UNIVERSIDADE ESTADUAL PAULISTA
"JÚLIO DE MESQUITA FILHO"

Instituto de Biociências Letras e Ciências Exatas - São José do Rio Preto

VIVIANE BRITO DIAS

EFEITO DA PERDA DE FLORESTA E DOS TIPOS DE MATRIZES SOBRE AS COMUNIDADES DE PEQUENOS MAMÍFEROS EM PAISAGENS ANTROPIZADAS NA MATA ATLÂNTICA

São José do Rio Preto - São Paulo
2025

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Tese apresentada à Universidade Estadual Paulista (UNESP), Instituto de Biociências Letras e Ciências Exatas - São José do Rio Preto, para obtenção do título de Doutora em Biodiversidade.

Orientadora: Prof. Dr. Rita de Cassia Bianchi

Coorientador: Prof. Dr. Milton Cezar Ribeiro

São José do Rio Preto - São Paulo

2025

Brito Dias, Viviane

B862e

Efeito da perda de floresta e dos tipos de matrizes sobre as comunidades de pequenos mamíferos em paisagens antropizadas na Mata Atlântica / Viviane Brito Dias. -- São José do Rio Preto, 2025

128 p.

Tese (doutorado) - Universidade Estadual Paulista (UNESP), Instituto de Biociências Letras e Ciências Exatas, São José do Rio Preto

Orientadora: Rita de Cassia Bianchi

Coorientador: Milton Cezar Ribeiro

1. Rodentia e Didelphimorphia. 2. modelos hierárquicos multiespécie. 3. biodiversidade. 4. agroecossistemas. 5. paisagens dinâmicas. I. Título.

Sistema de geração automática de fichas catalográficas da Unesp. Dados fornecidos pelo autor(a).

IMPACTO POTENCIAL DESTA PESQUISA

Esta pesquisa apresenta elevado potencial científico ao contribuir para o aprofundamento do entendimento sobre os efeitos das alterações antrópicas nas paisagens, decorrentes de atividades agrícolas, sobre a biodiversidade, o que se refletirá na participação em eventos internacionais de prestígio, ampliando a visibilidade da UNESP no cenário global, bem como na publicação de resultados em periódicos internacionais de alto impacto. Do ponto de vista inovador, esta tese incorpora a aplicação e difusão de análises avançadas, ainda incipientes no contexto nacional, como os modelos hierárquicos multiespécies e métricas de variação espaço-temporal da vegetação obtidas a partir de imagens de satélite de alta resolução. Tais abordagens metodológicas têm o potencial de estimular sua adoção em diferentes contextos científicos, fortalecendo a interdisciplinaridade e ampliando as fronteiras da pesquisa em biodiversidade. No âmbito da internacionalização, essa pesquisa fomentou o estabelecimento e a consolidação de colaborações com instituições de excelência, como o CSIC (Espanha) e a Universidade de Oxford (Reino Unido), promovendo intercâmbio científico e ampliando a inserção da pesquisa brasileira no cenário internacional. Adicionalmente, os resultados alcançados possuem relevância direta para o desenvolvimento sustentável, uma vez que podem subsidiar estratégias de manejo capazes de conciliar produção agrícola e conservação da biodiversidade. Dessa forma, espera-se gerar impactos não apenas na esfera acadêmica, mas também em níveis local, regional e nacional, oferecendo subsídios técnicos e científicos para políticas públicas e práticas de uso da terra que equilibrem as necessidades humanas e a preservação da biodiversidade.

POTENTIAL IMPACT OF THIS RESEARCH

This research presents significant scientific potential by contributing to a deeper understanding of the effects of human-induced landscape changes, resulting from agricultural activities, on biodiversity. This will be reflected in participation at prestigious international events, enhancing UNESP’s visibility in the global arena, as well as in the publication of results in high-impact international journals. From an innovative perspective, this thesis incorporates the application and dissemination of

advanced analyses, still incipient in the national context, such as multi-species hierarchical models and spatiotemporal variation metrics of vegetation derived from high-resolution satellite imagery. These methodological approaches have the potential to stimulate their adoption in different scientific contexts, strengthening interdisciplinarity and expanding the frontiers of biodiversity research. In terms of internationalization, this research fostered the establishment and consolidation of collaborations with leading institutions, such as CSIC (Spain) and the University of Oxford (United Kingdom), promoting scientific exchange and broadening the insertion of Brazilian research into the international arena. Additionally, the results obtained have direct relevance for sustainable development, as they can support management strategies capable of reconciling agricultural production with biodiversity conservation. Thus, this research is expected to generate impacts not only in the academic sphere but also at local, regional, and national levels, providing technical and scientific support for public policies and land-use practices that balance human needs with biodiversity preservation.

VIVIANE BRITO DIAS

EFEITO DA PERDA DE FLORESTA E DOS TIPOS DE MATRIZES SOBRE AS COMUNIDADES DE PEQUENOS MAMÍFEROS EM PAISAGENS ANTROPIZADAS NA MATA ATLÂNTICA

Tese apresentada à Universidade Estadual Paulista (UNESP), Instituto de Biociências Letras e Ciências Exatas - São José do Rio Preto, para obtenção do título de Doutora em Biodiversidade.

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Dedico este trabalho à minha mãe Silvana, minha irmã Thaís e seus filhos maravilhosos, Antônio e Cecília, meu irmão José, aos meus avós maternos e à memória sempre viva do meu pai Zenilton.

AGRADECIMENTOS

Este doutorado foi só possível graças à ajuda e presença de muitas na minha vida. Agradeço primeiramente aos meus orientadores, Rita e Miltinho pela oportunidade e confiança que ofereceram de realizar este doutorado. Agradeço especialmente à professora Rita, que confiou em me orientar sem mesmo me conhecer e por todas as orientações, conselhos e suporte que me deu durante o doutorado. Agradeço ao meu companheiro, de vida e trabalho, Felipe, por toda sua ajuda em todos os aspectos do doutorado e de vida, por tudo que me ensinou e pela paciência comigo nos momentos mais difíceis. Agradeço ao Lucas Zordan por toda ajuda no campo, que mesmo diante de todos os problemas e dificuldades que enfrentamos, esteve sempre comigo até o final. Agradeço também imensamente a todos os auxiliares de campo que voluntariamente me ajudaram nas amostragens dos pequenos mamíferos. Sem Lucas e eles esta pesquisa não teria acontecido. Agradeço ao Urucum e aos técnicos da UNESP que me ajudaram e me ensinaram muito em campo, especialmente ao Sérgio Nazareth, que além de toda ajuda braçal e de tudo que me ensinou, aliviava os dias pesados de campo com suas piadas, risadas e sua comida maravilhosa. Sou extremamente grata aos professores Renata Pardini e Alexandre Percequillo, pelo empréstimo das armadilhas e por compartilhar conhecimentos essenciais para que eu realizasse as atividades de campo. À todos os amigos fiz durante meu intercâmbio na Espanha, que mesmo distantes vou levar para sempre comigo. Agradeço especialmente à Guru (Gurutzeta Guillera-Arroita), que aceitou me receber na Espanha, e ao querido Pachi, por tudo que me ensinaram e por nunca duvidarem que eu seria capaz. Sou grata à todos os amigos que me acompanham em todas as jornadas da minha vida, sempre me apoiando, presencialmente ou à distância, e que sempre acreditaram em mim, muitas vezes quando nem eu mesmo acreditava que seria capaz. Agradeço à minha família, que mesmo não entendo o motivo das minhas escolhas de carreira, sempre me apoiam em qualquer uma delas. Agradeço aos pais e avó do Felipe (também minha família) por todo o suporte a apoio que me deram em todas as fases desse doutorado. Sou grata aos membros da minha comissão avaliadora, que prontamente e gentilmente aceitaram fazer parta da minha avaliação. Todos vocês foram essenciais para que esta pesquisa acontecesse. Muito obrigada!

O presente trabalho foi realizado com apoio da Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) - Código de Financiamento 001

“O homem é parte da natureza, e sua guerra contra a natureza é inevitavelmente uma guerra contra si mesmo.”
(Rachel Carson, atribuído).

RESUMO

A redução e a fragmentação de habitat nativo causadas por atividades humanas são as principais ameaças à biodiversidade em hotspots como a Mata Atlântica. Nesse bioma altamente alterado, os remanescentes florestais ocorrem como pequenas manchas imersas em matrizes antrópicas (i.e. áreas de não-habita) diversas. Embora historicamente negligenciadas, as características de diferentes usos do solo influenciam diretamente a persistência das espécies e a integridade das comunidades. Ainda assim, abordagens binárias (habitat/não-habitat) ainda são dominantes enquanto que a heterogeneidade espacial e temporal das paisagens antropizadas é geralmente ignorada em estudos de paisagens fragmentadas. No Brasil, perda e a fragmentação de habitats decorrentes principalmente das atividades agrícolas são reconhecidas como as principais ameaças às espécies de mamíferos na Mata Atlântica. Os pequenos mamíferos não-voadores (< 2kg; ordens Didelphimorphia e Rodentia) formam um grupo funcionalmente relevante nos ecossistemas e sensível a perturbações ambientais. Vários estudos têm demonstrado que a perda e a fragmentação do habitat na escala de paisagem afeta a integridade das comunidades de pequenos mamíferos na Mata Atlântica. No entanto, pouco se sabe sobre os efeitos de diferentes usos de solo e da heterogeneidade espaço-temporal de matrizes sobre a ocorrência e diversidade do grupo na região. A compreensão adequada dos impactos da perda de habitat e da influência da matriz em paisagens fragmentadas requer ainda análises que incluam diferentes componentes da biodiversidade e lidem com o problema da detecção imperfeita das espécies. Para isso, o uso de ferramentas analíticas como os modelos hierárquicos multiespécie (MHM) tem sido apontado como uma abordagem eficaz para realizar estimativas precisas da diversidade de espécies. Esta tese, (1) realizou uma revisão sistemática da literatura para avaliar se estudos realizados na Mata Atlântica brasileira têm considerado a heterogeneidade e composição das matrizes antrópicas em pesquisas com esse grupo. Resultados mostraram que os estudos tem sido focados principalmente em áreas florestas e escalas locais, com pouco foco e esforço despendido à áreas de matriz antrópica ou na investigação dos efeitos da composição e estrutura de paisagens; (2) realizou amostragens de pequenos mamíferos em diferentes ambientes de paisagens agrícolas e utilizou métricas tradicionais de estrutura de paisagens derivadas de mapas classes e métricas contínuas derivadas de índice de vegetação combinados com MHMs para investigar os efeitos das variações espaço-temporais nessas paisagens sobre aspectos taxonômicos e funcionais (ocorrência, abundância, e diversidade e composição funcional) da diversidade das comunidades. Os resultados evidenciam que os efeitos de paisagens fragmentadas sobre aspectos taxonômicos e funcionais da diversidade são moldados pela variação espacial e temporal da produtividade da vegetação e pela variação temporal da matriz. Respostas das espécies à essa variabilidade dependeram de seus traços ecológicos e mudanças temporais na em caracteríticas da vegetação moldam as comunidades de acordo com traços funcionais. Os resultados desta tese reforçam que incorporar múltiplos aspectos da diversidade biológica e considerar explicitamente a heterogeneidade e dinamismo das paisagens é essencial para entender os efeitos de diferente usos de solo sobre a biodiversidade em paisagens fragmentadas e, assim, orientar ações de manejo para preservar a resiliência dos ecossistemas em agroecossistemas.

Palavras-chave: Rodentia; Didelphimorphia; biodiversidade; agroecossistemas; paisagens dinâmicas; sensoriamento remoto; modelos hierárquicos multiespécie.

ABSTRACT

The loss and fragmentation of native habitats caused by human activities are among the main threats to biodiversity in hotspots such as the Atlantic Forest. In this highly altered biome, forest remnants occur as small patches embedded within diverse anthropogenic matrices (i.e., non-habitat areas). Although historically overlooked, land-use characteristics directly influence species persistence and community integrity. Nevertheless, binary habitat/non-habitat approaches remain dominant in studies of fragmented landscapes, while the spatial and temporal heterogeneity of anthropogenic landscapes is generally disregarded. In Brazil, habitat loss and fragmentation, mainly driven by agricultural activities, are recognized as the primary threats to mammal species in the Atlantic Forest. Non-volant small mammals (< 2 kg; orders Didelphimorphia and Rodentia) form a functionally relevant group in ecosystems and are sensitive to environmental disturbances. Several studies have shown that habitat loss and fragmentation at the landscape scale affect the integrity of small mammal communities in the Atlantic Forest. However, little is known about the effects of different land uses and the spatiotemporal heterogeneity of matrices on the occurrence and diversity of this group in the region. A proper understanding of the impacts of habitat loss and matrix influence in fragmented landscapes also requires analytical approaches that incorporate different biodiversity components and address the issue of imperfect species detection. In this context, the use of analytical tools such as multispecies hierarchical models (MHMs) has been recognized as an effective approach for accurately estimating species diversity. This thesis: (1) conducted a systematic literature review to evaluate whether studies carried out in the Brazilian Atlantic Forest have considered matrix heterogeneity and composition in research involving this group. The results showed that studies have mainly focused on forest areas and local scales, with limited attention given to anthropogenic matrix areas or to the effects of landscape composition and structure; (2) conducted field sampling of small mammals in different environments across agricultural landscapes and used traditional landscape structure metrics derived from land cover maps, as well as continuous metrics derived from vegetation indices, combined with MHMs to investigate the effects of spatiotemporal variations in these landscapes on taxonomic and functional aspects (occurrence, abundance, and functional diversity and composition) of community diversity. The results highlight that the effects of fragmented landscapes on taxonomic and functional diversity are shaped by spatial and temporal variation in vegetation productivity and by temporal variation in the surrounding matrix. Species responses to this variability depended on their ecological traits, and temporal changes in vegetation characteristics shaped communities according to functional traits. The findings of this thesis reinforce that incorporating multiple aspects of biodiversity and explicitly accounting for landscape heterogeneity and dynamism is essential for understanding the effects of different land uses on biodiversity in fragmented landscapes, thereby guiding management actions to preserve ecosystem resilience in agroecosystems.

Keywords: Rodentia; Didelphimorphia; biodiversity; agroecosystems; dynamic landscapes; remote sensing; multispecies hierarchical models.

SUMÁRIO

1 INTRODUÇÃO

A perda e a fragmentação de habitat nativo causada pela expansão agrícola e urbana são as principais ameaças à biodiversidade em hotspots como a Mata Atlântica (Newbold et al., 2016; Püttker et al., 2020). Nesse bioma altamente alterado, os remanescentes florestais representam apenas 23% da cobertura original e estão imersos em matrizes antrópicas diversas (Vancini et al., 2024). Embora historicamente negligenciadas, as características de diferentes usos do solo influenciam diretamente a persistência das espécies e a integridade das comunidades (Chetcuti et al., 2021; Driscoll et al., 2013). Ainda assim, a maioria dos estudos focados no efeito de paisagens fragmentadas sobre a biodiversidade adota abordagens binárias (habita/não-habitat) e ignora a heterogeneidade espacial e temporal das paisagens fragmentadas (Lindenmayer et al., 2008; Santos et al., 2021; Watling et al., 2011). Mapas de cobertura do solo derivados de dados de sensoriamento remoto podem fornecer informações sobre padrões espaciais e dinâmica temporal de tipos gerais de uso e cobertura, mas seu formato geralmente categórico ignora a heterogeneidade em escala fina dentro de cada tipo (St-louis et al., 2014; Tuanmu; Jetz, 2015). Atualmente o uso de índices de vegetação obtidos por sensoriamento remoto têm sido reconhecidos e recomendados para capturar a heterogeneidade de habitat em escala fina, até mesmo dentro de tipos únicos de cobertura do solo considerados homogêneos em classificações tradicionais (Tuanmu; Jetz, 2015). Índices de vegetação derivados de imagens de satélite medem características biofísicas da superfície terrestre que estão intimamente relacionadas à estrutura e composição da vegetação, por exemplo, a produtividade da vegetação ou biomassa verde (Phillips et al., 2008). Medidas de textura das imagens derivadas desses índices podem assim capturar a diferença e as transições de heterogeneidade de habitat em escala fina, dentro e entre os tipos de cobertura do solo em grandes extensões de área e fornecer uma indicação adequada da heterogeneidade em locais considerados homogêneos por classificações tradicionais (Farwell et al., 2021; Tuanmu; Jetz, 2015). Além de espacialmente heterogêneas, paisagens agrícolas podem ter uma grande variação temporal em sua composição de acordo com, o ciclo de fenologia das culturas, o sistema de cultivo e o gerenciamento de cultivos (Santos et al., 2021). Desse modo, considerar a heterogeneidade da matriz baseada unicamente em um momento instantâneo ignora essa variação espaço-temporal de paisagens dinâmicas e pode superestimar o isolamento e as probabilidades de extinção das populações nessas paisagens (Martensen et al., 2017; Santos et al., 2021).

No Brasil, a Mata Atlântica abriga o maior número de espécies ameaçadas do país, sendo que 38,5% delas são endêmicas desse bioma. A perda e a fragmentação de habitats, decorrentes principalmente das atividades agrícolas, são reconhecidas como as principais ameaças às espécies de mamíferos na região (ICMBIO, 2018a; ICMBIO, 2018b). Os pequenos mamíferos não-voadores (> 2kg; ordens Didelphimorphie e Rodentia) constituem um grupo de vertebrados que possuem características e estratégias que lhes permitem responder rapidamente a perturbações ambientais, em escalas espaciais relativamente pequenas (Bonvicino et al., 2002; Lira et al., 2012; Vieira et al., 2018). Eles estão formam um grupo multitrófico e desempenham importantes papéis nos processos naturais e no equilíbrio ecológico em regiões tropicais (Galetti et al., 2016; Loft et al., 2024; Paine; Beck, 2007; Terborgh et al., 2001). Vários estudos têm demonstrado que a perda e a fragmentação do habitat na escala de paisagem afeta a integridade das comunidades de pequenos mamíferos, sendo os requisitos de habitat das espécies um fator determinante das suas respostas à perda de vegetação nativa (Estavillo et al., 2013; Pardini et al., 2010). No entanto, apesar de estudos com pequenos mamíferos terem sido desenvolvidos ao longo dos anos em toda a extensão da Mata Atlântica brasileira, investigações sobre os efeitos de diferentes usos de solo e da heterogeneidade espaço-temporal de matrizes em toda a extensão de paisagens fragmentadas, sobre a ocorrência e diversidade de pequenos mamíferos não-voadores ainda são escassas na região da Mata Atlântica brasileira.

A compreensão adequada dos impactos da perda de habitat e da influência da matriz em paisagens fragmentadas requer ainda análises que incluam diferentes componentes da biodiversidade (Bełcik et al., 2020; Boesing et al., 2018). Focar apenas em um componente pode levar a conclusões imprecisas, uma vez que componentes diferentes podem responder de maneira diferente à mesma variável estudada (Anunciação et al., 2021; Bełcik et al., 2020). Além disso, a detectabilidade da biodiversidade depende do local, das condições do levantamento das espécies e também das características das espécies individuais que compõem a comunidade (Iknayan, et al., 2024). Contabilizar a probabilidade de detecção das espécies em cada local nas estimativas dos diferentes componentes da biodiversidade tem o potencial de representar melhor a distribuição das diferentes características e funções e, assim, fornecer uma estimativa mais precisa das funções e serviços do ecossistema (Jarzina; Jetz, 2016). Para lidar com o problema da detecção imperfeita em estudos ecológicos, o uso de ferramentas analíticas que fornecem estimativas de distribuição e abundância de espécies, ao mesmo tempo em que consideram a detecção imperfeita, como os modelos hierárquicos

multiespécie (MHM), tem sido apontado como uma abordagem eficaz para realizar estimativas precisas da diversidade de espécies (Iknayan et al., 2014; Jarzina; Jetz, 2016). Apesar de todos os recursos e avanços nesse sentido, a detecção imperfeita das espécies ainda tem sido considerada em uma pequena parcela de estudos com dados ecológicos (Guillera-Arroita, 2017).

Esta tese aborda lacunas fundamentais na compreensão dos efeitos da matriz sobre comunidades de pequenos mamíferos não-voadores, um grupo funcionalmente relevante nos ecossistemas e sensível a perturbações ambientais. No Capítulo 1, realizo uma revisão sistemática da literatura para avaliar se e como estudos realizados na Mata Atlântica têm considerado a heterogeneidade e composição das matrizes antrópicas em pesquisas com esse grupo. No Capítulo 2, utilizo métricas tradicionais de estrutura de paisagens derivadas de mapas classes e métricas contínuas derivadas de índices de vegetação combinados com dados de ocorrência das espécies de pequenos mamíferos em diferentes ambientes de paisagens agrícolas (floresta, pasto, agricultura e silvicultura) em modelos de ocupação multiespécie (um tipo de MHM) para investigar os efeitos das variações espaço-temporais nessas paisagens sobre a ocupação das espécies de pequenos mamíferos. Além disso, analiso o quanto métricas de classes e derivadas de índices de vegetação são eficazes para explicar os padrões de ocorrência das espécies nessas regiões. Por fim, no Capítulo 3, utilizo MHMs para investigar o efeito da variação espaço-temporal das paisagens (utilizando metricas tradionais e derivadas de indice de vegetação) sobre aspectos taxonômicos e funcionais da diversidade das comunidades de pequenos mamíferos (ocorrência, abundância, e diversidade e composição funcional).

Ao integrar dados de sensoriamento remoto para gerar métricas tradicionais e contínuas caracterizando paisagens agrícolas da Mata Atlântica, combinados com modelagem hierárquica de comunidades, esta tese contribui com novas abordagens para estudos em paisagens antropizadas, amplia a compreensão dos efeitos da variabilidade temporal na vegetação em paisagens agrícolas sobre diferentes aspectos da diversidade biológica e propõe alternativas robustas para avaliar como paisagens dinâmicas influenciam a biodiversidade e o funcionamento dos ecossistemas.

2 PEQUENOS MAMÍFEROS NÃO-VOADORES EM PAISAGENS FRAGMENTADAS DA MATA ATLÂNTICA: focos de pesquisa e lacunas frente às paisagens antrópicas

RESUMO

Ambientes naturais em hotspots de biodiversidade, como a Mata Atlântica, se encontram atualmente reduzidos e fragmentados pela expansão de atividades humanas, imersos em paisagens altamente heterogêneas. Nessas áreas, a disponibilidade de habitat e as condições na matriz são fundamentalmente importantes para a persistencia de populações de mamíferos. Pequenos mamíferos não-voadores compreendem um grupo bem amostrado através de toda extensão da Mata Atlântica. No entanto, pouco se sabe se essas pesquisas têm focado em aspectos importantes de toda extensão de paisagens fragmentadas, como em diferentes tipos de matrizes e composição e estrutura dos ambientes que compõem as paisagens. Nesse estudo eu realizei uma revisão sistemática da literatura buscando investigar os aspectos de paisagens antropizadas que têm sido incorporados em pesquisas com pequenos mamíferos na região da Mata Atlântica brasileira. Analisando 53 artigos, eu encontrei que os estudos tem sido focados principalmente em áreas florestas e escalas locais, com pouco foco e esforço despendido à áreas de matriz antrópica ou na investigação dos efeitos da composição e estrutura de paisagens. Além disso, recursos modernos que permitem a obtenção de métricas que capturam heterogeneidade do habitat em escala fina ainda não tem sido utilizados em estudos com esse grupo. A diversidade taxonômica foi o aspecto dominante na maioria dos estudos. Futuros estudos envolvendo comunidades de pequenos mamíferos nesta região deveriam focar em diferentes aspectos da diversidade do grupo, fornecendo assim informações importantes sobre as consequências de mudanças nas comunidades sobre o funcionamento e a estabilidade dos ecossistemas nessas paisagens.

Palavras-chave: Rodentia. Didelphimorphia. Usos do solo. Sensoriamento remoto. Diversidade. Agroecossistemas.

1 INTRODUÇÃO

A perda e a fragmentação do habitat causadas pelas mudanças no uso do solo são as maiores causas de perda de espécies em *hotspots* de biodiversidade (Kong; Zhou; Jiao, 2021). Mesmo que importantes para a manutenção da biodiversidade e para diversas funções e serviços do ecossistema (Banks-Leite et al., 2014), os ambientes naturais continuam sendo convertidos de forma intensa em áreas agrícolas e urbanas, ficando reduzidos à manchas imersas em um mosaico de ambientes antrópicos (Hobbs; Higgs; Harris, 2009). A Mata Atlântica, por exemplo, cobre atualmente cerca de 23% de sua cobertura original, onde mais de 90% dos seus fragmentos remanescentes se encontram isolados e com menos de 50 ha (Vancini et al., 2024), imersos em mosaico de diferentes ambientes antrópicos (i.e. matrizes).

Atualmente, muitas paisagens da Mata Atlântica estão passando por uma mudança de diminuição para expansão da cobertura florestal por meio da regeneração florestal (Vancini et al., 2024). Dessa forma, entender o efeito de diferentes matrizes e estrutura de paisagens fragmentadas sobre a biodiversidade em paisagens da Mata Atlântica são essenciais para orientar esforços de conservação da biodiversidade e estratégias de recuperação para populações ameaçadas (Crouzeilles et al., 2019a; Driscoll et al., 2013; Kong; Zhou; Jiao, 2021).

Em paisagens fragmentadas, tanto a quantidade de vegetação nativa como as condições da matriz são fundamentalmente importantes para manutenção da biodiversidade remanescente e merecem igual atenção na pesquisa e manejo (Chetcuti; Kunin; Bullock, 2021; Driscoll et al., 2013). Paisagens fragmentadas podem ser compostas por uma variedade de ambientes na matriz, com diferentes níveis de qualidade, riscos e disponibilidade de recursos, que podem influenciar na dinâmica espacial das populações e na ocorrência de espécies (Driscoll et al., 2013; Chetcuti; Kunin; Bullock, 2021). Convencionalmente, a estrutura e composição de habitats é medida em ambientes naturais por meio de pesquisas de campo com uso intensivo de mão de obra (e.g. Delciellos et al., 2016; Hannibal et al., 2019). Embora possa ser adequado para determinadas questões, essa informação é limitada a pequenas regiões e escalas. Atualmente, a disponibilização gratuita de dados oriundos de sensoriamento remoto permitiu que muitos estudos em larga escala começassem a quantificar a heterogeneidade tanto em escala locais (ex: Serafini; Priotto; Gomez, 2019), regionais (Walder et al., 2025), ou globais (Tuanmu; Jetz, 2015). Embora em estudos que buscam entender o efeito de paisagens alteradas sobre a biodiversidade comumente sejam utilizados mapas classificados de uso e cobertura do solo, a pelo menos uma década o uso de dados não-classificados de sensoriamento remoto (dados espectrais), como índices de vegetação, têm sido reconhecidos e recomendados para capturar a heterogeneidade uma ampla variedade de escalas, até mesmo dentro de tipos únicos de cobertura do solo considerados homogêneos em mapas de classes (St-Louis et al., 2009; Tuanmu; Jetz, 2015).

Os pequenos mamíferos não-voadores (< 3kg) (Ordens Didelphimorphia e Rodentia) constituem um grupo de vertebrados que possuem características e estratégias que lhes permitem responder rapidamente a perturbações ambientais, em escalas espaciais relativamente pequenas (Lira et al., 2012; Serafini; Priotto; Gomez, 2019). Eles formam um grupo multi-trófico e estão entre as principais presas de carnívoros, desempenhando assim importantes papéis ecológicos em ecossistemas tropicais (Galetti et al., 2015; Loft et al., 2024; Terborgh et al., 2001). Vários estudos têm demonstrado que a perda e a fragmentação do

habitat na escala de paisagem afetam a integridade das comunidades de pequenos mamíferos, por exemplo, levando à reduções na riqueza dos especialistas de floresta e favorecendo a proliferação de espécies generalistas e adaptadas a distúrbios (Estavillo; Pardini; Rocha, 2013; Bovendorp et al., 2019; Pardini et al., 2010). Além da quantidade de habitat na paisagem, a estrutura da vegetação e os diferentes de tipos de usos do solo na paisagem também tem efeitos consideravelmente importantes sobre a ocorrência de pequenos mamíferos em paisagens fragmentadas (Bajaru; Kulavmode; Manakadan, 2019; Delcielos et al., 2016; Hannibal et al., 2019; Serafini; Priotto; Gomez, 2019). Apesar dessas evidências, e de que os pequenos mamíferos são um grupo relativamente bem amostrados na região da Mata Atlantica Brasileira (Bovendorp et al., 2017), investigações sobre o efeito de diferentes de diferentes usos de solo e contextos de paisagem sobre a ocorrência e diversidade de pequenos mamíferos não-voadores em paisagens fragmentadas ainda parecem ser pouco realizadas.

A fim de fornecer uma visão geral de quais aspectos da estrutura de paisagens antropizadas tem sido incorporados em pesquisas com pequenos mamíferos na região da Mata Atlântica brasileira, eu realizei uma revisão sistemática da literatura para (1) investigar a quantidade de pesquisas desenvolvidas na região da Mata Atlântica que incluíram variáveis espaciais, (2) identificar as as matrizes amostradas e o esforço amostral empregado nessas matrizes (3) investigar os aspectos da diversidade estudados (4) e quantificar os estudos que utilizaram informações da estrutura da vegetação obtidas manualmente ou por sensoriamento remoto (usando dados de classes ou espectrais).

2 MÉTODOS

2.1 Pesquisa bibliográfica

Eu realizei uma revisão sistemática de artigos científicos publicados até 27 de setembro de 2021, utilizando as bases de dados Scielo (www.scielo.org) e Scopus (www.scopus.com) com as seguintes combinações de palavras-chave: ("pequenos mamíferos" OR mamíferos OR Didelphimorphia OR Rodentia) AND (floresta OR fragmento OR mancha OR matriz OR agroecossistema OR agrícola OR agricultura OR antropogênico OR plantação OR monocultura OR agrofloresta OR cacau OR café OR Eucalipto OR Pinus OR soja OR cana-de-açúcar OR silvicultura OR palmeiral OR seringueira OR pasto OR milho OR "floresta secundária" OR reflorestamento OR regeneração OR restauração) AND ("Mata Atlântica" OR "Floresta Atlântica") usando as palavras-chave em português na Scielo e ("small mammals" OR Didelphimorphia OR Rodentia OR mammals*) AND (forest OR fragment OR patch OR

matrix OR agroecosystem OR agriculture * OR anthropogenic* OR plantation OR crop* OR monoculture OR agroforest OR cocoa OR coffee OR Eucalyptus OR Pinus OR palm OR rubber OR pasture OR grassland OR corn* OR soy OR sugar-cane OR forestry OR "secondary forest" OR reforestation OR regeneration OR restoration) AND ("Atlantic Forest") usando as palavras-chave em inglês na Scopus. Eu restringi a pesquisa ao título, resumo e palavras-chave dos artigos. Adicionalmente, eu incluí no conjunto de artigos selecionados aqueles artigos que eu já conhecia e atendiam aos critérios de seleção, mas não foram retornados pelas buscas nas bases de dados.

2.2 Compilação de dados

Minha pesquisa retornou um total de 204 artigos científicos, entre os quais eu selecionei apenas aqueles que atendiam a todos os seguintes critérios: 1) ser um estudo desenvolvido com protocolo padrão para capturar pequenos mamíferos não-voadroes (< 3kg) (Ex: Bovendorp; MCCleery; Galetti, 2017). Estudos com registros de pequenos mamíferos obtidos por outros métodos (ex: câmera trap e observação de comportamento) não foram consideradados; 2) artigos desenvolvidos apenas na Mata Atlântica brasileira, incluindo áreas de transição com outros biomas, desde que uma fitofisionomia da Mata Atlântica também tenha sido amostrada; 3) artigos que não utilizaram dados de outro trabalho publicado ou de base de dados; 4) não ser uma pesquisa de teste de métodos (ex: eficiência de amostragem); 5) não ser meta-análise, revisão ou *datapaper*; .

Após a filtragem, eu obtive 47 artigos das buscas nas bases de dados e incluí seis artigos já conhecidos, resultando em 53 artigos utilizados nas análises. De cada artigo selecionado eu registrei a localidade geográfica (Estado do Brasil), o ano de realização da amostragem, o tipo de ambiente amostrado (fitofisionomia da Mata Atlântica e os tipos de matrizes antrópicas), o esforço amostral despendido em cada tipo de ambiente, quais aspectos das diversidade foram medidos, se complexidade estrutural da vegetal foi amostrada e o método (manual ou sensoriamento remoto), se características da escala de paisagem foram avaliadas e quais características.

3 RESULTADOS

Os 53 trabalhos incluídos foram desenvolvidos entre os anos 1985 e 2019. Embora em quase todos os estados onde a Mata Atlântica brasileira se estende pelo menos um estudo

tenha sido realizado, a maioria das pesquisas ocorreu nos estados de São Paulo, Minas Gerais, Rio de Janeiro e Bahia.

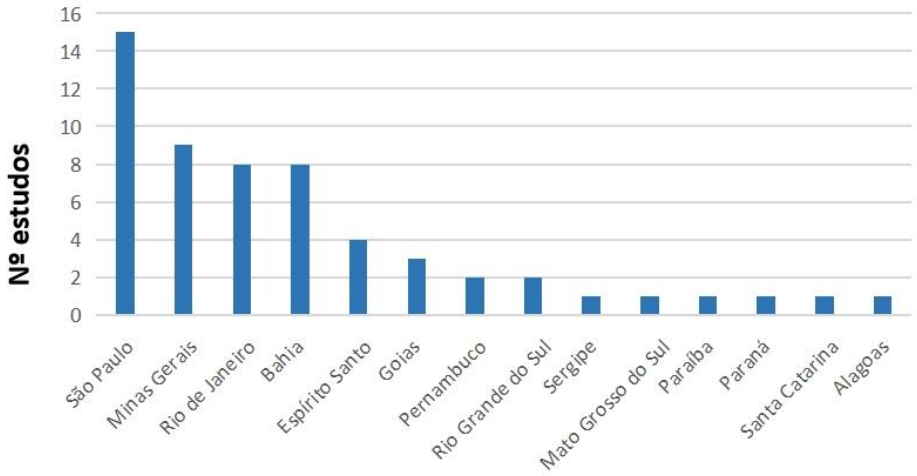

Figura 1. Número de estudos por estado brasileiro que amostraram pequenos mamíferos não-voadores na região da Mata Atlântica, entre os anos de 1985 e 2019.

A maioria dos estudos (83%) não inlcuiu varáveis espaciais como variáveis preditoras em suas análises. Entre os que incluíram, o tamanho do fragmento de floresta foi a métrica mais utilizada (n=5), seguida por dados categóricos de atividades antrópicas na paisagem (n=3). O efeito da quantidade de floresta na paisagem foi avaliado apenas em dois estudos (Estavillo; Pardini; Rocha, 2013 e Pardini et al., 2010).

A maior parte das pesquisas conduzidas com pequenos mamíferos não-voadores na região da Mata Atlântica focaram em ambientes florestais, enquanto que poucas ocorreram em ambientes de matriz antrópica (Figura 2). No entanto, a partir do ano de 1999 houve aumento na proporção de estudos realizados em floresta e matriz, bem como no número de tipos de matrizes antrópicas amostradas (Figura 3). Estudos com que amostraram áreas de restauração/regeneração foram mais desenvolvidos entre 2006 e 2012, porém este aumento não permaneceu nos anos mais recentes (2013-2019) (Figura 3).

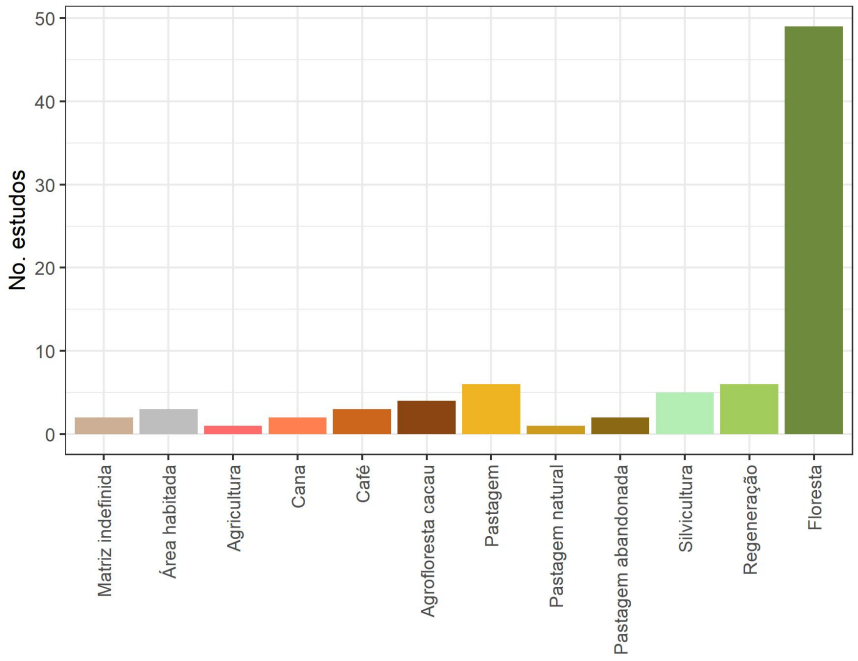

Figura 2. Tipos de uso e cobertura do solo amostrados em estudos que amostraram pequenos mamíferos em ambientes na região da Mata Atlântica brasileira, entre 1985 e 2019.

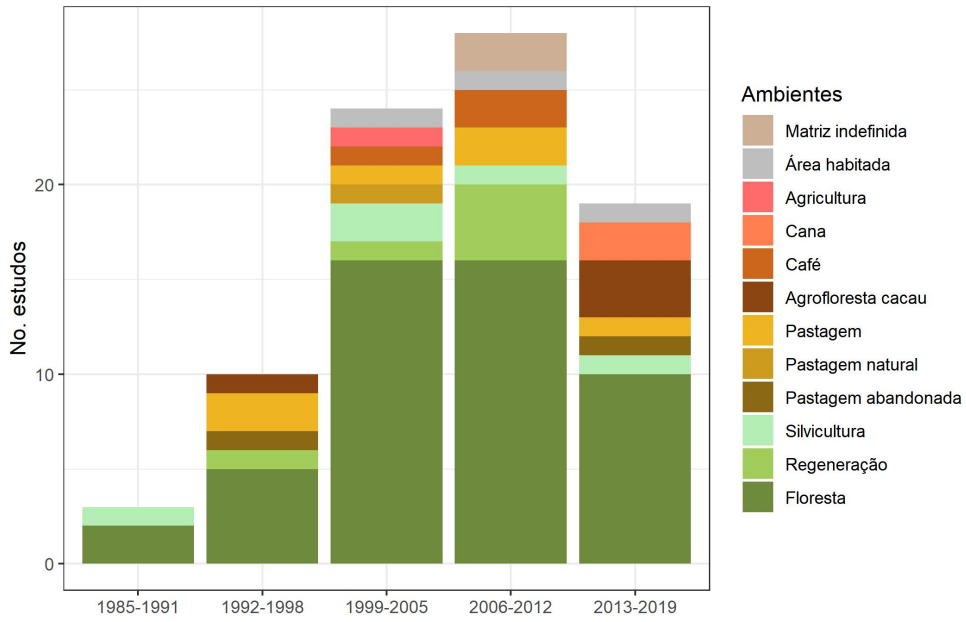

Figura 3. Ambientes focados em estudos que amostraram pequenos mamíferos na região Mata Atlântica brasileira entre 1985 e 2019.

Os ambientes com maior esforço amostral médio empregado foram as fitofisionomias florestais da Mata Atlântica, seguidos de um tipo de matriz indefinida (que apareceu em um único estudo: Estavillo; Pardini; Rocha, 2013), agrofloresta de cacau e cana-de-açúcar (Figura 4).

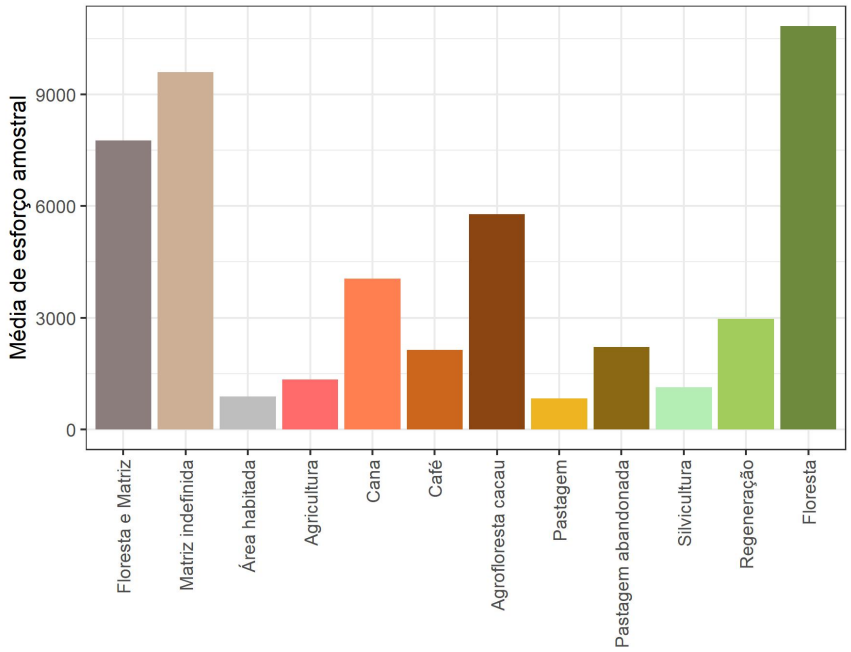

Figura 4. Esforço amostral médio empregado em cada tipo de ambiente amostrado em estudos desenvolvidos para captura de pequenos mamíferos na região da Mata Atlântica brasileira, entre 1985 e 2019. Esforço amostral foi dado em *trap-nights, trap-days, bucket-nights* ou *bucket-days.* A classe Floresta e Matriz corresponde a esforço amostral não especificado para cada ambiente amostrado no estudo.

Composição, riqueza e abundância foram os aspectos da diversidade focados em 90% dos estudos realizados enquanto que outros aspectos como diversidade funcional e filogenética foram analisados em apenas um estudo em área de ecótone Mata Atlântica e Pampas (Luza; Gonçalves; Hartz, 2015). Apenas 21 % (n=11) dos estudos analisados utilizaram a estrutura da vegetação como variável preditora, nos quais os dados foram obtidos de forma manual, apenas no entorno dos sítios de amostragem. Nenhum dos estudos utilizou dados espectrais de sensoriamento para obter indicadores da estrutura da vegetação.

4 DISCUSSÃO

Essa revisão sistemática forneceu uma visão geral dos aspectos de paisagens fragmentadas estudados em pesquisas envolvendo levantamentos de pequenos mamíferos não-voadores na região da Mata Atlântica brasileira e identificou que porporcionalmente muito menos atenção é dada ao estudo dos efeitos de diferentes ambientes da matriz, comparada às áreas florestais. Além disso, apesar da importância amplamente conhecida da composição e estrutura de paisagens sobre a biodiversidade em paisagens antropizadas (Santos et al., 2021), estudos

investigando os efeitos de diferentes aspectos dessas paisagens sobre a diversidade de pequenos mamíferos ainda são escassos e concentram- se principalmente em poucas métricas baseadas em classes de uso e cobertura do solo. Além disso, ainda que os pequenos mamíferos sejam bem amostrados através de toda extensão da Mata Atlântica (Bovendorp et al., 2017), nossos resultados indicam que o foco dessa pesquisas permanece principalmente em aspectos taxonômicos da diversidade (composição, riqueza e abundância), enquanto outros aspectos como diversidade funcional e filogenética não tem sido estudados localmente (mas ver Boverndorp et al., 2019 para um estudo utilizando *datapaper* para investigar a diversidade funcional de pequenos mamíferos na região na Mata Atlântica). Apesar dos avanços tecnológicos e da crescente assecibilidade à diferentes fontes de imagens de satélite e softwares de SIG, minha revisão indica que abordagens tradicionais de obtenção de métricas de paisagem e estrutura da vegetação ainda são as predominante nos estudos com pequenos mamíferos não-voadores na Mata Atlântica brasileira.

Embora as condições da matriz sejam fundamentalmente importantes para persistencia de animais em paisagens modificadas (Chetcuti; Kunin; Bullock, 2021) e apesar da grande heterogeneidade presente na maior parte das paisagens da Mata Atlântica, resultante da diversidade de usos do solo (MAPBIOMAS BRASIL, 2022), minha revisão indica que a importância das matrizes antrópicas ainda não tem sido devidamente levada em conta nos estudos com pequenos mamíferos nessa região. Uma possível razão para o foco em estudos locais e áreas florestais pode estar relacionado à quantidade de esforço amostral, financeiro e humano, necessário para a obtenção de amostras suficientes para descrever adequadamente a diversidade de espécies em comunidades de pequenos mamíferos altamente diversas, como as que ocorrem na Mata Atlântica (Bovendorp; MCCleery; Galetti, 2017; Rocha et al., 2023). Essa limitação logística possivelmente direciona a maioria das pesquisas a ambientes e locais da Mata Atlântica que otimizem o aproveitamento de recursos financeiros, materiais e equipamento disponíveis. Nesse sentido, o pequeno número estudos que avaliou a influência de variáveis na escala de paisagem pode ser em parte devido à quantidade de paisagens e da extensão espacial que geralmente são necessários em estudos envolvendo análises esse tipo de estudo (Fahrig et al. 2011; Vieira et al. 2018), que para muitos pesquisadores brasileiros pode ser impraticável devido à limitações logísticas. No entanto, uma revisão da literatura existente sobre a ocorrência de mamíferos carnívoros em diferentes usos de solo em agroecossistemas em todo o mundo, também encontrou que informações sobre as paisagens circundando esses agroecossistemas não estavam presentes na maioria dos estudos (Ferreira et al., 2018). Esses resultados combinados sinalizam que ainda pouco interesse tem sido dado à investigação dos

efeitos de diferentes aspectos de paisagens agrícolas sobre a ocorrência de mamíferos em paisagens fragmentadas.

Estudos recentes apontam um aumento na cobertura floresta na região da Mata Atlântica brasileira (Crouzeilles et al., 2019a; Vancini et al., 2024). Apesar disso, o número de estudos focados em áreas de restauração não aumentou entre as pesquisas mais recentes (2013-2019). O aumento da biodiversidade pela restauração do ecossistema - e potencialmente as chances de regeneração natural, sustentabilidade ecológica e funcionalidade a longo prazo - tem sido positivamente associado à proporção da vegetação nativa remanescente na paisagem (Banks-Leite et al., 2014; Crouzeilles et al., 2019b; Leite et al., 2013). No entanto, os estudos que amostraram pequenos mamíferos em áreas de regeneração florestal não avaliaram a influência da estrutura da paisagem sobre as variáveis resposta analisadas (Beltrão-Mendes et al., 2020; Pinotti; Pagotto; Pardini, 2015; Umetsu; Pardini 2007; Vera Y Conde; Rocha, 2006). Esses resultados vão em linha com a revisão de LEITE et al. (2013) que forneceu uma visão geral de como a ecologia da paisagem estava sendo usada em projetos de restauração, onde os autores identificaram que poucos estudos enfocando a relação entre as características da paisagem e os resultados da restauração foram conduzidos no Brasil.

4.1 Conclusão

A perda e fragmentação de habitats decorrentes das atividades agrícolas representam as principais ameaças as espécies de mamíferos da Mata Atlântica brasileira (ICMBio, 2018). Embora a estrutura da paisagem e as condições na matriz sejam fundamentalmente importantes para a permanência de populações de mamíferos em paisagens fragmentadas (Brady et al., 2011), minha revisão aponta que esses fatores têm sido pouco abordados em pesquisas com pequenos mamíferos não voadores na região da Mata Atlântica brasileira. Assim, estudos futuros deveriam desenvolver pesquisas com desenhos amostrais apropriados para amostrar pequenos mamíferos em áreas de regeneração florestal, em diferentes tipos de matrizes, bem como avaliar o efeito de diferentes aspectos da composição e estrutura de paisagens na ocorrência dessas espécies (Chetcuti; Kunin; Bullock, 2021). O acesso gratuito a dados classificados e espectrais provenientes de sensoriamento remoto viabiliza a quantificação precisa de características de paisagens heterogêneas em diferentes escalas espaciais e temporais, com reduzido custo financeiro e esforço físico. Tais recursos, portanto, representam uma oportunidade a ser explorada em estudos futuros com pequenos mamíferos. Medições detalhadas de diferentes aspectos de paisagens antropizadas podem fornecer

informações valiosas para explicar a ocorrência de pequenos mamíferos (Marston et al., 2023) e, assim, orientar estratégias de conservação desse grupo altamente ameaçado na Mata Atlântica. Diante das atuais mudanças na cobertura do solo impulsionadas por atividades humanas, além das abordagens de focadas em medidas taxonômicas da diversidade, futuros estudos também deveriam focar nos aspectos funcionais e filogenéticos da diversidade do grupo, uma vez que estes podem fornecer informações importantes sobre as consequências de mudanças nas comunidades sobre o funcionamento e a estabilidade dos ecossistemas em paisagens antropizadas (Cadotte; Carscadden; Mirotchnick, 2011; Flynn et al., 2011).

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3 Temporal stability of vegetation across agricultural land uses enhances small non-volant mammal occurrence in the Brazilian Atlantic Forest

Abstract

Agricultural landscapes are inherently dynamic and comprise a variety of land uses which can influence species persistence in fragmented landscapes of biodiversity hotspots, such as the Atlantic Forest. Although land use and land cover (LULC) maps may provide useful information for investigations on the effects of landscape changes on biodiversity, they overlook heterogeneity and ignore temporal variation within land cover classes. Meanwhile, vegetation indices derived from satellite imagery capture aspects of habitat heterogeneity at fine scales deemed homogeneous by traditional land-cover classifications. Here, we modelled the occupancy of 21 species of small non-volant mammals captured in agricultural landscapes in a region of the Brazilian Atlantic Forest, using both landscape metrics derived from a standard LULC map and metrics of spatial and temporal variability in vegetation productivity and heterogeneity (contrast) derived from the Enhanced Vegetation Index (EVI). Small mammal occupancy was predicted equally well by models based either on LULC map or on EVI derived metrics. We found strong evidence for a positive effect of forest patch density, and negative effects of mosaic of uses cover (LULC map-derived metrics) and of contrast temporal variation (EVI-derived metric). However, consistent evidence across models was observed only for contrast temporal variation. Our results indicate that landscapes where land uses maintain more stable vegetation characteristics throughout the year can support a greater number of species with diverse habitat requirements. Using EVI-derived metrics to capture detailed spatiotemporal changes in vegetation provided complementary insights about the aspects of anthropogenic land use driving biodiversity patterns in these agroecosystems.

Keywords: Rodentia; Didelphimorphia; spectral indices; landscape heterogeneity; dynamic landscapes; agroecosystems; multispecies occupancy models.

1. Introduction

Habitat loss and fragmentation caused by land-use change are the leading drivers of species loss in biodiversity hotspots (Newbold et al., 2016; Püttker et al., 2020). In Brazil, the Atlantic Forest harbors the highest number of threatened species in the country, with 38.5% of them being endemic to this biome (ICMBio, 2018). Currently, forest vegetation within the Atlantic Forest biome covers about 23% of its original extent, with more than 97% of the remaining fragments smaller than 50 hectares (Vancini et al., 2024). In addition to the amount of native forest, studies have shown that in fragmented landscapes, the conditions of the matrix (i.e., human-modified areas) play a fundamental role in sustaining biodiversity and therefore deserve equal attention in both biodiversity research and management (Chetcuti et al., 2021; Driscoll et al., 2013; Lindenmayer et al., 2008). The matrix can comprise a variety of environments with differing quality, levels of risk, and resource availability, which may influence species responses to habitat loss and fragmentation (Driscoll et al., 2013; Boesing et al. 2018; Chetcuti et al., 2021). For mammal species, for example, some matrix types can offer complementary food resources and facilitate dispersal across fragmented landscapes (Brady et al., 2011; Magioli et al., 2019). Brady et al. (2011) found that within human-modified, highly fragmented landscapes in subtropical Australia, vegetation structural complexity of the matrix can increase the probability of mammals movement across the landscape, increasing mammal species richness. Therefore, detailed information on land-cover heterogeneity has the potential to enhance our understanding of how different land uses affect biodiversity patterns, ultimately contributing to more effective management and conservation strategies (Chetcuti et al., 2021; Santos et al., 2021).

Niche theory predicts a positive relationship between habitat heterogeneity and species diversity, as more heterogeneous areas can provide greater niche space and allow for species coexistence through resource partitioning (Fink and Snyder, 2008; Hutchinson, 1957). Both local vegetation heterogeneity, due to plant composition and structural diversity and landscape-level heterogeneity, resulting from land-cover diversity, can influence positively the diversity of various taxonomic groups at both local and landscape levels (Le provost et al., 2021; Schuldt et al., 2019). In addition to spatial heterogeneity, incorporating detailed descriptions of agricultural systems across temporal scales into studies of biodiversity patterns has also been recommended (Martensen et al., 2017; Santos et al., 2021), since temporal dynamic of matrix, for example crop changes, can influence local biodiversity (Lee et al., 2024). Agricultural landscapes can exhibit substantial temporal variation in their composition due to crop phenology cycles, cropping systems, and management practices (Santos et al.,

2021). Assessing matrix heterogeneity based only on a single time snapshot, such as annual land cover maps, ignores this variation and may overestimate population isolation and extinction risks (Martensen et al., 2017; Santos et al., 2021).

Conventionally, habitat heterogeneity is measured in natural environments at local scales through labor-intensive field surveys (e.g., Delciellos et al., 2016; Hannibal et al., 2019; Santos-Filho et al., 2024). While this may be suitable for certain questions, its application is generally limited to small regions and scales, due to economic and logistic costs. The increasing availability of free remote sensing data has enabled many large-scale studies to begin quantifying heterogeneity at landscape scales, generally using categorical land-cover maps (e.g., Le Provost et al., 2021; Serafini et al., 2019; Vieira et al., 2018). Such maps can provide information on spatial patterns and temporal dynamics of general habitat types, but their categorical nature overlooks heterogeneity within land-cover classes (St-Louis et al., 2014; Tuanmu and Jetz 2015). In this context, vegetation indices derived from remote sensing have been used to access aspects of habitat heterogeneity at fine scales, including areas that appear homogeneous under traditional land-cover classifications (Farwell et al. 2021; Tuanmu and Jetz, 2015; Wood et al., 2012). Vegetation indices derived from satellite imagery measure biophysical surface characteristics closely related to vegetation structure and composition (Farwell et al., 2021; Phillips et al., 2008). Texture measures derived from these indices can capture variation of the spatial vegetation structure and habitat heterogeneity transitions across broad areas, and offer suitable indicators of heterogeneity at both local and landscape extents (Farwell et al., 2021; Tuanmu and Jetz, 2015).

In the Brazilian Atlantic Forest, habitat loss and fragmentation caused by agricultural activities are the main threats to 52% of mainland mammal taxa officially listed as threatened with extinction (ICMBio, 2018). Small non-volant mammals (body mass < 2 kg; orders Didelphimorphia and Rodentia) display traits and strategies that allow them to respond rapidly to environmental disturbances at relatively small spatial scales (Escobar and Estades, 2021; Lira et al., 2012; Vieira et al., 2018). They form a multitrophic group and play essential roles in natural processes and the ecological balance of tropical ecosystems (Loft et al., 2024; Paine and Beck, 2007; Terborgh et al., 2001). Several studies have shown that habitat loss and fragmentation affect small mammal community integrity, with species' habitat requirements being a major factor in their responses to native vegetation loss (Estavillo et al., 2013; Pardini et al., 2010). For example, forest loss decreases forest specialist richness while favoring generalist species proliferation (Banks-Leite et al., 2014; Pardini et al., 2010). Additional

studies have shown that both local vegetation structure and land-use type also influence small mammal occurrence in these fragmented landscapes (Delciellos et al., 2016; Püttker et al., 2008; Hannibal et al., 2019; Umetsu and Pardini, 2007). However, further investigation is still needed into the patterns of small mammal diversity across forest and matrix in agricultural landscapes within the Atlantic Forest region, especially regarding the effects of spatiotemporal variability in vegetation characteristics.

Vegetation indices, such as Enhanced Vegetation Index – EVI and Normalized Difference Vegetation Index – NDVI, have been proved to successfully explain small mammal species distribution and abundance in agricultural landscapes (Andreo et al., 2019). These indices have a strong correlation with photosynthesis and biomass, and are historically used as surrogates for ecosystem productivity or general ecosystem energy (Phillips et al., 2008). The positive relationship between productivity and both mammal species richness and abundance has been consistently observed worldwide, irrespective of body mass (De Souza Ferreira Neto et al., 2022). Meanwhile, a negative effect of annual variability in productivity - measured by dynamic habitat indices derived from time series of satellite-derived vegetation metrics - on species richness has also been supported for different taxa globally, including mammals (Radeloff et al., 2019). Environmental instability driven by human activities, such as land-use or climate change, is expected to reduce species occurrence and abundance due to increased and stochastic fluctuations in resource availability (Janova and Heroldova, 2016; Tao et al., 2024; Williams and Midleton, 2007). In addition, measures of fine-scale spatial vegetation heterogeneity, accessed by image texture of vegetation indices may better explain species diversity than conventional measures of habitat composition (St-Louis et al., 2014; Tuanmu and Jetz, 2015), once they capture microhabitat features of vegetation structure and composition (Farwell et al., 2021; Silveira et al., 2023).

Here, we investigated the effects of the spatial and temporal characteristics of agricultural landscapes on small non-volant mammal communities in a region of the Brazilian Atlantic Forest. Our goal was to assess the degree to which species occurrence across landscapes is influenced by (1) broad land use and land cover (LULC) composition and forest fragmentation, quantified using metrics derived from a classified LULC map; and (2) the spatiotemporal variation in fine-scale vegetation productivity and heterogeneity, captured through a vegetation index (EVI) and its associated texture metric (contrast), at both site and landscape levels. We examined the evidence for the effects of site and landscape metrics and assessed whether they provide complementary information for modeling small mammal

occupancy. We expected that: (1) intermediately forested and highly fragmented landscapes would host a greater proportion of the regional species pool than more forested or matrix dominated ones, due to the presence of generalist and disturbance-adapted species from the matrix, in addition to the more specialized forest species (De La Sancha et al., 2023; Estavillo et al., 2013; Umetsu and Pardini, 2007); (2) species occurrence would be higher in sites and landscapes with greater spatial productivity (EVI) (De Souza Ferreira Neto et al., 2022) and vegetation heterogeneity (contrast) (Schuldt et al., 2019; Silveira et al., 2023); and (3) species occurrence would decline in areas with greater temporal variability in landscape productivity and heterogeneity (Radeloff et al., 2019; Tao et al., 2024). Considering that both landscape-level and within-habitat disturbances contribute to biodiversity loss in tropical regions (Barlow et al., 2016), and given the well-established role of habitat structure and composition in shaping small mammal communities in fragmented Atlantic Forest landscapes (Delciellos et al., 2016; Hannibal et al., 2019), we expect that metrics and models based exclusively on EVI (capturing fine-scale vegetation variability), or models incorporating both metrics derived from LULC map (capturing broad land cover variability) and from EVI, will better explain species occurrence than metrics and models based solely on the LULC map (Prajzlerová et al., 2024; Suttidate et al., 2023).

2. Methods

2.1. Study area and Sampling design

The study area is located in the northeastern region of São Paulo state and the southern region of Minas Gerais state in Brazil, within the Atlantic Forest biome (Figure 1). Sampling sites were distributed across 13 circular landscapes with a radius of 1000m, selected to include a gradient of forest cover (ranging from 6% to 96%) and in the matrix (i.e., human-modified areas) including the most common types of land use in the region (pasture, mosaic of agriculture-pasture uses, and silviculture) (Figure 1).

The small mammal sampling was typically conducted over a period of 10 consecutive nights at each landscape, between December 2022 and October 2023. For logistical reasons, however, the sampling duration was shorter at some sites, with a minimum of six trap-nights. This variation in sampling effort was accounted for in the modeling. In each landscape, we established four to five sampling sites, which were spatially distributed according to the proportion of forest cover and the availability of pasture, agriculture, and silviculture in the matrix. In total, we sampled 63 sites: 35 in forests and 28 in matrix sites (16 in pastures, six in agricultural fields, and six in eucalyptus plantations). A minimum distance of 100 meters was

maintained between sampling sites, with an average spacing of 207 meters. Each sampling site consisted of a grid of 50 live traps arranged in five parallel lines, with five trapping stations per line spaced approximately 10 meters apart. Each trapping station was equipped with two live traps: in matrix sites both traps were placed on the ground, whereas in forest sites, one trap was set on the ground and the other in the understory vegetation at a height of 1.5 – 2 m. All traps used were of the 'Sherman' model, of three sizes (small: Trap1 [23.5 x 8 x 9 cm], large: Trap2 [38 x 10 x 12 cm] and Trap3 [43 x 12.5 x 14 cm]), made of aluminum. The traps were baited with a mixture of peanut butter, banana, sardines, vanilla essence and cornmeal. The distribution of the different sizes in trapping stations was standardized to always include 25 small traps (Trap1) and 25 large traps (Trap2 and Trap3). For logistical reasons, Trap3 was used only in samplings that occurred from December 2022 until May 2023. This difference in arrangement due to the lack of Trap3 was considered during the analyses, as described in the Methods section. During a sampling period, traps were kept open for 6-10 consecutive nights and checked daily to identify captured species and replace baits. We aimed to establish longer than usual trapping sessions - exceeding the common 4–8-night standard - to obtain a more representative sample of small mammals in species-rich assemblages such as those found in the Atlantic Forest (Bovendorp et al., 2017b; Palmeirim et al., 2020), as rare species may only be detected during the second week of trapping (Palmeirim et al., 2020). Some individuals of each species were euthanized to assist with species identification (following appropriate ethical protocols and prior authorization from the responsible authorities (UNESP's Ethics Committee and ICMBio authorization). We sent the collected material to a taxonomic team at ESALq/USP, where they are currently housed in their zoological collection.

2.2. Site and Landscape metrics

2.2.1. Metrics based on land cover classes

To calculate traditional land cover and fragmentation metrics for each landscape we used the land cover map from the MapBiomas - Collection 2 (beta), at a 10 m resolution (MapBiomas, 2023) (Figure 1A). Besides the forest cover, four main land use types (classes) predominated in our study area: agriculture, pasture, mosaic of uses, and silviculture. Since the amount of pasture was consistently highly negatively correlated with forest cover in the landscapes (Pearson's correlation coefficient > 0.70), we excluded this class from our analysis. Additionally, the area covered by agriculture was unrepresentative in most landscapes. For

this reason, we grouped it with the mosaic of uses class, which predominates in the region (Figure 1) (Table 1).

2.2.2. Metrics based on vegetation index

We calculated Enhanced Vegetation Index (EVI) rasters using the red and near-infrared bands from 3 m resolution PlanetScope SuperDove imagery (Planet Team, 2024), which we then used to derive metrics for each sampling site and landscape. We calculated mean EVI at the site level using a circular area with a 50 m radius from the center of the sampling grid, and at the landscape level using four circular buffer sizes (1, 3, 5 and 7 km radii) centered on the sampling sites. Using the EVI rasters for each site and landscape, we derived the texture measure contrast, calculated as the exponentially weighted difference in EVI values between adjacent pixels within a 3 × 3 moving window (Haralick et al., 1973) (Figure 1B-C). We then averaged the contrast values to obtain a metric of mean contrast at both site and landscape levels, after masking out water bodies and urban areas from the EVI rasters using the LULC map. We chose contrast as a proxy of site and landscape heterogeneity, since it has been recommended as suitable to capture landscape heterogeneity in human-dominated areas (Tuanmu and Jetz, 2015). We calculated mean EVI and contrast values using the available satellite image corresponding to the date closest to the sampling date as a proxy for instantaneous spatial productivity/heterogeneity of each sampling site and landscape.

To capture the temporal variability in landscape productivity and heterogeneity (i.e. spatial variability in structural and compositional features of vegetation), we calculated the coefficient of variation of the mean EVI and contrast from a total of 12 satellite images, corresponding to the sampling month and the 11 previous months. To do this, we calculated the monthly mean of EVI and contrast for each site, and then computed the coefficient of variation by dividing the standard deviation of each index by its respective 12-month mean. This temporal window was defined to detect changes in vegetation cover resulting from the various land-use management practices in the region (e.g., planting, harvesting, etc.) (Santos et al., 2021), as well as seasonal variations that may affect vegetation in these landscapes.

We computed all predictor metrics in R (version 4.3.2) (R Core Team, 2023), through several packages, including “terra” (Hijmans et al., 2023a) and “raster” (Hijmans et al., 2023b) for handling raster data, “sf” (Pebesma, 2018) for vector data operations, “landscapemetrics” (Hesselbarth et al., 2020) for calculating land cover metrics, and “rgrass” (Bivand, 2022) for accessing GRASS GIS functionalities (GRASS version 8.2 - GRASS Development Team, 2022) to calculate texture and manipulating geospatial data.

Table 1. Metrics based on a classified land use and land cover (LULC) map and unclassified Enhanced vegetation index rasters (EVI), used as predictors of small mammals occupancy in agricultural landscapes of Atlantic Forest, Brazil. Site-level metrics were calculated within a 50 m radius buffer from the center on each sampling site. Landscape-level metrics were calculated within circular buffers with radii of 1, 3, 5 and 7 km, centered on the centroid of the sampling sites within each landscape.

Metric name	Description	Unit	Source
Forest cover	Proportion of land covered by forest, including different types of Atlantic Forest formations.	Percentage	LULC map
Silviculture cover	Proportion of land covered by tree species planted for commercial purposes (e.g. pine, eucalyptus, araucaria)	Percentage	LULC map
Mosaic of uses cover	Proportion of land covered by different types of agriculture and agricultural use where it was not possible to distinguish between pasture and agriculture (i.e. a single predominant use)	Percentage	LULC map
Forest patch density	Fragmentation of the "Forest" class, standardized for the landscape area (quantified as number of patches per 100 hectares)	Density	LULC map
mean EVI	Average enhanced vegetation index, calculated from 3 m resolution PlanetScope satellite imagery. Used as a proxy for site and landscape spatial productivity (i.e. amount of green biomass)	Continuous numeric: $\geq -1; \leq 1$	EVI
EVI temporal variation	Coefficient of variation of mean EVI values from a total of 12 satellite images corresponding to the sampling month and the 11 previous months. Used as a proxy for annual variation in landscape productivity	Continuous numeric: ≥ 0	EVI
mean Contrast	Metric based on the textural characteristics of EVI (exponentially weighted difference of EVI between adjacent pixels), used as a proxy for spatial vegetation heterogeneity at site and landscape scales	Continuous numeric: ≥ 0	Image texture of EVI
Contrast temporal variation	Coefficient of variation of Contrast values from a total of 12 satellite images corresponding to the sampling month and the 11 previous months. Used as a proxy for annual variation in vegetation heterogeneity within landscapes	Continuous numeric: ≥ 0	Image texture of EVI

2.3. Modelling framework

2.3.1. Multiscale Multispecies Occupancy modeling

To test the effects of agricultural landscapes characteristics on species occurrence, we fitted multispecies occupancy models within a modelling framework that accounts for imperfect detection (Guillera-Arroita, 2017), and taking into account our multiscale sampling design. The multispecies occupancy model structure assumes that species-specific effects are drawn from a common probability distribution. Under this approach species are assumed to respond to environmental conditions in a somewhat similar way, allowing more precise estimates, particularly for rare or elusive species that are infrequently detected during surveys (Kéry and

Royle, 2016). Following our multiscale design, we describe the detection/non-detection data of each species k at the landscape i (main unit), and at the site level j (subunits) using a three level hierarchical model. Let z_{ik} be a latent variable indicating the presence (1) or absence (0) of species k in landscape i, and a_{ijk} the latent occupancy state (1 or 0) of species k at site j within landscape i. A site can only be occupied ($a_{ijk} = 1$) when the species is present in the landscape it belongs to ($z_{ik} = 1$). The observed data (i.e., detections and non-detections), y_{ijlk} , for species k, at site j, in landscape i, on sampling occasion l, are modeled as imperfect observations of the true latent occupancy state at site level, a_{ijk}, given a detection probability, p_{ijlk}. The occurrence state at landscape, $z_{ik,}$ site level, $a_{ijk,}$ and the observed detection/non-detection data, y_{ijlk}, are modeled as the outcome of Bernoulli processes:

Landscape-level presence/absence: $z_{ik} \sim$ Bernoulli (ψ_{ik})
Site-level presence/absence: $a_{ijk}|z_{ik} \sim$ Bernoulli ($z_{ik} * \theta_{ijk}$)
Survey-level detection/non-detection data: $y_{ijlk}|a_{ijk} \sim$ Bernoulli ($a_{ijk} * p_{ijlk}$)

where, ψ_{ik} is the landscape-level occupancy probability, θ_{ijk} *is* the site-level occupancy probability, and p_{ijlk} is the detection probability associated with the actual replicated detection/non-detection data y taken at a site (Kery and Royle, 2016). These probabilities were modeled as functions of landscape, site, and survey covariates using logistic regression (logit link). Intercepts and slopes (β_0s and βs) in each process were modeled as species-specific random effects drawn from community-level (hyper)distributions with estimated means and variances. This hierarchical structure allows for partial pooling of information across species, enabling inference about both individual and community-level responses. The community-level hyperparameters mean and variance were assigned semi-informative priors, Normal (0,1) for means and Inverse-Gamma (2,1) for variances, aiming to regularize species-level estimates and mitigate overfitting (Hooten and Hobbs, 2015).

Landscape-level occupancy probability was modeled as a linear function of the landscape metrics derived from the LULC map and EVI rasters (Table 1). Site-level occupancy was modeled only using EVI-derived metrics (Table 1), which capture fine-scale vegetation characteristics not accounted for by land cover classes (Silveira et al., 2023). To reduce the correlation among consecutive detections and facilitate the estimation of detection probability within each sampling occasion, we collapsed each 6–10-nights sampling period into two sampling occasions of 1-5 days interval (Pautrel et al., 2024). The probability of detection was

modeled as a function of the sampling effort (trap-nights) during each sampling occasion, the types of traps used at the sites (all three types or solely Trap1 and Trap2), and the meteorological conditions during the sampling occasion (mean temperature and mean precipitation). Temperature and precipitation data were obtained from the National Institute of Meteorology (INMET, 2024), using information from the meteorological stations closest to the sampled locations. All continuous predictors were standardized to have mean zero and variance of one.

We estimated model parameters using JAGS version 4.3.1 (Plummer, 2003), via the "R2Jags" package (Su and Yajima, 2015) in R version 4.2.3 (R Core Team, 2023). We ran three parallel chains of length 50,000, discarding the first 5,000 iterations as burn-in, and used a thinning rate of 10. We assessed MCMC convergence using the R-hat statistic, with values falling below 1.1 indicating adequate convergence (Gelman and Rubin, 1992).

2.3.2. Model selection and inference on covariate effects

We used the Watanabe-Akaike Information Criterion (WAIC) to estimate out-of-sample predictive performance of models and to select among competing models (Hooten and Hobbs, 2015). We conducted model selection using a two-step approach. In the first step, we fitted single-source metric models, each including a different subset of landscape-level covariates to represent our distinct hypotheses about the main drivers of species occupancy: (1) occupancy is primarily influenced by forest amount and fragmentation (forest patch density) (derived from LULC map), (2) occupancy responds mainly to the amount of forest and dominant land use types in the surrounding matrix (silviculture and mosaic of uses cover) (derived from LULC map), (3) occupancy is driven by spatial and temporal variation in vegetation productivity (EVI), and (4) occupancy is driven by spatial and temporal variation in vegetation heterogeneity (texture of EVI). We fitted all models using the landscape metrics calculated within the four buffer sizes (1, 3, 5, and 10 km radius), resulting in four models for each alternative hypothesis. The objectives of this step were to identify, for each model, the spatial scale that fitted the best predictions of small mammal occupancy (i.e. lowest WAIC), to assess the estimated effects of landscape covariates in these models, and to determine the spatial scale at which landscape variables most strongly influenced species occupancy, i.e. scale of effect (Jackson and Fahrig, 204) (Full procedure described in Supplementary S1). We included the landscape covariates at their respective scale of effect when fitting the multiple-metric models in the second step of model comparison. In cases where the spatial scale with the lowest WAIC did not match the scale where a given metric showed the strongest

inferential support (based on pd and ROPE, as described below), we prioritized the latter (Supplementary S1).

In the second step of model selection, we built models combining predictors derived from both LULC map and EVI-based metrics, with the aim of testing whether these models would produce improved estimates of species distributions, compared to the simpler models fitted in the first step (Prajzlerová et al., 2024; Suttidate et al., 2023). Prior to model fitting, we assessed pairwise correlations among all landscape covariates using Pearson's correlation test, and used together in a model only those not highly correlated (correlation coefficients $|r| \leq 0.70$; Dormann et al., 2013) (Supplementary Figure S1). Metrics of vegetation heterogeneity (mean Contrast and Contrast temporal variation) were highly correlated with land cover metrics, at their respective scale of effect. Mean contrast had a positive correlation with forest cover ($r = 0.73$), and contrast temporal variation was correlated with the land cover of matrix environments (positive correlation with mosaic of uses cover, $r = 0.72$; negative correlation with silviculture cover, $r = -0.83$). Given these high values of correlation, and attempting not to exclude arbitrarily any covariate, in the second step we fitted five multiple-metric models, ranging from those based solely on LULC-derived metrics to those based solely on EVI-derived metrics. To evaluate whether models combining multiple landscape metrics improved predictive performance, we compared them to simpler models containing metrics derived from a single data source using WAIC. To assess whether the estimated effect sizes and levels of support for each metric changed when included alongside other variables in a multiple-metric model, we examined the strength of evidence for each metric across both single-source and multiple-metric models.

To assess the strength of estimated covariate effects at the landscape, site, or detection level, we report the mode, the highest density credible intervals (HDIs) at 95% of the posterior distributions, and summarized the posterior distribution of each metric into Bayesian indices: probability of direction (*pd*) and Region of Practical Equivalence (ROPE) (Makowski et al., 2019). Probability of direction is defined as the proportion of the posterior distribution that has the same sign as the median. It ranges from 0.5 to 1.0 and is interpreted as the probability that a parameter effect goes in a particular direction (i.e., is positive or negative), and thus the presence of an effect (Makowski et al., 2019). The ROPE is a proportion of the HDI of a posterior distribution that lies within a region of practical relevance i.e., it outlines a range around the null value (zero) (Makowski et al., 2019). If the effect falls within this range, the magnitude of the effect is likely to be too small for practical reasons. We defined ROPE as

±0.10 (logit scale), in an attempt to treat only very small coefficients as "negligible" effect size (Makowski et al., 2019).

The site-level covariates (mean EVI and mean contrast), and survey-specific covariates (trap type, sampling effort, and meteorological conditions) were included in all candidate model formulations, but we assessed their effects using only the top-ranked models based on the WAIC. We summarized overall metacommunity patterns by estimating the mean occupancy probability and mean detection probability across species, based on posterior simulations of community-level intercepts from the top-ranked models, transforming back to the probability scales (Kéry and Royle, 2016).

2.3.3. Model Checking and Validation

In order to assess model fit, we performed Bayesian p-value goodness-of-fit tests for each of the fitted models (Broms et al., 2016). The Bayesian p-value test was calculated as the proportion of times that the deviance of the observed data was greater than the deviance of detection data predicted from the model. For a model that fits well, the Bayesian p-value should be close to 0.5, and if it is greater than 0.95 or less than 0.05, the model does not fit the data well (Broms et al., 2016). To assess model predictive performance, we computed the posterior distribution of the area under the receiver operating characteristic curve (AUC-ROC) using training data. The AUC is a rank-based metric that quantifies the model's ability to distinguish between observed detections and non-detections. In this context, it evaluates how well the predicted (unconditional) detection probabilities - derived from landscape-level occupancy (ψ), site-level occupancy (θ), and conditional detection (p) probabilities- correspond to the observed detection patterns. Higher AUC values indicate better discriminative ability, with 1.0 representing perfect prediction and 0.5 indicating prediction no better than chance.

We performed all model assessment and comparison analysis in R version 4.3.2 (R Core Team, 2023), using the "pROC" package (Robin et al., 2011) to calculate AUC, the "loo" package (Vehtari et al., 2017) to calculate WAIC, and "bayestestR" package (Makowski et al., 2024) to calculate the mode values, HDIs, and the indices *pd* and ROPE. All figures were created using the "ggplot2" package (Wickham, 2016).

3. Results

With a total sampling effort of 29,160 trap-nights, we captured 616 individuals of 23 small mammal species, seven belonging to the order Didelphimorphia and 16 to order Rodentia. Among them, 10 species are endemic to the Atlantic Forest, including two marsupials (*Monodelphis iheringi*, *Monodelphis scalops*) and eight rodents (*Delomys sublineatus*, *Brucepattersonius cf. nebulosus* [*Brucepattersonius* sp. 1], *Brucepattersonius cf. soricinus* [*Brucepattersonius sp*. 2], *Juliomys pictipes*, *Juliomys ossitenuis*, *Thaptomys nigrita*, *Euryoryzomys russatus*, *Sooretamys angouya*) (Abreu et al., 2024). Other species are typical of open formations, secondary vegetation, and agricultural fields (*Calomys tener*, *Necromys lasiurus*), or grasslands *(Monodelphis dimidiata*) (Patton et al., 2015; Vilela et al., 2010). Two of the rodent species were exotic invasive (*Rattus rattus* and *Mus musculus*). We excluded these exotic species from our analyses to avoid violating the assumptions of the multispecies occupancy model (i.e., that species respond to environmental conditions in a relatively similar manner), as their presence in the study area is likely a direct result of human introduction rather than natural habitat use.

The scales of effect for landscape metrics differed between LULC map-based and EVI-based metrics (Supplementary Table S1). The effects of forest cover and fragmentation had stronger evidence at the smaller landscape scale (1 km radius), while the amount of silviculture and mosaic of uses had the strongest support at a 3 km and 5 km radius, respectively. For EVI-based metrics, mean productivity (EVI) and vegetation heterogeneity (contrast) had the strongest support at the 3 km scale, whereas their temporal variability was best supported at 7 km and 5 km scales, respectively. In LULC map-based models, the estimates indicate a positive effect of forest cover and fragmentation, silviculture cover, and a negative effect of increased cover of mosaic of uses (Supplementary Table S1). In EVI-based models, the estimates indicate a positive effect of landscape productivity, but negative of vegetation heterogeneity, and of temporal variation in vegetation productivity and heterogeneity (Supplementary Table S1). The strength of evidence for the significance of these effects in the simpler single-source models varied from strong to weak (Supplementary Table S1), with the strongest support for mosaic of uses cover (Mode = -0.72, 95% HDI [-1.50, 0.06]; pd=96.78%; 3.33% in ROPE), and the weakest for EVI temporal variation (Mode = -0.18, 95% HDI [-0.95, 0.56]; pd=69.10%; 20.08% in ROPE).

When comparing simpler single-source models with multiple-metric models, three models received similar support based on WAIC (ΔWAIC $\leq$ 2.1):(1) a multiple covariate model including forest cover, forest patch density, and land cover of silviculture and mosaic of uses classes; (2) a simpler single-source model at 1 km radius, including forest cover and land

cover of silviculture and mosaic of uses classes; and (3) a simpler single-source model including mean contrast and its temporal variability (Table 2). The metrics with the strongest support in these models were mosaic of uses cover (Mode = -0.78, 95% HDI [-1.76, 0.23]; pd=93.14%; 5.88% in ROPE), contrast temporal variation (Mode = -0.58, 89% HDI [-1.24, 0.08]; pd=92.29%; 7.19% in ROPE), and silviculture cover (Mode = 0.51, 89% HDI [-0.34, 1.45]; pd=83.78%; 9.53% in ROPE). The WAIC estimates of all models exhibited relatively large standard errors (SE > 35), indicating substantial uncertainty in the estimates (Table 2). Therefore, it is not possible to assert with confidence that the top-ranked models are clearly better than the others based solely on WAIC (Gelman et al., 2014). All models showed adequate fit to the data and good predictive performance, as indicated by AUC and Bayesian p-values (Table 2).

Table 2: Model selection results for assessing the effects of landscape metrics derived from both classified (LULC map-based) and unclassified (EVI-based) remotely sensed data using multispecies occupancy models of small mammals. Models were fitted using landscape metrics calculated within four spatial buffers (1, 3, 5, and 7 km radii) evaluate predictive performance and determine each metric's scale of effect. We present the scale of effect of each landscape metric combined into multiple-metric models including uncorrelated predictors (|r|<0.70). Results include the central tendency (mode), 95% credible intervals, and Bayesian indices: probability of direction (pd), and the proportion of the posterior within the Region of Practical Equivalence (ROPE). Model fit and predictive performance were assessed using the Area Under the Curve (AUC) and the Bayesian p-value; We used Watanabe-Akaike Information Criterion (WAIC) and its standard error (SE) to compare models. Bolded entries indicate models with ΔWAIC < 2.1, and metrics with the stronger evidence within the respective multiple-metric model. Table of model comparison including all candidate models is available in Supplementary Table S1.

	Landscape metric	Mode	pd	ROPE (-0.10, 0.10)	HDI 95%	AUC	Bayesian p-value	WAIC (SE)
SINGLE-SOURCE MODELS								
Forest cover and fragmentation								
1km	*Forest cover*	0.39	84.95	12.88	-0.39, 1.15	0.88	0.12	873.6 (35.5)
	Forest patch density	0.53	93.91	7.03	-0.16, 1.23			
Landscape composition								
1km	*Forest cover*	-0.27	68.59	15.08	-1.28, 0.70	0.89	0.12	**869.3 (35.2)**
	Silviculture cover	0.21	71.90	14.81	-0.66, 1.27			
	Mosaic of uses cover	-0.78	93.14	5.88	-1.76, 0.23			
Productivity (EVI)								
3km	*mean EVI*	0.35	84.57	14.86	-0.34, 1.07	0.86	0.12	892.1 (36.9)
	EVI temporal variation	0.05	52.08	21.24	-0.82, 0.77			
Contrast								
5km	*mean Contrast*	-0.08	61.39	21.82	-0.88, 0.67	0.88	0.12	**871.2 (35.3)**
	Contrast temporal variation	-0.58	92.29	7.19	-1.42, 0.23			

MULTIPLE-METRIC MODELS								
M01: Class map - based						0.90	0.11	**869.1 (35.2)**
	Forest_1km	0.14	68.84	16.79	-0.69, 1.16			
	Forest patch density_1km	0.30	73.40	15.18	-0.58, 1.21			
	Silviculture_3km	**0.49**	**83.35**	**9.74**	**-0.56, 1.77**			
	Mosaic of uses_5km	-0.21	70.64	15.18	-1.19, 0.68			
M02: Class map and EVI-based						0.90	0.11	877.2 (35.6)
	Forest_1km	0.32	76.84	13.62	-0.57, 1.33			
	Forest patch density_1km	0.17	63.91	16.22	-0.80, 1.11			
	Contrast temporal variation_5km	**-0.68**	**90.30**	**6.22**	**-1.72, 0.39**			
	mean EVI_3km	0.43	86.36	10.09	-0.41, 1.38			
	EVI temporal variation_7km	-0.07	61.74	19.28	-1.06, 0.71			
M03: EVI-based						0.90	0.12	878.4 (35.7)
	mean Contrast_3km	-0.11	59.11	19.67	-0.99, 0.74			
	Contrast temporal variation_5km	**-0.82**	**95.34**	**4.19**	**-1.76, 0.14**			
	Mean EVI_3km	0.43	83.92	11.65	-0.42, 1.35			
	EVI temporal variation_7km	-0.15	63.72	17.91	-1.11, 0.70			
M04: Class map and EVI-based						0.90	0.12	879.4 (35.7)
	Forest_1km	0.34	72.99	14.29	-0.67, 1.34			
	Forest patch density_1km	0.17	63.40	16.07	-0.83, 1.15			
	Silviculture_3km	0.65	85.76	7.33	-0.58, 2.01			
	mean EVI_3km	**0.55**	**89.95**	**8.04**	**-0.30, 1.60**			

	EVI temporal variation_7km	0.17	64.69	16.40	-0.81, 1.12			
	Mosaic of uses_5km	-0.39	75.30	13.36	-1.38, 0.67			
M05: Class map and EVI-based						0.90	0.12	881.0 (35.8)
	mean Contrast_3km	-0.13	58.93	17.53	-1.03, 0.80			
	Forest patch density_1km	-0.07	56.60	19.73	-0.90, 0.84			
	Contrast temporal variation_5km	**-0.86**	**93.69**	**4.72**	**-1.90, 0.24**			
	mean EVI_3km	0.44	83.59	11.28	-0.48, 1.45			
	EVI temporal variation_7km	-0.19	64.50	17.09	-1.12, 0.77			

Comparing the coefficients of all landscape metrics - each at its respective scale of effect - across the simpler and multiple-metric models, we found that some metrics - silviculture, mean EVI, EVI temporal variation, and contrast temporal variation - showed consistent estimated effects and strength of evidence, even when included alongside other predictors . In contrast, other metrics exhibited reduced estimated effects and lower levels of support in the multiple covariate models: forest cover, forest patch density, mosaic of uses cover, and mean contrast (Table 2). Among the metrics with consistent support, contrast temporal variation showed the highest *pd*, ranging from 90.30% to 95.35% across models, indicating a high probability of its negative effect. Additionally, less than 7.5% of its posterior distribution fell within the ROPE across these models, suggesting that the effect size is meaningful (Table 2).

The high correlation between contrast temporal variation and both mosaic of uses cover and silviculture cover, suggests that contrast temporal variation effectively reflects temporal variation in vegetation structure resulting from land-use dynamics in the agricultural matrix. Therefore, we used the simpler contrast-based model to summarize overall metacommunity patterns, estimate community-level and species-specific responses to landscape-level temporal variability in vegetation heterogeneity. Additionally, we also use this model to assess the effects of site-level productivity and vegetation heterogeneity, and of survey-specific covariates on detection probability. Based on this model, we found that most species in the metacommunity are moderately likely to occur across landscapes (mean $\psi = 0.54$; median = 0.55; Q1 = 0.35, Q3 = 0.73), while a few exhibit more restricted distributions, with low occupancy probabilities. Site-level occupancy probability per species was also moderate (mean $\theta = 0.50$; median = 0.50; Q1 = 0.37, Q3 = 0.63), and the average detection probability as well (mean $p = 0.45$; median = 0.44; Q1 = 0.32, Q3 = 0.58). Variation among species was lower at the site-level and detection probabilities compared to the landscape-level expected occupancy.

The community-level effect of temporal variability in vegetation heterogeneity (contrast) indicates a decrease in mean occupancy as temporal variation increases, with average occupancy dropping from approximately 65% in more stable landscapes to around 40% in highly variable ones (Figure 2).

At species level, estimates of our selected model demonstrated that, in general, species-specific responses to temporal variation on landscape contrast vary around the mean response of the community with no clear pattern related to their taxonomic group (Didelphimorphia [marsupials] or Rodentia) (Figure 3). However, and despite the substantial credible intervals, we notice that four species show a greater deviation from the common mean: the marsupials

Didelphis aurita and *Monodelphis dimidiata* presented a higher positive response to temporal variation of contrast, whereas the marsupial *Gracilinanus microtarsus* and the rodent *Thaptomys nigrita* presented higher negative response (Figure 3).

Species-specific occupancy estimates across all landscapes showed that most species had higher estimated occupancy probability in landscapes with lower temporal variation in vegetation heterogeneity (contrast) along the year (Figure 4). That includes common generalist species, such as *Calomys tener*, *Olygoryzomys nigripes*, and *Gracilinanus microtarsus,* as well as Atlantic Forest endemic species, *Delomys sublineatus*, *Euryoryzomys russatus, Sooretamys angouya* and *Thaptomys nigrita* (Figure 4). Two species of marsupials, *Didelphis aurita* and *Monodelphis dimidiata* had an opposite response, being more likely to occur in landscapes with higher temporal variation of contrast (Figure 4).

We did not find evidence for the effects of site-level mean EVI and mean contrast on community mean occupancy (Supplementary Table S2). However, we found strong evidence of a negative effect of using Trap3 during the first months of sampling on the mean detection of the community (Mode = -1.03; 89% HDI [-1.61, -0.38]; *pd*[99.41]; ROPE[0.00]). Sampling effort and meteorological conditions during sampling occasions did not have a clear effect on community mean detection (Supplementary Table S2).

4. Discussion

Contrary to our expectations, our results indicate that small mammal occupancy in the study region can be predicted equally well by broad LULC classes and by fine-scale measures of variation in vegetation productivity and heterogeneity. However, spatiotemporal measures of fine-scale vegetation variation captured effects of dynamic aspects of matrix land use that would not be discernible from LULC map-based metrics alone. We found strong evidence that community mean occupancy increases in more fragmented landscapes (high forest patch density) and decreases in those dominated by agropastoral activities, as expected. However, the weight of evidence for these class metrics (forest patch density and mosaic of uses cover) was strong only when tested in models that included other LULC map-based landscape metrics, indicating that they do not fully capture the complexity of these agroecosystems.

Among the EVI-based metrics, we found consistent evidence for a negative effect of contrast temporal variation across all models in which it was included. Given its high collinearity with land cover of matrix classes (mosaic of uses and silviculture), the temporal variability in

contrast seems to reflect the effects of annual variation in vegetation characteristics resulting from different farming systems in these landscapes. Both broad land cover characteristics and fine-scale spatial and temporal variability in vegetation characteristics can play important roles in determining biodiversity patterns (Delciellos et al., 2016; Silveira et al., 2023). Similarly to our findings, previous studies comparing the predictive ability of classified and unclassified remote-sensing metrics for explaining bird distribution and richness have reported comparable support for predictors derived from both sources (Prajzlerová et al., 2024), or even improved performance when these predictors were combined (Suttidate et al., 2023). Our results suggest that using high-resolution satellite imagery to capture detailed spatio-temporal variability in vegetation within fragmented landscapes may lead to a better understanding of which aspects of anthropogenic land-uses are driving biodiversity change.

Agricultural landscapes are inherently dynamic due to crop phenology cycles, cropping systems, and management practices (Santos et al., 2021). In fragmented landscapes, environmental noise is expected to promote faster extinction of species that disperse and compete over short distances, but delays extinction of species that disperse and compete over longer distances (Tao et al., 2024). Most of the small mammal species recorded have small body size, and are not expected to disperse over large distances (Pires et al., 2002), especially through pasture and agricultural matrices (Pires et al., 2002; Santos-Filho et al., 2012; Umetsu and Pardini, 2007). This low dispersion capability can explain the estimated reduction in community mean occupancy with the increase in temporal variation of vegetation heterogeneity (contrast temporal variation) across the landscapes in our study area. High temporal variability in vegetation characteristics, particularly that resulting from the management of agricultural areas, may reduce both occupancy and population sizes of less mobile species potentially driving some of them to local extinction (Escobar and Estades, 2021; Tao et al., 2024). Escobar and Estades (2021) showed that the survival of mobile mice species almost doubled that of the less mobile mice species after forest plantation clearcutting. More mobile individuals survived by leaving the clear-cutting area and relocating to undisturbed ones, allowing them to persist in neighboring habitats after clearcutting operations (Escobar and Estades, 2021). In our study, the species with the highest dispersal capacity among the detected small mammals was the marsupial *Didelphis aurita* (Pires et al., 2002), which showed a positive estimated coefficient for contrast temporal variation, in contrast to the negative average estimate at the community level. The ability of long distance dispersers, as *D. aurita,* to move across different areas of the fragmented landscapes may

allow some individuals to randomly encounter suitable habitats, albeit temporary, thus favoring their persistence in these landscapes (Tao et al., 2024; Umetsu et al., 2008).

By analyzing individual occupancy probabilities across landscapes with different levels of temporal variation in vegetation heterogeneity, we observed that both Atlantic Forest endemics and disturbance-adapted species showed high occupancy probability in landscapes with lower temporal variability in vegetation heterogeneity. The opposite pattern was observed in landscapes with the highest variability, where the occupancy probability of endemic species such as *Euryoryzomys russatus*, *Sooretamys angouya*, and *Thaptomys nigrita* appeared to be particularly reduced. This may relate to the reduced cover of forest environments (natural or plantations) in more temporally varying landscapes (Umetsu and Pardini, 2007). In our study, in addition to native forest sites, we detected four Atlantic Forest endemic species (*Brucepatersonius* sp1., *Thaptomys nigrita*, *Monodelphis scalops*, and *Monodelphis iheringi*) in eucalyptus plantations within two of the landscapes with lowest contrast temporal variation, one of which had only 16% of forest cover (at 1km radius). Such results contrast those by Estavillo et al. (2013), who captured forest specialists in the matrix only in landscapes with forest cover above 30%. The use of the matrix by forest-dependent species in fragmented landscapes may help explain the unclear effects of forest cover and fragmentation observed in our models when analyzed alongside either land cover of matrix classes or EVI-derived metrics (Umetsu et al., 2008). Our findings reinforce the importance of matrix characteristics in complementing habitat or enhancing connectivity to support the persistence of small mammals in fragmented landscapes (Umetsu et al., 2008).

Although we hypothesized that the differences in occupancy across sites would be driven by differences in local vegetation productivity or heterogeneity, we found no clear evidence that either site-level mean EVI and mean contrast influenced species occupancy at sites within the landscapes. Andreo et al. (2019) found that metrics derived from vegetation indices (EVI and NDVI) were more effective to predict mice abundance and distribution in agroecosystems of central Argentina when measured one or two months before trapping than those measured at the time of trapping. In our analysis, we evaluated only the mean EVI and mean contrast of one point in time of the sampling month, but not their temporal variation. At smaller spatial scales within fragmented landscapes, the persistence of low dispersal species may exhibit a pattern opposite to that observed in larger landscapes, that is, a delayed metapopulation extinction in more variable areas (Tao et al., 2024). Therefore, some unexpected occurrences at landscape scale may actually reflect smaller scale processes not captured by our

instantaneous site-level predictors. For example, we detected an endemic small arboreal rodent, *Juliomys pictipes*, in forest fragments located within a highly variable landscape. According to the trend in model estimates and theoretical expectations for large areas (Tao et al., 2024), it should present low probabilities of occurrence in this landscape, but our model estimated high occupancy probability, although with high uncertainty (Supplementary Figure S2). Notably, the expected occupancy probability of *J. ossitenuis,* also endemic small arboreal rodent, can be either low or high in highly variable landscapes (Figure 4). Such ambiguous and uncertain estimates may be explained by opposing effects of environmental variability at smaller spatial scales around isolated forest patches (Tao et al., 2024), which were not accounted for in this study. Considering our results along with recent findings, we suggest that future studies in agricultural landscapes should investigate the effects of temporal variability in vegetation characteristics as a predictor of species occurrence in both local and landscape scales (Lee et al., 2024; Marston et al., 2023).

The marsupial *Monodelphis dimidiata* is another species that deviated from the overall community-level occupancy pattern, showing a positive response to increased temporal variability in vegetation heterogeneity at the landscape level. *M. dimidiata* is generally associated with open habitats across its distribution in the Pampas and Atlantic Forest domains (Vilela et al., 2010). In our study, the species was detected exclusively at pasture sites (not used for grazing), located in landscapes with the highest levels of temporal contrast variability. We believe that in our study region, this species is restricted to pasture areas with specific characteristics, such as ungrazed sites dominated by dense grass cover (VBD personal observation). Therefore, although heterogenous spatio-temporally variable landscapes may lead to local extinctions of many species of the region pool, they can still offer favorable stable microhabitats that allow the persistence of *M. dimidiata*. This may be possible due to its preference to avoid dispersal into unsuitable temporary habitats (Tao et al., 2024).

While we found no evidence that meteorological conditions or the differences in sampling effort at some sites influenced the community-level detection probability, we found strong evidence that using Trap3 during the first months of sampling reduced the community's mean detection probability. This trap was the largest among those we used, and we suspect that its trigger mechanism may be less sensitive to light species (Barros et al., 2015), which include many of the species recorded during sampling. However, we cannot confidently attribute the lower detection of communities to Trap3 design, as we did not perform a specific test to isolate its effect from other potential causes. Future studies targeting small non-volant

mammals, particularly in areas where very small species are expected should carefully consider the potential effects of larger traps and trigger sensitivity on species detectability, since it can affect biodiversity estimates (Barros et al., 2015; Rocha et al., 2023). The most recommended methodological strategy to capture a higher diversity of species in small mammal communities is to combine live traps with pitfall traps (Bovendorp et al., 2017a; Palmeirim et al., 2020). However, the cost of deploying both trap types across a large number of sites and landscapes can be impractical, often limiting their use to forested areas and few landscapes. Although our model estimates suggest that most species from the regional pool tend to be widespread across the region, some species show more restricted occurrences, both across landscapes and within specific ones. Therefore, to improve cost-efficiency in future studies that rely solely on live traps to sample small non-volant mammals in highly heterogeneous regions, such as much of the Atlantic Forest, a valuable strategy would be to sample communities across a broader range of locations within the region of interest, with particular attention to the focal landscapes, including matrix environments (Umetsu and Pardini, 2008).

Since agricultural land use is the main driver of habitat loss in biodiversity hotspots, it becomes imperative to understand its effects on biodiversity in order to define effective management strategies that reconcile biodiversity conservation with agricultural production (Kong et al., 2021). In this study we showed that indices derived from high resolution satellite imagery capture spatiotemporal variability in vegetation characteristics resulting from anthropogenic land uses, and can explain the occurrence of small mammals in fragmented landscapes of Atlantic Forest. Our results indicate that fragmented landscapes, where land uses maintain more stable vegetation characteristics throughout the year, can support the occurrence of species with diverse habitat requirements, including generalists and forest dependent ones. Thus, conservation planning in heterogeneous fragmented landscapes can benefit from the complementary insights offered by spatiotemporal metrics derived from vegetation indices along with standard LULC maps. These additional metrics can be particularly valuable for refining information within broad classes such as mosaics of uses, where the difference between pasture and agriculture farming areas is not distinguishable (MapBiomas, 2022). Future studies should also evaluate the impacts of temporal variability of vegetation within fragmented landscapes on different aspects of biodiversity of the Atlantic Forest, including phylogenetic and functional diversity.

Acknowledgements

We thank small mammal taxonomist Prof. Dr. Alexandre Reis Percequillo (ESALq – Piracicaba/SP) and his team for their support with the identification and curation of the collected specimens, as well as for lending part of the traps used during sampling. We also thank Prof. Dr. Renata Pardini (USP – São Paulo/SP) for lending additional traps used in this study. We are grateful to Lucas Zordan, Rafael Souza, technicians from UNESP, and all field assistants who were essential to the success of the fieldwork. We are deeply thankful to all farm owners and protected area managers who kindly allowed our team to carry out the sampling on their properties. This study had the collaboration of infrastructure and support from the Pierre Kaufmann Observatory Radio, located in the city of Atibaia, Sao Paulo. The Pierre Kaufmann Radio Observatory is an institution maintained and operated by the Mackenzie Presbyterian University through its Mackenzie Radio Astronomy and Astrophysics Center (CRAAM) in collaboration with the National Institute for Space Research (INPE). We kindly thank Guilherme Alaia for all the support that he gives to the LTER CCM team.

Funding: This work was supported by the Coordination for the Improvement of Higher Education Personnel – Brazil (CAPES) (Finance Codes: 88887.817847/2023-00 and 88887.899640/2023-00); the Sao Paulo Research Foundation - FAPESP (Finance Codes: #2013/50421-2; #2020/01779-5; #2021/06668-0; #2021/08322-3; #2021/08534-0; #2021/10195-0; #2021/10639-5; #2022/10760-1) and National Council for Scientific and Technological Development - CNPq (Finance Codes: #442147/2020-1; #402765/2021-4; #313016/2021-6; #440145/2022-8; 420094/2023-7; 446029/2024-6; 421464/2025-9), and São Paulo State University - UNESP; ´Ramón y Cajal´ fellowship (RYC2020-028826-I) funded by MCIN/AEI/10.13039/501100011033 and “ESF Investing in your future”; CSIC (Proyecto Intramural-20223AT013 to GGA); and Leverhulme Centre for Nature Recovery (University of Oxford). This study is also part of the Center for Research on Biodiversity Dynamics and Climate Change, which is financed by the Sao Paulo Research Foundation - FAPESP.

Declaration of generative AI and AI-assisted technologies in the writing process

During the preparation of this work the authors used ChatGPT in order to improve English language, grammar and readability. After using this tool/service, the authors reviewed and edited the content as needed and take full responsibility for the content of the publication.

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Highlights

- Small mammal occupancy in agroecosystems of Atlantic Forest can be predicted equally well by broad land use and land cover classes or by fine-scale measures of vegetation characteristics derived from vegetation index
- Metrics derived from a vegetation index provided complementary insights into the effects of spatiotemporal variability in vegetation characteristics driven by anthropogenic land uses that are not discernible from land cover classes alone
- Fragmented landscapes in which land uses maintain more stable vegetation characteristics throughout the year can support a greater number of species with diverse habitat requirements, including generalists and endemic forest-dependent species

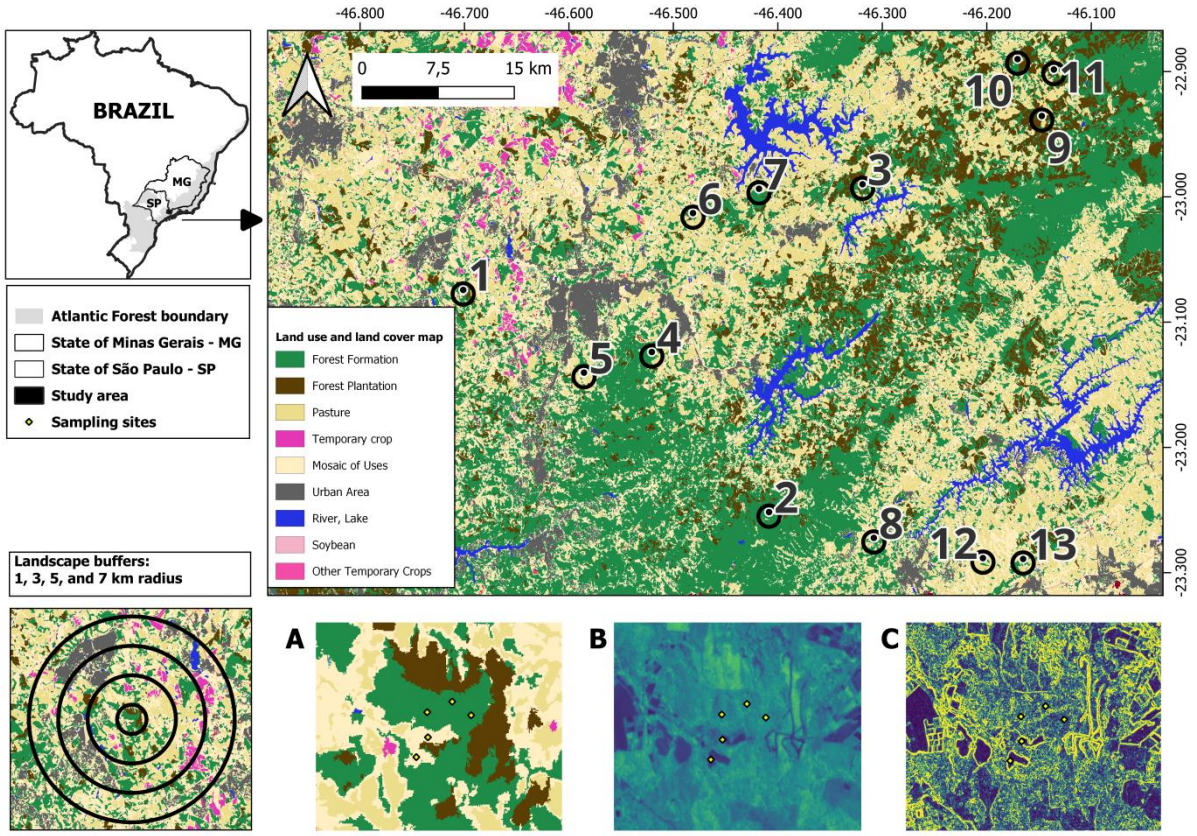

Figure1: Map of the study area showing the 13 agricultural landscapes where small non-volant mammals were sampled within an Atlantic Forest region located between the states of São Paulo (SP) and southern Minas Gerais (MG), Brazil. Standard classified and unclassified landscape metrics were calculated within circular buffers with radii of 1,000 to 7,000 meters, centered on the centroid of 4-5 sampling sites in each landscape. A) Landscape 1 and the location of its respective sampling sites shown over the standard land use and land cover class map (MapBiomas – Collection 2 (beta)); B) Landscape 1 and the location of its respective sampling sites shown over the Enhanced Vegetation Index (EVI) raster from September 2023, derived from PlanetScope satellite imagery (Planet Team, 2024); C) Landscape 1 and the location of its respective sampling sites shown over the image texture of EVI (Contrast) from September 2023.

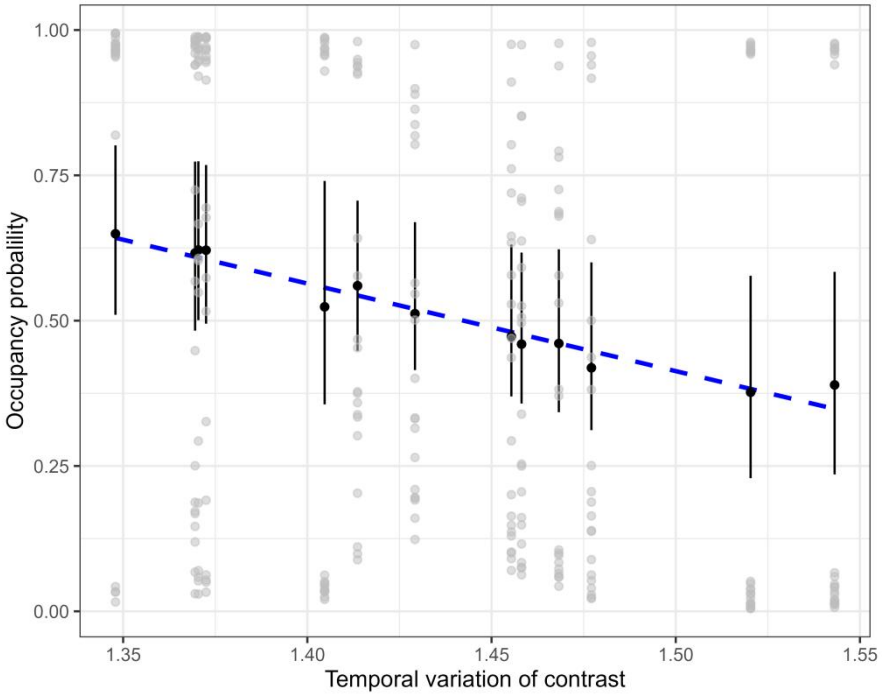

Figure 2: Small mammal community mean occupancy estimated across 13 agricultural landscapes in a region of Atlantic Forest, Brazil, in response to temporal variability of vegetation heterogeneity (contrast) at a 5 km buffer. Estimated mode (black dots) and 95% (black line) credible intervals are presented. The dashed blue line represents the linear trend between contrast temporal variation at the landscape and the community mean occupancy. Gray dots are the estimated occupancy probabilities of the 21 species within each landscape.

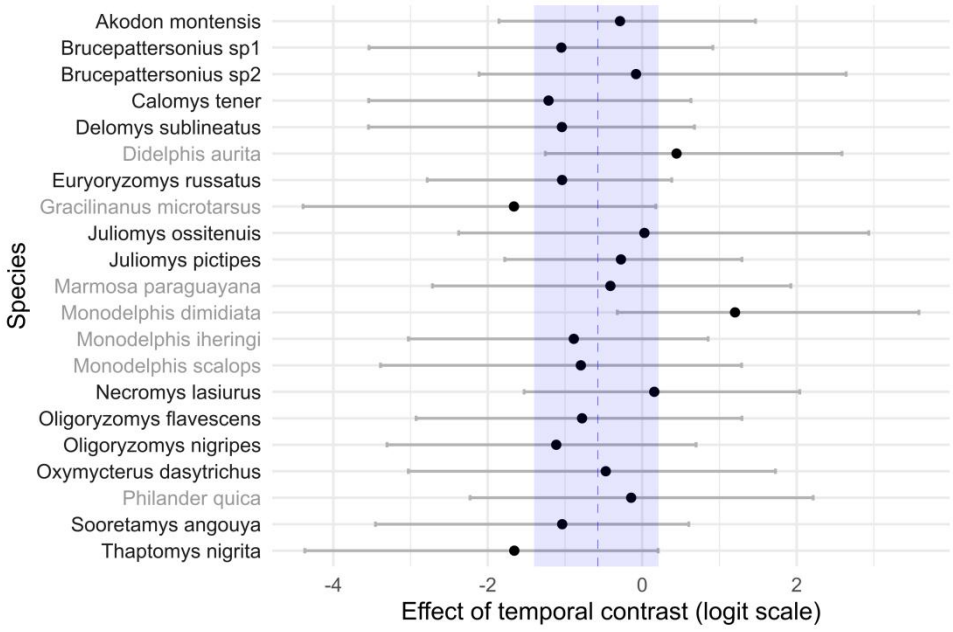

Figure 3: Community-level mean effect (mean of the distribution of species-specific regression coefficients) and species-specific effects (estimated regression coefficients) of temporal variability in vegetation heterogeneity (contrast) on small mammals' occupancy in

agricultural landscapes of the Atlantic Forest, Brazil. We present the mode (black dots) for species-specific effects, along with their 95% (grey line) credible intervals. Community-level mean effect (dashed blue line) and its associated 95% credible intervals are represented in the shaded (blue) background. .

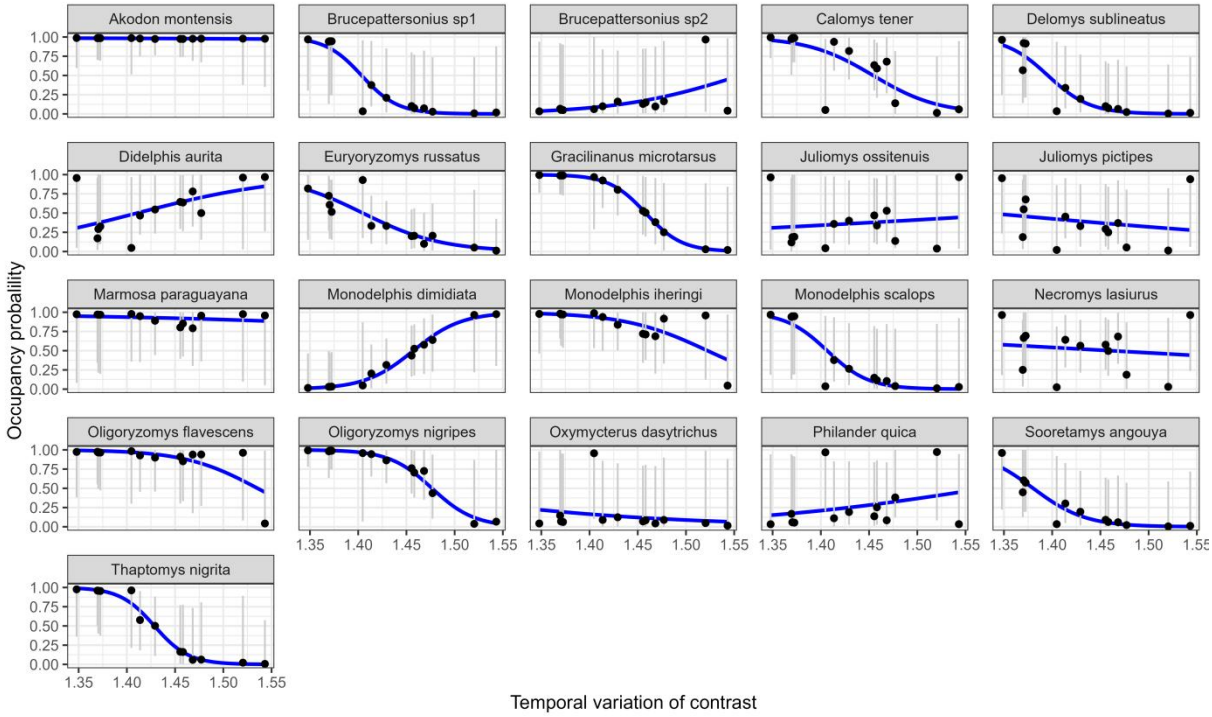

Figure 4: Species-specific occupancy probability estimates and their 95% credible intervals (gray lines) in response to temporal variability in vegetation heterogeneity within landscapes (contrast). The blue line represents the linear trend between contrast temporal variation at the landscape and the species occupancy estimate.

Temporal stability of vegetation across agricultural land uses enhances small non-volant mammal occurrence in the Brazilian Atlantic Forest

SUPPLEMENTARY MATERIAL

S1. Scale of effect selection

To determine the spatial scale at which each landscape predictor better explains the occurrence of small mammals (Jackson and Fahrig, 2012), we tested our models in four spatial scales, i.e., concentric circles with 1, 3, 5 and 7 kilometers of radii. These range of scales were chosen based on the minimum size necessary to include all sampling sites (1km) and 0.5 * the maximum dispersal distance of the largest captured species, *Didelphis albiventris* and *Philander quica* (Jackson and Fahrig, 2012). We estimated potential dispersal distances for these species based on their maximum reported home ranges, converting these values using the approach proposed by Bowman et al. (2002). Following Jackson and Fahrig (2012), we used these estimates to define the upper limit of scales, and plausible range of spatial scales to test for landscape effects (Table 1). Thus, we treated the estimated dispersal distance as an upper limit (7 km radius) and additionally tested intermediate scales (3 km and 5 km radii), along with a lower bound of 1 km. The scale of the predictor effect was chosen as the one where the estimated parameter of the metric had the clearest effect on the community mean occupancy, based on the Bayesian indices: probability of direction (*pd*) and region of practical equivalence (ROPE) (Makowski et al., 2019). Probability of direction is defined as the proportion of the posterior distribution that has the same sign as the median. It ranges from 0.5 to 1.0 and is interpreted as the probability that a parameter effect goes in a particular direction (i.e., is positive or negative), and thus the presence of an effect (Makowski et al., 2019). The ROPE is a proportion of the HDI (89%) of a posterior distribution that lies within a region of practical relevance e.g., it outlines a range around the null value (zero), thus indicating if the magnitude of the effect is practically meaningful (Makowski et al., 2019).

Table 1: Determination of the upper limit of the spatial scales used for estimating the scale of effect of landscape covariates on small non-volant mammals in the Brazilian Atlantic Forest cover region. Home range references: *Didelphis aurita*: Cerbocini et al., 2011; *Philander quica*: Lira and Fernandez, 2009. MDD – Maximal dispersal distance (Bowman et al., 2002).

Species	Home range (m²)	√Home range (m)	MDD	0.3*MDD	0.5*MDD
Philander quica	121000	347,85	13914	4174,20	6957
Didelphis aurita	95200	308,54	12341,6	3702,48	6170,55

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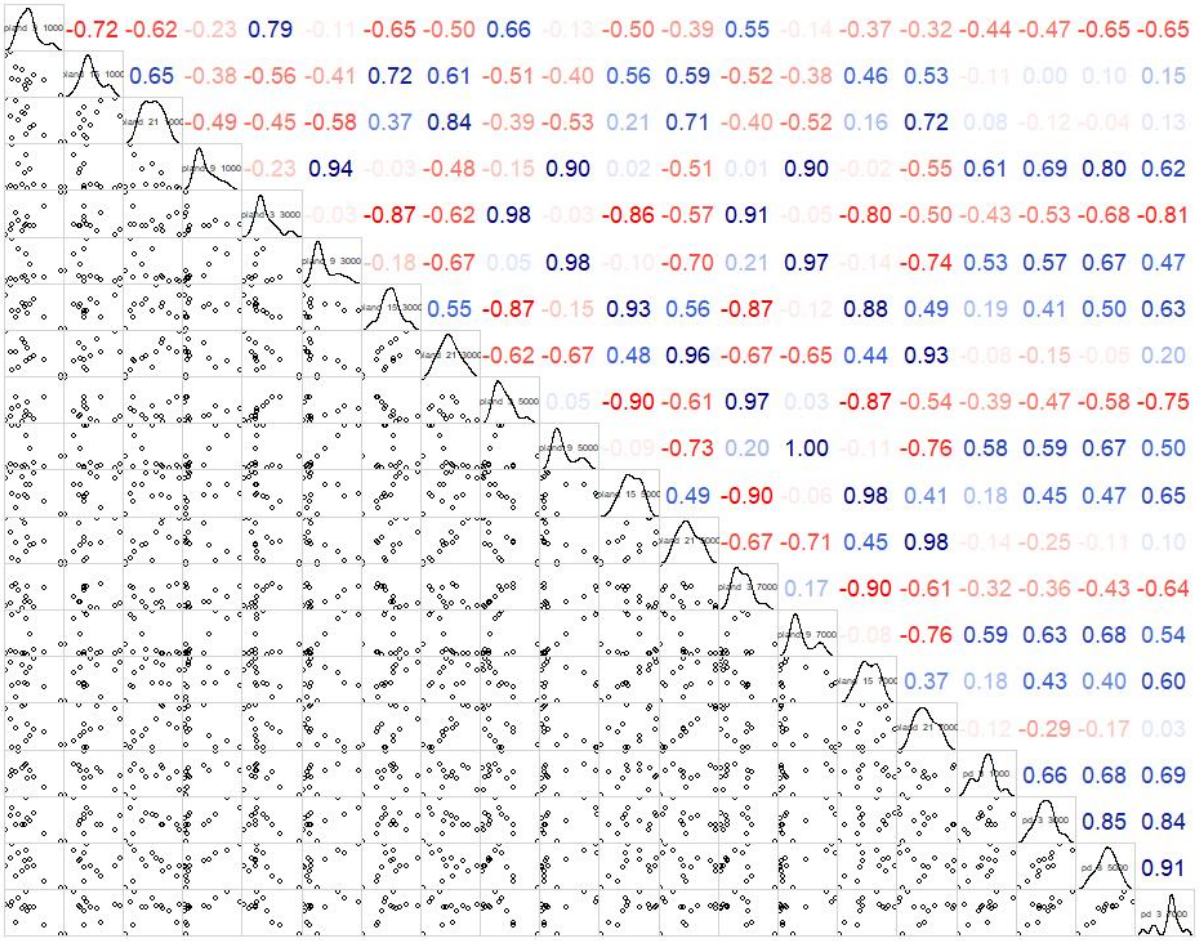
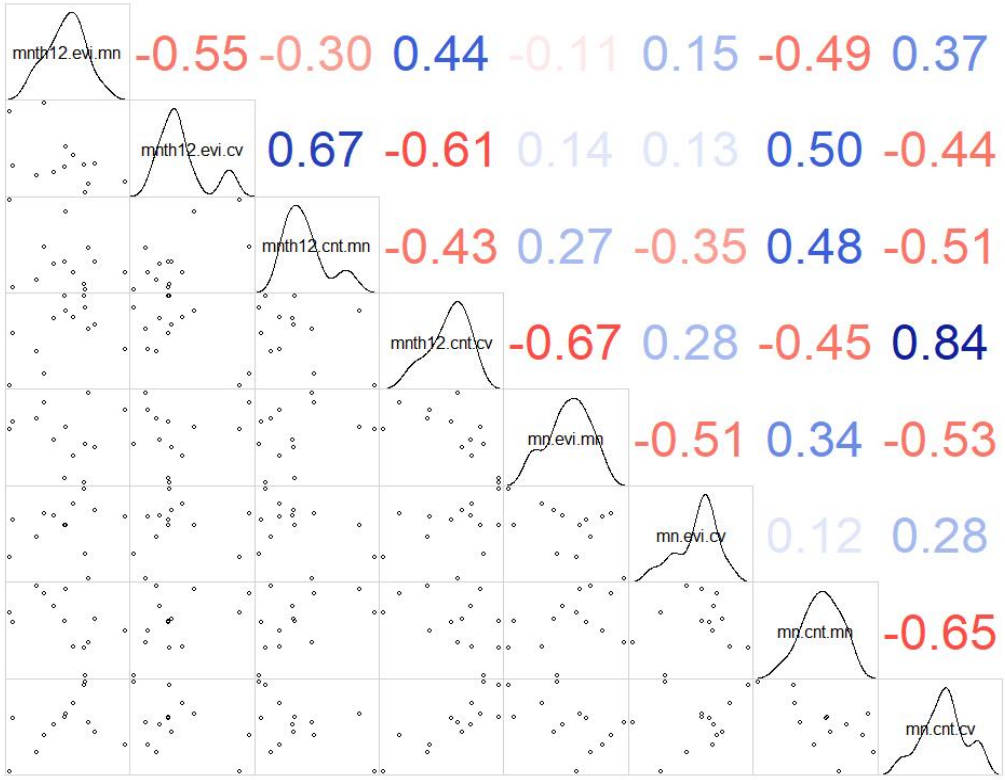
Figure S1. Pearson's correlation between landscape metrics derived from land use and land cover map and a vegetation index (EVI), calculated across four spatial scales (1, 3, 5, and 7 km radii). Abbreviations: Class metrics: pland = percentage of land cover; pd = forest patch density; Unclassified (EVI-based) metrics: mnth12.metric.mn = mean value of the metric in a given month (EVI or Contrast); mn.metric.cv = coefficient of variation of the monthly mean values (temporal variation).

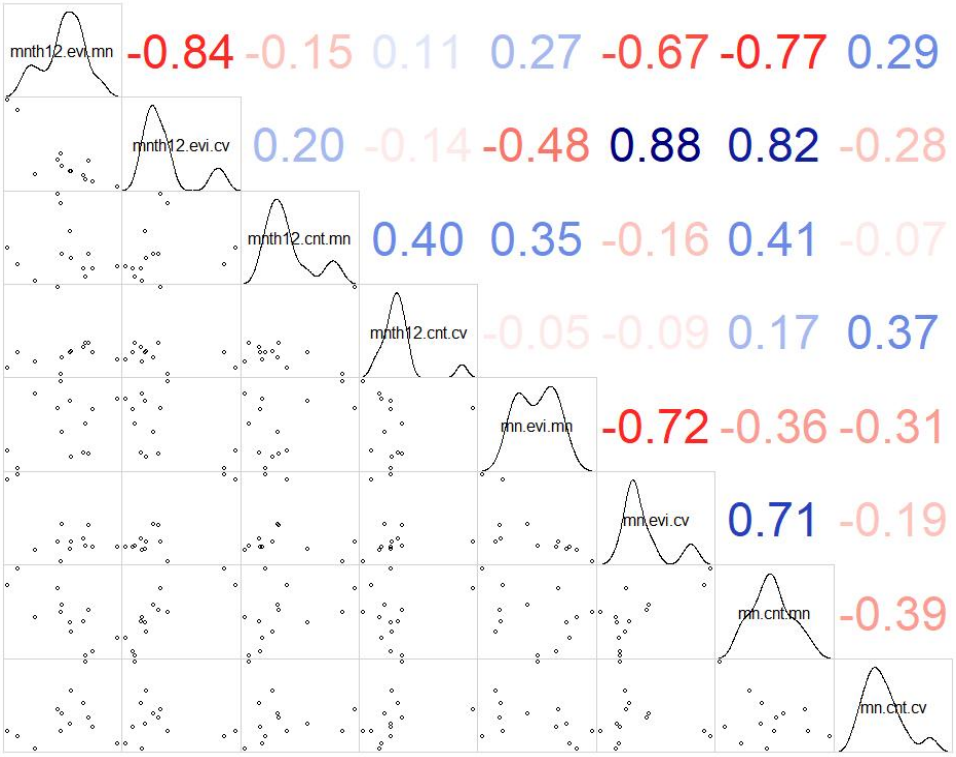
(A) Correlations among all metrics derived from a classified land cover map (pland, pd) across the four tested spatial scales.



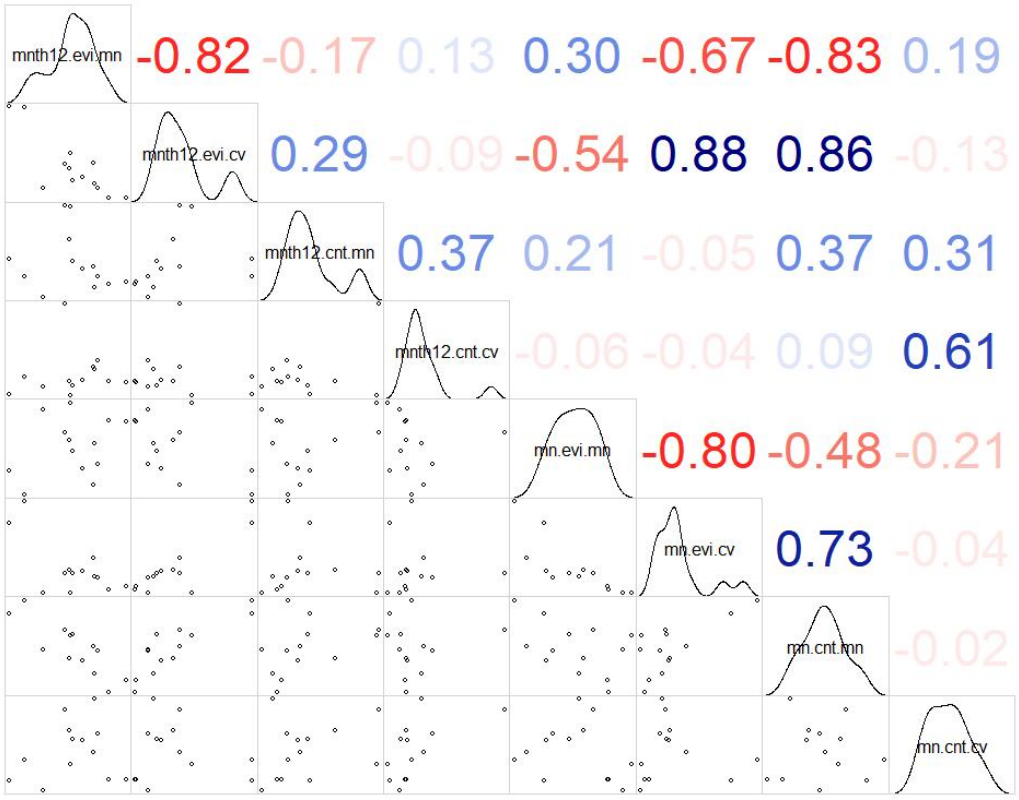
(B) Correlation among EVI-based metrics at a 1 km radius.



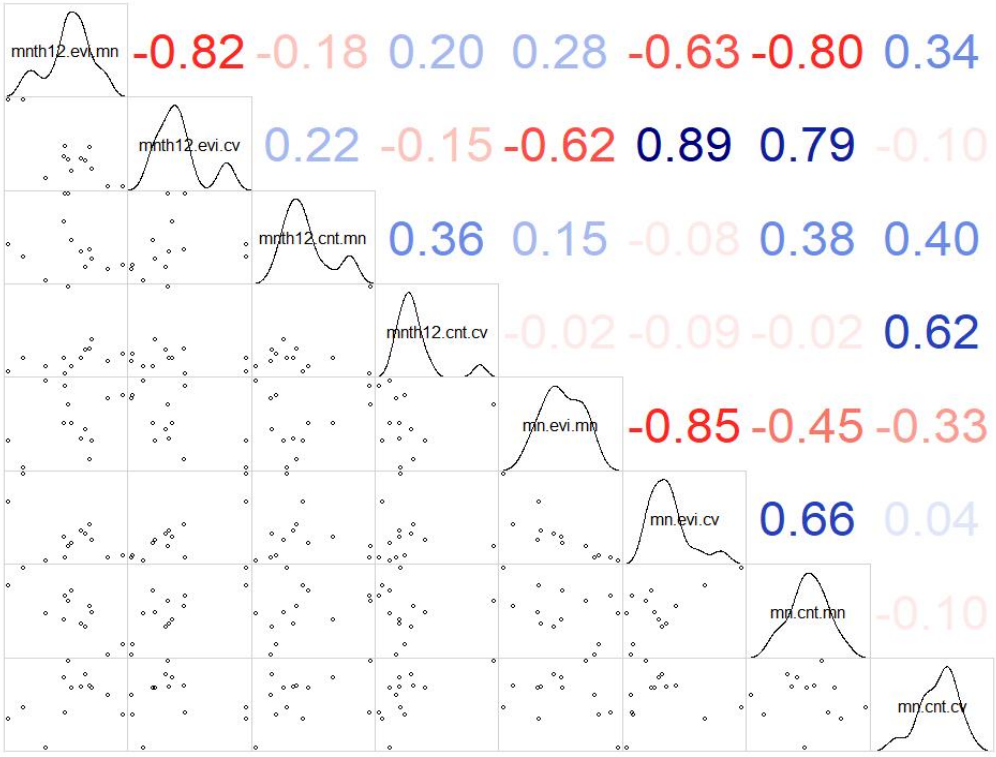
(C) Correlation among EVI-based metrics at a 3 km radius.



(D) Correlation among EVI-based metrics at a 5 km radius.



(E) Correlation among EVI-based metrics at a 5 km radius.



(F) Correlations among landscape metrics selected at their respective scale of effect, used in the multiple-metric models.

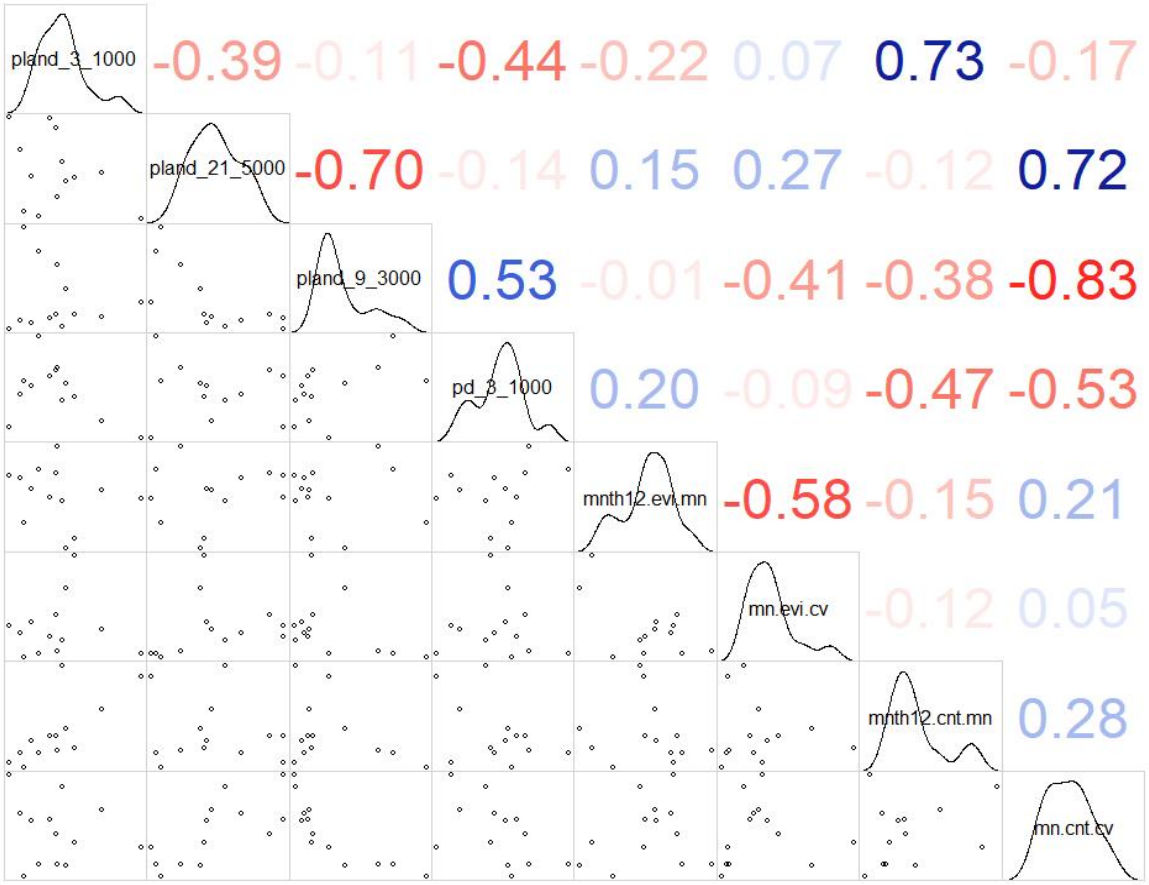


Table S1. Posterior estimates of multispecies occupancy models fitted for assessing the effects of landscape metrics derived from both land use and land cover map and Enhanced vegetation index (EVI) data on small mammals occurrence in a region of Brazilian Atlantic Forest. We present model results for each set of landscape metrics derived at the four spatial scales (1, 3, 5, and 7 km radii), fitted separately to assess the effects of each group of variables and identify their scale of effect. Results include the central tendency (mode), 95% credible intervals, and Bayesian indices: probability of direction (pd), and the proportion of the posterior within the Region of Practical Equivalence (ROPE). Model fit and predictive performance were assessed using the Area Under the Curve (AUC) and the Bayesian p-value; We used Watanabe-Akaike Information Criterion (WAIC) and its standard error (SE) to compare models. Bolded entries indicate landscape metrics at their respective scale of effect.

Simpler Models	**Landscape metric**	**Mode**	**pd**	**ROPE** (-0.10, 0.10)	**HDI 95%**	**AUC**	**Bayesian p-value**	**WAIC (SE)**
Forest cover cover and fragmentation								
1km	***Forest cover***	**0.39**	**84.95**	**12.88**	**-0.39, 1.15**	0.8855	0.12	873.6 (35.5)
	Forest patch density	**0.53**	**93.91**	**7.03**	**-0.16, 1.23**			
3km	*Forest cover*	0.30	82.04	14.73	-0.42, 1.15	0.8789	0.12	882.9 (36.2)
	Forest patch density	0.38	85.19	13.79	-0.36, 1.13			
5km	*Forest cover*	0.40	83.75	13.95	-0.40, 1.13	0.8796	0.12	878.6 (36.0)
	Forest patch density	0.50	88.91	10.17	-0.29, 1.34			

7km	*Forest cover*	0.30	84.24	13.42	-0.42, 1.12	0.8838	0.12	878.5 (35.8)
	Forest patch density	0.46	89.11	9.89	-0.32, 1.34			
Landscape composition								
1km	*Forest cover*	-0.27	68.59	15.08	-1.28, 0.70	0.8923	0.12	869.3 (35.2)
	Silviculture cover	0.21	71.90	14.81	-0.66, 1.27			
	Mosaic of uses cover	-0.78	93.14	5.88	-1.76, 0.23			
3km	*Forest cover*	-0.15	63.60	17.26	-1.05, 0.76	0.8935	0.12	870.6 (35.4)
	Silviculture cover	**0.51**	**83.78**	**9.53**	**-0.51, 1.69**			
	Mosaic of uses cover	-0.49	86.07	9.09	-1.64, 0.48			
5km	*Forest cover*	-0.29	72.61	16.68	-1.07, 0.59	0.8805	0.12	876.8 (35.8)
	Mosaic of uses cover	**-0.72**	**96.78**	**3.33**	**-1.50, 0.06**			
7km	*Forest cover*	-0.22	71.60	18.01	-1.02, 0.57	0.8795	0.12	879.6 (36.1)
	Mosaic of uses cover	-0.63	96.63	3.42	-1.41, 0.08			

Productivity (EVI)								
1km	*mean EVI*	0.14	71.68	25.20	-0.43, 0.75	0.8676	0.12	887.2 (36.6)
	EVI temporal variation	0.07	63.07	24.09	-0.55, 0.77			
3km	***mean EVI***	**0.35**	**84.57**	**14.86**	**-0.34, 1.07**	0.8675	0.12	892.1 (36.9)
	EVI temporal variation	0.05	52.08	21.24	-0.82, 0.77			
5km	*mean EVI*	0.28	81.93	15.85	-0.40, 1.03	0.8673	0.12	890.6 (36.9)
	EVI temporal variation	-0.16	62.33	20.92	-0.91, 0.64			
7km	*mean EVI*	0.30	79.17	17.70	-0.44, 0.96	0.8684	0.12	894.0 (37.1)
	EVI temporal variation	**-0.18**	**69.10**	**20.08**	**-0.95, 0.56**			
Contrast								
1km	*mean Contrast*	-0.27	76.53	17.94	-0.99, 0.44	0.8776	0.12	875.5 (35.6)
	Contrast temporal variation	-0.10	60.35	21.35	-0.85, 0.65			
3km	***mean Contrast***	**-0.34**	**80.19**	**16.00**	**-1.04, 0.43**	0.8839	0.12	874.4 (35.5)
	Contrast temporal variation	-0.57	91.93	6.98	-1.46, 0.26			

5km	*mean Contrast*	-0.08	61.39	21.82	-0.88, 0.67	0.8878	0.12	871.2 (35.3)
	Contrast temporal variation	**-0.58**	**92.29**	**7.19**	**-1.42, 0.23**			
7km	*mean Contrast*	-0.27	74.93	17.68	-1.03, 0.46	0.8772	0.12	878.2 (35.8)
	Contrast temporal variation	-0.26	74.89	17.52	-1.08, 0.49			

Table S2. Posterior estimates of site-level and survey-specific covariates included in Contrast_5km model for small mammal occupancy and detection. We present the mode (central tendency) of the posterior distribution of the effect size (coefficient), along with the 89% and 95% Highest Density Intervals (HDI). We also report the probability of direction (pd), which indicates the certainty about the sign of the effect, and the Region of Practical Equivalence (ROPE), representing the proportion of the posterior distribution considered practically equivalent to zero.

Model Contrast_5km	**Variable**	**Mean**	**Mode**	**pd**	**ROPE** (-0.10, 0.10)	**HDI 89%**	**HDI 95%**
Site-level	*mean EVI*	0.07	0.06	61.29	33.35	-0.34, 0.45	-0.41, 0.57
	mean Contrast	0.12	0.12	70.31	30.53	-0.26, 0.50	-0.34, 0.61
Survey-specific	***Trap-type***	-0.99	-1.03	99.41	0.00	-1.61, -0.38	-1.75, -0.23
	Sampling effort	0.16	0.15	75.79	28.66	-0.22, 0.52	-0.30, 0.63
	Temperature	-0.07	-0.02	60.57	29.91	-0.52, 0.35	-0.61, 0.47
	Rainfall	-0.06	-0.06	62.63	35.93	-0.42, 0.28	-0.52, 0.36

4 Temporal variability in vegetation affects the body mass of small non-flyng mammals communities in agricultural atlantic forest landscapes

Abstract

In the face of rapid land-cover changes driven by human activities, combining functional and taxonomic approaches is essential to better understand the effects of heterogeneous and dynamic landscapes on biodiversity and ecosystem functioning. This is particularly relevant in biodiversity hotspots. Since functionally distinct species are generally rare, functional diversity metrics can be biased by imperfect detection. Multispecies hierarchical models (MHMs) offer an effective solution to this issue by providing reliable estimates of species occurrence and abundance while accounting for detection errors. Here applied MHMs to investigate how occurrence, abundance, and functional diversity (FDis) and composition (CWM-body mass) of small non-flyng mammal communities respond to spatial and temporal characteristics of agricultural landscapes in a region of Brazilian Atlantic Forest. We used the estimates of species presence-absence, occupancy probability and abundance derived from MHMs and calculated three alternatives of the metrics functional dispersion (FDis) and community-weighted means of body mass (CWM-body mass). We examined how changes in FDis values were driven by species composition or shifts in the occupancy probability and abundance, in combination with how species were distributed in the community's functional space. Our results show that landscape productivity and temporal variation in productivity and vegetation heterogeneity influence species occupancy, abundance, and CWM-body mass, but not FDis. CWM-body mass consistently decreased with increasing temporal variability in productivity and increased with variability in vegetation heterogeneity, regardless of the input type. These findings suggest that temporal changes in vegetation characteristics shape communities according to functional traits. Given the established link between CWM traits and ecosystem processes, and the potential for paradoxical responses in FDis, we propose that CWM-based metrics offer a more interpretable and robust strategy to assess how landscape dynamics affect biodiversity and ecosystem functioning.

Keywords: Rodentia; Didelphimorphia; dynamic landscapes; landscape heterogeneity; funcitonal diversity; functional composition; multispecies hierarchical models

1. Introduction

Habitat loss and related pressures of land use are major drivers of ongoing species loss worldwide (Newbold et al., 2016), and consequently, of the erosion of the diversity of ecological roles species play in natural communities (Brodie et al., 2021; Flynn et al., 2009). The relationships between biodiversity, landscape fragmentation, and land-use types are primarily addressed through metrics of species occurrence, abundance, or richness (Chetcuti et al., 2021; Watling et al., 2011). While such metrics underscore the intrinsic value of species, they may not be directly linked to ecosystem functioning. In the face of current land cover changes driven by human activities, studies using trait-based approaches, which place species-specific characteristics (traits) at the center of analyses, alongside taxonomic-oriented

approaches, are important for improving our understanding of the consequences of biodiversity loss on ecosystem functioning and stability in anthropized landscapes (Cadotte et al., 2011; Flynn et al., 2011; Fry et al., 2018).

A focus on traits of communities can be particularly valuable in biodiversity hotspots - biogeographic regions rich in endemic species but with high levels of the primary vegetation loss - where remaining original vegetation cover is surrounded by heterogeneous and dynamic land use changes (Kobayashi et al., 2019). In the Atlantic Forest domain, a recognized biodiversity hotspot, native forest cover has been reduced to about 23% of its original extent and over 97% of remaining fragments are smaller than 50 hectares and embedded within a mosaic of anthropogenic matrices, mainly for agricultural purposes (Vancini et al., 2024; MapBiomas, 2022). As a consequence, local communities in these areas have been altered through the local species extinction, reduced abundance of native species, as well as the influx of novel species from other regions (De La Sancha et al., 2023; Kobayashi et al., 2019; Püttker et al., 2020), with potential impacts on ecosystem functions (Flynn et al., 2011; Fry et al., 2018). The importance of matrix characteristics to the persistence of biodiversity in fragmented landscapes has been widely demonstrated (Chetcuti et al., 2021; Umetsu et al., 2008; Watling et al., 2011). However, although agricultural landscapes are inherently dynamic (Santos et al., 2021), the effects of temporal variability in vegetation on the biodiversity in agricultural landscapes of the Atlantic Forest remain underexplored.

Functional diversity and functional composition encompass a variety of measures that characterize the functional trait structure of communities, capturing how traits are represented and distributed across species (Laliberté & Legendre, 2010; Mammola et al., 2021), and linking species diversity with ecosystem function (Cadotte et al., 2011). Although the fundamental unit of functional diversity metrics usually is the presence or abundance of a species detected over an area and time (Mammola et al., 2021), the detection of species in an area depends on several factors, such as, the conditions under which species surveys are conducted, the individual behaviour of the species and the environment of a given site (Iknayan et al., 2014). Thus, surveys rarely detect all species or individuals in a community or population, resulting in either false species absences or unrealistic estimates of diversity (Guillera-Arroita et al., 2014; Richter et al., 2021). Studies have shown that functionally distinct species often have different probabilities of detection, since rarity is often associated with low species distribution and abundance, so that functional diversity and composition can be biased by imperfect detection (Jarzina & Jetz, 2016; Roth et al., 2018). To address this

issue, the use of analytical tools that provide estimates of species distribution and abundance while accounting for imperfect detection, such as multispecies hierarchical models (MHM), has been pointed out as an effective approach to perform accurate estimates of species diversity (Iknayan et al., 2014; Jarzina & Jetz, 2016). There are growing number of studies that have applied HMM to evaluate community-level data (Iknayan et al., 2014; Devajaran et al., 2020) wherein, beyond distributions and abundances of species in communities (i.e., taxonomic diversity), it can also be used to account for imperfect detection in estimates of other facets of biodiversity, including functional diversity (Jarzina & Jetz, 2016). With regard to functional diversity (FD), Jarzina & Jetz (2016) suggested that functional dendrograms, or distance-based metrics, can be constructed for all species in the regional species pool and corrected for detection bias by using the true probabilities of occurrence estimated for each species-site combination to weight either the branch lengths of the dendrogram or the mean distance in multidimensional trait space in the FD calculation . Although this method has not yet been widely applied, it has the potential of improving the accuracy of functional diversity estimates, especially in species-rich ecosystems, such as the Atlantic Forest, where high levels of rarity (Bovendorp et al., 2017) can amplify the effects of imperfect detection.

Reliable estimates of species presence–absence, occupancy probabilities, or abundance at a locality can be obtained from MHMs and used as input to calculate functional diversity (FD) metrics for a region of interest (Iknayan et al., 2014). Among studies that account for imperfect detection using MHMs to calculate functional diversity metrics, it is more common to use species presence–absence matrices estimated from multispecies occupancy models (e.g., Cook et al., 2020; Bohnett et al., 2022; Gorczynski et al., 2023; Jones et al., 2021), while using estimated abundances or occupancy probabilities as weights has been less explored (e.g. Gorczynski et al., 2021). One of the challenges of distance-based FD metrics is that, depending on the data and the ecological question, they can sometimes produce counterintuitive changes in their values (Guillerme et al., 2025; Laliberté & Legendre, 2010; Petchey & Gaston, 2006), affecting the interpretation of changes in FD across different environmental conditions (Guillerme et al., 2025). Therefore, changes in FD values may differ and require distinct interpretation depending on whether they are calculated using species presence–absence data or weighted by occupancy probabilities or species abundance.

In this work we investigated how occurrence, abundance and functional diversity and composition of small mammal communities respond to spatial and temporal characteristics of land cover types in these landscapes. Small non-flying mammals (body mass > 2 kg) form a

vertebrate group with traits and strategies that allow them to respond rapidly to environmental disturbances at relatively small spatial scales (Lira et al., 2012; Serafini et al., 2019; Vieira et al., 2018). They form a multitrophic group - feeding on a variety of resources such as plant material, invertebrates, and even small vertebrates - while serving as prey for higher-level predators (Galetti et al., 2016). Their ecological roles and high metabolic rates make them key conduits of energy flow from lower to higher trophic levels, being particularly useful to express ecosystem functioning in tropical ecosystems (Loft et al., 2024). In Brazil, 53 of the 102 mainland mammal taxa officially listed as threatened with extinction are from the Atlantic Forest, where habitat loss and fragmentation caused by agricultural activities represent the main threats to these species (ICMBio, 2018). Several studies have shown that habitat loss and fragmentation at the landscape scale affect small mammal communities in Atlantic Forest regions in different manners (Estavillo et al., 2013; Bovendorp et al., 2019; Pardini et al., 2010), such as reducing forest specialist richness while favoring generalist species proliferation (Pardini et al., 2010; De La Sancha et al., 2023) or changing species diets, habitat use, and trophic structure (Magioli et al., 2019). Beyond habitat amount, vegetation composition, structure, and productivity are already known to affect the occurrence and abundance of small mammals in fragmented landscapes (Andreo et al., 2019; Hannibal et al., 2019; Serafini et al., 2019; Püttker et al., 2008;). The effects of habitat loss and fragmentation on small mammals diversity in the Atlantic Forest region have been explored in a few studies (Pardini et al. 2010; Vieira et al. 2018; Bovendorp et al. 2019), but further investigation is still needed across agricultural landscapes, especially regarding the effects of spatiotemporal variability in vegetation characteristics. Since temporal dynamic of agricultural land uses in fragmented landscapes can affect organisms' responses to resource variability (Escobar & Estades, 2021; Mezzini et al., 2025), and influence the morphological structure of small mammal assemblages at landscape scale (Luza et al., 2015), we aimed to move beyond coarse categorical classifications of land cover by accounting for stochastic resource variation, seeking a more comprehensive understanding of how biodiversity is influenced by temporally dynamic land uses in agricultural landscapes.

We sampled small non-flying mammal communities (orders Didelphimorphia and Rodentia), across sites of forest and matrix within 13 agricultural landscapes in a region of the Brazilian Atlantic Forest, and used multispecies occupancy models and community N-mixture models (Kéry & Royle, 2016) to investigate the effects of local and landscape variables on small mammals occurrence and abundance.We used the estimates of species presence-absence,

occupancy probability and abundance derived from the models to calculate three alternatives of two complementary functional traits based metrics: the functional dispersion, as a metric of functional diversity, and an index of community-weighted means of body mass (CWM-Body mass), as a proxy of functional composition (Laliberté & Legendre, 2010). Given that temporal variability in fragmented landscapes affect species persistence and abundance differently, depending on their traits (Escobar & Estades, 2021; Tao et al., 2024), we hypothesize that, (1) forest loss and fragmentation will reduce functional diversity of communities, due to the loss species with unique traits in this areas (e.g. frugivores and forest specialists), and that this effect will be intensified by increased temporal variation within landscapes (Flynn et al., 2009; Tao et al., 2024; Umetsu et al., 2008); (2) community-level mean body mass will be higher in temporally more variable landscapes, given the ability of larger-bodied species to move longer distances in response to locally unstable resources (Escobar & Estades, 2021; Ferreira et al., 2018; Tao et al., 2024). To aid interpretation of each alternative functional dispersion metric, we examined how changes in the metric value were driven by species composition or shifts in the occupancy probability and abundance, in combination with how species were distributed in the community's functional space. We hypothesize that the type of input data (presence-absence, occupancy probability and abundance) will influence the outcomes of functional diversity, reflecting distinct patterns of community organization under landscape change (Petchey & Gaston, 2006). Based on this analysis, we provide recommendations for use and interpretation of functional dispersion in altered landscapes, depending on the context and data extracted from MHMs.

2. Methods

2.1. Study area

Small mammals were sampled across 63 sites distributed among 13 landscapes (four to five sites per landscapes) within the Atlantic Forest biome, located between the northeast of São Paulo state and the south of Minas Gerais state, in Brazil (Figure 1). Sampled landscapes were pre-selected to include, within 1000-m radius, a gradient of forest cover (6% to 96%) and the most common matrix (i.e., anthropogenic non-habitat areas) of agricultural land use in the region: pasture, agriculture, and silviculture (Figure 1). In total, we sampled 35 sites in forest fragments, 16 in pastures, six in agricultural fields, and six in eucalyptus plantations (total of 28 matrix sites) (Figure 1).

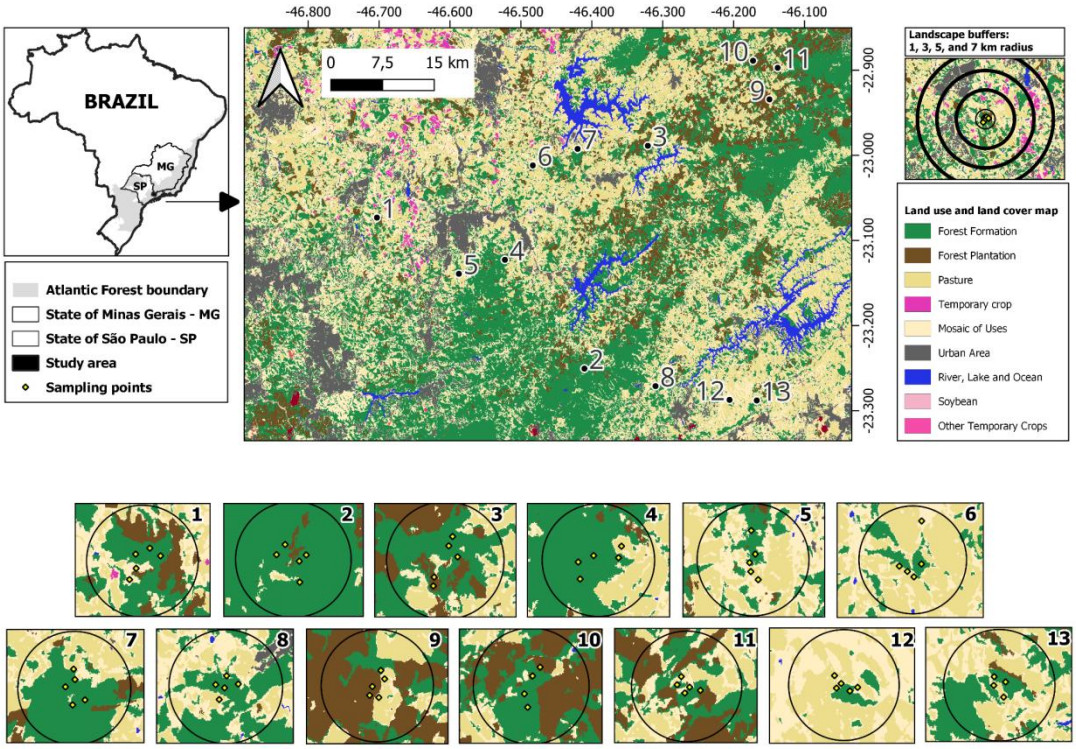


Figure 1: Map of the study area showing land use and land cover types (MapBiomas - Collection 2 (beta)) and distribution of the 63 sampling sites within 1,000m radius landscapes. Landscape metrics were calculated within circular buffers with radii of 1,000 to 7,000 meters, centered on the centroid of sampling sites in each landscape. Site-level metrics were calculated within a 50 m radius circular buffer centered on each sampling site.

2.2. Small mammals sampling

In each landscape, we established four to five trapping sites, which were distributed in different environments according to the proportion of forest cover and matrix type. Small mammal communities were sampled on a single survey at each site, over 6 to 10 consecutive nights, between December 2022 and October 2023, totaling 29,160 trap-nights. We set a minimum distance of 100 meters between sampling sites, with an average spacing of 207 meters. Each site was surveyed using 50 live traps 'Sherman' type, of three sizes (small: Trap1 [23.5 x 8 x 9 cm], large: Trap2 [38 x 10 x 12 cm] and Trap3 [43 x 12.5 x 14 cm]). Traps were arranged in a grid consisting of five parallel lines, each containing five trapping stations spaced approximately 10 meters apart. At each station, two traps were placed either on the ground or, if forest sites, one on the ground and one in the understory vegetation at a height of 1.5 – 2 m. The distribution of the different sizes was standardized to always contain 25 small traps (Trap1) and 25 large traps (Trap2 and Trap3). Due to logistical reasons, Trap3 was used only in samplings that occurred until May 2023. The absence of Trap3 was explicitly accounted for during the modeling procedure. Traps were baited with a mixture of peanut

butter, banana, sardines, vanilla essence and cornmeal, and checked daily to identify captured species and replace baits. Captured individuals were marked using numbered stainless steel ear tags or by clipping fur on the upper hind leg region. Some individuals of each species were euthanized to assist with species identification (following appropriate ethical protocols and prior authorization from the responsible authorities (UNESP's Ethics Committee and ICMBio authorization). We sent the collected materials from these individuals to the taxonomist Alexandre Reis Percequillo at ESALq/USP- Piraciacaba, where they are deposited in the zoological collection.

2.3. Landscape and site variables

We used a land cover map at a 10 m resolution from MapBiomas - Collection 2 (beta) (MapBiomas Project, 2023) to calculate the forest cover and density of forest patches, for each landscape. Forest cover includes different types of Atlantic Forest forest formations, while Forest patch density describes the fragmentation of the Forest class, standardized for the landscape area (Number of patches per 100 hectares). To derive metrics of site and landscape spatiotemporal variability of productivity (i.e. amount of green biomass) and fine-scale heterogeneity (i.e. spatial variability in structural and compositional features of vegetation), we used a vegetation index - the Enhanced Vegetation Index (EVI) - calculated from high-resolution satellite imagery (spectral metrics). Vegetation indices derived from satellite imagery measure biophysical surface characteristics closely related to vegetation structure and composition (Phillips et al. 2008; St-Louis et al., 2009). Thus, metrics derived from these indices can capture variation and habitat heterogeneity across both local and broader spatial and temporal scales, providing effective indicators of within-habitat heterogeneity of vegetation even in areas considered homogeneous in class maps (Farwell et al., 2021; St-Louis et al., 2009). EVI rasters were calculated for each landscape using the red and near-infrared bands from 3-meter resolution PlanetScope SuperDove imagery (Planet Team, 2024). For each landscape, EVI-derived metrics were calculated to capture both spatial and temporal variation of vegetation productivity. Spatial metrics were based on EVI values from the sampling month, while temporal metrics reflected EVI variation over a 12-month period encompassing the sampling month and the preceding 11 months. This temporal window was defined to detect changes in vegetation cover resulting from the various land-use management practices in the region (e.g., planting, harvesting, etc.), as well as the seasonal variations that may affect different types of vegetation in these landscapes (Santos et al., 2021).

We calculated all landscape-level variables within four circular buffer sizes (1 km, 3 km, 5 km, and 7 km radii) centered on the centroid of sampling sites. Site-level variables were calculated within a circular area of 50 meters radius from the center of each sampling site, using only EVI rasters. To calculate a metric of spatial productivity of each sampling site and landscape, we averaged EVI values within each respective buffer radius (mean EVI). As a metric of spatial heterogeneity, we calculated a texture measure from EVI rasters: Contrast. Contrast was calculated as the exponentially weighted difference in EVI values between adjacent pixels within a 3 × 3 moving window (Haralick et al., 1973). We then averaged the contrast values to obtain a metric of mean contrast at both site and landscape levels, after masking out water bodies and urban areas from the EVI rasters using the land cover class map. We then averaged the contrast values to obtain a metric of mean contrast at both site and landscape levels, after masking out water bodies and urban areas from the EVI rasters using the land cover classes map. To derive metrics of temporal variability in landscape productivity (mean EVI) and heterogeneity (mean contrast) for each landscape, we calculated the coefficient of variation of mean EVI and mean contrast obtained from the sampling month and 11 previous months, hereafter named "EVI.cv" and "Contrast.cv", respectively.

All predictor metrics were computed in R (version 4.3.2) (R Core Team, 2023), through packages "terra" (Hijmans et al., 2023a) and "raster" (Hijmans et al., 2023b) for handling raster data, "sf" (Pebesma, 2018) for vector data operations, "landscapemetrics" (Hesselbarth et al., 2020) for calculating land cover metrics, and "rgrass" (Bivand, 2022) for accessing, calculating texture and manipulating geospatial data formats and GRASS GIS (version 8.2) (GRASS Development Team, 2022) functionalities. The study area map was produced using QGIS (version 3.28.0) and a class map from MapBiomas - Collection 2 (beta) (MapBiomas Project, 2024)

2.3.1. Scales of effect and correlation between among landscape metrics

The scale of effect (i.e. the spatial scale at which a landscape predictor best explained the occurrence of the species) of each landscape metric was determined in a previous study, where the full procedure is described (Chapter 1), being: forest cover and patch density at a 1 km radius; mean EVI and mean Contrast at a 3 km radius; EVI.cv at a 7 km radius; and Contrast.cv at a 5 km radius. Pearson's pairwise correlations among landscape metrics revealed a strong positive correlation between mean contrast and forest cover ($r = 0.73$), as well as between contrast temporal variation (Contrast.cv) and mosaic of uses cover ($r = 0.72$),

and a strong negative correlation with silviculture cover (r = - 0.83). Considering these correlations, and that in our previous study (Chapter 2) metrics derived from vegetation indices successfully explained small mammal species distribution in agricultural landscapes, we used only the EVI-derived metrics to fit the multispecies hierarchical models. However, to answer our question regarding the effects of environmental variability in fragmented landscapes on functional diversity and composition, we used the class metrics forest cover and forest patch density (as proxies for fragmentation), and EVI.cv at and Contrast.cv (as proxies for landscape temporal variability) as predictors on Bayesian linear models.

2.4. Multispecies hierarchical models

We used two types of multispecies hierarchical models (MHM) to estimate community-level responses to environmental predictors: multispecies occupancy model (MSOM) was applied to model the occupancy of species within communities, while community N-mixture model (CNMM) to model species abundance. Both models share a similar structure, with a latent ecological process (i.e., the true but imperfectly observed presence-absence or abundance) and an observation process that accounts for imperfect detection (Kéry & Royle, 2016). We combined observational data (i.e., detections/non-detections or species counts) of each species at landscape and site level using a three level model (i.e., a multiscale design). This hierarchical structure defines the relationship between latent ecological states (presence-absence or abundance) across scales. For detailed model specifications, see Supplementary Material (Supplementary S1).

Landscape-level occupancy probability and abundance were modeled as linear functions of the variability in productivity (mean EVI) and fine-scale vegetation heterogeneity (mean contrast) during the sampling month, as well as their annual variability (EVI.cv and Contrast.cv). Site-level occupancy probability and abundance were modeled solely as linear functions of mean EVI and mean contrast.

To build the detection histories (sampling replicates), we divided each sampling survey into two sampling occasions by aggregating detection/non-detection data into two consecutive 5-day intervals. The probability of detection was modeled as a function of the types of traps used at the sites (all three types or solely Trap1 and Trap2), the sampling effort during each sampling occasion (trap-nights), and the meteorological conditions during each sampling occasion (mean temperature and mean precipitation). Temperature and precipitation data were

obtained from the INMET database (INMET, 2024), using information from the meteorological stations closest to the sampled locations. All continuous predictors were standardized to have mean zero e variance one, using the function “decostand” from the “vegan” package in R environment (R Core Team, 2023).

We assessed model fit using Bayesian p-values for each fitted model. For the MSOM, we calculated the Bayesian p-value as the proportion of MCMC iterations in which the deviance of the observed data exceeded the deviance of data predicted by the model (Broms et al., 2016). For the CNMM, we applied a posterior predictive check (Gelman et al., 1996), which involved calculating a test statistic by summing the predicted values (posterior predictive counts) across sites and species for each MCMC iteration and comparing it to the corresponding statistic from the observed data. The Bayesian p-value was then computed as the proportion of iterations in which the predicted statistic exceeded the observed one. A well-fitting model is expected to yield a Bayesian p-value close to 0.5, while values below 0.05 or above 0.95 indicate poor model fit.

To assess the MSOM’s ability to distinguish between observed detections and non-detections, we computed the posterior distribution of the area under the receiver operating characteristic curve (AUC-ROC) using training data. Higher AUC values indicate better discriminative ability, with 1.0 representing perfect prediction and 0.5 indicating no better than chance.

We summarized overall metacommunity patterns by estimating the mean occupancy probability, mean abundance and mean detection probability across species, based on posterior simulations of community-level intercepts from the MSOM and CNMM, transforming back to the probability and abundance scales to the real scales (Kéry & Royle, 2016). The strength of support for each covariate effect was assessed by examining the posterior distribution of each parameter, including the mode, the 95% and 89% highest density intervals (HDIs), and Bayesian indices probability of direction (pd) and Region of Practical Equivalence (ROPE). Probability of direction is defined as the proportion of the posterior distribution that has the same sign as the median. It ranges from 0.5 to 1.0 and is interpreted as the probability that a parameter effect goes in a particular direction (i.e., is positive or negative), and thus the presence of an effect (Makowski et al., 2019). The ROPE index is a proportion of the HDI (89%) of a posterior distribution that lies within a region related to the practical relevance of the effect, i.e., it outlines a range around the null value (zero) (Makowski et al., 2019). If the effect falls within this range, the magnitude of the effect

is likely to be too small for practical reasons. We defined ROPE as ±0.10, in an attempt to treat only very small coefficients as "negligible" effect size (Makowski et al., 2019).
We estimated model parameters using JAGS version 4.3.1 (Plummer, 2003), via the "R2Jags" package (Su & Yajima, 2015) in R version 4.2.3 (R Core Team, 2023). We performed model assessment an inference analysis using the "pROC" package to calculate AUC, "bayestestR" package (Makowski et al., 2019b) to calculate the mode values, HDIs, and the indices *pd* and ROPE. All graphics were created using the "ggplot2" package (Wickham, 2016).

2.5. Functional diversity

2.5.1.Species traits

We selected six functional traits related to resource use, the timing and location of resource acquisition, locomotion and dispersal capacity. These traits were chosen because the coexistence of small non-flying mammals in heterogeneous landscapes may result from microhabitat selection and segregation, combined with efficient resource partitioning (Luza et al., 2015). Moreover functional diversity may be more informative when capturing finer functional differences within broader ecological functions (Petchey & Gaston, 2006). Categorical and binary traits were obtained from open-access trait databases and published literature, while continuous traits were measured directly from all sampled individuals. For each species, trait values were aggregated by calculating the mean, resulting in a single representative value per trait per species (Table 1). We provide parwaise correlations among traits in Supplementary Figure S1.

Table 1. Trait data used to calculate functional diversity of small non-flying mammals communities in a region of Brazilian Atlantic forest.

Functional component	Type	Measure	Description	Source
Diet	Fuzzy	Relative proportion of food items on diet*: Invertebrates general; Mammals and Birds; Reptiles and Amphibians; Vertebrates general or unknown; Scavenge and carcasses; Fruit and drupes; Nectar; Seed; Other plant material. (%)	Proportional diet composition across food items. Reflects dietary specialization when dominated by few items, or indicates generalist feeding behavior when more evenly distributed.	Willman et al., (2014)
Foraging strata	Categorical	Arboreal; Scansorial; Terrestrial; Semifossorial.	Preferred vertical strata used. Indicate where a species spends its time foraging.	Abreu et al., (2024)

Activity time	Binary	Nocturnal; Diurnal; Crepuscular. (yes/no)	Indicator of time of resource acquisition.	Willman et al., (2014)
Body mass	Continuous	Average body mass obtained from captured individuals. (g)	Indicator of species foraging strategies and dispersal capacity.	Field measurements
Tail-to-body length ratio	Continuous	The ratio between tail length to total head-body lenght.	Indicator of modes of locomotion and location of resource acquisition. Reflects a species' ability to use vertical strata.	Field measurements
Foot-to-body length ratio	Continuous	The ratio between hindfoot length and total head-body length.	Indicator of modes of locomotion and location of resource acquisition. Reflects a species' ability to use vertical strata.	Field measurements

2.5.2. Modeling functional diversity and composition in a two-step analysis (Meta-analysis)

We modeled functional diversity and composition using a two-step modelling approach, referred to as a meta-analysis. In the first step, we generated 2,000 values of functional diversity and composition based on posterior estimates of species presence–absence, occupancy probability and abundance from the MHMs. In the second step, we used Bayesian modelling to evaluate how landscape predictors influenced the estimated functional diversity and composition. We calculated the Functional dispersion index (FDis) as a metric of functional diversity of communities, which quantifies the spread of species within the occupied trait space (Laliberté & Legendre, 2010). We calculate the community-weighted means of body mass (CWM-Body Mass) as a proxy of functional composition of communities, i.e., the dominant trait value in a community (Laliberté & Legendre, 2010). We choose the body mass since it is established in the literature as a key functional attribute reflecting species' metabolic rates, ecological strategies, and responses to environmental gradients (Woodward et al., 2005). Additionally, we calculated the community-weighted means of all numerical traits and performed Pearson correlation among the CWMs of the proportion of each dietary items and modes of locomotion, to explore their relationship with community-level mean body mass.

In the first-step we calculated both functional metrics using the three input data predicted by the MHMs: species presence–absence (PA) and occupancy probabilities (psi) estimated via MSOM, and species abundances (abd) estimated via CNMM. For each landscape we sampled 2,000 random samples of each latente variable (PA, psi and abd) from posterior distribution

for each combination species-landscape. For each of the 2,000 samples, we calculated the posterior mean and standard deviation of each functional metric per landscape. These values, along with their associated uncertainty, were then used as inputs in a subsequent Bayesian linear regression.

In the second step, the mean and standard deviation of each functional metric were modeled as a function of landscape forest cover, fragmentation, and vegetation variability metrics. This regression incorporates two residual components: one reflects the estimation uncertainty from the first-step analysis (i.e., standard deviation of the functional diversity indices), and the other represents the usual residual variation estimated from the data. This two-steps modeling approach (Bayesian meta-analysis) ensures appropriate propagation of uncertainty from the MHMs into the meta-analytic framework (Kéry & Royle, 2016). The second-step regression was fitted using Bayesian methods consistent with those applied in the MSOM and CNMM. Model definitions and priors are detailed in the Supplementary S2. Inference on the effects of covariates was performed similarly, by examining mode values, highest density intervals (HDIs), and the probability of direction index. Model fit was evaluated through the Bayesian p-value, which involved calculating a test statistic by summing the predicted values (posterior predictive means of the FDis and CWM–Body Mass across all sampling units for each MCMC iteration and comparing it to the corresponding statistic from the observed data. The Bayesian p-value was computed as the proportion of iterations in which the predicted statistic exceeded the observed one.

2.5.2. Examining trait-based community structure underlying functional dispersion

To examine the community-level trait structure underlying FDis values, we conducted an analysis aimed at unpacking the components contributing to FDis indices derived from the mean estimates of each input data type. Specifically, we performed a principal coordinates analysis (PCoA) on a Gower's distance matrix constructed from species traits (Laliberté & Legendre, 2010). Using the resulting species coordinates in the reduced trait space, we then calculated the community-level functional centroid for each landscape. When using estimates of occupancy probabilities (*ψ-psi*) or estimated abundances, species coordinates were weighted to reflect their relative importance within each landscape. In contrast, for presence–absence data, all species present contributed equally to the centroid calculation. We then calculated the Euclidean distance between each species and the corresponding landscape centroid, generating a matrix of distances (Z-values) that quantify how far each species lies

from the functional center of its respective community (Laliberté & Legendre, 2010). This analysis aimed to explore how community-level trait structure contributes to overall functional dispersion and whether particular community configurations, such as dominance by species with peripheral (high distance to the centroid) versus central (low distance to the centroid) trait values, were associated with higher or lower FDis values. We generated visual plots of the distribution of species-to-centroid distances within each community (i.e., landscape), alongside the respective FDis, occupancy, and abundance estimates. This graphical inspection enabled the identification of trait-based community patterns that may underlie variation in functional structure across landscapes.

All analyses and visualizations were performed using R version 4.2.3 (R Core Team, 2023). Functional diversity and composition metrics were calculated using the "FD" package (Laliberté et al., 2014). Principal coordinates analysis (PCoA) was conducted with the "ape" package (Paradis & Schliep, 2019). All figures were created using the "ggplot2" package (Wickham, 2016).

3. Results

We captured 616 individuals of 23 small mammal species, seven belonging to the order Didelphimorphia and 16 to order Rodentia. Two of the rodent species were exotic invasive (*Rattus rattus* and *Mus musculus*). We excluded these species from our analyses to avoid violating the assumptions of the MHMs (i.e., that species respond to environmental conditions in a similar manner), as their presence in the study area is likely a direct result of human introduction rather than natural habitat use.

Among the 21 species analyzed in this study, 10 were endemic to the Atlantic Forest, including two marsupials (*Monodelphis iheringi*, *Monodelphis scalops*) and eight rodents (*Delomys sublineatus*, *Brucepattersonius cf. nebulosus* [Brucepattersonius sp. 1], *Brucepattersonius cf. soricinus* [Brucepattersonius sp. 2], *Juliomys pictipes*, *Juliomys ossitenuis*, *Thaptomys nigrita*, *Euryoryzomys russatus*, *Sooretamys angouya*) (Abreu et al., 2024). Other species were typical of open formations, secondary vegetation, agricultural fields (*Calomys tener*, *Necromys lasiurus*), or grasslands *(Monodelphis dimidiata*) (Patton et al., 2015; Vilela et al., 2010). Most species were habitat generalists, widely distributed across different biomes and vegetation types, including both natural and human-modified landscapes.

3.1. Variables effects on species occupancy, abundance and detection

At landscape level, the predictions shows that most species in the metacommunity are moderately likely to occur across landscapes (μ_{psi} = 0.55, 95% CRI = 0.06 - 0.96), while their expected abundance tends to be low (μ_{abd} = 0.95, 95% CRI = 0.09 - 3.94). However, one or a few species can be dominant in certain landscapes, as mean abundance could reach up to 49.41 individuals in extreme cases (maximum across species). At the site level, the expected probability of occupancy for a species is slightly lower than at the landscape level (MSOM: μ_{psi} = 0.50, 95% CRI = 0.37 - 0.98), while expected species abundance was similar to that observed at the landscape level (CNMM: μ_{adb} = 1.12, 95% CRI = 0.10 - 4.63). Predictions also revealed considerable variation in species abundance across sites, indicating a general metacommunity pattern characterized by a few species reaching relatively high local abundances (up to 58.75 individuals in some sites), while most species remain in low abundances. The mean probability of detecting a species in the metacommunity is moderated (MSOM: μ_{p} = 0.44, 95% CRI = 0.13 - 0.79), whereas at the individual level, it was predicted to be considerably lower (CNMM: μ_{p} = 0.15, 95% CRI = 0.03 - 0.38).

The the effect of landscape productivity (mean EVI) on community mean abundance was clearly positive (Mode = 0.47, pd = 99.67% ; ROPE = 0.00%) (Figure 2), but the positive effect on community mean occupancy (i.e., expected proportion of species occurring within the community) was uncertain (Mode = 0.43, pd = 83.92% ; ROPE = 11.65%). Although the models estimated a negative effect of landscape vegetation heterogeneity (mean contrast) on community mean occupancy and a positive effect on community mean abundance, the evidence for these effects was weak (See Supplementary Table S1 for a summary of the posterior estimates).

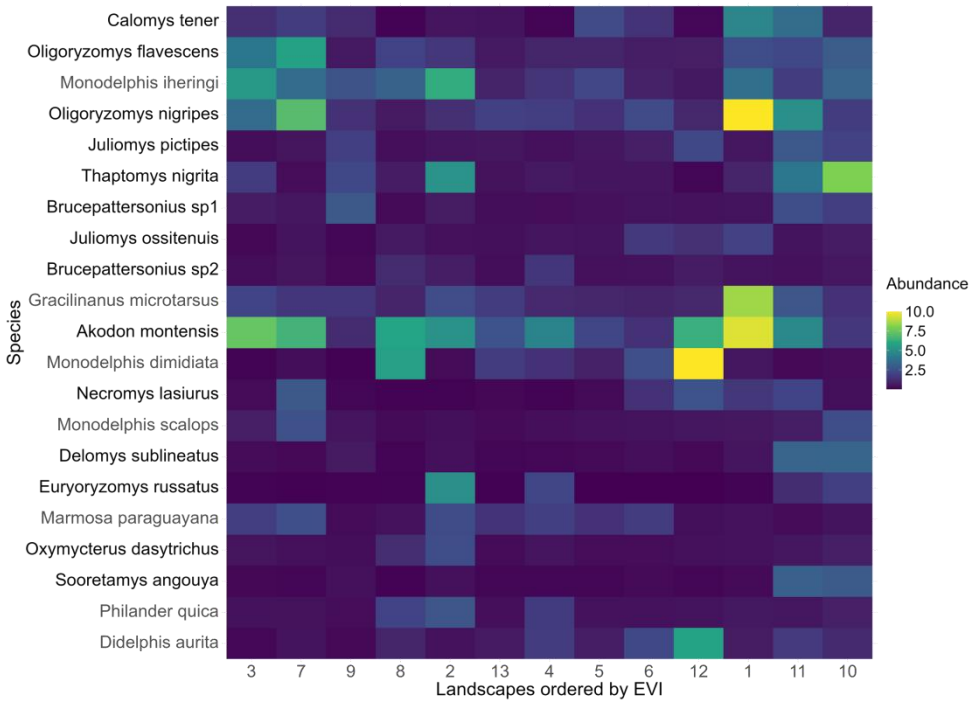


Figure 2: CNMM mean estimates of small mammal abundance across agricultural landscapes in a region of Brazilian Atlantic Forest. The Y-axis shows species ordered by increasing body mass. The X-axis represents landscapes ordered by mean productivity (EVI) in 3-km radius landscapes. Species named in black are rodents and dark gray are marsupials.

We found strong evidence for a negative effect of temporal variability of landscape heterogeneity (Contrast.cv) on community mean occupancy (Mode = -0.82, pd = 95.34% ; ROPE = 4.19%), and moderate evidence for a negative effect on abundance (Mode = -0.26, pd = 90.41% ; ROPE = 17.92%) (Supplementary Table S1) (Figure 3).

At site level, we found no evidence that site productivity (mean EVI) or vegetation heterogeneity (mean contrast) affected community mean occupancy or abundance (Supplementary Table S1). All models showed good fit to the data and predictive performance, as indicated by AUC values and Bayesian p-values (Supplementary Table S1).

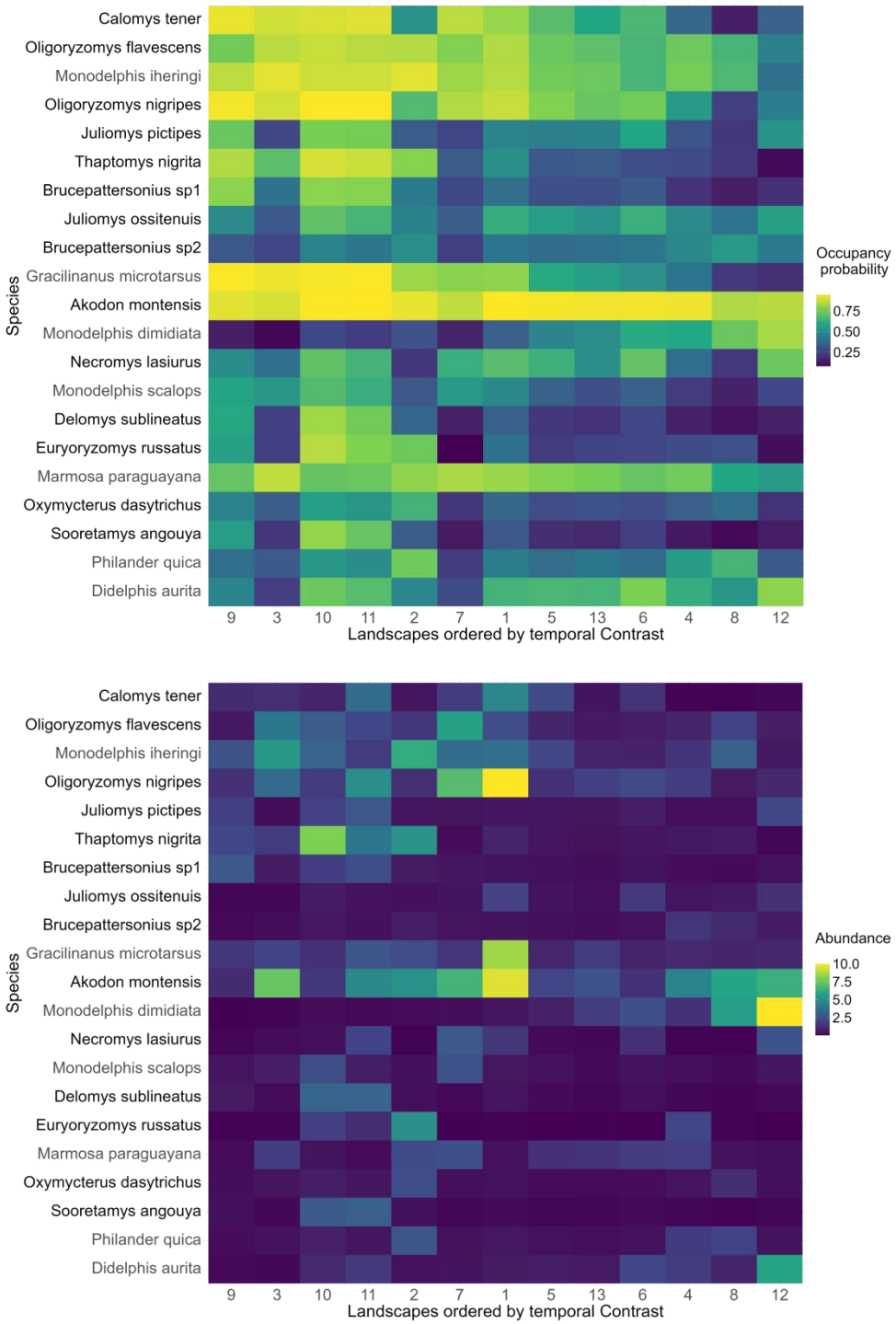


Figure 3: MSOM mean estimates of species occupancy probability (top) and CNMM mean estimates of small mammal abundance across agricultural landscapes in a region of Brazilian Atlantic Forest. The Y-axis shows species ordered by increasing body mass. The X-axis represents landscapes ordered by annual variability in vegetation heterogeneity (Contrast) in 5-km radius landscapes. Species named in black are rodents and dark gray are marsupials.

3.2. Effects of landscape metrics on functional diversity and composition

We found no evidence that any landscape predictor (forest cover, forest patch density and EVI.cv and Contrast.cv) influenced FDis, regardless of the input type used (presence–absence, occupancy probability, or abundance) (Table 1). In contrast, models with CWM-Body Mass consistently indicated a negative effect of temporal variation of landscape productivity (EVI.cv) but a positive effect of temporal variation of vegetation heterogeneity (Contrast.cv) on CWM-Body Mass, differing only in the strength of the evidence (Table 1; Figure 4). Using presence–absence data to derive CWM–Body Mass yielded the strongest evidence for the effects of these covariates (pd values: 98% and 99%), whereas models based on estimated abundances showed the weakest support (pd values: 92% and 86%) (Table 1). Similarly, effect sizes (coefficient estimates) were approximately twice as large when CWM–Body Mass was calculated using presence–absence data (Table 1). All models exhibited adequate fit based on Bayesian p-values (Table 1).

Pearson's correlations between CWMs based on occupancy probability (CWMs-psi) and abundance (CWMs-abd) data indicated that communities with higher mean body mass also tended to include more species or individuals with more terrestrial habits (i.e., lower tail-to-body length ratio). Correlations in CWMs-psi and presence-absence (CWMs-PA) showed that communities with higher mean body mass tended to include species with lower mean proportions of fruits or other plant-derived items in their diet (Supplementary Figure S2).

Table 1: Bayesian linear models of the relationship between functional dispersion and community-weighted means of body mass (CWM-Body mass) indices and landscape scale variables in an Atlantic Forest region, Brazil. We present model posterior summaries (mode, HDI - high density intervals of 95% and 89%, pd - probability of direction) and posterior predictive check (Bayesian p-value). Bolded entries indicate metrics with the strongest evidence.

Input type and Functional diversity metric	Landscape metrics	Mode	pd	HDI 89%	HDI 95%	Bayesian p-value
Presence-Absence						
Functional Dispersion	*Forest cover_1km*	0.01	51.30	-0.27, 0.26	-0.34, 0.33	0.49
	Patch density_1km	-0.01	50.03	-0.32, 0.30	-0.40, 0.41	
	EVI temporal_7km	-0.007	50.55	-0.22, 0.19	-0.27, 0.24	
	Contrast temporal_5km	0.02	51.03	-0.28, 0.29	-0.35, 0.37	
CWM-Body mass	*Forest cover_1km*	7.54	87.08	-3.39, 20.35	-6.79, 22.44	0.75
	Patch density_1km	2.48	66.17	-8.51, 17.02	-11.68, 19.72	
	EVI temporal_7km	**-13.80**	**98.55**	-24.00, -3.90	-26.22, -1.70	
	Contrast temporal_5km	**24.44**	**99.18**	7.36, 37.69	3.65, 41.03	
Occupancy probability						
Functional Dispersion	*Forest cover_1km*	0.02	51.62	-0.25, 0.28	-0.32, 0.37	0.49
	Patch density_1km	-0.03	50.27	-0.31, 0.31	-0.38, 0.41	
	EVI temporal_7km	-0.007	50.28	-0.19, 0.21	-0.24, 0.28	
	Contrast temporal_5km	-0.007	51.13	-0.28, 0.29	-0.35, 0.36	
CWM-Body mass	*Forest cover_1km*	1.89	60.58	-8.43, 11.51	-10.95, 13.51	0.34
	Patch density_1km	0.79	55.72	-9.31, 12.51	-13.39, 13.57	
	EVI temporal_7km	**-8.46**	**92.48**	-16.58, 0.21	-17.65, 2.43	
	Contrast temporal_5km	**12.61**	**96.13**	1.60, 24.18	-1.43, 26.28	

Abundance						
Functional Dispersion	*Forest cover_1km*	0.009	51.20	-0.27, 0.26	-0.35, 0.32	0.50
	Patch density_1km	0.03	50.35	-0.30, 0.32	-0.40, 0.39	
	EVI temporal_7km	0.001	50.90	-0.20, 0.20	-0.25, 0.26	
	Contrast temporal_5km	0.005	50.95	-0.28, 0.28	-0.37, 0.35	
CWM-Body mass	*Forest cover_1km*	4.08	64.30	-13.80, 22.14	-18.08, 26.35	0.18
	Patch density_1km	-3.23	59.07	-18.54, 13.64	-21.84, 17.50	
	EVI temporal_7km	**-9.73**	**91.90**	-18.02, 1.21	-20.28, 3.44	
	Contrast temporal_5km	**10.24**	**86.12**	-4.37, 28.49	-8.36, 31.50	

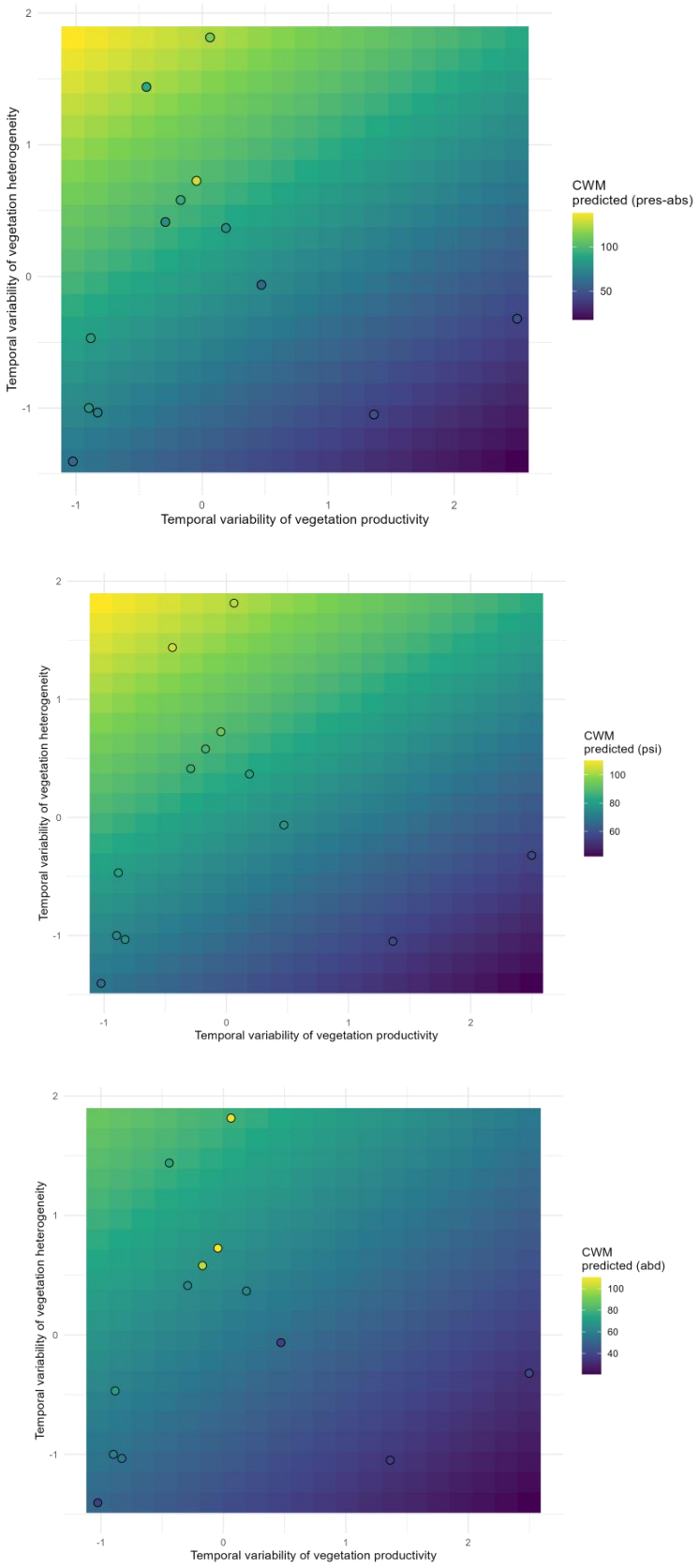


Figure 4: Effects of annual variability in landscape productivity (EVI.cv) and vegetation heterogeneity (Contrast.cv) (z-transformed) on expected small mammals community-weighted means of body mass (CWM) derived from three data types (presence-absence: pres-abs; occupancy probability: psi; abundance: abd). Dots are observed values.

3.3. Community trait structure underlying functional dispersion

Estimated FDis values varied little across landscapes and input types, with the largest range observed for FDis derived from species abundance (0.179 - 0.214) (Figure 5). For FDis-PA, the highest values were found in communities with either a few species spanned across a wide range of distance from community centroid (e.g. landscape 8 (n=4)) or intermediate number of species, where species were mostly distributed at intermediate to high distances from the centroid (e.g. landscapes 2 (n=8) and 4 (n=7)) (Figure 5). In contrast, the lowest FDis-PA values occurred in communities with a high number of species distributed across a wide range of distances (from low to high) (e.g. landscapes 10 (n=10) and 11(n=13)), or in communities with an intermediate number of species showing similar intermediate distances to the centroid (e.g. landscape 9 (n=7)) (Figure 5) (Supplementary Figure S3).

The highest FDis-psi values were observed in landscapes where an intermediate number of species from the regional pool had high occupancy probabilities ($\psi > 0.5$) and spanned across intermediate to high distances from the centroid (e.g. landscapes 8 and 4) (Figure 3 and 5). Conversely, the lowest FDis-psi values were found in communities where most species had high occupancy probabilities, spanned across low to high distances from the centroid (e.g. landscapes 8 and 4) (Figure 3 and 5). When comparing landscapes with similarly low FDis-psi values - landscapes 10 and 11 (0.207) with landscape 3 (0.211) - we found that in landscape 3, the slightly higher index value was driven by a much smaller number of species with high occupancy probabilities, compared to a much higher number at landscapes 10 and 11 (Figure 3), which were more centered at intermediate distances from the centroid (Figure 5) (Supplementary Figure S3).

The highest values of FDis-abd were associated with communities in which a few species spanned across intermediate distances to the community centroid had the highest abundances, which was consistently relatively low (typically up to 3 individuals) (Figure 3 and 5). In contrast, the lowest FDis-abd values were observed in communities where species with the highest abundances spanned from low to high distance to centroid (e.g., landscapes 10 and 11), or where abundances were similarly low and evenly distributed among species more centered in closer distances to centroid (e.g., landscape 9) (Figure 3 and 5).

Interesting contrasting results emerge when comparing community structures driving FDis values among the most preserved landscapes (landscapes 2 and 4 - both are part of highly forested protected areas) with more fragmented landscapes (landscapes with few amount of forest cover, dominated by pasture and mosaic of uses: e.g. 5, 6, 12, 13). When presence–

absence data were used as input, the preserved landscapes had the highest FDis values compared to the more fragmented landscapes. When occupancy probability was used, preserved and fragmented landscapes had very similar FDis values, although values were slightly smaller in fragmented landscapes (Figure 5). However, when species abundance was used, fragmented landscapes showed higher FDis values than one of the most preserved landscapes (landscape 2) (Figure 5). Another contrasting result emerged when comparing FDis values of the most fragmented landscape (landscape 12). When presence–absence data or occupancy probabilities were used as input to derive FDis, landscapes 12 showed intermediate-high index values (Figure 5). However, when species abundance was used, landscape 12 was among the lowest FDis landscapes (Figure 5).

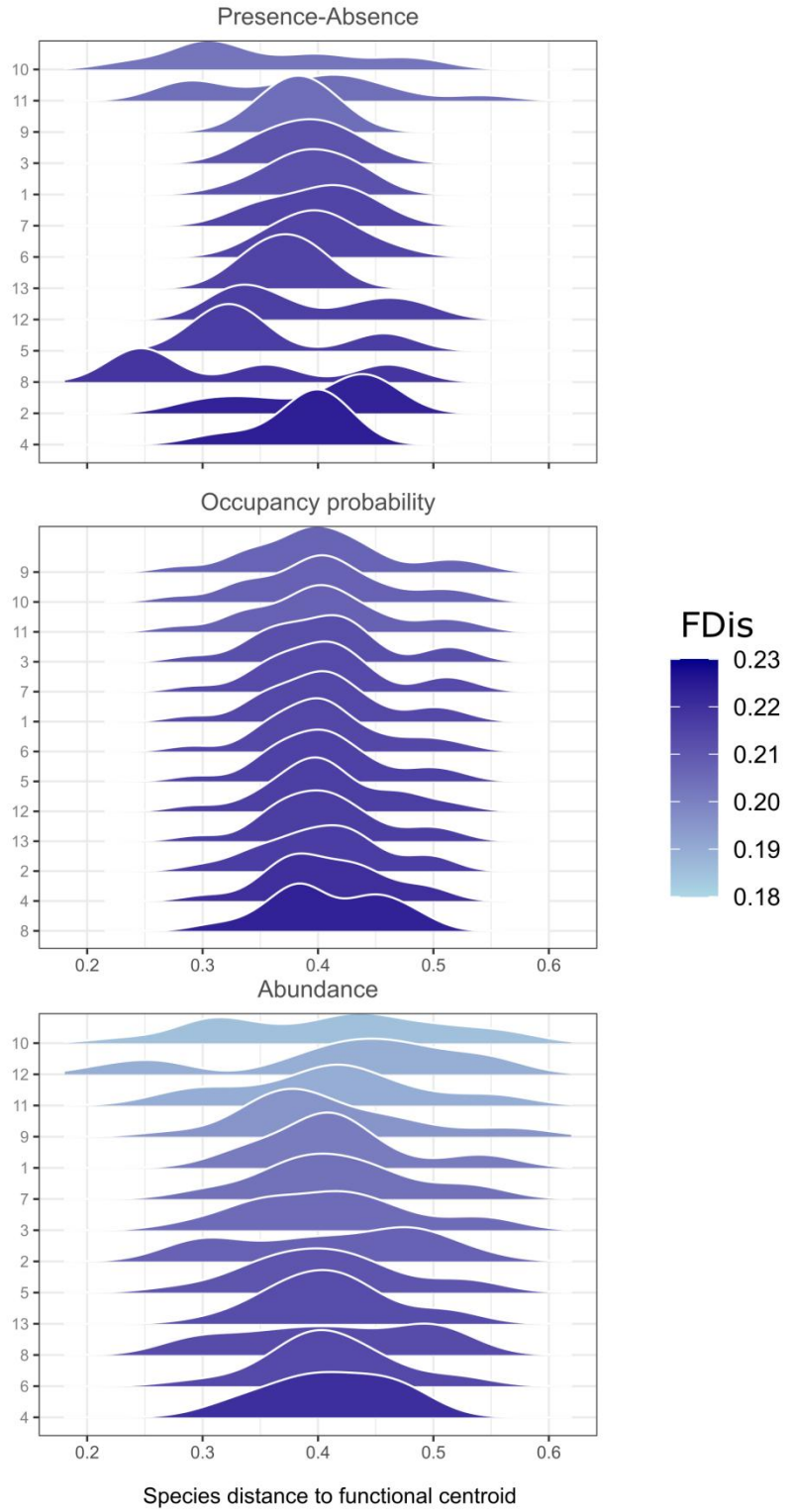


Figure 5: Distribution of species-to-centroid distances within each community (i.e., landscape) and their respective estimated Functional Dispersion (FDis) index. The three alternatives of FDis were calculated using three data types as input: species presence-absence, occupancy probability and abundance estimates.

4. Discussion

Our study indicates that landscape productivity and spatiotemporal variations in vegetation heterogeneity influence different facets of small mammals diversity in agricultural landscapes of the Atlantic Forest. Contrary to our expectations, we found no evidence for the effects of forest loss, fragmentation and temporal variability of vegetation characteristics on the functional diversity (FDis) of communities, regardless of the input data used (presence-absence, occupancy probability or abundance). Similar FDis values were associated with divergent organizational patterns of species within communities, regardless of the input data, and underscore the need for a deeper understanding of how agricultural landscape structure influences multiple dimensions of biodiversity. We found that the functional composition (CWM-Body mass) across all input data types was consistently negatively affected by temporal variability in landscape productivity (EVI.cv), and positively by temporal variability in vegetation heterogeneity (contrast.cv) at the landscape, indicating that temporal variation in vegetation characteristics in agricultural landscapes acts as an ecological filter, deferentially shaping communities according to their functional characteristics (Guillerme et al., 2025). Our results highlight the importance of examining temporal aspects of agricultural landscapes on biodiversity.

A widely known general pattern of species abundance and range size distribution in ecological assemblages is that most species are narrowly distributed and few are abundant (Gaston et al., 2000). Similarly, we found that most species of small mammal metacommunity had low abundances, while a few were highly abundant across landscapes or within specific landscapes. However, this pattern did not appear the same for occupancy: most species of small mammal assemblage were expected to be widespread, while only a small proportion were rare. This may be due to the occurrence of many species that are common in the fragmented landscapes of the Atlantic Forest, such as *Akodon montensis*, *Oligoryzomys spp*., *Gracilinanus microtarsus*, *Marmosa paraguayana* and *Didelphis aurita*, including primarily non-Atlantic Forest species *Calomys tener* and *Necromys lasiurus,* which can benefit from forest edges and the non-forested matrix (Bonvicino et al., 2002; De La Sancha et al., 2023, Estavillo et al., 2013; Umetsu & Pardini 2007).

Species distribution and abundance are consistently found to be influenced by productivity, typically assumed to reflect resource availability (Mittelbach & McGill, 2019). The positive effect of productivity on terrestrial mammal richness and abundance has been reported as a consistent pattern worldwide (De Souza Ferreira Neto et al., 2022). Our results clearly

supported a positive effect of landscape productivity on community mean abundance, but its positive effect on expected species richness (i.e., community mean occupancy) was not clear. This lack of clear support for a positive effect of productivity on community mean occupancy may be due to diverging species responses linked to landscape productivity, depending on their habits and ecological requirements. For example, in a meta-analysis investigating the diversity–productivity relationship across mammal trait groups, De Souza Ferreira Neto et al., 2022 found that the richness and abundance of insectivorous and arboreal mammals were not correlated with productivity. In our study, six species had equally high expected occupancy probabilities in landscapes with low and high productivity: *A. montensis*, *C. tener*, *O. flavescens*, *O. nigripes, G. microtarsus*, and *M. paraguayana.* Besides being widespread in conserved and altered vegetation in Atlantic forest landscapes, these species can feed on multiple basal food sources, from invertebrates to fruits (Bonvicino et al., 2002; Galetti et al., 2016; Wilman et al., 2014), which may allow them to occur even in less productive landscapes. On the other hand, both endemic and non-endemic species were highly likely to occur and tended to reach higher estimated abundances in the most productive landscapes. We did not find evidence that productivity or vegetation heterogeneity at site-level affected communities mean occupancy or abundance. Considering that most of our study area consists of heterogeneous and dynamic agricultural environments, we hypothesized that other site-level characteristics, such as spatiotemporal variations in vegetation, may be influencing the diversity of local communities. Actually, temporal variation in site-level vegetation has already been found to influence species diversity (Lee et al., 2024) and abundance (Andreo et al., 2019; Marston et al., 2023) in agroecosystems. Future studies in agroecosystems should also investigate the effects of spatiotemporal variation in vegetation characteristics at the site level on different aspects of species diversity.

As expected, temporal variability of vegetation heterogeneity negatively affected both community mean occupancy and abundance, although the evidence for the negative effect on abundance was weaker compared to that for occupancy. The observed consistency in the response of species occupancy and abundance may indicate that temporal variation in the amount and type of resources available to a species, resulting either from weather conditions or agricultural management, lead to concomitant variations in the distribution and abundance of many species in the communities (Gaston et al., 2000). In large landscapes, environmental stochastic is expected to accelerate the extinction of species that disperse and compete over short distances (Tao et al., 2024). In our study, smaller-bodied species from the regional pool

showed the highest occupancy probabilities in landscapes with lower temporal variability. Since body size is a well-established proxy for dispersal capacity (Bowman et al., 2002), high temporal variability in vegetation may reduce both occupancy and population sizes of small-bodied species, potentially driving some of them to local extinction (Escobar & Estades, 2021; Tao et al., 2024). The moderate evidence for an effect on abundance may be explained by high estimated abundances of the marsupials *Didelphis aurita* and *Monodelphis dimidiata* and the widespread rodent *Akodon montensis* on the most temporally varying landscapes. The combination of omnivorous behavior and long-distance dispersal ability in *D. aurita* may enable it to move across different areas within fragmented landscapes and locate suitable habitats, even if temporary, thus favoring its occurrence in temporally variable landscapes (Magioli et al., 2019; Umetsu et al., 2008). On the other hand, *M.dimidiata* appears to be most associated with open habitats throughout its distribution range in the Pampas and Atlantic Forest domains (Vilela et al., 2010). In our study, we detected this species only in sites of non-grazed pasture areas, which were located in landscapes with highest annual variability in contrast. Notably, it was extremely abundant in the most degraded landscape of our study (landscape 12), the one with the highest value of temporal variation in vegetation heterogeneity along the year.

In addition to affecting species occurrence and abundance, our results suggest that temporal variability in characteristics of vegetation in agricultural landscapes can shape the functional composition of communities, through effects on the body mass of local assemblages. Communities within landscapes with high temporal variability in productivity had, on average, smaller species and individuals than those in more stable landscapes. Larger individuals require more energy, according to their metabolic rates, which limits how many can exist per unit area (Brown & Maurer, 1987). Thus, highly variable landscapes in terms of productivity may reflect instability in the availability of food resources needed to sustain many larger animals, or multiple trophic levels, leading to communities composed mainly of smaller ground-dwelling species that primarily feed on plant-based items. By contrast, communities within landscapes exhibiting high temporal variability in vegetation heterogeneity had, on average, larger species and individuals. Our findings suggest that temporal variability in the agricultural matrix of fragmented landscapes favors communities with larger-bodied species. These findings corroborate a consistent pattern observed for carnivorous mammals in agroecosystems worldwide, where larger species tend to be more common in agricultural matrices (Ferreira et al., 2018). Larger animals may be able to disperse over broader areas

(Bowman et al., 2002), enabling them to locate new suitable habitats when faced with temporarily shifting food resources, favoring their persistence in highly variable environments (Mezzini et al., 2025; Tao et al., 2024). Additionally, correlation analyses revealed that increases in community-level mean body mass were positively associated with broader vertebrate-based diets and reduced reliance on plant-based resources. This pattern aligns with previous findings showing that omnivorous species capable of relying on animal-based diets are favored in anthropogenic landscapes of the Atlantic Forest (Magioli et al., 2019).

The negative effect of temporal variability in landscape productivity and the positive effect of temporal variability in vegetation heterogeneity of landscape on community mean body mass were consistent across models of CWM-Body Mass derived from the three data types. Differences emerged in the magnitude of the estimated effects (coefficients), which were larger when using unweighted presence–absence data, and similar between occupancy probability and abundance data. The similarity of coefficients between occupancy probability and abundance may also reflect concomitant variation in the distribution and abundance of many species within communities (Gaston et al., 2000). When using presence–absence data, coefficients were about twice as large, possibly due to the stronger influence of simply considering the presence of larger-bodied species on the metric, without accounting for their relative contribution (weights) to the community's functional space (Petchey & Gaston 2006). Additionally, evidence supporting the positive effect of temporal variability in vegetation heterogeneity at the landscape level was weaker for CWM–abd than for CWM–PA or CWM–psi. This may be related to the lower number of individuals estimated for very larger-bodied species occurring in these landscapes compared to that for smaller ones (e.g. landscape 12 where *M. dimidiata* was desprortionaly abundante). Thus, when weighted by abundance, the proportional contribution of species to the community can reduce the influence of those with highly contrasting body mass but low individual numbers, reflecting on the functional dominance of communities (Petchey & Gaston, 2006).

Mean FDis values varied little across landscapes and data types. This pattern is consistent with global patterns of mammalian functional diversity in the tropics (Gorczynski et al., 2021; Safi et al., 2011). More similar functional traits of coexisting species in the tropics is attributed to high density of ecologically similar species coexisting within limited geographical space (“ecological packing”), allowing for a high functional redundancy in species-rich environments (Safi et al., 2011). Additionally, it has been shown that landscape disturbances can act as an environmental filter leading to morphological similarities among

the species and individuals coexisting in small non-flying mammal assemblages in a region of Atlantic Forest (Luza et al., 2015). Our results may reflect an ecological packing in landscapes with high richness or wherein most of species has high occurrence probability. In such cases, a high number of species may be functionally similar, occupying similar positions within the community's trait space, which can result in low functional dispersion (FDis) (Petchey & Gaston 2006; Safi et al., 2011; Villéger et al., 2010). In contrast, communities with low species richness, either in highly fragmented landscapes or most forested protected areas, maybe composed of functionally dissimilar species, often resulted in the highest FDis values.

The similarly high FDis values observed in both preserved and agriculture dominated landscapes contrast with expectations for functional diversity in agroecosystems (Flynn et al., 2009). However, previous research has shown that, when measured with the FDis index, high values of functional diversity may also occur in disturbed environments (Colombo et al., 2022). In Colombo et al. (2022), high values of FDis of bat communities in degraded Amazonian islands were attributed to the occurrence of few trait-dominant species (Colombo et al., 2022), highlighting that high functional dispersion can occur even in disturbed landscapes. The divergent organizational patterns of communities along the gradient of landscape disturbance, which nonetheless result in similar FDis values, suggest that the functional structuring of species dissimilarities and abundances within communities may buffer functional diversity against the impacts of species loss (Petchey & Gaston, 2006). However, despite similar FDis values in species-rich and species-poor communities, landscapes with high functional redundancy (due to the presence of several functionally similar species) may be more resilient to the loss of ecosystem functioning following species loss (Flynn et al., 2009; Marsh et al., 2025). In contrast, in landscapes with low functional redundancy (where few functionally unique species dominate), the loss of even a small number of species could have a large impact on ecosystem functioning (Flynn et al., 2009). In light of these paradoxical responses of FDis to species occurrence and abundance in highly spatially and temporally heterogeneous landscapes, the combined use of varied measures of the components of biodiversity seems essential to accurately detect the true effects of biodiversity changes driven by anthropogenic landscapes (Brodie et al., 2021; Mouchet el al., 2010; Villéger et al., 2010).

In this study, we found no evidence that the functional dispersion (FDis) of small mammal communities changed in response to forest loss and fragmentation, or to temporal variation in

vegetation characteristics within landscapes, regardless of the community attribute used as input (i.e., species occurrences, occupancy probabilities, or abundances). Our analysis of these other attributes suggests that the apparent stability in FDis may result from different mechanisms shaping the distribution and dominance of functional traits across landscapes (Guillerme et al., 2025; Petchey & Gaston, 2006). For instance, in well-preserved, highly forested landscapes, high FDis values may reflect the presence of species with a wide range of traits, likely structured by niche partitioning in complex forest environments (Gorczynski et al., 2023; Guillerme et al., 2025). In contrast, in highly fragmented or temporally dynamic landscapes, similarly high FDis values may emerge due to strong environmental filtering, which favors a few species with specific trait combinations that confer advantages under those particular conditions (Guillerme et al., 2025). Thus, in accordance with previous studies showing that different functional diversity metrics may lead to paradoxical responses to disturbance (Villéger et al., 2010), our results highlight the importance of using multiple diversity facets to better capture the true impact of biodiversity loss on ecosystem functioning. In contrast to FDis, our functional composition measure (CWM-Body mass) consistently responded to temporal variability in the landscape. We found that considering only species presence–absence, rather than their relative contributions to community functions (i.e., occupancy probabilities or abundances), yielded stronger evidence of compositional shifts. However, the mere presence of a specific trait within a community does not guarantee the maintenance of ecosystem functioning (Laliberté & Legendre, 2010). Therefore, we recommend, whenever possible, incorporating species abundances to better capture the effects related to the functional composition of communities. Because abundance data are often more difficult to obtain than detection/non-detection data, we suggest using species occupancy probabilities, derived from MSOMs, as a proxy (Gaston et al., 2000). These probabilities may better approximate species contributions to ecosystem functioning than binary occurrence data. Finally, considering the established link between community-weighted mean (CWM) trait values and ecosystem processes (Díaz et al., 2007; Fry et al., 2018), and the potential for paradoxical or inconsistent results from functional diversity indices (Villéger et al., 2010), CWM-based metrics may offer a more interpretable and advantageous strategy. They can effectively represent dominant traits within communities and help understanding of the ecological consequences of heterogeneous and dynamics landscapes on biodiversity and ecosystem functioning.

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Temporal variability in vegetation affects the body mass of small non-flyng mammals communities in agricultural atlantic forest landscapes

SUPPLEMENTARY MATERIAL

S1. Model Specifications: Multi-Species Occupancy Model (MSOM) and Community N-Mixture Model (CNMM)

In the MSOM, the presence-absence z for each species k at the landscape i is the latent state, which follows a Bernoulli distribution:

$$\text{Landscape-level presence-absence: } z_{ik} \sim \text{Bernoulli}(\psi_{ik})$$

where ψ_{ik} is the probability of occurrence in a landscape.

In the CNMM, the abundance N for each species k at the landscape i is the latent state, which follows a Poisson distribution:

$$\text{Landscape-level abundance: } N_{ik} \sim \text{Poisson}\ (\lambda_{ik})$$

where λ_{ik} is the expected abundance in a landscape.

We combined observational data (i.e., detections/non-detections or species counts) of each species k at the landscape i (main unit), and at the site level j (subunits) using a three level model (i.e., a multiscale design). This hierarchical structure defines the relationship between latent ecological states across scales.

In the MSOM, a site j can only be occupied by species k ($a_{ijk} = 1$) if the corresponding landscape i is occupied ($z_{ik} = 1$):

$$\text{Site-level presence-absence: } a_{ijk}|z_{ik} \sim \text{Bernoulli}\ (z_{ik} * \theta_{ijk})$$

$$\text{Observed detection/non-detection data: } y_{ijlk}|a_{ijk} \sim \text{Bernoulli}\ (a_{ijk} * p_{ijlk})$$

where, θ_{ijk} represents the availability probability of species k at site j, given that the species is present in landscape i. The parameter p_{ijlk} denotes the detection probability of a species during replicate l, conditional on the species being available at the site.

In the CNMM, the latent abundance at site level (n_{ijk}) is drawn from a Poisson distribution conditional on the landscape-level abundance (N_{ik}):

Site-level abundance: $n_{ijk}|N_{ik} \sim$ Poisson ($N_{ik} * \theta_{ijk}$)

Observed species counts: $yc_{ijlk}|n_{ijk} \sim$ Binomial ($n_{ijk} * p_{ijlk}$)

where, θ_{ijk} corresponds to the proportion of the total landscape-level abundance N_{ik} allocated to site j, while p_{ijlk} represents the detection probability of an individual present at that site during replicate l. The observed species counts yc_{ijlk} were modeled using a binomial distribution, where n_{ijk} is the latent number of individuals of species k at site j. We modeled species abundance using a log-link function and species occupancy and detectability using a logit function, as follows:

Landscape-level occupancy: $logit\ (\psi_{ik}) = \beta 0_k + \beta 1_k *$ mean $EVI_i + \beta 2_k *$ $EVI.cv_i + \beta 3_k *$ mean $Contrast_i + \beta 4_k *$ $Contrast.cv_i$

Landscape-level abundance: $log\ (\lambda_{ik}) = \beta 0_k + \beta 1_k *$ mean $EVI_i + \beta 2_k *$ $EVI.cv_i + \beta 3_k *$ mean $Contrast_i + \beta 4_k *$ $Contrast.cv_i$

Site-level occupancy: $logit\ (\theta_{ijk}) = \beta 0_k + \beta 1_k *$ mean $EVI_{ij} + \beta 2_k *$ mean $Contrast_{ij}$

Site-level abundance: $log\ (\theta_{ijk}) = \beta 0_k + \beta 1_k *$ mean $EVI_{ij} + \beta 2_k *$ mean $Contrast_{ij}$

Detection probability: $logit(p_{ijlk}) = \beta 0_k + \beta 1_k *$ trap-type$_{ijl} + \beta 2_k *$ sampling effort$_{ijl} + \beta 3_k *$ rainfall$_{ijl} + \beta 4_k *$ temperature$_{ijl}$

The probability of species k occurring at a landscape (ψ_{ik}), a site (θ_{ijk}), and the probability of detecting the species/individual (p_{ijlk}), were modeled as functions of landscape (mean EVI, EVI.cv, mean Contrast, Contrast.cv), site (mean EVI, mean Contrast), and survey covariates (trap-type, sampling effort, rainfall,temperature). For each site ij, we divided the the total

sampling period (6 to 10 trap-nights) two sampling occasions (replicates, l) by collapsing detection/non-detection data into two 5-day intervals. All continuous predictors were standardized to have mean zero e variance one.

Species-specific intercepts and slopes (β) were treated as random effects drawn from community-level prior distributions, assumed to follow a normal distribution with mean (μ_β) and variance (σ^2_β) hyperparameters. These represent, respectively, the average and variability of species responses to landscape, site, and survey-level variables (Kéry & Royle, 2016a).

Model of species-specific response: $\beta^{\psi}_k \sim Normal\ (\mu_\beta\ ,\ \sigma^2_\beta)$

$$\beta^{\theta}_k \sim Normal\ (\mu_\beta\ ,\ \sigma^2_\beta)$$

$$\beta^{p}_k \sim Normal\ (\mu_\beta\ ,\ \sigma^2_\beta)$$

We used semi-informative N (0,1) hyperpriors for community-level hyperparameters and regression coefficients and a semi-informative Inverse-gamma (2,1) hyperprior for variance, in order to regularize parameter estimates while allowing the model sufficient flexibility to reflect variation across species (Gelman, 2006; Hooten & Hobbs, 2015).

We ran three parallel chains of length 50,000, discarding the first 5,000 iterations as burn-in, and used a thinning rate of 10. Convergence was assessed using the Gelman-Rubin convergence diagnostic, with values falling below 1.1 indicating adequate convergence (Gelman & Rubin, 1992).

S2. Model Specifications for the Bayesian Meta-Analysis

To properly propagate uncertainty from the first-step analysis, we implemented a Bayesian measurement error model in which the functional metric, i (Functional Dispersion - FDis and Community-weighted means of body mass - CWM), was modeled as a normal distribution centered on its expected value (μ_i), with variance (σ^2_i) defined by the posterior standard deviation from the first step:

$$FDis/CWM \sim N(\mu_i\ ,\ \sigma^2_i)$$

The expected value μ_i was modeled as a linear function of the landscape metrics, and we included an additional residual error term to account for unexplained variation (ϵ_i):

$$\mu_i = \beta_0 + \beta 1 * \text{forest cover}_i + \beta 2 * \text{pacth density}_i + \beta 3 * \text{mean EVI}_i + \beta 4 * \text{mean Contrast.cv}_i + \epsilon_i$$

$$\epsilon_i \sim N(0, \tau_{resid})$$

We used weakly informative priors N(0,1000) for the regression intercepts and slopes, β, to provide mild regularization while allowing flexibility in estimating the effects of landscape covariates on functional diversity indices (Hooten & Hobbs, 2015). For the variance parameters, τ_{resid} , we applied a semi-informative Inverse-gamma (2,1) prior to balance shrinkage and flexibility in capturing variation across landscapes (Gelman, 2006). We ran three parallel chains of length 25,000, discarding the first 5,000 iterations as burn-in, and used a thinning rate of 10. Convergence was assessed using the Gelman-Rubin convergence diagnostic, with values falling below 1.1 indicating adequate convergence (Gelman & Rubin, 1992). This approach accounts for both sources of uncertainty - estimation error from the functional metric calculated from posterior samples in the first-step and residual model error - ensuring valid inference in the second-stage analysis (Kéry & Royle, 2016b).

Figure S1. Correlation matrix of the fuzzy-coded dietary traits and continuous traits used to calculate functional diversity indices (FDis and CWM-Body mass) for small non-flying mammal communities. The included traits are: The traits included were: body mass (average adult body mass in grams), foot-to-body length ratio (ratio between hindfoot length and total head-body length), tail-to-body length ratio (ratio between tail length and total head-body length), and dietary proportions including: fruit (Diet–Fruit), nectar and plant exudates (Diet–Nect), seeds and grains (Diet–Seed), invertebrates (Diet–Inv), endothermic vertebrates such as mammals and birds (Diet–Vend), ectothermic vertebrates such as reptiles and amphibians (Diet–Vect), carrion or remains (Diet–Scav), and vegetative plant parts such as leaves, roots, grasses, and sprouts (Diet–PlantO).

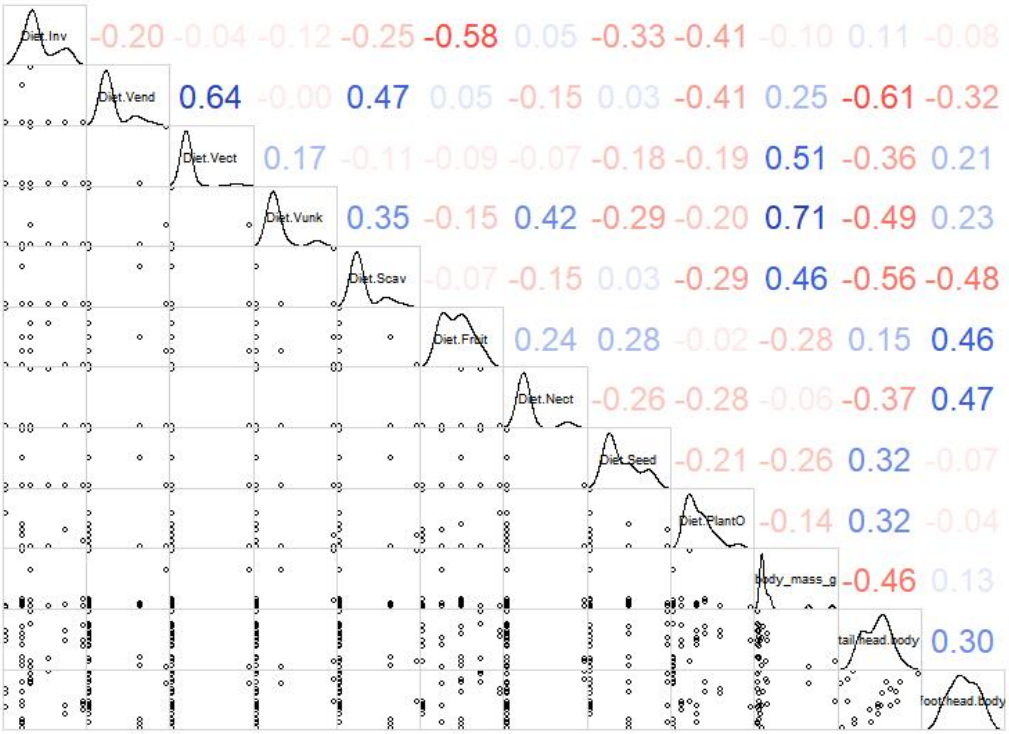
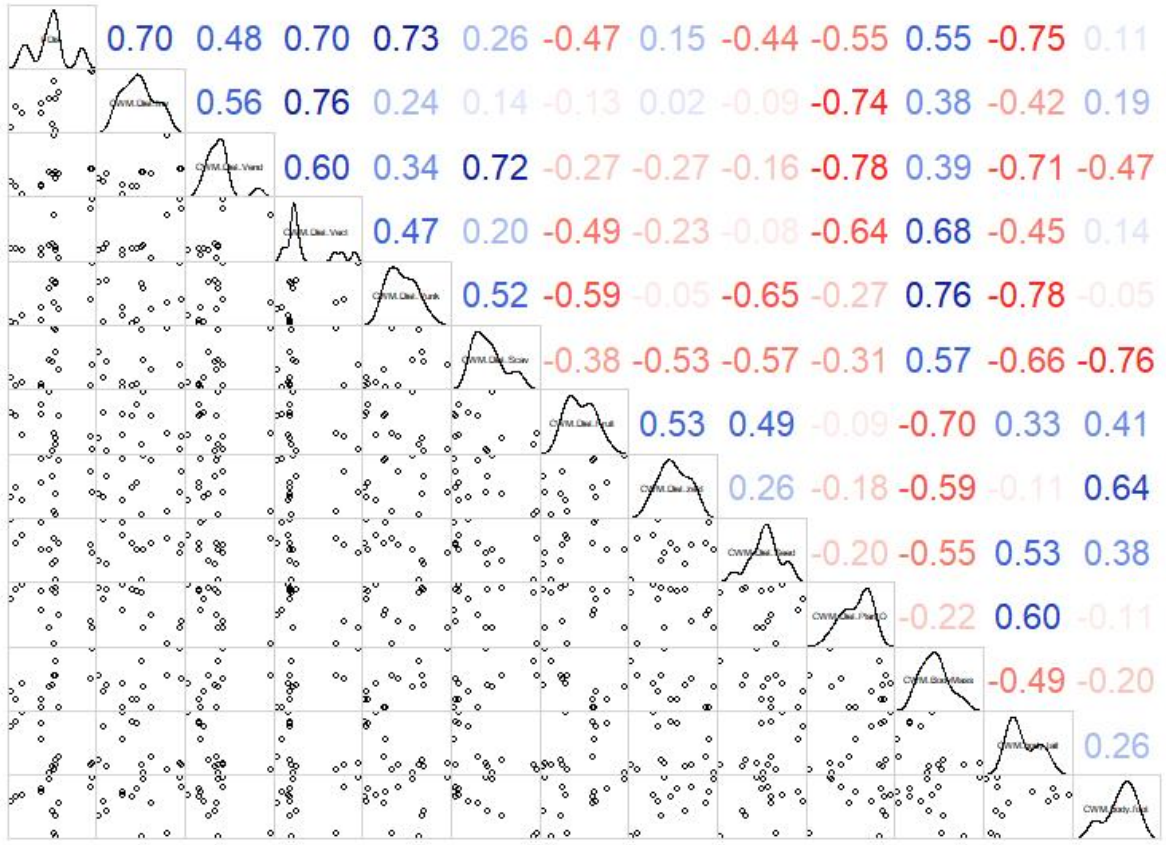
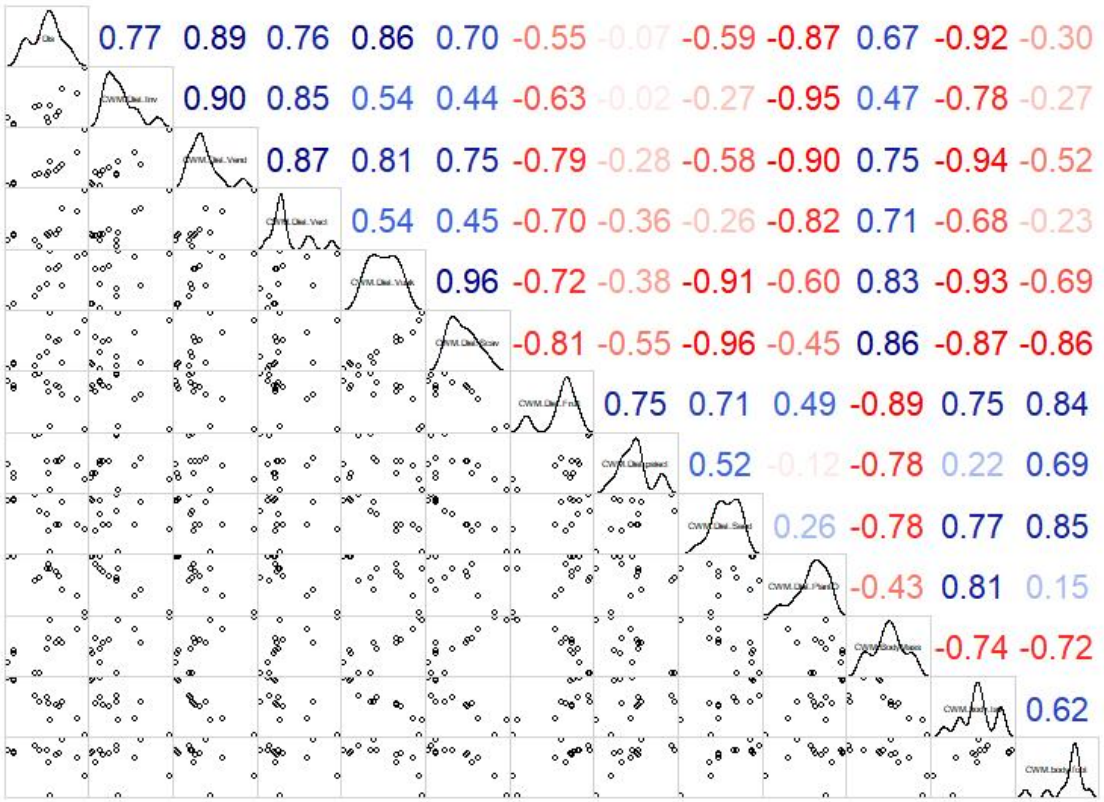


Figure S2. Correlation matrix of community-weighted means of body mass (CWM-Body mass) of small non-flying mammal communities, calculated using three types of input data (A: species presence-absence; B: species occupancy probability; C: species abundance). The included traits are: The traits included were: body mass (average adult body mass in grams), foot-to-body length ratio (ratio between hindfoot length and total head-body length), tail-to-body length ratio (ratio between tail length and total head-body length), and dietary proportions including: fruit (Diet–Fruit), nectar and plant exudates (Diet–Nect), seeds and grains (Diet–Seed), invertebrates (Diet–Inv), endothermic vertebrates such as mammals and birds (Diet–Vend), ectothermic vertebrates such as reptiles and amphibians (Diet–Vect), carrion or remains (Diet–Scav), and vegetative plant parts such as leaves, roots, grasses, and sprouts (Diet–PlantO):

A. CWM-Body mass calculated using species presence-absence as input data.



B. CWM-Body mass calculated using species occupancy probability as input data.



C. WM-Body mass calculated using species abundance as input data.

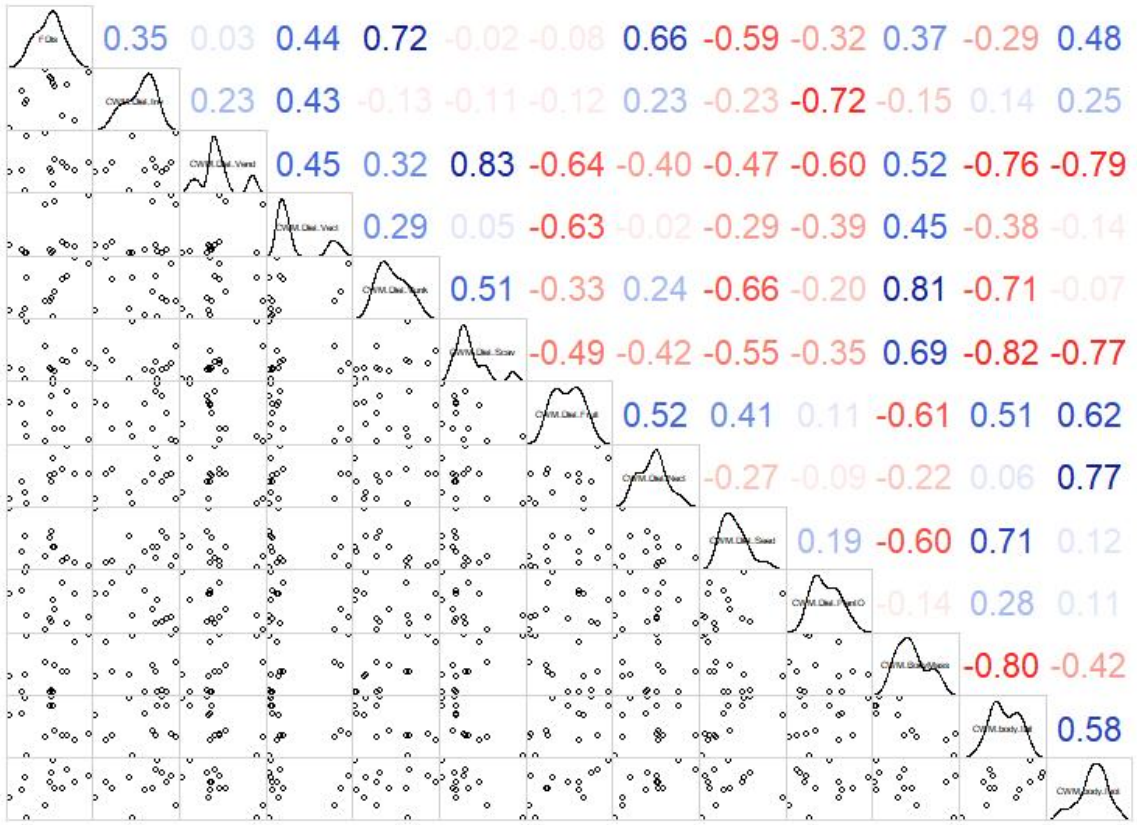
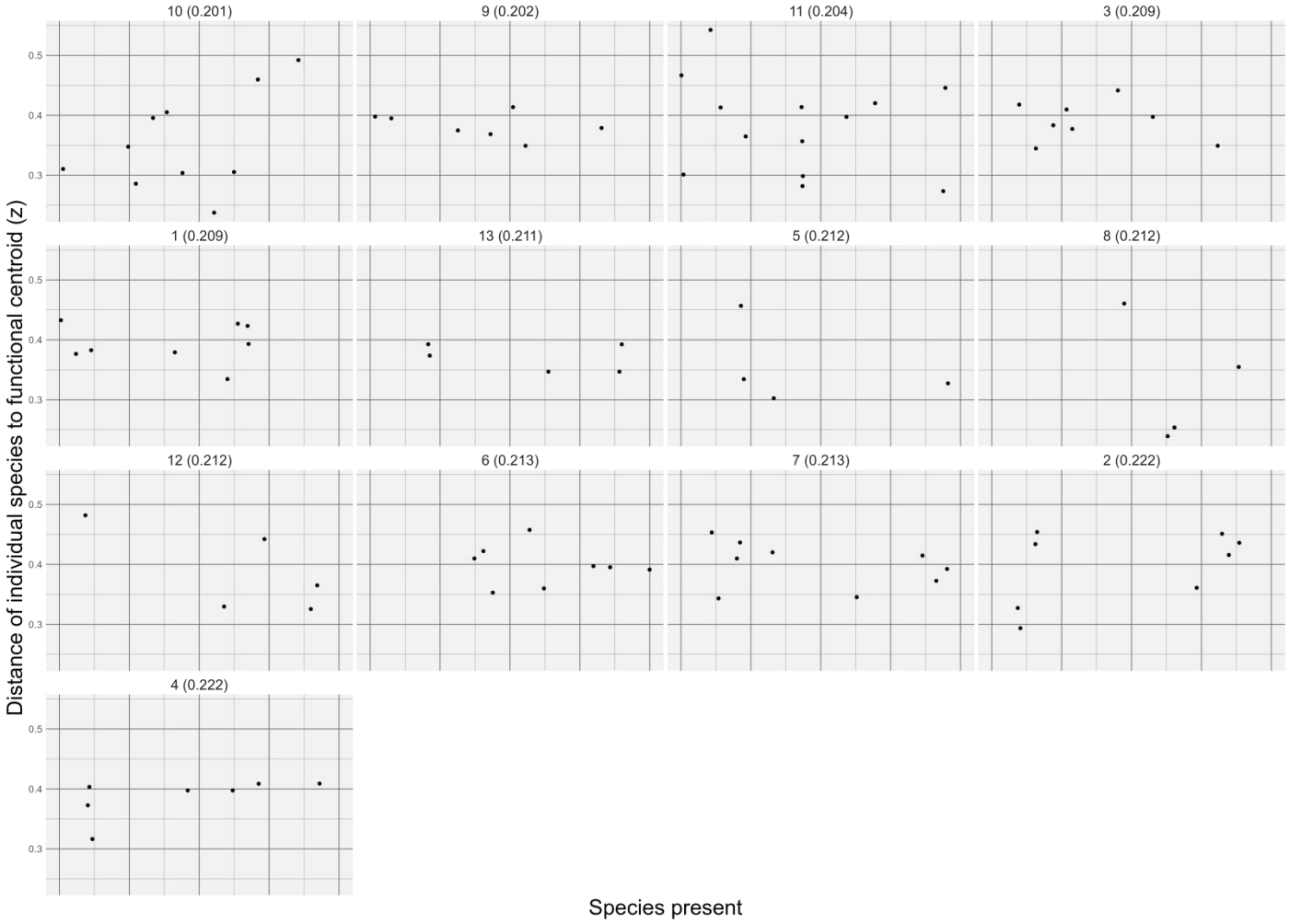
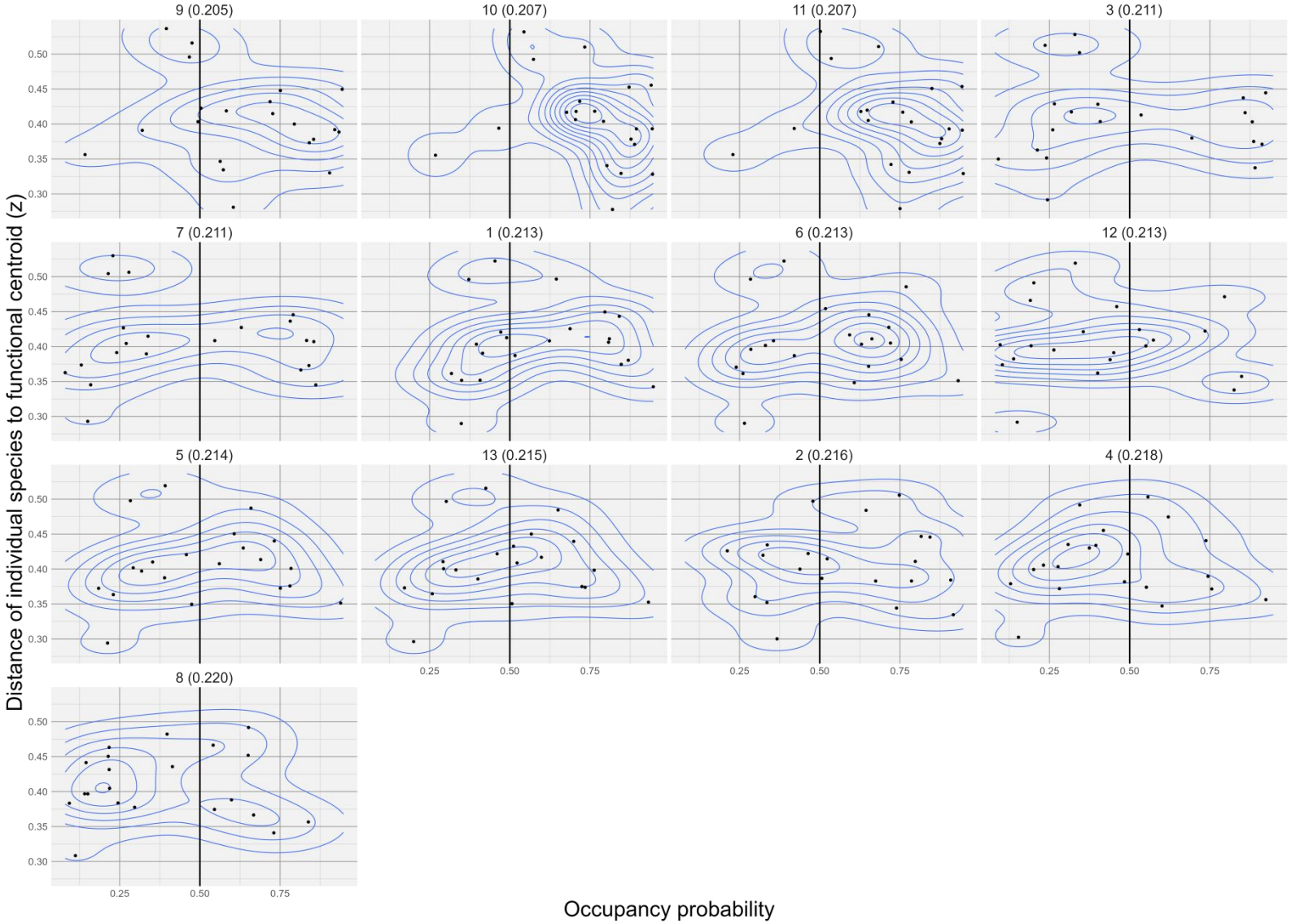


Figure S3. Distribution of species-to-centroid distances within each community (i.e., landscapes 1-13) and their respective estimated Functional Dispersion (FDis) index. The three alternatives of FDis were calculated using three data types as input: species presence-absence (A), occupancy probability (B) and abundance estimates (C).

A. FDis using presence-absence data



B. FDis using occupancy probability data



C. FDis using abundace data

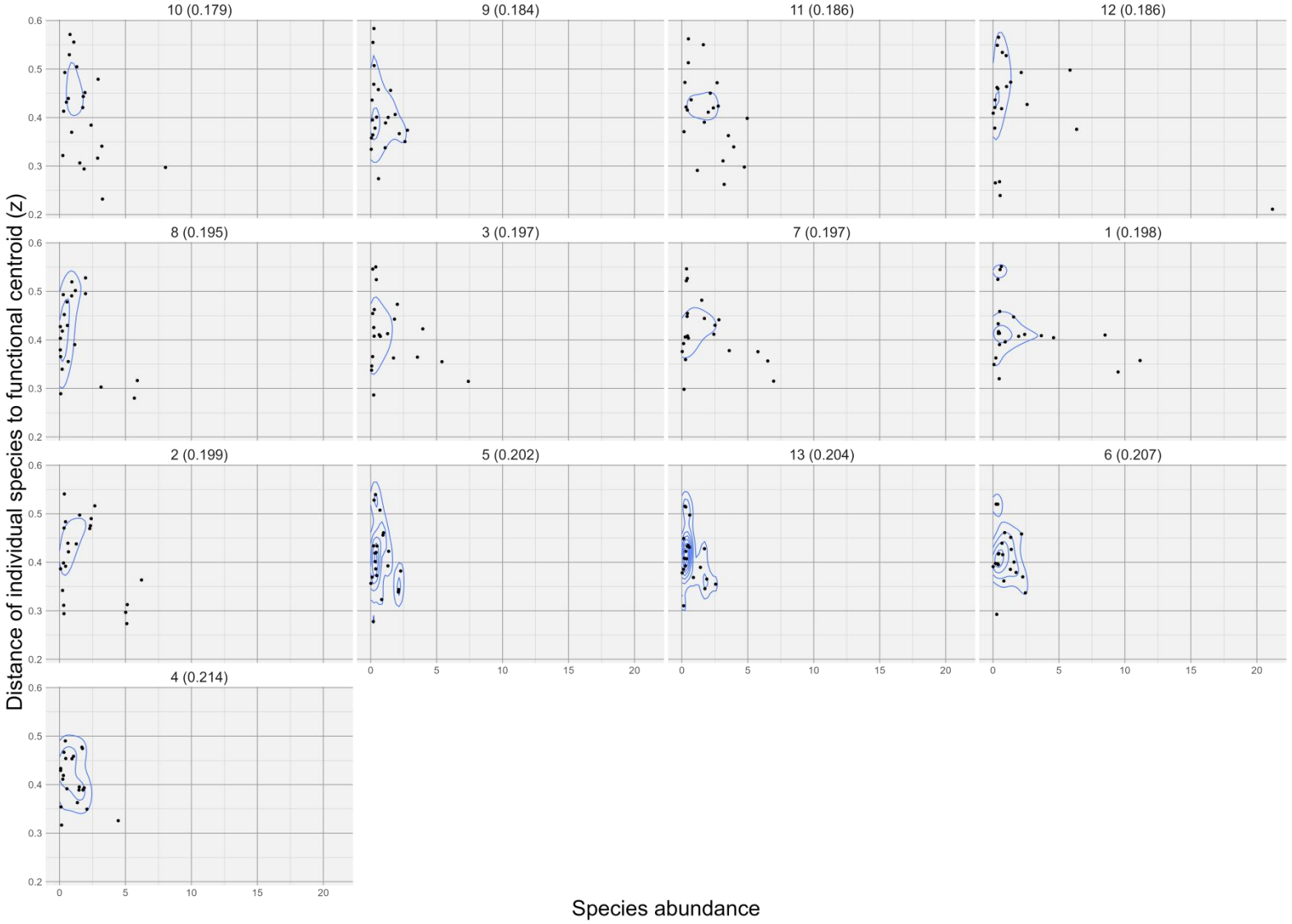


Table S1. Multispecies hierarquical models (multispecies occupancy models - MSOM; Community N-mixuture models - CNMM) fitted to assess the effects of landscape mean productivity (mean EVI) and vegetation heterogeneity (mean Contrast) and their temporal variation (EVI.cv and Contrast.cv) on small mammals occupancy em abundance in a region of the Brazilian Atlantic Forest. Scale of effect of landscape metrics (1, 3, 5, or 7 km radius) were chosen in a previous study. Site-level and survey-specific covariates are presented. We present model posterior summaries (mode, HDI - high density intervals of 95% and 89%, pd - probability of direction) and posterior predictive check (Bayesian p-value). Bolded entries indicate metrics with the strongest evidence.Model fit and predictive performance were assessed using the Area Under the Curve (AUC) (for MSOM) and the Bayesian p-value. Bolded entries indicate metrics with the stronger evidence. NA - not applicable.

Multispecies hierarchical models	**Variable**	**Mode**	**pd**	**ROPE** (-0.10, 0.10)	**HDI 89%**	**HDI 95%**	**AUC**	**Bayesian p-value**
MSOM-occupancy							0.90	0.12
Landscape-level	*mean Contrast_3km*	-0.11	59.11	19.67	-0.81, 0.57	-0.99, 0.74		
	Contrast.cv_5km	**-0.82**	**95.34**	**4.19**	**-1.54, -0.02**	**-1.76, 0.14**		
	mean EVI_3km	0.43	83.92	11.65	-0.26, 1.19	-0.42, 1.35		
	EVI.cv_7km	-0.15	63.72	17.91	-0.89, 0.58	-1.11, 0.70		
Site-level	*mean EVI*	0.06	60.47	32.91	-0.34, 0.45	-0.44, 0.55		
	mean Contrast	0.07	69.61	31.49	-0.25, 0.51	-0.35, 0.60		
Survey-specific	***Trap-type***	**-0.94**	**99.33**	**0.00**	**-1.60, -0.37**	**-1.73, -0.20**		
	Sampling effort	0.15	78.37	27.44	-0.18, 0.54	-0.29, 0.63		
	Temperature	-0.02	51.63	30.92	-0.45, 0.41	-0.53, 0.54		
	Rainfall	-0.12	66.75	34.39	-0.44, 0.26	-0.54, 0.33		
CNMM-abundance							NA	0.44
Landscape-level	*mean Contrast_3km*	0.15	73.71	33.09	-0.19, 0.43	-0.28, 0.50		
	Contrast.cv_5km	**-0.26**	**90.41**	**17.92**	**-0.62, 0.05**	**-0.69, 0.14**		
	mean EVI_3km	**0.47**	**99.67**	**0.00**	**0.21, 0.78**	**0.14, 0.84**		
	EVI.cv_7km	0.28	88.33	18.29	-0.19, 0.43	-0.17, 0.67		
Site-level	*mean EVI*	0.14	76.18	38.11	-0.16, 0.39	-0.22, 0.45		
	mean Contrast	0.08	72.45	46.93	-0.14, 0.32	-0.21, 0.36		

Survey-specific	***Trap-type***	**-0.67**	**95.74**	**4.95**	**-1.27, -0.07**	**-1.41, 0.08**		
	Sampling effort	**0.43**	**98.45**	**2.32**	**0.11, 0.78**	**0.01, 0.86**		
	Temperature	-0.30	87.87	17.38	-0.68, 0.09	-0.75, 0.20		
	Rainfall	-0.08	62.92	37.52	-0.40, 0.26	-0.48, 0.35		

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5 CONCLUSÃO

Esta tese abordou, de forma integrada, como diferentes características espaciais e temporais de paisagens agrícolas influenciam a biodiversidade de pequenos mamíferos não-voadores na Mata Atlântica, um dos principais hotspots de biodiversidade do mundo. A partir de uma revisão sistemática e de análises empíricas utilizando dados amostragens em campo e de sensoriamento remoto, este trabalho evidencia que os efeitos de paisagens fragmentadas sobre a biodiversidade são moldados por atributos espaço-temporais da vegetação, com destaque para variação temporal da vegetação medida em escala fina nesses ambientes.

Os resultados demonstraram que as paisagens agrícolas não são homogêneas nem estáticas, e que sua variação espaço-temporal, especialmente em termos de produtividade e heterogeneidade estrutural da vegetação, exerce influência significativa sobre a ocupação, abundância e composição funcional das comunidades de pequenos mamíferos. A adoção de métricas contínuas derivadas de dados de sensoriamento remoto – como índices de vegetação e métricas de textura – permitiu capturar nuances de ambientes considerados homogêneos por classificações tradicionais, revelando efeitos da matriz não detectados com métricas de classes de uso e cobertura do solo. Além disso, o uso de modelos hierárquicos multiespécie (MHMs) possibilitou integrar diferentes componentes da diversidade (taxonômica e funcional), lidando com a detecção imperfeita e fornecendo estimativas confiáveis sobre como as comunidades se organizam frente à alteração das paisagens. Os resultados indicam que a resposta das espécies às características da paisagem depende de seus traços ecológicos, e que mudanças temporais nas características da vegetação (produtividade e heterogeneidade espacial) moldam as comunidades de acordo com traços funcionais, especialmente ao determinar o tamanho corporal das espécies dominantes.

Desse modo, os resultados aqui apresentados destacam que estratégias de conservação e manejo em paisagens agrícolas da Mata Atlântica devem considerar não apenas a quantidade de floresta, mas também variações de caraterísticas em escala fina da vegetação, inclusive sua variação temporal. Incorporar múltiplos aspectos da diversidade biológica e medidas da heterogeneidade e do dinamismo das paisagens e estudos de paisagens agrícolas é essencial para um melhor entendimento dos efeitos de diferente usos de solo sobre a biodiversidade e orientar ações de manejo para preservar os processos ecológicos e garantir a resiliência em agroecossistemas.

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