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Da dispersão de sementes ao estabelecimento de plantas: como a fauna modula a regeneração natural de florestas tropicais degradadas?

José Eduardo Teixeira Falcon
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JOSÉ EDUARDO TEIXEIRA FALCON

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Orientador: Lucas Navarro Paolucci

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RESUMO

FALCON, José Eduardo Teixeira, D.Sc., Universidade Federal de Viçosa, junho de 2025. **Da dispersão de sementes ao estabelecimento de plantas: como a fauna modula a regeneração natural de florestas tropicais degradadas?**. Orientador: Lucas Navarro Paolucci.

Distúrbios antrópicos degradam florestas tropicais e causam a perda de biodiversidade e serviços ecossistêmicos essenciais para o bem-estar humano. A proporção de florestas degradadas na Amazônia tem aumentado nos últimos anos e há perspectivas de crescimento para as próximas décadas. Assim, o controle da degradação florestal e a regeneração de florestas degradadas se tornam essenciais. A regeneração natural é uma maneira eficiente e barata de se recuperar florestas degradadas. Porém, distúrbios antrópicos impõem filtros ecológicos que inibem a regeneração natural, como a limitação da dispersão de sementes e a limitação no estabelecimento de plantas. A fauna é fundamental para atenuar tais filtros, dispersando sementes, predando insetos herbívoros e melhorando a saúde do solo. No entanto, a fauna também limita a regeneração natural por meio da predação de sementes pós-dispersão. Nesta tese, investiguei funções ecossistêmicas desempenhadas pela fauna e relevantes para a regeneração natural de florestas em dois capítulos. No primeiro, quantifiquei a contribuição de antas, importantes dispersoras de sementes, para a regeneração de florestas que sofrem impactos crônicos de incêndios florestais e vizinhas de plantações de soja. Também quantifiquei os mecanismos subsequentes à dispersão realizada pelas antas e que podem contribuir para a regeneração, como a dispersão secundária e a predação de sementes, e a modulação da saúde do solo abaixo das fezes. A disponibilidade de soja no entorno da área de estudos foi determinante para o papel das antas como dispersoras de sementes. Durante a época de soja, as antas se alimentaram deste recurso e não foram encontradas sementes nativas em suas fezes, o que inibiu a regeneração de plantas por meio da dispersão de sementes. No entanto, observei maior biomassa microbiana, proporção de fungos e fósforo disponível no solo abaixo das fezes de antas. Na ausência de soja da paisagem, o consumo de frutos e sementes nativas pelas antas resultou no recrutamento de 33 plântulas, que podem ser extrapoladas para 223 plântulas por ano em florestas degradadas. Os papéis das antas não diferiram entre florestas degradadas e florestas intactas. No segundo capítulo, investiguei por que há menor riqueza de plantas em florestas ripárias circundadas por plantações, quantificando a frugivoria, a predação de sementes pós-dispersão e a predação de insetos herbívoros em comparação com florestas ripárias sem distúrbios. As florestas ripárias degradadas apresentaram apenas a frugivoria por aves menor do que em florestas ripárias não degradadas. Isso sugere que a menor riqueza de plantas nessas florestas pode ser atribuída a limitações de dispersão, já que filtros de estabelecimento, como a predação de sementes e de insetos herbívoros, não diferiram entre os tipos de floresta. Assim, as antas desempenham um papel crucial na promoção da regeneração, mas sua eficácia é dependente da presença de plantações no entorno. Já a diminuição da frugivoria por aves em florestas circundadas por plantações aponta para a limitação de sementes como um filtro ecológico chave. Portanto, de maneira geral, as funções ecossistêmicas foram pouco sensíveis aos distúrbios antrópicos, o que reforça o papel da fauna como aliada importante para a regeneração natural de florestas degradadas.

Palavras-chave: ecologia do distúrbio; distúrbios florestais; funções ecossistêmicas; regeneração natural; dispersão de sementes; predação de sementes; herbivoria; ecologia do solo

ABSTRACT

FALCON, José Eduardo Teixeira, D.Sc., Universidade Federal de Viçosa, June, 2025. **From seed dispersal to plant establishment: how does fauna modulate the natural regeneration of degraded tropical forests?**. Adviser: Lucas Navarro Paolucci.

Anthropogenic disturbances degrade tropical forests, causing biodiversity loss and essential ecosystem services vital for human well-being. The proportion of degraded forests in the Amazon has increased in recent years, with projections for continued growth in the coming decades. Thus, controlling forest degradation and regenerating degraded forests becomes essential. Natural regeneration is an efficient and inexpensive way to recover degraded forests. However, anthropogenic disturbances impose ecological filters that inhibit natural regeneration, such as limitations in seed dispersal and plant establishment. Fauna is fundamental to mitigating such filters by dispersing seeds, preying on herbivorous insects, and improving soil health. Nevertheless, fauna also limit natural regeneration through post-dispersal seed predation. In this thesis, I investigated ecosystem functions performed by fauna that are relevant to the natural regeneration of forests across two chapters. In the first, I quantified the contribution of tapirs, important seed dispersers, to the regeneration of forests suffering chronic impacts from wildfires and adjacent to soybean croplands. I also quantified the mechanisms subsequent to tapir-mediated dispersal that can contribute to regeneration, such as secondary dispersal and seed predation, and the modulation of soil health beneath their feces. The availability of soybeans in the study area's surroundings was determinant for the tapirs' role as seed dispersers. During the soybean season, tapirs fed on this resource, and no native seeds were found in their feces, which inhibited plant regeneration through seed dispersal. However, I observed increased microbial biomass, fungal proportion, and available phosphorus in the soil beneath tapir feces. In the absence of soybeans from the landscape, the consumption of native fruits and seeds by tapirs resulted in the recruitment of 33 seedlings, which can be extrapolated to 223 seedlings per year in degraded forests. The roles of tapirs did not differ between degraded and intact forests. In the second chapter, I investigated why there is lower plant richness in riparian forests surrounded by croplands, quantifying frugivory, post-dispersal seed predation, and herbivorous insect predation in comparison to undisturbed riparian forests. Degraded riparian forests exhibited only lower bird frugivory than undisturbed riparian forests. This suggests that the lower plant richness in these forests can be attributed to dispersal limitations, as establishment filters, such as seed predation and herbivorous insect predation, did not differ between forest types. Thus, tapirs play a crucial role in promoting regeneration, but their effectiveness depends on the presence of croplands in the surroundings. Meanwhile, the decrease in bird frugivory in forests surrounded by croplands points to seed limitation as a key ecological filter. Therefore, overall, ecosystem functions were not very sensitive to anthropogenic disturbances, which reinforces the role of fauna as an important ally for the natural regeneration of degraded forests.

Keywords: disturbance ecology; forest disturbances; ecosystems functions; natural regeneration; seed dispersal; seed predation; herbivory; soil ecology

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1 INTRODUÇÃO GERAL

A Amazônia é a maior floresta tropical do mundo com cerca de 5.8 milhões de km² (Science Panel for the Amazon, 2021). A extensão da Amazônia cobre 0,5% da superfície terrestre, onde é possível encontrar mais de 10% de todas as plantas e vertebrados conhecidos, o que torna essa a região mais biodiversa do planeta (Guayasamin et al., 2021). A Amazônia é fundamental para regulação dos ciclos de carbono e da água em escala regional e mundial, uma vez que é responsável por 16% da produtividade primária global e por um quinto da água doce lançada nos oceanos (Costa et al., 2021; Malhi et al., 2021). Esses números demonstram a importância da Amazônia como uma grande reserva de biodiversidade e fornecedora de serviços ecossistêmicos. Contudo, a Amazônia está ameaçada por ações antrópicas para a expansão de atividades industriais e agropecuárias que geram desmatamento e degradação ambiental (Albert et al., 2023).

Enquanto o desmatamento é um estado binário de uso do solo, desmatado ou não desmatado (Putz; Redford, 2010), a degradação ambiental é uma mudança deletéria gradual, transitória ou de longo prazo em estruturas, funções e processos florestais (Lapola et al., 2023). Entre os principais distúrbios antrópicos que causam a degradação florestal da Amazônia estão os incêndios florestais e o efeito de borda (Berenguer et al., 2024). Os incêndios geralmente se originam em áreas agrícolas ou de desmatamento e, eventualmente, escapam para as florestas adjacentes (Cammelli; Coudel; De Freitas Navegantes Alves, 2019; Ray; Nepstad; Moutinho, 2005). Já o efeito de bora resulta do processo de fragmentação causado pelo desmatamento, que altera condições microclimáticas nas bordas das florestas (Berenguer et al., 2024; Lapola et al., 2023). Isso leva à diminuição da umidade do ar e do solo, ao aumento da temperatura, da intensidade luminosa e da exposição ao vento (Berenguer et al., 2024; Lapola et al., 2023). Esses distúrbios geram alterações de composição e funcionais em comunidades de fauna e flora, menor produtividade primária e armazenamento de carbono (Berenguer et al., 2024; Lapola et al., 2023). A degradação florestal prolongada leva ainda a perdas de conectividade do dossel, de funções ecológicas e da capacidade de regeneração da floresta, resultando em um tipo de desmatamento específico por decaimento gradual (De Almeida et al., 2022).

Recentemente, as taxas de desmatamento da Amazônia diminuíram graças à reinstauração do Plano de Ação para Prevenção e Controle do Desmatamento na Amazônia Legal (MMA, 2023). Por exemplo, em 2024 a área desmatada na Amazônia brasileira foi de 5.816 km², o menor incremento anual de desmatamento em uma década e 26,4% inferior à média do período entre 2008 e 2024 (INPE, 2025). No entanto, as áreas degradadas da Amazônia aumentaram 44% em 2024 (25.023 km²) quando comparadas a 2023 e 163% quando comparadas com 2022, contrariando a redução no desmatamento (INPE, 2025; Mataveli et al., 2025). Projeções apontam que até 2050 distúrbios antrópicos podem converter entre 10 e 47% da Amazônia em estados florestais alternativos, os quais não são equivalentes funcionais aos seus estados naturais de conservação (Flores et al., 2024). Diante disso, a Amazônia pode se aproximar de seu ponto de inflexão, onde a resiliência da floresta é comprometida (Lovejoy; Nobre, 2018).

Para conter o avanço da degradação florestal, é essencial controlar o avanço do desmatamento e estabelecer projetos de restauração e reflorestamento em larga escala (Mataveli et al., 2025), sendo a regeneração natural de áreas degradadas o método de melhor custo-benefício para isso (Chazdon; Guariguata, 2016). Porém, a regeneração natural pode ser influenciada por filtros ecológicos que limitam a chegada de sementes (limitação de sementes) e/ou o estabelecimento de plantas regenerantes nos locais degradados (limitação de estabelecimento; Jakovac et al., 2021; Myers; Harms, 2009). A limitação de sementes ocorre quando há escassez ou limitação na chegada de sementes por falta de fontes locais, produção insuficiente ou restrição na dispersão, dificultando o recrutamento de novas plantas (Turnbull; Crawley; Rees, 2000). Já os filtros de estabelecimento restringem a regeneração por meio de processos que ocorrem após a chegada das sementes, como a disponibilidade de micrositíos adequados, a predação de sementes e plântulas e a competição por recursos, que determinam se as sementes que chegaram conseguem germinar e se estabelecer (Clark et al., 1999).

A fauna auxilia a regeneração natural ao desempenhar funções ecológicas que atenuam filtros ecológicos. A dispersão de sementes por animais é fundamental em áreas degradadas, dada a alta proporção de plantas zoocóricas na região neotropical (Gardner et al., 2019). Predadores de sementes, embora causem alguma mortalidade, podem aumentar a diversidade vegetal ao controlar espécies dominantes (Comita et al., 2014). Animais insetívoros, por meio da predação, reduzem indiretamente os danos foliares causados por insetos herbívoros (Karp; Daily, 2014), favorecendo o crescimento das plantas. Além disso, a atividade animal melhora a qualidade do solo através da deposição de excretas ricas em nutrientes no solo (Hooper et al., 2005).

Assim, o objetivo geral desse trabalho foi investigar os mecanismos de regeneração natural mediados pela fauna em florestas degradadas por múltiplos distúrbios antrópicos na Amazônia. No primeiro capítulo, nós quantificamos os efeitos da deposição de fezes de antas – o maior mamífero da América do Sul e um herbívoro voraz – em florestas degradadas pelo fogo. Adicionalmente, mensuramos os mecanismos subjacentes à dispersão de sementes pelas antas, como a dispersão secundária de sementes, predação de sementes nas fezes e enriquecimento nutricional do solo abaixo das fezes. No segundo capítulo, nós investigamos os mecanismos regeneração natural de florestas secundárias circundadas por plantações e impactadas principalmente por efeito de borda. Especificamente, nós mensuramos a frugivoria, predação de insetos herbívoros e predação de sementes.

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2 CAPÍTULO 1

Tapir dung boosts natural regeneration and soil enrichment of Amazonian forests

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2.1 Abstract

Lowland tapir (*Tapirus terrestris*) plays a significant role in forest regeneration by dispersing three times more seeds in disturbed forests than in undisturbed forests. Our study investigates how tapir dung deposition shapes seedling recruitment and its implications for forest regeneration. Additionally, we investigated underlying mechanisms potentially linked with seedling recruitment, including secondary seed dispersal, seed predation within dung, and soil nutritional quality beneath dung. We collected and deposited dung piles in undisturbed and in severely disturbed forests bordering soybean crops in the southeastern Brazilian Amazon in February and September 2023, during soybean productive and fallow periods, respectively. We assessed the dung beetle community and their seed and dung removal in tapir dung, and also seedling recruitment and survival in dung addition plots with and without dung beetle access. We also measured seed removal by all fauna within and outside the dung. Finally, we quantified soil microbial biomass, phosphorus content of soils and seedlings beneath and around dung clumps. We recorded a high abundance of soybean parts and no native seeds in the dung when there were soy crops in the surroundings, which led to zero native seedling recruitment. However, when soybean was absent in the landscape (fallow period), we found 33 established seedlings, all in plots with dung addition. Dung beetle community and their ecosystem functions did not differ across forests. Seed predation within dung was 31.1% lower than outside, suggesting a protective role for seeds within dung. Soil beneath dung had 60% higher microbial biomass and 30% higher phosphorus content than soils without dung. This highlights the crucial role of tapirs as forest fertilizers, as their dung increase soil nutritional content and biological activity, despite the lack of native seed dispersal in the presence of soybean. However, tapirs are key seed dispersers and directly contribute to seedling establishment across disturbed forests during the fallow period in their surroundings.

Key words: seedling recruitment, seed removal, secondary seed dispersal, soil microbiota, soil phosphorus, wildfire.

2.2 Introduction

The southeastern Brazilian Amazon rainforest, one of the world's largest agricultural frontiers, faces significant pressure from anthropogenic activities that degrade forests (Balch et al., 2015; Brando et al., 2020). Wildfires, logging and edge effects degrade forests (Silvério et al., 2019; Trumbore et al., 2015) and potentialize the effects of natural disturbances, like droughts and windthrows (Brando, Paolucci, et al., 2019). These disturbances act synergistically, pushing forests into a severe state of degradation, resulting in impacts on the plant (P. M. Brando et al., 2014, 2024; Silvério et al., 2019) and animal communities (Andrade et al., 2014; Barlow & Peres, 2004; Lourenço et al., 2024; Paolucci et al., 2017), ecological interactions (Massad et al., 2013; Paolucci et al., 2016; Queiroz et al., 2022), and biogeochemical cycles (Brando et al., 2019). With future scenarios of climate and land use changes, interactions between forest disturbances will be more frequent and intense in the following years (Brando et al., 2020; Nobre et al., 2016), which urges for a greater understanding of mechanisms that contribute to forest regeneration.

Natural forest regeneration is one of the most cost-effective strategies for forest recovery (Chazdon & Guariguata, 2016; Chazdon & Uriarte, 2016) and can restore biological communities and ecosystem functions impacted by human disturbances (Jakovac et al., 2021a). However, natural regeneration is highly limited by ecological filters that inhibit or reduce plant establishment (Jakovac et al., 2021a; J. A. Myers & Harms, 2009). Some of these filters, such as dispersal limitation, restrict the propagule's arrival to degraded habitats, while others impede seed germination and plant establishment, causing establishment limitation (Holl et al., 2000; Jakovac et al., 2021a; Martínez-Ramos et al., 2016). Animals are crucial to seed dispersal and plant establishment (Wunderle, 1997), increasing the richness, abundance and evenness of seed species in the seed rain (Camargo et al., 2021; Carlo & Morales, 2016; González-Castro et al., 2019). However, frugivores are frequently depleted in disturbed forests, particularly large-bodied species, which reduces seed dispersal, forest regeneration and carbon storage (Culot et al., 2017; Gardner et al., 2019; Kurten, 2013).

The lowland tapir (*Tapirus terrestris* Linnaeus 1758; hereafter tapir) can be a nature-based solution for natural forest regeneration by providing ecosystem functions that preserve and restore ecosystem structure (Villar & Medici, 2021). Tapirs are the largest South American land mammal (100-250 kg; Padilla & Dowler, 1994) and are voracious herbivores that disperse large quantities of native seeds from approximately 300 species (Barcelos et al., 2013; O'Farrill et al., 2013). As tapirs inhabit undisturbed and disturbed habitats, they attend orchards and croplands, where they raid at least 22 cultivars, like soy and maize (Flesher & Medici, 2022). Tapirs can move over 20 km per day, potentially dispersing seeds along their home range (mean of 8.3 Km^2), highlighting their role as long-distance seed dispersers (Fragoso et al., 2003; Medici et al., 2021). Some tapir individuals can modulate their movement patterns to feed in locations with more abundant resources; however, their home ranges show low plasticity and are stable across climatic seasons and habitat structure (Medici et al., 2021). While the contributions of tapirs to seed dispersal, plant recruitment, and survival are well-documented in undisturbed forests (Fragoso, 1997; Fragoso et al., 2003; Fragoso & Huffman, 2000; but see Villar et al., 2020), their actual contribution for the natural regeneration of disturbed forests remains unclear. Previous research suggests this role can be important and positive, as tapirs can disperse up to three times more seeds in disturbed than undisturbed Amazon forests surrounded by croplands (Paolucci et al., 2019). Therefore, tapirs can contribute disproportionately to plant recruitment in disturbed forests and play a key role in natural forest regeneration.

In addition to their direct role in seed dispersal, tapirs' dung is an important resource for secondary dispersers, like dung beetles (Lugon et al., 2017). Dung beetles can maximize tapir seed dispersal by redistributing seeds from the dung clump onto the ground, which reduces seedling mortality by density-dependent effects and potentially increases plant recruitment (Andresen & Urrea-Galeano, 2022; Nichols et al., 2008). Dung beetles' activity is positively influenced by the amount of dung available in their habitat (Peck & Howden, 1984; Rodrigues et al., 2013), as locations with higher herbivore biomass allow for a greater dung beetle species richness and average body size (which in turn is an indicative of higher seed dispersal capability; Andresen & Laurance, 2007). On the other hand, dung beetles are negatively impacted by forest disturbances, which reduce their species richness, abundance, biomass, and ecosystem functions like secondary seed dispersal (Andrade et al., 2014; R. F. Braga et al., 2013) – and may limit plant recruitment mediated by these animals in disturbed forests.

Secondary seed dispersal from dung also protects the seeds from predators by redistributing them onto the ground, since the dung odor attracts seed predators (Janzen, 1982; McConkey, 2005). Seed predation within vertebrates' dung is prevalent across several ecosystems, dung types, and predator species (Andresen, 2002; Feer & Forget, 2002; Martínez-Mota et al., 2004; Sekar et al., 2016; Srbek-Araujo et al., 2017), and can offset both primary and secondary seed dispersal by killing propagules (Andresen & Levey, 2004). Forest disturbance also influences the abundance of seed predators. For example, the abundance of small rodents increases in disturbed rainforests (Palmeirim et al., 2020), intensifying seed predation and reducing plant recruitment (Krishnan et al., 2022). Conversely, ants – the main resource removers in tropical forests and important seed predators (Fernandes et al., 2020; Griffiths et al., 2018) – are less abundant, remove fewer seeds (Paolucci et al., 2016), and take longer to find seeds in disturbed rainforests (Ribeiro et al. 2024). While some ant species are granivorous, others are good-quality secondary seed dispersers, so the outcomes of such interactions may affect seeds' fate (Passos & Oliveira, 2003; Pizo & Oliveira, 1998). Both rodents and ants prefer to feed on seeds exposed outside of dung, probably because of the ease of access to this resource (Bermejo et al., 1998; Martínez-Mota et al., 2004). Their different responses in the face of forest disturbances exemplify how complex the indirect contributions of tapirs to forest natural regeneration can be.

Besides seed dispersal, tapirs can promote plant recruitment by enhancing soil nutritional conditions (Villar et al., 2021). Large herbivores (e.g., tapirs and peccaries) in neotropical rainforests increase the available nitrogen in the soil through excreta and trampling, modifying soil physicochemical properties and potentially enhancing forest primary productivity (Villar et al., 2021). Animal excreta provide readily available nutrients for plants and soil microbiota, and organic matter for microbial decomposition (Hobbs, 1996), which also releases nutrients for microbial and plant uptake (Berg & McClaugherty, 2003). Soil microbial biomass can decrease due to indirect modifications of soil properties caused by forest disturbances, reducing nutrient cycling and available phosphorus (Mataix-Solera et al., 2009). Phosphorus is the main element constraining Amazon's productivity (Cunha et al., 2022; Dionizio et al., 2018), so the higher input of tapir dung in disturbed forests (Paolucci et al., 2019), with its nutrient content and potential to stimulate microbial activity, may mitigate the phosphorus limitation and help to promote forest recovery.

In this study, we quantified the contributions of tapirs to plant recruitment across both undisturbed and highly disturbed southeastern Amazonian forest surrounded by croplands, as well as investigated abiotic and biotic filters that may explain such contributions. For this, we tested whether tapirs' dung increases plant recruitment in the presence and absence of plantations in the landscape. Additionally, we quantified the following underlying mechanisms: I) dung beetle ecosystem functions of dung removal and secondary seed dispersal activity; II) seed predation in tapirs' dung; and III) soil nutritional quality (nutrients and microbial biomass), and plant nutrient uptake due to tapirs' dung presence onto soil. Our study area encompassed three adjacent forest blocks bordering croplands, each subjected to different experimental fire regimes between 2004 and 2010. The fires, combined with extreme drought events, blowdowns, and edge effects, resulted in significant forest degradation, including high tree mortality, canopy cover openness, grass invasion, and herbivory compared to undisturbed forests (Balch et al., 2015; P. M. Brando, Paolucci, et al., 2019; Queiroz et al., 2022). These long-term experimental burns in southeastern Amazonia provided a unique opportunity to quantify the role of tapir dung in plant recruitment within a disturbed landscape. Moreover, the interface between forest × cropland, with seasonal plantations, present in our study area, integrates and mirrors the major agricultural frontier of the World. Thus, the results of this research can be extrapolated to a large scale.

2.3 Methods

2.3.1 Study area

We conducted this study at Tanguro Field Station (state of Mato Grosso, Brazil; 13°04'S, 52°23''W), located in the southeastern Amazon basin, in a transitional zone between the Cerrado (tropical savanna) and Amazon (tropical rainforest) biomes. The native vegetation is a tropical evergreen forest with lower stature, biomass and diversity than the Northern Amazon forest (Balch et al., 2008, 2015). The climate is tropical humid, with average temperature varying between 24 to 26°C, a prolonged dry season (May to September), and annual precipitation is around 1,700 mm (Balch et al., 2008; Maracahipes-Santos et al., 2020; Rocha et al., 2013). The soils are Oxisols with a water table at 12 – 15 m depth (Balch et al., 2008).

The experimental burns were set in three adjacent forest plots (fire treatments) edging a soybean field, each one with 50 hectares (500 × 1000 m). The plots were subjected to different fire regimes: one plot was burned annually between 2004 and 2010 (except 2008; B1*yr*), one was burned triennially (2004, 2007, and 2010; B3*yr*), and a third was left unburned (Control; Figure S1). The burnings were initiated with kerosene drip torches at the end of each year's dry season (Balch et al., 2008). The intensity and severity of fires were greater in the B3*yr* plot than in the B1*yr* plot due to the higher fuel accumulation during the non-burning years (Balch et al., 2015). The fires increased the mortality of large trees, especially during drought years (2007 and 2010; Brando et al., 2014) and after a windstorm event in 2012 (Silvério et al., 2019). These combined disturbances caused in the burned plots a prominent reduction in canopy cover, above-ground biomass, abundance, and diversity of fruits and seeds in the seed rain and litter (Brando et al., 2014, 2024). Our plots were not replicated due to logistical, ethical, and financial constraints. However, several vegetation and microclimate metrics obtained before the experiment indicated no significant differences between the plots (Balch et al., 2008, 2013), which suggests that observed differences are associated with fire treatments.

2.3.2 Plant recruitment from tapir dung quantification

We collected 25 Kg of fresh tapir dung (~1 day old) from our study area and nearby forest fragments. We stored the dung in coolers with ice for a maximum of two days before the beginning of the experiment in February 2023 (which was a soybean harvest period). We took a sample of 18 Kg of homogenized dung for the experiments and seven kilograms to count the seed number per kilogram (adapted from Lugon et al., 2017).

To assess seed germination and seedling establishment promoted by tapirs, as well as the effects of dung beetles, we established six sampling points of 50 × 50 m within each fire treatment (Control, B1*yr*, and B3*yr*; N = 18), at least 150 m apart. At each sampling point, we established a block consisting of three regeneration parcels, one meter in diameter each and ten meters apart, from which we removed the litter layer to control the effects of the seed bank on regeneration. Each regeneration parcel received one of the following treatments: I) 500 g of tapir dung with free access for dung beetles (free dung beetle access regeneration treatment), II) 500 g of tapir dung excluding dung beetle (dung beetle exclusion regeneration treatment) and III) without dung addition (control regeneration treatment; Figure S2-A; Figure S3-S5). The experiment was monitored monthly from February until September 2023 (seven months) for counting seedlings growing within the regeneration parcels.

To prevent dung beetles from accessing the dung, we removed the bottoms of 10-liter buckets (28 cm in diameter) and buried them approximately 15 cm deep in the soil at the center of 18 regeneration parcels (one per sampling point, six per fire treatment). We deposited the dung inside these buckets, covered with a nylon net (0.08 × 0.08 mm), and applied a layer of Tanglefoot® around them. We removed the exclusion on the third day after setting up the experiment, when the dung was dry and had crusts around, to minimize its effects on dung beetle attraction. Dung beetle colonization reduces according to dung drying and crusting formation, probably due to reduced emissions of volatile compounds that attract dung beetles (Dormont et al., 2004; Gittings & Giller, 1998).

We replicated this experiment in September 2023 during the soybean fallow period in Mato Grosso state to assess seed germination and seedling establishment from tapirs' dung in the absence of soybean in the landscape. All procedures of feces collection, homogenization and storage were followed as in the previous experiment. However, we did not replicate the dung beetle exclusion experiment because the abundance and richness of these insects decrease significantly during the dry season in the Amazon (Correa et al., 2021; Noriega et al., 2021). We deposited the same amount of dung (500 g) in new regeneration parcels, ~5 m from regeneration parcels of the previous experiment, at the same sampling points. We counted the seedlings from this experiment in February 2024, five months later.

2.3.3 Dung beetle sampling

All experiments to assess the role of dung beetles were performed in January 2023, before the plant recruitment experiment, since adding dung in the sampling points could interfere with the dung beetle activity. We sampled dung beetles attracted by tapir dung in the same six points of the plant recruitment experiments in each fire treatment. The dung beetles were collected with three pitfall traps (15 cm in diameter each), arranged 5 m apart and baited with 100 g of fresh tapir dung (18 pitfall traps per fire treatment, 54 in the whole area). All pitfall traps were buried with ground-level openings, filled with approximately 250 ml of saline solution, and collected 48 h later (França et al., 2018; Figure S2-B; Figure S6). We sorted the beetles and weighed the dry biomass on a precision scale. The identification was made by a specialist (MSc. Glauco L. Martins) at the Laboratório de Sistemática e Biologia de Coleoptera, from Universidade Federal de Viçosa (UFV), MG, Brazil. All specimens are deposited in the Laboratório de Ecologia de Comunidades e Ecossistemas Tropicais (EcoTrop) collection at UFV, MG, Brazil.

We evaluated the dung beetle ecosystem functions – dung consumption and seed dispersal – at the same sampling points in all fire treatments (Control, B1*yr*, and B3*yr*; N = 18). At each sampling point, we removed the litter layer over the soil to set a one-meter-diameter mesocosm arena, fenced by a nylon net (~15 cm high) and fixed to the ground with bamboo sticks. At each arena, we deposited a sample of 200 g of homogenized fresh tapir dung mixed with 60 plastic beads (5 mm; Figure S2-B). To control for dung weight loss by drying, we set up 30 g of the same dung sample of tapirs suspended in a bag next to each arena to prevent dung beetle access (moisture control; Figure S2-B; Figure S7). We collected the remaining dung from the arenas and moisture control after 24 h, counted the remaining beads to estimate secondary seed dispersal, and weighed the feces on a precision scale to calculate the amount of dung consumed (Braga et al., 2013; França et al., 2018).

2.3.4 Quantification of seed predation from tapir dung

We quantified seed predation from tapir dung in February 2023. For this, we set pairs of treatments: one with 20 sunflower seeds (shelled and sterilized following Hargreaves et al., 2024) added to 50 g portions of homogenized fresh dung (seeds within dung treatment), and another with the same amount of seeds but without tapir dung (seeds outside dung treatment; Figure S2-C; Figure S8), totaling 320 seeds per treatment (adapted from Velez et al., 2016). We deposited one treatment pair (N = 18/treatment) directly onto the soil, 50 cm apart, at each sampling point of each fire treatment. We counted the remaining number of seeds after 24 h and classified the seeds' condition as: intact (without predation signals), and partially predated (with predation signals; e.g., teeth and mandible marks and/or broken seeds). We calculated seed removal by subtracting the number of seeds offered from the sum of intact and predated seeds found per sampling unit. While acknowledging that seeds removed from the ground and dung can sometimes be secondarily dispersed rather than predated (Falcon et al., 2024), we classified all missing seeds as predated in our study (following Hargreaves et al., 2024). This decision was based on two considerations: (1) the high probability of seed consumption following removal, with over 90% of removed seeds typically being eaten (Hulme, 1998) and (2) the lack of specific adaptations in our model species to facilitate secondary dispersal (e.g., elaiosomes or thick seed coats), making this outcome less likely (Vander Wall, 2010).

2.3.5 Quantification of soil microbial biomass and phosphorus and phosphorus content in seedlings

To evaluate the soil phosphorous content (SPC) and microbial biomass (SMB) after the tapir dung deposition in February 2023, we used decomposition tubes at all sampling points of the three fire treatments. The tubes were made with plastic containers (14 cm in diameter, 16.5 cm in height) perforated on the sides and bottom, allowing soil organisms and water passage. We buried three tubes per sampling point (~10 cm deep), two meters apart, triangularly, and filled them with the previously removed soil without a litter layer and topsoil. We added 200 g of tapir dung in each tube and collected one of three tubes after 7, 15, and 30 days of dung deposition (respectively: T_7, T_{15} and T_{30}; Figure S2-D; Figure S9-S10), discarding the soil's first layer in contact with dung (~1 cm). We control for the effects of dung addition by collecting a sample in the center of these triangular arrangements on the day of the experiment setup (T_0 samples; Figure S2-D). We included soil samples from the control and dung beetle exclusion regeneration parcels (treatments II and III, section 2.2) collected in September 2023, 230 days after the setup of the previous experiment. Each soil collection was considered a soil sampling event. These samples were collected at the center of regeneration parcels, excluding the litter layer and topsoil. All samples varied between one and two kilograms, depending on soil humidity, and were maintained frozen (-20°C) until analyses were carried out (Boone et al., 1999). Additionally, we collected all seedlings within the control and dung beetle exclusion regeneration parcels to quantify plant phosphorus content in September 2023.

For the soil microbial biomass and soil phosphorus content analyses, we thawed the samples at room temperature, homogenized, sieved (4 mm and 2 mm, respectively), and maintained them with controlled moisture at 60% of the maximum water holding capacity (Campos et al., 2015). We separated 100 g of each sample for microbial biomass and 300 g for phosphorus analysis. The whole seedlings were dried in an oven (60°C for 48 h), pulverized in a ball mill, weighed, and stored in microtubes.

We quantified the soil microbial biomass and the percentage of fungi in the sample using microbial biomass quantification kits (microBIOMETER®). The soil phosphorus content was quantified by extraction with hydrochloric acid and sulfuric acid (Mehlich-1 method; Mehlich 1953), and plant tissue samples by digestion with nitric and perchloric acids (Zarcinas et al., 1987). Both were quantified by colorimetry in Inductively Coupled Spectrometer (ICP; Mylavarapu et al., 2002).

2.3.6 Data analysis

We built generalized linear models (GLMs) to separately compare the abundances of seedlings in regeneration parcels across fire treatments in September 2023 and February 2024. We used seedling abundance as the response variable and forest plot as predictor variables in GLMs with a Poisson error distribution and a “quasi” correction for overdispersion. The seedling abundance in the regeneration parcels treatments with and without tapir dung addition was not used as a predictor variable because we only observed seedlings in the regeneration parcels with tapir dung addition in February 2024. Therefore, we compare the seedling abundance across regeneration parcel treatments with descriptive analysis. Additionally, we estimated the number of seedlings recruiting per hectare per year in unburned and burned plots. First, we estimated the number of seeds in 500 g of tapir dung (the dung quantity used in the regeneration experiments; see Section 2.2). Next, we used the average number of seedlings in the regeneration parcels as a proxy to calculate the number of seedlings recruited per the estimated number of seeds in 500 g of dung. Finally, we extrapolated this seedling recruitment rate to estimate how many seedlings would be expected from 4130 seeds dispersed by tapirs per hectare per year in the unburned plot, and from 13750 seeds, on average, in burned plots. The estimates of seeds dispersed by tapirs per hectare per year in the different forest plots were obtained from Paolucci et al. (2019) and corrected by adding 40%, as indicated by the authors.

We used GLMs to analyze the effects of dung beetle activity on seedling recruitment, with fire treatment as the predictor variable for all analyses. We combined data from the three pitfalls at each sampling point (sampling unit) to assess species richness, abundance, and biomass of dung beetles. We applied Poisson error distribution to analyze counting response variables (species richness, abundance, and number of seeds removed), using a “quasi” correction for models with overdispersion. We fitted models with continuous response variables (dung beetle biomass and dung removal) using Gaussian error distribution.

The number of predated seeds (response variable) was analyzed in relation to fire treatments and seed treatment (within/outside tapir dung; response variables) using generalized linear mixed models (GLMMs). Seed predation was quantified as the total of removed plus partially predated seeds. Seed treatment pair identity (within/outside dung) was included as a random factor. We employed Poisson errors for intact and predated seed models and Negative Binomial errors for seed removal analyses.

To assess the effects of fire treatments, tapir dung addition, and soil sampling events (predictor variables) on the total phosphorus content, total soil microbial biomass, proportion of fungi and bacteria in the soil (response variables), we used three GLMMs. For that, we fitted a GLMM for each response variable and included in each one, the sampling point identity and the weight of added dung were treated as random variables. The weight of dung was included because samples collected in February 2023 received 200 g of dung, whereas samples collected in September 2023 received 500 g. Finally, we used a GLMM to analyze the total phosphorus content in seedling samples (response variable) with tapir dung addition treatment and fire treatment as predictor variables. The random variables were the sampling point identity and the seedling dry mass used for acid digestion. All models were conducted with Gaussian error structure, except for the model of fungal proportion, where we used the Betabinomial distribution, and for the model of bacterial proportion, where we used Ordbeta distribution.

All analyses were performed using the R software (R Core Team, 2023). We used the glmmTMB package v1.1.9 (Brooks et al., 2017) to fit mixed models. We analyzed residuals to verify the distribution suitability and fit in all models. The differences between levels of fire treatments and time from the addition of dung and collection of soil were evaluated through pairwise contrast tests (Crawley, 2013).

2.4 Results

We did not find any seed in tapir dung during the first monitoring cycle, however, we counted 1581 seeds from seven kg of tapir dung used in the experiment during the fallow period (~113 seeds/500 g), belonging to five morphospecies. No seedlings emerged in any regeneration parcels during the first monitoring cycle (February-September 2023). However, we recorded a total of 33 seedlings from five morphospecies (1.83 ± 0.34; mean ± SE; Figure 1) by the end of the second cycle (September 2023 - February 2024), all within regeneration parcels with tapir dung addition. From these total, ten seedlings were recorded in B1*yr* (1.67 ± 0.49), 13 seedlings in B3*yr* (2.17 ± 0.60), and ten seedlings in Control (1.67 ± 0.76; Figure 1). We estimated that tapirs directly contribute to the recruitment of approximately 223 and 67 seedlings per ha/year across burned and unburned forests, respectively. Thus, tapir dung addition increased seedling abundance, which was consistent across fire treatments (*χ2* [2, N = 36] = 0.53, *P* = 0.76). The absence of seedlings in regeneration parcels without tapir dung addition precluded statistical comparison between dung addition treatments.

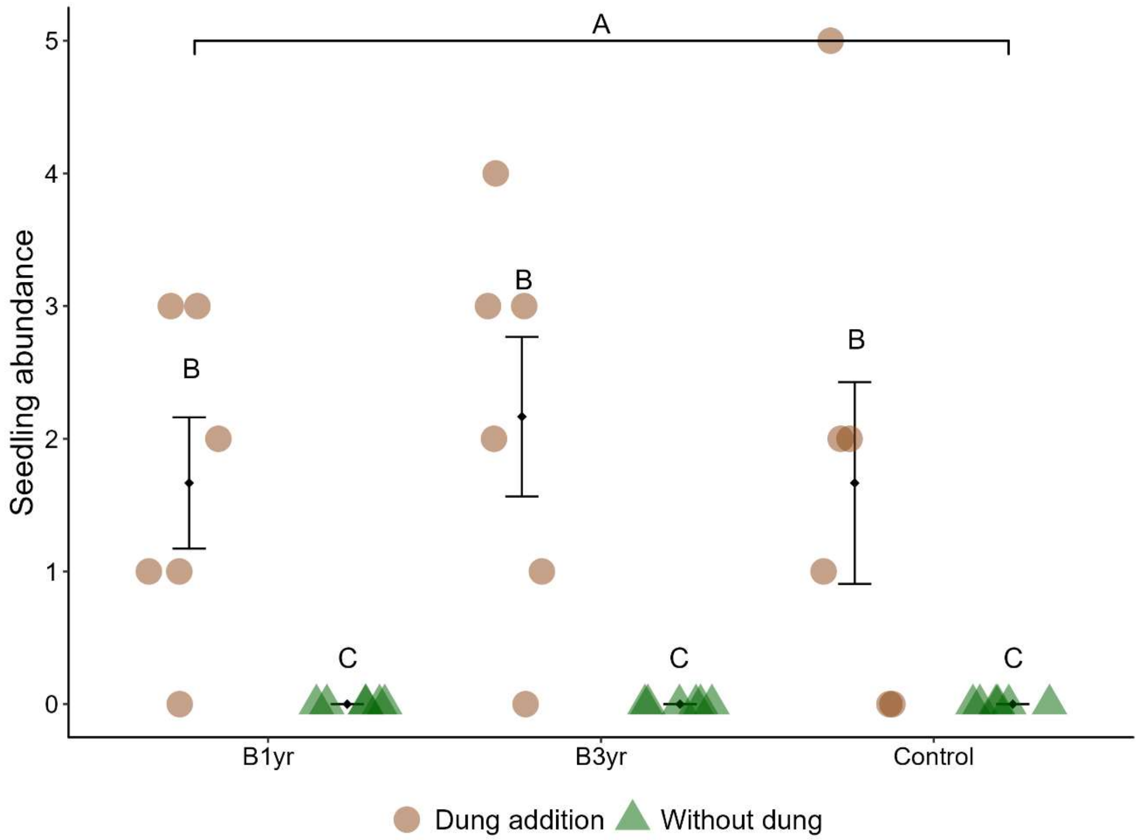

Figure 1. Seedling abundance in one-meter diameter regeneration parcels with (1.83 ± 0.34; mean ± SE) and without (0.00 ± 0.00) tapir dung addition in the southeastern Amazon forest (B1yr = annually burned; B3yr = triennially burned; Control = unburned). The black dots represent the mean, and the bars represent the SE.

We sampled 68 individuals of dung beetles belonging to four genera (*Dichotomius* spp., *Eurysternus* spp., *Canthon* spp. and *Deltochilum* spp.; Table S1) and 15 morphospecies across all plots. Species richness, abundance, and biomass did not differ among fire treatments (richness: $F_{1,16}$ = 2.53, *P* = 0.13; abundance: $F_{1,16}$ = 0.99, *P* = 0.33; biomass: $F_{1,16}$ = 0.007, *P* = 0.93; Figure 2 A-C). Ecosystem functions provided by dung beetles also did not differ between fire treatments (secondary seed dispersal: $F_{1,16}$ = 0.11, *P* = 0.74; dung removal: $F_{1,14}$ = 1.69, P = 0.21; Figure 2 D-E).

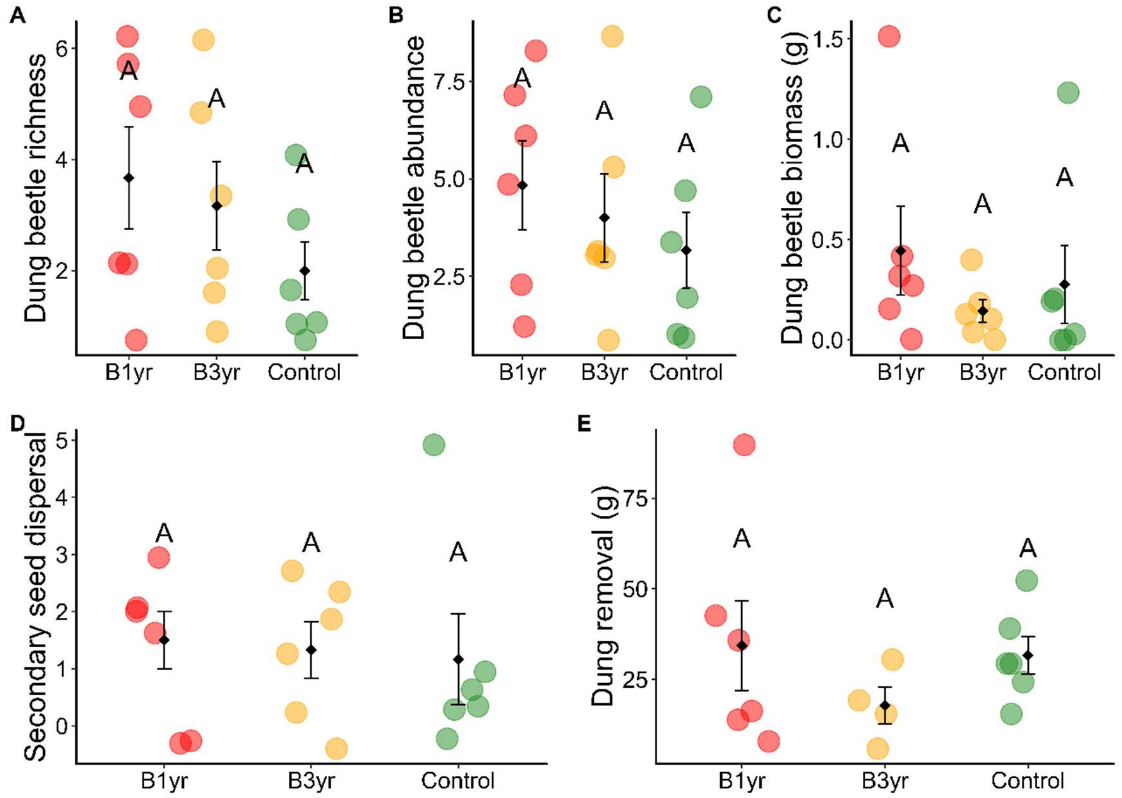

Figure 2. Variation in dung beetle community metrics and ecosystem functions in southeastern Amazon forest (B1yr = annually burned; B3yr = triennially burned; Control = unburned). (**A**) species richness (Control: 1.67 ± 0.66; B3yr: 3.00 ± 0.89; B1yr: 3.50 ± 1.02; mean ± SE), (**B**) abundance (Control: 2.83 ± 1.14; B3yr: 3.83 ± 1.22; B1yr: 4.67 ± 1.26), (**C**) biomass (g) (Control: 0.27 ± 0.19; B3yr: 0.14 ± 0.05; B1yr: 0.44 ± 0.22), (**D**) number of mimetics seeds secondary dispersed (Control: 1.16 ± 0.79; B3yr: 1.50 ± 0.50; B1yr: 1.33 ± 0.49) and (**E**) tapir dung removal (g) (Control: 31.63 ± 5.18; B3yr: 17.78 ± 5.08; B1yr: 34.36 ± 12.35). The bars represent the SE; the letters indicate significant differences between the parcels at alfa = 5%.

From a total of 360 seeds per treatment, we observed 68.90% more predation of seeds located outside dungs (19.61 ± 0.38; N = 353) compared to seeds within dungs (11.61 ± 1.41; N = 209; $\chi 2$ [1, N = 36] = 25.35, *P* = < 0.001). This higher seed predation outside dungs was consistent across all fire treatments ($\chi 2$ [2, N = 36] = 0.44, *P* = 0.80; **Erro! Fonte de referência não encontrada.**). From the remaining seeds sampled outside dung, we recorded only four predated and three intact seeds in two replicates, so the mean values and deviations were not calculated. From the remaining seeds within dung, we recorded 53 predated (2.94 ± 0.53) and 98 intact seeds (5.44 ± 2.11).

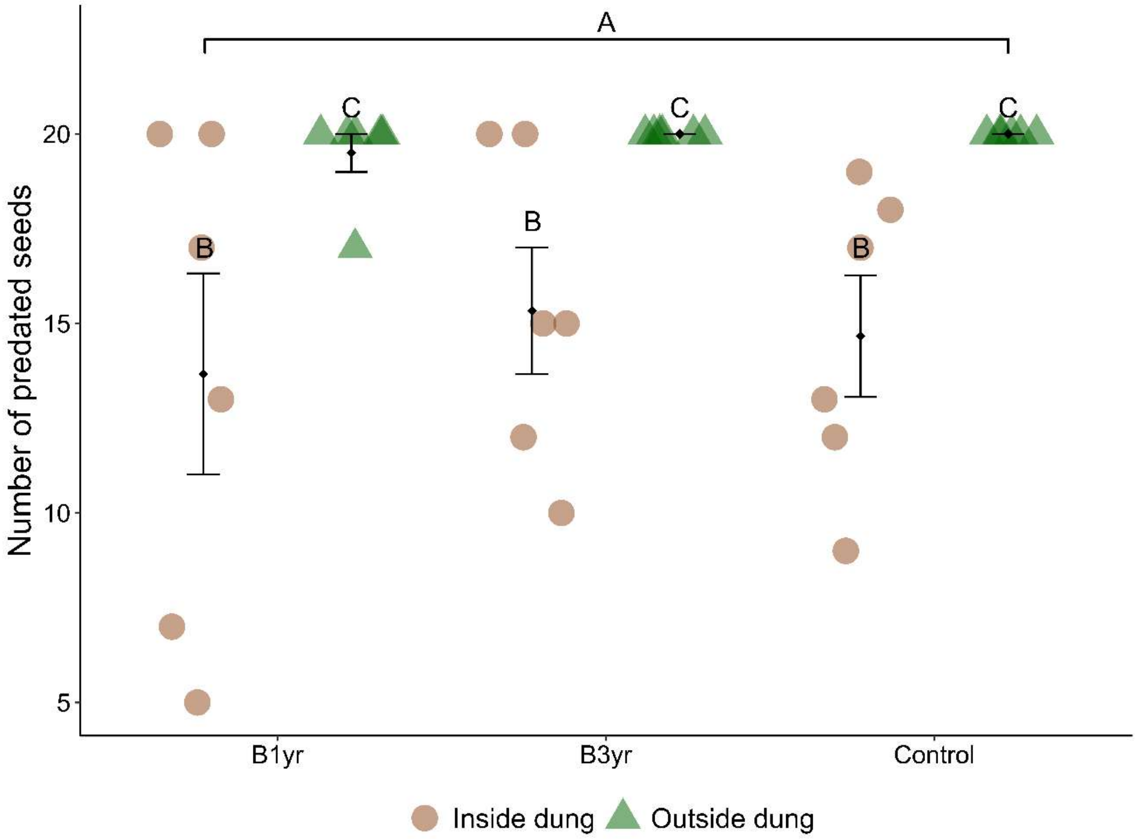

Figure 3. Variation among the number of removed seeds located within (11.61 ± 1.41; mean ± SE) and outside (19.61 ± 0.38; mean ± SE) of tapir dung in the southeastern Amazon forest (B1yr = annually burned; B3yr = triennially burned; Control = unburned). The bars represent the SE; the letters indicate significant differences between the parcels at alfa = 5%.

Soils with tapir dung addition had ~60% more total microbial biomass and a proportion of fungi 109% higher (205 ± 11.2; 0.23 ± 0.015 µg C/g, respectively) than treatments without dung addition (120 ± 15.7 µg C/g; 0.11 ± 0.02, respectively; total microbial biomass: $\chi 2$ [1, N = 80] = 18.82, $P < 0.0001$; fungi proportion: $\chi 2$ [1, N = 80] = 9.55, $P = 0.001$; Figure 4 A-B). The proportion of bacteria was 17% lower in treatments with dung addition (0.77 ± 0.015 µg C/g) compared to treatments without dung addition (0.89 ± 0.02 µg C/g; $\chi 2$ [1, N = 80] = 9.87, $P = 0.001$). However, total microbial biomass, fungi and bacteria proportions did not differ across fire treatments (microbial biomass: $\chi 2$ [2, N = 80] = 2.16, $P = 0.33$; fungi proportion: $\chi 2$ [2, N = 80] = 1.71, $P = 0.42$; bacteria proportion: $\chi 2$ [2, N = 80] = 1.71, $P = 0.42$), and with time since dung deposition (microbial biomass: $\chi2$ [4, N = 80] = 0.11, P = 0.13; fungi proportion: $\chi2$ [4, N = 80] = 8.20, P = 0.08; bacteria proportion: $\chi2$ [4, N = 80] = 7.84, P = 0.09).

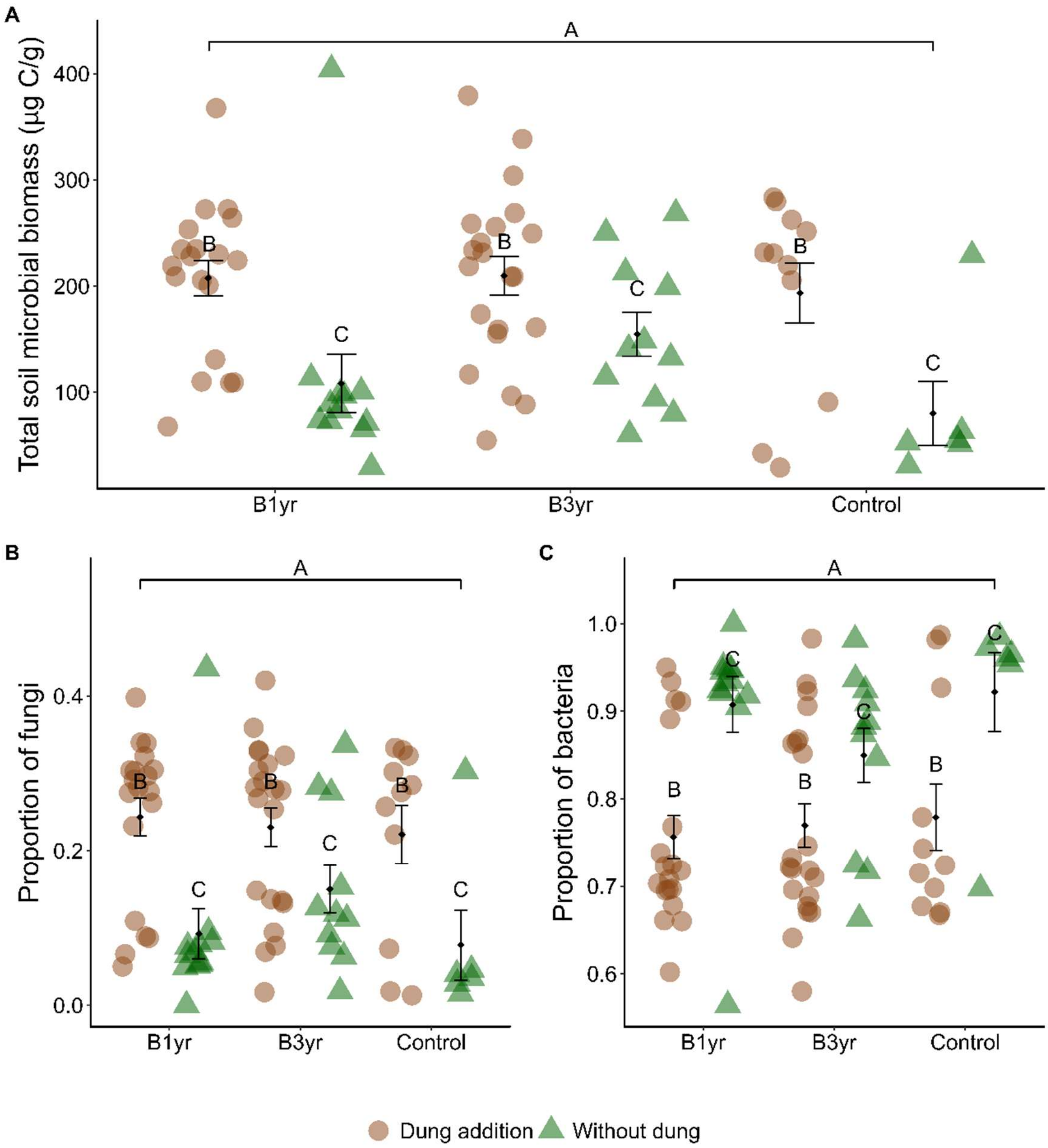

Figure 4. Variation in (**A**) total soil microbial biomass expressed in micrograms (µg) of microbial carbon per gram of soil (tapir dung addition: 205 ± 11.2 µg C/g; and without tapir dung addition: 120 ± 15.7 µg C/g; mean ± SE), (**B**) proportion of fungi in the soil with and without tapir dung addition (tapir dung addition: 0.23 ± 0.015; and without tapir dung: 0.11 ± 0.02) (**C**) proportion of bacteria in the soil with and without tapir dung addition (tapir dung addition: 0.77 ± 0.015; and without tapir dung: 0.89 ± 0.02 %) in the southeastern Amazon forest (B1yr = annually burned; B3yr = triennially burned; Control = unburned). The bars represent the SE; the letters indicate significant differences between the parcels at alfa = 5%.

Tapir dung addition increased total soil phosphorus content ($\chi2$ [1, N = 81] = 16.81, P < 0.001;

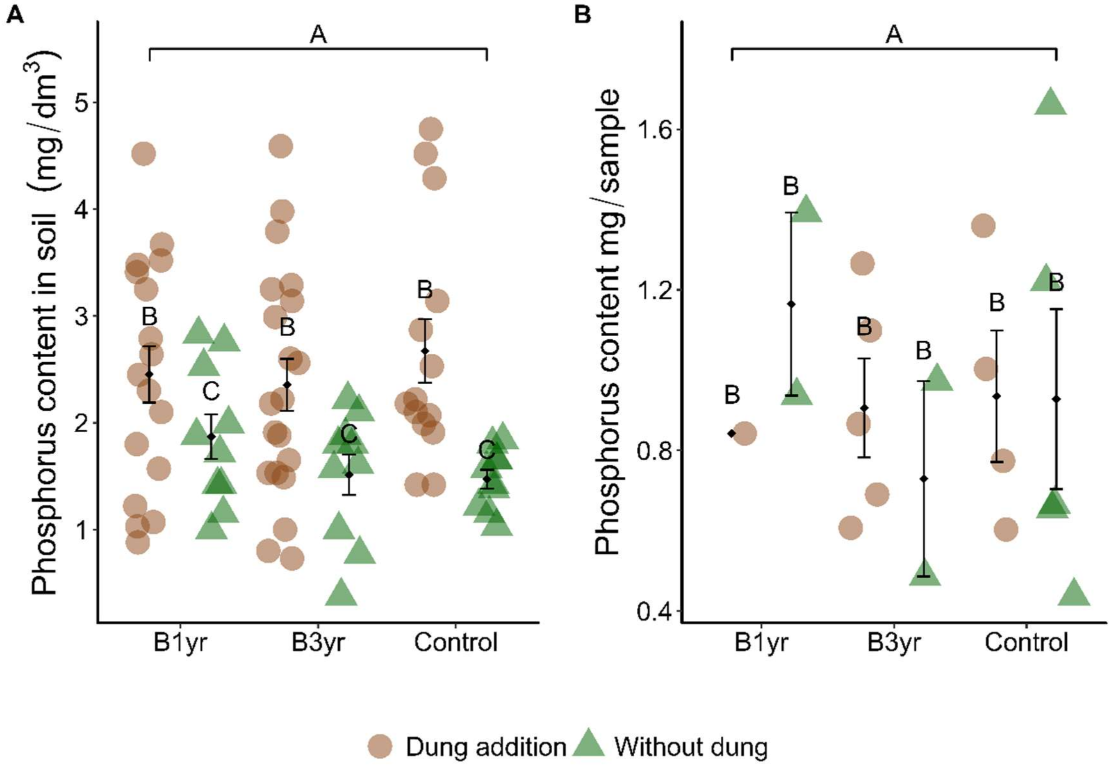

Figure ***5*** A), with an average increase of 30% per cubic decimeter (dm³) of soil compared to the treatment without dung addition (2.63 ± 0.18 mg P/dm³ vs. 1.88 ± 0.20 mg P/dm³, respectively). Neither fire treatment ($\chi2$ [2, N = 81] = 0.67, P = 0.71) nor time since tapir dung deposition ($\chi2$ [4, N = 81] = 2.65, P = 0.61) affected soil phosphorus content.

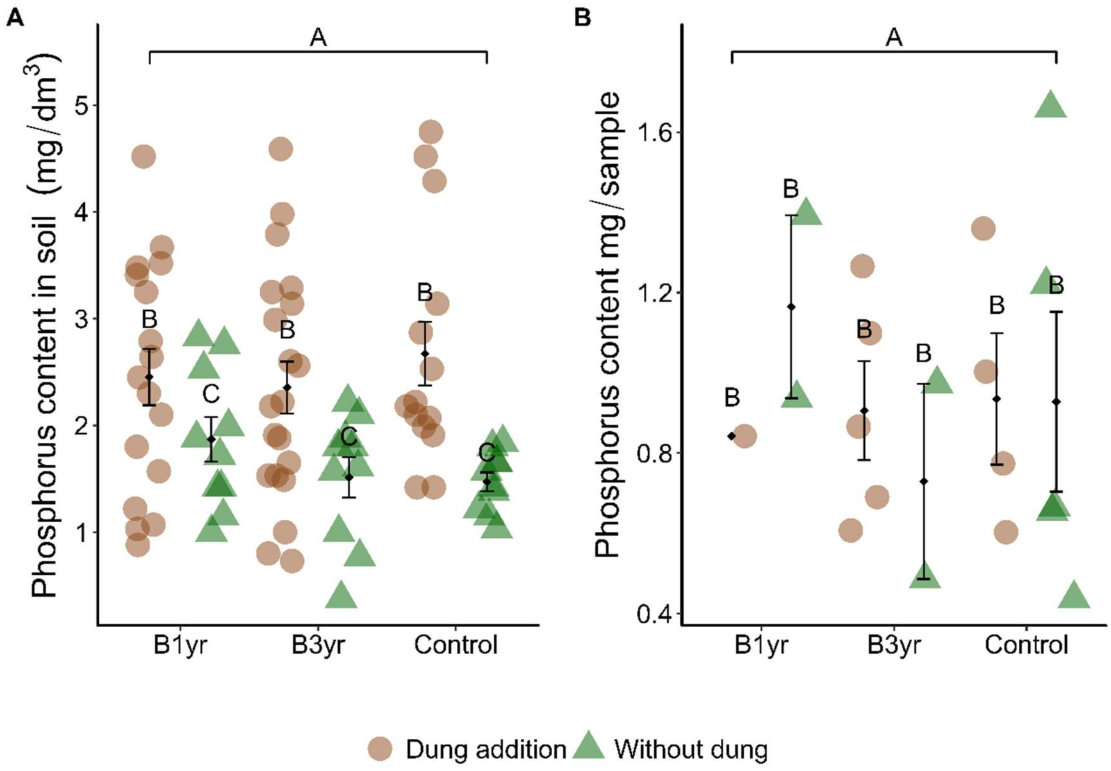

Figure 5. Variation in phosphorus content among treatments with and without tapir dung addition in southeastern Amazon forest (B1yr = annually burned; B3yr = triennially burned; Control = unburned). **A.** Total phosphorus content in the soil in milligrams per decimeter cubic (dm^3) (Tapir dung addition: 2.63 ± 0.18; Without tapir dung addition: 1.88 ± 0.20), and **B.** Total phosphorus content in seedling tissues (Tapir dung addition: 0.91 ± 0.08; Without tapir dung: 0.94 ± 0.14). The bars represent the SE, and the letters indicate significant differences between the parcels at α = 5%.

Finally, by the end of first monitoring cycle (February-September 2023), we collected 111 seedlings from 19 regeneration parcels – 45 from ten parcels with tapir dung addition (seedlings/parcel: 4.50 ± 2.32; seedling dry mass: 0.12 ± 0.01 mg) and 66 from nine parcels without tapir dung addition (seedlings/parcel: 7.33 ± 2.44; seedling dry mass: 0.12 ± 0.01 mg). As we did not find seeds in the dung used to set up the experiment, these seedlings probably came from other dispersal agents or resprout. Neither tapir dung addition ($\chi 2$ [1, N = 18] = 0.18, *P* = 0.66;

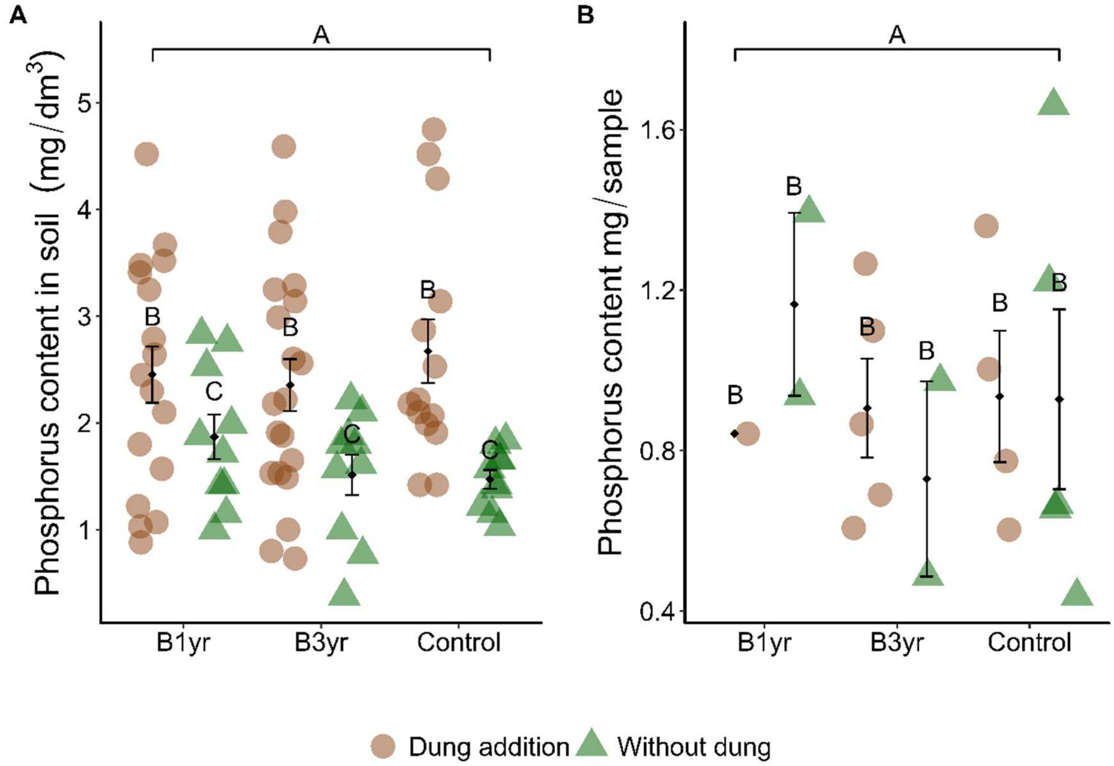

Figure **5**B) nor fire treatment ($\chi 2$ [2, N = 18] = 0.49, *P* = 0.77) affected phosphorus content in seedling tissues.

2.5 Discussion

Our study quantified the role of tapirs in promoting plant recruitment across Amazonian forests, according to seasonal changes in the availability of local food resources. In our study area, tapirs frequently have access to abundant non-native food resources like soybean and corn in our study area. During the soybean cultivation period, tapir dung contained mainly soybean stems and leaves, which prevented the recruitment of native forest species. However, when there was no soybean cultivation, we found 1581 native seeds in the dung, resulting in the recruitment of 33 seedlings. From these results, we extrapolate a potential recruitment of 223 and 67 seedlings per hectare in burned and unburned forests, respectively. The high abundance of seedlings germinating from tapirs dung suggests that tapirs provide seeds and favorable conditions for plant recruitment – as the increase of microbial biomass by 60%, of fungi in the soil by 109%, and of nutritional soil content by 30%. Furthermore, as forest degradation did not affect seedling recruitment from tapir dung, it seems that plant recruitment from tapir dung is contingent on the availability of native seeds in the dung, which in turn depends on crop availability in the landscape. Given that tapirs may deposit approximately three times more seeds in disturbed forests than undisturbed forests (Paolucci et al., 2019), seedling recruitment from tapirs dung is expected to be three times higher across disturbed forests.

Seedling recruitment from tapirs dung was not potentialized by dung beetle activity neither in disturbed nor in undisturbed forests. As dung beetle exclusion experiments were only conducted when soybean plantations were available, the scarcity of forest seeds and the predominance of soybean parts in tapir dung may have flattened the effects of dung beetle on seedling recruitment. Additionally, dung beetle diversity (species richness, abundance and biomass) and functions (secondary seed dispersal and dung removal) were not affected by forest degradation, indicating similar ecosystem functionality across disturbed and undisturbed forests (but see Andrade et al., 2014). Compared to other studies in the Amazon (Braga et al., 2013; França et al., 2020; Ribeiro et al., 2024), we recorded lower dung beetle diversity and ecosystem functions. This difference may be attributed to the baits we used – tapir's dung, as we were interested in the roles of tapirs in plant recruitment – contrasting with previous studies that used omnivore dung, which is a more attractive resource for dung beetles (Bogoni & Hernández, 2014; Gigliotti et al., 2023). However, as dung beetle activity is positively affected by the local dung amount and dung density in an area (Andresen, 2001, 2002), the large amount of dung deposited by tapirs across disturbed forests could offset its lower attractiveness (Lugon et al., 2017). In our study, we standardized dung amounts used in the experiments and did not directly assess the effects of dung densities on dung beetle activity. Nevertheless, given the comparable dung beetle activity between forests we observed, it is plausible that high dung densities in areas like tapir latrines and disturbed forests could amplify the effects of dung beetles on seedling recruitment (Lugon et al., 2017).

The limited secondary seed dispersal and dung removal we observed across all forest plots suggest that seeds within dung clumps may undergo reduced manipulation after tapirs' primary dispersal. This is reinforced by the higher number of remaining seeds found within tapir dung compared to seeds found outside dung, regardless of the forest plots. Tapir dung reduces the rates of seed predation and, indirectly, increases the rates of seed germination, because the vegetable fibers in dung form a mechanical barrier that may prevent seed predators from accessing seeds (Fragoso, 1997; Quiroga-Castro & Roldán, 2001). Viable seeds within dung clumps may remain aggregated and still susceptible to mortality due to density-dependent factors (competition with siblings and herbivory; Howe, 1989). However, we observed differential seed predation depending on the seeds' location in the dung clumps. Most remaining seeds were in the inner part of clumps, while a few remaining seeds were in the outer portion (J. E. Falcon, pers. obs.). This seed predation pattern reduces seed densities in the dung clumps, may alleviate seed mortality through density-dependent factors (Hulme, 1998), and benefits the plant recruitment of seeds from dung clumps.

Remaining seeds in tapir's dung can establish in a nutrient-rich microhabitat, as we found tapirs dung enriched phosphorus content in the soil. Herbivore’s dung, such as tapir’s, are rich in recalcitrant compounds (e.g. lignin and cellulose; Holter, 2016; Jastrow et al., 2007), which are decomposed mainly by fungi in the soil (Sitters et al., 2014; Wang et al., 2023). The higher fungi biomass in the soil due to tapirs dung we found likely enhanced organic matter decomposition and nutrients release, as phosphorus (Bardgett et al., 1998; Bardgett & Wardle, 2003; Wang et al., 2023). The carbon:phosphorus (C:P) ratio in herbivores dung is low (Sitters et al., 2014; Valdés-Correcher et al., 2019); under such conditions, microbiota immobilizes phosphorus directly in the organic matter during decomposition, leaving the mineralized nutrient available in the soil (Enwezor, 1976). Despite tapirs dung increased phosphorus content in the soil, phosphorus content in plant tissues was similar across seedlings growing next to and outside dungs. Phosphorus diffuses in the soil only a few micrometers from its origin (Keyes et al., 2013). As we sampled seedlings up to 50 cm from the dung clumps, only seedlings on dung clumps or with developed radicular system may have accessed this nutrient (McGrath et al., 2001). Hence, the higher soil phosphorus content available from tapir dung probably contributed for the higher local plant recruitment and growth we observed.

The net primary productivity (NPP) of the Amazon forest, especially along its borders with the Cerrado, is highly limited by phosphorus (Dionizio et al., 2018;

Vitousek, 1984), but soils with a major fraction of phosphorus promote higher NPP (Dionizio et al., 2018; Mercado et al., 2011; Quesada et al., 2010, 2012). For example, artificial fertilizations in the Central Amazon found that NPP increased 15,6% after two years of phosphorus supplementation (Cunha et al., 2022). Because tapirs commonly defecate in latrines and, at least in our study region, three times more in disturbed forests (Paolucci et al., 2019), the phosphorus distribution is probably heterogeneous, forming soil nutritional hotspots. Since plant diversity and density are positively related to nutritional soil conditions (S. Albert et al., 2020; Vourlitis et al., 2013), these hotspots may act synergistically with the increase of propagule apport to form a core of recruitment and major NPP in the landscapes. This reinforces the dual role of large herbivores in nutrient cycling and promoting NPP: one at local scales, within forest patches where they preferentially forage and defecate; another at the landscape scale, reducing spatial variability in soil nutrients due to their extensive home ranges and high mobility (Villar et al., 2021). Furthermore, the nutritional composition of herbivore dung varies according to food resource (Chaudhary et al., 2020). Considering that tapirs in our study area feed on artificially fertilized plantations at least during parts of the year, the effect of their behavior as soil fertilizers is likely variable over time. Future investigations could focus on exploring this relationship.

The roles of tapirs in the regeneration of disturbed tropical rainforests immersed in an agricultural landscape are multiple and partially associated with food resource availability. Tapirs were effective seed dispersers of native forest species and promoted plant recruitment only when exogenous food resources (soybean crops) were absent in the landscape. Additionally, we only observed plant recruitment under dung addition, which reinforces the role of tapirs in overcoming seed dispersal limitations. Furthermore, seeds within tapirs dung were more protected and experienced lower predation rates than seeds outside the dung. These seeds can develop and recruit under improved soil nutrient conditions, since the tapirs acted as forest fertilizers, enhancing soil nutritional conditions through their dung. Therefore, in the face of the ongoing global biodiversity crisis, where large vertebrates face elevated extinction risks (Dirzo et al., 2014), tapirs emerge as a potentially cost-effective agent of forest recovery.

Tapirs not only dispersed seeds but also decreased filters of plant recruitment – i.e., their dung decreased seed predation and increased soil nutrients, making them a valuable asset in restoration efforts. Their crucial roles in forest restoration are increasingly recognized, particularly within the context of the UN Decade on Ecosystem Restoration (United Nations, 2019), which emphasizes the urgency of restoring degraded ecosystems for biodiversity conservation.

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2.7 Apêndice A

Tapir dung boosts natural regeneration and soil enrichment of Amazonian forests

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2.7.1 Supplementary information

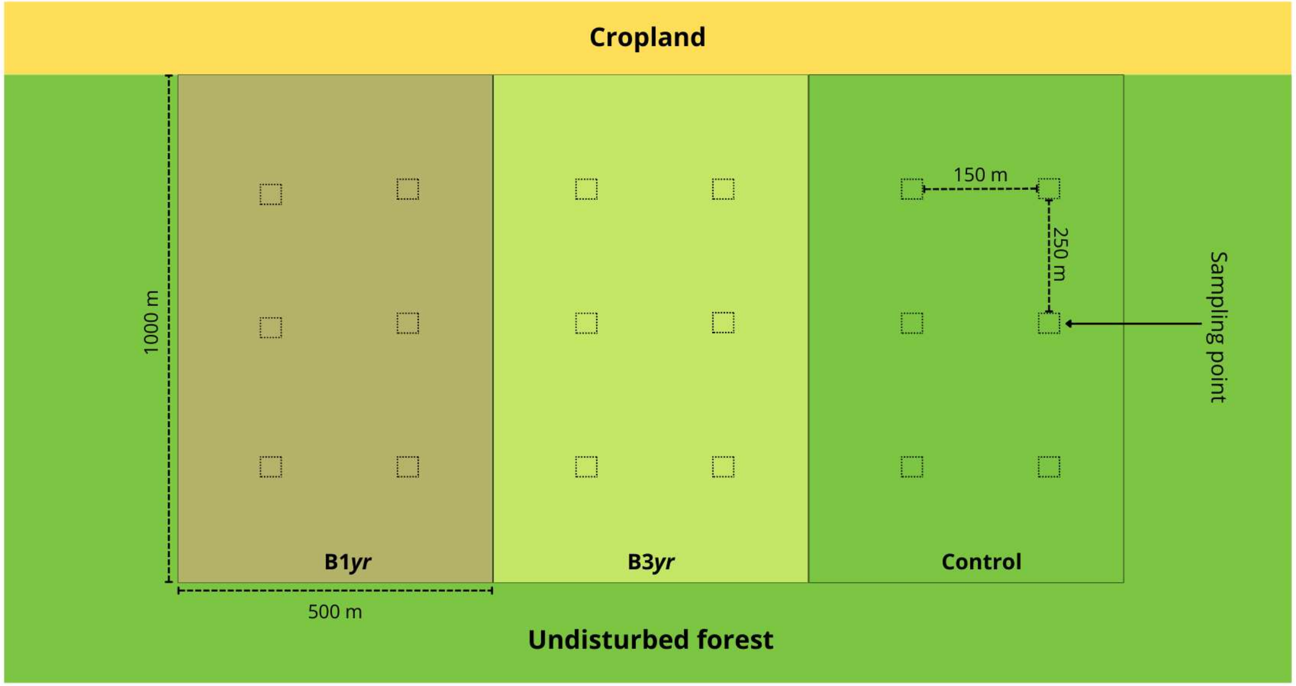

FIGURE S1. The study area is located at Tanguro Field Station (state of Mato Grosso, Brazil; 13°04’S, 52°23’’W), southeastern Amazon basin, in a transitional zone between the Cerrado (tropical savanna) and Amazon (tropical rainforest) biomes. The diagram represents the three forest treatments submitted to different fire regimes between 2004 and 2010, with the B1*yr* treatment submitted to one fire event per year (except 2008), the B3*yr* treatment submitted to one fire event every three years, and the unburned control treatment. All treatments have an area of 50 hectares and exact dimensions (500 x 1000 m). The experiments were conducted within each sampling point (50 x 50 m), represented by the squares distributed by each fire treatment. The diagram is not shown on a realistic scale.

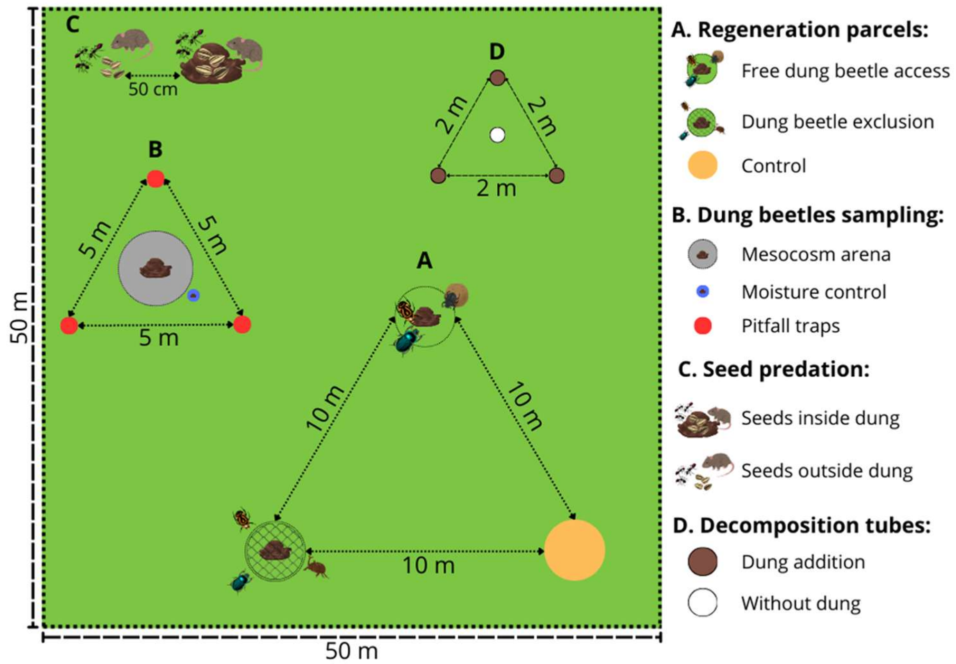

FIGURE S2. All experiments were performed in a replicate of a sampling point (N = 18 sampling points) located at Tanguro Field Station (state of Mato Grosso, Brazil; 13°04'S, 52°23''W), southeastern Amazon basin; the arrangement of experiments varied along the sampling points. **A. Regeneration parcels**: 1-m diameter parcels that were established treatments of tapir dung addition to measuring the plant recruitment with free dung beetle access, with dung beetle exclusion and without dung addition (control). **B. Dung beetle sampling**: two experiments were performed to sample dung beetle richness and abundance using pitfall traps and dung beetle ecosystem functions (secondary seed dispersal and dung removal) using mesocosm arenas. These experiments were conducted on different days at the exact location of sampling points. **C. Seed predation**: paired experiment used to measure the predation of seeds inside and outside tapir dung. **D. Decomposition tubes**: 14-cm diameter decomposition tubes used to measure the soil's microbial biomass and phosphorus content beneath 200 g of dung addition. The white dot represents the T_0 samples, samples collected at the beginning of the experiment as control samples; the brown dots represent T_7, T_{15}, and T_{30}, samples collected after seven, 15 and 30 days after dung addition. The diagram is not shown on a realistic scale.

Figure S3. Regeneration parcel with free access to dung beetles.

Figure S4. Regeneration parcel with dung beetle exclusion.

Figure S5. Control regeneration parcel, without tapir dung addition.

Figure S6. Pitfall trap baited with tapir dung.

Figure S7. Mesocosm arena used to measure dung beetle ecosystem functions (secondary seed dispersal and dung removal).

Figure S8. The paired experiment was used to measure seed predation inside tapir dung (red arrow) and outside tapir dung (yellow arrow).

Figure S9. Decomposition tube installation.

Figure S10. Arrangement of installed decomposition tubes.

Table S1. Dung beetle species collected in Tanguro Field Station (state of Mato Grosso, Brazil; 13°04'S, 52°23''W), southeastern Amazon basin. Dung beetles were collected using the pitfall trap method (N = 54 pitfalls; 18/fire treatment). Each pitfall was baited with 100 g of tapir dung in February 2023 and collected after 48 hours of exposition at the field. **Fire treatment** – Fire treatment that forest plot was applied: Control = unburned forest; B1*yr* = annual fires; B3*yr* = triannual fires.

Fire treatment	Sampling point	Fuse	Coordinate X	Coordinate Y	Family	Subfamily	Species	Biomass (mg)
Control	p1	22	350677	8553737	Scarabaeidae	Scarabaeinae	*Dichotomius* sp. 7	24
Control	p1	22	350677	8553737	Scarabaeidae	Scarabaeinae	*Dichotomius* sp. 7	3
Control	k5	22	350476	8553736	Scarabaeidae	Scarabaeinae	Dichotomius sp. 6	12
Control	k5	22	350476	8553736	Scarabaeidae	Scarabaeinae	Dichotomius sp. 7	7
Control	k5	22	350476	8553736	Scarabaeidae	Scarabaeinae	*Eurysternus* sp. 2	21
Control	k5	22	350476	8553736	Scarabaeidae	Scarabaeinae	*Eurysternus* sp. 2	37
Control	k5	22	350476	8553736	Scarabaeidae	Scarabaeinae	*Eurysternus* sp. 2	40
Control	k5	22	350476	8553736	Scarabaeidae	Scarabaeinae	*Eurysternus* sp. 2	38
Control	k5	22	350476	8553736	Scarabaeidae	Scarabaeinae	*Eurysternus* sp. 1	37
Control	f5	22	350478	8553994	Scarabaeidae	Scarabaeinae	*Dichotomius* sp. 1	62
Control	f5	22	350478	8553994	Scarabaeidae	Scarabaeinae	*Dichotomius* sp. 1	82
Control	f5	22	350478	8553994	Scarabaeidae	Scarabaeinae	*Dichotomius* sp. 3	1088
Control	p5	22	350532	8553491	Scarabaeidae	Scarabaeinae	*Dichotomius* sp. 6	9
Control	p5	22	350532	8553491	Scarabaeidae	Scarabaeinae	*Dichotomius* sp. 6	12
Control	p5	22	350532	8553491	Scarabaeidae	Scarabaeinae	*Dichotomius* sp. 1	39

Fire treatment	Sampling point	Fuse	Coordinate X	Coordinate Y	Family	Subfamily	Species	Biomass (mg)
Control	p5	22	350532	8553491	Scarabaeidae	Scarabaeinae	*Eurysternus* sp. 2	38
Control	p5	22	350532	8553491	Scarabaeidae	Scarabaeinae	*Dichotomius* sp. 1	106
B1*yr*	k26	22	349444	8553723	Scarabaeidae	Scarabaeinae	*Dichotomius* sp. 6	11
B1*yr*	k26	22	349444	8553723	Scarabaeidae	Scarabaeinae	*Dichotomius* sp. 6	11
B1*yr*	k26	22	349444	8553723	Scarabaeidae	Scarabaeinae	*Eurysternus* sp. 1	55
B1*yr*	k26	22	349444	8553723	Scarabaeidae	Scarabaeinae	*Dichotomius* sp. 1	30
B1*yr*	k26	22	349444	8553723	Scarabaeidae	Scarabaeinae	*Deltochilum* sp. 2	807
B1*yr*	k26	22	349444	8553723	Scarabaeidae	Scarabaeinae	*Deltochilum* sp. 1	238
B1*yr*	k26	22	349444	8553723	Scarabaeidae	Scarabaeinae	*Dichotomius* sp. 4	360
B1*yr*	p22	22	349613	8553464	Scarabaeidae	Scarabaeinae	*Dichotomius* sp. 6	13
B1*yr*	p22	22	349613	8553464	Scarabaeidae	Scarabaeinae	*Dichotomius* sp. 6	11
B1*yr*	p22	22	349613	8553464	Scarabaeidae	Scarabaeinae	*Dichotomius* sp. 6	11
B1*yr*	p22	22	349613	8553464	Scarabaeidae	Scarabaeinae	*Dichotomius* sp. 6	10
B1*yr*	p22	22	349613	8553464	Scarabaeidae	Scarabaeinae	*Dichotomius* sp. 2	371
B1*yr*	f22	22	349604	8553980	Scarabaeidae	Scarabaeinae	*Dichotomius* sp. 7	5
B1*yr*	f22	22	349604	8553980	Scarabaeidae	Scarabaeinae	*Canthon* sp. 1	17
B1*yr*	f22	22	349604	8553980	Scarabaeidae	Scarabaeinae	*Dichotomius* sp. 5	34
B1*yr*	f22	22	349604	8553980	Scarabaeidae	Scarabaeinae	*Dichotomius* sp. 1	63
B1*yr*	f22	22	349604	8553980	Scarabaeidae	Scarabaeinae	*Eurysternus* sp. 1	60

Fire treatment	Sampling point	Fuse	Coordinate X	Coordinate Y	Family	Subfamily	Species	Biomass (mg)
B1*yr*	f22	22	349604	8553980	Scarabaeidae	Scarabaeinae	*Dichotomius* sp. 8	13
B1*yr*	f22	22	349604	8553980	Scarabaeidae	Scarabaeinae	*Dichotomius* sp. 1	21
B1*yr*	f22	22	349604	8553980	Scarabaeidae	Scarabaeinae	*Eurysternus* sp. 1	105
B1*yr*	p26	22	349425	8553460	Scarabaeidae	Scarabaeinae	*Dichotomius* sp. 6	4
B1*yr*	p26	22	349425	8553460	Scarabaeidae	Scarabaeinae	*Dichotomius* sp. 6	13
B1*yr*	p26	22	349425	8553460	Scarabaeidae	Scarabaeinae	*Deltochilum* sp. 1	174
B1*yr*	p26	22	349425	8553460	Scarabaeidae	Scarabaeinae	*Dichotomius* sp. 7	15
B1*yr*	p26	22	349425	8553460	Scarabaeidae	Scarabaeinae	*Dichotomius* sp. 1	30
B1*yr*	p26	22	349425	8553460	Scarabaeidae	Scarabaeinae	*Eurysternus* sp. 2	37
B1*yr*	k22	22	349613	8553723	Scarabaeidae	Scarabaeinae	*Dichotomius* sp. 1	75
B1*yr*	k22	22	349613	8553723	Scarabaeidae	Scarabaeinae	*Eurysternus* sp. 1	79
B3*yr*	p15	22	349978	8553468	Scarabaeidae	Scarabaeinae	*Dichotomius* sp. 6	9
B3*yr*	p15	22	349978	8553468	Scarabaeidae	Scarabaeinae	*Dichotomius* sp. 7	1
B3*yr*	p15	22	349978	8553468	Scarabaeidae	Scarabaeinae	*Canthon* sp. 2	4
B3*yr*	p15	22	349978	8553468	Scarabaeidae	Scarabaeinae	*Dichotomius* sp. 7	16
B3*yr*	p15	22	349978	8553468	Scarabaeidae	Scarabaeinae	*Canthon* sp. 1	14
B3*yr*	p15	22	349978	8553468	Scarabaeidae	Scarabaeinae	Dichotomius sp. 6	17
B3*yr*	p15	22	349978	8553468	Scarabaeidae	Scarabaeinae	*Eurysternus* sp. 2	31
B3*yr*	p15	22	349978	8553468	Scarabaeidae	Scarabaeinae	*Eurysternus* sp. 2	27

Fire treatment	Sampling point	Fuse	Coordinate X	Coordinate Y	Family	Subfamily	Species	Biomass (mg)
B3*yr*	p15	22	349978	8553468	Scarabaeidae	Scarabaeinae	*Eurysternus* sp. 1	66
B3*yr*	k19	22	349798	8553724	Scarabaeidae	Scarabaeinae	*Dichotomius* sp. 6	13
B3*yr*	k19	22	349798	8553724	Scarabaeidae	Scarabaeinae	*Dichotomius* sp. 6	10
B3*yr*	k19	22	349798	8553724	Scarabaeidae	Scarabaeinae	*Eurysternus* sp. 1	82
B3*yr*	f15	22	349973	8553978	Scarabaeidae	Scarabaeinae	*Dichotomius* sp. 6	6
B3*yr*	f15	22	349973	8553978	Scarabaeidae	Scarabaeinae	*Dichotomius* sp. 7	27
B3*yr*	f15	22	349973	8553978	Scarabaeidae	Scarabaeinae	*Dichotomius* sp. 6	8
B3*yr*	p19	22	349810	8553468	Scarabaeidae	Scarabaeinae	*Deltochilum* sp. 1	247
B3*yr*	p19	22	349810	8553468	Scarabaeidae	Scarabaeinae	*Dichotomius* sp. 1	34
B3*yr*	p19	22	349810	8553468	Scarabaeidae	Scarabaeinae	*Eurysternus* sp. 1	11
B3*yr*	p19	22	349810	8553468	Scarabaeidae	Scarabaeinae	*Dichotomius* sp. 7	5
B3*yr*	p19	22	349810	8553468	Scarabaeidae	Scarabaeinae	*Dichotomius* sp. 8	103
B3*yr*	k15	22	349985	8553730	Scarabaeidae	Scarabaeinae	*Dichotomius* sp. 8	11
B3*yr*	k15	22	349985	8553730	Scarabaeidae	Scarabaeinae	*Eurysternus* sp. 2	46
B3*yr*	k15	22	349985	8553730	Scarabaeidae	Scarabaeinae	*Eurysternus* sp. 1	72

3 Capítulo 2

Why does plant diversity decline in degraded Amazonian riparian forests? The role of fauna

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Target journals: Forest Ecology and Management, Journal of Applied Ecology, Biotropica, Oecologia.

3.1 Abstract

Riparian forests are ecotonal areas that connect aquatic and terrestrial ecosystems and have various ecosystem functions crucial for the maintenance and stabilization of both. Anthropogenic impacts such as fragmentation and edge effects degrade riparian forests, leading to lower species richness of plant communities compared to conserved riparian forests. Frugivory, predation of herbivorous insects, and seed predation are functions performed by fauna that may explain plant diversity in a given locality. Here, we explored these functions to answer why the plant richness in degraded riparian forests is lower compared to conserved riparian forests. To this, we measured frugivory, predation of herbivorous insects, and postdispersal seed predation in degraded and conserved riparian forests. Our results demonstrated that the levels of these three ecosystem functions did not differ between the evaluated riparian forests. Possibly, changes in species composition and abundance among these forests maintain ecosystem functions stable through functional redundancy. This indicates that the low plant richness in degraded riparian forests may be related to factors extrinsic to fauna. Once identified and managed, if necessary, fauna can maintain both forests functionally stable.

3.2 Introduction

Riparian forests are ecotonal zones growing along watercourses that provide essential ecosystem functions for maintaining aquatic and terrestrial biodiversity (Naiman et al., 1993; Riis et al., 2020). In aquatic ecosystems, riparian forests drive the physical-chemical parameters of the water (Macedo et al., 2013; Souza et al., 2013) and provide organic matter that sustains aquatic food webs (Lorion & Kennedy, 2009). In terrestrial ecosystems, they stabilize the soil, control floods, and provide habitat for fauna and flora (Lees & Peres, 2008; Maracahipes-Santos et al., 2020; Riis et al., 2020). Brazilian riparian forests are protected by law, which establishes a vegetation strip of at least 30 meters in width on each bank of watercourses (Brasil, 2012). However, riparian forests in the eastern Brazilian Amazon experience higher deforestation rates than non-riparian forests, driven mainly by agricultural expansion (Macedo et al., 2013; Nunes et al., 2019). Disturbed riparian forests surrounded by croplands have lower plant species richness than undisturbed riparian forests (Maracahipes-Santos et al., 2020). Therefore, it is crucial to understand the mechanisms that promote natural forest regeneration in disturbed riparian forests.

Deforestation, along with forest degradation and edge effects, are some causes of structural and functional modifications in ecosystems (*e.g.*, habitat loss, canopy openness and biological invasions) that promote the reduction and loss of biodiversity (Faria et al., 2023; Lapola et al., 2023; Magrach et al., 2014). Several ecosystem functions result from the ecological interaction between organisms and depend on biodiversity (Hooper et al., 2005). Consequently, losses in biodiversity impact ecological interactions and their net results. For example, biodiversity loss in fragmented landscapes decreases mutualistic interactions, such as seed dispersal, and increases antagonistic interactions, such as seed predation and herbivory (Magrach et al., 2014). Seed limitation, when seeds do not arrive in the suitable sites for establishment, and establishment limitation, when abiotic and biotic filters (seed predation and herbivory, for example) limit plant establishment (Muller-Landau et al., 2002; Schupp et al., 2002) – and therefore impact forest maintenance and regeneration (Chazdon, 2013; Rodriguez-Perez & Traveset, 2007).

In Amazonian riparian forests, the width of the forest strip plays a critical role in shaping seed-disperser fauna richness and functional diversity. Narrow forests (<200 m wide) in degraded landscapes are particularly vulnerable to edge effects and exhibit simplified forest structures (Maracahipes-Santos et al., 2020), supporting less diverse bird and mammal communities than conserved forests (Lees & Peres, 2008). For example, the scarcity of resources and simplified habitats reduce the species richness of frugivorous birds and small mammals, ultimately diminishing the functional diversity of these groups (Hannibal et al., 2020; Maure et al., 2018). Since animal seed dispersal may increase the richness and abundance of plant species in the seed rain (Camargo et al., 2021; Carlo & Morales, 2016) and potentialize the arrival of propagules in suitable sites for establishment (Clark et al., 2007; Myers & Harms, 2009), such forest degradation may decrease seed germination and plant recruitment. Thus, the loss of frugivores prevents seed dispersal, hindering the regeneration of degraded forests (Gardner et al., 2019).

Post-dispersal seed predation (hereafter seed predation) can regulate plant recruitment and diversity through top-down control in areas with high conspecific plant densities (i.e., negative density dependence mechanism; Comita et al., 2014; Terborgh, 2012), while elevated seed predation can reduce natural forest regeneration (Chazdon, 2013). Seed predation is a highly variable process and is dependent on several factors, such as seed morphological traits (e.g., seeds' size, hardness, weight; Béllo Carvalho & Pizo, 2023; Chen et al., 2017), the abundance and dynamic of seed's predators (Chen et al., 2017; Mendes et al., 2016; Tabeni et al., 2018). The combination of these factors makes predicting patterns of seed predation difficult. However, the populations of seed predators, as generalist small rodents, birds and ants, increase in forest edges (C. Braga et al., 2020; Farji-Brener, 2001; Gray et al., 2007; Ribeiro et al., 2024). Therefore, frequently there are higher rates of seed predation at fragment edges and degraded areas (Chen et al., 2017). Thus, seed predation can filter plant establishment (Muller-Landau et al., 2002) and can limit the natural forest regeneration of degraded riparian forests.

Insectivorous birds and small mammals also decline in degraded forests (Hannibal et al., 2020; Maure et al., 2018). This can disrupt the top-down control of herbivorous insects, leading to increased herbivory (Karp & Daily, 2014; Maas et al., 2013; but see Morante-Filho et al., 2016), which is another important biotic filter for natural forest regeneration (Muller-Landau et al., 2002). Subsequent to seed predation, herbivory promotes the diversity of plant communities by reducing the survival of plants in areas with high conspecific density (Comita et al., 2014; Terborgh, 2012). Although severe insect herbivory can kill the host plant, more often it reduces plant size, growth, and seed production, thus impairing natural forest regeneration (Massad et al., 2013; Myers & Sarfraz, 2017; but see Garcia & Eubanks, 2019). Predation by arthropods on herbivorous insects is high in the tropics, partly due to the abundance of predatory arthropods (Roslin et al., 2017; Zvereva et al., 2020). Although the biodiversity of predatory arthropods usually decreases in degraded native forests (Queiroz et al., 2022; Tscharntke et al., 2008, 2012), recent studies indicate that the abundance of predatory ants and spiders in degraded riparian forests does not differ from their reference forests (Pires et al., 2022; Ribeiro et al., 2024). This may lead to stable insect predation levels regardless of the conservation status of the riparian forest (Ribeiro et al., 2024). The complex interactions across different groups of predators and their responses to forest degradation adds further challenges to our understanding of mechanisms underlying the natural recovery of Amazonian riparian forests.

Other factors as landscape configuration, land-use history, and local floristic composition also shape the possible pathways of regenerating forests (Chazdon, 2013; Jakovac et al., 2021b). This multitude of factors makes ecological regeneration a process with a high degree of uncertainty and variability among locations (Norden et al., 2015), and poses an important challenge for ecologists and conservationist practitioners to understand mechanisms governing the natural recovery of riparian tropical forests. Here we investigate why disturbed Amazonian riparian forests surrounded by croplands have a lower natural recovery – i.e., fewer species of trees, seedlings and saplings than undisturbed riparian forests (Maracahipes-Santos et al., 2020). Our overarching hypothesis is that animals play a crucial role in this process, through both positive and negative animal-plant interactions. Specifically, we hypothesized that: (1) frugivory decreases and (2) seed predation increases in the riparian forests surrounded by croplands compared to intact riparian forests. The frequency of frugivory is an essential proxy for seed dispersal efficiency and, potentially, for plant recruitment (Campagnoli et al., 2024), while the seed predation kills the seed embryo, thus limits the plant gemination (Muller-Landau et al., 2002). Additionally, we quantified the predation pressure over herbivorous insects across riparian forests surrounded by croplands and undisturbed riparian forests, and the role of predatory birds and arthropods in herbivorous insect control in both sites.

3.3 Methods

3.3.1 Study area

We conducted the study at Tanguro Field Station (state of Mato Grosso, Brazil; 13°04’S, 52°23’’W), in the transition zone between the Cerrado and Amazon biomes. The average temperature in the region varies between 24 to 26°C (Maracahipes-Santos et al., 2020), and the average annual precipitation is 1,700 mm (Balch et al., 2008). The farm covers about 96,000 hectares, from which approximately half is occupied by plantations, while the remaining portion is covered by a lower, drier, and less diverse transitional Amazon Forest compared to central regions in the Amazon (Balch et al., 2008; Massad et al., 2013). The land-use history on the farm began in the early 1980s with deforestation for pasture establishment. In the 2000s, cattle farming was discontinued, making way for corn, soy, and cotton plantations (Macedo et al., 2012; Maracahipes-Santos et al., 2020).

3.3.2 Experimental design and compilation of fauna data

We selected ten riparian forests for ecosystem function sampling, six forests surrounded by cropland fields and four undisturbed riparian forests. In all riparian forests, we delimited a 40-meter-wide plot starting from the watercourse's edge. The length of these plots in forests surrounded by cropland ranged from 100 to 160 meters due to the varying width of the riparian vegetation strip in each riparian forest. For undisturbed riparian forests, we established a limit of 100 meters in length from the water body, as these forests were immersed in a forest matrix (Maracahipes-Santos et al., 2020; Figure 6; Table S1).

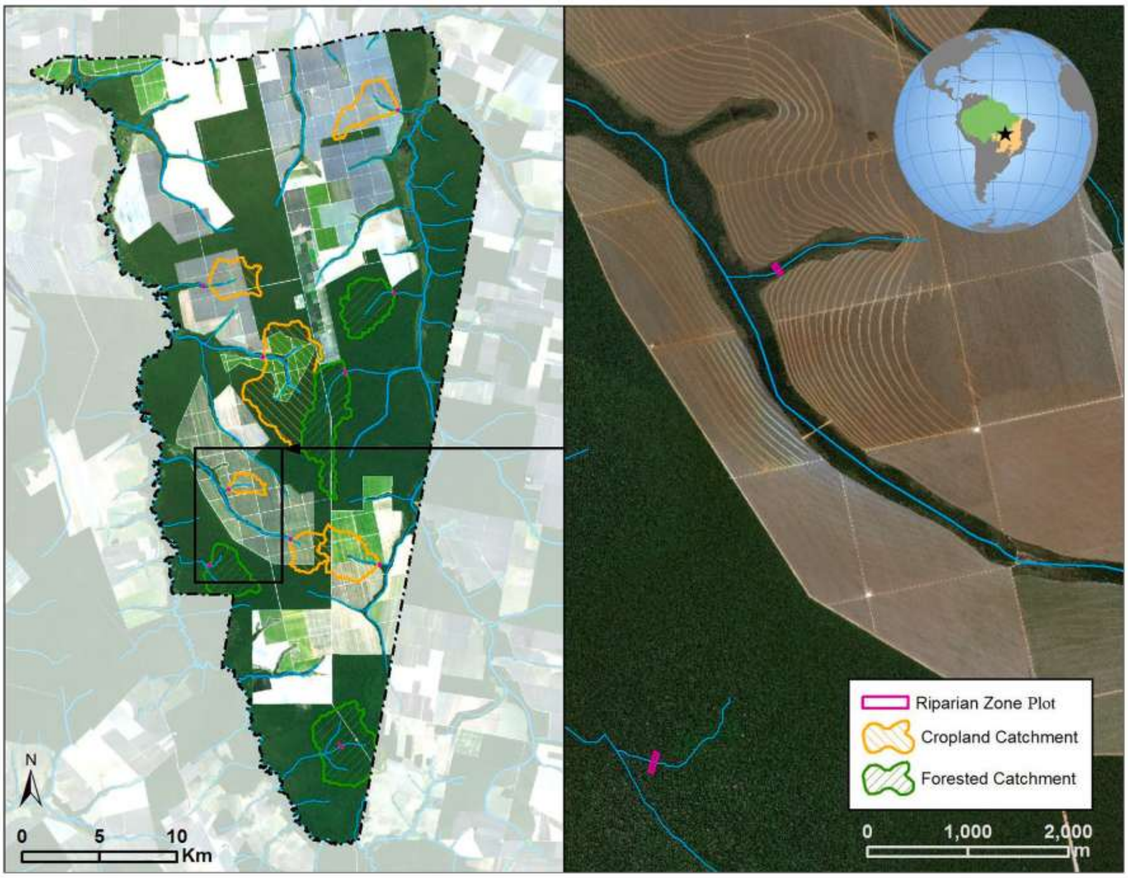

Figure 6. On the left is Tanguro Field Station (Querência, Mato Grosso, Brazil), with the location of the ten riparian forests used for the experiment. Undisturbed riparian forests are highlighted with green lines, and forests surrounded by cropland fields are highlighted with yellow lines. The exact points where we conducted the experiments are marked with pink lines. On the right is an approximate view of the sampling points. Adapted from Maracahipes-Santos et al. (2020).

To investigate the impacts of riparian forest degradation on frugivory, we selected ten non-fruiting and non-flowering adult trees spaced at least ten meters apart in each riparian forest. For each of these trees, we installed ten round artificial fruits (diameter between 1.3 and 1.6 cm) made of red modeling clay (Corfix®), odorless, and non-toxic, at 1.5 - 2.0 m height, totaling 100 fruits per riparian forest and 1000 fruits in the entire sampled area. We visited each riparian forest between 12 and 32 days (average = 20 days) after installing the fruits to count the number of fruits marked by animals. We also categorized the type of marks on the fruits according to Low et al. (2014) into marks by birds, rodents and marsupials (Figure S1).

To investigate the impacts of riparian forest degradation on seed removal, we conducted a paired experiment beneath each tree from the frugivory experiment. This experiment consisted of a vertebrate exclusion treatment (exclusion treatment) and an open treatment for all fauna (open treatment) arranged on the ground, 1.0 to 1.5 m apart from each other. In both treatments, we placed ten intact sunflower seeds, husk-free and heat-sterilized at 110˚C for one hour (average ± SD: height = 7.95 ± 0.70, weight = 0.04 ± 0.01). We covered the exclusion treatment with a conical metal grid (approximately 12 cm in height, 15 cm in diameter, and mesh size 2.5 × 2.5 cm) to prevent vertebrates' access to the seeds. The seeds were directly deposited in shallow soil depressions to prevent loss for reasons other than animal predation. The experiment was left in the field for 24 hours, and after this period, we returned to count the number of seeds with no apparent manipulation, partially predated, and removed (Figure S2). We recognize that some removed seeds may be secondarily dispersed rather than predated by ants (Falcon et al., 2024) and rodents (Zhang et al., 2025), for example. However, we considered all removed seeds as predated in our study (following Hargreaves et al., 2024) because there is a high probability of removed seeds being eaten after the removal event (Hulme, 1998), and there is no adaptations in the sunflower seeds, like elaiosomes or thick seed coats, that facilitate secondary dispersal or prevent seed predation, respectively (Vander Wall & Longland, 2004).

Finally, to assess the effects of riparian forest degradation on predation pressure over herbivorous insects, we selected ten adult trees without fruits and flowers, spaced at least ten meters apart from each other and from the trees of the previous experiment. For each tree, we installed an artificial caterpillar made of green modeling clay (Corfix®), odorless and non-toxic, measuring 3.0 cm in length and 0.5 cm in diameter. The caterpillars were placed on a robust and exposed branch between 1.5 and 2.0 m in height. In total, ten artificial caterpillars were installed per riparian forest, and 100 caterpillars in the entire sampled area. We visited the riparian forests between 12 and 32 days (average = 20 days) after installing the caterpillars to count the number of caterpillars with predation marks. We classified the predation marks on the caterpillars following Low et al. (2014) into marks by birds, mammals, and insects (Figure S3).

We used the data available in the Tanguro Field Station database (PELD/TANG, 2021) to conduct a descriptive comparison of bird (Table S2) and mammal communities (Table S3), and data from Ribeiro et al. (2024) for ant community comparisons (Table S4). All communities were investigated in three riparian forests surrounded by croplands (APP 4, APP Cascavel, and APP Nascente) and three undisturbed riparian forests (APP 2, APP 2A, and APP M), using data from 2018 for the ant community, and from 2021 for the bird and mammal communities. We followed the categorization of birds' trophic niche and primary lifestyle (i.e., habitat strata used preferentially) as suggested by Tobias et al. (2022). For mammals, we categorized the trophic niche and primary lifestyle following Wilman et al. (2014). This reference does not categorize trophic niches directly but provides percentages of food resources consumed by each mammal species. We used this to classify trophic niches based on the most abundant food item utilized for each species.

3.3.3 Data analysis

To test the effects of riparian forest types (predictor variable) on frugivory, we counted the number of fruits with animal marks per tree and calculated the proportion of frugivory in each tree (response variable). Then, we fitted mixed-effects Generalized Linear Regression Models (GLMMs) using a betabinomial error distribution, monitoring time interval of each riparian forest as covariate and the identities of the riparian forests as a random variable. Additionally, we conducted the same analysis protocol to test the effects of riparian forest types on the proportion of attacks carried out by birds, rodents and marsupials (response variables).

To determine the number of predated seeds, we summed the number of intact and partially predated seeds and then subtracted this sum from the total number of seeds used in each depot. Then, we assessed the general proportion of predated seeds (response variable) among different riparian forests and treatments (exclusion and open; predictor variables) using a GLMM. We used riparian forest and treatment-paired identities (exclusion-open pair) as random variables. We also tested the effects of invertebrates and vertebrates on seed predation using two GLMMs, with riparian forest type as the predictor and riparian forest identity as a random variable. The response variables were the proportion of seeds predated by invertebrates, obtained from the proportion of predated seeds in the exclusion treatment, and the proportion of predated seeds by vertebrates. This was calculated as the difference between total predation in the open treatment and exclusion treatment. We built all GLMMs using binomial error distribution.

Finally, we compared predation on herbivorous insects among riparian forest types (predictor variable) by categorizing the condition of the model caterpillar as preyed (with animal marks; 1) and non-preyed (without animal marks; 0) on each tree (response variable), and built a GLMM using a binomial error distribution. We included the time between caterpillar deployment and monitoring as a covariate and the identity of the riparian forests as random variable. We also tested whether herbivorous predation by birds and insects (response variables), separately, varied across riparian forest types following the same analytical process.

We conducted all analyses using the R software (R CORE TEAM, 2023) and the glmmTMB package (Brooks et al., 2017). We verified the fit of all models for residual dispersion, outliers, and zero inflation using the DHARMa package (Hartig & Hartig, 2017).

3.4 Results

From a total of one thousand fruits placed in the riparian forests, we found 475 intact fruits, 418 manipulated by frugivores vertebrates, 113 by insects, and 64 removed. The total count was 1070 records because some fruits exhibited more than one type of animal mark. The average proportion of frugivory in undisturbed riparian forests was 0.46 ± 0.04 (average ± standard error) compared to 0.43 ± 0.03 in riparian forests surrounded by croplands fields; there was no difference in the proportion of frugivory between both types of riparian forests ($\chi2$ [1, N = 95] = 0.43; P = 0.50; Figure 7A). The proportion of frugivory by birds was higher in undisturbed than in riparian forests surrounded by croplands ($\chi2$ [1, N = 93] = 5.03; P = 0.02), with a frugivory average of 0.32 ± 0.02 in undisturbed riparian forests (N = 131; 32% of total fruits placed in undisturbed riparian forests) and 0.23 ± 0.02 in riparian forests surrounded by croplands (N = 96; 24% of total fruits placed in riparian forests surrounded by croplands fields; Figure 7B). The frugivory driven by marsupials and rodents was 0.08 ± 0.02 and 0.07 ± 0.02 in riparian forests surrounded by croplands, and 0.06 ± 0.02

and 0.04 ± 0.01 in undisturbed riparian forests, respectively. We did not observe differences in the frugivory among riparian forests for rodents ($\chi2$ [1, N = 94] = 0.34; *P* = 0.55) and marsupials ($\chi2$ [1, N = 94] = 0.12; *P* = 0.72).

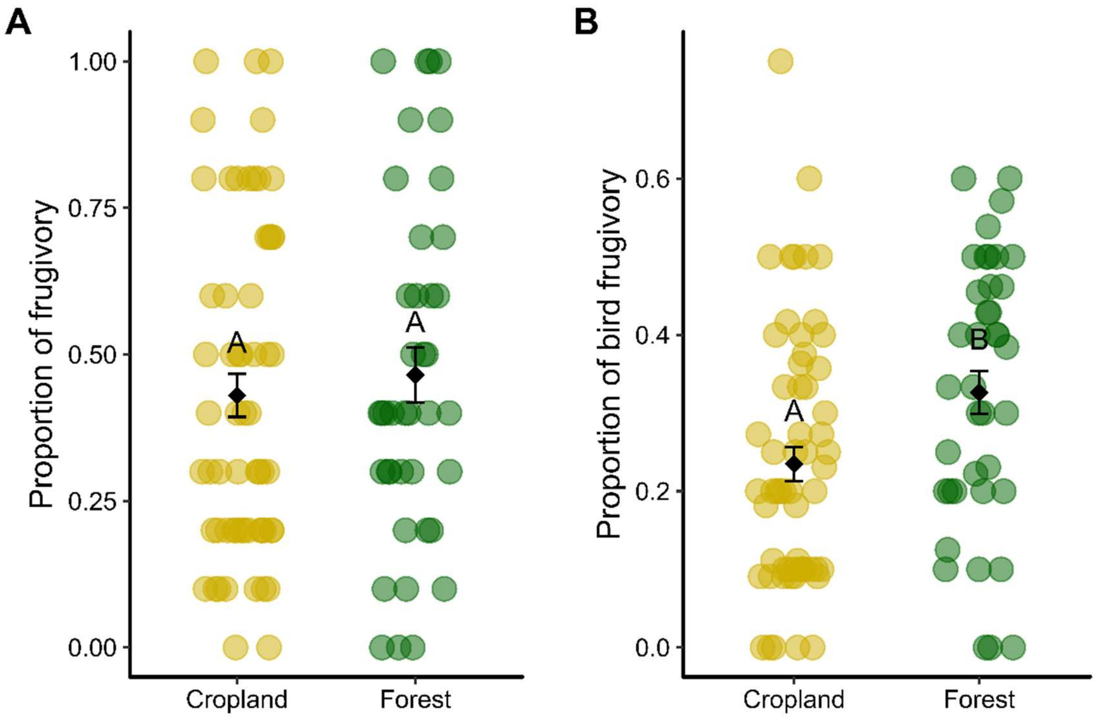

Figure 7. Variation between frugivory proportion in the undisturbed riparian forests and riparian forests surrounded by croplands fields at Tanguro Field Station (Querência, Mato Grosso, Brazil). A. Total frugivory proportion; B. Frugivory proportion by birds. The bars represent the SE, and the letters indicate significant differences between the parcels at alfa = 5%.

We recorded high seed predation rates in all treatments in both riparian forest types. In riparian forests surrounded by croplands, 570 seeds were predated in the exclusion treatment (0.95 ± 0.01) and 580 seeds in the open treatment (0.98 ± 0.01). In undisturbed riparian forests, 393 seeds were predated in the exclusion treatment (0.98 ± 0.01) and 378 in the open treatment (0.94 ± 0.02). In total, 1921 seeds (0.96) out of the 2000 seeds placed in the study area were preyed on, with a proportional average of 0.95 ± 0.01 seed predation in riparian forests surrounded by cropland and 0.96 ± 0.01 in undisturbed riparian forests. The proportion of total seed predation did not differ across riparian forests ($\chi2$ [1, N = 195] = 0.001; *P* = 0.97) and treatments ($\chi2$ [1, N = 196] = 0.384; *P* = 0.53; Figure 3). Seed predation in exclusion treatment was driven exclusively by invertebrates, which did not differ across riparian forest types ($\chi2$

[1, N = 95] = 1.96; *P* = 0.160). We estimated 22 seeds predated by vertebrates in the riparian forests surrounded by croplands (0.04 ± 0.01) and six seeds in the undisturbed riparian forests (0.01 ± 0.009); this difference was not significant (χ2 [1, N = 85] = 1.54; *P* = 0.213).

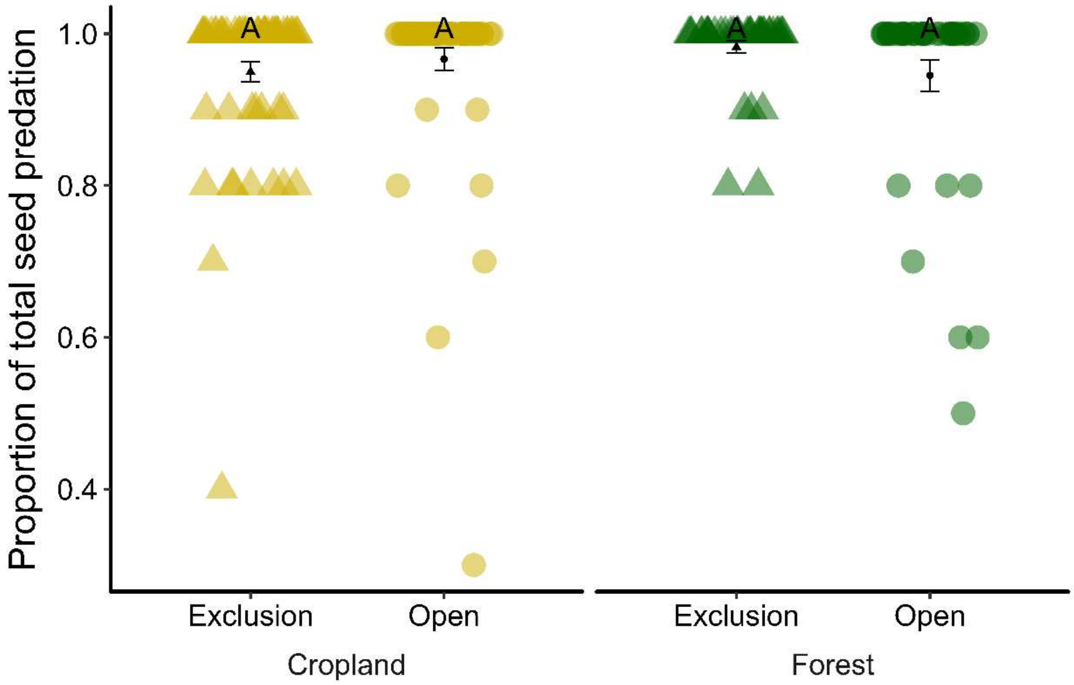

Figure 8. Variation in total seed predation between undisturbed riparian forests and riparian forests surrounded by cropland fields at Tanguro Field Station (Querência, Mato Grosso, Brazil). Exclusion: vertebrate exclusion treatment; Open: open to all fauna treatments; the bars represent the SE, and the letters indicate significant differences between the parcels at alfa = 5%.

We did not find 12 caterpillars out of the 100 placed in the riparian forests, so we removed them from the analysis, thus remaining 88 caterpillars. We did not observe differences in overall predation pressure between riparian forest types (χ2 [1, N = 84] = 1.59; *P* = 0.20; Figure 9), although we recorded a higher proportion of attacks on caterpillars in riparian forests surrounded by croplands fields (0.62 ± 0.07; N = 31) than in undisturbed riparian forests (0.51 ± 0.08; N = 20). There were no differences across riparian forests in attacks carried out by birds (χ2 [1, N = 84] = 0.64; *P* = 0.42) and arthropods (χ2 [1, N = 84] = 0.07; *P* = 0.77). Birds attacked more caterpillar models in riparian forests surrounded by croplands (0.22 ± 0.06; N = 11) than in undisturbed riparian forests (0.15 ± 0.05; N = 6). Conversely, arthropods were more representative in the herbivore predation in undisturbed riparian forests (0.35 ± 0.07; N = 14) than in riparian forests surrounded by croplands (0.32 ± 0.06; N = 16). We did not analyze predation carried out by mammals because we recorded only four caterpillars with mammal' marks.

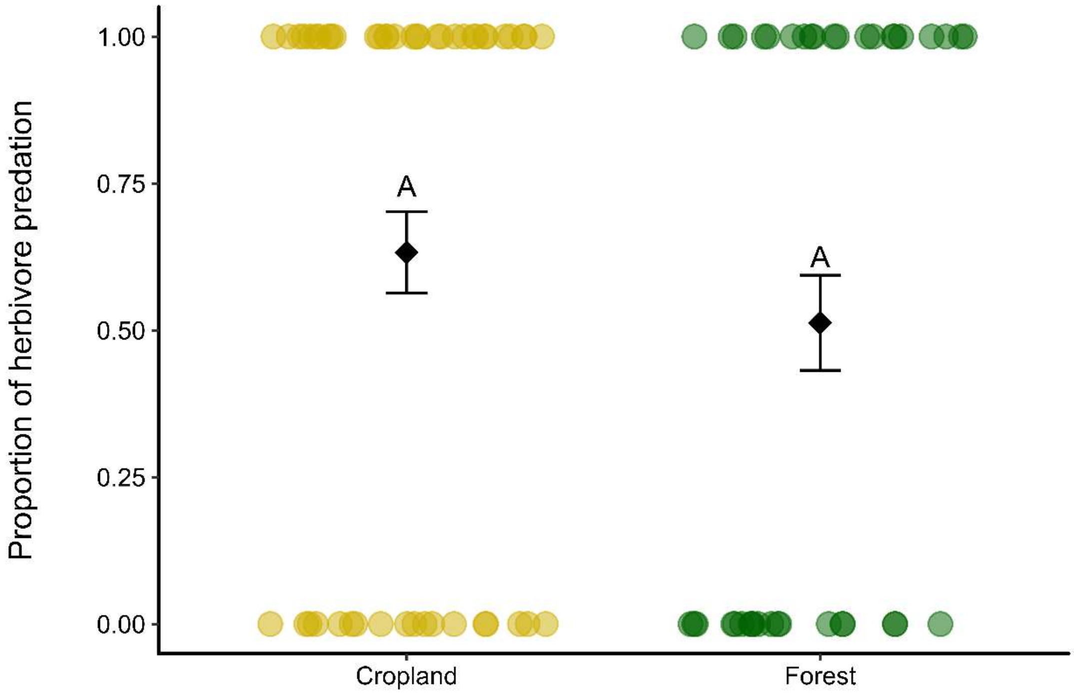

Figure 9. Variation between the total proportion of predator attacks on herbivorous insect models in the undisturbed riparian forests and riparian forests surrounded by cropland fields at Tanguro Field Station (Querência, Mato Grosso, Brazil). The bars represent the SE, and the letters indicate significant differences between the parcels at alfa = 5%.

3.5 Discussion

Contrary to our initial hypothesis, we did not find lower frugivory, predation of herbivorous insects, and higher seed predation in riparian forests surrounded by croplands than in undisturbed riparian forests. These results indicate that the ecosystem services provided by the fauna remain equivalent across disturbed and undisturbed Amazonian riparian forests. However, we observed lower frugivory by birds in riparian forests surrounded by croplands compared to undisturbed riparian forests, which may have important implications for the natural recovery of these forests.

The decline in birds' seed dispersal across degraded riparian forests may be due to reductions in bird species' abundance, taxonomic and functional richness (Lees & Peres, 2008; Maure et al., 2018; Ramos & Anjos, 2014). While in our study area frugivorous birds species richness was slightly lower in undisturbed riparian forests (S = 17) than in riparian forests surrounded by croplands (S = 19), with 44% of species composition similar among them (S = 11; PELD/TANG, 2021), their abundances was almost twice as high in undisturbed forests (N = 116) compared to riparian forests near croplands (N = 66; PELD/TANG, 2021; Table S2). This higher abundance of frugivorous birds in undisturbed forests was likely a key mechanism for the higher bird frugivory we observed (Pizo et al., 2022), which likely increases seeds abundance and species richness in the seed rain (Pejchar et al., 2008; Camargo et al., 2021), an essential step to overcome the seed limitation that increases plant recruitment (Barbosa & Pizo, 2006; Caughlin et al., 2016). Thus, the abundance of frugivores drives the quantitative component of seed dispersal effectiveness (contribution of a disperser, a group of dispersers, or a dispersal phase to plant recruitment; sensu Schupp et al., 2010) and disproportionately contributes to plant recruitment (Campagnoli et al., 2024). We acknowledge that results must be interpreted cautiously because bird community data were collected one year before our experiments (PELD/TANG, 2021), as the community can undergo interannual changes (Menger et al., 2017). However, the recovery of bird communities is slow after anthropogenic disturbances and does not recover the original abundance ten years after the impacts, for example (Mestre et al., 2013). Therefore, this difference in the frugivore birds' abundance is a potential explanatory mechanism for a lower species richness of plants, seedlings and saplings in Amazonian riparian forests surrounded by croplands (Maracahipes-Santos et al., 2020).

Additionally, the species richness and abundance of understory generalist birds, which are less sensitive to forest disturbance (Morante-Filho et al., 2015), were higher in riparian forests surrounded by croplands (S = 13; N = 102; PELD/TANG, 2021) than in undisturbed riparian forests (S = 8; N = 35; PELD/TANG, 2021; Table S2), with 24% of species similarity (S = 4). This higher abundance in riparian forests surrounded by croplands was caused by a high abundance of species like picazuro pigeon (*Patagioenas picazuro*; N = 31) and smooth-billed ani (*Crotophaga ani*; N = 23) – species that fill a small part of their diets with fruits (10% - 30%), which is complemented with seeds and/or invertebrates (WILMAN et al., 2014). Although generalist birds can increase frugivory, seed dispersal, and plant recruitment (Carlo & Morales, 2016; Palacio et al., 2016; Pizo et al., 2022), the lower frugivory by birds in riparian forests surrounded by croplands suggest that the higher abundance of generalists did not offset the decline of frugivores abundance in these sites. This reinforces the potential role of frugivore birds in promoting a higher plant species richness in undisturbed riparian forests (Maracahipes-Santos et al., 2020).

The equivalence of total frugivory (driven jointly by birds and mammals) across riparian forest types suggests that mammals could offset the frugivory loss by birds. Previous data on arboreal and scansorial small mammals (marsupials and rodents) from our study area reported low richness and abundance across all guilds with some fruits in their diets (frugivores, herbivores, and omnivores; PELD/TANG, 2021; Table S3), which constrains interpretations of mammal frugivory. Nevertheless, the communities of small mammals in Amazon forest fragments, including fragments surrounded by grain plantations, like our study area, are dominated by generalist species (C. Braga et al., 2020; Santos-Filho et al., 2012). Small generalist marsupials can disperse seeds (Cáceres & Monteiro-Filho, 2007; Cantor et al., 2010), but their diets are composed mainly of animals (vertebrates and invertebrates), with a small part of fruits (Cantor et al., 2010; Lessa & da Costa, 2010). Although granivorous rodents occasionally disperse seeds (Zwolak et al., 2024), their predation rates exceed 70% in tropical forests (Fleury et al., 2014; Notman & Gorchov, 2001). The high density of generalist small rodents can increase seed predation, decreasing plant recruitment and forest regeneration (Fleury et al., 2014; Galetti et al., 2015). Hence, in addition with the low frugivory by small mammals we found, it seems unlikely that small mammals compensated for the loss of frugivorous birds in riparian forests surrounded by croplands.

Despite the potential increase of generalist granivorous vertebrates in forest fragments (C. Braga et al., 2020; Gray et al., 2007), our results demonstrated that seed predation by them was low in both riparian forest types. Nonetheless, the total seed predation rate was high in both riparian forests and in open to all fauna and exclusion of vertebrate treatments. The consistency of high seed predation across both treatments suggests substantial seed predation by invertebrates, aligned with the pattern of seed predation in the tropics (Hargreaves et al., 2019). A previous study in the same forests also did not find differences between seed removal by invertebrates across riparian forests surrounded by croplands and undisturbed riparian forests (Ribeiro et al., 2024). Also, they found that leaf-cutting ants are three times more representative in riparian forests surrounded by croplands than in undisturbed riparian forests (Ribeiro et al., 2024; Table S4). Leaf-cutting ants reduce the availability of seeds and increase plant mortality, impacting the natural forest regeneration (A. N. Costa et al., 2017; Dohm et al., 2011). Conversely, other research from our study region found that seed predation is reduced in the edges compared to the interior of burned forests, probably due to impacts on seed predator communities (Penido et al., 2015). Although the abundance and richness of the ant community did not differ, the species composition changed between riparian forests surrounded by croplands (S = 56; N = 146) and undisturbed riparian forests (S = 52; N = 130), with 27% of similarity between them (Ribeiro et al., 2024). Taken together with our results – considering the equivalence of seed predation and the changes in ant species composition, we suggest a functional redundancy of seed predator communities between riparian forest types (Naeem, 1998; Walker, 1992). Thus, seed predation potentially remains functional across degraded riparian forests, regulating the density of abundant plants through top-down control and capable of promoting plant diversity (Connell, 1971; Hulme, 1998; Janzen, 1970).

The functional redundancy can also explain the maintenance of predation pressure on herbivorous arthropods across riparian forests, as the species composition of birds (PELD/TANG, 2021) and ants (Ribeiro et al., 2024) varies across riparian forest types. Following the same pattern of ants and omnivorous birds, the richness and abundance of insectivorous birds were similar between riparian forests surrounded by croplands (S = 45; N = 157) and undisturbed riparian forests (S = 40; N = 138; Table S2), with 39% of species composition similar between them. Birds and ants are two of the main predators of herbivorous arthropods in the Neotropic region (Roslin et al., 2017; Van Bael et al., 2003). Birds may increase the predation pressure on herbivorous arthropods in undisturbed riparian forests due to an increase in forest coverage, followed by an increase in the abundance of prey, and consequent increase in predation success (Morrison et al., 2010). Conversely, the increase of generalist birds in degraded forests and the simplified structure of this environment, which facilitates the encounter of prey by predators, may increase predation rates (Barlow & Peres, 2004; Queiroz et al., 2022). In turn, predation by arthropods on herbivorous insects is high in the tropics, in part due to the high abundance of predatory arthropods in this region (Roslin et al., 2017; Zvereva et al., 2020). Thus, the stability in the predation of herbivorous insects in both riparian forest types can maintain the top-down control of plant populations and also promote species diversity (Connell, 1971; Janzen, 1970; Pacala & Crawley, 1992).

Considering that seed and herbivore predation remained similar across riparian forests surrounded by croplands and undisturbed riparian forests, it seems that the main mechanism driving tree, seedling, and sapling diversity on degraded Amazonian riparian forests is related to seed limitation. We did not estimate herbivory directly, but the top-down control of herbivorous insects, which inversely correlates with herbivory in our study region (Queiroz et al. 2022). Although herbivory in forest edges can be high (Urbas et al., 2007), our results demonstrated that predation of herbivorous arthropods, conducted by multiple taxa (birds and arthropods), can control populations of herbivorous arthropods, and likely reduces the herbivory. Seed predation and herbivory are relevant biotic filters that limit the establishment and survival of plants (Muller-Landau et al., 2002; Vargas & Stevenson, 2013). The lack of impact on these filters in disturbed riparian forest contrasts with the lower frugivory by birds on these forests. Seed dispersal by birds, inferred through frugivory, seems to be a key ecological filter for the arrival of seeds in riparian forests surrounded by croplands, which limits tree, seedling, and sampling diversity at these sites. However, we highlight that extrinsic factors to the fauna may also contribute to explain this pattern, including the distance to a propagule source, the identity and functional characteristics of initial plant species in regeneration sites.

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3.7 Apêndice B

Why does plant diversity decline in degraded Amazonian riparian forests? The role of fauna

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3.7.1 Supplementary information

Table S1. List of the ten riparian forests used for sampling ecosystem functions at Tanguro Field Station (Querência, Mato Grosso, Brazil). The length of the vegetation strip on each bank of the riparian forests is presented separately, with the first value corresponding to the right bank (R), followed by the left bank (L). Source: Maracahipes-Santos et al., 2020.

Riparian forest	Matrix	Treatment	Margin length (R/L)
APP 2	Forest	Undisturberd	100/100
APP 2A	Forest	Undisturberd	100/100
APP CN	Forest	Undisturberd	100/100
APP M	Forest	Undisturberd	100/100
APP 4	Cropland	Disturbed	60/140
APP 5	Cropland	Disturbed	130/60
APP 6	Cropland	Disturbed	50/70
APP AR3	Cropland	Disturbed	80/40
APP Cascavel	Cropland	Disturbed	160/50
APP Nascente	Cropland	Disturbed	100/50

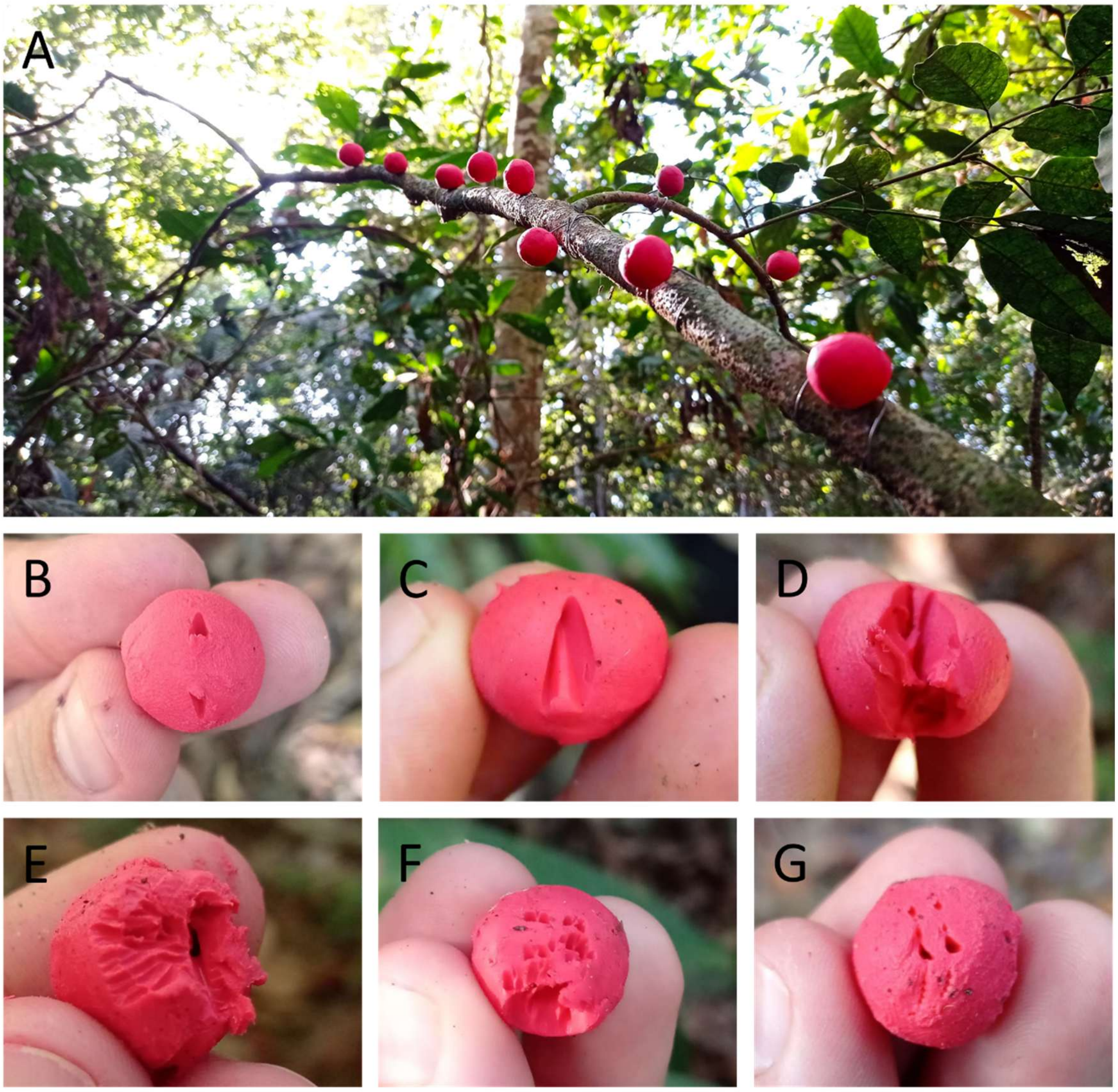

Figure S1. Models of plasticine fruits used for sampling frugivory in disturbed and undisturbed riparian forests at Tanguro Field Station (Querência, Mato Grosso, Brazil). A) Fruits installed on a tree branch (N = 10); B-J) Fruits attacked by different frugivores, being: B-D) birds; E-F) Rodents; G) Marsupial.

Figure S2. Experiment of seed predation in disturbed and undisturbed riparian forests at Tanguro Field Station (Querência, Mato Grosso, Brazil). A) Vertebrate exclusion treatment (exclusion treatment) with wire cage with sunflower seed beneath (N = 10 seeds); B) Open to all fauna experiment (open treatment), sunflower seeds placed directly on the ground (N = 10 seeds); C) Arrange of two treatment in the riparian forest ground 1.0 to 1.5 m apart.

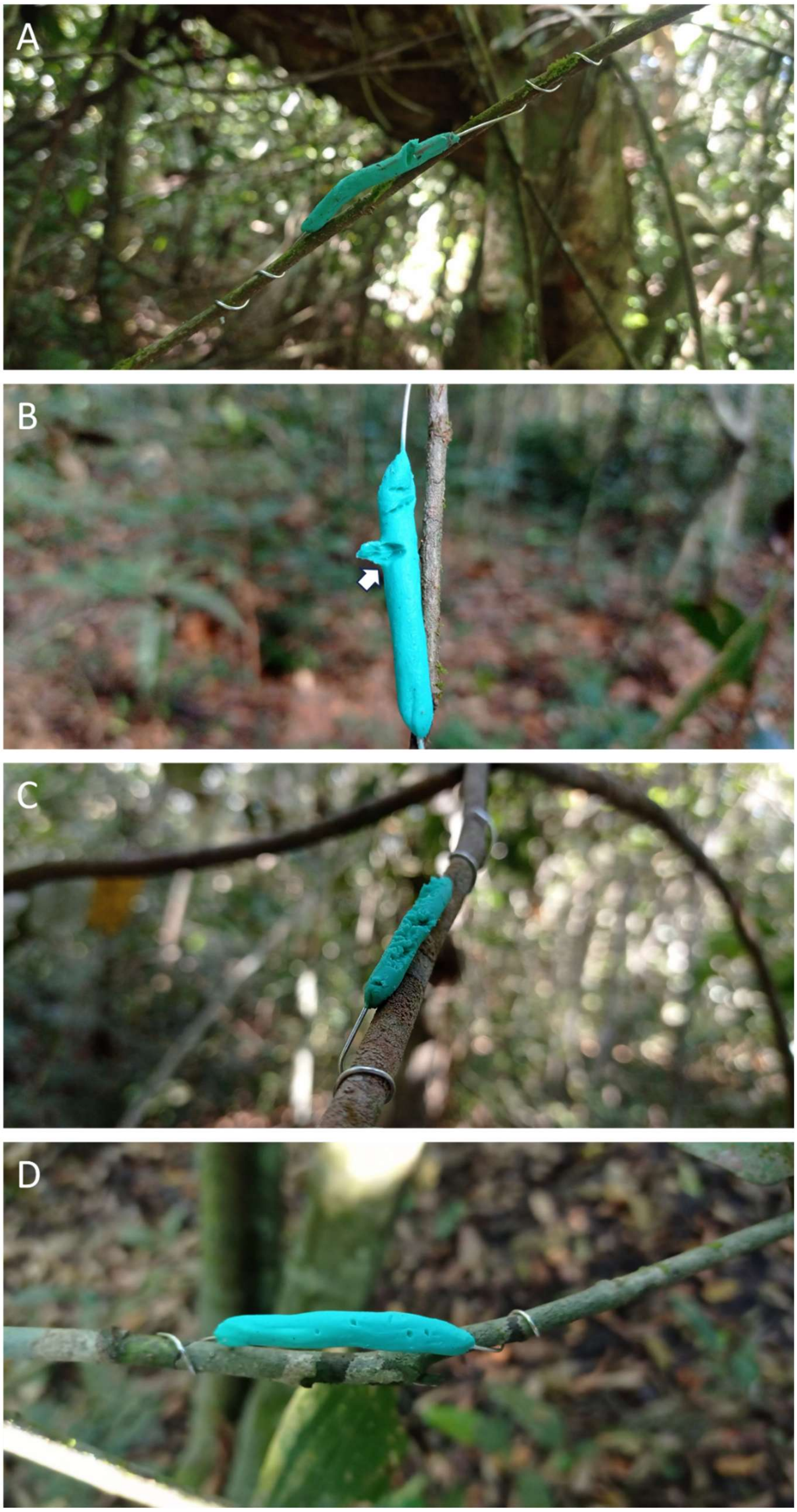

Figure S3. Models of plasticine caterpillars used for sampling predation upon herbivore insects in disturbed and undisturbed riparian forests at Tanguro Field Station (Querência, Mato Grosso, Brazil). A-D) Marks of predators on caterpillars, beeing: A) Birds; B) Birds and rodent (pointed by white arrow); C-D) Arthropods.

Table S2. Frugivore, invertivore, and omnivore bird assembly in disturbed riparian forests surrounded by croplands (Cropland) and undisturbed riparian forests (Forest) at Tanguro Field Station (Querência, Mato Grosso, Brazil). Source: Database Peld/Tang (2021).

Species	Riparian forest treatment	Functional Group	Lifestyle	N
Aburria cujubi	Cropland	Frugivore	Insessorial	2
Ortalis guttata	Cropland	Frugivore	Insessorial	7
Ramphastos tucanus	Cropland	Frugivore	Insessorial	6
Pteroglossus castanotis	Cropland	Frugivore	Insessorial	2
Pteroglossus bitorquatus	Cropland	Frugivore	Insessorial	4
Patagioenas cayennensis	Cropland	Frugivore	Insessorial	6
Tyranneutes stolzmanni	Cropland	Frugivore	Insessorial	3
Manacus manacus	Cropland	Frugivore	Insessorial	1
Machaeropterus pyrocephalus	Cropland	Frugivore	Insessorial	2
Ceratopipra rubrocapilla	Cropland	Frugivore	Insessorial	6
Tityra cayana	Cropland	Frugivore	Insessorial	1
Legatus leucophaius	Cropland	Frugivore	Insessorial	2
Turdus leucomelas	Cropland	Frugivore	Insessorial	5
Euphonia chlorotica	Cropland	Frugivore	Insessorial	1
Tersina viridis	Cropland	Frugivore	Insessorial	6
Dacnis cayana	Cropland	Frugivore	Insessorial	4
Dacnis lineata	Cropland	Frugivore	Insessorial	2
Saltator maximus	Cropland	Frugivore	Insessorial	3
Stilpnia cyanicollis	Cropland	Frugivore	Insessorial	3
Ictinia plumbea	Cropland	Invertivore	Generalist	8
Brachygalba lugubris	Cropland	Invertivore	Insessorial	4
Galbula ruficauda	Cropland	Invertivore	Insessorial	9
Galbula dea	Cropland	Invertivore	Insessorial	2
Chelidoptera tenebrosa	Cropland	Invertivore	Insessorial	10
Monasa nigrifrons	Cropland	Invertivore	Insessorial	7
Picumnus albosquamatus	Cropland	Invertivore	Insessorial	6
Melanerpes cruentatus	Cropland	Invertivore	Insessorial	11
Myrmophylax atrothorax	Cropland	Invertivore	Insessorial	5
Myrmotherula axillaris	Cropland	Invertivore	Insessorial	1
Herpsilochmus frater	Cropland	Invertivore	Insessorial	6
Thamnophilus doliatus	Cropland	Invertivore	Generalist	9
Thamnophilus murinus	Cropland	Invertivore	Insessorial	2
Thamnophilus aethiops	Cropland	Invertivore	Insessorial	1
Cymbilaimus lineatus	Cropland	Invertivore	Insessorial	1
Sclateria naevia	Cropland	Invertivore	Insessorial	1
Myrmoborus myotherinus	Cropland	Invertivore	Insessorial	1
Myrmoborus leucophrys	Cropland	Invertivore	Insessorial	1
Cercomacra cinerascens	Cropland	Invertivore	Insessorial	3
Hypocnemis cantator	Cropland	Invertivore	Insessorial	6
Dendrocincla fuliginosa	Cropland	Invertivore	Insessorial	1

Species	Riparian forest treatment	Functional Group	Lifestyle	N
Dendrocolaptes certhia	Cropland	Invertivore	Insessorial	4
Xiphorhynchus elegans	Cropland	Invertivore	Insessorial	1
Xiphorhynchus guttatoides	Cropland	Invertivore	Insessorial	1
Dendroplex picus	Cropland	Invertivore	Insessorial	1
Xenops minutus	Cropland	Invertivore	Insessorial	1
Piaya cayana	Cropland	Invertivore	Insessorial	3
Hemitriccus minor	Cropland	Invertivore	Insessorial	2
Camptostoma obsoletum	Cropland	Invertivore	Insessorial	3
Ramphotrigon ruficauda	Cropland	Invertivore	Insessorial	2
Myiarchus ferox	Cropland	Invertivore	Insessorial	2
Megarynchus pitangua	Cropland	Invertivore	Insessorial	1
Myiozetetes cayanensis	Cropland	Invertivore	Insessorial	8
Arundinicola leucocephala	Cropland	Invertivore	Insessorial	2
Cyclarhis gujanensis	Cropland	Invertivore	Insessorial	2
Nyctidromus albicollis	Cropland	Invertivore	Insessorial	1
Vireo chivi	Cropland	Invertivore	Insessorial	1
Pheugopedius genibarbis	Cropland	Invertivore	Insessorial	10
Cantorchilus leucotis	Cropland	Invertivore	Insessorial	1
Polioptila dumicola	Cropland	Invertivore	Insessorial	4
Turdus albicollis	Cropland	Invertivore	Generalist	5
Basileuterus culicivorus	Cropland	Invertivore	Insessorial	2
Hemithraupis flavicollis	Cropland	Invertivore	Insessorial	2
Tachyphonus phoenicius	Cropland	Invertivore	Insessorial	1
Conirostrum speciosum	Cropland	Invertivore	Insessorial	2
Trogon rufus	Cropland	Ominivore	Insessorial	1
Momotus momota	Cropland	Ominivore	Insessorial	12
Patagioenas picazuro	Cropland	Ominivore	Generalist	31
Crotophaga major	Cropland	Ominivore	Insessorial	1
Crotophaga ani	Cropland	Ominivore	Insessorial	23
Pitangus sulphuratus	Cropland	Ominivore	Insessorial	5
Arremon taciturnus	Cropland	Ominivore	Insessorial	2
Cacicus cela	Cropland	Ominivore	Insessorial	7
Molothrus oryzivorus	Cropland	Ominivore	Terrestrial	1
Ramphocelus carbo	Cropland	Ominivore	Insessorial	5
Schistochlamys melanopis	Cropland	Ominivore	Insessorial	2
Thraupis sayaca	Cropland	Ominivore	Insessorial	2
Thraupis palmarum	Cropland	Ominivore	Insessorial	10
Penelope superciliaris	Forest	Frugivore	Insessorial	2
Ramphastos tucanus	Forest	Frugivore	Insessorial	8
Ramphastos vitellinus	Forest	Frugivore	Insessorial	4
Pteroglossus castanotis	Forest	Frugivore	Insessorial	6
Patagioenas speciosa	Forest	Frugivore	Insessorial	3
Patagioenas cayennensis	Forest	Frugivore	Insessorial	4
Tyranneutes stolzmanni	Forest	Frugivore	Insessorial	12
Machaeropterus pyrocephalus	Forest	Frugivore	Insessorial	1

Species	Riparian forest treatment	Functional Group	Lifestyle	N
Ceratopipra rubrocapilla	Forest	Frugivore	Insessorial	12
Querula purpurata	Forest	Frugivore	Insessorial	11
Lipaugus vociferans	Forest	Frugivore	Insessorial	34
Mionectes oleagineus	Forest	Frugivore	Insessorial	1
Legatus leucophaius	Forest	Frugivore	Insessorial	6
Turdus leucomelas	Forest	Frugivore	Insessorial	2
Euphonia chlorotica	Forest	Frugivore	Insessorial	2
Tersina viridis	Forest	Frugivore	Insessorial	4
Stilpnia cyanicollis	Forest	Frugivore	Insessorial	4
Ictinia plumbea	Forest	Invertivore	Generalist	1
Glaucidium brasilianum	Forest	Invertivore	Insessorial	2
Trogon curucui	Forest	Invertivore	Insessorial	2
Galbula ruficauda	Forest	Invertivore	Insessorial	2
Monasa nigrifrons	Forest	Invertivore	Insessorial	2
Picumnus albosquamatus	Forest	Invertivore	Insessorial	1
Melanerpes cruentatus	Forest	Invertivore	Insessorial	8
Epinecrophylla leucophthalma	Forest	Invertivore	Insessorial	2
Myrmophylax atrothorax	Forest	Invertivore	Insessorial	7
Myrmotherula axillaris	Forest	Invertivore	Insessorial	4
Myrmotherula menetriesii	Forest	Invertivore	Insessorial	3
Thamnomanes caesius	Forest	Invertivore	Insessorial	5
Herpsilochmus frater	Forest	Invertivore	Insessorial	9
Thamnophilus doliatus	Forest	Invertivore	Generalist	1
Cymbilaimus lineatus	Forest	Invertivore	Insessorial	1
Myrmoborus myotherinus	Forest	Invertivore	Insessorial	2
Akletos melanoceps	Forest	Invertivore	Insessorial	1
Cercomacra cinerascens	Forest	Invertivore	Insessorial	7
Hypocnemis cantator	Forest	Invertivore	Insessorial	10
Willisornis vidua	Forest	Invertivore	Insessorial	10
Dendrocolaptes certhia	Forest	Invertivore	Insessorial	3
Xiphorhynchus elegans	Forest	Invertivore	Insessorial	7
Dendroplex picus	Forest	Invertivore	Insessorial	1
Automolus infuscatus	Forest	Invertivore	Insessorial	1
Onychorhynchus coronatus	Forest	Invertivore	Insessorial	1
Camptostoma obsoletum	Forest	Invertivore	Insessorial	1
Myiopagis viridicata	Forest	Invertivore	Insessorial	3
Ramphotrigon ruficauda	Forest	Invertivore	Insessorial	7
Rhytipterna simplex	Forest	Invertivore	Insessorial	2
Cyclarhis gujanensis	Forest	Invertivore	Insessorial	1
Nyctidromus albicollis	Forest	Invertivore	Insessorial	1
Pachysylvia muscicapina	Forest	Invertivore	Insessorial	1
Pheugopedius genibarbis	Forest	Invertivore	Insessorial	6
Turdus albicollis	Forest	Invertivore	Generalist	10
Psarocolius viridis	Forest	Invertivore	Insessorial	6
Cacicus solitarius	Forest	Invertivore	Insessorial	2

Species	Riparian forest treatment	Functional Group	Lifestyle	N
Basileuterus culicivorus	Forest	Invertivore	Insessorial	1
Habia rubica	Forest	Invertivore	Insessorial	2
Hemithraupis flavicollis	Forest	Invertivore	Insessorial	1
Lanio versicolor	Forest	Invertivore	Insessorial	1
Trogon rufus	Forest	Ominivore	Insessorial	7
Momotus momota	Forest	Ominivore	Insessorial	6
Patagioenas picazuro	Forest	Ominivore	Generalist	4
Lepidothrix nattereri	Forest	Ominivore	Insessorial	7
Schiffornis turdina	Forest	Ominivore	Insessorial	2
Pachyramphus marginatus	Forest	Ominivore	Insessorial	1
Arremon taciturnus	Forest	Ominivore	Insessorial	4
Cyanerpes caeruleus	Forest	Ominivore	Insessorial	4

Table S3. Frugivore, omnivore, and herbivore mammal assembly in disturbed riparian forests surrounded by croplands (Cropland) and undisturbed riparian forests (Forest) at Tanguro Field Station (Querência, Mato Grosso, Brazil). Source: Database Peld/Tang (2021).

Species	Riparian forest treatment	Functional Group	Lifestyle	Fruits in diet (%)	N
Nasua nasua	Cropland	Frugivore	Scansorial	70	1
Rhipidomys emiliae	Cropland	Herbivore	Arboreal	20	3
Sapajus apella	Cropland	Herbivore	Arboreal	20	1
Didelphis marsupialis	Cropland	Omnivore	Scansorial	0	2
Rhipidomys emiliae	Forest	Herbivore	Arboreal	20	2
Didelphis marsupialis	Forest	Omnivore	Scansorial	0	4

Table S4. Ant community in disturbed riparian forests surrounded by croplands (Cropland) and undisturbed riparian forests (Forest) at Tanguro Field Station (Querência, Mato Grosso, Brazil). Source: Database Peld/Tang (2021).

Species	Riparian forest treatment	Functional Group	N
Acromyrmex sp.A	Cropland	Leaf cutting Attini	1
Acromyrmex sp.B	Cropland	Leaf cutting Attini	5
Acromyrmex sp.C	Cropland	Leaf cutting Attini	4
Acromyrmex sp.D	Cropland	Leaf cutting Attini	2
Apterostigma megacephala	Cropland	Non leaf cutting Fungus growing Ants	1
Atta cephalotes	Cropland	Leaf cutting Fungus growing Ants	3
Atta sexdens	Cropland	Leaf cutting Fungus growing Ants	6
Brachymyrmex sp.B	Cropland	Non leaf cutting Fungus growing Ants	1
Camponotus sp.10	Cropland	Epigaeic Omnivores	1
Camponotus sp.15	Cropland	Epigaeic Omnivores	1
Camponotus sp.20	Cropland	Epigaeic Omnivores	2
Camponotus sp.21	Cropland	Epigaeic Omnivores	1
Camponotus sp.23	Cropland	Epigaeic Omnivores	1
Camponotus sp.3	Cropland	Epigaeic Omnivores	9
Camponotus sp.5	Cropland	Epigaeic Omnivores	3
Camponotus sp.6	Cropland	Epigaeic Omnivores	1
Camponotus sp.7	Cropland	Epigaeic Omnivores	5
Crematogaster sp.A	Cropland	Arboreal Dominants	1
Cyphomyrmex sp.1	Cropland	Non leaf cutting Fungus growing Ants	1
Dolichoderus imitator	Cropland	Arboreal Dominants	1
Ectatomma edentatum	Cropland	Epigaeic Predators	2
Ectatomma sp.2	Cropland	Epigaeic Predators	1
Gigantiops destructor	Cropland	Epigaeic Omnivores	14
Mayaponera constricta	Cropland	Epigaeic Predators	7
Neivamyrmex sp.1	Cropland	Army Ants	1
Neoponera sp.1	Cropland	Epigaeic Predators	1
Neoponera sp.2	Cropland	Epigaeic Predators	1
Nylanderia sp.1	Cropland	Epigaeic Omnivores	4
Nylanderia sp.3	Cropland	Epigaeic Omnivores	2
Ochetomyrmex semipolitus	Cropland	Epigaeic Omnivores	1
Octostruma sp.1	Cropland	Cryptobiotic Predators	1
Pachycondyla sp.2	Cropland	Epigaeic Predators	2
Pheidole sp.8	Cropland	Epigaeic Omnivores	1
Pheidole sp.A	Cropland	Epigaeic Omnivores	1
Pheidole sp.B	Cropland	Epigaeic Omnivores	6
Pheidole sp.C	Cropland	Epigaeic Omnivores	1
Pheidole sp.K	Cropland	Epigaeic Omnivores	5
Pheidole sp.O	Cropland	Epigaeic Omnivores	1
Pheidole sp.Q	Cropland	Epigaeic Omnivores	4
Pheidole sp.R	Cropland	Epigaeic Omnivores	7
Pheidole sp.T	Cropland	Epigaeic Omnivores	2

Species	Riparian forest treatment	Functional Group	N
Pheidole sp.X	Cropland	Epigaeic Omnivores	1
Pheidole sp.Y	Cropland	Epigaeic Omnivores	1
Pseudomyrmex sp.2	Cropland	Arboreal Predators	2
Rogeria sp.1	Cropland	Cryptobiotic Omnivores	1
Sericomyrmex sp.2	Cropland	Non leaf cutting Fungus growing Ants	3
Sericomyrmex sp.3	Cropland	Non leaf cutting Fungus growing Ants	2
Solenopsis sp.B	Cropland	Epigaeic Omnivores	1
Solenopsis sp.C	Cropland	Epigaeic Omnivores	1
Solenopsis sp.F	Cropland	Epigaeic Omnivores	5
Solenopsis sp.G	Cropland	Epigaeic Omnivores	1
Trachymyrmex sp.B	Cropland	Non leaf cutting Fungus growing Ants	4
Trachymyrmex sp.C	Cropland	Non leaf cutting Fungus growing Ants	2
Trachymyrmex sp.E	Cropland	Non leaf cutting Fungus growing Ants	2
Trachymyrmex sp.F	Cropland	Non leaf cutting Fungus growing Ants	4
Wasmannia auropunctata	Cropland	Epigaeic Omnivores	1
Acromyrmex sp.A	Forest	Leaf cutting Attini	1
Acromyrmex sp.B	Forest	Leaf cutting Attini	8
Apterostigma sp.1	Forest	Non leaf cutting Fungus growing Ants	1
Atta cephalotes	Forest	Leaf cutting Fungus growing Ants	5
Atta laevigata	Forest	Leaf cutting Fungus growing Ants	1
Atta sp.7	Forest	Leaf cutting Fungus growing Ants	1
Atta sp.8	Forest	Leaf cutting Fungus growing Ants	1
Brachymyrmex sp.1	Forest	Opportunists	1
Camponotus sp.11	Forest	Epigaeic Omnivores	2
Camponotus sp.12	Forest	Epigaeic Omnivores	3
Camponotus sp.13	Forest	Epigaeic Omnivores	1
Camponotus sp.16	Forest	Epigaeic Omnivores	1
Camponotus sp.17	Forest	Epigaeic Omnivores	1
Camponotus sp.2	Forest	Epigaeic Omnivores	1
Camponotus sp.3	Forest	Epigaeic Omnivores	1
Camponotus sp.4	Forest	Epigaeic Omnivores	1
Camponotus sp.5	Forest	Epigaeic Omnivores	3
Camponotus sp.6	Forest	Epigaeic Omnivores	1
Camponotus sp.7	Forest	Epigaeic Omnivores	4
Camponotus sp.9	Forest	Epigaeic Omnivores	3
Crematogaster sp.A	Forest	Arboreal Dominants	3
Dolichoderus imitator	Forest	Arboreal Dominants	2
Ectatomma edentatum	Forest	Epigaeic Predators	2
Ectatomma sp.1	Forest	Epigaeic Predators	1
Gigantiops destructor	Forest	Epigaeic Omnivores	8
Gnamptogenys sp.1	Forest	Epigaeic Predators	2
Hypoponera sp.1	Forest	Cryptobiotic Predators	1
Linepithema sp.1	Forest	Epigaeic Omnivores	1
Mayaponera constricta	Forest	Epigaeic Predators	1
Neoponera sp.1	Forest	Epigaeic Predators	10

Species	Riparian forest treatment	Functional Group	N
Nylanderia sp.1	Forest	Epigaeic Omnivores	6
Nylanderia sp.2	Forest	Epigaeic Omnivores	1
Odontomachus sp.1	Forest	Epigaeic Predators	1
Pachycondyla sp.1	Forest	Epigaeic Predators	7
Pachycondyla sp.2	Forest	Epigaeic Predators	4
Pachycondyla sp.3	Forest	Epigaeic Predators	1
Pheidole sp.A	Forest	Epigaeic Omnivores	4
Pheidole sp.B	Forest	Epigaeic Omnivores	3
Pheidole sp.H	Forest	Epigaeic Omnivores	1
Pheidole sp.i	Forest	Epigaeic Omnivores	1
Pheidole sp.J	Forest	Epigaeic Omnivores	1
Pheidole sp.K	Forest	Epigaeic Omnivores	2
Pheidole sp.Q	Forest	Epigaeic Omnivores	8
Pheidole sp.R	Forest	Epigaeic Omnivores	5
Pheidole sp.U	Forest	Epigaeic Omnivores	1
Pheidole sp.V	Forest	Epigaeic Omnivores	2
Sericomyrmex sp.3	Forest	Non leaf cutting Fungus growing Ants	1
Solenopsis sp.B	Forest	Epigaeic Omnivores	1
Solenopsis sp.C	Forest	Epigaeic Omnivores	1
Solenopsis sp.D	Forest	Epigaeic Omnivores	5
Solenopsis sp.E	Forest	Epigaeic Omnivores	1
Trachymyrmex sp.D	Forest	Non leaf cutting Fungus growing Ants	1

4 CONCLUSÃO GERAL

Nesta tese investiguei as funções ecossistêmicas desempenhadas pela fauna que contribuem para a regeneração natural de florestas degradadas da Amazônia. Para isso, comparei florestas degradadas por múltiplos distúrbios com florestas de referência. Embora a literatura aponte para diferenças notórias entre essas florestas nas comunidades de fauna e flora, as funções ecossistêmicas foram pouco sensíveis ao estágio de conservação florestal.

No primeiro capítulo, eu e meus colaboradores investigamos os efeitos da adição de fezes de antas e dos mecanismos subjacentes a essa adição sobre o recrutamento de plântulas. Nossos resultados indicam que, independentemente do estado de degradação florestal, as antas são capazes de promover a regeneração natural de florestas degradadas por mecanismos complementares: a melhora na saúde do solo e o recrutamento de plantas. A abundância de plantações de soja na paisagem da área de estudos foi determinante para nossos resultados. Quando presente, as antas tinham livre acesso às plantações e se alimentaram de partes vegetais dessas plantas, o que fez com que as suas fezes fossem formadas exclusivamente por partes de soja. As sementes de plantas nativas foram ausentes nas fezes durante esse período, o que limitou o recrutamento de plantas. No entanto, as fezes ainda foram responsáveis pela melhora na saúde do solo abaixo delas, com os aumentos de fósforo, biomassa microbiana e proporção de fungos. As antas se alimentaram de plantas nativas durante o período sem soja na paisagem, o que resultou no recrutamento de plantas a partir de sementes contidas em suas fezes. Portanto, destacamos a importância bivalente das antas como ferramentas para atenuar limitações de dispersão de sementes e de estabelecimento de plantas.

No segundo capítulo, nós exploramos funções ecossistêmicas relacionadas à dispersão de sementes e ao estabelecimento de plantas para responder porque a riqueza de plantas em florestas ripárias circundadas por plantações é menor do que em florestas ripárias sem distúrbios. Para isso, investigamos a frugivoria (como indicador potencial de dispersão de sementes), a predação de sementes pós-dispersão e a predação de insetos herbívoros. De maneira geral, não observamos efeitos do tipo de floresta ripária, se circundada por plantações ou sem distúrbios, sobre as funções ecossistêmicas. No entanto, nós observamos uma menor frugivoria por aves em florestas ripárias circundadas por plantações, resultados que são correlacionados com a menor abundâncias de aves frugívoras nesses locais. A dispersão de sementes por aves é uma das principais maneiras de superar a limitação de sementes em florestas degradadas. Assim, a menor riqueza de plantas em florestas ripárias circundadas por plantações pode ser devida à baixa dispersão de sementes por aves nesses locais. Considerando que a predação de sementes e a herbivoria – função que controla populações de herbívoros e indiretamente diminui a herbivoria – foram equivalentes entre as florestas ripárias, é provável que a riqueza de plantas seja limitada pela dispersão de sementes, já que esses filtros de estabelecimento tendem a se manterem em níveis próximos.

Em um contexto de preocupação crescente para mitigar impactos antrópicos sobre ecossistemas naturais e frear mudanças climáticas, nossos resultados demonstram que a fauna pode contribuir significativamente para esse fim. A baixa sensibilidade das funções ecossistêmicas frente a distúrbios reforça que a fauna pode ser uma importante ferramenta para regeneração de florestas degradadas. Deste modo, passivos ambientas e programas de restauração de áreas degradadas podem incluir e potencializar a fauna como promovedoras e auxiliares de regeneração natural.