VANESSA SOARES RIBEIRO

LAND USE CHANGE AND FIRE IN AMAZONIA: IMPACTS ON INVERTEBRATES AND THEIR ECOSYSTEM FUNCTIONS

Tese apresentada à Universidade Federal de Viçosa, como parte das exigências do Programa de Pós-Graduação em Ecologia, para obtenção do título de *Doctor Scientiae*.

Orientador: José Henrique Schoereder

Coorientadores: Lucas Navarro Paolucci
Ricardo Ildefonso Campos

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RESUMO

RIBEIRO, Vanessa Soares, D.Sc., Universidade Federal de Viçosa, agosto de 2021. **Land use change and fire in Amazonia: impacts on invertebrates and their ecosystem functions**. Orientador: José Henrique Schoereder. Coorientadores: Lucas Navarro Paolucci e Ricardo Ildefonso Campos.

Distúrbios antrópicos como a mudança no uso da terra e os incêndios florestais são responsáveis por modificar a estrutura de paisagens naturais. Na região sul da bacia Amazônica, as modificações da estrutura da paisagem devido às ações antrópicas ocorrem de forma intensa. Nessa região, a conversão de florestas naturais para agricultura e o aumento de incêndios florestais, acidentais ou não, são responsáveis por modificar características ambientais. A modificação de características ambientais é responsável por mudança na estrutura de comunidades capazes de alterar as funções e serviços ecossistêmicos prestados por diversos organismos. Os invertebrados são responsáveis por promoverem diversas funções ecossistêmicas, como dispersão secundária de sementes, ciclagem de nutrientes e decomposição de matéria orgânica. Nesta tese, eu abordei como os distúrbios antrópicos no sul da Amazônia podem afetar funções ecossistêmicas desempenhadas por diferentes grupos de invertebrados. No primeiro capítulo, eu investiguei como a conversão de florestas em agricultura alteram as funções ecossistêmicas desempenhadas por formigas e besouros rola-bosta em florestas ripárias. Eu avaliei as funções de predação promovida por formigas, dispersão de sementes por formigas e besouros rola-bosta e remoção de fezes em florestas ripárias com entorno de floresta e com entorno de agricultura. Eu mostrei que os dois grupos sofrem mudanças na composição de espécies, mas apenas em formigas essas mudanças alteram as funções ecossistêmicas (dispersão de sementes). No segundo capítulo, eu investiguei o papel dos cupins para a decomposição de matéria orgânica em florestas queimadas, buscando entender quais os mecanismos explicam possíveis variações nesta função ecossistêmica. Eu encontrei aumento na abundância de cupins, menor predação de cupins por formigas e maior decomposição de matéria orgânica em florestas queimadas em relação as florestas preservadas. Essas mudanças nas comunidades de cupins ajudam a aumentar a função de decomposição de matéria orgânica. Concluí que distúrbios antrópicos alteram as funções ecossistêmicas desempenhadas por invertebrados após distúrbio antrópico, e tais funções são importantes para a manutenção de florestas e da biodiversidade.

Palavras-chave: Distúrbio antrópico. Funções ecossistêmicas. Formigas. Rola-bosta. Cupins.

ABSTRACT

RIBEIRO, Vanessa Soares, D.Sc., Universidade Federal de Viçosa, June, 2021. **Land use change and fire in Amazonia: impacts on invertebrates and their ecosystem functions**. Adviser: José Henrique Schoereder. Co-advisers: Lucas Navarro Paolucci and Ricardo Ildefonso Campos.

Anthropic disturbances such as land-use change and forest fires are responsible for modifying natural landscape structure. In the Southern part of the Amazon basin, changes in landscape structure due to anthropic actions occur intensely. In this region, the conversion of natural forests to agricultural lands and the increase of fires, either accidental or not, are responsible for modifying environmental characteristics. Changes in environmental characteristics are responsible for changes in the structure of communities and, consequently, altering ecosystem functions and services provided by different organisms. Invertebrates promote several ecosystem functions, such as secondary seed dispersal, nutrient cycling and organic matter decomposition. In this thesis, I investigated how anthropic disturbances in southern Amazonia affect ecosystem functions performed by different invertebrate groups. In the first chapter, I investigated how conversion of forests to agriculture alter ecosystem functions performed by ants and dung beetles in riparian forests. I evaluated predation promoted by ants, seed dispersal by ants and dung beetles, and dung removal in forested and cropland catchments. I showed that both groups suffered changes in species composition, but only in ants these changes altered ecosystem functions (seed dispersal). In the second chapter, I investigated the role of termites to organic matter decomposition in burned forests to understand which mechanisms explain possible variations in this ecosystem function. I showed increase in termite abundance, decrease of termite predation by ants, accompanied by increase in organic matter decomposition in burned forests. I concluded that anthropic disturbances altered ecosystem functions performed by invertebrates after anthropic disturbances, and these functions are an important factor for maintenance of forests and biodiversity.

Keywords: Anthropic disturbance Ecosystem functions. Ants. Dung beetles. Termites.

SUMÁRIO

INTRODUÇÃO GERAL

A região sul da bacia Amazônica tem sofrido com intensos distúrbios antrópicos, como mudanças no uso da terra e aumento da incidência de incêndios florestais (Balch et al. 2015; Macedo et al. 2012). Esses distúrbios são capazes de modificar a estrutura do habitat, e podem ocorrer de forma simultânea, uma vez que habitats fragmentados são mais susceptíveis a incêndios do que florestas intactas (Alencar et al. 2015; Kelly et al. 2020) (Fig. 1). Tanto as florestas fragmentadas devido a mudança no uso da terra, como as florestas queimadas sofrem alteração na biodiversidade (Chase et al. 2020; Sales et al. 2020) capazes de promover mudanças em funções ecossistêmicas.

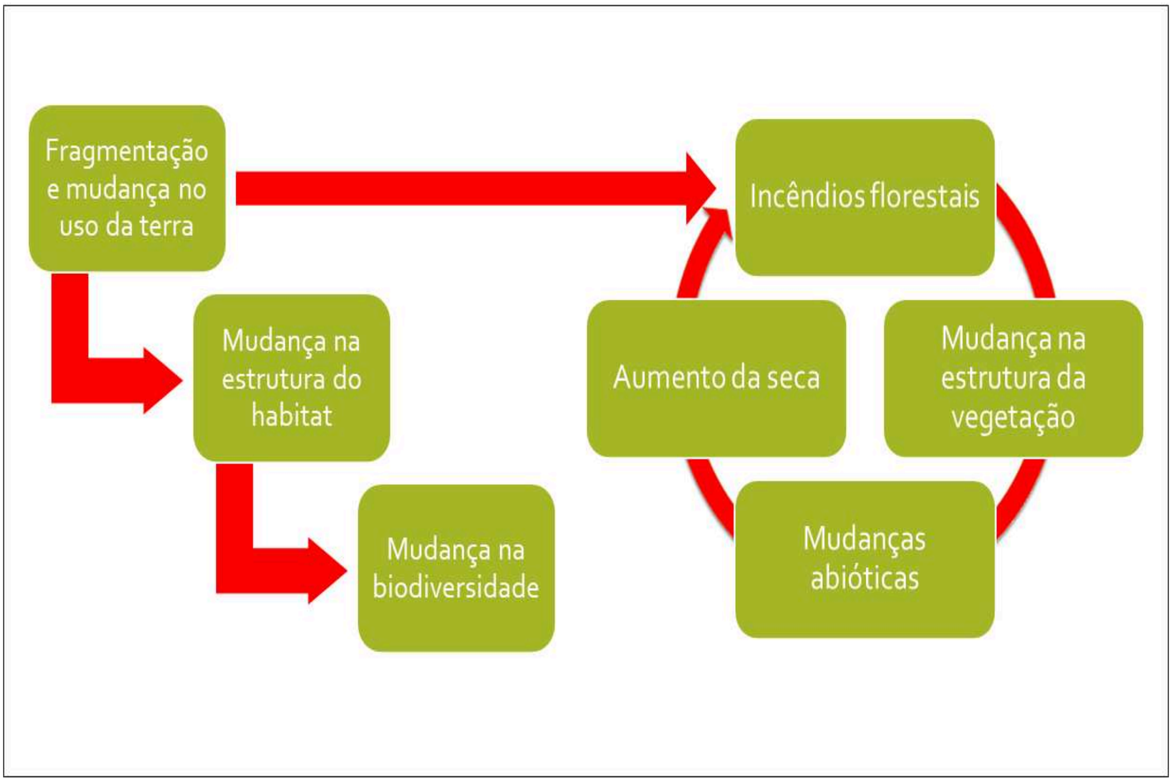

Figura 1. Efeitos da mudança no uso da terra e de incêndios florestais. As setas indicam quais as consequências de cada um dos eventos. Após a fragmentação ocorre um efeito em cascata que leva a mudanças na biodiversidade. Fragmentação pode levar ao aumento de incêndios florestais e aos efeitos cíclicos de tais incêndios.

Com o avanço do desmatamento, as florestas ripárias são em geral, o tipo de vegetação mais comum que permanece na paisagem, geralmente como fragmentos estreitos que acompanham os cursos d'água (Macedo et al. 2013). Florestas ripárias fragmentadas e com estrutura da vegetação alterada inseridas na agricultura possuem riqueza e composição vegetal modificadas, seguidas do aumento de diferentes tipos de espécies generalistas, capazes de promover uma heterogeneização biótica (Maracahipes-Santos et al. 2020). Além disso, devido a fragmentação, essas florestas estão sujeitas aos efeitos de borda, como o aumento da temperatura e diminuição da umidade (Laurance et al. 2007). Consequentemente, as mudanças na estrutura da vegetação que ocorrem pela conversão de florestas ripárias em agricultura podem levar à alteração em funções ecossistêmicas desempenhadas por diversos organismos, por exemplo formigas e besouros rola-bosta.

Formigas e besouros rola-bosta são amplamente usados como indicadores de mudanças ambientais devido as diferentes respostas que esses dois grupos possuem após um distúrbio. Esses organismos são responsáveis por funções ecossistêmicas, como ciclagem de nutrientes, bioturbação do solo e dispersão secundária de sementes (Andersen 2019; Nichols et al. 2008). A mirmecocoria aumenta a dispersão e diminui a predação das sementes por predadores (Giladi 2006), sendo que a manipulação de sementes pelas formigas é capaz de influenciar a comunidade de plantas devido ao aumento na taxa de germinação (Fernandes et al. 2018). Os besouros rola-bosta também são capazes de influenciar a estrutura das comunidades de plantas, pois além de removerem as sementes presentes nas fezes de mamíferos, muitas espécies enterram essas fezes, auxiliando ainda mais na germinação das sementes (Griffiths et al. 2016). No entanto, tanto formigas, quanto besouros rola-bosta podem sofrer mudanças nas comunidades e consequentemente nas funções ecossistêmicas desempenhadas devido à mudanças na estrutura do habitat (Barragán et al. 2011; Carvalho et al. 2020; Gray et al. 2016; Gray et al. 2014; Griffiths et al. 2015; Leal et al. 2012; Solar et al. 2016).

A mudança no uso da terra é também responsável pelo aumento da ocorrência de incêndios florestais em florestas tropicais (Bradshaw et al. 2009). A queima das florestas aumenta a quantidade de combustível disponível, devido ao aumento na mortalidade de árvores, aumento na abertura do dossel, maior quantidade de serapilheira, aumento da temperatura, diminuição da umidade e invasão de gramíneas (Brando et al. 2008, 2014; Barlow et al. 2020). Tais características das florestas queimadas as tornam semelhantes a florestas que sofrem com eventos de seca extrema (Ashton et al. 2019; Corlett 2016).

Um estudo mostrou que após um evento de seca extrema em uma floresta tropical da Malásia, o aumento na abundância de cupins possibilitou que aumentassem funções ecossistêmica como o aumento da decomposição de matéria orgânica e da taxa de germinação de sementes que mitigaram alguns dos efeitos da seca nesta floresta (Ashton et al. 2019). Nós sabemos que os incêndios florestais e as mudanças na estrutura do habitat diminuem a abundância de artrópodes em florestas queimadas (Silveira et al. 2010). No entanto, nós não sabemos se as semelhanças ambientais que existem entre florestas tropicais que sofrem um evento de seca extrema e uma floresta tropical queimada também é capaz de alterar a resposta das comunidades de cupins e aumentar algumas das funções ecossistêmicas que esses organismos promovem.

Tendo em vista o aumento da ocorrência de mudança no uso da terra e de incêndios florestais na região sul da bacia Amazônica e as alterações que a estrutura do habitat sofre devido a esse tipo de ação antrópica. Nesta tese, constituída de dois capítulos, eu investiguei como os diferentes tipos de distúrbios antrópicos na região sul da floresta Amazônica alteraram funções ecossistêmicas desempenhadas por formigas, besouros rola-bosta e cupins.

No primeiro capítulo, eu avaliei os impactos da mudança no uso da terra de florestas ripárias na Amazônia na eficiência das funções ecossistêmicas de formigas e besouros rola-bosta. Primeiro eu investiguei se as comunidades de formigas e besouros rola-bosta sofrem algum tipo de mudança na estrutura devido à conversão das florestas ripárias em agricultura. Em seguida eu avaliei se as mudanças na estrutura das comunidades alteram a eficácia das funções ecossistêmicas prestadas por formigas e besouros rola-bosta. Eu avaliei quatro florestas ripárias com entorno intacto e seis florestas ripárias com entorno degradado, composto de agricultura (Fig. 2). Como métrica para avaliar a estrutura das comunidades eu utilizei riqueza, abundância e composição de espécies. Adicionalmente, eu separei as formigas em grupos funcionais e utilizei a biomassa de besouros rola-bosta. Para avaliar se as funções ecossistêmicas das formigas são alteradas devido as mudanças na estrutura da comunidade eu medi a dispersão de sementes mirmecocóricas e a predação de cupins por formigas. Já para avaliar as funções ecossistêmicas de besouros rola-bosta, eu medi a quantidade de fezes de anta removida e a quantidade de sementes presentes nas fezes removidas.

No segundo capítulo, eu investiguei o papel dos cupins para a decomposição de matéria orgânica em florestas queimadas. Eu parti do fato que após um evento de seca extrema em uma floresta tropical na Malásia os cupins aumentaram a abundância e a decomposição de matéria orgânica (Ashton et al. 2019), e que floretas queimadas possuem características ambientais semelhantes a seca. Portanto, primeiro eu avaliei se há maior abundância de cupins em florestas queimadas e quais os mecanismos podem levar a esse aumento. Eu investiguei dois possíveis mecanismos capazes de influenciar a abundância de cupins. O primeiro a alteração de fatores ambientais como temperatura, umidade e altura da serapilheira, e o segundo a diminuição da predação de cupins por formigas. Eu medi a decomposição de matéria orgânica usando sacos de decomposição com e sem acesso de invertebrados. Eu utilizei dois experimentos de fogo, o primeiro com grandes parcelas de 500 × 1000 m que sofreram queimas anuais (B1*yr*) e queimas a cada três anos (B3*yr*) (Fig. 3), o segundo experimento é formado por blocos aleatórios de 40 × 40 m que queimados apenas uma vez (Fig. 4).

Figura 2. Florestas ripárias localizadas na Fazenda Tanguro, Querência - MT. Bacias em amarelo representam florestas ripárias com entorno de cultivo agrícola, bacias em verde representam as florestas ripárias com entorno de floresta intacta.

Figura 3. Experimento de fogo composto três grandes parcelas (500 × 1000 m). B1*yr* sofreu queimas anualmente de 2004 à 2010, exceto 2008; B3*yr* sofreu queimas a cada três anos, nos anos de 2004, 2007 e 2010; e a terceira parcela não foi queimada – controle.

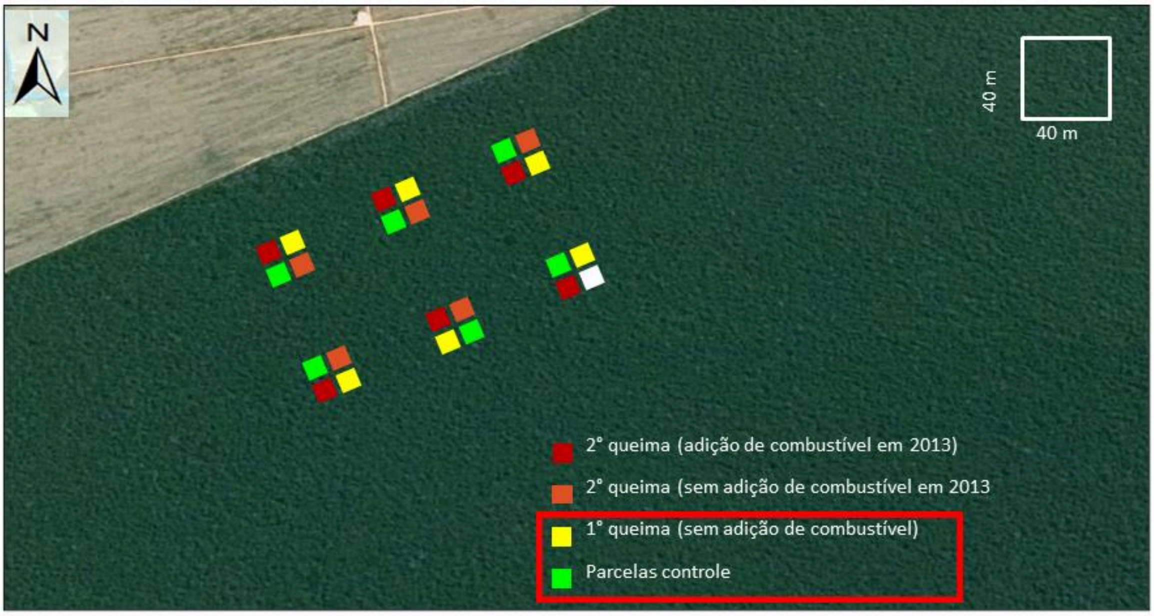

Figura 4. Experimento composto por seis blocos de parcelas aleatórias de 40 × 40 m. As parcelas amarelas sofreram queima sem a adição de combustível nos anos de 2013 e 2016; as parcelas verdes não foram queimados. Somente essas duas parcelas de cada bloco foram utilizadas.

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CAPÍTULO UM

IMPACT OF CHANGE IN LAND-USE OF AMAZON RIPARIAN FORESTS ON ECOSYSTEM FUNCTIONS PERFORMED BY ANTS AND DUNG BEETLES

Impact of change in land-use of Amazon riparian forests on ecosystem functions performed by ants and dung beetles

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Abstract

Habitat fragmentation promotes changes in biodiversity and alters ecosystem functions of ants and dung beetles. We investigated whether natural forest conversion to cropland promotes changes in community structure and in the effectiveness of ecosystem processes performed by ants and dung beetles in the southern region of the Amazon. For this, we surveyed the two insects' groups in two types of forests: riparian forests within forests (e.g. forested catchments) and riparian forests embedded within croplands (cropland catchments), obtaining data of community structure through pitfalls. We evaluated the ecosystem functions performed by ants and dung beetles such as seed removal, predation by ants and feces removal by dung beetles. Although ant and dung beetle richness and abundance did not differ between riparian forests in forested and cropland catchments, species composition in both groups differed between the two types of riparian forests. Ants find seeds faster in forested catchments and the proportion of seed cheating (i.e. cleaning seeds without removing them) was higher. However, the proportion of removed seeds, number of termites preyed by ants and time to find termites did not differ. Dung beetle biomass was higher in forested catchments, but no significant differences were found in dung beetle-mediated processes between forested and cropland catchments. Although most functions estimated did not differ, ants and dung beetles showed altered community structure. Changes in ant species composition within cropland catchments is probably responsible for promoted modifications in ecosystem functions and services.

Keywords: Amazon Forest, riparian forests, ecosystem functions, ants, dung beetles.

Introduction

Since early 1970s the southern region of the Amazon basin suffers extensive losses of native forest first to pasture and later to soybean fields (Macedo et al. 2012). Known as "arc of deforestation", this region displays one of highest global rates of forest loss and fragmentation (Brando et al. 2013; Morton et al. 2006). The Brazilian Forestry Code imposes that, riparian forests must be preserved, at least 30 m of vegetation along riversides (Federal Law nº 12.651/2012). Fortunately, riparian forests preserved in the Southern Amazon are usually larger than required by law due to the difficulties in applying mechanized agriculture in these places. As a result, the region is currently a mosaic landscape with pristine forests, riparian forests, and agriculture land.

Riparian forests buffer the impacts of intensive agriculture, maintaining biodiversity, ecological functions and ecosystem services (Lowrance et al. 1984; Macedo et al. 2013; Maracahipes-Santos et al. 2020; Nagy et al. 2015; Silvério et al. 2015). Riparian forests maintain streams by regulating air and water temperature, shadowing, intercepting and transporting nutrients, and serving as corridors for animal flux (Macedo et al. 2013; Nagy et al. 2015; Neill et al. 2013). Riparian forests fragments within croplands catchments tend to have heterogeneous plant composition, with high pioneer species occurrence and lower tree and native seedling density when compared to continuous riparian forests (Maracahipes-Santos et al. 2020). Riparian forest fragments in croplands are exposed to edge effects wind, drought, parasites (Laurance et al. 2000; 2007), increased air and water temperature, humidity decrease (Kapos 1989; Macedo et al. 2013; Nagy et al. 2015), changes in aquatic macroinvertebrate communities (Neill et al. 2013), and losses of ecosystem services such as pest control and pollination (Tilman et al. 2002). Riparian forests fragmentation alters ants (Hymenoptera: Formicidae) and dung beetles (Coleoptera: Scarabaeidae) communities, which are often not able to disperse in surrounding agricultural matrix (Gray et al. 2016).

Ants are a dominant group in tropical ecosystems, represent 20 to 52% of animal biomass in the tropics (Dial et al. 2006). They play several ecological roles (Andersen and Majer 2004; Folgarait 1998) and occupy different niches above and belowground (Tuma et al. 2020). Ants have an important role in ecosystem processes such as nutrient cycling, predation, herbivory, plant recruitment and germination, and seed dispersal (Del Toro et al. 2012; Fernandes et al. 2018). They prey on several animal groups (Hölldobler and Wilson. 1990), shaping other insect community (Tuma et al. 2020) and contributing to increased plant diversity via top-down control (Leles et al. 2017). Some ant species control the amount of herbivores in plants, and many of them have a mutualistic relationship with plants that offer shelter and food (Schmitz et al. 2000; Styrsky and Eubanks 2007). On another hand, some ant species of the Attini tribe are herbivores, as they use large amounts of fresh leaves to feed the fungus garden (Vasconcelos and Cherrett 1997). Ants are also important seed dispersers – and the seeds they disperse tend to become less exposed to granivorous (Giladi 2006; Leal et al. 2015). Ants have a positive impact on plant growth in forests and agriculture because they increase soil water infiltration and improve soil nitrogen due to their tunnels (Evans et al. 2011). Additionally, ants are classified into different functional groups, used in environmental impact assessment (Andersen 1995; Andersen 1997; Andersen and Majer 2004).

Dung beetles perform various ecosystem functions and services such as nutrient cycling, bioturbation, parasite control, fly control, dung removal and decomposition and secondary seed dispersal (Andresen 2002; Nichols et al. 2008). Dung beetles bioturbation modifies soil biota and promotes aeration, affecting plant productivity (Nichols et al. 2008). The amount of soil removed by dung beetles depends on beetle body size, as larger beetles can remove more soil (Edwards and Aschenborn 1987). When removing feces, they displace organic material, rich in nutrients and promote chemical changes in the soil, which also has implications for plant productivity (Nichols et al. 2007; 2008). Dung displacement promotes secondary seed dispersal, reducing seed predation and directing the seed to a more favorable microclimate (Andresen and Levey 2004). The quality of secondary seed dispersal services by dung beetle is linked to depth at which seeds are buried (Griffiths et al. 2015). The depth which seeds are buried depends on dung beetle community structure, dung beetle body size and seed size (Andresen 2002; Andresen and Levey 2004). As well as ants, dung beetles are sensitive to environmental changes (Griffiths et al. 2015). Different dung beetles functional groups can perform different functions, and the loss of any these groups can lead to negative changes in the ecosystem function performed (Barragán et al. 2011).

Environmental changes in riparian forests associated with fragmentation can promote a cascade effect, modifying ant and dung beetle community structure and the associated ecosystem functions. Here, we investigate how agricultural land-use changes alters ant (Hymenoptera: Formicidae) and dung beetles (Coleoptera: Scarabaeidae) community structure in Amazon riparian forests. We expect a decrease in species richness and abundance in riparian forest fragments within cropland fields, in addition to change in species composition. We also expect change in ant functional groups, and decrease in dung beetle biomass in riparian forest fragments within cropland fields. In addition, we investigate whether changes in community structure alters ecosystem processes effectiveness performed by ants and dung beetles.

Methods

Study area

We conducted this study at Fazenda Tanguro, located in Southern Amazon, Mato Grosso, Brazil (12°49′S, 52°21′W). The air temperature varies from 24 to 26 ºC, and the mean annual precipitation varies from 1700 to 2200 mm, with dry season from May to September (Alvares et al. 2013). The site is located in the transition zone between savanna (Cerrado) and Amazon rainforest and has a 40-year history of changes in land use and vegetation cover. This farm was initially exploited by the partial removal of pristine forest and pasture establishment. From between 2004 and 2009 onwards the farm was partially converted to soybean plantations, and double crop of soybean and corn, with approximately 60% of primary forest remaining today (Nagy et al. 2015). Some riparian forest remained isolated within an agricultural matrix, while others constitute continuous block of pristine forests.

Ant and dung-beetle sampling

We sampled ten riparian forests between March and April 2018: four riparian forests within forests (forested catchments) and six riparian forest fragments within cropland fields (cropland catchments) (see Fig. 1 in Maracahipes-Santos et al. 2020). In each riparian forest we sampled ants and dung beetles in one 750 m transect. Each transect had ten non-baited pitfall traps of 5 cm in diameter for ant sampling, and five baited pitfall traps with 15 cm in diameter containing 20 g of human feces for dung beetle sampling (Andresen 2002; Marsh et al. 2013). We placed pitfalls every 50 m, interspersing two ant pitfalls with one dung beetle pitfall, so that dung beetle pitfalls were 150 m away from each other (Silva and Hernández 2015). All pitfalls remained in the field for 48 hours. Ant samples were sorted and identified at the Community Ecology Laboratory at the Federal University of Viçosa, while dung beetles were sorted and identified by a specialist (Dr. Fernando Vaz-de-Melo) at the Scarabaeoidologia Laboratory of Federal University of Mato Grosso. We deposited ants and dung beetles in reference collections at the Scarabaeoidologia Laboratory of the Federal University of Mato Grosso, and Community Ecology and Tropical Ecosystems Laboratory of Federal University of Viçosa, respectively.

Ant functional groups

We classified ants into functional groups according to Leal et al. (2012) and Paolucci et al. (2016). We adopted primarily the classification made by Paolucci et al. (2016), who also carried their study in the Amazon. There was only one change: we defined cryptic predatory and cryptic omnivorous species as cryptobiont species, following criteria established for classification in a previous meta-analysis (Bickford et al. 2007). Thus, we established ten groups: Arboreal Dominant, Arboreal Predators, Army Ants, Camponotini Subordinate, Cryptobiont, Epigeic Omnivores, Epigeic Predators, Leaf-cutting Fung-growing Ants, Non-leaf-cutting Fungi-growing Ants and Opportunists (Table S1). We included in statistical analyses only functional groups that presented more than one species in both forested and cropland catchments.

Dung beetle biomass

We estimated dung beetle biomass. We oven-dried individuals for at least 72 hours at 40° C and weighed each one on precision scale. After, we obtained the average biomass of beetles in each riparian at forest forested and cropland catchments.

Seed removal by ants

We established a grid of 5 × 5 stations 2 m apart from each other in each riparian forest to estimate removal rate of seeds by ants, following Paolucci et al (2016). We used *Mabea fistulifera* seeds (globular 0.8 × 0.5 mm; Euphorbiaceae) because it is myrmecochorous and occurs naturally in the studied region. We set a sheet of paper (10 × 15 cm) in each station containing a seed in center. After setting the 25 stations, we walked for 1 hour, taking note of removal events (greater than 5 cm distance) and cheating, when ants ingested only the elaiosome without removing the seed (Leal et al. 2012; Leal et al. 2014). The shorter seed exposure time, the lower the predation risk and the higher the quality of dispersal services provided by ants (Leal et al. 2012; Leal et al. 2014). We recorded cheating events only after ants stayed more than 15 min eating the elaiosome. We sampled ants for subsequent identification when they removed the seed for more than 5 cm or remained eating elaisome for more than 15 min. In cases in which the actual removal has not been observed, we established that removal had happened and placed another seed for possible capture of species for identification. We carried out experiment in the periods of highest ant activity, between 9 and 11 am and 3 and 5 pm.

Termite predation by ants

We established three stations 3 m apart from each other in each riparian forest. Each station received a sheet of paper (10 × 15 cm) with a live termite attached with white glue. We picked up termites in nests minutes before experiment started. We recorded termite predation events by ants for 10 min. We only recorded predation events when termites were captured, removed, or killed in place.

Feces and seeds removal by dung beetles

We used fresh tapir (*Tapirus terrestres*) feces for the experiment of feces and mimetic seed removal by dung beetles. Tapirs are large and abundant mammals at the experimental site, they deposit large amounts of feces, and are good seed dispersers, especially in degraded forests (Paolucci et al. 2019). First, we homogenized the tapir feces collected and then separated 500 g for each sample. We placed 20 colored plastic beads (diameter 3 to 4 mm) in each 500 g sample, so that we could count the number of seeds that dung beetles disperse along with feces removal. We froze the samples after ready until placed them in fields. We placed three samples of feces separated by 150 m from each other in each riparian forest and left all samples in the field for 24 hours. After this period, we collected the samples, weighed, and counted the remaining beads. We determined if the natural weight loss affected significantly the samples weight. To control for natural weight loss, we placed smaller samples (20 g of tapir feces) next to each 500 g sample, suspended to impede the access by dung beetles and weighed them after 24 hours.

Statistical analysis

In all analyses, we used the forested and cropland catchments as explanatory variable. To test whether changes in species richness and abundance of ants and dung beetles, and in ant functional groups abundance, we used GLM (Generalized Linear Model), with Poisson error distribution. We obtained species and functional group abundances as the sum of frequencies of any species and component species of each group, respectively. We tested the prediction that species composition differs between treatments using PERMANOVA, based on Jaccard's dissimilarity (Anderson 2001), and plotted the results graphically with a PCoA (Principal Coordinates Analysis).

We used a survival analysis to compare the time for the seeds and termites to be discovered in each treatment, using Weibull error distribution. In seed removal analysis, we used time for occurrence of each event (either removal or cheating) as the response variable. In termite predation, we used time for occurrence of each event (predation) as the response variable.

We used seed proportion as response variable and as predictors: seed removal by ants, seed cheating by ants, termite predation by ants, natural weight loss in feces, feces removal by dung beetles and seed removal by dung beetles. We calculate dung beetle biomass using the mean weight per individual as a response variable. We used GLM with binomial distribution for data of proportion and mean. We checked for overdispersion in all GLMs, using the R package DHARMa V 0.4.1 (Hartig, 2021).

Results

Community structure

We sampled 87 ant species, distributed in 28 genera and seven subfamilies, the subfamily Myrmicinae had the highest species richness (Table S1). Ant species richness and abundance in riparian forests did not differ between forested and cropland catchments (richness: χ^2 [1, N = 10] = 0.46, P = 0.83; abundance: χ^2 [1, N = 10] = 0.36, P = 0.76). Ant species composition differed between riparian forest in forested and cropland catchments ($F_{1,8}$ = 1.92, R^2 = 0.19, P = 0.02, Fig. 1). Leaf-cutting fungi-growing ant abundance was higher in cropland than in forested catchments (χ^2 [1, N = 10] = 5.01, P = 0.03, Fig. 2), while other functional groups did not differ between riparian forest in forested and cropland catchments.

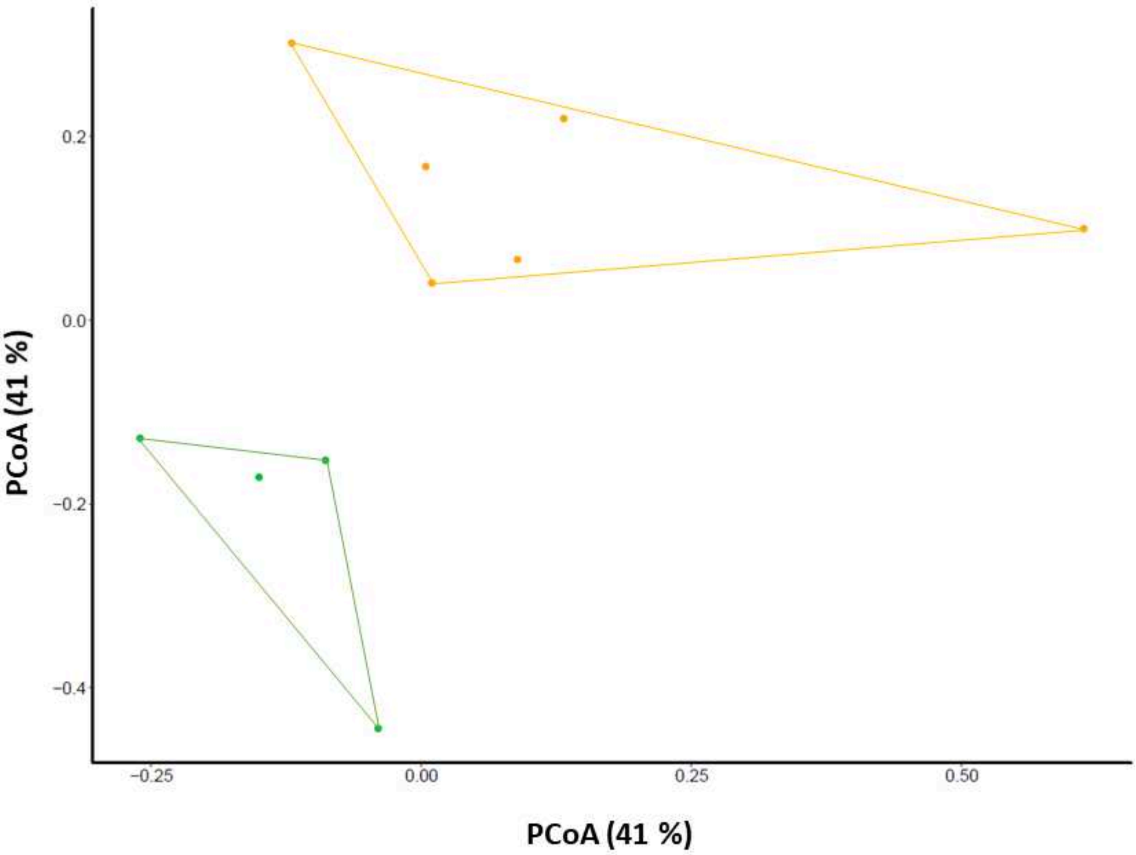

Figure 1. PCoA plots of ant species composition according to riparian forests type: forested (green) and cropland catchments (yellow). Statistical significances were tested through PERMANOVA - $F_{1,8} = 1.92$, $R^2 = 0.19$, $P = 0.02$.

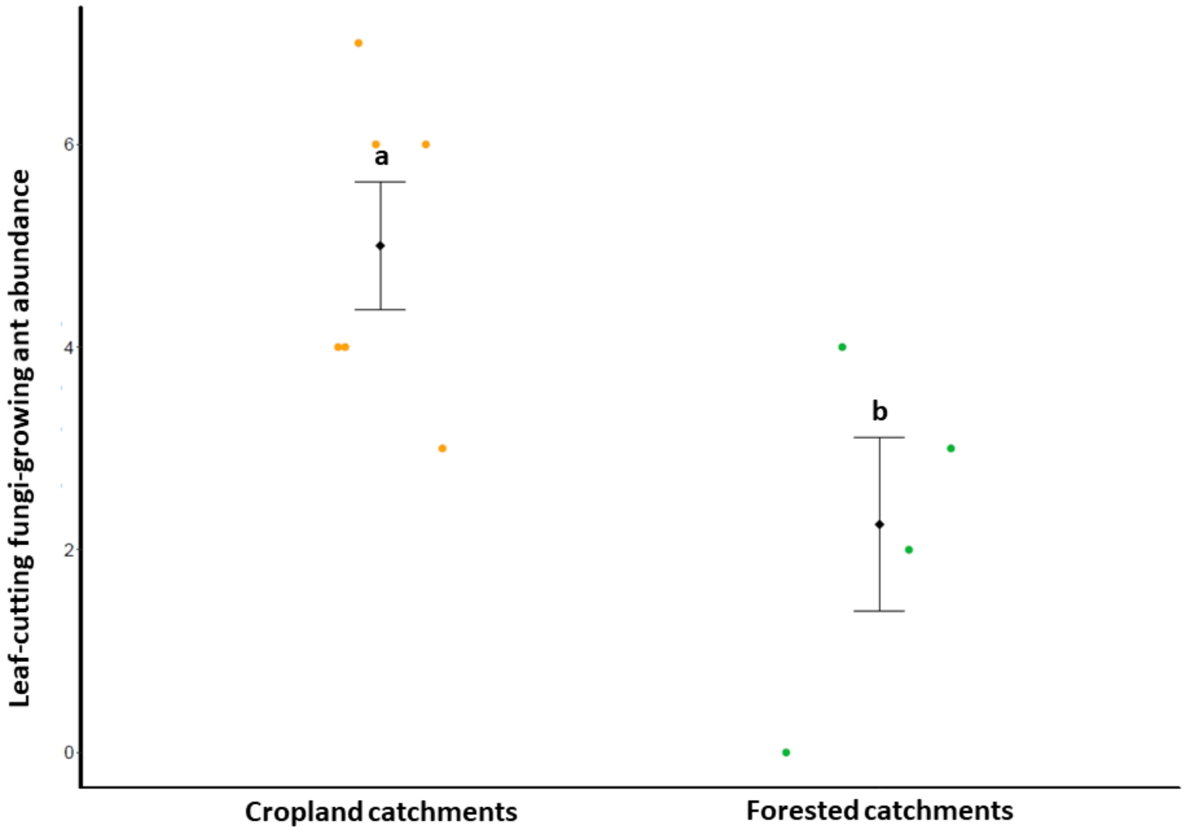

Figure 2. Variation in abundances of leaf-cutting fungus-growing ant functional group. Different letters indicate significant differences, according to ANOVA. Bars represent standard error.

We sampled 1543 individuals of 33 dung beetle species, distributed in 15 genera (Table S2). Dung beetle richness and abundance did not differ between riparian forest in forested and cropland catchments (richness: χ^2 [1, N = 10] = 2.45, P = 0.12; abundance: χ^2 [1, N = 10] = 32.37, P < 0.37). Dung beetle species composition differed between riparian forests in forested and cropland catchments ($F_{1,8}$ = 3.40, R^2 = 0.30, P = 0.006, Fig. 3). Dung beetle biomass was higher in riparian forests within forested rather than in cropland catchments (χ^2 (1, N = 10) = 0.07, P = 0.003, Fig. 4).

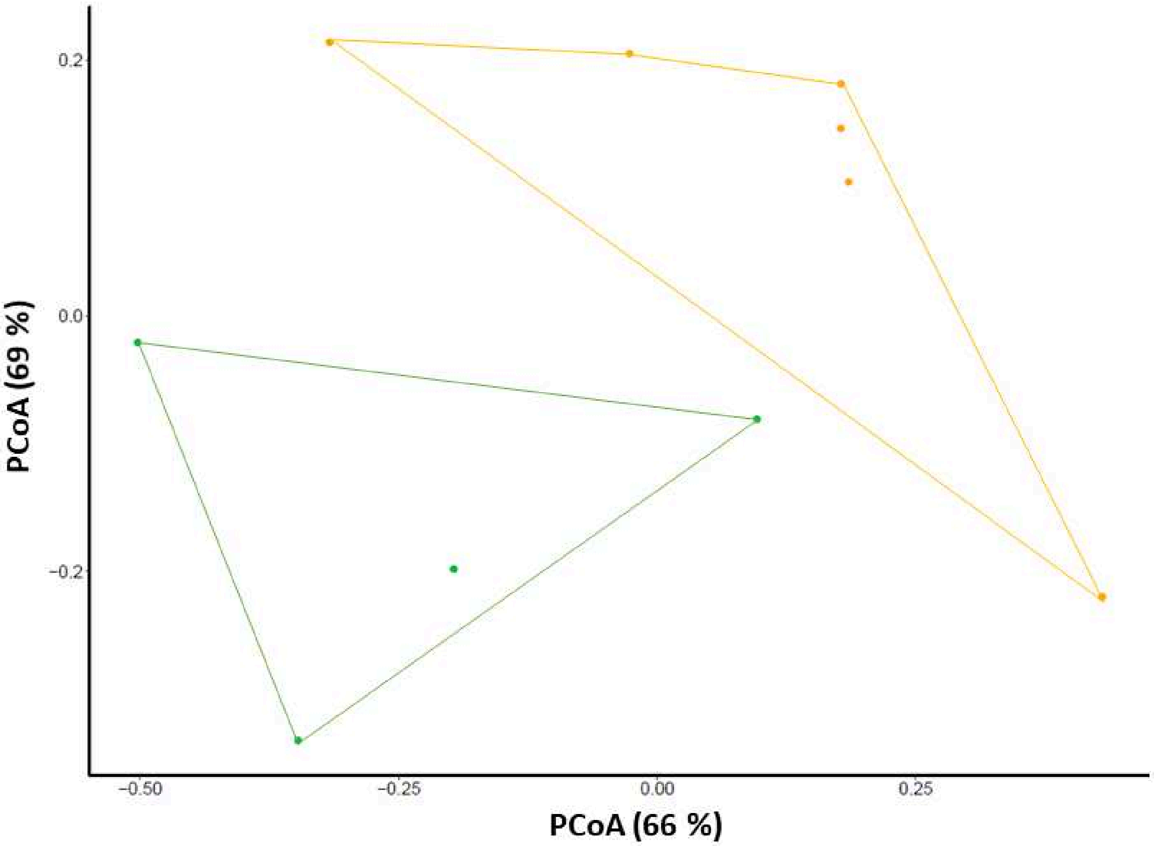

Figure 3. PCoA plots of dung beetle species composition according to riparian forests type: forested (green) and cropland catchments (yellow). Statistical significances were tested through PERMANOVA - $F_{1,8} = 3.40$, $R^2 = 0.30$, $P = 0.006$.

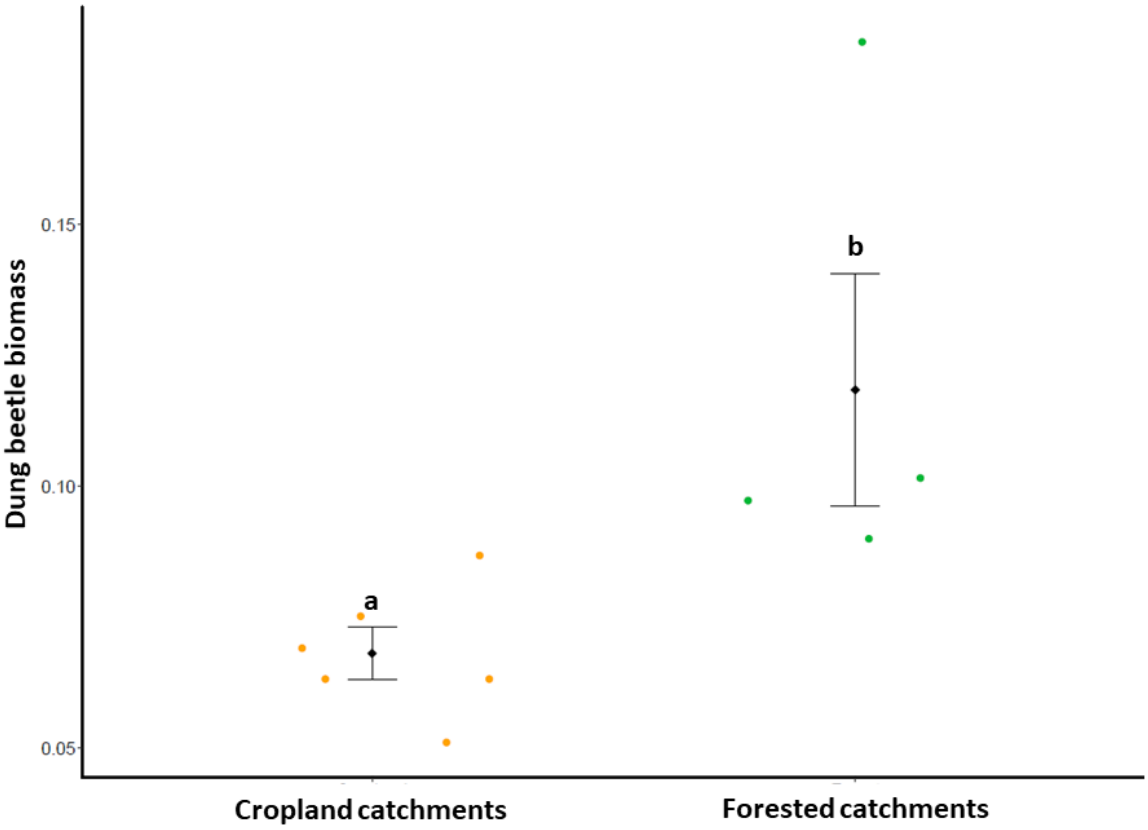

Figure 4. Variation in biomass of dung beetle species between riparian forests in forested and cropland catchments. Different letters indicate significant differences, according to ANOVA. Bars represent standard error.

Ecosystem functions by ants and dung beetles

Seed cheating by ants was higher in forested than in cropland catchments (χ^2 [1, N = 10] = 4.60, P = 0.032, Fig. 5). The number of seeds removed by ants did not differ between riparian forest in forested and cropland catchments (χ^2 [1, N = 10] = 0.02, P = 0.88). Ants found seeds faster in riparian forest in forested than in cropland catchments [χ^2 (1, N = 10] = 7.38, P = 0.007, Fig. 6).

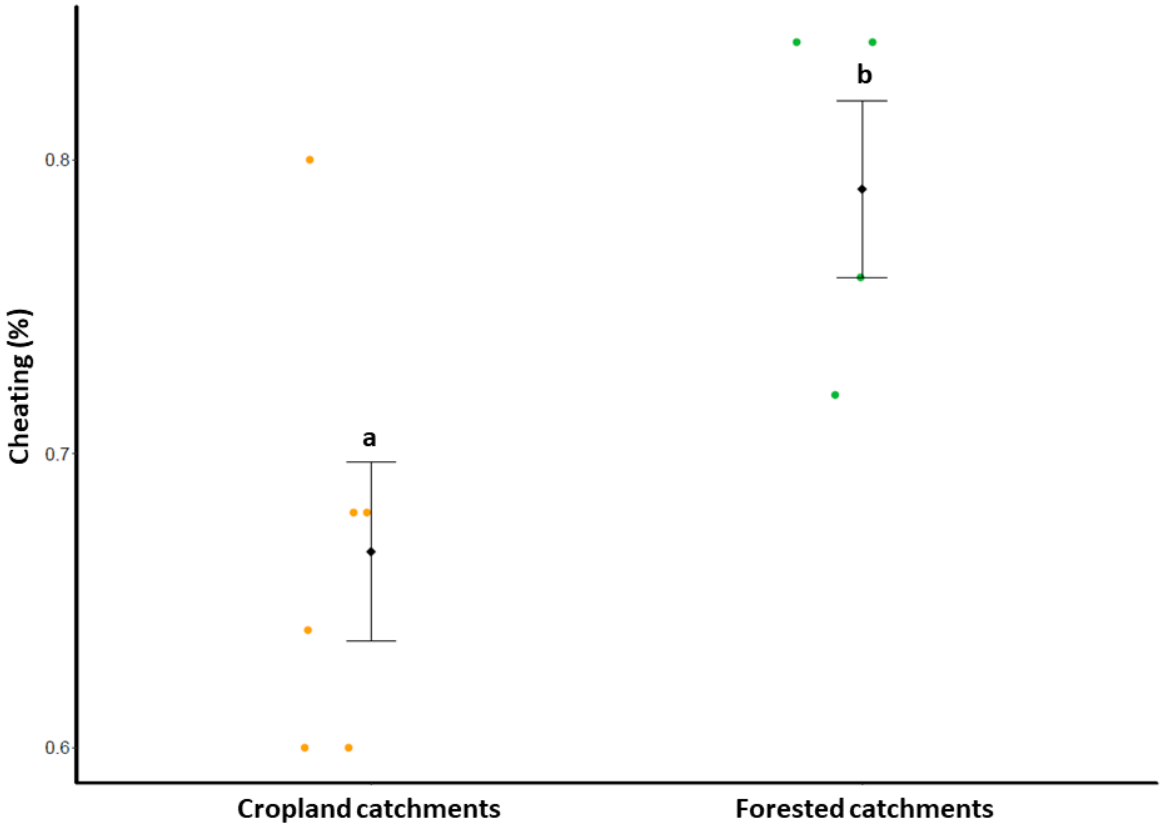

Figure 5. Variation of cheating in riparian forest in forested and cropland catchments. Different letters indicate significant differences, according to ANOVA. Bars represent standard error.

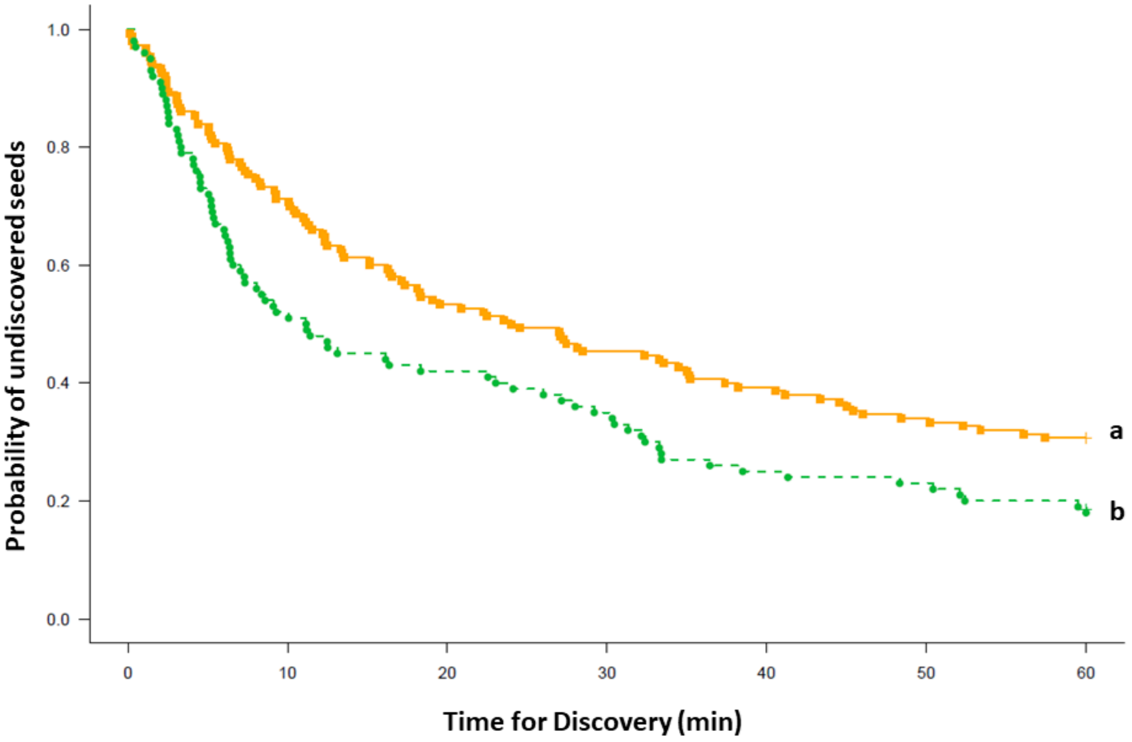

Figure 6. Variation in seed discovery time by ants. Seeds were discovered faster in riparian forests with forested catchments (green) than in cropland catchments (yellow). Different letters indicate significant differences, according to survival analysis.

The proportion of termites predated by ants and the time for ants to prey on termites did not differ between riparian forest in forested and cropland catchments (proportion termites predated: χ^2 (1, N = 10) = 0.82, P = 0.48; time to prey: χ^2 (1, N = 10) = 0.70, P = 0.40). The amount of tapir feces removed, and the number of seeds (beads) removed by dung beetles did not differ between riparian forest in forested and cropland catchments (feces: χ^2 (1, N = 10) = 1.14, P = 0.86; beads: χ^2 (1, N = 10) = 0.12, P = 0.89).

Discussion

Riparian forests within cropland catchments hold different ant and dung beetle community species composition compared with riparian forests within forested catchments, but similar species richness and abundance. These changes in species composition can promote modifications in ecosystem functions and services, as different species play different roles in ecosystem. For instance, the higher abundances of leaf-cutting fungus-growing ant functional group in riparian forest in cropland catchments potentially increase herbivory (Leal et al. 2014).

The difference in ant species composition in riparian forest in cropland catchments probably caused the lower cheating and increase in time ants took to find the seeds. Lower biomass of dung beetles in riparian forest in cropland catchments probably reduced the efficiency of seed removal, due the presence of dung beetles with a smaller body (Culot et al. 2013). However, dung beetle ecosystem functions were maintained in cropland catchments.

Species more adapted to environmental conditions within riparian forests surrounded by croplands can increase their distribution and maintain species richness and abundance of the community. Although metrics such as species richness and abundance are typically used to assess biological communities, species composition usually correlates better with habitat quality (Barlow et al. 2007; Del Toro et al. 2012; Solar et al. 2016). Species play different roles in the ecosystem and the identity of individuals makes it possible to assess losses of ecosystem functions (Carvalho et al. 2018; Del Toro et al. 2012), and of the ability of remnant species to compensate for those functions. . Land-use changes can filter species adapted to disturbance followed by declines in species sensitive to disturbances (Lugo et al. 2020). Thus, change in the pattern of winners and losers species established in riparian forests may be related to changes in habitat quality.

Among the ant functional groups, only leaf-cutting fungi-growing ants were more abundant in riparian forests within cropland than in forested catchments. These ant species tend to be more abundant in disturbed ecosystems because they have large colonies able to use different types of fresh plant material as a resource (Leal et al. 2014), leading to increased fresh leaves consumption (Urbas et al. 2007). Thus, the increased in leaf-cutting fungi-growing ant abundance in cropland catchments may have negative effects, because they need larger amount fresh leaves for colony maintenance (Leal et al. 2014). Leaf-cutting fungi-growing ants also enlarge open habitats due to cleaning and defoliating the places where the nests are present, forming extensive clearings (Corrêa et al. 2010; Farji-Brener and Illes 2000; Leal et al. 2014). The increase in cutting behavior in the riparian forest in cropland catchments affect the regeneration process due to damage caused on local vegetation and consequent higher canopy opening (Leal et al. 2014; Leal et al. 2014).

Even though the proportion of removed seeds did not differ between studied riparian forests, the proportion of cheating was higher and the time required to ants discover seeds was lower in riparian forest in forested catchments, what indicate lower quality of this service in cropland catchments. The ant behaviour to consume the elaiosome without seed removal can either has a neutral effect or be an ecosystem disservice (Arnan et al. 2012; Leal et al. 2015), as it can increase infection by pathogens and decrease germination (Fernandes et al. 2018), although it may also increase seed water absorption and germination (Leal et al. 2007). Thus, change in ant species composition may be able to benefit riparian forests in cropland catchments by reducing cheating behaviour, what can be beneficial to regeneration. On the other hand, ants discovered seeds faster in riparian forest in forested catchments than in cropland catchments, so seeds were more exposed to granivorous in the latter (Giladi 2006; Leal et al. 2015), what can indicate that quality of this service decreased in cropland catchments. Similar to our results, ants also needed a longer time to find the seeds in burned Amazonian forests, but in burned forests they have a decrease in seed removal behaviour, and did not alter the cheating behaviour (Paolucci et al. 2016). The difference in behaviour in these different disturbances shows that forest fires and fragmentation may lead to similar patterns in time of seed discovery, but different patterns in type of ant-seed interaction. Contrary to reduction in seeds removal in burned forests, which reduces service efficiency, the reduction cheating behaviour in riparian forest fragments can be beneficial to forest restoration.

Despite changes in plant structure in the studied cropland riparian forests (Maracahipes-Santos et al. 2020), the proportion of termite preyed by ants did not differ between riparian forest in forested and cropland catchments. This result indicates that plant biomass consumed by herbivores is not affected by change in ant composition change in cropland catchments.

Dung beetle biomass was larger in riparian forests within forested than cropland catchments. Dung beetles body size changes are usually correlated to defaunation. Defaunated sites have smaller dung beetles due to a higher occurrence of small mammals (Culot et al. 2013). Usually, forests are populated by large-bodied beetles (Filgueiras et al. 2015), which are able to bury larger seeds. However, seed removal by dung beetles were maintained in cropland catchments when compared to forested catchments. Although some studies reported a high sensitivity of dung beetle functions to human impacts as logging (França et al. 2017), in modified riparian forests their services may hold, due to the structural complexity of such forests (Gray et al. 2014). The decrease in dispersal of large seeds may affect forest structure and regeneration (Griffiths et al. 2016), but in our study this impact may have been mitigated by the species present in cropland catchments, even after changes in composition.

We showed that ants and dung beetles have similar responses to habitat fragmentation in relation to community structure: no impacts in species richness and abundance, but changes in species composition. Changes in ant species composition in riparian forests located in cropland catchments probably caused lesser cheating and more time for seeds to be found. The seeds not found in riparian forests at cropland catchments reduce the disservice caused by cheating behavior, and can help or promote a neutral effect on restoration. Additionally, predation by ant is not affected by change on species composition, indicating that there is no alteration in herbivore control by ants in riparian forests in cropland catchments. Changes in dung beetle species composition and biomass did not impacted seed and dung removal. The conversion of riparian forests into cropland similarly affects community structure of ants and dung beetles, but not necessarily their functions in the ecosystem. Thus, the new species composition in riparian forests in cropland catchments may be able to maintain or improve ecosystem services with positive benefits for forest recovery.

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Supplementary material

Table S1. Ant species in each treatment and classification of functional group.

Treatment	Species	Functional group
Cropland	*Acromyrmex sp.2*	Leaf-cutting Fungus-growing Ants
Cropland	*Acromyrmex sp.3*	Leaf-cutting Fungus-growing Ants
Cropland	*Acromyrmex sp.4*	Leaf-cutting Fungus-growing Ants
Cropland	*Apterostigma megacephala*	Non-leaf-cutting Fungus-growing Ants
Cropland	*Atta cephalotes*	Leaf-cutting Fungus-growing Ants
Cropland	*Atta laevigata*	Leaf-cutting Fungus-growing Ants
Cropland	*Atta sexdens*	Leaf-cutting Fungus-growing Ants
Cropland	*Brachymyrmex sp.1*	Opportunists
Cropland	*Brachymyrmex sp.A*	Opportunists
Cropland	*Camponotus crassus*	Subordinate Camponotini
Cropland	*Camponotus sp.10*	Subordinate Camponotini
Cropland	*Camponotus sp.13*	Subordinate Camponotini
Cropland	*Camponotus sp.15*	Subordinate Camponotini
Cropland	*Camponotus sp.22*	Subordinate Camponotini
Cropland	*Camponotus sp.28*	Subordinate Camponotini
Cropland	*Camponotus sp.3*	Subordinate Camponotini
Cropland	*Camponotus sp.36 aff crassus*	Subordinate Camponotini
Cropland	*Camponotus sp.6*	Subordinate Camponotini
Cropland	*Camponotus sp.7*	Subordinate Camponotini
Cropland	*Crematogaster sp.10*	Arboreal Dominants
Cropland	*Crematogaster sp.17*	Arboreal Dominants
Cropland	*Crematogaster sp.2*	Arboreal Dominants
Cropland	*Cyphomyrmex sp.1*	Non-leaf-cutting Fungus-growing Ants
Cropland	*Dolichoderus imitator*	Arboreal Dominants
Cropland	*Ectatomma edentatum*	Epigaeic Predators
Cropland	*Ectatomma tuberculatum*	Epigaeic Predators
Cropland	*Gigantiops destructor*	Epigaeic Omnivores
Cropland	*Gnamptogenys striatula*	Epigaeic Predators
Cropland	*Mayaponera constricta*	Epigaeic Predators
Cropland	*Neivamyrmex sp.1*	Army Ants
Cropland	*Neoponera carinulata*	Epigaeic Predators
Cropland	*Nylanderia sp.2*	Epigaeic Omnivores
Cropland	*Nylanderia sp.3*	Epigaeic Omnivores
Cropland	*Ochetomyrmex semipolitus*	Epigaeic Omnivores
Cropland	*Octostruma sp.1*	Cryptobiotic
Cropland	*Pachychondyla harpax*	Epigaeic Predators
Cropland	*Pheidole sp.1*	Epigaeic Omnivores
Cropland	*Pheidole sp.14*	Epigaeic Omnivores
Cropland	*Pheidole sp.17*	Epigaeic Omnivores

Cropland	*Pheidole sp.2*	Epigaeic Omnivores
Cropland	*Pheidole sp.29*	Epigaeic Omnivores
Cropland	*Pheidole sp.37*	Epigaeic Omnivores
Cropland	*Pheidole sp.55*	Epigaeic Omnivores
Cropland	*Pheidole sp.7*	Epigaeic Omnivores
Cropland	*Pheidole sp.8*	Epigaeic Omnivores
Cropland	*Pheidole sp.macho*	Epigaeic Omnivores
Cropland	*Pheidole sp.Y*	Epigaeic Omnivores
Cropland	*Pseudomyrmex sp.10*	Arboreal Predators
Cropland	*Pseudomyrmex sp.2*	Arboreal Predators
Cropland	*Rogeria sp.1*	Cryptobiotic
Cropland	*Sericomyrmex sp.2*	Non-leaf-cutting Fungus-growing Ants
Cropland	*Sericomyrmex sp.4*	Non-leaf-cutting Fungus-growing Ants
Cropland	*Sericomyrmex sp.5*	Non-leaf-cutting Fungus-growing Ants
Cropland	*Solenopsis sp.1*	Epigaeic Omnivores
Cropland	*Solenopsis sp.2*	Epigaeic Omnivores
Cropland	*Solenopsis sp.22*	Epigaeic Omnivores
Cropland	*Solenopsis sp.35*	Epigaeic Omnivores
Cropland	*Solenopsis sp.4*	Epigaeic Omnivores
Cropland	*Solenopsis sp.A*	Epigaeic Omnivores
Cropland	*Trachymyrmex sp.1*	Non-leaf-cutting Fungus-growing Ants
Cropland	*Trachymyrmex sp.6*	Non-leaf-cutting Fungus-growing Ants
Cropland	*Trachymyrmex sp.9*	Non-leaf-cutting Fungus-growing Ants
Cropland	*Trachymyrmex sp.B aff sp.6*	Non-leaf-cutting Fungus-growing Ants
Cropland	*Wasmannia auropunctata*	Epigaeic Omnivores
Forest	*Acromyrmex sp.3*	Leaf-cutting Fungus-growing Ants
Forest	*Apterostigma carinatum*	Non-leaf-cutting Fungus-growing Ants
Forest	*Apterostigma megacephala*	Non-leaf-cutting Fungus-growing Ants
Forest	*Atta cephalotes*	Leaf-cutting Fungus-growing Ants
Forest	*Atta laevigata*	Leaf-cutting Fungus-growing Ants
Forest	*Brachymyrmex sp.1*	Opportunists
Forest	*Camponotus atriceps*	Subordinate Camponotini
Forest	*Camponotus crassus*	Subordinate Camponotini
Forest	*Camponotus sp.10*	Subordinate Camponotini
Forest	*Camponotus sp.11*	Subordinate Camponotini
Forest	*Camponotus sp.22*	Subordinate Camponotini
Forest	*Camponotus sp.3*	Subordinate Camponotini
Forest	*Camponotus sp.5*	Subordinate Camponotini
Forest	*Camponotus sp.6*	Subordinate Camponotini
Forest	*Camponotus sp.7*	Subordinate Camponotini
Forest	*Camponotus sp.8*	Subordinate Camponotini
Forest	*Camponotus sp.9*	Subordinate Camponotini
Forest	*Crematogaster sp.10*	Arboreal Dominants
Forest	*Dolichoderus imitator*	Arboreal Dominants

Forest	*Ectatomma edentatum*	Epigaeic Predators
Forest	*Ectatomma sp.1*	Epigaeic Predators
Forest	*Gigantiops destructor*	Epigaeic Omnivores
Forest	*Gnamptogenys striatula*	Epigaeic Predators
Forest	*Hypoponera sp.1*	Cryptobiotic
Forest	*Linepithema aztecoides*	Epigaeic Omnivores
Forest	*Mayaponera constricta*	Epigaeic Predators
Forest	*Neoponera verenae*	Epigaeic Predators
Forest	*Nylanderia sp.2*	Epigaeic Omnivores
Forest	*Ochetomyrmex semipolitus*	Epigaeic Omnivores
Forest	*Odontomachus menerti*	Epigaeic Predators
Forest	*Pachychondyla harpax*	Epigaeic Predators
Forest	*Pachycondyla crassinoda*	Epigaeic Predators
Forest	*Pheidole sp.1*	Epigaeic Omnivores
Forest	*Pheidole sp.14*	Epigaeic Omnivores
Forest	*Pheidole sp.17*	Epigaeic Omnivores
Forest	*Pheidole sp.2*	Epigaeic Omnivores
Forest	*Pheidole sp.29*	Epigaeic Omnivores
Forest	*Pheidole sp.31*	Epigaeic Omnivores
Forest	*Pheidole sp.49*	Epigaeic Omnivores
Forest	*Pheidole sp.7*	Epigaeic Omnivores
Forest	*Pheidole sp.9*	Epigaeic Omnivores
Forest	*Pheidole sp.H*	Epigaeic Omnivores
Forest	*Pheidole sp.I*	Epigaeic Omnivores
Forest	*Pheidole sp.S*	Epigaeic Omnivores
Forest	*Sericomyrmex sp.2*	Non-leaf-cutting Fungus-growing Ants
Forest	*Solenopsis sp.1*	Epigaeic Omnivores
Forest	*Solenopsis sp.2*	Epigaeic Omnivores
Forest	*Solenopsis sp.22*	Epigaeic Omnivores
Forest	*Trachymyrmex sp.2*	Non-leaf-cutting Fungus-growing Ants
Forest	*Trachymyrmex sp.6*	Non-leaf-cutting Fungus-growing Ants

Table S2. Dung beetle species in each treatment and classification.

Treatment	**Species**
Cropland	*Ateuchus azteca*
Cropland	*Ateuchus pygidialis*
Cropland	*Canthidium aff. lentum*
Cropland	*Canthon conformis*
Cropland	*Canthon triangularis*
Cropland	*Coprophanaeus dardanus*
Cropland	*Deltochilum amazonicum*
Cropland	*Deltochilum orbiculare*
Cropland	*Deltorrhinum sp1*
Cropland	*Dichotomius aff.lucasi*
Cropland	*Dichotomius aff.zikani*
Cropland	*Dichotomius mamillatus*
Cropland	*Dichotomius nisus*
Cropland	*Dichotomius robustus*
Cropland	*Dichotomius worontzowi*
Cropland	*Eurysternus caribaeus*
Cropland	*Eurysternus howdeni*
Cropland	*Onthophagus osculatii*
Cropland	*Onthophagus ptox*
Cropland	*Oxysternon macleayi*
Cropland	*Oxysternon silenus aeneum*
Cropland	*Scybalocanthon sp1*
Cropland	*Scybalocanthon sp2*
Cropland	*Sylvicanthon bridarollii*
Cropland	*Sylvicanthon candezei*
Forest	*Ateuchus azteca*
Forest	*Ateuchus pygidialis*
Forest	*Canthidium aff. gerstaeckeri*
Forest	*Canthidium aff. lentum*
Forest	*Coprophanaeus (Megaphanaeus) ensifer*
Forest	*Coprophа-eus dardanus*
Forest	*Cryptocanthon campbellorum*
Forest	*Deltochilum amazonicum*
Forest	*Deltochilum orbiculare*
Forest	*Dichotomius aff. lucasi*
Forest	*Dichotomius aff. zikani*
Forest	*Dichotomius mamillatus*
Forest	*Dichotomius opacus*
Forest	*Dichotomius robustus*
Forest	*Dichotomius sp1*
Forest	*Dichotomius worontzowi*

Forest	*Eurysternus caribaeus*
Forest	*Eurysternus foedus*
Forest	*Isocopris nitidus*
Forest	*Onthophagus osculatii*
Forest	*Oxysternon macleayi*
Forest	*Oxysternon silenus aeneum*
Forest	*Phanaeus bispinus*
Forest	*Scybalocanthon sp1*
Forest	*Sylvicanthon bridarollii*
Forest	*Sylvicanthon candezei*

CAPÍTULO DOIS

FOREST FIRES: IMPACT ON TERMITE COMMUNITIES AND THEIR ECOSYSTEM FUNCTIONS

Forest fires: impact on termite communities and their ecosystem functions

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Abstract

Termites are invertebrates responsible for performing ecosystem functions related to organic matter decomposition, bioturbation and carbon cycle. Here, we investigate whether termites can mitigate the effects of fire, increasing organic matter decomposition in Amazonian forests, exploring which are the possible mechanisms involved in the increase of termites. We formulate four hypotheses: (i) termites have greater abundance in burned forests; (ii) termite abundance increase is related to environmental factors; (iii) termites are less predated in burned forests; (iv) burned forests have greater organic matter decomposition rates. We sampled in two different fire experiments in the Southern Amazon region. The first is a big-plot experiment, consisting of a forest burned annually (B1*yr*) and every three years (B3*yr*), both recovering for 10 years, and a third unburned forest (control). The second is a block experiment, consisting of random blocks burned only twice and in recovery for five years. We evaluated, termite abundance and activity, environmental changes, ant-termite interactions, and decomposition rates. The increase in termite abundance may be related to environmental factors and decreases in termite predation by ants. Fire treatments had higher decomposition rates and termite abundance. We reason that higher decomposition of organic matter is due to the increase in termite abundance, which is a response to environmental changes and altered ant-termite interactions.

Keywords: Burned forests; ecosystem functions; termites.

Introduction

Tropical forests tend to not burn naturally, so fire ignition is predominantly associated with human activities, mainly deforestation and land use management (Barlow et al. 2020). The southern edge of Amazon basin is the largest Brazilian agricultural frontier, and forests degraded by fires have become part of the landscape since 1970's (Morton et al. 2013). Recurrent fires tend to reduces forest regeneration capacity and changes forest structure (Balch et al. 2013) by increasing tree mortality and changing microclimate (Brando et al. 2014), impacting the diversity and functioning of the forest (Balch et al. 2015; Brando et al. 2014; 2016; 2019). Fire-driven changes in forest structure are frequently followed a parallel fauna conversion – i.e., local extinctions of forest species and an influx of open-habitat species (de Andrade et al. 2017; Paolucci et al. 2017; Sales et al. 2020).

Drought in tropical forests promotes higher temperature and soil water deficit, capable of alter vegetation structure and promote higher plant mortality (Ashton et al. 2019; Corlett 2016). Forest fires and extreme drought events in tropical forests have similar impacts on forest structure, such as decreased evapotranspiration and humidity, and increased canopy openness, understory temperature and CO_2 emissions (Brando et al. 2008, 2014; Barlow et al. 2020). Termites can mitigate extreme drought effects in tropical forests, which can cause an increase in their abundance and in rates of organic matter decomposition, promoting higher survival of seedlings due to the maintenance of moisture and nutrient heterogeneity (Ashton et al. 2019).

Termites are responsible for several ecosystem functions and services, especially in the tropics. In tropical soils, they represent 40 to 60% of the biomass of macro invertebrates (Dahlsjö et al. 2014), and are responsible for nutrient mineralization generated from intestinal transit and feces deposition (Brauman 2000). Due to their complex and effective intestinal biota, termites are considered the main invertebrates decomposing organic matter (Griffiths et al. 2019; Tuma et al. 2020). Environmental factors such as drier soil and lower leaf litter depth are able to alter the foraging capacity, and increase decomposition functions of termites, as in the case of extreme drought (Ashton et al. 2019). Physical and chemical changes in the soil promoted by termites can support plant growth due to organic matter and nutrient deposition, with further consequences for vegetation structure (Muvengwi et al. 2017). Termites are also able to influence carbon flows in open environments by increasing dead wood decomposition rates up to 63% (Griffiths et al. 2021).

Termites represent an important food source for ants, providing lipids, proteins, minerals, sugars and micronutrients (Tuma et al. 2020). Together, ants and termites represent more than half of invertebrate biomass in tropical forests (Stork 1996; Tuma et al. 2020). Predation and top-down control by ant may be responsible for shaping the termite distribution and activity (Gonçalves et al. 2005; Tuma et al. 2020). Fire in tropical forests changes the structure of insect communities, causing decreases in species abundance and richness, especially of predatory ants (Paolucci et al. 2016; 2017).

Environmental changes caused by fire and extreme drought in tropical forests are similar (Barlow et al. 2020; Ashton et al. 2019). However, the responses of termite communities to forest fires have not been explored in the tropics and we lack an understanding of the mechanisms driving community changes. Additionally, we do not know if changes in termite communities could explain changes in the function of organic matter decomposition in burned forests. Here, we investigated whether termites can mitigate the effects of fire in southern Amazonian forests through increased decomposition of organic matter, as previously observed for drought in other tropical forests (Ashton et al. 2019), and also what are the possible mechanisms involved. For this, we tested four hypotheses: (i) termites have greater abundance in burned forests; (ii) termite abundance increase is related to environmental factors; (iii) termites are less predated in burned forests; (iv) burned forests have greater organic matter decomposition.

Methods

Study area

Field work was carried out from January to May 2020 in two different fire experiments within the “Fazenda Tanguro”, southern Amazon, Mato Grosso, Brazil. The local vegetation is typical of transition between Cerrado (savanna) and Amazon Forest, with vegetation height relatively low when compared to forest of the central Amazon (Balch et al. 2008). The climate is tropical humid, with average annual rainfall of 1770 mm and dry season between May and September (Rocha et al. 2014).

We conducted this study in two different prescribed fire experiments located in the Fazenda Tanguro: the “Big-plot”, and the “Block” experiment. The Big-plot experiment (13°04’S, 52°23’W), composed of three 50 ha (0.5 × 1.0 Km, see Fig. 2c in Balch et al. 2015) plots established in 2004. The first plot was kept unburned (control), the second plot was burned annually (B1*yr*) from 2004 to 2010, with the exception of the year 2008, and the third plot was burned every three years (B3*yr*), in 2004, 2007 and 2010 (Balch et al. 2008). In the big-plot experiment, fire was intense and had high flames, mainly in the B3*yr* treatment, due to fuel accumulation between fires (Balch et al. 2015). In addition, two of the fires (2007 and 2010) occurred in drought years (Brando et al. 2014). In the B3*yr* treatment, there was a higher post-fire tree mortality, larger loss of aboveground biomass (Brando et al. 2014), and increased grasses invasion (Silvério et al. 2013). We established 18 sub-plots of 30 × 30 m in each big-plot, six per big-plot, with minimum distance of 160 m among them.

The Block experiment (12 ° 49'S, 52 ° 21'W) followed a randomized block design, with a total of six blocks and four plots of 40 m × 40 m within each block. Blocks were 250 to 550 m distant from surrounding soybean fields. In the block experiment, understory fires were less intense (Brando et al. 2016) and mostly impacted small plants and thin-bark species (Valle et al. 2021). The experimental design of the blocks is detailed in (Brando et al. 2016): we sampled two blocks, having (i) plots burned in 2013 (without fuel addition) and in 2016, and (ii) control unburned plots. Within each of 40 × 40 m plots we delimited 30 × 30 m sub-plots as our experimental units. Fires in both experiments were set in the end of dry season (August - September).

Termite abundance

We sampled termites through active sampling in 54 5 × 2 m plots in the Big-plot and 36 in the Block experiment. For the Big-plot, we established three plots within each sub-plot of 30 × 30 m, totaling 54 plots within the big-plot experiment – 18 in each prescribed fire treatment (Control, B1*yr* and B3*yr*). For the Block experiment we established 36 plots, 18 in each treatment (Control and Burned). We sampled in four different micro-habitats inhabited by termites (trees, epigaeic, subsoil, and dead wood), with a sampling effort of one hour per plot adapted from the protocol of Jones and Eggleton (2000). We stored the sampled material in 70% alcohol, and termite abundance was screened in each microhabitat in the lab.

Environmental variables

We measured all environmental variables directly on the ground in the same day and period of termite sampling. We set a transect in the center of each 30 × 30 m sub-plot, both in the big-plot experiment and block experiment. We measured soil temperature using a thermometer, soil humidity with a humidity sensor, and litter height through a ruler at every five meters along this transect, obtaining six measurements per sub-plot and the mean of each variable per sub-plot.

Termite predation experiment

We assess termite predation through three white paper stations (10 × 10 cm), separated by three meters from each other in each sub-plot (both in the big-plot and block experiments). In each station, we put a live termite attached with white glue and counted the elapsed time ants took to prey the termite. We observed this interaction for up to 10 minutes, and after this period obtained the proportion of predated termites.

Decomposition measurement

We chose the plant species *Amaioua guianesis* for decomposition experiments because it is present in all experimental plots. We sampled fresh leaves of *A. guianesis* and dried in oven at 60° C for 72 hours. We placed ~ 5 g of dried leaves in two types of decomposition bags: open bags (mesh containing holes of about one cm in diameter, allowing invertebrate access to the leaves) and closed bags (mesh without holes to avoid invertebrate access). We placed four open bags and four closed bags in each sub-plot of 30 × 30 m, totaling 16 open bags and 16 closed bags in each treatment of the big-plot experiment, and 16 open bags and 16 closed bags in each treatment in the block experiment. We removed one decomposition bag of each type from each sub-plot after 112 days. and oven-dried the material again at 60° for 72 hours. Dried leaves were weighted to establish the weight loss.

Termite activity

We placed 10 toilet paper rolls in each sub-plot to monitor termite activity temporally and spatially in the field (Davies et al. 2021). We photographed each of toilet paper after 30 days and exchanged them for new toilet paper, totaling three sampling periods (90 days). We determined classes of consumption to estimate toilet paper loss, from 1 to 5: 1 represented a loss of 0 to 20% of toilet paper, 2 represented a loss of 21 to 40%, 3 represented a loss of 41 to 60%, 4 represented a loss of 61 to 80% and 5 represented a loss of 81 to 100%. All photos were analyzed by three different scientists to decrease bias; when the three person did not agree on the classification, we considered the value estimated by at least two people. We calculated the average loss of the ten toilet papers per sub-plot through the number mean that each interval represented.

Statistical analysis

We used the sub-plot as sample units in all analyses. We built two different models for termite abundance and environment variables, depending on the fire experiment (big-plot or block). To test differences in termite abundance in the big-plot experiment, we used GLM (Generalized Linear Model) with Poisson error distribution. To test differences in termite abundance in the block experiment, we used GLMM (Generalized Mixed Model), with the block as a random effect, and a Poisson error distribution. To test the effect of treatments on environmental variables in the big-plot experiment we used GLM model, and for the block experiment we used GLMM model, with block as a random variable. We used Poisson or Gaussian error distribution according to model fit.

We did a survival analysis to compare the time for termites to be discovered in each treatment, with Weibull error distribution, where the time for occurrence of each event (predation) was the response variable. We also measured the mean proportion of termite predated by ants in each treatment, analyzed with binomial distribution.

We analyzed the data from decomposition bags through model comparison with the package glmmTMB (Boorks et al. 2017). We measured the total leaf mass loss after 112 days as a response variable, and fire treatment and bag type (open or closed) as explanatory variables. In the block experiment, all closed bags were lost in the control forest, and could not be analyzed. We used sub-plot as a random variable in all models, and for the block experiment we also used the blocks as random variables, with Gaussian error distribution. We compared the models and used the model with lowest AIC. We used the package emmeans vs 1.5.1 (Lenth, 2021) to obtain the results of pairwise comparisons.

For testing termite activity, we considered the toilet paper mean loss as a response variable and treatment as an explanatory variable. We used the sampled period as a random variable in all models and, in the block experiment we also use the blocks as a random variable.

We performed all analyses in the R software (R-core team 2020), and the packages vegan 2.5-6 (Oksanen et al., 2020) for pairwise comparisons, lme4 V 1.1-23 (Bates et al., 2015) and glmmTMB V 1.0.2.1 (Boorks, et al. 2017) to perform GLMMs, and DHARMa V 0.4.1 (Hartig, 2021) to perform residual analysis, check model suitability and distribution.

Results

Termite abundance and activity

In big-plot experiment, the B1*yr* plot had the higher termite abundance, while not differences were found between B3*yr* and control plots (χ^2 [1, N = 18] = 5.46, P = 0.02, Fig. 1A). In the block experiment, the burned treatment had higher termite abundance than the control (χ^2_{10} = 56.27, P < 0.001, Fig. 1B).

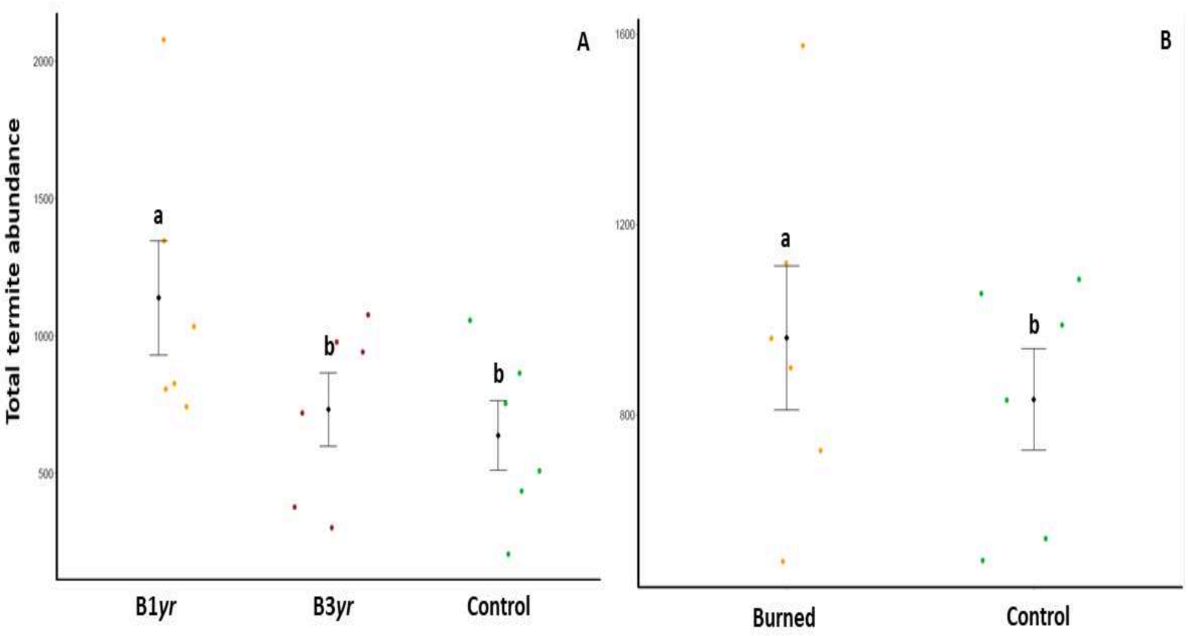


Figure 1. Total termite abundance in the big-plot (A) block (B) experiment. Bars represent standard error. Different letters indicate significant differences among treatments, according to ANOVA. B1*yr* = Annually burned; B3*yr* = Triennially burned; Control = control non burned plot.

In the big plot experiment, termite abundance in dead wood was higher in the B1*yr* treatment (χ^2 [1, N = 18] = 7.57, $P < 0.006$, Fig. 2), while it was similar across all other strata ($P > 0.05$). In the block experiment, tree termite abundance was higher in the control treatment ($\chi^2_{10} = 36.91$, $P < 0.001$, Fig. 3A), while epigaeic ($\chi^2_{10} = 21.54$, $P < 0.001$, Fig. 3B), and subsoil termite abundance ($\chi^2_{10} = 236.13$, $P < 0.001$, Fig. 3C) was higher in burned treatment. Decomposition of toilet paper rolls did not differ among treatments in big-plot experiment ($\chi^2_{13} = 2.2503$, $P = 0.32$) or between treatments in block experiment ($\chi^2_{10} = 0.0014$, $P = 0.97$).

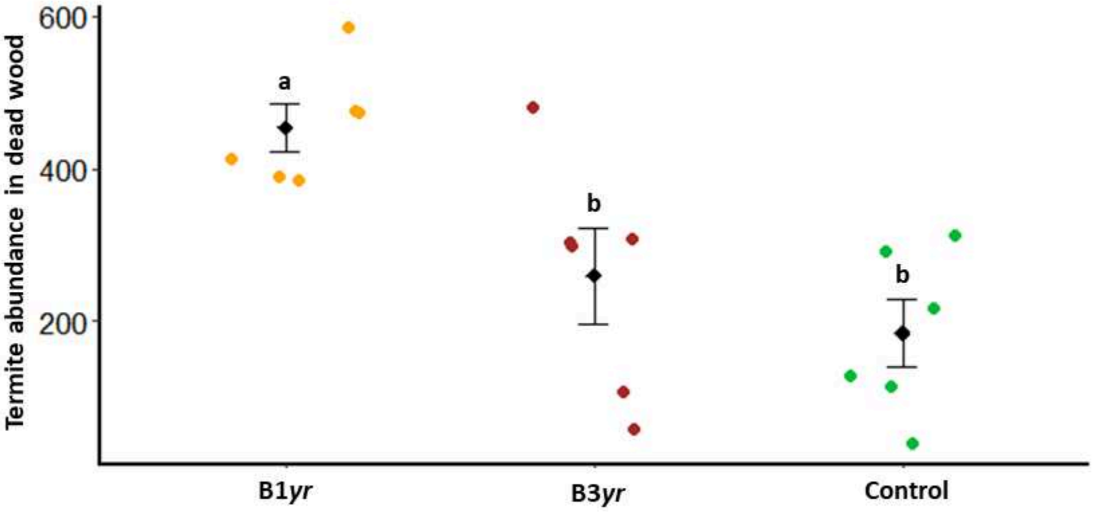
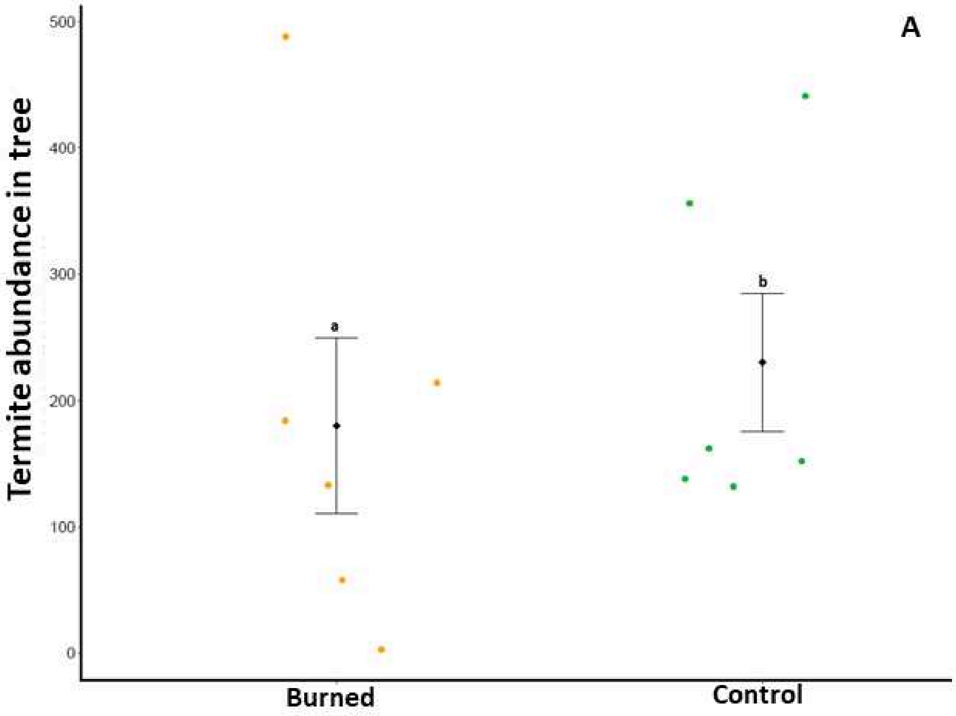
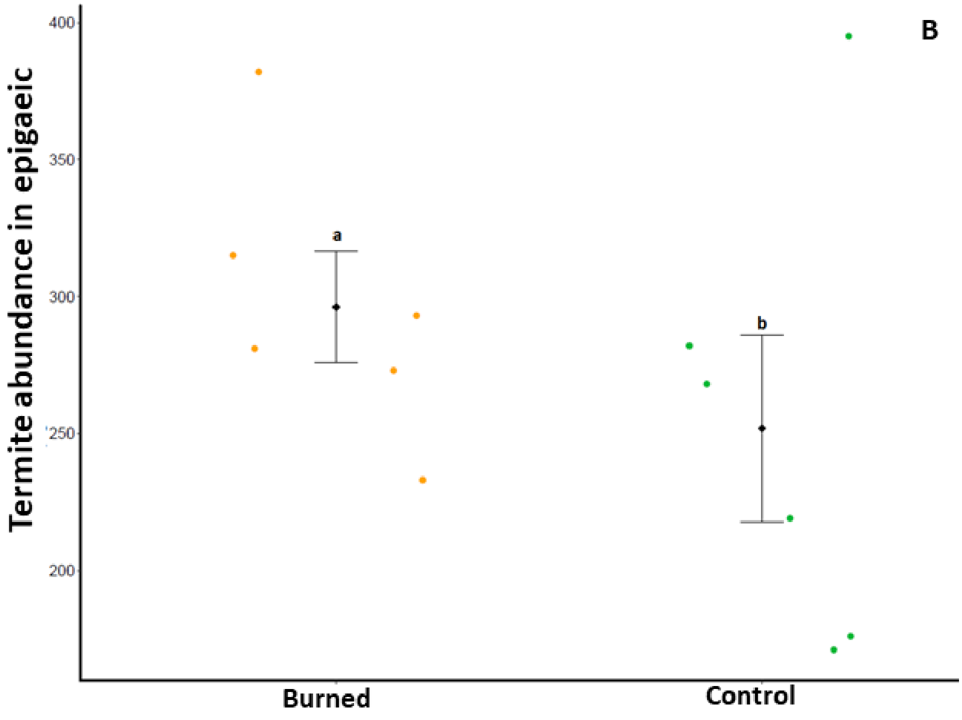


Figure 2. Termite abundance in dead wood in big-plot experiment (B1*yr* = Annually burned; B3*yr* = Triennially burned). Bars represent standard error. Different letters indicate significant differences among treatments, according to ANOVA.


A
Termite abundance in tree
500
400
300
200
100
0
a
b
Burned
Control


B
Termite abundance in epigaeic
400
350
300
250
200
a
b
Burned
Control

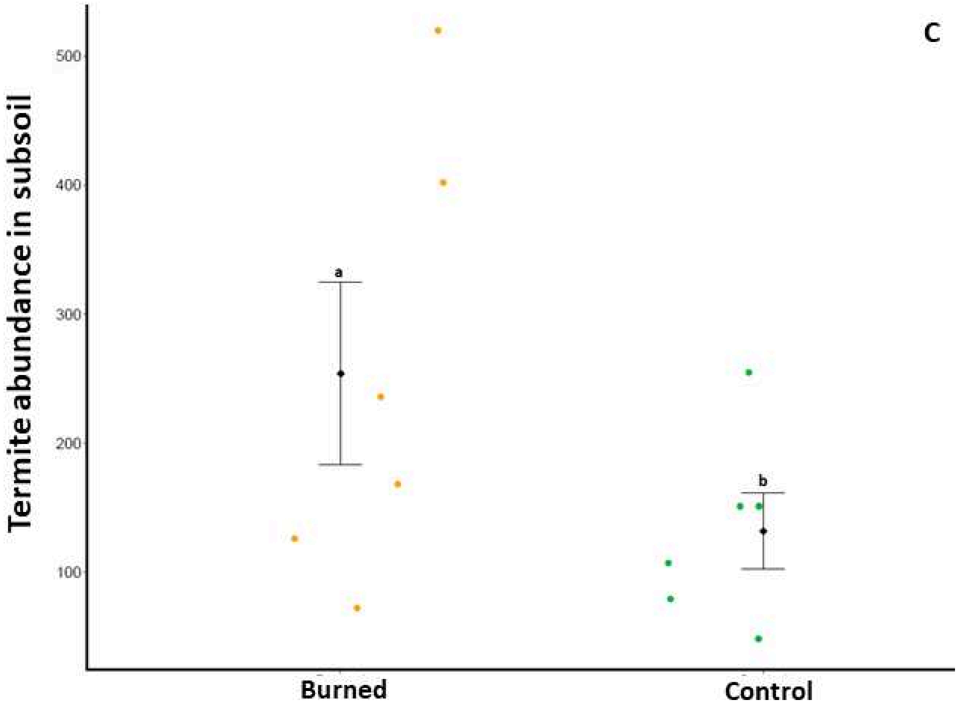


Figure 3. Termite abundance in A) tree, B) epigaeic and C) subsoil in block experiment. Bars represent standard error. Different letters indicate significant differences among treatments, according to ANOVA.

Environmental variables

In the big-plot experiment, B1*yr* and B3*yr* had lower soil moisture (χ^2 [1, N = 18] = 31.7, P < 0.001, Fig. 4A) and higher soil temperature (χ^2 [1, N = 18] = 8.5, P < 0.001, Fig. 4B) than the control forest, but litter height was similar across all treatments (χ^2 [2, N = 18] = 0.85, P = 0.36). In the block experiment, burned plots had higher soil moisture (χ^2_{10} = 7.08, P < 0.008, Fig. 5), while soil temperature (χ^2_{10} = 1.17, P = 0.28) and litter height (χ^2_{10} = 2,51, P = 0.11) were similar across treatments.

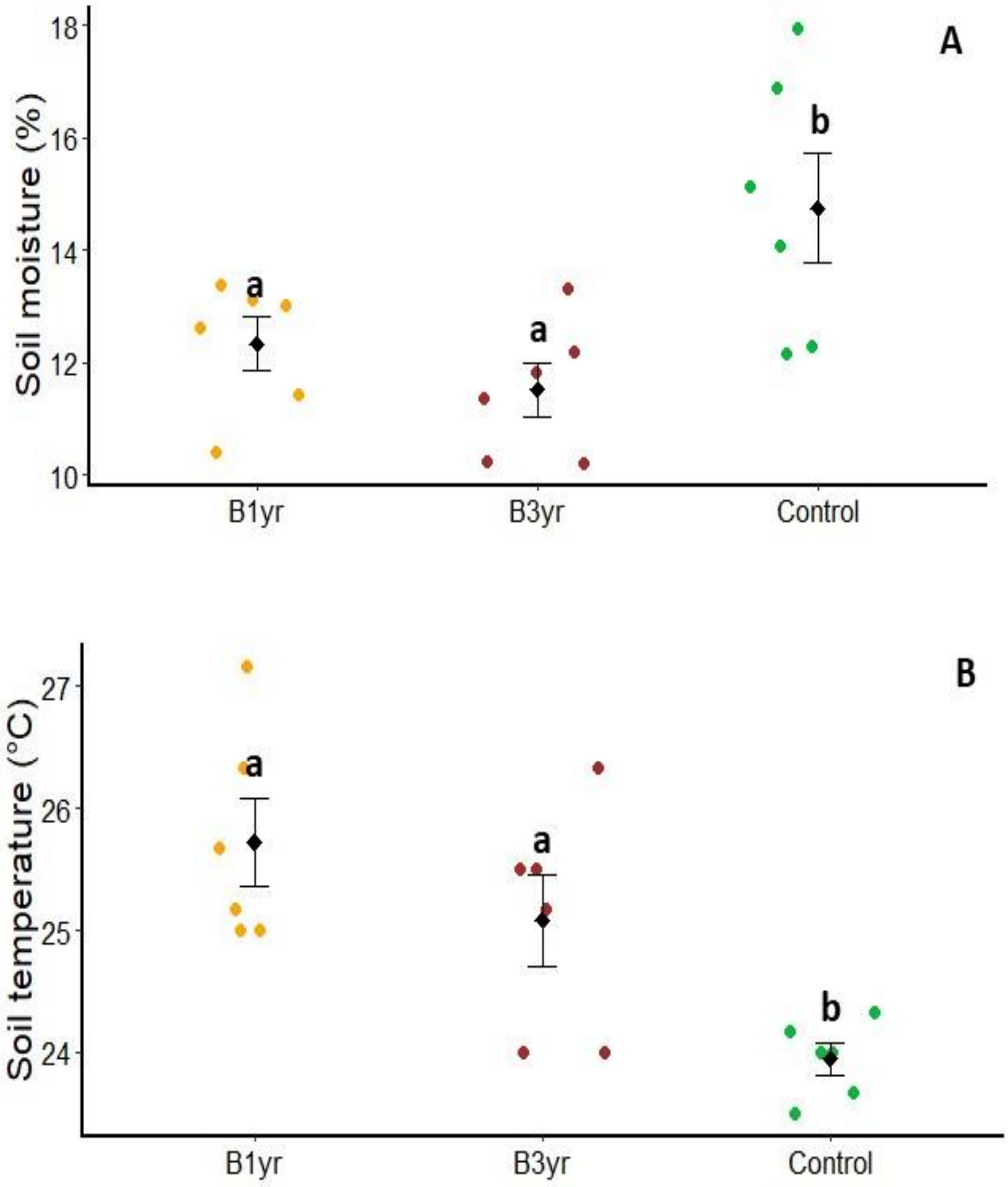


Figure 4. Soil A) moisture and B) temperature in big-plot experiment (B1*yr* = Annually burned; B3*yr* = Triennially burned). Bars represent standard error. Different letters indicate significant differences among treatments, according to ANOVA.

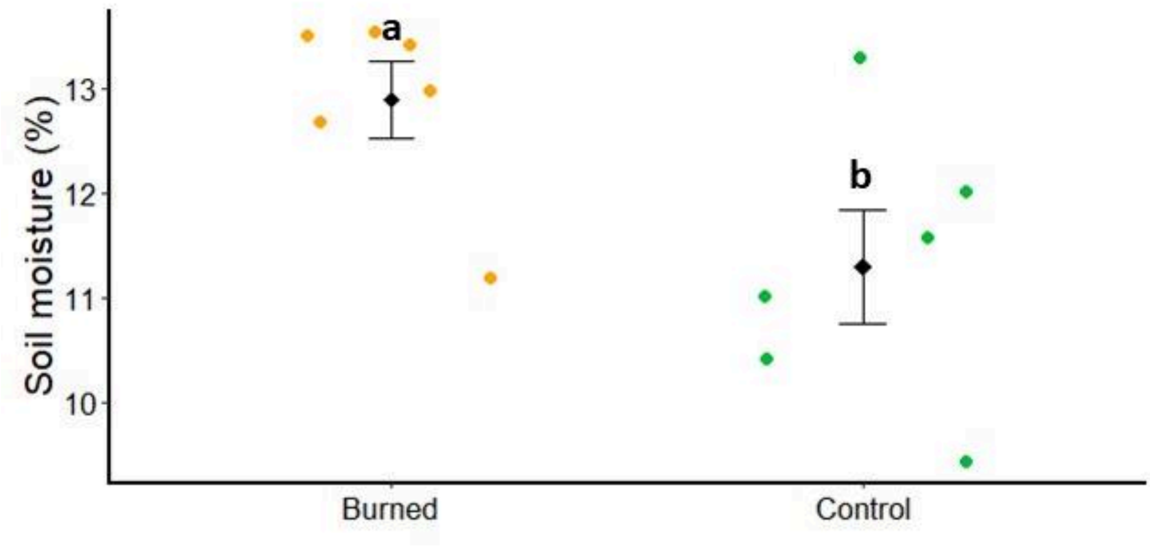
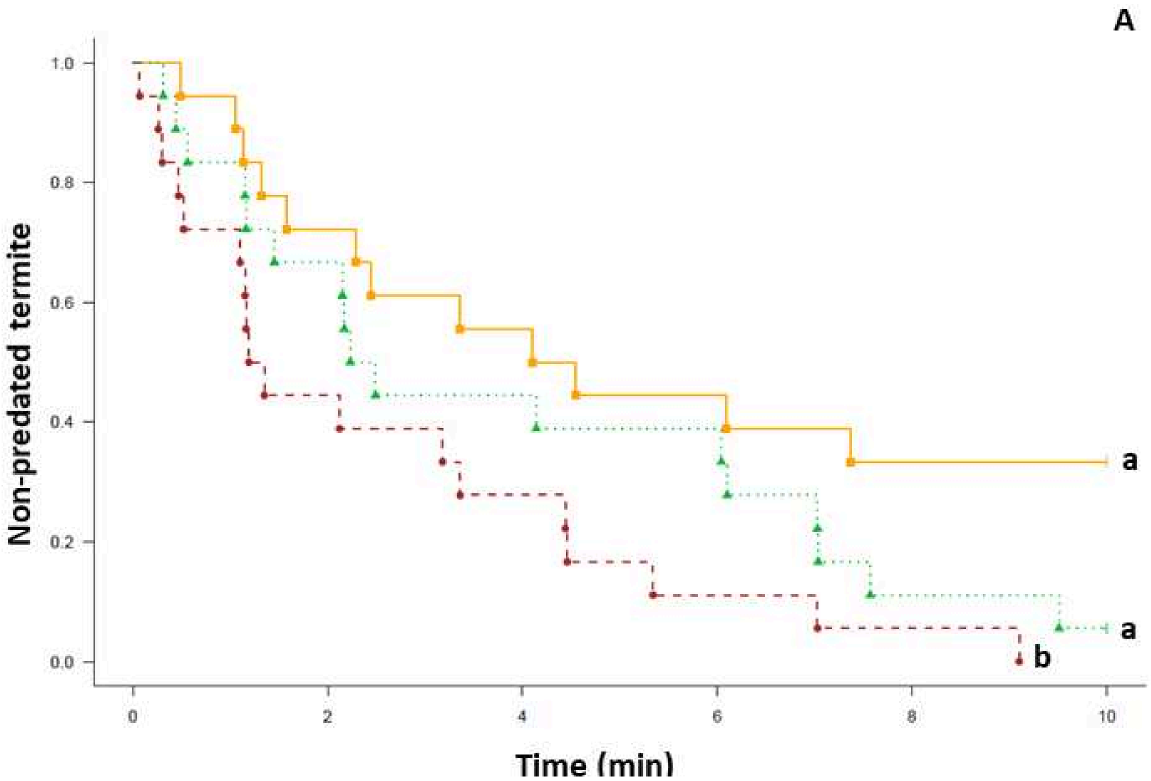


Figure 5. Soil moisture in block experiment. Bars represent standard error. Different letters indicate significant differences among treatments, according to ANOVA.

Termite predation experiment

In the big-plot experiment, the time elapsed for termites to be predated by ants was shorter in B3*yr*, and did not differ between B1*yr* and control plots (χ^2 [1, N = 18] = 6.31, P = 0.01, Fig. 6A). The proportion of termites predated by ants was higher in B3*yr* (100% of individuals preyed) and in the control than in the B1*yr* plot (χ^2 [1, N = 18] = 9.14, P = 0.02, Fig. 6B). In the block experiment, the time elapsed to termites to be predated by ants (χ^2 [2, N = 12] = 0.004, P = 0.2), and proportion of termites predated by ants (χ^2_{10} = 1.64, P = 0.2) did not differ between treatments.


A
Non-predated termite
1.0
0.8
0.6
0.4
0.2
0.0
0
2
4
6
8
10
Time (min)
a
a
b

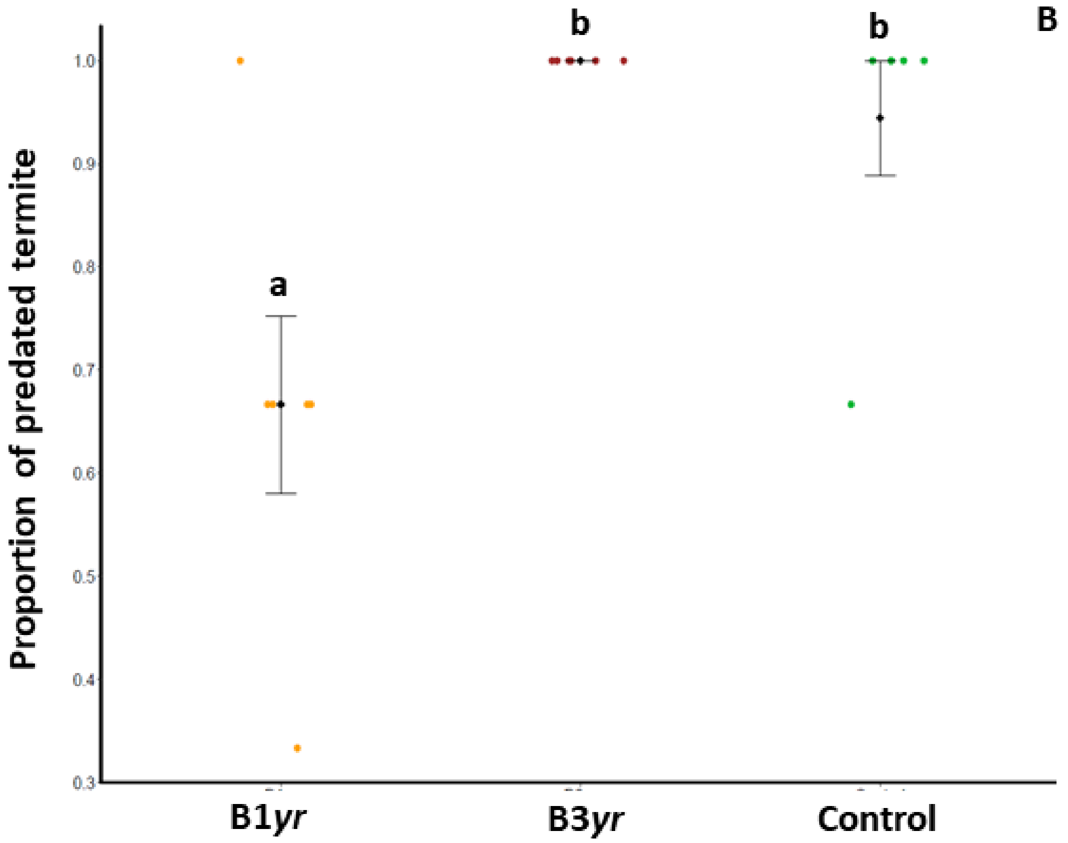

B
Proportion of predated termite
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
a
b
b
B1yr
B3yr
Control

Figure 6. A) Time elapsed to termite predated by ants (yellow – B1*yr* = Annually burned; brown – B3*yr* = Triennially burned and green – control). B) proportion of termite predated by ants in big-plot experiment (B1*yr* = Annually burned; B3*yr* = Triennially burned). Bars represent standard error. Different letters indicate significant differences among treatments, according to ANOVA.

Decomposition

In the big-plot experiment, open bags experienced higher weight loss than closed bags in B1*yr* and less weight loss in control, but B3*yr* treatment did not differ among B1*yr* treatment and control (χ^2_{15} = 11.63, P = 0.003, Fig. 7). The weight loss in closed bags did not differ among treatments. In fire treatments of the big-plot experiment (B1*yr* and B3*yr*), weight loss was higher in open bags when compared to closed bags in the same treatment, but in the control plots the weight loss was similar across open and closed bags (χ^2_{15} = 25.2, $P < 0.001$, Fig. 7). In the block experiment, the weight loss in open bags did not differ across treatments (χ^2_{10} = 0.65, P = 0.42, Fig. 8), and open bags had higher weight loss than closed bags in burned treatment (χ^2_{10} = 12.32, $P < 0.001$, Fig. 2).

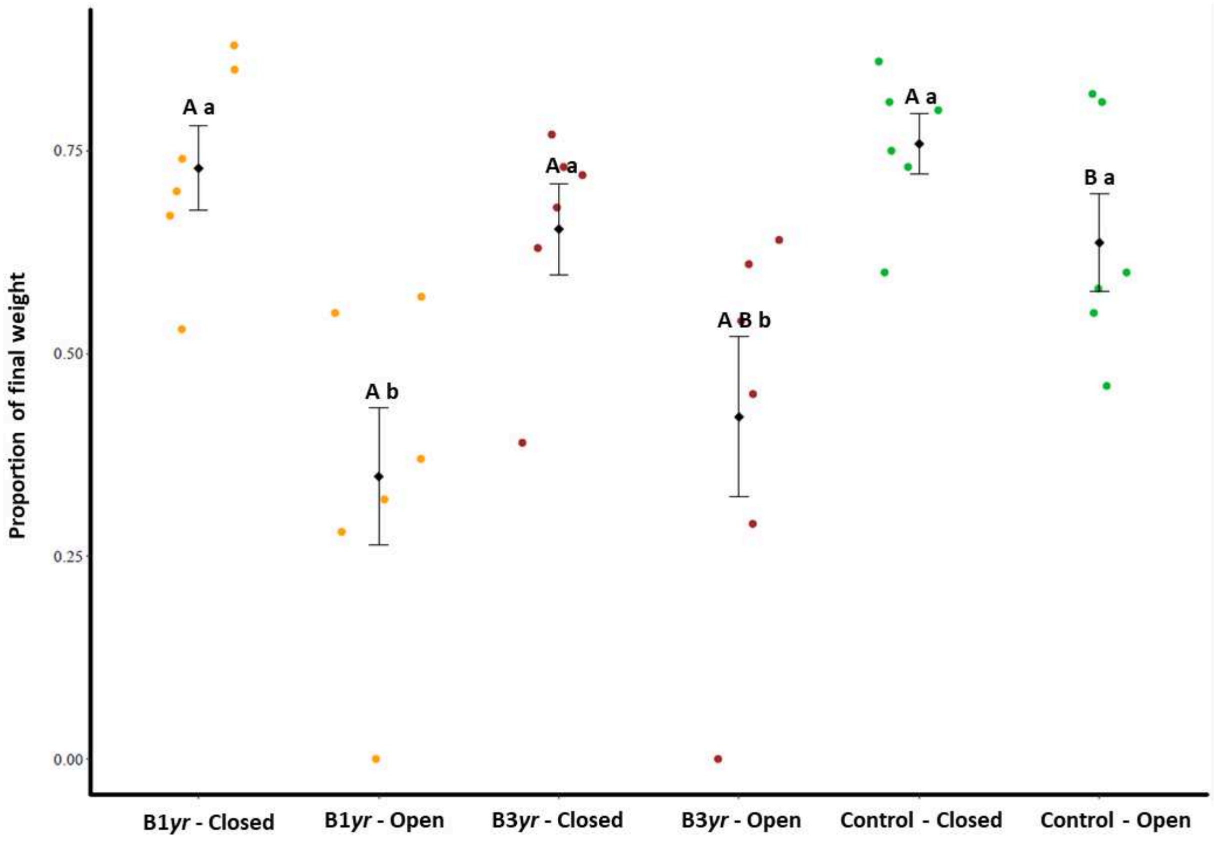


Figure 7. Litter bag decomposition in the big-plot experiment. Capital letters indicate significant differences among treatments (B1*yr* = Annually burned; B3*yr* = Triennially

burned). Lower letters represent the differences between open bags (mesh containing holes about one cm in diameter, allowing invertebrate access to the leaves) and closed bags (mesh without holes, not allowing invertebrate access) in the same treatment, according to two-way ANOVA. Bars represent standard error.

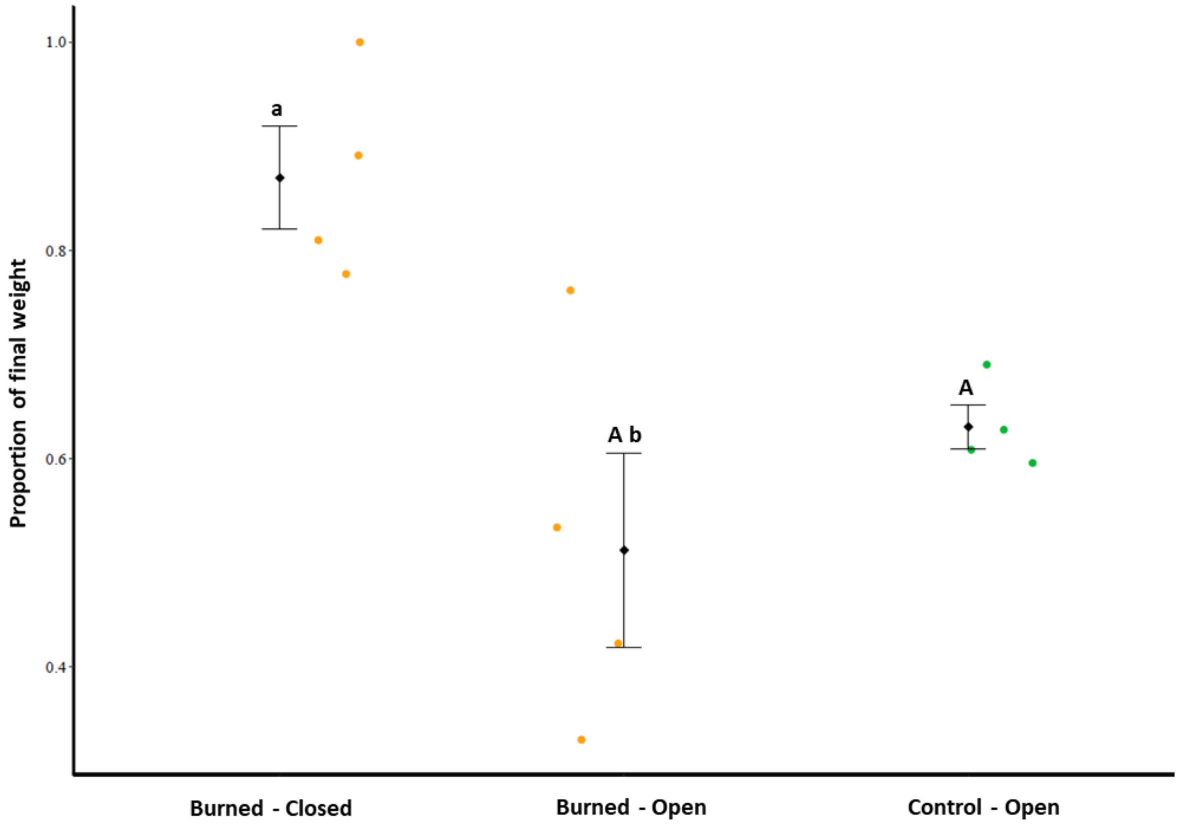


Figure 8. Litter bag decomposition in the big-plot experiment. Capital letters indicate significant differences between treatments. Lower letters represent the differences between open bags (mesh containing holes about one cm in diameter, allowing invertebrate access to the leaves) and closed bags (mesh without holes, not allowing invertebrate access) in the same treatment, according to two-way ANOVA. Bars represent standard error.

Discussion

Our results indicate that a higher termite abundance in forest burned multiple times in the southern Amazonia may be a key mechanism responsible for the increase in organic matter decomposition. In the big-plot experiment, termite abundance in the annually burned plot was 1.55-fold higher than in the triennially burned plot, and 1.78-fold higher than in the control plot. Accordingly, the annually burned plot had 1.2-fold higher decomposition than the triennially burned, and 1.83-fold higher decomposition of organic matter than litterbags in the control with invertebrate access. However, this pattern of higher decomposition in burned forest did not hold in the block experiment, although termite abundance increased 1.15 times in burned plots compared to the unburned control. We reason that these organisms are capable to increase the decomposition of organic matter only in burned forests with a large increase in termite abundance, which occurred in our large-scale, recurrent big-plot experiment.

The increase in termite abundance may be related to changes in forest structure following fire, as it was correlated with higher temperature and decreased soil moisture in the big-plot experiment. Similar results were found after an extreme drought event in a Malaysian tropical forest, where higher temperature and lower soil moisture also occurred, followed by an increase in termite abundance (Ashton et al. 2019). However, in our block experiment there was no variation in temperature between treatments – but contrary to what we expected, soil moisture was higher in the burned treatment. However, environmental changes alone may not be able to alter the termite functions.

Additionally, top-down control in ant-termite interactions seems to be one of the main mechanisms shaping termite communities in burned forests. In the annually burned treatment of the big-plot experiment, we found the highest termite abundance and the lowest predation of termites. Lower ant predation pressure increases termite abundance and organic matter decomposition. Lower ant predation pressure on termites can also explain the increased termite abundance and decomposition of organic matter in Malaysian tropical forest after an extreme drought (Ashton et al. 2019).

Our results also indicated that invertebrates have important roles in organic matter decomposition within Amazonian burned forests. Unlike in the burned plots, leaf decomposition due invertebrate activity and microorganisms was the same in the control plot of our big-plot experiment. However, invertebrates were responsible for promoting higher decomposition of organic matter in all our burned plots when compared with the control in both experiments. Leaf mass loss in decomposition bags with invertebrate access in burned forest is about 2-fold higher than in decomposition bags without invertebrate access. Our results therefore corroborate that decomposition in burned forests is slower when invertebrates are excluded (Silveira et al. 2009). Several groups of invertebrates influence decomposition of organic matter (Vasconcelos and Laurance 2005) and termites are a key group in this process after fire in certain environments, such as savannas (Davies et al. 2021; DeSouza et al. 2003). Although other invertebrate groups are also important to organic matter decomposition, our results indicate that termites are especially important to this process due to increase of abundance in burned plots. They become particularly more relevant to decomposition after fires in tropical forests, helping to mitigate the effect of burning. Additionally, we found a higher termite abundance in dead wood in the burnt forests, which can contribute for an increase in dead wood decomposition. Carbon in aboveground biomass is lost after fires due to an increased tree mortality (Brando et al. 2014), and a study in Malaysia tropical forest showed that termites increase carbon flux in glades formed by falling trees (Griffiths et al. 2021). Thus, termites are also likely to contribute to the increase of carbon flux in burned forests.

We showed that an increase in termite abundance can contribute to higher decomposition of organic matter in burned tropical forests. Studies that showed the implications of termite abundance increase for organic matter decomposition also demonstrate that termite are important to nutrient cycle and seed survival after disturbance in tropical forest (Ashton et al. 2019). Thus, increases in decomposition can promotes a cascade effect in burned forests by enhancing soil nutrients, and structuring vegetation, and eventually boosting forest recovery. In addition, burned forests have higher dead wood levels, and intense losses in carbon stock. Termites are important for carbon stock increase (Griffiths et al. 2021), and increase in termite abundance can mitigate lose process present in dead wood.

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CONCLUSÃO GERAL

Nesta tese, nós demostramos como diferentes tipos de distúrbios antrópicos, como a fragmentação de habitat e incêndios florestais, na região sul da Amazônia podem afetar funções ecossistêmicas desempenhadas por três grupos de invertebrados. Nós mostramos que a conversão de florestas em agricultura pode levar a mudanças na estrutura das comunidades de formigas e besouros rola-bosta de florestas ripárias, e que essas mudanças são responsáveis por alterar funções ecossistêmicas. Nós apontamos alguns resultados inesperados, como a manutenção das funções ecossistêmicas de besouros rola-bosta mesmo em florestas ripárias presentes na agricultura. No entanto, é possível que as mudanças na composição de espécies de besouros rola-bosta possam impactar funções ecossistêmicas que não medimos.

Nós também demostramos a importância de invertebrados, especialmente os cupins, na decomposição de matéria orgânica em florestas queimadas. Nós identificamos os possíveis mecanismos que permitem que os cupins aumentem a decomposição de matéria orgânica após incêndios florestais. Contudo, nós entendemos a necessidade de mais estudos que liguem esses invertebrados às funções ecossistêmicas. Os cupins são capazes de promover um efeito positivo em outras funções ecossistêmicas em florestas queimadas devido ao aumento de sua abundância e mudanças nas interações com outros grupos de predadores, como formigas. De maneira geral, os resultados chamam atenção por mostrar como as ações antrópicas recorrentes na região amazônica são capazes de promover um efeito cascata que vai desde a modificação do ambiente até alteração em funções ecossistêmicas, as quais têm implicações para a recuperação natural destas florestas.