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Edge effects on ant diversity and functional composition in a forest fragment in the Central Amazon

Talitha F. Santos[1], Vanessa P. Mesquita[2], Juliana S. Araújo[3], Fabricio B. Baccaro[3]

1 - Programa de Pós-graduação em Zoologia, Universidade Federal do Amazonas, Manaus-AM, Brazil

2 - Instituto Nacional de Pesquisas da Amazônia, Manaus-AM, Brazil

3 - Departamento de Biologia, Universidade Federal do Amazonas, Manaus-AM, Brazil

Corresponding author
Talitha Ferreira dos Santos
Universidade Federal do Amazonas
Av. General Rodrigo Octavio Jordão Ramos, 1200, CEP: 69067-005 - Coroado I, Manaus, Amazônia, Brasil.
E-Mail: talitha.fs@gmail.com

Abstract

The process of human-induced forest fragmentation increases the degree of isolation and causes biodiversity loss. Abrupt changes occur mainly near the edge of the fragment, where the average temperature is relatively higher and the humidity is lower. However, some natural environmental characteristics, such as higher air moisture in riparian areas, may buffer or minimize the edge effects. Here, we studied how the edge effect may affect ant species diversity and functional composition on valleys dissected by small streams (mesic areas). We categorized ant assemblages into the functional groups based on foraging, nesting habits, natural history information, and phylogeny. Ants were sampled using pitfalls and the Winkler extractor in ten riparian plots in a fragment of the Central Amazon. We individually fit the ant species richness, occurrence, and composition against two edge measures: forest edge distance and road-building distance. We recorded 99 species/morphospecies. Forest edge distance and road-building distance did not influence the occurrence and number of ant species per plot but were related to ant species composition. Moreover, there was not a clear pattern between functional groups distribution, except by leaf-cutters and generalist omnivorous species. Our results suggest a limited effect of forest edge distance and road-building distance on ant diversity.

Introduction

The process of human-induced forest fragmentation increases the degree of isolation and biomass loss, and it is one of the most severe threats to biodiversity conservation (Laurance & Williamson, 2001; Laurance & Vasconcelos, 2009; Betts et al., 2019). Overall, biodiversity reduction in the forest fragments responds to variations in the physical environment, including an increase in air temperature and luminosity closer to the forest edge (Vasconcelos & Laurance, 2005). The edge effect is among the most striking changes in fragmented areas since they form an abrupt transition between the forest and the adjacent landscape (Laurance, 2004; Ries et al., 2004). Moreover, the changes caused by the edge effect can shape ecological processes and community structure well

beyond the border of the fragment (Laurance & Vasconcelos, 2009; Ruffell & Didham, 2016; Luther et al., 2020).

At the edge, the environment is typically drier with greater thermal variation and more susceptible to heavy winds than areas inside the forest fragment (Laurance et al., 2000; Laurance & Williamson, 2001; Laurance & Vasconcelos, 2009; Marcon et al., 2012). Microclimate changes caused by forest fragmentation were evident up to 100 m into the forest interior (Corlett & Primack, 2011), but the effects on assemblage structure varied with taxa. Lower species diversity in forest edges was reported for frogs (Tsuji-Nishikido & Menin, 2011), birds (Nogueira et al., 2021), and small mammals (Pardini et al., 2005; Palmeirim et al., 2020). In the Central Amazon, soil invertebrates such as termites (Dambros et al., 2013), beetles (Silva et al., 2017), and ants (Carvalho & Vasconcelos, 1999;

Vasconcelos et al., 2006) also respond negatively to habitat fragmentation with a decrease of abundance and richness due to vulnerability and the changes in microclimate conditions along forest edges.

Ants are key ecosystems engineers (Folgarait, 1998) and have been used as bioindicators to evaluate habitat conditions resulting from land management actions or long-term ecosystem changes (Underwood & Fisher, 2006; Griffiths et al., 2018). Factors such as higher light incidence, lower quantity of litter and the decrease in humidity closer to the fragment edge are correlated with a reduction of ant species diversity and variations in foraging activities (Carvalho & Vasconcelos, 1999; Vasconcelos & Laurance, 2005).

However, ant species resilience is related to water availability, being higher in moist environments (Levings, 1983; DeLabie & Fowler, 1993; Baccaro et al., 2013). In a Panamanian rainforest, Kaspari and Weiser (2000) found a 25 percent increase in ant visitation at baits in the wet season compared to the dry season and an over 200 percent increase in activity in a topographic gradient. Similar patterns of activity and diversity were found by Vasconcelos et al. (2003) and Baccaro et al. (2010) for ant communities in the Central Amazon. There is a natural moisture gradient related to topography in the Terra-firme forests of Central Amazonia. The valleys (lower areas) are more humid and sandier than the clayed soils of the plateaus (higher areas) (Kaspari & Weiser, 2000; Baccaro et al., 2010). However, it is unclear how the constant moisture of valleys can minimize the disturbances caused by edge effects over the ant species.

To predict the species resilience and how they interact, the functional diversity approach has been used to provide more mechanistic predictions of species responses (McGill et al., 2006; Petchey & Gaston, 2006; Mouillot et al., 2013). Trait patterns may be evaluated through functional groups or guilds according to their life history, to understand evolutionary processes and aspects of community ecology (Violle et al., 2007). Ant functional group are often used to explore responses to environmental disturbances (Leal et al., 2012; Baccaro et al., 2013, González et al., 2018) and to predict local species co-occurrence patterns (Silva & Brandão, 2010).

In this context, our study evaluated how the diversity of ant species and functional composition of riparian areas (next to valleys) varied along with the distance from the forest and road-building edges in a Central Amazon fragmented forest. We expect that taxonomic diversity (occurrence and richness) of ant species would not be related to both edge distances (distance from the forest and road-building edges) in these riparian areas, suggesting that the greater humidity in the valleys could be acting as a buffer, decreasing the negative edge effects in the ant assemblages. We also hypothesize that changes in taxonomic composition of ant species along the forest gradient would be subtle. However, related to functional groups, we expect that   generalist species would be more abundant close to the edge of the fragment due to

the adaptation to highly variable abiotic conditions (Wilson, 1987; Vasconcelos et al., 2006). In contrast, the abundance of specialist species would decrease closer to the forest edges, considering the sensibility of specialist species in fragmented forests (Leal et al., 2012).

Material and Methods

Study site

The study was conducted in a forest fragment at the campus of the Universidade Federal do Amazonas (03º 04 '34 "S, 59º 57' 30" W), municipality of Manaus, Amazonas, Brazil (Figure 1). The total area is approximately 776 ha and comprises 592 ha managed for conservation (Marcon et al., 2012). The fragment harbors areas of Terra-firme (including valleys and plateaus) and white-sand forests. The rainy season is between November and May, and the dry season is between June and October (Marcon et al., 2012).

Sampling design

The Program for Biodiversity Research (Programa de Pesquisa em Biodiversidade) installed and maintained 10 riparian plots at the Universidade Federal do Amazonas forest fragment (Figure 1). The riparian plots (next to valleys) are 250 m-long and were installed at 3 meters from the streams. The valley width, where the riparian plots were installed, ranged from 9.90 to 36.67 m. Valley width was based on the lowland areas around streams subject to flooding (Tsuji-Nishikido & Menin, 2011). For more information about the riparian plots habitat, see Tsuji-Nishikido and Menin (2011).

Environmental predictors

We use edge distance and road-building distance as environmental variables to evaluate the edge effect on ant assemblages in the mesic environments. The plot distance to the nearest fragment edge and the nearest construction/road was measured using Google Earth tools. The forest edge distance varied from 73 to 1114 m, and the road-building distance ranged from 65 to 499 m (Appendix - Supplementary material). Both distances were based on the center point of each plot.

Ant sampling

Ants were sampled using pitfall traps (Yi et al., 2012) and Winkler extractor methods (Lopes & Vasconcelos, 2008). We sampled ants in ten pitfalls and collected ten samples of 1 m² of leaf-litter in each plot. The sampling stations were regularly spaced every 25 m. Pitfalls consisted of 500 mL plastic cups buried to the ground level, partially filled with alcohol 70% and detergent and were left in the field for 48 hours. Each litter sample was sifted through a coarse sieve (1 cm² mesh size). Posteriorly the leaf-litter material was placed into a mesh bag and suspended vertically for 48 hours. Ants and other arthropods fell in a small cup partially filled with 70%
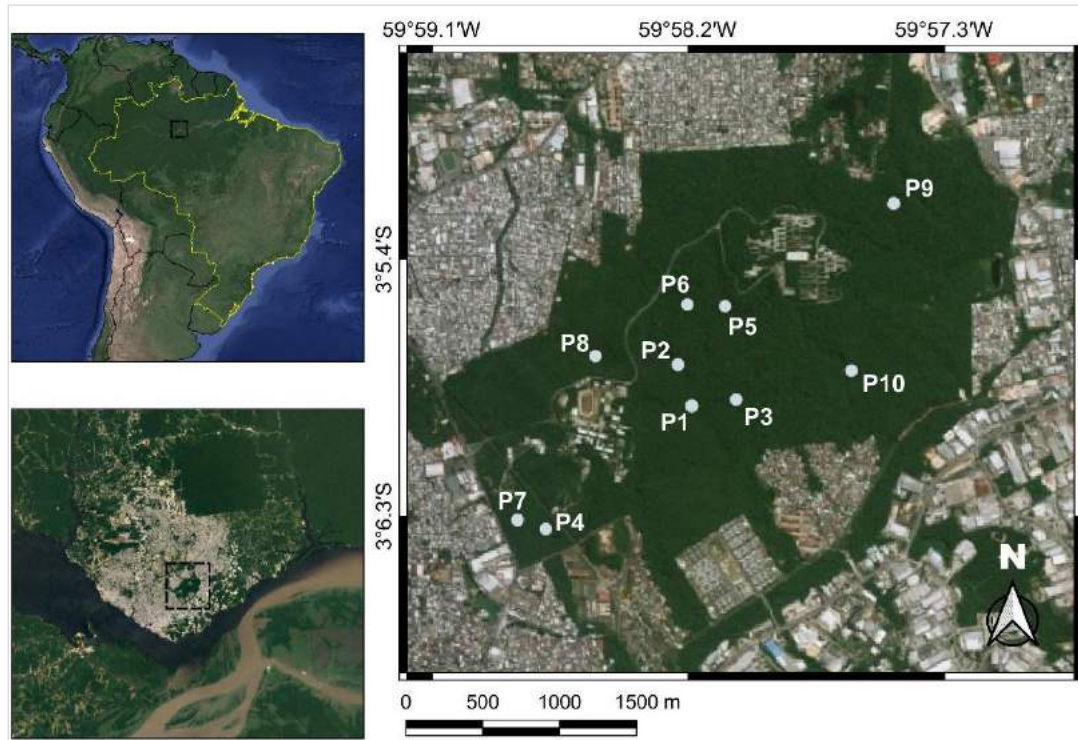
Fig 1. Geographical location of the study area, campus of the Universidade Federal do Amazonas, Brazil with permanent riparian plots installed by the Program for Biodiversity Research (Programa de Pesquisa em Biodiversidade).

alcohol, fixed at the bottom of the bag. Ants were sorted to genus level using identification keys (Baccaro et al., 2015) and to species level by comparing with specimens deposited in entomological collections and checking specific literature. Voucher specimens were deposited in the Invertebrates Collection of Universidade Federal do Amazonas. Ants were sampled in September 2012 in 10 permanent plots installed in riparian areas, next to valleys and small streams of Terra-firme forests.

Functional group classification

Ant species were placed into functional groups from classifications for Neotropical ants (Groc et al., 2014). The functional group approach was based on foraging behavior, food choice, nesting sites, natural history information, and phylogeny of each group species with potentially similar lifestyles. The matrix was composed of seven groups comprising two groups of fungus-growers, three groups of omnivores, and two groups of predators (Groc et al., 2014): (1) Leaf-cutters, (2) Cryptobiotc attines, (3) Ground-dwelling omnivores, (4) Generalist omnivores, (5) Arboreal omnivores, (6) Ground dwelling generalist predators and (7) Ground dwelling specialist predators.

Statistical analysis

We combined the Winkler and pitfall data to give a more reliable view of ant species richness and composition per plot. Given that ants are colonial organisms, we used the number of occurrences per plot as a measure of ant abundance (Gotelli & Chao, 2013). We used multiple linear regressions to detect the effects of the independent variables (both edge distance and road-building distance) over ant abundance and richness per plot. Sample-based rarefaction curves was constructed to estimate species richness using plots as sampling units (Colwell et al., 2012). Sample completeness was measured by sample coverage, the proportion of the total number of individuals that belong to the species detected in the sample (Chao & Jost, 2012). Interpolated and extrapolated values are based on Hill numbers generated in the iNEXT package (Hsieh et al., 2016).

We used Permutational Multivariate Analysis of Variance (PERMANOVA) (Anderson 2001) and non-metric multidimensional scaling (Kruskal, 1964), based on Bray-Curtis (occurrence data) and Sorensen (presence-absence data) distance measure to relate ant composition with both edge distance and road-building distance. While occurrence data give more weight to abundant species, presence-absence data gives more weight to rare or uncommon species. The p-value analysis was based on 999 permutations. Both PERMANOVA and NMDS (metaMDS function) were made using vegan package (Oksanen et al., 2013).

We converted the occurrence numbers to proportions for controlling the abundance variation per functional group among plots. Posteriorly, we used the proportion of each functional group per plot as a dependent variable against sampling edge distance and road-building distance in beta regressions models. Beta regression models are less prone to distortions caused by lower and upper bounds of proportions (Espinheira et al., 2008). All statistical analyses were done in R (R Core Team, 2022).

Results

We found 99 ant species/morphospecies belonging to 34 genera from eight subfamilies in pitfall traps and Winkler extractor combined (Appendix – Supplementary material). The most representative subfamilies collected with the Winkler extractor were Myrmicinae (52 species/morphospecies), followed by Ponerinae (6), Formicinae (6), and Ectatomminae (5). For pitfall traps, the most representative subfamilies were Myrmicinae (43 species/morphospecies), followed by Ponerinae (8), Ectatomminae (6), and Formicinae (5).

Species richness was higher using the Winkler extractor (73 species). *Pheidole* was the richest genera (12 species), followed by *Strumigenys* (9 species) and *Crematogaster* (8 species). The most frequent species was *Solenopsis* sp. 1, with 49 occurrences. A total of 63 ant species were recorded from

Pitfall traps, with the richest genera being *Pheidole* (14 species), *Solenopsis* (6 species), and *Crematogaster* (5 species). The most frequent species was *Ectatomma lugens,* with 26 occurrences.

Ant occurrence did not vary over the edge distance or road-building distance ($R^2 < 0.01$; $F_{2,7} = 0.57$; $P = 0.58$). Similarly, the number of species remained stable according to edge and road-building distance ($R^2 = 0.11$; $F_{2,7} = 1.58$; $P = 0.27$). However, rarefaction curves with sample and coverage-based show that Winkler extractor and Pitfall traps combined have an accentuated increase in estimated number of species (~95%) than isolated methods to access sampling effort (Appendix – Supplementary material).

The distance of forest edge and road-building distance were both related with ant species composition (Table 1), for presence-absence (Figure 2 and 3) and abundance data (Appendix – Supplementary material).

Table 1. Summary statistics of PERMANOVA using abundance (occurrence) and presence-absence data of ant composition. The results were based on 999 permutations.

Dependent variable	Predictors	R^2	F	P
Abundance data	Road-building distance	0.157	1.530	0.029
	Forest edge distance	0.174	1.699	0.010
Presence-absence data	Road-building distance	0.162	1.733	0.045
	Forest edge distance	0.249	2.657	0.001

We grouped our species in seven of the nine functional groups proposed by Groc et al. (2014). We did not sample predatory ants belonging to raid-hunting predators and arboreal predators functional groups. In general, there was not a clear pattern between functional groups distribution, except by leaf-cutters and generalist omnivorous species. We found relatively more leaf-cutters ants on plots further from road-

building constructions. Contrary to our hypothesis, we found relatively fewer generalist omnivores closer to the forest edge (Table 2). There is an evident species turnover in the other functional groups along forest and road-building edge distances (Figures 2 and 3). However, it is not associated with an increase or decrease of a particular guild.

Table 2. Summary of beta regression models for the relative abundance of ants for each functional group. Significative results are in bold.

| Functional groups	R^2	Predictors	*b* coefficient	P
Arboreal omnivores		Forest edge distance	-0.001	0.112
	0.275	Road-building distance	0.001	0.508
Cryptobiotic attines		Forest edge distance	< 0.001	0.120
	0.287	Road-building distance	< 0.001	0.953
Leaf cutters		Forest edge distance	< 0.001	0.135
	0.434	Road-building distance	0.002	**0.003**
Generalist omnivores		Forest edge distance	0.001	**0.018**
	0.375	Road-building distance	-0.001	0.053
Ground dwelling omnivores		Forest edge distance	< 0.001	0.475
	0.061	Road-building distance	< 0.001	0.925
Ground dwelling generalist predators		Forest edge distance	< 0.001	0.537
	0.065	Road-building distance	< 0.001	0.988
Ground dwelling specialist predators		Forest edge distance	< 0.001	0.838
	0.049	Road-building distance	0.001	0.467
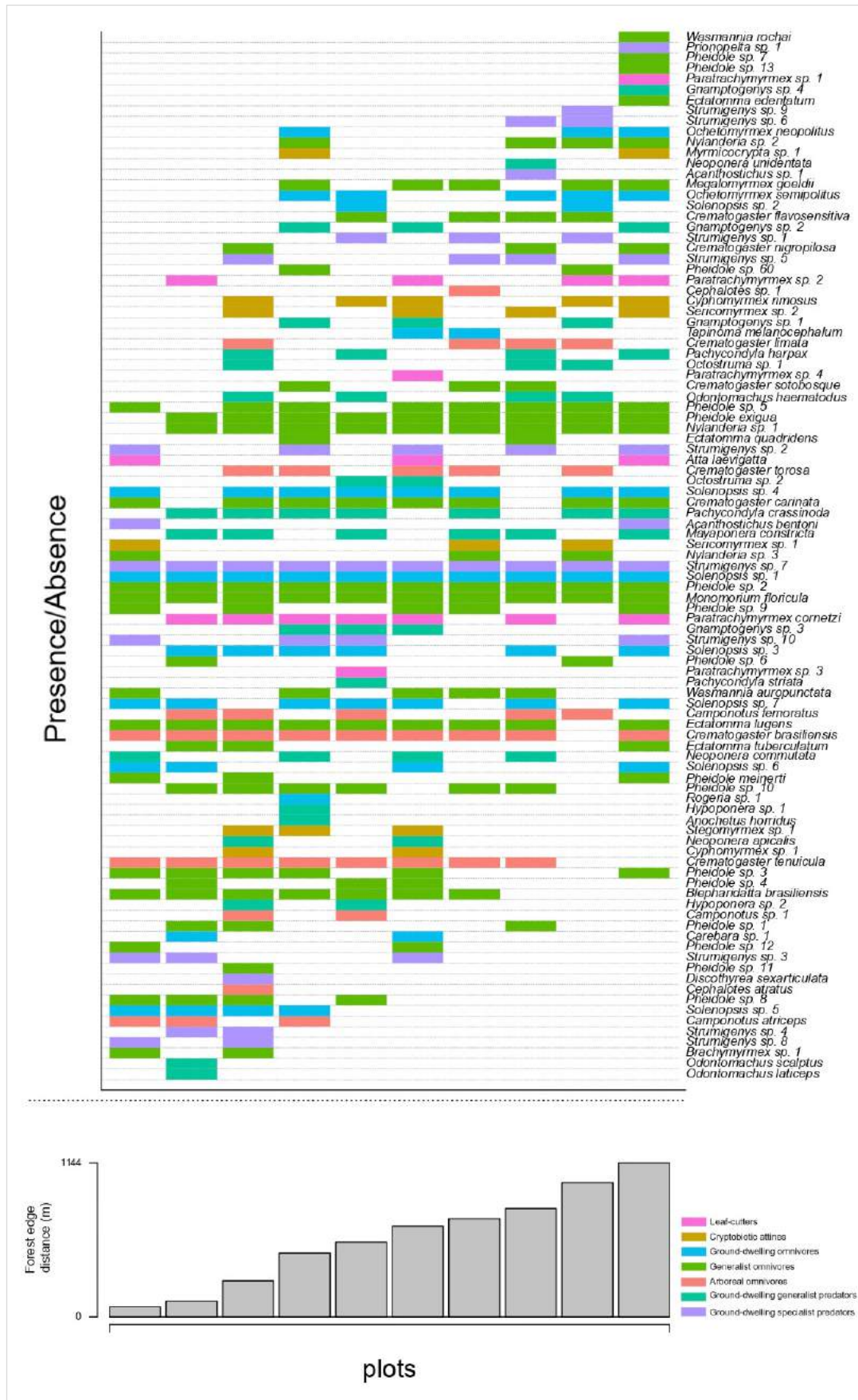
Fig 2. Turnover of ant species along a gradient of edge distance, showing species turnover from the forest edge to the inside of the forest, using presence-absence data. The x axis represents our plots and the y axis represents our dependent variables.
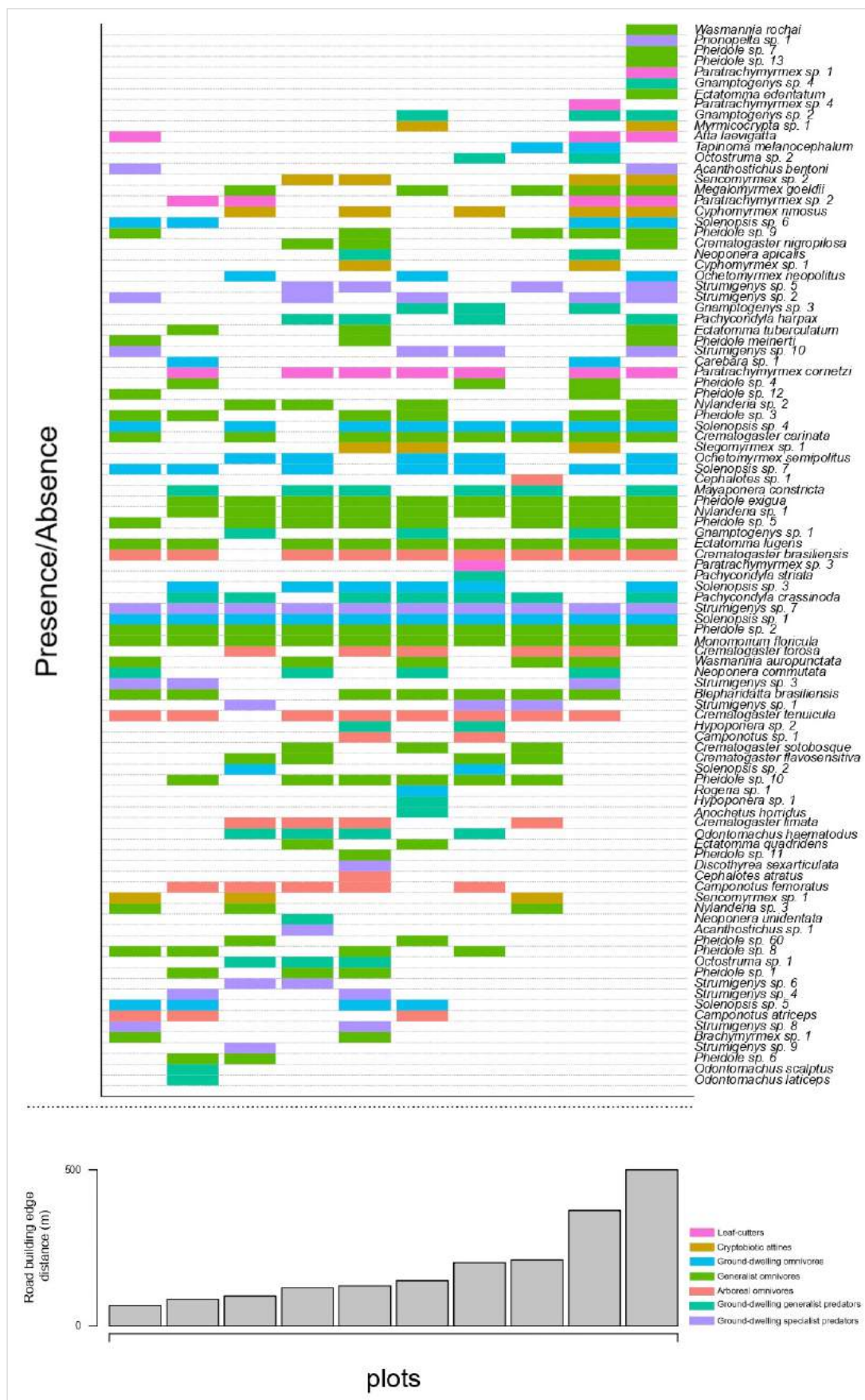
Fig 3. Turnover of ant species along a gradient of road-building distance, with presence-absence data. The x axis represents our plots and the y axis represents our dependent variables.

Discussion

Overall, our results suggest a limited effect of forest or road-building edge effects on ant diversity. Only ant assemblage composition was related to forest and road-building edge distance. There was also no strong pattern associated with functional group abundance. Both generalist and specialist predators were common along the edge distances investigated. Edge effects in fragmented forests are caused by biotic and abiotic factors that influence species diversity, and such changes depend on the fragment edge's severity (Laurance et al., 2002; Laurance & Vasconcelos, 2009). Some environmental predictors, such as moisture and temperature, are more variable 10 m from the forest fragment edge (Laurance et al., 2002). Both in forest edge or clearings next to road construction, tree falls are more frequent due to abrupt variations in microclimate as elevated wind turbulence and temperature variability (Kapos et al., 1997; Laurance et al., 1997), and consequently greater solar incidence (Laurance et al., 1997; Carvalho & Vasconcelos, 1999). These environmental changes can be even higher in urban forest fragments due to direct contact with city buildings and pavement (Dambros et al., 2013). However, in our study, we observed that the abundance and number of ant species did not vary according to the edge distance or road-building distance. Given that many ant species follow or are constrained by humidity (Kaspari & Weiser, 2000), moisture of riparian areas may be buffering the edge effects on ant diversity.

Species composition was related to both forest edge and road-building distances. By assessing isolated and continuous fragments in Central Amazonia, Carvalho and Vasconcelos (1999) found that ant composition was related to distance to the forest edge in fragmented areas. Physical factors such as litter depth decrease considerably at the forest edge, reducing indispensable nesting and foraging resources for ant species (Carvalho & Vasconcelos, 1999; Vasconcelos & Laurance, 2005) and may explain the high species turnover detected along the forest or road-build edge gradient in our study. However, the lack of pattern of functional group distribution suggests that forest or road-build edge effects in valley areas are more subtle than in typical Terra-firme forests, in plateus gradient.

Moisture can influence the composition and activity of ant species, with an increase in ant activity and diversity in more humid seasons and habitats (Levings, 1983; Kaspari & Weiser, 2000; Vasconcelos et al., 2003). However, in valleys, the temporary accumulation or lateral percolation of water near small streams (Chauvel et al., 1987) may limit the establishment and growth of some ground-nesting species (Baccaro et al., 2013). Therefore, higher ant species richness found in more humid habitats may be related to an increase of generalist species associated with a decrease in the specialist predators, litter nest fungus growers, and other functional guilds (Baccaro et al., 2013). At the site scale, disturbance resulting from water-table fluctuation may account in part for only seven out of nine functional groups recorded. Part of the variation in species composition is related to forest edge or road-building distances, but there is no clear pattern of functional group distribution along these gradients. Species with very different habitat, nesting, and resource requirements, such as Cryptobiotic attines, Generalist omnivores, and Ground dwelling specialist predators, were found along the gradient. These results suggest a limited effect of forest or road-building edge distances on ant species assemblages in this fragment.

The forest and road-build edge effects show subtle effects on ant diversity, not related to ant species richness and abundance. The general lack of abundance patterns of functional groups along the gradient also reinforces a weak relation of forest or road-build edge effects on ant assemblages in these riparian areas. The well-known strong link between ants and humidity associated with higher and stable moisture found in valleys suggests that moisture may be buffering the pervasive effects of forest and road-building edge effects. Additional experimental studies are needed to elucidate and decouple the possible interactions between moisture and edge effects.

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