

Universidade de São Paulo - USP
Instituto de Biociências
Programa de Pós-graduação em Ecologia

Complex impacts of habitat loss on community assembly

Impactos da perda de habitat na montagem de comunidades

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ABSTRACT

Although the loss of native habitat is the primary cause of biodiversity change worldwide, understanding biodiversity's response to habitat loss requires considering the influence of introduced anthropogenic habitats in modified landscapes. My thesis examined how the loss of native habitat and the gain of anthropogenic habitat affected biodiversity patterns, using Scarabaeinae beetles (aka dung beetles) as a study system. I analyzed various dimensions of biodiversity response to the reduction of native tropical forest in a paired habitat study along a forest loss gradient in the Brazilian Atlantic Forest. In a first chapter, I observed changes in Scarabaeinae beetle diversity in the forest along this gradient. Deforestation was associated with patterns of biotic differentiation, with increases in alpha and gamma richness, "positive" responses that can be partly understood in light of the history of anthropogenic changes in the Brazilian Atlantic Forest and the proximity to taxa sources associated with open areas. In the second chapter, I explored how changes in the composition and structure of biotic communities in one habitat type may be related to those in adjacent habitat types. The interaction between native and anthropogenic habitats along gradients of environmental change influences community responses to habitat cover reduction. Findings reveal a complex interplay of factors shaping biotic communities within and between native and anthropogenic habitats. Landscape structure, species habitat associations, and habitat conversion significantly impacted community composition, owing to the combined influences of spillover, invasion, and extinction. Landscape configuration, such as increased edges between forest and pasture, can influence species turnover, underscoring the importance of managing habitat edges between native and anthropogenic areas to preserve landscape biodiversity. This research brings crucial contributions to understanding biodiversity's response to anthropogenic influence, transcending prevalent geographical and taxonomic biases. These findings guide strategies for the conservation and restoration of modified landscapes, essential for fundamental ecological processes.

Keywords: Habitat loss and change, community assembly, landscape-level sampling,

Scarabaeidae: Scarabaeinae, biodiversity, β -diversity

RESUMO

Embora a perda de habitat nativo seja a principal causa de mudança na biodiversidade em todo o mundo, compreender a resposta da biodiversidade à perda de habitat requer considerar a influência de habitats antropogênicos introduzidos em paisagens modificadas. Minha tese examinou como a perda de habitat nativo e o ganho de habitat antropogênico afetaram os padrões de biodiversidade, utilizando besouros Scarabaeinae (rola-bostas) como sistema de estudo. Analisei várias dimensões da resposta da biodiversidade à redução da floresta tropical nativa em um estudo de habitat emparelhado ao longo de um gradiente de perda de floresta na Mata Atlântica brasileira. No primeiro capítulo, observei mudanças na diversidade de rola-bostas na floresta ao longo desse gradiente. O desmatamento foi associado a padrões de diferenciação biótica, com aumentos na riqueza alfa e gama, respostas "positivas" que podem ser parcialmente compreendidas à luz do histórico das mudanças antropogênicas na Mata Atlântica brasileira e da proximidade a fontes de táxons associados a áreas abertas. No segundo capítulo, explorei como as mudanças na composição e estrutura das comunidades bióticas em um tipo de habitat podem estar relacionadas com aquelas do habitat adjacente. Resultados revelam uma interação complexa de fatores que moldam as comunidades bióticas dentro e entre habitats nativos e antropogênicos. A estrutura da paisagem, as associações de habitat das espécies e a conversão de habitat impactaram significativamente a composição da comunidade, devido às influências combinadas de *spillover*, invasão e extinção. A configuração da paisagem, como o aumento das bordas entre floresta e pastagem, pode influenciar a troca de espécies, destacando a importância de gerenciar as bordas dos habitats entre áreas nativas e antropogênicas para preservar a biodiversidade da paisagem. Esta pesquisa traz contribuições cruciais da resposta da biodiversidade à influência antropogênica, transcendendo vieses geográficos e taxonômicos prevalentes. Esses resultados direcionam estratégias de conservação e restauração de paisagens modificadas, fundamentais para processos ecológicos essenciais.

Palavras-chave: Perda e mudança de habitat, montagem da comunidade, amostragem em nível de paisagem, Scarabaeidae: Scarabaeinae, biodiversidade, β -diversidade.

INTRODUÇÃO GERAL

Entender os efeitos da perda de habitat na biodiversidade é essencial para direcionar estratégias de conservação em face das pressões humanas (Pardini et al. 2018). Mais de quatro décadas de pesquisa ecológica aplicada têm demonstrado efeitos da perda e fragmentação de habitats naturais resultam em mudanças na biodiversidade (MEA 2005; Hooper et al. 2012; Haddad et al. 2015; IPBES 2019). Globalmente as populações biológicas e biodiversidade vêm passando por mudanças que não são triviais (Dornelas et al. 2014; Hillebrand et al. 2018; Magurran et al. 2018; Antão et al. 2020), que incluem tanto declínios, aumentos, variações ou não na abundância e riqueza de espécies ao longo do tempo e gradientes ambientais (Vellend et al. 2013; Elahi et al. 2015; Newbold et al. 2015, Blowes et al. 2019; Chase et al. 2019; Daskalova et al. 2020). Diante de um cenário de mudanças globais aceleradas, sobretudo em regiões tropicais (Bradshaw et al. 2009; Gibson et al. 2011; Giam 2017), é urgente e essencial compreender os padrões complexos de mudanças biodiversidade e embasar políticas de conservação para conter tais impactos.

Ao reconhecer a importância de entender as respostas bióticas à perda e modificação de habitat, esbarramos na questão da escala de observação. Ao passo que se enfrenta uma limitação de dados finos o suficiente para entender como as espécies de menor capacidade dispersiva respondem a perturbações, sabe-se que o efeito das mudanças de uso do solo pode ser atenuada conforme a área de estudo aumenta (Chase et al. 2018), enquanto os efeitos das mudanças climáticas provavelmente são mais fortes em escalas espaciais maiores (Carvalho et al. 2013). Por exemplo, as espécies podem se refugiar em remanescentes de habitat ou microclimas adequados, mesmo em face as mudanças no habitat em escala espacial de paisagem, de maneira que nem sempre olhar para a biodiversidade numa escala local reflete o como ela responde em escalas espaciais mais amplas.

Uma maneira de incorporar a questão da escala, é analisar a biodiversidade em seus níveis complementares de organização no espaço – local ou alfa, regional ou beta e global ou gama. Como descrito classicamente por Whittaker (1960), a partição mais ampla da diversidade se define como diversidade 'gama' (ou regional, γ) e a diversidade média na unidade espacial menor como diversidade 'alfa' (ou local, α). Contudo, medir

apenas a diversidade local ou regional não reflete mudanças nas identidades das espécies (Hillebrand et al. 2018; Magurran et al. 2019) e não são suficientes para quantificar a homogeneização ou diferenciação biótica (Olden and Rooney 2006). Para isso, há a diversidade 'beta' (β -diversidade) é então definida como o grau em que a diversidade regional excede a diversidade local e pode ser medida tanto multiplicativamente ($\beta = \gamma / \alpha$) quanto aditivamente ($\beta = \gamma - \alpha$) (Lande 1996; Crist and Veech 2006). Acessar essas dimensões da diversidade é essencial para revelar padrões que só seriam capturados quando em conjunto (McKnight et al. 2007).

A β -diversidade é útil para examinar mudança direcional nas diferenças composicionais (Socolar et al. 2016), como a diminuição da dissimilaridade (ou seja, aumento da similaridade) na composição entre unidades amostrais (aka "homogeneização biótica") ou mesmo o aumento da dissimilaridade na composição (aka "diferenciação biótica") (Rolls et al. 2023). Entender mais proximamente os mecanismos que levam a esses padrões de mudança direcional na β -diversidade pode revelar e ajudar a atenuar impactos das mudanças composicionais na biota, por exemplo através das diferenças na riqueza e/ou substituição de táxons entre unidades de amostragem (Baselga 2010). Diferenças de riqueza (i.e. *nestedness*) ocorrem quando um conjunto em uma unidade de amostragem é composto por um subconjunto dos táxons em comparação com outro conjunto. Enquanto a substituição (i.e. *turnover*) se refere ao caso de, mesmo a riqueza permanecer constante - as espécies presentes em uma unidade podem estar ausentes em outra, sendo substituídas por uma nova espécie.

A escala espacial de padrões e processos é central para a ecologia e a perda e a fragmentação do habitat também são fenômenos espacialmente explícitos. Dessa maneira, compreender seus impactos na biodiversidade também requer atenção à escala adequada. Mudanças na estrutura da paisagem (i.e., a quantidade, qualidade e disposição de habitat), que afetam a sobrevivência e a dispersão de populações estruturadas espacialmente, são processos que agem em múltiplas escalas, tanto amplas quanto locais. Por exemplo, os principais aspectos da estrutura da escala da paisagem (e.g. cobertura total do habitat) estão relacionados de maneira não linear aos principais aspectos da estrutura em escala local (e.g. número, tamanho e distância entre fragmentos) (Fahrig 2003). Dessa forma, entender as relações da biodiversidade com a

perda de habitat e fragmentação exige estudos de desenho hierárquico que abordem múltiplas escalas, com replicação ao nível da paisagem e pseudo-replicação adequada ao nível local dentro de cada paisagem (Fardila et al. 2017).

A perda de habitat nativo é acompanhada do ganho de habitat antropogênico, contudo a interação entre habitats naturais e não nativos também desempenha um papel crucial, embora ainda não completamente compreendido (Boesing et al. 2017; Reider et al. 2018; Habel et al. 2020; de Souza Leite et al. 2022). Para isso, é essencial realizar estudos que não só abordem a biodiversidade em diferentes níveis de organização, como considerem a paisagem como um todo, é também necessário entender como a biodiversidade responde a múltiplos tipos de habitat (e.g. nativo e antropogênico, ou matriz), e como essas respostas são interdependentes (Kareiva et al. 2007). Fragmentos de habitat nativo estão geralmente rodeados por não nativos (matriz) resultando em mosaicos complexos de remanescentes de habitats de vários tipos (e.g. agrícolas). Tais manchas de habitat podem variar muito em termos de oferta de recursos e permeabilidade a dispersão das espécies (Villard and Metzger 2014), afetando a conectividade e modificando a biodiversidade dentro de cada tipo de habitat.

As informações sobre as associações de habitat das espécies são também essenciais para interpretar padrões de resposta à mudança no uso da terra, uma vez que a resposta das espécies à perda de habitat depende da preferência por habitat ou recursos (Ewers and Didham 2006). A extinção de espécies especialistas em habitat e sua substituição por generalistas contribuem para os padrões gerais de homogeneização ou diferenciação biótica (McKinney and Lockwood 1999; Rooney et al. 2004; Olden and Rooney 2006; Rolls et al. 2023) ou ganho de α -diversidade (Toussaint et al. 2016). A perda de habitat nativo tende a afetar mais fortemente as espécies especialistas em habitat com uso de habitat restrito ou distribuições mais estreitas, enquanto espera-se impactar de maneira neutra ou mesmo positiva as espécies com uso de habitat generalista ou distribuições mais amplas (Pardini et al. 2010; Estavillo et al. 2013; Banks-Leite et al. 2014; De Coster et al. 2015). Para o caso da β -diversidade, mudanças podem ser resultado da extinção de espécies especialistas (i.e. espécies de nichos mais estreitos, Britton et al. 2017), aumentos de espécies generalistas (i.e. espécies de mais amplas tolerâncias ecológicas, Johnson et al. 2014), ou ambos (Heinrichs and Schmidt

2017). Embora as informações sobre associação de habitat sejam cruciais para discernir tendências subjacentes em respostas divergentes de especialistas e generalistas de habitat (Sax et al., 2002; Banks-Leite et al., 2014), os dados sobre associações de habitat podem ser difíceis de estabelecer, especialmente para biotas tropicais diversas e para a maioria dos táxons não-vertebrados.

Mudanças estrutura da paisagem resultam em manchas de habitat nativo imersas em matrizes de usos da terra antropogênicos que pode influenciar o movimento de organismos entre habitats de diferentes tipos (i.e. *cross-habitat spillover*; Blitzer et al. 2012; Bagueette et al. 2013). Entender as relações de mudanças na composição e estrutura das comunidades bióticas requer incluir a influência do habitat antropogênico introduzido, entando, pouco se sabe sobre esse impacto nas comunidades biológicas em manchas de ambos habitats nativo e antropogênicos, e a interação entre tais comunidades (*spillover*). Enquanto espera-se que a biodiversidade de habitats nativos diminua e a biodiversidade em habitats antropogênicos aumente ao longo dos gradientes de mudança ambiental, sabe-se pouco sobre como o compartilhamento de espécies entre tais habitats se altera e interage com dinâmica dentro de remanescentes e resultando em influenciar a biodiversidade ao nível de paisagem. Acessar tais mecanismos, parece crítico para entender como tanto o declínio e extinção de espécies de habitat nativo quanto a invasão e proliferação de espécies adaptadas à distúrbio se traduzem em mudanças na composição das comunidades ao nível da paisagem. Um indicador potencial é a β -diversidade, que pode contribuir para desvendar os mecanismos que promovem as diferenças ou similaridades entre comunidades locais, além de útil para quantificar a diferenciação ou homogeneização biótica, também funciona como indicador de conectividade ecológica e *spillover* (Barros et al. 2019).

As evidências delineadas acima demonstram que entender como a biodiversidade responde à perda e modificação do habitat nativo requer dados coletados (1) nos níveis distintos de organização da biodiversidade, (2) incorporando informação sobre as diferentes respostas das espécies, (3) mensurando essa resposta em escala tanto locais quanto de paisagem ao longo de um gradiente de perda de vegetação nativa com replicação na ampla escalas de paisagem em que os processos de fragmentação e perda de habitat operam, e (4) usando um desenho de estudo que permita entender como os

habitats nativos e antrópicos interagem. Para entender as respostas da biodiversidade à perda e modificação de habitats no nível da paisagem, a presente tese examinou padrões de diversidade dentro e entre habitat nativo e antropogênico. Especificamente, desenvolvi dois capítulos. No capítulo 1, busco entender como a perda de habitat influencia a biodiversidade dentro dos remanescentes nativos na paisagem e, no capítulo 2, como a perda de habitat nativo influencia a relação entre comunidades biológicas comparando habitats nativo e antropogênico. Para isso, uso dados empíricos de besouros coprófagos como sistema de estudo ao longo de um gradiente de perda de mata nativa na Mata Atlântica. Besouros rola-bosta (Coleoptera: Scarabaeidae: Scarabaeinae) são um grupo de insetos coprófagos e cosmopolitas que são frequentemente utilizados como indicadores ecológicos (Nichols and Gardner 2011), respondendo a mudanças ambientais. Suas comunidades frequentemente apresentam uma ampla diversidade de respostas à perda e mudança de habitat nativo (Larsen et al. 2008; Nichols et al. 2013), na escala local e da paisagem (Souza et al. 2020; Rivera et al. 2021; Carvalho et al. 2023), ao nível das espécies (e.g. Fuzessy et al. 2021; Franco et al. 2023), preferências de recursos fecais (e.g. Frank et al. 2018) e por meio de um framework de atributos das espécies (Nichols et al. 2013; de Castro-Arrazola et al. 2023). Espera-se que, em conjunto, os resultados dessa tese trazem esclarecimentos robustos dos processos ecológicos que sucedem a mudança de habitat ao nível da paisagem e auxiliar estratégias de conservação e restauração de paisagens modificadas.

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CAPÍTULO 1

When forest loss leads to biodiversity gain: Insights from the Brazilian Atlantic Forest



When forest loss leads to biodiversity gain: Insights from the Brazilian Atlantic Forest*

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Abstract

Decades of research indicate that while native habitat loss often drives biodiversity loss and biotic homogenization, there are frequent exceptions. Relying on a multi-level landscape design, multiple biodiversity metrics and species habitat associations we explored one such exception. We investigated dung beetle responses to Atlantic Forest loss by modeling for both specialist and generalist species abundance, alpha and gamma diversities, and beta diversity through a null-model approach (β_{RC}) that permits comparing observed values to those expected by chance. We found that both native forest specialist and habitat generalist communities gained species with native forest loss at local (α -diversity) and landscape (γ -diversity) levels, while community composition became increasingly dissimilar (β -diversity). Yet, abundance response to forest loss varied between groups. While for generalists, forest loss led to increased overall abundance and abundance distribution across species remained random among communities, for specialists, overall abundance did not change and abundance distribution across species became dissimilar. Such findings suggest that habitat loss does not always drive a decrease in the number of specialist species that compensate for the gain of generalist species, adding to evidence that habitat loss can drive biodiversity gain and biotic differentiation. These responses may be common in particular biogeographical contexts, where contemporary and/or historical regional dynamics may have influenced the resilience of forest biota and contribute to the availability of disturbance-adapted species. Our study highlights the importance of sampling across multiple spatial scales to understand the effects of habitat loss on biodiversity and suggest caution to silver-bullet conservation guidelines.

Keywords: deforestation, community assembly, landscape-level sampling, Scarabaeidae: Scarabaeinae, biotic differentiation, biotic homogenization.

Introduction

Understanding biodiversity responses to anthropogenic change is crucial to guide conservation planning (Pardini et al., 2018). Four decades of applied ecological research indicate that native habitat loss and fragmentation drive biodiversity loss and change (IPBES, 2019a, 2019b), often resulting in an increase in similarity among communities over time (i.e. biotic homogenization; Püttker et al., 2015; Olden et al., 2018).

Even as biodiversity continues to decline at global (Barnosky et al., 2011) and often regional scales (e.g. Estavillo et al., 2013), native habitat loss may result in localized increases in species richness (Arroyo-Rodríguez et al., 2013) depending on the availability of disturbance-resilient taxa (Karp et al., 2012) and degree of connectivity within landscapes (Barros et al., 2019). Additionally, empirical evidence suggests that native habitat loss can lead to biotic heterogenization (Rahel, 2010) as well as increased diversity at larger spatial scales (e.g. Rooney et al., 2004; Carvalheiro et al., 2013; Davey et al., 2013; Eskildsen et al., 2015; Daskalova et al., 2020). These observations suggest that quantifying biodiversity response – and contributing to clarifying the factors that underpin the observed exceptions associated with positive biodiversity responses to habitat loss – requires sampling across spatial scales, examining multiple metrics of biodiversity (e.g. abundance, alpha, beta and gamma), and incorporating information on species' habitat association. Surprisingly few empirical studies to date have addressed the consequences of habitat loss fully combining these three key aspects (but see Hendrickx et al., 2009; Dormann et al., 2007; Chetcuti et al., 2020; Daskalova et al., 2020).

Sampling across spatial scales is crucial as the effects of habitat loss on biodiversity are affected by processes occurring at multiple scales. As a landscape undergoes native habitat loss, the decrease in total habitat coverage is nonlinearly related to the number, size, and distance between local native habitat remnants (Andrén, 1994; Fahrig, 2003). The biodiversity persisting within those local remnants is in turn influenced by characteristics of the landscape (Pardini et al., 2010), including how the number, size and isolation of remaining patches affect connectivity and organismal movement across the landscape, and across landscapes at the regional level (Villard and Metzger, 2014). Examinations of biodiversity response to habitat loss therefore require multi-level study designs with replication both within and across landscapes to capture patterns of α -, β - and γ -diversity. Despite the importance of such multi-level studies, the

challenges inherent in designing field studies with sufficient replication (Hurlbert, 1984) and controlled collinearity between local, landscape and regional explanatory variables (Eigenbrod et al., 2011; Cunningham and Lindenmayer, 2017) has resulted in relatively few empirical multi-level datasets upon which to base our understanding of biodiversity response to native habitat loss (Resasco et al., 2017).

Because different measures of biodiversity correspond to distinct spatial scales, understanding responses to landscape change requires the use of multiple biodiversity metrics. While early models of biodiversity response often examined a single metric at one spatial scale (mostly the examination of species richness within local communities), biodiversity research now commonly examines multiple diversity metrics, including the number of species in a local community (alpha, $\bar{\alpha}$), compositional differences between local communities (beta, β) and the total species diversity within landscapes (gamma, γ) (Anderson et al., 2011). β -diversity is particularly useful to uncover the processes behind overall measures of biodiversity change (Tuomisto, 2010), especially when calculated using a null model approach that can discern if dissimilarity in composition and structure across communities is lower or higher than expected by chance (Chase, 2011). For example, stochastic extinctions should decrease diversity within patches ($\bar{\alpha}$), and increase diversity across patches (β), with γ -diversity depending on the balance between these effects. When extinctions are instead deterministic, $\bar{\alpha}$ -diversity may decline in similar ways across multiple patches, leading to decreased β - and γ -diversity and contributing to biotic homogenization.

Finally, information on species habitat associations is also critical to interpret assemblage-level patterns in response to land-use change because species response to habitat loss depends on habitat or resource preference (Ewers and Didham, 2006). The extinction of habitat specialist species and replacement by habitat generalists contribute to overall patterns of biotic homogenization (loss of β -diversity in addition to loss of α -diversity (Toussaint et al., 2016; Villéger et al., 2011)) – a process by which distinct communities become increasingly similar over time. Native habitat loss tends to more heavily impact those habitat specialist species with restricted habitat use or narrower distributions, while impacting neutrally or positively those species with generalist habitat use or broader distributions (Pardini et al., 2010; Estavillo et al., 2013; Banks-Leite et al., 2014; de Coster et al., 2015). While information on habitat association is critical to discern

underlying trends in divergent responses by habitat specialists and generalists (Sax et al., 2002; Banks-Leite et al., 2014) data on habitat associations may be difficult to establish, particularly for diverse tropical biotas and for most non-vertebrate taxa.

In this study we unpack a positive biodiversity response of dung beetle communities to native habitat loss by using a multi-level landscape design that allows quantifying diversity at multiple spatial scales (abundance, α -, β - and γ -diversities). We also use a null-model approach that allows comparing observed changes in composition to those expected by chance, and considering different habitat association groups. Dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae) are a cosmopolitan and primarily coprophagous insect group that is frequently used as an ecological indicator taxa (Nichols and Gardner, 2011). Dung beetle communities often display a wide diversity of response to native habitat loss and change (Beiroz et al., 2017; Larsen et al., 2008; Nichols et al., 2013; Nunes et al., 2016), with consistent species-level responses to habitat change (e.g. Fuzessy et al., 2021) and strongly consistent and often narrow fecal resource preferences (Frank et al., 2017) that are increasingly understood through a species trait framework (deCastro-Arazola et al., 2022; Nichols et al., 2013). We aim to address two questions: (1) whether biodiversity response to native habitat loss is necessarily negative, and (2) how species' habitat associations modulate this response.

Materials and methods

Study region

We collected land cover and biodiversity samples in the Cantareira-Mantiqueira region of São Paulo state (23° 01' S and 46° 15' W'), within the Brazilian Atlantic Forest (Fig. 1a). The Atlantic Forest phytogeographic domain is composed of five forest types (Oliveira-Filho and Fontes, 2000), with lower montane ombrophilous dense forest the most representative across the study region (IBGE, 2012). The region has a humid subtropical climate (annual minimum mean 14.9 ± 0.90 °C; annual maximum mean 26.3 ± 1.15 °C), mean annual rainfall of 1440 ± 120 mm, and an elevation between 800 and 1200 m (<http://www.cpa.unicamp.br/>).

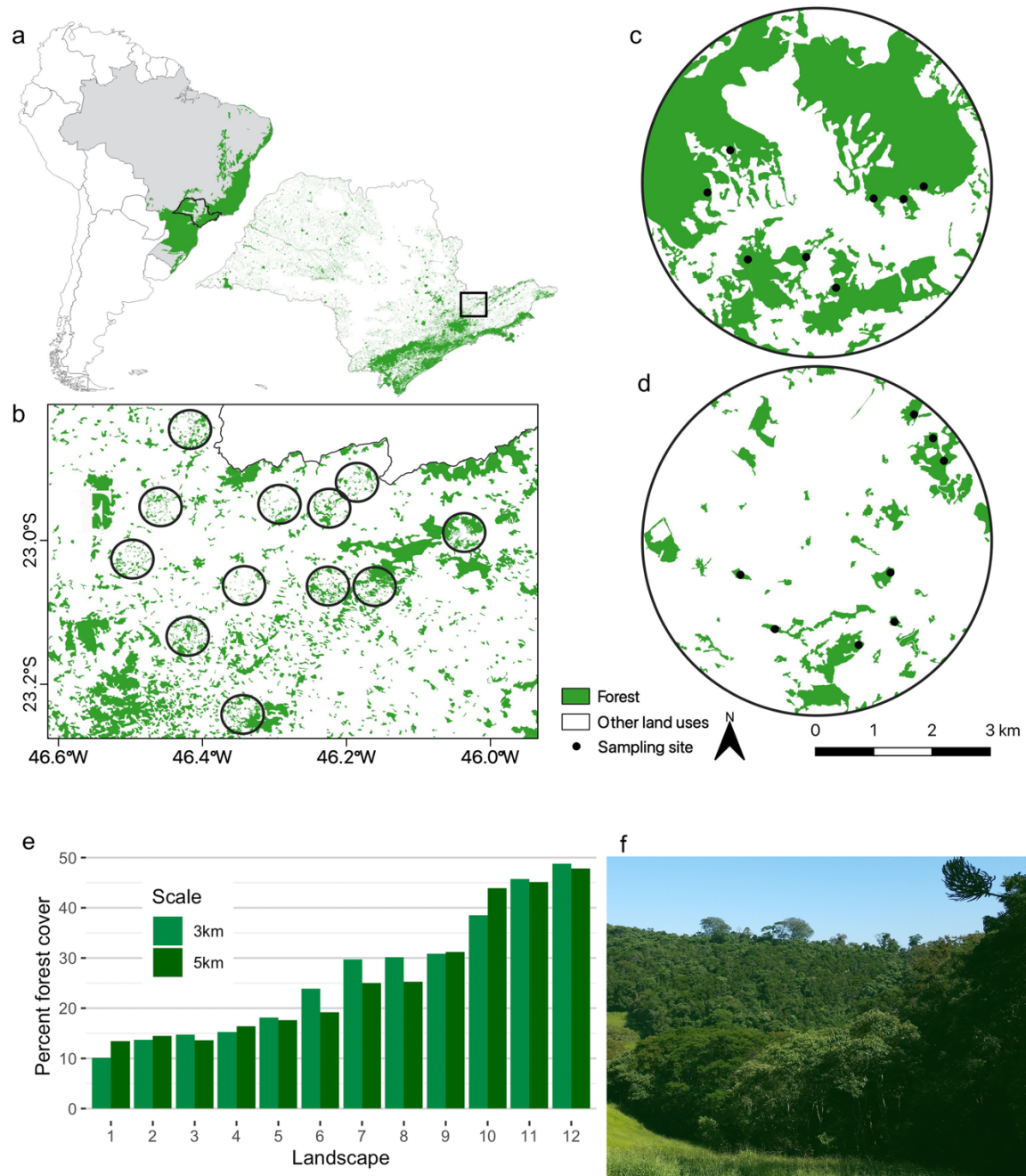


Figure 1 Location and design of the study to examine biodiversity response to forest loss, including (a) Map of Brazil with the original Atlantic Forest biome, and the state of São Paulo, in detail showing the study region within the current Atlantic Forest domain; (b) study region and 12 focal landscapes with 3 km radius (7854 ha) selected to represent the deforestation gradient; (c, d) sample landscapes with high (c: 48 %) and low (d: 10 %) native forest cover; (e) forest cover percentage of the 12 focal landscapes measured at a 3 and 5 km radius, displayed in light and dark green, respectively; and (f) photo displaying one of the forest plots (credit: Andrea Larissa Boesing). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

This region was originally covered by the Atlantic Forest domain, with globally high rates of species diversity and endemism (Myers et al., 2000). However, after five centuries of deforestation and fragmentation following European colonization (Joly et al.,

2014), only 28 % of this biome remains (Rezende et al., 2018), with the remaining forest cover predominantly reduced to fragments in early to medium stages of succession (Lira et al., 2012; Rosa et al., 2021), and with >80 % of fragments smaller than 50 ha (Ribeiro et al., 2009), contributing to the status of the Atlantic Forest as a critical biodiversity hotspot (Myers et al., 2000). The Cantareira-Mantiqueira region is an ecological corridor that provides critical connectivity for the remaining Atlantic Forest fragments in the region, contributing to the region's status as a biodiversity conservation priority at the state level (Joly et al., 2010). Landscapes in this region are characterized by small secondary forest fragments surrounded by open-habitat matrices, dominated mostly by cattle pasture systems in small properties and reforestation and *Eucalyptus* spp. plantations (Joly et al. 2014). Approximately 50–90 km to the north and west of the Cantareira-Mantiqueira corridor lays the biome Cerrado (Fig. S1); a Brazilian savanna phytogeographic domain comprised of a mosaic of vegetation types including grasslands, savanna woodlands and semi-deciduous forests (Bueno et al., 2018).

Nested sampling design

We selected 12, 3-km radius focal landscapes (7854 ha; Fig. 1b). All landscapes were constrained within 800 and 1300 m.a.s.l. (meters above sea level), on ferric red latosol or argisol soil, and to exclude major interstate highways and water reservoirs (Pasher et al., 2013). We used the Sampling Design tool in ArcGIS 10.1 to calculate the percentage of land use defined as native forest cover in circular buffers of 3-km radii around the landscape's centroids, and further restricted the selection of focal landscapes to areas where native forest cover did not vary >5 % within 1, 2, or 3-km radius from each landscape centroid, to avoid the potential influence of larger patch on ecological processes (Pasher et al., 2013). We mapped each landscape land use using high-resolution images (ArcGis 10.3 basemap imagery, Digital Globe satellites 2010–2011). We defined as forest only those native forest remnants at an intermediate (ca 10 years) or advanced successional stages. The 12 focal landscapes vary from 10.1 to 48.8 % (Mean (SD) = 26.35 (12.64); Fig. 1c and d) native forest cover at 3-km radii (Fig. 1f). We used this resulting gradient in landscape-level native forest cover across the 12 focal landscapes to explore patterns of biodiversity response to deforestation.

To distribute eight biodiversity sampling sites within the forest remnants of each focal landscape we used a stratified, random, and proportional selection process based on

the largest fragment in the landscape ($n = 95$ sites in total, as one site was lost due to heavy rain flooding of these pitfall traps). As the size of the largest forest fragment is an important landscape structure feature related to the proportion of total forest remaining in a landscape (Fahrig, 2003), we assigned sampling sites in the largest fragment according to the proportion of its cover in the landscape while remaining sites were assigned to smaller fragments larger than 2.5 ha. All sampling sites within a landscape were randomly assigned to these two categories within an inner radius of 3- km and respecting a minimum distance of 300 m between them.

Biodiversity data collection

Dung beetle sampling followed a standardized protocol using pitfall traps (20 cm diameter, 15 cm depth). In each of the 95 forest sampling sites, we placed four traps at 50, 70, 90 and 100 m from the forest edge, along a transect oriented towards the fragment center. Feces from omnivorous mammals (i.e. humans and swine) are often used in neotropical biodiversity studies of dung beetles (Nichols et al., 2009; Frank et al., 2018), as they attract species known to use primate, herbivore and omnivorous feces (Larsen et al., 2006) and are commonly reported to attract a wider variety of species than other types of baits (Bogoni et al., 2014). Pitfall traps were buried flush with the ground, baited with 20 g of a 10 % human, 90 % pig dung bait (Marsh et al., 2013) and operated for one 48-hour period at each site, sampling three to four landscapes at a time during the wet season (December 2014–March 2015).

Habitat association categorization

Specimens were identified to species by an expert dung beetle taxonomist (F.A.B. Silva, Federal University of Pará) with extensive collection experience in the dung beetle fauna of the Atlantic Forest and Cerrado domains. The same taxonomist then classified all species according to habitat association, integrating published information on biogeographical distribution, habitat use and preference based on occurrence data. Forest specialists (FS) are defined as those species with both a biogeographical distribution restricted to the Atlantic Forest and with a clear preference for forested habitats, based on occurrence data. Non-forest specialists (NFS) are defined as those species with a biogeographical distribution not limited to the Atlantic Forest (including distributions inclusive of the Cerrado domain, or broader distributions inclusive of the Cerrado and

Amazon), and/or with habitat preferences not limited to forested habitats (see supplementary material S1).

Data analyses

Alpha diversity ($\bar{\alpha}$) represents the local diversity in a given site, estimated here as the observed mean species richness across the eight sampling sites per landscape. Gamma diversity (γ) is the total number of species in the landscape. Beta-diversity (β) is a measure of dissimilarity in species composition between sites within each landscape, estimated here as the mean number of species that cannot be found in each local unit and quantified using the additive approach ($\beta = \gamma - \bar{\alpha}$; Lande, 1996; Crist and Veech, 2006; Veech and Crist, 2007). The additive β -diversity is useful for its simple interpretability, as it places alpha and β -diversity in the same units and allows the calculation of the relative contributions of alpha and β -diversity to overall gamma diversity (Lande, 1996).

Null model-based calculations of beta diversity are a helpful complement to additive beta diversity, as they can be calculated without influence by the changes in local species richness that typically accompany habitat loss (Kraft et al., 2011). Null model approaches to β -diversity can additionally be used to infer possible mechanisms of community assembly, including those deterministic processes that lead to communities structured by species sorting, and those neutral and stochastic processes that generate more random assemblages (Chase and Myers, 2011). To this end we also calculated β -diversity using the null model approach proposed by Raup and Crick (1979), which accounts for species richness differences between localities. The Raup–Crick metric (hereafter β_{RC}) tests the probability of two communities being more or less dissimilar compared to a null expectation (random sampling from a pool) considering the number of species present at each community. This metric of compositional dissimilarity between communities in different sites complements the results of additive β -diversity metrics both by providing a measure of changing community composition that is free from underlying changes in species richness, and by permitting inference on the influence of random or deterministic processes on observed differences in species composition (Baeten et al., 2012). β_{RC} can be used with a helpful scaling proposed by Chase (2011), leading to a β_{RC} metric that ranges from -1 to 1 , and indicates if communities share fewer species (β_{RC} values approaching 1), as many species as (β_{RC} approaching 0), or more species than expected

by chance (β_{RC} approaching -1). To calculate β_{RC} , we defined the species pool as all species captured in the study region, following Chase (2011). As species' absence critically informs the degree of similarity among sites, for the β_{RC} calculations we removed the few sites with occurrence zero from the analysis ($n=3$ for FS and $n=7$ for NFS).

Abundance-based measures are also an important measure of biodiversity change that function as a proxy of the changes in species performance that precede local species extinction. We calculated the total number of individuals (total abundance) in each landscape. We also calculated the abundance-based version of the β_{RC} , as proposed by Stegen et al. (2013a, 2013b). This metric (hereafter $\beta_{RC\text{-abundance}}$) quantifies if the dissimilarity in community structure (i.e., differences in abundance distribution across species) between sites within landscapes is lower, higher or as expected by chance. Following the procedure performed by Püttker et al. (2015), we used all species and individuals captured in the study region to define the regional pool and drew from that pool random draws of individuals, instead of species. We then constructed random communities by shuffling individuals of each species among sites, while maintaining each species total abundance. For both β_{RC} and $\beta_{RC\text{-abundance}}$, we ran random samples without replacement from the theoretical pool for each pair of sites, after which we computed the mean $\beta_{RC\text{-abundance}}$ per landscape.

To investigate the response to habitat loss of these six biodiversity metrics at the landscape level, we used generalized linear models (GLM) with appropriate error distributions (poisson for γ -diversity; gamma for $\bar{\alpha}$ - and β -diversity; gaussian for β_{RC} and $\beta_{RC\text{-abundance}}$; negative binomial for total abundance). We modeled each variable separately as a function of the percent of landscape-level forest cover calculated at both 3-km and 5-km radii. We also examined the quadratic forms of these predictors to account for potentially non-linear relationships with forest cover, as well as a reference model without predictors. We used an AICc model selection approach to select the best model (including the spatial scale of landscape-level forest cover) for each dependent variable, considering models with $\Delta AICc \leq 2$ as having the strongest empirical support. To understand how habitat association modulates biodiversity response, we ran the analyses listed above separately for both forest specialists (FS) and non-forest specialists (NFS). We ran all analyses in R version 4.2.0 (R Core Team, 2023) with the packages: *stats* for linear and

generalized linear models; *bbmle* for model selection (Bolker, 2017), *car* for model collinearity tests (Fox and Weisberg, 2019), *DHARMA* for residual diagnostics, including spatial autocorrelation (Hartig, 2019); and *MASS* for fitting negative binomial models (Venables and Ripley, 2002). All analyses (including preliminary analyses and model validation) are fully reproducible, with code and data available in an online repository (Figshare: DOI: <https://doi.org/10.6084/m9.figshare.21572217>; Github: https://github.com/barretoju/Landscape_Diversity_DungBeetles).

Results

We sampled a total of 4002 individuals of 50 dung beetle species, in 17 genera. Of these, 2482 individuals of 28 species were forest specialists (FS, Table S1), and 1520 individuals of 22 species were non-forest specialists (NFS; Table S1). For all subsequent analyses, we removed six singleton species found only once in forest habitats (Table S1). We detected forest specialists and non-forest specialists in all landscapes, across the forest cover gradient.

We found that forest specialist (FS) species increased in γ -, $\bar{\alpha}$ - and β -diversity with forest loss (Fig. 2a–c), and that the diversity of FS communities responded better to forest cover at a larger spatial scale (5- km) (Table 1a–c). The total abundance of FS species demonstrated no response to forest loss, and the abundance of FS species was better represented by models of forest cover at the 5-km scale (Fig. 2d, Table 1e). Community compositional similarity (β_{RC}) for FS communities was similar to that observed for NFS, with both habitat association groups demonstrating little responsiveness to forest loss (β_{RC} ; Fig. 2e, Table 1d). For forest specialists, the abundance distribution across species between communities in more forested landscapes was as similar as expected by chance and became more different than expected by chance as deforestation progressed (β_{RC} -abundance; Fig. 2f, Table 1f). This implies that between-community differences in which forest specialists were common or rare in deforested landscapes were greater than expected, despite the lack of relationship between forest loss and total abundance loss (Fig. 2d).

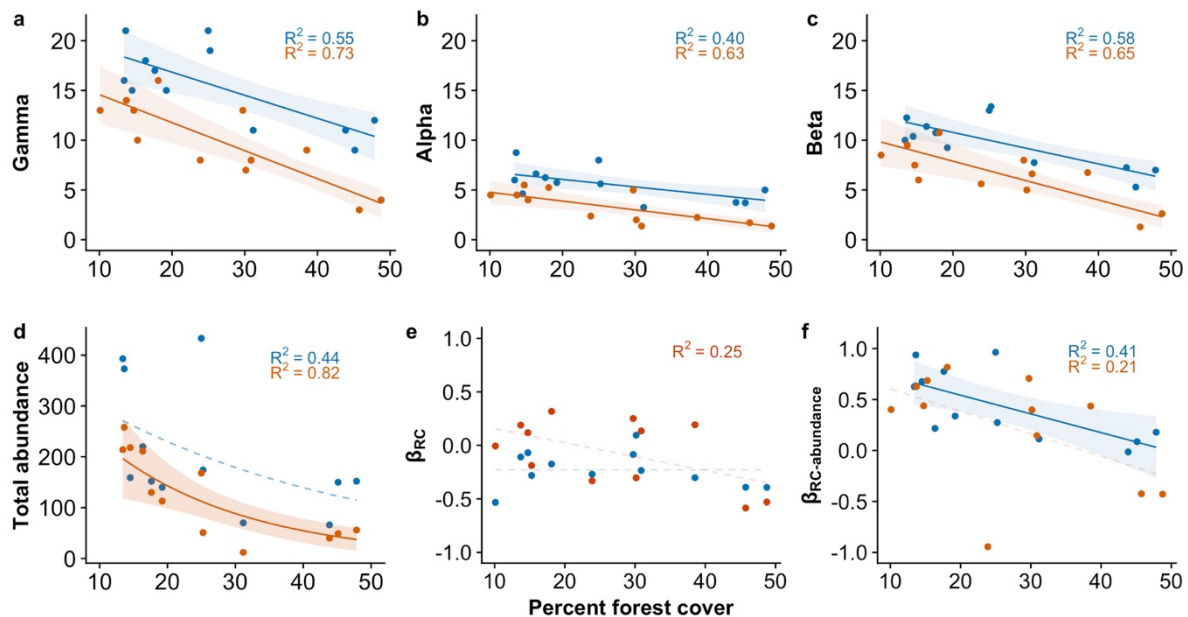


Figure 2. Top AIC models of three complementary biodiversity metrics for forest specialists (FS, in blue) and non-forest specialist (NFS, in red) species across a gradient of native forest cover, including the three complementary metrics of diversity - (a) gamma, (b) alpha, and (c) beta diversities-; (d) total abundance; (e) β -diversity calculated with the Raup-Crick method for presence-absence data; and (f) β -diversity calculated with the Raup-Crick method for abundance data across a gradient of native forest cover. Following the best spatial scale selected for each biodiversity metric (Table S2), data are plotted each against the best spatial scale of forest cover, at the 5 km radius scale for FS species and abundance of NFS, and at the 3 km radius scale for all other metrics of NFS species. Solid lines represent relationships between variables following the top selected model; shaded areas represent 95% confidence intervals; dashed lines with no shading represent when the model of absence of effect (null) was ranked among the candidate model set (defined as all models with $\Delta\text{AICc} \leq 2$). All model plots contain their respective estimated explained variance (R^2).

We found that non-forest specialist (NFS) species also showed an increase in γ -, $\bar{\alpha}$ - and β -diversity with forest loss (Fig. 2a–c), and that the diversity of NFS communities was better represented by models of landscape-level forest cover measured at the 3-km scale (Table 1g–i). NFS species also showed an increase in both total abundance across sites with forest loss, and the abundance of NFS species was better represented by models of forest cover at the 5-km scale (Fig. 2d, Table 1k). NFS communities contrasted from FS communities in their abundance response to deforestation, with an increase in total abundance with forest loss for NFS taxa (Fig. 2d, Table 1k) but no clear response in total abundance for FS taxa. The patterns of community similarity across the deforestation gradient also differed between NFS and FS communities, as neither the community compositional similarity (β_{RC} ; Fig. 2e, Table 1j) nor the abundance distribution across species between communities for non-forest specialists ($\beta_{\text{RC-abundance}}$; Fig. 2f, Table 1l) presented any clear response to forest loss.

Table 1 The top AIC-selected models ($\Delta AIC_c = 0$) and their regression model coefficients for each response variable: gamma (γ), alpha (α), and additive beta (β) diversities, as well as total abundance, and β -diversity calculated from the Raup-Crick null model approach calculated for both presence/absence (β_{RC}) and abundance (β_{RC} -abundance). For both forest specialists (a-f) and non-forest specialists (g-l) we present the selected model predictor, degrees of freedom (df), Akaike weight (w_i), model variance explained (r^2), model estimates and standard error (Estimate, SD) and 95 % confidence intervals (CI). The full model selection table can be found in the supporting material (Table S2). (*) Asterisks indicate when null model also ranked among the selected models $\Delta AIC_c \leq 2$ for that response variable.

Forest specialists (FS)			
a) Gamma γ			
Top AIC model: Forest cover at 5km ($\Delta AIC = 0$, $w_i = 0.58$, $df = 3$; $r^2 = 0.58$)		Estimate (SD)	CI
	Intercept	21.47 (2.02)	17.69 – 25.70
	FC at 5km	-0.23 (0.06)	-0.35 – -0.11
b) Alpha α			
Top AIC model: Forest cover at 5km ($\Delta AIC = 0$, $w_i = 0.54$, $df = 3$; $r^2 = 0.4$)		Estimate (SD)	CI
	Intercept	7.57 (0.96)	5.84 – 9.57
	FC at 5km	-0.08 (0.03)	-0.13 – -0.02
c) Beta β			
Top AIC model: Forest cover at 5km ($\Delta AIC = 0$, $w_i = 0.71$, $df = 3$; $r^2 = 0.61$)		Estimate (SD)	CI
	Intercept	13.94 (1.28)	11.50 – 16.66
	FC at 5km	-0.16 (0.04)	-0.23 – -0.08
d) β_{RC} (P/A-based) *			
Top AIC model: Null ($\Delta AIC = 0$, $w_i = 0.45$, $df = 2$)		Estimate (SD)	CI
	Intercept	-0.23 (0.05)	-0.34 – -0.12
	~ 1 (NULL)	-	-
e) Total abundance *			
Top AIC model: Forest cover at 5km ($\Delta AIC = 0$, $w_i = 0.4$, $df = 3$; $r^2 = 0.44$)		Estimate (SD)	CI
	Intercept	379.43 (120.98)	208.54 – 714.06
	FC at 5km	0.98 (0.01)	0.96 – 1.00
f) β_{RC} -abundance			
Top AIC model: Forest cover at 5km ($\Delta AIC = 0$, $w_i = 0.6$, $df = 3$; $r^2 = 0.42$)		Estimate (SD)	CI
	Intercept	0.91 (0.18)	0.52 – 1.30
	FC at 5km	-0.02 (0.01)	-0.03 – -0.00
Non-forest specialists (NFS)			
g) Gamma γ			
Top AIC model: Forest cover at 3km ($\Delta AIC = 0$, $w_i = 0.8$, $df = 3$; $r^2 = 0.73$)		Estimate (SD)	CI
	Intercept	17.39 (1.95)	13.79 – 21.65
	FC at 3km	-0.28 (0.05)	-0.38 – -0.18
h) Alpha α			
Top AIC model: Forest cover at 3km ($\Delta AIC = 0$, $w_i = 0.5$, $df = 3$; $r^2 = 0.63$)		Estimate (SD)	CI
	Intercept	5.66 (0.80)	4.28 – 7.39
	FC at 3km	-0.09 (0.02)	-0.13 – -0.05

i) Beta β

Top AIC model: Forest cover at 3km ($\Delta AIC = 0$, $w_i = 0.71$, $df = 3$; $r^2 = 0.61$)		Estimate (SD)	CI
	Intercept	11.78 (1.59)	8.81 – 15.36
	FC at 3km	-0.19 (0.04)	-0.28 – -0.11

j) β RC (P/A-based) *

Top AIC model: Forest cover at 3km ($\Delta AIC = 0$, $w_i = 0.37$, $df = 3$; $r^2 = 0.22$)		Estimate (SD)	CI
	Intercept	0.28 (0.19)	-0.14 – 0.70
	FC at 3km	-0.01 (0.01)	-0.03 – 0.00

k) Total abundance

Top AIC model: Forest cover at 5km ($\Delta AIC = 0$, $w_i = 0.4$, $df = 3$; $r^2 = 0.82$)		Estimate (SD)	CI
	Intercept	374.47 (125.81)	204.76 – 711.73
	FC at 5km	0.95 (0.01)	0.93 – 0.97

l) β RC-abundance *

Top AIC model: Forest cover at 3km ($\Delta AIC = 0$, $w_i = 0.36$, $df = 3$; $r^2 = 0.19$)		Estimate (SD)	CI
	Intercept	0.82 (0.34)	0.06 – 1.57
	FC at 3km	-0.02 (0.01)	-0.05 – 0.00

Discussion

We found that loss of native tropical forest led to a consistent increase in both dung beetles abundance and diversity, at all scales, for both forest specialists and non-forest specialists. Our findings echo others (e.g. Rahel, 2010; Daskalova et al., 2020) that challenge the widely-held assumption that native habitat loss universally leads to biodiversity decline (Newbold et al., 2015; Ceballos et al., 2017), including for dung beetles (e.g. Gibson et al., 2011; Barlow et al., 2016), and that habitat loss disproportionately impacts habitat specialists, relative to generalists (Estavillo et al., 2013; Pinto Leite et al., 2018). Our findings highlight that habitat loss does not always drive a decrease in the number of specialist species that offsets the gain of generalist specialists. We show that biodiversity can increase in deforested landscapes.

While we found that the local gain of species outpaced local extinction for both habitat specialists and generalists, we only detected a clear signal of generalists increasing in abundance as forest declined at the landscape scale. Hence, despite the increase in species richness in both groups, we observed an abundance-based signal that deforestation favors habitat generalists, but not all forest specialist species. This result aligns with the common observation that environmental disturbance decreases the population size of habitat specialists while favoring habitat generalists (Pardini et al., 2009), across taxa as diverse as birds (Morante-Filho et al., 2015) mammals (Pardini et

al., 2010) and dung beetles (Silva et al., 2016) to anthropogenic landscapes in tropical forest.

Generally, when the extinction process initiated by native habitat loss is random, it should lead to increased biotic differentiation between communities in different patches (increase in additive β -diversity; Baselga et al., 2015). However, extinctions from anthropogenic disturbance are often deterministic, not neutral, leading instead to a process of biotic homogenization (loss of β -diversity) (de Araújo et al., 2014; Püttker et al., 2015; Gossner et al., 2016; Collins et al., 2017; Finderup Nielsen et al., 2019). In addition to the increase in local and landscape diversity with deforestation, we observed an increase in differentiation for both generalists and specialists. This signal of differentiation disappeared when we controlled for difference in species richness by using beta diversity in the null model approach (β_{RC}) for both generalists and specialists. We observe no clear change in dissimilarity and communities are as similar as expected by chance. In our study, forest loss did not induce the pattern of communities becoming more different than expected by chance – a pattern expected to happen in highly deforested landscapes from either increased effect of drift (not expected here as abundance did not decline) or strong and variable deterministic factors that vary across fragments. Hence, although deforestation led to increased richness, this species gain seems random, and we did not find a clear sign of deterministic factors associated with the gain of the same species across fragments.

Studying β -diversity requires a sampling design with replication at multiple spatial scales, and the interpretation of β -diversity is affected by the variation in α -diversity, which is not common (but see Dormann et al., 2007). While the null-model metric proposed by Raup-Crick that corrects for α -diversity has been used in some studies along environmental gradients (Rocha et al., 2016; Martins et al., 2018; González-Trujillo and Alonso-Moreno, 2020), most do not explore the relative influence of deterministic and stochastic process. Those that do, have observed β -diversity changes to be explained by both deterministic and stochastic processes. For instance, González-Trujillo and Alonso-Moreno (2020) found beta diversity of Raup-Crick of invertebrate communities to become more dissimilar than expected by chance as a response of habitat simplification in a high-Andean stream. Püttker et al. (2015) found habitat loss to act as a strong ecological filter leading to less rich, homogenized

small mammal communities more similar than expected by chance in the Atlantic Forest. In contrast, in a study of Atlantic intertidal assemblages, Martins et al. (2018) found higher disturbance intensity to be associated with higher, and more random, community dissimilarity as well as higher species richness.

Examining a β -diversity metric that instead considers differences in community structure ($\beta_{RC\text{-abundance}}$), we observed that abundance distribution across generalists was as similar as expected by chance (random) between forest patches, irrespective of deforestation. In contrast, abundance distribution across specialists became more dissimilar than expected by chance as forest cover declined. Hence, the increased beta diversity (differentiation) in deforested landscapes is stronger and more deterministic for specialists than for generalists. This suggests both that specialist communities are indeed more sensitive to the increased - and variable across patches - disturbance pressures associated with greater forest habitat loss and fragmentation, and that community structure may offer a clearer signal of the biotic response to these disturbance pressures than community composition can. Despite an increase in the use of abundance-based null model approaches for beta diversity (e.g., Stegen et al., 2013a; Segre et al., 2014; Püttker et al., 2015; Tucker et al., 2016; Mori et al., 2018), we know of no study to date that also reported similarly clear patterns of biotic differentiation on the community structure of specialist species (i.e., an increase in $\beta_{RC\text{-abundance}}$).

Potential explanatory mechanisms

Our observation that deforestation was associated with an increase in diversity may be influenced by the historical biogeographical context of our study region. Current biotic responses to environmental change are often conditioned by biogeographical processes (Turvey and Fritz, 2011), including historical exposure to forest–savannah transitions (Williamson, 1996; Nichols et al., 2013). For example, forest-dwelling Amazonian dung beetle fauna are more sensitive to forest conversion than Afrotropical taxa (Nichols et al., 2013), potentially as they have been less exposed (Scholtz et al., 2009) to the forest–savannah transitions associated with the Quaternary-period glacial cycles (Prentice et al., 2011; Oliveras and Malhi, 2016) that were more extensive and frequent in Africa (Colinvaux et al., 2000; Malhi et al., 2013) than in Amazonia (Furley and Metcalfe, 2007). This biogeographical context may contribute to explaining the contrast between our results and those from the only comparable, multi-scale dung

beetle study in the Atlantic Forest. From the Brazilian northeastern state of Bahia, Pinto Leite et al. (2018) report that gamma and alpha diversity of forest specialist species declined with deforestation, while generalist and open-area affiliated species remained rare across all levels of forest cover. While both studies were carried out within the Atlantic Forest, the two study regions differ significantly in their historic exposure to forest–savannah transitions (Carnaval et al., 2009; Pinto-Sánchez et al., 2014), with our southern study region characterized by frequent savanna transitions (Anadón et al., 2014), and the northern study region of Pinto Leite et al. (2018) characterized by climatic stability and lack of associated transitions (Carnaval and Moritz, 2008). Greater historical exposure to shifts between closed and open-area physiognomies may have therefore contributed to a underlying greater resiliency to forest conversion across both forest specialists and generalists in the southern Brazilian Atlantic Forest from our study region.

The contemporary ecological context of our study sites may further contribute to the regional availability of both forest specialist and generalist species in our landscapes. As our study region is adjacent to both a significant Atlantic Forest ecological corridor to the north and east (Joly et al., 2010, 2014) and the predominantly open vegetation physiognomy of the Brazilian Cerrado to the west (Marino-Junior, 2004; Bueno et al., 2018), it is exposed to regional availability of both forest specialists and non-forest specialists. Mixture of these two assemblages is likely facilitated by the significant regional connectivity provided by the network of forest remnants and by dung beetle use of introduced exotic pastures (Correa et al., 2020, 2021). Overall, these observations of a likely regional availability of a disturbance-adapted pool of species suggest that ecological and biogeographical context can strongly influence biotic response to contemporary anthropogenic disturbance.

Conservation implications

Effective conservation planning in anthropogenic landscapes requires a robust understanding of the effects of land-use change on biodiversity. This is not a trivial task given that complex and variable responses to environmental change are likely the rule (Hillebrand et al., 2018; Magurran et al., 2018; Daskalova et al., 2020; Antão et al., 2020). In this context, this study contributes to mounting evidence that habitat change may not always lead to biodiversity loss (Sax and Gaines, 2003; Elahi et al., 2015;

Hillebrand et al., 2018; Finderup Nielsen et al., 2019; van Schalkwyk et al., 2020), but rather to complex biodiversity change that include negative (Kormann et al., 2018), neutral (Antão et al., 2020) or positive (Arroyo-Rodríguez et al., 2013) responses, and which are likely modulated by biogeographic context (Nichols et al., 2013) and the history and temporality of anthropogenic habitat change (Daskalova et al., 2020).

We also note that we would not have observed the full spectrum of biodiversity response to forest loss, including numerous qualitative differences in the response patterns of forest specialists and generalists, without the combined methodological approaches used here, such as a landscape-scale study design, use of multiple and complementary biodiversity metrics including null model approaches, and information on species' habitat associations. While these are methodological approaches that we recommend are applied in efforts to quantify biodiversity response to environmental change, we recognize that use of a landscape-scale study design present tradeoffs, including logistical difficulties in achieving a sufficiently large number of landscape replicates. Our findings therefore highlight that unpacking complex biodiversity response to environmental change – critical to support conservation and management – can require significant effort.

A robust understanding of biodiversity responses to land-use change underpins our understanding of the conservation value of both area-based and management-based conservation measures. Well-managed and connected protected areas and other effective area-based conservation are an important component of a wider conservation strategy and are recognized as a critical element of effective sustainable landscape management (IPBES, 2019a, 2019b). However, results from this study and others that demonstrate the complex and potentially context-dependent consequences of native habitat loss for biodiversity also suggest that higher native habitat cover cannot always effectively proxy for greater biodiversity in some areas. It is also clear that many anthropogenic land-uses outside of conservation areas are compatible with conserving at least part of the native biota of a given region (e.g. Chazdon et al., 2009). Understanding and predicting the conservation value of different management approaches is therefore a critical complement to exclusively area-based approaches and depends on reliable and interpretable information on biodiversity responses to a range to land-use change (Nichols and Gardner, 2011). Conservation strategies will therefore

generally benefit from a stronger understanding of the patterns and underlying mechanisms of the full spectrum of biotic consequences of land-use change.

Our results further underpin the importance of taking into account ecological variability and context dependency to the success of conservation efforts, especially in complex tropical landscapes (Boedhihartono et al., 2018). Decades of effort to delineate general or universal conservation suggest that ‘silver bullet’ conservation strategies are rarely effective across multiple contexts (Wells et al., 2020), and are more effective when conservation actions are rooted in the peculiarities of local contexts (Meyfroidt et al., 2022). Overall, our findings underscore the importance of understanding how biotic responses may be modulated by ecological and biogeographic context, and reinforce the relevance of well-designed field studies to evaluate the results of potential conservation interventions.

CRedit authorship contribution statement

JRB compiled the dataset, performed all analyses, and wrote the manuscript. RP contributed to funding, sampling design, and manuscript revision. FABS contributed to data collection, and manuscript revision. ESN contributed to funding, sampling design, data collection, and manuscript revision. JPM contributed to funding and manuscript revision.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data accessibility statement

Original data and analytical code are available in Figshare Repository (DOI: <https://doi.org/10.6084/m9.figshare.21743339>) and Github (https://github.com/barretoju/Landscape_Diversity_DungBeetles).

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2023.109957>.

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Supplementary material

S1 Species habitat association list

Table S1. Species habitat classifications developed from data on dung beetle habitat preference and biogeographic association, based on published literature and collection data from an expert dung beetle taxonomist (F. Silva, Universidade Federal do Pará). Habitat preference abbreviations include: F, forest; O, open areas; and, G, habitat generalist (found in both forest and open areas). Biogeographic association abbreviations include: AF, Atlantic Forest; WIDE, widely distributed; TRANS, Atlantic Forest transition to Cerrado; CE, Cerrado. Habitat association abbreviations include: FS, forest specialists; and NSF, non-forest specialists. These classifications were defined by combining information on habitat preference and biogeographic association, with forest specialists defined as species with a clear preference for forest habitats and a distribution restricted to the Atlantic Forest, and, non-forest specialists defined as species collected in either open areas or open areas and forest habitats, and a distribution not restricted the Atlantic Forest. To run the analyses we removed six singletons found only once in forest habitats, including *Canthon histrio*, *Canthon podagricus*, *Coprophanaeus bellicosus*, *Deltochilum* (*Deltohyboma*) sp., *Dichotomius bos* and *Uroxys aff brevis*. The final column (Ref.) specifies the associated references, with all citations listed below.

Species	Habitat preference	Biogeographic association	Habitat association	Ref.
<i>Ateuchus carbonarius</i> (Harold, 1868)	F	AF	FS	1
<i>Ateuchus volxemi</i> (Preudhomme de Borre, 1886)	F	AF	FS	1
<i>Canthidium</i> sp.	F	AF	FS	*
<i>Canthon</i> aff. <i>angularis</i> Harold, 1868	G	AF	NFS	2, 3, 4, *
<i>Canthon</i> aff. <i>luctuosus</i> Harold, 1868	F	AF	FS	*
<i>Canthon</i> aff. <i>semiopacus</i> Harold, 1868	F	AF	FS	*
<i>Canthon ibarragrassoi</i> (Martínez, 1952)	F	AF	FS	2, 5
<i>Chalcocoprís hesperus</i> (Olivier, 1789)	G	TRANS	NFS	3, 7, 8
<i>Coprophanaeus cerberus</i> (Harold, 1869)	F	AF	FS	3, 9
<i>Coprophanaeus saphirinus</i> (Stürm, 1828)	F	AF	FS	3, 8, 9, 10

<i>Deltochilum brasiliense</i> (Castelnau, 1840)	F	AF	FS	2, 3, 5, 11, 12, *
<i>Deltochilum dentipes</i> Eschscholtz, 1822	F	AF	FS	3, 13
<i>Deltochilum furcatum</i> (Castelnau, 1840)	F	AF	FS	3, 12, *
<i>Deltochilum morbillosum</i> Burmeister, 1848	F	TRANS	NFS	2, 3, *
<i>Deltochilum rubripenne</i> (Gory, 1831)	F	TRANS	NFS	2, 12, *
<i>Dichotomius</i> aff. <i>carbonarius</i> sp.1 (Mannerheim, 1829)	G	CE	NFS	3, 14
<i>Dichotomius</i> aff. <i>carbonarius</i> sp.2 (Mannerheim, 1829)	F	TRANS	NFS	3, 8, 14, *
<i>Dichotomius assifer</i> (Eschscholtz, 1822)	G	AF	NFS	3, 8, 14, *
<i>Dichotomius depressicollis</i> (Harold, 1867)	F	AF	FS	3, 8, 14, *
<i>Dichotomius fissus</i> (Harold, 1867)	G	AF	NFS	3, 14, 15
<i>Dichotomius mormon</i> (Ljungh, 1799)	F	AF	FS	4, 8, 16
<i>Dichotomius quadrinodosus</i> (Felsche, 1901)	F	AF	FS	3, 4, 17
<i>Dichotomius</i> sp.1	F	AF	FS	*
<i>Dichotomius</i> sp.2	F	AF	FS	*
<i>Dichotomius</i> sp3	G	TRANS	NFS	*
<i>Dichotomius</i> sp.4	G	TRANS	NFS	*
<i>Dichotomius</i> sp.5	F	AF	FS	*
<i>Eurysternus cyanescens</i> Balthasar, 1939	F	TRANS	NFS	3, 18, 19
<i>Eurysternus francinae</i> Génier, 2009	F	AF	FS	3, 5, 18, 19
<i>Eurysternus hirtellus</i> Dalman, 1824	F	TRANS	NFS	3, 18, 19

<i>Eurysternus inflexus</i> (Germar, 1824)	F	AF	FS	3, 18, 19
<i>Eurysternus parallelus</i> Castelnau, 1840	G	TRANS	NFS	2, 3, 5, 11, 14, 18, 19
<i>Ontherus sulcator</i> (Fabricius, 1775)	G	WIDE	NFS	2, 3, 8, 14, 18
<i>Onthophagus</i> sp.1	F	AF	FS	*
<i>Onthophagus</i> sp.2	F	AF	FS	*
<i>Onthophagus</i> sp.3	F	AF	FS	*
<i>Onthophagus</i> sp.4	O	CE	NFS	*
<i>Paracanthon monteiroorum</i> Pacheco & Vaz-de-Mello, 2019	F	AF	FS	20
<i>Paracanthon rosinae</i> Balthasar, 1942	F	AF	FS	20
<i>Phanaeus dejeani</i> Harold, 1868	F	AF	FS	3, 21
<i>Phanaeus splendidulus</i> (Fabricius, 1781)	F	AF	FS	3, 11, 21
<i>Pseudocanthon xanthurus</i> (Blanchard, 1847)	G	TRANS	NFS	8, 15, 22
<i>Scybalocanthon nigriceps</i> (Harold, 1868)	F	AF	FS	2, 23
<i>Sylvicanthon foveiventris</i> (Schmidt, 1920)	F	AF	FS	24
<i>Trichillum</i> sp.	O	TRANS	NFS	*
<i>Uroxys</i> sp.1	F	TRANS	NFS	*
<i>Uroxys</i> sp.2	F	TRANS	NFS	*
<i>Uroxys</i> sp.3	F	TRANS	NFS	*
<i>Uroxys</i> sp.4	F	TRANS	NFS	*

* F. Silva personal data and MZUFPA (Zoological Museum of the Federal University of Pará) collection data (Coleção de Scarabaeinae do Setor de Zoologia, Instituto de Ciências Biológicas, Universidade Federal do Pará, Belém, Brazil (Fernando A.B. Silva)).

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S2 Model selection table

Table S2. AICc-based selected models table containing the models of gamma (γ), alpha (α), additive beta (β) diversities followed by abundance at landscape total, and β -diversity calculated from the Raup-Crick null model approach, for both presence/absence (β_{RC}) and abundance-based (β_{RC} -abundance) that scored below $\Delta AIC_c=2$. All tested as a function of Atlantic Forest loss for each group of species, first models separated into forest specialists species (FS; Table 1a), followed by non-forest species (NFS; Table 1b). We show all models in a candidate set with ordered from the lowest to the highest AICc values $\Delta AIC_c \leq 2$. We present information regarding the diversity metric tested (Diversity), model terms for forest loss predictors (Model), Akaike information criterion corrected for small samples (AICc), AICc difference from the first-ranked model (ΔAIC_c), degrees of freedom (df), Akaike weight (ω_i) and model variance explained (r^2).

Diversity	Model	AICc	ΔAIC_c	df	ω_i	r^2
a) Forest Specialists (FS)						
Gamma γ	FC at 5km	65.36	0	3	0.8	0.58
Alpha α	FC at 5km	47.99	0	3	0.5	0.4
	FC at 3km	49.97	2	3	0.2	0.29
Beta β	FC at 5km	53.97	0	3	0.7	0.61
Total abundance	FC at 5km	150.1	0	3	0.4	0.44
	~ 1 (NULL)	150.7	0.5	2	0.3	-
	FC at 3km	151.4	1.2	3	0.2	0.33
β RC (P/A-based)	~ 1 (NULL)	-3.97	0	2	0.5	-
	Non-linear FC at 3km	-2.48	1.5	4	0.2	0.31
β RC-abundance	FC at 5km	8.78	0	3	0.6	0.42
	FC at 3km	10.67	1.9	3	0.2	0.32
b) Non-forest specialists (NFS)						
Gamma γ	FC at 3km	61.65	0	3	0.8	0.73
Alpha α	FC at 3km	41.18	0	3	0.5	0.63
	FC at 5km	41.8	0.6	3	0.4	0.61
Beta β	FC at 3km	57.73	0	3	0.7	0.62
Total abundance	FC at 5km	136.7	0	3	0.4	0.82
	FC at 3km	137.4	0.7	3	0.3	0.79
	Non-linear FC at 5km	137.7	0.9	4	0.3	0.93
β RC (P/A-based)	FC at 3km	9.75	0	3	0.4	0.22
	~ 1 (NULL)	10.22	0.5	2	0.3	-
	FC at 5km	10.9	1.1	3	0.2	0.14
β RC-abundance	FC at 3km	23.92	0	3	0.4	0.19
	~ 1 (NULL)	23.92	0	2	0.4	-
	FC at 5km	24.98	1.06	3	0.2	0.12

S3 Cerrado biome adjacent to study region

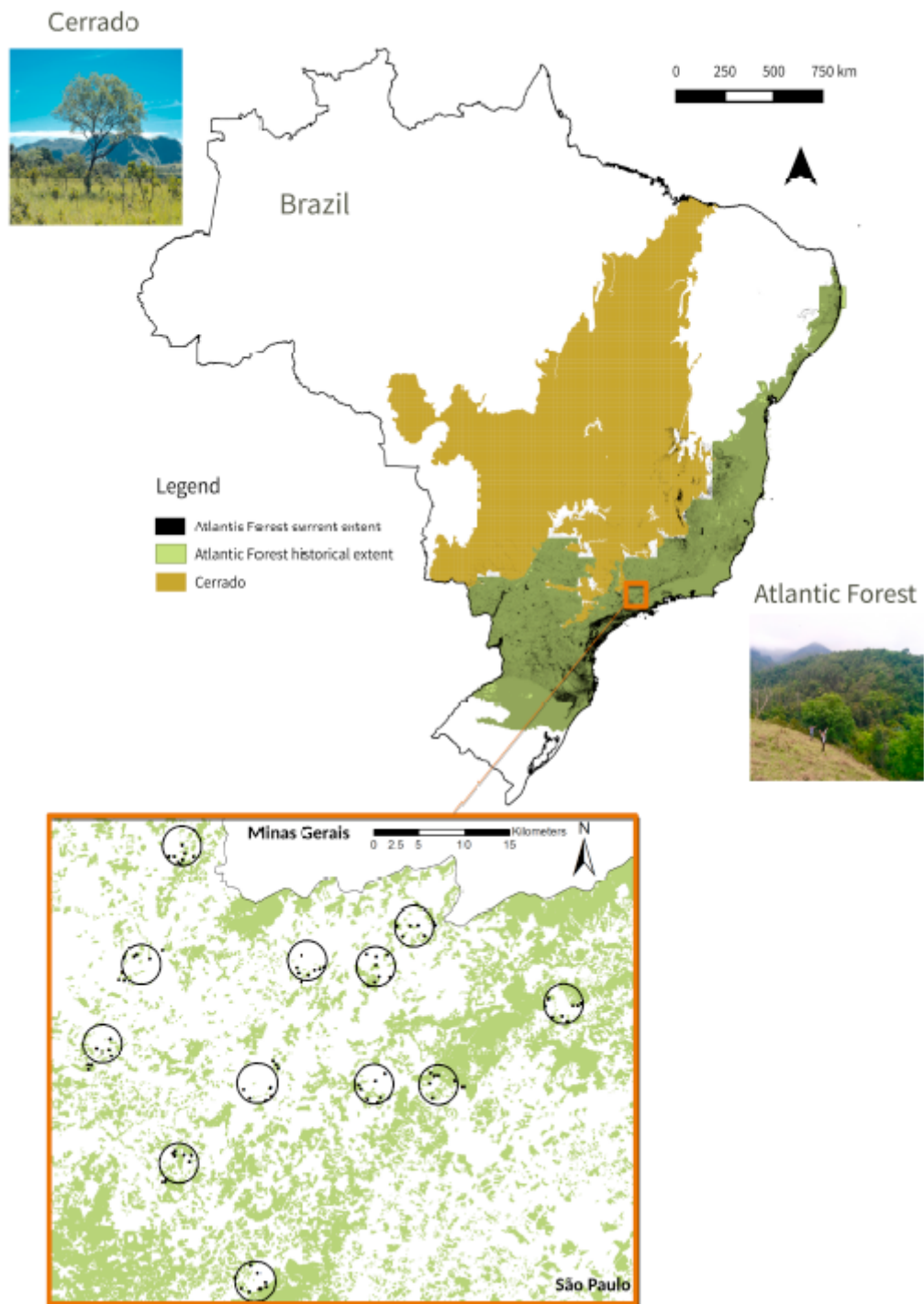


Figure S1. Brazil, with the original extent of the Cerrado and Atlantic Forest phytogeographic domains, study region, and the locations of 12 focal landscapes.

CAPÍTULO 2

Context-dependent drivers of biodiversity response to anthropogenic change



Context-dependent drivers of biodiversity response to anthropogenic change

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Abstract

Landscape-level changes in native habitat composition and configuration are relatively well characterized as key drivers of ongoing biodiversity change. However, how biodiversity in the non-native habitat matrices in these landscapes responds to changes in landscape structure, or influence the response of biodiversity in remaining native habitat, is less clear. A multi-level landscape design with paired biodiversity sampling in both native and matrix habitats examined the influence of species' habitat associations and landscape structure on the response of tropical dung beetle communities to conversion of native forests into anthropogenic cattle pasture. We modeled landscape-level species richness, abundance and β -diversity of dung beetle communities captured in both native and anthropogenic habitats along a gradient of native forest cover as a function of species' habitat association, and multiple metrics of landscape structure. Our findings indicate that community abundance and richness were significantly affected by habitat type and species' habitat preferences, as well as native habitat cover at the landscape scale. While differences in β -diversity between adjacent native and anthropogenic habitats were also influenced by species' habitat associations, the impacts of landscape structure differed for different β -diversity components, with turnover for generalists largely responding to the density of forest-pasture edges and nestedness responding only to species' habitat association. Finally, our study identified an additional impact of landscape structure, indicating the homogenization of native forest specialist and habitat generalist communities with an increase in edge density. This evidence highlights the importance of sampling in multiple habitats to understand the interplay between environmental change at broader spatial scales and biological traits on key biodiversity responses, including biotic homogenization. Our findings have clear implications for both area-based and management-based landscape conservation practices.

Keywords: biodiversity, β -diversity, deforestation, biotic homogenization, Scarabaeidae: Scarabaeinae, species assemblage, turnover.

Introduction

While native habitat loss and change remain the major driver of ongoing biodiversity loss globally (Barnosky et al., 2011; Díaz et al., 2019; Purvis et al., 2022) and often regionally (Estavillo et al. 2013; Horváth et al. 2019). However,, an expanding body of evidence demonstrates that biodiversity response to more localized native habitat change can be highly context-dependent (Vellend et al. 2013; Hillebrand et al. 2018; Blowes et al. 2023), influenced by factors including the availability of disturbance-resilient taxa (Barreto et al., 2021; Bregman et al., 2014; Karp et al., 2012) and overall landscape structure (Fischer and Lindenmayer 2007; de Castro Solar et al. 2015; Pfeifer et al. 2017; Barros et al. 2019). An increasing body of work has additionally examined the influence of non-native matrix habitats on biodiversity native habitats (Boesing et al., 2018; de Souza Leite et al., 2022; Habel et al., 2020; Reider et al., 2018). Still, how biological communities found in the landscape matrix themselves respond to changes in landscape structure, or influence the response of biodiversity in native habitats, remains less clear (de Souza Leite et al. 2022a; Valente et al. 2023).

Matrix communities may particularly influence local biodiversity response and regional biodiversity patterns through their role in biotic homogenization, increasing similarity between communities in different habitats (McKinney & Lockwood, 1999; Olden & Rooney, 2006). The increased similarity of communities in native and anthropogenic habitats typically involves the gradual replacement of habitat specialists by disturbance resilient or habitat generalist taxa, and is generally of conservation concern (Olden et al., 2004). Understanding the process of biotic homogenization is critical for predicting future biodiversity trends and informing conservation and management strategies across various scales and contexts (Chase et al., 2020; Rolls et al., 2023; Socolar et al., 2016). Community similarity between native and matrix habitats is likely influenced by the composition of biological communities (including the availability of disturbance-resilient taxa in both habitat types), and the degree of species exchange between communities (cross-habitat spillover). Landscape structure should further influence biotic homogenization, as both community composition within habitats and species exchange between habitats are affected by habitat type, amount, and connectivity between habitats (Fahrig 2003; Boesing et al. 2018; de Souza Leite et al. 2022).

Across the Tropical Americas, native habitat conversions into high-contrast matrix types (e.g. exotic cattle pasture), often results in biological communities characterized by low species richness and abundance (Boesing et al., 2018; de Souza Leite et al., 2022; Maciel et al., 2023; Silva et al., 2017), particularly in regions where open vegetation physiogamies are a comparative biogeographic novelty (Carnaval et al., 2009; Nichols et al. 2013). However, the role of species traits in modulating biodiversity responses to conversions to this habitat type remains unclear. For example, while species' habitat association (i.e. a tendency to be forest specialists or habitat generalists) is understood to strongly determine the response of forest-dwelling species to landscape change (Banks-Leite et al., 2014; Barreto et al., 2023), fewer efforts have been dedicated to understand these patterns across non-native habitats (*but see* Estavillo et al 2013; de Souza Leite et al., 2022). Sampling across native and anthropogenic habitats is critical to how trait-dependencies in biodiversity response to changes in native habitat cover or configuration might influence biotic homogenization, including through processes like the spread of disturbance-resilient taxa, the loss of habitat specialist species, or both.

Landscape structure is expected to further influence such trait-dependencies in biodiversity response to habitat change (Newbold et al. 2014; de Souza Leite et al. 2022). As landscapes undergo native habitat loss, declining native habitat cover is inversely related to matrix habitat cover, and nonlinearly related to the size, number and distance of native habitat remnants (Andr n 1994) as well as the amount of edge between native and matrix habitats (Fahrig 2003). The biodiversity persisting within local habitat remnants is, in turn, modulated by structural landscape characteristics (Pardini et al., 2010, Souza et al. 2020), including through effects associated with the amount of remaining habitats (Martensen et al., 2012), and connectivity across both landscape and regional scales (Villard & Metzger, 2014). Higher habitat cover is generally understood to be associated with increased species richness and abundance within habitat patches (Hanski, 2011; Pardini et al., 2010, though see Barreto et al., 2023), often with differential effects on habitat specialists and generalists (Devictor et al., 2008; Estavillo et al., 2013). Increased edges between matrix and native habitats should increase the rate at which individuals encounter edges (Boesing et al., 2017) which may influence rates of species exchange (cross-habitat spillover) between native and matrix habitats (Frost et al., 2015; Schneider et al., 2016), often in a trait-dependent manner (Boesing et al., 2017). For instance, dispersal abilities play a crucial role in this context, where species exhibiting

stronger mobility can more easily cross habitats, therefore shaping the dynamics of species exchange. These influences of landscape structure on biodiversity likely apply to biodiversity in matrix habitats as well as within native remnants, though their effects on matrix biodiversity have been less well-characterized.

Increasing number of empirical efforts to quantify biodiversity response to landscape change are integrating biological sampling across multiple spatial scales, with several metrics of biodiversity, and incorporating information on disturbance resilience (e.g. species' habitat association) (Estavillo et al., 2013; Newbold et al., 2015; Pinto Leite et al., 2018; Püttker et al., 2015). These initiatives are contributing to unpacking important nuances in biodiversity response (Barreto et al., 2023; Daskalova et al., 2020). However, multiscale investigations of biodiversity responses are often limited to a single (typically native) habitat type (*but see* Estavillo et al., 2013; Pinto Leite et al., 2018; Püttker et al., 2015). This may limit our understanding of context dependencies of biodiversity responses in real landscapes, which are typically composed of mosaics of native and matrix habitats (Chazdon et al., 2009; Fahrig et al., 2019). Investigating how landscape structure shapes trait-dependencies in biodiversity responses in both native and matrix habitats is therefore essential for improving the understanding of key biodiversity patterns, including the drivers of biotic homogenization (Filgueiras et al., 2016; Marsh et al., 2018; Martínez-Falcón et al., 2018; Orme et al., 2019). Efforts to quantify biodiversity response are particularly important in complex tropical landscapes (Boedhihartono et al., 2018) where a robust understanding the ecological impacts of land-use change often underpins our comprehension of the conservation value of both area- based and management-based conservation measures.

Dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae) are an ideal model taxon to explore the influences of species' habitat association and landscape structure on community composition in both native and matrix habitats. Dung beetles are a cosmopolitan and primarily coprophagous insect group that is frequently used as an ecological indicator taxa (Nichols & Gardner, 2011). Their communities often display a wide diversity of response to native habitat loss and change (Barreto et al., 2023; Larsen et al., 2008; Nichols et al., 2013), that are increasingly understood through a species trait framework (e.g. Barreto et al. 2023; deCastro-Arrazola et al., 2023; Nichols et al., 2013). Despite an improving understanding of the response of dung beetles in native habitat

patches to forest cover loss at broader spatial scales (Pinto Leite et al. 2018; Torppa et al. 2020; Carvalho et al. 2023; Barreto et al. 2023), how landscape structure influences cross-habitat community composition has not yet been rigorously explored.

In this study we examine the influence of species' habitat association and landscape structure on tropical dung beetle communities in both native and anthropogenic habitats by using a multi-level landscape design with paired sampling in both habitat types. We aim to address two questions: (1) are the differences in biotic communities between native and anthropogenic habitats modulated by species' habitat associations, and (2) does landscape structure further influence these trait-dependent differences in response.

Materials and methods

Study region

We collected land cover and biodiversity samples in the Cantareira-Mantiqueira region of São Paulo state (23° 01' S and 46° 15' W'), within the Brazilian Atlantic Forest (Figure 1a). The Atlantic Forest phytogeographic domain is composed of five forest types (Oliveira-Filho and Fontes, 2000), with lower montane ombrophilous dense forest the most representative across the study region (IBGE, 2012). The region has a humid subtropical climate (annual minimum mean 14.9 ± 0.90 °C; annual maximum mean 26.3 ± 1.15 °C), mean annual rainfall of 1440 ± 120 mm, and an elevation between 800 and 1200 m (<http://www.cpa.unicamp.br/>).

The Atlantic Forest has globally high rates of species diversity and endemism (Myers et al. 2000). However, five centuries of deforestation and fragmentation following European colonization (Joly et al. 2014) have resulted in only 28% of the biome remaining (Rezende et al., 2018). The remaining forest cover consists mainly of small fragments in early to medium stages of succession (Lira et al., 2012; Rosa et al., 2021), with more than 80% of fragments smaller than 50 ha (Ribeiro et al., 2009), contributing to the status of the Atlantic Forest as a critical biodiversity hotspot (Myers et al., 2000). The Cantareira-Mantiqueira region is a crucial ecological corridor that provides connectivity for the remaining Atlantic Forest fragments in the area, and hence is considered a biodiversity conservation priority at the state level (Joly et al., 2010). Landscapes in the region are characterized by small secondary forest fragments surrounded by matrices dominated by

cattle pasture systems in small properties (mean 46.9% \pm 11.1; Figure 1e). Other land uses are also present, though in lower proportions, including *Eucalyptus spp.* plantations (18.1% \pm 8.7), urban areas (7.4% \pm 7.5), water (0.9% \pm 1.9) or else (1.4% \pm 2.5).

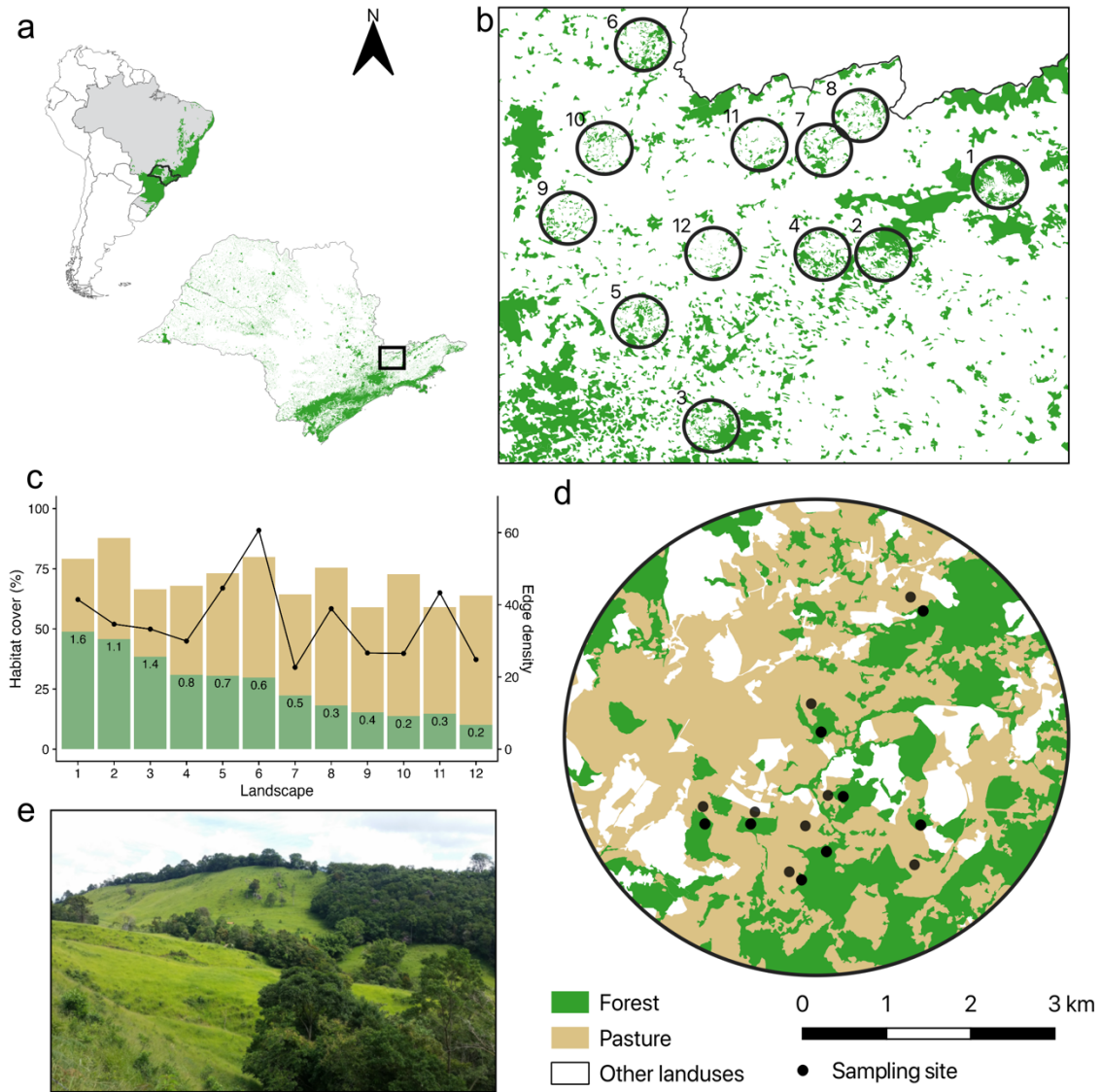


Figure 1. Location and design of the study to examine the influence of species' habitat association and landscape structure on tropical dung beetle communities in adjacent native and anthropogenic habitats. Including: (a) map of Brazil with original Atlantic Forest domain in green, the state of São Paulo, in detail showing the study region within the current Atlantic Forest; (b) study area with 12 focal landscapes with 3 km radius (7,854 ha) selected to represent the deforestation gradient, (c) percentages of forest (green) and pasture (yellow) cover in each landscape, with values of the ratio of forest to pasture in black text and edge density (black line and dots) measured at a 3 km radius for each landscape (see Figure S1 for the version of 5km radius and landscape shape index (LSI) values); (d) sample landscape (#6) with 29.7% of native forest and 50.2% pasture cover, showing habitat sampling points (black), within forest (green) and pasture (yellow); and (e) photo displaying one of the sampling plots (credit: Andrea Larissa Boesing).

Nested sampling design

We selected 12, 3-km radius focal landscapes dominated by either native forest or pastures (7,854 ha; Figure 1b). All selected landscapes were constrained within 800 and 1,300 m.a.s.l. (meters above sea level), on ferric red latosol or argisol soil, and to exclude major interstate highways and water reservoirs (Pasher et al., 2013). We used the Sampling Design tool in ArcGIS 10.1 to calculate the percentage of land use defined as native forest cover in circular buffers of 3-km radii around the landscape's centroids, and further restricted the selection of focal landscapes to areas where native forest cover did not vary more than 5 percent within 1, 2, or 3-km radius from each landscape centroid, to avoid the potential influence of larger patch on ecological processes (Pasher et al., 2013). We mapped each landscape land use using high-resolution images (ArcGIS 10.3 basemap imagery, Digital Globe satellites 2010-2011). We defined as forest only those native forest remnants at an intermediate (ca 10 years) or advanced successional stages. We defined pastures as areas of active cattle raising, without scattered trees, or regenerating forest, or aquatic ecosystems, and verified both habitat types through field observation. The resulting 12 focal landscapes vary from 10.1–48.8% native forest cover ($26.4\% \pm 12.6$); Figure 1c) and 28–59% pasture cover ($44.2\% \pm 9.7$) at 3-km radii (Figure 1c). We used this resulting gradient in landscape-level native forest and corresponding variation pasture cover across the 12 focal landscapes to explore the effects of landscape structure on the differences in ecological communities between native forests and pastures.

To distribute sampling sites across each focal landscape – eight within native forest remnants and eight within pastures – we used a stratified, random, and proportional selection process based on the largest forest fragment in the landscape. As the size of the largest forest fragment is an important landscape structure feature related to the proportion of total forest remaining in a landscape (Fahrig, 2003), we randomly assigned eight sampling points to the largest fragment according to the proportion of its cover in the landscape while remaining points were assigned to smaller fragments larger than 2.5ha. All sampling points were within the radius of 3-km of each landscape, at least 300 meters apart, but within 400 m of an access road. At each sampling point, we placed an approximately 100-m transect towards the interior of each habitat type, one in native forest and the other in pasture habitats (Figure 1d).

Landscape structure predictors

We estimated landscape structure for each landscape using metrics of landscape composition (percent native forest and anthropogenic pasture cover) and configuration (forest-pasture edge density, ED_{F-P} , and landscape shape index, LSI; see Table S1 for additional details). We found a strong correlation between native forest and pasture cover in our landscapes (Figure S2a) and therefore combined the two measures of habitat types into a single forest-pasture cover ratio (FP_{ratio}) by dividing the percentage of native forest cover by percentage of pasture cover. To represent landscape configuration as a function of the density of edges between forest and pasture habitats, we calculated ED_{F-P} as the total sum of the lengths of all forest-pasture edge segments in the landscape divided by the total landscape area. To additionally represent landscape configuration through the landscape shape index, we calculated LSI as the total forest-pasture edge in the landscape divided by the hypothetical minimum total edge possible (i.e., if the landscape consists of a single forest patch). These two landscape configuration variables were selected for their relative independence from habitat type (Figure S2b). As the units and boundaries of any ‘landscape’ depend on the species assemblage under consideration (Wiens, 1989) and the spatial definition of landscape can vary across taxa (Metzger, 2001), we calculated all landscape-level composition and configuration metrics at landscapes defined by both a 3 km and 5km radius.

Biodiversity data collection and species’ habitat association categorization

We sampled dung beetle communities following a standardized protocol using pitfall traps (20 cm diameter, 15 cm depth). In each of the 95 forest and pasture sampling sites, we placed four traps at 50, 70, 90 and 100 m from the edge, along an transect oriented towards the forest fragment center. Feces from omnivorous mammals (i.e., humans and swine) are often used in neotropical biodiversity studies of dung beetles (Frank et al., 2018; Nichols et al., 2009), as they attract species known to use primate, herbivore and omnivorous feces (Larsen et al., 2006) and are commonly reported to attract a wider variety of species than other types of baits (Bogoni et al., 2014). Pitfall traps were buried flush with the ground, baited with 20 g of a 10% human, 90% pig dung bait (Marsh et al., 2013) and operated for one 48-hour period at each site, sampling three to four landscapes concurrently during the wet season (December 2014–March 2015).

Specimens were identified to species by an expert dung beetle taxonomist (F.A.B. Silva, Federal University of Pará) with extensive collection experience in the dung beetle fauna of the Atlantic Forest and Cerrado domains. The same taxonomist then identified all species according to species' habitat associations. Our approach involved integrating published information on biogeographical distribution, habitat use, and preference using extensive occurrence data. We defined forest specialists (henceforth, specialists), as those species with both a biogeographical distribution restricted to the Atlantic Forest and with a clear preference for forested habitats, based on occurrence data. Conversely, we characterized as non-forest specialists (henceforth, generalists) as those species with biogeographical distributions extending beyond the Atlantic Forest (including broader distributions inclusive of the Cerrado and Amazon domain) and/or exhibiting habitat preferences not limited to forested habitats. While there are certain drawbacks to relying on observational data as a proxy for species' habitat association, it is often the most feasible approach for invertebrates such as dung beetles, which are a diverse tropical group with less robust and publicly accessible occurrence data (e.g. compared to avian biodiversity data in the same region (Boesing et al., 2017)). Recent work by Barreto et al. (2023) demonstrates that these species' habitat association groups may influence dung beetle response to habitat changes – similar to evidence from other taxonomic groups (Banks-Leite et al., 2014; Ewers & Didham, 2006; Pardini et al., 2010). More details on the species' habitat association classifications used here can be found in Barreto et al. (2023).

Data analyses

To explore if the differences in dung beetle community structure and composition between native and anthropogenic habitats are modulated by species' habitat association, we first calculated a series of biodiversity metrics for each of the 12 focal landscapes, including total species richness and abundance within each habitat type, as well as β -diversity between the two habitat types. The total β -diversity between two communities may reflect two different pathways towards community dissimilarity, species turnover (β_{SIM} , species replacement) and nestedness (β_{SNE} , species loss/gain; Baselga, 2010). We used the approach proposed by (Baselga, 2010), to decompose total β -diversity (pairwise Sørensen dissimilarity indices, β_{SOR}) into turnover (β_{SIM}) and nestedness (β_{SNE}) components using the *betapair* function from the R-package 'betapart' (Baselga et al., 2023). β -diversity metrics are continuous variables that assume values in

the interval $[0,1]$, and indicate if communities share fewer species (β values approaching 1) or many species (β approaching 0). When there is a perfect contrast in community composition between two habitat types (i.e. zero species overlap), β_{SOR} can assume an extreme value of 1, which can prevent reliable model fit in a beta distribution model (also defined on the interval $[0,1]$). To avoid this issue in the few instances of such non-overlap at the sampling site level in our data ($n=3$), we applied the data transformation recommended by Cribari-Neto & Achim Zeileis (2010) as $(y \cdot (n - 1) + 0.5)/n$; where n is the sample size.

We then modeled species richness and abundance as a function of habitat type and species' habitat association, using generalized linear mixed models (Poisson and Negative Binomial distribution, respectively). In all models, we used landscape as a random intercept because dependent variables were calculated separately for specialist and generalist species, i.e., two samples per landscape. We build a set of five candidate models using the variables of habitat type (forest or pasture) and species' habitat association (specialist or generalist) alone, in additive or interactive combinations, together with a null model. We used an AIC model selection approach corrected for small sample sizes (AICc), considering models with $\Delta AICc < 2$ as having the strongest empirical support. We modeled β -diversity as a function of species' habitat association only (as habitat type is intrinsically incorporated in the β -diversity metric), using generalized linear mixed models (Beta distribution) and landscape as a random intercept.

To explore how landscape structure may further influence any trait-dependent differences in biodiversity response between native and anthropogenic habitats, we built upon the top models ($\Delta AICc = 0$) for total species richness, abundance, and β -diversities obtained as outcomes from Question 1 and added landscape structure as predictors. To do this we modeled species richness, abundance, and β -diversities as a function of landscape cover and configuration, including forest-pasture percentage ratio ($F-P_{ratio}$), edge density (ED_{F-p}) and the landscape shape index (LSI), in addition to the selected term of species' habitat association*habitat type (i.e. species' habitat association:habitat type + species' habitat association + habitat type) for models of species richness and abundance, and to species' habitat association term for model of β -diversity (Table S2). We ran all models at both the 3-km and 5-km spatial scale. As with Question 1, we selected best models (including spatial scale) with AICc model

selection considering models with $\Delta AICc < 2$ as having the strongest empirical support. We calculated the r-squared from mixed models (Nakagawa et al., 2013), including both marginal (fixed effects only, R^2_m) and conditional values (fixed and random effects, R^2_c). The candidate model set tested for Question 2 can be found in Table S2.

We ran all analyses in R version 4.2.3 (R Development Core Team, 2023) using the following packages: *bbmle* for model selection (Bolker 2023), *betapart* for pairwise β -diversity calculations (Baselga et al. 2023), *glmmTMB* for fitting mixed effect beta regression models (Mollie et al., 2017), *car* for model collinearity tests (Fox & Weisberg, 2019), *DHARMA* for residual diagnostics, including spatial autocorrelation (Hartig, 2022), *performance* for extracting r-squared from mixed effect models (Lüdecke et al. 2021); and *ggeffects* (Lüdecke, 2018) for predictions and model 95% confidence intervals. All analyses (including data management, preliminary explorations and model validation) are fully reproducible, with code and data available in an online repository (*add referred repo DOI when ready*).

Results

In the 12 focal landscapes, we sampled a total of 4,392 dung beetle individuals of 58 species. Of these, 2,466 individuals of 26 species were habitat specialists, and 1,926 individuals of 32 species habitat generalists. We recorded 1,156 individuals of 26 species exclusively in forest habitats, of which 18 were specialists and eight generalists. We also captured 38 individuals of four generalist species exclusively in pasture habitats and caught no specialist species uniquely in pasture habitats (Table S3). We found 3,198 individuals of 28 species occupying both habitat types, including eight specialist (1,459 individuals) and 20 generalist species (1,739 individuals). While at the landscape level, at least nine species of specialist and generalists were represented in all landscapes, specialists were not observed in the sampled pasture habitats of all landscapes. This included two focal landscapes with zero specialist species representation in any sampled pasture (Table S4), and six landscapes with specialists represented by a single species found in extremely low abundance across all sampled pastures (Table S4).

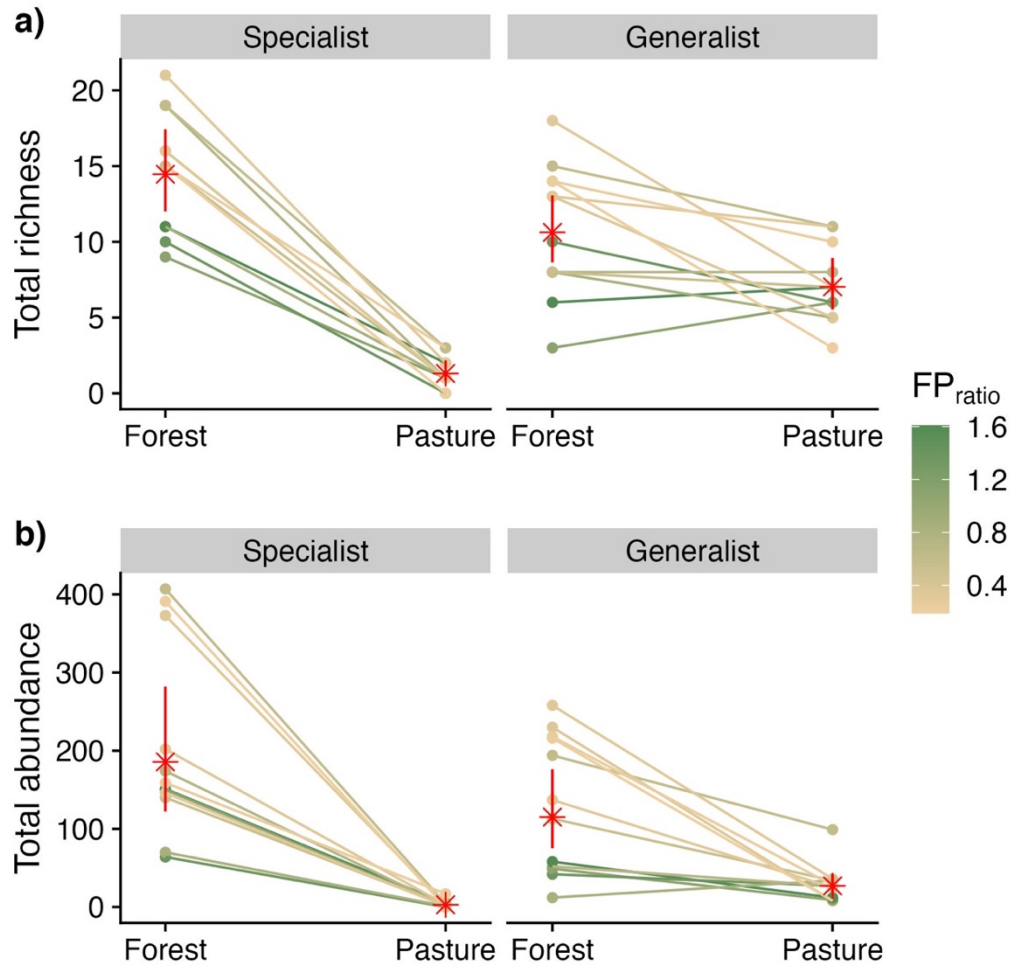


Figure 2. Total (a) richness and (b) abundance of dung beetle communities collected in native (forest) and anthropogenic (cattle pasture) habitats in each of 12 focal landscapes, separated by species' habitat associations (specialist, left and generalists right) and the habitat in which communities were sampled. Line colors indicate the value of the forest-pasture cover ratio gradient of the focal landscape where collections occurred, at the 3-km scale. Asterisks and bars represent predicted values of each response variables and confidence intervals for the top selected model ($\Delta AIC_c = 0$), respectively.

Are the differences in biotic communities between native and anthropogenic habitats modulated by species' habitat association? (Question 1)

The total (landscape-level) species richness and abundance of dung beetle communities captured in forest and pasture habitats were strongly influenced by the interaction of species' habitat association and habitat type (Figure 2; Table S5). Overall, pasture habitats supported fewer species ($R^2_m = 0.85$, $R^2_c = 0.89$, Figure 2a) and individuals ($R^2_m = 0.9$, $R^2_c = 0.85$, Figure 2b) than forest habitats. However, this difference in biodiversity response between habitat types was stronger for specialists than for generalists. We found that specialist species richness was on average 11 times

higher in forests (14.75 ± 4 ; mean \pm SD) compared to pastures (1.33 ± 1 ; Figure 2a left). Generalist species richness was 1.5 times higher in forests (10.83 ± 4 ; mean \pm SD) compared to pastures (7.17 ± 2 ; Figure 2a right). In contrast, even though generalists generally had higher and much more variable species richness compared to specialists in pastures, both specialists and generalists were less abundant in pastures than forests (Figure 2b). Specialist individuals were only occasionally recorded in pastures and in very low abundances (3.25 ± 5 ; Figure S3b). Generalists' abundance in pastures (28.92 ± 24 individuals; Figure 2b) were also lower than forests (131.58 ± 88), though this difference was less marked than for specialists, with generalist's abundance being on average 4.6 times higher in forests (Figure 2b).

Overall, the β -diversity (β_{SOR}) of forest and pasture communities exhibited a remarkably low degree of overlap in community composition between the two habitat types, with differences in community composition strongly influenced by species' habitat association (Figure 3). We found that the composition of specialist communities was less similar between habitat types than generalist communities (specialists: 0.84 ± 0.1 , $0.67 - 1$; generalists: 0.71 ± 0.2 , $0.44 - 1$; mean \pm SD; range, Figure 3, Table S5c-e).

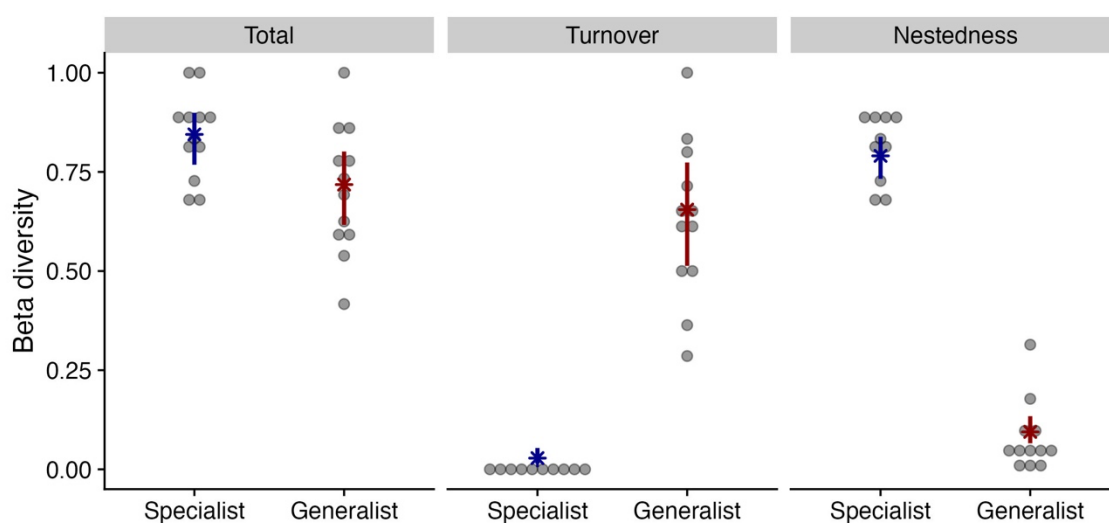


Figure 3. β -diversities of dung beetle communities collected in native and anthropogenic habitats in the 12 focal landscapes. Plots are separated by β -diversity components, including total β -diversity (β_{SOR}), and its two partitions: turnover (β_{SIM}) and nestedness (β_{SNE}). β -diversity values approaching 1 indicate maximum difference in community composition between habitats, and values approaching 0, maximum similarity. Species' habitat associations are represented on the x-axes. Grey dots are observed data, and asterisks and bars represent predicted values of each response variables and confidence intervals for the selected model, respectively.

Decomposing total β -diversity (β_{SOR}) into its components, we found that species' habitat association played an even stronger role in the differences in both turnover and nestedness of communities between habitats (Figure 3, Table S5c-e). For generalist communities, turnover (β_{SIM}) across habitats was both high and variable, while nestedness (β_{SNE}) was relatively low. In contrast, specialist communities were only associated with high nestedness, due to a absence of turnover (Figure 3). Given the extremely low representation of specialist species in pasture habitats and absence of any specialist taxa in two landscapes (see Table S4), the values for specialist turnover were all either zero or NA, for those landscapes without specialist representation.

Does landscape structure further influence these trait-dependent differences in response? (Question 2)

Across the gradient of landscape-level native forest cover, we found dung beetle total richness and abundance to consistently respond to landscape structure (Table 2a-b), while β -diversity instead primarily responded to species' habitat association (Table 2c-e). Species richness declined as the forest-pasture cover ratio increased at both 3km and 5km spatial scales (Table S6; Figure 4a), indicating that landscapes with higher forest cover, and consequently reduced pasture, tended to harbor less rich communities. This general pattern occurred for both specialist and generalist species, and within both habitat types (Table S6). The total abundance of both specialists and generalists in both forest and pasture habitats also declined with greater forest cover (Figures 4b and S3b; Table S6). Albeit significant diversity response of specialists in pasture habitat (Table S6), it is important to note the limitations in drawing conclusive findings for that subset of the data, given the above-mentioned limitations of low occurrence and variable abundance (Figure 2, left).

Table 1. Model selection table with selected models ($\Delta AICc < 2$) for (a) total richness, (b) total abundance, and compositional β -diversities, including: (c) total β -diversity, (d) turnover, and nestedness, as a function of landscape structure variables (in bold): landscape cover (forest-pasture ratio; FP) and configuration (edge density; ED, and landscape shape index; LSI), as well as species' habitat association (SHA), and habitat type (HT). See Table S6 for details of the top model ($\Delta AICc = 0$) coefficients for total richness and abundance.

MODELS	AICc	$\Delta AICc$	df	R2_m	R2_c
<i>a) Total richness</i>					
~ FP ratio (5km) + SHA + HT + SHA:HT	223	0	6	0.89	0.89
~ FP ratio (3km) + FP ratio (3km):HT + SHA + HT + SHA:HT	224	1.1	6	0.89	0.89
~ FP ratio (5km) + FP ratio (5km):HT + SHA + HT + SHA:HT	225	1.3	7	0.88	0.89
~ FP ratio (3km) + FP ratio (3km):HT + SHA + HT + SHA:HT	225	1.7	7	0.88	0.88
<i>b) Total abundance</i>					
~ FP ratio (5km) + SHA + HT + SHA:HT	449	0	7	0.89	0.91
~ FP ratio (3km) + SHA + HT + SHA:HT	460	0.6	7	0.89	0.91
~ FP ratio (3km) + FP ratio (5km):HT + SHA + HT + SHA:HT	450	0.9	8	0.89	0.91
~ FP ratio (3km) + FP ratio (3km):HT + SHA + HT + SHA:HT	450	1.2	8	0.89	0.91
<i>c) Total β diversity (β_{sor})</i>					
~ SHA	-29.5	0	4	0.25	0.25
~ EDG (3km) + SHA	-29	0.5	5	0.45	0.45
~ EDG (5km) + SHA	-27.9	1.6	5	0.38	0.38
<i>d) Turnover (β_{sim})</i>					
~ SHA	-52	0	4	0.81	0.81
~ EDG (3km) + SHA	-50.5	1.4	5	0.84	0.84
~ EDG (5km) + SHA	-50	2	5	0.83	0.83
<i>e) Nestedness (β_{sne})</i>					
~ SHA	-47	0	4	0.99	0.99

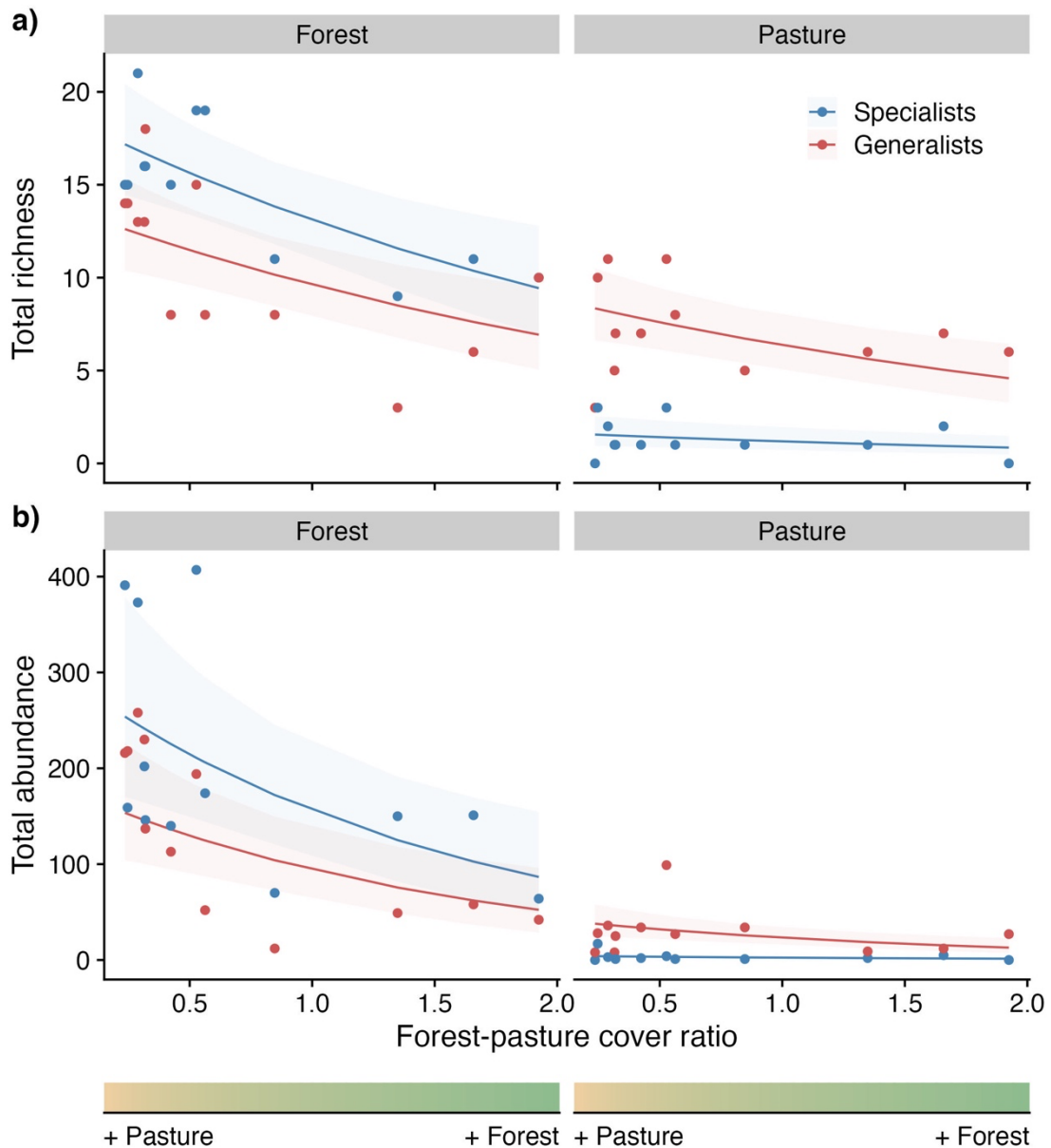


Figure 4. Model predictions and observed data for (a) total richness and (b) total abundance of dung beetles in native (forest) and anthropogenic (pasture) habitats in each of the 12 focal landscapes, separated by species' habitat associations. Generalists are represented in red, and specialists in blue. For each metric, lines represent the top model ($\Delta\text{AICc}=0$) in the candidate model set from Table 2, and shaded areas represent 95 % confidence intervals.

In contrast to species richness and total abundance, β -diversity (β_{SOR}) did not respond to landscape-level habitat cover, and instead was primarily influenced by species' habitat association (Table 2c) and also by edge density. The β_{SOR} of both specialists and generalists declined with increasing edge density at both spatial scales (Figure 5a), suggesting that as the density of pasture-forest edges increased, dung beetle communities in those two habitats become more similar overall (Table S6). However, decomposing β_{SOR} into its components

revealed important differences in the responses reveal by both components and between specialists and generalists. First, we found that the turnover component of β -diversity (β_{SIM}) declined with increasing edge for generalists, but not specialists (Table 2d-e; in red, Figure 5b). Because this result could have emerged from the frequency of zeros in the turnover metric for specialist communities, we ran the same set of models for the subset of generalist species only, with qualitatively similar results (Table S7 and Figure S4, solid vs dashed line). Second, we found that the nestedness component of β -diversity (β_{SNE}) responded to species' habitat association alone, with no model including landscape structure predictors emerging in the top selected model set ($\Delta AICc < 2$) set. Taken together, these results suggest that different drivers may influence the processes that result in species turnover and exchange between biological communities, and those resulting in species loss from biological communities.

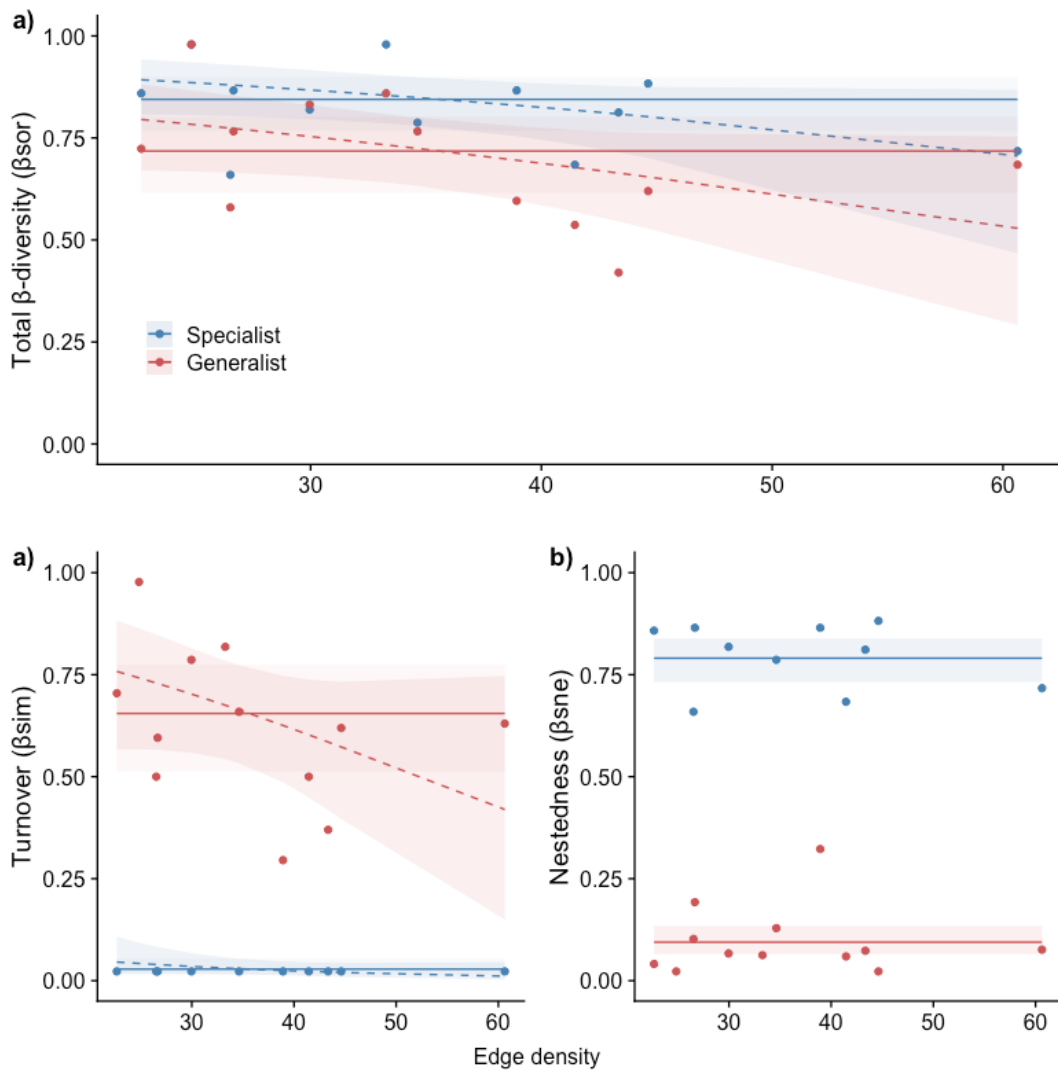


Figure 5. Model predictions and observed data for three measures of β -diversity as a function of edge density: (a) total β -diversity, (b) turnover and (c) nestedness. Solid lines represent the top selected model ($\Delta AICc = 0$) from Table 3; and dashed lines represent the equally plausible 2nd-best model ($\Delta AICc < 2$) in the candidate model set. Generalists are represented in red, and specialists in blue.

Shaded areas around model prediction lines represent 95 % confidence intervals. All observed values for turnover (β_{SIM}) of specialists were zero. See methods for details on how these zeros were handled.

Discussion

We found that both landscape structure and species' habitat associations play key roles in influencing differences in the structure and composition of biotic communities within and between adjacent native and anthropogenic habitats. First, the abundance and richness of communities was strongly influenced by habitat type and species' habitat association, as well as landscape structure. Second, we also observed that differences in community composition (β -diversity) between adjacent native and anthropogenic habitats were influenced by species' habitat association, as well as by landscape structure, with communities of habitat generalists (but not specialists) found in native and matrix habitats becoming more similar as landscape-level edge density increased. Finally, we found that these differences were driven by marked contrasts in the response of the turnover and nestedness components of β -diversity between specialists and generalists, with generalists being mainly driven by turnover and specialists' communities being only associated with nestedness. Beyond adding to the body of evidence demonstrating that landscape change impacts biodiversity differently depending on their degree of habitat specialization (Barreto et al., 2023; Devictor et al., 2008; Tscharrntke et al., 2005), our findings illustrate how the combined effects of environmental change at broader spatial scales and the biological traits of the organisms being examined modulate patterns of community composition and help clarify the underlying mechanisms driving homogenization or differentiation in light of the ecological context (Rolls et al., 2023).

Consistent with previous studies, the replacement of native forest by cattle pastures strongly reduced the total species richness and abundance of dung beetle communities (Nichols et al. 2013; Carrara et al. 2015; Fuzessy et al. 2021). While previous studies have explored the responses of either taxonomic or functional diversity of dung beetles to forest conversion to pasture, few have explored the differences in response across species' habitat association groups or other trait-based classifications (Audino et al. 2014; Carvalho et al. 2022; Arellano et al. 2023). We observed that even within these depauperate pasture communities, species' habitat association strongly modulated response, with higher richness and abundance of habitat generalists relative to specialists in pasture habitats. The strongly different biotic and abiotic conditions resulting from the loss of tree cover, soil changes including compaction, parasiticide use (Carvalho et al. 2020) and significant simplification of the faunal communities providing fecal resources likely influence the environmental filters

(Kraft et al. 2014) which affect the abundance, richness, and composition of pasture-dwelling dung beetle communities by preventing species with certain ranges of physiological or ecological requirements from establishing or persisting (Reider et al. 2018; de Souza Leite et al. 2022). These ecological filters generally select for, or filter, a subset of species sharing response traits from the local or regional pool (deCastro-Arrazola et al., 2023). While the species' habitat association classifications used here serve as only a proxy for a diverse set of dung beetle response traits, our findings suggest that the broader trait-environment-response frameworks can offer valuable insights into the assembly of even extremely depauperate communities.

We found that the species richness and abundance of dung beetle communities in anthropogenic pastures was influenced by the composition, but not configuration, of the surrounding landscape. We found even fewer species and individuals of both groups in landscapes with higher forest cover in relation to pasture (FP_{ratio}) and at both habitat types (Table S6). These effects were strongest for specialists in forests, and for generalists in pasture. This exploration of the response of matrix fauna to landscape structure complements the results reported here for forest, and which are additionally evaluated in Barreto et al. 2023, wherein the loss of native tropical forest led to a consistent increase in both dung beetle abundance and diversity, at all scales, for both forest specialists and habitat generalists. Our findings highlight the complex relationships between environmental change and biodiversity (Daskalova et al., 2020; Hillebrand et al., 2018; Magurran et al., 2018), and that habitat change can lead to a variety of biodiversity responses (Antão et al., 2020; Arroyo-Rodríguez et al., 2013; Elahi et al., 2015; Sax & Gaines, 2003; van Schalkwyk et al., 2020) in different biogeographic and the historical contexts (Barreto et al., 2023; Daskalova et al., 2020; Nichols et al., 2013).

We also found that the degree to which dung beetle communities in forest and adjacent pasture habitats were similar in composition was strongly dependent on species' habitat association. Overall, generalist communities demonstrated higher shared community composition across habitats than did specialist communities. When exploring the components of β -diversity, we found that these differences in specialist communities were primarily driven by nestedness, while generalist β -diversity was mainly due to turnover. These patterns suggest that very different processes may be at play in structuring the response of specialists and generalists to habitat change. Nestedness occurs when species loss causes species-poor sites to resemble a strict subset of species-rich sites (Baselga, 2010; Ulrich W. & Gotelli,

2007). That specialist communities in cattle pasture resembled a strict subset of communities in adjacent forest fragments reinforces the idea that non-random processes, such as ecological filtering, may a strong role in the assembly of communities (Britton et al. 2017) composed of species with narrower niches (Carscadden et al., 2020) or lower tolerances to environmental condition (Qian, 2009) following conversion of forests into pasture. Turnover occurs when species are replaced across communities through by the addition of new species pulled from the regional species pool. The low turnover seen for specialist communities may reflect the extreme paucity of specialist species in pasture habitats, limiting the capacity for species replacement to play a significant role in driving differences in specialist community composition between habitats. That generalist communities in cattle pasture demonstrated higher values for turnover is likely linked to the better representation of generalists in both habitat types and suggests an important role for the regional availability of these disturbance-resilient taxa. The biotic response to habitat loss is contingent to traits, such as the ability to move (e.g. Newbold et al. 2013, 2014; de Souza Leite et al. 2022), and the ecological and biogeographical context (Nichols et al., 2013), such regional context can influence the regional availability of disturbance-adapted taxa (Barreto et al., 2023). Taken together, these results suggest that even within the same ecological and disturbance context, the impacts of processes that drive species turnover and exchange between biological communities, and those resulting in species loss from biological communities may be largely trait-dependent.

The turnover associated with generalist communities was also negatively influenced by density of forest-pasture edges, suggesting that generalist communities in forest fragments and their adjacent cattle pastures were more alike in those landscapes with a higher density of edges between these two habitat types. While previous research has hinted at the influence of ecological traits, such as dispersal abilities, on turnover and nestedness patterns (Soininen et al., 2018), to our knowledge, none explore turnover and nestedness as a function of species' habitat associations (but see Leboucher et al., 2019). While the body of empirical evidence evaluating β -diversity components as a function landscape structure is also limited (Legendre, 2014; Rolls et al., 2023), our results align with the idea that landscape-level edge density may play a key role in biotic homogenization processes, as edges facilitate the exchange of generalist species between even these extremely distinct habitats.

Our findings contribute to the limited empirical basis for understanding the drivers of biotic homogenization (Rolls et al., 2023), which requires superseding the inherent challenges in designing field studies, such as sampling in more than one habitat type, and adequate

landscape-level replication. From the same study sites across forest-dwelling dung beetle communities, Barreto et al. (2023) demonstrated a relationship between the level of biotic differentiation and landscape-level native habitat loss. The same study revealed that specialists and generalists in forest fragments also demonstrated distinct responses to forest loss, with specialist communities demonstrating increased structural dissimilarity with declining forest cover, while the abundance distribution of generalist communities remained consistent (Barreto et al. 2023). Those results do not conflict with those from the present study, given the non-linear relationship between landscape-level edge density and habitat cover (Fahrig, 2003), which peaks at intermediate levels of landscape-level habitat loss and declines under both high and low levels of habitat cover. Besides, the present study focused on examining similarities in composition between communities in forest and adjacent pasture habitats. Using a subset of these same sampling sites and with an avian model system, Boesing *et al.* (2017) also explored questions related to community composition across pasture and forest habitats, and demonstrated that habitat generalists constituted most of the species actively crossing forest-pasture edges. While we did not directly sample spillover (i.e. cross-habitat movement), our results are similarly commensurate with a higher rate of exchange of generalist species across forest-pasture edges, as well as persistence in both habitats. Previous studies of the influence of edge on β -diversity suggest a complex relationship (Filgueiras et al., 2016; Krishnadas et al., 2019; Stone et al., 2018). Edge effects could reduce β -diversity due to environmental constraints or by promoting the dominance of some species or increase β -diversity, attributed to varying abiotic conditions (Krishnadas et al., 2019), or even remain irresponsive in case there is an unclear interplay of both scenarios.

We note that we would not have observed the differential influences of landscape structure and species' habitat association on various aspects biodiversity response to forest loss without the combination of methodological approaches used here, including a landscape-scale study design, sampling in multiple habitats, consideration of multiple biodiversity metrics and information on species' habitat associations. We acknowledge limitations of habitat association classification, particularly when exacerbated by limited occurrence data for diverse tropical taxa (*see* Lima 2013, expanded upon by Vale et al. 2018), and encourage future efforts to apply species trait-frameworks to explorations of the context-dependency of biodiversity response.

While effective conservation planning requires a clear understanding of biodiversity response to anthropogenic drivers of biodiversity decline including land-use change,

interpreting the conservation implications of positive biodiversity responses to anthropogenic change (Sax and Gaines 2003; Arroyo-Rodríguez et al. 2013; van Schalkwyk et al. 2020; Davey et al., 2013; Funderup Nielsen et al., 2019; Barreto et al. 2023) is less straightforward. For example, the findings presented here suggests that increased edges between forest and pasture may contribute to biotic homogenization by fostering exchange of generalist taxa between forests and pastures. Reducing this contributor to biotic homogenization may therefore involve management actions to reduce landscape-level edge, which can be achieved at both high and at low levels of native habitat cover (Fahrig 2003). We also detected higher species diversity of both generalist and specialist taxa at lower levels of native forest cover, suggesting that large patches should be preserved alongside the smaller ones, where different processes and effect of landscape structure play out in different ways. This could arguably imply that reducing edge through reducing native forest coverage could be the optimal solution, which clearly cannot be universally applied across all taxa, even from the same study sites (e.g. Boesing et al. 2018, de Souza Leite et al. 2022). Ultimately, our findings underscore the understanding that biodiversity responses to native habitat loss may be complex and context-dependent and challenge efforts to delineate general or universal ‘silver-bullet’ conservation strategies (Wells et al., 2020). We furthermore challenge many of the international frameworks on which conservation efforts have mostly been predicated on, e.g. national plans, area-based conservation, or the '30x30' goal (EOP 2021; WWF, 2020).

Conclusions

Our study explored a nuanced interplay of factors that shape biotic communities within and between native and anthropogenic habitats. Landscape structure and species' habitat associations emerged as crucial drivers of community composition, with generalists and specialists responding markedly differently to these influences. Forest conversion to low-quality anthropogenic habitat significantly impacted community composition and structure, particularly for specialists. While landscape composition affected community diversity it did not influence compositional similarity between habitats. Instead, we found that a key proxy for landscape configuration – edge density – did drive compositional changes, with stronger effects on generalists. These results suggest that future attention should be paid to the role of edge density on driving species exchange between habitats, and potentially contributing to biotic homogenization. Overall, our study contributes valuable insights to the understanding of community assembly processes and their implications for conservation in landscapes undergoing environmental change.

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Supplementary Material

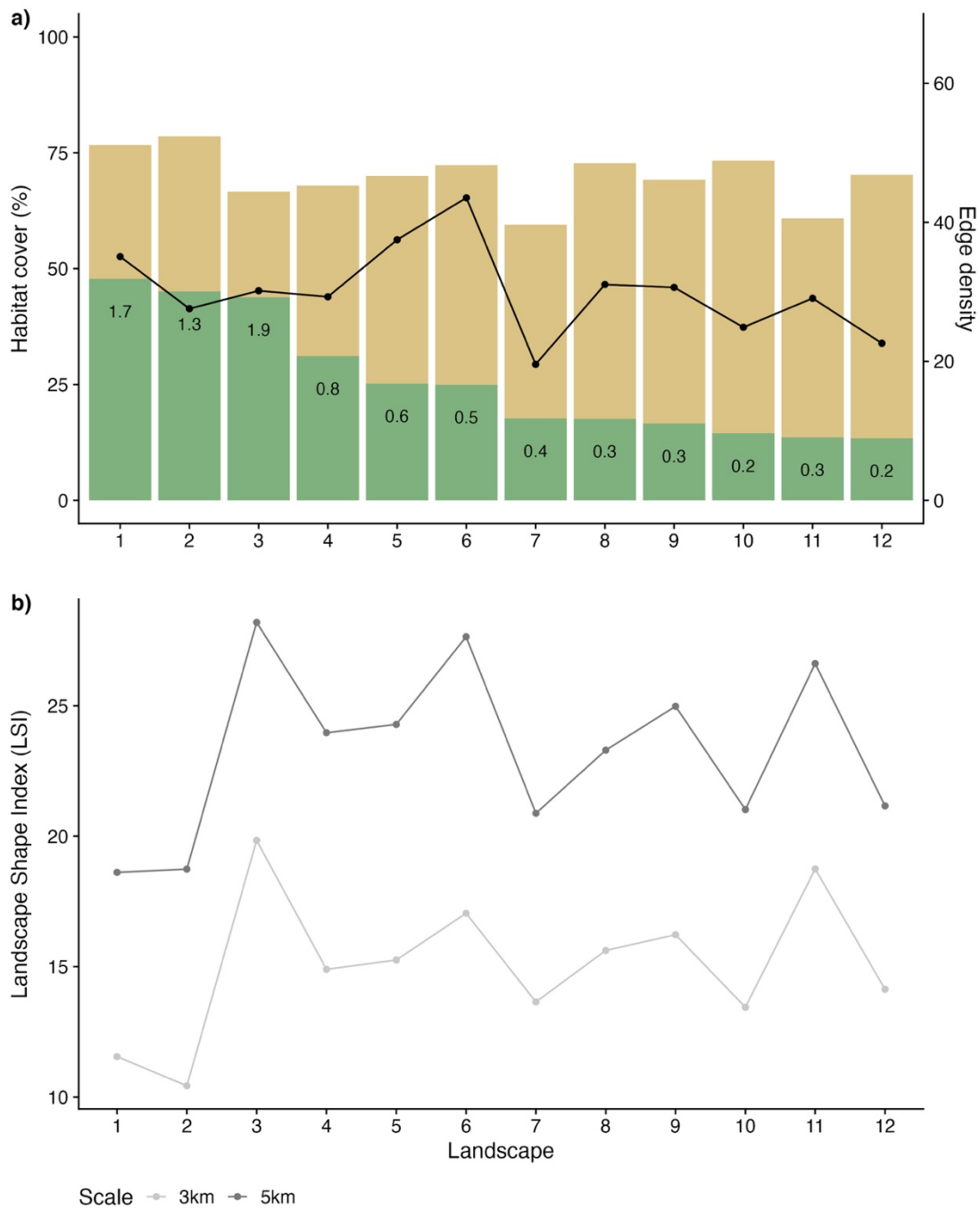


Figure S1. Landscape structure metrics in each focal landscape, including (a) the observed percent cover of native forest (green) and anthropogenic pasture cover (yellow), calculated ratio of forest-pasture cover (black text) and edge density (black line) measured at a 5 km radius, and (b) the landscape shape index (LSI) measured at both 3 km (light grey) and 5 km (dark grey) radius.

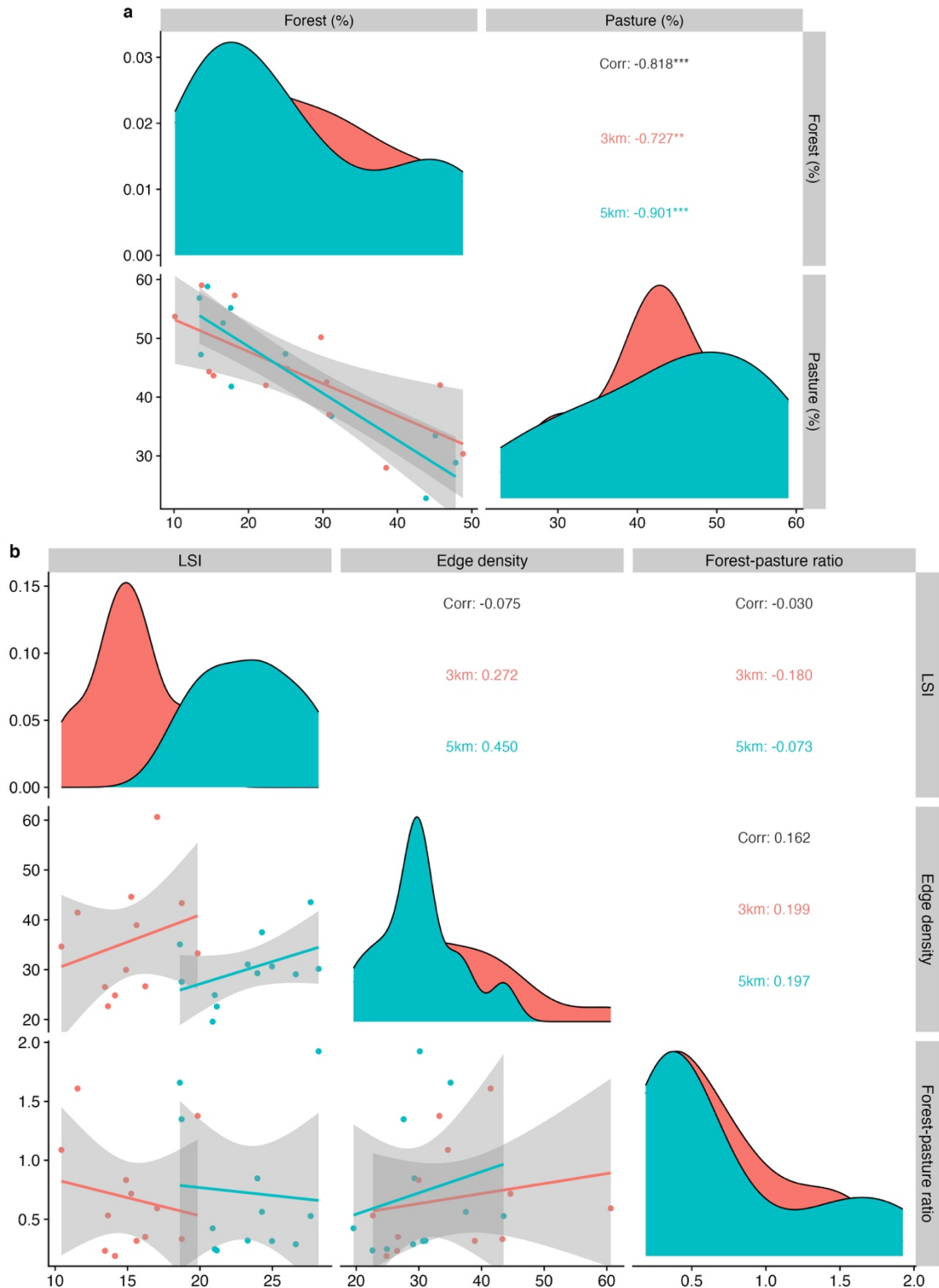


Figure S2. Correlation among landscape structure metrics, including (a) percent native forest and anthropogenic pasture cover, (b) forest-pasture cover ratio, edge density and the Landscape Shape Index (LSI). All predictors presented in two spatial scales (3k; red and 5km; blue). See Table S1 for expanded description of landscape configuration metrics.

Table S1. Landscape configuration metrics of forest and pasture edge density, including acronyms, formulas and descriptions. See Figure 2 for correlations between metrics.

Metric (acronym)	Formula	Description
Edge Density	EDG= E/A (10000) Where E is the total edge length (m) in the landscape and A is the total landscape area (m ²).	ED equals the sum of the lengths (m) of all forest-pasture edge segments in the landscape, divided by the total landscape area (m ²), multiplied by 10,000 (to convert to hectares)
Landscape shape index (LSI)	LSI = E/min E Where E is the total edge length (m) in cell surfaces and min E is the minimum total edge length in cell surfaces.	LSI equals the total length of edge in the landscape (given in number of cell surfaces) divided by the minimum total length of edge possible (also given in number of cell surfaces) achieved when the landscape consists of a single patch.

Table S2. Candidate model set used to explore the influence of landscape structure at both 3 and 5km scales on (a) total richness and abundance, and (b) β -diversities, including total β -diversity, turnover and nestedness (Question 2). For each model, fixed effects selected from Question 1 results were retained including species' habitat association:habitat type for models of (a) species richness and abundance and (b) species' habitat association for model of β -diversities. For all models, landscape was included as a random effect. Acronyms include: species' habitat association (SHA), habitat type (HT), forest-pasture cover ratio (FP ratio) and edge density (EDG).

a) Models for total richness and abundance

- ~ 1 + (1|Landscape)
- ~ SHA:HT + SHA + HT + (1|Landscape)
- ~ FP ratio + SHA:HT + SHA + HT + (1|Landscape)
- ~ EDG + SHA:HT + SHA + HT + (1|Landscape)
- ~ LSI + SHA:HT + SHA + HT + (1|Landscape)
- ~ FP ratio:SHA + FP ratio + SHA:HT + SHA + HT + (1|Landscape)
- ~ EDG:SHA + EDG + SHA:HT + SHA + HT + (1|Landscape)
- ~ LSI:SHA + LSI + SHA:HT + SHA + HT + (1|Landscape)
- ~ FP ratio:HT + FP ratio + SHA:HT + SHA + HT + (1|Landscape)
- ~ EDG:HT + EDG + SHA:HT + SHA + HT + (1|Landscape)
- ~ LSI:HT + LSI + SHA:HT + SHA + HT + (1|Landscape)
- ~ FP ratio:SHA + FP ratio:HT + FP ratio + SHA:HT + SHA + HT + (1|Landscape)
- ~ EDG:SHA + EDG:HT + EDG + SHA:HT + SHA + HT + (1|Landscape)
- ~ LSI:SHA + LSI:HT + LSI + SHA:HT + SHA + HT + (1|Landscape)

b) Models for β -diversities

- ~ 1 + (1|Landscape)
 ~ SHA + (1|Landscape)
 ~ FP ratio + SHA + (1|Landscape)
 ~ EDG + SHA + (1|Landscape)
 ~ LSI + SHA + (1|Landscape)
 ~ FP ratio:SHA + FP ratio + SHA + (1|Landscape)
 ~ EDG:SHA + EDG + SHA + (1|Landscape)
 ~ LSI:SHA + LSI + SHA + (1|Landscape)
 ~ FP ratio + EDG + SHA + (1|Landscape)
 ~ FP ratio + LSI + SHA + (1|Landscape)
 ~ FP ratio:SHA + FP ratio + EDG:SHA + EDG + SHA + (1|Landscape)
 ~ FP ratio:SHA + FP ratio + LSI:SHA + LSI + SHA + (1|Landscape)
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Table S3. Observed total species richness and abundance of dung beetles classified as forest specialists (S) or habitat generalists (G) collected exclusively in native forest, in anthropogenic pasture habitats, or collected in both habitat types.

Habitat	Richness		Totals	Abundance		Totals
	S	G		S	G	
Exclusively collected in forests	18	8	26	1007	149	1,156
Exclusively collected in pastures	0	4	4	0	38	38
Collected in both habitat types	8	20	28	1,459	1,739	3,198
Totals	26	32	58	2,466	1,926	4,392

Table S4. Landscape-level total species richness and abundance of specialists and generalists dung beetle communities captured in forest and pasture habitats (n=8 each). Native forest cover percent for each landscape is shown in parenthesis.

Landscape ID	Richness				Abundance			
	Forest		Pasture		Forest		Pasture	
	S	G	S	G	S	G	S	G
1 (48.8%)	11	6	2	7	151	58	5	12
2 (45.8%)	9	3	1	6	150	49	2	9
3 (38.5%)	10	10	0	6	64	42	0	27
4 (30.8%)	11	8	1	5	70	12	1	34
5 (30.5%)	19	8	1	8	174	52	1	27
6 (29.7%)	19	15	3	11	407	194	4	99
7 (22.3%)	15	8	1	7	140	113	2	34
8 (18.1%)	16	18	1	7	146	137	1	25
9 (15.3%)	16	13	1	5	202	230	3	8
10 (14.7%)	21	13	2	11	373	258	3	36

11 (13.7%)	15	14	3	10	159	218	17	28
12 (10.1%)	15	14	0	3	391	216	0	8

Table S5. Model selection table for (a) total richness, (b) total abundance modeled as a function of species' habitat association and habitat type. and (c) β -diversities, including (d) total (β_{SOR}), (e) turnover (β_{SIM}) and (f) nestedness (β_{SNE}) modeled as a function of species' habitat association. AICc top models ($\Delta AICc = 0$) in bold, columns show the Akaike Information Criteria corrected for small sample sizes (AICc), $\Delta AICc$, degrees of freedom (df) and marginal (R^2m) and conditional (R^2c) R^2 . Abbreviations as follows: "SHA"(species' habitat association), and "HT" (habitat type).

Models	AICc	$\Delta AICc$	df	R^2m	R^2c
a) Total richness					
~ SHA : HT + SHA + HT	229.3	0	5	0.85	0.9
~ HT	284.4	55.1	3	0.67	0.8
~ SHA + HT	285.5	56.2	4	0.67	0.8
~ 1	389.7	160.4	2	-	-
~ SHA	390.7	161.4	3	0.02	0.3
b) Total abundance					
~ SHA : HT + SHA + HT	453.7	0	6	0.85	0.9
~ SHA + HT	482.1	28.4	5	0.76	0.8
~ HT	485.3	31.6	4	0.67	0.7
~ 1	522	68.3	3	-	-
~ SHA	524	70.3	4	0.01	0
c) Total beta diversity (β_{sor})					
~ SHA	-29.5	0	4	0.26	-
~ 1	-22.9	6.6	3	-	-
d) Turnover (β_{sim})					
~ SHA	-52	0	4	0.81	1
~ 1	-6.4	45.5	3	-	-
e) Nestedness (β_{sne})					
~ SHA	-47	0	4	0.99	-
~ 1	2.5	49.5	3	-	-

Table S6. Coefficients for the top models ($\Delta\text{AICc}=0$) selected for total richness, total abundance and β -diversities, including total (β_{SOR}), turnover (β_{SIM}) and nestedness (β_{SNE}) (see Table 2). Abbreviations as follow: “Est.” (Estimate), “SE” (Standard Error), “t” (Statistic), “P” (P-value), and “95%CI” (Lower and Upper Confidence Interval).

Diversity	Term	Est.	SE	t	P	95% CI
Total Richness	(Intercept)	2.67	0.079	34.004	0	(2.516, 2.824)
	Forest-pasture ratio	-0.203	0.06	-3.411	0.001	(-0.32, -0.087)
	Generalist	-0.309	0.115	-2.672	0.008	(-0.535, -0.082)
	Pasture	-2.404	0.261	-9.208	0	(-2.915, -1.892)
	Generalist:Pasture	1.99	0.296	6.731	0	(1.411, 2.57)
	RE Landscape sd_(Intercept)	0.067				
Total Abundance	(Intercept)	5.226	0.179	29.131	0	(4.874, 5.577)
	Forest-pasture ratio	-0.365	0.112	-3.246	0.001	(-0.585, -0.145)
	Generalist	-0.503	0.238	-2.118	0.034	(-0.969, -0.038)
	Pasture	-4.159	0.292	-14.245	0	(-4.731, -3.587)
	Generalist:Pasture	2.759	0.384	7.188	0	(2.007, 3.512)
	RE Landscape sd_(Intercept)	0.215				
Total β -diversity (β_{SOR})	(Intercept)	1.694	0.232	7.301	0	(1.239, 2.148)
	Edge density	-0.347	0.2	-1.734	0.083	(-0.74, 0.045)
	Generalist	-0.761	0.192	-3.953	0	(-1.138, -0.383)
	RE Landscape sd_(Intercept)	0.595				
Turnover (β_{SIM})	(Intercept)	-3.538	0.322	-10.99	0	(-4.169, -2.907)
	Edge density	-0.41	0.282	-1.451	0.147	(-0.964, 0.144)
	Generalist	4.179	0.182	22.987	0	(3.822, 4.535)
	RE Landscape sd_(Intercept)	0.939				
Nestedness (β_{SNE})	(Intercept)	1.327	0.163	8.135	0	(1.008, 1.647)
	Generalist	-3.588	0.265	-13.527	0	(-4.108, -3.068)
	RE Landscape sd_(Intercept)	0				0

Generalists' community change

Similar to total β -diversity, the turnover component of β -diversity (β_{sim}) responded in the same way, to species' habitat association as well as to edge density at both spatial scales (Table 3b). The relationship between β_{sim} and edge density was negative for habitat generalists communities (in red, Figure 5b) and non-existent for specialists, as overall beta diversity for specialists was driven entirely by nestedness, and not turnover. Given that this turnover component of β -diversity was zero for specialists species across all landscapes, we performed an additional analysis of turnover for the subset of generalists species only (Table S7). These results were qualitatively similar (Figure S4, solid and dashed line), meaning our initial approach is robust, despite the values of zero for specialist turnover.

Table S7. Model selection table containing the first five models for turnover subset for generalists communities only. Equally plausible models ($\Delta\text{AICc} < 2$) in bold.

Generalists' turnover models	AICc	ΔAICc	df	pseudoR2
~ 1	-0.5	0	2	-
~ Edge density (3km)	0.6	1.1	3	0.17
~ Edge density (5km)	1.3	1.8	3	0.13
~ LSI (5km)	3.1	3.6	3	0.01
~ Forest-pasture ratio (5km)	3.1	3.6	3	0.01

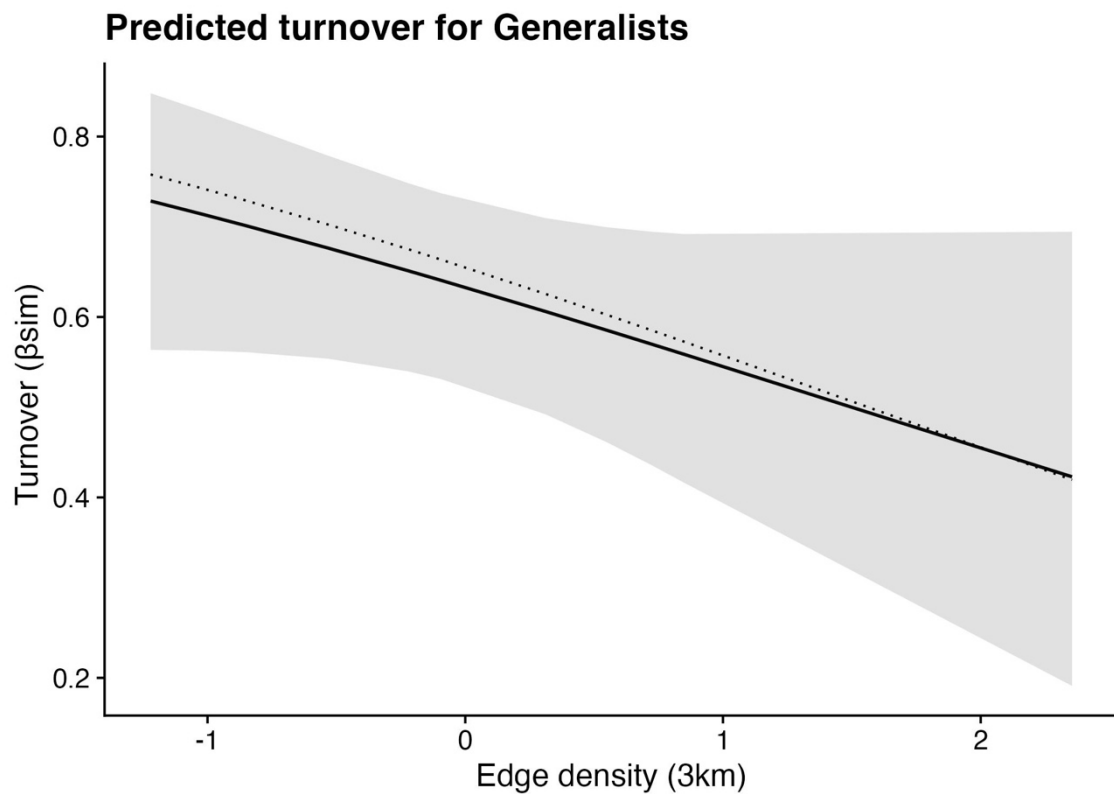


Figure S3. Model predictions for the turnover (β_{sim}) component of beta diversity for habitat generalists as a function of edge density at the 3km scale. Lines represent the 2nd top model: edge density comparing subset data for generalists (solid) and original selected model including turnover of specialists (dashed).

CONSIDERAÇÕES FINAIS

O objetivo principal da minha tese foi analisar como a biodiversidade responde a mudanças antropogênicas. Para isso, olhei diversidade em suas várias dimensões de resposta, utilizando besouros Scarabaeinae como sistema de estudo em um desenho de amostragem robusto a nível de paisagem na Mata Atlântica brasileira com habitats nativo e antropogênicos pareados. Esta pesquisa contribuiu com interpretações das respostas complexas da biodiversidade, positivas inclusive, moduladas pela associação de habitat das espécies, da estrutura da paisagem e contexto biogeográfico.

Na tese, foquei nas seguintes questões específicas:

- 1) Se a resposta da biodiversidade à perda de habitat nativo é necessariamente negativa (Capítulo 1);
- 2) Como as associações de habitat das espécies modulam essa resposta (Capítulo 1);
- 3) Se as diferenças nas comunidades bióticas entre habitats nativo e antropogênico são moduladas pelas associações de habitat das espécies (Capítulo 2);
- 4) Se a estrutura da paisagem adiciona explicação a essas diferenças (Capítulo 2).

Juntos, os dois capítulos se debruçam em resultados robustos das respostas bióticas a perda e alteração no habitat. Respostas que são complexas, sutis e dependentes do contexto. Nossos achados agregam desafios e esforços para delinear estratégias de conservação, sugerindo complementação e cautela com as diretrizes simplistas ou gerais, como muitos dos instrumentos internacionais de conservação se fundamentam hoje (e.g. planos nacionais, conservação baseada em área, ou a meta '30x30').

No capítulo 1, examinei mudanças na diversidade de besouros Scarabaeinae que habitam a floresta ao longo de gradiente de perda de floresta nativo da Mata Atlântica. Relatei que o desmatamento estava associado a maior diversidade local e de paisagem, tanto de comunidades especializadas em florestas nativas quanto das generalistas de habitat. Encontramos também um sinal de composição de comunidade cada vez mais dissimilar. Contudo, a resposta de abundância à perda de floresta variou entre os grupos, onde apenas generalistas aumentaram em número de indivíduos, e com distribuição aleatória entre as

espécies nas comunidades; enquanto os especialistas não variaram em abundância geral, contudo a distribuição da abundância entre as espécies ficou mais dissimilar. Essas descobertas sugerem que a perda de habitat nativo nem sempre leva a uma diminuição no número de espécies especialistas, que compensam o ganho de espécies generalistas. Tal resultado agrega evidências de que a perda de habitat pode impulsionar o ganho de biodiversidade e diferenciação biótica, sobretudo em contextos biogeográficos específicos, onde dinâmicas regionais contemporâneas e/ou históricas podem ter influenciado a resiliência da biota florestal e contribuído para a disponibilidade de espécies adaptadas a perturbações.

Em habitats modificados pelo ser humano, a maioria dos remanescentes de habitat nativo está inserida em matrizes de uso da terra antropogênicas, por isso é necessário entender a biodiversidade também do habitat antropogênico introduzido, além do habitat nativo sendo perdido, e de como tais habitat interagem. Em um segundo capítulo, meu objetivo foi explorar como as mudanças na composição e estrutura das comunidades bióticas dentro de um determinado tipo de habitat (e.g. floresta nativa) podem estar relacionadas com aquelas nos tipos de habitat adjacentes (e.g. habitats antropogênicos). Encontrei uma interação complexa de fatores que moldam as comunidades bióticas dentro e entre habitats nativos e antropogênicos. As associações de habitat das espécies e também a estrutura da paisagem e desempenham papel na composição da comunidade, com generalistas e especialistas respondendo de maneira marcadamente diferente a essas influências. A conversão de florestas para habitats antropogênicos de baixa qualidade impactou significativamente a composição e a estrutura da comunidade, especialmente para os especialistas. Embora a composição da paisagem tenha afetado a diversidade, ela não influenciou a similaridade de composição das comunidades entre os habitats. Em vez disso, encontrei sinais da densidade de borda como um indicador-chave para a configuração da paisagem, levando as mudanças na similaridade de composição, com efeitos mais fortes em táxons generalistas. Em resumo, os achados enfatizam a importância de considerar tanto as características do ambiente quanto os atributos ecológicos das espécies ao avaliar a biodiversidade e desenvolver estratégias de conservação em paisagens em mudança.