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Selective logging does not alter termite response to soil gradients in Amazonia

Renato Almeida de Azevedo[1,*], Quézia Cristina Lima Santos[2], Isadora Essig Fluck[4], Domingos J. Rodrigues[2], Leandro D. Battirola[3] and Cristian de Sales Dambros[4]

[1]Instituto Nacional de Pesquisas da Amazônia - INPA, Coordenação de Biodiversidade - COBIO, Av. André Araújo, 2936, Petrópolis, Manaus, AM, Brazil; [2]Universidade Federal de Mato Grosso, Programa de Pós-Graduação em Ecologia e Conservação da Biodiversidade (PPGECB), Instituto de Biociência, Cuiabá, Mato Grosso, Brazil; [3]Universidade Federal de Mato Grosso, Campus Universitário de Sinop, Programa de Pós-Graduação em Ciências Ambientais (PPGCAM), Instituto de Ciências Naturais, Humanas e Sociais, Sinop, Mato Grosso, Brazil and [4]Universidade Federal de Santa Maria, Departamento de Ecologia e Evolução, Santa Maria, RS, Brazil

Research Article

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Author for correspondence:
*Renato Almeida de Azevedo,
Email: azevedo.inpa@gmail.com

Abstract

Selective logging has been widely employed as a management practice in tropical forests due to its reduced impact on biodiversity. However, by altering microclimatic conditions, logging could affect soil fauna responsible for nutrient cycling and the long-term dynamic of the forest. We investigated how selective logging affected termite species richness, composition, and the distribution of species in trophic groups, as well as the natural response of termites to gradients of soil conditions. Termites and edaphic variables were sampled in 32 permanent plots in southern Amazonia. Plots were subject to selective logging for 10–31 years before termite sampling. Time post-management was associated with changes in termite species composition, and wood-feeding termites were more abundant in recently logged areas. Nevertheless, most of the variation in termite species richness and composition can be attributed to the natural variation in soil clay content. Moreover, soil-dweller species, a vulnerable group strongly linked to soil decomposition, were present in all plots. These results suggest that the impact of selective logging on termite communities might be milder compared with other types of disturbance. It is likely that the decomposition process performed by termites, and consequently long-term ecosystem functioning, is preserved under selective logging.

Introduction

Selective logging became one of the main forest management practices in the last decades, and the method is thought to have a relatively low short-term impact on biodiversity (Sabogal et al. 2006). However, tropical forest degradation alters forest structure, species composition, and successional processes, causing impacts that may last for several years or even decades (Blanc et al. 2009). In the long run, in addition to the effects on predators and herbivores, selective logging could still have major impacts on forest dynamics by affecting the soil fauna responsible for nutrient cycling and ecosystem functioning. Decomposing organisms, such as termites, are the main drivers of nutrient cycling and are important for the maintenance of the vegetation structure in tropical forests over long periods (Jouquet et al. 2011).

Even though forest management has a low impact on vegetation structure (Silva 1996), the fundamental processes such as canopy-gap dynamics, predation, and carbon storage will be altered or disrupted (Laurence et al. 2002). In tropical regions, ectotherms have a low tolerance to changes in temperature (Sunday et al. 2011), and even slight temperature increases can have a major impact on the survival and reproduction of these organisms (Walther et al. 2002). Moreover, the reduction in soil moisture is likely to have a strong impact on animals adapted to high levels of soil moisture (Oberst et al. 2019), such as soil-dweller species that have a unique role in the decomposition of soil organic matter (Lavelle et al. 1997). Therefore, by changing microclimatic conditions, selective logging may alter the decomposition process by altering the abundance and diversity of the soil fauna.

Termites are among the most abundant animals in tropical forests (Fittkau & Klinge 1973) and play an important role in nutrient cycling and the dynamics of organic matter (Griffiths et al. 2019; Lavelle et al. 1997). Near forest borders, the higher sunlight incidence and the reduction in moisture alter the composition of termite species (Dambros et al. 2013). For example, areas as far as 90 m from roads are dominated by generalist wood-feeding termites, and compared with the intact forest, these areas have fewer species specialized in the decomposition of soil organic matter (Dambros et al. 2013). These results suggest that even minor changes in microclimatic conditions, such as those observed in managed areas, can have an impact on the distribution of termite species.

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In addition to the direct impact of management on termite communities, disturbances could also alter the response of termites to the natural variation in soil conditions (Dambros *et al.* 2013). Many termite species use soil to build nests (Pie et al. 2004), which are used to precisely control microclimatic conditions inside the nest (Hu et al. 2012). Because only highly tolerant species survive under disturbance regimes, specialists tend to be impacted most (biotic homogenization; McKinney & Lockwood 1999). Forest disturbance may reduce the natural variation in termite species composition that occurs along the environmental gradient of soil granulometry because only species that build specific types of nests can survive. However, the impact of logging on the reduction of species turnover along gradients has not been investigated.

We analyzed how termite species richness, abundance, the taxonomic and trophic composition changed in an experiment of selective logging analyzing how this management strategy affected the composition of termites along natural environmental gradients. We hypothesized that: (1) selective logging reduces the diversity of termites, especially the diversity of species that inhabit the soil, and (2) the removal of habitat specialists homogenizes communities along the natural gradient of soil granulometry.

Material and methods

Study area

The study was conducted in Claudia, Mato Grosso state, Brazil. The region is characterized by dry Amazonian forests (Ferreira et al. 1999), which correspond to approximately 10% of the Amazonian biome. The climate in the region is classified as moist and warm (Am in the Köppen scale) with two marked seasons: a rainy season from September to April and a dry season from May to August. The mean precipitation is 2200 mm, and the mean annual temperature is 24°C (Vourlitis et al. 2002).

The region is considered as a transition forest among Cerrado and Semideciduous Forests (Brasil 1979), and the vegetation is rapidly disappearing due to high deforestation rates caused by livestock activity (Kunz et al. 2008). The deforestation process created a mosaic of areas in the landscape with several types of land uses and regeneration regimes, from old impacted forests to recently impacted (Wang et al. 2019).

Sampling design and data collection

Data collection was performed in three units, denominated as 'modules' distant 20 km from one another. The modules are located in forests with different management histories (selective cutting of wood). Module I is located in an area that has been managed for 10 years previous to termite sampling (2002), module II for 17 years (1995), and module III for 31 years (1981). Modules I and II were installed in a continuous forest area, whereas module III was installed in a forest section surrounded the west and the east by plantations, being connected to a single large area of native vegetation.

In each module, termite sampling was conducted in several plots following the method used in the Biodiversity Research Program (PPBio). PPBio uses a standardized survey in permanent grids of plots, which allows for rapid and long biodiversity monitoring in Amazonia (Magnusson et al. 2005). Modules I and II are formed by grids composed of six Northeast-southwest and two northwest-southeast 1 km equidistant tracks, forming a rectangle of 12 km^2. Each kilometer along the northwest-southeast tracks has a transect of 250 m, resulting in 12 plots in each of these modules. Module III has the same sample design as the first two but has only eight plots because of the forest fragment small size (Figure S1 in Supplementary material). Plots of all modules were installed according to the criteria stipulated by Magnusson et al. (2005), following relief level curves to minimize soil variation within the plots. This procedure reduces soil and elevation variation and ensures that the data will not be directly influenced by variation in these factors. All plots were installed at a distance of at least 200 m from the forest edge to avoid edge effects. This minimum distance is much higher than the edge effect previously reported for termites (Dambros et al. 2013) and other groups (Forman & Alexander 1998).

Termites were sampled in the 31 plots (12 in module I, 11 in module II, and 8 in module III), following a modification of the protocol proposed by Jones & Eggleton (2000). Each plot was subdivided into five sections of 5 × 2 m spaced 50 m apart, totaling 155 sections. This division into sections allows detecting trophic groups and species to associate species composition with the environment (Dambros et al. 2020). The sampling effort in each section was 1 hour/person of active search. Sampling was carried out in August, September, and October 2010 and August 2011. These months are characterized by the end of the dry period and the beginning of the rainy season in the region.

Termites were collected manually with entomological tweezers and pickaxes, which were used to dig the ground and to break larger trunks. In each section, all possible termite habitats were surveyed for termites, such as soil, dead wood, nests (epigeal, hypogeal, and arboreal up to 2 m height), foraging galleries, plant roots, animal feces, fallen fruits, and litter. The collected material was conditioned in plastic collecting bottles containing 70% EtOH. The individual colonies were screened in the laboratory and identified using identification keys (Constantino 1999) and compared with the material deposited at the Museum of Zoology of the University of São Paulo (MZUSP). All material was stored in 80% EtOH and deposited in the Entomological Collection of the Biological Collection of the Southern Amazon maintained by the Biodiversity Studies Center of the Mato Grosso (NEBAM-UFMT/Sinop) and MZUSP.

In each plot, we measured variables related to soil, canopy cover, litter volume, and time post-management. Soil samples were taken with the aid of a Dutch survey (Moulatlet & Emilio 2011). The samples presented a depth of 0–10 cm and were arranged in six points distant at 50 m each. The sampling design allowed a homogenization of the plot, resulting in a single composite sample. Four canopy readings were performed every 50 m (north, south, east, and west) using a concave spherodensiometer (Concave-Model 1C-Forest Densiometers). The readings were performed between 9 a.m. and 2 p.m. Moreover, we collected litter volume (liters) at five points every 50 m in the plot. The litter contained in an area of 1 m^2 was collected and compressed three times in a graduated bucket, using wood press launched at a distance of 1.5 m from the bucket. For the analyses, we used the mean value of the five measures of volume per plot. Finally, we obtained the time post-management of each plot through an interview with the owners of the areas. These areas have been left without other disturbances since the time post-management.

Data analysis

Because sections were not independent of each other due to the short distance between them, we used data at the plot (i.e., transects of 250 m each) and used plots as sampling units in all analyses. The

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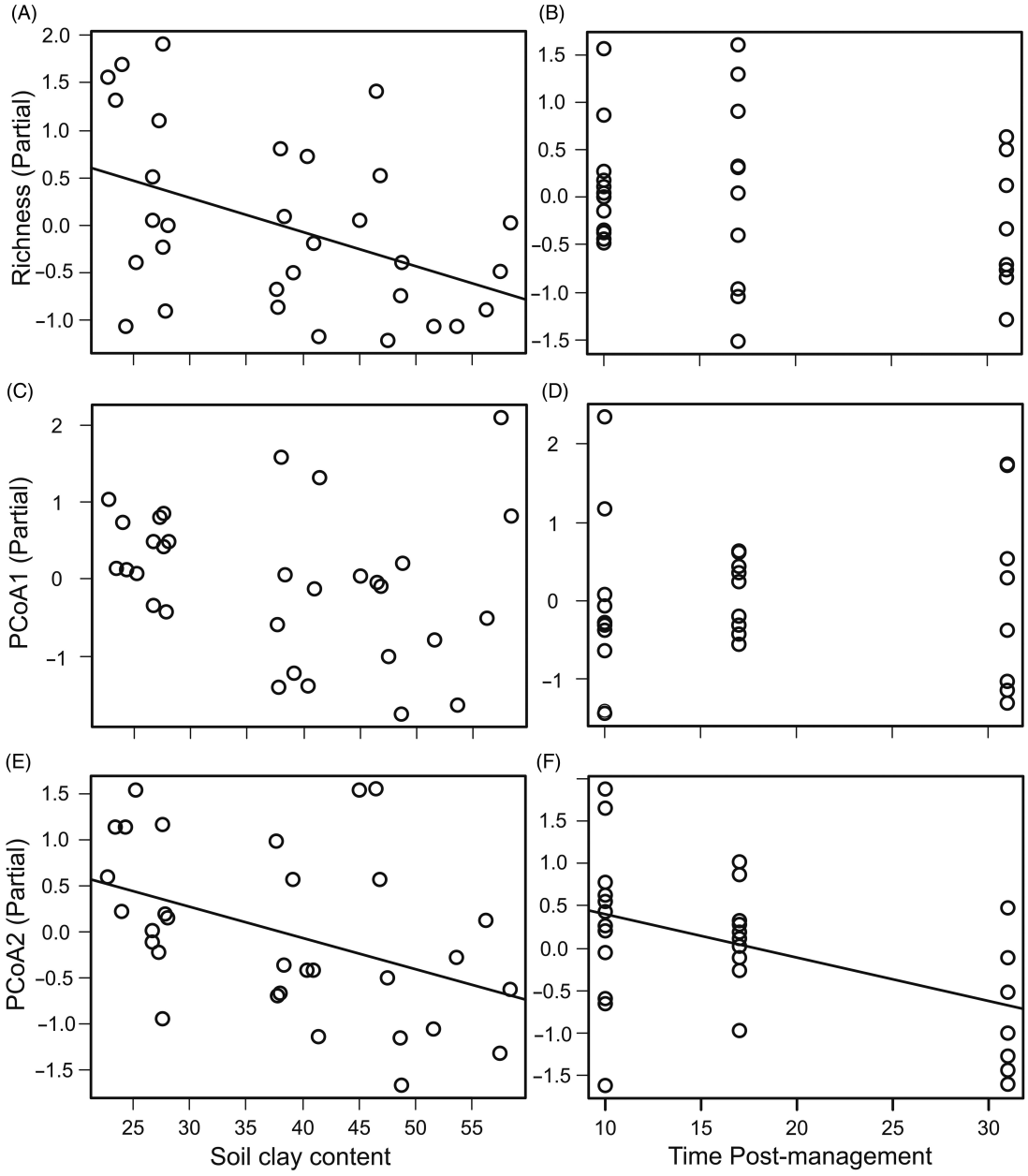


Figure 1. Partial regression analysis testing the effect of soil clay content and time post-management on species richness (A and B) and composition variation (C and F).

relative frequency of each species in each section within a transect was used as a proxy for abundance in each plot. As the total of sections per transect was five, the maximum frequency that each species was bounded between zero and five. Species richness was measured as the number of species found in each plot.

The functional composition was measured as the change in the distribution of species in trophic groups. Termite species were categorized into trophic groups (Constantino 1999; Roisin & Leponce 2004): (I) wood-feeders: species that feed on dead wood; (II) humus-feeders: species that feed on mineral soil and humus; (III) litter-feeders: species that feed on leaf and small woody litter; and (IV) intermediary-feeders: species that feed on largely decayed wood that has become soil-like. Termites inhabiting and feeding in distinct substrates, such as soil, litter, and wood, are likely to respond differently to disturbances (Ackerman et al. 2009).

Differences in species composition between plots were measured by the Jaccard dissimilarity index. We applied a Principal Component Analysis (PCoA) to summarize the dissimilarity values in two ordination axes. The first two axes captured 20% of the variation in the Jaccard dissimilarity index. Each additional axis increased the variance explained by less than 8%. The two ordination axes were used as response variables in statistical models. The Jaccard index considers only species presence/absences in transects, not species abundances. Because termites are modular organisms, tallying the number of individuals to calculate abundance might overestimate the abundance of species with larger colonies. Although we obtained occurrence frequency in sections within transects, the Jaccard index is more sensitive to rare species than indexes weighted by abundance (Jost 2007). These species are the most

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Table 1. Coefficients of the association of environmental predictor variables with termite species richness, overall abundance (occurrence frequency), and species composition on multiple regression models. Species composition was measured as the first two ordination axes of a Principal Coordinate Analysis (PCoA) using the pairwise Jaccard similarity index. R^2 represents adjusted values.

	Time post-management	Soil clay content	Canopy height	Litter	*F*	*df*	R^2
Species richness (S)	−0.21	−0.68**	0.37	−0.26	4.515	26	0.32**
Abundance	−0.33	−0.69**	0.49*	−0.21	4.425	26	0.31**
Composition (PCoA1)	0.29	0.02	−0.02	−0.06	0.722	26	˜0
Composition (PCoA2)	0.38*	0.66**	−0.12	0.11	4.395	26	0.31**

**$p < 0.01$.
*$p < 0.05$.

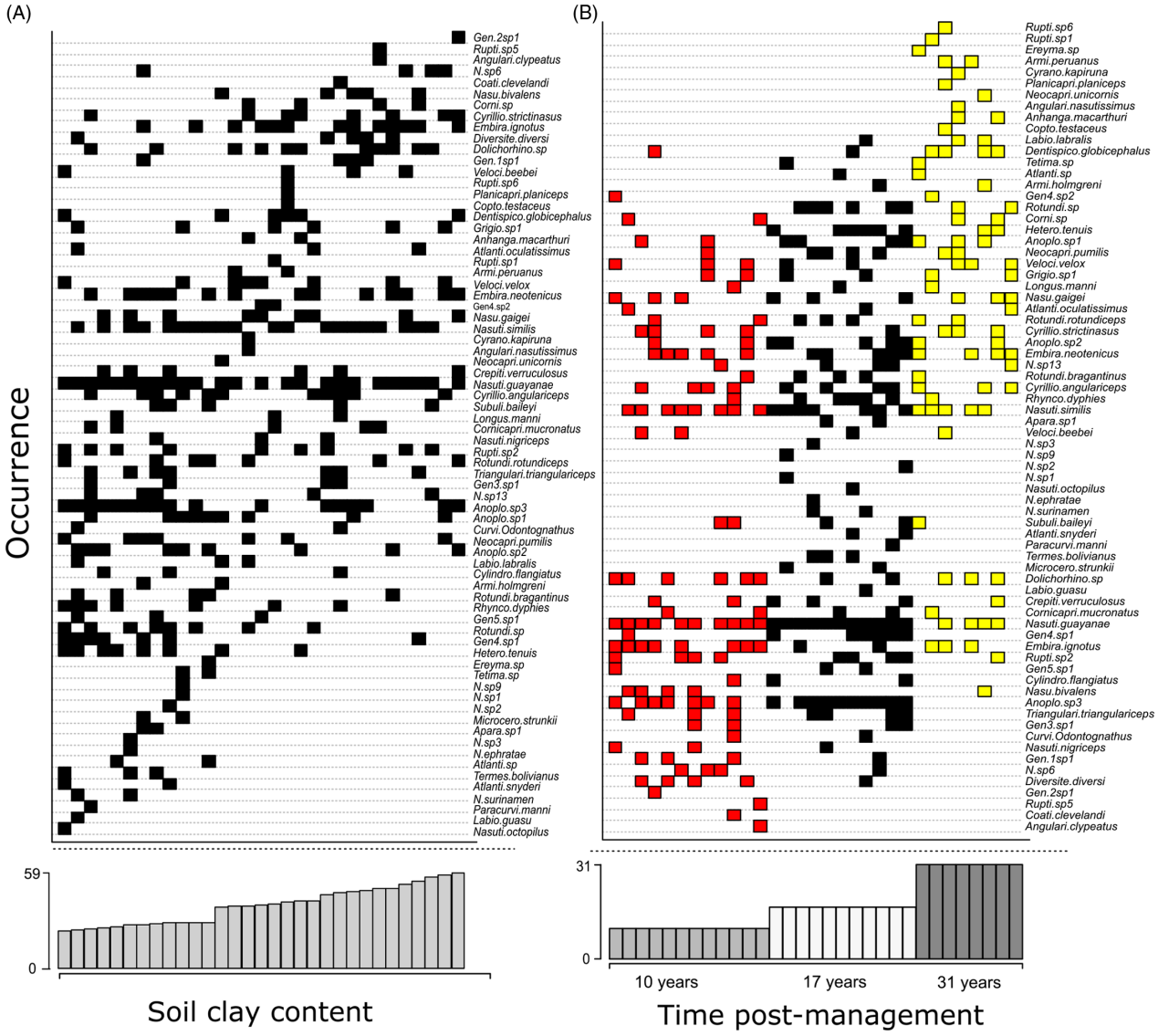


Figure 2. Presence and absence of each termite species along the soil clay content gradient (A) and time post-management (red: 10, black: 17, yellow: 31) (B).

likely to be affected by changes in the environment. Therefore, we only used metrics based on the presence/absence data for the species composition analyses.

To evaluate the association between soil clay content, time post-management, litter volume and canopy cover (predictor variables) and termite abundance, species richness, and species composition (response variables), we used multiple linear regression. These regression models were run for all species and using each trophic group separately. In addition to the multiple regression models using the PCoA axes of species composition, we also investigated

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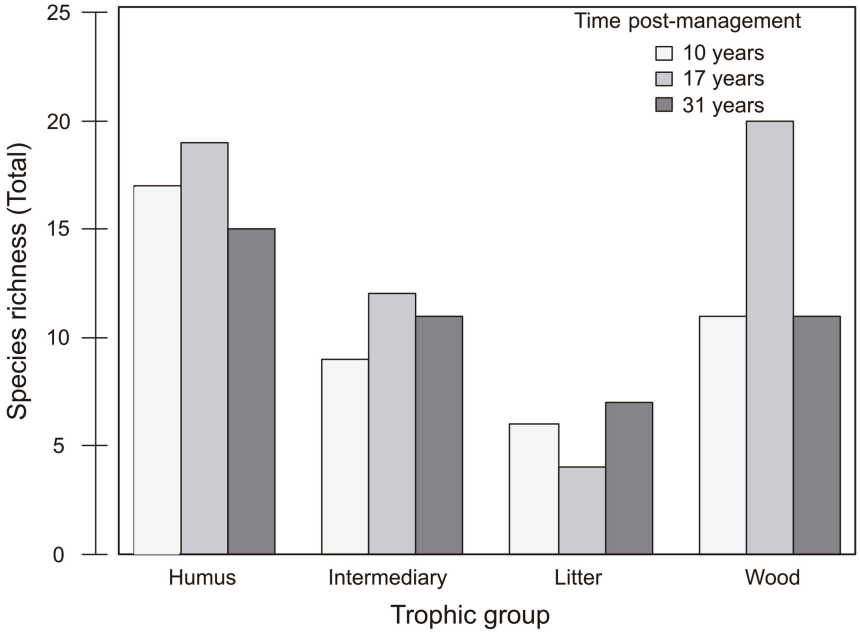


Figure 3. Total termite species richness of each trophic group per time post-management (10, 17, and 31).

changes in species composition against the predictor variables using a Redundancy Analysis (RDA), which uses the raw species counts instead of the Jaccard similarity matrix.

All analyses were performed using the Vegan (Oksanen et al. 2018) and Betapart (Baselga et al. 2017) packages in R (R Development Core Team).

Results

We observed a total of 72 species in the three studied modules. The 17-year post-management area had the highest species richness (55 species compared with 43–44 species in the 10 and 31 years post-management modules; Table S1 in Supplementary material). Species richness and abundance were lower in areas of high soil clay content (Figure 1A; Table 1), but there was no evidence of change in species richness with time post-management in multiple regression models (Figure 1B; Table 1). Species richness was positively related to species abundance (Figure S1 in Supplementary material).

Changes in termite species composition were associated with both soil clay content and time post-management, as measured by the second PCoA ordination axis (Figure 1C–F, Table 1) and the RDA analysis ($p < 0.01$; Figure S2 in Supplementary material). Therefore, termite species replaced each other along these gradients (Figure 2).

Concerning trophic groups, litter-feeders represented the termite group with the lowest species richness in all post-management treatments (Figure 3). Humus and wood-feeding termites were the groups with the highest species richness, and the contribution of each of these groups changed over time – the most species-rich termite group after 10 and 31 years of management was humus-feeding termites, whereas in the area managed 17 years ago, the termite group with the highest species richness was the wood-feeding group (Figure 3).

When species richness was correlated against predictor variables separately for each trophic group, time post-management, soil clay content, and leaf-litter were associated with a decrease in wood-feeding termite species richness (partial regression model: when the effect of other variables is removed; Table S2 in Supplementary material). However, we have not detected effects of soil clay content, time post-management, canopy cover, or leaf-litter on termite species richness for other groups.

Discussion

In contrast to expectations of an effect of selective logging on canopy openness, time post-management (minimum 10 to maximum 31 years) was not associated with termite richness or abundance. Instead, we found the percentage of soil clay to be strongly associated with termite abundance, species richness, and composition. These results may indicate that the medium and long-term impact of selective logging on the termite community is low and does not change the response of species to natural environmental gradients. It is possible that the 10-year interval is enough for the forest to recover and that it is not possible to detect this impact over longer periods.

Wood-feeding termites were the group with the highest diversity 17 years post-management. These termites may have high richness after selective logging because the fall of entire trees, branches, and leaves increases food availability (Sizer et al. 2000). A similar increase of wood-feeding termites is also observed in agroforests (Ackerman et al. 2009), where vegetation cover is dissimilar to the natural environment, but the availability of wood increases. These results suggest that restricted logging impacts resource availability, but has a minor impact on the delicate response of termites to microclimatic conditions. The soil-feeding termites were not associated with time post-management or with changes in canopy cover. Several soil-feeding termite species are highly specialized and occur only when environmental conditions are favorable (Eggleton et al. 2002). The change in vegetation cover is generally associated with reduced soil moisture (Dambros et al. 2013), which impacts the abundance of species sensible to drought (Dambros et al. 2013; Okwakol 2000).

Although species composition changed as a function of time post-management, the temporal turnover of termite species was less pronounced than the natural spatial turnover along the soil

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clay gradient. Clay is used by many species to build nests (Jouquet et al. 2011) and is associated with vegetation structure (e.g., palm density; Costa et al. 2009), which causes turnover in termite species composition (Dambros et al. 2017). In highly disturbed areas, the natural variation in species composition tends to be relatively weak because species with narrow environmental requirements (specialists) are replaced by species with broader requirements (generalists; Mckinney & Lockwood 1999). We have not observed this drastic change from specialist to generalist species in disturbed areas. Even in recently logged areas (10 years), we observed species and trophic groups common to pristine environments (e.g., humus consumers; Ackerman et al. 2009). More importantly, the soil clay gradient continued to be the main factor responsible for changes in species composition between plots. These results may indicate that selective logging management was unable to homogenize the soil biota, differently from observation in highly disturbed areas (Ackerman et al. 2009).

Termites are among the most abundant animals in tropical forests and are the main decomposers of plant material in these regions (Eggleton et al. 1996). While termites in high abundance can rapidly decompose organic material, the high diversity of species in several trophic groups allows most of the decomposition chain to occur (Griffiths et al. 2019). In one extreme, wood-feeding termites decompose dry and recently fallen trees and branches; in the other extreme, soil-feeding termites decompose organic matter already incorporated into the soil (Donovan et al. 2001). The maintenance of termites in high abundance and diversity observed in this study suggest that most of the decomposition process is likely to be preserved.

Although time post-management influences species composition, this effect is weak compared with the natural variation in composition along the soil clay gradient. These results suggest that forest management with selective logging has a much lower impact on species diversity than observed by road construction (Dambros et al. 2013), burning (Dawes-Gromadzki 2007), conversion of areas to pastures (Bandeira & Vasconcellos 2002), or agroforestry (Ackerman et al., 2009). Also, all decomposition groups, including those most vulnerable and responsible for maintaining soil fertility (Dibog et al. 1999), were found 10 years post-management. The soil fauna is largely responsible for organic matter decomposition (Lavelle et al., 1997), and the maintenance of the high abundance and species diversity in managed areas may indicate that selective logging has a low long-term impact on nutrient cycling and decomposition.

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Supplementary material. To view supplementary material for this article, please visit https://doi.org/10.1017/S0266467421000080

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