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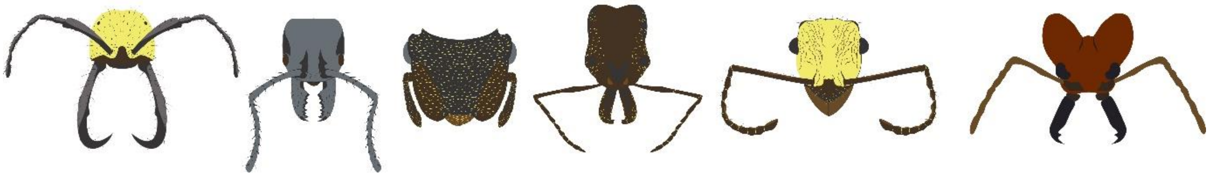
RELAÇÃO ENTRE TRAÇOS FUNCIONAIS DE INSETOS COM CARACTERÍSTICAS DA PAISAGEM. UM DESTAQUE PARA FORMIGAS NA MATA ATLÂNTICA



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Área de concentração: Ecologia e Conservação da Biodiversidade.

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O limite entre o espaço e a Terra é puramente arbitrário. E eu provavelmente sempre estarei interessado nesse planeta – é o meu favorito.

Carl Sagan

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RESUMO

A atividade antrópica gera impactos na comunidade dos insetos de diversas formas. A remoção do habitat original e a modificação na paisagem são um dos principais impulsionadores da extinção do grupo. As respostas das espécies às mudanças no habitat estão ligadas, principalmente, às suas características morfológicas e comportamentais. Dessa forma, é possível reconhecer quais conjuntos de traços morfológicos as tornam mais vulneráveis aos efeitos antrópicos. Nesse contexto, esta tese teve como objetivo entender como a perda de habitat e o efeito de borda estruturam as comunidades de insetos e como atuam na seleção de características funcionais/comportamentais do grupo. No primeiro capítulo, avaliei as respostas de diferentes grupos de insetos e seus traços de história de vida às bordas antropogênicas. Para este este capítulo, realizei uma meta-análise global a partir de buscas de artigos na plataforma Web of Science. Examinei 712 comparações, extraídas de 62 estudos, que avaliaram o efeito de bordas antrópicas sobre insetos. Os resultados demonstram que insetos sociais e que forrageiam pelo solo são afetados negativamente pelas bordas antrópicas. Por outro lado, as espécies que forrageiam pelo ar e espécies invasoras são favorecidas pelas bordas. A partir desses resultados, foquei em investigar, de forma empírica, os efeitos antrópicos em escala de paisagem sobre as assembleias de formigas. Dessa forma, os dois últimos capítulos da tese englobam o estudo de 20 fragmentos florestais imersos em duas regiões que são distintas na intensidade do uso do solo e tipo de matriz circundante. Uma região apresenta maior cobertura florestal, menor isolamento entre fragmentos e menor densidade de borda. Opostamente, a outra região abriga fragmentos com baixa cobertura florestal, maior densidade de borda e matrizes não permeáveis. Ambas regiões estão localizadas na Mata Atlântica do sul do Estado da Bahia, Brasil. Dessa forma, no segundo capítulo, avaliei como a perda de cobertura florestal e densidade de borda podem afetar os traços funcionais e a riqueza taxonômica e funcional das formigas. O objetivo principal foi identificar qual conjunto de características funcionais desse grupo o torna vulnerável à mudanças estruturais na paisagem. Os resultados indicam que formigas com pernas, escapos antenais e clipeus menores são mais sensíveis às mudanças na paisagem. Por outro lado, não detectei a influência dessas modificações na riqueza taxonômica e funcional das formigas. No terceiro capítulo, avaliei como diferenças entre as duas regiões afetam a diversidade beta (β) funcional e taxonômica de formigas. Os resultados demonstram que as duas regiões possuem composição funcional e taxonômica distintas. O escapo antenal e o clipeus foram os traços motores na diferenciação funcional entre as regiões, enquanto que as espécies *Ectatomma permagnum*, *Odontomachus haemadotus* e *Cephalotes atratus* foram responsáveis pela distinção taxonômica. O turnover foi o principal componente na estruturação funcional e taxonômica das assembleias de formigas nas duas regiões. Os fragmentos imersos em matrizes não permeáveis, com baixa cobertura florestal e maior densidade de borda apresentaram maiores taxas de turnover taxonômico. Por fim, esses resultados revelam que existe seleção das características morfológicas dos insetos às mudanças na paisagem. Essa seleção pode ser refletida na organização e na composição funcional das comunidades. Estudos como estes, que identificam quais características morfológicas dos insetos os tornam mais vulneráveis à antropização, são indispensáveis e também diretamente aplicáveis para compreendermos a influência da atividade humana no funcionamento dos ecossistemas.

Palavras-chave: Floretas tropicais, Perda de habitat, Efeito de borda, Formicidae, Diversidade beta

ABSTRACT

Human activity generates impacts on the insect community in several ways. Removal of original habitat and landscape modification is one of the main drivers of extinction of the group. Habitat removal and landscape modification is one of the main drivers of the group's extinction. The responses of species to habitat changes are linked mainly to their morphological and behavioral characteristics. Thus, it is possible to recognize which sets of morphological traits make them more vulnerable to anthropogenic effects. In this context, this thesis aimed to understand how habitat loss and the edge effect structure insect communities and how they act on the selection of functional/behavioral traits of the group. In the first chapter, I evaluated the responses of different insect groups and their life history traits to anthropogenic edges. For this chapter, I conducted a global meta-analysis from searches of articles on the Web of Science platform. I examined 712 comparisons, extracted from 62 studies, that evaluated the effect of anthropogenic edges on insects. The results show that social and ground foraging insects are negatively affected by anthropogenic edges. On the other hand, air foraging and invasive species are favored by edges. From these results, I focused on empirically investigating landscape-scale anthropogenic effects on ant assemblages. Thus, the last two chapters of the thesis encompass the study of 20 forest fragments immersed in two regions that are distinct in land use intensity and type of surrounding matrix. One region has greater forest cover, less isolation between fragments, and lower edge density. Oppositely, the other region is harboring fragments with low forest cover, higher edge density, and non-permeable matrices. Both regions are located in the Atlantic Forest of Southern Bahia State, Brazil. Thus, in the second chapter, I evaluated how loss of forest cover and edge density can affect the functional traits and taxonomic and functional richness of ants. The main objective was to identify which set of functional traits of this group makes it vulnerable to structural changes in the landscape. The results indicate that ants with legs, antennal scapes, and smaller clypeus are more sensitive to changes in the landscape. On the other hand, I did not detect the influence of these changes on the taxonomic and functional richness of ants. In the third chapter, I evaluated how differences between the two regions affect the functional and taxonomic beta (β) diversity of ants. The results show that the two regions have distinct functional and taxonomic composition. The antennal scape and clypeus were the driving traits in functional differentiation between the regions, while the species *Ectatomma permagnum*, *Odontomachus haemadotus*, and *Cephalotes atratus* were responsible for taxonomic distinction. Turnover was the main component in the functional and taxonomic structuring of the ant assemblages in the two regions. The fragments immersed in non-permeable matrices, with low forest cover and higher edge density showed higher rates of taxonomic turnover. Finally, these results reveal that there is selection of morphological characteristics of insects to changes in the landscape. This selection can be reflected in the organization and functional composition of the communities. studies such as these, which identify which morphological characteristics of insects make them more vulnerable to anthropization, are indispensable and also directly applicable for understanding the influence of human activity on ecosystem functioning.

Key-words: Tropical forests, Habitat loss, Edge effect, Formicidae, Functional traits, Beta diversity.

Sumário

INTRODUÇÃO GERAL

A perda de habitat é uma das principais ameaças à biodiversidade. Este processo caracteriza-se pela supressão de áreas do habitat original e seus efeitos têm sido, por muito tempo, o foco central nos debates sobre a ecologia de comunidades e paisagem, com objetivo central de promover a conservação da biodiversidade (Fahrig, 2003; Watling et al., 2020). A diminuição da quantidade do habitat original é capaz de reduzir drasticamente populações e levar à extinção de numerosas espécies nativas. Isso ocorre porque estas espécies, por vezes especialistas de florestas, são cada vez mais susceptíveis à endogamia, tendo sua área de vida reduzida devido ao isolamento das populações decorrendo do processo de perda e fragmentação de sua área de distribuição original (Kerr & Deguise, 2004; Pardini, Nichols, & Püttker, 2017).

As áreas que circundam remanescentes florestais são conhecidas como matrizes e podem ser de origem natural ou antrópica (Berry, Tocher, Gleeson, & Sarre, 2005). A influência dessas áreas de matrizes adjacentes às florestas resulta em uma diferença detectável na função, composição ou estrutura perto da borda, conhecida como efeito de borda (Harper et al., 2005). Este efeito, diretamente relacionado ao aumento das bordas nas florestas através da fragmentação, tem como principais características a diminuição na umidade, aumento da amplitude térmica, mudanças nas interações entre espécies e distribuição local das mesmas (*resource mapping*) (Ries e t al., 2004).

Globalmente existem aproximadamente 5,5 milhões de insetos no mundo (Stork, 2018). Os organismos pertencentes a esta Classe são essenciais para o funcionamento dos ecossistemas (Gullan & Cranston, 2014; New & Samways, 2014) por desempenharem inúmeras funções ecológicas, o que inclui: dispersão de sementes, ciclagem de nutrientes, polinização, regulagem das populações de animais e plantas através da predação ou do parasitismo, e alterações na estrutura física dos ecossistemas com espécies comumente chamadas de engenheiras ambientais (Gullan & Cranston, 2014). No entanto, devido às altas taxas de declínio dos insetos, tais funções estão ameaçadas (Hallmann et al., 2017). A perda de habitat causada pelo desmatamento, conversão das florestas em áreas agrícolas e urbanas como os principais motores na perda global dos insetos (Sánchez-Bayo & Wyckhuys, 2019; Wagner, 2020).

As mudanças causadas pelas ações antrópicas ao exercerem diferentes pressões seletivas podem gerar respostas divergentes dentro de um mesmo grupo taxonômico. Isso sugere que a causa no declínio das espécies está vinculada aos traços similares compartilhados entre os insetos (Caitano et.al, 2020). Os traços de história de vida são características morfológicas ou comportamentais ligadas ao modo como as espécies se relacionam com o meio (Caitano et al., 2020). A integração dessa informação na abordagem de estudos conservacionistas permite preencher lacunas, por exemplo, em uma meta-análise que avaliou o efeito sobre formigas e besouros, a conversão de florestas em plantios de palmeira de óleo (dendezeiro, *Elaeis guineensis* Jacq., Arecaceae) favoreceu espécies de pequeno porte e de níveis tróficos mais baixos, as quais eram menos abundantes em áreas florestais (Senior et al., 2013).

Além das mudanças na seleção de características morfológicas das espécies, a antropização de áreas florestais tem por consequência a composição taxonômica e funcional das comunidades. Comumente as alterações na composição das comunidades são avaliadas a partir da análise de β-diversidade. A β-diversidade pode ser particionada em dois processos: turnover e aninhamento (Baselga, 2010). O turnover é a substituição ou troca de espécies e/ou funções entre dois locais. Por sua vez, o aninhamento é a perda ou ganho de espécies e/ou funções na comparação entre dois ambientes, sendo que, num dado local, ocorre um subconjunto de espécies e/ou de funções do outro. O uso da β-diversidade tem sido cada vez mais explorado para comunidade de insetos (Bishop et. al, 2015; da Silva et al., 2019; Schmidt et al., 2017). No entanto, nosso conhecimento das consequências da perda de habitat e efeito de borda sobre a β-diversidade taxonômica e funcional dos insetos ainda encontra-se bastante fragmentário (Dianzinga, Moutoussamy, Sadeyen, Ravaomanarivo, & Frago, 2020; R. J. Silva, Storck-Tonon, & Vaz-de-Mello, 2016; Stone, Catterall, & Stork, 2018).

Recentemente, Saunders e colaboradores (2020) listaram as linhas prioritárias de estudos para a conservação do grupo. Dentre elas, destaca-se o uso dos traços morfológicos das espécies para compreender o impacto humano nas comunidades de insetos e o estudo da dinâmica da substituição ou de troca de espécies dentro das comunidades e metacomunidades. Dentre os insetos, as formigas se destacam pela sua relevância e representatividade nos ecossistemas. Nas florestas tropicais, estima-se que sua biomassa ultrapassa até quatro vezes a de todos os vertebrados juntos, incluindo mamíferos, anfíbios e répteis (Fittkau & Klinge, 1973; Tuma, Eggleton, & Fayle, 2020). As formigas estão presentes em todos os continentes, exceto Antártica, desempenham numerosas funções em todos os níveis tróficos e são extremamente sensíveis às mudanças ambientais (Gerlach et al., 2013; Hölldobler & Wilson, 1990)

O uso dos traços funcionais de formigas tem se mostrado uma ferramenta útil em biomonitoramento para compreender os gradientes ambientais (Arnan, Cerdá, & Retana, 2014), mudanças no uso da terra (Heuss, Grevé, Schäfer, Busch, & Feldhaar, 2019; Salas-Lopez, Violle, Mallia, & Orivel, 2018; Yates, Andrew, Binns, & Gibb, 2014), efeito do fogo (Arnan, Cerdá, Rodrigo, & Retana, 2013) e acompanhar ou antecipar as mudanças climáticas (Arnan, Arcoverde, Pie, Ribeiro-Neto, & Leal, 2018). O uso do tamanho corporal e posição trófica são os traços de formigas mais utilizados pelos ecólogos. O tamanho corporal, por exemplo é associado à distância de dispersão de sementes (Ness, Bronstein, Andersen, & Holland, 2004) e complexidade do habitat (Kaspari & Weiser, 1999). Com base em variáveis morfológicas, Silva e Brandão (2010) conseguiram fornecer uma lista das guildas de formigas de serapilheira para a Mata Atlântica. Adicionalmente, Parr e colaboradres (2017) elaboraram um data base que reúne mais de vinte características morfológicas de formigas, que estão conectadas com as funções que esses insetos executam e com seu modo de interação com o ambiente. A partir desse compilado de informações é possível gerar hipóteses sobre como mudanças no ambiente podem estruturar assembleias de formigas, bem como as funções desempenhadas por elas.

Diante do cenário exposto, a tese está estruturada em torno de três questões centrais, as quais compõe os três capítulos: i) Quais traços de história de vida comuns compartilhados entre os insetos os tornam mais vulneráveis ao efeito de bordas antrópicas? ii) Como os traços funcionais de formigas respondem à perda de habitat e efeito de bordas em áreas de florestas tropicais? iii) Como diferentes cenários de uso da terra podem afetar a composição funcional e taxonômica de formigas na Mata Atlântica? O primeiro capítulo "*Edge effects on insects depend on life history traits: a global metaanalysis*" foi publicado na revista Journal of Insect Conservation em 2020. O segundo capítulo "*Effects of habitat amount and configuration on ant functional traits in a Neotropical rainforest*" será submetido à revista Functional Ecology. Por fim, o terceiro capítulo "β-Diversidade Taxonômica e funcional de formigas em diferentes cenários de uso da terra. Um exemplo na Hilea Baiana" será submetido à revista Sociobiology.

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CAPÍTULO I

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EDGE EFFECTS ON INSECTS DEPEND ON LIFE HISTORY TRAITS: A GLOBAL META-ANALYSIS

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Abstract

Some species are more affected than others by edge effects resultant from habitat loss and fragmentation, generally due to human activities. As these specific responses depend on biophysical and behavioral traits of organisms, it is expected that the occurrence of species with particular traits will vary between fragment edges and interiors. Edges are also known to often harbor many invasive species. We performed a meta-analysis of the responses of insect species with different life history traits to anthropogenic edges, focusing on the species' behavioral characteristics and whether they are considered invasive or not. We systematically searched the Web of Science database for papers on this subject published until May 2018. We examined response ratios for 712 comparisons of anthropogenic edge effects on insects. As expected, the responses differed according to the traits evaluated. Soil-foraging and social insects were negatively affected by anthropogenic edges. Conversely, flying and invasive species were favored by edges. Our analyses suggest that edges, by differently affecting different insect groups, have an important role in structuring local insect communities. Finally, the importance of functional traits in studies of edge effects must be highlighted.

Keywords: bioindicators; edge influence; invasive species, social insects.

Introduction

Habitat loss and fragmentation are among the main threats to biodiversity worldwide (Laurance et al. 2002; Tabarelli and Gascon 2005; Sánchez-Bayo and Wyckhuys 2019) due to, among other mechanisms, edge effects that occur at the interface between natural and anthropogenic environments (Murcia 1995; Harper et al. 2005). Edge effects, also called edge influence, may be understood as "the effect of processes (both abiotic and biotic) at the edge that result in a detectable difference in composition, structure, or function near the edge, as compared with the ecosystem on either side of the edge" (Harper et al. 2005). They are a much studied phenomenon, with a recent review having detected 674 empirical studies on edge responses (Ries et al. 2017), and have been studied in a variety of terrestrial biomes on different continents and with different organisms (Harper et al. 2005; Ries et al. 2017). Common responses to edge effects include changes in vegetation structure and composition, commonly with an increase in invasive species abundance; increased wind damage; changes in microclimate, with edges often (but not always) being warmer and drier than interior areas; altered species interactions; and changes in the composition of animal species (Murcia 1995; Fagan et al. 1999; Ries et al. 2004; Harper et al. 2005; Laurance and Curran 2008; Arroyo-Rodríguez et al. 2017; Magura et al. 2017).

The mechanisms responsible for such effects may be broadly classified into ecological flows (including energy, materials, organisms, and information), heterogeneous distribution of resources and access to resources located on different sides of the edge, resource mapping (i.e. distribution of organisms according to the distribution of the resources they require), species interactions, and geometric restrictions to the movement of organisms (Cadenasso et al. 2003; Ries et al. 2004; Prevedello et al. 2013).

Species sensitivity to anthropic disturbances is related to their life history traits, such as dispersal capacity (Bommarco et al. 2010), nesting strategy (Martello et al. 2016), body mass (Bovo et al. 2018), diet breadth (Swihart et al. 2002; Batáry et al. 2007), and activity time (Barber et al. 2017). Similarly, edge effects often differ among taxonomic groups (Barbaro and Van Halder 2009; Delgado et al. 2013; Pfeifer et al. 2017). Abiotic and biotic factors can serve as filters for life history traits, enabling predictions on how different species will respond to edges. For example, species that live almost exclusively on the soil may have their dispersal and foraging capacity limited by humidity, amount of litter and temperature (Arbea and Blasco-Zumeta 2001; Silva et al. 2011; Robinson et al. 2018), whereas organisms that forage and/or disperse primarily by air can be affected more heavily by changes in wind direction and speed and air temperature (Burnett and Hays 1974; Vale 1983; Kearney et al. 2010). In addition, as edge gradients in microclimate may differ among the vertical strata in a forest (Didham and Ewers 2014), and so may the gradients in air and soil temperature (Dodonov et al. 2019), organisms that occupy different strata may be affected differently, and this difference may be especially strong when comparing insects with predominantly terrestrial foraging to those that forage by flight.

The same abiotic change can have distinct effects on different species. For instance, in some social bees, the higher the temperature, the greater the colony size and longevity (Holland and Bourke 2015). Conversely, for ants, increased temperature alters the reproductive phenology, limiting mating between populations under different abiotic conditions (Chick et al. 2019). Even so, some ant species appear to be favored by edges (Majer et al. 1997; Siqueira et al. 2017), such is the case of some leafcutter ants (Siqueira et al. 2017), which may be favored by the increased abundance of pioneer plant species at edges with a concomitant decrease in dietary restrictions for these ant species (Falcão et al. 2011). Species responses to edges also vary widely among non-social insects (e.g. Martello et al. 2016). Thus, it is of interest to assess whether edge effects differ among social and non-social insects, or whether the results are mostly idiosyncratic.

Additionally, edges can have a great influence on biological communities by favoring invasive species, considered one of the greatest threats to biodiversity and ecosystem maintenance (Porter and Savignano 1990; Lebrun et al. 2012). Invasive species may have high phenotypic plasticity, easy association with humans, and short reproductive cycles (Sakai et al. 2001), and often have higher abundances at edges (Lustig et al. 2017). When favored by one or more environmental conditions, these species often exclude native species from the system, resulting in drastic changes in their functioning (Porter and Savignano 1990; Heterick et al. 2000). Therefore, although it is not a life trait, evaluating edge effects on invasive species can help us to better understand community changes at edges, for example due to competitive exclusion of non-invasive (either native or introduced) by invasive species.

Insects are terrestrial organisms with an extremely large biogeographic distribution and encompass countless taxa with a variety of life history traits, and thus are excellent models to assess how edges affect species' biophysical and behavioral traits. They are also highly threatened by habitat loss and fragmentation (Sánchez-Bayo and Wyckhuys 2019), in part due to the high susceptibility of this group to edge effects (but see Caitano et al. 2018). One of the mechanisms of edge effects that directly affect insects is linked to the availability and quality of key resources (Ries and Sisk 2004; Ries et al. 2004). For example, some utterfly and bee species are attracted by the complementary features at the edges (Morandin et al. 2007; Ries and Sisk 2008), as well as some herbivores, which benefit from the rapid growth of early successional and pioneering plant species (Tabarelli et al. 2012). However, insect responses can be neutral or even negative if the edge offers supplementary resources or few attractions, respectively (Ries and Sisk 2008). Thus, a better understanding of how insects respond to anthropogenic edges may aid in their conservation.

We investigated which characteristics shared between different insect taxa make them more vulnerable to edge effects. Our initial hypothesis was that groups of insects with different foraging characteristics (flight or ground-dwelling), social organization (eusocial or non-social), and invasiveness (invasive or native) would respond differently to anthropogenic edges (Fig.1). Our assumption was that flying species in general can search for resources at much greater distances and are less impacted by microclimatic changes than species whose foraging is predominantly terrestrial. Therefore, we expected litter-dwelling and ground-dwelling insects to be adversely affected, whereas flying insects respond neutrally or positively to edges. In addition, it is reasonable to think that species living exclusively in colonies need more food resources for their survival. Furthermore, social insects, either flying (social bees and wasps) or walking (ants and termites), usually have a permanent site for nesting and are active throughout the year. Non-social insects do not have these qualities and their occurrence can be casual, seasonal, or limited by time or resources. The expression of edge effects may therefore be dependent of insect sociality. Thus, we expected social insects to be affected negatively by edges (even though some social insects such as leaf-cutting ants, have been shown to be more abundant at edges – Siqueira et al. 2017 -, our hypothesis was that social species in general would be negatively affected). Finally, due to the high adaptive capacity and/or low food selectivity and because of studies showing such patterns for other groups, we expected that invasive insects would be more successful at edges, unlike non-invasive species.

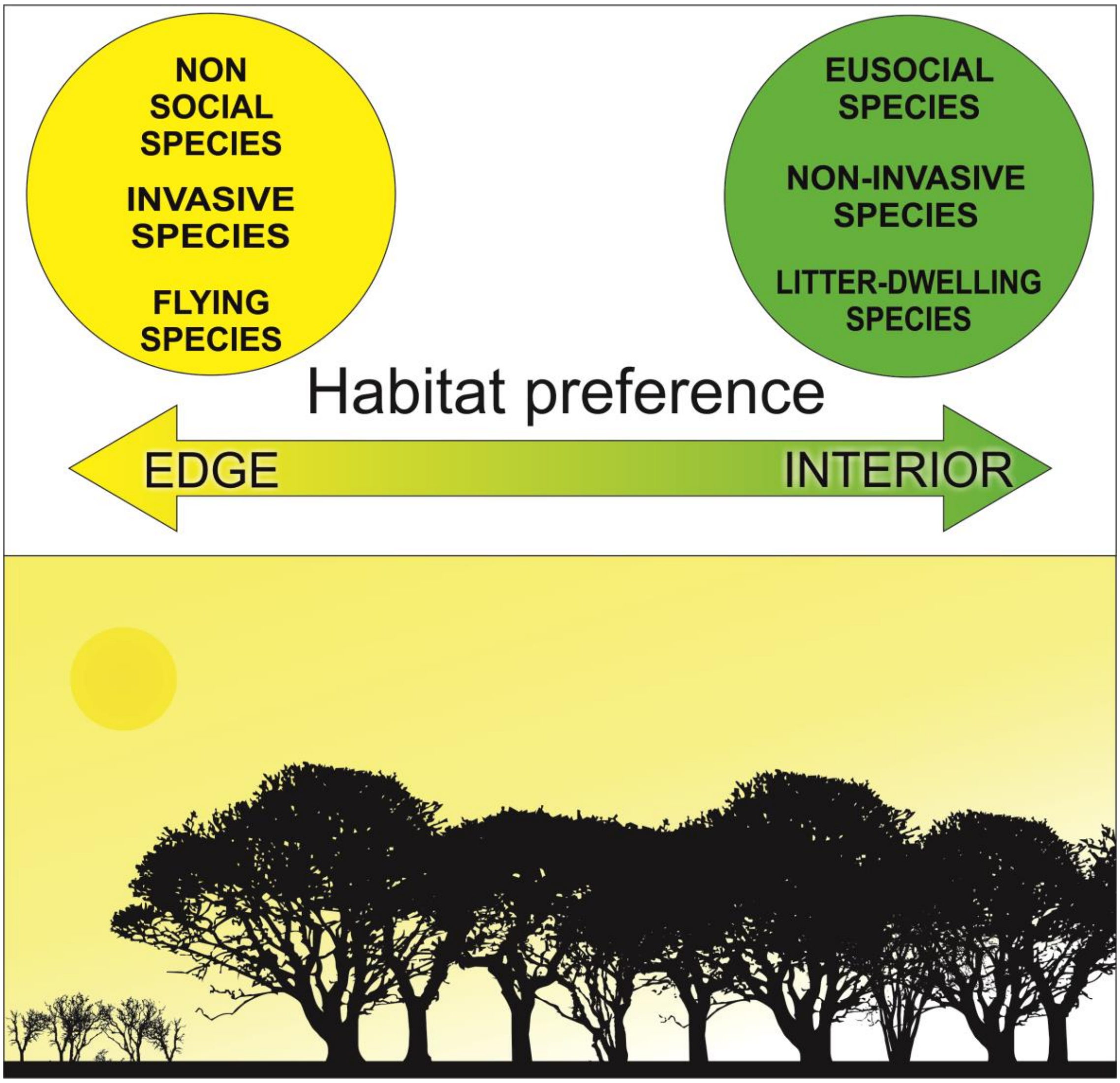

Fig.1. Synthetic view of the hypothesized responses of insects to edge effects according to foraging mode, sociability, and invasiveness.

Material and Methods

Dataset

We conducted a search in the ISI Web of Science database to identify publications on how edge effects affect the insect community. We systematically searched all research articles published until May, 2018, using the queries: Topic: (edge effect*) OR Topic: (edge influence), defined for the areas: Biodiversity Conservation; Ecology; Biology; Entomology; Environmental Sciences; Soil Science; Zoology; Agronomy.

Our selection criteria of these studies were as follows: a) publications in English; b) on insects; c) including replicates for both edge and interior areas; d) presenting data information including mean values and sample size for both treatments (edge and interior); and e) specifically concerning anthropogenic edges. We excluded articles that: a) evaluated only ecological processes, such as seed dispersal or predation; b) on immature insects only; c) studied only natural edges; d) dealed only with aquatic insects; e) assessed only behavior.

Among the papers focusing on insects along edge-interior transects, only data from the innermost points of the “habitat” area were used for comparison with the interior. These points were located 20 to 2000m from the edge. Edge sampling points were those located in the zone between 0-15m, where 0 represents the line of separation between the studied environment and the adjacent matrix. When the data were only available as figures, we retrieved them using the Web Plot Digitilizer software (Rohatgi 2011).

Meta-analytical procedure

When the study simultaneously presented data with error estimates and data without estimation, we prioritized the data with error estimates. As an alternative to perform the meta-analysis without discarding valuable data, we used the response ratio (RR) as an index of effect size (Hedges et al. 1999): $RR = \ln(X_{edge} / X_{\mathrm{reference}})$, where X_{edge} and $X_{reference}$ represent the average richness and abundance value per treatment. Negative RR values indicate negative edge effects on the response variable (i.e. lower values at the edge than in the reference samples), whereas positive RR indicate positive edge effects. A median RR was calculated over all comparisons and a 95% confidence interval (CI) was estimated from 10,000 bootstrap samples (with replacement) (Almeida-Rocha et al. 2017). To translate these values into percentage change, we used the equation $(e^{RR} - 1) \cdot 100$.

Since studies usually presented more than one comparison, we attempted to avoid pseudo-replication by subsampling the dataset by sorting a single comparison per study, creating 10,000 subsampled datasets to generate a median effect size and a 95% CI. We considered the effect to be significant when 95% CI did not include zero. We evaluated how the effects of anthropogenic edges affected the abundance and richness of insects classified according to two life history traits which we expected to be related to fitness at edge areas, namely i) foraging mode(flying or walking) and ii) social behavioral (eusocial or non-social), and also compared between non-invasive and invasive species (as classified by the studies’ authors). We conducted separate analyzes for abundance and richness. We didn’t perfomed analysis for richness regarding invasiveness. We didn’t have enough studies to perform a robust analysis on this aspect.

We used the Trim-and-Fill method to evaluate publication bias from the Hedges'g effect size. This method estimates the number of missing studies and verifies whether there would be a difference in overall effect size outcome if such studies were included in the analysis (Duval and Tweedie 2000). All analyzes were performed in R (R Core Team, 2018). We used the "Metafor" package (Viechtbauer 2010) to perform the meta-analysis with Hedge's effect size and to check for publication bias.

Results

We have previously selected 9,540 articles that complied with the search criteria. Of these, only 474 met the criteria of the second screening process. Finally, 62 studies met our inclusion criteria and were included in the meta-analytical review, with 710 comparisons (Table S1). The most representative categories were non-social, non-invasive organisms that access the resource by walking (Table S2). The results were robust to publication biases (Table S3).

The richness of flying insects was greater at edges than in interior areas (5% increase; 95%CI: 2%-6%), whereas their abundance did not differ between edge and interior areas (7% decrease; CI: 70% decrease to 7% increase). The richness of ground insects was not affected by edges (0% change; CI: 2% decrease to 4% increase), but their abundance was lower at edges (decrease 20%; CI: 6%-30%) (Fig. 2a).

Edge effects also differed greatly between eusocial and non-social insects (Fig. 2b). Eusocial insects had a 10% decrease in their richness and a 22% decrease in their abundance at edges (CI of 10%-10% and 35%-8%, respectively). In turn, the richness of non-social insects increased at edges (6%; CI: 3–7%), whereas their abundance was not affected (0; decrease 9% to 9% increase, Fig. 2b).

Although there were no significant overall edge effect on non-invasive species abundance (19% decrease; CI: 48% decrease to 10% increase, Fig. 2c), there was an increase in invasive species abundance at edges (132%; CI: 123%-143%). All results were robust to publication biases (Table S2).

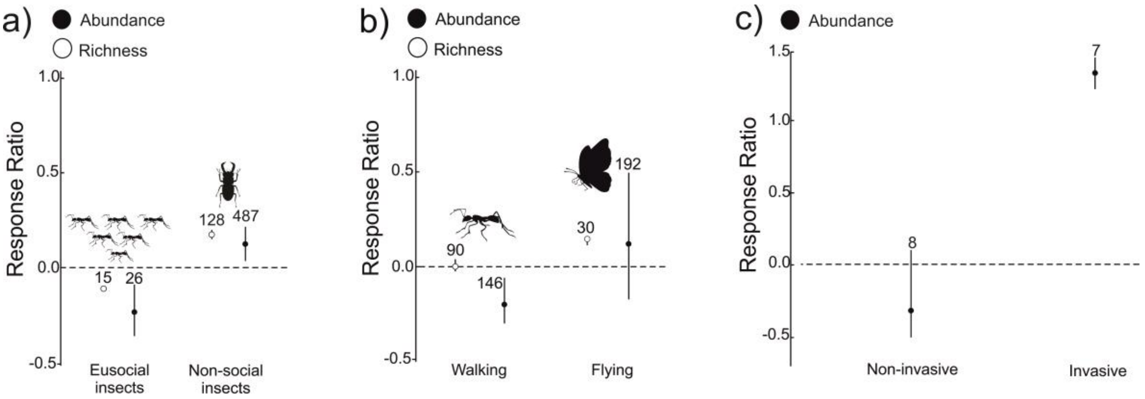

Fig2. Edge effects on the insects a) Foraging mode (by flight or walking), b) social behavioral (eusocial or non-social) and c) invasiveness (invasive or non-invasive). Numbers above the effects indicate the numbers of comparisons evaluated for each effect. Effects are significant if confidence intervals do not overlap with zero.

Discussion

We found significant edge effects on different insect groups, and observed that these effects differ widely among groups with different life history traits. Thus, socials insects and insects foraging primarily on the ground were negatively affected by anthropogenic edges. On the other hand, invasive species and those that forage by flight appear to benefit from edges. These findings are consistent with our hypotheses and highlight the role of edges as ecological filters for insect life history traits.

In general, complementary resources and more movement space may be beneficial for insects that forage by flight (Monkkonen and Mutanen 2003; Stephen and Sánchez 2014). Open areas sometimes serve as reproductive habitats and/or dispersion routes for flying insects (see Haddad and Baum 1999; French and McCauley 2019). The microclimatic changes observed at the edges, the greater facility of locating resources, as well as the availability of habitat for reproduction, may be attractive to numerous species that forage flying (Kuussaari et al. 2007; Gadelha et al. 2015). Usually, flying species have high dispersal capacity and are particularly efficient in locating resources when they are scarce or distant (Jennings and Pocock 2009). Such resource use strategies can be advantageous and more efficient at edge areas.

In contrast, species with predominantly terrestrial foraging have a narrower living area with much more limited dispersion capacity. These characteristics, added to altered environmental conditions at the edge (Murcia 1995; Didham and Lawton 1999; Harper et al. 2005), can make these species more susceptible and explain the negative response of this group of insects to anthropogenic edges. Edge effects on temperature vary among the different vertical strata of a forest, and the temperatures experienced by the soil fauna are different from those experienced by the canopy organisms (Didham and Ewers 2014). Groups of organisms that spend much of their life in the soil or litter may thus be strongly affected by microclimatic gradients (Foley et al. 2008; Pinheiro et al. 2010). Edge areas commonly suffer increased exposure to solar radiation, higher temperatures and lower humidity than the forest interior (Dodonov et al. 2013; Arroyo-Rodríguez et al. 2017), which in turn can compromise the physiology and foraging activity of several species. For example, some termites have their distribution affected by soil temperature, which results in variations in the occurrence of this group at different landscape scales (Davies et al. 2003; Palin et al. 2011). This limitation in relation to temperature can be one of the factors responsible for the low number of records of these among other species at edges.

Social insects showed a preference for interior habitats, which was not observed for non-social species. This is in contrast with studies observing greater leaf-cutting ant abundance at edges (e.g. Siqueira et al. 2017). Although a colony structure is more efficient for resource searching and defense, its maintenance obviously requires larger and/or more constantly provisioned amounts of food (Wilson 1971, 1975). In addition to this competition for food resources, there is also a demand for favorable places for colony foundation (Winfree et al. 2009), which has direct implications on the perpetuation of the species (Banschbach et al. 2012). All these factors can be intensified by the proximity between nests, as the same types of resources are used simultaneously. In addition, social insects usually have a permanent nesting site and are active all year round, which can become a downside when under strong environmental disturbance. In this way, edge environments, as previously mentioned, would be strongly stressful and unattractive due to larger abiotic variations capable of affecting the health of the colonies, as well as due to a lack of resources which would be found in interior areas. On the other hand, species of non-social bees may prefer edge habitats since they are less affected by the environmental filters found and usually build their nests in open areas or hollow structures (such as logs) (Michener 2000; Morandin et al. 2007), common and easier to find in edge environments (Franklin et al. 2015).

However, reporting of eusocial insects on anthropogenic edges is rather common (Ramos and Santos 2006; Wirth et al. 2007; Barrera et al. 2015). In addition, some groups are thought to be strongly associated with edges. For example, the honey bee *Apis melifera* is commonly found at anthropogenic edges (Aizen and Feinsinger 1994; Morales and Aizen 2002) because of its ability to nest on a wide variety of conditions and its foraging contemplates great diversity both native and alien flowers (Villanueva-G and Roubik 2004). However, other numerous species of social bees avoid edge areas (Ramos and Santos 2006). In addition, leaf-cutting ants are considered almost unanimously benefited by the perturbation provoked by anthropogenic areas (Meyer et al.

2009; Siqueira et al. 2017). However, despite being a group well recognized for its economic importance and for the maintenance of ecosystems, it corresponds to only approximately 0.05% of ant species (AntWeb 2020). From our findings, the general pattern is that social insects are negatively affected, and that species that have higher frequency at the edges are actually the exception to the rule.

As indicated in our study, invasive insect species are highly favored by edges. This is probably due to this group's ability to tolerate a great range of variation in several environmental factors such as temperature, humidity, and luminosity, which are important environmental filters near edges (Murcia 1995), and thus make extensive use of the available resources (Parker et al. 1999). Additionally, the lack of natural predators favors the establishment and population growth of these species (Fox and Fox 1986; Petren and Case 1996). Thus, the consistent increase in invasive species is alarming. Several studies have shown that, in the vast majority of environments, the most common observations are the expulsion or population decline of native species by competition with invasive ones (Huenneke and Thomson 1995; Hingston and McQuillan 1999; Hoffmann et al. 1999). For example, in different areas where Argentine ants (*Linepithema humile*) were introduced, the native ant community was initially strongly altered (Human et al. 1998; Suarez et al. 1998).

In conclusion, the results of our meta-analysis suggest that edge effects on insect can be partially predicted from a small set of life history traits. We have seen that insects that forage on the ground and social insects are more vulnerable to edge effects, which indicates that termites and ants are more susceptible to threats than other groups. Finally, we encourage future research to go beyond simple presence-absence of different species, but to also focus on the species' life history traits, such as foraging habits, reproduction mode, biogeography, mobility and social structure, which may modulate their responses to anthropogenic edges. This approach can also help to predict the changes induced by edge formation to the system functioning and suggest more sensitive insect groups whose life history traits indicate them to be of greater conservation concern.

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Compliance with ethical standards Conflict of interest

The authors declare that they have no conflict of interest.

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SUPPLEMENTARY MATERIAL

EDGE INFLUENCE ON INSECTS DEPEND ON LIFE HISTORY TRAITS: A GLOBAL META-ANALYSIS

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S1. Publications used in the meta-analysis.

Title	**Periodic**	**Study**
Do leaf-cutting ants benefit from forest fragmentation? Insights from community and species-specific responses in a fragmented dry forest	Insect Conservation and Diversity	Barrera et al. 2015
Species-specific distribution of two sympatric Maculinea butterflies across different meadow edges	Journal of Insect Conservation	Batáry et al. 2009
Spatial and temporal variation in the Argentine ant edge effect: Implications for the mechanism of edge limitation	Biological Conservation	Bolger 2007
Remarkable fly (Diptera) diversity in a patch of	Zootaxa	Borkent et al. 2018

Costa Rican cloud forest: Why inventory is a vital science		
Distance from Edge Determines Fruit-Feeding Butterfly Community Diversity in Afrotropical Forest Fragments	Community and Ecosystem Ecology	Bossart and Opuni-Frimpong 2009
Cerrado ground-dwelling ants (Hymenoptera: Formicidae) as indicators of edge effects	Zoologia	Brandão et al. 2011
Responses of wasp communities to urbanization: effects on community resilience and species diversity	Journal of Insect Conservation	Christie and Hochuli 2009
Cavity-nesting bees and wasps (Hymenoptera: Aculeata) in a semi-deciduous Atlantic forest fragment immersed in a matrix of agricultural land	Journal of Insect Conservation	da Rocha-Filho et al. 2017
Effects of habitat fragmentation on carabid beetles: experimental evidence	Journal of Animal Ecology	Davis and Margules 1998
The impact of coffee and pasture agriculture on predatory and omnivorous leaf-litter ants	Journal of Insect Science	Dias et al. 2012
The effect of the landscape matrix on the distribution of dung and carrion beetles in a fragmented tropical rain forest	Journal of Insect Science	Díaz et al. 2010
Effects of Habitat Type and Trap Placement on Captures of Bark (Coleoptera: Scolytidae) and Longhorned (Coleoptera: Cerambycidae) Beetles in Semiochemical-Baited Traps	Journal of Economic Entomology	Dodds 2011
The impact of logging roads on dung beetle assemblages in a tropical rainforest reserve	Biological Conservation	Edwards et al. 2017
Dung and carrion beetles in tropical rain forest fragments and agricultural habitats at Los Tuxtlas, Mexico	Journal of Tropical Ecology	Estrada et al. 1998
Fruit-feeding butterflies in edge-dominated habitats: community structure, species persistence and cascade effect	Journal of Insect Conservation	Filgueiras et al. 2016a
Spatial replacement of dung beetles in edge-affected habitats: biotic homogenization or	Diversity and	Filgueiras et al. 2016b

divergence in fragmented tropical forest landscapes?	Distributions	
Butterfly distribution in fragmented landscapes containing agroforestry practices in Southeastern Brazil	Agroforestry Systems	Francesconi et al. 2013
Edge effects on the blowfly fauna (Diptera, Calliphoridae) of the Tijuca National Park, Rio de Janeiro, Brazil	Brazilian Journal of Biology	Gadelha et al. 2015a
Mesembrinellinae (Diptera: Calliphoridae) to edge effects in the Tingua Biological Reserve, Rio de Janeiro, Brazil	Brazilian Journal of Biology	Gadelha et al. 2015b
Functioning of ecotones - spiders and ants of edges between native and non-native forest plantations	Polish Journal of Ecology	Gallè et al. 2014
Beetle species' responses suggest that microclimate mediates fragmentation effects in tropical Australian rainforest	Austral Ecology	Grimbacher et al. 2006
Detecting the effects of environmental change above the species level with beetles in a fragmented tropical rainforest landscape	Ecological Entomology	Grimbacher et al. 2008
Mosquito Communities and Avian Malaria Prevalence in Silvereyes (Zosterops lateralis) Within Forest Edge and Interior Habitats in a New Zealand Regional Park	Ecohealth	Gudex-Cross et al. 2015
An experimental test of corridor effects on butterfly densities	Ecological Applications	Haddad and Baum 1999
Carabid beetles in fragments of coniferous forest	Annales Zoologici Fennici	Halme and Niemelä 1993
Distribution of carabid beetles (Coleoptera, Carabidae) across a boreal forest-clearcut ecotone	Conservation Biology	Heliola et al. 2001
Population density, sex ratio, body size and fluctuating asymmetry of Ceroglossus chilensis (Carabidae) in the fragmented Maulino forest and surrounding pine plantations	Acta Oecologica-International Journal of Ecology	Henríquez et al. 2009

The habitat-specific effects of highway proximity on ground-dwelling arthropods: Implications for biodiversity conservation	Biological Conservation	Knapp et al. 2013
Ground beetle responses to patch retention harvesting in high elevation forests of British Columbia	Ecography	Lemieux and Lindgren 2004
The effects of urbanization on ant assemblages (Hymenoptera : Formicidae) associated with the Molson Nature Reserve, Quebec	Canadian Entomologist	Lessard and Christopher 2005
Spillover of arthropods from cropland to protected calcareous grassland - the neighbouring habitat matters	Agriculture Ecosystems & Environment	Madeira et al. 2016
Ant litter fauna of forest, forest edges and adjacent grassland in the Atlantic rain forest region of Bahia, Brazil	Insectes Sociaux	Majer et al. 1997
The effect of habitat configuration on arboreal insects in fragmented woodlands of south-eastern Australia	Biological Conservation	Major et al. 2003
Forest edge and carabid diversity in a Carpathian beech forest	Community Ecology	Máthé 2006
Habitat preferences of the invasive harlequin ladybeetle Harmonia axyridis (Coleoptera: Coccinellidae) in the Western Cape Province, South Africa	African Entomology	Mukwevho et al. 2017
Beetle's responses to edges in fragmented landscapes are driven by adjacent farmland use, season and cross-habitat movement	Landscape Ecology	Ng et al. 2017
The influence of abrupt forest edges on praying mantid populations	Insect Conservation and Diversity	O'Hanlon and Holwell 2011
The challenge of maintaining Atlantic forest biodiversity: A multi-taxa conservation assessment of specialist and generalist species in an agro-forestry mosaic in southern Bahia	Biological Conservation	Pardini et al. 2009

Habitat characteristics shaping ant species assemblages in a mixed deciduous forest in Eastern India	Journal of Tropical Ecology	Parui et al. 2015
Profiling crop pollinators: life history traits predict habitat use and crop visitation by Mediterranean wild bees	Ecological Applications	Pisanty and Mandelik 2017
Environmental Determinants on the Assemblage Structure of Drosophilidae Flies in a Temperate-Subtropical Region	Neotropical Entomology	Poppe et al. 2015
Floral visitors and pollination of Psychotria tenuinervis (Rubiaceae): Distance from the anthropogenic and natural edges of an Atlantic forest fragment	Biotropica	Ramos and Santos 2006
Roadside habitats: effects on diversity and composition of plant, arthropod, and small mammal communities	Biodiversity And Conservation	Rotholz and Mandelik 2013
Landscape parameters explain the distribution and abundance of Episyrphus balteatus (Diptera : Syrphidae)	European Journal of Entomology	Sarthou et al. 2005
Abrupt species loss of the Amazonian dung beetle in pastures adjacent to species-rich forests	Journal of Insect Conservation	Silva et al. 2017
Oil pipeline corridor through an intact forest alters ground beetle (Coleoptera : Carabidae) assemblages in southeastern Ohio	Environmental Entomology	Silverman et al. 2008
Edge and shape effects on ant (Hymenoptera : Formicidae) species richness and composition in forest fragments	Biodiversity and Conservation	Sobrinho and Schoereder 2007
Patch size determines the strength of edge effects on carabid beetle assemblages in urban remnant forests	Journal of Insect Conservation	Soga and Koike 2013
Interactive effects of habitat fragmentation and microclimate on trap-nesting Hymenoptera and their trophic interactions in small secondary rainforest remnants	Biodiversity and Conservation	Stangler et al. 2015

Interactive effects of habitat fragmentation and microclimate on trap-nesting Hymenoptera and their trophic interactions in small secondary rainforest remnants	Biodiversity and Conservation	Stangler et al. 2015
Effects of landscape disturbance on mosquito community composition in tropical Australia	Journal of Vector Ecology	Steiger et al. 2012
Species richness and relative species abundance of Nymphalidae (Lepidoptera) in three forests with different perturbations in the North-Central Caribbean of Costa Rica	Revista de Biologia Tropical	Stephen and Sánchez 2014
Effects of fragmentation and invasion on native ant communities in coastal southern California	Ecology	Suarez et al. 1998
Arthropod assemblages deep in natural forests show different responses to surrounding land use	Biodiversity and Conservation	Swart et al. 2017
High cover of forest increases the abundance of most grassland butterflies in boreal farmland	Insect Conservation and Diversity	Toivonen et al. 2017
The response of ground beetles (Coleoptera : Carabidae) to selection cutting in a South Carolina bottomland hardwood forest	Biodiversity and Conservation	Ulyshen et al. 2006
Patterns of arthropod abundance, vegetation, and microclimate at boreal forest edge and interior in two landscapes: Implications for forest birds	Ecoscience	Van Wilgenburg et al. 2001
Edge effects on dung beetle assemblages in an Andean mosaic of forest and coffee plantations	Biotropica	Villada-Bedoya et al. 2016
Use of remnant boreal forest habitats by saproxylic beetle assemblages in even-aged managed landscapes	Biological Conservation	Webb et al. 2008
Distribution of Carabid Beetles (Coleoptera: Carabidae) Across a Forest-Grassland Ecotone in Southwestern China	Environmental Entomology	Yu et al. 2007
Distribution of Carabid Beetles (Coleoptera: Carabidae) Across Ecotones Between Regenerating and Mature Forests in Southwestern China	Environmental Entomology	Yu et al. 2009

Distribution of ground-dwelling beetle assemblages (Coleoptera) across ecotones between natural oak forests and mature pine plantations in North China	Journal of Insect Conservation	Yu et al. 2010

S2. Numbers of studies and observations for each subgroup.

	Number of studies	**N° of Observations**
Social behavioral (eusocial)	13	44
Social behavioral (non-social)	50	615
Foraging mode (walking)	32	239
Foraging mode (flying)	20	222
Non-invasive	4	10
Invasive species	4	7

S3. Analysis of Bias using Hedges' G with publications that reported means and dispersion measures.

	Estimate	**Confidence Interval**	**Number of studies**	**N° of Observation**	**Z value**	**P_Value**	**Trim Fill**	**Estimate Trim-Fill**	**Confidence Interval Trim-Fill**
Anthropogenic Edges	-0.07	-0.55 0.41	46	265	-0.1430	0.76	0-12 missing studies	-0.02	-0.68 1.64
Social behavioral (eusocial or non-social)	-0.07	-0.35 0.20	46	263	-0.52	0.6	0 – 12 missing studies	-0.02	-0.68 1.6
Foraging mode (flying or walking)	-0.62	-1.12 -0.12	37	131	-2.46	0.01	0 – 10 missing studies	-0.15	-1.1 1.7
Non-invasive and invasive species	-0.99	-2.97 0.97	4	11	-0.99	0.32	0 – 10 missing studies	0.18	-3.74 3.2

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CAPÍTULO II

EFFECTS OF HABITAT AMOUNT AND CONFIGURATION ON ANT FUNCTIONAL TRAITS IN A NEOTROPICAL RAIN FOREST

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Authors' contributions

BC, IM, DF, PD and JD conceived the ideas; IM and DF designed methodology; IM collected the data; BC and PD analysed the data; BC led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Data availability statement

Effects of habitat amount and configuration on ant functional traits in a Neotropical rain forest

Abstract

1. Habitat loss and fragmentation are synergetic drivers reshaping and threatening the alive biodiversity. Although several studies have evaluated the effects of habitat loss and fragmentation on species diversity, the understanding of how functional traits are linked to these responses are a recent approach. This applies mainly to the assessment of how species diversity and their morphological characteristics directly associated with their ecological functions are influenced by anthropic processes.

2. Ants are fundamental components of different ecosystems, especially in tropical forests where they are dominant. However, the relationship between landscape structure, i.e., composition and configuration, and ant functional traits is still poorly documented in tropical rainforests. We analyze how different dimensions of species diversity - taxonomic and functional richness - and functional traits of ants respond to forest cover loss and the increasing in edge density in 20 forest sites located within anthropogenic landscapes in the Brazilian Atlantic Forest.

4. Taxonomic and functional richness were not affected by neither forest amount nor landscape configuration. However, we found a strong relationship between functional traits and both predictors. Specifically, ants in forest fragments immersed within landscapes with higher edge density showed species with legs, antennal scape and clypeus larger than species with small edge. In addition, forest amount and the overall context the anthropic occupation of the landscapes jointly affected ant species with larger mandibles.

5. Altogether, our study identified a set of morphological traits correlated with the higher vulnerability of ant species to changes in landscape structure; Information on the variation in ant morphological trait is necessary and applicable to fully understand anthropogenic effects on ant assemblages over large scales. We have seen that species with smaller clypeus, femur and antennal scape are more susceptible to edge effects. Identifying which key sets of species' characteristics make them more susceptible to the impacts of habitat loss and edge effects will help to set more precise conservation goals for vulnerable ecosystems such as tropical rainforests.

Keywords: Edge effects, Formicidae, fragmentation, habitat loss.

Introduction

The conversion of tropical rainforests into areas for agriculture, pasture, and urbanization has drastically reduced the amount of habitat for native species (Laurance, 2007; Laurance, Sayer, & Cassman, 2014; Morante-filho, Benchimol, & Faria, 2020). Thus, as continuous forests are reduced, becoming more fragmented and isolated, these profound changes in landscape composition and configuration – triggering can accelerate the process of species extinction (Fletcher, Jr. et al., 2018; Morante-filho et al., 2020; Püttker et al., 2020). Indeed, according to the habitat amount hypothesis (HAH), species richness can be predicted exclusively by the amount of habitat remaining in the landscape (Fahrig, 2013). However, other landscape features, such as the configuration or spatial arrangement of forest remnants, must be considered when dealing from the perspective of conservation effort (Hanski, 2015). For example, in human-modified landscapes, forest remnants are increasingly surrounded by matrices of non-forest vegetation (Lindell et al., 2007; Turner, 1996). The effect of the adjacent matrix results in a detectable difference in function, composition, or structure near the forest edge, known as the edge effect or edge influence (Harper et al., 2005).

Edge effects can lead to serious impacts on species diversity and composition, ultimately affecting ecosystem functioning. (Murcia, 1995). This can occur due to changes in abiotic conditions, such as increased air circulation and wider temperature ranges, greater solar incidence and lower humidity (Murcia, 1995), as well as changes in ecological flows such as energy, organisms and matter (Ries, Fletcher, Jr., Battin, & Sisk, 2004). These changes can act as environmental filters leading to a decrease in species richness and functionally, ultimately homogenizing biological communities (Thier & Wesenberg, 2016). Thus, understanding how habitat loss and edge effects affect biodiversity is one of the most challenging issues in conservation ecology.

While community responses to habitat loss and fragmentation have been assessed primarily through species richness and abundance, another recent approach that has been widely used is to assess the morphological traits of organisms that are related to certain functions of these species in the systems (Cianciaruso, Silva, & Batalha, 2009). The functional trait-based approach can add information not captured by other diversity metrics, such as purely taxonomic ones, helping us to better understand how species reassembling occurs and which characteristics make them more sensitive in different landscape contexts (Mouchet, Villéger, Mason, & Mouillot, 2010). Recent studies show that structural changes in the landscape can act as important environmental filters, selecting certain functional characteristics in the remaining assemblages. For example, species attributes such as body size, diet type, and dispersal ability are commonly related to greater sensitivity to forest loss and fragmentation (Cleary et al., 2007; Kotze & O'Hara, 2003; Rainio & Niemela, 2003). Specifically, a recent review indicated that the response of insects to edge effects varies according to some life history traits, with species that move on the ground surface and social species being especially vulnerable (Caitano, Chaves, Dodonov, & Delabie, 2020).

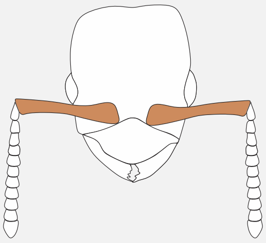
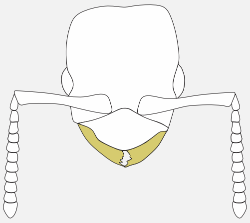
Among the social insects, ants represent a significant part of the total biomass of species present in tropical forests, adding is a group very related to environmental changes (Fittkau & Klinge, 1973). Ants also play crucial roles in maintaining ecosystems by a series of functioning, such as dispersing seeds and contributing to soil cycling and aeration (Del Toro, Ribbons, & Pelini, 2012). The use of ant functional traits has proven a valuable tool to assess the underlying mechanisms that influence management and land use changes (Hevia, Ortega, Azcárate, López, & González, 2019; Martello et al., 2018; Salas-Lopez, Violle, Mallia, & Orivel, 2018; Yates, Andrew, Binns, & Gibb, 2014), the effect of fire regimes (Arnan, Cerdá, & Rodrigo, 2020), and environmental complexity (Fichaux et al., 2019; Guilherme et al., 2019) and climatic factors (Arnan, Cerdá, & Retana, 2014; Fichaux et al., 2020). In this context, several hypotheses have been formulated to link ant morphological traits with environmental characteristics, including changes in landscape structure. For instance, ants with longer legs move faster and have a larger foraging areas, allowing these species to resist in more disturbed, deforested and fragmented landscapes, althgough this trait restrict their use of some types of shelters and foraging niches (Kaspari & Weiser, 1999). In addition, ants with longer legs can resist high temperatures longer due to the convection movement of the air while walking (Hurlbert, Ballantyne IV, & Powell, 2008; Sommer & Wehner, 2012). Another trait often related to environmental characteristics is the antennal scape, one of the segments of the antenna. The size of the scape strongly defines the capacity of the chemical-sensory and tactile perceptions of a chemically-oriented species (Weiser & Kaspari, 2006; Yates et al., 2014). Ants with proportionally larger antennal scape are often associated with more complex environments and therefore with higher demands on their sensory perception capacity (Fichaux et al., 2019; Nooten, Schultheiss, Rowe, Facey, & Cook, 2019; Yates et al., 2014).

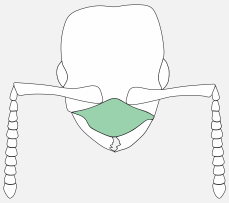
In addition to filtering species according to their locomotion mode and sensory perception, changes in the landscape structure, which lead to changes in the quality and composition of the remaining habitats, can select species based on how they acquire resources. For example, ants with proportionally larger mandibles are associated with habitats with greater resource availability (Fowler, Forti, Brandão, Delabie, & Vasconcelos, 1991). Environments with a greater quantity and variety of potential prey items can increase the probability of survival of predator species at these sites (Campiolo, Rosário, Strenzel, Feitosa, & Delabie, 2015). Also, species that feed on extrafloral nectaries and on the sugary secretion of hemiptera, have longer clypeus (structures related to obtaining liquid resources) (Davidson, Cook, & Snelling, 2004). Here we focus on these four functional traits, which, among the numerous functional attributes of ants, are the ones most directly related to locomotion, sensory capacity and resource acquisition mode.

We assessed how changes in landscape composition and configuration, specifically how the loss of forest cover and the increasing's in edge density (i.e. the quantity of edges between forest and non-forest in the landscape) in human-modified landscapes affect ant diversity and functional traits. We predicted that 1) forest cover would be positively correlated with mean mandible size, as well as with functional and taxonomic richness, and 2) landscapes with higher edge density would harbor ant species with larger clypeus, antennae, and legs, and assemblages with lower functional and taxonomic richness. These expectations are detailed explained in Table 1. Our primary goal was to identify which set of ant functional characteristics make them vulnerable to structural changes in human-modified landscapes.

Table 1. Hypothesis summary. The table shows the hypothesis and the expected signs for each response variable.

VARIABLES	FOREST COVER	EDGE DENSITY	EXPLANATION
Taxonomic Richness	↑	↓	Taxonomic richness of ants is commonly associated with environmental complexity and heterogeneity. Sites with a greater variety of habitats provide shelter and food resources for a greater number of species (Ribas, Schoereder, Pic, & Soares, 2003). Thus, landscapes with greater forest cover may have higher ant species richness. On the other hand, remnants that are immersed in non-forest matrices, with high susceptibility to edge effects and fluctuations in abiotic conditions, may favor the entry and permanence of opportunistic ant species (Berman, Andersen, & Ibanez, 2013).
Functional Richness	↑	↓	Environments with more available niches can harbor species with different functions in the systems (Mason, Mouillot, Lee, & Wilson, 2005). Thus, we predict that landscapes with more forest habitats have a greater diversity of microhabitats and favor the occurrence of species with different habitat requirements, which is a factor that provides greater functional

			richness. On the other hand, ant assemblages in landscapes with higher edge density may be functionally homogenized due to environmental filters promoted by changes in abiotic conditions and alterations in biotic interactions (Thier & Wesenberg, 2016).
Antennal Scape 	↓	↑	Ants depend on chemical markers (e.g. pheromones, kairomones) for communication, foraging, and orientation. The size of the scape, therefore, is related to the capacity for chemo-sensory and tactile perceptions of a given species (Weiser & Kaspari, 2006). We expect that in landscapes with higher structural complexity, ants with small antennal scape are more sensory limited, thus reducing, for example, their foraging ability. In more deforested landscapes, forests tend to be less complex: smaller trees and a more open canopy (Rocha-Santos et al., 2016). Thus, in environments more exposed to the edge and with less forest cover, the ants will present longer antennal scape due to the arrangement of elements found on the surface in these areas. Thus, we expect a shorter relative length of the antennal scape in environments with lower edge density and less forest cover.
Mandible 	↑	↓	Predatory species, on average, have larger mandibles (Fowler et al., 1991). Sites in landscapes with greater forest cover and low anthropogenic disturbance may harbor a greater quantity and variety of potential prey, making them more attractive environments for predatory ants (Campiolo et al., 2015; Leal, Filgueiras, Gomes, Iannuzzi, & Andersen, 2012b), which increases the probability of survival of predatory species in these sites. We expect that ants in areas with more forest cover and lower edge densities will exhibit larger mandible sizes.
Femur	↓	↑	Ants with longer legs are tolerant to higher temperatures due to the convection movement

			of air on the ground surface during walking (Sommer & Wehner, 2012). Species more exposed to insolation need to avoid overheating. In turn, ants with smaller legs are more sensitive to higher temperatures and therefore tend to forage near the nest or in more humid locations (Kaspari, 1993). So, we expect that in areas with less forest cover and higher edge density, ants have larger legs on average.
Clypeus 	⇩	⇧	The clypeus is a morphological structure associated with the use of liquid resources by species. In general, species that feed on extrafloral nectaries and on the sugar secretion of hemiptera, have longer clypeus (Davidson et al., 2004). Forest fragments embedded in more deforested landscapes tend to have higher edge representation and a higher proportion of pioneer plants, which invest more in nectaries in these environments (Blüthgen N. & Reifenrath 2003, Bentley, 1976). So we expect that landscapes with higher edge density and less forest cover will harbor species with larger clypeus.

Methods

Study Area

We sampled ants between April 2017 and May 2018 in twenty Atlantic forest remnants in southern Bahia, Northeastern Brazil (Figure 1). These areas have similar soil types, floristic composition, and topography (Benchimol et al., 2017). The average annual temperature is 24°C and the annual rainfall average is 2000 mm/yr (Thomas, De Carvalho, Amorim, Garrison, & Arbeláez, 1998). According to the Köppen classification, the climate is hot and humid without a dry season.

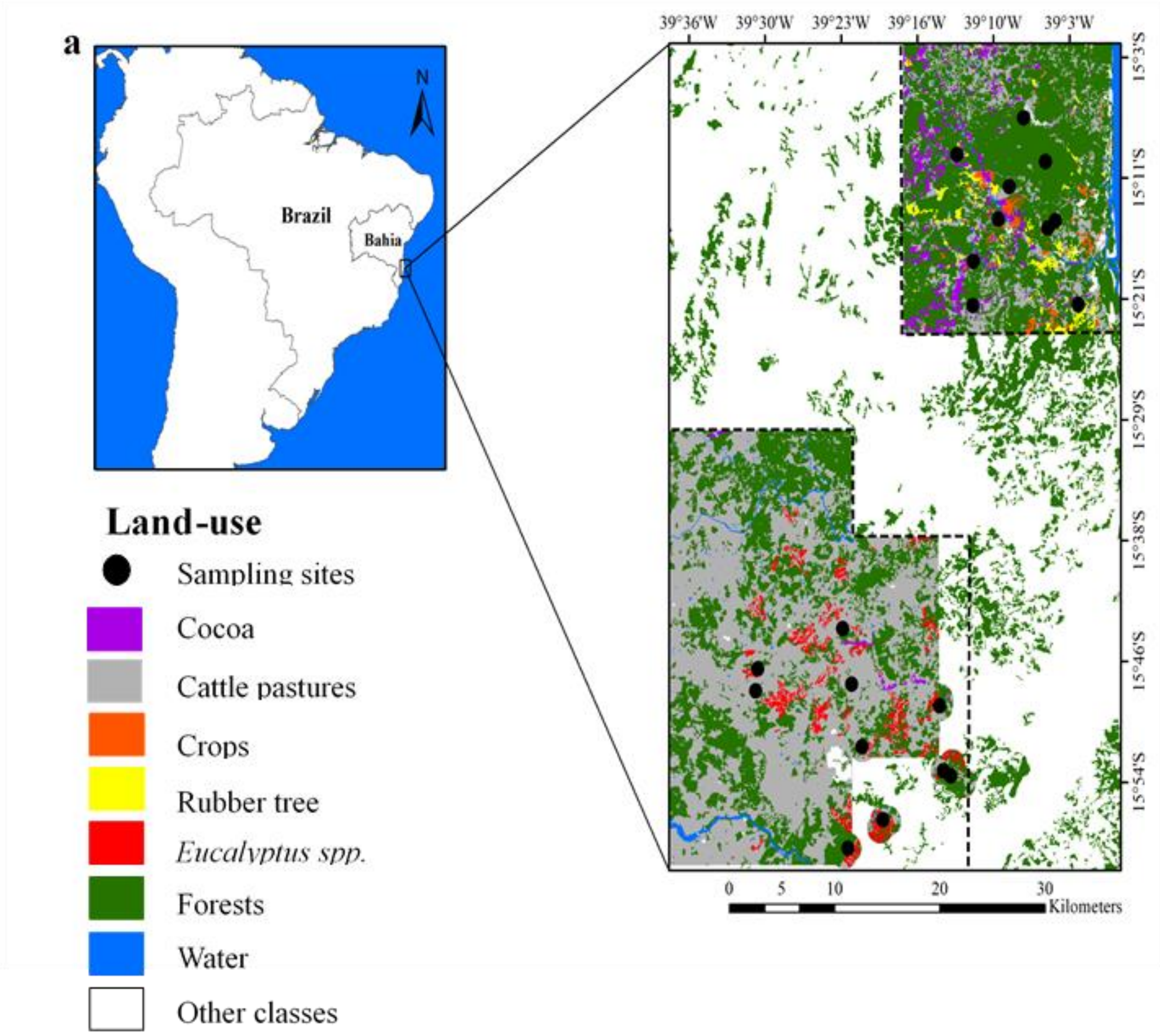


Fig1. Sampled forest sites (black points) in the southeastern Bahia State, Brazil. Location of the 20 sampling sites and land cover classification used for the calculation of landscape descriptors.

We selected twenty landscapes covering a forest cover gradient from 2.5 to 100% (Figure 1) according to the patch-landscape approach (Tischendorf & Fahrig, 2000). All landscapes were mapped for land use using satellite images (RapidEye 2009-2010, QuickBird e World View from 2011). Among the twenty landscapes in our study, ten are less isolated and surrounded by low-contrast matrices, including: agroforestry systems (corresponding to 22% of the matrix landscape) and rubber trees (10%) (Morante-Filho, Arroyo-Rodriguez, & Faria, 2016); these landscapes are found in the northernmost part of the study region, and have been categorized as high forest cover (HFC, hereafter). The other ten remaining fragments, located in the southern part of the studied region, are immersed in high-contrast matrices, mainly pastures (86% of the matrix) and eucalypt (7%) (Morante-Filho et al., 2016), thus more isolated from each other, and have been classified as a region of low forest cover (LFC, hereafter). We considered as forest cover the set of secondary and mature native forests, but excluded plantations and agroforestry systems. We used FRAGSTATS 4.2 software (McGarigal & Marks, 1995) to estimate forest cover and edge density, with buffers from 100m to 1000m (with 100m increments).

Ant Sampling

We sampled ants on shrubs using the "branch-clipping" technique, a method that consists of pruning branches of plants wrapped in plastic collection bags (40 x 60 cm) to capture invertebrates that are in the foliage (Cooper & Whitmore, 1990). For the application of the method, five (5) transects of 25 m each were allocated in each sampling site, at a minimum distance of 25 m from each other (Fig2). In each transect, we randomly selected five (5) plants in the forest understory with height between 50 and 200 cm (Manhães & Dias, 2011), totaling 25 plants sampled per sampling site. The capture of leaf litter and ground-dwelling ants was carried out using pitfalls. The pitfalls were systematically distributed along the transects at a minimum distance of 10 m between one trap and another, three pitfalls per transect, totaling 15 traps per sampling site. The pitfalls were set for a total period of 68hrs. All ants collected were fixed in 90% alcohol and taken to the Myrmecology Laboratory of the Cacao Research Center (Centro de Pesquisas do Cacau – CEPEC; Ilhéus, BA, Brazil) for identification. All ants were identified whenever possible to the species level; nomenclature follows (Bolton, 2003, 2016). Vouchers are deposited in the Collection of the CEPEC Myrmecology Laboratory.

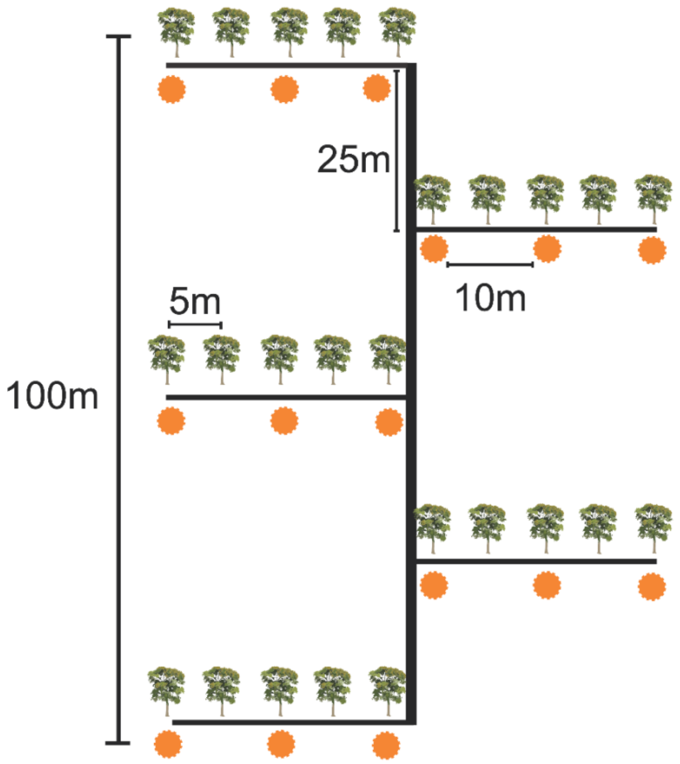


Fig2. In each landscape, ants were collected, in the trees and on the ground, using the branch-clipping and pitfall methods, respectively. Orange circles represent pitfall traps, in total there were 25 plants and 15 pitfalls per landscape.

Functional traits

We measured eight morphological attributes (Fig 3, Table 2). We selected these traits as they are highly associated with the capacity of a given species to use and explore the available resources, to resource use and because they have been observed to respond to changes in the landscape (Yates et al., 2014). For each species collected, six workers were randomly selected where possible (average = 4.2 specimens measured per species). In species that are dimorphic or polymorphic, only the minor caste was measured. This approach is performed to avoid confounding environmental effects with caste differences. We measured the ants using a ocular micrometer accurate to 0.01 mm mounted on a stereomicroscope Leica M80 (Leica Microsystems, Ilhéus, Brazil). The functional traits were standardized by Weber's measure (trait value/Weber's length), the longest rigid length on an ant's body, in order to reduce errors regarding the measurement of body size. All features were standardized by Weber's length, except for the mandible, which was standardized by head width (see Bishop et al., 2015; Fowler et al., 1991; Guilherme et al., 2019).

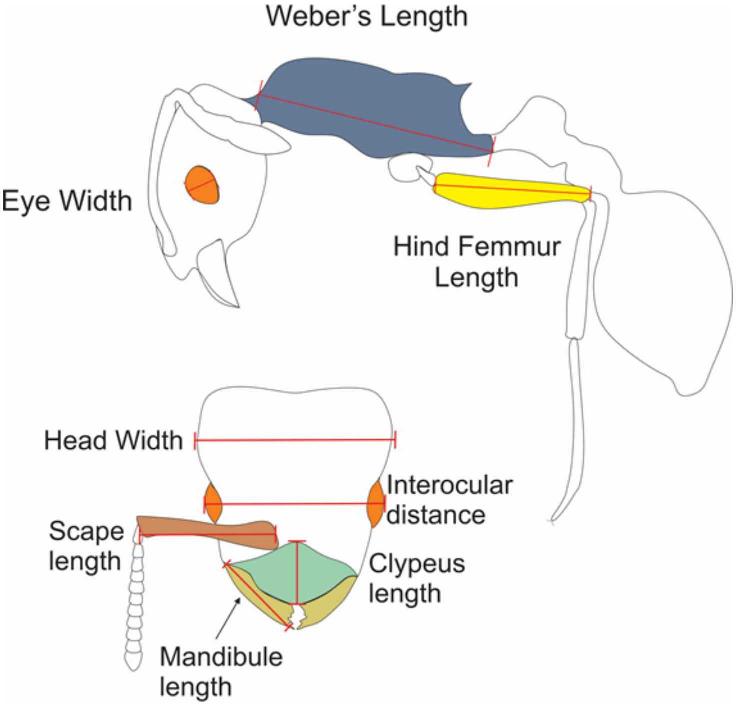


Fig3. Morphological traits used to calculate functional diversity for ant communities sampled in 20 forest patches within Atlantic Forest in Bahia State, Brazil.

Table2. Functional traits used to calculate functional diversity and their hypothesized ecological functions for ant communities sampled in 20 forest patches within Atlantic Forest in Bahia State, Brazil.

Traits	Ecological functions
Weber's length	Related to body size, also associated with habitat complexity (Kaspari & Weiser, 1999)
Head width	Predictor of mandibular musculature (Weiser & Kaspari, 2006)
Antennal Scape length	Related to sensory abilities, perception, and ability to move between locations (Weiser & Kaspari, 2006; Yates et al., 2014)
Eye width	Larger eyes are found in predatory species and/or species that forage in nocturnal or low-light environments (Weiser & Kaspari, 2006)
Clypeus length	Associated with eating habits using liquid resources (Davidson et al., 2004)
Mandible length	Related to foraging strategy, larger mandibles are associated with predator species and prey size (Fowler et al., 1991)
Femur length	Associated with environmental complexity, foraging speed, and thermal tolerance. (Hurlbert et al., 2008; M. Kaspari & Weiser, 1999; Sommer & Wehner,

	2012)
Inter ocular distance	Related to habitat complexity (Gibb et al., 2014). In general, predatory ant species have eyes that are more distant from each other than other species (Silvestre, Brandão, & Rosa da Silva, 2003)

Data Analysis

We used forest cover and edge density as predictor variables. Our response variables were taxonomic richness, standardized functional richness, and mean values of mandible, antennal scape, clypeus, and femur length of ants collected by pitfall and branch-clipping. Functional richness was calculated using all traits (Table 2), measured with the DBFD package (Villéger et al., 2008). We calculated the Standartized Effect Size Functional Richness (sesFRic) to minimize the relationship with taxonomic richness. Functional richness was standardized as follows: [(Observed FRic value - Mean of randomized FRic value) / SD of randomized FRic values], with the independent swap algorithm and 999 randomizations (Gotelli, 2000). To analyze how traits are affected, we calculated the community-trait mean (CTM) in each landscape: (Sum of mean trait values of co-occurring species/number of species) (Guilherme et al., 2019). We used for the calculation of the CTM only the traits most related to feeding, foraging mode and sensory ability (mandible, femur, clypeus and antennal scape lengths).

When the appropriate landscape scale is unknown or there is no consensus in the literature, the most appropriate approach to decide which scale is most relevant to predict the effect of landscape context is the multi-scale analysis, i.e., by drawing buffers of different radius around each sampling site to identify species response to multiple scales (Huais, 2018). We selected the best buffer size for each response variable via the smallest value of Akaike's Information Criterion corrected for small samples (AICc) (supplementary material). All models were fitted using Additive Models (GAM).

We also used GAM to test the relationship between the response and predictor variables. We fit different models (Table 3), after defining the best buffer for each response variable, with a smoothing degree with an upper limit set to 4 to avoid overfitting. Then, based on our initial hypotheses (Table 1) we contrasted different models (Table3). To evaluate the effect of edge density, we use the Null, Edge, Edge with Region Interaction and Forest Cover and Edge models. For forest cover, we contrasted the models Null, Forest Cover, Forest Cover with Region Interaction e Forest Cover and Edge. The AICc was used for model selection (Burnham & Anderson, 2002). Models with ΔAICc < 2.0 were considered the most plausible; when one of the selected models included interaction, we opted for the simplest one and when the null model was among the selected models, we opted for the null model. All statistical analyses and graphics were performed in R Core Team (2020) supported by the packages "mgcv", "visreg", "gamm4", "bbmle", "mgcViz" and "tidymv".

Table 3. Models

	Explanation
Null Model	*Contains only the intercept and assumes that the response variable is unrelated to the predictor variables*
Edge	*The response variable is affected by edge density.*
Edge with Region interaction	*The response variable is influenced by edge density and the effect depends on the region sampled.*
Forest Cover	*The response variable depends on forest cover.*
Forest Cover with Region interaction	*The response variable is affected by forest cover and the effect depends on the region sampled.*
Forest Cover and Edge	*Forest cover and edge density have effects on the response variable.*

Results

We sampled 123 ant morphospecies from 39 genera and 8 subfamilies (Table 4). The subfamily Myrmicinae (64 species) and Ponerinae (20 species) were the best represented in samples. The most frequent species were *Crematogaster limata* and *Ectatomma tuberculatum*. A total of 4,021 ant morphological measurements were performed in different gradients of forest cover and edge density. The scales selected varied from 200 to 1000 m, depending on the response variable (Supplementary Material). We found no evidence of a relationship of functional and taxonomic richness neither with edge density (Table 5) on forest cover (Table 6), with the null model having a ΔAIC < 2 (Table 5). However, landscapes with higher edge densities comprised ant species with significantly larger femur, antennal scape and clypeus (Figure 4d,e,f). We also detected significant differences in trait sizes between the two regions.

In the High Forest Cover (HFC) region, which is characterized by more connected fragments and low contrast matrices, forest cover was negatively related with the size of mandibles and clypeus (Figure 5e,f), i.e., ant species with average larger mandibles and clypeus in landscapes with less forest cover. Although the average size of mandibles and clypeus was smaller in the other region, no relationship with forest cover was detected.

Table 4. List of ant species collected during the study in 20 Atlantic forest landscapes located in Southern Bahia State, Brazil. HFC: High Forest Cover; LFC: Low Forest Cover. Values represent the number of landscapes in which each species was recorded.

Subfamiy/species	HFC	LFC	Frequency
Subfamily Ambyoponinae			
Prionopelta sp		1	1
Subfamily Dolichoderinae			
Dolichoderus imitator	5	7	12
Dolichoderus lutosus	1	1	2
Subfamily Dorylinae			
Eciton burchellii		2	2
Labidus praedator		5	5
Neivamyrmex gibbatus		1	1
Subfamily Ectatomminae			
Gnamptogenys sp		1	1
Ectatomma edentatum		1	1
Ectatomma permagnum	2	7	9
Ectatomma tuberculatum	10	8	18
Gnamptogenys acuminata	1		1
Gnamptogenys horni	1	1	2
Gnamptogenys moelleri	1	5	6
Gnamptogenys regularis	1		1
Gnamptogenys striatula	1		1
Subfamily Formicinae			
Azteca sp	2	5	7
Brachymyrmex heeri	1	1	2
Camponotus agra		1	1
Camponotus atriceps	2		2
Camponotus bidens	2		2
Camponotus canescens	1		1
Camponotus cingulatus	4	6	10
Camponotus crassus		1	1
Camponotus egregius	1	3	4
Camponotus fastigatus	2		2
Camponotus latangulus	2	2	4
Camponotus melanoticus		1	1

Camponotus myrma sp		1	1
Camponotus novogranadensis	2	1	3
Camponotus punctulatus andigenus	1		1
Camponotus rectangularis	3	2	5
Camponotus renggeri		1	1
Camponotus scissus		2	2
Camponotus trapezoideus	1	1	2
Linepithema neotropicum		2	2
Nylanderia fulva	1	2	3
Nylanderia guatemalensis	4	1	5
Nylanderia sp		3	3
Paratrechina longicornis		1	1
Subfamily Myrmicinae			
Acromyrmex subterraneus		1	1
Apterostigma sp1		1	1
Apterostigma sp2		1	1
Apterostigma sp3	1	3	4
Apterostigma sp4		1	1
Apterostigma sp5	1		1
Atta sexdens		4	4
Cephalotes atratus	4		4
Cephalotes grandinosus	1		1
Cephalotes minutus		1	1
Cephalotes opacus	2	2	4
Cephalotes pavonii		1	1
Cephalotes pinelii		1	1
Crematogaster acuta	1	1	2
Crematogaster erecta		2	2
Crematogaster limata	10	9	19
Crematogaster longispina	1	1	2
Crematogaster nigropilosa		1	1
Crematogaster tenuicula	4	2	6
Cyphomyrmex transversus		3	3
Hylomyrma balzani		1	1
Hylomyrma immanis	1	1	2
Megalomyrmex drifti	3	3	6
Mycocepurus goeldii	1	6	7
Ochetomyrmex semipolitus	2		2
Pheidole diligens sp.1	3		3
Pheidole diligens sp.2		1	1
Pheidole fallax sp.1	1	2	3
Pheidole fallax sp.2		1	1
Pheidole fallax sp.3	1	1	2
Pheidole fallax sp.4	5	4	9
Pheidole fallax sp.5		1	1
Pheidole fallax sp.6	1	1	2

Pheidole fimbriata		1	1
Pheidole flavens sp.1	3	1	4
Pheidole flavens sp.2	5	3	8
Pheidole flavens sp.3		1	1
Pheidole flavens sp.4	4	1	5
Pheidole radoszkowskii	3	7	10
Pheidole tristis sp.1	7	6	13
Pheidole tristis sp.2		1	1
Pheidole tristis sp.3	1		1
Pheidole tristis sp.4	2	1	3
Procryptocerus pictipes	1		1
Rogeria subarmata		1	1
Sericomyrmex sp	1	1	2
Sericomyrmex bondari	5	6	11
Sericomyrmex mayri	2	3	5
Sericomyrmex saussurei	9	5	14
Solenopsis sp	2	1	3
Solenopsis geminata	1	1	2
Solenopsis saevissima	1		1
Solenopsis sp.2		1	1
Solenopsis sp.3		1	1
Solenopsis sp.4	2	2	4
Solenopsis sp.5	1		1
Solenopsis virulens	3	1	4
Trachymyrmex pruinosus	3	1	4
Trachymyrmex relictus	1	2	3
Trachymyrmex sp.1	3	1	4
Trachymyrmex sp.2	1	1	2
Trachymyrmex sp.3		1	1
Wasmannia auropunctata	8	7	15
Subfamília Ponerinae			
Anochetus sp		2	2
Hypoponera sp1	1		1
Hypoponera sp2		1	1
Hypoponera sp3		1	1
Leptogenys luederwaldti	2		2
Mayaponera constricta	2	2	4
Neoponera apicalis	1	2	3
Neoponera cavinodis	1		1
Neoponera concava	8	2	10
Neoponera inversa	3		3
Neoponera striatinodis		1	1
Neoponera unidentata		1	1
Neoponera verenae	3	5	8
Neoponera villosa		1	1
Odontomachus chelifer		2	2

Odontomachus haematodus	3	10	13
Odontomachus meinerti	3	5	8
Pachycondyla crassinoda	7	5	12
Pachycondyla harpax	2	6	8
Rasopone ahuacan		1	1
Subfamily Pseudomyrmicinae			
Pseudomyrmex filiformis		1	1
Pseudomyrmex oculatus	7	4	11
Pseudomyrmex pallidus	1	2	3
Pseudomyrmex stigma	1		1
Pseudomyrmex tenuis	3	8	11
Pseudomyrmex venustus		2	2

Table 5. Generalized additive models (GAM) testing for a relationship between functional and taxonomic richness and functional traits of ants with edge density. The selected model for each response variable is highlighted in bold.

	Taxonomic Richness		**Functional Richness (SES)**		**Femur**	
Models	Deviance Explained (%)	dAiCc model	Deviance Explained (%)	dAiCc model	Deviance Explained (%)	dAiCc model
Null	-	0.0	-	**0.0**	-	3.8
Edge Density	5.25	**1.8**	1.64	2.5	33.4	**1.1**
Edge Density with Region	19.2	3.6	35	2.9	48.2	2.5
Forest Cover + Edge	37.9	6	14.8	2.8	47.7	0.0

	Mandible		**Antennal Scape**		**Clypeus**	
Models	Deviance Explained (%)	dAiCc model	Deviance Explained (%)	dAiCc model	Deviance Explained (%)	dAiCc model
Null	-	**0.6**	-	2	-	3.4
Edge Density	12.4	0.8	20.9	**0.0**	26.7	**0.0**
Edge Density with Region	46.8	0.0	23.6	2.7	28.9	2.6
Forest Cover + Edge	15.6	3.2	27.7	3	33.6	1.2

Table 6. Generalized additive models (GAM) testing for a relationship between functional and taxonomic richness and functional traits of ants in forest cover.

	Taxonomic Richness		**Functional Richness (SES)**		**Femur**	
Null		**1.8**		**0.0**		3.8
Forest Cover	20.6	0.0	2.0	2.4	15.6	3.2
Forest Cover with Region	36.2	0.4	17.4	5.0	28.8	5.1
Forest Cover + Edge	37.9	7.8	14.8	2.8	47.7	**0.0**

	Mandible		**Antennal Scape**		**Clypeus**	
Null		5.1		**1.1**		13.3
Forest Cover	12.4	4.7	26.3	0.0	23.4	13.3
Forest Cover with Region	52	**0.0**	26.2	0.9	72	**0.0**
Forest Cover + Edge	15.6	7.7	27.7	2.1	33.6	11.1

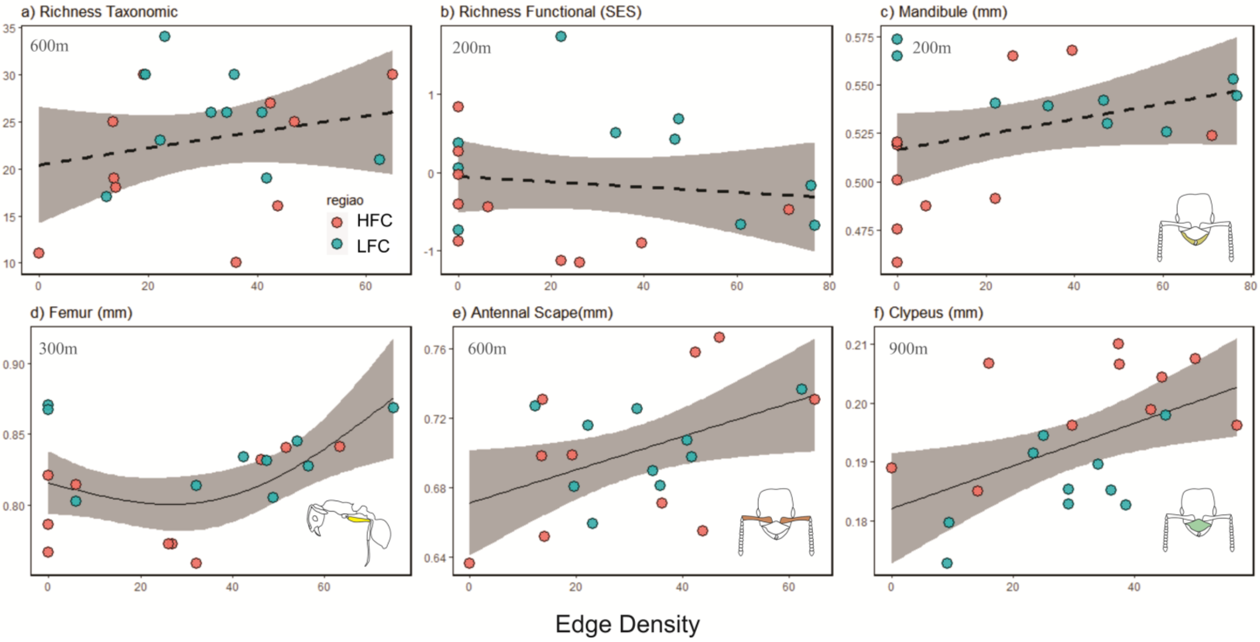


Fig4.Relationship between edge density within within 1-km landscape buffer at 20 surveyed forest sites and taxonomic richness (a), Functional richness (SES) (b) and functionals traits (d,e,f). Blue dots correspond to the region with low forest cover (LFC), while pink dots represent sites in the region with high forest cover (HFC). When a null model was selected (without the effects of edge density), we represent it by the dashed line.

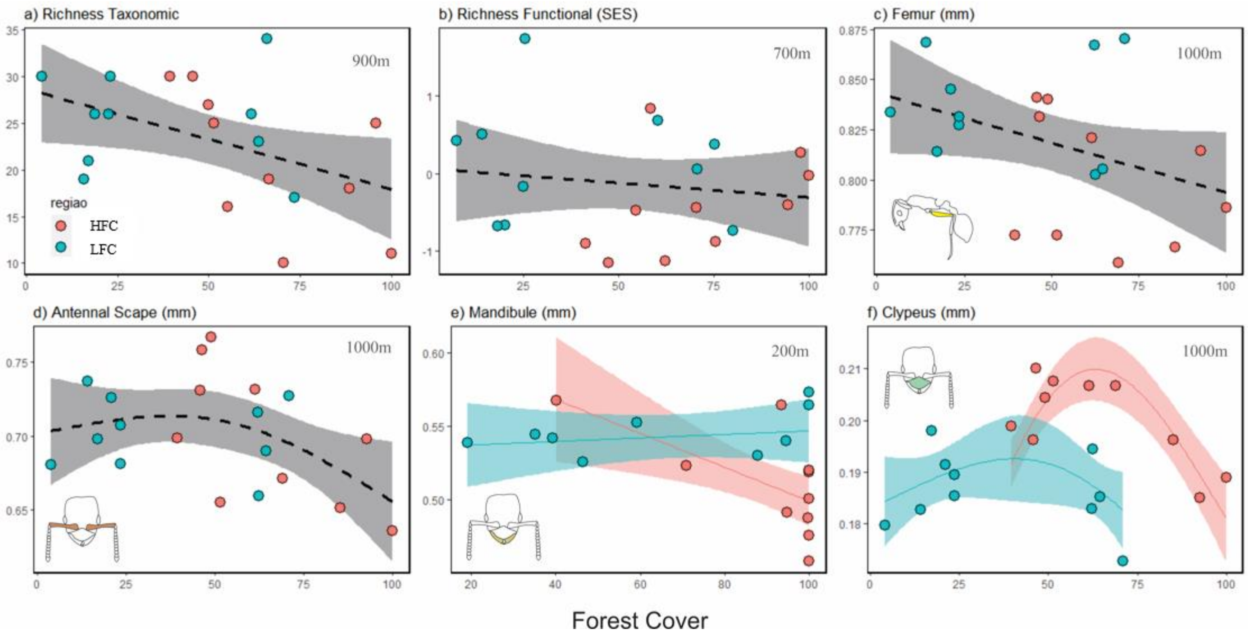


Fig5. Relationships between taxonomic richness (a), Functional richness (SES) (b), mandibule (c) and fEmur(d) according to forest cover loss at the landscape-scale. Blue dots correspond to the region with low forest cover (LFC), while pink dots represent sites in the region with high forest cover (HFC). When a null model was selected (without the effects of edge density), we represent it by the dashed line.

Discussion

Our study showed how landscape changes can promote significant changes in the functional composition of ants in the Atlantic Forest. We found that landscape composition and configuration are key filters of ant functional traits. In remnants inserted in landscapes with higher edge density, ants, on average, have larger legs, antennal scape, and clypeus. Furthermore, we show the pervasive role of deforestation at the landscape scale in shaping important ant functional traits, as demonstrated by the difference in mandible and clypeus size between two nearby regions, one less and the other more forested. Despite such striking and specific functional responses to landscape-scale structural changes, both taxonomic and functional richness were maintained, indicating the importance of assessing a broader spectrum of response variables in order to more adequately detect pivotal changes triggered by landscape alterations.

The morphological characters that were favored by increased edge density (larger antennal scape, clypeus and legs) are typical of habitat-generalist ant species with omnivorous diet (Silva & Brandão, 1999). The presence of generalist species is commonly associated with landscapes with high exposure to anthropogenic edge effects (Caitano et al., 2020). Landscapes exposed to higher edge density are more susceptible to changes in climatic factors, such as low humidity, high solar radiation and high temperature ranges (Harper et al., 2005; Murcia, 1995). These factors together directly interfere with the ants' nesting and foraging strategy. Small-legged ants generally have a preference for nesting on twigs on the ground or in the leaf litter, with little exposure to direct sunlight, and rarely cover distances greater than one meter from the nest (Kaspari, 1993). On the other hand, ants with longer legs have an advantage in places where resources are scarce because they can save foraging time and explore more distant areas (Silva & Brandão, 1999; Sommer & Wehner, 2012). Additionally, the higher foraging speed allows ants with long legs to cool their bodies by convection by decreasing the distance between their bodies and warmer air surfaces (Sommer & Wehner, 2012), which can be a valuable strategy in environments more exposed to solar incidence. A good example of this are ants of the genus *Dorymyrmex*, virtually the only ant species in the Neotropical Region that can forage at midday on the beach (Jaffe, 1993).

The positive relationship between antennal scape size and increased edge exposure may be related to the three-dimensional surface configuration of the fragments. As ants forage mostly on the ground, the arrangement of elements found on the surface can act as barriers to their sensory perception (Kaspari & Weiser, 1999). The spatial configuration of these elements is different between fragmented and continuous areas (Rodrigues & Nascimento, 2006). In tropical environments with greater exposure to the edge, the amount of fallen woody litter can be up to 60% greater than sites with less edge influence (Rodrigues & Nascimento, 2006). This dense cover on the soil surface may contribute to the dispersion of the semiochemical substances in the habitat, leaving the olfactory environment of the insects more confused, which may favor ants with long antennal scapes, which are more efficient in their chemical communication. In addition, trails left by the ants may be more easily lost in areas more exposed to sunlight, since the rate of evaporation and decomposition of track pheromones increases under these conditions (Van Oudenhove, Billoir, Boulay, Bernstein, & Cerdá, 2011), such as fragments with higher edge density.

We hypothesized that ants in more preserved areas - in landscapes with smaller edge density and more forest - would have larger mandibles on average, a characteristic probably related to a greater variety and abundance of prey in these locations. However, this relationship was negative and influenced by the regional context in which each fragment is inserted. This can be explained by the high occurrence of predatory species, like those of the Ponerinae subfamily, in fragments with less forest cover in the less anthropized region. In this region, the remnants have a matrix of low contrast, such as agroforestry systems, besides being relatively less isolated. This indicates that species that can capture large prey can establish themselves in landscapes with less forest cover in which the remnants are more connected, immersed in more "friendly" matrices (Dias, Zanetti, Santos, Louzada, & Delabie, 2008). It has already been seen in this same region that such species tend to use areas with forest cover closer to the original vegetation, because they are highly dependent on the vegetation strata where their potential prey predominates (Campiolo et al., 2015).

Therefore, forest remnants in this region, and thus in landscapes with lower forest cover and fragments with higher edge density, harbor ants with larger clypeus. Ants with longer clypeus are generally nectarivorous and commonly feed on sugary liquids secreted by homopterans or have interactions with plants with extrafloral nectaries (Fowler et al., 1991). The size of the clypeus is associated with the feeding habit in which ants use liquid resources. Extrafloral nectaries are typical of pioneer plant species, which have high growth rates and an affinity for total light (Bentley 1976; Blüthgen & Reifenrath 2003). Forest cover loss and increased exposure to edge effects may favor the establishment of these plants and this resource at these sites, which attracts nectarivorous ant species, such as those of the subfamilies Dolichoderinae and Formicinae (Bentley, 1976; Pereyra, Pol, & Galetto, 2015).

In our study, we saw that landscape descriptors such as edge density and remaining forest cover are not particularly good predictors of ant taxonomic richness. This richness, thus, is likely to be related to local attributes of each patch, such as tree density and richness (Ribas et al., 2003), depth, and heterogeneity of the leaf litter (Queiroz, Ribas, & França, 2013). It is apparently more difficult to detect a general pattern in the taxonomic richness of ants at larger scales. Responses to deforestation may prove positive (Ahuatzin et al., 2019) or often neutral (Caitano, Dodonov, & Delabie, 2018; Leal et al., 2012a). The responses of total ant richness may also be masked because of the large functional diversity existing in the group. For example, Leal et al. (2012) recorded no influence of forest cover on total ant richness in anthropic landscapes of the northeastern Atlantic Forest; however, for some groups such as Myrmicinae, this is a key factor in their abundance. Thus, we sought answers with functional richness by calculating the functional space filled by species in each landscape type, and similarly did not find an influence of landscape descriptors on this functional metric. This reveals that, in general, variation in functional traits when assessed together do not reveal clear patterns linked to loss of forest cover and edge density.

Although we did not detect an influence of edge density and forest cover on ant taxonomic and functional richness, these variables operate on each trait in unique ways. This study highlights the importance of landscape-scale anthropogenic effects on ant functional traits in tropical forests. Another factor that can be investigated in the future within the context of landscapes is the degree of isolation and the type of surrounding matrix. Consistent responses from traits reveal to us that it is possible to use this tool to help us to decide which ant species may be most vulnerable to effects caused by changes in tropical rainforests. Here we encourage that effects generated by changing landscapes are also studied in other taxonomic groups using a functional approach.

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SUPPLEMENTARY MATERIAL

EFFECTS OF HABITAT AMOUNT AND CONFIGURATION ON ANT FUNCTIONAL TRAITS IN A NEOTROPICAL RAIN FOREST

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Scale Selection

Taxonomic Richness

Forest Cover

Buffer	dAICc	df
900	**0.0**	**2.49213859496784**
1000	0.0	2.50223455518959
800	0.4	2.36954154218363
700	1.2	2.28941361726383
600	1.8	2.23251397816748
500	2.0	2.05387021536159
400	2.6	2.20529043015968
300	3.0	2.6517869954066
200	4.3	2.68319355096665
100	5.0	2.81651084978827

Edge Density

Buffer	dAICc	df
600	**0.0**	**3.88414259220345**
500	0.4	3.89897192936829
700	2.1	3.84597335818128

200	3.0	2.82726999263718
800	3.3	3.83150333769055
1000	3.5	3.8560969856614
300	4.5	2.00001261037233
900	5.0	3.80095509581652
100	5.5	2.00000637074514
400	6.8	2.84306888138019

Functional Richness

Forest Cover

Buffer	dAICc	df
700	**0.0**	**3.00000000011309**
800	0.0	3.00000000028101
600	0.1	3.00000000008399
900	0.2	3.05537658553574
500	0.2	3.00000000005375
1000	0.3	3.1500452256714
200	0.3	3.00000000006984
400	0.4	3.00000000004709
300	0.4	3.00000000002144
100	0.5	3.36976193429088

Edge Density

Buffer	dAICc	df
200	**0.0**	**3.00000000004897**
100	0.7	3.00000000006219
1000	0.8	3.00000000009656
800	0.8	3.00000000007309
900	0.9	3.00000000005947
400	0.9	3.00000000012096
300	1.0	3.00000000006918

600	1.0	3.42014641075509
500	1.0	3.0351587140632
700	1.1	3.32705261434344

Femur

Forest Cover

Buffer	dAICc	df
1000	**0.0**	**3.00000001801206**
900	0.2	3.00000001822172
800	0.6	3.00000001822868
700	1.0	3.00000001812865
600	1.4	3.00000001917503
500	1.9	3.00000000723682
400	2.5	3.00000001457121
300	2.6	3.00000002104858
200	2.9	3.47052969306593
100	3.6	3.33971005405842

Edge Density

Buffer	dAICc	df
300	**0.0**	**4.50060732058313**
200	3.3	3.00000002619175
400	3.7	3.0000000347933
600	4.6	3.00000002909299
500	4.8	3.00000003122609
100	5.2	3.00000001771517
700	5.6	3.00000005017543
1000	5.8	3.0000000222135
900	5.9	3.00000001460818
800	6.2	3.00000001631988

Antennal Scape

Forest Cover

Buffer	dAICc	df
1000	0.0	3.76373244146238
900	0.2	3.78727022233583
800	0.5	3.77176560791019
200	0.9	4.34407559628423
700	0.9	3.74575096202479
600	1.2	3.71186824009724
500	1.9	3.64018165948509
300	2.4	3.49834302970698
400	2.7	3.38501795262763
100	3.2	4.47195535352515

Edge Density

Buffer	dAICc	df
600	0.0	3.0000000210753
200	0.3	3.00000001760657
700	0.8	3.00000002062939
300	1.1	3.04624772194162
500	1.7	3.00000002508567
400	1.7	3.00000001375396
800	2.2	3.00000001821346
100	3.5	3.10051154990544
900	3.6	3.0000000206449
1000	3.7	3.00000001849707

Mandibule

Forest Cover

Buffer	dAICc	df
200	0.0	3.07740955507147
100	0.1	3.00000003779298
300	2.0	3.31057837201751
400	2.5	3.00000003009381
1000	2.8	3.00000002723939
700	2.8	3.00000003168204
800	2.8	3.00000001910209
900	2.8	3.00000000777253
500	3.3	4.6825403875315
600	3.6	4.2666853770204

Edge Density

Buffer	dAICc	df
200	0.0	3.00000001617407
300	0.2	3.00000002280098
400	0.3	3.00000002105962
500	0.6	3.00000001831419
800	0.7	3.0000000176932
700	0.8	3.00000001689207
600	0.9	3.00000001563635
100	0.9	3.0000000226439
900	1.0	3.00000002015212
1000	1.4	3.00000002337781

Clypeus

Forest Cover

Buffer	dAICc	df
1000	0.0	4.3089929752173
900	0.5	4.0037539512755
600	0.8	3.86249686153823

800	1.0	3.83836094576172
500	1.0	4.11144356476965
700	1.0	3.79720237596654
400	2.4	4.55711783800178
200	2.5	3.00000013650161
300	2.6	3.00000012215563
100	2.7	3.00000015400653

Edge Density

Buffer	dAICc	df
900	0.0	3.00000015003246
1000	0.1	3.00000012708615
800	1.2	3.00000013954238
700	3.6	3.00000015958558
600	4.8	3.00000157463665
300	5.2	3.78894798807893
500	5.4	3.08252581018644
100	5.9	3.00000013116837
200	6.0	3.00000025438852
400	6.2	3.3263703669074

CAPÍTULO III

B-DIVERSIDADE TAXONÔMICA E FUNCIONAL DE FORMIGAS EM DIFERENTES CENÁRIOS DE USO DA TERRA.

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Trabalho proposto para a Sociobiology

Abstract

The profound changes generated through urban and agricultural expansion have reduced areas of original forests and increasingly threaten biological communities. Little is known about how habitat loss can affect the patterns of taxonomic and functional composition of ants in the Brazilian Atlantic Forest. We sampled ants in 10 landscapes immersed in a region with high forest cover (HFC) and another 10 landscapes located in a region with low cover (LFC). We analyzed the taxonomic and functional composition and beta diversity of each region and investigated which functional traits and species drive the dissimilarities between locations. The two regions differed in functional and taxonomic composition. The functional composition is mainly directed by femur length and antennal scapula length. The species *Cephalotes atrattus* was associated with the region with high forest cover, while the species *Ectatomma permagnum* and *Odontomachus haemadotus* with the region with low forest cover. The main process in assembling taxonomic and functional biodiversity was turnover. There were no differences in beta functional diversity between regions. We have seen that taxonomic turnover is greater in areas with low forest cover and is responsible for up to 90% of dissimilarity. Our results reveal the importance of inserting fragments with low forest cover in management plans. We highlight that profound changes in landscapes in the Atlantic Forest lead to changes in functional and taxonomic structuring in ant assemblages.

Keywords: habitat loss, functional traits, formicidae, community dissimilarity, tropical forest, turnover.

Resumo

As profundas modificações geradas através da expansão urbana e agrícola têm reduzido áreas de florestas originais e ameaçado cada vez mais as comunidades biológicas. Pouco sabemos como a perda de habitat pode afetar os padrões de composição taxonômica e funcional das formigas na Mata Atlântica. Nós amostramos formigas em 10 paisagens imersas em uma região com alta cobertura florestal (HFC) e outras 10 paisagens localizadas em uma região com baixa cobertura (LFC). Analisamos a composição e a beta diversidade, taxonômica e funcional, de cada região e investigamos quais traços funcionais e espécies são os motores das dissimilaridades entre os locais. Nós observamos que as duas regiões diferem na composição funcional e taxonômica. A composição funcional é dirigida, principalmente, pelo fêmur e escapo antenal. A espécie *Cephalotes atrattus* foi associada à região de alta cobertura florestal, enquanto que as espécies *Ectatomma permagnum e Odontomachus haemadotus* à região de baixa cobertura florestal. O principal processo na montagem da biodiversidade taxonômica e funcional foi o turnover. Não houve diferenças na beta diversidade funcional entre os ambientes. Vimos que o turnover taxonômico é maior em áreas de baixa cobertura florestal e responsável por até 90% da dissimilaridade. Nossos resultados revelam a importância da inserção dos fragmentos com baixa cobertura florestal nos planos de manejo. Destacamos que mudanças profundas nas paisagens da Mata Atlântica levam à mudanças na estruturação funcional e taxonômica nas assembleias de formigas.

Palavras-chave: perda de habitat, traços funcionais, formicidae, dissimilaridade da comunidade, floresta tropical, turnover.

Introdução

A Floresta Atlântica da América do Sul já perdeu cerca de 93% de suas áreas nativas (Galindo-Leal & Câmara, 2003), e as áreas remanescentes estão isoladas e imersas em matrizes de alto contraste, tais como pastagens, agroflorestas e agricultura intensiva (Faria, Delabie, & Dias, 2020). A conversão de florestas e a perda de habitat são uma das principais ameaças a diversidade biológica e seus efeitos podem provocar mudanças profundas na composição das espécies entre os remanescentes. A β-diversidade é um dos componentes principais da biodiversidade, sendo que essa medida permite inferir quais são os processos que estruturam a organização das espécies numa comunidade (Andrés Baselga, Orme, Villeger, De Bortoli, & Leprieur, 2017). A dissimilaridade entre locais pode ser fruto de processos históricos naturais, tais como barreiras biogeográficas, e/ou resultar de mudanças desencadeadas por ações antrópicas (Andrés Baselga, 2010).

Na escala de paisagem, fatores como isolamento e perda de habitat podem prejudicar a dispersão das espécies e aumentar a β-diversidade. Uma região mais conectada, com matrizes mais permeáveis (baixo contraste com a vegetação nativa) e com maior taxa de cobertura florestal, favorece o fluxo de espécies nativas entre ambientes, o que culmina na maior similaridade na composição taxonômica entre sítios (Morante-Filho, Arroyo-Rodriguez, & Faria, 2016). Nesse cenário, a substituição da cobertura florestal por matrizes pouco permeáveis pode contribuir significativamente para a variação da composição de espécies. Esse aumento da beta diversidade pode ser resultado tanto da perda (aninhamento ou *nestedness*) quanto da substituição (*turnover*) de espécies. Algumas espécies podem responder positivamente à medida que os distúrbios antrópicos alteram as paisagens naturais (*winner species* ou "espécies vencedoras"), enquanto que espécies mais sensíveis são desfavorecidas por essas alterações (*loser species* ou "espécies perdedoras") (McKinney & Lockwood, 1999).

Além da substituição ou perda de espécies, as mudanças antrópicas também podem afetar a composição funcional da comunidade. Estudos que utilizam da abordagem funcional frequentemente mostram uma ligação entre as condições ambientais com traços funcionais das espécies. Logo, mudanças na paisagem decorrentes da intervenção humana podem servir como filtros e selecionar certas características funcionais das espécies. Esse tipo de pressão seletiva pode desencadear substituições e/ou perdas de funções. Ações antrópicas, tais como queimadas (Arnan, Cerdá, Rodrigo, & Retana, 2013), mudanças climáticas (Arnan et al., 2018), conversão do uso da terra (Salas-Lopez, Violle, Mallia, & Orivel, 2018), interferem diretamente na estruturação funcional das comunidades. Por exemplo, a conversão de florestas subtropicais em plantações promove a substituição de espécies florestais por aquelas presentes nas matrizes e torna o ambiente mais pobre funcionalmente (Santoandré, Filloy, Zurita, & Bellocq, 2019a).

Assim, a β-diversidade funcional é uma ferramenta chave para ajudar a desvendar os processos estruturantes das comunidades. Por exemplo, duas comunidades podem ter alta dissimilaridade taxonômica, porém baixa dissimilaridade funcional. Nesse caso, embora as espécies sejam diferentes, essas desempenham funções similares no ecossistema. Isso significa que a perda de algumas espécies não está necessariamente atrelada à perda de funções. Por outro lado, ambientes com baixa redundância funcional apresentam muitas espécies com funções únicas; nesse cenário, cada ambiente é um conjunto único de funções e a perda de espécies pode afetar diretamente o funcionamento dos ecossistemas. Logo, ambientes com baixa redundância funcional são mais sujeitos ao colapso em sua estrutura funcional.

As formigas (Insecta: Formicidae) são fundamentais para o funcionamento dos ecossistemas: elas atuam na ciclagem de nutrientes, são dispersoras de semente, predadoras e diversas espécies podem ser consideradas engenheiras de ecossistema atuando na estruturação dos solos (Agosti, Majer, Alonso, & Schultz, 2000; Crist, 2009; Folgarait, 1998). Por serem sensíveis às mudanças ambientais, as formigas são amplamente utilizadas na busca de respostas sobre as mudanças de origens antrópicas (Caitano, Dodonov, & Delabie, 2018; Delabie, Paim, Nascimento, Campiolo, & Mariano, 2006; Queiroz et al., 2020). Estudos prévios com o grupo já demonstraram que o clima (Arnan et al., 2018), fogo (Arnan et al., 2013) e agricultura (Santoandré, Filloy, Zurita, & Bellocq, 2019b) modificam a estrutura da composição funcional e taxonômica da assembleia de formigas. No entanto, estudos direcionados sobre a forma com que as mudanças no uso da terra afetam o padrão de diversidade beta funcional e taxonômica ainda são escassos.

Aqui nós avaliamos os padrões de β-diversidade taxonômica e funcional de formigas em 20 paisagens na Mata Atlântica em duas regiões que contrastam em cobertura florestal e tipo de matriz. Procuramos entender quais mecanismos são mais importantes em cada cenário: a) substituição de espécies ou perda/ganho de espécies? e b) substituição funcional ou perda/ganho de funções? Considerando os efeitos negativos da perda de cobertura de floresta e mudanças drásticas no uso da terra, esperávamos observar diferenças na composição das assembleias de formigas entre paisagens com maior e menor cobertura florestal. Além disso, predizemos que espécies presentes em paisagens mais isoladas e com baixa cobertura florestal encontrarão dificuldades de dispersão, o que incrementará o valor da diversidade beta. Adicionalmente, predizemos que a maior exposição a matrizes de alto contraste facilitaria a substituição ou perda de determinadas espécies ou funções, devido à troca de espécies especialistas de habitat por espécies provindas das matrizes.

Métodos

Área de estudo

O estudo foi conduzido em 20 sítios florestais abrangendo 3.500 km^2, inseridos na mesma sub-região biogeográfica, delimitada pelos rios Jequitinhonha e de Contas. Essa é uma região originalmente coberta por floresta tropical úmida de planície (Faria, Delabie, & Dias, 2021; Thomas, De Carvalho, Amorim, Garrison, & Arbeláez, 1998) com média anual de temperatura de 24°C e a média anual de chuva é próxima de 2.000mm.

Apesar dos sítios amostrados apresentarem solo, topografia e composição florística próximos (Benchimol et al., 2017), esses estão inseridos em duas regiões distintas pela taxa de cobertura florestal e tipo de matriz circundante. A região de alta cobertura florestal (HFC) possui 50% de mata nativa e floresta secundária com matriz altamente heterogênea: plantações de cacau à sombra (22% da matriz da paisagem) e seringueiras (10%). Por sua vez, a região de baixa cobertura florestal (LFC) possui apenas 30% dos quais corresponde a florestas primárias e secundárias imersas em matrizes de pastagens de gado (86% à matriz paisagística) e plantações de *Eucalyptus* sp. (7%) (Fig1).

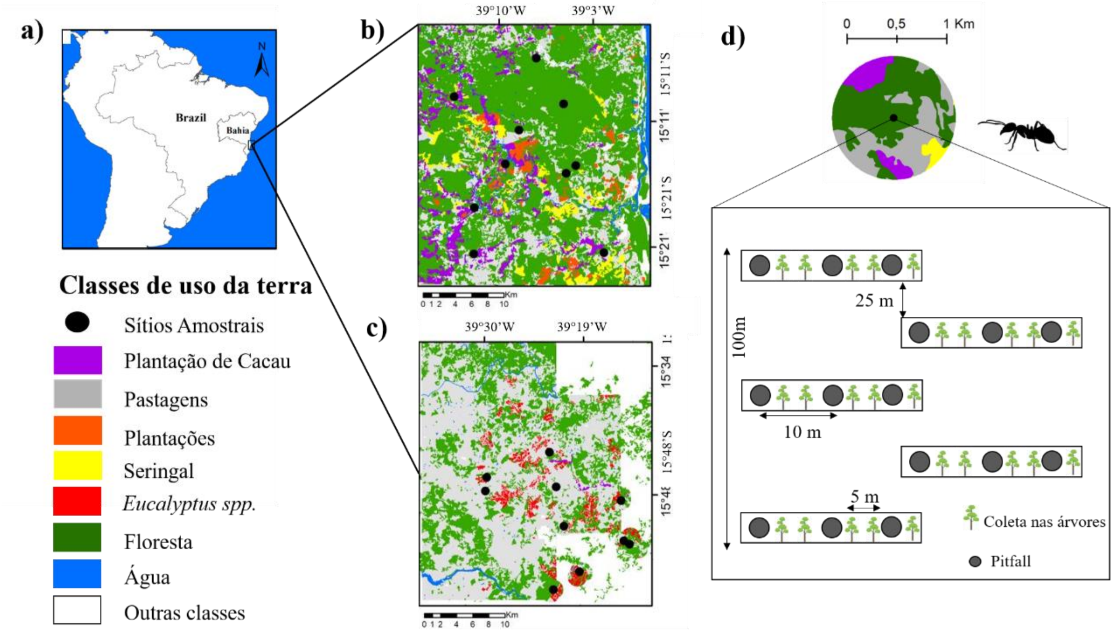

Fig1. Área de estudo no sul da Bahia, Brasil a). Mapa com as duas regiões que diferem na cobertura florestal e classes de cobertura da terra. Região com alta cobertura florestal (HFC) b) e região com baixa cobertura florestal (LFC) c). Os pontos pretos indicam os sítios florestais dentro de cada paisagem. Em cada sítio, as formigas foram coletadas nas árvores e no solo, com auxílio do método branch-clipping e pitfall d).

Coleta das Formigas

As formigas foram coletadas no período de Abril de 2017 a Maio de 2018. Nós coletamos formigas em ramos de 25 plantas do sub-bosque para cada sítio amostral através do método *branch clipping* (ver Cooper & Whitmore, 1990). As plantas estavam distribuídas em cinco transectos de 25 metros a intervalo mínimo de 5 metros entre dois indivíduos sucessivos. Para a captura das formigas de solo, distribuímos três pitfalls ao longo de cada transecto, totalizando 15 armadilhas por sítio amostral. Os pitfalls ficaram instalados por 68 horas. Todas as formigas coletadas foram fixadas em álcool 90% e encaminhadas ao Laboratório de Mirmecologia do Centro de Pesquisas do Cacau (CEPEC; Ilhéus, BA, Brasil) para identificação e deposição dos vouchers (Delabie et al 2020). Todas as formigas foram identificadas sempre que possível até o nível de espécie, seguindo a nomenclatura de Bolton (2003, 2016).

Análise de Dados

Foram selecionados seis traços funcionais que visam descrever o nicho funcional das formigas, considerando em particular o modo de aquisição de alimentos e uso do habitat: Comprimento do fêmur, associado à habilidade de locomoção, resistência térmica e complexidade do habitat (Kaspari & Weiser, 1999; Sommer & Wehner, 2012); Comprimento de mandíbula, relacionado diretamente ao tipo de dieta (Fowler, Forti, Brandão, Delabie, & Vasconcelos, 1991); Comprimento do clípeo, associado ao modo de aquisição de recursos líquidos (Davidson, Cook, & Snelling, 2004); Comprimento do escapo antenal, relacionado à percepção sensorial (Weiser & Kaspari, 2006; Yates, Andrew, Binns, & Gibb, 2014); Largura do olho, indicativo de comportamento de busca por recursos e período de forrageio (Weiser & Kaspari, 2006); e Distância Interocular, que está associado ao método de caça e tipo de habitat (Gibb et al., 2014). Quando possível, medimos quatro indivíduos por espécie, somente operárias menores foram usados (Bihn, Gebauer, & Brandl, 2010). Medimos as formigas usando um micrómetro ocular com precisão de 0,01 mm montado num estereomicroscópio Leica M80 (Leica Microsystems). O tamanho do corpo foi estimado a partir da medida do comprimento de Weber (distância da margem anterodorsal do pronoto à margem posteroventral do propodeu**)** (Weber, 1938) e os demais traços foram padronizados de acordo com essa medida, com exceção da mandíbula cujo tamanho foi padronizado pela largura da cabeça (ver Bishop et al., 2015; Fowler et al., 1991; Guilherme et al., 2019).

Foi utilizada a Análise Multivariada Permutacional de Variância (PERMANOVA) para avaliar diferenças taxonômicas e funcionais nas assembleias de formigas entre as duas regiões. Utilizamos a similaridade de Jaccard e a distância Euclidiana para a abordagem taxonômica e funcional, respectivamente.

Para ilustrar diferenças na composição funcional e taxonômica realizamos uma Análise de Componentes Principais (PCA) e Escalonamento Multidimensional Não–Métrico (NMDS), respectivamente. Excluímos as espécies *singletons* (espécies com um único registro) do NMDS. Para identificar quais espécies são as principais motoras da dissimilaridade na composição taxonômica, usamos a função *envfit* (com 9999 permutações). Essa função ajusta vetores em uma ordenação, consideramos apenas as espécies que obtiveram valor de $p<0,01$.

Para avaliar quais são os principais processos que regem a β-diversidade taxonômica nas regiões, nós usamos o índice de dissimilaridade de Jaccard baseado numa matriz de presença e ausência. Para calcular os componentes de turnover e aninhamento da β-diversidade funcional, nós calculamos a distância funcional da matriz entre os pares de espécies usando distância Euclideana. Então, usamos a matriz gerada pela distância Euclideana para realizar uma Análise de Coordenadas Principais (PCoA) a fim de gerar o espaço funcional multivariado para cada paisagem estudada. Os dois primeiros eixos do PCoA foram retidos e utilizados para estimar os componentes da β diversidade funcional para cada região.

Nós calculamos seis matrizes para cada região com as métricas de beta diversidade: i) β-diversidade total (taxonômica e funcional), ii) componente de aninhamento da β-diversidade (taxonômica e funcional)) e iii) componente de substituição ou *turnover* da β-diversidade (taxonômica e funcional). Comparamos os valores da beta diversidade taxonômica e funcional entre as regiões a partir da função *betadisper*, usada para comparar a dispersão entre dois ou mais conjuntos de dados multivariados e baseada na análise PERMDISP (Anderson, Ellingsen, & McArdle, 2006), com 9999 permutações. Essa análise consiste em verificar a homogeneidade multivariada de dispersões, permitindo visualizar a variação na diversidade beta dentro e entre as regiões. Por fim, o teste de permutação (9999 permutações) é feito para verificar se existe diferenças nos dados de dispersão entre os grupos. Todas as análises foram realizadas no software R (R Core Team, 2020) usando os pacotes *Betapart* (Baselga et al., 2018) para β-matrizes de diversidade e *Vegan* (Oksanen et al., 2013) para PCoA, PCA, NMDS e Envfit.

Resultados

Foram coletadas 128 morfoespécies de formigas pertencentes a 39 gêneros. As subfamílias Myrmicinae (64 espécies) e Ponerinae (20 espécies) foram as que mais tiveram espécies. Foram 81 morfoespécies para a região de alta cobertura florestal (HFC) e 107 morfoespécies para a região de baixa cobertura (LFC). Dentre essas, 22 são exclusivas da HFC, enquanto 47 somente ocorreram na região LFC. Os dois sistemas têm 59 espécies em comum (tabela1).

Tabela1. Lista das espécies de formigas compartilhadas e exclusivas em duas regiões na Mata Atlântica, estado da Bahia, Brasil.

LFC/HFC	HFC	LFC
Apterostigma sp.3	*Apterostigma* sp.5	*Acromyrmex subterraneus*
Azteca sp	*Camponotus atriceps*	*Anochetus sp*
Brachymyrmex heeri	*Camponotus bidens*	*Apterostigma* sp.1
Camponotus cingulatus	*Camponotus canescens*	*Apterostigma* sp.2
Camponotus egregius	*Camponotus fastigatus*	*Apterostigma* sp.4
Camponotus latangulus	*Camponotus punctulatus andigenus*	*Atta sexdens*
Camponotus novagrandensis	*Cephalotes atratus*	*Camponotus agra*
Camponotus rectangularis	*Cephalotes grandinosus*	*Camponotus crassus*

Camponotus trapezoideus
Cephalotes opacus
Crematogaster acuta
Mayaponera constricta
Crematogaster limata
Crematogaster longispina
Crematogaster tenuicula
Dolichoderus imitator
Dolichoderus lutosus
Ectatomma permagnum
Ectatomma tuberculatum
Gnamptogenys horni
Hylomyrma immanis
Gnamptogenys moelleri
Megalomyrmex drifti
Mycocepurus goeldii
Neoponera apicalis
Neoponera concava
Neoponera verenae
Nylanderia fulva
Nylanderia guatemalensis
Odontomachus haematodus
Odontomachus meinerti
Pachycondyla crassinoda
Pachycondyla harpax
Pheidole flavens sp.3
Pheidole fallax sp.1
Pheidole fallax sp.3
Pheidole fallax sp.4
Pheidole fallax sp.6
Pheidole flavens sp.1
Pheidole flavens sp.2
Pheidole radoszkowskii
Pheidole tristis sp.1
Pheidole tristis sp.4
Pseudomyrmex oculatus
Pseudomyrmex pallidus
Pseudomyrmex tenuis
Sericomyrmex bondari
Sericomyrmex mayri
Sericomyrmex saussurei
Sericomyrmex sp
Solenopsis geminata
Solenopsis sp
Solenopsis sp.4
Solenopsis virulens
Gnamptogenys acuminata
Gnamptogenys regularis
Gnamptogenys striatula
Hypoponera sp1
Leptogenys luederwaldti
Neoponera cavinodis
Neoponera inversa
Ochetomyrmex semipolitus
Pheidole diligens sp.1
Pheidole tristis sp.3
Procryptocerus pictipes
Pseudomyrmex stigma
Solenopsis saevissima
Solenopsis sp.5
Camponotus melanoticus
Camponotus myrma sp
Camponotus renggeri
Camponotus scissus
Cephalotes minutus
Cephalotes pavonii
Cephalotes pinelii
Crematogaster erecta
Crematogaster nigropilosa
Cyphomyrmex transversus
Eciton burchellii
Ectatomma edentatum
Gnamptogenys sp
Hylomyrma balzani
Hypoponera sp.2
Hypoponera sp.3
Labidus praedator
Linepithema neotropicum
Neivamyrmex gibbatus
Neoponera striatinodis
Neoponera unidentata
Neoponera villosa
Nylanderia sp
Odontomachus chelifer
Paratrechina longicornis
Pheidole diligens sp.2
Pheidole fallax sp.2
Pheidole fallax sp.5
Pheidole fimbriata
Pheidole flavens sp.3
Pheidole tristis sp.2
Prionopelta sp
Pseudomyrmex filiformis
Pseudomyrmex venustus
Rasopone ahuacan
Rogeria subarmata
Solenopsis sp.2
Solenopsis sp.3
Trachymyrmex sp.3

Trachymyrmex pruinosus
Trachymyrmex relictus
Trachymyrmex sp.1
Trachymyrmex sp.2
Wasmannia auropunctata

A análise de PERMANOVA revelou diferenças significativas entre a composição taxonômica e funcional das assembleias de formigas entre regiões com diferentes cenários de uso da terra (Tabela 2). Neste caso, ficou evidente que paisagens com maior cobertura florestal e com menor exposição às bordas de alto contraste (na região LFC) apresentam um conjunto de espécies dissimilares funcionalmente e taxonomicamente em comparação às paisagens com baixa cobertura florestal.

Tabela 2. Resultados da PEMANOVA para composição da assembleia (taxonômica e funcional) de formigas entre regiões com baixa cobertura florestal com densa cobertura florestal, no bioma Mata Atlântica, norte da Bahia, Brasil.

Variável Resposta	**F-modelo**	**R^2**	**p-valor**
Composição Taxonômica	2.1	0.10	>0.0001
Composição Funcional	4.07	0.18	0.02

As dissimilaridades observadas na composição taxonômica entre as duas regiões se devem principalmente a três espécies de formigas (Fig 2). Dentre essas, *Odontomachus haemadotus* (p<0,001) e *Ectatomma permagnum* (p<0,004) são as espécies mais comuns na região LFC e menos frequentes nas áreas HFC. Por outro lado, a espécie *Cephalotes atratus* (p<0,002) foi mais frequentes nas áreas de HFC e com nenhuma ocorrência na região LFC.

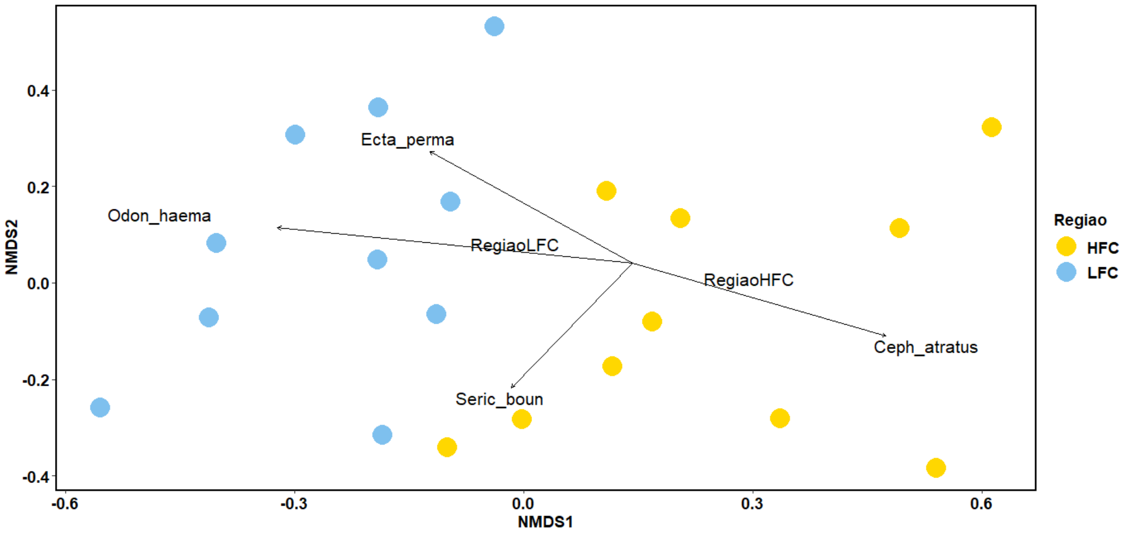

Fig2. Biplot de dimensionamento multidimensional não-métrico (NMDS) de assembléias de formigas amostradas em duas regiões que contrastam no uso da terra e cobertura florestal. Os pontos representam amostras das assembleias de formigas e as setas são vetores que representam a força e a direção da correlação da abundância de cada espécie com o espaço NMDS (ou seja, carregamentos de espécies). Apenas espécies com cargas significativas (P <0,01) foram plotadas (Ecta_perma= *Ectatomma permagnum*, Odon_haema= *O. haemadotus*, Seric_boun = *Sericomyrmex boundari* e Ceph_atratus= *C. atratus*).

As diferenças na composição funcional entre as regiões são regidas principalmente pelo tamanho dos escapos antenais, fêmur e distância interocular (Fig 3). Formigas encontradas em paisagens com menor cobertura e expostas a matrizes de alto contraste (LFC) possuem pernas e escapos antenais maiores. Por sua vez, formigas da região HFC tem a distância interocular mais pronunciada e menor tamanho de escapo e fêmur.

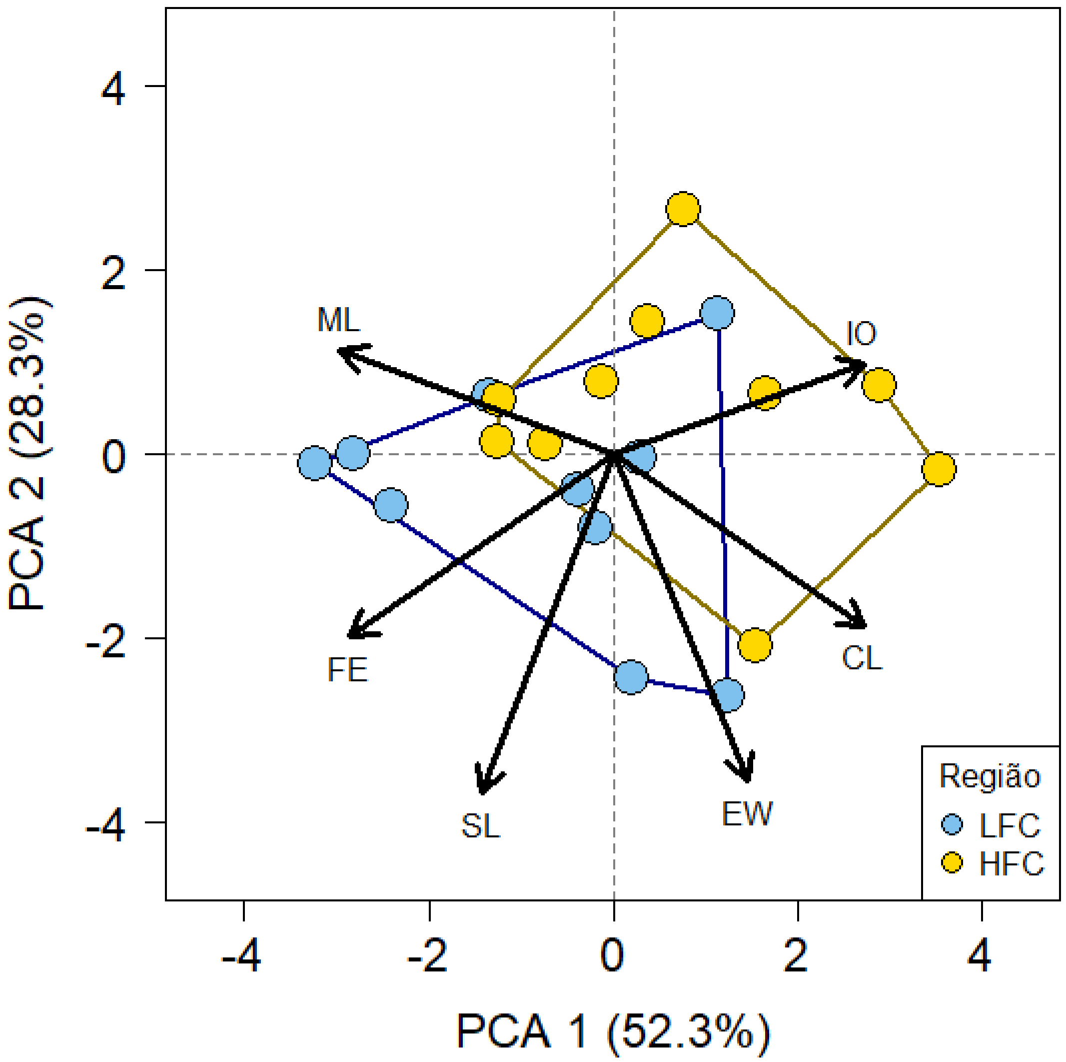

Fig 3. Análise de Ordenação de Componente Principal (PCA) da composição funcional das regiões HFC (alta cobertura florestal) e LFC (baixa cobertura florestal). Biplot representando o primeiro (PC1) e o segundo (PC2) eixos da análise do componente principal; a porcentagem de variação explicada por cada eixo é indicada entre parêntesis. *FE* comprimento do fêmur, *SL* comprimento do escapo antenal, *EW* comprimento do olho, *CL* comprimento do clípeo, *ML* comprimento da mandíbula, *IO* distância interocular.

Apesar de apresentarem composições taxonômicas e funcionais distintas, ambos cenários apresentaram altos valores de β-diversidade (tabela 3). As análises de partição das betas diversidades taxonômica e funcional, para ambas regiões, revelaram um padrão similar, sendo o principal motor das diferenças observadas na composição das espécies nos ambientes o turnover, embora a substituição de espécies tenha se revelado superior à substituição funcional (tabela 3).

A partir dos valores particionados de β-diversidade taxonômica, foi encontrado que 95.5% e 97.7% do padrão observado é o resultado do processo de substituição para a região de baixa cobertura florestal (LFC) e alta cobertura florestal (HFC), respectivamente (Tabela 3). O turnover também foi o processo dominante na contribuição da b-diversidade funcional das duas regiões, sendo 73.6% para região HFC e 82.4% para região LFC. Diferente da beta taxonômica, o aninhamento teve maior participação na organização na assembleia de formigas, com 25% e 17.5% para HFC e LFC, respectivamente (table3).

Tabela 3. β-diversidade (usando o índice Jaccard) entre as duas regiões com diferentes cenários de uso do solo.

		HFC	**LFC**
Taxonômica	β-diversidade total	0.89	0.90
	Turn/Total	95.5%	97.7%
	Ani/Total	4.5%	2.2%
Funcional	β-diversidade total	0.72	0.74
	Turn/Total	73.6%	82,4%
	Ani/Total	25%	17.5%

A diferença entre o turnover taxonômico nas duas regiões é significativo, sendo que fragmentos na região de baixa cobertura florestal apresentam maiores taxas de substituição de espécies do que fragmento em regiões de baixa cobertura (Fig 4). Enquanto que para aninhamento o padrão foi o oposto, sendo que regiões com cobertura florestal mais densa e com fragmentos mais conectados tiveram aninhamento superior aos fragmentos das paisagens LFC. Por outro lado, nenhuma diferença foi detectada para a β-diversidade funcional.

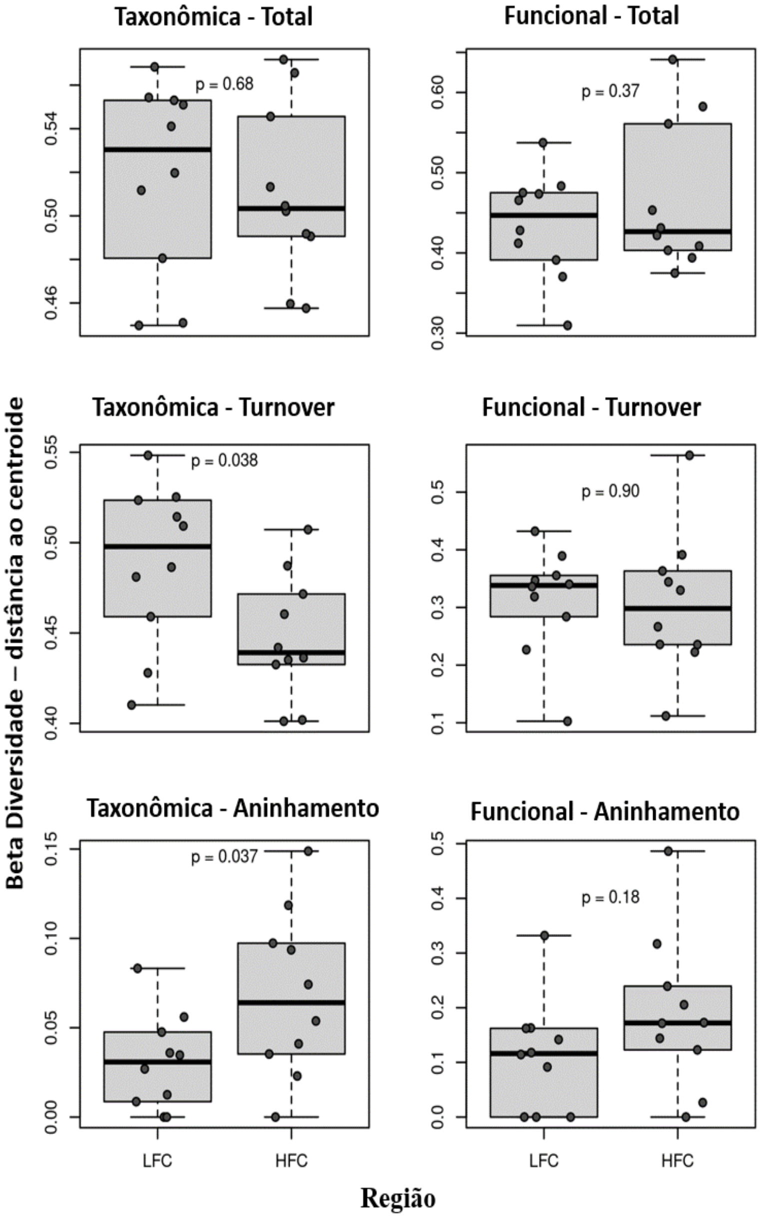

Fig 4. Boxplot com as diferenças da beta diversidade taxonômica e funcional entre regiões com base na distância ao centroide.

Discussão

Neste estudo, buscamos identificar e avaliar a composição taxonômica e funcional das assembleias de formigas presentes em duas regiões que diferem na cobertura florestal e tipo de matriz circundante. Primeiramente, nossos resultados mostraram que as assembleias de formigas destes dois tipos de cenários (HFC e LFC) diferem entre si de forma significativa e apontamos quais traços e espécies são os principais responsáveis dessas diferenças. Além disto, constatamos que embora tenham estruturas de floresta (e.g. cobertura florestal) discrepantes, os processos que estruturam a composição taxonômica e funcional destas comunidades são os mesmos e em proporções semelhantes. Neste caso, independentemente da quantidade de cobertura florestal e contexto da paisagem, o turnover atua como o processo majoritário, tanto na estruturação taxonômica quanto funcional.

Os fatores que afetam a diversidade tanto taxonômica quanto funcional de formigas normalmente têm relação direta com a estrutura do habitat (i.e. densidade de árvores, estrutura da serapilheira, estrutura da vegetação quanto à altura e tamanho do fragmento). Todos estes fatores, comumente utilizados para a caracterização local, sofreram ou podem estar sofrendo impactos diretos e indiretos dos processos regionais naturais ou antrópicos. Neste caso, dado que não há registros ou evidências de processos naturais históricos como de derivas ou barreiras biogeográficas na região considerada, a ação antrópica aparece como sendo a principal força atuante para a diferenciação das assembleias de formigas, tanto da região de Alta Cobertura Florestal (HFC) e da Baixa Cobertura Florestal (LFC). Neste sentido, a conversão de florestas tropicais em pastagens, silvicultura e agricultura, transformou paisagem que era outrora de floresta contínua em paisagens distintas com remanescentes florestais isolados e circundados por diferentes tipos de matrizes antrópicas. Essas alterações, em escala regional, têm efeito direto na composição das assembleias de formigas, ao favorecerem a substituição das espécies florestais por aquelas com requerimentos de habitat similares aos que são encontrados nas matrizes (Tathiana G. Sobrinho, Schoereder, Sperber, & Madureira, 2003)

Em nosso estudo, as formigas *Ectatomma permagnum* e *Odontomachus haemadotus*, foram fundamentais na montagem da assembleia de formigas da região LFC. *E. permagnum* é bastante comum em áreas de eucalipto (Braga, Louzada, Zanetti, & Delabie, 2010; Marinho, Zanetti, Delabie, Schlindwein, & Ramos, 2002). Assim também, *O. haemadotus* é comum em áreas antropizadas como pastos (Talaga et al., 2015) e em restingas queimadas (Bonicenha Endringer, Santos, Da Cunha Teixeira, & Schoereder, 2008). Essas duas espécies são frequentemente associadas com ambientes antropizados e são consideradas formigas indicadoras de ambientes perturbados (Ribas, Campos, Schmidt, & Solar, 2012). Esse resultado demonstra o papel relevante das matrizes adjacentes aos remanescentes da região LFC. Essa região é caraterizada principalmente por ter matrizes de pasto e eucalipto em sua composição, isso indica que as espécies de formigas que são típicas desses ambientes estão se estabelecendo com sucesso nas florestas remanescentes. Por outro lado, a espécie C*ephalotes atratus* ocorreu apenas nas paisagens florestais da região HFC. Paisagens da região HFC abrigam uma maior quantidade de espécies arbóreas (Rocha-Santos et al., 2017) e esse fator pode explicar a preferência da *C. atratus* por essa região. Isso porque essa espécie nidifica preferencialmente em ramos de árvores (Mann, 1916).

Adicionalmente, os traços responsáveis pela diferença funcional entre habitats foram melhor explicados pela variação no escapo antenal, fêmur e distância interocular. Os dois primeiros traços provavelmente refletem como as matrizes (pasto e eucalipto) e raleamento da cobertura florestal podem beneficiar formigas com características de espécies generalistas e com dieta onívora. Essa distinção nesses caracteres morfológicos podem ser respostas do aumento de espécies especialistas de bordas e comuns na matriz e uma diminuição de espécies mais vulneráveis aos efeitos da perda de habitat nos fragmentos da região LFC.

Embora distintas em composição taxonômica e funcional, podemos constatar que tanto regiões compostas por fragmentos com alta cobertura florestal (HFC) quanto aquelas compostas por fragmentos com baixa cobertura florestal (LFC), possuem altos valores de beta diversidades taxonômica e funcional. Os valores de diversidade beta em ambos os casos tem como principal processo o turnover. O turnover pode ser explicado tanto por fatores biogeográficos quanto através do contexto de antropização. A primeira proposta é pouco provável, uma vez que, as paisagens amostradas estão todas inseridas numa mesma sub-região geográfica. Por outro lado, apesar de possuírem *a priori* características bióticas similares por terem a mesma origem biogeográfica, cada fragmento pode apresentar recursos e condições abióticas diferentes, os quais são potencialmente ocupados por espécies diferentes, levando a acentuar a dissimilaridade das assembleias aos níveis dos fragmentos e das próprias unidades de paisagem (Liu, Yunhong, & Slik, 2014; Morante-Filho et al., 2016; Solar et al., 2016). A maior exposição dos fragmentos às matrizes circundantes potencializam essa divergência taxonômica na comunidade de formigas, ao favorecer a troca/substituição de espécies especialistas de florestas por outras espécies já presentes na matriz (Sobrinho & Schoereder, 2007; Sobrinho et al., 2003).

Em conformidade com nossas hipóteses iniciais, a taxa de substituição de espécies e de funções é superior entre fragmentos com baixa cobertura florestal. Nessa mesma área de estudo, um padrão de substituição similar foi observado para aves (Morante-Filho et al., 2016), onde sites isolados um dos outros sustentavam altas taxas de diversidade beta em paisagens com menos cobertura florestal. Em outras palavras, a aptidão à dispersão era mais limitante para espécies especialistas da floresta do que para espécies generalistas.

Esse padrão também foi detectado em outros estudos em regiões distintas, os quais deixaram claro que ambientes menos similares entre si devido a níveis elevados de antropização, geram estruturas de assembleias taxonomicamente e funcionalmente distintas (Rabello et al., 2021; Santoandré et al., 2019b). Os efeitos dessa antropização, nas assembleias de formigas, podem resultar em uma queda do compartilhamento de espécies na escala de paisagem, principalmente devido à dificuldade de dispersão (i.e. devido a matrizes mais inóspitas) e aumento da heterogeneidade de paisagem (Arnan, Cerdá, & Retana, 2015; Schmidt et al., 2017). Assim, nas condições de cobertura florestal rala, temos um cenário onde a assembleia de formigas é composta por diferentes espécies e com baixa redundância funcional entre fragmentos. Nesse contexto, alguns fragmentos podem conter funções ecossistêmicas únicas, as quais podem ser perdidas e extintas no próprio ambiente, em caso de perturbações ambientais que as atinjam diretamente. De forma contrária, regiões com paisagens com cobertura florestal densa apresentam maior sobreposição de funções. Essa estrutura das assembleias de formigas pode resultar em uma maior resiliência das funções diante de perturbações, pois, caso eventualmente haja perda de espécies, estas são substituídas e funções ecossistêmicas serão mantidas (Petchey & Gaston, 2002).

A partir desse cenário e da caracterização das espécies e características morfológicas responsáveis por essas diferenças e que caracterizam cada região, conseguimos ver como a qualidade ambiental de uma paisagem pode ser severamente comprometida devido à exposição a matrizes de alto contraste e pelo raleamento da cobertura florestal. A alta taxa de substituição de espécies e de suas funções revela o quanto as áreas de florestas tropicais estão ameaçadas por mudanças na paisagem. Isso indica que é necessária a priorização de um grande número de áreas para a conservação de espécies nesse ambiente. Deste modo, ressaltamos a importância também da preservação dos fragmentos com baixa cobertura florestal, pois esses podem abrigar funções únicas e estão mais susceptíveis aos eventos de extinção. Adicionalmente, nosso estudo evidencia que a perda destas áreas ou seu fracionamento também influencia a composição funcional das espécies. Assim, recomendamos fortemente a inclusão da abordagem funcional na avaliação das mudanças desencadeadas pelas alterações na paisagem.

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CONSIDERAÇÕES FINAIS

As mudanças causadas pela perda e fragmentação de habitat, incluindo os impactos provocados pelos efeitos de borda, representam uma forte ameaça à biodiversidade em ecossistemas terrestres. No cenário atual, tanto a expansão agrícola e urbana, quanto a conversão de florestas em pastagens, têm afetado diretamente a entomofauna. A partir dos estudos realizados nessa tese, consegui ampliar o conhecimento sobre os impactos antrópicos na comunidade de insetos, especialmente para a família Formicidae. É de conhecimento geral que a avaliação de questões e processos em larga escala nos ajuda a compreender de forma holística os padrões de resposta da biodiversidade.

Dentro deste propósito, a partir de uma meta-análise global, observei que as bordas de origem antrópica tem exercido uma pressão direta sobre os insetos que vivem nesse tipo de ambiente e em sua história de vida. Em particular, revelei que a crescente exposição aos efeitos de borda pode fornecer ambientes ideais para as espécies invasoras. Isso pode causar o deslocamento de espécies nativas, bem como, alterar a estrutura e funcionamento das comunidades ecológicas. Esse aumento das espécies invasoras em ambientes em áreas de borda é alarmante e merece maior atenção nos estudos conservacionistas. Dentre os traços que são afetados negativamente, destacamos a socialidade. Dessa forma, esse estudo nos alerta sobre uma parcela importante da diversidade de insetos que merece e deve ser investigada a fim de tornar mais claro o real efeito da antropização e o futuro das bordas antrópicas em áreas naturais. Sendo assim, destaco no final do primeiro capítulo, dois grandes grupos de insetos que reúnem as duas características (socialidade e forrageio pelo chão) apontadas como fator de vulnerabilidade às bordas antrópicas, os cupins e as formigas. A partir desse apontamento, foquei em entender a importância dos efeitos antrópicos em escala de paisagem sobre as assembleias de formigas.

No segundo capítulo, constatei que a perda de cobertura florestal e a densidade de borda atuam na seleção de traços ecológicos das formigas em áreas de Mata Atlântica, embora não tenha sido detectado nenhum efeito sobre a riqueza taxonômica ou funcional. Além disso, foi observado que a cobertura florestal e o contexto de ocupação antrópica atuam de forma conjunta na seleção das características funcionais das formigas. Essa seleção de características funcionais é refletida na organização e na composição funcional das espécies de formigas entre áreas que contrastam em cobertura, isolamento dos fragmentos de vegetação nativa e tipo de matriz. Ou seja, as mudanças na paisagem também interferem na composição das assembleias de formigas. A partir das respostas obtidas sobre quais espécies caracterizam cada região e de suas características morfológicas, podemos observar como a exposição às matrizes contrastantes comprometem o funcionamento dos remanescentes da Mata Atlântica. Neste sentido, foi revelado que cada fragmento apresenta um conjunto de espécies e funções com alto nível de especialização (alta taxa de turnover). Além disso, essas assembleias compostas por espécies quase que totalmente exclusivas, é mais expressiva em fragmentos mais isolados e com menor cobertura florestal. Isso indica que fragmentos pequenos dessa região devem ser incorporados aos planos de conservação. Logo, os esforços conservacionistas precisam abranger um maior conjunto de fragmentos da Mata Atlântica dessa região.

Por fim, os resultados desta tese destacam a acuidade de ir além dos estudos conservacionistas mais clássicos, e de neles incorporar também caracteres morfológicos funcionais das espécies. Dentre os traços funcionais do grupo Formicidae, destacamos o fêmur, clipeus e escapo antenal. Vimos que formigas com pernas, clipeus e escapo antenal menores, estão mais vulneráveis aos impactos da perda de habitat e efeitos de borda. Essas informações nos ajudam na tomada de decisões relacionadas às espécies de formigas cuja biologia é ainda pouco conhecida. Além disso, identificar quais características das formigas as tornam vulneráveis, ajudará a traçar metas conservacionistas mais precisas para as espécies que vivem em ecossistemas ameaçados, como a Mata Atlântica. Além disto, temos cada vez mais evidências de que a variação das características morfológicas dos insetos são indispensáveis e diretamente aplicáveis para compreender plenamente as consequências dos efeitos antrópicos sobre o funcionamento dos ecossistemas.