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**INFLUÊNCIA DA PERDA DE MAMÍFEROS TERRESTRES DE
MÉDIO E GRANDE PORTE NA PERDA DE INTERAÇÕES
ECOLÓGICAS EM UMA ÁREA DE FLORESTA AMAZÔNICA**

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**Influência da defaunação de mamíferos terrestres na perda de
interações ecológicas em uma área de floresta amazônica**

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Sinopse:

Esta tese investiga as complexas interações entre a fauna de mamíferos, as comunidades de insetos coprófagos e os processos de regeneração florestal em florestas de terra firme na Amazônia Central. O trabalho articula dois eixos principais: o efeito da perda de fauna (defaunação) no recrutamento de árvores de valor comercial e os determinantes bióticos e abióticos que moldam as comunidades de besouros coprófagos (Scarabaeidae).

Palavras-chave: Floresta de terra firme, Amazônia, Co-declínio, Mamíferos, Gradiente ambiental, Remoção de sementes, Besouros rola-bosta.

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RESUMO GERAL

Os mamíferos desempenham um papel fundamental para o equilíbrio de processos ecológicos em florestas tropicais, tanto por meio de interações entre animais e plantas, a exemplo a remoção de sementes, até interações com outros animais, como o fornecimento de recursos para os besouros coprófagos que se alimentam das fezes e carcaças de mamíferos. Nesse contexto, a defaunação, caracterizada pela perda de mamíferos de médio e grande porte, pode comprometer múltiplas interações ecológicas e, consequentemente, o funcionamento dos ecossistemas. Neste estudo, investigamos como a perda de mamíferos de médio e grande porte afeta interações ecológicas chave, incluindo aquelas entre mamíferos e plantas, e entre mamíferos e besouros coprófagos. No primeiro capítulo, realizamos na Floresta Nacional do Tapajós (FLONA Tapajós) um experimento de exclusão de mamíferos para simular experimentalmente um gradiente de defaunação, monitorando a remoção de 1.800 sementes de seis espécies vegetais de interesse comercial na Floresta Amazônica. Nossos resultados, mostram que a exclusão de mamíferos reduziu significativamente a remoção de sementes, particularmente sob condições de exclusão severa (quando nenhum mamífero terrestre tinha acesso às sementes). O roedor *Proechimys spp.* interagiu com a maioria das sementes em todos os tratamentos experimentais, exceto com *Lecythis lurida*, cujas sementes foram removidas apenas por *Dasyprocta croconota*. Assim, esse efeito foi mais proeminente apenas para *L. lurida*, a espécie com as sementes maiores. Dessa forma, embora a defaunação impacte a remoção de sementes, seus efeitos dependem dos atributos das plantas e da identidade dos dispersores. No segundo capítulo, avaliamos o papel da biomassa de mamíferos terrestres e dos gradientes ambientais na estruturação taxonômica e funcional da assembleia de besouros rola-bosta, em áreas com diferentes níveis de defaunação da FLONA Tapajós. Amostramos simultaneamente, utilizando armadilhas fotográficas e armadilhas de queda do tipo *pitfall*, as assembleias de mamíferos e besouros, respectivamente. Além disso, medimos variáveis de estrutura florestal e do solo em 34 parcelas. Nossos resultados mostram que a riqueza taxonômica de besouros rola-bosta apresentou uma relação positiva com a biomassa de mamíferos, padrão consistente com a forte dependência trófica dos besouros com os recursos derivados de mamíferos. Em contrapartida, o gradiente ambiental desempenhou um papel dominante na abundância, nos padrões de guildas e em dimensões específicas da diversidade funcional dos besouros. Por outro lado, a biomassa de mamíferos

influenciou ainda dimensões específicas da riqueza e diversidade funcional de besouros, revelando um padrão complementar. A riqueza e a divergência funcional aumentaram conforme a biomassa de mamíferos, enquanto a dispersão e a equitabilidade funcional foram moldadas primordialmente pela textura do solo e estrutura da vegetação. Assim, nossos resultados demonstram que a perda de mamíferos atua como um filtro ecológico que reduz a diversidade e altera a estrutura funcional das assembleias de besouros rola-bosta, evidenciando a importância dos mamíferos na manutenção de processos ecológicos associados a esses organismos. Em conjunto, os capítulos evidenciam que a defaunação afeta múltiplas dimensões das interações ecológicas, tanto entre mamíferos e plantas quanto entre mamíferos e outros animais, com consequências diretas e indiretas para o funcionamento dos ecossistemas, incluindo a remoção de sementes e a ciclagem de nutrientes (indiretamente através da influência dos mamíferos sobre os besouros rola-bosta). Portanto, a conservação eficaz na Amazônia deve incluir estratégias que protejam os ecossistemas do processo de defaunação, incluindo o fortalecimento da fiscalização contra a caça ilegal, a priorização da integridade estrutural da floresta e a integração da diversidade funcional no planejamento de conservação para áreas florestais na Amazônia.

Palavras-Chave: Amazônia, co-declínio, interações ecológicas, sistema florestal, floresta tropical.

GENERAL ABSTRACT

Mammals play a fundamental role in balancing ecological processes in tropical forests, through interactions between animals and plants, such as seed removal, as well as interactions with other animals, such as providing resources for dung beetles that feed on mammal feces and carcasses. In this context, defaunation, characterized by the loss of medium and large-sized mammals, can compromise multiple ecological interactions and, consequently, ecosystem functioning. In this study, we investigate how the loss of medium and large-sized mammals affects key ecological interactions, including those between mammals and plants, and between mammals and dung beetles. In the first chapter, we conducted a mammal exclusion experiment in the Tapajós National Forest (FLONA Tapajós) to experimentally simulate a defaunation gradient, monitoring the removal of 1,800 seeds from six plant species of commercial interest in the Amazon Forest. Our results show that mammal exclusion significantly reduced seed removal, particularly under severe exclusion conditions (where no terrestrial mammals had access to the seeds). The rodent *Proechimys spp.* interacted with most seeds across all experimental treatments, except for *Lecythis lurida*, whose seeds were removed only by *Dasyprocta croconota*. Thus, this effect was more prominent only for *L. lurida*, the species with the largest seeds. Therefore, although defaunation impacts seed removal, its effects depend on plant traits and the identity of the dispersers. In the second chapter, we evaluated the role of terrestrial mammal biomass and environmental gradients in structuring the taxonomic and functional assembly of dung beetle communities, in areas with different levels of defaunation within the FLONA Tapajós. We simultaneously sampled mammal and beetle assemblages using camera traps and pitfall traps, respectively. Additionally, we measured forest structure and soil variables across 34 plots. Our results show that the taxonomic richness of dung beetles presented a positive relationship with mammal biomass, a pattern consistent with the strong trophic dependence of beetles on mammal-derived resources. In contrast, the environmental gradient played a dominant role in abundance, guild patterns, and specific dimensions of the functional diversity of beetles. On the other hand, mammal biomass also influenced specific dimensions of beetle functional richness and diversity, revealing a complementary pattern. Functional richness and divergence increased with mammal biomass, while functional dispersion and evenness were shaped primarily by soil texture and vegetation structure. Thus, our results demonstrate that mammal loss acts as an

ecological filter that reduces diversity and alters the functional structure of dung beetle assemblages, highlighting the importance of mammals in maintaining ecological processes associated with these organisms. Together, the chapters show that defaunation affects multiple dimensions of ecological interactions, both between mammals and plants and between mammals and other animals, with direct and indirect consequences for ecosystem functioning, including seed removal and nutrient cycling (indirectly through the influence of mammals on dung beetles). Therefore, effective conservation in the Amazon must include strategies that protect ecosystems from the defaunation process, including strengthening enforcement against illegal hunting, prioritizing the structural integrity of the forest, and integrating functional diversity into conservation planning for forested areas in the Amazon.

Key-words: Tropical forest, Amazon, co-decline, forest system, ecological interactions.

1 INTRODUÇÃO GERAL

A integridade dos processos ecossistêmicos em florestas tropicais é sustentada principalmente por interações ecológicas cruciais. Os vertebrados interagem com cerca de 94% das espécies de plantas (Jordano, 2000) e seu declínio pode levar a efeitos em cascata devastadores, resultando no declínio de populações e comunidades biológicas que deles dependem. Assim, a manutenção da biodiversidade está intimamente ligada à persistência dessas interações ecológicas, que conectam diferentes níveis tróficos e regulam o funcionamento dos ecossistemas. Este cenário tem sido evidenciado e estima-se que nos últimos 115 anos pelo menos 32% das populações de vertebrados têm entrado em declínio populacional, em uma taxa de redução de 2 espécies ao ano (Ceballos et al., 2017). Além disso, 177 espécies de mamíferos tiveram redução em suas distribuições geográficas, devido a perda de áreas, com mais de 40% dessas espécies sofrendo declínios populacionais severos (Ceballos et al., 2017).

Alterações humanas, lideradas pelo desmatamento e degradação, associado a à caça furtiva, têm afetado seletivamente várias espécies da fauna, podendo causar severas reduções populacionais ou extinções locais, gerando o fenômeno das “florestas vazias”. Nessas florestas a estrutura da vegetação permanece aparentemente intacta, mas as funções ecológicas das interações entre animal-planta são perdidas devido a perda de espécies-chave da fauna (Redford, 1992), processo esse que mais tarde ficou conhecido como defaunação (Dirzo et al., 2014). Nesse contexto, a defaunação emerge como um dos principais processos capazes de romper interações ecológicas chave, afetando simultaneamente diferentes componentes da biodiversidade e suas funções associadas.

O conceito de defaunação foi discutido pela primeira vez em 1988, no Simpósio Internacional de Interação Animal-Planta na UNICAMP (Galetti e Dirzo, 2013), e detalhado posteriormente por Dirzo e Miranda (1990). Desde então, diversos estudos

têm identificado fatores como a caça (Stafford et al., 2017), a expansão agrícola e urbana (Ribeiro et al., 2009) e a perda e fragmentação do habitat (Fahrig, 2003) como vetores desse processo. No entanto, embora esses fatores sejam amplamente reconhecidos, seus efeitos sobre as interações ecológicas e o funcionamento dos ecossistemas ainda demandam maior investigação. Nesse contexto, mais do que quantificar suas causas ou intensidade, torna-se fundamental compreender como a defaunação altera processos ecológicos e interações entre espécies ao longo do tempo.

Em florestas tropicais, a defaunação atinge principalmente os mamíferos, como os grandes herbívoros, frugívoros e predadores, que estão entre os principais animais ameaçados de extinção (Peres e Palácios, 2007; Bogoni et al., 2018). A perda desses grupos é particularmente crítica, pois eles desempenham papéis centrais tanto em interações planta–animal (como dispersão e predação de sementes) quanto em interações com outros organismos, sustentando redes ecológicas complexas (Culot et al., 2015; Bogoni et al., 2019).

No Brasil, estudos concentram-se principalmente na Mata Atlântica, apresentando resultados variados. Por exemplo, pesquisas experimentais têm demonstrado que a exclusão experimental de mamíferos terrestres não alterou a demografia de plântulas (Brocardo et al., 2013). Outras pesquisas, utilizando a mesma abordagem experimental, relataram que a perda de grandes herbívoros acelera a redução da diversidade, altera a composição da comunidade e a diversidade funcional de plântulas (Souza et al., 2020; Villar e Medici, 2021), sendo sugerido que o declínio de espécies de grande porte pode impactar a capacidade de sequestro de carbono das florestas (Bello et al., 2015; Peres et al., 2016), devido a limitação na dispersão de espécies de plantas com sementes grandes, que possuem madeira de alta densidade e dependem desses frugívoros para sua remoção (Chen et al., 2021). Muitas dessas espécies também apresentam elevado valor econômico na Amazônia, sendo amplamente

exploradas para madeira e outros produtos florestais, o que reforça a importância de compreender como a defaunação pode afetar sua regeneração natural.

No entanto, em biomas como o da Amazônia, esses estudos têm recebido pouca atenção, apesar das fortes pressões que a região enfrenta, como o avanço da grilagem e do agronegócio que fortemente ameaçam a biodiversidade (Fearnside, 2005). Essa lacuna é particularmente relevante quando consideramos que os efeitos da defaunação podem se manifestar em múltiplas dimensões das interações ecológicas, ainda pouco exploradas de forma integrada na região. Até onde sabemos, existem apenas dois estudos experimentais que investigam esses efeitos da perda de espécies sobre a perda de interações no bioma amazônico, o primeiro revelou que quando mamíferos são excluídos localmente há um aumento significativo na densidade e no recrutamento de plântulas próximo a planta-mãe, chegando a ser de três a quase seis vezes maior nas áreas isoladas em comparação aos controles (Beck et al., 2013). Esse aumento na densidade de plântulas está associado à redução na dispersão de sementes, com potenciais consequências negativas para o recrutamento a longo prazo devido a processos dependentes de densidade (Camargo-Sanabria et al., 2015). Já o segundo trabalho, evidenciou que a exclusão de mamíferos de médio e grande porte pode provocar um colapso funcional superior a 95% em processos vitais, como a bioturbação e a ciclagem de nutrientes (Batista et al., 2025).

Adicionalmente, estudos observacionais têm demonstrado que distintos níveis de defaunação podem afetar criticamente outras populações de animais silvestres (Bogoni et al., 2019; Fuzessy et al., 2021), uma vez que o declínio de espécies pode ocorrer associado a um efeito em cascata (Dirzo et al., 2014). Isso ocorre porque diferentes grupos faunísticos estão frequentemente vinculados a relações de co-ocorrência com outros grupos (Culot et al., 2013; Raine et al., 2018). Por exemplo, em locais intensamente caçados, há aumento na densidade de pequenos mamíferos em resposta à

redução de espécies de maior porte (Galetti et al., 2017; Bovendorp et al., 2018), o que resulta em menor distância de dispersão de sementes e alterações na dinâmica das interações ecológicas (Galetti et al., 2015b; Fuzessy et al., 2018).

De forma semelhante, essas alterações na comunidade de mamíferos também afetam outros grupos, provocando redução na diversidade funcional de besouros coprófagos (Bogoni et al., 2020). Nesse caso, a relação entre mamíferos e besouros representa uma via adicional pela qual a defaunação pode afetar o funcionamento dos ecossistemas, conectando diferentes níveis tróficos além das interações planta–animal. Tais alterações, podem afetar funções chaves no ecossistema, como a dispersão de sementes e estoque de carbono (Galetti et al., 2015a; Fuzessy et al., 2018). Nesse sentido, recentemente alguns estudos têm indicado que a população de algumas espécies de besouros-rola-bosta (Scarabaeinae) podem declinar devido à extinção ou declínio de populações de mamíferos (Iida et al., 2018; Nichols et al., 2009; Raine et al., 2018; Raine e Slade, 2019), uma vez que eles coevoluíram estreitamente com mamíferos de médio e grande porte, os quais fornecem os principais recursos tróficos (fezes e carcaças), necessários para sua alimentação e reprodução (Barlow et al., 2007).

Embora o co-declínio seja conhecido (Bogoni et al., 2014; Culot et al., 2013; Nichols et al., 2013), estudos recentes também têm indicado respostas relacionadas a variações na condição e no tamanho corporal de besouros em função de alterações na estrutura do habitat (Salomão et al., 2018). Embora se saiba que gradientes ambientais filtram o *pool* regional de espécies e geram variação espacial nessas assembleias (Raine, 2019), pouco se sabe sobre como essas comunidades na Amazônia respondem simultaneamente a mudanças no ambiente e à perda de mamíferos. Essa abordagem integrada é essencial para compreender como fatores bióticos (perda de mamíferos) e abióticos (gradientes ambientais) interagem na estruturação dessas assembleias, uma vez que a perda da mastofauna, combinada à degradação do habitat, pode gerar

impactos em cascata que reduzem drasticamente a abundância de invertebrados decompositores (Lamperty et al., 2020).

Contudo, apesar dessas evidências gerais, para o bioma amazônico pouco se têm explorado como a perda específica de mamíferos combinado ao gradiente ambiental modulam as respostas funcionais e os processos ecológicos desempenhados pela comunidade de besouros-rola-bosta (Nichols et al., 2013). Portanto, há uma urgência em compreender como o declínio das populações de mamíferos afeta a fauna associada e suas funções, para que sejam definidas estratégias que visem frear a perda de processos ecossistêmicos essenciais, como os desempenhados pelos besouros rola-bosta.

Diante desse cenário, esta tese adota uma abordagem integrada para investigar como a defaunação afeta diferentes tipos de interações ecológicas mediadas por mamíferos, conectando processos planta-animal e animal-animal. Nesse contexto, essa tese está estruturada em dois capítulos que foram realizados na Floresta Nacional do Tapajós (FLONA Tapajós) no Pará. No primeiro capítulo, focamos nas interações entre mamíferos e plantas, por meio de um experimento de exclusão de mamíferos que simula um gradiente de defaunação e permite avaliar seus efeitos sobre a remoção de sementes. No segundo capítulo, ampliamos essa abordagem para interações entre mamíferos e outros organismos, avaliando, em áreas com diferentes níveis de defaunação de mamíferos, como a biomassa de mamíferos e os gradientes ambientais estruturam taxonomicamente e funcionalmente a assembleia de besouros rola-bosta. Para tanto, amostramos simultaneamente, utilizando armadilhas fotográficas e armadilhas *pitfall*, as assembleias de mamíferos e besouros, respectivamente. Complementarmente, medimos variáveis de estrutura florestal e do solo, permitindo avaliar de forma conjunta os efeitos da defaunação em múltiplas dimensões das interações ecológicas.

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1.1 A Floresta Nacional do Tapajós e a defaunação de mamíferos

No Brasil, as Unidades de Conservação (UCs) foram criadas com o objetivo de conter o avanço do desmatamento e a ocupação desordenada do território, promovendo o uso sustentável dos recursos naturais. Embora apresentem limitações no controle da caça, essas áreas estão entre as estratégias mais eficazes para a conservação da biodiversidade e da integridade dos processos ecossistêmicos (Bruner et al., 2001), especialmente por manterem extensas áreas de florestas maduras em melhor estado de conservação quando comparadas a áreas não protegidas.

No estado do Pará, a Floresta Nacional do Tapajós (FLONA Tapajós), criada pelo Decreto nº 73.684 de 19/02/1974, constitui uma Unidade de Conservação de uso sustentável, permitindo a exploração de madeira e de produtos florestais não madeireiros (BRASIL, 1974). Esse modelo de uso múltiplo, aliado à presença de comunidades tradicionais e à implementação de manejo florestal de impacto reduzido (RIL), torna a área particularmente relevante para investigar como atividades humanas influenciam a fauna e os processos ecológicos associados. A gestão da área é realizada, em parte, pela Cooperativa Mista da Flona do Tapajós (COOMFLONA), que opera sob

um rigoroso arcabouço legal, incluindo o Decreto 5.975/2006 e resoluções do CONAMA 406/2009.

Adicionalmente, a FLONA Tapajós se destaca como uma das Unidades de Conservação com maior histórico de pesquisas científicas no Brasil, impulsionado pela instalação de módulos do sistema RAPELD a partir de 2010. Apesar desse histórico, estudos focados na mastofauna de médio e grande porte são relativamente recentes e têm revelado padrões importantes sobre o estado de conservação dessas comunidades. Rosa et al. (2021) indicaram que áreas da porção norte da FLONA apresentam redução na riqueza e na biomassa de mamíferos terrestres, especialmente de espécies de maior porte, como a anta (*Tapirus terrestris*) e a onça-pintada (*Panthera onca*), sugerindo um cenário de defaunação. Em contraste, áreas da porção sul apresentam maior integridade faunística, configurando um gradiente espacial de defaunação dentro da própria unidade de conservação.

Dando sequência a esse diagnóstico, Brocardo et al. (2023) demonstraram que a estrutura das comunidades de vertebrados é fortemente influenciada por variáveis ambientais, com respostas distintas entre grupos, e que a baixa ocorrência de espécies de grande porte indica pressão de caça na região. Dessa forma, enquanto Rosa et al. (2021) evidenciam o padrão espacial da defaunação, Brocardo et al. (2023) contribuem para a compreensão dos fatores que estruturam essas comunidades e possivelmente intensificam esse processo. Esses estudos, em conjunto, indicam que a FLONA Tapajós apresenta variação espacial tanto na estrutura das comunidades de mamíferos quanto na intensidade da defaunação, criando uma oportunidade única para investigar seus efeitos ecológicos.

Nesse contexto, a existência de áreas mais e menos defaunadas dentro da FLONA Tapajós permite a avaliação de como diferentes níveis de perda de mamíferos influenciam interações ecológicas mediadas por esses organismos. Essa abordagem

possibilita testar, de forma complementar, como a defaunação afeta tanto interações planta–animal, por meio de um experimento de exclusão de mamíferos que simula diferentes níveis de defaunação, quanto interações entre animais, avaliadas ao longo de um gradiente natural de defaunação, como aquelas envolvendo besouros coprófagos.

Dando continuidade aos estudos anteriores que evidenciaram o padrão espacial da defaunação e seus potenciais determinantes, esta tese avança ao investigar suas consequências ecológicas, integrando diferentes abordagens e níveis de organização biológica. Assim, a FLONA Tapajós configura-se como um sistema modelo para investigar os efeitos da defaunação sobre múltiplas dimensões das interações ecológicas, integrando variação na biomassa de mamíferos e gradientes ambientais.

Dessa forma, os resultados desta tese contribuem para compreender como a perda de mamíferos pode comprometer processos ecossistêmicos essenciais, como a dispersão de sementes e a ciclagem de nutrientes, a partir de evidências experimentais e observacionais, ao alterar interações ecológicas chave entre mamíferos, plantas e outros organismos, com implicações diretas para a conservação da biodiversidade e para a sustentabilidade de práticas de manejo florestal comunitário na região.

2 OBJETIVOS

2.1 Objetivo geral

Avaliar os efeitos da perda (a exemplo, defaunação) de mamíferos de médio e grande porte sobre interações ecológicas mediadas por esses organismos, bem como suas consequências para processos ecológicos e comunidades biológicas em uma floresta amazônica de terra firme.

2.2 Objetivos específicos

- Testar como a defaunação de mamíferos de médio e grande porte afeta interações ecológicas entre mamíferos e plantas, por meio da remoção de sementes de espécies vegetais de interesse comercial, especialmente aquelas que possuem sementes maiores.
- Examinar como a defaunação, expressa pela biomassa de mamíferos terrestres >1Kg, e a complexidade ambiental, caracterizada pela estrutura da vegetação e do solo, influenciam interações ecológicas entre mamíferos e besouros coprófagos, refletidas na estrutura taxonômica e funcional da comunidade de besouros rola-bosta.

3 REFERÊNCIAS

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CAPÍTULO 1

Castro, A., R. Fadini, M. Pires, C. Brocardo, I. Wilker, and C. Rosa., 2026.

“Animal–Plant Interactions Under Defaunation: Consequences for Amazonian Trees of Commercial Interest.” *Biotropica*. 0:e70183.

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Animal–Plant Interactions Under Defaunation: Consequences for Amazonian Trees of Commercial Interest

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ABSTRACT

The decline of medium- and large-bodied terrestrial mammal populations can compromise key ecological processes such as seed dispersal. We conducted an exclusion experiment simulate a defaunation gradient, monitoring the removal of 1,800 seeds from six plant species of commercial interest in the Amazon Forest. Overall, mammal exclusion significantly reduced seed removal, particularly under severe exclusion conditions. However, this effect was species-specific. Only *Lecythis lurida*, the species with the largest seeds, showed a significant reduction in removal under severe defaunation. *Proechimys* spp. interacted with most seeds in all experimental treatments, except for *L. lurida*, whose seeds were removed only by *Dasyprocta croconota*. While *Proechimys* spp. likely acts as a seed predator for all tested species, *D. croconota* can contribute to seed dispersal and consequently to the recruitment of a variety of plant species. Our findings reinforce that while defaunation impacts seed removal, its effects depend on plant traits and the identity of dispersers. The loss of terrestrial mammals may compromise long-term plant recruitment, especially for species that rely on larger mammals for effective seed removal. The loss of ecological interactions may jeopardize the sustainable supply of timber and non-timber products, directly affecting the income and food security of local traditional cooperatives in the Amazon.

Keywords: Amazon, extinction risk, rodents, seeds removal, seed size.

1 INTRODUCTION

Tropical forests harbor more than twice as many known species as any other terrestrial biome on Earth (Pillay et al. 2022). However, in recent decades, they have experienced severe biodiversity losses, primarily due to population declines and local extinctions of vertebrates, a process known as defaunation (Dirzo et al. 2014; Galetti et al. 2017; Gardner et al. 2019). Defaunation can disrupt ecological interactions and compromise key functions that regulate critical ecosystem functions, such as seed dispersal and predation (Galetti et al. 2015; Fedriani et al. 2020), ultimately affecting plant mortality and recruitment (Villar et al. 2021). Despite its vastness and biodiversity, the Amazon has not been exempt from this process, with reports of defaunation driven by expanding anthropogenic activities (Peres and Palacios 2007; Rosa et al. 2021).

In tropical forests, approximately 94% of plant species depend primarily or exclusively on frugivorous animals for seed removal (Jordano 2000). Seed removal by animals typically leads to two possible outcomes: dispersal, when the seed is transported and deposited away from the parent plant (with or without prior ingestion) or predation, when the seed's embryo is damaged during consumption (Howe and Smallwood 1982). While frugivores may act as seed predators when consuming fruits, they often provide the service of seed dispersal by moving viable seeds over long distances, which can enhance germination and recruitment success (Jordano and Godoy 2002; Beck et al. 2013; Squinzani et al. 2022). Medium- and large-bodied mammals play a crucial role in this process, as many species ingest whole fruits and seeds and defecate the seeds intact, often far from the parent plant (Beckman and Sullivan 2023). This ability to handle and transport large seeds is closely linked to body size, as smaller animals typically cannot consume large seeds without damaging them through mastication (Chen et al. 2017). However, small mammals can also carry seeds without

ingestion, eventually dropping or caching the seeds, thus dispersing them through stomatochory (McConkey et al. (2024). Additionally, larger seeds are expected to be more attractive to frugivores and seed predators due to the higher nutrient content of the fruits or seeds themselves (Dirzo et al. 2007; Dylewski 2020). Therefore, the absence of medium and large bodied mammals may compromise the dispersal and recruitment of large-seeded plant species in defaunated areas (De Paula et al. 2018). In Afrotropical forests, for instance, Rosin et al. (2016) observed that the removal of terrestrial mammals significantly reduced seed removal and increased predation rates, leading to lower seedling establishment. Studies in Neotropical forests have shown that the absence of large mammals may favor an increase in the abundance of small rodents (Wright 2003; Galetti et al. 2015a; Bovendorp et al. 2018). These animals tend to act more as seed predators than as dispersers (De Mattia et al. 2004), which can intensify predation pressure and negatively impact plant recruitment, especially for species whose seeds are primarily dispersed by large terrestrial mammals.

Reductions in seed dispersal in defaunated areas can, in the medium term, affect several vital ecological processes for plant life, such as establishment, recruitment, and consequently, impact the populations of many plant species (Villar and Medici 2021; Beck et al. 2013), including those of high commercial value such as timber species (Rosin and Poulsen 2016). Changes in plant recruitment may lead to the replacement of species whose seeds are removed by medium- and large-bodied frugivores, often of greater commercial value, by species of lower commercial interest, whose seeds are dispersed by wind, small mammals, or birds (Peres et al. 2016). This shift may have negative economic consequences for local and traditional communities that depend on both timber and non-timber forest products.

The effects of defaunation have been widely studied in highly fragmented biomes such as the Atlantic Forest (Brocardo et al. 2013; Souza et al. 2020; Villar et al.

2021), where successive local extinctions have already altered ecological interactions. These studies have found consistent evidence of the direct and indirect impacts of fauna loss on seed removal and forest regeneration, such as reduced seed removal (Culot et al. 2017) and increased seed mortality (Galetti et al. 2015). However, most of this research has focused on a narrow set of plant groups, particularly palms and conifers (Culot et al. 2017; Galetti et al. 2015; Brocardo et al. 2018; Meiga et al. 2020; Squinzani et al. 2022).

Despite the Amazon's high biodiversity, experimental studies assessing how terrestrial mammal defaunation alters key ecological processes remain scarce. To our knowledge, only two studies have addressed this issue using defaunation experiments. Beck et al. (2013), working in the Peruvian Amazon, found that defaunation increased seedling density and cover, indicating long-term shifts in forest dynamics and tree community structure. More recently, Batista et al. (2025) observed a substantial reduction in ungulate behaviors such as trampling, feeding, defecation, and bioturbation in defaunated areas. They also found that small mammals could not compensate for the loss of these functions, pointing to significant disruptions in ecosystem processes. However, no study to date has assessed how defaunation affects seed removal of plant species with commercial value in the Amazon. Understanding these interactions is essential for anticipating the ecological impacts of fauna loss, especially in a biome that remains relatively intact but is under increasing pressure. This knowledge is particularly relevant for assessing how reduced seed removal in defaunated areas may affect plant recruitment, with direct implications for fauna conservation and the sustainability of forest management practices, both timber and non-timber, involving commercial species in the region.

In this study, we employed a well-established exclusion plot model, experimentally simulating the exclusion of medium and large-sized terrestrial mammals.

Plots followed an exclusion gradient, from control (no exclusion) to the most severe (total exclusion) (Galetti et al. 2015; Souza et al. 2022; Villar and Medici 2021; Batista et al. 2025), that experimentally evaluate the effects of terrestrial mammal defaunation on seed removal of commercially important Amazonian plant species. Generally, seeds are considered as removed when it is not possible to determine whether it had been dispersed or preyed upon by vertebrates during each survey. However, with the aid of camera traps, we were able to describe the behavior of animals interacting with seeds and infer whether they could have been dispersed or preyed upon.

Specifically, our objectives were: (1) to test how defaunation affects the removal of seeds from plant species of commercial interest, especially for species with larger seeds, and (2) to evaluate how the small-size rodent *Proechimys* spp. interact with seeds of plant species with different sizes, an understudied aspect of seed removal dynamics. We hypothesized that in environments where we experimentally simulated defaunation, the dispersal and successful germination of seeds of commercially valuable plant species would be negatively affected, resulting in reduced seedling recruitment because of the absence of medium and large-bodied mammals. We also expected that in the absence of seed removal, the probability of seeds being removed to suitable germination sites, whereas the remaining seeds would end up being attacked by other biotic agents, such as fungi and borer insects, especially for species with larger seeds.

2 METHODS

2.1 Study area

We conducted this study in the Tapajós National Forest (FNT), Pará, Brazil (Figure 1). The FNT is a sustainable-use protected area covering 527,319 ha, predominantly composed of dense terra firme rainforest, characterized by emergent

trees reaching over 50 meters in height, such as the *Bertholletia excelsa* and *Hymenolobium petraeum* (ICMBio, 2019). The climate is classified as Am (tropical monsoon) under the Köppen system, with a mean annual temperature of 25°C and average precipitation of 2,110 mm (INMET 2021).

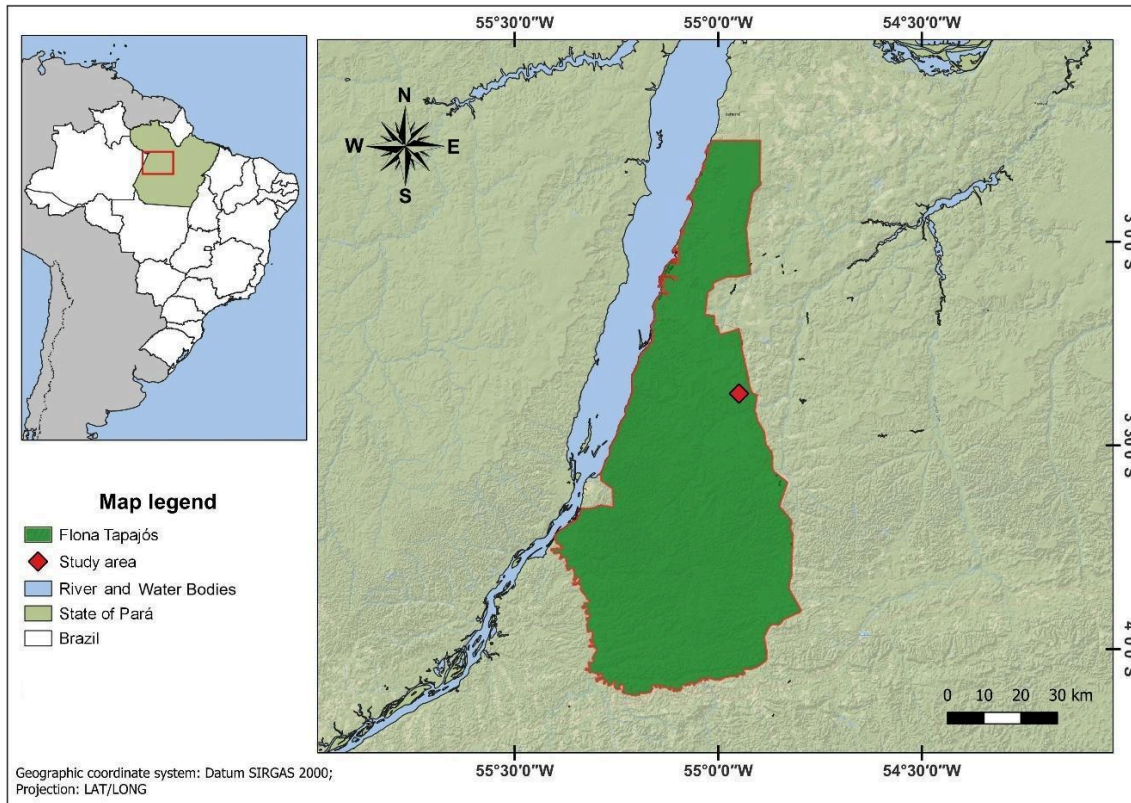


Figure 1. Location of the study area within the Tapajós National Forest (FLONA Tapajós), Brazilian Amazon.

Although mature forest predominates in the FNT, it is influenced by selective logging through a Reduced Impact Logging (RIL) forest management plan implemented by the Tapajós National Forest Mixed Cooperative (COOMFLONA). Commercially harvested species include *Hymenaea* spp., *Lecythis lurida*, and *Manilkara* spp. Additionally, non-timber products such as *Carapa guianensis* and *Bertholletia excelsa* are collected, along with essential oils, including *Copaifera* spp. (ICMBio 2019).

We established our experiment to simulate experimental defaunation in a non-managed forest area, located approximately 2 km from the nearest logging zone,

near the COOMFLONA operational base (3°22'01.29"S, 54°57'04.73"W). Previous studies at the site have documented a diverse community of medium- and large-bodied granivorous and herbivorous mammals, including *Cuniculus paca*, *Dasyprocta croconota*, *Dicotyles tajacu*, *Mazama americana*, *Passalites nemorivagus*, and *Tapirus terrestris*, as well as top predators such as *Panthera onca* and *Puma concolor* (Rosa et al. 2021; Brocardo et al. 2023).

2.2 Plant species selection

We assessed the effects of terrestrial mammal defaunation on seed removal from six commercially important plant species: *B. excelsa*, *Carapa guianensis*, *Euterpe oleracea*, *Hymenaea courbaril*, *L. lurida*, and *Manilkara huberi* (see, Table 1; Supplementary material 2). Species selection was based on (1) commercial importance (timber and non-timber) in the Amazon (ICMBio 2019); (2) local availability of viable seeds (minimum of five adult trees, with at least 700 viable seeds per species); (3) known use as food resources by local fauna (Bodmer 1991; Galetti et al. 2015b); and (4) variation in seed size and weight, ranging from 1.1 g (*M. huberi*) to 30 g (*L. lurida*), and from 1.2 cm (*E. oleracea*) to 9 cm (*L. lurida*), respectively (Table 1).

Seed mass and size for *B. excelsa*, *C. guianensis*, and *L. lurida* were obtained from published sources (Carvalho 2014). For *E. oleracea*, *M. huberi*, and *H. courbaril*, we measured seeds in the laboratory. For each species, 100 depulped and cleaned seeds from at least five individuals were weighed using a precision scale and measured using a digital caliper.

TABLE 1. Seed traits of commercially important plant species used in the seed removal experiment across a gradient of terrestrial mammal defaunation in the Tapajós National Forest. Commercial use of the studied species: nut consumption (NC), essential oils (EO), pulp and palm heart consumption (PPC), timber harvesting (TH).

Scientific name	Common name	Commercial use	Length (~cm)	Mass (~g)	Fruiting period (month)	Germination (day)
<i>Bertholletia excelsa</i>	Brazil nut	NC	4.1 (3.2–5.8)	5	January to May	~18 (month)
<i>Carapa guianensis</i>	Crabwood	EO	4.8 (3.8 – 6.2)	25	April to July	~30 (day)
<i>Euterpe oleracea</i>	Açaí palm	PPC	1.2 (0.7–1.5)	1.5	all year	~20 (day)
<i>Hymenaea courbaril</i>	Brazilian cherry	TH	3.5 (3–4)	3.5	June to September	~15 (day)
<i>Lecythis lurida</i>	Jarana	TH	8 (6–9)	30	March to May	~30 (day)
<i>Manilkara huberi</i>	Maçaranduba	TH	1.8 (1.2–2.4)	1.7	January to May	~6 (month)

2.3 Exclusion plots

We used experimental exclusion plots (5×10 m) to assess the effects of medium- and large-bodied mammal defaunation on seed removal. The experiment included 10 blocks spaced at least 500 m apart. Each block contained three plots representing defaunation treatments: (1) Control – plot marked with stakes at the corners and freely accessible to all terrestrial species; (2) Partial exclusion – plot fenced with steel mesh (5×10 cm), suspended 20 cm above the ground to allow access by medium-sized mammals (e.g., *C. paca*, *D. croconota*) while excluding large mammals (e.g., *T. terrestris*, *M. americana*); and (3) Severe exclusion – plot fenced with mesh buried 30 cm deep, excluding both medium- and large-bodied mammals (*T. terrestris*, *M. americana*, *T. pecari*, *D. tajacu*), (Figure 2).

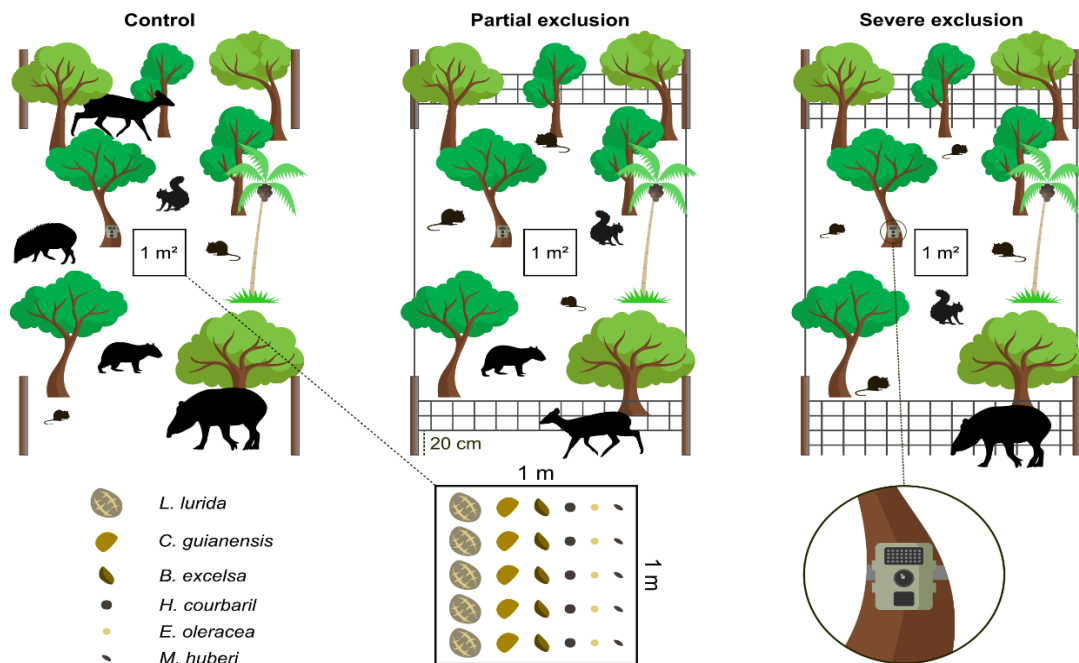


Figure 2. Schematic representation of the exclusion experiment to experimentally simulate a defaunation gradient in the Tapajós National Forest.

Only arboreal and climbing mammals (e.g., *primates*, *Guerlinguetus* spp., *Didelphis* spp.), as well as small rodents (e.g., *Proechimys* spp.), had access to all

treatments, including severe exclusion. The three plots within each block were 10–30 m apart to ensure similar abiotic conditions (Figure 2). Each plot contained a 1×1 m subplot marked with PVC pipes where seed experiments were conducted.

2.4 Seed removal and fate experiment

We conducted the experiment during the rainy season (April–July 2022), coinciding with the fruiting period of selected species. We collected seeds in FNT, from at least five fruiting trees per species. For *H. courbaril* seeds, which have pulp adhered to them, we removed the pulp manually after water immersion and then sun-dried the seeds for approximately six hours. *E. oleracea* seeds were collected from a plantation near the FNT and mechanically depulped without visible damage. The seeds of the remaining species (*B. excelsa*, *C. guianensis*, *L. lurida*, and *M. huberi*) were collected after being naturally shed and required no depulping, as they are dry seeds. We excluded all damaged or infested seeds.

Our experiment included a total of 1,800 seeds from six plant species. Initially (April to July of 2022), the experiment started with 1,500 seeds from five species, distributed in plots with 50 seeds each (10 seeds per species per 1m² subplot). The seeds were arranged in parallel rows on bare soil, spaced 10 cm apart within and between rows, with each row corresponding to a different species. Because fruits of *H. courbaril* were not available simultaneously with the other species, we added 300 seeds (10 seeds per plot, with two rows of five seeds each) of this species to the experiment in August. Although the availability of more seeds/species can attract more consumers or satiate frugivores, the similarity of the results among plant species in our experiments suggests that this is unlikely (see results).

We inspected plots every 10 days for 70 days. For each seed, we recorded its fate: (1) removed; (2) predated by invertebrates (e.g., boring insects); (3) infected by

fungi; or (4) germinated. Seeds were considered removed if missing or found with mammal tooth marks. For small seeds, shell fragments inside exclusion treatments helped confirm mammal removal. Germination was recorded when the radicle exceeded 2 cm or showed leaf sprouting. Frequently, seeds that were considered germinated were also later removed or still predated by fungi or insects. Thus, they were included in more than one category in the study. However, germination was not the primary focus of this study, as the experiment duration was insufficient to evaluate all species. For example, among the studied species, germination can take an average of up to 20 days for *E. oleracea* seeds (personal observation), to six months for *M. huberi* seeds (Cruz 2016) and 18 months for *B. excelsa* (Carvalho 2014). The experiment ended after two consecutive visits with no seed removal, and the remaining seeds were considered unviable due to fungal or invertebrate predation.

2.5 Terrestrial mammal-seed interactions

We installed one camera trap (Bushnell 12Mp NatureView Cam Essential HD Low Glow®) per subplot, directed at the seed area (Figure 2). With only 15 cameras available, we randomly selected five blocks (15 plots) for each monitoring cycle. Every 10 days, corresponding with seed inspections, we rotated the cameras to ensure coverage across all blocks. Cameras alternated between sets of five blocks every 10 days, repeating the cycle throughout the 70-day study. In total, we accumulated 660 camera trap-days. Cameras were set to record 20-second videos with 10-second intervals. Species were identified using Rosa et al. (2021).

The animals' behavior was categorized into four classes, based on video data from camera traps: Non-interactive behavior (NB) - animals passing by without interacting with seeds; Interactive behavior (IB) - animals sniffing or handling seeds without removal; Dispersal behavior (DB) - seed removal from the plot (Which could or

could not result in seed dispersal); and Predation behavior (PB) - consumption of seeds within the plot. Notably, seeds that had interactive behavior were subsequently counted as removed after their removal.

2.6 Data analysis

To test whether defaunation influenced seed removal, we used generalized linear mixed models (GLMMs). First, we analyzed total seed removal (all species combined), followed by separate analyses per species. The response variable was the number of seeds removed per plot, and the predictor was defaunation treatment (control, intermediate, severe). Block was included as a random effect, as each block contained all three treatments. Analyses were performed using the `glmmTMB` function from the `glmmTMB` package (Bolker 2023).

To evaluate interactions between mammals and seeds, we focused solely on *Proechimys* spp. due to the limited number of video records. These small-sized rodents weigh on average 250g (Paglia et al. 2011). And are known to interact with various plant species in tropical forests via seed removal (Carreira et al. 2020). Specifically, for this analysis, the cameras allowed us to categorize the records into dispersed seeds and predated seeds and additionally classified seeds by size: (1) Small (≤ 2 cm): *E. oleracea*, *M. huberi*; (2) Medium (2.1–5 cm): *B. excelsa*, *C. guianensis*, *H. courbaril*; and (3) Large (> 5.1 cm): *L. lurida*. We built three GLMMs, one per seed size class, with number of *Proechimys* spp. interactions as the response and defaunation treatment as the predictor. Block was included as a random effect. We used the `glmer.nb` function from the `lme4` package with negative binomial distribution, which best fit the data. All analyses were conducted in R version 4.1.2 (R Development Core Team 2024), and plots were created using `ggplot2` (Wickham 2016).

3 RESULTS

3.1 Seed removal and fate

Of the 1,800 seeds monitored over 70 days, 89.6% ($n = 1,614$) were removed by terrestrial mammals. Overall, seed removal was highest in the control (571 seeds; 95.1%) and partial exclusion plots (563 seeds; 93.8%), and considerably lower in the severe exclusion plots (480 seeds; 80%), (Figura 3).

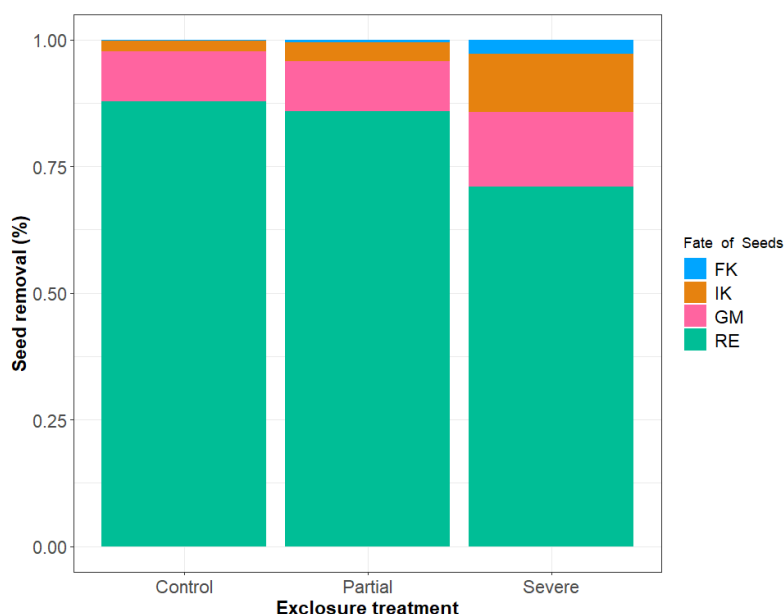


Figure 3. Proportion of seed fates along the experimental gradient simulating defaunation (Control, Partial Exclusion, Severe Exclusion). Seeds were categorized as: Removed (RE), Invertebrate-Killed (IK), Fungal-Killed (FK), or Germinated (GM).

Seed removal by terrestrial mammals occurred mostly within the first 10 days of the experiment for most small- and medium-seeded species, with an average of 50% removed during this initial period. Exceptions were *E. oleracea*, with only 24.6% removal in the first 10 days, and *L. lurida*, with just 13% removed.

Among the seeds remaining after this period, most were later removed by mammals or attacked by fungi or invertebrates, with no evidence of germination. Exceptions were again *E. oleracea*, which had 36.6% of its seeds germinate between

days 20 and 30, and *L. lurida*, with 16.3% germinating between days 30 and 40 (Figure 4).

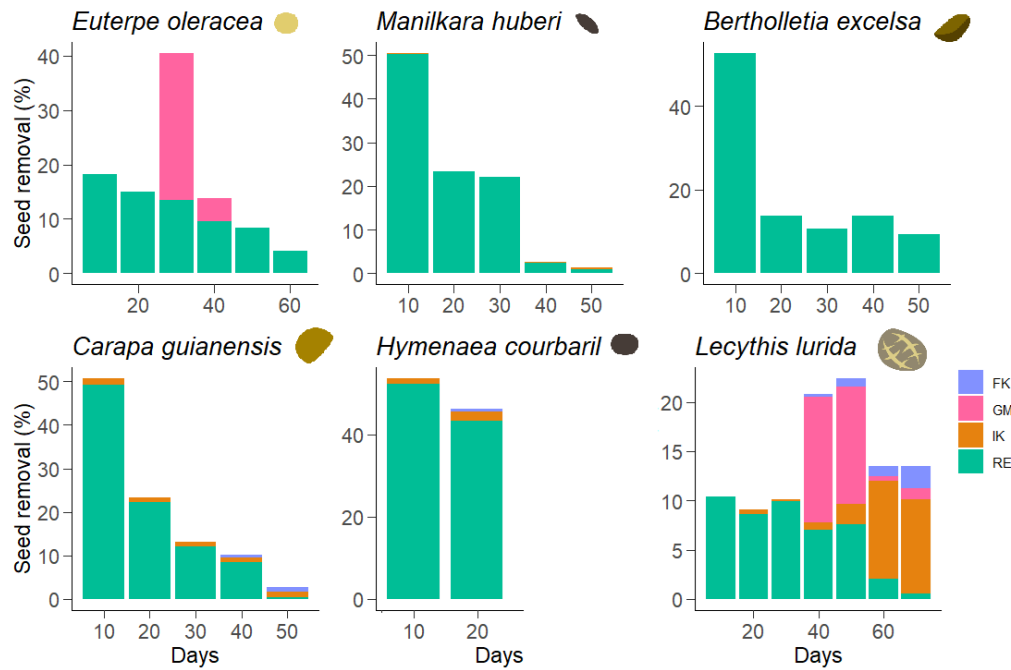


Figure 4. Fate of seeds within the experiment simulating defaunation over 70 days by plant species. Seeds were categorized as: Removed (RE), Invertebrate-Killed (IK), Fungal-Killed (FK), or Germinated (GM).

Our analysis revealed that defaunation had a significant effect on seed removal, with a marked reduction in the proportion of removed seeds in areas with lower terrestrial mammal presence ($\chi^2 = 63.403$; $df = 2$; $p < 0.001$; Figure 5).

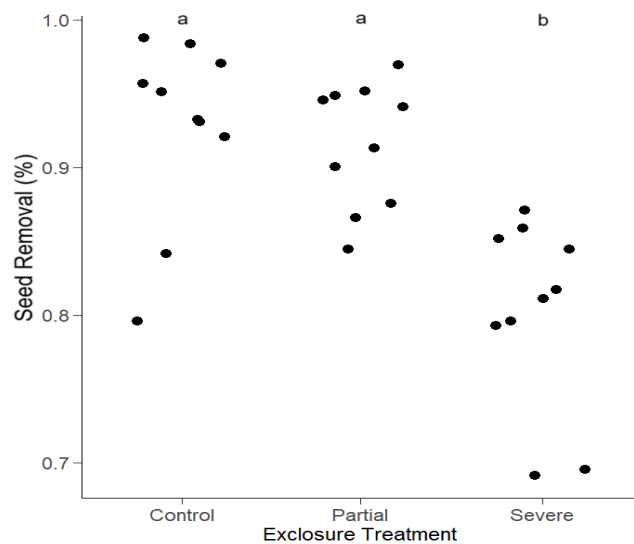


Figure 5. Proportion of seeds removed by terrestrial mammals in each treatment of the defaunation gradient (Control, Partial Exclusion, Severe Exclusion). Each dot represents seed removal in one experimental plot ($n = 10$ per treatment). Identical letters indicate non-significant differences; different letters indicate significant differences.

In control plots, consumption by invertebrates (13 seeds; 2.1%), fungi (2 seeds; 0.3%), and germination (64 seeds; 10.6%) accounted for only a small fraction of the total. Partial exclusion showed a similar pattern: 4% ($n = 24$) of seeds were consumed by invertebrates, 0.6% ($n = 4$) by fungi, and 10.8% ($n = 65$) germinated. In contrast, in severe exclusion plots, the proportion of seeds with evidence of attack by invertebrates 13% ($n = 78$), fungi (3.1%; $n = 19$), as well as those that germinated (16.5%; $n = 99$), was higher (Figure 3). Notably, however, 76.7% ($n = 76$) of germinated seeds in severe exclusion plots were later removed, indicating that initial germination does not guarantee protection from predation by either terrestrial mammals or invertebrates (see Supplementary Material 1).

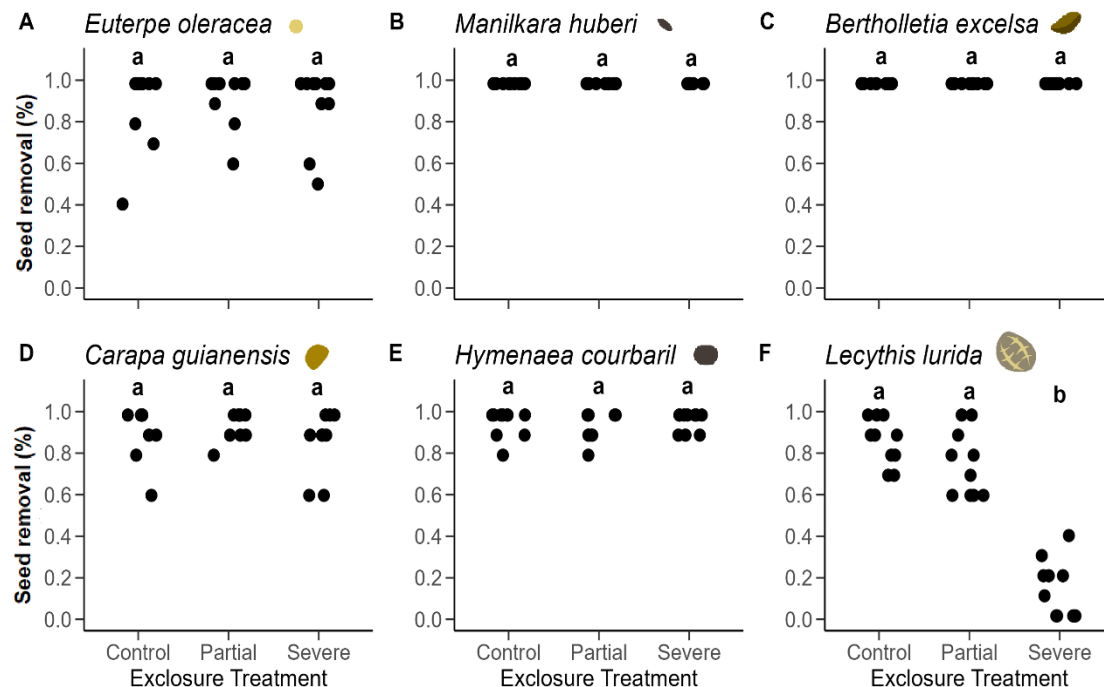


Figure 6. Proportion of seeds removed by terrestrial mammals for each plant species across the experimental gradient simulating defaunation (Control, Partial Exclusion, Severe Exclusion). Black dots represent observed values per plot ($n = 10$ per treatment).

Identical letters indicate non-significant differences; different letters indicate significant differences.

Except for *L. lurida*, seed removal for all plant species showed no significant variation across treatments: *E. oleracea* ($\chi^2 = 0.183$; $df = 2$; $p = 0.911$), *M. huberi* ($\chi^2 = 0.000$; $df = 2$; $p = 1.000$), *H. courbaril* ($\chi^2 = 0.001$; $df = 2$; $p = 0.968$), *B. excelsa* ($\chi^2 = 0.000$; $df = 2$; $p = 1.000$), and *C. guianensis* ($\chi^2 = 4.010$; $df = 2$; $p = 0.134$), *L. lurida* ($\chi^2 = 108.861$; $df = 2$; $p < 0.001$), (Figure 6). Overall, seed removal was high throughout the experiment, although this result was largely driven by the significantly lower removal of *L. lurida*, the species with the largest and heaviest seeds, in severe exclusion plots compared to control and partial exclusion plots. (Figure 6).

3.2 Terrestrial mammal-seed interactions

We recorded 469 videos during the experiment simulating defaunation, identifying seven terrestrial mammal groups: small marsupials (Didelphidae), *Cuniculus paca*, *D. croconota*, *Dasypus* sp., *Didelphis* sp., *Guerlinguetus* spp., and *Proechymys* spp. Of these, only three taxa actively interacted with seeds: *D. croconota*, *Guerlinguetus* spp., and *Proechymys* spp., with a total of 205 interactions.

Of the total videos recorded, 43.9% ($n = 206$) consisted of non-interactive behaviors, in which animals only moved through the plots without engaging with the seeds. Interactive behavior (sniffing or handling, without dispersal) accounted for 12.4% ($n = 58$). Seed dispersal and predation behaviors accounted for 33% ($n = 155$) and 10.7% ($n = 50$), respectively (Figure 7).

Among the species observed interacting with seeds, *Proechimys* spp., showed both dispersal and local predation behaviors ($n = 143$) and interacted with all six plant species. We recorded 29 dispersal events and 26 predation events with small-seeded species (*E. oleracea*, *M. huberi*), (26.8%). For medium-sized seeds (*B. excelsa*, *C.*

guianensis), we recorded 41 dispersal events (29.2%) and 19 predation events. For large seeds (*L. lurida*), We observed 28 dispersal events (13.6%) and one predation event. (Figure 7).

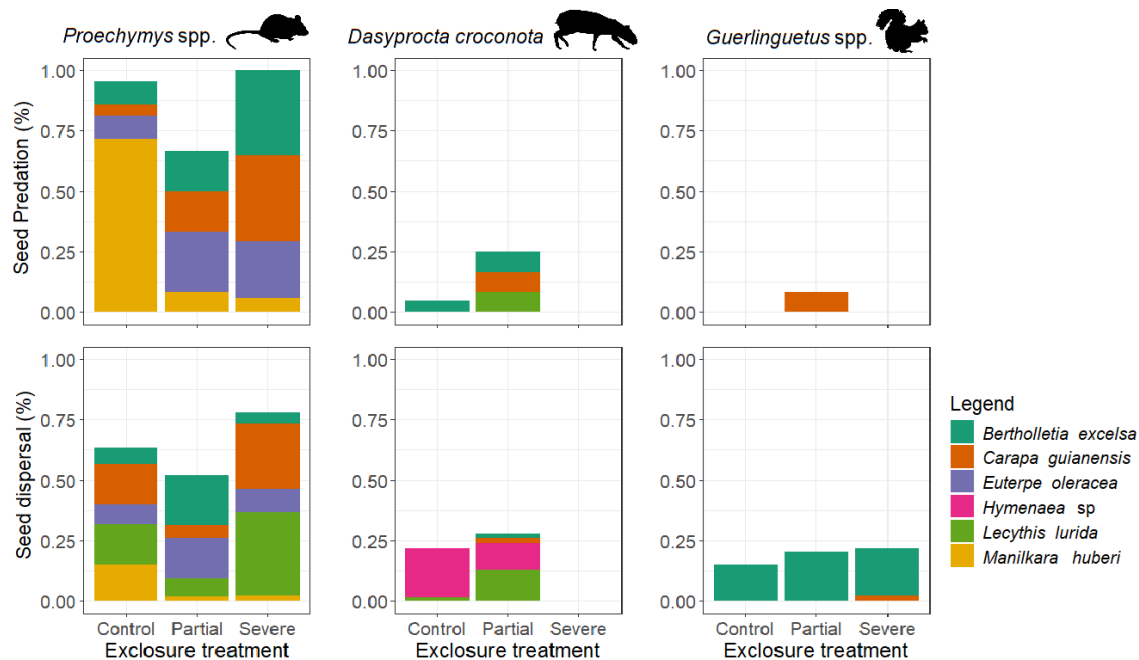


Figure 7. Proportion of recorded dispersal and predation interactions between terrestrial mammals and seeds of different plant species along the experimental gradient simulating defaunation. (Control, Partial Exclusion, Severe Exclusion).

We observed Squirrels (*Guerlinguetus* spp.) interacting only with two medium-seeded species, with a strong preference for *B. excelsa* (29 dispersal events; 14.4%), as indicated by a frequency nearly 15 times higher than interactions with *C. guianensis*. As expected, considering their arboreal habits, they showed no difference in interaction frequency between treatments. Agoutis *D. croconota* also interacted with multiple species showed generalist behavior, removing 28 seeds and preying upon four species, all from medium- to large-seeded species. However, agoutis were only able to interact with seeds in the control and partial exclusion plots. We note that in partial exclusion plots, we observed fewer *Proechimys* spp. interactions and more frequent interactions with *D. croconota* (Figure 7).

Among the recorded mammals, only *Proechimys* spp. had enough interaction records for statistical analysis testing differences among seeds of different sizes. Despite frequent interactions, we found no significant effect of defaunation on the frequency of *Proechimys* spp. interactions with seeds of different sizes: small ($\chi^2 = 3.732$; $df = 2$; $p = 0.154$), medium ($\chi^2 = 0.193$; $df = 2$; $p = 0.907$), and large ($\chi^2 = 0.000$; $df = 2$; $p = 1.000$). These results suggest that the presence or absence of medium- and large-bodied mammals did not significantly influence the behavior of this small rodent in seed handling across the defaunation gradient.

4 DISCUSSION

In this study, we used a terrestrial mammal exclusion experiment to experimentally simulate a defaunation gradient to assess, for the first time in the Amazon rainforest, the effects of defaunation on the early stages of recruitment in plant species of commercial interest. Our results support the hypothesis that the exclusion of medium- and large-bodied mammals significantly reduces seed removal, but only for larger seeds. The reduction observed in severe exclusion plots reinforces the central hypothesis of this study and aligns with patterns documented in tropical forests on other continents (Rosin and Poulsen 2016; Williams et al. 2021). These findings underscore the ecological importance of terrestrial mammals in plant regeneration dynamics, although the effects of defaunation may vary depending on the ecological context and the species involved (Galetti et al. 2015; Williams et al. 2022).

When examining each plant species individually, we found that defaunation did not significantly affect seed removal in five of the six species evaluated. The exception was *L. lurida*, whose seeds, the largest in our study, experience significantly reduced removal rates in severe exclusion plots. This result is consistent with studies showing

that larger seeds depend more heavily on large-bodied mammals for removal and dispersal (De Mattia and Rathcke 2006; Chen et al. 2021). Furthermore, when large vertebrates were experimentally absent, *L. lurida* seeds exhibited high rates of predation by invertebrates (66%) and attack by fungi (16%), suggesting that the absence of seed removal may substantially increase seed mortality (but see Cuny et al. (2022) that reported cases where insect predation can even increase plant germination). Similar results were reported by Williams et al. (2021), who demonstrated in a Bornean rainforest exclusion experiment that in the absence of removal by large vertebrates seeds were subjected to increased levels of seed predation by insects and fungi, maintaining high seed mortality rates. However, despite this functional compensation in mortality, it is important to note while insects and fungi act mostly as predators for large seeds, vertebrates such as agoutis, in addition to frequently acting as predators, also have the potential to disperse larger seeds through removal and caching. This process allows plant establishment away from the source and influences the spatial distribution of plant populations (Jansen et al. 2012, Mittelman et al. 2020). Thus, even when mortality rates remain constant, the absence of vertebrates capable of removing and eventually disperse large seeds can impair regenerative processes and affect long-term seedling recruitment dynamics for large-seeded plants.

Although more frequent in large-seeded species, partial compensation by invertebrates and fungi was a general pattern in severe exclusion plots, where invertebrate predation increased across several species. For instance, while combined mortality from fungi and invertebrates ranged from 2% to 14% in control and partial exclusion plots, it exceeded 30% for some species in the severe exclusion treatment. This reinforces the idea that the absence of vertebrates not only reduces potential seed dispersal but also leaves seeds more vulnerable to pathogenic and specialized herbivore attacks. These interactions are rarely considered in defaunation studies but may have

direct effects on seed survival and forest regeneration (Williams et al. 2021; Rosin et al. 2018). The intensification of post-dispersal mortality by these agents suggests that vertebrates play a broader ecological role, acting also as indirect modulators of biotic pressure on viable seeds.

Although our results highlight the importance of mammals in seed removal, we did not record interactions with large-bodied species such as tapirs (*T. terrestris*) and white-lipped peccaries (*T. pecari*) along the defaunation gradient. These mammals are widely recognized as key frugivores that can both predate and disperse seeds in tropical forests (Galetti et al. 2015; Peres et al. 2016; Fedriani et al. 2020), and their presence has been previously documented in our study area (Brocardo et al. 2023; Batista et al. 2025). However, the primary agents of seed removal in our experiment were small- and medium-bodied rodents, particularly *Proechimys* spp. We observed that in the absence of medium-sized rodents such as *D. croconota*, seed removal by smaller rodents, increased considerably, suggesting a potential mechanism of functional compensation. Nonetheless, our observations also indicate that the ability of these small rodents to handle seeds may be constrained by seed size: small and medium seeds were removed more frequently than large seeds, indicating possible physical limitations in handling and transporting heavier seeds (Dylewski et al. 2020; Meiga et al. 2020).

These findings support the hypothesis of a potential trade-off between disperser body size and seed size (Dirzo et al. 2007; Maron et al. 2018; Dylewski et al. 2020). Still, our statistical analyses did not detect significant differences in removal rates by *Proechimys* spp. across seed size classes, suggesting that other factors, such as seed coat texture, chemical composition, or position on the forest floor, may also influence disperser choice. Additionally, although small-sized rodents generally have lower movement capacity than larger rodents such as agoutis and pacas, many act primarily as seed predators rather than dispersers (Adler and Kestell 1998). They often lack

behaviors such as caching or burying seeds, which enhance the chances of successful dispersal. Thus, even if small rodents quantitatively compensate for seed removal, it is unlikely that they provide qualitative benefits equivalent to those of larger mammals. Therefore, it is unrealistic to expect that a single trait can explain the complexity of plant–animal interactions or the dynamics of seed removal. (Chen et al. 2021).

The combined use of camera traps and seed removal experiments also revealed behaviors rarely documented in previous studies, despite their important implications for recruitment limitation (Rosin and Poulsen 2016; Rosin et al. 2018). For instance, *Proechimys* spp. was recorded consuming sprouts of *E. oleracea* and germinated seeds of *C. guianensis* (see Supplementary Material 1), indicating that even germinated seeds may fail to reach the seedling stage due to post-germination herbivory. These findings highlight *Proechimys* spp. as the predominant species removing seeds throughout the experiment, except for *L. lurida* seeds. However, it is crucial to emphasize that *Proechimys* spp. is primarily a seed predator rather than a disperser (see Adler and Kestell 1998). Whereas *D. croconota* can contribute extensively to seed dispersal and consequently to the recruitment of a variety of plant species. Thus, the absence of *D. croconota* in areas with severe exclusions may have reduced the ratio between seeds dispersed and predated, with fewer seeds being dispersed and more seeds being preyed upon. This, in the long term, may result in a decrease in the density and diversity of commercially important trees, which may have significant economic impacts on both traditional communities, that depend on these species for their subsistence, as well as the timber industry, which relies on the exploitation of these tree species. Therefore, our findings support that considering the implications of defaunation is crucial for sustainable forest management and conservation of commercially important plant species.

Our findings contribute to a better understanding of the effects of defaunation on seed removal and fate which affect seed germination and seedling recruitment. We suggest that future studies experimentally manipulate access by different groups of seed removers under realistic seed availability conditions, incorporating a broader set of seed traits. This approach may help clarify how defaunation influences seed removal and fate, and how these effects vary with plant morphological, chemical, and functional characteristics (Williams et al. 2021; Chen et al. 2021).

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7 SUPPLEMENTARY MATERIAL 1 - Capítulo 1

Supplementary Material 1: Records of evidence indicating animal–seed interactions and seeds affected by fungi and insects along an experimental defaunation gradient. Includes documentation of the main animal species observed interacting with seeds in the exclusion treatments.

	
A- <i>Carapa guianensis</i> seed removed post-germination	B- <i>Carapa guianensis</i> seed predated post-germination
	
C- <i>Euterpe oleracea</i> seed and leaf sprout removed post-germination	D- <i>Carapa guianensis</i> seed initially damaged by biting and subsequently infected by fungus

	
E- <i>C. guianensis</i> seed damaged by insect boring	F- Seed of <i>Lecythis lurida</i> predated (red circle) and fungus-infected (blue circle)
	
G- <i>Carapa guianensis</i> seed under predation	H- <i>Carapa guianensis</i> seed being removed
	
I- <i>Carapa guianensis</i> seed being removed	J- <i>Bertholletia excelsa</i> seed being removed



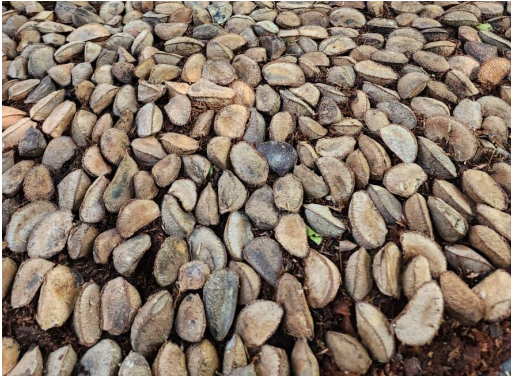
K- *Lecythis lurida* seed being removed



L- *Bertholletia excelsa* seed being removed

8 SUPPLEMENTARY MATERIAL 2 - Capítulo 1

Supplementary Material 2: Records of the seeds and fruits of the plant species used to experimentally simulate a defaunation gradient.

	
<i>A- Carapa guianensis</i> fruit with predated seeds. Image: Daniela Pauletto.	<i>B- Carapa guianensis</i> seed. Image: adapted from Carvalho., 2014, Embrapa florestas.
	
<i>C- Image of a Euterpe oleracea</i> individual, characterizing its fruits in bunches.	<i>D- Left: Fruits with pulp. Right: Fruit with mechanically removed pulp.</i>
	

E- Fruit of *Bertholletia excelsa*.



F- Seeds of *Bertholletia excelsa*. Image: Dyennef Morais.



G- Fruit of *Hymenaea courbaril*.



H- *Hymenaea courbaril* seed being manually processed for pulp removal.



I- Fruit *Lecythis lurida*.



J- Seed *Lecythis lurida*.



K- Fruit of <i>Manilkara huberi</i> . Image: adapted from Cruz, E. (2016).	L- Seed of <i>Manilkara huberi</i> , with the pulp manually removed. Image: adapted from Cruz, E. (2016).
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CAPÍTULO 2

CASTRO, Arlison; WILKER, Icaro; FADINI, Rodrigo; BROCARD, Carlos; COSTA, Maria K. S.; PIRES, Mathias M.; COSTA, Maria K. S.; MALDANER, Maria E.; MAIA, Laís F.; BORDIN, Bruna R.; VAZ-DE-MELLO, F. Z.; POPPY, Lane.; FRANÇA, Filipe M.; ROSA, Clarissa. **Defaunation and environmental filtering shape dung beetle communities in the Amazon.**

Defaunation and environmental filtering shape dung beetle communities in the Amazon

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ABSTRACT

The rapid land-use transformation in recent decades has driven an unprecedented biodiversity crisis, amplifying the co-decline of species and the imbalance within tropical ecosystems. In this context, defaunation of medium and large-bodied mammals has emerged as a key process affecting ecological interactions and ecosystem functioning. Our study assessed the role of terrestrial mammal biomass and environmental gradients in structuring the dung beetle assemblage in Amazon. We conducted joint sampling using camera traps and pitfall traps to collect data on mammal and dung beetle communities. Additionally, we quantified environmental gradients based on vegetation structure and soil properties across 34 plots. By integrating resource-based (mammal biomass), vegetation structure, and soil perspectives, our results show that environmental variables, particularly soil texture and forest structure, play a dominant role in shaping dung beetle abundance, guild composition, and specific dimensions of functional diversity, whereas mammal biomass primarily influences taxonomic richness and selected functional metrics. These findings indicate that defaunation and environmental gradients exert complementary but distinct effects on dung beetle communities, with implications for ecosystem functioning. Our results underscore that conserving dung beetle diversity, and the ecosystem functions they support, requires the protection of both mammal populations and habitat integrity. Therefore, effective conservation strategies in the Amazon should integrate measures to mitigate defaunation, such as controlling illegal hunting, with actions that maintain forest structure, soil integrity, and functional diversity within ecological communities.

Keywords: co-decline, scarabeidae, vegetation, traits functional, forest system, tropical forests, soil.

1 INTRODUCTION

Over the past three decades, at least 420 million hectares of forest have been converted to other land uses worldwide (FAO, 2020). This rapid transformation has intensified biodiversity loss, especially in tropical forests, where approximately 60% of animal populations have declined or become threatened with extinction in the last half-century (WWF, 2020; Ceballos et al., 2017). Continued land-use change and habitat degradation facilitate the poaching of game animals (Brocardo et al., 2023), driving the process of defaunation, characterized by the decline or local extinction of medium- and large-bodied vertebrates (Dirzo et al., 2014). Since large terrestrial vertebrates are a vital protein source for traditional populations living in tropical ecosystems worldwide (Jerozolinski and Peres 2003), they are disproportionately targeted by hunting, making them particularly vulnerable to defaunation.

In this scenario, Amazonian tropical forests emerge as a critical ecosystem for studying species decline. Evident signs of degradation in these areas, influenced by both the history of human occupation and forest management, have intensified hunting pressure in the region (Rosa et al., 2021; Brocardo et al., 2023). In these landscapes, although vertebrate abundance is still shaped by local variables such as fruit biomass, the scarcity of preferred game species, such as the lowland tapir (*Tapirus terrestris*) and the white-lipped peccary (*Tayassu pecari*), reveals an omnipresent anthropogenic pressure that alters the availability of biotic resources on the forest floor (Brocardo et al., 2023). Thus, defaunation not only reduces mammal abundance but also reshapes the structure of vertebrate communities, with cascading effects on other trophic levels. Such structural changes in the mammal community not only reduce food supply but also modify the dynamics of competition (Bovendorp et al., 2018), and coexistence among dependent groups, such as dung beetles (Bogoni et al., 2019). This process can directly

or indirectly disrupt various ecological processes, altering ecosystem functions and services, such as nutrient cycling and seed dispersal and consequently increasing forest vulnerability (Barlow et al., 2018; Raine et al., 2018).

Dung beetles (Coleoptera: Scarabaeidae) have coevolved closely with medium- and large-bodied mammals, as their community structure is shaped by biotic and abiotic factors associated with resource availability and habitat conditions, respectively (Cajaiba et al., 2017; Bogoni et al., 2020; Fuzessy et al., 2021). Because of this tight trophic dependence, dung beetles are particularly sensitive to defaunation, which directly reduces the availability and diversity of dung resources. However, the widespread decline of mammal assemblages across the Neotropics reduces resource availability (Bogoni et al., 2016), intensifies competition among beetle species, and may drive the local extinction of more specialized taxa (Culot et al., 2013; C3mbita et al., 2025).

Such changes can compromise multiple ecological functions; for instance, by reducing nutrient cycling, which aids the incorporation of organic matter (e.g., nitrogen and phosphate) into the soil profile (Maldonado et al., 2019). Furthermore, the decline of these assemblages disrupts secondary seed dispersal, a process that is particularly vulnerable to the loss of its invertebrate mediators (Culot et al., 2015; Griffiths et al., 2016; Urrea-Galeano et al., 2019). In this context, assessing biodiversity loss in ecologically important groups such as dung beetles is essential, as defaunation-driven declines in mammal communities can propagate across trophic levels, leading to reductions in dung beetle diversity and associated ecosystem functions (Nichols et al., 2008).

Additionally, Amazonian tropical forests are heterogeneous landscapes where environmental characteristics vary both spatially and temporally, often as a result of human-driven disturbances (Alves et al., 2010; Fadini et al., 2021). Consequently,

abiotic factors, particularly soil characteristics and vegetation structure, further influence the functional groups and traits of dung beetle assemblages, driving their specific resource removal strategies (Griffiths et al., 2015; Silva et al., 2015; Salomão et al., 2018). However, these environmental filters operate alongside defaunation, and their relative importance compared to biotic drivers such as mammal biomass remains poorly understood. For instance, soil compaction can influence the abundance of paracoprid beetles, as drier and more compacted soils restrict their tunneling activity (Salomão et al., 2022). Meanwhile, soil texture can positively influence the abundance of telecoprids, as they exhibit ball-rolling behavior and bury them in shallower nests (Ahungu et al., 2025). Additionally, endocoprid beetles may be more influenced by forest structure, which likewise modulates habitat quality: deeper leaf litter enhances nesting opportunities and refuge availability, whereas greater canopy openness can accelerate dung desiccation and reduce resource suitability (Silva et al., 2015; Farias and Hernandez, 2017; Costa et al., 2022).

Furthermore, the use of functional traits (measured by the FRic, FDis, FEve, and FDiv indices) is fundamental to understanding how individuals perceive and respond to environmental variations (Violle et al., 2007) and resource availability, such as the presence of mammals (Bogoni et al., 2019). For example, soil compaction and texture can select for specific morphological traits; larger individuals with greater digging strength may have their activity restricted in dense soils, demonstrating how habitat shapes the functional structure of the assemblage (Raine et al., 2018; Salomão et al., 2022). In parallel, the decline of large mammals promotes a filter that favors generalist and resilient species, reducing the diversity of attributes essential for critical ecosystem functions (Bogoni et al., 2019). In this sense, traits such as body size (length and biomass) become key predictors, as they determine the efficiency of excrement removal and, consequently, the maintenance of nutrient cycling at the local level

(Noriega et al., 2023), but see (Priky et al., 2022). These findings highlight that the functional response of dung beetle assemblages is not explained by a single factor, but rather by a combination of biotic and abiotic conditions.

However, it remains unclear how defaunation and environmental gradients jointly shape the functional integrity of Amazonian dung beetle communities. Given the ecological roles dung beetles perform, understanding how resource availability and environmental complexity shape their communities is fundamental for informing conservation. Although environmental gradients are known to filter regional species pools and generate spatial variation in dung beetle assemblages (Raine and Slade, 2019), little is known about how Amazonian dung beetle communities respond to degradation and mammal species declines.

Here, we investigate how defaunation intensity, using mammal biomass as a proxy, interacts with environmental gradients (vegetation and soil structure) to shape dung beetle community patterns in upland Amazonian forests, encompassing areas with different levels of defaunation. Specifically, we assess how these predictors explain variation in dung beetle species richness, abundance, and composition, as well as differences across behavioural guilds and functional diversity metrics. We expect that: (1) dung beetle richness and abundance will be positively affected by mammal biomass, and that community composition will be driven by mammal biomass, while environmental variables exert secondary effects due to the strong trophic dependence of dung beetles on mammals (Bogoni et al., 2019); (2) endocoprid abundance will be positively associated with mammal biomass and vegetation structure, reflecting resource and habitat availability, whereas paracoprid and telecoprid guilds will respond primarily to soil structure; and (3) functional diversity will decline with decreasing mammal biomass (i.e., increasing defaunation), as the loss of large-bodied mammals

reduces resource availability and acts as an ecological filter favouring generalist species; additionally, environmental constraints such as vegetation structure and soil compaction are expected to further modulate these patterns by limiting the performance of traits poorly adapted to local conditions (Salomão et al., 2022).

2 METHODS

2.1 Study area

Our study was conducted in the Tapajós National Forest (Floresta Nacional do Tapajós – FNT), a protected area of approximately 523,000 ha located in the municipality of Belterra, Pará, Brazil (Figure 1). According to the Köppen classification, the regional climate is Am, with a mean annual temperature of 25.6 °C (INMET, 2020) and mean annual precipitation of 1,820 mm. Two well-defined seasons occur: a rainy season from December to May and a dry season from June to November (ICMBio, 2019). The predominant vegetation type is evergreen dense rainforest (Floresta Ombrófila Densa in Portuguese), and the dominant soil is dystrophic yellow latosol, which has variable texture and is generally deep, acidic, and friable (Espírito-Santo et al., 2005).

2.2 Sampling design

We worked in four RAPELD modules (Rapid Assessment and Long-Term Ecological Research; Magnusson et al., 2013), previously established for biodiversity monitoring in the FNT (Figure 1). Each module has a rectangular layout (1 km × 5 km). Within each module, a 5 km trail contains five plots of 250 m in length. All plots follow contour lines to minimise variation in topography and soil properties within each plot (Magnusson et al., 2013).

These modules are distributed across different portions of the FLONA Tapajós that encompass a gradient of defaunaion, with northern areas (with two modules) showing reduced mammal richness, particularly of large-bodied species, and southern areas (another two modules) presenting higher faunal integrity (Rosa et al., 2021). This spatial variation allows the comparison of sites with different levels of defaunaion within the same forest landscape.

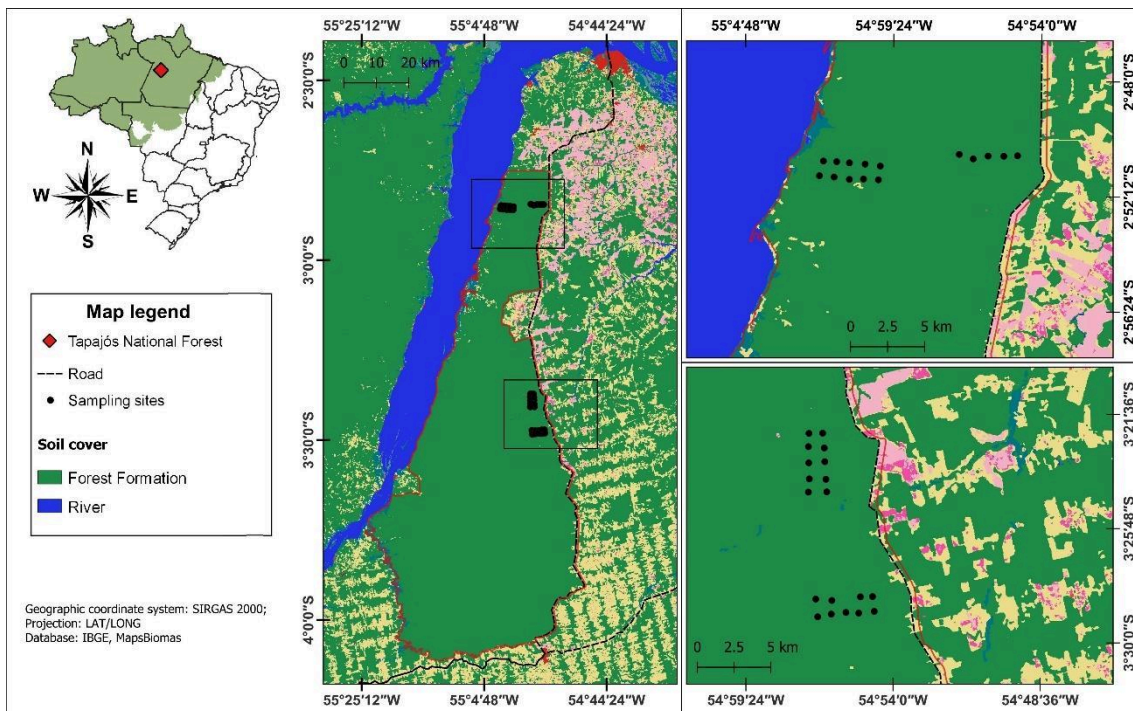


Figure 1: Location of the study area in the Tapajós National Forest. Centre image shows RAPELD modules' distribution, while right panels show distribution of sampling plots within each module.

2.3 Dung beetle sampling

We sampled dung beetles between June 2019 and January 2020, during the dry season of that year. In each of the 34 plots, we established six sampling points at 50 m intervals along the 250 m plot. At each point, we installed a pitfall trap consisting of a

1L plastic container buried at ground level and filled with 200 ml of killing solution (water, detergent, and salt) (Rodrigues et al., 2025a).

Each trap contained a bait holder with 40 g of mixed human and pig faeces (1:4 ratio), wrapped in gauze and suspended above the solution so that beetles were attracted but did not directly contact the faeces (Marsh et al., 2013; Rodrigues et al., 2025a). To protect traps from rainfall, we placed a plastic cover 10-15 cm above each pitfall. Traps remained active for 48 h, after which we collected all beetles, preserved in 70% ethanol, and later sorted in the laboratory. We identified specimens to species, or to morphospecies when species-level identification was not possible, using the reference material of Vaz-de-Mello et al. (2011) and Maldaner et al. (2024), and later validated by a taxonomic specialist (Vaz-de-Mello, F.). Voucher specimens were deposited in the Eurides Furtado Entomological Collection (CEMT), Cuiabá, Mato Grosso.

2.4 Functional groups and traits

We assigned species to three functional groups based on their resource removal strategies and nesting behaviour: endocoprids (nesting within dung), paracoprids (tunnelers), and telecoprids (rollers), for description see (Maldaner et al., 2024; Table S1). To characterize functional traits, we measured morphological attributes and biomass that are likely to affect dung beetle performance under local environmental conditions (Violle et al., 2007).

For a subset of individuals per species ($n = 30$), we taken morphometric measurements with a digital calliper with 3 digits of precision. For species with fewer than 30 individuals collected, we considered only the measurements from the individuals found. We measured body length and width, anterior tibia length and width, and posterior tibia length and width (Griffiths et al., 2015). However, measured morphological traits are usually highly correlated, but correlated traits shouldn't be used

in calculating functional diversity indices (Cadotte et al., 2011). To address this, we divided the hind leg measurements by the corresponding front leg measurements (Griffiths et al., 2015). Biomass was obtained by weighing individuals with a precision balance before and after oven-drying all specimens for 96 hours at 40-50 °C. For each species, we calculated mean trait values based on measurements of multiple individuals and used both fresh and dry biomass.

2.5 Mammal sampling

We sampled medium and large bodied terrestrial mammals using non-baited camera traps that were deployed previously to the dung beetle sampling. We installed one camera within a 10 m radius of the central line plot of each of the 34 plots, forming independent sampling stations, close to paths used by animals. Cameras were mounted on trees, 30–40 cm above the ground, near animal paths, and programmed to record photographs. Each camera operated continuously (24 h day⁻¹) for 35 days, yielding a total effort of 1,868 camera-trap days (Rosa et al., 2021). Records of the same species at the same station were considered independent when separated by at least 24 h (Brocardo et al., 2023). Species identifications were confirmed by specialists using a field guide (Reis et al., 2010; Table S1). We estimated mammal biomass per station by multiplying the number of independent records of each species by its mean body mass from Paglia et al. (2012) and then summing across species.

2.6 Environmental variables

Vegetation structure data were made in 2019 and is obtained from Torralvo et al. (2019). Measurements were collected using a portable terrestrial LiDAR device (LD90-3100VHS-FLP, Riegl, Horn, Austria), which scans the environment with a laser to derive structural metrics. Vegetation structure metrics were extracted between 0–15 m

to represent the understory leaf area. For canopy forest, clearing forest, leaf area and tree height, measurements were obtained at heights >15 m. All metrics were collected along each 250 m plot. Additionally, we established four points 1 m from each pitfall in the four cardinal directions (N, S, E, W) and measured litter depth with a ruler placed on the soil surface, recording the maximum height of the litter layer. We used mean litter depth per plot, calculated from the six points (at each 50 m) along each 250 m plot.

To assess soil structure, we performed two different soil measurements. First, we measured soil compaction at the same points used for litter depth using a FALKER digital penetrometer (PenetroLOG–PLG 1020). The penetrometer records soil resistance to penetration, providing an index of compaction. Measurements (in kPa units) were taken for the 0–20 cm depth layer, and we calculated mean compaction for each plot (mean of six points per plot). Additionally, for each plot, we measured soil texture by collecting a soil sample (up to 20 cm deep) using a Dutch auger. At each plot, we defined six collection points spaced 50 m apart. We then mixed the six samples from each plot to represent a composite soil texture sample for each plot (clay, silt, and sand fractions). We used data on clay and sand content (g kg^{-1} ; sand as the sum of fine and coarse fractions) from the top 0–20 cm, assuming that this layer most strongly affects dung beetle activity. Soil sampling and laboratory procedures followed PPBio protocols (Rodrigues et al., 2025b), with granulometric analyses performed at the Laboratory of Soil, Plant Tissue, and Fertilizer Analysis of the Federal University of Viçosa.

2.7 Data Analysis

We used plots as the sampling units, with richness, abundance, overall composition, guild abundance (endocoprids, paracoprids, and telecoprids) and traits functions represented by functional richness (FRic), functional dispersion (FDis), functional evenness (FEve), and functional divergence (FDiv) as response variables. To

select explanatory variables, we assessed multicollinearity among environmental predictors included: 1) mammal biomass; 2) vegetation structure, represented by canopy forest, clearing forest, leaf area and tree height; 3) soil structure, represented by (soil compaction, clay, silt, and sand); and 4) litter depth. We use the *rcorr* function in the Hmisc package to calculate a correlation matrix and visualised pairwise correlations using *corrplot* (corrplot package), (Harrell, 2025). We adopted an exclusion criterion for pairs of variables displaying a Pearson correlation coefficient ($r > 0.7$ or -0.7) to ensure model stability (Taiyun and Viliam, 2024). We ensured that only independent, non-collinear variables were included in all our models: canopy forest, forest clearings, soil compaction, sand, and litter depth (Supplementary material, figure S1).

To evaluate whether the composition of the beetle community is affected by mammal biomass, soil structure variables (soil compaction, sand), and vegetation structure (canopy cover, forest clearings, and litter depth), we performed a distance-based Redundancy Analysis (dbRDA) using the *capscale* function from the *vegan* R package, (Oksanen et al., 2025). The dbRDA was based on the Bray-Curtis distance, given the abundance data. To control for the potential effect of the Module on the beetle composition structure, this variable was included as a conditioning factor in the model using the *Condition* function. The significance of the axes and predictor variables was evaluated through permutation tests using the *anova.cca* function with 9,999 permutations. We also extracted the adjusted coefficient of determination (adjusted R^2) using the *RsquareAdj* function.

We modelled dung beetle species richness, total abundance and abundance of each guild (endocoprid, paracoprid, and telecoprid) as functions of the explanatory variables using generalised linear mixed models (GLMMs) with a negative binomial error distribution, fitted with the *glmmTMB* package, version 1.1.10 (Brooks et al., 2017).

To quantify functional traits, we first calculated species-level median values for six continuous traits (biomass, dorsal body size, anterior tibia length and width, posterior tibia length and width). Because morphological traits were highly correlated, we derived two ratio traits: posterior/anterior tibia length and posterior/anterior tibia width (Supplementary material, figures S2, S3). We then calculated functional metrics for each plot using the *FDiversity* package, version 1.1.1 (Casanoves et al., 2011). All functional metrics were modelled using GLMM, having mammal biomass, vegetation structure, and soil structure as fixed effects and RAPELD module as a random effect. While *FRic* and *FDis* models were fitted with *lme4*, version 1.1-36 (Bates et al., 2015), while *FEve* and *FDiv* were analysed using negative-binomial GLMMs (*nbinom2*) fitted with *glmmTMB*, version 1.1.10 (Brooks et al., 2017).

For all response variables taxonomic and functional, we began with full models including all non-collinear predictors and RAPELD module as a random effect. We then applied a top-down model selection approach, sequentially removing non-significant predictors based on likelihood ratio tests (χ^2) with the *Anova* function in the *car* package, version 3.1 (Fox and Weisberg, 2019) and retaining predictors with $P < 0.05$. We used the negative binomial distribution with a log link function instead of the Poisson distribution due to overdispersion. We evaluated model fit and residual diagnostics using the *performance* package (Lüdtke et al., 2021). All analyses were conducted in R version 4.1.2 (R Development Core Team 2024), and plots were created using *ggplot2* (Wickham 2016).

3 RESULTS

We collected 4,223 dung beetles belonging to 60 species or morphospecies. Paracoprids comprised 34 species and 82% of all individuals, followed by endocoprids

(16 species; 7.4% of individuals) and telecoprids (10 species; 10.6% of individuals), (Supplementary material, table S1). Species richness per plot ranged from 5 to 19 (12.2 ± 3.6 ; mean $\pm$ SD), whereas the number of individuals ranged from 15 to 429 (124.2 ± 103.6), (Supplementary material, table S2 and S3).

Mammal monitoring efforts, using camera traps, resulted in 724 independent observations of 22 species. The number of species per plot ranged from 5 to 8 (5.17 ± 2.3), and the number of records per plot ranged from 4 to 53 (21.3 ± 12.9). Mammal biomass per plot varied from 12.3 to 683.6 kg (141.88 ± 141.92). Soil structure varied among plots, with particularly marked variation in sand content, which ranged from 21.0 to 659.5 g/ kg⁻¹ (141.88 ± 141.92 ; mean $\pm$ SD). The litter depth per station varied from 0.7 to 2.2 cm (1 ± 0 ; mean $\pm$ SD). Furthermore, the vegetation structure varied among plots, with particularly marked variation in forest clearing 0.71 to 0.97 % (0.85 ± 0.05 ; mean $\pm$ SD).

3.1 Effects of mammal biomass and environmental variables on richness, abundance, and composition

Dung beetle species richness was positively influenced by mammal biomass, suggesting that areas with higher biomass support a greater number of beetle species, explaining 11% of its variation ($\chi^2 = 4.328$; df = 1; p = 0.008; $r^2 = 0.11$; Figure 2A). In contrast, total dung beetle abundance was unrelated to mammal biomass but increased with soil sand content, which explained 17% of variation in abundance ($\chi^2 = 6.9514$; df = 1; p = 0.03; $r^2 = 0.17$; Figure 2B). No other predictors had significant effects on richness or abundance. We found that beetle composition was weakly affected by mammal biomass, soil structure, and vegetation (adjusted $R^2=0.055$), with the first axis showing no significant effect ($F=3.8980$; $p=0.0788$), nor did the subsequent axes.

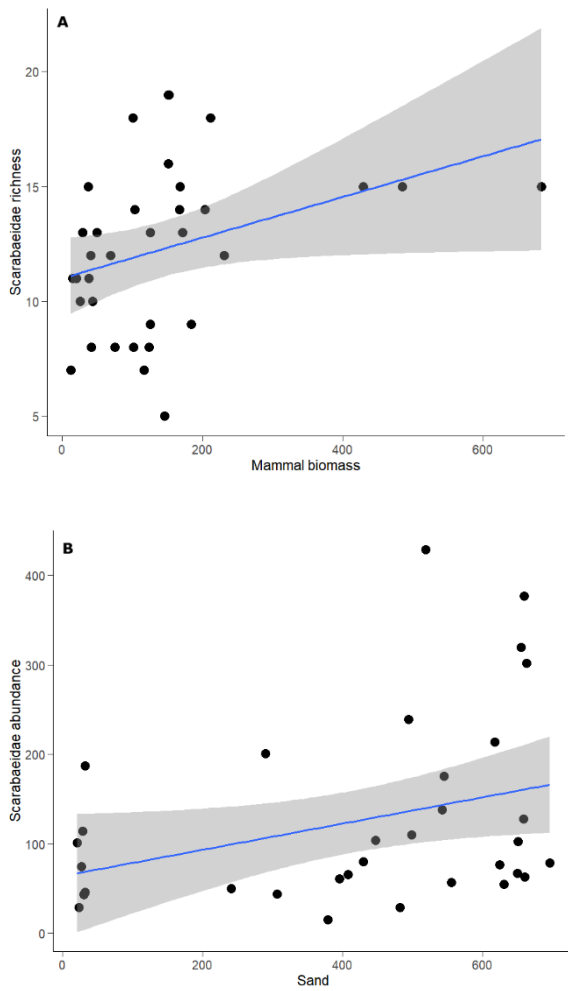


Figure 2: The positive effect of (A) mammal biomass on dung beetle species richness and of (B) soil sand content on dung beetle abundance. Black points represent the 34 sampling sites where dung beetles were collected.

3.2 Dung beetle functional groups and diversity metrics:

Behavioral guilds exhibited distinct responses to environmental predictors. For paracoprids and telecoprids, soil sand content was the main driver for the increase and decrease in their abundance, respectively. Explaining 24% of the variance in paracoprids ($\chi^2 = 10.40$, $df = 1$, $p = 0.001$, $R^2 = 0.24$) and 21% in telecoprids ($\chi^2 = 4.52$, $df = 1$, $p = 0.03$, $R^2 = 0.21$; Figure 3A–B). In contrast, endocoprid abundance responded

positively to increased litter depth, showing higher population density in sites with deeper leaf litter ($\chi^2 = 4.45$, $df = 1$, $p = 0.03$, $R^2 = 0.17$, Figure 4).

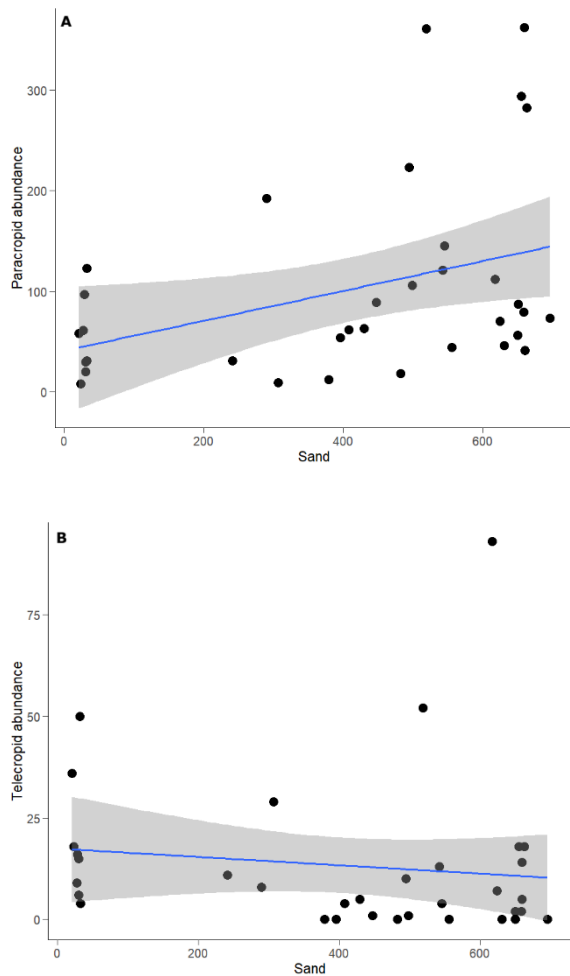


Figure 3: (A) The positive relationship between paracoprid abundance and soil sand content, and (B) the negative relationship between telecoprid abundance and soil sand content. Black points represent the 34 sampling sites where dung beetles were collected.

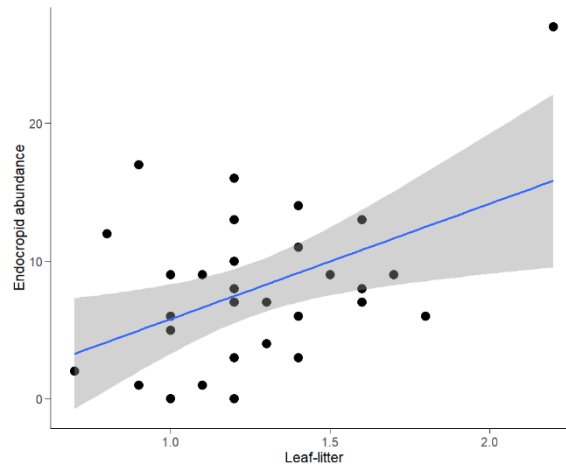


Figure 4: Endocoprid behavioural guild showing the positive relationship with an increase in litter depth. Black points represent the 34 sampling sites where dung beetles were collected.

Functional diversity metrics responded to both mammal biomass and habitat structure. Functional richness (FRic) increased with mammal biomass, whereas functional divergence (FDiv) showed a negative relationship, explaining 15% ($\chi^2 = 7.462$; $df = 1$; $p = 0.006$; $r^2 = 0.15$) and 31% ($\chi^2 = 6.262$; $df = 1$; $p = 0.01$; $r^2 = 0.31$) of their variation, respectively (Figure 5A–B).

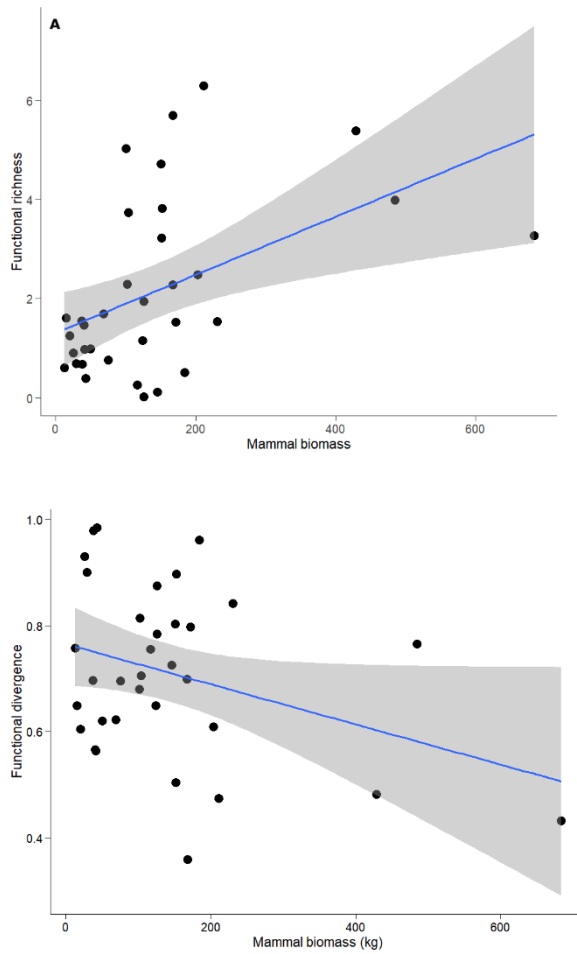


Figure 5: Effects of terrestrial mammal biomass on dung beetle functional diversity, showing (A) a positive effect on functional richness (FRic) and (B) a negative effect on functional divergence (FDiv). Black points represent the 34 sampling sites where dung beetles were collected.

Functional dispersion (FDis) decreased with increasing sand content, which explained 14% of its variation ($\chi^2 = 5.071$; $df = 1$; $p = 0.02$; $r^2 = 0.14$; Figure 6A). Functional evenness (FEve) declined with higher gap fraction, with gap fraction explaining 15% of its variation ($\chi^2 = 6.328$; $df = 1$; $p = 0.01$; $r^2 = 0.15$; Figure 6B), (Supplementary material, table S5).

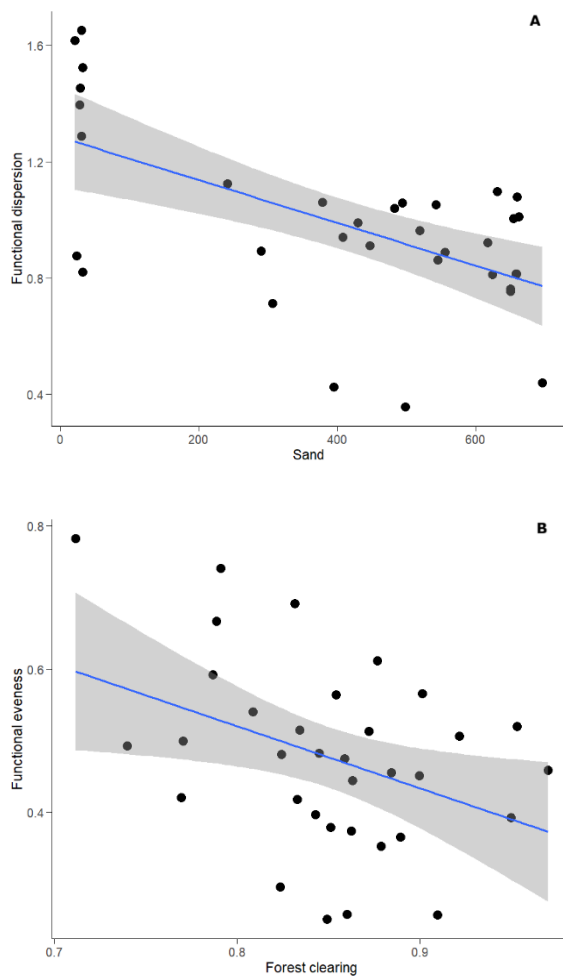


Figure 6: Effects of environmental predictors on dung beetle functional diversity, showing (A) the negative relationship between functional dispersion (FDis) and soil sand content, and (B) the negative relationship between functional evenness (FEve) and vegetation structure (gap fraction). Black points represent the 34 sampling sites where dung beetles were collected.

4 DISCUSSION

In this study, we evaluated the relative importance of mammal biomass and habitat attributes in shaping dung beetle taxonomic, functional trait and behavioral guild-level responses. To our knowledge this study represents one of the first integrative

quantitative assessments linking dung beetle assemblages, terrestrial mammal biomass, and fine-scale environmental variation in Amazonian upland forests (but see Nichols et al., 2009). By explicitly framing mammal biomass as a proxy for defaunation, our results highlight how the loss of mammals acts as a key driver of dung beetle community structure and function.

Overall, our findings indicate that defaunation influences dung beetle communities in a non-uniform manner, strongly affecting taxonomic richness and functional dimensions, while environmental factors modulate specific aspects of abundance, guild structure, and functional distribution. As predicted, mammal biomass was positively associated with dung beetle species richness, indicating that areas with higher mammal biomass harbor a broader set of species, likely through increased resource diversity and availability. Importantly, the contrasting responses of functional diversity metrics, namely increased functional richness but reduced functional divergence with increasing mammal biomass, suggest that defaunation acts as an ecological filter, constraining the distribution of functional strategies within assemblages rather than uniformly reducing trait diversity.

In contrast, mammal biomass did not emerge as the dominant driver of all community attributes. Contrary to our expectation, dung beetle abundance were not primarily explained by mammal biomass, but instead were strongly influenced by physical soil properties. Specifically, abundance varied significantly along the soil sand content gradient, highlighting the key role of edaphic constraints in regulating beetle populations. Similarly, functional responses exhibited complementary patterns across dimensions, functional richness increased with mammal biomass and divergence decreased, whereas functional dispersion and evenness were primarily shaped by soil and vegetation structure. This decoupling indicates that defaunation and environmental gradients operate on different components of biodiversity, with mammal biomass

influencing the breadth of functional traits and environmental factors structuring their distribution and evenness. Together, these findings align with recent work emphasizing that tropical forest invertebrate communities often respond to a combination of resource availability and habitat structure, with the relative importance of each factor varying across ecosystems (Barlow et al., 2016; Feer et al., 2015; Carvalho et al., 2020).

The positive association between dung beetle richness and mammal biomass is consistent with the strong trophic dependence of dung beetles on mammal-derived resources (Nichols et al., 2009; Bogoni et al., 2016; Bogoni et al., 2018). In many tropical forests, reductions in mammal biomass through hunting or fragmentation trigger declines in dung beetle diversity, biomass and ecosystem functioning (Culot et al., 2013; Noriega et al., 2021; Davies et al., 2020). Our findings reinforce this link but also indicate that richness may respond more sensitively than abundance under moderate levels of defaunation. Top-down effects on dung beetles can propagate further, leading to reduced bioturbation, secondary seed dispersal, and nutrient cycling. (Andresen and Feer, 2005; Nichols et al., 2008, Noriega et al., 2023). Thus, even when abundance remains stable, erosion of taxonomic and functional diversity may compromise long-term ecosystem resilience.

The absence of a relationship between mammal biomass and either abundance or composition in our Amazonian sites contrasts with findings from heavily defaunated landscapes in the Atlantic Forest (Bogoni et al., 2019; Braga et al., 2013). One plausible explanation is that mammal biomass in our study system remains above a functional threshold necessary to sustain dung beetle populations, even under ongoing defaunation, as previously suggested for the FNT (see Rosa et al., 2021). This suggests that defaunation in the study area may still be at an early or intermediate stage, where reductions in mammal populations have not yet translated into strong changes in dung beetle abundance or composition. In addition, a compensatory effect may be occurring,

whereby generalist and disturbance-tolerant medium-sized mammals (e.g., *Dasyprocta croconota*, *Cuniculus paca*) maintain overall dung supply despite the decline of large-bodied, functionally unique species (e.g., *Tapirus terrestris*, *Mazama* spp., *Dicotyles tajacu*). Under such conditions, dung beetle assemblages may maintain stable abundance while undergoing subtle taxonomic and functional reorganization, rather than abrupt declines.

This threshold-dependent and compensatory response indicates that early stages of defaunation may not be detectable through abundance metrics alone, underscoring the importance of multidimensional biodiversity assessments (Culot et al., 2017; Nichols et al., 2013). Finally, the relatively continuous forest structure of the Tapajós National Forest may further buffer the effects of defaunation by maintaining habitat connectivity and microclimatic stability, allowing dung beetle assemblages to persist even in areas with reduced mammal biomass.

Regarding environmental gradients, contrary to our initial expectation that vegetation structure would be a key determinant of dung beetle richness, abundance, and composition, it did not affect our response variables. Instead, responses varied primarily according to soil structure metrics; particularly, soil sand content emerged as a strong determinant of dung beetle abundance, and guild-level responses. This finding underscores the fundamental role of belowground physical properties in structuring aboveground detritivore communities (França et al., 2018; Costa et al., 2022; Salomão et al., 2022). Soil texture likely mediates beetle movement, nesting success, brood survival excavation costs, brood chamber stability, and moisture retention (Sowig, 1995; Halffter and Edmonds, 1982; Yamada et al., 2007, Griffiths et al., 2015). Sandy soils may facilitate tunnelling for some species but increase desiccation risk and brood mortality for others, thereby filtering assemblages according to nesting strategy and

physiological tolerance (Sowig et al., 1995; Yamada et al., 2007; Costa et al., 2022; Salomão et al., 2022).

Guild-specific responses further support this interpretation. Paracoprids increased with sand content, while telecoprids declined (Costa et al., 2022), indicating contrasting sensitivities linked to nesting depth, brood provisioning strategies, and susceptibility to microclimatic stress. It also supports the idea that environmental filtering can be a major mechanism structuring dung beetle communities even in relatively intact forests (Gardner et al., 2008; Griffiths et al., 2016). The positive association between endocoprids and litter depth suggests that microhabitat buffering, via moisture retention that prolong dung hydration, increased larval survival (Anduaga, 2004) and species persistence in humid forests (Larsen and Forsyth, 2005). These results highlight that environmental filtering operates across behavioral guilds, reinforcing the role of habitat structure in maintaining functional heterogeneity.

The functional approach revealed complex and partly contrasting effects of resource availability and habitat structure on dung beetle trait organization. Functional richness increased with mammal biomass, indicating an expansion of trait space under greater resource availability. Similar patterns have been reported in tropical forests where resource pulses promote broader functional spaces in detritivorous communities (Fukami et al., 2006). This pattern suggests that a greater diversity and quantity of dung inputs may facilitate the coexistence of species with distinct morphologies and nesting strategies. In contrast, functional divergence decreased with increasing mammal biomass, indicating that although more functional strategies are present, species tend to cluster around particular trait combinations. This apparent convergence suggests that increased resource availability may intensify competition or favour dominant functional strategies, leading to a non-random occupation of trait space (Fuzessy et al., 2021).

We also found clear evidence that abiotic filters shape dung beetle functional structure. Functional dispersion declined with increasing sand content, consistent with edaphic filtering favouring species with similar, excavation-efficient morphologies (Griffiths et al., 2015; Salomão et al., 2018). Likewise, functional evenness decreased with increasing canopy gaps, likely reflecting warmer and drier microclimatic conditions that disproportionately constrain certain functional strategies (Slade et al., 2007; Costa et al., 2022; Bicknell and Peres, 2010; França et al., 2016). Together, these results indicate that abiotic constraints can compress trait distributions even when taxonomic richness is maintained, potentially reducing functional redundancy and ecosystem stability.

In summary, our findings demonstrate that defaunation and environmental gradients play complementary but distinct roles in structuring dung beetle communities. Mammal biomass primarily influences species richness and specific functional dimensions, whereas soil and vegetation characteristics regulate abundance, guild structure, and trait distribution. This division of ecological roles highlights the importance of considering both biotic and abiotic drivers to fully understand community responses to environmental change.

Conserving dung beetle diversity, and the ecosystem functions they perform, requires protecting both mammal populations and habitat quality in Amazonia. Disruption of resource availability through defaunation or alteration of soil and forest structure through logging, fire, and fragmentation can independently and interactively undermine ecosystem functioning (Peres et al., 2016; Barlow et al., 2016; Zeng et al., 2019). Effective conservation strategies should therefore integrate the control of defaunation with the maintenance of environmental integrity, explicitly incorporating functional diversity metrics to anticipate ecosystem-level consequences of biodiversity loss.

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Author Contributions

Conceptualization: ABC, CAR and RFF; Data collection: ABC, CAR (mammals), FMF, LFM, MEM, EC (beetles). Data processing: ABC, CAR (mammals), LFM, MEM, EC, FZVdM (beetles). Writing - original draft preparation: ABC, CAR, CRB, IW, RFF, and FMF; Data analysis: ABC, IW, and PL with support from all authors; writing - review and editing: ABC, CAR, IW, FMF and RFF; visualization and supervision, with extensive contribution of all authors. Supervision: CAR, RFF, and FMF. All authors have read and agreed to the final version of the manuscript.

Declaration of Competing Interest

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

Disclosure Statements

The corresponding author confirms, on behalf of all authors, that there have been no involvements that might raise the question of bias in the work reported or in the conclusions, implications, or opinions stated.

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7 SUPPLEMENTARY MATERIAL

DEFAUNATION AND ENVIRONMENTAL FILTERING SHAPE DUNG BEETLE COMMUNITIES IN THE AMAZON.

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Appendix A. Supplementary figures.

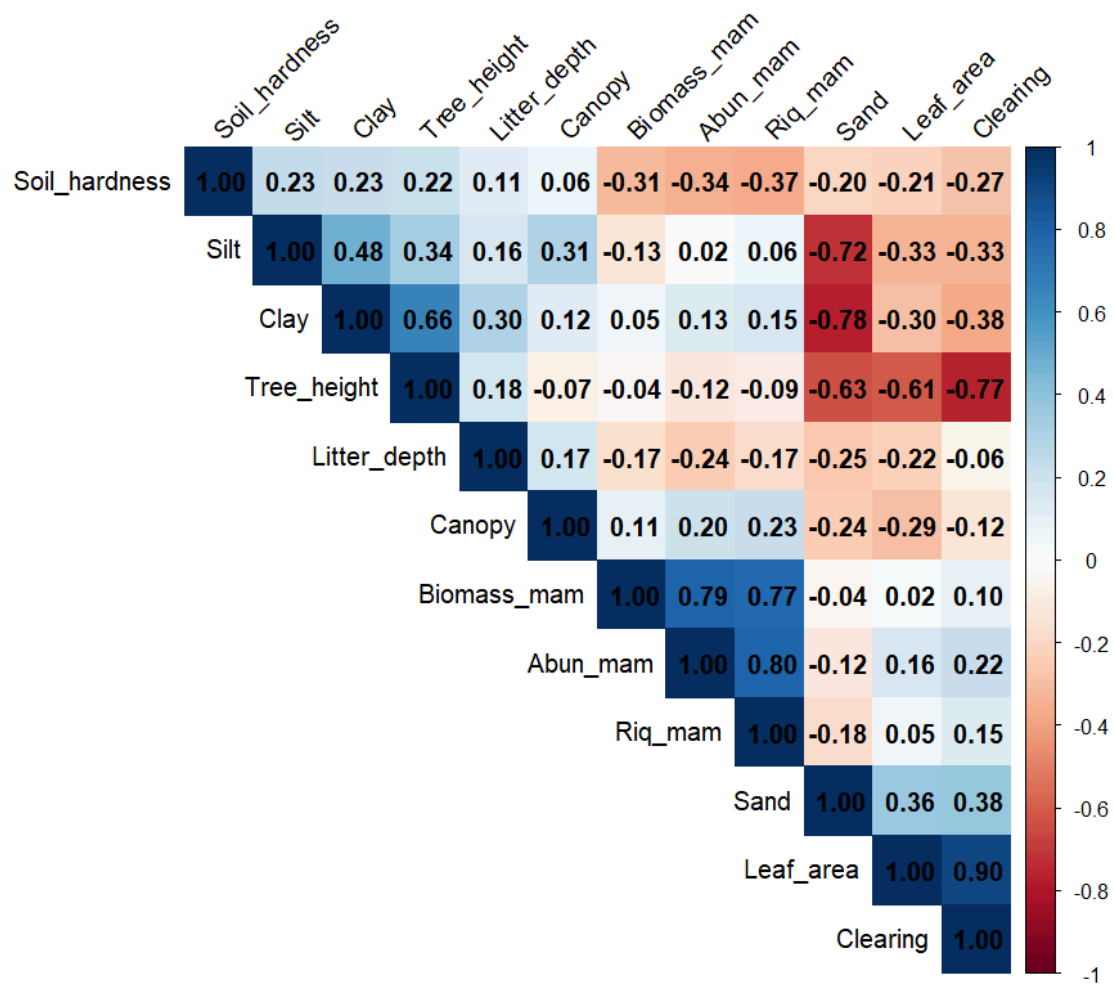


Fig S1. Calculate multicollinearity and visualize the correlation matrix, occurred in rcorr function from the Hmisc package and the corrplot function from the corrplot package, respectively. analysis results showed that variables with correlation coefficients above 0.70 or below -0.70 were considered highly collinear and excluded from further analysis. The 'Mam' suffix in the predictor variables denotes data from mammals.

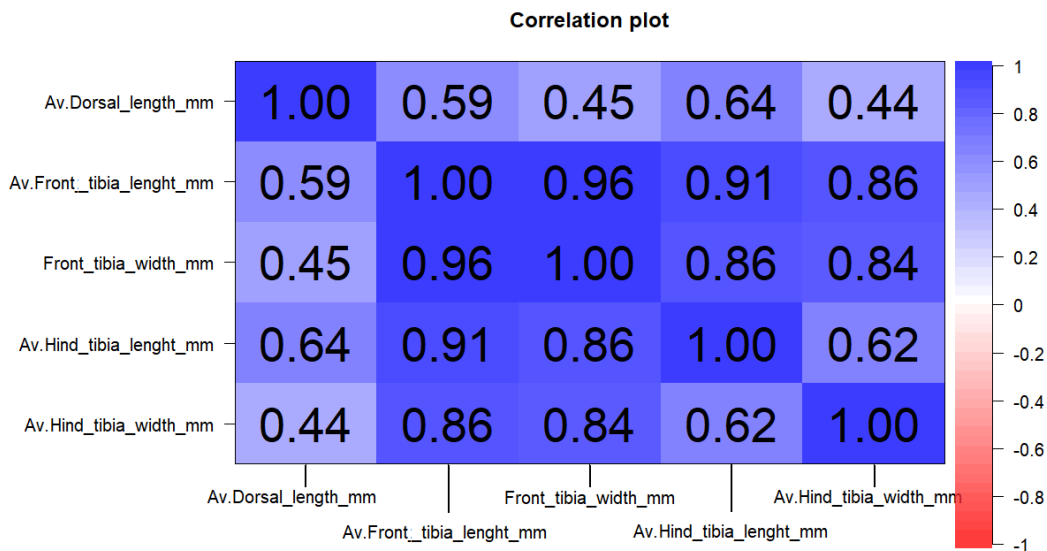


Fig S2. Analysis results showed high collinearity among the morphological traits presented, requiring adjustment.



Fig S3. Results after adjusting the morphological traits by dividing the hind leg measurements by the corresponding front leg measurements (Griffiths et al., 2015), the analysis result showed low collinearity between the variables.

Appendix B. Supplementary Tables

Table S1. Species and total abundances (N) surveyed across 34 plots where the beetles were sampled, Pará state, Brazilian Amazon.

Behavioral guild (GC), into three categories: endocoprid (E), paracoprid (P), telecoprid (T).

Species	N	GC	Species	N	GC
<i>Anomiopus.sp1</i>	1	P	<i>Deltochilum.sp3</i>	7	E
<i>Ateuchus.aff.ovalis</i>	1	P	<i>Dichotomius.leopoldinae</i>	2	P
<i>Ateuchus.aff.pygidialis</i>	24	P	<i>Deltochilum.orbignyi.amazonicum</i>	4	E
<i>Ateuchus.sp1</i>	134	P	<i>Dichotomius.aff.lucasi</i>	1796	P
<i>Ateuchus.sp2</i>	23	P	<i>Dichotomius.carinatus</i>	11	P
<i>Ateuchus.sp3</i>	1	P	<i>Dichotomius.melzeri</i>	4	P
<i>Ateuchus.substriatus</i>	5	P	<i>Dichotomius.sp1</i>	12	P
<i>Blackburneus.sp1</i>	2	P	<i>Dichotomius.worontzowi</i>	4	P
<i>Canthidium.aff.deyrollei</i>	551	P	<i>Eurysternus.arnaudi</i>	4	E
<i>Canthidium.melanocephalum</i>	10	P	<i>Eurysternu.atrosericus</i>	112	E
<i>Canthidium.aff.metallicum</i>	58	P	<i>Eurysternus.balachowskyi</i>	1	E
<i>Canthidium.sp1</i>	14	P	<i>Eurysternus.caribaeus</i>	40	E
<i>Canthidium.sp2</i>	15	P	<i>Eurysternus.cyanescens</i>	1	E
<i>Canthidium.sp3</i>	7	P	<i>Eurysternus.cyclops</i>	7	E
<i>Canthidium.sp4</i>	7	P	<i>Eurysternus.plebejus</i>	1	E

<i>Canthidium.sp5</i>	1	<i>P</i>	<i>Eurysternus.sp</i>	1	<i>E</i>
<i>Canthidium.sp6</i>	7	<i>P</i>	<i>Eurysternus.vastiorum</i>	2	<i>E</i>
<i>Canthidium.sp7</i>	3	<i>P</i>	<i>Eurysternus.wittmerorum</i>	2	<i>E</i>
<i>Canthon.aff.quadriguttatus</i>	5	<i>T</i>	<i>Ontherus.carinifrons</i>	84	<i>P</i>
<i>Canthon.aff.xantophus</i>	2	<i>T</i>	<i>Onthophagus.rubrescens</i>	113	<i>P</i>
<i>Canthon.conformis</i>	1	<i>T</i>	<i>Onthophagus.onorei</i>	19	<i>P</i>
<i>Canthon.delpontei</i>	1	<i>T</i>	<i>Onthophagus.osculatii</i>	164	<i>P</i>
<i>Canthon.fulgidus</i>	318	<i>T</i>	<i>Oxysternon.macleayi</i>	29	<i>P</i>
<i>Canthon.semiopacus</i>	2	<i>T</i>	<i>Scybalocanthon.sp</i>	21	<i>T</i>
<i>Coprophanaeus.dedegallieri</i>	2	<i>P</i>	<i>Scybalocanthon.candezei</i>	37	<i>T</i>
<i>Coprophanaeus.lancifer</i>	2	<i>P</i>	<i>Sylvicanthon.proseni</i>	53	<i>T</i>
<i>Cryptocanthon.sp</i>	2	<i>P</i>	<i>Sylvicanthon.sp</i>	11	<i>T</i>
<i>Deltochilum.sp</i>	63	<i>E</i>	<i>Trichillum</i>	1	<i>E</i>
<i>Deltochilum.sp1</i>	14	<i>E</i>	<i>Uroxys.sp1</i>	354	<i>P</i>
<i>Deltochilum.sp2</i>	49	<i>E</i>	<i>Uroxys.sp2</i>	1	<i>P</i>

Table S2. Total, mean, and standard deviation of dung beetle species richness surveyed across 34 plots where the beetles were sampled, Pará state, Brazilian Amazon.

Site	Modulo	Plot	Group	Richnes		
				s	Mean	Standard Deviation
FNT	Acarating a	AC_N_500	Scarabaeidae	18	0.300	0.462
FNT	Acarating a	AC_N_1500	Scarabaeidae	15	0.250	0.437
FNT	Acarating a	AC_N_2500	Scarabaeidae	18	0.300	0.462
FNT	Acarating a	AC_N_3500	Scarabaeidae	14	0.233	0.427
FNT	Acarating a	AC_N_4500	Scarabaeidae	15	0.250	0.437
FNT	Acarating a	AC_S_500	Scarabaeidae	5	0.083	0.279
FNT	Acarating a	AC_S_1500	Scarabaeidae	14	0.233	0.427
FNT	Acarating a	AC_S_2500	Scarabaeidae	7	0.117	0.324

Acarating						
FNT	a	AC_S_3500	Scarabaeidae	14	0.233	0.427
Acarating						
FNT	a	AC_S_4500	Scarabaeidae	8	0.133	0.343
FNT	M117	M117_NS1_500	Scarabaeidae	10	0.167	0.376
M117_NS1_150						
FNT	M117	0	Scarabaeidae	11	0.183	0.390
M117_NS1_250						
FNT	M117	0	Scarabaeidae	13	0.217	0.415
M117_NS1_350						
FNT	M117	0	Scarabaeidae	13	0.217	0.415
M117_NS1_450						
FNT	M117	0	Scarabaeidae	13	0.217	0.415
FNT	M117	M117_NS2_500	Scarabaeidae	13	0.217	0.415
M117_NS2_150						
FNT	M117	0	Scarabaeidae	9	0.150	0.360
M117_NS2_250						
FNT	M117	0	Scarabaeidae	15	0.250	0.437
M117_NS2_350						
FNT	M117	0	Scarabaeidae	11	0.183	0.390

M117_NS2_450						
FNT	M117	0	Scarabaeidae	10	0.167	0.376
FNT	M134	M134_LO2_500	Scarabaeidae	15	0.250	0.437
M134_LO2_150						
FNT	M134	0	Scarabaeidae	11	0.183	0.390
M134_LO2_250						
FNT	M134	0	Scarabaeidae	8	0.133	0.343
M134_LO2_350						
FNT	M134	0	Scarabaeidae	7	0.117	0.324
M134_LO2_450						
FNT	M134	0	Scarabaeidae	12	0.200	0.403
FNT	M134	M134_LO1_500	Scarabaeidae	8	0.133	0.343
M134_LO1_150						
FNT	M134	0	Scarabaeidae	12	0.200	0.403
M134_LO1_350						
FNT	M134	0	Scarabaeidae	9	0.150	0.360
M134_LO1_450						
FNT	M134	0	Scarabaeidae	19	0.317	0.469
FNT	M67	M67_S_500	Scarabaeidae	15	0.250	0.437
FNT	M67	M67_S_1500	Scarabaeidae	19	0.317	0.469

FNT	M67	M67_S_2500	Scarabaeidae	16	0.267	0.446
FNT	M67	M67_S_3500	Scarabaeidae	11	0.183	0.390
FNT	M67	M67_S_4500	Scarabaeidae	8	0.133	0.343

Table S3. Total, mean, and standard deviation of dung beetle species abundance surveyed across 34 plots where the beetles were sampled, Pará state, Brazilian Amazon.

Site	Modulo	Plot	Group	Abundanc		
				e	Mean	Standard Deviation
FN	Acarating					
T	a	AC_N_500	Scarabaeidae	429	7.150	29.738
FN	Acarating					
T	a	AC_N_1500	Scarabaeidae	377	6.283	32.656
FN	Acarating					
T	a	AC_N_2500	Scarabaeidae	239	3.983	13.065
FN	Acarating					
T	a	AC_N_3500	Scarabaeidae	302	5.033	21.864
FN	Acarating					
T	a	AC_N_4500	Scarabaeidae	214	3.567	15.120

FN	Acarating					
T	a	AC_S_500	Scarabaeidae	66	1.100	5.376
FN	Acarating					
T	a	AC_S_1500	Scarabaeidae	201	3.350	14.261
FN	Acarating					
T	a	AC_S_2500	Scarabaeidae	77	1.283	6.236
FN	Acarating					
T	a	AC_S_3500	Scarabaeidae	320	5.333	19.413
FN	Acarating					
T	a	AC_S_4500	Scarabaeidae	138	2.300	10.326
FN						
T	M117	M117_NS1_500	Scarabaeidae	29	0.483	2.111
FN	M117_NS1_150					
T	M117	0	Scarabaeidae	46	0.767	3.094
FN	M117_NS1_250					
T	M117	0	Scarabaeidae	55	0.917	3.132
FN	M117_NS1_350					
T	M117	0	Scarabaeidae	67	1.117	4.833
FN	M117_NS1_450					
T	M117	0	Scarabaeidae	103	1.717	8.267

FN						
T	M117	M117_NS2_500	Scarabaeidae	44	0.733	2.170
FN		M117_NS2_150				
T	M117	0	Scarabaeidae	44	0.733	3.808
FN		M117_NS2_250				
T	M117	0	Scarabaeidae	128	2.133	8.819
FN		M117_NS2_350				
T	M117	0	Scarabaeidae	61	1.017	6.080
FN		M117_NS2_450				
T	M117	0	Scarabaeidae	79	1.317	7.886
FN						
T	M134	M134_LO2_500	Scarabaeidae	80	1.333	4.905
FN		M134_LO2_150				
T	M134	0	Scarabaeidae	63	1.050	3.132
FN		M134_LO2_250				
T	M134	0	Scarabaeidae	50	0.833	2.970
FN		M134_LO2_350				
T	M134	0	Scarabaeidae	15	0.250	0.816
FN		M134_LO2_450				
T	M134	0	Scarabaeidae	29	0.483	1.600

FN						
T	M134	M134_LO1_500	Scarabaeidae	110	1.833	12.160
FN		M134_LO1_150				
T	M134	0	Scarabaeidae	104	1.733	7.508
FN		M134_LO1_350				
T	M134	0	Scarabaeidae	57	0.950	3.868
FN		M134_LO1_450				
T	M134	0	Scarabaeidae	176	2.933	12.915
FN						
T	M67	M67_S_500	Scarabaeidae	75	1.250	3.939
FN						
T	M67	M67_S_1500	Scarabaeidae	187	3.117	9.776
FN						
T	M67	M67_S_2500	Scarabaeidae	101	1.683	5.625
FN						
T	M67	M67_S_3500	Scarabaeidae	114	1.900	6.483
FN						
T	M67	M67_S_4500	Scarabaeidae	43	0.717	2.100

Table S4. Results of analysis. model including mammalian biomass (BM, kg), litter depth (LD, cm), sand (SA, g/kg), soil hardness (SH, kPa), canopy openness (CA, %) and clearing openness (CL, %), as explanatory predictors (Pred). Response metrics (Resp) included observed species richness, abundance and behavioural guild level (paracropid, telecropid e endocropid); (X^2) indicates valour de Chi-quadrado; **P** indicates deviance analysis (P-value); total deviance explained by the model (R^2_{dev}). Significant predictors (*) based on upper 0.95.

Resp.	Pred.	X^2	P_{dev}	R²_{dev}
Observed richness (Total assemblage)	BM	4.3283	0.03*	0.11
	LD	0.1120	0.73	-
	SA	0.1242	0.72	-
	SH	0.0695	0.79	-
	CA	0.2517	0.61	-
	CL	0.6270	0.42	-
Abundance (Total assemblage)	BM	1.8819	0.17	-
	LD	2.2882	0.13	-
	SA	6.9514	0.008*	0.17
	SH	0.4643	0.50	-
	CA	0.4681	0.49	-
	CL	0.6499	0.42	-
Abundance (Paracropid)	BM	0.5509	0.45	-
	LD	1.5579	0.21	-
	SA	10.402	0.001*	0.24
	SH	0.1761	0.67	-
	CA	0.1222	0.72	-
	CL	1.4294	0.23	-
Abundance (Telecropid)	BM	2.3030	0.12	-
	LD	0.1180	0.73	-
	SA	4.5223	0.03	0.21
	SH	0.0010	0.97	-
	CA	1.5242	0.21	-

	CL	0.2277	0.63	-
	BM	0.0371	0.84	-
	LD	4.4517	0.03*	0.17
Abundance	SA	1.6512	0.19	-
(Endocropid)	SH	0.9927	0.31	-
	CA	0.0307	0.86	-
	CL	0.5457	0.45	-

Table S5. Results of analysis. Models included mammal biomass (BM; kg), litter depth (LD; cm), sand (SA; g/kg), soil hardness (SH; kPa), canopy openness (CA; %) and clearing openness (CL; %), as explanatory predictors (Pred). Response metrics (Resp) included observed traits functions (FRic, FDis, FEve e FDiv); (X^2) indicates valor de Chi-quadrado; **P** indicates deviance analysis (P-value); total deviance explained by the model (R^2_{dev}). Asterisk (*) indicates predictors statistical significance ($P < 0.05$).

Resp.	Pred.	X^2	P_{dev}	R^2_{dev}
	BM	7.4622	0.006*	0.15
	LD	0.2672	0.60	-
Observed	SA	0.0089	0.92	-
richness (FRic)	SH	0.0794	0.77	-
	CA	0.0360	0.84	-
	CL	0.8671	0.35	-
	BM	0.8383	0.35	-
	LD	0.0480	0.82	-
Observed	SA	0.9902	0.02*	0.14
dispersion	SH	0.1234	0.72	-
(FDis)	CA	0.2609	0.60	-
	CL	0.9152	0.33	-

	BM	0.1502	0.69	-
	LD	0.4728	0.49	-
Observed	SA	0.1301	0.71	-
Eveness (FEve)	SH	2.1003	0.14	-
	CA	3.4873	0.06	-
	CL	6.3285	0.01*	0.15
	BM	7.6627	0.005*	0.31
	LD	0.6295	0.42	-
Observed	SA	0.8851	0.34	-
divergence	SH	0.1128	0.73	-
(FDiv)	CA	1.3262	0.24	-
	CL	1.2579	0.26	-

8 CONCLUSÃO GERAL

A presente tese investigou como a defaunação de mamíferos de médio e grande porte afeta interações ecológicas chave e suas consequências para a biodiversidade e o funcionamento de florestas de terra firme na Amazônia Central, por meio de uma abordagem integrativa que combina experimentos de exclusão de fauna e levantamentos de comunidades de invertebrados, permitindo avaliar desde interações planta–animal até a estruturação de comunidades biológicas.

No capítulo 1, evidenciamos que a defaunação de mamíferos de médio e grande porte desencadeia um efeito cascata que compromete o recrutamento inicial de espécies arbóreas de interesse comercial. O experimento de exclusão revelou que a ausência desses vertebrados reduz drasticamente a remoção de sementes de maior tamanho, como as da espécie *L. lurida*, deixando-as vulneráveis a altas taxas de predação por invertebrados e ataques fúngicos. Embora tenha havido uma compensação funcional quantitativa por pequenos roedores (como *Proechimys* spp.), essa compensação foi

funcionalmente limitada, uma vez que tais espécies atuam predominantemente como predadoras e possuem restrições no transporte de sementes maiores. Esses resultados demonstram que a perda de grandes mamíferos compromete interações planta-animal fundamentais, com implicações diretas para a manutenção da diversidade arbórea e para a sustentabilidade econômica de recursos florestais utilizados por comunidades tradicionais e pela atividade madeireira.

No capítulo 2, expandimos a análise para as comunidades de besouros rola-bosta (Scarabaeinae), evidenciando que a manutenção da biodiversidade desse grupo depende de uma interação complementar entre a disponibilidade de recursos de origem animal (fezes e carcaças) e filtros ambientais abióticos. Confirmamos que a biomassa de mamíferos é um preditor positivo da riqueza de espécies e da diversidade funcional (FRic), reforçando a forte dependência trófica desse grupo. Contudo, variáveis ambientais, como a textura do solo e a estrutura da vegetação, desempenham papel dominante na regulação da abundância, dos padrões de guildas e de dimensões específicas da diversidade funcional.

Em conjunto, os resultados demonstram que a defaunação atua como um filtro ecológico que reconfigura interações tróficas e funcionais, com o potencial de simplificar a composição das comunidades e comprometer a resiliência dos ecossistemas a longo prazo. Além disso, evidenciam que os efeitos da defaunação são modulados por condições ambientais, resultando em respostas não uniformes entre diferentes níveis de organização biológica. Assim, esta tese reforça a importância da conservação das florestas amazônicas para a manutenção da integridade de seus processos ecológicos, destacando que estratégias eficazes devem integrar a proteção da fauna, a preservação da estrutura do habitat e a manutenção da diversidade funcional como pilares da sustentabilidade ecológica e socioeconômica da região.