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Anthropogenic impacts on animal-plant interactions and their ecosystem functions in tropical forests

Jefferson Bruno Bretas de Souza Oliveira
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JEFFERSON BRUNO BRETAS DE SOUZA OLIVEIRA

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Thesis submitted to the Ecology Graduate Program of the Universidade Federal de Viçosa in partial fulfillment of the requirements for the degree of *Doctor Scientiae*.

Adviser: Lucas Navarro Paolucci

Co-advisers: Wesley F. D. da Cruz
Hernani F. M. de Oliveira

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Assent:

Jefferson Bruno Bretas de Souza Oliveira
Author

Lucas Navarro Paolucci
Adviser

A todos aqueles que buscam algo mais... sim, é possível.

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Fazer ciência é algo maravilhoso e enriquecedor, ao mesmo tempo que pode ser conturbado e assustador. Apesar do nosso nome estar como primeiro autor, este trabalho é tão nosso quanto dos et al. Portanto, agradeço ao meu orientador **Lucas Paolucci**, o qual sei que aceitou me orientar acreditando ser um trabalho fácil e que se mostrou ser mais desafiador do que o esperado. Agradeço imensamente a ajuda e compreensão quando precisei e pela resiliência e paciência em continuar me ensinando mesmo quando não mais parecia ter jeito. Ao **Hernani**

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É interessante contemplar uma margem emaranhada, coberta com muitas plantas de vários tipos, com pássaros cantando nos arbustos, com vários insetos voando e com vermes rastejando pela terra úmida, e refletir que essas formas elaboradamente construídas, tão diferentes umas das outras, e dependentes uns dos outros de uma maneira tão complexa, todos foram produzidos por leis que atuam ao nosso redor
(Charlie Darwin) ...
e sabendo disso... a vida, ela sempre encontra um meio (Dr. Ian Malcolm).

ABSTRACT

OLIVEIRA, Jefferson Bruno Bretas de Souza, D.Sc., Universidade Federal de Viçosa, March, 2025. **Anthropogenic impacts on animal-plant interactions and their ecosystem functions in tropical forests**. Adviser: Lucas Navarro Paolucci. Co-advisers: Wesley Francisco Dáttilo da Cruz and Hernani Fernandes Magalhães de Oliveira.

Tropical forests are fundamental for providing ecosystem services essential to human subsistence, socioeconomic development, and the maintenance of biodiversity. These services depend on ecological interactions, especially between plants and animals, sustaining ecosystem functionality and resilience. However, the increasing intensification of land use — driven by both human population growth and capital accumulation — has led to severe disturbances in these forests. As a result, the advancement of anthropogenic pressures has caused continuous degradation of forest habitats, thereby altering their structure and dynamics. Such changes have increased forest vulnerability to new disturbances, leading to a rise in the frequency and intensity of fire. Consequently, habitat structure modifications and biodiversity loss resulting from these impacts can disrupt species interaction patterns and compromise ecological processes related to reproduction, seed dispersal, and the structuring of plant communities. As a result, forest regeneration and functionality may be impaired, even years after the initial impacts. Therefore, to better understand the effects of anthropogenic impacts on tropical forests, it is necessary to assess how human activities influence ecological interactions. In this thesis, I investigate the effects of different anthropogenic disturbances on animal–plant interactions mediated by pollinators, frugivores, and secondary post-dispersal agents in tropical forests. To this, I developed two chapters that evaluate the impacts of land-use change and fire on these interactions. In the first chapter, I used data from the literature on plant–pollinator networks in different tropical forests to assess the effects of land-use change on pollinator interaction patterns and their resistance to the extinction of floral partners. I found that pollinators in disturbed forests interacted with fewer partners and were less resistant to coextinctions than pollinators in old-growth forests. However, there was no difference in these metrics between pollinators in converted forests and those in either disturbed or old-growth forests. Despite these differences, I found no difference across treatments in network structural organization as measured by nestedness. In the second chapter, I evaluated the long-term impacts of fire and edge effects, or they synergy, on frugivory frequency and secondary seed removal by fauna, 12 years after a forest fire event. Arboreal frugivory was not affected by fire or edge effects, but terrestrial frugivory was intensified in unburned edges. There was a general reduction in seed manipulation by the entire fauna in burned treatments. However, when only invertebrates were considered, there was no difference in seed manipulation between the unburned edge and the burned interior. These findings indicate that forest habitat changes caused by anthropogenic disturbances lead to shifts in animal–plant interaction patterns, with potential implications for the functioning of forest ecosystem processes — even long after the initial disturbances. Therefore, despite the resilience observed in certain interactions, continued anthropogenic pressures in tropical forests may increase their vulnerability by disrupting key ecological interactions and altering interaction patterns.

Keywords: ecological disturbances; ecological dynamics; ecological networks; forest fires; forest resilience

RESUMO

OLIVEIRA, Jefferson Bruno Bretas de Souza, D.Sc., Universidade Federal de Viçosa, março de 2025. **Impactos antrópicos em interações animal-planta e suas funções ecossistêmicas em florestas tropicas**. Orientador: Lucas Navarro Paolucci. Coorientadores: Wesley Francisco Dáttilo da Cruz e Hernani Fernandes Magalhães de Oliveira.

As florestas tropicais são fundamentais para a provisão de serviços ecossistêmicos essenciais à subsistência humana, ao desenvolvimento socioeconômico e à manutenção da biodiversidade. Esses serviços dependem, em grande parte, de interações ecológicas, especialmente daquelas entre plantas e animais, que sustentam a funcionalidade e resiliência dos ecossistemas. Contudo, a crescente intensificação do uso da terra , impulsionado tanto pelo crescimento populacional humano quanto pelo aumento na acumulação por capital, tem provocado perturbações intensas nestas florestas. Logo, o avanço da antropização tem resultado na degradação contínua de habitats florestais, alterando assim a estrutura e a dinâmica dessas florestas. Tais mudanças aumentaram a vulnerabilidade das florestas a distúrbios, acarretando no aumento da frequência e intensidade do fogo. Consequentemente, modificações na estrutura do habitat e a perda da biodiversidade decorrentes destes impactos podem alterar os padrões de interações entre espécies e comprometer os processos ecológicos relacionados a reprodução, dispersão e estruturação da comunidade vegetal. Como resultado, a regeneração e funcionalidade das florestas são potencialmente comprometidas, mesmo anos após os impactos. Portanto, para melhor entendermos os efeitos dos impactos antropogênicos em florestas tropicais, é necessário avaliarmos como as atividades humanas influenciam interações ecológicas. Nesta tese, investigo os impactos de diferentes perturbações antropogênicas em interações animal-planta mediados por polinizadores, frugívoros e agentes secundários pós-dispersão em florestas tropicais. Para isto, elaborei dois capítulos que avaliam os impactos de mudanças no uso da terra e do fogo nessas interações. No primeiro capítulo utilizei dados da literatura sobre redes planta-polinizador de diferentes florestas tropicais para avaliar os efeitos das mudanças no uso da terra sobre os padrões de interação de polinizadores e sua resistência à extinção de parceiros florais. Observei que os polinizadores em florestas perturbadas estabeleceram interações com menos parceiros e foram menos resistentes às coextinções do que os polinizadores em florestas antigas. Entretanto, não houve diferença em tais métricas entre polinizadores em florestas convertidas e os polinizadores em florestas antigas ou perturbadas. Apesar disso, não observei diferença entre os tratamentos na organização estrutural das redes medida pelo aninhamento. No segundo capítulo, avaliei os impactos crônicos do fogo em sinergia com os efeitos de borda na frequência de frugivoria e na manipulação secundária de sementes pela fauna 12 anos após a queima florestal. A frugivoria arbórea não foi afetada pelo fogo ou pela borda, mas a frugivoria terrestre foi intensificada pela borda não queimada. Houve redução na manipulação de sementes por toda a fauna nos tratamentos queimados. Entretanto, quando apenas os invertebrados foram avaliados, não houve diferença na manipulação de sementes entre a borda não queimada e o interior queimado. Esses resultados indicam que mudanças em habitats florestais devido a distúrbios antrópicos causam mudanças nos padrões em interações animal-planta, com possíveis implicações para o funcionamento dos processos ecossistêmicos florestais, mesmo em longos períodos após os impactos. Portanto, apesar da resiliência de determinadas interações, a antropização contínua de florestas tropicais pode aumentar sua vulnerabilidade ao interromper parte das interações ecológicas e alterar os padrões de interações.

Palavras-chave: distúrbios ecológicos; dinâmicas ecológicas; incêndios florestais; redes ecológicas; resiliência florestal

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SUMÁRIO

1 GENERAL INTRODUCTION

Tropical forests comprise the most extensive forests globally, accounting for 45% of all forested areas (PAN *et al.* 2013; FAO 2020). They are a complex mosaic of habitats ranging from herbaceous layers to high-canopy arboreal strata, resulting in highly heterogeneous and biodiverse systems (BARLOW *et al.* 2007; DE BRUYN *et al.* 2014; SLIK *et al.* 2015). Despite their limited geographical distribution, tropical forests are crucial for supporting essential ecosystem functions and services for wildlife and human populations. They are important stores of atmospheric carbon globally (PUTZ *et al.* 2008; SAATCHI *et al.* 2011), and are key for climate regulation, biogeochemical, nutrient and hydrological cycles (ARTAXO *et al.* 2022; LEFEUVRE *et al.* 2022). Furthermore, tropical forests provide critical resources for human subsistence and socioeconomic production, such as food provision and raw materials, mainly for developing countries (REED *et al.* 2017; SEIFERT *et al.* 2022). These services underline the importance of tropical forests for human well-being and position them as a target for conservation efforts and a sustainable future (EDWARDS *et al.* 2019; BOUL LEFEUVRE *et al.* 2022).

Tropical forests' complexity is critical for their functionality (BARLOW *et al.* 2007; GIBSON *et al.* 2011; SEIFERT *et al.* 2022). Ecological interactions, for example, are key mechanisms for the dynamics and maintenance of these forests: they are limiting factors responsible for the heterogeneity and diversity of plants due to the control over the establishment of new individuals (JORDANO, 2000; MULLER-LANDAU and HARDESTY, 2005). For instance, pollination is essential for most wild flowering plants' fruit and seed production (BAWA, 1990) and to increase agricultural yields (RICKETTS, 2004; BLANCHE *et al.* 2006; VERGARA and BADANO, 2009). Similarly, frugivory is the primary seed dispersal mechanism that contributes to the distribution and diversity maintenance of plant species and, consequently, improve ecosystem functions supported by the vegetation community such as carbon storage, nutrient cycling, and the regeneration of degraded areas (HEYMANN *et al.* 2019; VILLAR *et al.* 2021; BELLO *et al.* 2024). In addition, post-dispersal manipulation of seeds — whether through predation or secondary dispersal — acts as a complementary mechanism to primary seed dispersal: it helps to regulate the distribution and heterogeneity of plant species by controlling the establishment, composition and structure of vegetation (PAINE and BECK, 2007; TERBORGH, 2012). Thus, plant-animal interactions are a key factor for tropical forests due to a cascade of ecological processes that ensure their conservation (MORRIS, 2010; TERBORGH, 2012; CULOT *et al.* 2017). Therefore, understanding how multiple threats affect plant-animal interactions can result in appropriate conservation guidelines (TEIXIDO *et al.* 2022).

The ecological dynamics and high biodiversity of tropical forests are central factors for forest resilience to disturbances (SILVER *et al.* 1996; COLE *et al.* 2014; CIEMER *et al.* 2019). However, the increasing demand for resources, primarily driven by human population growth and capital accumulation, mainly based on illegal or non-sustainable practices, has intensified land-use changes globally such that most tropical forests have some history of disturbance (WRIGHT and MULLER-LANDAU, 2006; TYUKAVINA *et al.* 2016; LAPOLA *et al.* 2023). As a result, the different threats faced by tropical forests have altered their dynamics and reduced their functionality, mainly due to impacts on their ecosystem functions (RISWAN and HARTANTI, 1995; BOWMAN *et al.* 2020). For instance, fragmentation due to intensive deforestation in recent decades - whether due to agricultural practices, livestock farming or urbanization - has drastically reduced forest cover, increased isolation and expanded edges, characterized by higher temperatures and lower humidity (LAURANCE, 2004; BROADBENT *et al.* 2008; TABARELLI *et al.* 2008). These impacts have resulted in forest simplification through the loss of late-successional tree species and the proliferation of small pioneer species (LOPES *et al.* 2009), as well as the loss of specialized forest fauna and an increase of exotic generalists adapted to open habitats (SALES *et al.* 2020).

The ongoing simplification of tropical forests, in conjunction with extreme weather events—such as increasingly prolonged and frequent drought periods—has significantly altered wildfire dynamics (SILVÉRIO *et al.* 2019; BRANDO *et al.* 2020a). For instance, fires in tropical forests can occur naturally, but with a very long interval (500–1000 years) (PIVELLO, 2011). However, deforestation by agricultural intensification and logging has increased the intensity and frequency of fires, even in remote and isolated forests (SILVA *et al.* 2023; BOURGOIN *et al.* 2024). Despite the isolated impacts of both anthropogenic mechanisms, the effects of fragmentation, such as forest edges, can act as a catalyst for fire and intensify the effects of disturbances (MENEZES *et al.* 2019; DRISCOLL *et al.* 2021), such as increased tree mortality, canopy opening, high temperatures, and invasion of exotic species (BALCH *et al.* 2008, 2009; BRANDO *et al.* 2012). In the Arc of Deforestation in the southern Brazilian Amazon, for example, logging and forest fires are the main disturbance agents, with 16 % of forest areas expected to be burned in the coming years (BRANDO *et al.* 2020b). Consequently, the synergy of recurrent anthropogenic actions may drive the conversion of tropical forests into a state increasingly vulnerable to disturbances (SIlVÉRIO *et al.* 2013; BALCH *et al.* 2015; ARASA-GISBERT *et al.* 2024), which also increases the vulnerability of forest species (STORK *et al.* 2009; FENG *et al.* 2021).

Anthropogenic environmental changes are the main drivers of biodiversity loss in tropical forests (WRIGHT and MULLER-LANDAU, 2006; SALES *et al.* 2020). Additionally, the effects of anthropization on forest functionality ultimately result from impacts on the ecological interactions mediated by species' responses to changes in their habitat (MORRIS, 2010; NEUSCHULZ et al., 2016), leading to loss of ecological functions (FRANÇA *et al.* 2017). For pollinators, changes in landscape structure due to land-use influences affect the availability of essential resources such as flower species (MOREIRA *et al.* 2018). These changes can affect the foraging strategies of pollinators, lead to the loss of species sensitive to habitat changes, and promote the dominance of generalist species, thereby reshaping interaction patterns (FERREIRA *et al.* 2015, 2020). Such shifts in plant-pollinator communities and their interactions have significant implications for the resilience of pollinators to the loss of floral partners (SRITONGCHUAY *et al.* 2019; LÓPEZ-FLORES *et al.* 2023). Consequently, less efficient pollination systems may emerge in disturbed forests or for dependent crops (LOPES *et al.* 2009; VERGARA and BADANO, 2009; SOARES *et al.* 2022). Therefore, understanding the impacts of land-use change on pollinator interaction patterns is crucial for the persistence of species and forest ecosystems (NEUSCHULZ *et al.* 2016; SRITONGCHUAY *et al.* 2019; LÓPEZ-FLORES *et al.* 2023).

In a similar way, fire can shape the plant-animal interactions through changes in the forest community and influence the associated ecological processes (BALLARIN *et al.* 2023; JONES *et al.* 2023). For instance, fire can reduce the diversity of fruiting species and limit the availability of fruits and seeds, especially at forest edges where the effects of fire are more severe (CURY *et al.* 2020; SHI *et al.* 2022; BRANDO *et al.* 2024). Furthermore, in addition to the increased mortality of vertebrates (BARLOW and PERES, 2004, 2006) and invertebrates (HAUGAASEN *et al.* 2003; SILVEIRA *et al.* 2010, 2012), structural changes in the forest due to vegetation loss by fire tricky the movement and persistence of dense-dependent species on vegetation (LAPPAN *et al.* 2020). This may lead to immediate or long-term population declines and even extinctions of less resilient species to habitat changes, and favor generalist species adapted to open habitats. These shifts can affect the establishment of plant-animal interactions mediated by frugivores (BARLOW and PERES, 2006; CHAVES *et al.* 2022; ROSSI *et al.* 2024) and secondary agents (PAOLUCCI *et al.* 2016; CAZETTA and VIEIRA, 2021), and limit forest restoration (AIDE and CAVELIER, 1994). Although previous studies have investigated the impacts of fire on forest species, our understanding of how these changes affect plant-animal interactions remains limited (e.g., BALLARIN *et al.* 2023), particularly when considering the synergistic effects of fire with forest edge dynamics (but see ROSSI *et al.* 2024).

1.1 OBJECTIVES

One of the central goals of ecology has been to understand how anthropogenic environmental disturbances influence species interaction patterns and, consequently, their ecological processes (WARDLE *et al.* 2011; VALIENTE-BANUET *et al.* 2014; TEIXIDO *et al.* 2022). Although the ongoing forest anthropization drives changes in plant-animal interaction and the consequent decline of forest functions (SOARES *et al.* 2015), disturbed forests can retain high ecological value by providing essential ecological services (MALHI *et al.* 2022). Therefore, due to the increasing human encroachment into natural habitats, understanding how anthropogenic disturbances affect ecological interactions in tropical forests is crucial for developing effective conservation strategies for forests under land-use changes (MALHI *et al.* 2014). Thus, the objective of this thesis was to evaluate the impacts of different anthropogenic disturbances on plant-animal interactions performed by pollinators, frugivores, and post-dispersal secondary agents in tropical forests. For this purpose, this thesis was organized into two chapters:

Chapter 1 - Anthropogenic impacts on plant-pollinator networks of Tropical Forests: implications for pollinator coextinction: Using ecological networks, we investigated the impacts of land-use changes in tropical forests on pollinator interaction patterns and their resistance to the extinction of their floral partners. For this, we used data compiled from the literature on forests in different regions.

Chapter 2 - Fire and edges in the Amazon: impacts on key animal-plant interactions to forest regeneration: Using a controlled burn experiment in a southern Amazonian forest, we investigated the impacts of fire and its synergistic effects with forest edges on the establishment of plant-animal interactions mediated by frugivorous animals and post-dispersal secondary agents.

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2 CHAPTER 1

Anthropogenic impacts on plant-pollinator networks of tropical forests: implications for pollinators coextinction

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Anthropogenic impacts on plant-pollinator networks of tropical forests: implications for pollinators coextinction

Jefferson Bruno B. S. Oliveira[1], **Hernani F. M. Oliveira**[2], **Wesley Dáttilo**[3], **Lucas N. Paolucci**[4]

[1] Programa de Pós-Graduação em Ecologia, Departamento de Biologia Geral, Universidade Federal de Viçosa, Viçosa, MG, Brazil. ORCID 0000-0002-5392-6080

[2] Departamento de Zoologia, Universidade Federal do Paraná, UFPR, Curitiba, PR, Brazil. ORCID 0000-0001-7040-8317

[3] Red de Ecoetología, Instituto de Ecología AC, Xalapa, Veracruz, Mexico. ORCID 0000-0002-4758-4379

[4] Departamento de Biologia Geral, Universidade Federal de Viçosa, Viçosa, MG, Brazil. ORCID 0000-0001-6403-5200

Correspondence author: Jefferson Bruno B. S. Oliveira - jeffersonbrunoxd@gmail.com; jefferson.oliveira@ufv.br

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2.2 Abstract

Anthropogenic changes in natural habitats are one of the main causes of disruptions in plant-pollinator interaction due to plant community alterations, which can affect pollinator persistence. However, pollinators can expand their interactions by exploring alternative resources to compensate for already-established partners' loss. Ecological networks have been used to investigate interactions between species and the effects of environmental impacts on them. However, although tropical forests are threatened by anthropogenic activities worldwide, there is a limited representation of tropical pollination networks in existing evidence. We surveyed literature data for plant-pollinator networks from different tropical regions to assess the impacts of land-use changes on pollinator interaction patterns and their resistance to coextinctions. We hypothesized that pollinators in anthropized tropical forests establish interactions with more partner plants than pollinators in old-growth forests; pollinator networks in anthropized tropical forests are more nested than networks in old-growth forests; pollinators in anthropized tropical forests are more resistant to the extinction of their partners than pollinators in old-growth forests. Contrary to our expectations, we did not observe an effect of anthropization on the structural organization of networks. Furthermore, pollinators in disturbed forests established interactions with fewer partners and were less robust to coextinctions than in old-growth forests. However, there was no difference in the establishment of interactions or the resistance to coextinctions between pollinators in converted forests and pollinators in old-growth or disturbed forests. These results indicate the negative effects of anthropization on establishing interactions and pollinator resistance to coextinctions despite no impact on network assembly.

Keywords: Ecological interactions; Network topology; Plant-pollinator dynamics; Species loss; Tropical forest disturbances

2.3 Introduction

Tropical forests play a key role in providing ecosystem services such as carbon sequestration and climate regulation (Putz et al. 2008; Artaxo et al. 2022), as well as in food provision (Reed et al. 2017; Lefeuvre et al. 2022). For that, these forests depend on species and their interactions - such as those carried out by pollinators (Ollerton et al. 2011; Silva et al. 2021) - which are sensitive to anthropogenic changes (Bello et al. 2015; Neuschulz et al. 2016). Currently, land-use changes are quickly transforming tropical forests: anthropization has resulted in a rise in disturbed forests and habitats extensively used for human activities (Turubanova et al. 2018; Edwards et al. 2019). Hence, these changes can trigger species loss, leading to an impoverishment of ecosystem services (Murphy et al. 2022; Millard et al. 2023) and a decrease in forest regeneration (Neuschulz et al. 2016).

The decline of pollinators has become a critical issue for their conservation (Dicks et al. 2021). The conversion of natural habitats to semi-natural states or anthropogenic habitats, such as urbanization and agricultural use, is a key driver of pollinator extinction (Potts et al. 2010; Harrison and Winfree 2015). These activities caused significant environmental changes, including habitat loss and a reduction in floral resources (Wenzel et al. 2020; Millard et al.

2021). As pollinators depend on interactions with their plant partners (Ghazoul 2006; Tinoco et al. 2017), changes in floral composition due to land-use changes can modulate the risk of coextinction among pollinators (Ferreira et al. 2013; Sánchez-Bayo and Wyckhuys 2019). Therefore, the resistance of pollinators to coextinctions in anthropogenic habitats depends on how land-use changes impact plant-pollinator interaction patterns (Morris 2010; López-Flores et al. 2023).

Ecological networks can be used to investigate the impacts of anthropization on how species interact and how these impacts can affect coextinction events (Weiner et al. 2014; Araújo et al. 2016; Adedoja and Kehinde 2018). For example, in natural conditions, networks as those of pollination, are frequently nested: species that engage in few interactions are connected to the rest of the community by their interactions with a subset of highly interactive species, while interactions between specialists rarely occur (Bascompte et al. 2003). In addition, models with large-scale networks found that mutualistic networks become increasingly nested as human influence increases (Sebastián-González et al. 2015; Takemoto and Kajihara 2016). How nested networks arise or influence the diversity or persistence of species is a subject of extensive and controversial debate (Thebault and Fontaine 2010; Saavedra et al. 2016; Valdovinos et al. 2016; Strona 2022). However, nestedness can reflect some processes in network dynamics, such as species coexistence and interaction asymmetry (Bascompte et al. 2006; Bascompte and Jordano 2007; Bastolla et al. 2009). Thus, this structural property can unravel mechanisms that explain how environmental changes affect species interactions and their resistance to coextinction (Burgos et al. 2007; Vanbergen et al. 2017; Ren et al. 2023).

Land-use changes can alter ecological networks through disturbance-adapted species influencing the architecture of these networks (Doré et al. 2021; Agüero et al. 2022). For example, the initial loss of species mainly affects specialized pollinators sensitive to the loss of specific partners (Rader 2014; Weiner et al. 2014). In contrast, generalist pollinators are more resistant to disturbance due to their flexibility in rewiring interactions with available plants, thereby avoiding coextinctions (Valdovinos et al. 2013; Sheykhali et al. 2020; Vizentin-Bugoni et al. 2020). As a result, generalist pollinators often dominate and contribute to an increase in the number of interactions within plant-pollinator networks in anthropogenic habitats (Burkle et al. 2013; Doré et al. 2021). Consequently, the pollinator community in these habitats tends to comprise highly connected species, forming networks resistant to coextinctions (Deguines et al. 2012; Baldock et al. 2019).

Despite advances in the study of ecological networks, much of the research has focused on non-tropical regions (Vizentin-Bugoni et al. 2018). Few studies have addressed pollinator persistence patterns (e.g., Millard et al. 2021, 2023) or the effects of human disturbances on pollination networks across tropical regions (but see Sebastián-González et al. 2015; Takemoto and Kajihara 2016; Doré et al. 2021). As a result, our understanding of the consequences of anthropization on plant-pollinator tropical forest networks remains limited and underrepresented (Moreira et al. 2018; Wenzel et al. 2020). This underrepresentation may confound our understanding of pollinator persistence in tropical forests, mainly due to habitat differences. For example, temperate forests have a longer history of land-use change compared to tropical forests (Klein Goldewijk et al. 2011), giving more time for species and their interactions to adapt to changes (Burkle et al. 2013; Newbold et al. 2020). Due to such differences, recent studies have shown that pollinators in temperate habitats are adapting to land-use changes, while tropical pollinators are negatively impacted (Millard et al. 2021, 2023).

Based on a dataset compilation of tropical forests' pollination networks documented across different regions, we investigated if land-use changes affect pollinator-plant interactions and the resistance of pollinators to coextinctions. We hypothesized that: (i) pollinators in anthropized tropical forests establish interactions with more partner plants than pollinators in old-growth forests; (ii) pollinator networks in anthropized tropical forests are more nested than pollinator networks in old-growth forests; (iii) pollinators in anthropized tropical forests are more resistant to the extinction of their partner plants compared to pollinators in old-growth forests (Fig. 1).

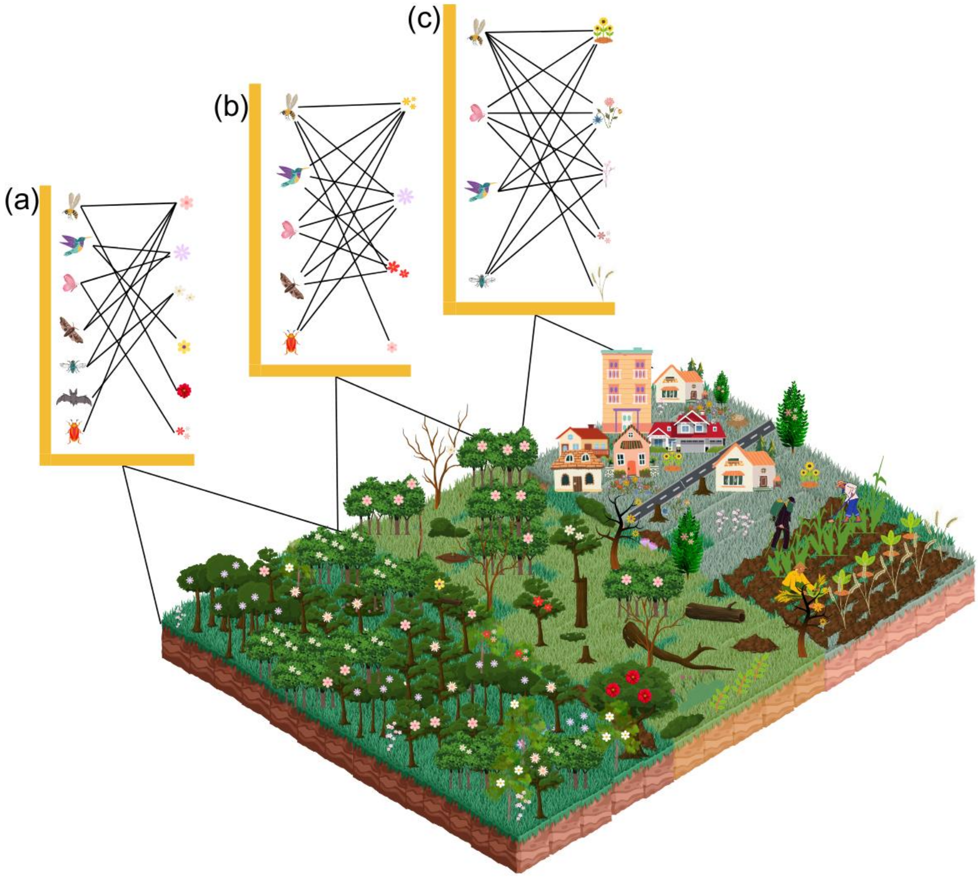

Fig. 1 Schematic representation of the different land-use categories we studied and their expected effects on the patterns of interactions in pollination networks: (a) old-growth forest; (b) disturbed forest; (c) converted forest. Pollination networks in anthropogenic forests, including disturbed forests and those converted to urban areas or agricultural land, are expected to establish more interactions and become more nested and more resistant to coextinctions

2.4 Methods

2.4.1 Data compilation

We sampled pollinator networks from tropical forests compiled from published papers, dissertations, and theses. To compile the data, we used the following search terms on Google Scholar and Web of Science with Boolean operators: network* OR interaction* AND plant* AND pollination OR pollinator* AND tropical forest OR rainforest. We considered the first 500 articles from each search engine, yielding 1,000 studies. The search was conducted in October 2021, and all studies from previous years up to that date were included. To expand our search, we compiled data from previous reviews that used similar search methods:

Schleuning et al. (2012), Takemoto and Kajihara (2016), and Moreira et al. (2020). These studies searched networks in different years and included other search engines and broadly searched networks in databases such as GlobalWeb (www.globalwebdb.com) and Interaction Web Database (www.nceas.ucsb.edu/interactionweb). This inclusion added 134 studies to our sample.

Most of the studies collected considered any interaction between the visitor and the flower as a sign of potential pollination. Therefore, we also considered all the networks presented here to be pollination networks, given the potential of flower visitors to pollinate when interacting with a flower (Vieira et al. 2013). There is a continuum in pollination networks: even if a particular visitor species has low pollination effectiveness for a particular flower species, that visitor species may still contribute to the pollination of that flower, even to a lesser degree. Furthermore, visitor species may effectively pollinate other flowers in the network. Thus, plant-visitor networks represent a pollination system in which pollinators interact with and depend on flowers they do not pollinate (see Rosas-Guerrero et al. 2014; Santiago-Hernández et al. 2019; Lima et al. 2020). Therefore, encompassing all interactions provides a more comprehensive description of the responses of pollinators to environmental changes.

2.4.2 Data filtering

We filtered studies based on a four-step selection criterion that we established (Table S1; Fig. S1). This filtering consisted of: (1) the exclusion of repeated studies; (2) exclusion based on the title review; (3) exclusion based on the abstract review; (4) exclusion based on the full paper review. From these steps, we selected only studies that: (a) were conducted in tropical forests; (b) represented interactions between pollinator species and their respective partner plants (e.g., through tables or graphs; studies with graphs where we could not extract which species interacted were not included); (c) included networks with at least five plant species and five pollinator species (e.g., Moreira et al. 2020; Doré et al. 2021); (d) described the habitat conservation or provided ways for its assessment (e.g., geographic coordinates or cited studies describing the studied habitat). Because some studies had more than one network, to ensure independence and avoid spatial correlation in our analysis, we treated networks located within less than 1 km of each other as a single network. Additionally, to increase the scope and representation of our study, we included studies with different pollinator groups (e.g., Apoidea, Lepidoptera, and Trochilidae).

2.4.3 Land-use categories

We classified the selected networks according to the type of forest conservation: old-growth forests: defined here as a primary tropical forest or a secondary tropical forest in an advanced stage of regeneration; disturbed forests: defined here as a tropical forest impacted by anthropogenic activities (secondary forests in the initial regeneration stage or under anthropogenic pressure such as deforestation and fragmentation); and converted forest: defined here has an area that was a tropical forest, but has been completely converted to human use (i.e., cropland, urban areas such as urban gardens, residential gardens, etc.). We classified primary forests and secondary forests in an advanced stage of regeneration in the same category because, in addition to their ecological proximity, a large proportion of tropical forests are not pristine (i.e., without any human intervention) or are rarely sampled, which makes difficult to distinguish between these two forests types (Tyukavina et al. 2016; Turubanova et al. 2018; Grantham et al. 2020).

We classified the locations where networks were observed based on the descriptions provided in the respective study from which the networks were extracted or verified by reviewing the characteristics of the sites in studies conducted in the same place. To ensure the conservation status of all studied sites, we utilized the Global Forest Watch (GFW) online platform (www.globalforestwatch.org). GFW provides a map and several tools to monitor global forest change based on geographic coordinates. To check the categorization of each location, we used the Forest Landscape Integrity Index (FLII). The FLII uses several indicators of anthropogenic change, including forest loss, fragmentation, and human disturbance, which provide information that reflects the level of forest integrity (Grantham et al. 2020). Additionally, we used the Primary Forest Extent Map provided by the GWF. This map supplies a dataset indicating the extent of regions featuring primary forests characterized by low or no human interference within the tropical region (Turubanova et al. 2018).

2.4.4 Networks construction

Due to the limited availability of weighted data in the studies (number of interactions between two species), we created a binary adjacency matrix for each selected network (presence and absence of interactions). Binary matrices indicate only the interactions between species without considering the weight of these interactions. This is an approach used in previous studies to avoid data loss as many network studies have only binary data (e.g., Takemoto and Kajihara 2016; Moreira et al. 2020). In addition, most of the assembled studies focused only on a specific group of pollinators (e.g., only Apoidea or only Trochilidae). As comprehensive networks and partial networks can differ in their established patterns (Vizentin-Bugoni et al. 2018), we separated networks that included mixed groups of pollinators into individual networks for each taxonomically related group to control for biases in the effects. These new networks were also subject to the previously mentioned selection criteria.

2.4.5 Network metrics

We analyzed network descriptors for binary networks to test whether pollinator species in anthropized tropical forests establish a greater number of interactions than those in old-growth forests. In binary networks, a species' number of interactions directly indicates its number of partners. Therefore, the number of interactions is a helpful metric for quantifying partners per pollinator, offering a simple and interpretable measure of interactions (Dunne et al., 2002; Jacquemin et al., 2020). We used the mean degree of pollinators to quantify the interactions per pollinator in the networks. This descriptor calculates the mean connections among species: the degree represents the partners a species interacts with, while the mean degree represents the mean interactions within the evaluated group (i.e., the mean number of pollinator partners in the network). A higher mean degree indicates a greater number of interactions per species. The mean degree was estimated by averaging interactions across all pollinator species and their partner plants in each network. The metric was calculated using the *grouplevel* function from the *bipartite* package in the R software (R Core Team, 2022).

To test whether pollination networks in anthropized forests (post-disturbance networks) are more nested than those in old-growth forests, we calculated the nestedness of networks using the *bipartite* package (Dormann et al. 2008). We used the NODF metric because, unlike other metrics, NODF tends not to overestimate the degree of nestedness in networks (Almeida-Neto et al. 2008). NODF returns values between 0 and 100, where 0 represents a non-nested network, and 100 represents a fully nested network. To allow comparisons between different networks and reduce biases such as network size, we standardized the nestedness of the networks using z-score values, as recommended (e.g., Dáttilo et al. 2016; Takemoto and Kajihara 2016). The z-score values are obtained by comparing the observed networks with the mean of the permutation of 1,000 null models, which is calculated as

$$z = \frac{observed\ nestedness\ - mean\ (null\ network)}{SD\ (null\ network)}.$$

For this, we used the *shuffle.web* null model. This model keeps two properties of networks constant: the number of interactions and the number of links (connectance).

To test whether pollinators in anthropized tropical forests are more resistant to the loss of partner species than those in old-growth forests, we assessed the ability of pollinators to cope with simulated coextinction events by calculating the robustness index (Memmott et al. 2004; Burgos et al. 2007). The robustness index is a network descriptor that measures the rate at which species at one level of the network become coextinct when their interaction partners at the other trophic level of the network become extinct (Dunne et al. 2002; Gaiarsa and Guimarães 2019). The robustness index ranges from 0 to 1: the greater the robustness, the higher the capacity of species from one trophic level to resist extinction of another trophic level. For example, a value of 1 suggests that most pollinator species would not become coextinct, even if a large proportion of plant species were eliminated. On the other hand, a value of 0 suggests that most pollinator species would be coextinct even if a small proportion of the plant species were eliminated. We calculated the robustness of pollinators to random extinction of their partner plants (hereafter "pollinators robustness") by randomizing 100 coextinction models using the *robustness* function of the *bipartite* package (Dormann et al. 2008) of the R software (R Core Team 2022).

2.4.6 Data analysis

We used generalized linear mixed models (GLMM's) to test whether tropical forest degradation affects network metrics. We used the mean degree, pollinators robustness, and nestedness (z-score) as response variables and forest degradation degree as an explanatory variable. We used each study as a random factor to avoid sampling bias due to networks in the same study and sampling region (i,e. observer bias and sampling region variability) (Luna et al. 2022). To compare network metrics between land-use categories, we used the *glmmTMB* package (Brooks et al. 2017) with a gamma distribution for the mean degree of pollinators, gaussian distribution to nestedness (z-score), and beta distribution for pollinators robustness.

To control for residuals and confounding effects, we included network size, plant family richness, latitude, and elevation as covariables in our models. Network size (the total number of species in the network) may influence some interaction network patterns (Rivera-Hutinel et al. 2012; Landi et al. 2018). The richness of plant families may influence species fluctuation (i.e., the more families of sampled plants, the more species of pollinators in the networks) (e.g., Ebeling et al. 2008; Moreira et al. 2020). Latitude and elevation may influence species diversity and patterns of pollinator networks (Ollerton and Cranmer, 2002;

Trøjelsgaard and Olesen, 2013). We tested the models' assumptions using the *DHARMa* package (Hartig et al., 2022). To compare the effects in the models, we use ANOVA with the *car* package (Fox and Weisberg 2019). When the effect of the treatments was observed, we performed post hoc comparisons with the means adjusted by the models using the *emmeans* package (Lenth 2021), applying Tukey's adjustment for comparisons.

2.5 Results

2.5.1 Distribution of pollination networks

After filtering the data (see Methods), our searches returned 28 studies (Fig. S1; Table S2). However, two of these studies were excluded from our analyses, as the samples used in these studies were responsible for an excessive increase in the metrics tested. This probably occurred because one study had an unusually long sampling duration (approximately 32 months), while the other sampled pollen from the bodies of pollinators, which expands both the foraging area and the number of pollinator partners (Wilms et al. (1996) and Chupil (2013), respectively).

We analyzed 49 pollinator networks in tropical forests, compiled from 26 studies conducted across nine countries and three continents (Fig. 2; Table S2; Table S3). Of these studies, 22 were conducted in the Neotropical region (America), one in the Afrotropical region (Africa), and three in the Indomalaya region (Asia). Among all the networks, 18 originated from old-growth forests, 15 from disturbed forests, and 16 from converted forests. These included 27 Apoidea networks (five in old-growth forests, 10 in disturbed forests, and 12 in converted forests), 18 Trochilidae networks (12 in old-growth forests, five in disturbed forests, and one in converted forest), three Lepidoptera networks (one in an old-growth and two in converted forest), and one Diptera network (in a converted forest), (Table S3).

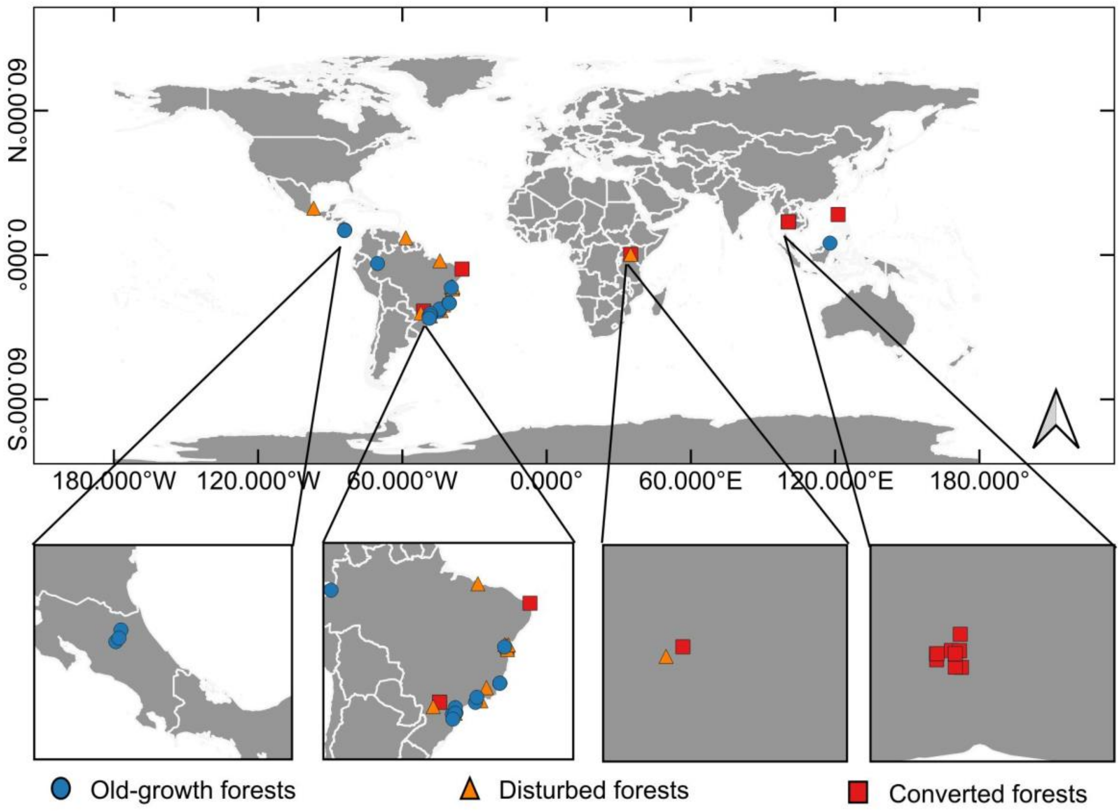

Fig. 2 This map shows the locations of the 49 plant-pollinator networks. A zoom feature is used to focus on areas where points overlap due to the scale of the map. Different colors and shapes represent networks in different land-use categories: blue circles for networks in old-growth forests, orange triangles for networks in disturbed forests, and red squares for networks in converted forests

2.5.2 Effect of anthropization on network metrics

We observed an effect of land-use change on the mean degree of pollinators (Chi = 8.76; DF = 2; $p < 0.02$; Table 1; Figure 3a). Pollinators had a lower mean degree in disturbed forests than in old-growth forests ($p = 0.008$); however, there were no differences with pollinators in converted forests ($p = 0.67$). Furthermore, there were no differences in mean degree between pollinators in old-growth forests and converted forests ($p = 0.27$). Additionally, we did not find an effect of land-use change on network nestedness (Chi = 1.20; DF = 2; $p > 0.54$; Table 1; Figure 3b). Finally, we found an effect of anthropization on pollinators robustness (Chi = 7.94; DF = 2; $p < 0.02$; Table 1; Figure 3c). We observed that pollinators in disturbed forests were less robust than those in old-growth forests ($p = 0.014$), but there was no difference with pollinators in converted forests ($p = 0.85$). We also found no differences in robustness between pollinators in old-growth forests and converted forests (p = 0.12).

Table 1 Minimum, maximum, mean, and standard deviation value of response variables (mean degree of pollinators; network nestedness, and pollinator robustness) across the tested land-use categories (old-growth forests, disturbed forests, and converted forests)

	Land-use categories	Min	Max	Mean	SD
Mean degree of pollinators	Old-growth forests	1.2	13.5	4.8	3.08
	Disturbed forests	1.3	4.6	2.5	0.99
	Converted forests	1.2	15.4	4.6	3.38
Nestedness (z-score)	Old-growth forests	0.25	38.02	8.49	8.64
	Disturbed forests	0.78	33.11	7.72	9.17
	Converted forests	-3.25	50.97	13.80	15.49
Pollinator robustness	Old-growth forests	0.452	0.885	0.643	0.110
	Disturbed forests	0.415	0.669	0.548	0.07
	Converted forests	0.368	0.824	0.622	0.121

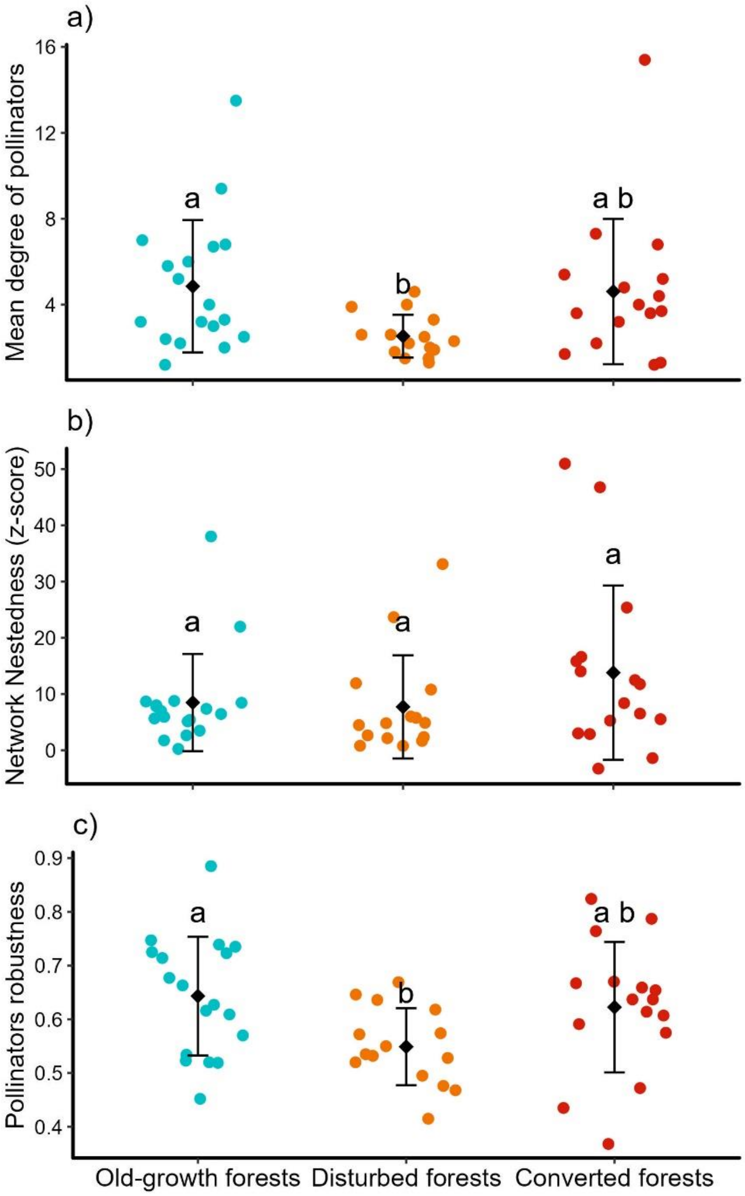

Fig. 3 Mean and variation in our response variables across land-use categories (old-growth forests, disturbed forests, and converted forests) are presented as follows: a) mean degree of pollinators, b) pollinators networks nestedness (z-score), and c) robustness of pollinators to the random loss of partner plants. Each dot corresponds to a network. The diamonds indicate the mean, and the bars show the standard deviation for each treatment category. Different letters represent significant differences at alfa = 0.05

2.6 Discussion

We used pollination networks as a model to investigate the impacts of land-use changes in tropical forests on pollinator interaction patterns and resistance to the loss of their partners. Specifically, although our results do not indicate differences in network patterns between disturbed and converted forests (our categories of anthropization), we observed that pollinators in disturbed forests establish interactions with fewer partner plants and are less resistant to coextinctions than pollinators in old-growth forests. On the other hand, pollinators in converted forests showed no differences in the number of interactions established or resistance to coextinction compared to pollinators in old-growth forests. Furthermore, we did not observe differences in network nestedness between the land-use categories. These findings reflect the complexity of the anthropization on pollination networks and suggest that different factors associated with the type of land-use change can modulate pollinator interaction patterns differently.

In general, the establishment of interactions and the resistance of pollinators to coextinctions are determined by the ability of pollinators to coexist and reorganize their interactions to compensate for the loss of their initial partners (Vizentin-Bugoni et al. 2020; Wang et al. 2020; Zaninotto et al. 2023). However, pollinators respond primarily to changes in the diversity and availability of floral resources and the complexity of the environment (Ebeling et al. 2008; Papanikolaou et al. 2017), which can vary with forest conservation status (Theodorou et al. 2017; Escobedo-Kenefic et al. 2022). We found that pollinators interact with fewer partners in disturbed forests than in old-growth forests, suggesting a decline in interactions established by pollinators in these habitats. Previous studies have shown that fragmentation and deforestation in disturbed forests, characterized by habitat loss, have led to a reduction in floral partners and interactions by pollinators (Smith and Mayfield 2018; Montoya-Pfeieiffer et al. 2020; Pereira et al. 2022), as well as in other plant-animal mutualistic networks (Marjakangas et al. 2020). Thus, disturbed forests may represent significantly simplified habitats with a limited distribution of floral partners, which hinders pollinator foraging (Ferreira et al. 2013, 2020; Moreira et al. 2018). Therefore, our results indicate that pollinators in these forests may have struggle to reorganize or expand their interactions, leading to interacting with fewer partners. Consequently, since pollinators tend to go extinct due to the decline of their floral partners (Biesmeijer et al. 2006; Bain et al. 2022), the lower resistance of pollinators to coextinction in disturbed forests compared to old-growth forests is probably related to the simplification and loss of interactions observed.

On the other hand, we found no difference in the number of interactions or resistance to coextinctions between pollinators in converted forests and those in old-growth forests or with pollinators in disturbed forests. This pattern can be explained by the diverse spatial heterogeneity of converted habitats, which can trigger unique responses in pollinator interaction patterns. Although habitat conversion is a significant driver of landscape change, converted habitats may provide favorable conditions for the establishment of pollinator interactions due to the presence of gardens, plantations, or remaining forest fragments (Hagen and Kraemer 2010; Nascimento et al. 2020; Stewart and Waitayachart 2020). However, there are significant differences in the composition of these habitats, which differ in extent, intensity of disturbance, and landscape heterogeneity (Wenzel et al. 2020; Escobedo-Kenefic et al. 2022; Ruas et al. 2022). Impacts on these attributes of habitats can decrease the availability and diversity of partners, and increase the loss of interactions and the risk of coextinction (see Sritongchuay et al., 2019; Escobedo-Kenefic et al. 2022; Proesmans et al. 2024). Therefore, unique environmental pressures across converted habitats may lead to high variation in network patterns (Wenzel et al. 2020; Maruyama et al. 2021), particularly considering how these pressures have influenced the composition of the remaining species (Marcacci et al. 2022). Indeed, generalist pollinators have more partners available in converted habitats, which confers higher number of interactions and resistance to interaction loss, unlike specialized pollinators that depend more on specific partners (Maruyama et al. 2019; 2021; Proesmans et al. 2024). Therefore, converted forests may represent an intermediate point in the effects of anthropization on pollinators by maintaining networks with a similar number of plant-pollinator interactions as in old-growth forests, but may also promote interaction loss and lower resistance to coextinction, as observed in disturbed forests.

Mutualistic networks are not formed by random patterns but follow a nested structure due to the hierarchical organization of their interactions, where more specialized species interact with a subset of more generalist species (Dáttilo et al., 2016; Rohr et al., 2014). Although we observed that pollinators in disturbed forests established interactions with fewer partners and lower resistance to coextinctions in disturbed forests than in old-growth forests, we did not observe any effect of land-use change on the nestedness of networks. This result indicates that pollinators tend to follow a constant pattern of foraging despite the effects of anthropization. This can be explained by the role of central species that act as the core of networks and contribute to nestedness, mainly generalist species that tend to compensate for the loss of species and their interactions - thus maintaining the structure of networks (Bascompte et al. 2003; Ramos-Jiliberto et al. 2012; Vizentin-Bugoni et al. 2020). For example, due to the role played by generalist pollinators, the structure of networks based on a palm species was maintained despite the fragmentation gradient in a Mexican forest, even with changes in species composition (Dáttilo et al. 2015). Therefore, our observations highlight the hierarchical role in the interaction patterns of pollination networks, even resulting from environmental changes.

We highlight that additional results in our models can reinforce our understanding of how different factors influence the organization of pollinator interactions and persistence (Table S4). We observed that plant family richness positively influenced the number of interactions, nestedness, and pollinator robustness to coextinction, while the nestedness was also positively influenced by the network size (Table S4). These results can be attributed to the role of taxonomic diversity in fostering interactions and species resilience, which suggests that the capacity of species to establish interactions varies primarily with network diversity and resource availability. For instance, the diversity of floral partners can increase pollinator diversity and positively influence the establishment of interactions and the resistance of pollinators to coextinctions (Laha et al. 2020; Ren et al. 2023). Additionally, network size reflects the heterogeneity of the network species, leading to more opportunities for interaction: larger networks tend to have a higher diversity of species, allowing generalist species to interact with specialists, thereby promoting nestedness (Bascompte et al. 2003; Bascompte and Jordano, 2007). Therefore, since factors intrinsic to the different habitats addressed can influence the taxonomic heterogeneity of the networks due to the intensity of the disturbance, this would lead the different land-use categories to vary their network patterns (López-Vázquez et al. 2024; Proesmans et al. 2024), which may explain the high variability in the studied metrics in different treatments (Table 1 and Figure 3).

There is currently an intense debate about interaction patterns in pollination networks along geographic gradients (Trøjelsgaard and Olesen, 2013; Liu et al. 2021; Wang et al. 2024). However, we did not find a relationship between the evaluated metrics and latitude or elevation (Table S4). Network structural changes due to geographic variation are generally attributed to environmental, climatic or evolutionary changes over broader gradients (Schleuning et al. 2012; Albrecht et al. 2018; Chartier et al. 2021). Therefore, how spatial gradients shape interactions is inherently linked to environmental conditions across these gradients (Luna et al. 2022). First, our data include networks at narrower latitudes (Fig.2), where climatic and environmental conditions are less contrasting than broader gradients. Consequently, the lack of a latitudinal relationship in the network metrics can be observed through the restricted latitudinal variation where environmental and climatic conditions are less contrasting (see Dáttilo and Vasconcelos, 2019; Moreira et al. 2020; Luna et al. 2022). Second, it is important to highlight that our data include networks in habitats subject to anthropogenic environmental change. Therefore, changes in interaction patterns along geographic gradients may have been masked due to anthropogenic interventions in the habitats studied, suggesting complex interactions between geographic constraints and anthropogenic pressures.

2.6.1 Limitations and considerations

Tropical forests are the most biodiverse ecosystems on Earth, with a high diversity of species and interactions (Dáttilo and Rico Gray 2018). However, limited research investment and methodological challenges have resulted in uneven and scarce coverage of pollination networks and groups across tropical forests of different biogeographic regions (Cagnolo 2018; Vizentin-Bugoni et al. 2018). Our data reflects this heterogeneity, with more data of Neotropical networks, an underrepresentation of Afrotropical and Indomalayan regions, and a lack of data from Australasia. We also observed an uneven distribution of land-use categories, with a lack of networks in old-growth forests from the Afrotropical region, and of disturbed forests from the Indomalayan region. Furthermore, networks in converted forests were predominant in the Indomalayan region, and underrepresented in other regions. Finally, our dataset were mainly consisted of bee and hummingbird networks (this last group is endemic to the Americas); Lepidoptera and Diptera were underrepresented, and important vertebrate pollinators such as sunbirds (Afrotropical region) and bats (all regions) were absent, as were other invertebrate groups. The undersampling or lack of data from some regions and taxa may bias our results, given species' different ecological and evolutionary responses to land use changes (Fleming and Muchhala 2008; De Palma et al. 2016). Specifically, we may underestimate the impact of land-use change on networks of underrepresented regions and groups, particularly endemic or rare taxa to these regions. Addressing these gaps is critical for a more comprehensive understanding of pollination network dynamics across tropical forests, and may improve our knowledge of how land-use change affects species interactions (Cagnolo 2018; Moreira et al. 2018; Maruyama et al. 2021).

The use of binary networks in our study, as opposed to weighted networks, which more accurately reflect natural interactions, may have led to an over- or underestimation of nestedness and robustness in the networks (e.g., Kaiser-Bunbury et al. 2010; Gaiarsa and Guimarães 2019). This may have limited our understanding of network patterns influenced by the strength of interactions (weighted measure) or species' ability to reorganize their interactions, which is influenced by abundance (see Winfree et al. 2014). Additionally, given that network structure can be influenced by sampling effort (Doré et al. 2021), the methodological differences and non-standardized descriptions of sampling effort across studies make it challenging to control for sampling in our models, constraining our understanding of the results (Vizentin-Bugoni et al. 2015). This limitation is especially pronounced in tropical forests, where the vast diversity of pollinator-plant interactions makes comprehensive network studies difficult, often resulting in research toward partial networks (Vizentin-Bugoni et al. 2018).

We emphasize that this study's focus was to assess anthropisation's impact on the structure of tropical forest networks rather than on functions related to species interactions. However, based on the lower number of interactions and robustness by pollinators observed in disturbed forests, it is important to emphasize that there is a disturbance threshold beyond which networks cannot maintain stability and may collapse, impairing functions (Fortuna and Bascompte 2006; Bascompte and Scheffer 2023). For example, anthropogenic changes can make it difficult for pollinators to locate floral partners and reduce the frequency of interactions (Harrison and Winfree 2015; Jürgens and Bischoff 2017; Hou et al. 2019). This could lead to pollinators' extinction even before their partners' loss (Santamaría et al. 2016) and can decrease effective pollination (Soares et al. 2022; Hernández-Rivera et al. 2024) . In addition, homogenization of the network may occur due to the loss of rare specialized species and due to the persistence of common generalists (Maruyama et al. 2019; Ruas et al. 2022). This homogenization can cause less effective pollen exchange between flowers of the same species and consequently decrease pollination (Gómez et al. 2007; Anderson et al. 2011). Therefore, to better understand the impact of land use changes on networks, future studies should consider the impact of environmental changes on the synergistic effects between network structure and the effectiveness of pollinator functions.

2.7 Conclusion

Although previous studies have demonstrated species loss due to anthropogenic changes, our approach reflects the importance of considering ecological networks to better understand how land-use change affects species persistence through their interactions. There were no effects of land-use change on the organization of networks through nestedness. However, pollinators in disturbed forests established interactions with fewer partners and were less robust to coextinctions than in old-growth forests, indicating that pollinators in disturbed forests are vulnerable to environmental change. Furthermore, we observed no differences in the establishment of interactions or robustness of pollinators between converted and old-growth forests; however, there were no differences between both anthropogenic categories (disturbed and converted forests), highlighting the complexity of pollinator responses in converted habitats (urban and agricultural areas). Therefore, our findings suggest that pollinator interaction patterns and their resistance to partner loss in tropical forests depend primarily on environmental factors associated with network patterns, such as resource availability as measured by the number of interactions and the diversity of partners in the networks. Future studies and decision-makers should consider the impacts of land-use change on environmental factors that help to establish interactions between pollinators and their floral partners and thus promote the persistence of pollinators in anthropized habitats that can serve as pollinator refugia under strict conservation guidelines (Klein et al. 2008; Baldock et al. 2019).

Supplementary information

Table 1 Filtering method employed to select studies on pollinator networks in tropical forests. The filtering process consisted of four stages: (1 and 2) filtering based on title information; (3) filtering based on abstract information; (4) filtering based on full study information

Fig. 1 A diagram illustrating the stages of selecting studies focusing on tropical forest pollinator networks. It displays the number of studies excluded and selected at each step and the corresponding reasons for exclusion. The diagram concludes by showing the total number of studies excluded and the final count of studies selected

Table 2 Studies with pollinator networks in tropical forests that were found in this study. The table presents each study's identification number in our database alongside the reference in the original language

Table 3 Study identification number, along with the number of networks used in our analysis, the pollinator group, the land-use categories, and the country where the networks are located

Table 4 Complete results of the models assessing the effects of covariates (network size, plant family richness, pollinator group, latitude, and elevation) on evaluated network metrics (mean degree of pollinators, network nestedness, and pollinator robustness) in tropical forest pollination networks

Statements and Declarations

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Competing Interests

The authors have no relevant financial or non-financial interests to disclose.

Author Contributions

JBBSO and LNP carried out the conception and initial design of the study. JBBSO performed material preparation, data collection, and analysis under LNP supervision. JBBSO wrote the manuscript under LNP supervision. All authors reviewed and commented on previous versions of the manuscript. JBBSO edited this manuscript. All authors have read and approved the final manuscript.

Data Availability

The datasets obtained during the current study are available in the supplementary information or from the corresponding author on reasonable request. The datasets generated and/or analyzed during the current study are available from the corresponding author on reasonable request.

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2.9 APÊNDICE A

Anthropogenic impacts on plant-pollinator networks of tropical forests: implications for pollinators coextinction

Biodiversity and Conservation

Jefferson Bruno B. S. Oliveira[1], Hernani F. M. Oliveira[2], Wesley Dáttilo[3], Lucas N. Paolucci[4]

[1] Programa de Pós-Graduação em Ecologia, Departamento de Biologia Geral, Universidade Federal de Viçosa, Viçosa, MG, Brazil.

[2] Departamento de Zoologia, Universidade do Paraná, UFPR, Curitiba, PR, Brazil.

[3] Red de Ecoetología, Instituto de Ecología AC, Xalapa, Veracruz, Mexico.

[4] Departamento de Biologia Geral, Universidade Federal de Viçosa, Viçosa, MG, Brazil.

Correspondence author: Jefferson Bruno B. S. Oliveira - jeffersonbrunoxd@gmail.com; jefferson.oliveira@ufv.br

2.9.1 Supplementary information

Table 1 Filtering method employed to select studies on pollinator networks in tropical forests. The filtering process consisted of four stages: (1 and 2) filtering based on title information; (3) filtering based on abstract information; (4) filtering based on full study information

Exclusion from the first stage (exclusion by title)	
Exclusion terms	**Reason for exclusion**
It is a duplicate	It means that the study is a duplicate.
Exclusion from the second stage (exclusion by title)	
Exclusion terms	**Reason for exclusion**
It is a review	The title showed that the study is a review
It is not a tropical forest area	The title showed that the study did not take place in a tropical forest area.
It is not a valid network	The title showed some information that the study does not present a valid network for our study. Examples:

	The study focused on the visitation of only four plant species or less. The study focused only on four species or less of pollinators. The study is not about floral visitation. The study is not about visitation by animals.
It is an oceanic island	The title showed that the study took place on an island
Exclusion from the third stage (exclusion by abstract)	
Exclusion terms	**Reason for exclusion**
It is not a valid network	The title showed some information that the study does not present a valid network for our study. Examples: The study focused on the visitation of only four plants species or less. The study focused only four species or less of pollinators. The study is not about floral visitation. The study is not about visitation by animals.
It is not a tropical forest area	The abstract showed that the study did not occur in a tropical forest area.

	Examples: (1) The study occurred in a tropical area but was in any biome other than tropical forest area. (2) The study was done in nurseries or greenhouses (controlled environments)
It is a review	The abstract showed that the study is a review
It is an oceanic island	The abstract showed that the study took place on an oceanic island
Exclusion from the fourth stage (exclusion for the complete study)	
Exclusion terms	**Reason for exclusion**
It is not a tropical forest area	The study showed that it did not occur in a tropical forest. Examples: (1) The study occurred in a tropical area but was in any biome other than a tropical forest area. (2) The study was done in nurseries or greenhouses (controlled environments)
It is not a valid network	The study showed some information that does not present a valid network for our study. Examples: The study focused on the visitation of only four plant species or less.

	The study focused only on four species or less of pollinators. (3) The study does not show interactions between species or does not show interactions clearly. (4) The study used networks with simulated interactions.
It is a review	The study is a review.
It is an oceanic island	The study showed that the study took place on an island.
There are repeated data	The study uses data from another work already selected.
Link not found	Studies that could not be accessed.
Natural disturb	The study occurred in a place that has experienced recent natural disturbances such as hurricanes or fires.

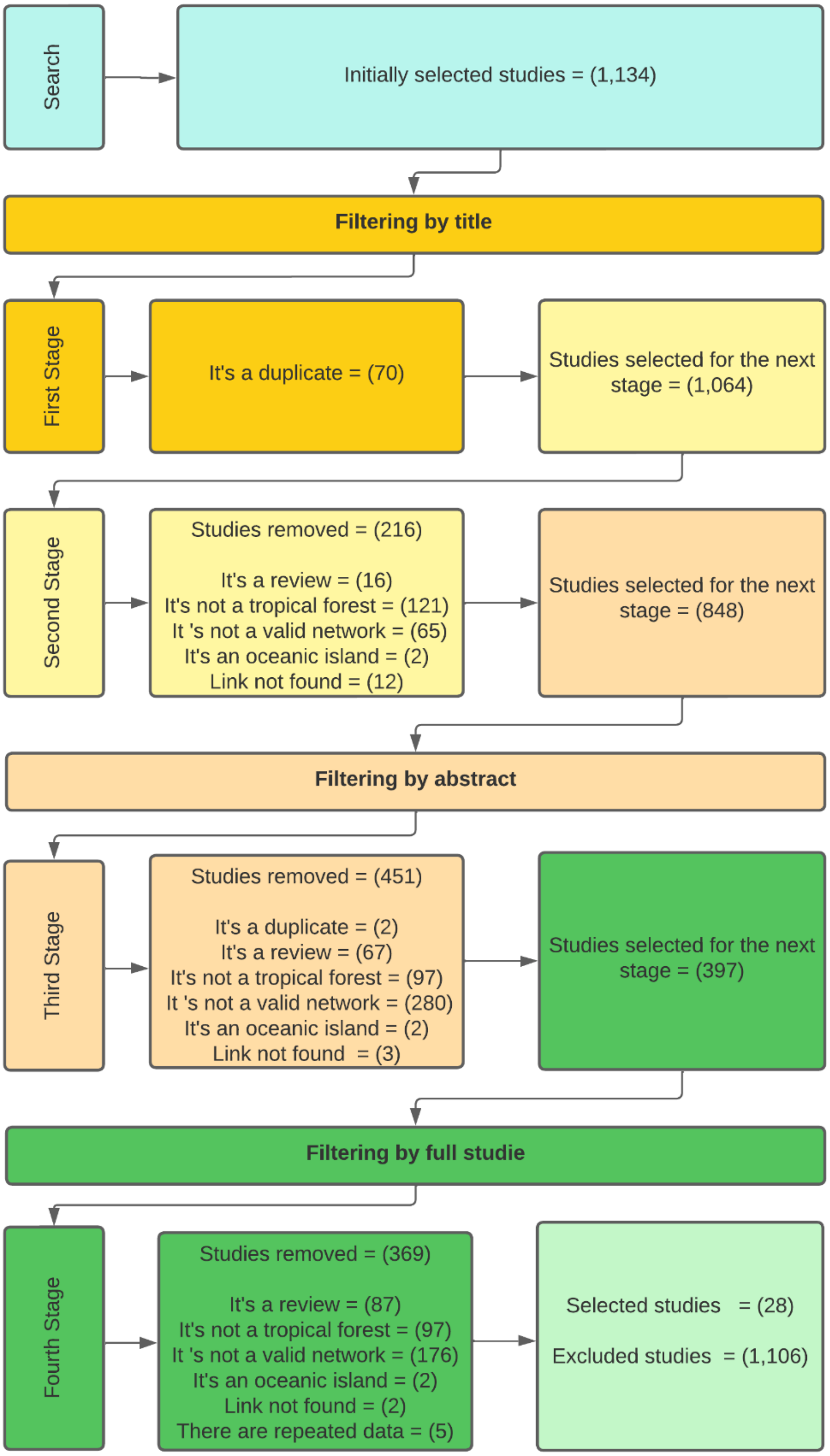

Fig. 1 A diagram illustrating the stages of selecting studies focusing on tropical forest pollinator networks. It displays the number of studies excluded and selected at each step and the corresponding reasons for exclusion. The diagram concludes by showing the total number of studies excluded and the final count of studies selected

Table 2 Studies with pollinator networks in tropical forests that were found in this study. The table presents each study's identification number in our database alongside the reference in the original language

Study ID	Study reference
4	Ferreira, PA et al. (2020) Forest and connectivity loss simplify tropical pollination networks. Oecologia 192:577–590. https://doi.org/10.1007/s00442-019-04579-7
13	Stewart AB, Waitayachart P (2020) Year-round temporal stability of a tropical, urban plant-pollinator network. PLoS ONE 15:e0230490. https://doi.org/10.1371/journal.pone.0230490
38	González-Vanegas PA et al (2021) Buzz-Pollination in a Tropical Montane Cloud Forest: Compositional Similarity and Plant-Pollinator Interactions. Neotrop Entomol 50:524–536. https://doi.org/10.1007/s13744-021-00867-1
41	Hagen M, Kraemer M (2010) Agricultural surroundings support flower–visitor networks in an Afrotropical rain forest. Biological Conservation 143:1654–1663. https://doi.org/10.1016/j.biocon.2010.03.036
83	Schrader J, Franzén M, Sattler C, Ferderer P, Westphal C (2018) Woody habitats promote pollinators and complexity of plant–pollinator interactions in homegardens located in rice terraces of the Philippine Cordilleras. Paddy Water Environ 16:253–263. https://doi.org/10.1007/s10333-017-0612-0
144	Wolowski M, Ashman TL, Freitas L (2013) Community-wide assessment of pollen limitation in hummingbird-pollinated plants of a tropical montane rain forest. Annals of Botany 112:903–910. https://doi.org/10.1093/aob/mct140
179	Maglianesi MA, Blüthgen N, Böhning-Gaese K, Schleuning M (2014) Morphological traits determine specialization and resource use in plant–hummingbird networks in the neotropics. Ecology 95:3325–3334. https://doi.org/10.1890/13-2261.1
203	Rodríguez-Flores C, Stiles FG, Arizmendi MC (2012) Pollination network of a hermit hummingbird community (Trochilidae, Phaethornithinae) and their nectar resources in the Colombian Amazon. Ornitologia

	Neotropical 23: 63–78.
243	Vizentin-Bugoni J, Maruyama PK, Sazima M (2014) Processes entangling interactions in communities: forbidden links are more important than abundance in a hummingbird–plant network. Proc R Soc B 281:20132397. https://doi.org/10.1098/rspb.2013.2397
262	Mouga DM et al. (2012) Bees and plants in a transition area between Atlantic rain forest and Araucaria forest in Southern Brazil. revec 67:313–327. https://doi.org/10.3406/revec.2012.1970
280	Piacentini VQ, Varassin IG (2007) Interaction Network and the Relationships between Bromeliads and Hummingbirds in an Area of Secondary Atlantic Rain Forest in Southern Brazil. Journal of Tropical Ecology 23:663–671.
330	Pinheiro M, Brito VLGD, Sazima M (2018) Pollination biology of melittophilous legume tree species in the Atlantic Forest in Southeast Brazil. Acta Bot Bras 32:410–425. https://doi.org/10.1590/0102-33062018abb0078
1044	Abreu CRM, Vieira MF (2004) Os beija-flores e seus recursos florais em um fragmento florestal de Viçosa, sudeste brasileiro. Lundiana 5:129–134. https://doi.org/10.35699/2675-5327.2004.22014
1047	Bueno RO (2012) Fatores que influenciam interações entre beija-flores e plantas em Mata Atlântica: disponibilidade de recursos e ajustes morfológicos. Thesis, Programa de Pós-Graduação em Ecologia e Conservação, Universidade Federal do Paraná
1049	Chupil H (2013) Uso de grãos de pólen na identificação de plantas e para examinar a partição de nicho alimentar entre beija-flores no sul do Brasil. Dissertation, Programa de Pós-Graduação em Ecologia e Conservação, Setor de Ciências Biológicas, Universidade Federal do Paraná
1051	Kaehler M, Varassin IG, Goldenberg R (2005) Polinização em uma comunidade de bromélias em floresta atlântica alto-montana no estado do Paraná, Brasil. Rev. bras. Bot. 28:219–228. https://doi.org/10.1590/S0100-84042005000200003

1055	Machado CG, Semir J (2006) Fenologia da floração e biologia floral de bromeliáceas ornitófilas de uma área da Mata Atlântica do Sudeste brasileiro. Rev. bras. Bot. 29, 163–174. https://doi.org/10.1590/S0100-84042006000100014
1060	Malucelli ST (2014) Fatores envolvidos na estruturação das redes de polinização beija flor-planta em um gradiente sucessional. Dissertation, Programa de Pós-Graduação em Ecologia e Conservação, Setor de Ciências Biológicas, Universidade Federal do Paraná
1064	Rodrigues MS (2008) Partilha de recursos florais por beija-flores em uma área de Mata Atlântica na Ilha da Marambaia, RJ. Dissertation, Programa de Pós-Graduação em Biologia Animal, Instituto de Biologia, Universidade Federal Rural do Rio de Janeiro
1067	Varassin IG, Sazima M (2012) Spatial heterogeneity and the distribution of bromeliad pollinators in the Atlantic Forest Acta Oecologica 43:104–112. https://doi.org/10.1016/j.actao.2012.06.001
1076	Cunha LC (2014) Os apidae corbiculados e suas fontes florais em uma área urbana. Dissertation, Programa de Pós-Graduação em Ciências Biológicas, Departamento de Biologia Animal e Vegetal, Área de Concentração: Biodiversidade e Conservação de Hábitats e Fragmentos, Universidade Estadual de Londrina
1078	Gonçalves SJM, Rêgo M, Araújo A (1996) Abelhas sociais (Hymenoptera: Apidae) e seus recursos florais em uma região de mata secundária, Alcântara, MA, Brasil. ACTA AMAZÔNICA 26:55-68
1085	Wilms W, Imperatriz-Fonseca VL, Engels W (1996) Resource Partitioning between Highly Eusocial Bees and Possible Impact of the Introduced Africanized Honey Bee on Native Stingless Bees in the Brazilian Atlantic Rainforest. Studies on Neotropical Fauna and Environment 31:137–151. https://doi.org/10.1076/snfe.31.3.137.13336
1103	Dworschak K, Blüthgen N (2010) Networks and dominance hierarchies: does interspecific aggression explain flower partitioning among stingless bees? Ecological Entomology 35:216–225. https://doi.org/10.1111/j.1365-2311.2010.01174.x
1128	Stiles FG 1975 Ecology, Flowering Phenology, and Hummingbird Pol-

	lination of Some Costa Rican Heliconia Species. Ecology 56:285–301. https://doi.org/10.2307/1934961
1132	Williams NH, Dodson CH (1972) Selective attraction of male Euglossine bees to orchid floral fragrances and its importance in long distance pollen flow. Evolution 26:84–95. https://doi.org/10.1111/j.1558-5646.1972.tb00176.x
1133	Mendonça LB, Anjos LD (2005) Beija-flores (Aves, Trochilidae) e seus recursos florais em uma área urbana do Sul do Brasil. Rev Bras Zool 22:51–59. https://doi.org/10.1590/S0101-81752005000100007
1134	Braga RCP (2021) Abelhas e PANC: uso de espécies não convencionais como estratégia para manter a polinização em um sistema agroecológico urbano. Universidade Federal do Rio Grande do Norte

Table 3 Study identification number, along with the number of networks used in our analysis, the pollinator group, the land-use categories, and the country where the networks are located

Study ID	Network ID	Pollinators	Land-use categories	Country
4	2	Apoidea	Disturbed forest	Brazil
4	3	Apoidea	Disturbed forest	Brazil
4	4	Apoidea	Disturbed forest	Brazil
4	5	Apoidea	Disturbed forest	Brazil
4	6	Apoidea	Old-growth forests	Brazil
4	7	Apoidea	Disturbed forest	Brazil
4	8	Apoidea	Disturbed forest	Brazil
13	10	Apoidea	Converted forest	Thailand
13	11	Apoidea	Converted forest	Thailand
13	12	Apoidea	Converted forest	Thailand
13	13	Apoidea	Converted forest	Thailand
13	14	Apoidea	Converted forest	Thailand
13	15	Apoidea	Converted forest	Thailand
13	17	Apoidea	Converted forest	Thailand
13	18	Apoidea	Converted forest	Thailand

13	54	Diptera	Converted forest	Thailand
13	55	Lepidoptera	Converted forest	Thailand
13	56	Lepidoptera	Converted forest	Thailand
38	19	Apoidea	Disturbed forest	Mexico
41	35	Apoidea	Converted forest	Kenya
41	36	Apoidea	Disturbed forest	Kenya
83	24	Apoidea	Converted forest	Philippines
144	25	Trochilidae	Old-growth forests	Brazil
179	27	Trochilidae	Old-growth forests	Costa Rica
179	28	Trochilidae	Old-growth forests	Costa Rica
179	29	Trochilidae	Old-growth forests	Costa Rica
203	30	Trochilidae	Old-growth forests	Colombia
243	31	Trochilidae	Old-growth forests	Brazil
262	32	Apoidea	Old-growth forests	Brazil
280	1	Trochilidae	Old-growth forests	Brazil
330	33	Apoidea	Old-growth forests	Brazil
1044	38	Trochilidae	Disturbed forest	Brazil
1047	59	Trochilidae	Disturbed forest	Brazil
1051	41	Trochilidae	Old-growth forests	Brazil
1055	42	Trochilidae	Old-growth forests	Brazil
1060	43	Trochilidae	Disturbed forest	Brazil
1060	44	Trochilidae	Disturbed forest	Brazil
1060	45	Trochilidae	Old-growth forests	Brazil
1064	58	Trochilidae	Disturbed forest	Brazil
1067	46	Trochilidae	Old-growth forests	Brazil
1067	47	Lepidoptera	Old-growth forests	Brazil
1067	48	Apoidea	Old-growth forests	Brazil
1076	49	Apoidea	Converted forest	Brazil
1078	50	Apoidea	Disturbed forest	Brazil
1103	60	Apoidea	Old-growth forests	Malaysia
1128	52	Trochilidae	Old-growth forests	Costa Rica
1132	37	Apoidea	Disturbed forest	Guyana
1133	39	Trochilidae	Converted forest	Brazil

1134	57	Apoidea	Converted forest	Brazil

Table 4 Complete results of the models assessing the effects of covariates (network size, plant family richness, pollinator group, latitude, and elevation) on evaluated network metrics (mean degree of pollinators, network nestedness, and pollinator robustness) in tropical forest pollination networks

	Covariables	Estimate	Chi	DF	p
Mean degree of pollinators	Network size	-0.004	0.43	1	0.5
	Plant family richness	0.057	8.48	1	**0.003***
	Latitude	-0.006	0.01	1	0.99
	Elevation	0.091	0.96	1	0.32
Network nestedness (z-score)	Network size	0.226	14.86	1	**<0.001***
	Plant family richness	0.612	10.30	1	**<0.001***
	Latitude	1.417	2.14	1	0.14
	Elevation	0.855	0.76	1	0.38
Pollinator robustness	Network size	-0.003	0.46	1	0.49
	Plant family richness	0.038	7.53	1	**0.006***
	Latitude	-0.062	0.82	1	0.36
	Elevation	0.089	1.41	1	0.23

Significant values are indicated with asterisks

3 CHAPTER 2

Fire and edges in the Amazon: impacts on key animal-plant interactions to forest regeneration

Fire and edges in the Amazon: impacts on key animal-plant interactions to forest regeneration

Jefferson Bruno B. S. Oliveira[1] et al.

[1] Programa de Pós-Graduação em Ecologia, Departamento de Biologia Geral, Universidade Federal de Viçosa, Viçosa, MG, Brazil. ORCID 0000-0002-5392-6080

Correspondence author: Jefferson Bruno B. S. Oliveira - jeffersonbrunoxd@gmail.com; jefferson.oliveira@ufv.br

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3.2 Abstract

Ecosystem functions mediated by animal-plant interactions play a crucial role in forest maintenance. However, the increase of edges in the Amazon and the consequent new fire dynamics put the forest into a novel degradation scenario. These impacts can lead to the loss of ecological interactions by frugivorous animals and post-dispersal agents, driven by forest simplification resulting from structural changes, reduced resource availability, and species loss. As a result, burned forests exhibit reduced regeneration, mainly at their edges. We investigated the extent to which edges and frequent fires in an Amazonian forest impact arboreal and terrestrial frugivory and secondary seed manipulation by animals using artificial fruits and agricultural seeds as models in interaction experiments. We also examined whether the impacts are more severe due to fire-edge synergies. Additionally, we assessed the key groups responsible for these interactions. We predicted that burned forest would reduce the frequency of animal-plant interactions, with greater losses due to fire-edge synergies. Arboreal frugivory did not differ between treatments, but terrestrial frugivory was higher at the unburned edge. Additionally, fire reduced seed manipulation by the entire faunal community, while seed manipulation by invertebrates was not different between the unburned edge and the interior of the burned forest. Furthermore, we observed the potential dominance of invertebrates in terrestrial frugivory and seed manipulation between the different treatments, which may indicate a potential complementarity of interactions by invertebrates. We conclude that forest disturbances affect plant-animal interactions through indirect reductions in interaction frequency by key agents, which may ultimately impact forest regeneration.

Keywords: Ecological interactions, ecological processes, fire disturbances, forest services, tropical forests

3.3 Introduction

Tropical forests increasingly face the multiple impacts of human activities due to land-use changes for logging, agricultural and livestock practices (Turubanova et al. 2018; Edwards et al. 2019; Grantham et al. 2020). For instance, an estimated 38% of the Amazon is under the effects of anthropogenic disturbances (Lapola et al. 2023), potentially increasing to 47% by 2050 (Flores et al. 2024). Such disturbances have simplified and modified the structure of Amazonian forest habitats through deforestation and fragmentation (Berenguer et al. 2024). Notably, ongoing forest fragmentation has led to the formation of forest patches and the expansion of edge areas (Vedovato et al. 2016). Just between 2001 and 2015, approximately 180,000 km² of new forest edges were formed, resulting in impacts on forest dynamics (Silva Junior et al. 2015). For example, environmental changes triggered by forest edges, such as increased temperature, wind intensity, and dryness, can intensify large tree mortality, reduce plant diversity, and facilitate grass invasion – mainly adjacent to pastures or croplands (Silvério et al. 2013; 2019; Maracahips-Santos et al. 2020). Even though fire is not a regular natural disturbance in the Amazon rainforest, the edge effects increase forests' flammability, further altering the forest's microclimate, structure, and composition (Aragão et al. 2018; Barlow et al. 2020; Brando et al. 2020), with cascading effects on biodiversity (Sales et al. 2020; Feng et al. 2021). Natural forest regeneration is crucial for attenuating the impacts of disturbances (Rodrigues et al. 2004; Jakovac et al. 2021), but it is frequently limited burned forests (Cury et al 2020) – mainly in burned edges where more severe environmental filters occur (Balch et al. 2015; Brando et al. 2019; Drüke et al. 2023). Known mechanisms responsible for the limited regeneration of burned forests include lower seed rain, seed bank and resprout, which decreases seedling density (Cury et al. 2020a; Brando et al. 2024). Therefore, impacts on processes that drive seed availability and distribution may reduce vegetation reproduction and contribute to limited forest regeneration (Nevo et al. 2023; Hatfield et al. 2024).

Animals play central roles in forest maintenance, functioning, and dynamics (Bello et al. 2015, 2024; Quintero et al. 2024) – particularly in the tropics, where 90% of plant species depend on them to complete their life cycles (Jordano 2000; 2016; Tong et al. 2023). For example, the distribution of vegetation is determined by both primary seed dispersal by frugivorous animals and secondary post-dispersal agents, as they control the arrival and distribution of new individuals (Camargo et al. 2019; Falcon et al. 2024). Furthermore, although seed predation can decrease reproductive success (Rosin and Poulsen 2018; Dylewski et al. 2020), it may act as a selective filter by promoting assembly, diversity and coexistence of vegetation, mainly controlling overabundant species (Paine and Beck 2007; Comita et al. 2014). These biotic processes play a pivotal role in tropical forests regeneration, and are frequently more influential than abiotic filtering processes: they facilitate plant establishment in suitable sites for recruitment and help regulate competition, thereby mitigating the pressure of environmental filters (Wunderle Jr 1997; Estrada-Villegas et al. 2023; Selwyn et al. 2023). Therefore, losing plant-animal interactions due to anthropogenic disturbances can ultimately limit forest regeneration and functionality (Neuschulz et al. 2016; Faria et al. 2023; Bello et al. 2024).

Anthropogenic impacts on ecological interactions are mainly driven by species' responses to habitat changes, which determine the susceptibility of their interactions (Morris 2010; Emer et al. 2019). For instance, fire simplifies forest structure, which decreases resources for fauna, such as vegetation cover and diversity of fruits and seeds—especially at forest edges (Cury et al. 2020a; Shi et al. 2022; Brando et al. 2024). Additionally, whether due to forest degradation, resource loss, or direct mortality, fire reduces species or population of forest specialists, both among vertebrates (Peres et al. 2003; Barlow and Peres 2004a, 2006) and invertebrates (Haugaasen et al. 2003; Paolucci et al. 2017). Furthermore, the simplification of forest structure, combined with changes in environmental filters, hinders both the movement and occurrence of fauna adapted to forest habitats (Silveira et al. 2010, 2013; Lappan et al. 2020). Thus, as species co-occurrence is key for the establishment of interactions (see Pizo and Oliveira 2000; Campagnoli et al. 2024), indirect effects of forest fires or edges can limit species encounters and cause a loss of interactions, both by frugivores (Chaves et al. 2022; Lee et al. 2022; Rossi et al. 2024) and secondary post-dispersal agents (Paolucci et al. 2016). These impacts can result in less efficient ecosystem functions, such as poor dispersion, establishment, and recruitment of post-fire vegetation (Lappan et al. 2020; da Silva Rocha et al. 2022; Lourenço et al. 2024). Therefore, due to the complementarity of these interactions, exploring how fire and edge effects influence animal-plant interactions is crucial to understanding processes underlying forest resilience (see Ballarin et al. 2023).

Vertical stratification is central in frugivore-plant interactions and vegetation establishment, as different species are adapted to distinct forest strata (Thiel et al. 2021, 2023). For instance, arboreal frugivores from the understory and terrestrial frugivores are key seed dispersers in regenerating forests. Arboreal frugivores exert intense fruit consumption and seed dispersion (Camargo et al. 2021; Chaves et al. 2018; 2022), while terrestrial frugivores expand plant-frugivore interactions by accessing lower fruits, including those on the forest ground (Bueno et al. 2013; Carreira et al. 2020). The arboreal understory is dominated by opportunistic frugivores with fragile and specialized interactions (Schleuning et al. 2011), with species vulnerable to fire and deforestation (Barlow and Peres 2002; Slik and Van Balen 2006), and good indicators of environmental changes (Barlow et al. 2006). Meanwhile, terrestrial frugivores are particularly sensitive to environmental disturbances (Arévalo-Sandi et al. 2018). Although the impact of forest fires on species loss across strata has been widely studied (e.g., Barlow et al. 2002; Barlow and Peres 2004a; Slik and Van Balen 2006), its direct effects on plant-frugivore interactions — especially in lower strata or in combination with edge effects — remain understudied (but see Rossi et al. 2024). Current research focuses on a limited number of faunal species or related taxonomic groups (e.g., Paolucci et al. 2019).

Vertebrates are the primary seed dispersers in tropical habitats (Wandrag et al. 2015; Corlett 2017). However, invertebrates play an active role in diaspore interactions on the forest ground (Pizo and Oliveira 2000; 2001; Santana et al. 2016), and may provide complementary services to plant reproductive success (diplocory) (Christianini and Oliveira 2010; Falcon et al. 2024) or act as the only disperser agent (Corlett 2021). As opportunistic fruit consumers, ants, for example, can benefit non-myrmecochorous species as a primary dispersal agent by reducing seed predation through cleaning or dispersing to suitable sites for recruitment (Pizo and Oliveira 2001; Anjos et al. 2018; Fernandes et al. 2018). Therefore, the negative impacts of vertebrate interaction loss on plant recovery can be partially mitigated by invertebrates

(Christianini and Oliveira 2009; Anjos et al. 2020). Nonetheless, the impacts of disturbances on fruit-invertebrate interactions across anthropogenically disturbed forests are often overlooked (see Anjos et al. 2020; Marques Dracxler and Kissiling 2021; Bona et al. 2023). These interactions are particularly important across burned forests, where invertebrate communities are sensitive to habitat changes (Silveira et al. 2010; 2013), and there is an influx of generalist species (Paolucci et al. 2017).

Here, we investigated how the indirect effects of fire impact animal-plant interactions in Amazon forests, particularly at forest edges — where fire is typically more intense and frequent — and impair forest recovery more severely (Figure 1). Specifically, we investigated whether the plant-animal interactions, such as frugivory or direct seed manipulation by secondary post-dispersal agents, are reduced in an Amazonian forest with limited post-fire regeneration (see Methods). We hypothesized that fire reduces plant-animal interactions, with greater losses due to fire-edge synergies. Environmental changes driven by edge effects and fire are expected to reduce the frequency of interactions in disturbed areas compared to undisturbed areas. Additionally, we investigated how the impacts on interactions vary across strata and examined the contribution of animal groups to these interactions.

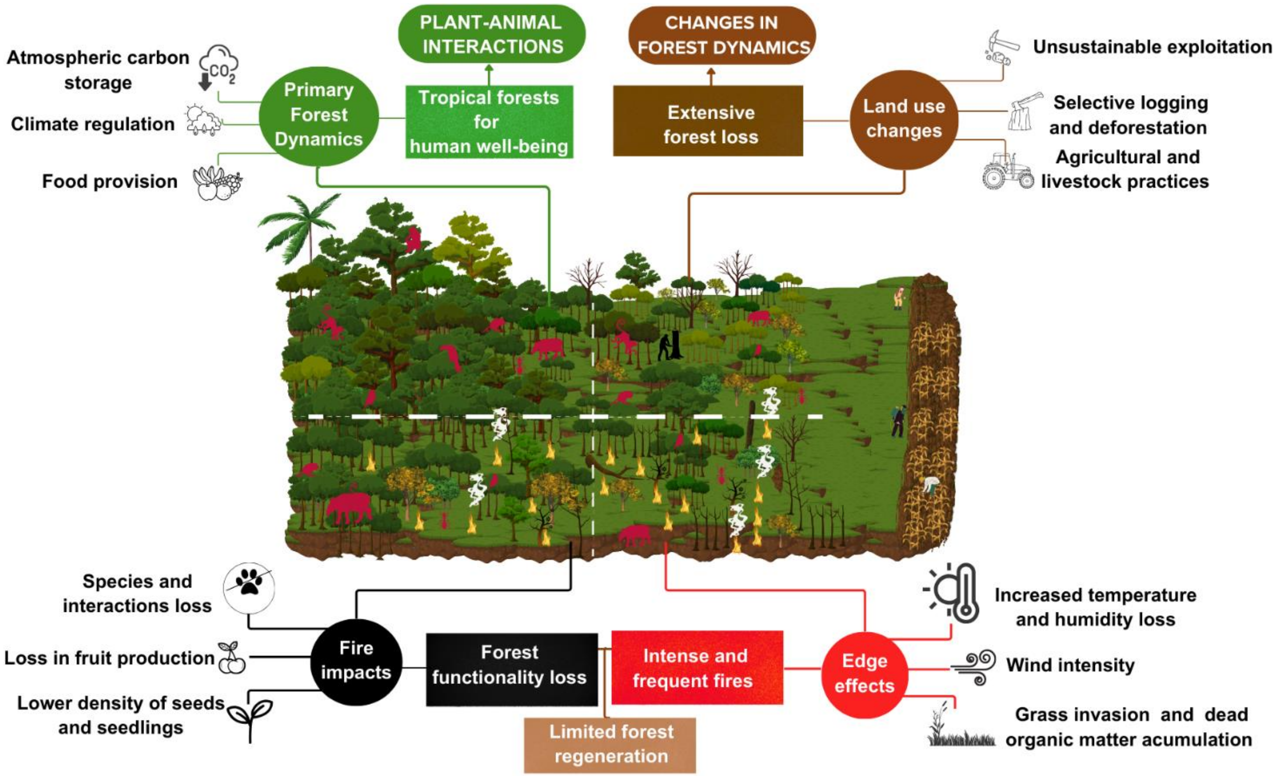

Fig. 1 A model of the degradation processes in the Amazonian tropical forest. The model illustrates the three main disturbances and their main impacts that drive forest functionality

loss, ultimately leading to limited regeneration: forest edges, fire spread, and their synergistic effects.

3.4 Methods

3.4.1 Study area

The study was conducted in a southeastern Amazonian forest located in Tanguro ranch (83,000 ha) in the municipality of Querência in Mato Grosso State, Brazil (13°4'27.31 "S / 52°22'37.34 "W; Figure 2a, b). Our study area is part of a region known as the "Arc of Deforestation", which comprises one of the main deforestation frontiers of the Amazon region. This region is frequently affected by both direct and indirect anthropogenic fires (Morton et al. 2013; Marques et al. 2020; Silva et al. 2023). The forest studied has a lower canopy height (average 20 m) and lower plant diversity (97 tree and liana species) compared to the humid Amazon forests in the north, with nine tree species representing 50% of the Importance Value Index (IVI) for the site (Balch et al., 2008). In addition, the forest edges an area initially cleared for pasture (in 80's) that was later converted to agricultural cultivation (in 2004) (Figure S1). The region has a mean annual rainfall of 1,739 mm and a mean temperature during the dry season of 25ºC (Balch et al. 2008; 2013), and the mean annual temperature is between 24ºC and 26ºC.

3.4.2 Sampling design

Experimental burns were conducted in paired forest plots (1 km × 500 m each) within a large-scale experiment surrounded by an additional primary forest (Figure 2b, c). Two of the plots were experimentally burned at different frequencies at the end of the dry season (between September and October): one plot was burned annually from 2004 to 2010, except in 2008 (annually burned), and the other one was burned triennially in 2004, 2007, and 2010 (triennially burned). The third plot was left unburned as a control. After the burn, the plots were left to regenerate naturally to study the effects of fire on the forest. There was no logging or burning before the controlled burning.

Our experiments were conducted only in control and triennially burned plots (hereafter unburned and burned plots, respectively; Figure 2d). Previous studies indicated greater negative effects of fire in the triennially burned than in the annually burned plot: more intense fire, higher tree mortality, reduced plant and seedling diversity, and consequently lower regeneration density, especially at the edges (Balch et al. 2008, 2013; Cury et al. 2020a, b).

Additionally, fruit-bearing plants were less diverse, with lower fruit and seed production (Brando et al. 2024).

To assess the influence of fire-edge interaction, we divided each plot into two subplots: forest edge (from 50 m to 200 m from the edge of the plots) and forest interior (from 500 m to 650 m from the edge of the plots), so we had four treatments: unburned interior (our control), unburned edge, burned interior, and burned edge (Figure S1). In each subplot, we established three sampling transects: 50 m, 100 m, and 150 m (edge treatments) and 500 m, 550 m, and 600 m (interior treatments). In each sampling transect, we established ten sampling points 50 m apart, totaling 30 sampling points in each treatment (Figure 2d). The experiments were set at the end of the dry season, between the flowering peak and the beginning of the forest fruiting season (September 2022).

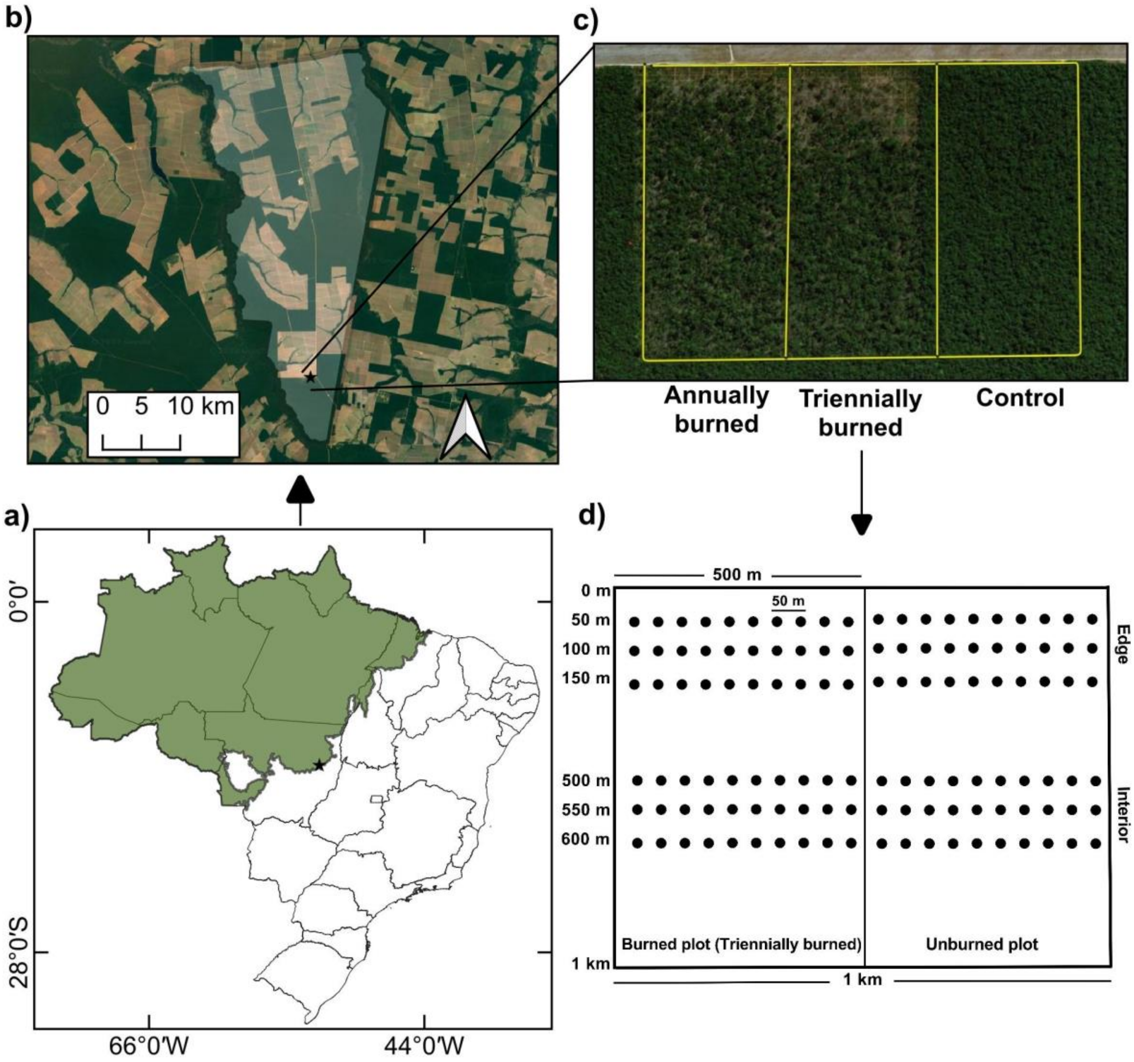

Fig. 2 Map showing the location of the experimental area in the southern Amazon rainforest (Querência, Mato Grosso, Brazil): a) Brazil, highlighting the states within the Amazon rainforest (green), with the black star representing the sampled forest; b) a satellite

image of Tanguro ranch (opaque area) and its surroundings. The black star shows the location of the experimental plots; c) a satellite image of the experimental plots; d) a schematic representation of the sampling points within the plots (burned (triennially) and unburned (control)) and subplots (edge and interior)

3.4.3 Fruit interaction experiment

To assess the effects of the disturbances on fruit-animal interactions, we conducted frugivory experiments at two sampling lines in each treatment: 50 m and 150 m (edges treatments) and 500 m and 600 m (interior treatments), with 20 sampling points in each treatment. We used artificial red fruits with a diameter of 1.5 cm made from non-toxic plasticine to estimate the interactions. Red artificial fruits are an effective alternative for understanding patterns and behaviors regarding frugivory, as they effectively simulate natural fruits that are attractive to most animals (Duan et al. 2014; Balasa et al. 2023; Hazell et al. 2023). These experiments were conducted in two vegetation strata: vegetation branches (arboreal frugivory) and forest ground (terrestrial frugivory). We arbitrarily selected two trees 10 m apart at each sampling point. We avoided trees with natural fruits within a two-meter radius to reduce interference from other attractants or sampling bias due to the already-established behavior of a frugivore visiting the site. We deposited 10 fruits on branches approximately 1.8 m high on one of the trees and 10 fruits on the forest ground around the base of the trunk of the other tree using wire simulating the fruit stalks (Figure S2). To prevent the fruits from being covered by litter, the fruits were placed 3 cm above the ground, at the base of the trunk, with the wires facing downwards for invertebrate access.

We exposed a total of 1,600 artificial fruits, with 800 fruits for arboreal frugivory and 800 for terrestrial frugivory. We deposited 200 fruits in the arboreal stratum and 200 on the forest ground for each treatment. We examined each sampling point 96 hours after the exposure of the fruits to evaluate signs of interaction with the local fauna. We considered any fruit found with marks left by fauna or absent fruits as an interaction (i.e., a frugivory event) (Figure S2 and S3). We searched for the missing fruits around the tree to ensure their absence was not due to accidental falls. Missing fruits found around the focal plant without the presence of marks were not counted as frugivory. Multiple marks on the same fruit were considered as a single interaction.

To improve our understanding of the potential effects of forest disturbances on frugivory, we identified the main faunal groups that contributed to the interactions. We recorded and categorized the marks on fruits as made by birds, mammals, or invertebrates

(Figure S3 for more information). We considered each fruit found with one or multiple marks from a particular group as a single interaction event of frugivory for that group. Marks from different groups found on the same fruits were counted for both groups.

3.4.4 Seed interaction experiment

To assess the effects of the disturbances on seed-animal interactions, we conducted experiments at three sampling lines in each treatment: 50 m, 100 m and 150 m (edges treatments) and 500 m, 550 m and 600 m (interior treatments), with 30 sampling points in each treatment (Figure 2d). We used sunflower seeds, a non-native agricultural species (10 seeds - mean ± SD: height = 7.95 ± 0.70 mm, weight = 0.04 ± 0.01 g). Hulled sunflower seeds are nutritious and have few chemical or physical protective mechanisms, ensuring attraction to a wide range of granivores and consistent predation behavior. This choice excluded any factors that might favor interactions of a native seed with a specific group of seed predators, mainly behaviors of specific granivorous species acquired within one of the treatment plots (e.g., Christianini and Galetti 2007; Hargreaves et al. 2024). We used a batch of organic seed purchased from the same supplier to ensure seed consistency. Only seeds without visible damage were selected so that we could attribute any observed damage to predators. To inhibit the germination, we sterilized them in an oven at 110ºC for 1h.

We established two seed depots at each sampling point to evaluate the interactions from entire fauna and only invertebrates: one depot consisted of 10 seeds accessible to all fauna (open-access), and another consisted of 10 seeds enclosed in a conical metal cage (12 cm in high, 15 cm in diameter, and mesh size 2.5 × 2.5 cm, with metal hooks anchoring it to the ground) to exclude vertebrates and allow access only to invertebrates (invertebrates-only). The depots were located within one meter of each other in previously cleaned soil. This experimental design allows for evaluating interactions across the entire fauna while isolating the contributions of vertebrates and invertebrates (Figure S4).

We exposed a total of 2,400 seeds, with 1,200 seeds for the open-access experiment and 1,200 for the invertebrates-only, 300 seeds per experiment in each treatment. We inspected each depot 24 hours after seed deposition to check interactions with fauna. We acknowledge that the seeds used in our study are 'artificial' lipid-rich models, lacking other structures that might be of interest for consumption. This may suggest that most of the seeds used were probably predated rather than dispersed. However, using the missing seeds as a proxy solely for predation or dispersal without evaluating the seed fate could be biased (see Vander Wall et al. 2015), primarily due to the different traits of fauna and seed species that can lead to different fates to missing seeds (see Chang and Zhang 2014; Penn and Crist 2018). Therefore, we highlight that our seeds serve as a model to assess the impacts of forest disturbances on animal-seed interactions (from now on, seed manipulation – following Fernandes et al. 2018), regardless of the seeds' final fate. So, we recorded all events indicating seed manipulation by fauna. We considered an interaction as any seed found with consumption marks or seeds missing from the deposits. Additionally, we registered the seeds with consumption marks as predated seeds and missing seeds as removed for descriptive purposes.

3.4.5 Statistical analysis

To investigate the effects of fire and forest edge on frugivory and seed manipulation, we calculated the proportion of observed interactions = attacked fruits or manipulated seeds/available fruits and seeds. We fitted generalized linear models to analysis (GLMs). We developed a model for each experiment for the frugivory analysis: one for arboreal and one for terrestrial frugivory. We also created two models for seed manipulation: one for open-access and one for invertebrates-only. Our response variables were the proportion of fruits attacked and the proportion of seeds manipulated by fauna, with forest treatments (unburned interior, unburned edge, burned interior, and burned edge) as the predictor variable. We used a beta-binomial distribution for proportional data using the *glmmTMB* package (Brooks et al. 2017). We analyzed the residuals to check the distribution's adequacy and the models' fit using the *DHARMa* package (Hartig et al. 2022). The significance of the models was tested using type II Anova from the *car* package (Fox and Weisberg 2019). When models were significant, we performed contrast tests with pairwise comparisons separately, combining treatment categories within models.

3.5 Results

Frugivory occurred in 28% (448) of all artificial fruits (Figure 3). Invertebrates attacked 14% (224), with ants responsible for 87.5% (196) of the invertebrates' interactions. Birds and mammals attacked 7.75% (124) and 5.06% (81) of the fruits, respectively. Among arboreal fruits, 26.5% (212) were attacked, with birds attacking the largest proportion (54.2%; 115), while mammals attacked 13.6% (29) and invertebrates attacked 21.2% (45). Ants were responsible for 73.33% (33) of the invertebrate attacks. Among the terrestrial frugivory, 29.5% (236) were attacked. Invertebrates attacked 75.8% (179), with ants accounting for 91.06% (163); mammals and birds attacked 22.03% (52) and 3.8% (9), respectively.

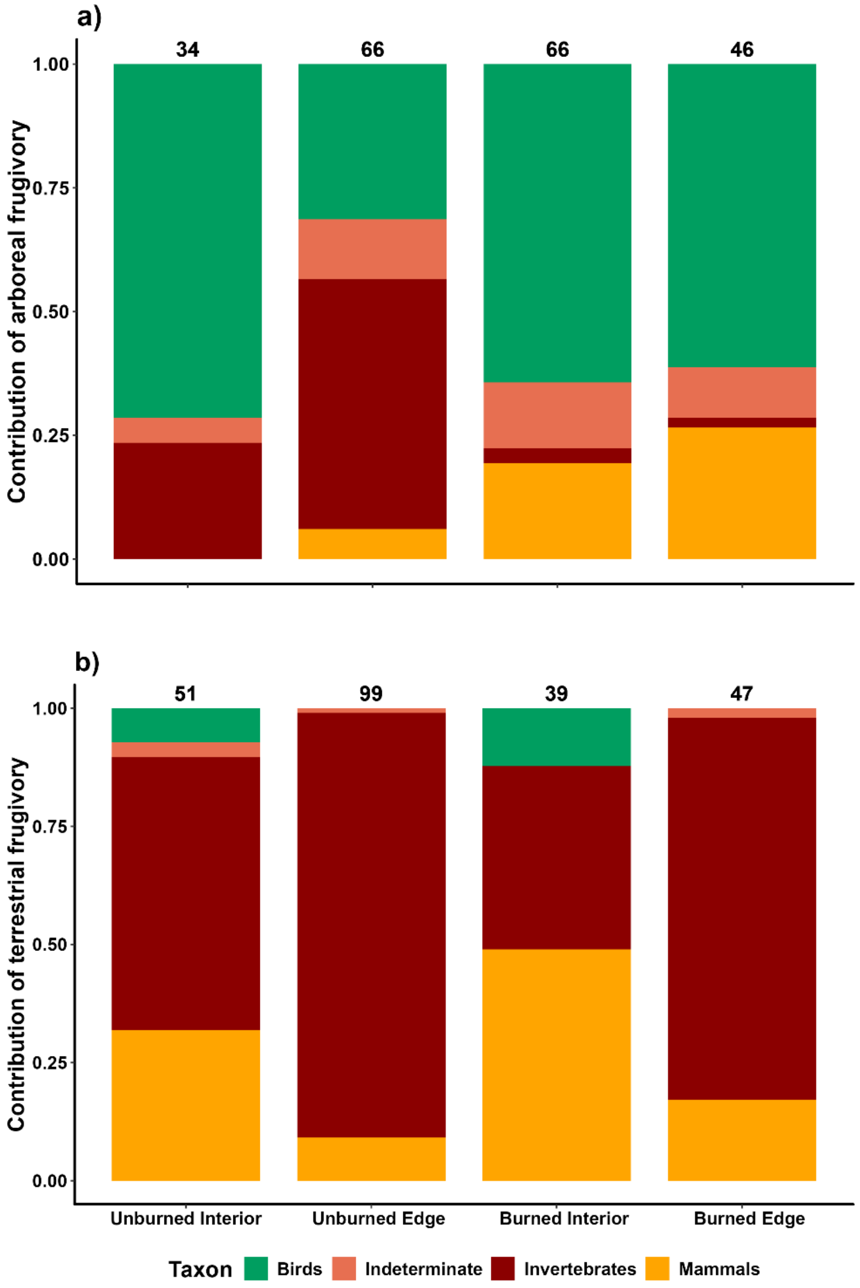

Fig. 3 The relative contribution of fauna to arboreal (a) and terrestrial (b) frugivory based on total interactions between treatments. The treatments include unburned interior, unburned edge, burned interior and burned edge. Faunal groups include birds (green) indetermined (salmon), invertebrates (red), and mammals (yellow). The number of attacked fruits is above the bars

Frugivory exhibited a wide range of variation from 0 % to 100 % across arboreal and terrestrial experiments. There were no differences in the proportion of arboreal frugivory between treatments (Chi = 4.94; df = 3; p = 0.17; Table 1; Table S1; Figure 4a). However, the unburned edge exhibited approximately twice as many attacked fruits as the other treatments in terrestrial frugivory (Chi = 7.41; df = 3; p = 0.05; Tables 1; Table S1; Figure 4b); there were no differences between the unburned interior, burned interior, and burned edge treatments.

Table 1 Minimum, maximum, mean, and standard error values of the proportion of attacked fruits (arboreal and terrestrial frugivory) among treatments: unburned interior, unburned edge, burned interior, and burned edge

Experiment	Treatments	Min	Max	Mean	SE
Arboreal frugivory	unburned interior	0	1	0.17	0.04
	unburned edge	0	1	0.33	0.06
	burned interior	0	1	0.33	0.07
	burned edge	0	1	0.23	0.06
Terrestrial frugivory	unburned interior	0	1	0.25	0.08
	unburned edge	0	1	0.49	0.09
	burned interior	0	1	0.19	0.05
	burned edge	0	1	0.23	0.08

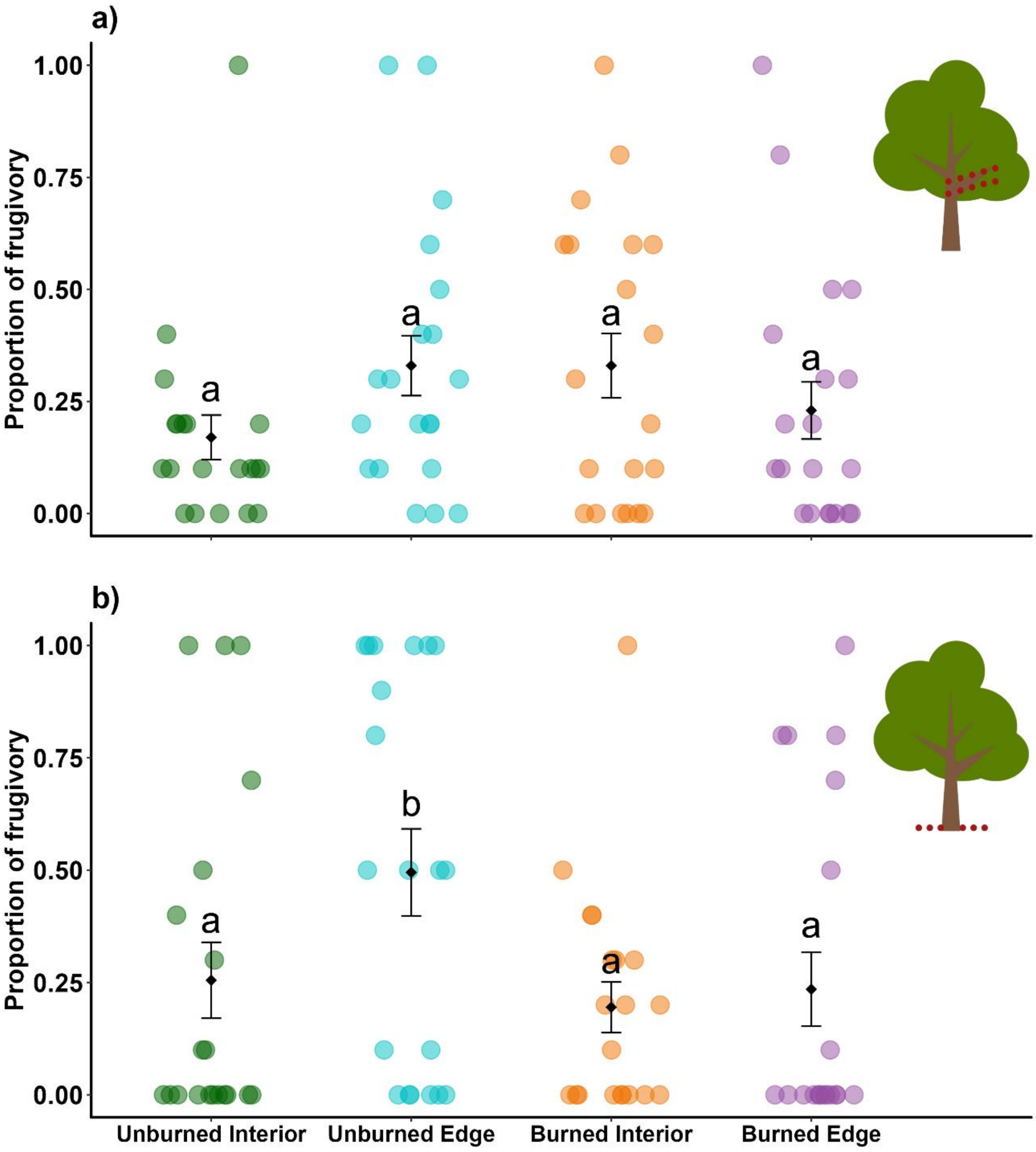

Fig. 4 Variation in the proportion of frugivory by fauna among treatments: unburned interior, unburned edge, burned interior, and burned edge. The experiments were conducted (a) on branches (arboreal frugivory), and (b) on the ground (terrestrial frugivory). Different letters represent significant differences at alfa = 5%. Black diamonds represent mean values. Bars represent standard errors (SEs). Colored dots indicate sample points. Some samples are not visible due to overlaps

We observed that 90.41% (2,170) of the exposed seeds were manipulated, with a range of 0% to 100% (Figure 5). While 89.5% (1,074) of the seeds were manipulated in open-access, 91.33% (1,096) were manipulated in the invertebrates-only. We observed that 95.5%

(2,051) of the manipulated seeds were removed, including 94.50% (1,015) in the open-access, and 94.52% (1,036) in the invertebrates-only. Additionally, 5.48% (119) of the manipulated seeds were effectively predated, from which 5.49% (59) were in the open-access, and 5.47% (60) were in the invertebrates-only.

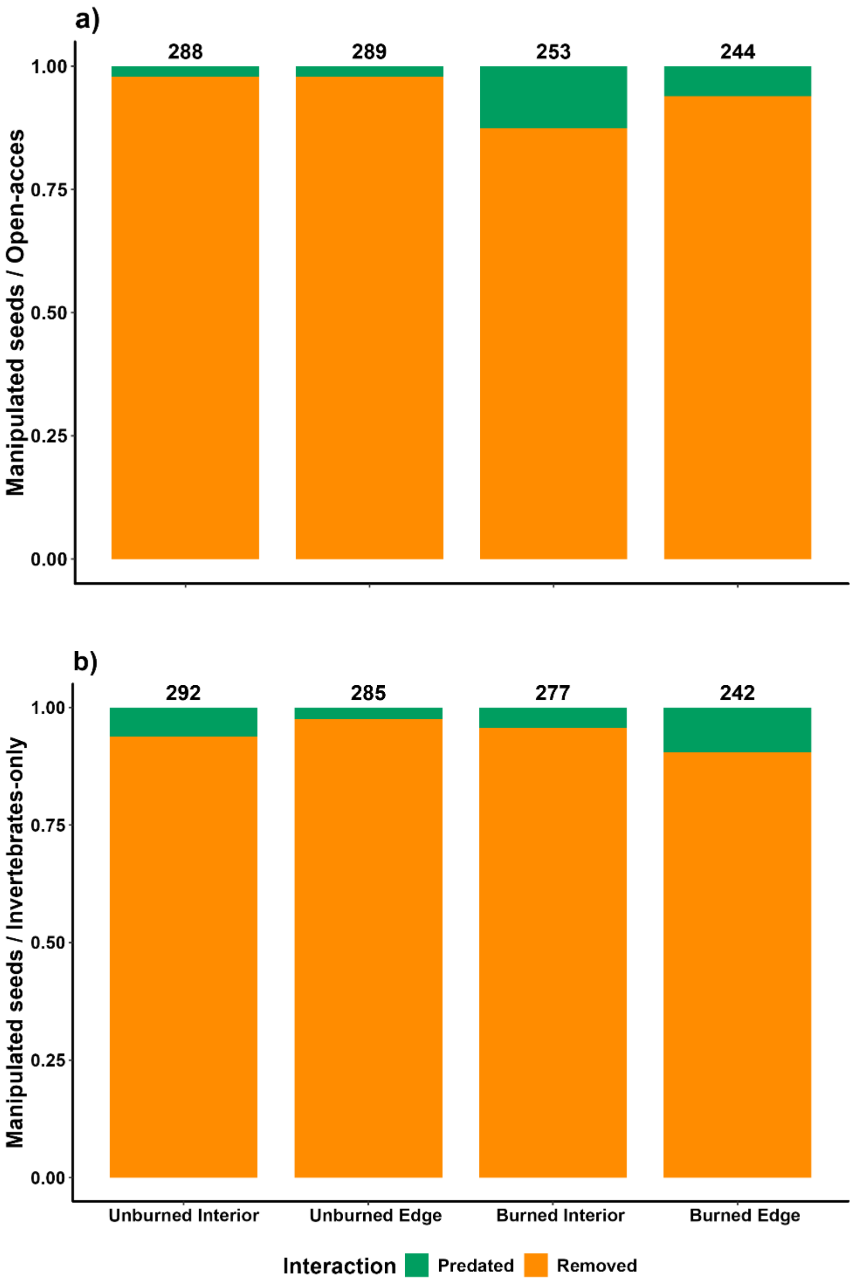

Fig. 5 Contribution of the observed interactions between treatments in seed manipulation by fauna for the open-access (a) and invertebrates-only (b). The treatments include unburned interior, unburned edge, burned interior and burned edge. Interactions include predated seeds (seen with predation marks; green) and removed seeds (missing; orange). The number of manipulated seeds is above the bars

Although we found an effect of the treatment on seed manipulation for the open-access (Chi = 14.86, df = 3; $p < 0.002$; Table 2; Table S2; Figure 6a) and the invertebrates-only (Chi = 9.34, df = 3; p = 0.02; Table 2; Table S2; Figure 6b), we observed different responses between the experiments. In the open-access, 16% more seeds were manipulated in the unburned than in the burned treatments, but there were no differences between the edge and interior within each plot. However, we obtained contrasting results for invertebrates-only. We observed that 5.42% and 20% more seeds were manipulated in the unburned interior compared to burned interior and burned edge, respectively, and that 17% more seeds were manipulated in the unburned edge compared to burned edge. However, we did not observe differences in the proportion of manipulated seeds between the burned interior and unburned edge (Table 4).

Table 2 Minimum, maximum, mean and standard error values of the proportion of manipulated seeds exposed on open-access and on invertebrates-only across treatments: unburned interior, unburned edge, burned interior and burned edge

Experiment	Treatments	Min	Max	Mean	SE
Open-access	unburned interior	0.3	1	0.96	0.02
	unburned edge	0.5	1	0.96	0.02
	burned interior	0.2	1	0.84	0.03
	burned edge	0.0	1	0.81	0.05
Invertebrates-only	unburned interior	0.7	1	0.97	0.01
	unburned edge	0.4	1	0.95	0.02
	burned interior	0.4	1	0.92	0.02
	burned edge	0.2	1	0.80	0.04

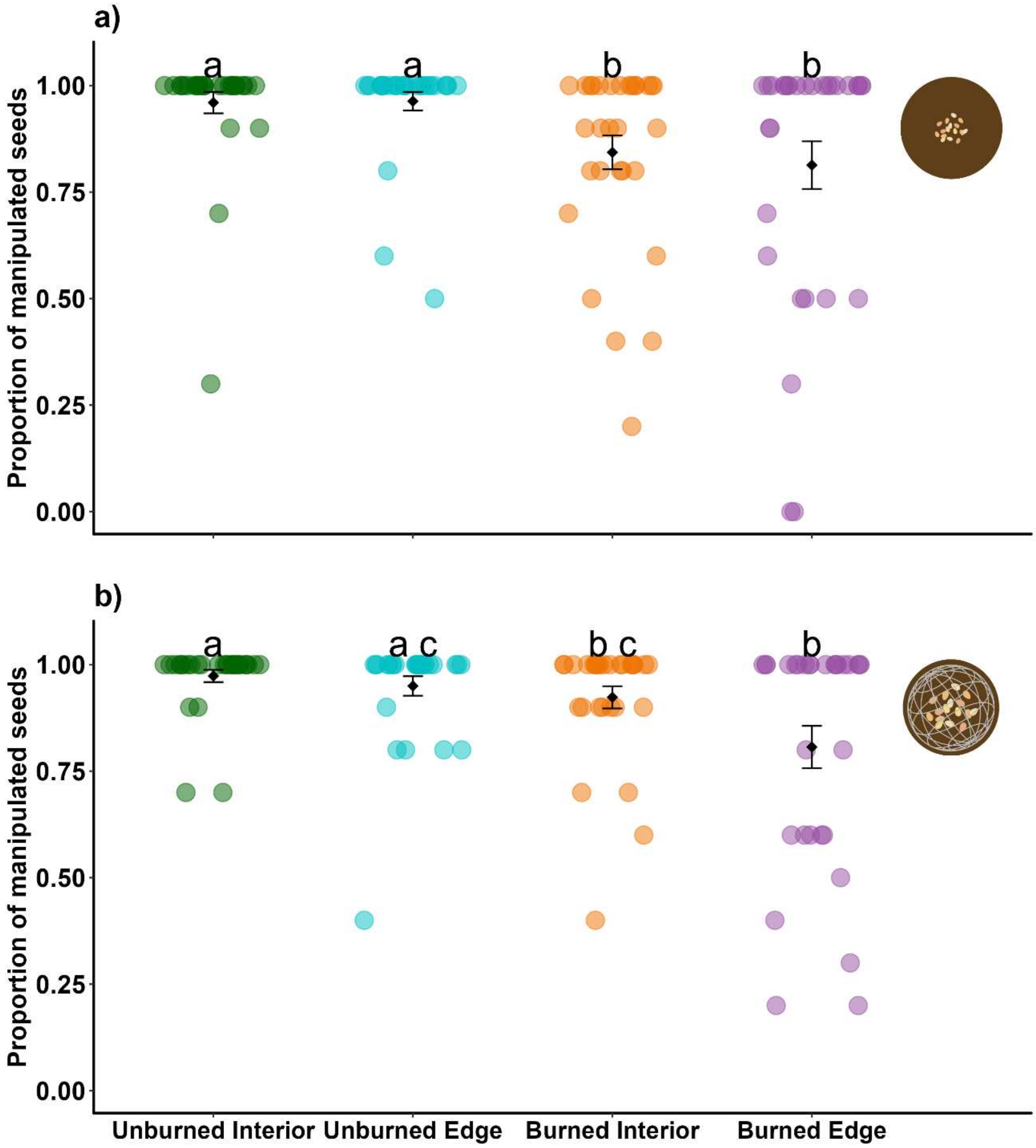

Fig. 6 Variation in the proportion of manipulated seeds in the open-access experiment for all fauna (a) and the invertebrates-only (b) among treatments: unburned interior, unburned edge, burned interior and the burned edge. Different letters represent significant differences at alfa = 5%. Black diamonds represent mean values. Bars represent standard errors (SEs). Colored dots indicate sample points. Some samples are not visible due to overlaps

3.6 Discussion

We observed distinct responses to fire and forest edge impacts in frugivory across arboreal and terrestrial strata, and in seed manipulation between full faunal access and invertebrate-only. Arboreal frugivory was not reduced by fire, edge or their synergy, but terrestrial frugivory was higher at unburned edge. Additionally, fire decreased seed manipulation by all organisms in both interior and edge, but edge alone did not impact it. Finally, fire also decreased seed manipulation by invertebrates in burned interior and burned edge compared to unburned interior, but edge alone did not impact this interaction. We also emphasize the role of invertebrates in animal-plant interactions, even in burned forests and at the forest edge, as they may help support interactions with diaspores on the ground in disturbed forests. Therefore, we observed intricate patterns in animal-plant interactions, indicating fire and edge impacts over animal-plant interaction dynamics in an Amazonian forest even 12 years after the last fire.

Species filtering is one of the main drivers of interaction patterns in an ecosystem (Camargo et al. 2020; González-Varo et al. 2023), with generalist species turnover enhancing post-fire interaction resilience (Barlow and Peres 2004b; Rossi et al. 2024). We observed that different faunal groups contributed to frugivory — with different contribution degrees by groups across strata — even in forest areas impacted by fire and edge effects. For instance, arboreal frugivory was mainly driven by vertebrates, particularly birds, accounting for 67.9% of interactions in this stratum (Figure 3a). While intact forests serve as refuges for fauna occurrence (Robinson et al. 2013; Berry et al. 2015), the growth of pioneer and exotic vegetation in burned forests and edges may compensate for reduced fruit production (Brando et al. 2024) and provide support to generalist frugivores (Mestre et al. 2013; Hawes et al. 2020). Additionally, generalist birds' mobility, foraging adaptability (Lees and Peres 2009; Ramos et al. 2020) and fruit color perception, in addition to vegetation openness (Galetti et al. 2003), facilitate their persistence in disturbed habitats, promoting seed dispersal (Carlo and Morales 2016). For instance, a similar result was observed in our study area with increased caterpillar predation by birds eight years post-fire (Queiroz et al. 2022). Therefore, more persistent species, mainly generalist birds, may be among the main groups contributing to the resilience of frugivory, and consequently, to subsequent ecological functions.

On the other hand, invertebrates — particularly ants — contributed to 75% of terrestrial frugivory (Figure 3b). Additionally, as vertebrate access appears to have little influence on overall seed manipulation (similar between entire fauna and invertebrates alone - 89.5% and 91.3%, respectively), invertebrates seemed to dominate post-dispersal processes not only in the undisturbed interior, but also in burned forest and edge. Ants actively forage for diaspores on the forest ground, driving primary and secondary dispersal (Passos and Oliveira 2003, 2004; Rico-Gray and Oliveira 2007). In addition, generalist ant species, which dominate post-fire communities (Paolucci et al. 2017), forage for diverse resources in disturbed forests, particularly at edges (Meyr et al. 2009; Gerhold et al. 2019) and may outcompete vertebrates for resource access in burned forests (Rossi et al. 2022). These findings highlight the dominant role of invertebrates such as ants in primary and secondary animal-plant interactions, even in burned and edge forests, suggesting they could partially compensate for reduced vertebrate interactions with diaspores in a lower stratum (see Rico-Gray and Oliveira 2007; Griffiths et al. 2017; Anjos et al. 2020).

The frequency of arboreal frugivory in the forest understory was not reduced by fire and edge effects or their synergies, but the edge effect increased the terrestrial frugivory frequency twice. While losses of species and unique interactions are expected due to deforestation or fire (Lee et al. 2022; Rossi et al. 2024), our results indicate that frugivory frequency can persist despite fire and edge effects, suggesting that frugivory can be maintained in disturbed tropical forests (e.g., Malhi et al. 2022). As frugivory frequency is an important mechanism for successful interaction and seed dispersal (Vázquez and Jordano 2005; Campagnoli et al. 2024), the sustained frugivory we observed in disturbed forests may support seed dispersal, drive plant species reproduction (Chaves et al. 2018; Camargo et al. 2021) – and therefore promote forest resilience (Camargo et al. 2021). Furthermore, dropping fruits accumulate on the forest ground and cause seed mortality by fungal activity or competition (Kluger et al. 2008). However, terrestrial frugivory can decrease such mortality by increasing the likelihood of seed dispersal by vertebrates (Tobler et al. 2010; Camargo-Sanabria et al. 2016) or invertebrates (Pizo and Oliveira 2001; Christianini et al. 2012). As invertebrates showed an increase of about four times in terrestrial frugivory compared to arboreal frugivory, while vertebrates decreased about two times (Figure 3), the similar frugivory rates between strata (29.5% and 26.5%, respectively) demonstrate the complementarity role between arboreal vertebrates and terrestrial invertebrates (e.g., Pizo et al. 2005; Christianini and Oliveira 2009, 2010; Camargo 2016). This highlights the key role of invertebrates in frugivory, even in burned forests and edges and that invertebrates may be the main group for primary diaspore dispersal on forest ground in scenarios of vertebrate loss.

Fire decreased seed manipulation by all fauna and invertebrates-only – both in the edge and forest interior. As invertebrates were the main group manipulating seeds, changes in vegetation openness by fire — a key factor driving variation in ant activity and species distribution — may explain this pattern (see Andersen 2019). For instance, fire generated a mosaic of environmental conditions in our study area, with varied impacts on vegetation and, consequently, different microclimate conditions (Brando et al. 2019; Silvério et al. 2019). This mosaic may increase seed manipulation variations, with sites impacted by fire due to higher organic matter loads reducing seed detection by ants more than sites less impacted (Paolucci et al. 2016). These results contrast with fire-adapted habitats, where seed interactions increase due to post-dispersal agent resilience, especially ants (e.g., Andersen 1988; Parr et al. 2007; Alcolea et al. 2022), and support a previous study in a nearby area, where ant-seed interaction decreased in burned forests (Paolucci et al. 2016). Additionally, forest edges and burned forests share environmental variations, such as vegetation openness, moisture loss and temperature increase, which may explain the similar seed manipulation by invertebrates between the unburned edge and burned interior. However, the consistently lower seed manipulation by fire-edge synergy — by all groups and invertebrates-only — along with the increase in terrestrial frugivory at the unburned edge but not at the burned one, could be an indication that fire-edge synergy may drive the reduced diaspore interactions in the lower strata forest. For instance, the effect of fire alone in reducing seed manipulation by invertebrates was smaller than the fire-edge synergy compared to undisturbed forests (a reduction of 5% and 20%, respectively). Thus, our findings highlight the fragility of animal-diaspore interactions by fire in tropical forest ground, even 12 years after fire, highlighting the strong influence of environmental changes in disturbed forests.

Although vegetation establishment is shaped by different environmental factors like luminosity, temperature and soil moisture, secondary interactions — through seed predation and dispersal — play a crucial role in plant community assembly (Culot et al. 2017; Larios et al. 2017). Thus, the negative fire impacts observed in seed manipulation may contribute to shifts in vegetation assembly and lower forest regeneration. For instance, reduced seed predation can increase competition and structural homogenization by favoring pioneer or invasive species (Paine & Beck 2007; Terborgh 2012). Similarly, limited secondary dispersal may restrict seed access to suitable recruitment sites while increasing seed competition and mortality due to seed accumulation (Vander Wall & Longland 2004; Gallegos et al. 2014). Therefore, reduced animal interactions in disturbed forests can negatively impact regeneration by altering seed distribution and composition (Fiedler et al. 2021).

3.6.1 Directions and next steps for forest regeneration

Despite the beneficial role promoted by invertebrates, invertebrate-mediated interactions cannot fully replace vertebrate services (Camargo et al. 2019). For example, invertebrates are constrained by diaspore size (Pizo and Oliveira 2001; Christianini et al. 2012; Anjos et al. 2018), and tend to facilitate exotic or pioneer species recruitment (Fernandes et al. 2020; Pereyra et al. 2022) (Figure S5g). In contrast, vertebrates disperse a broader range of seeds over longer distances, enhance germination via digestion, fertilize seeds and attract secondary dispersers by their feces (Jansen et al. 2008; Valenta and Fedigan 2009; Soltani et al. 2018; Marques Dracxler and Kissling 2021). Vertebrates are, therefore, a key factor for seed dispersion across degraded tropical forests (e.g., Paolucci et al. 2019) (Figure S5 e,f,h). In our study areas, vegetation homogenization occurred in burned and edge forests, primarily due to the invasion of grass species and the dominance of pioneers such as *Mabea fistulifera* (see Balch et al. 2008; Silvério et al. 2013; Brando et al. 2019, 2024), a myrmecochorous species commonly found at forest edges (Fernandes et al. 2020) (Figure S5 d, g). The dominance of invertebrates — particularly ants — in terrestrial frugivory and seed manipulation could partially explain these vegetation shifts. Thus, future research should explore the influence of invertebrate dominance in interactions by vertebrates (e.g., Davis et al. 2010; Dáttilo et al. 2016) and, consequently, the impact on forest regeneration by fires and edges.

Fruit nutritional composition (Quintero et al. 2020; Pizo et al. 2021), abundance, species richness, co-occurrence, and morphological traits (Burns 2002; Camargo et al. 2019; Campagnoli et al. 2024) are key factors influencing frugivory and seed dispersal effectiveness. Additionally, direct seed manipulation can lead to immediate consumption, transport for later use, handling damage, or effective dispersal. However, seed fate depends on traits such as palatability, toxicity, hardness, size, structural features, and the size and behavior of dispersing animals (Chang and Zhang 2014; Fernandes et al. 2018; Penn and Crist 2018). Our study used artificial fruits and agricultural seeds as models to assess how forest disturbances affect animal-plant interaction frequencies; thus, our results should be interpreted within this context. Future research should explore how widespread anthropogenic impacts such as fires and edges effects influence interactions across species with different traits, particularly those crucial for forest regeneration (e.g., Fiedler et al. 2021; Boone et al. 2022).

3.7 Conclusion

Different animal groups may drive frugivory, with vertebrates and invertebrates playing complementary roles in arboreal and terrestrial interactions, respectively. Because invertebrates were the primary agents of terrestrial frugivory and seed manipulation, they may be critical for maintaining animal-diaspore interactions in the lower forest strata, even under disturbances such as fire and edge. The resilience and adaptability of different animals to environmental changes likely contributed to the maintenance of frugivory frequency despite fire and edge effects, with increases at the edges due to invertebrate-driven terrestrial frugivory. While invertebrates are important secondary agents and can partially compensate for vertebrate-driven interactions, they did not wholly prevent the fire-induced decline in seed manipulation. Therefore, secondary interactions may be more negatively impacted by fire than frugivory. Furthermore, the consistently lower seed manipulation by fire-edge synergies across all animal groups and for invertebrates alone, together with the lack of increase in terrestrial frugivory at burned edges, highlights the synergistic effect of fire and edge disturbance on animal-diaspore interactions in forest ground.

Our data were collected 12 years after the fire; therefore, the observed effects are primarily due to indirect consequences of structural changes in the forest. The different impacts on different ecological interactions we observed illustrate the complex dynamics shaping tropical forests under anthropogenic pressure (e.g. Schleuning 2011). Including vertebrate and invertebrate interactions may provide more comprehensive responses to fire and edge impacts on animal-plant interactions. Future conservation strategies should consider the dynamic impacts of fire and edges on animal-plant interactions, adopt targeted approaches to primary and secondary interactions, and integrate invertebrate interactions in frugivory (mainly terrestrial frugivory) to develop a more robust response to fire impacts.

Suplementar Information

Fig. 1 Forest areas studied 12 years after a controlled fire experiment: a) unburned forest edge; b) burned forest edge; c) the interior of the unburned forest; d) the interior of the burned forest; e-f) transition of the control and burned forest with the agricultural cultivation area, respectively

Fig. 2 Demonstration of the artificial fruits deposited to evaluate the establishment of animal-plant interactions carried out by frugivorous animals: a) artificial fruits deposited on branches; b) frugivory marks made by birds; c-d) artificial fruits deposited on the ground with marks of attack by invertebrates (ants)

Fig. 3 Artificial fruits with the marks of frugivory by different faunal groups: a-b) invertebrates (ants and other invertebrates, respectively); c) birds; d-f) mammals (primates, rodents and marsupials, respectively). Birds: triangular marks or peck marks; mammals: bite marks with teeth; invertebrates: ants leave circular cut marks or small perforations, while other invertebrates leave small scraping marks or two converging scratches

Fig. 4 Demonstration of the seed deposition: a) seeds deposited in the experiment without a cage for free access by all groups; b) seeds deposited using cages to exclude vertebrates and allow exclusive access by invertebrates; c) demonstration of seed deposition with and without cages at each sampling point; d) seeds remaining after interaction with animals with seeds showing predation marks

Fig. 5 Natural fruits and seed found among the sample areas with evidence of interactions with local fauna: a) fruit with marks of attacks carried out by birds; b) fruit being accessed by ants on the forest floor; c) fruit after being consumed by primates; d) fruits of the pioneer species *Mabea fistulifera* found in abundance on forest edges and burned areas; e) feces with the presence of seeds deposited in a burned area; f) feces with the presence of diaspores deposited forest ground; g) seeds of *Mabea fistulifera* and other species present around an ant nest.; h) Tapir' feces with the presence of seeds; i) *Thraupis sayaca*, a low-quality disperser, in *Mabea fistulsifera* fruits

Table 1 Results of contrast tests for the terrestrial frugivory experiment by pairwise comparisons among treatments: unburned interior, unburned edge, burned interior, and burned edge

Table 2 Results of contrast tests for the seed manipulated experiments by pairwise comparisons among treatments: unburned interior, unburned edge, burned interior and burned edge

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3.9 APÊNDICE B

Fire and edges in the Amazon: impacts on key animal-plant interactions to forest regeneration

Jefferson Bruno B. S. Oliveira[1] et al.

[1] Programa de Pós-Graduação em Ecologia, Departamento de Biologia Geral, Universidade Federal de Viçosa, Viçosa, MG, Brazil. ORCID 0000-0002-5392-6080

Correspondence author: Jefferson Bruno B. S. Oliveira - jeffersonbrunoxd@gmail.com; jefferson.oliveira@ufv.br

3.9.1 Supplementary information

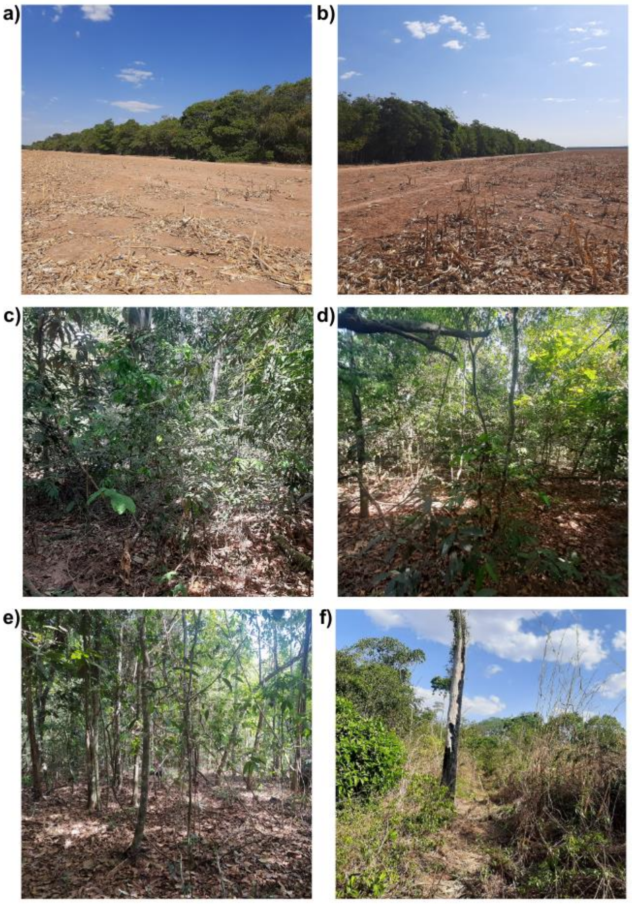

Fig. 1 Forest areas studied 12 years after a controlled fire experiment: a) unburned forest edge; b) burned forest edge; c) the interior of the unburned forest; d) the interior of the burned forest; e-f) transition of the control and burned forest with the agricultural cultivation area, respectively

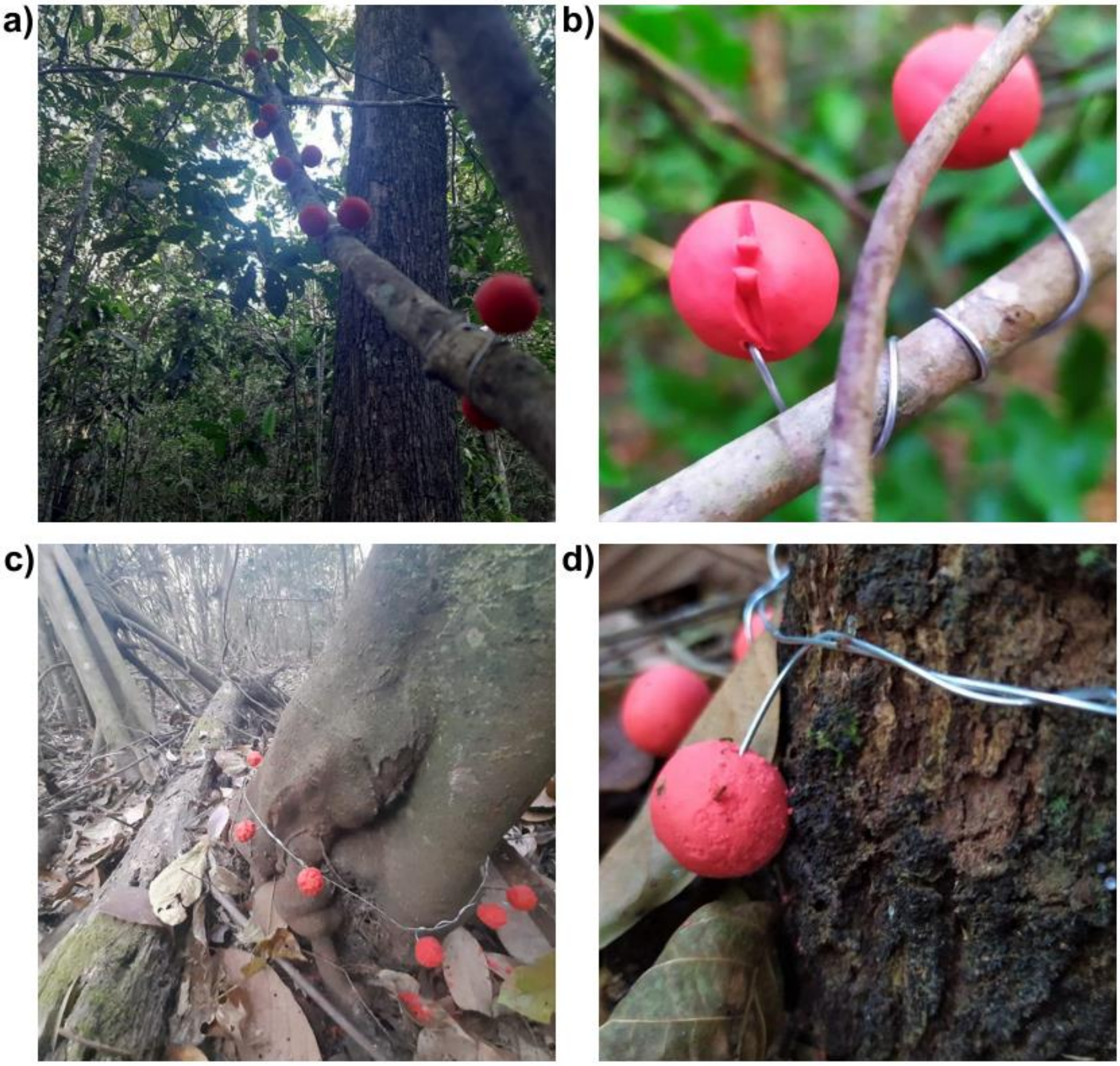

Fig. 2 Demonstration of the artificial fruits deposited to evaluate the establishment of animal-plant interactions carried out by frugivorous animals: a) artificial fruits deposited on branches; b) frugivory marks made by birds; c-d) artificial fruits deposited on the ground with marks of attack by invertebrates (ants)

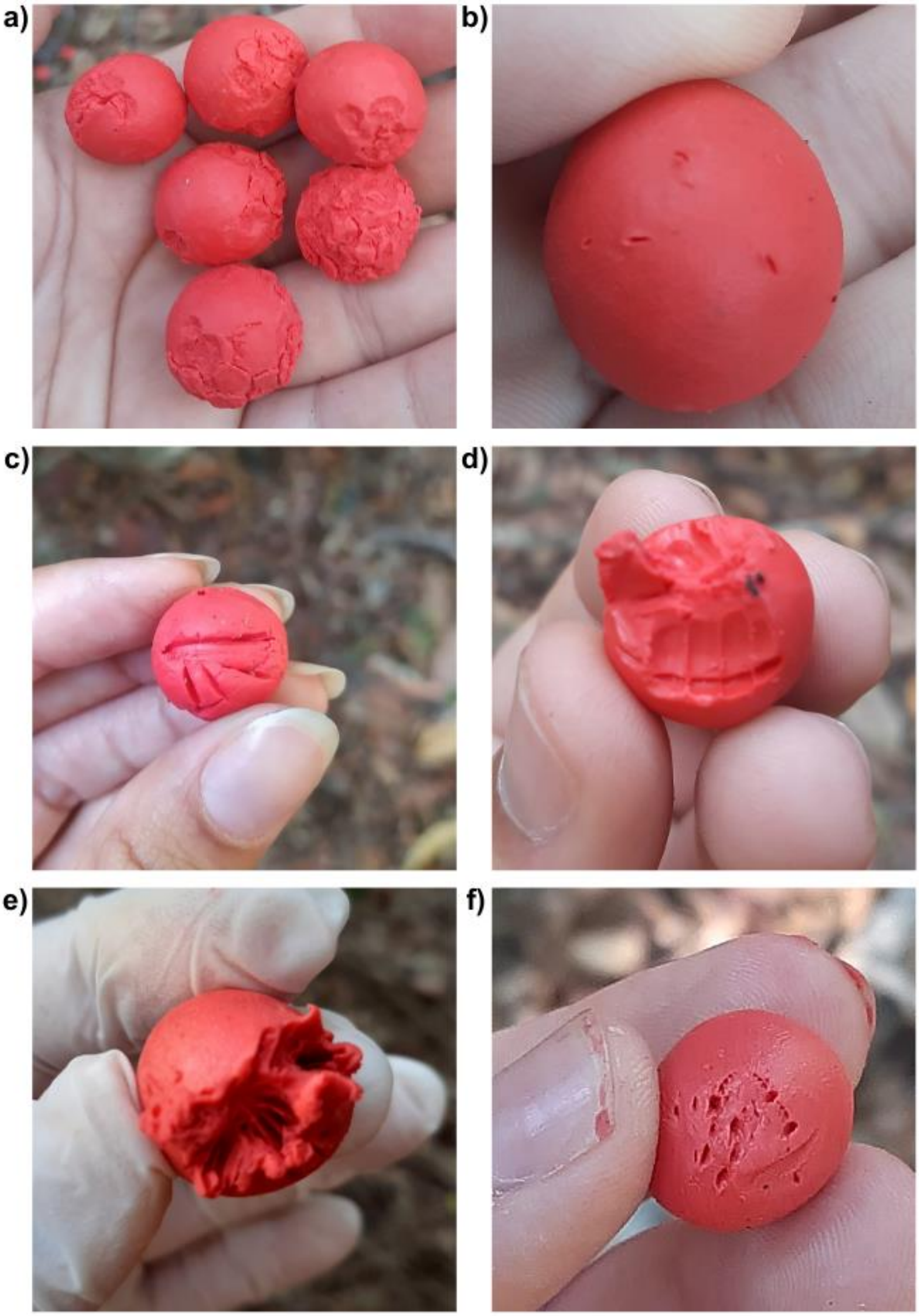

Fig. 3 Artificial fruits with the marks of frugivory by different faunal groups: a-b) invertebrates (ants and other invertebrates, respectively); c) birds; d-f) mammals (primates, rodents and marsupials, respectively). Birds: triangular marks or peck marks; mammals: bite

marks with teeth; invertebrates: ants leave circular cut marks or small perforations, while other invertebrates leave small scraping marks or two converging scratches.

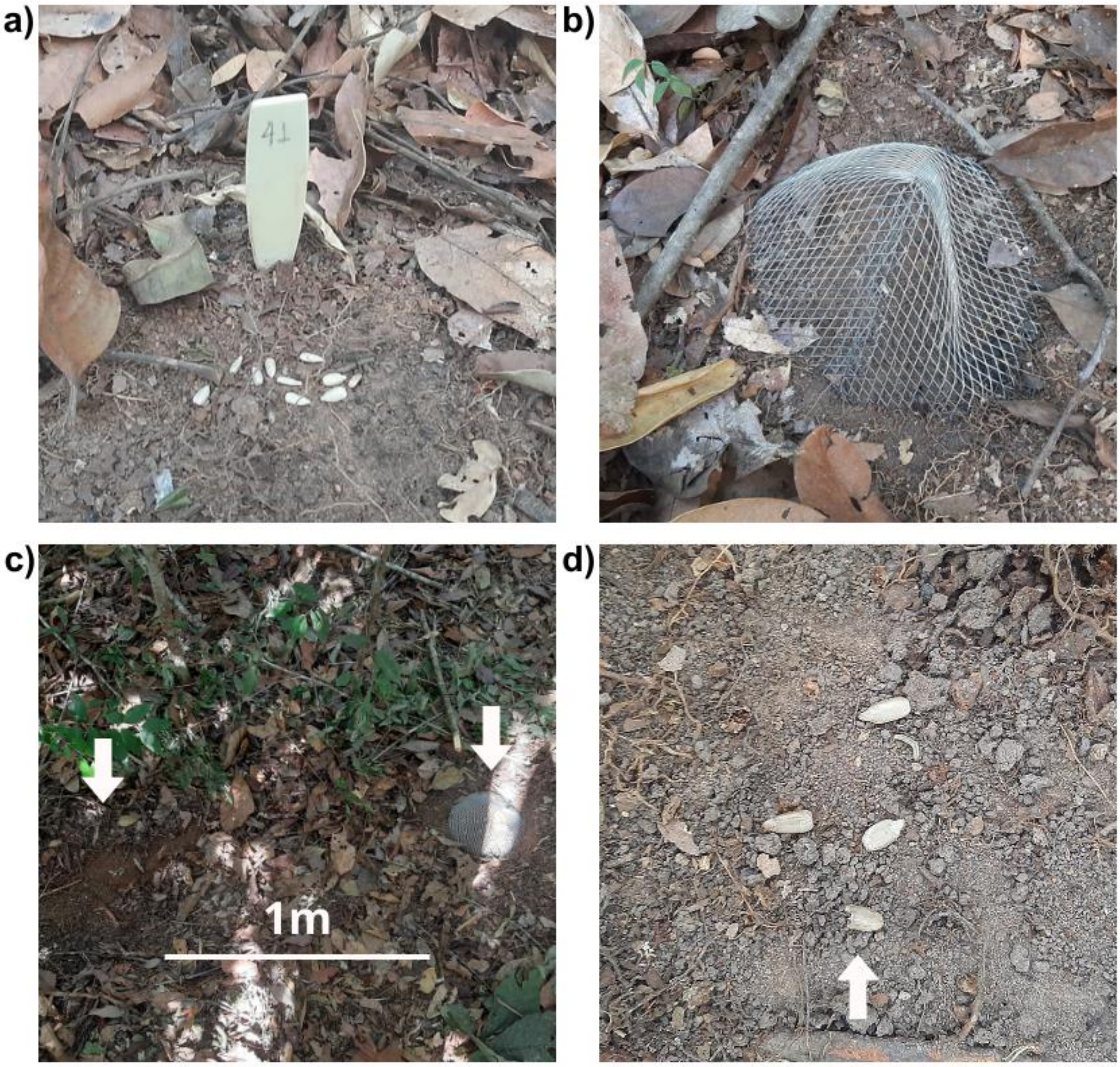

Fig. 4 Demonstration of the seed deposition: a) seeds deposited in the experiment without a cage for free access by all groups; b) seeds deposited using cages to exclude vertebrates and allow exclusive access by invertebrates; c) demonstration of seed deposition with and without cages at each sampling point; d) seeds remaining after interaction with animals with seeds showing predation marks

Fig. 5 Natural fruits and seed found among the sample areas with evidence of interactions with local fauna: a) fruit with marks of attacks carried out by birds; b) fruit being accessed by ants on the forest floor; c) fruit after being consumed by primates; d) fruits of the pioneer species *Mabea fistulifera* found in abundance on forest edges and burned areas; e) feces with the presence of seeds deposited in a burned area; f) feces with the presence of diaspores deposited forest ground; g) seeds of *Mabea fistulifera* and other species present around an ant nest.; h) Tapir' feces with the presence of seeds; i) *Thraupis sayaca*, a low-quality disperser, in *Mabea fistulsifera* fruits

Table 1 Results of contrast tests for the terrestrial frugivory experiment by pairwise comparisons among treatments: unburned interior, unburned edge, burned interior, and burned edge. Highlighted p-values represent significant differences

Pairwise comparisons	Chi	df	p
unburned interior × unburned edge	3.82	1	**0.05***
unburned interior × burned interior	0.01	1	0.90
unburned interior × burned edge	0.40	1	0.52
unburned edge × burned interior	3.65	1	**0.05***
unburned edge × burned edge	6.60	1	**0.01***
burned edge × burned interior	0.59	1	0.43

Table 2 Results of contrast tests for the seed manipulated experiments by pairwise comparisons among treatments: unburned interior, unburned edge, burned interior and burned edge. Highlighted p-values represent significant differences

Experiment	Pairwise comparisons	Chi	df	p
Open-access	unburned interior × unburned Edge	0.13	1	0.71
	unburned interior × burned Interior	9.98	1	**0.001***
	unburned interior × burned edge	5.94	1	**0.01***
	unburned edge × burned interior	12.05	1	**< 0.001***
	unburned edge × burned edge	7.58	1	**0.005***
	burned edge × burned interior	0.39	1	0.52
Invertebrates-only	unburned interior × unburned edge	0.53	1	0.46
	unburned interior × burned interior	3.91	1	**0.04***
	unburned interior × burned edge	8.44	1	**0.003***
	unburned edge × burned interior	1.5	1	0.21
	unburned edge × burned edge	4.96	1	**0.02***
	burned edge × burned interior	1.17	1	0.27

4 GENERAL CONCLUSION

This thesis investigated the impact of human activities in tropical forests on ecological interactions mediated by pollinators, frugivores and post-dispersal seed agents. The results highlight the consequences of anthropogenic disturbance on the establishment of fundamental interactions that support the conservation of forests, their resilience, and the persistence of their associated species. Thus, the observations presented here extend the understanding of forest impacts by highlighting their cascading effects on plant-animal interactions.

The effects of land-use change were observed to reduce the establishment of pollinator interactions in disturbed forests compared to old-growth forests. This loss of interactions may indicate that pollinators in anthropogenically disturbed forests may find it challenging to interact with adequate floral resources. Consequently, as pollinators in disturbed forests interacted with fewer floral partners, they were more sensitive to the random extinction of plants than pollinators in old-growth forests. This indicates a greater vulnerability of pollinators in disturbed forests and suggests that their prolonged anthropogenic disturbance could lead to the complete extinction of pollinators due to resource loss. Furthermore, no differences in the establishment of pollinator interactions were found between converted forests and old-growth or disturbed forests, possibly reflecting strong variation in pollinator responses to environmental differences between converted habitats. Despite these changes, the structure of plant-pollinator networks remained unchanged across land-use types, suggesting the resilience of their structural composition, which can persist even when interactions are less established.

It was also observed that plant-animal interactions related to frugivory and secondary seed manipulation could show differential responses to the effects of fire, with invertebrates — particularly ants — playing an active role in these interactions. Burned forest areas, both in the interior and along the forest edges, showed no differences in the frequency of arboreal frugivory compared to intact forests. This result suggests that the effects of fires and forest edges and their synergistic effects do not affect fauna's frequency of fruit access. However, the dominance of ants in interactions with fallen fruit resulted in a higher proportion of fruit attacked at unburned edges. These findings highlight the ants as an important group interacting with fallen fruit and emphasize that edge effects may favor foraging ants and their interactions with fruit in forest grounds. Additionally, burned areas showed reduced manipulation of seeds by fauna both in the interior and at the edges, demonstrating a negative effect of fire on access to seeds by secondary agents. However, less seed manipulation was observed only at the burned forest edges in interactions involving only invertebrates. This indicates variation in the responses by secondary agents, with invertebrate interactions showing greater resilience to the environmental changes caused by fire.

These findings demonstrate how environmental changes induced by different anthropogenic activities in tropical forests affect critical interactions that maintain their functioning. Therefore, this study contributes to understanding how ongoing anthropogenic disturbance of tropical forests could play a key role as the main driver of plant-animal interaction dynamics, potentially leading to severe impacts on the ecological functions they provide. Given the increasing demand for land use and the continued spread of fires in these forests worldwide, the findings presented here must be explored in a broader context, for example, by examining the intensity of different disturbances and linking these findings to the quality of the functions these interactions perform. Such findings may help decision-makers to develop effective forest management projects and conservation strategies that better ensure the protection of species and their interactions.