Digitonthophagus gazella* (Fabricius, 1787), have been deliberately introduced into several American countries (Nascimento et al., 1990; Noriega et al., 2017), raising concerns about the ecological risks associated with the dual pressures of pasture expansion and non-native species introductions.

Over the past few decades, numerous studies have addressed key aspects of dung beetle responses to forest loss and fragmentation (Nichols et al., 2007), trait–mediated responses to forest conversion (Nichols et al., 2013), and the effects of diverse anthropogenic drivers (Fuzessy et al., 2021). However, most of these studies do not explicitly consider pastures. More recent work has focused on the impacts of primary forest degradation (López–Bedoya et al., 2022), the efficiency of dung removal under experimental conditions (Noriega et al., 2023), taxonomic and functional diversity in Neotropical grazing systems (Arellano et al., 2023), the contribution of dung beetles to plant growth (Anderson et al., 2024), and their distribution across South American pasturelands (Maldaner et al., 2024). Although these studies have advanced our understanding, a critical knowledge gap remains regarding how dung beetles respond specifically to the conversion of native forests into pasturelands (but see Correa et al., 2025), and how these responses vary across biomes, regions, and functional groups. Livestock production in the Americas currently represents 35% of the global cattle population (FAO, 2025; Figure S2). In this context, a comprehensive meta–analysis is urgently needed to evaluate the consequences of pasture expansion for dung beetle assemblages. Here, we provide the first such synthesis for the Neotropical region. We analyze published data comparing dung beetle assemblages in native or less disturbed ecosystems (controls) and pasturelands (treatments), focusing on species richness, abundance, biomass, and functional composition. Specifically, we assess whether dung beetle responses vary according to native habitat type, pasture system (treeless vs shaded or silvopastoral), geographic position (north or south), or climate conditions (tropical/subtropical and Köppen–Geiger classifications). Given the long evolutionary association of Neotropical dung beetles with forested ecosystems (Gill, 1991), we predict consistent negative impacts of forest-to-pasture conversion on both taxonomic and functional diversity. Our general aim is therefore to corroborate that the transformation of natural forest biomes into pasturelands (i.e., vegetation structure simplification and changes in plant composition) has negative effects on American dung beetle assemblages. To this end, we assessed the impacts of ecosystem conversion on the taxonomic and functional diversity of dung beetles by examining: (i) whether different functional groups respond similarly to such environmental changes, (ii) whether stronger declines occur when primary forest are converted, (iii) whether treeless pastures produce more severe declines than shaded or silvopastoral systems, (iv) whether geographic position (latitude) and climate zone influence dung beetle responses, and (v) whether greater contrasts in vegetation structure between native ecosystems and pasturelands lead to more pronounced impacts on dung beetle assemblages.

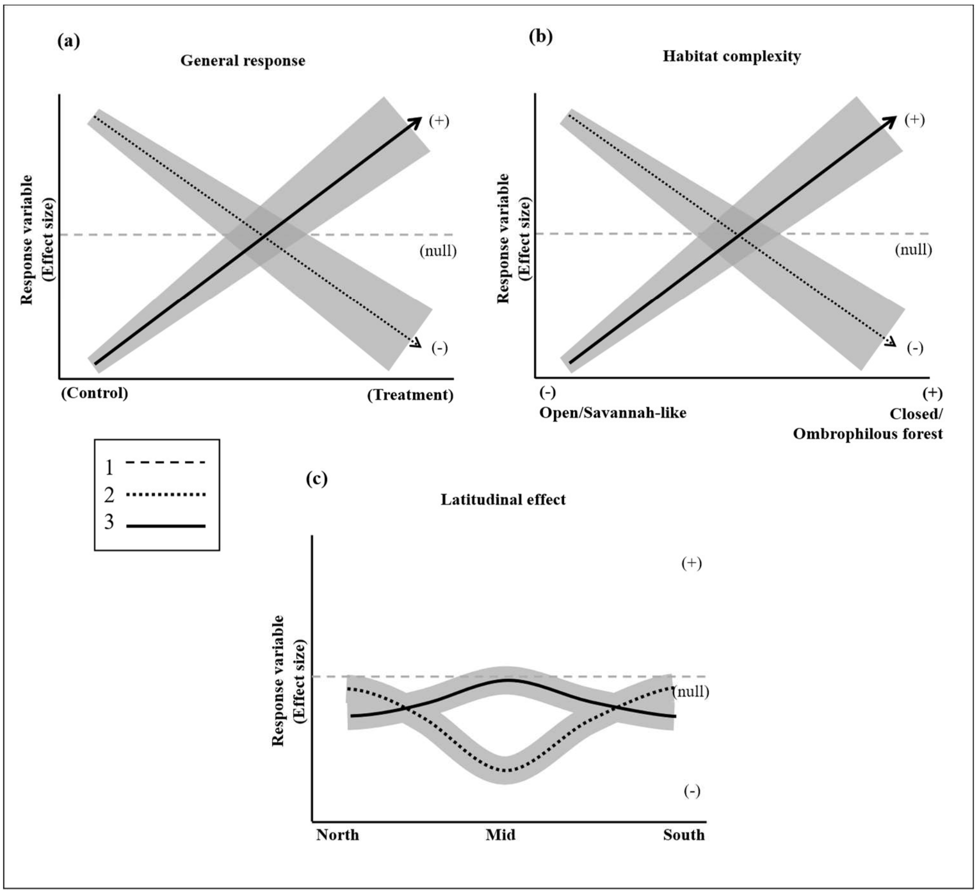

Fig. 1. Conceptual framework illustrating the expected responses of the considered dependent variables. In plot (a), the dotted line represents the expected negative response of dung beetle assemblages to habitat change, whereas the solid line depicts a potential positive response. In plot (b), a negative effect (dotted line) is expected as the contrast in vegetation structure between the original ecosystem and the derived pastureland increases, while the solid line shows the opposite pattern. In plot (c), the dotted line represents the expectation that lower latitudes nearer the equator experience stronger negative impacts owing to the greater contrast between historically stable habitats and pasturelands, whereas the solid line indicates a less pronounced, or opposite, but still negative trend. In all panels, gray shaded areas denote the margin of uncertainty, indicating variation in the magnitude of effect sizes, and the gray dashed line represents the null model, with a slope not significantly differing from zero.

Material and Methods

Search, inclusion and exclusion criteria

The effects of converting natural ecosystems into pasturelands on dung beetle assemblages were quantified using data extracted from peer–reviewed publications issued between 1961 and 2024. We performed a systematic search in three databases: Google Scholar, Clarivate–Web of Science (www.webofknowledge.com), and SCOPUS (www.scopus.com), using terms appearing in the paper title, abstract, or keywords. The search string applied was: [("dung beetle" OR scarabaei*) AND (pasture OR livestock OR “cattle raising” OR farming OR "cattle pasture" OR pastoralism OR "cattle management")]. Studies with inappropriate or missing data were excluded.

The search in the three databases (excluding Google Scholar) yielded 1,109 papers, which were reduced to 840 after removing duplicates (Fig. 2). A further 245 articles were excluded because they addressed non–target subjects (e.g., chemical effects, behavior, and species descriptions). The remaining papers were assessed for inclusion in the meta–analysis according to the following criteria: (a) The study must compare a native habitat or ecosystem (control) with any type of exotic pastureland (treatment), whether open or silvopastoral. (b) The paper must provide numerical data on assemblage composition, species richness, abundance and/or biomass at species, genus and/or morphospecies level, including mean and standard deviation, or data enabling calculation of the standard deviation. (c) The study must have been carried out in the Americas. Following this screening procedure, 31 papers (out of 595 assessed) were retained, to which we added five additional studies authored by us (C. Dos–Reis and F. Escobar). No eligible studies were found among the 100 initially extracted from Google Scholar. In total, 36 articles and 249 comparisons were included in the meta–analysis (see Fig. 2).

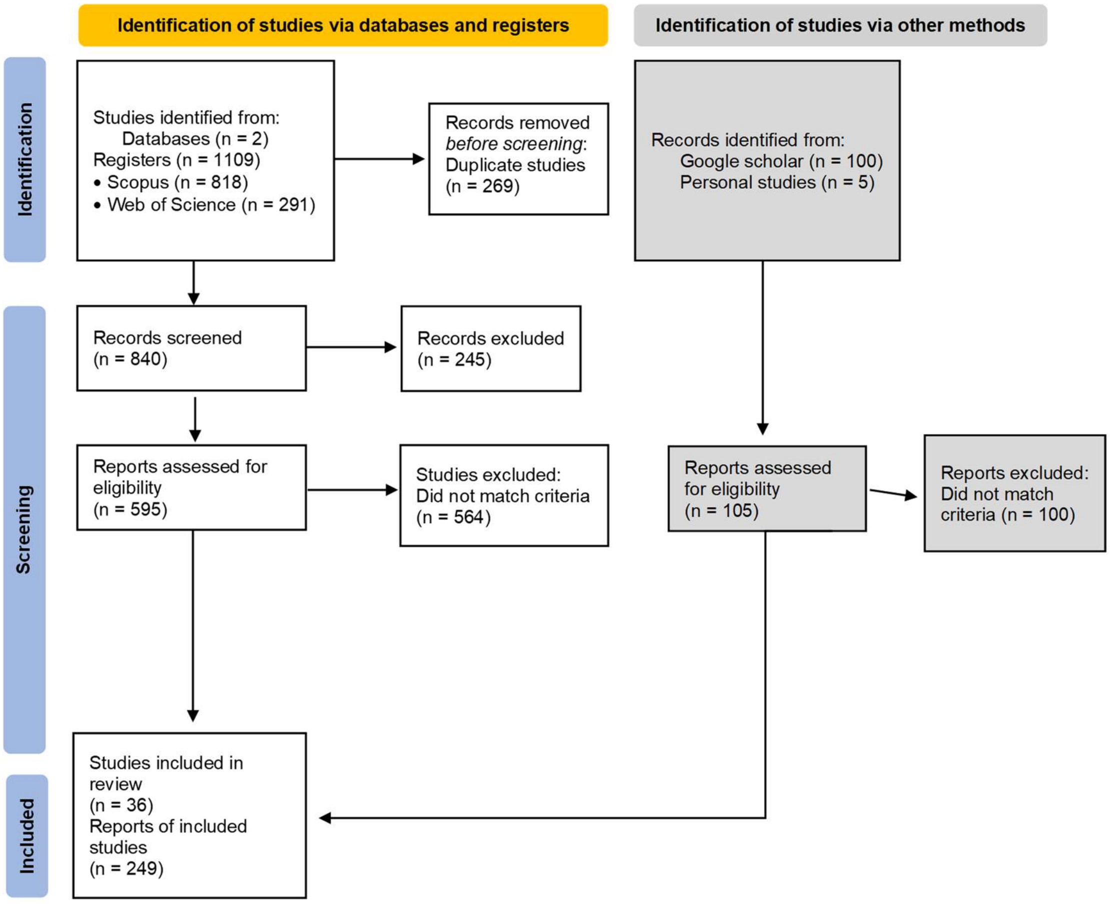

Fig. 2. Flow diagram summarizing the screening process applied to studies extracted from online scientific databases, showing the steps leading to inclusion or exclusion following the Preferred Reporting Items for Systematic reviews and Meta–Analyses (PRISMA 2000; see Page et al., 2021).

Effect size and robustness

As recommended by Buck et al. (2022), we used the *Hedges' d* to estimate the effect size of each study included in the meta–analysis, applying a random–effects model. This metric uses weighted standardized deviations and is appropriate for quantifying the magnitude of treatment effects (Borenstein et al., 2009). We calculated the mean effect size its 95% confidence interval for all comparisons, where negative and positive *Hedge's d* values indicate, respectively, a decrease or an increase in dung beetle species richness, abundance, or biomass. To assess the robustness of our meta–analysis to potential publication bias, we employed two complementary approaches. The Rosenthal Fail–Safe number (FSN) estimates the minimum number of non–significant and unpublished studies that would be required to nullify the observed effect. In addition, the Trim–and–Fill method was employed to detect and correct asymmetry in the funnel plot, as such asymmetry is often indicative of publication bias. This approach "trims" extreme effect sizes from one side of the funnel plot and then "fills" the plot by re–inserting them along with their imputed counterparts, providing an adjusted effect size estimate (Borenstein et al., 2009).

Data extraction and analysis

When necessary, we extracted and converted published values. Confidence intervals (CI 95%) were converted into standard deviations (SD) using the formula: $\mathrm{SD} = \sqrt{\mathrm{N}} * (\mathrm{upper\ limit} - \mathrm{lower\ limit})/3.92$. Standard errors (SE) were converted to standard deviations (SD) using the formula: $\mathrm{SD} = \mathrm{SE} * \sqrt{\mathrm{N}}$. When available, data were taken from supplementary material or digitized from published graphs using Web Plot Digitizer available at [https://apps.automeris.io/wpd/] (Drevon et al., 2017).

A comparative analysis was conducted for each case study. When variables differed among studies, each study was treated separately (Borenstein et al., 2009). Such variables included sampling periods (e.g., different years or seasons), bait type (e.g., human feces, cattle dung, carrion), and ecosystem types for both control and treatment conditions (e.g., primary or secondary forest, open pasture, pasture with scattered trees, silvopastoral systems). To evaluate how dung beetle assemblages respond to changes in vegetation structural complexity, we used the VSC index. This is a qualitative, arbitrary measure describing the structural contrast between the native ecosystem and the derived pastureland, based on vertical vegetation stratification as described by the authors of each study. The index ranks vegetation structure in anthropogenic (1–2) and native ecosystems (3–5) as follows: open pasture = 1; silvopastoral system= 2; Caatinga, Cerrado, Dry Chaco, Humid Chaco, Pine–oak forest = 3; Tropical deciduous forest, Riparian forests, Pantanal, Topical dry forest = 4; Brazilian Amazon, Tropical forest, Atlantic Forest, Tropical rainforest, Dense Ombrophilous Forest, Cloud Forest = 5. For each comparison, the value assigned to the pasture system was subtracted from that for the native ecosystem; thus, higher values indicate a greater structural contrast between pasture and natural habitat.

We used meta–regression to test for changes in the effect size due to Elevation, Latitude, and VSC index. We then performed *rma*() function, with Latitude as a moderator, to fit random effect meta-analysis. We fitted null, linear, quadratic, and cubic spline models, with spline parameters defined using knots at the 10th, 50th, and 90th percentiles (Harrell, 2015). Then, *rcs*() function was applied within *metafor* to obtain non–linear meta–regression (spline). Model performance was evaluated using AICc, selecting the model with the lowest value. Because most studies provided more than one comparison, we performed 10,000 bootstrap simulations (with replacement) to estimate the mean effect size. We also calculated the median effect size and its 95% confidence interval (Almeida-Rocha et al., 2017; Cervantes-López & Morante-Filho, 2024). Given the close similarity between bootstrapped and observed estimates, we retained the original results and presented the bootstrap validation in Table S7.

Dung beetle assemblage parameters

(i) Taxonomic diversity included species richness, number of individuals, and biomass. Metrics such as the amount of excavated soil and dung removal were also considered. However, due to the low number of available comparisons, these results are presented only in the supplementary material.

(ii) Functional groups were classified according to dung relocation behavior: *endocoprids* (beetles that live and breed within the dung pat), *paracoprids* (beetles that excavate galleries beneath the dung), and *telecoprids* (beetles that shape dung into balls, roll them away, and bury them in shallow tunnels) (Halffter & Matthews, 1966; Halffter & Edmonds, 1982; Tonelli, 2021; Maldaner et al., 2024).

(iib) Body size categories were defined as large beetles (≥10 mm in length) and small beetles (<10 mm) (Cambefort & Hanski, 1991).

(iii) Geographic descriptors were categorized as “North” or “South,” depending on whether the study was conducted above or below the equator.

(iv) Biogeographical regions were assigned following Wallace’s classification, namely Neotropical or Nearctic.

(v) Climate zones were categorized as tropical or subtropical following the Köppen–Geiger classification (Beck et al., 2018), with nine climate classes represented by: *Af* = Tropical rainforest*, Am* = Tropical monsoon, *Aw* = Tropical savanna*, BSh* = Arid steppe hot*, Cfa* = Temperate, no dry season, hot summer*,* Cfb = Temperate, no dry season, warm summer, *Cwa* = Temperate, dry winter, hot summer, Cwb = Temperate, dry winter, warm summer, Cwc = Temperate, dry winter, cold summer.

(vi) Habitat categories were defined based on the condition of the control and treatment sites. Control habitats were classified as primary or secondary forests, whereas treatment habitats were classified as open pastures or silvopastoral systems.

Results

Our comparisons were concentrated mainly in tropical latitudes, particularly in Brazil (n = 113) and Mexico (n = 66) (**Fig. 3**; Table S1), with comparatively fewer studies conducted in subtropical regions. The number of available comparisons ranged from 36 to 249 (**Fig. 2**). Species richness and number of individuals were the best represented metrics, with 113 and 106 comparisons respectively, whereas biomass was represented by only 15 comparisons.

Publication bias and extracted studies

The analyses indicate that our results are robust and statistically reliable. The Rosenthal Fail–Safe Number (FSN) show a number of unpublished null-effect studies equal to 318 times the original number of comparisons would be required to render the observed effects non–significant. Furthermore, the Trim–and–Fill analysis detected no missing studies on the right side of a funnel plot, suggesting that publication bias is unlikely (Table S2).

Diversity

Across the Americas, the conversion of natural forests to pastureland showed a consistent negative effect on dung beetle assemblages (**Fig. 4**). The overall mean effect size was significantly negative (*Hedges*' $d = -1.41$; 95% CI –1.79 to –1.03; $p < 0.001$). Similarly, species richness, number of individuals, and biomass each showed negative mean effect sizes in response to pasture creation. The strongest and statistically significant decline was observed for species richness, followed by the number of individuals, whereas the effect on biomass was negative but not statistically significant.

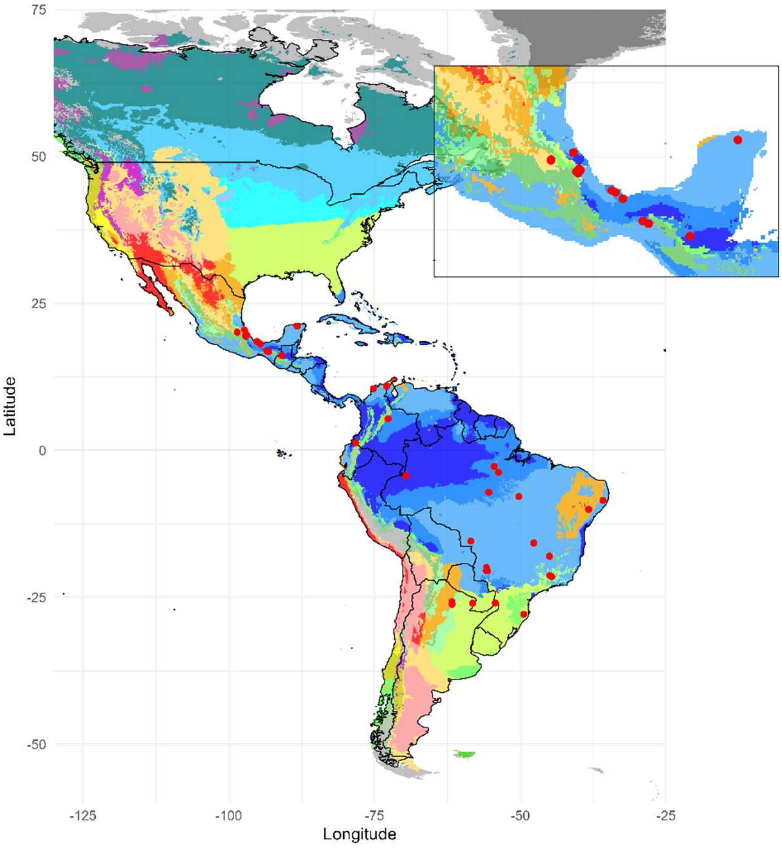

Fig. 3. Geographical distribution of study sites (red circles) included in the meta–analysis, plotted over the updated Köppen–Geiger climate classification (Beck et al. 2018).

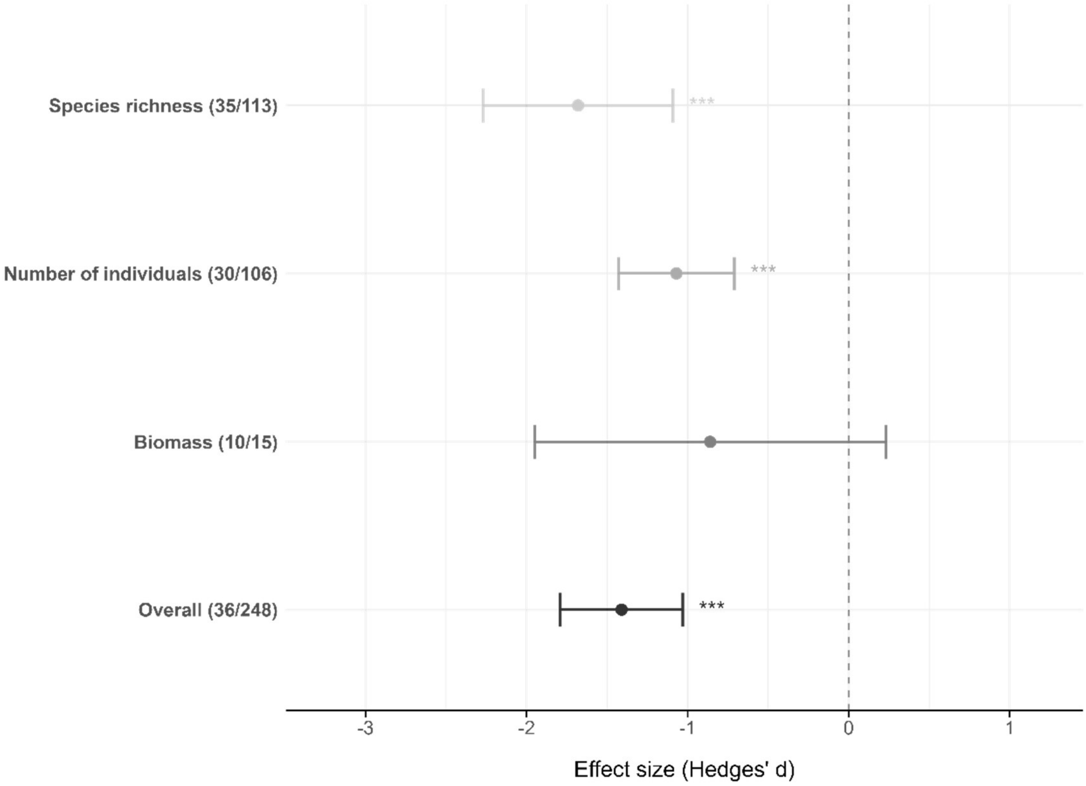

Fig. 4. Effect sizes for dung beetle diversity following the conversion of natural ecosystems into pasturelands, showing mean values and 95% confidence intervals. Significance levels are indicated as *p <0.05, **p <0.01, ***p <0.001. Numbers in parentheses refer to the number of studies/papers and the number of comparisons, respectively.

Functional groups

All functional groups showed a mean negative effect size in response to habitat conversion, although only some of these effects were statistically significant (**Figure S4**). Paracoprids showed a significant overall negative effect size, indicating a net loss, although neither species richness nor number of individuals showed significant changes. Telecoprids displayed significant declines in species richness and in the overall effect, whereas the number of individuals did not differ significantly from zero. In contrast, endocoprids exhibited no significant changes in species richness, number of individuals, or overall effect size. With respect to body size, effect sizes were negative across all categories. However, only large beetles (> 10 mm) were significantly affected by ecosystem conversion, whereas small beetles (< 10 mm) showed no significant response (**Figure S5**).

Habitat type

Dung beetles showed different effect size responses to forest-to-pasture conversion depending on habitat type (**Fig. 5**). Significant negative effect sizes were observed for assemblages from both native primary and secondary forests, as well as for their replacement by open pastures. In contrast, silvopastoral systems showed no significant effect, indicating that habitat conversion involving retained tree cover may mitigate the negative impacts on dung beetle assemblages.

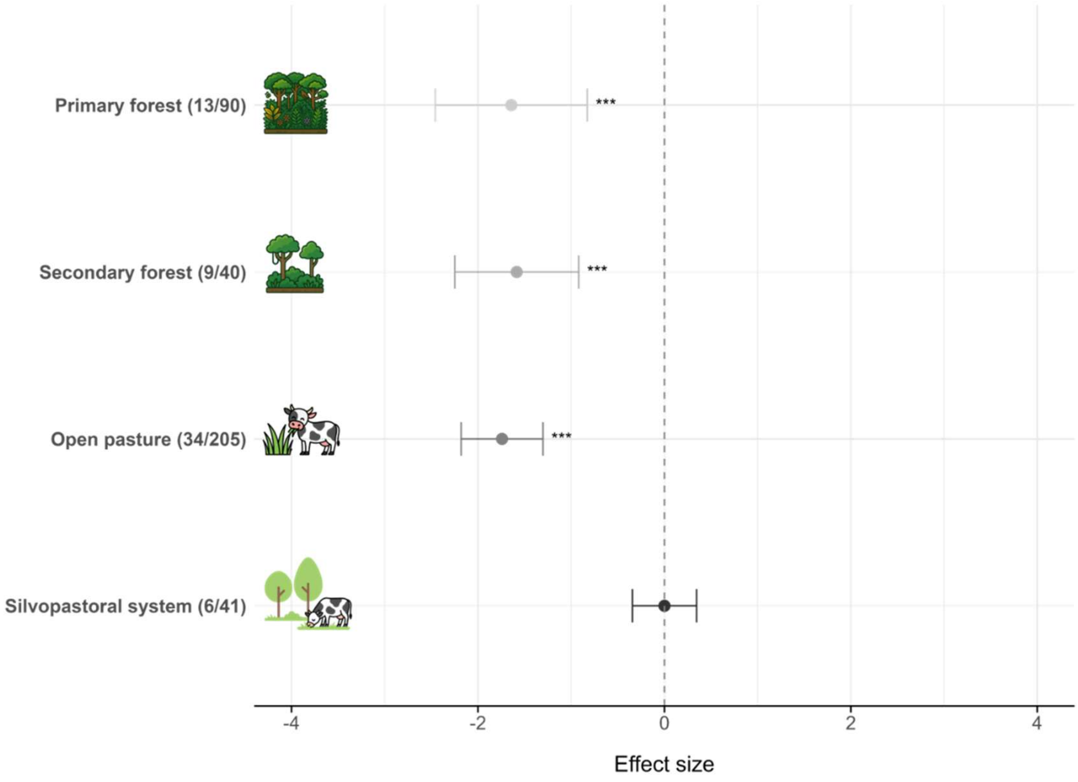

Fig. 5. Dung beetle responses (mean effect sizes and 95% confidence intervals) to habitat types as a moderator of land use change. Significance levels are indicated as ***p <0.001.

Biogeographical and Climate zones

The conversion of natural ecosystems into pasturelands had consistently significant negative effects on dung beetle assemblages across both the Northern and Southern hemispheres, as well as in tropical and subtropical zones and throughout the Neotropical region (**Erro! Fonte de referência não encontrada.**). With the single exception of the poorly studied Nearctic region, which showed a significant positive response, these findings indicate that the establishment and intensification of grazing areas generally exert negative impacts on dung beetle assemblages, irrespective of biogeographic or climate zone.

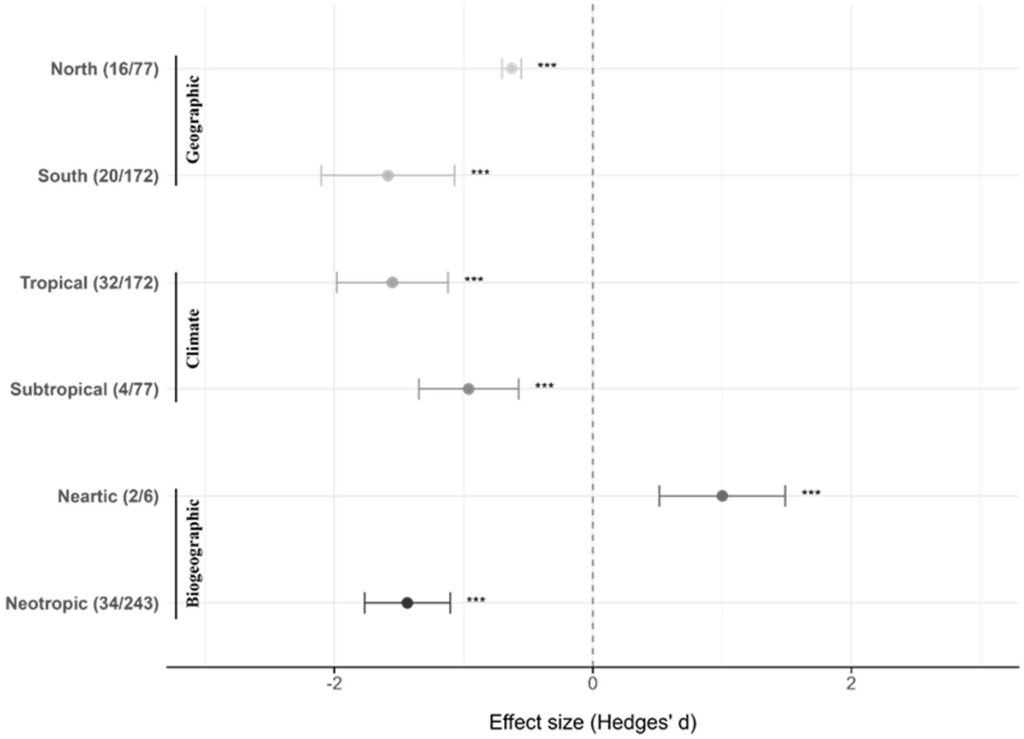

Fig. 6. Dung beetle responses (mean and 95% confidence intervals) across biogeographical and climatic regions following the conversion of natural ecosystems into pasturelands. Significance levels of the effect size are indicated as *p <0.05, **p <0.01, ***p <0.001.

Dung beetle assemblages exhibited significantly different responses to ecosystem conversion across the climatic zones of the Köppen–Geiger classification (**Fig. 7**). Species richness declined most sharply in tropical climates, particularly in rainforest regions (Af) (*Hedges*' *d* = –6.20; 95 % CI –8.90 to –3.52), followed by monsoon (Am) (*d* = –1.94; 95 % CI –3.44 to –0.44), and savanna climates (Aw) (*d* = –2.27; 95 % CI –3.41 to –1.12). No significant effects on species richness were detected in arid or temperate zones. A similar pattern emerged for the number of individuals: significant declines occurred in Af (*d* = –2.69; 95 % CI –4.32 to –1.05) and Aw (*d* = –0.98; 95 % CI –1.79 to –0.17) climates. Additionally, significant reductions were detected in two temperate climates: Cfa (*d* = –1.49; 95 % CI –2.53 to –0.45) and Cwa (*d* = –2.32; 95 % CI –4.09 to –0.55). All reported *p*–values were <0.05.

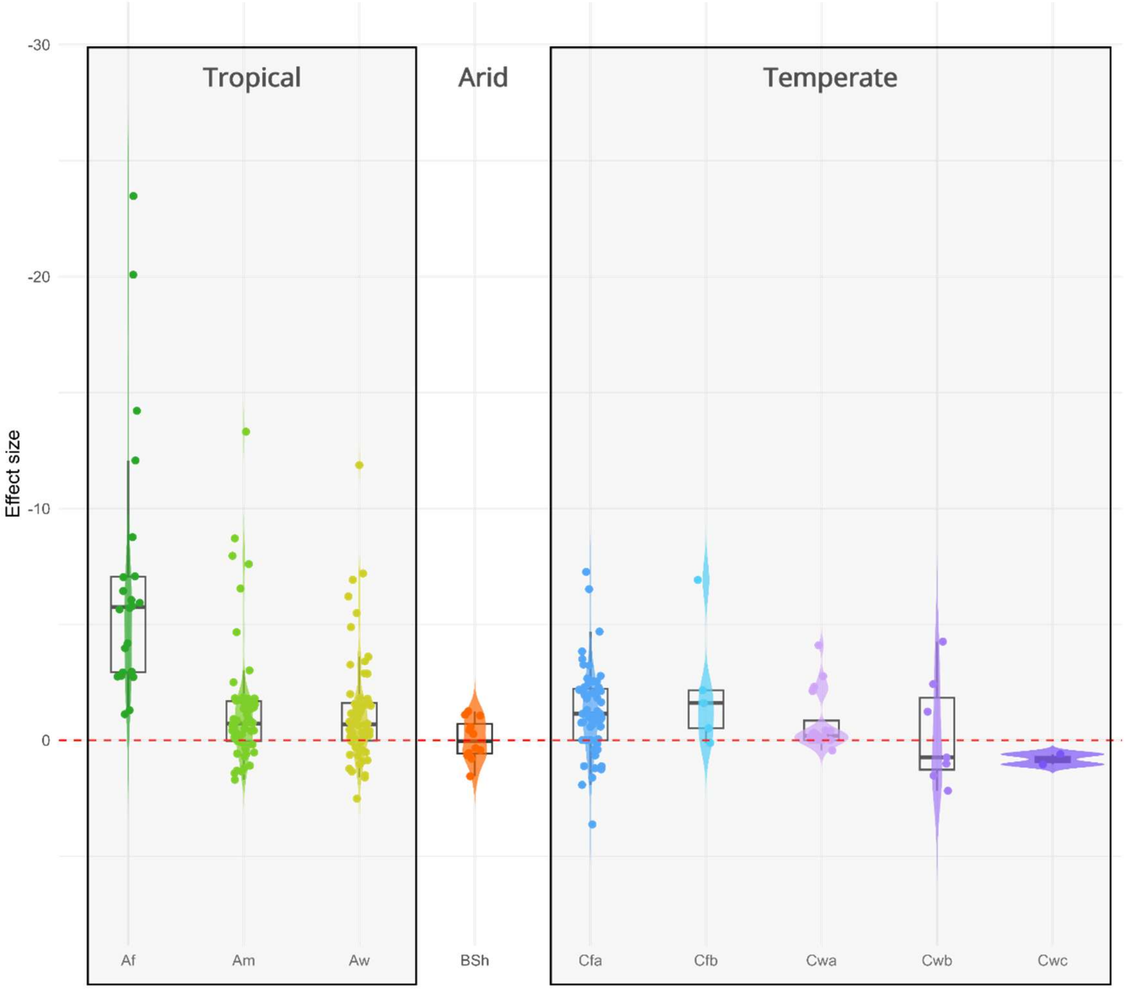

Fig. 7. Effect size bias representing the differing responses of dung beetle assemblages to the conversion of natural ecosystems into pasturelands updated Köppen–Geiger climate zones (Beck et al., 2018). *Af* = Tropical rainforest, *Am* = Tropical monsoon, *Aw* = Tropical savanna, *BSh* = Arid steppe hot, *Cfa* = Temperate, no dry season, hot summer, Cfb = Temperate, no dry season, warm summer, *Cwa* = Temperate, dry winter, hot summer, Cwb = Temperate, dry winter, warm summer, Cwc = Temperate, dry winter, cold summer. Each point represents an individual comparison extracted from the literature.

Meta–regression

Meta–regression using the VSC index revealed a significant negative effect size for dung beetle species richness, but no significant overall response for the number of individuals (**Fig. 8**). The VSC index reflects the contrast in vegetation structural complexity between pasturelands and the natural ecosystems they replace. Accordingly, our results indicate that converting structurally complex habitats into pasturelands has strong detrimental effects on dung beetle richness (VSC 4: β = –2.38; 95% CI–3.21 to –1.56; $p < 0.0001$). The significance of the VSC index was supported by a QM test (QM (df = 3) = 36.05; $p < 0.0001$). However, residual heterogeneity remained high ($I^2 = 98\%$), suggesting that a substantial proportion of unexplained variation persists beyond the model. Although the VSC index did not show an overall significant effect on the number of individuals (QM (df = 2) = 3.17; $p = 0.205$), significant negative responses were detected for VSC2 ($\beta = –0.81$; 95% CI –1.37 to –0.25; $p = 0.0048$) and, particularly, for VSC4 ($\beta = –1.39$; 95% CI –1.88 to –0.90; $p < 0.0001$. Again, heterogeneity was high ($I^2 = 94\%$). The overall non-significant result is likely driven by the small number of comparisons available for VSC 3, but the pattern nonetheless suggest that declines in abundance are also expected following pasture creation.

Meta–regression and QM tests indicated that elevation did not explain variation in effect sizes, consistently showing non–significant *p*–values >0.05. Although R^2 values were always < 5%, heterogeneity remained high ($I^2 > 95\%$).

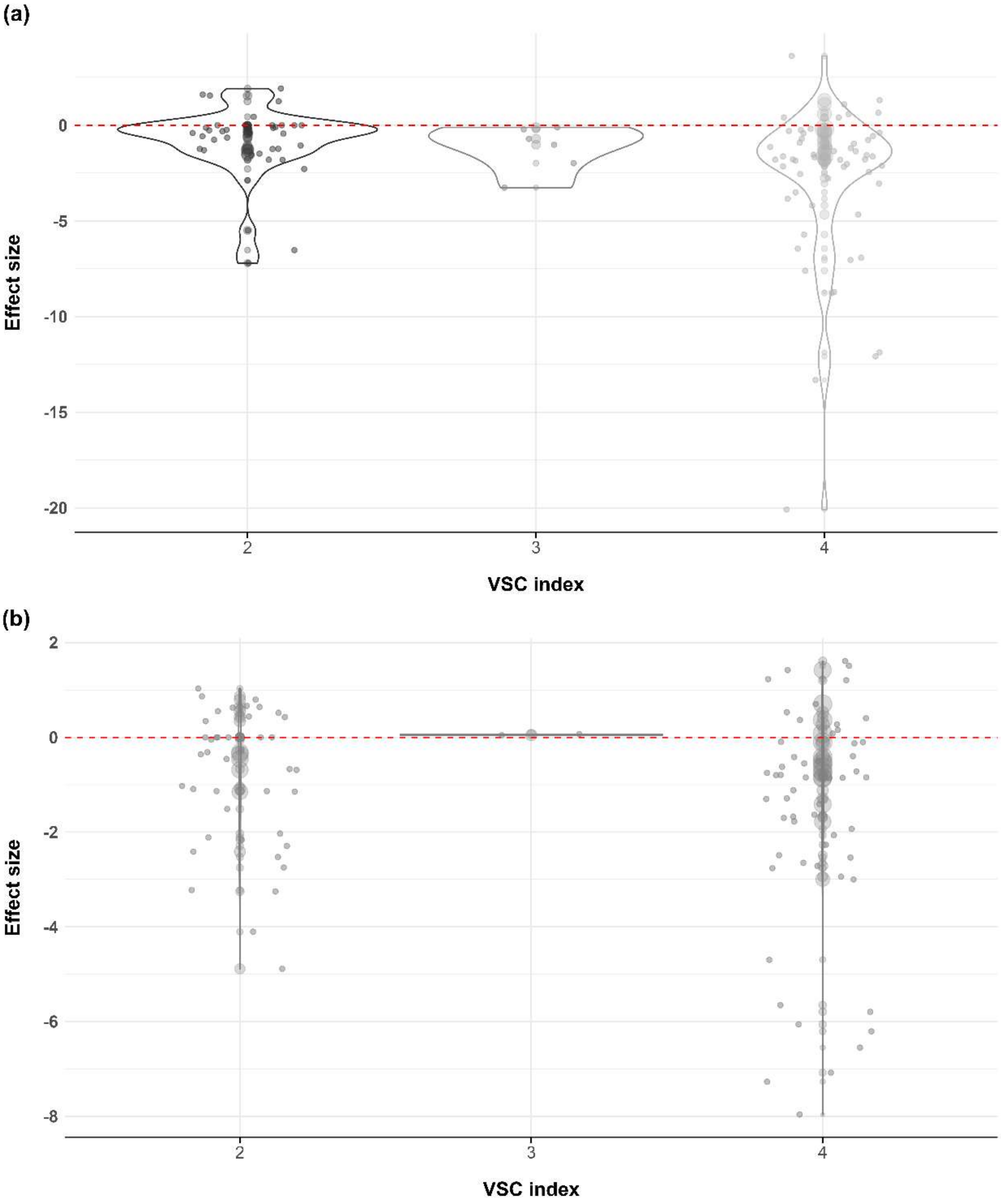

Fig. 8. Relationship between the vegetation structural complexity (VSC) index and effect size for (a) dung beetle species richness and (b) number of individuals. Boxplots show the distribution of effect sizes, while individual points represent study-level comparisons. Point size is proportional to the weight assigned to each comparison.

Nonlinear meta–regression provided the best explanation for the relationship between *Hedges' d* and latitude. The overall pattern was captured by a quadratic model (R^2 = 9.1%; $p < 0.05$; **Figure S6**). Latitude emerged as a significant predictor for both dung beetle species richness and number of individuals in pastures. In both cases, the response followed a curvilinear pattern, with declines peaking at mid–latitudes and diminishing towards lower, equatorial latitudes (**Fig. 9**). Spline regressions confirmed this trend, explaining 22.4% of the variance in species richness (QM SpRich = 12.45, p = 0.0020) and 17.0% of the variance in the number of individuals (QM

NofI = 6.91, $p = 0.032$). These findings indicate that the magnitude of dung beetle decline varies geographically across the Americas.

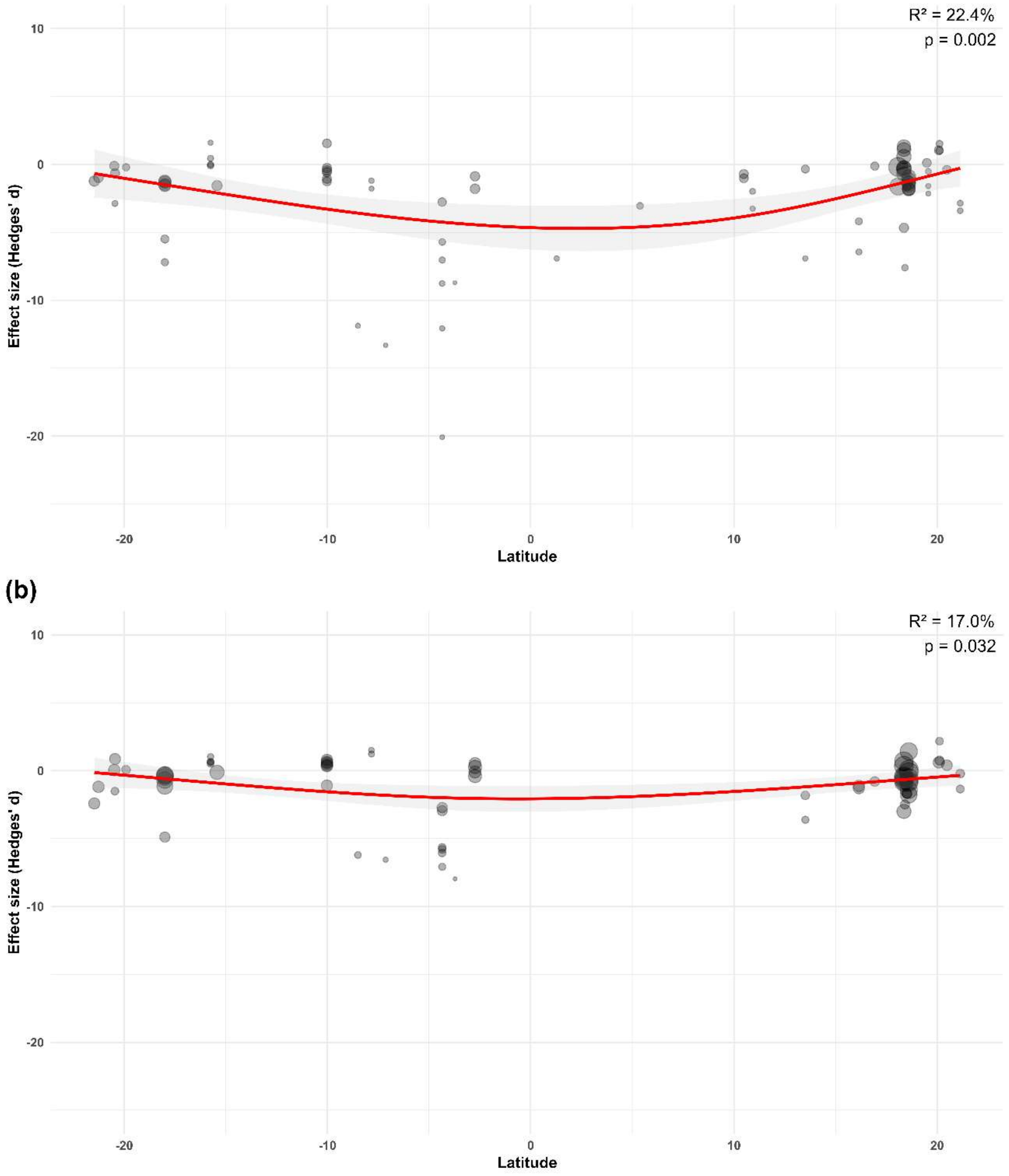

Fig. 9. Relationship between latitude and effect size (*Hedges' d*) for (a) dung beetle species richness and (b) number of individuals. The size of each data point is proportional to its sampling variance (*vi*), which reflects the weighting assigned to each comparison in the meta-analysis.

Discussion

Our meta–analysis demonstrated that the expansion of pasturelands at the expense of native ecosystems exerts a consistent overall effect on dung beetle assemblages across the Americas. Except for biomass, results for species richness and number of individuals showed that transforming natural ecosystems into pasturelands results in widespread losses of diversity, which may threaten the delivery of key environmental services performed by dung beetles. Different components of assemblage diversity, such as species richness, abundance, and biomass, all play a role in dung beetle–driven functional processes. Species richness is strongly correlated with functional richness, leading to low resilience in pasturelands where species richness is reduced (Tonelli et al., 2020). As many studies have shown, steep declines in dung beetle abundance can detrimentally affect ecosystem services. For example, a 33% decrease in abundance may result in a proportional reduction in dung removal (Manning & Cutler, 2018). Similar and even more consistent patterns have been observed for biomass (Alvarado et al., 2018; Amore et al., 2018; Sarmiento–Garcés & Hernández, 2021), because biomass and abundance do not always vary in parallel (Saint–Germain et al., 2007; Tonelli et al., 2018). Given the importance of biomass for explaining dung removal rates, an important question arises: why does biomass not decrease significantly following forest-to-pasture conversion? We suggest that the new environmental conditions favor a different set of species—often smaller, more abundant and generalist—that can reach high population sizes due to the continuous and abundant availability of livestock dung (Almeida et al., 2011; Nependa et al., 2021). Their numerical dominance can compensate for the loss of species, buffering functional declines. Ideally, therefore, both abundance and biomass should be evaluated simultaneously in biodiversity studies to better understand land–use effects (Cultid–Medina & Escobar, 2016). Compensatory processes, such as the hyperabundance of small–sized species documented in dry forest pastures of the Yucatan Peninsula (Alvarado et al., 2018, 2019), further illustrate that maintaining functional performance in modified landscapes does not necessarily imply preserving the original assemblage composition.

Our study also highlight that the magnitude and direction of responses to forest-to-pasture conversion were not uniform. Dung beetles respond idiosyncratically depending on both the original habitat type and the nature of the pasture system that replaces it, highlighting the need to evaluate land-use change within its environmental and biogeographical context. As expected, the effects of converting forest to pastures were consistently and strongly negative across studies conducted in tropical and most ombrophilous ecosystems. By contrast, in the Nearctic and temperate regions there was either no significant response or even a positive effect. Supporting evidence includes documented cases of abrupt dung beetle species loss in tropical and subtropical regions (Silva et al., 2017; Sarmiento–Garcés & Hernández, 2021). However, in the mountains of the Mexican Transition Zone, dung beetle diversity has been reported to be high in open pastures (Escobar et al., 2007; Barragan et al., 2014; Alvarado et al., 2020), particularly at the landscape scale in small pastures embedded within forest matrices (Ríos–Díaz et al., 2021). Thus, while forest conversion generally erodes biodiversity, the outcome ultimately depends on the ecological resilience of regional faunas and the spatial configuration of pastures within the landscape.

Dung beetle functional groups also responded differently to ecosystem changes across Americas. Combined with differences in beetle body–sizes, these idiosyncratic responses may disrupt key ecosystem services because dung removal and soil bioturbation capacity are closely linked to beetle size (Milotić et al., 2017; Stanbrook et al., 2022). Paracoprids are widely considered the most important functional group for livestock production systems (Yokoyama & Kai, 1993; Bang et al., 2005; Milotić et al., 2017; Maldaner et al., 2024) because they promote high rates of dung removal, soil excavation, and nitrogen cycling (Yokoyama & Kai, 1993; Nichols et al., 2008), even in highly compacted soils (Dabrowski et al., 2019). These processes are primarily driven by large–bodied species (Stanbrook et al., 2021). For example, the large paracoprid, *Dichotomius bos* (Blanchard, 1845), which reaches 28 mm in length, excavates tunnels exceeding one meter deep and removes substantial amounts of dung (Maldaner et al., 2024). When dominant, the species may contribute to remove up to 1kg of cattle dung in 24 hours (C. Dos–Reis, unpublished data). Amézquita & Favila (2011) found that large nocturnal taxa removed more dung than small diurnal species. Similarly, Slade et al. (2007) reported that large nocturnal paracoprids played a principal role in dung removal within a Bornean forest, as it decreased by 75% when they are absent. By contrast, telecoprids (rollers) and endocoprids (non-nesters) contribute relatively little to dung removal. Even large rollers bury dung in shallow galleries, limiting their overall impact on dung burial (Hanski & Cambefort, 1991; Maldaner et al., 2024). Endocoprid species may benefit from the abundance of livestock dung, but they contribute significantly to dung removal only when their populations reach extremely high densities (Lumaret et al., 1992; Tonelli et al., 2019).

Regardless of the original ecosystem, the conversion of primary or even protected forests into agricultural land is widely recognized as the most detrimental scenario for biodiversity (Giam 2017; Hedges et al., 2018; Leberger et al., 2020; López–Bedoya et al., 2022). Our results reinforce previous findings comparing dung beetles in forests and human–modified landscapes (Nichols et al., 2008; Fuzessy et al., 2021; López–Bedoya et al., 2022). We therefore emphasize the importance of preserving old–growth forest remnants throughout the Americas to maintain dung beetle diversity and associated ecosystem services (Bitencourt et al., 2019; Noriega et al., 2021). Restoration efforts may only partially recover dung beetle assemblages (González–Tokman et al., 2018). Thus, both local and landscape conservation initiatives should be considered to preserve native dung beetle assemblages (Sánchez–de–Jesús et al., 2016). These initiatives should aim to conserve at least 40% forest cover in the human–modified landscapes (Arroyo–Rodriguez et al., 2020) in order to guarantee dung beetle diversity (Cómbita et al., 2025).

A key result of our meta–analysis is the contrasting response of assemblages between open pastures and silvopastoral systems. Open pastures, which have low vegetation complexity (Rutten et al., 2015), typically experience steep declines in dung beetles (Silva et al., 2017) due to the reduced habitat heterogeneity, increased solar exposure, loss of thermal refuges, and reduced dung availability caused by mammal defaunation (Stanbrook & King, 2022; Cómbita et al., 2025). In contrast, silvopastoral systems showed no significant effects, supporting the idea that tree cover can buffer microclimatic changes and maintain assemblage structure. This pattern has been observed across multiple ecosystems, including dry forest in México (Arellano et al., 2013) and Colombia (Montoya–Molina et al., 2016), the Argentine Atlantic forest (Gómez–Cifuentes et al., 2020), and subtropical USA pastures (Stanbrook & King, 2022). These findings support the idea that silvopastoral systems serve as suitable refuges for dung beetle fauna (Giraldo et al., 2011), maintaining habitat heterogeneity and sustaining dung beetle diversity (Escobar, 2004; Rivera et al., 2020). However, the spatial context of the landscape is a key factor in determining diversity patterns in areas dominated by human activities (Alvarado et al., 2018; Edwards et al., 2021). When combined with forest remnants, riparian corridors, and live fences, these systems can contribute to conserving the integrity of key ecological services essential to the livestock industry in agricultural landscapes (Arellano et al., 2008a; Díaz et al., 2010; Giraldo et al., 2011; Gray et al., 2014; Souza et al., 2020). The role of silvopastoral systems is especially relevant given projections that climate change will drastically reduce native dung beetle occurrences in South American pastures (Maldaner et al., 2021), potentially compromising ecosystem services.

The VSC analysis further underscored that increasing structural contrast between natural ecosystems and pasturelands results in increasingly negative biodiversity responses. Species richness and abundance both exhibited increasingly negative responses from VSC 2 to

VSC 4, corresponding to a greater structural contrast. Neutral effects in silvopastoral systems reinforce the importance of structural complexity. These results align with the high specialization of tropical dung beetles, whose richness, abundance, and biomass remain high across vegetation types (Guerra–Alonso et al., 2020a; Nependa et al., 2021; Pessôa et al., 2021). The high overall species richness likely reflects intense local speciation within each habitat type, which in turn amplifies contrasts in species composition between undisturbed habitats and adjacent livestock pastures. For instance, in countries with high levels of livestock production, such as Brazil and Argentina, the growing global demand for food and the progressive conversion of natural habitats into pasturelands causes escalating threats to biodiversity hotspots (Crist et al. 2017; Molotoks et al., 2017). Consequently, regions of exceptional biodiversity in tropical America often coincide with areas at greatest risk of agricultural expansion (Molotoks et al., 2017).

Given the scarcity of studies evaluating dung beetle responses across latitudinal gradients (but see Lobo, 2000; Radtke et al., 2010; Errouissi et al., 2013; Arellano et al., 2023), our latitudinal analysis has yielded relevant results. Because dung beetle assemblages are strongly shaped by their historical and ecological contexts (Halffter & Matthews, 1966; Davis & Scholtz, 2001; Davis, 2009), their responses may vary idiosyncratically across regions. For instance, temperate assemblages exhibit greater average body–size than those in the tropics (Radtke et al., 2010) and are composed largely of eurytopic species capable of tolerating substantial microclimatic variation, such as that found in the Mexican Transition Zone (Halffter & Matthews, 1966; Escobar et al., 2007; Barragan et al., 2014). In contrast, assemblages in more stable biogeographic and evolutionary regions, such as tropical humid forests, are typically composed of stenotopic species (Halffter & Matthews, 1966). These species have a strong affinity for ombrophilous conditions and generally avoid open habitats or areas that are drastically disturbed by human activity. Such evolutionary patterns and, combined with contemporary responses to land-use change, may help explain our latitudinal findings. Alternatively, species inhabiting tropical dry forests may exhibit more eurytopic behavior, enabling them to tolerate substantial shifts in vegetation structure and microclimate (Halffter & Matthews, 1966; Montoya–Molina et al., 2016; Giménez–Gómez et al., 2025). This adaptability underscores the seasonal nature of their foraging behavior and their sensitivity to drought conditions.

Ultimately, the structural simplification of vegetation associated with the conversion of natural forest into pasturelands results in an average loss of approximately seven dung beetle species (SD ± 8.0, n = 57). Particularly drastic losses have been reported in pastures located within the Amazon rainforest (up to 33 species lost; Silva et al., 2017; Cajaiba et al., 2017) and in tropical forests of Mexico (23 species lost; Bourg et al., 2016). In contrast, some studies have reported no loss (Arellano et al., 2013) or slight gains of up to four species (Escobar et al., 2007; Ortega–Martínez et al., 2020; Ríos–Díaz et al., 2020; Oliveira et al., 2021). These modest increases typically occur when “savannah–like” habitats are converted into silvopastoral systems (Oliveira et al., 2021), where year–round availability of dung resources may help maintain dung beetle richness. A similar pattern emerges for abundance. On average, dung beetle assemblages showed a reduction of 303 individuals (SD ± 1371, n = 53) following habitat conversion, with severe reductions of up to 7,450 individuals in some studies (Guerra–Alonso et al., 2020b). By way of contrast, when gain was detected within the selected studies, abundance showed a mean increase of 500 specimens across 16 studies.

This scenario represents an ecological paradox, a question originally raised by G. Halffter (pers. comm.). Cattle dung is a novel resource, introduced into the Neotropical region by the Spanish roughly 500 years ago. Yet, despite the continuous availability of cattle manure in livestock pastures, resulting from large herds and high stocking densities, the presence of dung beetle species capable of exploiting this resource has not led to an increase in species richness or abundance of native beetles in these modified environments. The explanation likely lies in evolutionary and biogeographical constraints. Beyond the direct effects of reduced vegetation structural complexity associated with land-use change, the decline in dung beetle diversity observed in pasturelands may also reflect the loss of dung resource diversity characteristic of natural ecosystems. This reduction is closely linked to defaunation processes driven by habitat conversion (Ferreira et al., 2018; Gallego–Zamorano et al., 2020; Cómbita et al., 2025). At most, a local pasture typically receives a limited set of dung types—primarily from cattle, horses, and sheep—which is insufficient to compensate for the loss of the diverse dung resources provided by native mammals. Neotropical dung beetle assemblages are largely composed of stenotopic species with narrow habitat requirements, although some generalist species are able to colonize pasturelands. Even so, no more than 97 native dung beetle species have been documented using cattle dung in grazing areas across American pasturelands (Maldaner et al., 2024; C. Dos–Reis, unpublished data), representing only about 5.3% of the total species richness of the Neotropical dung beetle fauna.

Knowledge gaps and suggested research priorities

The findings of this study provide valuable insights that can guide the development of strategies to mitigate the consequences of livestock pastures expansion into natural ecosystems. This is particularly relevant for countries leading global livestock production (Alkemade et al., 2013; Morand, 2020). Among the top ten producers, only three countries (Brazil, Argentina, and Mexico) are represented in the available literature. Even when extending the scope to the top 20 producers, only five countries have conducted studies evaluating the effects of converting natural ecosystems to pasturelands on dung beetle assemblages (FAO, 2021). This gap is concerning and highlights the need to encourage further research. For example, aside from the studies of Conover et al. (2019) and Stanbrook & King (2022), there is a notable paucity of research comparing dung beetle assemblages in natural ecosystems versus pasturelands in North America, specifically in regions north of Mexico. Yet the United States is a major global producer of beef cattle and ranks second worldwide in milk production (FAO, 2021). Consequently, future research efforts should address not only taxonomic diversity but also the assessment of biomass and its impact on ecosystem services. This recommendation is reinforced by a recent review of dung beetle studies conducted in savanna environments (Reis et al., 2024), which underscores the need for a more comprehensive and integrative research agenda in this field.

Although our analysis yielded important insights regarding factors such as functional groups, biogeographical zones, and latitude, it is important to acknowledge that landscape context was not evaluated, as most of the included studies lacked detailed or consistent information at this spatial scale. Nevertheless, landscape structure—including matrix composition, habitat heterogeneity, spatial configuration, and the amount of remained native habitat— is known to be critical drivers in shaping dung beetle assemblages (Sanchez–de–Jesus et al., 2016; Montoya-Molina et al., 2016; Alvarado et al., 2018; Ratoni et al., 2023), especially in tropical regions. Therefore, we must incorporate landscape–scale variables to improve our understanding of dung beetle responses to rapid pasture expansion in American tropics. Previous studies have demonstrated that matrix composition influences dung beetle diversity and abundance by affecting resource availability and habitat connectivity (Nichols et al., 2007; Díaz et al., 2010; Alvarado et al., 2018). Similarly, landscape configuration may affect dispersal and population dynamics of dung beetles (Arellano et al., 2008b; Sánchez–de–Jesús et al., 2016; Barreto et al., 2024), whereas amounts of habitat have been identified as a key predictor of dung beetle assemblage structure, often more influential than fragmentation (Gardner et al., 2008; Fahrig, 2013; Cómbita et al., 2025).

The reliance on a single dung beetle sampling method and bait type (usually human feces, or a combination of human feces and carrion) can limit species detection and bias the inferences drawn from published studies. Although baited pitfall traps provide a reliable and widely used method for assessing dung beetle assemblages and allow robust inter–study comparisons (Mora–Aguilar et al., 2023), they may fail to detect rare, canopy-dwelling, or tramp species. Complementary techniques, such as flight intercept traps and manual collections, can help to capture these overlooked taxa (Puker et al., 2020; Mora–Aguilar et al., 2023; Bach et al., 2023). Furthermore, while human feces and carrion are effective attractants, the use of cattle dung as bait is imperative for identifying dung beetle species that specialize in exploiting this resource. Employing multiple bait types can also help detect forest species that are attracted to cattle dung but do not colonize pastures, as well as species capable of using open habitats but not necessarily preferring bovine dung. Such information is key for understanding which taxa contribute ecosystem services relevant to livestock systems. One important but often overlooked issue may affect results derived from pitfall-trap collections. These traps prevent the emigration of dung beetles and have an unknown, species-specific attraction range, thereby drawing individuals that may not originate from—or have emerged within—the locality where the pitfall-trap is placed. Comparing results obtained from conventional pitfall-traps with those from traps that allow both immigration and emigration may help identify the species that are truly effective in contributing to dung removal under specific local conditions (Amore et al., 2018).

Future studies should evaluate the ecosystem services provided by dung beetles in natural habitats and pasturelands across the Americas, as relatively few investigations have done so to date. A substantial knowledge gap persists in the Nearctic region, where more comprehensive research is particularly needed. Progress in understanding changes in biomass, functional groups, and body size following forest-to-pasture conversion has been limited by the scarcity of raw, species–level data. Improving data availability and standardization would enable robust testing of how assemblage structure responds to pasture conversion at continental scales. While some species appear to benefit from open pastures, it remains unclear whether they alter their breeding seasons in response to the increased food availability in pasturelands compared with natural habitats. For example, does the year–round availability of cattle dung modify the seasonality of nesting and reproductive cycles? Do species shift their typical breeding periods under these conditions? Ultimately, what are the demographic consequences, and what is the broader impact on population dynamics?

Although important insights have been gained into the effects of vegetation structural complexity on dung beetle assemblages since the seminal publication of Halffter & Matthews (1966), a pattern also supported by our meta–analysis, technological advances such as LiDAR now offer new opportunities to obtain more detailed and spatially explicit information on how habitat structure influences these assemblages.

Conclusions and recommendations

This study provides additional support for the prevailing hypothesis that the conversion of natural ecosystems into anthropogenic land uses has detrimental effect on dung beetle assemblages across the Americas. Furthermore, we offer novel evidence that responses to such transformations vary idiosyncratically across biogeographical regions, climatic zones, and functional groups. The magnitude of these effects also differs with latitude: declines are most pronounced in equatorial regions, where natural habitats—such as tropical rainforest—are structurally more distinct from pasturelands. Despite growing scientific recognition of the importance of ecosystem services and the urgent need to safeguard them, a comprehensive understanding of how habitat conversion affects dung beetle–mediated services remain limited. The scarcity of studies conducting paired comparisons between natural ecosystems and pasturelands severely restricts our capacity to draw firm conclusions. Such research is essential for assessing the consequences of habitat transformation on ecological functions and functional services that are critical to livestock production throughout the Americas.

As a practical alternative to mitigate the negative effects of converting natural forests into open pastures in tropical regions, the promotion of silvopastoral systems emerges as a robust management strategy at both local and landscape scales. This recommendation is grounded in one of the more significant findings of our study: while open pastures were associated with strong declines in dung beetle assemblages, silvopastoral systems exhibited no significant impacts. Consequently, policy-makers and land managers should prioritize the development and implementation of silvopastoral systems over the establishment of open pastures.

Acknowledgements

We are grateful to Cesar Murilo and Renato Salomao for valuable insights on early versions. C.R. expresses his thanks for a CAPES doctoral scholarship (Coordination for the Improvement of Higher Education Personnel – Brazil (CAPES) – Funding Code 001). His research was also supported by Rufford Small Grant (No. 36296–1). Laboratory support and infrastructure provided by CEPEC–CEPLAC, Brazilian Ministry of Agriculture is acknowledged. The Instituto of Ecology, A. C is thanked for providing laboratory support and infrastructure during his sandwich doctorate. Thanks are due to Raquel Carvalho for providing data. J.H.C.D. acknowledges their CNPq research productivity fellowship.

Authors' Contributions

C.R., J.D., and F.E. conceived and designed the study. C.R. collected and analyzed the data. C.R. wrote the first draft of the manuscript, under the supervision of J.D. and F.E. All authors reviewed and contributed substantially to the final version of the manuscript.

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Appendix A. Supplementary data

Dung beetles in a changing world: a comparative meta–analysis of effects on assemblages due to transformation from natural ecosystems to pasturelands in the Americas

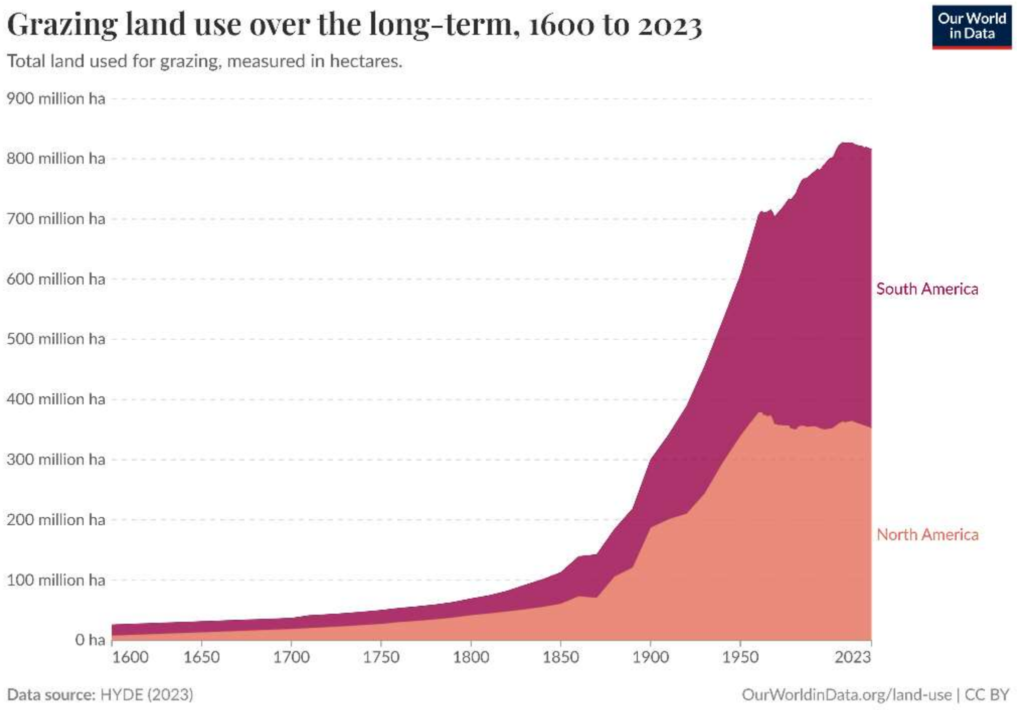

Figure S1. Grazing land use over time in the Americas.

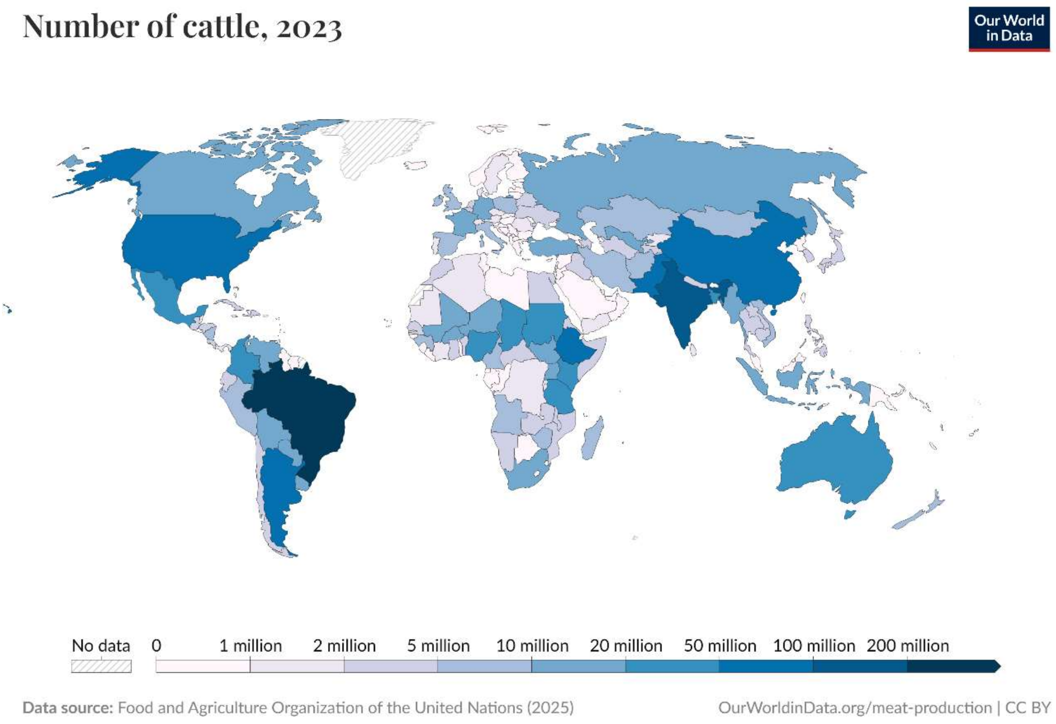

Figure S2. Map of cattle population density across the world. Source: Our World in Data.

Table S1. List of studies and comparisons by countries.

Countries	Study	Comparisons
Brazil	16	113
Mexico	13	66
Argentina	3	57
El Salvador	2	6
Colombia	3	6
Nicaragua	1	1
Total	**36**	**249**

Table S2. Publication bias – content for Fail–Safe Number Calculation Using the Rosenberg Approach (Borenstein et al., 2009).

Component	Effect size	Significant	Fail–safe number	Fsn_n	Trim and fill
Overall	–1.4116	<.0001	78843	1250	0 right side
Species richness	–1.6787	<.0001	23247	575	0 right side
Abundance	–1.0719	<.0001	10898	540	0 right side
Biomass	–0.8596	0.1232	131	85	3 left side
Primary forest	–1.6420	<.0001	15041	460	0 right side
Secondary forest	–1.5838	<.0001	2122	210	0 right side
Open pasture	–1.7414	<.0001	80358	1035	0 right side
Silvopastoral	0.0010	0.9953	0	215	0 left side
Paracoprid	–0.7044	0.0085	801	160	0 right side
Telecoprid	–0.6337	0.0027	496	160	4 right side
Endocoprid	–0.6101	0.0706	538	160	0 right side
Small beetle (< 10 mm)					
Large beetle (> 10 mm)					

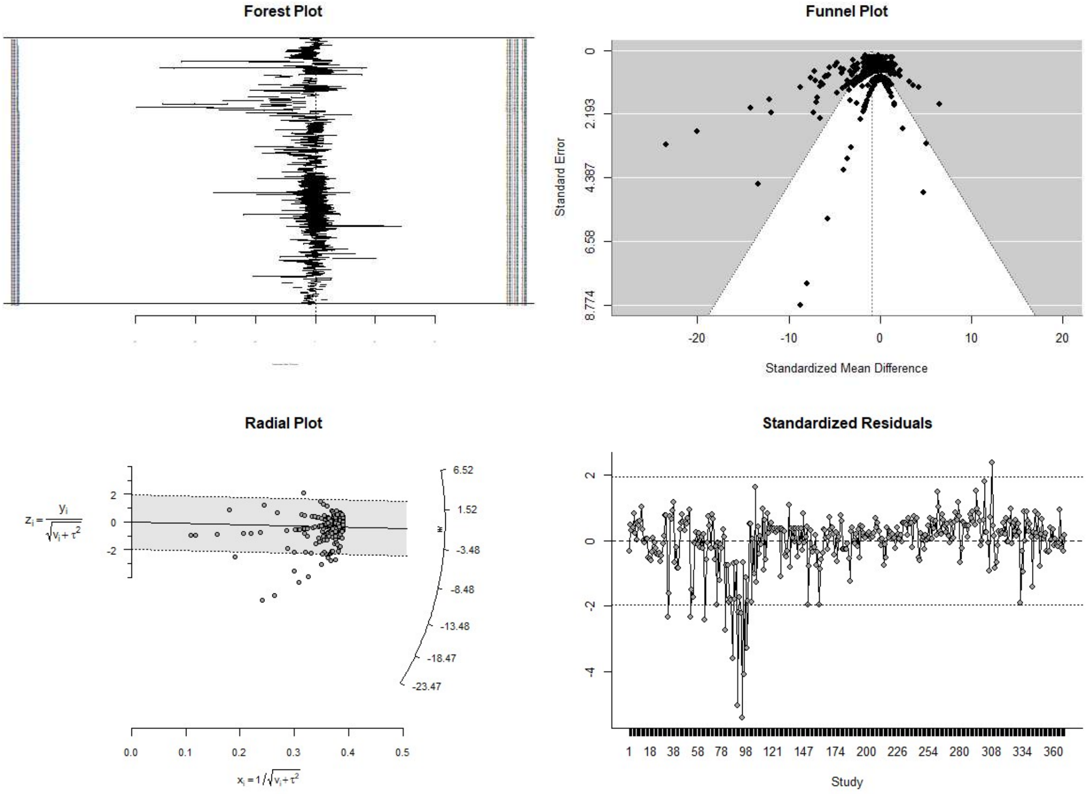

Figure S3. Publications bias plot for the main meta–analysis output.

Meta-analysis of dung beetle functional groups response

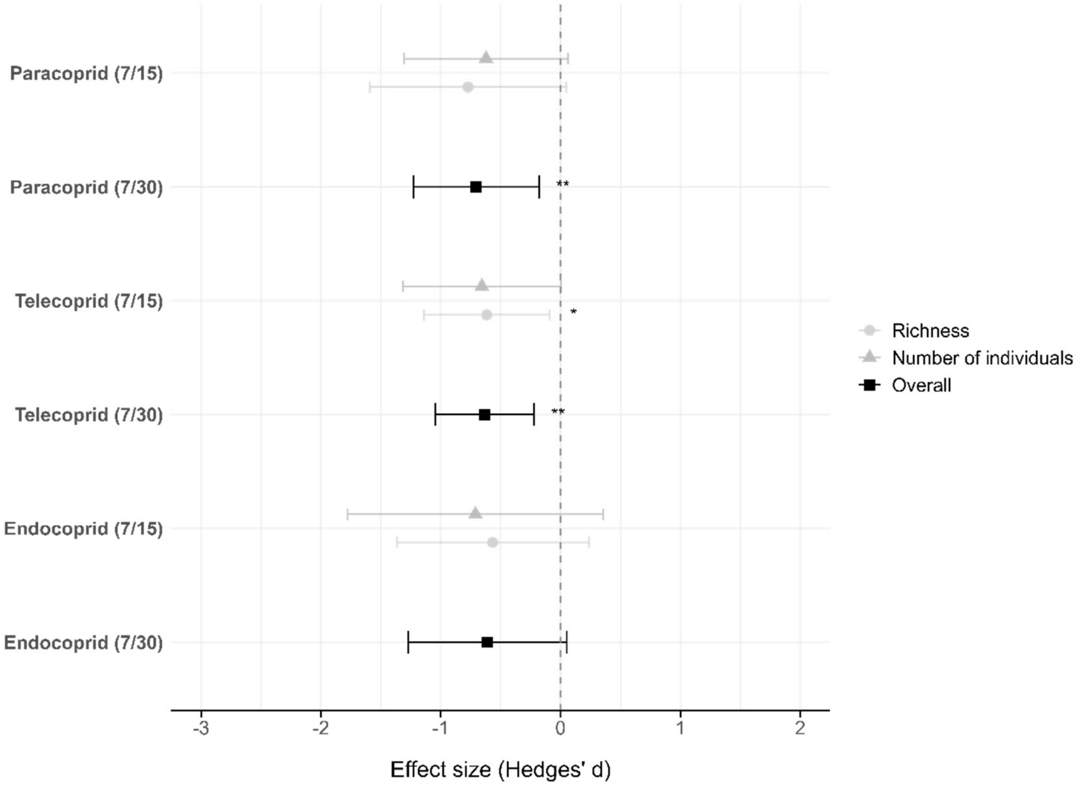

Figure S4. Overall impact on dung beetle functional groups of converting natural ecosystems to pasturelands. Negative values indicate a detrimental effect of habitat conversion. Asterisks denote statistical significance, as follows *= $p < 0.05$, **= $p < 0.01$, and ***= $p < 0.001$.

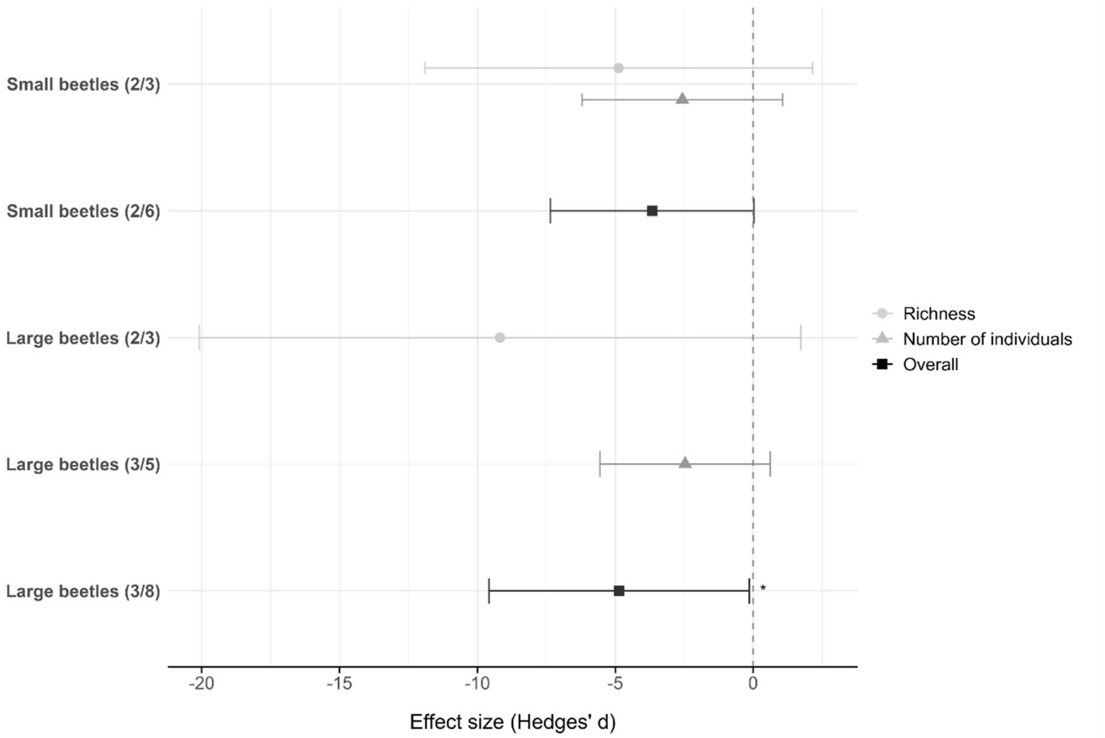

Figure S5. Dung beetle body–size responses to conversion of natural ecosystems to pasturelands. Asterisks denote statistical significance, as follows *= $p < 0.05$, **= $p < 0.01$, and ***= $p < 0.001$.

Meta–regression

Latitude

Global model:

fit_null <– rma(yi ~ Latitude, vi, data, method = "HE")
fit_linear   <– rma(yi ~ Latitude, vi, data, method = "HE")
fit_quadratic <– rma(yi ~ Latitude + I(Latitude^2), vi, data, method = "HE")
fit_spline <– rma(yi ~ rcs(Latitude, knots), vi, data, method = "HE")

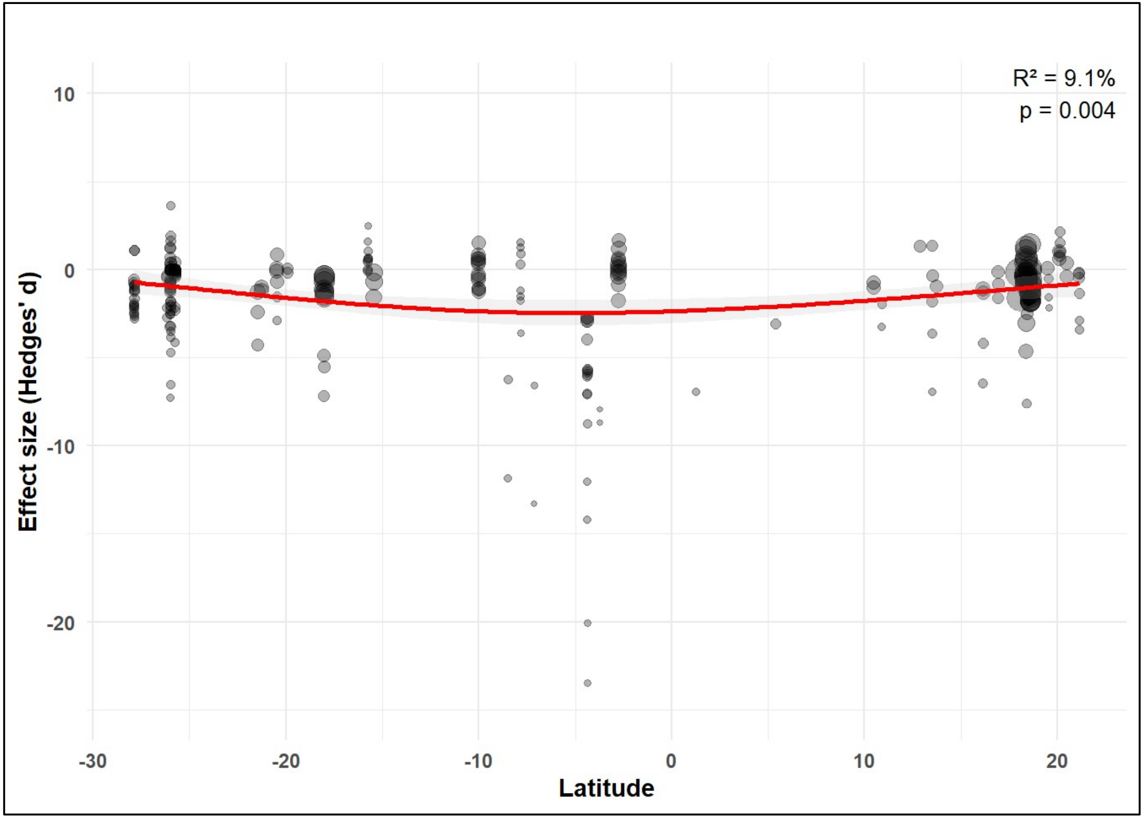

Figure S6. Meta-regression with a quadratic model.

Model	logLink	Deviance	AIC	BIC	AICc
Fit_null	–603.4077	965.2479	1210.8153	1217.8422	1210.8643
Fit_linear	–603.5825	965.5975	1213.1649	1223.7052	1213.2633
Fit_quadratic	**–593.9865**	**946.4055**	**1195.9729**	**1210.0266**	**1196.1375**
Fit_spline	–594.0392	946.5109	1196.0784	1210.1321	1196.2430

Tropical realm and richness
Models fitted with subset "Biogeographic.zone == "Tropical"; Descriptor == "Richness".

Model	logLink	Deviance	AIC	BIC	AICc
Fit_null	–204.6237	341.2626	413.2475	417.9609	413.4075
Fit_linear	–204.0934	340.2019	414.1868	421.2569	414.5111
Fit_quadratic	–196.5549	325.1250	401.1099	410.5367	401.6578
Fit_spline	**–196.2487**	**324.5126**	**400.4975**	**409.9243**	**401.0454**

Tropical realm and abundance
Models fitted with subset "Biogeographic.zone == "Tropical"; Descriptor == "Abundance".

Model	logLik	Deviance	AIC	BIC	AICc
Fit_null	–142.4582	252.8998	288.9164	293.3554	289.1010
Fit_linear	–142.3622	252.7078	290.7245	297.3830	291.0995
Fit_quadratic	–138.6885	245.3604	285.3771	294.2551	286.0120
Fit_spline	**–138.4739**	**244.9313**	**284.9479**	**293.8259**	**285.5828**

Subtropical realm abundance

Model	logLink	Deviance	AIC	BIC	AICc
Fit_null	**–70.15228**	**84.57455**	**144.30456**	**147.57973**	**144.64742**
Fit_linear	–69.62281	83.51562	145.24563	150.15838	145.95151
Fit_quadratic	–69.49682	83.26364	146.99365	153.54399	148.20577
Fit_spline	–69.50786	83.28572	147.01573	153.56607	148.22785

Subtropical realm richness

Model	logLink	Deviance	AIC	BIC	AICc
Fit_null	–66.71909	86.53773	137.43817	140.54887	137.81317
Fit_linear	–65.29644	83.69244	136.59288	141.25893	137.36708
Fit_quadratic	–65.34209	83.78373	138.68418	144.90557	140.01751
Fit_spline	**–65.33806**	**83.77568**	**138.67613**	**144.89752**	**140.00946**

Table S3. Outputs of meta–regression for latitudinal variation in species richness and number of individuals from Figure 6.

Response Variable	Statistic	Estimate	95% CI	p-value	R2
Species richness	QM (2)	12.45	-	0.002	22.4%
Species richness	Intercept	-5.77	[-7.99, -3.55]	< 0.0001	-
Species richness	Spline β1	-0.237	-	0.0032	-
Species richness	Spline β2	0.27	-	0.0007	-
Number of individuals	QM (2)	6.91	-	0.032	17.0%
Number of individuals	Intercept	-2.93	[-4.50, -1.37]	0.0002	-
Number of individuals	Spline β1	-0.13	[-0.239, -0.021]	0.0193	-
Number of individuals	Spline β2	0.201	[0.047, 0.354]	0.0103	-

Study distribution in the Americas

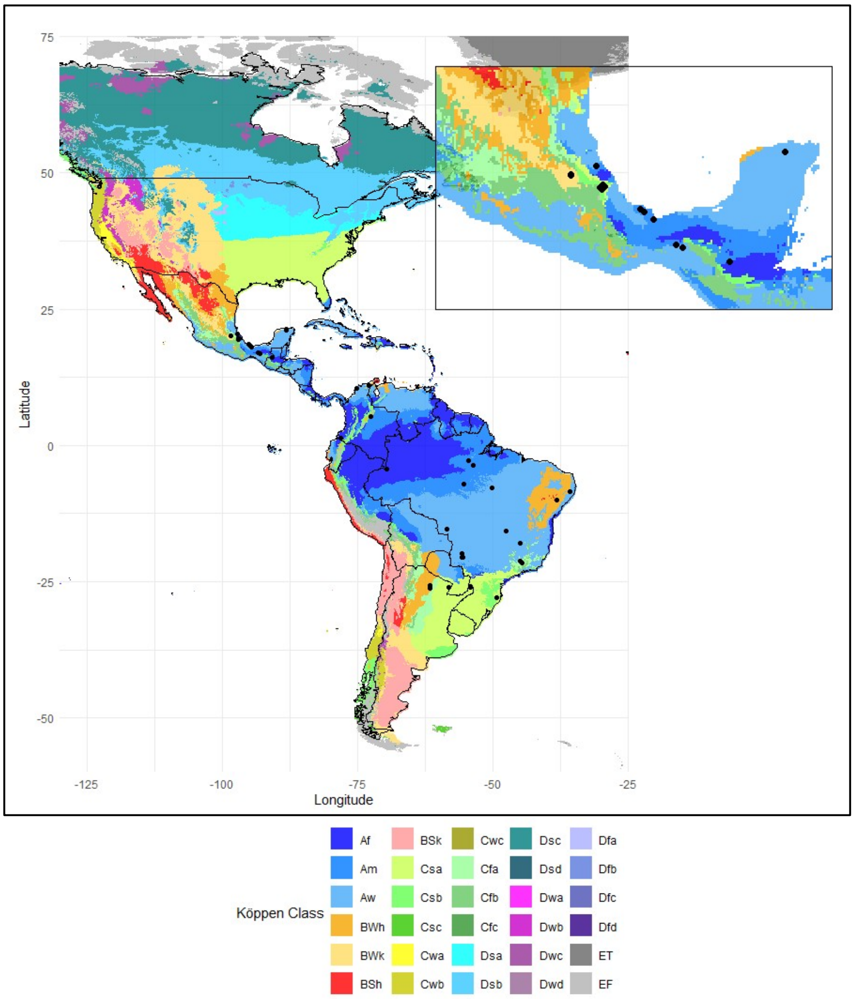

Figure S7. Köppen Geiger climate zones in the Americas and distribution of studies.

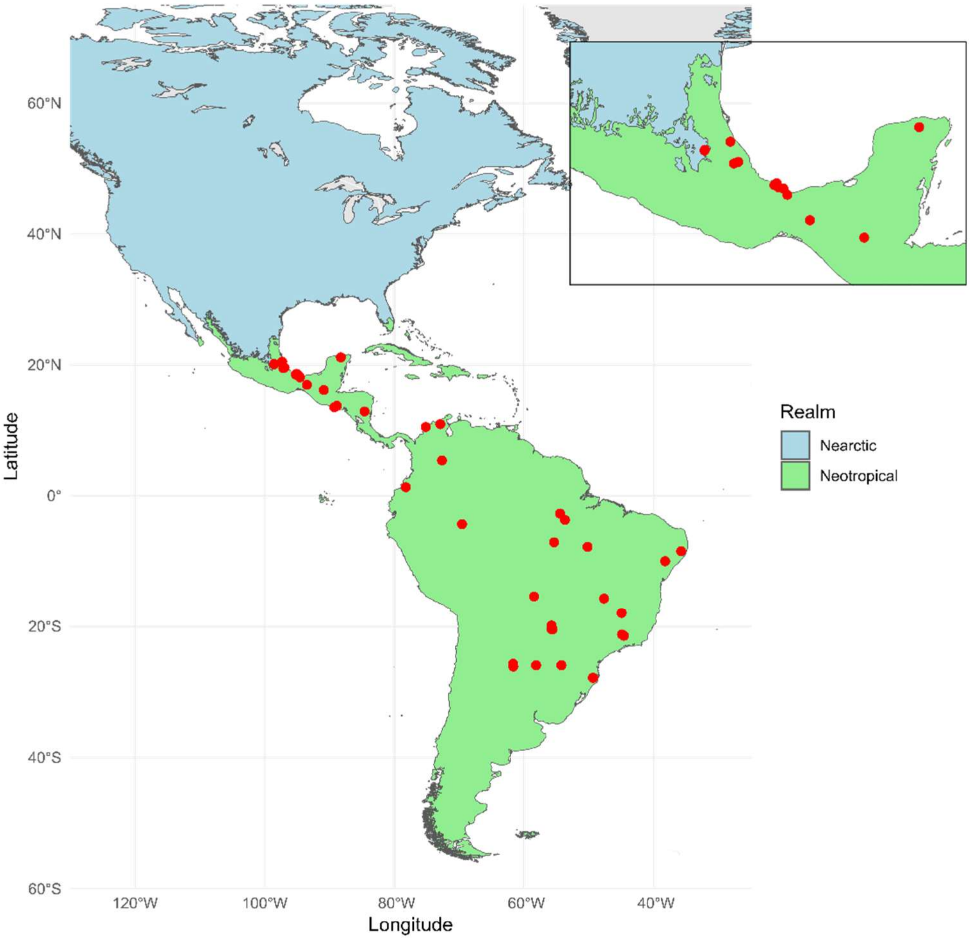

Figure S8. Distribution of studies in Neotropical and Nearctic realms.

Table S4. List of studies included on our meta-analysis.

ID	Year	Author	Title
01	2020	Carvalho et al.	Is dung removal a good proxy for other dung beetle functions when monitoring for conservation? A case study from the Brazilian Amazon
02	2021	Sarmiento-Garcés & Hernández	A decrease in taxonomic and functional diversity of dung beetles impacts the ecosystem function of manure removal in altered subtropical habitats
03	2017	Silva et al.	Abrupt species loss of the Amazonian dung beetle in pastures adjacent to species-rich forests
04	2020	Ortega-Martínez et al.	Assembly mechanisms of dung beetles in temperate forests and grazing pastures
05	2016	Correa et al.	Attractiveness of baits to dung beetles in Brazilian savanna and exotic pasturelands
06	2017	Cajaiba et al.	Can dung beetles (Scarabaeinae) indicate the status of Amazonia's ecosystems? Insights integrating anthropogenic disturbance with seasonal patterns
07	2021	Oliveira, et al.	Changes in land use affect dung beetle communities but do not affect ecosystem services in the Cerrado of Central Brazil
08	2020	Macedo et al.	Conversion of Cerrado savannas into exotic pastures: The relative importance of vegetation and food resources for dung beetle assemblages
09	1998	Estrada et al.	Dung and carrion beetles in tropical rain forest fragments and agricultural habitats at Los Tuxtlas, Mexico
10	2005	Scheffler P.Y.,	Dung beetle (Coleoptera: Scarabaeidae) diversity and community structure across three disturbance regimes in eastern Amazonia
11	2008	Navarrete D., Halffter G.,	Dung beetle (Coleoptera: Scarabaeidae: Scarabaeinae) diversity in continuous forest, forest fragments and cattle pastures in a landscape of Chiapas, Mexico: The effects of anthropogenic changes
12	2016	Silva et al.	Dung beetle (Coleoptera: Scarabaeinae) persistence in Amazonian forest fragments and adjacent pastures: biogeographic implications for alpha and beta diversity
13	2013	Braga et al.	Dung Beetle Community and Functions along a Habitat-Disturbance Gradient in the Amazon: A Rapid Assessment of Ecological Functions Associated to Biodiversity
14	2015	Filgueiras et al.	Dung beetle persistence in human-modified landscapes: Combining indicator species with anthropogenic land use and fragmentation-related effects
15	2020	Guerra Alonso et al.	Dung beetles response to livestock management in three different regional contexts
16	2007	Escobar et al.	From forest to pasture: an evaluation of the influence of environment and biogeography on the structure of dung beetle(Scarabaeinae) assemblages along three altitudinal gradients in the Neotropical region
17	2016	Bourg et al.	Got Dung? Resource Selection by Dung Beetles in Neotropical Forest Fragments and Cattle Pastures
18	2007	Halffter et al.	Instability of copronecrophagous beetle assemblages (Coleoptera : Scarabaeinae) in a mountainous tropical landscape of Mexico
19	2015	Montoya-Molina et al.	Land sharing vs. land sparing in the dry Caribbean lowlands: A dung beetles' perspective
20	2019	Guerra Alonso et al.	Livestock areas with canopy cover sustain dung beetle diversity in the humid subtropical Chaco forest
21	2020	Rivera et al.	Mechanisms of diversity maintenance in dung beetle assemblages in a heterogeneous tropical landscape
22	2019	Correa et al.	Patterns of taxonomic and functional diversity of dung beetles in a human-modified variegated landscape in Brazilian Cerrado

23	2021	Guerra Alonso et al.	Response of dung beetle taxonomic and functional diversity to livestock grazing in an arid ecosystem
24	2020	Rangel-Acosta et al.	Response of dung beetles (Scarabaeidae: Scarabaeinae) to habitat modification caused by a forest fire in the Bijibana Reserve, Atlantico-Colombia
25	2020	Ríos-Díaz et al	Sheep herding in small grasslands promotes dung beetle diversity in a mountain forest landscape
26	2020	Salomão et al.	Spatial and temporal changes in the dung beetle diversity of a protected, but fragmented, landscape of the northernmost Neotropical rainforest
27	2011	Almeida et al.	Subtle Land-Use Change and Tropical Biodiversity: Dung Beetle Communities in Cerrado Grasslands and Exotic Pastures
28	2016	de Albuquerque et al.	Using dung beetles to evaluate the conversion effects from native to introduced pasture in the Brazilian Pantanal
29	2017	Costa et al.	Variegated tropical landscapes conserve diverse dung beetle communities
30	2018	Alvarado et al.	The role of livestock intensification and landscape structure inmaintaining tropical biodiversity
31	2023	Gonzalez-Gomez et al.	Infuence of landscape and livestock management on dungbeetle diversity in tropical cattle pastures
32	NP	Dos-Reis et al.	Doctoral tesis
33	2008	Horgan, F. G.	Dung beetle assemblages in forests and pastures of El Salvador: a functional comparison
34	2007	Horgan, F. G.	Dung beetles in pasture landscapes of Central America:proliferation of synanthropogenic speciesand decline of forest specialists
35	FES	Escobar, F.	Data raw - Los Tuxlas - Magallanes
36	FES	Escobar, F.	Data raw - Los Tuxlas - Montepio

NP = Not published.

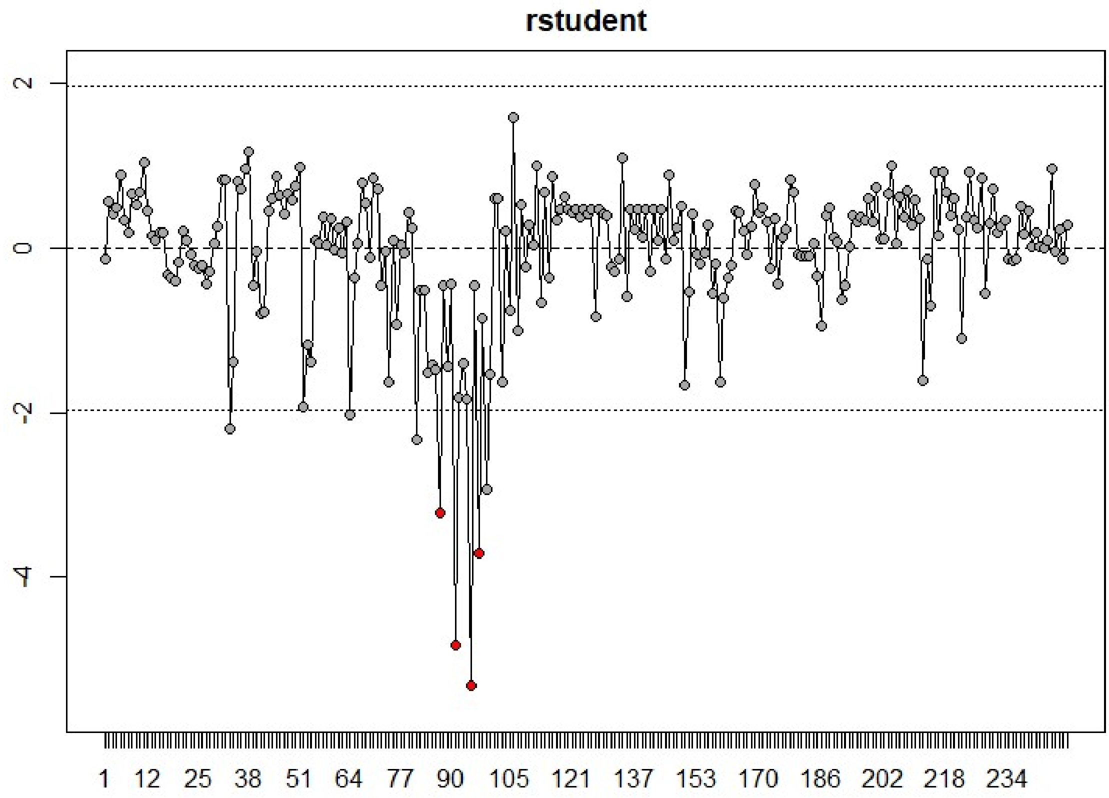

Figure S9. Outliers evaluation.

Table S4. General outputs for *hedges* d’ estimator and complete statistics for each descriptor level. Acronyms heading columns as in Borenstein et al. (2009) and metafor package. k = number of comparisons extracted from studies.

Data_level	**Descriptor**	**studies**	**k**	**estimate**	**se**	**zval**	**ci_lb**	**ci_ub**	**tau^2**	**tau**	**I^2**	**H^2**	**pval**	**signif**
General	Overall	36	248	–1,41	0,19	–7,26	–1,79	–1,03	8,58	2,93	97,68	43,04	<0,001	***
General	Abundance	30	106	–1,07	0,18	–5,86	–1,43	–0,71	3	1,73	94,05	16,8	<0,001	***
General	Biomass	10	15	–0,86	0,56	–1,54	–1,95	0,23	3,98	2	92,05	12,57	0,12	
General	Diversity (q=1)	2	3	–0,94	0,54	–1,72	–2	0,13	0	0	0	1	0,08	
General	Diversity (q=2)	2	3	0,73	0,78	0,93	–0,8	2,25	0,78	0,88	43,41	1,77	0,35	
General	Dung removed	2	4	–6,07	5,74	–1,06	–17,31	5,18	129,01	11,36	99,79	474,38	0,29	
General	Richness	35	113	–1,68	0,3	–5,55	–2,27	–1,09	9,45	3,07	97,93	48,24	<0,001	***
General	Soil excavated	2	4	–3,65	3,69	–0,99	–10,89	3,58	53,36	7,3	99,33	150,36	0,32	
Assemblage	Overall	36	144	–1,65	0,27	–6,16	–2,17	–1,12	9,3	3,05	97,33	37,44	<0,001	***
Assemblage	Richness	35	62	–2,04	0,37	–5,51	–2,76	–1,31	7,39	2,72	96,84	31,67	<0,001	***
Assemblage	Abundance	30	53	–1,2	0,25	–4,89	–1,68	–0,72	2,59	1,61	91,29	11,48	<0,001	***
Assemblage	Biomass	10	15	–0,86	0,56	–1,54	–1,95	0,23	3,98	2	92,05	12,57	0,12	
Assemblage	Dung removed	2	4	–6,07	5,74	–1,06	–17,31	5,18	129,01	11,36	99,79	474,38	0,29	
Assemblage	Soil excavated	2	4	–3,65	3,69	–0,99	–10,89	3,58	53,36	7,3	99,33	150,36	0,32	
Assemblage	Diversity (q=1)	2	3	–0,94	0,54	–1,72	–2	0,13	0	0	0	1	0,08	
Assemblage	Diversity (q=2)	2	3	0,73	0,78	0,93	–0,8	2,25	0,78	0,88	43,41	1,77	0,35	
Large beetles	Overall	3	8	–4,86	2,41	–2,02	–9,57	–0,14	45,01	6,71	99,27	137,07	0,04	*
Large beetles	Richness	2	3	–9,18	5,57	–1,65	–20,09	1,73	90,07	9,49	98,75	79,97	0,1	
Large beetles	Abundance	3	5	–2,47	1,58	–1,56	–5,55	0,62	11,96	3,46	97,84	46,36	0,12	
Small beetles	Overall	2	6	–3,66	1,89	–1,94	–7,36	0,03	20,59	4,54	98,4	62,37	0,05	
Small beetles	Richness	2	3	–4,88	3,59	–1,36	–11,91	2,16	37,55	6,13	98,89	90,07	0,17	
Small beetles	Abundance	2	3	–2,57	1,86	–1,38	–6,21	1,08	9,94	3,15	96,72	30,51	0,17	
Paracoprid	Overall	7	30	–0,7	0,27	–2,63	–1,23	–0,18	1,7	1,3	91,99	12,48	0,01	**
Paracoprid	Richness	7	15	–0,77	0,42	–1,84	–1,59	0,05	2,16	1,47	93,05	14,38	0,07	
Paracoprid	Abundance	7	15	–0,62	0,35	–1,79	–1,3	0,06	1,4	1,18	90,42	10,44	0,07	
Telecoprid	Overall	7	30	–0,63	0,21	–3	–1,05	–0,22	0,97	0,99	86,39	7,35	<0,001	**
Telecoprid	Richness	7	15	–0,62	0,27	–2,3	–1,14	–0,09	0,75	0,87	81,9	5,52	0,02	*
Telecoprid	Abundance	7	15	–0,66	0,34	–1,95	–1,32	0	1,29	1,14	89,39	9,42	0,05	
Endocoprid	Overall	7	30	–0,61	0,34	–1,81	–1,27	0,05	2,94	1,71	94,72	18,94	0,07	
Endocoprid	Richness	7	15	–0,57	0,41	–1,38	–1,37	0,24	2,09	1,44	92,22	12,85	0,17	
Endocoprid	Abundance	7	15	–0,71	0,54	–1,3	–1,78	0,36	3,91	1,98	95,92	24,5	0,19	

Table S5. *Hedges* d’ estimator and complete statistics for each moderator/modulator level. k = number of comparisons extracted from studies.

Moderator/modulator	**Level**	**studies**	**k**	**estimate**	**se**	**zval**	**ci_lb**	**ci_ub**	**tau^2**	**tau**	**I^2**	**H^2**	**pval**	**signif**
Pasture_type	Pasture	34	205	–1,74	0,22	–7,77	–2,18	–1,3	9,46	3,08	98,13	53,35	<0,001	***
Pasture_type	Silvopastoral system	6	41	0	0,18	0,01	–0,34	0,34	0,61	0,78	51,41	2,06	>0,1	
Forest_type	Primary	13	90	–1,64	0,42	–3,95	–2,46	–0,83	14,93	3,86	99,22	128,02	<0,001	***
Forest_type	Secondary	9	40	–1,58	0,34	–4,68	–2,25	–0,92	3,77	1,94	90,63	10,67	<0,001	***
Climate.zone	Tropical	32	171	–1,61	0,27	–6,05	–2,14	–1,09	11,25	3,35	98,62	72,26	<0,001	***
Climate.zone	Subtropical	4	77	–0,96	0,2	–4,87	–1,35	–0,57	2,31	1,52	79,83	4,96	<0,001	***
Biogeographic	Neotropic	34	242	–1,48	0,2	–7,5	–1,86	–1,09	8,59	2,93	97,7	43,57	<0,001	***
Biogeographic	Nearctic	2	6	1	0,25	4,03	0,51	1,49	0	0	0	1	<0,001	***
Hemisphere	South	20	172	–1,59	0,26	–6,04	–2,1	–1,07	10,85	3,29	97,01	33,47	<0,001	***
Hemisphere	North	16	76	–1,03	0,22	–4,74	–1,46	–0,61	3,2	1,79	96,71	30,36	<0,001	***

Table S6. Effect sizes estimated from 10 000 bootstrap simulations, with 95 % confidence intervals and meta-analysis validation metrics. Abbreviations: $\bar{g}$ = mean standardized mean difference; Fsn = fail-safe number; T&F = trim-and-fill estimate; k0 = estimated number of missing studies suggested by trim-and-fill; lb/ub = lower/upper bound of 95 % confidence interval.

Moderator/modulator	**$\bar{x}$_g**	**ci_g_lb**	**ci_g_ub**	**$\bar{x}$_Fsn**	**ci_Fsn_lb**	**ci_Fsn_ub**	**$\bar{x}$_k0**	**ci_k0_lb**	**ci_k0_ub**	**$\bar{x}$_T&F**	**ci_T&F_lb**	**ci_T&F_ub**
Richness	-1.91	-2.33	-1.55	3172.98	2200.98	4332.00	0.04	0	1	-1.91	-2.32	-1.55
Abundance	-1.13	-1.43	-0.89	1011.48	551.98	1584.00	0.20	0	1	-1.12	-1.43	-0.87
Biomass	-0.77	-1.07	-0.47	60.12	27.00	100.00	1.75	1	2	-1.26	-1.70	-0.70
Assemblage	-1.44	-1.89	-1.01	2175.32	1201.00	3281.07	0.48	0	6	-1.40	-1.88	-0.81
LargeDG	-2.93	-5.22	-1.67	27.08	12.00	46.00	0.00	0	0	-2.93	-5.22	-1.67
SmallDG	-2.77	-6.07	-1.03	12.11	4.00	23.00	NA	NA	NA	NA	NA	NA
Paracoprid	-0.66	-1.07	-0.25	53.44	9.00	116.00	0.24	0	1	-0.67	-1.05	-0.27
Telecoprid	-0.68	-1.14	-0.27	43.48	0.00	128.00	0.45	0	2	-0.65	-1.16	-0.16
Endocoprid	-0.45	-1.28	0.26	36.02	0.00	132.00	0.70	0	2	-0.61	-1.59	0.25
PrimaryF	-1.31	-2.12	-0.61	322.26	46.00	726.02	0.13	0	2	-1.30	-2.12	-0.48
SecondaryF	-0.99	-1.47	-0.50	58.97	13.00	117.00	0.36	0	3	-0.97	-1.47	-0.32
OpenPasture	-1.62	-2.12	-1.17	2456.32	1367.95	3749.00	1.44	0	9	-1.51	-2.07	-0.76
Silvopastoral	-0.69	-1.44	-0.04	7.42	0.00	33.00	0.32	0	2	-0.65	-1.44	0.08
Tropical	-1.39	-1.88	-0.95	1731.78	858.00	2801.00	0.42	0	5	-1.36	-1.87	-0.78
Subtropical	-1.52	-3.07	-0.21	20.31	0.00	60.00	0.37	0	1	-1.40	-3.05	-0.09
Neotropical	-1.56	-2.06	-1.10	2341.85	1249.00	3667.00	0.62	0	7	-1.52	-2.05	-0.85
Nearctic	1.01	0.65	1.43	3.62	1.00	7.00	NA	NA	NA	NA	NA	NA
North	-1.14	-1.82	-0.53	359.94	55.00	801.02	0.64	0	4	-1.05	-1.82	-0.34
South	-1.70	-2.40	-1.15	747.41	399.00	1182.02	0.24	0	2	-1.67	-2.35	-1.08

For subsets with very few studies (e.g., SmallDG, Neartic), bootstrap replicates often failed to converge due to insufficient data points, which is reported as NA in Table S6.

CAPÍTULO II

DUNG BEETLE (COLEOPTERA: SCARABAEINAE) ASSEMBLAGES' COMPOSITION AND STRUCTURE OF CAATINGA OF THE RASO DA CATARINA ECOREGION

Dung beetle (Coleoptera: Scarabaeinae) assemblages' composition and structure of Caatinga of the Raso da Catarina ecoregion

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Abstract

Dung beetles (Scarabaeinae) are key providers of ecosystem services in seasonally dry tropical forests (SDTFs), yet little is known about their assemblages in the Caatinga biome. Herein, we aimed to characterize the taxocenosis of Scarabaeinae across Caatinga forest fragments from the Raso da Catarina ecoregion. We sampled dung beetles in seven forest fragments of the Raso da Catarina ecoregion (Bahia, Brazil) using human feces and cattle dung as baits. A total of 4,068 individuals were collected, representing 31 species and 14 genera. Assemblages were dominated by paracoprids and small-bodied species, although some fragments were characterized by large-bodied taxa. Species richness varied between bait types, but abundance was consistently higher in cattle dung. NMDS ordinations revealed considerable dissimilarity among fragments, while bait type contributed to within-fragment variation. Despite some resource-specific occurrences, 77% of the species exploited both dung types, indicating high resource plasticity. Our findings refine baselines for Scarabaeinae in the Caatinga and highlight the ability of native assemblages to exploit livestock manure, a key resource in human-modified dry forests. This work also underscores the importance of forest fragments as reservoirs of dung beetle diversity in semi-arid landscapes.

Keywords: Scarabaeinae, Seasonally dry tropical forests, entomofauna, Biodiversity, Functional guilds.

Introduction

Seasonally dry tropical forests (SDTFs) remain among the least studied Neotropical biomes despite their extent and rapid transformation (Dirzo et al., 2011; Stan & Sanchez-Azofeifa, 2019; Lopez-Toledo et al., 2024). Among these, the Caatinga in northeastern Brazil is the largest continuous SDTF nucleus and an important endemism hotspot; yet it has been comparatively under-sampled and poorly protected compared with its area and biodiversity (Leal et al., 2005; Santos et al., 2011; de Albuquerque et al., 2012; Silva et al., 2017; Lessa et al., 2019). Knowledge gaps are especially acute for the entomofauna, with few baselines that integrate taxonomic diversity and their role in functioning ecosystems (de Albuquerque et al., 2012; Silva et al., 2017).

Dung beetles (Coleoptera: Scarabaeinae) are widely used as bioindicators of biodiversity (Halffter & Favila, 1993; Nichols & Gardner, 2011) because they couple community changes to key ecological processes that matter for both natural habitats and agroecosystems, like pastures, including dung removal, soil bioturbation, nutrient cycling, seed secondary dispersal, and mitigation of greenhouse gas emissions from cattle pats (Nichols et al., 2008; Slade et al., 2016; deCastro-Arrazola et al., 2023). Their functional roles are mediated by behavioral guilds and body size. Therefore, shifts in assemblage composition can scale up to altered ecosystem functioning (Milotić et al., 2017; Nervo et al., 2014). These properties make dung beetles an especially informative taxon for evaluating how pasture expansion and management intensity modify biodiversity and ecosystem services in the Neotropics (Arellano et al., 2023).

Dung beetles have a long-term evolutionary association with mammals' dung (Halffter & Matthews, 1966; Bogoni et al., 2019; Halffter & Favila, 2023), therefore they are specialized in a broad range of dung resources (Halffter & Matthews, 1966). As a result, preference in dung resources may arise from biological inventories from forested areas, because some species can deal better with herbivore dung than with carnivore or omnivore dung. Yet, in livestock-dominated Caatinga landscapes, comparisons still rarely evaluate resource filters alongside habitat type, which complicates the inference about how pasture conversion reshapes native dung beetle faunas. Addressing this gap is essential if we are to link observed taxonomic shifts to changes in function under real management regimes.

Available information on Scarabaeinae dung beetles in Caatinga is still incipient, with few published inventories that are geographically clustered and leave large portions of the region unsampled. Across Caatinga landscapes, native forest fragments are frequently used as emergency grazing areas during the dry season (Fortini et al., 2022), increasing the availability of cattle dung within native habitats and potentially reshaping resource regimes for dung beetles. Understanding how native dung beetles assemblages respond to cattle manure under these conditions is therefore essential. The aim of this study is to refine baselines for Caatinga fauna by describing assemblage composition and structure in forest fragments and evaluating their responses to contrasting dung resources.

Here we characterize the taxocenosis of Scarabaeinae across Caatinga forest fragments from the Raso da Catarina ecoregion, using a standardized sampling design that explicitly contrasts bait types commonly used in dung beetle diversity surveys. Specifically, we (i) describe alpha diversity (richness, number of individuals, evenness) and evaluate sampling coverage; (ii) quantify functional groups composition (paracoprids, telecoprids, endocoprids) and body-size classes (large and small); (iii) compare assemblage composition between fragments and between bait types; and (iv) identify indicator species associated with each bait type. This integrated approach allows us to distinguish habitat-driven differences among fragments from resource-driven differences attributable to bait use, thereby clarifying how each filter structures the assemblages.

Material and Methods

Our study was conducted in the northern region of the Bahia state, Brazil, within the municipalities of Jeremoabo, Antas, Paulo Afonso, and Sitio do Quinto. The fragments are within the Raso da Catarina ecoregion (Velloso et al., 2002). The region is in the Caatinga biome, a type of seasonal tropical dry forest, characterized by a hot and dry climate, it corresponds to *BSh,* Arid steppe hot from Köppen-Geiger (Beck et al., 2018), with average annual temperatures of 25 ºC and annual precipitation of 650 mm per year (Ab'Sáber, 1974; Velloso et al., 2002).

Dung beetle sampling

We sampled dung beetles from seven forest fragments of Caatinga from August to October 2023, a single field campaign per fragment (**Figure 1**). In each Caatinga fragment we established two transects of 300 m with at least 150 m from each other and at least 200 m from the edge to avoid forest edge influence (**Figure 1**d). Along each transect, six 1 L pitfall traps (12 cm diameter and 13 cm deep) were installed buried flush with the ground separated 50 m apart filled with ca. 200 mL of a lethal solution (saline solution with detergent and water). Each transect of traps were baited with either human feces or a mixture of cattle dung and pig manure (proportion of 3:1, respectively). The pitfall traps were covered with plastic protection to protect them from rain and drying out by exposure to the sun. The traps remained exposed for a total of 24 hours, and the collected insects were labeled, cleaned and preserved in containers with 70% alcohol. After screening in the laboratory, the specimens were dried. The beetles were identified to the lowest possible taxonomic level using taxonomic identification keys (Vaz-de-Mello et al., 2011) and verification with a taxonomist specialist in the group. The collected specimens were deposited in the following collections: Gregório Bondar entomological collection of the Cocoa Research Center (CEGB – CEPEC/CEPLAC), Ilhéus, Bahia; and Eurico Furtado Entomological Collection of UFMT, Cuiabá, Mato Grosso.

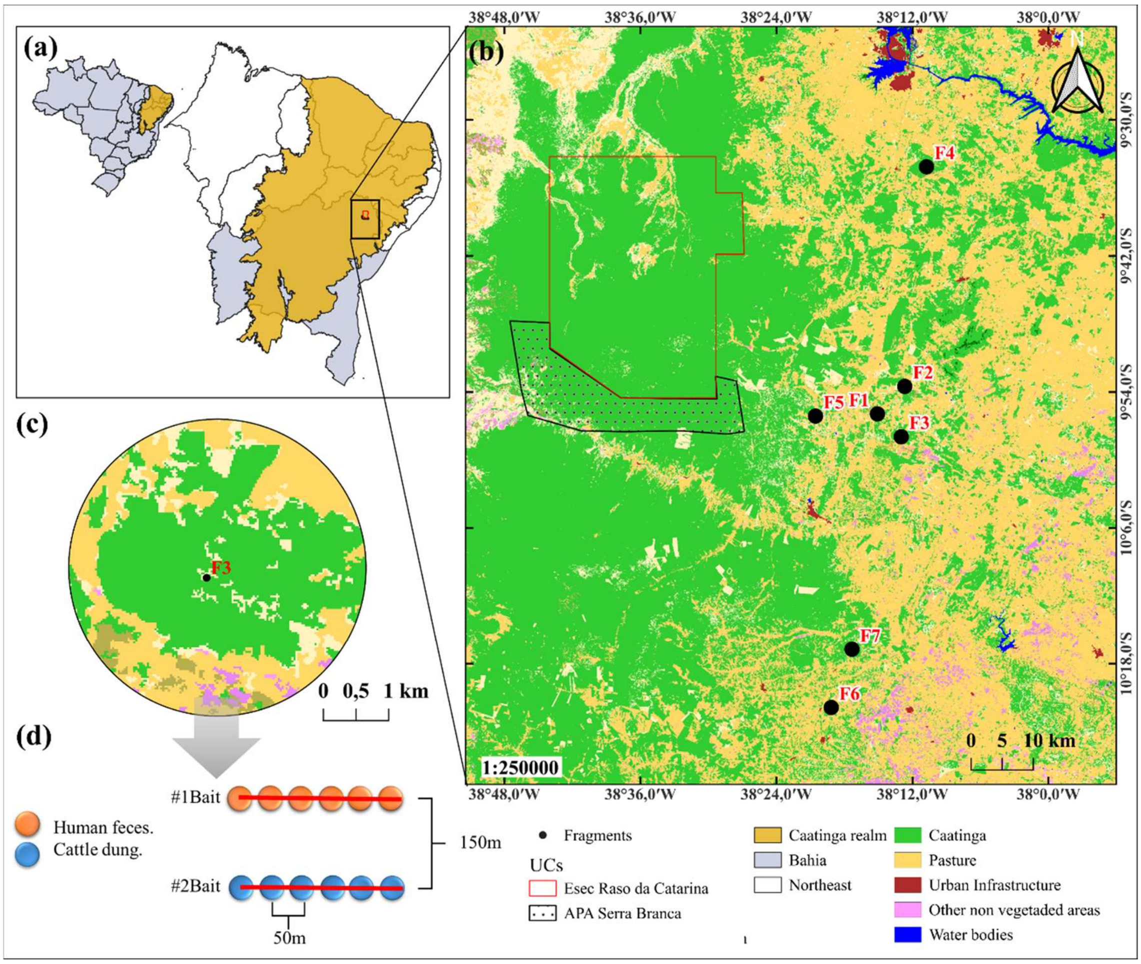

Figure 1. Map of sampling sites. (a) Brazil and northeast region in evidence. (b) sampling region. (c) forest fragment in 1km scale buffer. (d) sampling design.

Species were classified by food relocation behavior (hereafter as FRB) following the paracoprid, telecoprid, and endocoprid, following the literature (Halffter & Edmonds, 1982; Tonelli, 2021; Maldaner et al., 2024). Body size was defined as follows: beetles ≥ 10 mm were classified as large, and those < 10 mm as small beetles (Cambefort & Hanski, 1991). Body sizes were based on measurement of specimens captured in this research. To do so, measurements of pronotum plus elytra length were taken to compose body length using an average of five individuals per species.

Data analysis

We computed diversity estimates and standard errors (SE) using the iNEXT package and we calculated the sampling effort using rarefaction-extrapolation curves with an extrapolation based on the abundance of specimens collected (Hsieh et al., 2016). We drew rank-abundance curves for the evaluation of species dominance, rarity, and assemblage evenness among fragments and comparing baits. All analyses and plots were made using R software (R Core Team 2018). We constructed a Venn diagram to compare species richness among the different bait types, highlighting both shared and exclusive species. Additionally, we performed non-metric multidimensional scaling (NMDS) to visualize the arrangement among assemblages captured with each bait type and to assess patterns of species overlap.

Results

A total of 4,068 specimens of dung beetles (Scarabaeinae) were collected, representing 14 genera and 31 species (mean and standard deviation = 14.86 ± 5.98) (Table 7, **Figure 2**a). Sample coverage was reasonably accurate, as fragments were above 90% across baits (**Figure 2**b). Estimated species richness suggests that at least 38 species would be present, while a less conservative scenario would estimate 49 species (95% IC) (**Figure S10**). The genus *Canthidium* Erichson, 1847, was the most diverse, with six species, followed by *Dichotomius* Hope, 1838, with five species, and *Canthon* Hoffmannsegg, 1817, *Deltochilum* Eschscholtz, 1822, and *Ontherus* Erichson, 1847, each with three species. The most abundant species were *Genieridium margareteae* (Génier & Vaz-de-Mello, 2002) with 974 specimens, *Dichotomius irinus* (Harold, 1867) with 575 specimens, and *Ateuchus semicribratus* (Harold, 1868) with 522 specimens. The number of individuals varied across fragments and baits, averaging 581.14 ± 516.55 (mean and SD) (Table 7; **Figure 3**). Three species were singletons (Table 7).

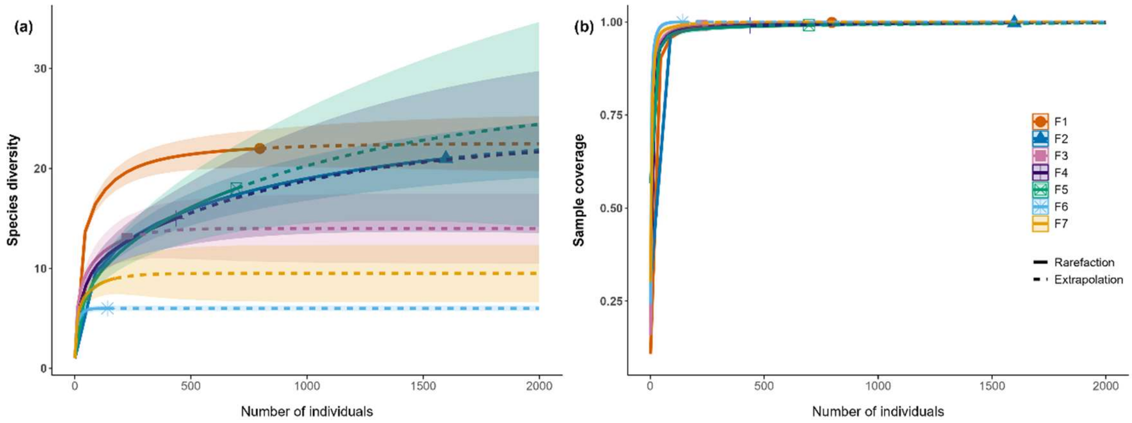

Figure 2. (a) Species richness curve of dung beetles (Scarabaeinae) observed (solid line) and extrapolated (dashed line) based on the number of individuals collected from forest fragments of Caatinga (i.e. seven fragments). Shaded projection corresponds to 95% IC. (b) sample coverage of our dung beetle assemblages from forest fragments of Caatinga. Endpoints or extrapolation defied by 2000.

Species richness sampled with human feces was not consistently higher than those sampled with mix cattle dung bait, as species of some fragments showed greater attraction to human feces while others to cattle dung (**Figure 3**a). In contrast, the number of individuals was consistently higher in fragments baited with cattle dung than with human feces (**Figure 3**b).

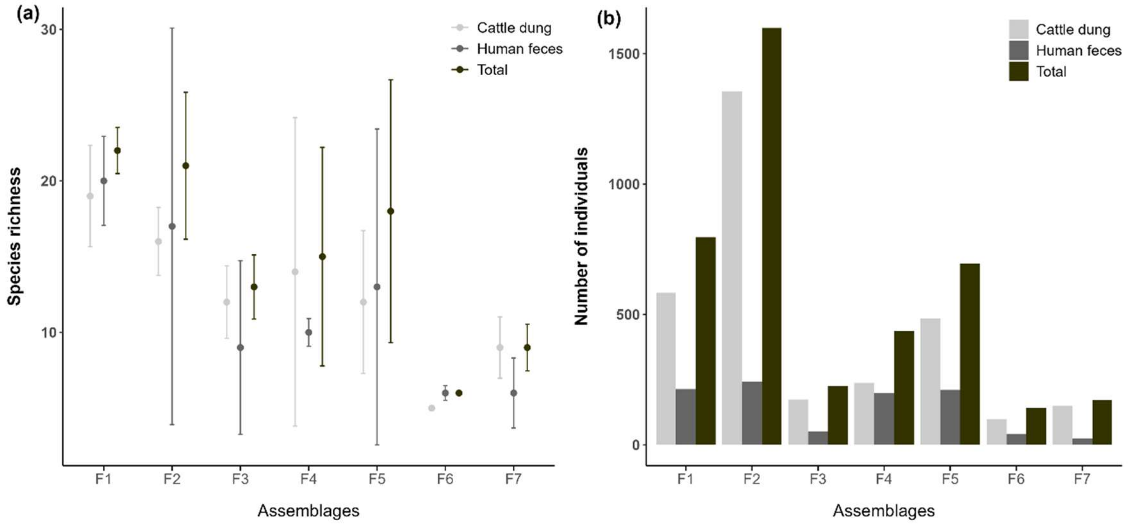

Figure 3. Species richness (a) and number of individuals (b) collected through seven Caatinga fragments sampled according to bait type.

Table 7. Dung beetle species recorded from seven Caatinga fragments in the Raso da Catarina ecoregion, northern of Bahia state, Brazil. Invasive alien species (§), new records (*), see methods cattle dung mixed with pig dung (3:1) (#). FRB = food relocation behavior, Par = paracoprid, Tel = telecoprid, End = endocoprid.

Species	FRB	Size	Human feces	Cattle dung$^{\#}$	Total
Ateuchus aff. ovalis	Par	Small	1	0	1
Ateuchus semicribratus (Harold, 1868)	Par	Small	27	495	522
Canthidium aff. manni	Par	Small	8	1	9
Canthidium sp. 1	Par	Small	13	7	20
Canthidium sp. 2	Par	Small	29	11	40
Canthidium sp. 3	Par	Small	17	6	23
Canthidium sp. 4	Par	Small	8	0	8
Canthidium sp. 5	Par	Small	0	1	1
Canthon aff. carbonarius	Tel	Small	10	7	17
Canthon sp. 1	Tel	Small	96	77	173
Canthon conformis Harold, 1869	Tel	Small	6	2	8
Deltochilum pseudoicarus Balthasar, 1939	Tel	Large	5	0	5
Deltochilum sp.1	Tel	Large	2	8	10
Deltochilum verruciferum Felsche, 1911	Tel	Large	139	125	264
Diabroctis mimas (Linnaeus, 1758)	Par	Large	0	1	1
Dichotomius bos (Blanchard, 1845)	Par	Large	0	5	5
Dichotomius geminatus (Arrow, 1913)	Par	Large	98	242	340
Dichotomius irinus (Harold, 1867)	Par	Large	135	440	575
Dichotomius nisus (Olivier, 1789)	Par	Large	81	173	254
Dichotomius puncticollis (Luederwaldt, 1935)	Par	Large	31	98	129
Digitonthophagus gazella (Fabricius, 1787)§	Par	Large	0	8	8
Genieridium margareteae (Génier & Vaz-de-Mello, 2002)	End	Small	86	888	974
Malagoniella astyanax (Olivier, 1789)	Tel	Large	14	13	27
Ontherus appendiculatus (Mannerheim, 1828)	Par	Small	1	6	7
Ontherus azteca Harold, 1869	Par	Large	8	26	34
Ontherus digitatus Harold, 1868	Par	Small	33	86	119
Onthophagus aff. ptox	Par	Small	2	49	51
Onthophagus hircus Billberg, 1815	Par	Small	23	136	159
Tetraechma liturata (Germar, 1813)	Tel	Small	4	4	8
Trichillum externepunctatum Preudhomme de Borre, 1880	End	Small	5	49	54
Uroxys bahianus Boucomont, 1928	Par	Small	102	120	222
Species richness	—	—	**27**	**28**	**31**
Number of individuals	—	—	**984**	**3084**	**4068**

The species *Ateuchus* aff. *ovalis*, *Canthidium* sp. 4, and *Deltochilum pseudoicarus* Balthasar, 1939, were restricted to human feces baits, while *Canthidium* sp. 5, *Diabroctis mimas* (Linnaeus, 1758), *Dichotomius bos* (Blanchard, 1845), and *Digitonthophagus gazella*

(Fabricius, 1787) were restricted to cattle dung. It is important to note that *D. gazella* is an invasive alien species. Finally, many species could use both baits (**Figure 4**).

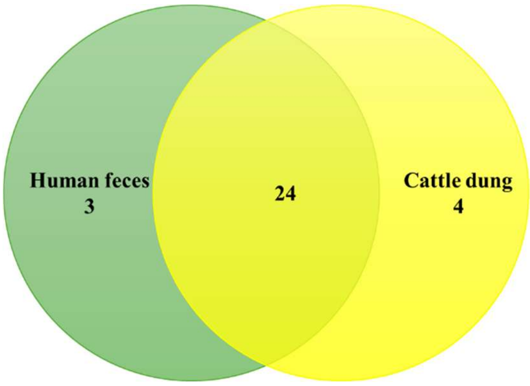

Figure 4. Veen diagram showing species shared and exclusive from each bait type.

The assemblages' evenness varied between baits as shown by the rank-abundance plot (**Figure 5**), while dung beetle assemblages associated with human feces were more even than those associated with cattle manure bait.

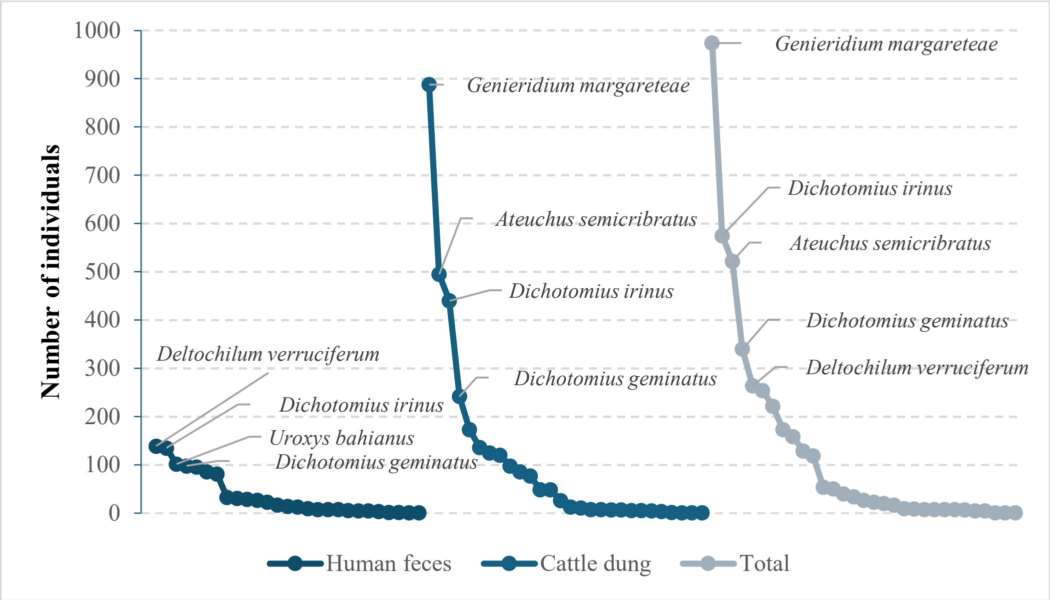

Figure 5. Rank-abundance curves showing species abundance distribution of dung beetles per bait type.

Non-metric multidimensional scaling (NMDS) ordinations showed that dung beetle assemblages responded both to bait type and to differences among fragments (**Figure 6**). In the Jaccard-based ordination across bait types (**Figure 6**a), assemblages that used cattle dung and human feces were partially differentiated within fragments, although considerable overlap was observed (stress = 0.11). When baits were combined (**Figure 6**b), assemblages separated clearly by fragment, indicating a considerable beta-diversity across sites (stress = 0.022). Ordinations based on the Bray–Curtis index revealed similar patterns, but with a stronger emphasis on species abundances. Across bait types (**Figure 6**c), pairs of points for each fragment tended to cluster, but differences between cattle dung and human feces remained evident in some cases (stress = 0.132). Finally, when both baits were combined (**Figure 6**d), fragments were distinctly separated, reinforcing the compositional and abundance differences among sites (stress = 0.025). Overall, these results demonstrate that bait type introduced within-fragment variation, while fragment identity remained the main driver of assemblage differentiation.

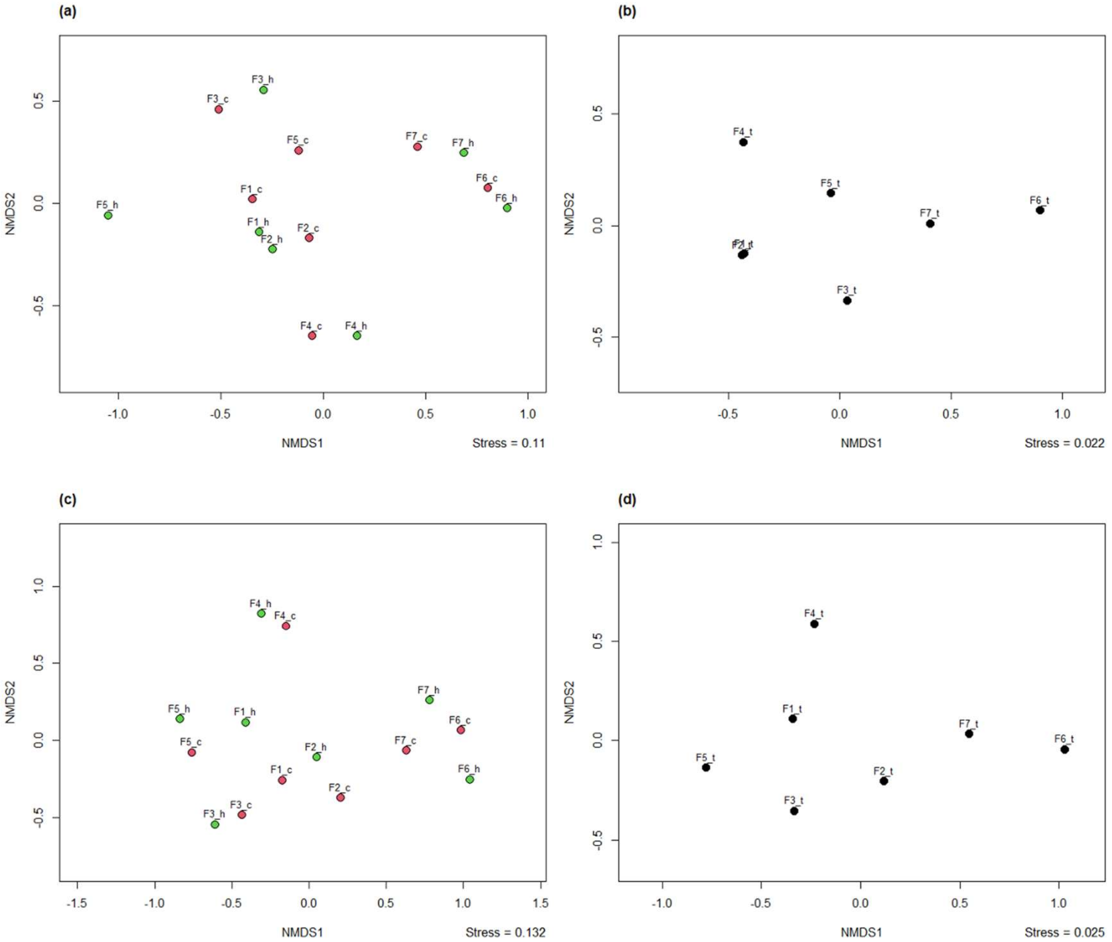

Figure 6. NMDS ordinations of dung beetle assemblages based on: (a) Jaccard index across bait types; (b) Jaccard index for the total assemblage; (c) Bray–Curtis index across bait types; (d) Bray–Curtis index combining both baits. Point colors: red = cattle dung, green = human feces.

The composition of species by functional group varied from forest fragment but assemblages are composed mostly by paracoprids (n = 21), followed by telecoprids (n = 8) and endocoprids (n = 2) (Figure 7a,c). Dung beetle body size analysis shows that assemblages are primarily composed of small species. However, some fragments included larger species (F6, F7, Figure 7b) and variations in abundance (F4 and F5, Figure 7d).

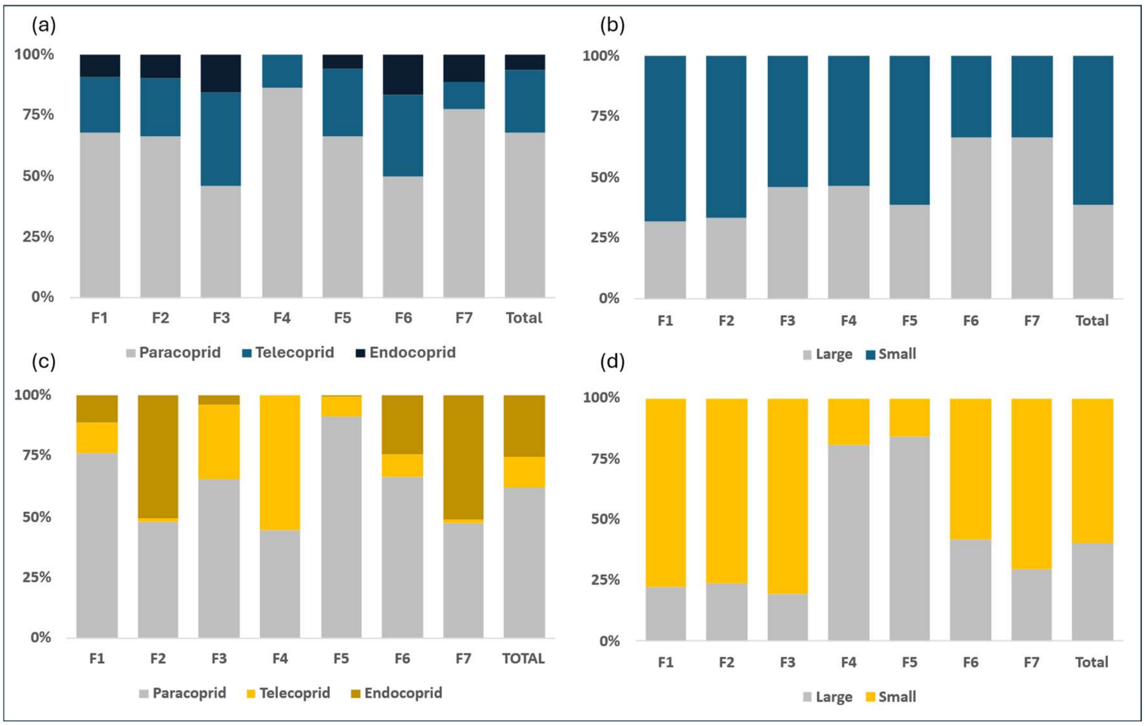

Figure 7. Proportional distribution of dung beetle species richness (a, b) and number of individuals (c, d) by functional group as food relocation behavior (a, c) and body size (b, d).

Ateuchus semicribratus (Harold, 1868) is a small paracoprid widely distributed in the region and was most abundant in cattle dung; it was also very abundant in the pastures of this region (see Chapter III). By contrast, its congener *Ateuchus* aff. *ovalis* was represented by a single individual captured in human feces bait. *Canthidium* spp. were more abundant in traps baited with human feces than with cattle dung. Large telecoprids of the genus *Deltochilum* were generally versatile in their use of resources; however, *Deltochilum pseudoicarus* Balthasar, 1939, one of the largest species (19.55 mm) encountered in this region, was recorded only with human feces bait and appeared to be largely restricted to native habitat, avoiding open areas. In contrast, *Deltochilum verruciferum* Felsche, 1911 behaved as a generalist, using both resources and habitats without much problem.

Dichotomius comprises paracoprids of particular relevance for pastures. *Dichotomius bos*, *Dichotomius geminatus* and *Dichotomius nisus* are frequently cited as important to the livestock industry (Maldaner et al., 2024). In our study, these species were more abundant in pitfall traps baited with cattle dung than with human feces. Notably, *Dichotomius bos* was recorded exclusively in cattle dung traps. In contrast, *Dichotomius irinus* and *Dichotomius puncticollis* were highly restricted to native Caatinga fragments. Regarding *D. irinus*, it is important to note that this species is the most abundant *Dichotomius* across our sampled fragments. In other words, is likely that the species replaces the role of *D. bos*, *D. nisus* and *D. geminatus* in this region with respect to the utilization of cattle manure in Caatinga fragments.

Ontherus Erichson, 1847 was represented by three species, most of which used cattle dung more frequently than human feces. Among them, *Ontherus appendiculatus* (Mannerheim, 1828) and *Ontherus digitatus* Harold, 1868, are commonly associated with pasturelands (Maldaner et al., 2024) and were also encountered in the pastures of Raso da Catarina.

Discussion

Our study contributes to the knowledge of the composition of native dung beetle assemblages from Caatinga fragments in the Raso da Catarina ecoregion. Furthermore, the results contribute to understanding how native assemblages can deal with cattle manure, as smallholders usually allow cattle herds in their fragments to graze, especially during the dry season. Previous studies on Caatinga are very sparse, with Bahia and Paraíba reporting much of the inventories we know for the biome (see **Table S1**). Generally, these inventories have used only human feces or occasionally carcasses as bait, but cattle manure is not commonly used. To our knowledge, our inventory represents the richest assemblage of dung beetle (Scarabaeinae) in Caatinga. Previous studies in Bahia showed 23 species in an ecotone in Feira de Santana (Lopes et al., 2006). Others have reported a mean of 17 species (n = 13, varying from 12 to 23 species; See **Table S1**). A rapid assessment of dung beetle fauna in the Raso da Catarina using carcasses as bait provided a total of 18 species (P.P. Lopes, personal communication).

Bait type influenced assemblage composition, but 77% of species exploited both resources, reflecting high trophic plasticity and the ability of native dung beetles to incorporate livestock manure. This flexibility is ecologically relevant, as free-ranging cattle often graze within Caatinga fragments (Fortini et al., 2022). Nevertheless, some species apparently exhibited resource specificity: *D. bos* was restricted to cattle dung, while *D. pseudoicarus* occurred only in human feces. Such preferences reveal that while many taxa adapt, others remain resource-limited, which may affect ecosystem functioning.

Digitonthophagus gazella is an introduced dung beetle deployed to support livestock production by enhancing dung removal and contributing to the suppression of horn flies and gastrointestinal parasites, as well as soil bioturbation. In Brazil, the species was introduced in 1989 by Empresa Brasileira de Pesquisa Agropecuária (EMBRAPA) (Nascimento et al., 1990) with the expectation of improving key ecosystem services in pasture systems. Although the species is present in the fragments, it is not capable of persist in there and records are dependent on proximity to cleared areas, trails rather than a direct capacity to colonize fragments of Caatinga. Additionally, it is very sensitive to the presence of native vegetation structure complexity in pastures as its abundance drops rapidly under native vegetation presence on pastures (Queiroz et al., 2023).

Fragment identity was the main driver of assemblage differentiation, as suggested by the NMDS results, but further research should explore in greater depth the landscape mechanisms underlying assemblage composition and the partitioning of diversity in SDTFs. Although not directly analyzed here, fragment identity may reflect the role of habitat heterogeneity and isolation in shaping dung beetle assemblages in our fragments of SDTFs, consistent with patterns from other tropical landscapes (Rivera et al., 2020; Storck-Tonon et al., 2020), including drylands (Estupiñan-Mojica et al., 2022), a matter that should be investigate. High dissimilarity across fragments indicates that conserving multiple sites is necessary to ensure the full regional pool is preserved. The prevalence of small-bodied paracoprids also suggests potential shifts in ecosystem service provision, as body size strongly influences dung removal efficiency (Nervo et al., 2014).

Although it is known that cattle grazing within native fragments can suppress, to some degree, ecological succession by reducing plant recruitment, an effect that intensifies in the dry season. Our results indicate that native dung beetle assemblages are capable of exploiting cattle manure, with multiple species from different sizes and FRB groups using it as a resource. However, population dynamics and the capacity to process cattle manure are likely to vary across seasons, particularly during the dry season, which we did not sample and compare here. Future work should consider to explicitly quantify seasonal effects through wet–dry comparisons that couple local assemblage’s metrics with ecosystem services (e.g., dung removal and soil excavation) to determine the extent to which seasonality modulates beetle activity on cattle manure on both pasturelands and Caatinga fragments. Finally, because dung beetles can be sensitive to vegetation structure complexity, we encourage the comparison of different Caatingas (i.e., phytophisiognomies) across the region under distinct elevations exploring different use of baits, but assuring the use of cattle manure, as cattle grazing on fragments is a cultural practice and a type of regional cattle management.

Conclusions

Dung beetle assemblages in Caatinga fragments of Raso da Catarina ecoregion show high diversity, with most species able to exploit both native and cattle dung resources. Each sampled fragment tends to host more distinct assemblage, underscoring that in this region, conserving multiple forest patches may be the best approach to preserve a regional pool of species. By providing new baselines for the Scarabaeinae in the Caatinga, our study highlights the ecological importance of forest fragments and the need to integrate grazing management into conservation strategies.

Acknowledgements

C. Dos-Reis thanks CAPES (Coordination for the Improvement of Higher Education Personnel - Brazil - Funding Code 001) for his doctoral scholarship. This research was supported by a Rufford Small Grant (No. 36296-1). C. Dos Reis is indebted to João Pedro and “Seu” Neo for their invaluable help in the field, bravely facing thorns and the dense vegetation when others wouldn't do. Iasmim Queiroz is thanked for her valuable help in laboratory. Thanks are due to CEPEC-CEPLAC, Brazilian Ministry of Agriculture, and Instituto de Ecología, A. C. for laboratory support and infrastructure. J.H.C. Delabie acknowledges his CNPq research productivity fellowship.

Authors’ Contributions

C. Dos-Reis, J.H.C. Delabie, and F. Escobar conceived and designed the study. C. Dos-Reis collected and analyzed the data. C. Dos-Reis wrote the first draft of the manuscript, under the supervision of J.H.C. Delabie and F. Escobar. All authors reviewed and contributed substantially to the final version of the manuscript.

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Supplementary material

Table S1. List of inventories and species richness reported from Caatinga.

Locality	Studies	Fieldwork	Richness	Reference
Bahia				
Boqueirão da Onça	1	1	14	Barreto et al., 2019
Contendas do Sincorá	1	1	21	Vieira & Silva, 2012
	1			Vieira, Silva & Louzada, 2017
Feira de Santana	1	1	23	Lopes et al., 2006
Milagres	2	1	15	Medina & Lopes, 2014a,b
Paraíba				
Cariri	1	1	19	Estupiñan-Mojica et al., 2022
Curimataú	1	1	20	Hernández, 2005
Santa Terezinha	1	1	17	Salomão & Iannuzzi, 2017
São José dos Cordeiros	1	1	20	Hernández, 2007
Pernambuco				
Catimbau	1	1	13	Liberal, 2008
	1			Liberal, 2011
	1	1	15	Filgueiras et al., 2021
Piauí				
Campo Maior	1	1	5*	Salomão et al., 2019
São Miguel do Fidalgo	1	1	15	Rocha et al., 2012
Sergipe				
Grota do Angico	1	1	12	Santos-Junior, 2014
Total Geral	**17**	**13**	—	—
Mean			**17**	—
Min-Max			**12 - 23**	—

(*) Traps were damaged and species richness is not accurate.

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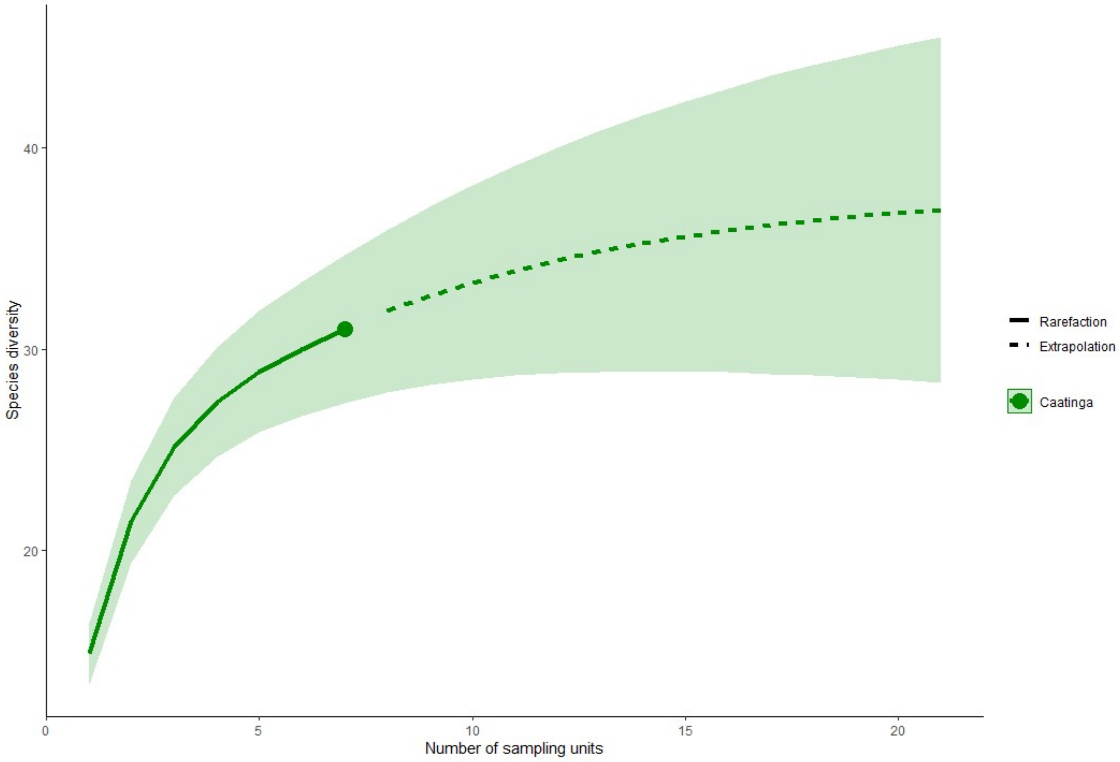

Figure S10. Species richness curve of dung beetles (Scarabaeinae) observed (solid line) and extrapolated (dashed line) based on the number of sampled forest fragments of Caatinga (i.e. seven fragments). Shaded projection corresponds to 95% IC.

CAPÍTULO III

LANDSCAPE CONTEXT IS A BETTER PREDICTOR OF DUNG BEETLE DIVERSITY THAN LOCAL MANAGEMENT IN PASTURES OF SEMI-ARID BRAZIL

Landscape context is a better predictor of dung beetle diversity than local management in pastures of semi-arid Brazil

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Abstract

The expansion of livestock is a major driver of land-use change in seasonally dry tropical forests (SDTFs), yet its impacts on insect biodiversity remain poorly understood. Dung beetles (Coleoptera: Scarabaeinae) are key providers of ecosystem services and sensitive bioindicators, making them ideal models to assess the effects of land use in semi-arid biomes. Here, we evaluated the relative importance of both landscape and local-scale predictors in shaping dung beetle assemblages in pastures within the Caatinga biome, Brazil's largest SDTF. We sampled 21 pastures during the rainy season and analyzed richness, abundance, diversity (Hill numbers), and functional group approach using multimodel inference. Sampling coverage exceeded 0.90 across all sites, ensuring robust comparisons. Our results show that landscape factors were stronger predictors than local management, with elevation exerting the most consistent positive effect, followed by edge density, which had a negative effect. Fragmentation per se (number of patches) was positively associated with assemblages, while forest cover showed a negative effect. At the local scale, ivermectin use reduced assemblages, whereas vegetation structure had modest positive effects. Dung beetle assemblages in pastures were dominated by small-bodied species, resulting in homogenized assemblages across sites. These findings suggest that in Caatinga pastures, the landscape scale features are more important in shaping assemblages from pasturelands in a dryland region and assemblages are dominated by small-bodied species structuring dung beetles during the rainy season. Our study highlights the need to incorporate both landscape planning and local management into conservation and livestock strategies to maintain biodiversity and ecosystem services in pasture from semi-arid regions of Brazil.

Keywords: Scarabaeinae, landscape ecology, diversity, seasonally tropical dry forests

Introduction

Humans have been profoundly altering ecosystems worldwide, particularly through deforestation driven by land-use change for livestock production in the Neotropics (Wassenaar et al., 2007; Aide et al., 2013). This process is expected to intensify in the coming decades, leading to biodiversity loss and ecosystem degradation, with direct consequences for the provision of ecosystem services (Dobson et al., 2006; Isbell et al., 2014). Simultaneously, scientists have highlighted the global decline of insects' populations caused by anthropogenic pressures, like habitat loss, pesticide use, light pollution, and climate change (Wagner et al., 2021). This scenario is particularly concerning for conservation aims because humans rely on a wide array of ecosystem services provided by biodiversity, and insects play a central role in maintaining these functions (Hill & Hamer, 2004; Elizalde et al., 2020).

Insects contribute to essential services that range from cultural and nutritional values to regulating and supporting processes of direct relevance to agriculture, such as pollination, natural pest control, and soil enhancement, among others (Losey & Vaughan, 2006; Nichols et al., 2008; Elizalde et al., 2020). Among them, dung beetles (Scarabaeidae) stand out as key providers of multiple ecological services, including nutrient cycling, soil aeration, pest suppression, and plant growth improving (Nichols et al., 2008; deCastro-Arrazola et al., 2023). Due to their taxonomic diversity, mammal dung dependence for feeding and reproduction, and high sensitivity to habitat disturbance via changes in vegetation structure (Halffter & Matthews, 1966; Reis et al., 2023), microclimatic changes (Halffter & Matthews, 1966), gradients of elevation (Escobar et al., 2005, 2006, 2007), dung beetles are widely recognized as reliable bioindicators (Halffter & Favila, 1993; Nichols & Gardner, 2011). More importantly, they contribute directly to pasture sustainability by influencing cattle productivity and soil health (deCastro-Arrazola et al., 2023). Despite advances in our understanding of dung beetle responses to anthropogenic pressures over the past decades (Nichols et al., 2007; Dos-Reis et al., Cap. II), important knowledge gaps remain. In particular, the responses of dung beetle assemblages to land-use change are still poorly understood in tropical arid and semi-arid biomes, where livestock production is rapidly expanding and ecosystem resilience to disturbance is comparatively low.

The Caatinga, a seasonally dry tropical forest (SDTF) covering most of Brazil's semi-arid region and constituting 11% of the Brazilian territory (Silva et al., 2017), is a unique and threatened biome characterized by high levels of endemism, pronounced climatic seasonality, and frequent drought events (Ferrer-Paris et al., 2019; Fernandes et al., 2020). Despite being recognized as a biodiverse seasonally dry forest (Fernandes et al., 2020), the Caatinga has historically received less scientific attention compared to other Brazilian biomes such as the Amazon and Cerrado. Significant knowledge gaps persist, particularly given their high potential for new species discoveries (Santos et al., 2011; Lessa et al., 2019; Gomes-da-Silva et al., 2025), especially regarding insects (Santos et al., 2011). Human pressures, including overgrazing, deforestation, and increasing climatic extremes, have intensified over the last few decades in the region, further threatening its biodiversity and ecosystem functioning (Albuquerque et al., 2017; Silva et al., 2017; Araujo et al., 2023).

Studies on dung beetle ecology in the Caatinga have progressed in recent decades, addressing topics such as diversity across different physiognomies (Barreto et al., 2020), responses to land-use change and exotic species (Liberal et al., 2011; Queiroz et al., 2023), successional dynamics (Lopes et al., 2006; Salomão & Iannuzzi, 2017), and seasonality (Medina & Lopes, 2014). More recently, landscape attributes shaping dung beetle diversity have also been investigated (Estupiñan-Mojica et al., 2022). Although this latter study explicitly addressed landscape ecology, most research has focused primarily on native habitats (i.e., Caatinga forest fragments). Consequently, studies on dung beetle assemblages in pastures remain scarce, particularly when compared to research conducted in other Brazilian biomes (see Maldaner et al., 2024). This gap limits our ability to understand how landscape attributes and local management practices interact to shape dung beetle assemblages, and how livestock production influences insect diversity and associated ecosystem services in semi-arid systems.

Dung beetle assemblages in agricultural landscapes are shaped by multiple drivers acting at different spatial scales. At the local scale, management practices such as grazing intensity, pesticide use, manure availability, and vegetation structure can directly affect dung beetle diversity and abundance, disturbing the ecological services in which they participate (González-Gómez et al., 2023; Queiroz et al., 2023; Morales-Trejo et al., 2024). At the landscape scale, factors such as forest cover, fragmentation, matrix heterogeneity, edge density, and connectivity are also known to influence dung beetle assemblages, particularly through their effects on dispersal and resource availability (Escobar, 2004; Rivera et al., 2020; Souza et al., 2020). In agricultural landscapes, landscape metrics may outweigh local practices because of dispersal limitations and reduced habitat availability constrain community assembly (Tscharntke et al., 2012). In semi-arid regions like the Caatinga, where climatic harshness and resource scarcity already impose strong environmental filters, the balance between local and landscape drivers is especially uncertain. Although interest in the scale-dependency of dung beetle responses to land use (González-Gómez et al., 2023), semi-arid pastures remain underrepresented in this debate (but see Barragán et al., 2014; in Mexico dry lands). Consequently, it is unclear whether local management or landscape-scale features exert stronger control over dung beetle assemblages in Caatinga pastures.

In this study, we provide, to our knowledge, the first assessment of dung beetle assemblages in Caatinga pastures, explicitly evaluating the effects of landscape attributes and local management practices. We examine the relative importance of local and landscape factors in shaping dung beetle assemblages in 21 pastures within the Caatinga biome. Specifically, we tested whether landscape-scale structure is a stronger predictor of dung beetle diversity and composition than local-scale management practices. We expected that: (i) species richness, abundance, and diversity within pastures would respond positively to native habitat amount, Caatinga patch numbers, and edges; (ii) elevation and annual precipitation (Bio12) would exert positive effects, whereas the mean diurnal range of temperature (Bio02) would have negative effects; (iii) at the local scale, vegetation structure, a proxy for vertical complexity, would help retain diversity in pastures, given the well-established positive relationship between dung beetles and vegetation heterogeneity (Halffter & Matthews, 1966; Reis et al., 2023), which has already been observed at a small scale in this region (Queiroz et al., 2023); (iv) pasture composition (clean versus mixed with native and exotic grasses and herbs) and the presence of shading trees would provide microclimatic buffering and favor persistence, and (v) agrochemical use, particularly ivermectin, would negatively affect dung beetles, as its detrimental impacts on beetle physiology, sensorial responses, and reproduction are well documented (Verdú et al., 2015). By addressing this question, we aim to fill an important knowledge gap in semi-arid systems, where livestock expansion poses growing threats to biodiversity. Beyond its theoretical contribution to the scale-dependency debate, our study has applied relevance: it can inform land-use planning and sustainable livestock management in the Caatinga, reconcile agricultural production with biodiversity conservation.

Material and Methods

Study area

We conducted this study in four municipalities in The Raso da Catarina ecoregion. This ecoregion is narrow and elongated in the N-S direction (**Figure 8**). Covering an area of 30,800 km², the region is a basin of very sandy, deep and infertile soils, with a very flat relief, but with canyons in the western part. The climate is semi-arid, quite hot and dry, with an average annual temperature of 24 ~ 27º C and precipitation of 650 mm/year (Ab'Sáber, 1974). The predominant type of vegetation is shrubby, very dense and less thorny than the Caatinga of crystalline soils (Velloso et al., 2002). The delimitation of the sample region was mainly based on - soil homogeneity; precipitation and vegetation- key conditions for the composition and abundance of dung beetle assemblies (Halffter & Matthews, 1966; Davis et al., 2016). However, other types of Caatinga phytophysiognomies can be found in the region. Therefore, vegetation comprised a Seasonally Dry Tropical Forest (Silva et al., 2017). The landscape is largely dichotomous, with land use dominated by pastures and forest cover. As a result of deforestation, suppression of vegetation through local management practices, and the long-term effects of intensive overgrazing, the region is also subject to desertification processes (Tomasella et al., 2018; Santos et al., 2022). This vulnerability is expected to worsen under climate change scenarios (Marengo et al., 2017).

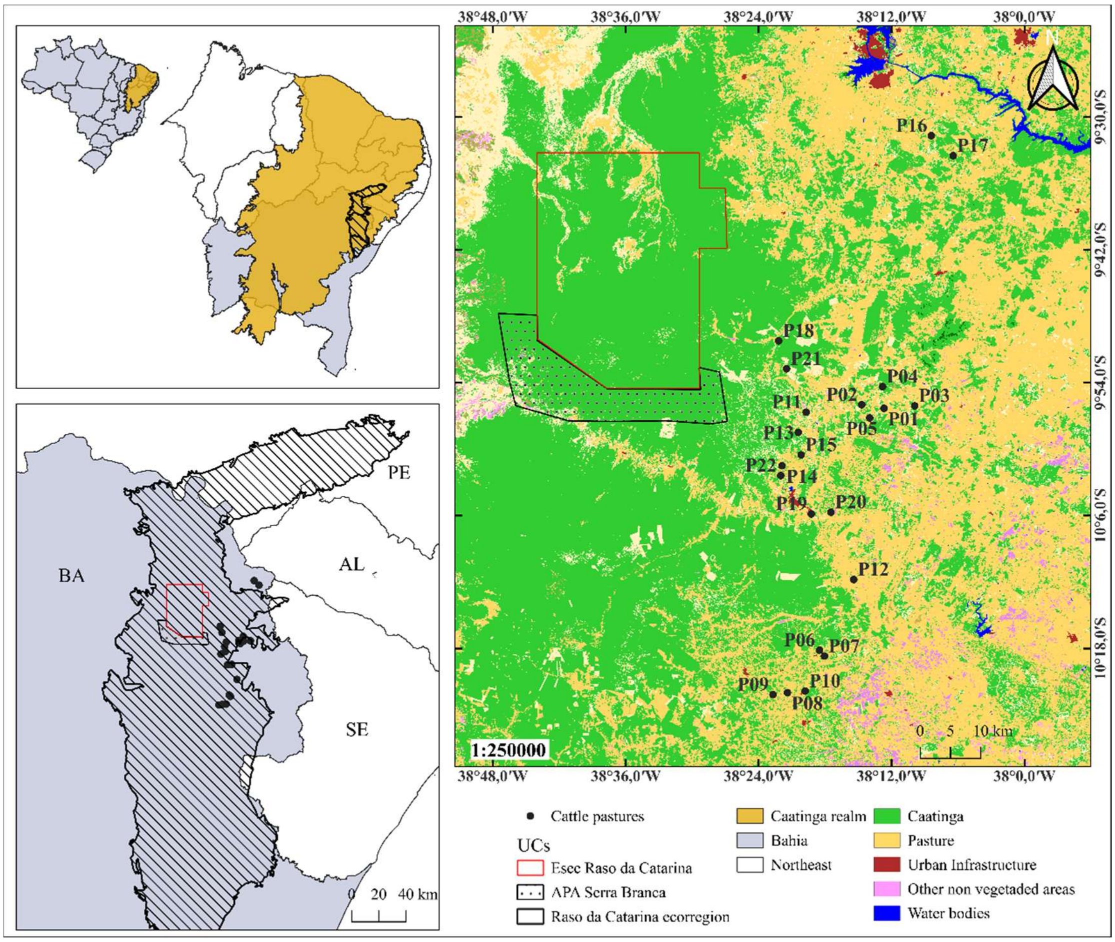


Figure 8. Map of the sampling areas. Land uses and ecoregion localization.

Dung beetle surveys

Sampling design

We sampled a total of 21 cattle ranches in the Raso da Catarina ecoregion. Sites were distant at least 2 Km apart from each other. The adopted distance was to ensure independence. In each pasture six 1 L pitfall traps (12 cm diameter, 12.8 cm depth) buried flush with the ground, separated by 50 m, partially filled (ca. 200 ml) with a solution composed of water, salt, and detergent to prevent the beetles from escaping (Sánchez-de-Jesús et al., 2016; Mora-Aguilar et al., 2023). Each trap was baited with 0.5 Kg of a mixture of cattle and pig dung (3:1) for 24 hours. The diet of bovine and pig that provided the manure was the same through the study in order to avoid difference in attraction effectiveness. The pitfalls were covered with plastic protection to protect from rain and drying out by exposure to the sun. The capture beetles were cleaned and preserved in recipients with 70 % alcohol. After screening in the laboratory and making the specimens in dry way. Beetles were identified to the lowest possible taxonomic level using identification keys (Vaz-de-Mello et al., 2011; Tissiani et al., 2017) and consultation with Dr. Fernando Vaz de Melo, specialist taxonomist in Neotropical dung beetles. The collected specimens were deposited in the collections Gregório Bondar entomological collection of the Cocoa Research Center (CEGB – CEPEC/CEPLAC), Ilhéus, Bahia and Eurico Furtado Entomological Collection of UFMT, Cuiabá, Mato Grosso.

Species were classified by food relocation behavior (hereafter as FRB) as paracoprid, telecoprid, and endocoprid, following the literature (Halffter & Edmonds, 1982; Maldaner et al., 2024; Tonelli, 2021). Body size was classified based on the length of beetle species, with species ≥ 10 mm categorized as large beetles and those < 10 mm categorized as small beetles (Cambefort & Hanski, 1991). Body sizes were based on measurement of specimens captured in this research. To do so, a measurement of pronotum plus elytra length was taken to compose body length using an average of five individuals per species.

To describe the landscapes, we use classified satellite imagery of 30 m resolution and at as a scale of 1:250,000. This imagery is sourced from the Landsat satellite, part of the MapBiomas collection (MapBiomas Project - Collection 8.0 of the Annual Series of Coverage and Land Use Maps of Brazil, accessed on 05/09/2024 via [http://www.mapbiomas.org]). Then, we used QGIS (QGIS Development Team 2016) and R-gui software version 4.4.1 to calculate landscape composition and configuration metrics. Subsequently, we calculated land use by applying different buffer scales to each landscape, ranging from 200 m to 1000 m radius in 200 m increments (see **Figure S11**). The selected scales are based on dung beetle species movement and previously studies (da Silva and Hernández, 2015; Rivera-Duarte et al., 2025). We consider the "Mosaic of Agriculture and Pasture" and "Pasture" categories of land use from MAPBIOMAS as pasture cover. This is because most landowners place cattle on corn plantations after harvest, and corn/pasture plantations are commonly found in this region. Both savanna and forest formations were considered as Caatinga vegetation in our landscape analysis.

Explanatory variables

Landscape composition and configuration

To calculate land-use cover, number of patches, and edge density, we used the R packages “landscapemetrics”, “sp”, and “raster” (Bivand et al., 2013; Hesselbarth et al., 2019; Hijmans, 2023). To elevation data we used elev() function from the “climenv” R package (Tsakalos et al., 2023) and values were extracted using the “terra” R package (Hijmans et al., 2024). We used data extracted from the WorldClim database which provides a 1 km^2 resolution and used the average year considering 1970–2000 for bioclimatic variables (see Fick and Hijmans, 2017). Correlation between explanatory variables were tested using the Pearson correlation test. We excluded mean annual temperature (Bio01) due to the high correlation with elevation ($r = -0.90$). Regarding the following variables elevation, Bio02 and Bio12 were calculated as mean within each scale. All variables were computed at each buffer scale (200, 400, 600, 800, and 1000 meters) using the central point as the reference location.

Local scale and cattle ranch management

To quantify local management at each ranch, we conducted a semi-structured questionnaire to gather information about practices for cattle and ranch management (Table SX). We interviewed owners or managers from each ranch to obtain information about: Herbicide use, Fertilize use, pesticide, vermicide, cattle density, cattle diet, and others. From these interviews, we derived the following explanatory variables: **Ivermectin (IV)**: indicates the usage of Ivermectin in the treatment or prevention of parasitic infections. **Pasture Composition (PC)**: categorizes pastures based on their vegetation characteristics. We define a "Clean" pasture as one that is predominantly composed of planted grasses, with minimal or no presence of native plants. In contrast, a "Mixed" pasture contains a diverse herbaceous stratum, featuring a combination of both planted grasses and native plant species. **Vegetation Structure index (VS):** indicates the number of vegetation strata present in the pasture, categorized as follows: S0: Indicates the absence of distinct strata, with vegetation primarily consisting of herbaceous plants provided by planted grasses. S1: Represents the presence of one stratum, which may include subshrubs, shrubs, or trees. S2: Denotes the presence of two distinct layers of vegetation. S3: Indicates the presence of three layers, including subshrubs, shrubs, and trees, reflecting a more complex vegetation structure. **Shading trees (ST)**: whether the pasture is shaded by native trees, providing a measure of the presence and influence of natural tree cover on the pasture environment.

Data analysis

We first estimated sample coverage for each ranch using the iNEXT package in R (Hsieh, Ma & Chao, 2016) to ensure that pastures were comparable based on observed diversity data. To determine the most appropriate spatial scale, we evaluated the scale of effect of landscape variables at five buffer radii (200, 400, 600, 800, and 1000 m). For this, we fitted generalized linear models with the 'Multifit' function (Huais, 2018), which automates the selection of the buffer that best explains each response variable (Martin & Fahrig, 2012; Fahrig, 2013). The best scale was selected based on AIC values.

Once the relevant scale was identified, we fitted generalized linear models (GLMs) to test the effects of landscape scale and local management on each response variable (Zuur et al., 2009). The diversity of species was analyzed using Hill numbers (^{q}D): species richness (^{0}D), Shannon diversity (^{1}D, Exponential of Shannon index), and Simpson diversity (^{2}D, Inverse of Simpson index) (see Jost 2006). Additionally, the following variables were evaluated: number of individuals and richness of paracoprid, telecoprid, and endocoprid beetles; and richness and number of individuals of large-bodied and small-bodied beetles.

Explanatory variables were checked for collinearity using Variance Inflation Factors (VIF < 5) with the "car" package (Fox & Weisberg, 2018) (see **Figure S13**). We transformed the following variables: elevation, number of patches, edge density, and Bio12 values into natural logarithm (log) to homogenize the spread of the data. GLMs were fitted following conventional family distributions for each type of data, applying *Poisson*, or negative binomial when necessary to deal with high residual deviation (Zuur et al., 2009). To perform GLM with binomial negative distribution, we used the "MASS" package (Venables & Ripley 2002). Model assumptions were validated using residual tests from DHARMa package (Hartig, 2024) and conventional validation through residual visualization (Zuur et al., 2009). A full list of response variables, explanatory variables, and error distributions is provided in Supplementary Table SX. Then, we performed Multimodel Inference (Burnham & Anderson, 2004) using the "dredge" function from the "MuMIn" package (Bartoń 2024) which compares all possible combinations of explanatory variables plus a null model for each response variable.

We used empirical cumulative distribution functions (ECDFs) to examine the distribution patterns of dung beetle richness and abundance across pastures, considering body size-based functional groups. This approach enabled a clear visualization and comparison of cumulative frequencies between small- and large-bodied species, facilitating the interpretation of how richness and abundance varied across sites. We employed paired Wilcoxon signed-rank tests to assess differences, specifying the alternative hypothesis that small-bodied beetles exceed large-bodied beetles by setting the argument [alternative = "greater"]. All analyses were performed in R version 4.4.1 (R Core Team, 2024).

Results

A total of 26,152 dung beetles belonging to 30 species (15 genera) were collected from 21 pastures. Number of individuals per site varied from 305 to 3,343 (1,245.3 ± 880 SD, whereas richness was from seven to 20 species (12.3 ± 3.61). The most abundant species were *Genieridium margareteae*, with 9,310 specimens (35.6 %), followed by the introduced *Digitonthophagus gazella* (19 %), and native species such as *Ateuchus semicribratus* (15 %), *Onthophagus* aff. *ptox* (10 %), and *Trichillum externepunctatum* (6 %) (**Table S4**). Together, these five species represented 67 % of the total individuals collected. Six species were identified as singletons: *Canthidium* sp. 1 and *Canthidium* sp. 5, *Canthon* sp.2 and *Canthon* sp.4, *Dichotomius puncticollis* and *Ontherus azteca* (see complete list in Supplementary material). Sample coverage across all sampled ranches was consistently high, exceeding 0.90 at each site, which indicates that our sampling effort was sufficient, and sites were comparable.

Landscape scale

Overall, the explanatory variables that best predicted changes in dung beetle diversity from pasture in the Caatinga were those associated with landscape scale, with models explaining from 14.37% to 46.76% (**Figure 10**). For species richness (**Figure 10a**), the models indicated that elevation is the most important predictor, with consistent positive effects, while temperature, edge density, and precipitation exerted negative effects. Together, these predictors accounted for 44.12% of the explained variation. In contrast, dung beetle abundance (**Figure 10b**) was negatively associated with forest cover and edge density, while elevation and the number of patches showed positive associations, explaining 44.57% of the variation. For Shannon diversity (^{1}D) (**Figure 10c**), edge density and forest cover emerged as the main positive predictors, explaining 14.37% of the variation. Simpson diversity (^{2}D) (**Figure 10d**) was positively influenced by the number of patches and negatively by forest cover, with models accounting for 15.64% of the variation.

All environmental variables, except for elevation and precipitation, significantly influenced total dung-beetle abundance; however, edge density and forest cover emerged as the most influential predictors (**Figure 10b**). Specifically, abundance increased with the number of forest patches but declined as forest cover increased, indicating that fragmentation *per se* may have a positive impact on the abundance of dung beetles that inhabit pastures in the Caatinga.

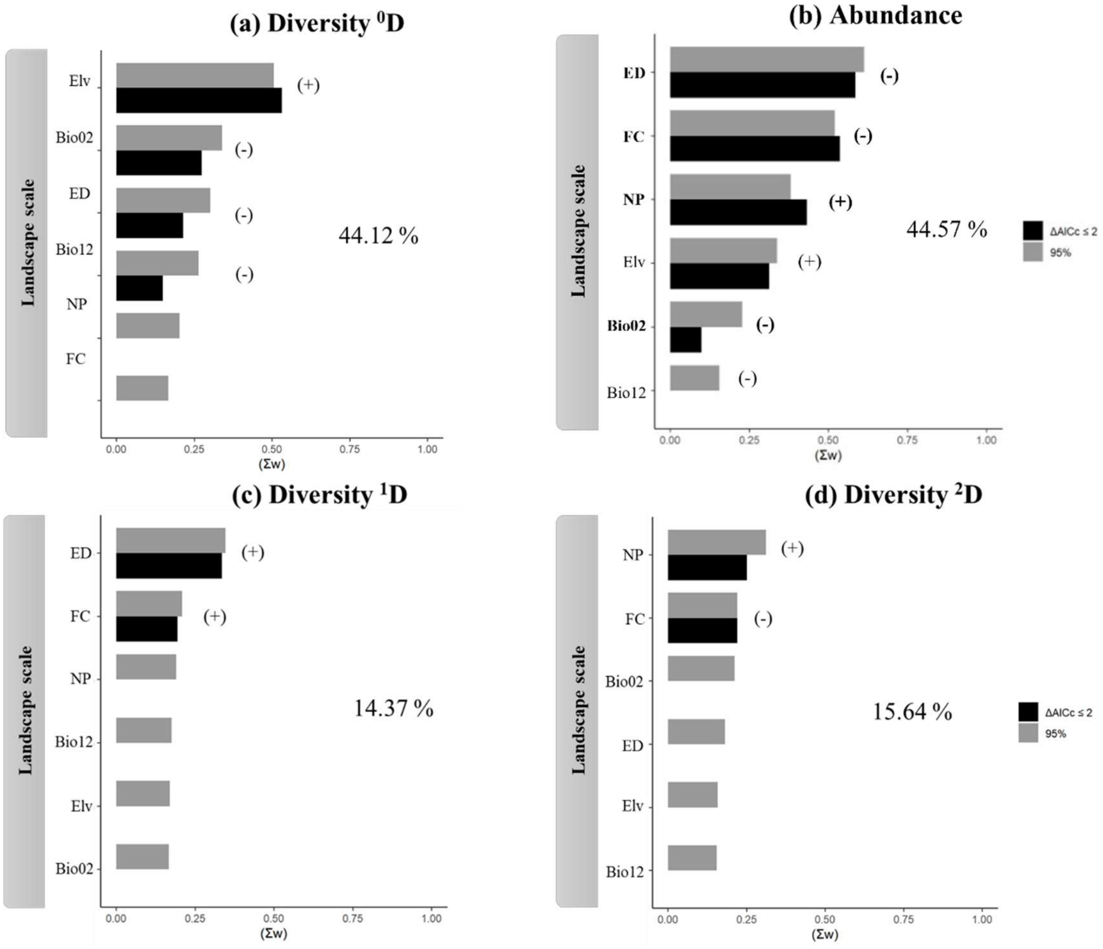
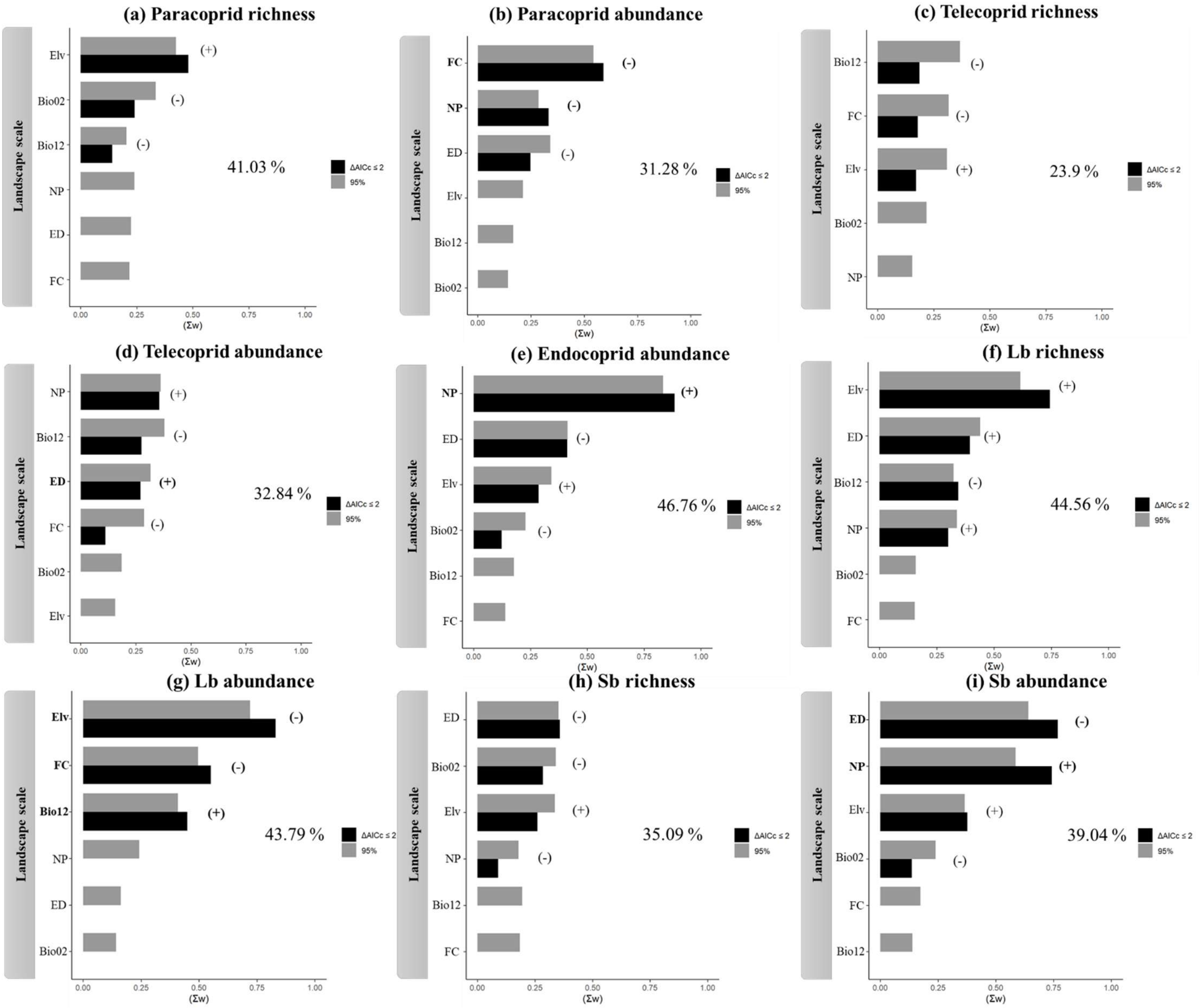


Figure 9. Landscape scale predictor variables included in the ΔAICc ≤ 2 set of models (black bars) and 95% set of models (gray bars) for species diversity (hill numbers 0, 1 and 2). The importance of each variable is shown by the sum of Akaike weights; parameters estimates (β) whether positive or negative is shown right after their respective variables’ bars. Acronyms correspond to [FC] Forest cover, [ED] Edge density, [NP] Number of patches, [Elv] Elevation above the sea level, [Bio02] Mean Diurnal Range, [Bio12] Annual Precipitation. Bold values in variables and parameter estimates correspond to significant values p-value ≤ 0.05.

Regarding the best response variables from complete models with high explained deviance (%), we found that the number of forest patches positively affected endocoprid abundance (47%, **Figure 10**e). Interestingly, elevation showed different patterns of effect depending on the response variable, especially regarding functional groups. For instance, large beetle richness was positively affected (**Figure 10**f), while abundance was negatively affected by elevation (**Figure 10**g). Forest cover appeared more consistently as a negative driver across metrics, notably reducing telecoprid richness and abundance (**Figure 10**c-d). Precipitation also negatively influenced telecoprid species responses (**Figure 10**c-d), but positively for large beetles' abundance (**Figure 10**g). The number of patches showed functional importance, favoring small-bodied beetles and endocoprid abundances (**Figure 10**i and 3e). Meanwhile, edge density acted as a suppressive factor across multiple responses, particularly reducing endocoprid abundances (**Figure 10**e), and small-bodied beetle richness and abundance (**Figure 10**h-i).


(a) Paracoprid richness

(b) Paracoprid abundance

(c) Telecoprid richness

(d) Telecoprid abundance

(e) Endocoprid abundance

(f) Lb richness

(g) Lb abundance

(h) Sb richness

(i) Sb abundance

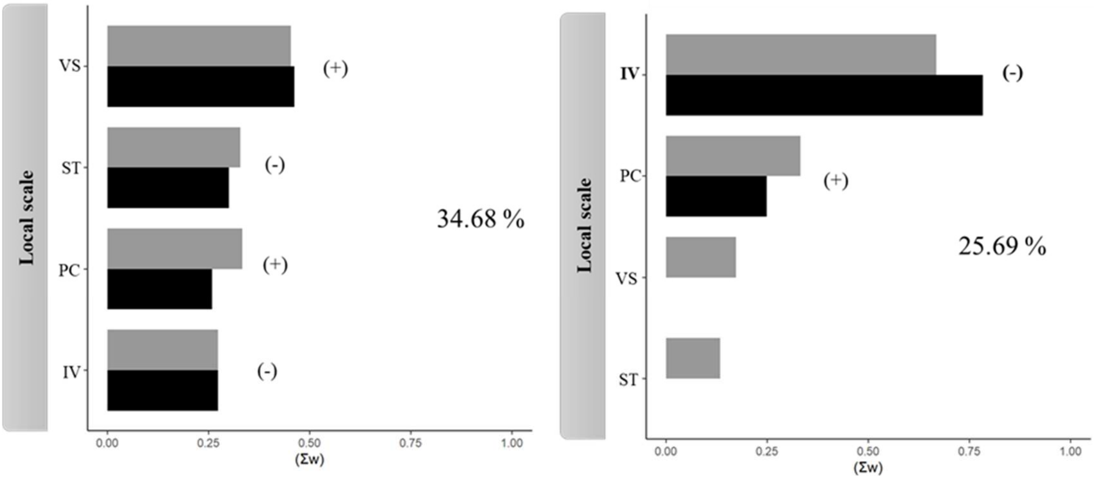
Figure 10. Landscape scale predictor variables included in the ΔAICc ≤ 2 set of models (black bars) and 95% set of models (gray bars) for richness and abundance of functional groups. The importance of each variable is shown by the sum of Akaike weights; parameters estimates (β) whether positive or negative is shown right after their respective variables' bars. Acronyms correspond to [FC] Forest cover, [ED] Edge density, [NP] Number of patches, [Elv] Elevation above the sea level, [Bio02] Mean Diurnal Range, [Bio12] Annual Precipitation. Bold values in variables and parameter estimates correspond to significant values p-value ≤ 0.05.

Local scale and ranch management

Local scale predictors accounted for a smaller but still significant portion of variation in dung beetle diversity, with models explaining between 3.01% and 43.47% of the variation (**Figure 4** and **Figure 5**). Ivermectin emerged as one of the strongest local predictors, showing negative effects on various aspects of dung beetle assemblages, including, richness, Hill numbers and functional groups, although the explanation was relatively low. Species richness is positively affected by vegetation structure and pasture composition while shading trees and ivermectin exerts a negative effect (**Figure 4a).** The number of individuals was best explained by the null model, indicating that no tested predictors had a strong influence on this response variable. In contrast, Shannon diversity was strongly and negatively affected by ivermectin use, whereas pasture composition had a positive effect (**Figure 4b**). Simpson diversity exhibited a similar pattern, although the effects were weaker (**Figure 4c**).

(a) Diversity ^{0}D

(b) Diversity ^{1}D



(c) Diversity ^{2}D

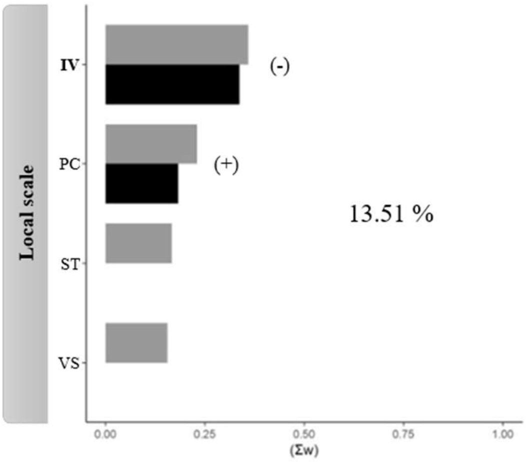


Figure 11. Local scale predictor variables included in the ΔAICc ≤ 2 set of models (black bars) and 95% set of models (gray bars) for species diversity (hill numbers 0, 1 and 2). The importance of each variable is shown by the sum of Akaike weights; parameters estimates (β) whether positive or negative is shown right after their respective variables' bars. Acronyms correspond to [VS] Vegetation structure, [ST] Shading trees, [PC] Pasture composition, [IV] Ivermectin. Bold values in variables and parameter

estimates correspond to significant values p-value ≤ 0.05. A model for number of individual was not shown because only the null model explained the variation.

While the number of common species was poorly explained by landscape-scale variables (**Figure 10**c), local scale management provided a better explanation (**Figure 11**b). Ivermectin usage exhibited consistent negative patterns across complete models and response variables (**Figure 11** and Figure 5). This impact was most evident in the reduction of overall species diversity (**Figure 11**a-c), and Paracoprid richness (**Figure 5a**). These findings indicate that while landscape-level factors are predominant, local management practices, particularly the use of agrichemicals, can influence and alter dung beetle populations.

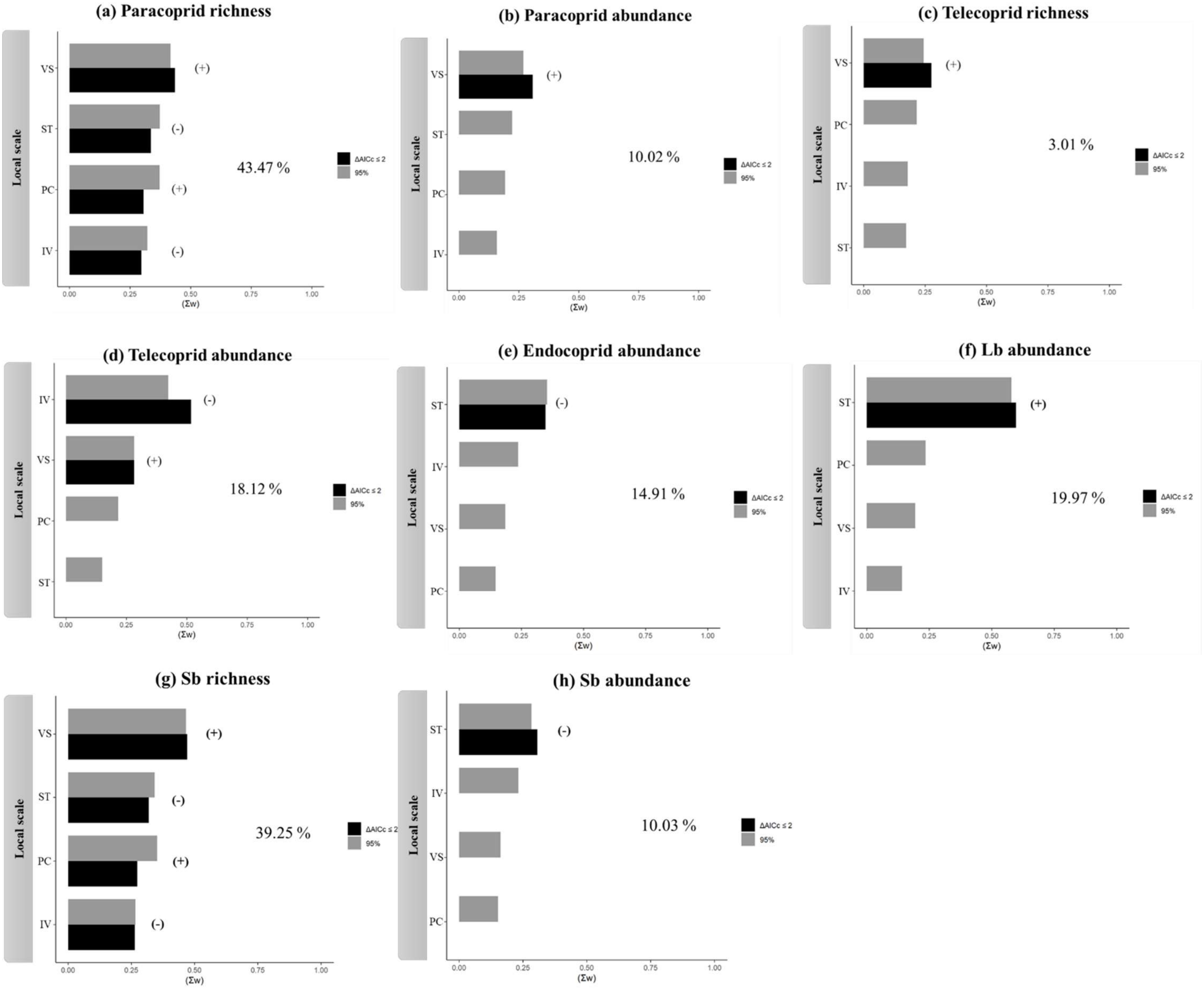


Figure 12. Local scale predictor variables included in the ΔAICc ≤ 2 set of models (black bars) and 95% set of models (gray bars) for richness and abundance of functional groups. The importance of each variable is shown by the sum of Akaike weights; parameters estimates (β) whether positive or negative is shown right after their respective variables' bars. Acronyms correspond to [VS] Vegetation structure, [ST] Shading trees, [PC] Pasture composition, [IV] Ivermectin. Bold values in variables and parameter estimates correspond to significant values p-value ≤ 0.05. A model for LB richness was not shown because only the null model explained the variation.

We found consistent evidence that small-bodied dung beetles dominate the assemblages across pastures by the total abundance per species. The empirical cumulative distribution functions (ECDFs) confirmed the patterns that both the richness and abundance of small-bodied species were higher throughout the sampled sites (**Figure 13** a-b). This pattern was statistically supported by Wilcoxon signed-rank tests: the richness of small-bodied species was significantly greater than that of large-bodied ones ($V = 188$, $p < 0.001$), and their abundance also significantly exceeded that of large species ($V = 175$, $p = 0.020$).

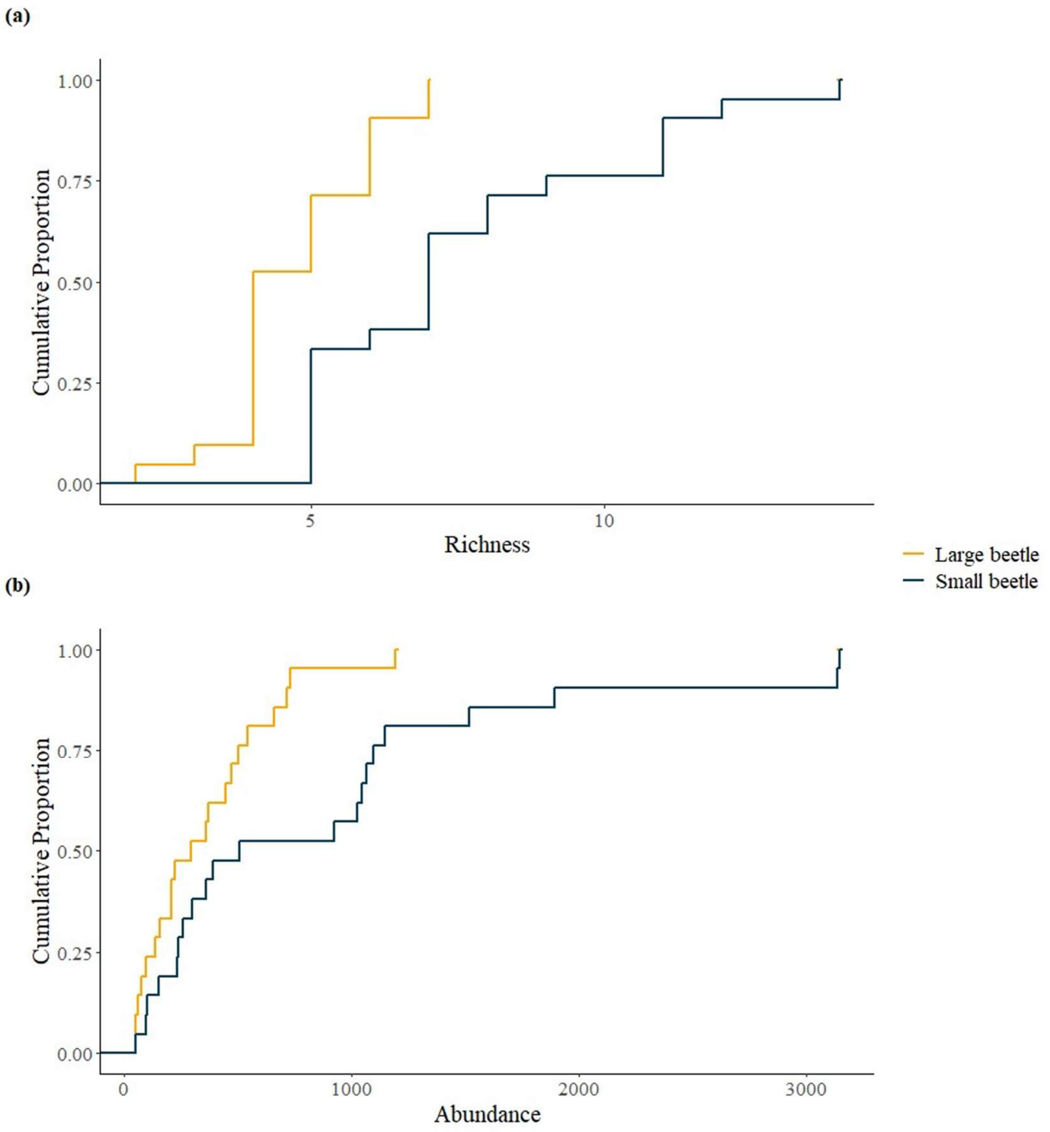


Figure 13. Empirical cumulative distribution function (ECDF) of dung beetle species richness (a) across 21 pasture sites, grouped by body size (small < 10mm vs. large > 10 mm). (b) ECDF of dung beetle abundance.

The percentage of small-bodied dung beetle species richness across the 21 pasture sites ranged from 45.5% at P06 to 73.3% at P05 (mean ± SD = 61.1% ± 7.2%; **Figure 14**a). Only one site (P06) showed a distinct dominance of large beetles, while the other 20 sites exceeded this threshold. Small beetle abundance exhibited even greater variability, two-thirds of the sites are dominated by small beetles in terms of abundance, ranging from 9.2 % at P12 to 98.5 % at P21 (mean ± SD = 60.9% ± 29.7%; **Figure 14**b). Moreover, in terms of the number of individuals, dominance reached values close to 100%. For example, in five pastures more than 90% of individuals were small-bodied species. Notably, most sites did not show parity in either abundance or richness, excepting for P07 and P16. This underscores a consistent asymmetry in body size structure across the grazing landscape, largely driven by the strong dominance of small-bodied beetles.

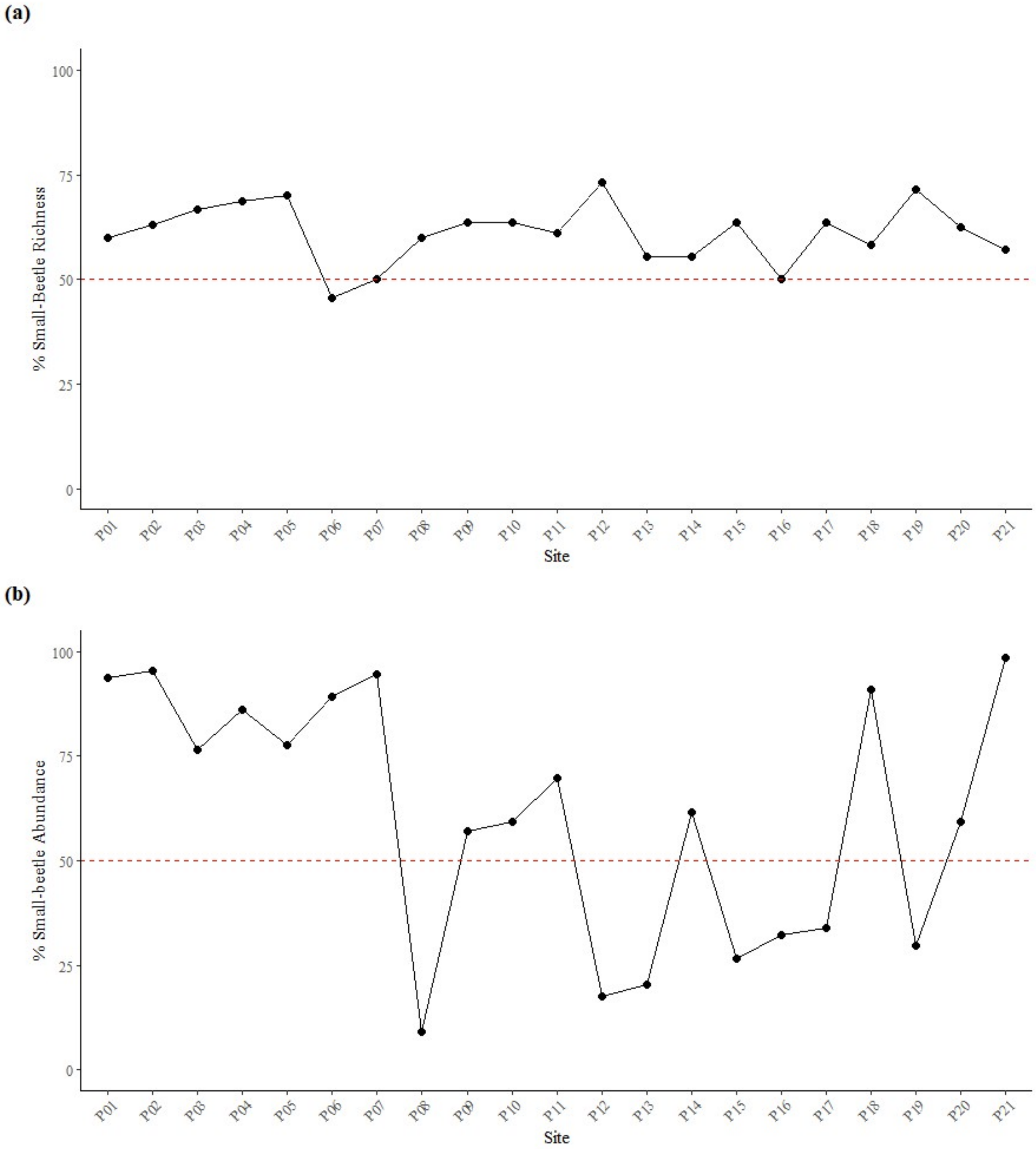


Figure 14. Dominance of small beetles across 21 pastures expressed as (a) percentage of total species richness and (b) percentage of total abundance. The red dashed line indicates the 50 % threshold. Values above this line highlight the dominance of small-bodied beetles, while values below indicate the dominance of large-bodied beetles.

Discussion

Our study provides the first evidence that dung beetle assemblages in Caatinga pastures are more strongly shaped by landscape-scale attributes than by local management factors. Among the predictors tested, forest cover and edge density had negative effects on assemblages, whereas the number of patches and elevation acted as positive predictors. However, at the local scale, ivermectin use consistently reduced diversity, while vegetation structure and pasture composition exerted positive influences and appeared in models that explained a substantial portion of the variation.

Landscape context importance

Contrary to our predictions, landscape attributes were not consistently strong positive predictors of dung beetle assemblages. Still, elevation and the number of patches showed positive effects across several response variables, while the temperature mean diurnal range (Bio02), forest cover, and edge density tended to have negative effects.

Although forest cover has often been identified as a key factor structuring dung beetle assemblages in tropical landscapes (Sánchez-de-Jesús et al., 2016), including SDTFs (Estupiñan-Mojica et al., 2022), our results suggest this effect may be more relevant to assemblages restricted to forest fragments. In pastures, dung beetle assemblages appear to benefit from open areas, indicating that matrix quality and resource continuity can outweigh the role of forest remnants in shaping community structure, at least during the rainy season. Even so, this does not imply that forest cover at the landscape scale is unnecessary or unimportant, as they likely function as spillover sources (Blitzer et al., 2012; Tscharntke et al., 2012), providing species that can recolonize pastures after disturbances such as slash-and-burn, pasture renewal, or drought events, all of which are common in the region.

Microclimatic factors are also expected to play a role in dung beetle ecology (Halffter & Matthews, 1966), although empirical evidence is mixed. Some studies have not detected strong responses to temperature or precipitation (Lobo et al., 1998; Calatayud et al., 2021), but future increases in temperature are predicted to alter dung beetle assemblages (Maldaner et al., 2021; Lobo et al., 2023). This is particularly relevant for the Caatinga, a venerable and threatened region which is projected to face significant climatic shifts (Marengo et al., 2017; Ferrer-Paris et al., 2019). Such changes may have profound consequences for dung beetle persistence in pastures and, consequently, for the ecosystem services they provide (Maldaner et al., 2021).

Species in SDTFs may exhibit eurytopic behavior that enables them to exploit open and disturbed habitats with little difficulty, possibly due to greater tolerance to high temperatures (Giménez Gómez et al., 2025; Halffter & Matthews, 1966). In this context, the paradox postulated by Dr. Halffter (see more discussion regarding this on Chapter I; G. Halffter, personal communication), namely "why does the constant input of cattle manure available year-round not sustain native species richness and abundance in the same proportion?", may not fully apply to Neotropical SDTFs. The difference between the original habitat and pastures is not as pronounced as in tropical rainforests, particularly regarding thermal conditions and vegetation structure. From an evolutionary perspective, these assemblages may be dominated by eurytopic species that are preadapted to cope with both open habitats and thermal variation (see Halffter & Matthews, 1966).

Moreover, the high availability of food resources in pastures (i.e., cattle manure) may contribute to the persistence of dung beetle species, at least those capable of using herbivore manure, and may contribute to the greater similarity between assemblages inhabiting pastures and forest fragments in SDTFs. This adaptability to manure resources is likely related to their close evolution with large mammals, many of which are now extinct. Despite these extinctions, extant dung beetle species and populations have demonstrated resilience and the capacity to exploit these resources effectively (Favila, 2012; Kohlmann et al., 2018). In fact, at some degree, the grazing my promote dung beetle diversity in xeric habitats (Verdú et a., 2007), and diversity can be even higher in grazing areas than in native vegetation from dry lands compared to tropical forest (Barragán et al., 2014).

Elevation has been reported as an important factor influencing dung beetle distributions in both tropical forests (Escobar et al., 2005) and seasonally dry tropical forests (SDTFs) (Domínguez et al., 2015), from natural habitat and pastures (Alvarado et al., 2020). This effect may be particularly relevant in dryland ecosystems, where higher-elevation sites likely provide more favorable microclimatic conditions, such as cooler temperatures and greater moisture retention, which can support dung beetle diversity and persistence. In our study region, we observed that pastures at higher elevations benefit from dawn dew, which helps maintain greener grass even during the early dry season, compared to lower-elevation pastures. Such local climatic phenomena represent an important mechanism for the persistence of organisms in SDTFs

(Reyes-García et al., 2012). In the Caatinga, higher elevations may provide critical microclimatic buffering, favoring herbaceous vegetation and, consequently, sustaining dung beetle assemblages during drought periods.

However, most studies on altitudinal effects in dung beetles have been conducted across wide elevation gradients, generally above 800 m (Escobar et al., 2005), with few including sites below 500 m. In SDTFs, available data come from higher ranges (1100–1700 m; Domínguez et al., 2015), which contrasts with the narrower gradient evaluated in our study (250–580 m).

Edge density had a negative effect on dung beetle assemblages. Because our focal habitat is pasture, this indicates that dung beetle abundance decreases as the interface between pasture and Caatinga habitat increases. In other words, a higher density of edges reflects greater presence of forest patches in large pastures, which seems to reduce the suitability of these open areas for dung beetles. This interpretation contrasts with the classic forest fragmentation framework, where edge proliferation is typically associated with negative effects on species in natural habitats (Fahrig, 2017; Fahrig et al., 2019). Here, the expected pattern is reversed: edge expansion reduces the continuity of open habitats and consequently lowers dung beetle abundance in pastures.

The importance of local management practices

Local management practices in ranches can strongly influence dung beetle assemblages and the ecosystem services they provide. For example, the duration of cattle ranching has been shown to negatively affect dung beetle diversity while increasing the relative abundance of exotic species in tropical dry forests of Mexico (Morales-Trejo et al., 2024). Another widespread practice in livestock management is the use of macrocyclic lactones, particularly ivermectin, to control helminth parasites and treat verminosis. In our study region, dosing practices often deviate from brand recommendations, as ranchers tend to rely on shared experiences rather than established protocols. Such practices not only reduce the efficiency of parasite control, resulting in economic losses, but also create unintended ecological consequences. Once administered, ivermectin is metabolized and excreted in manure, exposing dung beetles and other coprophagous organisms to its residues.

The detrimental effects of ivermectin on dung beetles have been well documented under both laboratory and field conditions (Villada-Bedoya et al., 2019). Reported impacts include reduced lipid reserves and overall body fitness, which compromise reproductive success (Martínez et al., 2017), as well as impairments to foraging behavior, sensory perception, and locomotor performance even at low doses (Verdú et al., 2015). Moreover, these effects can be cumulative and transgenerational (Baena-Díaz et al., 2018). In agreement with these findings, our study revealed that ivermectin use in cattle herds had negative consequences for dung beetle assemblages, particularly by reducing the number of common species, paracoprid richness, and telecoprid abundance. Importantly, ivermectin may affect different life stages in distinct ways. While adult beetles are still attracted to manure, egg and larval stages experience increased mortality (Finch et al., 2020), ultimately leading to declines in adult populations (González-Tokman et al., 2017).

Vegetation structure and the presence of shading trees demonstrated moderate effects across different metrics, with vegetation structure being slightly more influential. When pasture composition was identified as an important variable for the metric, it showed a positive effect; however, it did not exhibit strong overall effects. This suggests that the broader landscape context may overshadow local vegetation differences. Interestingly, paracoprid richness was benefited by mixed pastures and vegetation structure. In fact, tree cover is known to be the most influential factor determining dung beetle composition in assemblages (Halffter & Matthews, 1966), especially in pastures (Arellano et al., 2008; Giraldo et al., 2011). However, we did not find relationships between shading trees and dung beetle diversity; this may be due to the dichotomous nature of the variable. Instead, a more refined approach to this variable, treating it as a continuous measure (e.g., tree density), could better reflect the trends associated with the presence of shading trees in pastures. For instance, silvopastoral systems can enhance the relative abundance of dung beetle species richness (Duque-Vélez et al., 2022). In accordance with this, the vegetation structure index (VS) revealed a consistent positive effect on dung beetle assemblages. In other words, the more complex the structure in the cattle pasture, such as the presence of subshrubs, shrubs or a tree layer instead of a clear and opened pasture, the greater the vegetative complexity and the more beneficial it is to dung beetle assemblages. Previous result as have shown this in which “dirty pasture” with the presence of subshrubs reduce the dominance of exotic dung beetle and enhance native species (Queiroz et al., 2023). These results align with the idea that live fences (Arellano et al., 2008) and silvopastoral systems (Arellano et al., 2013; Giraldo et al., 2011) are reliable strategies for maintaining high diversity of dung beetles and their ecosystem services in American pastures (see Chapter I).

Small-bodied dominance

Dung beetle assemblages from highly modified habitats, such as open pastures, can experience a hyper-abundance of a few small-bodied species (Nichols et al., 2007; Rivera et al., 2021). In accordance with this, the most abundant species encountered was *G. margareteae* (length ± 4.55 mm). The distribution of *G. margareteae* in Caatinga pastures may represent a broad trend, similar to the pasture occupancy by *G. bidens* in the southern and central regions of Brazil (Maldaner et al., 2024). Therefore, hyper-abundance of *G. margareteae* might occur; however, this is not always the case. At least in our observations, we note that under high forest cover or under dominance of *D. gazella*, the abundance of *G. margareteae* tends to decrease drastically. The mechanisms behind the hyper-abundance of small-bodied species on pastures were not investigated or discussed by Nichols et al. (2007). However, we believe that, at least in our case, the dominance of small-bodied beetles could be attributed to some possibilities: (i) the effect of the introduced species *D. gazella* on native species populations, particularly through resource competition with larger beetles (e.g., *Dichotomius bos* and *D. nisus*) (see Filho et al., 2018; see Chapter IV); and (ii) the impact of long-term management practices on native dung beetle populations, for instance, long-term grazing in pastures reduce dung beetle diversity and increases dominance of exotic species (Morales-Trejo et al., 2024); (iii) thermal constraints associated with the seasonal harshness of Caatinga environments could favor assemblages dominated by small-bodied species, which are often more tolerant of temperature extremes. This last hypothesis warrants further testing across a broader pool of Caatinga species. It is important to note that the dominance of small-bodied species is likely linked to interspecific competition, functional group strategies, and nesting behavior (Halffter & Edmonds, 1982; Hanski & Cambefort, 1991). For instance, small species may outcompete larger ones due to their higher fecundity, faster development, and lower resource requirements. In contrast, large-bodied species, although often considered as superior competitors, depend on greater resource availability, exhibit lower reproductive rates, and have longer developmental periods (Hanski & Cambefort, 1991; Huerta et al., 2023).

These results indicate that small-bodied species not only contribute more to the taxonomic diversity of dung beetle communities in Caatinga pastures, but also numerically dominate them. The patterns across the sites can be visualized in **Figure 14**. This trend may reflect a greater tolerance or adaptability of smaller species to the ecological conditions of open and fragmented pasture landscapes.

Limitations and remaining knowledge gaps

Sampling solely performed during the rainy season (a relatively short window of time), combined with other factors such as the hyper-abundance of exotic species (i.e., *Digitonthophagus gazella*, see chapter IV) and soil characteristics, may have obscured underlying patterns. Under favorable conditions (i.e., rainy season with abundant cattle manure), species may move easily between forest fragments and pastures because climatic constraints are minimized. As result of this, there is a core of species, almost half of total pool, approximately 14 species that can be found possibility throughout any pasture sampled in such region (see **Figure S14** and **S5**). This makes it more difficult to detect effect of landscapes or local scale descriptors on dung beetle assemblages from SDTFs, as such a number of species have effect on most of assemblage descriptor variables measured here. In contrast, different patterns may emerge during the dry season or under drought conditions, when pastures are exposed to high temperatures and drastic reductions in vegetation biomass and soil cover. In such scenarios, forest fragments may function as refuges, since their vegetation structure provides shade and microclimatic buffering, creating less harsh environments that can sustain dung beetle persistence during unfavorable periods and provide alternative food resources during unfavorable periods (Salomão et al., 2018; Fuentes-Jacques et al., 2023).

Herein, we highlight important advances in the understanding of the ecology of dung beetles in the Caatinga. Notably, this is the first assessment of dung beetle assemblages from pasturelands in the Caatinga. Our study contributes to a broader understanding of the drivers of dung beetle diversity in tropical agricultural landscapes, particularly in SDTF regions. We emphasize the following key findings: (i) landscape-scale predictors are more effective than local management factors, showing a stronger impact on dung beetle assemblages; (ii) elevation was the best predictor, positively affecting dung beetle assemblages, followed by edge density, which revealed a more consistent negative effect; (iii) fragmentation *per se* may be beneficial to dung beetle assemblages in pastures of the Caatinga; (iv) although landscape-scale predictors are better, local management factors exhibited interesting patterns of effect on dung beetle assemblages, as seen with ivermectin acting as a harmful force; (v) in contrast to the use of ivermectin, vegetation structure can be a local driver that benefits dung beetle species; (vi) dung beetle assemblages in Caatinga pastures are dominated by small-bodied species in terms of both richness and abundance.

Contrary to the common assumption that forest cover is the major driver of dung beetle assemblages, our results suggest otherwise. Instead, a combination of factors appears to favor the reorganization of assemblages, leading to the dominance of some particular functional groups, which may directly affect the provision of ecosystem services.

Acknowledgements

C.R. thanks for the CAPES doctoral scholarship (Coordination for the Improvement of Higher Education Personnel - Brazil (CAPES) - Funding Code 001) and his research was supported by Rufford Small Grant (No. 36296-1), for laboratory support and infrastructure of CEPEC-CEPLAC, Brazilian Ministry of Agriculture. We are grateful to the smallholders who received us with full attention and hospitality. We acknowledge João Pedro (JP) for his invaluable support in field campaigns, Yohana Ocampo and Mª Betina Lima dos Reis for field campaigns and logistic support, and Iasmim Queiroz for valuable support in laboratory. C. Dos-Reis thanks to Dr. Fernando Vaz-de-Mello for his mentorship during Dos-Reis' stay in Cuiabá UFMT entomological collection. C. Dos-Reis thanks INECOL for lab and resources support during his Sandwich Doctorate internship. J.H.C.D. acknowledges their CNPq research productivity fellow.

Authors' Contributions

C. Dos-Reis, J.H.C. Delabie, and F. Escobar conceived and designed the study. C. Dos-Reis collected and analyzed the data. C. Dos-Reis wrote the first draft of the manuscript, under the supervision of J.H.C. Delabie and F. Escobar. All authors reviewed and contributed substantially to the final version of the manuscript.

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Supplementary material

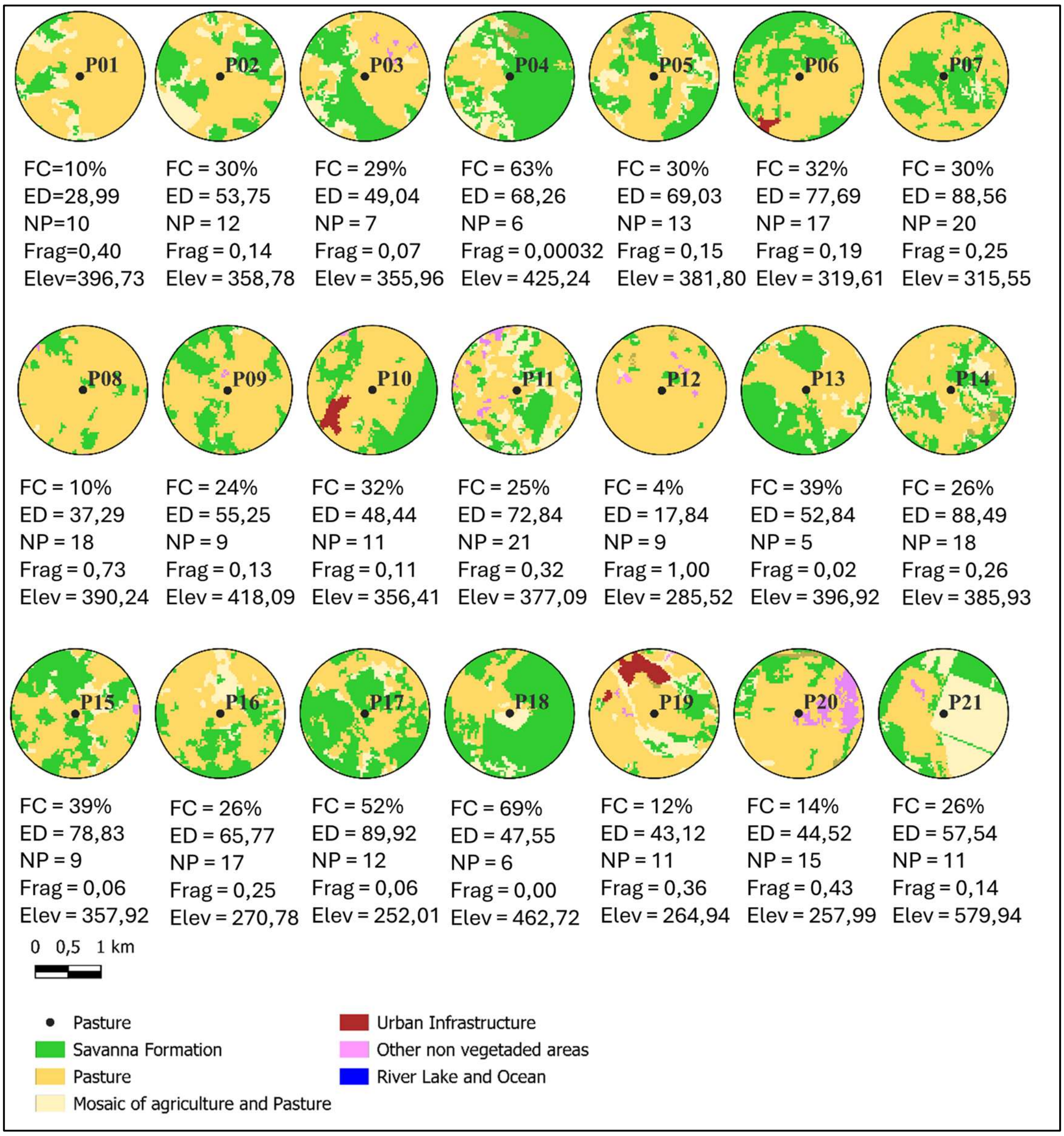


Figure S11. Sampled ranches and 1km radii landscapes. Landscape metrics are provided. FC= forest cover, ED= edge density, NP= number of fragments, Frag= fragmentation index, Elev= elevation.

Evaluating variable inclusion and removal

Correlation between landscape and climatic variables were evaluated because it is expected that some of them present high collinearity.

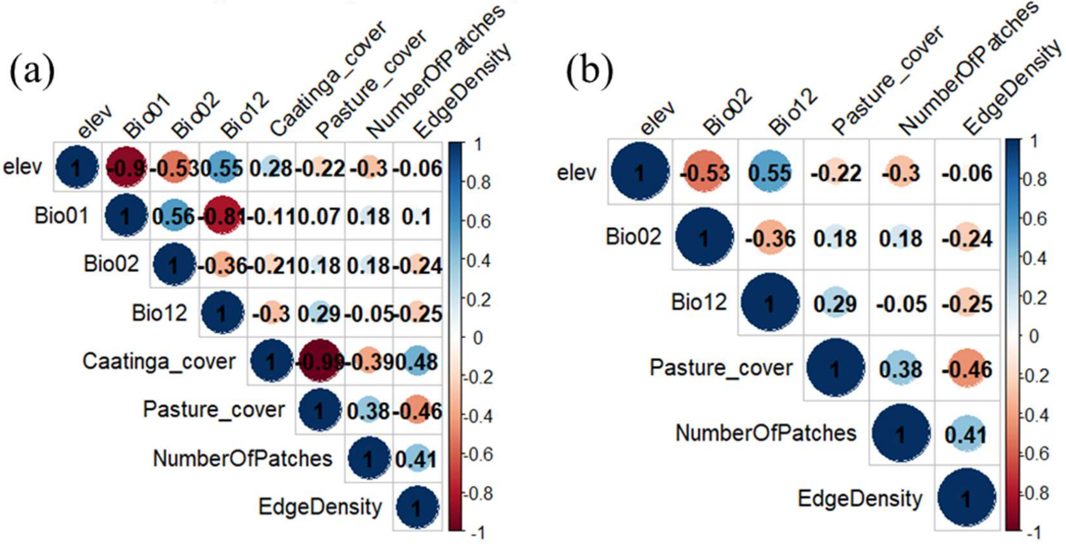


Figure S12. Correlation panels between landscape metrics and climatic variables: (a) initial set of variables; (b) after removing highly autocorrelated variables. Correlations plotted using the *corrplot* package.

Variance inflation factor (VIF) analysis to assess multicollinearity among predictor variables in a global model. Variables with VIF > 5 were considered highly collinear and were removed or combined.

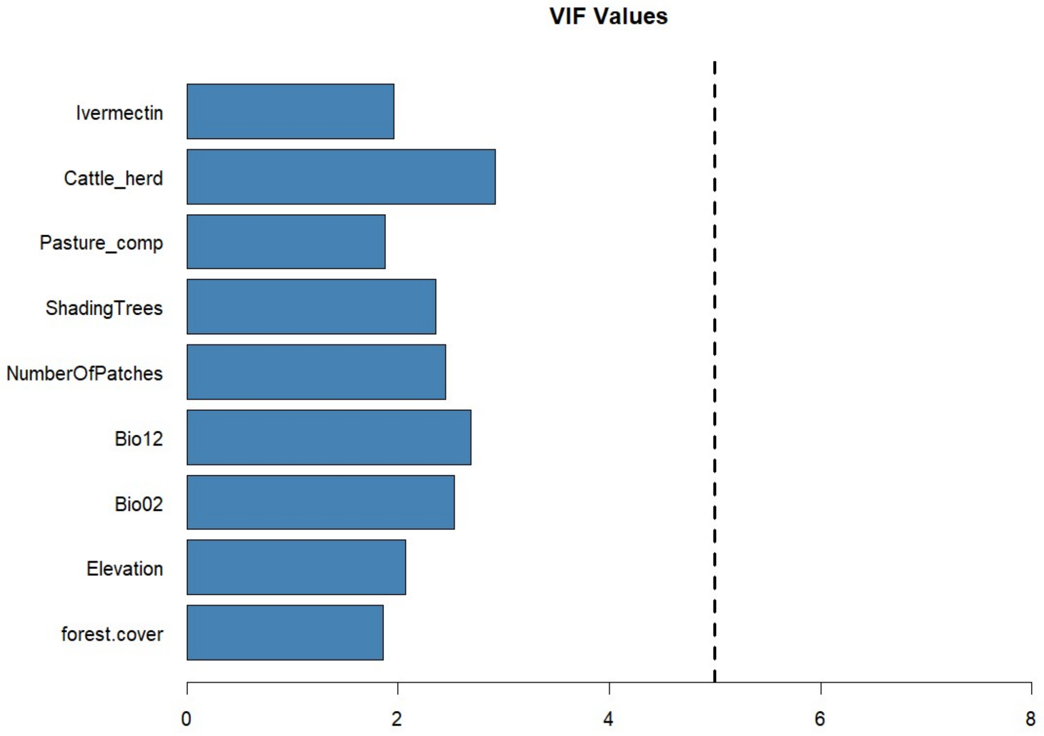
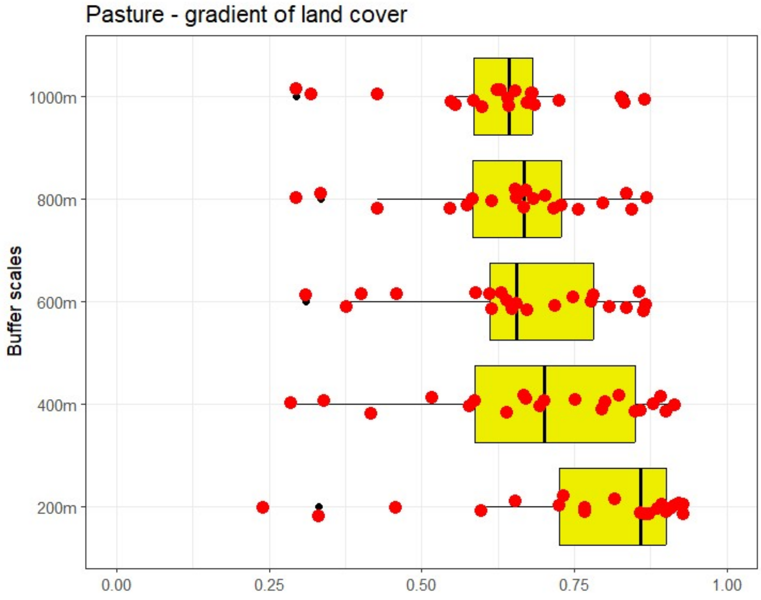
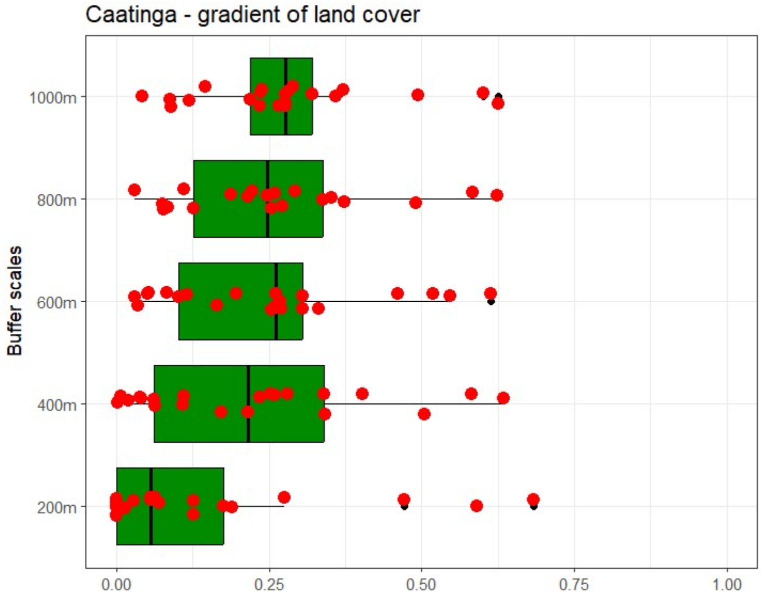


Figure S13. outputs for VIF to assess multicollinearity among predictor variables.

Forest cover and pasture cover, and elevation variation across ranches





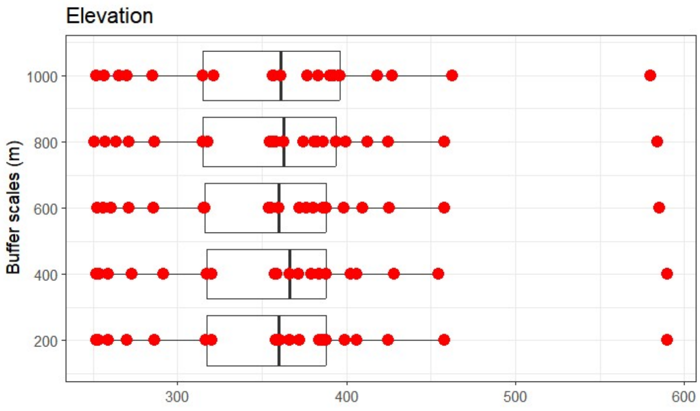


Table S2. Raw outputs of run models from each variable examined and its main statistics for landscape scale.

Landscape Scale				
Response Variable	**Explained**	**Best Predictor**	**Effect Direction**	**p-value**
^{0}D – Species richness	44.12%	log(Elevation_200)	Positive	> 0.05
Abundance	44.57%	log(NumberOfPatches_400)	Positive	<0.05
^{1}D – Shannon diversity	14.37%	Intercept	—	<0.01
^{2}D – Simpson diversity	15.64%	Intercept	—	> 0.05
Telecoprid richness	23.9%	log(Bio12_1000)	Negative	<0.05
Telecoprid abundance	32.84%	Number of patches	Positive	> 0.05
Paracoprid richness	41.03%	Elevation	Positive	> 0.05
Paracoprid abundance	31.28%	Forest cover	Negative	> 0.05
Endocoprid abundance	46.76%	log(NumberOfPatches_400)	Positive	<0.01
Large-bodied richness	44.56%	log(Elevation_200)	Positive	> 0.05
Large-bodied abundance	43.79%	log(Elevation_1000)	Negative	<0.01
Small-bodied richness	35.09%	log(EdgeDensity_200+1)	Negative	> 0.05
Small-bodied abundance	39.04%	log(NumberOfPatches_400)	Positive	<0.05

Table S3. Raw outputs of run models from each variable examined and its main statistics for local management scale.

Local Scale				
Response Variable	**Explained**	**Best predictor**	**Effect Direction**	**p-value**
^{0}D – Species richness	34.68 %	Intercept	—	<0.01
Abundance	8.12 %	Intercept	—	<0.01
^{1}D – Shannon diversity	25.69 %	Ivermectin	Negative	0.05
^{2}D – Simpson diversity	13.51 %	Intercept	—	<0.01
Telecoprid Richness	3.01 %	Intercept	—	<0.01
Telecoprid abundance	18.12 %	Intercept	—	<0.01
Paracoprid richness	43.47 %	Pasture composition	Positive	0.104
Paracoprid abundance	10.02 %	Intercept	—	<0.01
Endocoprid Abundance	14.91 %	Intercept	—	<0.01
Large-bodied richness	11.32 %	Intercept	—	<0.01
Large-bodied abundance	19.97 %	Shading trees	Positive	0.06
Small-bodied richness	39.25 %	Pasture composition	Positive	0.12
Small-bodied abundance	10.03 %	Intercept	—	<0.01

Table S4. Species abundance and frequency of occurrence in pasturelands of Raso da Catarina ecoregion. Min-Max= abundance range.

Species	**Abundance**	**Min-Max**	**Prop_abd**	**Freq**	**Frequency(%)**
Ateuchus semicribratus (Harold, 1868)	3958	0 - 1065	0,15	20	95%
Canthidium aff. manni	273	0 - 183	0,01	10	48%
Canthidium humerale (Germar, 1813)	53	0 - 32	0,00	4	19%
Canthidium prasinum (Blanchard, 1845)	11	0 - 7	0,00	2	10%
Canthidium sp. 1	1	0 - 1	0,00	1	5%
Canthidium sp. 2	8	0 - 4	0,00	5	24%
Canthidium sp. 3	5	0 - 3	0,00	3	14%
Canthidium sp. 5	1	0 - 1	0,00	1	5%
Canthon aff. carbonarius	20	0 - 12	0,00	3	14%
Canthon sp. 2	1	0 - 1	0,00	1	5%
Canthon sp. 4	1	0 - 1	0,00	1	5%
Deltochilum pseudoicarus Balthasar, 1939	4	0 - 4	0,00	1	5%
Deltochilum verruciferum Felsche, 1911	83	0 - 35	0,00	9	43%
Diabroctis mimas (Linnaeus, 1758)	14	0 - 13	0,00	2	10%
Dichotomius bos (Blanchard, 1845)	464	0 - 185	0,02	16	76%
Dichotomius geminatus (Arrow, 1913)	1182	0 - 551	0,05	17	81%
Dichotomius nisus (Olivier, 1789)	864	1 - 174	0,03	21	100%
Dichotomius puncticollis (Luederwaldt, 1935)	1	0 - 1	0,00	1	5%
Digitonthophagus gazella (Fabricius, 1787)	4858	1 - 1178	0,19	21	100%
Genieridium margareteae (Génier & Vaz-de-Mello, 2002)	9310	1 - 2749	0,36	21	100%
Malagoniella astyanax (Olivier, 1789)	41	0 - 11	0,00	10	48%
Ontherus appendiculatus (Mannerheim, 1828)	97	0 - 46	0,00	10	48%
Ontherus azteca Harold, 1869	1	0 - 1	0,00	1	5%
Ontherus digitatus Harold, 1868	149	0 - 40	0,01	12	57%
Onthophagus aff. ptox	2730	0 - 973	0,10	20	95%
Onthophagus hircus Billberg, 1815	123	0 - 87	0,00	10	48%
Pseudocanthon xanthurus (Blanchard, 1847)	43	0 - 28	0,00	4	19%
Tetraechma liturata (Germar, 1813)	199	0 - 90	0,01	10	48%
Trichillum externepunctatum Preudhomme de Borre, 1880	1655	0 - 381	0,06	20	95%
Uroxys bahianus Boucomont, 1928	2	0 - 1	0,00	2	10%
Abundance	**26152**	—	—	—	—
Species richness	**30**	—	—	—	—

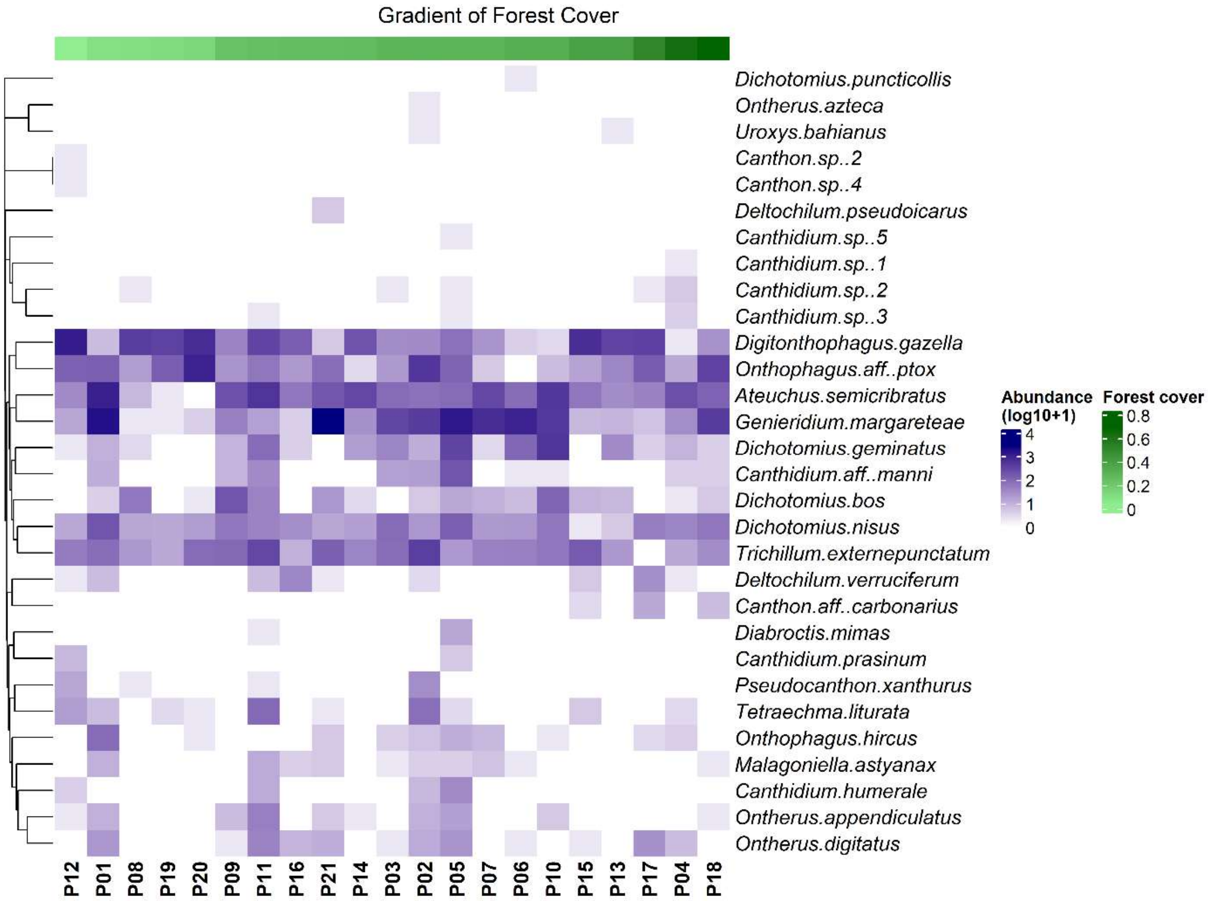


Figure S14. Heatmap showing species distribution of dung beetles recorded in 21 pastures sites. Pasture sites following a gradient of forest cover in a 1km^2 buffer.

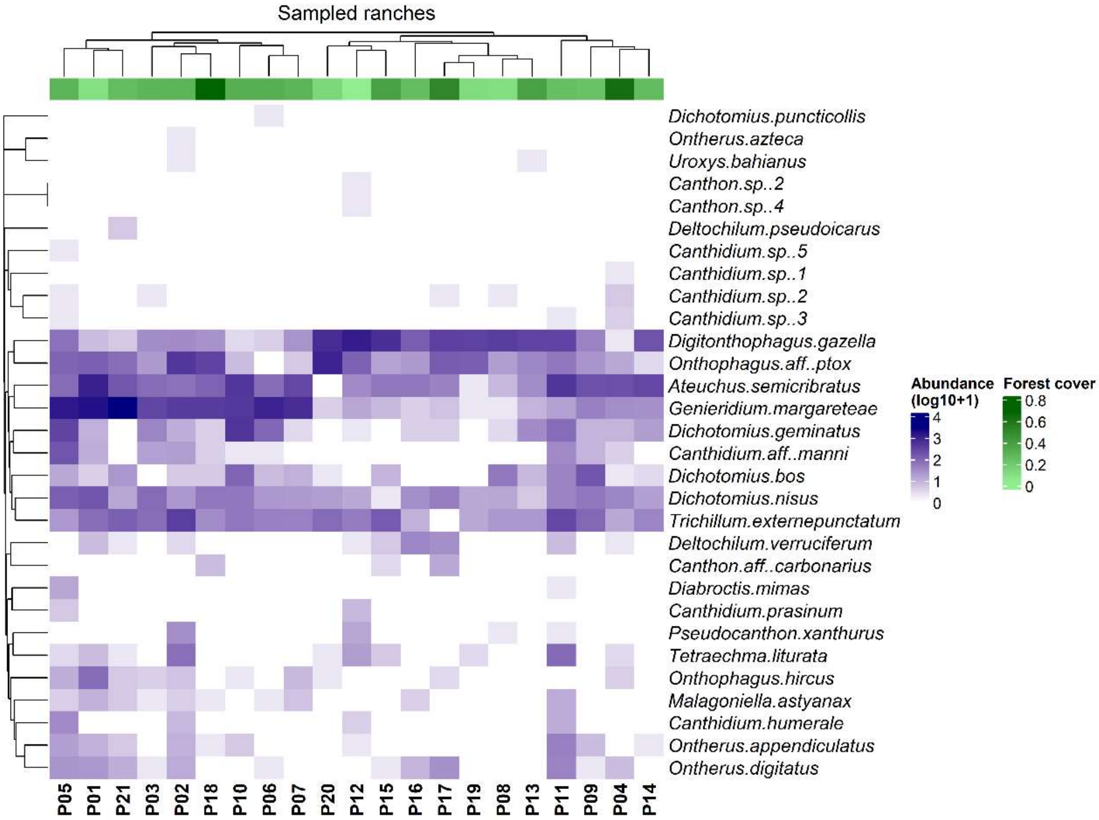


Figure S15. Heatmap showing species distribution of dung beetles recorded in 21 pastures sites.

CAPÍTULO IV

DOMINANCE OF THE EXOTIC AFRICAN DUNG BEETLE *Digitonthophagus gazella* (FABRICIUS, 1787) IN PASTURES SUPPRESSES NATIVE DUNG BEETLES FROM THE THREATENED CAATINGA BIOME

Manuscrito formatado nas normas da revista Biological invasions

Dominance of the exotic African dung beetle *Digitonthophagus gazella* (Fabricius, 1787) in pastures suppresses native dung beetles from the threatened Caatinga biome

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Abstract

The introduction of the exotic dung beetle *Digitonthophagus gazella* (Fabricius, 1787) into South American pastures has raised growing concerns about its impact on native dung beetle communities. In this study, we evaluated the effects of *D. gazella* dominance on the native dung beetle fauna in 21 pastures within the threatened Caatinga biome (Raso da Catarina ecoregion, Brazil). We examined how increasing dominance of *D. gazella* affects native species richness, abundance, diversity, evenness, community composition, and structure of different functional groups. Our results reveal strong negative effects of *D. gazella* predominance, including declines in species richness and abundance, significant losses in diversity of common and abundant species, and marked changes in species composition. Large–bodied and paracoprid functional groups were especially affected. Although *D. gazella* is efficient at removing cattle dung, its dominance in Neotropical pastures may lead to biotic homogenization due to suppression of native species, driving functional erosion with potential medium– and long–term environmental and economic impacts. These findings underscore the importance of long–term monitoring of *D. gazella* populations and native dung beetle–focused management in tropical ecosystems across South America.

Keywords: Scarabaeinae, Invasion ecology, Competition, Biotic homogenization, Tropical dry forests

Introduction

Among the most significant Anthropocene footprints are the drastic modification of natural ecosystems and the translocation of species by humans. This biological reshaping of the planet is the result of deliberate introductions for agriculture or conservation, as well as accidental spread through global trade and travel. It creates novel species combinations, thus affecting biodiversity and ecosystem functioning (Otto, 2018; Pyšek et al., 2020). To become invasive, exotic species must overcome a series of geographic barriers and ecological filters, including demographic, dispersal, and environmental factors, which determine their ability to establish and spread (Blackburn et al., 2011). Once established, and with population booms throughout the new environments, the invasive species can rapidly impact the recipient ecosystems, often leading to the decline of native populations and communities and incurring local extinctions (Bradley et al., 2019; Hui & Richardson, 2019; Kehoe et al., 2021) and subsequent functional disruptions due to cascading effects in the ecological interaction networks (Hui & Richardson, 2019; Sanders et al., 2003).

These impacts are frequently driven by direct competition with native species, particularly when overlap occurs at any level of niche use (Levine et al., 2003; Broennimann et al., 2012; Aravind et al., 2020). Typically, local extinctions occur when an introduced species overcomes interspecific (or life history) tradeoffs such as reproduction, survival, and growth of local species within a particular environment (Catford et al., 2018). The presence of an invasive alien species is often mediated by human activities, which makes it difficult to determine the direct effect of the alien species on native communities. Therefore, either biotic differentiation or homogenization can result from biological invasions, and the natural history of species may provide important insights into how the communities respond (Olden & Rooney, 2006). In native insect communities, it has been observed that they may respond to local displacement rather than species extinctions (Pyšek et al., 2017). Invasive alien species are, therefore, an ecological concern as they can drive environmental changes in protected areas, agroecosystems, and urban habitats, impacting many economic activities (Pyšek et al., 2020).

When deliberately introduced, the intention is usually that the alien species will contribute to solving specific environmental problems; for instance, pollination issues, pest population control, and habitat and soil improvement, among others (Kumschick et al., 2016). As a deliberate example of species introduction to provide ecosystem services, the dung beetles (Scarabaeinae) are highlighted. Dung beetles are key organisms in many terrestrial ecosystems due to their crucial ecological roles in dung removal, nutrient cycling, soil aeration, seed dispersal, and suppression of dung–breeding pests (Nichols et al., 2008; deCastro–Arrazola et al., 2023). These ecological services are of particular importance in cattle pastures, where the accumulation of cattle dung can hinder pasture productivity and facilitate the spread of parasites and disease harmful to livestock and human health, with significant economic consequences (Markin & Yoshioka, 1998; Nichols et al., 2008; deCastro–Arrazola et al., 2023).

To enhance dung removal and mitigate sanitary risks in extensive cattle–production systems, several countries have introduced exotic dung beetles, notably *Digitonthophagus gazella* (Fabricius, 1787), a species of Indo–African origin of generalist habits, with a rapid reproductive cycle and high ecological plasticity (Nascimento et al., 1990; Cambefort & Hanski, 1991; Doube et al., 1991; Saueressig & Alves, 1999; Floate et al., 2015; Noriega et al., 2017). *Digitonthophagus gazella* has successfully established populations across the Americas, from the United States to Argentina, including Brazil, where it was introduced for biological control and management of livestock feces due to its high dung removal capacity (Nascimento et al., 1990; Saueressig & Alves, 1999; Alvarez Bohle et al., 2009; Noriega et al., 2017; Noriega et al., 2020). Although programs of dung beetle introduction were an important matter in countries such as Australia and New Zealand that have faced ecosystem services disruption due to their native dung beetle species being incapable of dealing with the dung of introduced domestic animals (cows, horses, and sheep) during British colonization in the 19th century, because the dung beetle species native to these regions have evolved to use marsupial pellets (Emberson & Matthews, 1973; Doube et al., 1991; Edwards, 2009). Although the release of exotic dung beetle species into pastures was not considered a priority in Neotropical countries, the fear of what had happened with the ruin of the Australian cattle industry in the 1960s and the serious problems caused by horn fly (*Haematobia irritans*) encouraged these countries (Fincher et al., 1983; Markin & Yoshioka, 1998; Ridsdill-Smith & Edwards, 2011). Although efficient in terms of dung removal, *D. gazella* may impact native dung beetles by displacing them through competition, monopolizing dung resources, and potentially disrupting ecosystem functions, particularly those linked to large–bodied beetles that perform deep dung burial and intense soil bioturbation (Noriega et al., 2020; Maldaner et al., 2024).

Digitonthophagus gazella can access available resources rapidly and efficiently, and can utilize cattle dung, reproducing at a rate above the average (at least two generations per year) compared to native species of the same body size (Saueressig & Alves, 1999; Floate et al., 2015; Huerta et al., 2023). Under suitable environmental conditions, the species can disperse rapidly at rates of up to 220 km per year, as reported for Mexico (Kohlmann, 1994). Therefore, *D. gazella* can colonize a broad range of disturbed open areas, mainly utilized for livestock production

(Noriega et al., 2017; Noriega et al., 2020; Queiroz et al., 2023) and shows a preference for cattle pats (DBI, 2023). Despite the potential risks, the actual ecological role of *D. gazella* within native dung beetle communities remains poorly understood (but see Matavelli & Louzada, 2008; Queiroz et al., 2023; Maldaner et al., 2025). Two contrasting hypotheses have been proposed: (i) *D. gazella* may act as a strong competitor that suppresses populations of native species (Fincher et al., 1986; Howden & Scholtz, 1986; Young, 2007; Matavelli & Louzada, 2008; Noriega et al., 2017; Filho et al., 2018; Queiroz et al., 2023); or (ii) it may integrate into local communities through a process of functional naturalization, coexisting with native species (Lobo & Montes–de–Oca, 1994; Giraldo–Echeverri et al., 2024). It is therefore important to monitor and report the effects of *D. gazella* on native species in pastures of the Neotropical region (Noriega et al., 2017).

These uncertainties are of particular importance in tropical dry forests, such as the Caatinga biome in northeastern Brazil, a biodiverse, highly seasonal, and heterogeneous ecosystem that harbors a unique dung beetle fauna adapted to the scarce and variable availability of dung produced by vertebrates. Understanding how an introduced and invasive species such as *D. gazella* interacts with native communities in pastures embedded within this biome is critical for assessing the long–term impacts of the species on biodiversity and ecosystem resilience. In this study, we evaluate the effects of *D. gazella* dominance on native dung beetle communities in Caatinga pastures. Specifically, we expected the increasing dominance of *D. gazella* to negatively affect (i) species richness, (ii) abundance and diversity of native dung beetles, (iii) the structure of functional groups, and (iv) to drive community compositional changes. More specifically, we evaluated the effect of this exotic species on the abundance of three native species of similar or larger body–size from the genus *Dichotomius* Hope, 1838 (*D. bos*: 15–26 mm; *D. nisus*: 15–17 mm, and *D. geminatus*: 11–12 mm), chosen because they are paracoprids (as is *D. gazella*: 12–15 mm), widely distributed in pastures of the region and provide most of the ecosystem services in Caatinga pastures (Yokoyama & Kai, 1993; Bang et al., 2005; Milotić et al., 2017; Tissiani et al., 2017; Maldaner et al., 2024). Our study aimed to advance the debate on invasive alien species management and biodiversity conservation in tropical grazing systems.

Material and Methods

Study area

This study was conducted in 21 cattle pastures across four municipalities in the Raso da Catarina, located in the state of Bahia, within the Caatinga biome (Figure 1), a critically endangered ecosystem in Brazil according to the IUCN red list of ecosystems (Ferrer-Paris et al., 2019). This ecoregion is narrow and elongated in the N–S direction with an extension of 30,800 km². The region is a basin of very sandy, deep, and infertile soils, with very flat relief and canyons in the western part. The climate is semi–arid, quite hot and dry, with an average annual temperature ranging from 24 to 27 ºC and an average annual precipitation of around 650 mm, characterized by a markedly seasonal climate with severe droughts (Ab'Sáber, 1974). The predominant vegetation is shrubby and very dense with cacti and bromeliads, and is less thorny than the Caatinga of crystalline soils (Velloso et al., 2002). The vegetation therefore comprises a Seasonally Dry Tropical Forest (da Silva et al., 2017). The delimitation of the sample region was mainly based on soil homogeneity, precipitation regimen, and vegetation structure, which are important ecological conditions for the diversity and composition of native dung beetle communities. The region is considered a priority area for conservation and is known for being an important site for the study of biodiversity (Leal et al., 2003). Deforestation driven by livestock expansion, together with local management practices that promote soil degradation, are among the main threats to the region's wildlife diversity.

Sampling design

To ensure independence among sampling sites, we adopted a minimum distance of two km among pastures. Within each pasture, dung beetles were sampled using six 1 L pitfall traps (12 cm diameter, 12.8 cm depth) buried flush with the ground 50 m apart and partially filled with a solution of water, salt, and detergent to prevent the beetles from escaping. A plastic cover was placed above each trap to protect it from rainfall and direct sunlight. Each trap was baited with 500 g of a mixture of cattle and pig dung (3:1) for 24 hours.

Data analysis

We used Generalized Linear Models (GLMs) and Generalized Additive Models (GAMs) (Zuur et al., 2009) to test the effects of *D. gazella* dominance (considered as the proportion of abundance from the total number of individuals collected, ranging between 0 and 1) on different attributes of the native dung beetle community. We applied different regression approaches according to the nature and distribution of each response variable. First, we evaluated visual correlations to find the model type to apply to our model (GLM or GAM). The best model to test each relationship between the response variable and dominance of *D. gazella* was then compared with an equivalent null model using Akaike weights (wAICc). As attributes of the native dung beetle community, we computed Hill numbers: ${}^0D$ (species richness), ${}^1D$ (exponential of Shannon's index: which corresponds to the number of common or typical species in the community) and ${}^2D$ (inverse of Simpson's index: which corresponds to the number of very abundant or dominant species in the community) (Hill, 1973; Jost, 2006). In addition, we calculated evenness using the ratio ${}^1D/{}^0D$, as proposed by Jost (2010). To evaluate the effects of *D. gazella* on the functional groups of native dung beetles, we classified the species according to body size (Hanski & Cambefort, 1991): large (>10 mm) or small (<10 mm), as well as food relocation behavior (Halffter & Matthews, 1966): paracoprid, that digs tunnels directly beneath a dung pile; telecoprid, that forms dung into balls and rolls them away from the dung source to bury; and endocoprid, that lives, eats, and breeds within the dung pat itself. To run the analyses, we removed the abundance of *D. gazella* from the dataset in order to evaluate its dominance on only the native set of dung beetle species.

For count–based responses, such as species richness and number of individuals, we used Generalized Linear Models (GLMs) with Poisson or Negative Binomial distributions, depending on the presence of overdispersion (Zuur et al., 2009). Models were compared with null models through AICc computed from MuMIn (Bartoń, 2015). The lowest AICc model was considered plausible, but the significance of the p–value was adopted to determine the best model. For continuous community metrics, such as evenness and diversity (${}^1D$ and ${}^2D$ Hill numbers), which showed non–linear trends, we employed Generalized Additive Models (GAMs) using the mgcv package (Wood, 2011). To avoid overfitting and control model complexity, we used cross–validation to determine the optimal degree of smoothing, but setting a limit of five effective degrees of freedom (Zuur et al., 2009). The model fits were checked using the DHARMa package (Hartig, 2024) and conventional validation through residual visualization (Zuur et al., 2009). We followed conventional family distributions for each data type and tested the assumptions, adjusting the distribution where necessary (Zuur et al., 2009). To assess whether the proportional dominance of *D. gazella* influenced the composition of native dung beetle species, we performed a permutational multivariate analysis of variance (PERMANOVA) using the '*adonis2*()' function from the vegan package in R (Oksanen et al., 2013). The analysis was performed on a sites x species matrix considering Jaccard–based dissimilarity using presence–absence data and Bray–Curtis on abundance (excluding *D. gazella*). The proportional abundance of *D. gazella* at each site was used as a continuous predictor. A total of 999 permutations were performed under a reduced model. The amount of variance explained by the model (R^2), F–statistic, and significance level were recorded to evaluate the relationship between *D. gazella* dominance and native community composition changes.

Finally, we also conducted a non–metric multidimensional scaling (NMDS) ordination using the same dissimilarity matrix to visualize differences in species composition along the gradient of *D. gazella* dominance. Goodness–of–fit (stress value) was used to evaluate ordination quality, and the relationship between ordination scores and *D. gazella* proportions was assessed with the 'envfit()' function. All analyses were performed in R version 4.4.1 (R Core Team, 2024).

Results

We recorded a total of 4,858 individuals of *D. gazella* representing 19% of the total number of beetles collected (Table S1). The species was present in all surveyed cattle ranches, with a mean abundance (± SD) of 231.33 ± 306.30 individuals per site, ranging from 1 to 1,178 individuals (Table S1). *Digitonthophagus gazella* consistently exerted negative effects on native dung beetle communities composed of 29 species (Table S1), with species richness (Figure 2a) and total number of individuals (Figure 2b) both declining as the dominance of the exotic species increased (Table S2).

A significant non–linear relationship was found between the increased proportional dominance of *D. gazella* and native dung beetle diversity (Figure 3, Table S2). As the proportional abundance of *D. gazella* increased between 0.2 and 0.4, there was a more accentuated loss of typical or common (${}^{1}D$: edf = 3.55, F = 3.31, p = 0.0299, Figure 3a) and dominant (${}^{2}D$: edf = 3.43, F = 3.34, p = 0.0281, Figure 3b) effective species, suggesting that moderate to high levels of the exotic species dominance are associated with substantial losses in diversity. Although the relationship between *D. gazella* dominance and evenness was not significant (F = 3.08, p = 0.061, Table S2), evenness increased to a certain point and then began to drop when the dominance values exceeded 50% (Figure 3c).

The dominance of *D. gazella* affected both species richness and abundance of dung beetle functional groups according to their body size (Figure 4, Table S2). For large–bodied species, richness significantly declined with increasing dominance of *D. gazella* ($\beta = -3.209$, p = 0.004, Figure 4a). Similarly, large–bodied species abundance showed a strong negative relationship with *D. gazella* ($\beta = -2.513$, $p < 0.001$, Figure 4b). On the other hand, small–bodied species richness showed a negative trend and the relationship exhibited a weaker response ($\beta = -0.360$, p = 0.182, Figure 4c). However, small–bodied species abundance significantly declined in relation to the exotic species dominance (β = –2.960, p < 0.001; Figure 4b).

We observed strong negative responses of the functional groups related to food relocation behavior to the increasing dominance of *D. gazella* in pastures (Figure 5, Table S2). The richness of paracoprid species significantly declined as the proportional abundance of *D. gazella* increased (GLM, p < 0.05; Figure 5a). A similar pattern was found for paracoprid abundance, which presented a non–linear decline (GLM with negative binomial distribution, p < 0.01; Figure 5b). Endocoprid species were also negatively affected, with their total abundance dropping sharply in pastures where *D. gazella* was dominant (GLM, p < 0.01; Figure 5c). In contrast, telecoprid species showed no significant response (Figure S1).

NMDS ordination revealed consistent patterns of compositional differentiation in response to the predominance of the exotic species (Figure 6). Based on both Jaccard (stress = 0.195) and Bray–Curtis (stress = 0.181) dissimilarities, there were clear shifts in community composition across pastures, with the "prop_dgazella" vector pointing toward communities from sites with higher dominance of exotic species (e.g., P12, P13, P15). A clear separation of pastures was observed according to the presence of *D. gazella* (Figure 6a), but this trend was more pronounced in the abundance–based ordination (Bray–Curtis; Figure 6b). Communities from sites with low to intermediate dominance (yellow to orange) tended to cluster more closely, whereas those from high–dominance sites (red) appeared more distinct, indicating strong community species turnover. These visual patterns were supported by the PERMANOVA results. Using Bray–Curtis dissimilarity, the proportional abundance of *D. gazella* explained 20.1% of the variation in the native assemblage structure (F = 4.78, p = 0.001). With Jaccard dissimilarity, the effect remained significant, accounting for 16.8% of the variation (F = 3.84, p = 0.001). Altogether, these results indicate that the higher dominance of *D. gazella* is associated with pronounced shifts in the native dung beetle fauna composition.

The response of the three medium– and large–bodied species of the genus *Dichotomius* revealed that *Digitonthophagus gazella* dominance has an influence on those species of the genus *Dichotomius* which could represent shifts on dung beetles functioning in the cattle pastures of the study region (Figure 7, Table S2). For instance, the abundance of *D. nisus* was negatively affected by the dominance of *D. gazella* (β = –2.36, z = –4.41, p < 0.001, Figure 7a). Similarly, *D. geminatus*, of medium body size, also showed a significant negative response (β = –4.16, z = –3.33, p < 0.001, Figure 7b). In contrast, the dominance of *D. gazella* did not affect *D. bos* (β = –1.32, z = –1.02, p = 0.31), suggesting a weak or null effect on that particular species (Table 1; Figure 7c).

Discussion

Our results provide strong evidence that the introduced dung beetle *Digitonthophagus gazella* negatively impacts native dung beetle fauna from cattle pastures of the Raso da Catarina ecoregion within the threatened Caatinga biome of Brazil. Our results align with the hypothesis (i) in which *D. gazella* can be considered an important invasive alien species that affects native communities (Filho et al., 2018), rather than the naturalization proposed by hypothesis (ii), in which *D. gazella* could be considered a species that integrates into native dung beetle communities with no evident effect (Giraldo–Echeverri et al., 2024). This species exerts a marked influence on multiple community ecological attributes with significant reductions in species richness, abundance, diversity, and evenness, as well as changes in species composition and functional groups, particularly on large–bodied species of paracoprid habits. Although restricted to open pastures, *D. gazella* shows a high potential for ecological interference, likely through competitive exclusion and resource monopolization. Such a pattern could align with the process of biotic homogenization, in which an invasive alien species reduces the ecological distinctiveness of the preexisting local communities (Olden & Rooney, 2006; Florencio et al., 2013).

The distribution of *D. gazella* in the Neotropics is restricted to open habitats (Noriega et al., 2006; Noriega et al., 2010), avoiding forested areas, which represents a barrier to its dispersion (Lobo & Monte de Oca, 1994). The species seems to be incapable of colonizing native vegetation, even in savanna–like vegetation such as Caatinga. When collecting, the species is very rare (up to two individuals in occasional captures along trails or forest clearings) to absent from native vegetation, according to previous surveys (Queiroz et al., 2023; C. Dos–Reis, unpublished data) and confirming that observed by Giraldo–Echeverri et al. (2024) in a tropical dry forest livestock landscape in northern Colombia. In our study region, the exotic species is more strongly associated with cattle and pig excrement and seems to be sensitive to changes in the vegetation structure of livestock pastures, as its abundance drops drastically with increases in vegetation density. The mere presence of native shrubs is sufficient to reduce *D. gazella* abundance to less than half, thereby contributing to an increase in native species, adapted to forested areas (Queiroz et al., 2023; C. Dos–Reis, unpublished data).

The increasing dominance of *D. gazella* was also associated with marked declines in diversity of common (^{1}D) and dominant (^{2}D) species. Although the relationship was not linear, 40% dominance drives a drastic negative response in both diversity metrics, while an increased dominance of 60–80% implies the loss of two–thirds of the diversity, suggesting not only loss of the species that make up the core of the communities of native dung beetles that utilize pastures (comprising six species that account for about 75% of the total abundance, see Table S2), but also the erosion of pasture functioning. The displacement of dominant native fauna by *D. gazella* may compromise key ecological services such as deep dung burial, nutrient redistribution, and soil bioturbation (i.e., aeration and water infiltration), which are important for the sustainable management and health of pastures (Maldaner et al., 2024). In addition, evenness responds markedly when *D. gazella* dominance exceeds 50% in the pastures. This finding may reflect a trend toward the numerical homogenization of native dung beetle communities, suggesting that dominance of the exotic species likely suppresses the most abundant native taxa, resulting in relatively equal but lower abundances across the remaining species. Changes in species evenness within native communities merit attention, as an increased abundance of invaders can drive numerical restructuring of communities long before species are threatened with extinction (Chapin III et al., 2000; Bradley et al., 2019).

Digitonthophagus gazella utilizes fresh, firm to semi–liquid cattle dung, giving it a certain advantage over native beetle species, which are adapted to the use of drier, smaller mammalian excrement from ungulates, primates, and felines. Mammal defaunation due to land–use change related to the expansion of cattle farming drives changes in many tropical dung beetle communities (Fuzessy et al. 2021) and leads to a reduction in their biomass (Raine & Slade, 2019). Our results suggest that the impact of *D. gazella* varied according to body size, with large–bodied dung beetles being particularly affected. These species are relatively important due to the amount of excrement they can remove, added to having a single reproductive event per year and requiring more time to complete their life cycle, which can potentially impact population stability and make them more vulnerable to niche overlap (Hanski & Cambefort, 1991; Saueressig & Alves, 1999; Huerta et al., 2023). This contrasts with the findings of Giraldo–Echeverri et al. (2024), who reported that *D. gazella* shares resources and coexists for more than 96 hours with several native dung beetle species from the dry forests of northern Colombia. On the other hand, smaller species appeared tolerant of *D. gazella* dominance, suggesting a potential functional reshaping of dung beetle communities that inhabit the pastures. In fact, a hyper–dominance of small sized beetles in tropical pastures could be expected (Nichols et al., 2008), and cases have been already confirmed in this region (C. Dos–Reis, unpublished data), due to the suppression of large beetle species, as has also been observed in extensive treeless pastures in Yucatán, Mexico (Alvarado et al., 2019). However, we do not know if this is a result of community reorganization due to land–use changes, or whether the presence of this invasive exotic species synergistically modulates this reshaping.

The observed decline in both paracoprid and endocoprid dung beetles with increasing *D. gazella* abundance suggests a broad interference across the different food relocation behaviors. This pattern may reflect the fact that *D. gazella*, as a species of paracoprid habits, competes more directly with other species that exhibit similar behavior (Hanski & Cambefort, 1991). In contrast to the telecoprids, paracoprid and endocoprid species often exploit dung resources at or underneath the deposition site, leading to greater overlap in spatial and temporal resource use (Halffter & Edmonds, 1982; Hanski & Cambefort, 1991). The decline of paracoprid and endocoprid species may therefore indicate resource monopolization by *D. gazella*, a species known for its rapid colonization of cattle dung, short reproductive cycle, and high population growth (Saueressig & Alves, 1999; Floate et al., 2015; Noriega et al., 2020). A female of *D. gazella* can produce 100 offspring during her lifetime (Blume & Aga, 1978), with at least two generations produced per year. The telecoprids' lack of response may be attributed to their unique behavior of rolling and burying dung balls at a distance from the source. This relocation strategy effectively reduces direct competition and is recognized as a key mechanism promoting functional complementarity and species coexistence in dung beetle communities (Cambefort & Hanski, 1991).

As indicated by NMDS ordination and corroborated by PERMANOVA analyses, native dung beetle community composition changes were related to *D. gazella* dominance. Our results suggest that this species can act as an ecological filter, driving compositional homogeneity. The proportion of variance explained by *D. gazella* in native community structure (~16–20%) highlights its potential role as a modulator of taxonomic and functional shifts in dung beetle fauna inhabiting pastures of the Caatinga. In general, two patterns emerged with the presence of *D. gazella* in the pastures: (i) at low to intermediate dominance, competition may increase evenness and produce numerical homogenization, and (ii) at high dominance, communities apparently experience local extinctions and become more dissimilar from one another. These are aspects that require exploration in further studies.

In general, species of the genus *Dichotomius*, recognized for being of medium to large body size (ranging from 5 mm to 38 mm in length), are important in tropical pastures; 17 of the 170 valid species are common in Brazilian pastures (Tissiani et al., 2017). In our study, *D. nisus* and *D. geminatus*, known for their important role in dung removal in Caatinga pastures (C. Dos–Reis, unpublished data), exhibited marked declines under high *D. gazella* abundance. This raises concerns about the loss of essential ecosystem functions linked to native paracoprid activity. Interestingly, *D. bos* did not show a significant response, possibly due to niche differentiation, behavioral tolerance, or use of distinct microhabitats, factors that merit further investigation. However, *D. bos* is likely a direct competitor of *D. nisus*, which may already be under pressure from interspecific competition with other native species.

In general, few ecological studies have been conducted under field conditions to assess coexistence and interspecific competition in the presence of *D. gazella*. de Oca & Halffter (1995) documented the direct exclusion of *Onthophagus batesi*, a species smaller than *D. gazella*, in Mexico. In contrast, the abundance of *D. gazella* and *Onthophagus marginicollis*, a small–sized species (~ 7 mm long), was similar, and both species shared the resource (Giraldo–Echeverri et al., 2024). Interestingly, although *D. gazella* has also proven capable of competing successfully with larger species, this species can affect both large and small beetles at the community level. Similar patterns were reported by Filho et al. (2018) in Brazilian pastures. Although *D. gazella* was introduced into livestock systems for sanitary purposes, it is evident that rigorous monitoring and risk assessment programs were not implemented prior to its release in Neotropical countries, particularly when compared to the long–term monitoring efforts conducted in Australia (Edwards, 2009). Some native tropical dung beetles could have been considered from the outset as effective sanitary agents, avoiding the need for exotic introductions. Our findings underscore the potential ecological risks posed by *D. gazella*, particularly in pastures of the tropical dry forests.

Even though *D. gazella* is recognized as an efficient remover of dung, the reason it was introduced in many tropical and subtropical cattle pastures is that it rapidly digs numerous but shallow tunnels that do not reach 25 cm in depth, compared with native paracoprids that can easily dig tunnels deeper than 100 cm (DBI, 2023; Maldaner et al., 2024). However, even if the high abundance of *D. gazella* in pastures could compensate for the rate of cattle dung removal, other ecosystem services could be compromised. For instance, the quantity of soil removed in terms of burial depth impacts nutrient circulation, water infiltration, and soil aeration, with potential long–term effects on soil conditions.

Since government agencies selected certain morphological traits and released (or recommended the release of) only large, non-deformed individuals, they may have promoted populations with greater potential for invasion and establishment success (Nascimento et al., 1990; Duncan, 2016; Stanbrook–Buyer & Allen, 2025). Moreover, other factors, such as climatic changes related to temperature and relative humidity variation, may differentially regulate long–term shifts of the invasive species *D. gazella* and their impact on local dung beetle diversity (García et al., 2022). Long–term climate variations could prevent or favor the invasion of introduced species, modifying the structure of local communities and driving shifts in stability and resilience of ecosystems, which in turn could alter the relationships of species dominance and cause loss of biodiversity, with consequences for ecosystem functioning (García et al., 2022). Projections suggest that half of the native dung beetle species inhabiting South American pastures are expected to experience geographic range contractions, while *D. gazella* will expand its distribution, particularly under ongoing climate change (Maldaner et al., 2025). Recent evidence shows that the Brazilian Cerrado is becoming warmer and drier; conditions that should favor the dominance of *D. gazella*, since the increased temperatures can accelerate their metabolism and reproduction rate (García et al., 2022). Under such a scenario, *D. gazella* may expand without precedent through Neotropical tropical pastures, as their populations seem to be taking advantage of the low levels of competition from native dung beetle communities. In Neotropical pastures, such as those in Caatinga, it is likely that this invasive species will not occupy empty niches, increasing the realized trait space of the community, as proposed when it was introduced in Brazil during the 1990s (Noriega et al., 2020; Saueressig & Alves, 1999). Direct negative effects of *D. gazella* on native species have been reported in pastures in the state of Georgia, USA, where the species competes directly with local dung beetles (Young, 2007). In Texas, *D. gazella* accounted for 23% of all individuals captured in open pastures, and its abundance increased 3.6–fold in a single year, from 3,202 to 11,709 individuals, while the native species declined sharply (Fincher et al., 1986). Similar effects have also been documented in pastures of Colombia, where the species has altered native communities and competitive dynamics (Noriega et al., 2017).

The strength and nature of the impacts of invasive alien species often vary depending on the stage of invasion and the time elapsed since introduction. Since *D. gazella* was introduced relatively recently in South America (less than 40 years ago), with no monitoring or reporting of its spread in Brazil, native communities may still be undergoing a reassembly process, with lagged effects becoming more pronounced over time (Crooks, 2005). This process is likely dynamic and multifactorial rather than simple or direct and may depend on local features such as cattle density, retention of trees in pastures, management practices (e.g., use of antiparasitics), and landscape context (e.g., forest cover amount, fragmentation). Such factors may partially explain the idiosyncratic responses reported across different studies and countries (Noriega et al., 2020). It is known that Neotropical dung beetle diversity responds positively to vegetation structural complexity, facilitating colonization or recolonization by native species (Halffter & Matthews, 1966; Reis et al., 2023). For this reason, silvopastoral systems reinforced with patches of forest at the landscape scale may represent a reliable alternative to promote the retention of native species and their ecosystem services (Giraldo et al., 2011). Importantly, the outcome of invasion may also depend on the diversity of native dung beetle communities, which are expected to respond differently to the arrival and establishment of *D. gazella*. These responses range from invasive dynamics with strong negative effects (Fincher et al., 1986; Young, 2007; Matavelli & Louzada, 2008; Noriega et al., 2017; Filho et al., 2018; Queiroz et al., 2023) to apparent naturalization with no clear detriment to the native communities (Lobo & Montes–de–Oca, 1994; Giraldo–Echeverri et al., 2024). In such cases, competitive exclusion may act as a primary limiting factor for colonization success, of potentially greater importance than the species' own traits, as has been observed in both North American and Australian cattle pastures (Noriega et al., 2020).

Digitonthophagus gazella begins its activity with the first rains and, due to its rapid reproductive cycle, its populations can increase in size quickly during the wet season (de Oca & Halffter, 1995; Floate et al., 2015). In our study region, sampling was conducted during the rainy period, when dung beetle activity is highest, which means that our data represent only a specific time window of community dynamics. Year–round monitoring would therefore be valuable to assess how *D. gazella* dominance fluctuates over time and across seasons. For instance, Filho et al. (2018) reported that the response of communities and functional groups to *D. gazella* dominance can change over time. This is particularly relevant in regions such as the Caatinga biome, which are severely affected by drought, when dung beetle activity in the pastures is drastically reduced. However, during such dry periods, *D. gazella* and a few native species, such as *Ateuchus semicribratus* and *D. geminatus*, may remain active (C. Dos–Reis, pers. obs.).

In conclusion, our findings demonstrate that the increasing dominance of *D. gazella* has strong negative effects on native dung beetles in the Caatinga pastures. This study highlights the need for long–term monitoring of introduced species, especially in biodiverse yet fragile biomes such as the tropical dry forests. Conservation efforts should prioritize the preservation of native vegetation and consider sustainable cattle production practices such as silvopastoral systems and the regulation of the use of antiparasitics that may buffer the impacts of invasive species while promoting native species. Future research should assess the functional consequences of invasive alien species dominance across seasons and landscape contexts and determine the thresholds beyond which ecosystem services are irreversibly compromised.

Acknowledgements

C. Dos–Reis thanks CAPES (Coordination for the Improvement of Higher Education Personnel – Brazil – Funding Code 001) for his doctoral scholarship. This research was supported by a Rufford Small Grant (No. 36296–1). Thanks are due to CEPEC–CEPLAC, the Brazilian Ministry of Agriculture, and Instituto de Ecología, A. C., for laboratory support and infrastructure. J.H.C. Delabie acknowledges his CNPq research productivity fellowship.

Authors' Contributions

C. Dos–Reis, J.H.C. Delabie, and F. Escobar conceived and designed the study. C. Dos–Reis collected and analyzed the data. C. Dos–Reis wrote the first draft of the manuscript under the supervision of J.H.C. Delabie and F. Escobar. All authors reviewed and contributed substantially to the final version of the manuscript.

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Figures

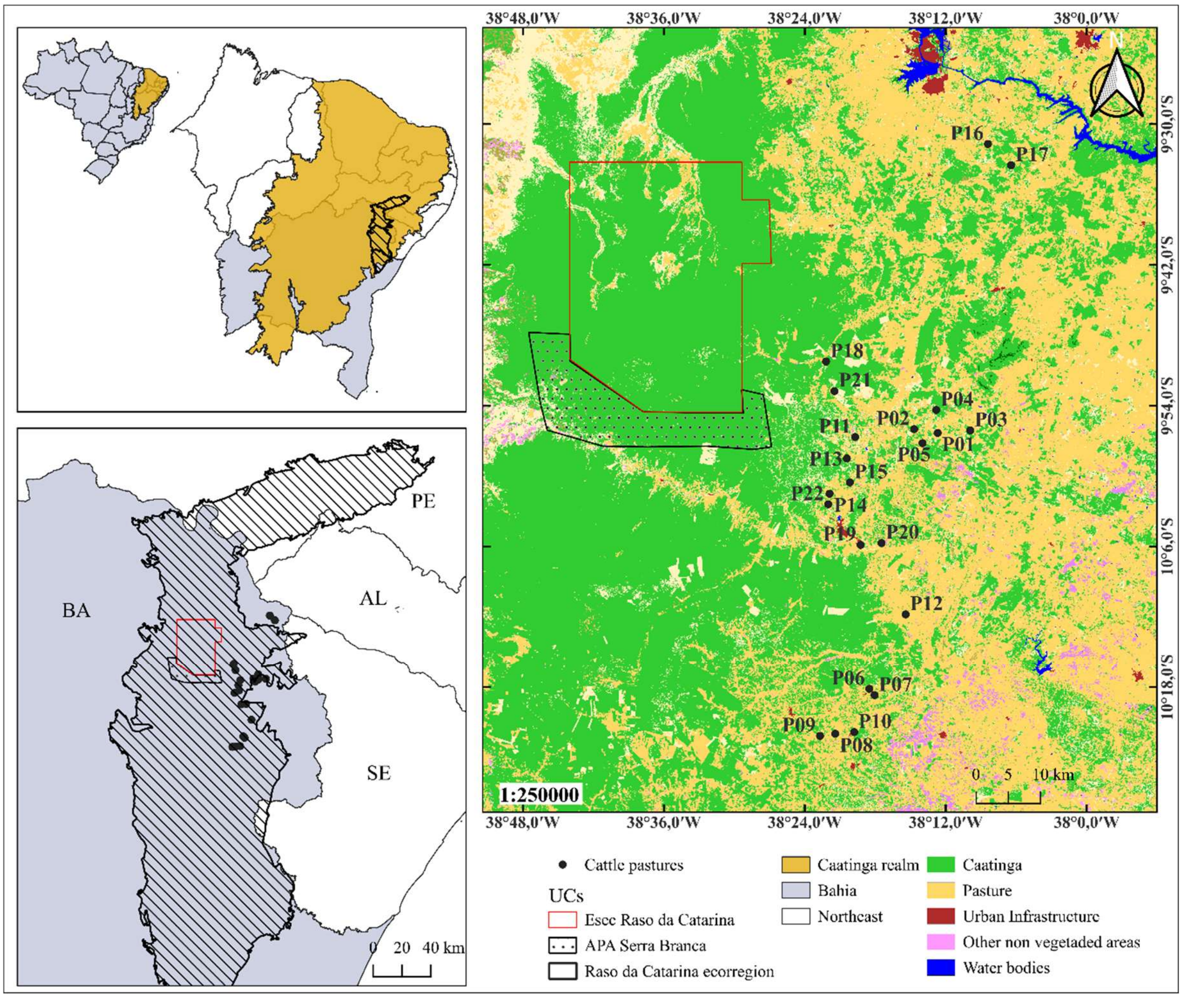

Figure 1. The study area, showing the location of the 21 cattle pastures in the Raso da Catarina ecoregion, Caatinga biome, Brazil.

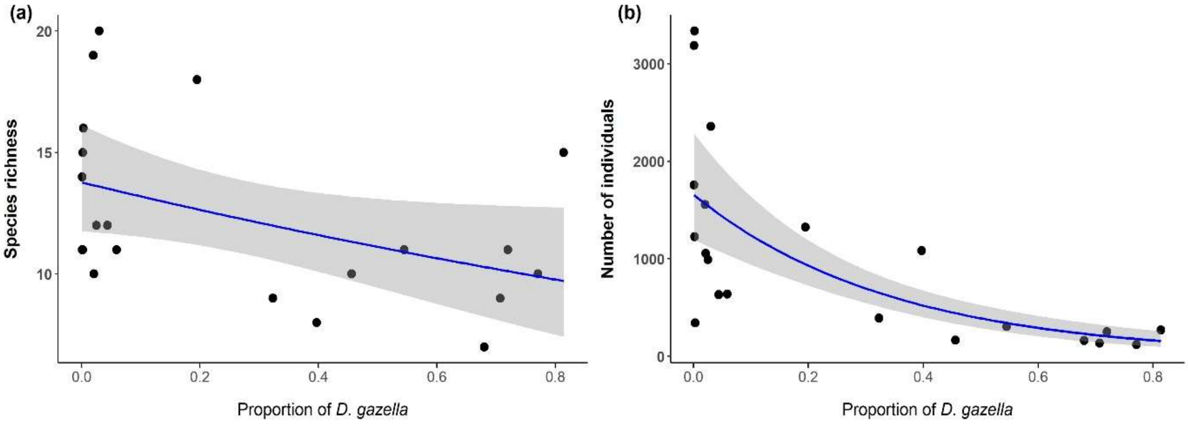

Figure 2. Response of species richness (a) and number of individuals (b) of native dung beetles to the dominance of *Digitonthophagus gazella*. The gray shaded area denotes the 95% confidence interval.

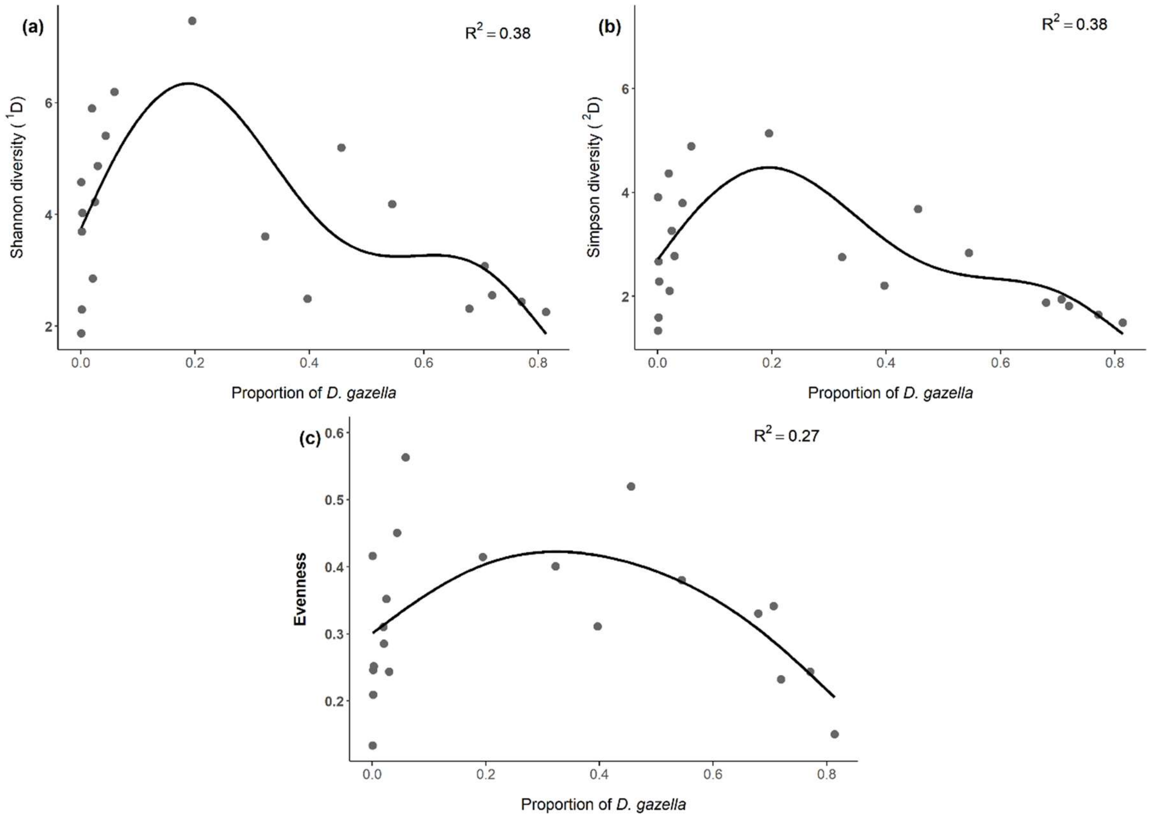

Figure 3. Response of (a) ^{1}D (Shannon diversity), (b) ^{2}D (Simpson diversity) and (c) evenness (^{1}D/^{0}D) of native dung beetle communities to the dominance of *Digitonthophagus gazella*.

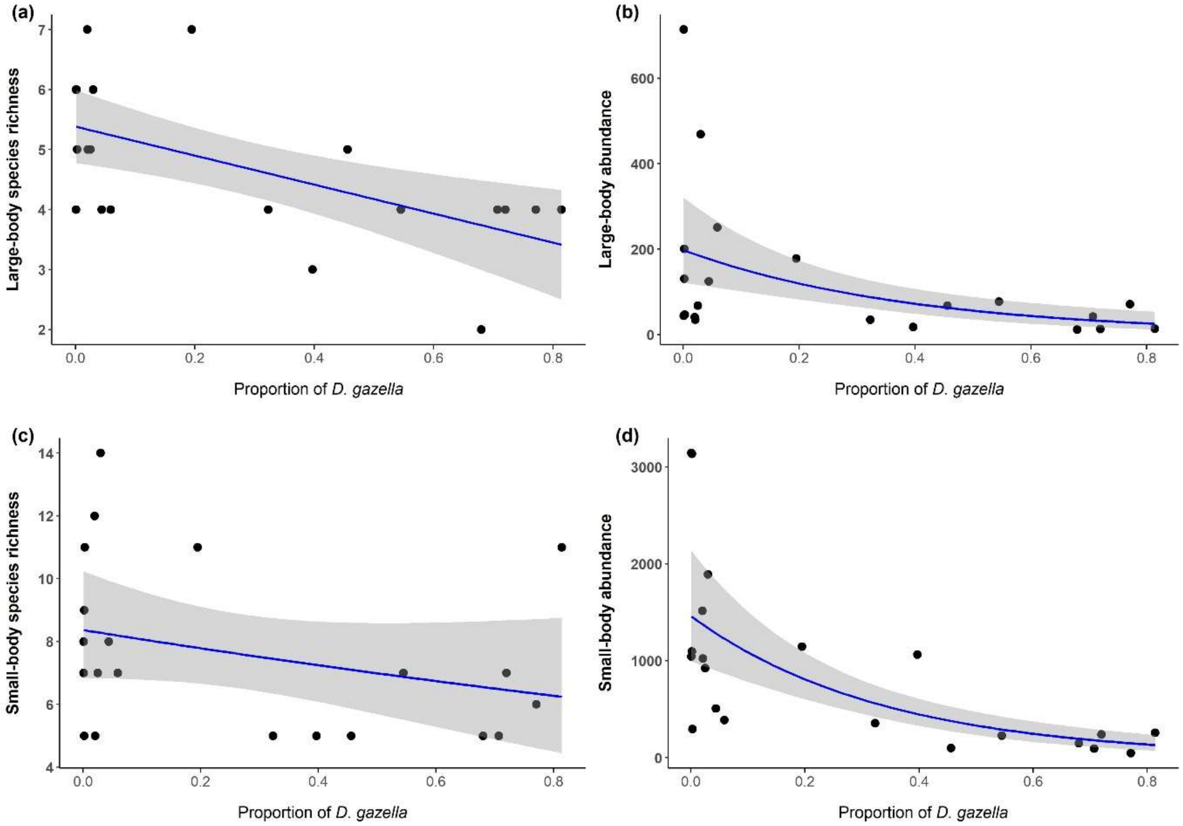

Figure 4. Body size and the response of native large–bodied dung beetle species richness (a) and abundance (b), and native small–bodied dung beetle species richness (c) and abundance (d) to the dominance of *Digitonthophagus gazella*. The gray shaded area denotes the 95% confidence interval.

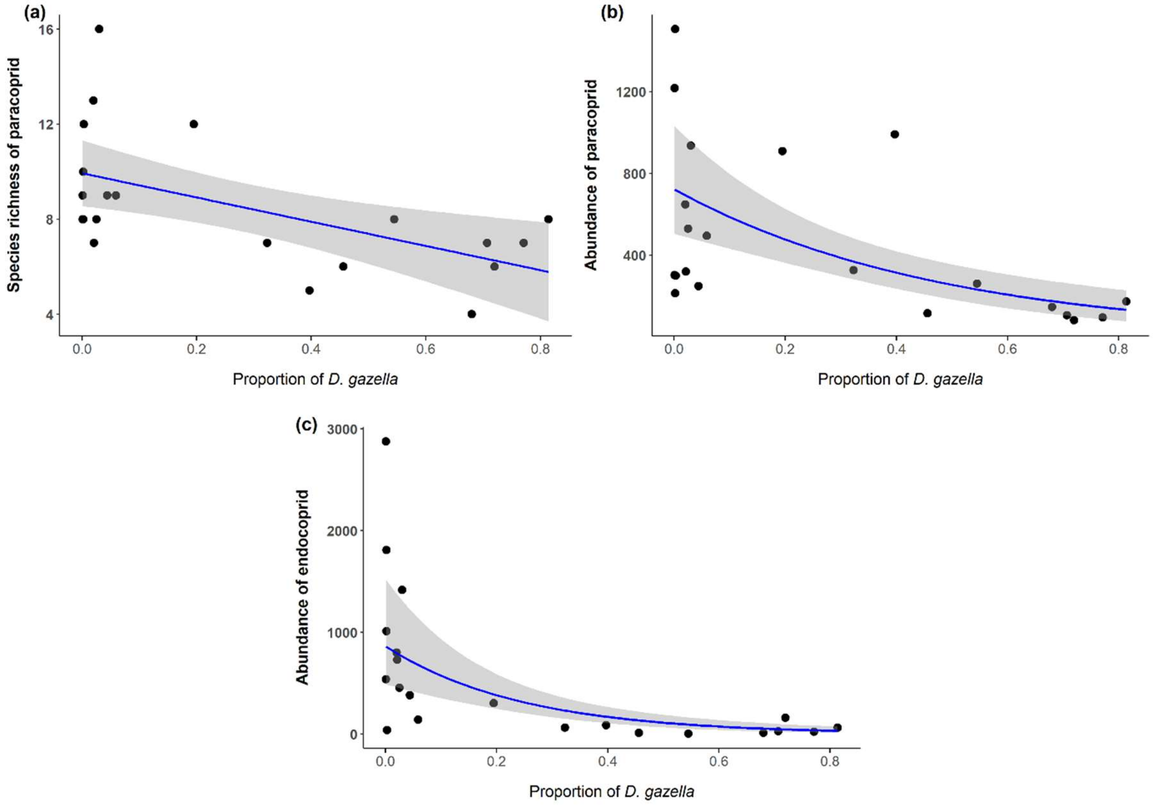

Figure 5. Food relocation behavior response of native paracoprid dung beetle species richness (a) and abundance (b), and native endocoprid dung beetle species abundance (c) to the dominance of *Digitonthophagus gazella*. The gray shaded area denotes the 95% confidence interval.

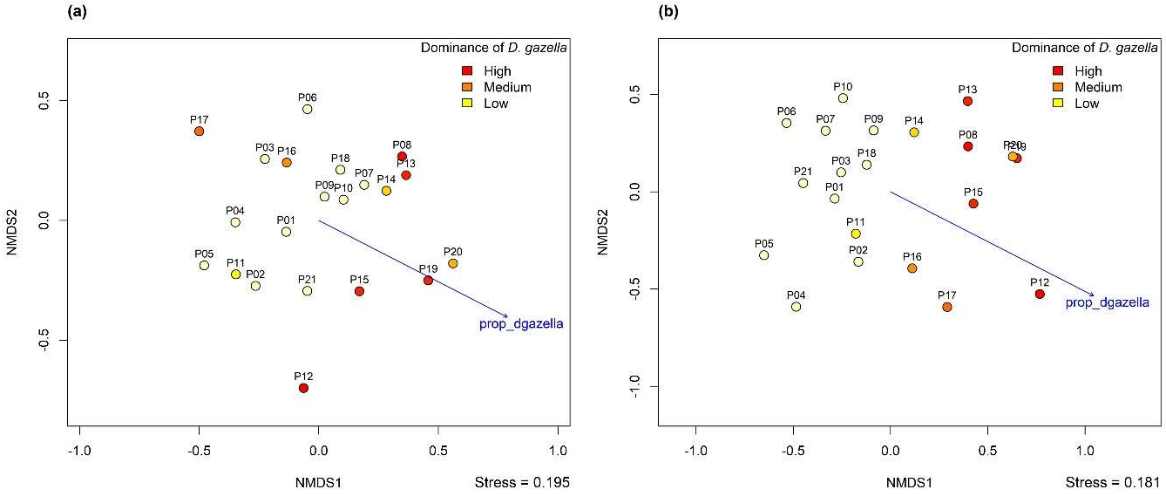

Figure 6. Non–metric multidimensional scaling (NMDS) ordination based on Jaccard (a) and Bray–Curtis (b) dissimilarities of native dung beetle communities across 21 Caatinga cattle pasture sites. Points represent pastures and are colored according to relative dominance (High, Medium, Low) of the exotic species *Digitonthophagus gazella*.

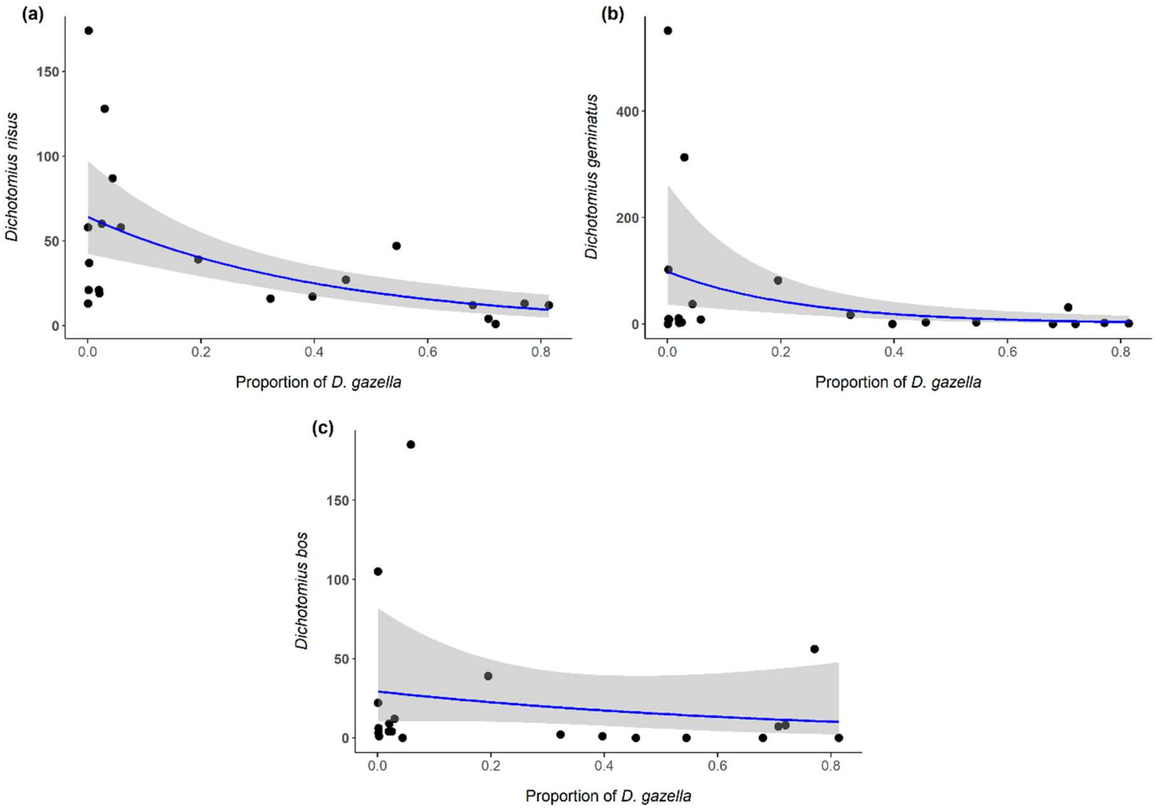

Figure 7. Abundance response of the three native paracoprid dung beetle species of the *Dichotomius* genus, *D. nisus* (a), *D. geminatus* (b) and *D. bos* (c), to the dominance of *Digitonthophagus gazella*. The gray shaded area denotes the 95% confidence interval.

Supplementary material

Table S1. Dung beetle species ordered from highest to lowest number of individuals collected in 21 pastures in the Raso da Catarina ecoregion, Caatinga biome, Brazil. Body size (Hanski & Cambefort, 1991) and food relocation behavior (Halffter & Matthews, 1966) are shown in parentheses: L = Large (>10 mm), S = small (<10 mm), P = Paracoprid, T = Telecoprid, E = Endocoprid. NI = Number of individuals.

Species / author	P1	P2	P3	P4	P5	P6	P7	P8	P9	P10	P11	P12	P13	P14	P15	P16	P17	P18	P19	P20	P21	NI
Genieridium margareteae (Génier & Vaz-de-Mello, 2002) (S, E)	1730	420	301	28	1398	966	688	1	45	478	15	13	8	26	7	3	5	425	1	3	2749	9310
Digitonthophagus gazella **(Fabricius, 1787) (L, P)**	**6**	**31**	**29**	**1**	**72**	**3**	**23**	**400**	**40**	**2**	**321**	**1178**	**328**	**187**	**647**	**139**	**366**	**25**	**344**	**712**	**4**	**4858**
Ateuchus semicribratus (Harold, 1868) (S, P)	1065	70	86	222	88	83	280	7	207	492	559	32	29	290	58	59	41	117	1	0	172	3958
Onthophagus aff. *ptox* (S, P)	128	492	19	12	112	0	4	17	23	6	60	118	35	2	14	19	142	342	134	973	78	2730
Trichillum externepunctatum Preudhomme de Borre, 1880 (S, E)	80	381	80	12	20	45	43	21	98	61	290	50	21	38	153	9	0	29	12	86	126	1655
Dichotomius geminatus (Arrow, 1913) (L, P)	9	10	37	8	313	102	2	2	8	551	82	1	31	17	0	3	3	3	0	0	0	1182
Dichotomius nisus (Olivier, 1789) (L, P)	174	21	87	37	128	21	19	13	58	58	39	12	4	16	1	27	47	60	12	17	13	864
Dichotomius bos (Blanchard, 1845) (L, P)	3	4	0	1	12	6	9	56	185	105	39	0	7	2	8	0	0	4	0	1	22	464
Canthidium aff. *manni* (S, P)	10	17	15	3	183	1	0	0	8	1	32	0	0	0	0	0	0	3	0	0	0	273
Tetraechma liturata (Germar, 1813) (S, T)	6	74	0	2	2	0	0	0	0	0	90	17	0	0	4	0	0	0	2	1	1	199
Ontherus digitatus Harold, 1868 (S, P)	21	11	1	6	23	1	0	0	1	0	40	0	0	0	1	8	26	0	0	0	10	149
Onthophagus hircus Billberg, 1815 (S, P)	87	5	3	3	10	0	7	0	0	1	0	0	0	0	0	0	2	0	0	1	4	123
Ontherus appendiculatus (Mannerheim, 1828) (S, P)	9	9	0	0	16	0	0	0	6	4	46	1	0	1	0	0	0	1	0	0	4	97

Deltochilum verruciferum Felsche, 1911 (L, T)	6	2	0	1	0	0	0	0	0	0	6	1	0	0	4	35	27	0	0	0	1	83
Canthidium humerale (Germar, 1813) (S, P)	0	7	0	0	32	0	0	0	0	0	11	3	0	0	0	0	0	0	0	0	0	53
Pseudocanthon xanthurus (Blanchard, 1847) (S, T)	0	28	0	0	0	0	0	1	0	0	1	13	0	0	0	0	0	0	0	0	0	43
Malagoniella astyanax (Olivier, 1789) (L, T)	9	3	1	0	3	1	5	0	0	0	11	0	0	0	0	3	0	1	0	0	4	41
Canthon aff. *carbonarius* (S, T)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	12	6	0	0	0	20
Diabroctis mimas (Linnaeus, 1758) (L, P)	0	0	0	0	13	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	14
Canthidium prasinum (Blanchard, 1845) (S, P)	0	0	0	0	4	0	0	0	0	0	0	7	0	0	0	0	0	0	0	0	0	11
Canthidium sp. 2 (S, P)	0	0	1	4	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	8
Canthidium sp. 3 (S, P)	0	0	0	3	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	5
Deltochilum pseudoicarus Balthasar, 1939 (L, T)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	4
Uroxys bahianus Boucomont, 1928 (S, P)	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	2
Canthidium sp. 1 (S, P)	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Canthidium sp. 5 (S, P)	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Canthon sp. 2 (S, T)	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
Canthon sp. 4 (S, T)	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
Dichotomius puncticollis (Luederwaldt, 1935) (L, P)	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Ontherus azteca Harold, 1869 (L, P)	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Species richness	**15**	**19**	**12**	**16**	**20**	**11**	**10**	**10**	**11**	**11**	**18**	**15**	**9**	**9**	**11**	**10**	**11**	**12**	**7**	**8**	**14**	**30**
Number of individuals	**3343**	**1587**	**660**	**344**	**2432**	**1230**	**1080**	**519**	**679**	**1759**	**1644**	**1448**	**464**	**579**	**899**	**305**	**672**	**1016**	**506**	**1794**	**3192**	**26152**

Table S2. Raw outputs of run models from each variable examined and its main statistics.

Variable	**β**	**P–value**	**AICc**		**Model/Distribution**
			Fitted	**Null**	
Species richness	**–0.428**	**0.045***	**114.420**	115.822	Glm poisson
Number of individuals	**–2.8969**	**<0.000*****	**315.688**	337.010	Glm.nb
Shannon diversity (^{1}D)	**NA**	**0.03***	**78.706**	81.282	GAM–Gaussian
Simpson diversity (^{2}D)	**NA**	**0.03***	**65.678**	68.593	GAM–Gaussian
Evenness (^{1}D/^{0}D)	*NA*	*0.06·*	*–31.258*	–28.590	GAM–Gaussian
Large–bodied_richness	**–3.209**	**0.004****	**66.946**	73.294	Glm–Gaussian
Large–bodied_abundance	**–2.5127**	**<0.000*****	**241.103**	249.989	Glm.nb
Small–bodied_richness	–0.3598	0.182	101.860	**103.686**	Glm poisson
Small–bodied_abundance	**–2.9604**	**<0.000*****	**314.485**	331.791	Glm.nb
Paracoprid_richness	**–0.6388**	**0.0156 ***	**99.265**	102.977	Glm poisson
Paracoprid_abundance	**–2.0766**	**<0.000*****	**293.349**	303.194	Glm.nb
Telecoprid_richness	0.0914	0.861	77.093	**74.667**	Glm poisson
Telecoprid_abundance	–0.3377	0.78	158.918	**156.235**	Glm.nb
Endocoprid_abundance	**–4.0721**	**<0.000*****	**286.205**	302.390	Glm.nb
*Dichotomius bos*_abundance	–1.316	0.306	159.146	**157.465**	Glm.nb
Dichotomius nisus abundance	**–2.3584**	**<0.000*****	**193.259**	203.020	Glm.nb
*Dichotomius geminatus*_abundance	**–4.1574**	**<0.000*****	**178.427**	183.007	Glm.nb

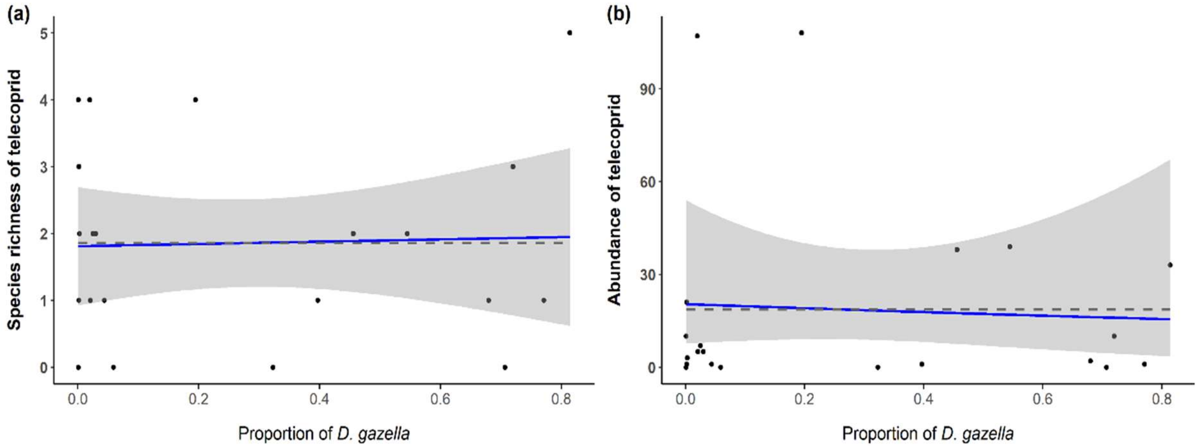

Figure S1. Telecoprid species richness (a) and abundance (b) response to *Digitonthophagus gazella* dominance is explained by the null model.

CONSIDERAÇÕES FINAIS

Esta tese investigou os efeitos da pecuária sobre a diversidade de besouros coprófagos (Scarabaeinae) em múltiplas escalas, desde análises de síntese continental com a meta-análise para as Américas, até estudos de campo no semiárido brasileiro, com foco na ecorregião do Raso da Catarina (Caatinga). Os resultados obtidos permitem algumas conclusões centrais:

1. Conversão de ecossistemas naturais em pastagens – A meta-análise para as Américas revelou que a transformação de ambientes naturais em pastagens exóticas gera efeitos consistentes e negativos sobre a riqueza, abundância e diversidade funcional de besouros coprófagos. Esses impactos são mais severos quando florestas primárias e ombrófilas tropicais são substituídas por pastagens abertas, enquanto sistemas silvipastoris por apresentarem estrutura vegetal mais complexa, apresentam efeitos atenuados e podem ser uma alternativa chave para a manutenção da diversidade em escala local e de paisagem.

2. Assembleias em fragmentos de Caatinga – Os fragmentos florestais do Raso da Catarina, mesmo sob forte pressão antrópica, ainda funcionam como refúgios importantes de diversidade, abrigando uma fauna plástica capaz de explorar tanto recursos nativos quanto esterco bovino.

3. Efeitos de escalas local e de paisagem – Nas pastagens da Caatinga, elementos da paisagem mostraram-se mais determinantes para alguns parâmetros das assembleias, como riqueza de espécies e abundância de besouros rola-bosta do que o manejo local. Práticas de manejo local, entretanto, foram mais influentes na diversidade de espécies comuns (q^1). Contudo, práticas invasivas como o uso de ivermectina tiveram efeitos negativos claros, reduzindo a diversidade das assembleias.

4. Invasão biológica por *Digitonthophagus gazella*, espécie de origem africana introduzida voluntariamente nos anos 1989 e que se tornou invasiva – Essa espécie exótica revelou forte dominância nos pastos do Raso da Catarina, promovendo supressão de espécies nativas, em especial paracoprídeos de tamanho grande, podendo resultar no comprometimento de funções ecológicas essenciais.

5. Integração entre biodiversidade e produção pecuária – Os resultados convergem para a importância de sistemas mais complexos (silvipastoris, ocorrência de árvores nativas remanescentes, mosaicos de vegetação) como alternativas viáveis para reduzir os impactos negativos da pecuária, conciliando conservação e produção.

Limitações do estudo, sugestões de expansão do estudo

Apesar dos avanços, permanecem algumas lacunas que não foram totalmente respondidas nesta tese: Por exemplo, no que tange ao capítulo de revisão, faltam estudos experimentais que comparem e reportem diretamente mudanças em assembleias a perda de serviços ecossistêmicos através de experimentos de campo, motivo pelo qual não foi possível avaliar a fundo e quantificar a perda de serviços em detrimento da transformação dos ambientes naturais em pastos nas Américas. Especificamente para os capítulos sobre a ecorregião do Raso da Catarina, não foi possível traçar um panorama geral sobre os efeitos de longo prazo. Em outras palavras, se faz necessária a amostragem de séries temporais em janelas que contemplem a variação sazonal da região na qual a Caatinga é tributária. Desta forma, seria possível avaliar a persistência ou reversibilidade dos efeitos da pecuária, do uso de ivermectina e da invasão de *D. gazella* sobre as assembleias de besouros rola-bosta. Há de se notar, então, que a interação entre eventos climáticos extremos (secas severas, chuvas erráticas) e a dinâmica das assembleias de rola-bostas permanece pouco explorada.

O que explica a hiperabundância de espécies pequenas e da espécie exótica *D. gazella* nos pastos do Raso da Catarina? Essa é uma lacuna não explorada que deve ser levada em conta. Saber quais características locais e de paisagem estão ligadas à hiperabundância de *D. gazella* poderia auxiliar na promoção de estratégias de conservação na região.

Em contexto de paisagem, é necessário compreender como arranjos mistos (fundo de pasto, silvipastoril, áreas de vegetação nativa de diferentes fitofisionomias) podem sustentar a biodiversidade e os serviços ecossistêmicos a longo prazo. Especificamente, fragmentos nativos usados ou não pelo pastoreio apresentam a mesma composição de espécies de rola-botas? Ou a presença de gado nos fragmentos altera a estrutura e composição das espécies de besouros?

CONCLUSÕES FINAIS

Em síntese, esta tese demonstra que a pecuária, embora vital para a subsistência e economia do semiárido, impõe pressões significativas sobre a biodiversidade, cenário esse que pode impactar no funcionamento dos ecossistemas. Ao mesmo tempo, aponta caminhos para a integração entre produção e conservação, reforçando a urgência de práticas sustentáveis que incorporem planejamento em escala de paisagem, redução do uso de insumos nocivos e valorização de sistemas silvipastoris. O avanço do conhecimento sobre besouros coprófagos no semiárido brasileiro não apenas preenche lacunas relevantes sobre a biodiversidade da Caatinga, mas também contribui para a construção de estratégias de manejo que conciliem a permanência da vida, da cultura regional e da produção pecuária com a conservação da diversidade biológica e dos serviços ecossistêmicos providos pelos besouros.

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