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Effects of Habitat Amount and Configuration on Ant Functional Traits in a Neotropical Rainforest

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Abstract

Habitat loss and fragmentation are synergetic drivers reshaping and threatening biodiversity. Although several studies have evaluated the effects of habitat loss and fragmentation on species diversity, understanding how functional traits are linked to these responses is a relatively recent approach. Ants are fundamental components of different ecosystems, especially in tropical forests where they are dominant. We analyze how functional traits of ants respond to forest cover loss and the increasing edge density in 20 forest sites in the Brazilian Atlantic Forest. We found a strong relationship between functional traits and both predictors. Specifically, forest fragments embedded in landscapes with higher edge density (i.e., a higher total length of habitat edges per unit area) showed ants with larger appendages (legs, antennal scape) and larger clypeus than those in landscapes with lower edge density. In addition, forest amount and the overall anthropic characteristics of the landscapes jointly affected ant species with larger mandibles. Altogether, our study identified a set of morphological traits correlated with the higher vulnerability of ant species to changes in landscape structure. Implications for insect conservation: we have seen that species with smaller clypeus, leg, and antennal scape are more susceptible to edge effects. Identifying the key species' attributes making 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 to agricultural land, pasture, and urban areas has drastically reduced the available habitat for native species (Laurance, 2007; Laurance et al., 2014; Morante-Filho et al., 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 et al., 2018; 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 from the perspective of conservation efforts (Hanski, 2015). For example, in human-modified landscapes, forest remnants are increasingly surrounded by matrices of non-forest vegetation (Turner, 1996; Lindell et al., 2007). The effects of the adjacent matrix result in detectable differences 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, wider temperature ranges, greater solar incidence, and lower humidity (Murcia, 1995), as well as changes in ecological flows, such as energy, organisms, and organic content (Ries et al., 2004). These changes can act as environmental filters, leading to a decrease in species richness and, ultimately, functionally 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 traditionally been assessed primarily through species richness and abundance, an approach that has gained increasing prominence over the last decades is the analysis of organisms' morphological traits related to their functional roles in ecosystems. The functional trait-based approach can provide information not captured by other diversity metrics, such as purely taxonomic ones, helping us to better understand how species reassembly occurs and which characteristics make species more sensitive under different landscape contexts. Recent studies show that structural changes in the landscape can serve as important environmental filters, selecting for specific functional characteristics within the remaining assemblages. For example, species attributes such as smaller body size and low dispersal ability are commonly associated with greater sensitivity to forest loss and fragmentation. Specifically, a recent review indicated that insect responses to edge effects vary with certain life-history traits, with species that move on the ground surface and social species being especially vulnerable (Caitano et al., 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 services, such as dispersing seeds and contributing to soil cycling and aeration (Del Toro et al., 2012). The use of ant functional traits has proven a valuable tool to assess the underlying mechanisms that influence management and land use changes (Sanabria et al., 2022; Zhang et al., 2022; Leong et al., 2022; Vasconcelos et al., 2024), the effect of fire regimes (Arnan et al., 2013), and environmental complexity (Fichaux et al., 2019; Guilherme et al., 2019) and climatic factors (Arnan et al., 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 area, allowing these species to resist in more disturbed, deforested, and fragmented landscapes, although this trait restricts their use of some types of shelters and foraging niches (Kaspari & Weiser, 1999). In addition, ants with longer legs can withstand high temperatures for longer due to convective air movement while walking (Hurlbert et al., 2008; Sommer & Wehner, 2012). Another trait often associated with environmental characteristics is the antennal scape, one of the antenna segments. The size of the scape strongly defines the capacity for chemical-sensory and tactile perception in a chemically oriented species (Weiser & Kaspari, 2006; Yates et al., 2014). Ants with proportionally larger antennal scapes are often associated with more complex environments and therefore with higher demands on their sensory perception capacity (Yates et al., 2014; Fichaux et al., 2019; Nooten et al., 2019).

In addition to filtering species by locomotion mode and sensory perception, changes in landscape structure that alter the quality and composition of remaining habitats can select for species based on how they acquire resources. In this study, we use the length of morphological structures as proxies for body size and functional performance. For example, ants with proportionally larger mandibles are associated with predatory habits (Gibb et al., 2014). Environments with a greater quantity and variety of potential prey items can increase the probability of survival of predator species at these sites (Campiolo et al., 2015). Also, species that feed on extrafloral nectaries and on the sugary secretions of hemiptera have larger clypeus (structures involved in obtaining liquid resources) (Davidson et al., 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.

Recent studies have focused on using ants' functional traits to assess the environmental impacts of anthropogenic activities. For example, environments that have undergone land-use modifications present ant assemblages with functional traits different from those of assemblages in unmodified forests (Nooten et al., 2019; Leong et al., 2022; Sanabria et al., 2022; Vasconcelos et al., 2024). Despite the great relevance of these studies, most focus on comparing highly contrasting environments. We still know little about more detailed responses regarding the gradual loss of forest and, eventually, the exposure of these fragments to edge density.

We assessed how changes in landscape composition and configuration, specifically forest cover loss and increases in edge density, affect ant diversity and functional traits. Edge density was defined as the total length of forest–non-forest edges per unit area of the landscape (e.g., meters per hectare), a standard metric in landscape ecology used to quantify fragmentation in human-modified landscapes. We predicted that 1) forest cover would be positively correlated with mean mandible size, and 2) landscapes with higher edge density would harbor ant species with larger clypeus, antennae, and legs. These expectations are detailed and explained in Table 1. Our primary goal was to investigate how ant functional traits influence species vulnerability to structural changes in human-modified landscapes.

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 et al., 1998). According to the Köppen classification, the climate is hot and humid, with no dry season.

We selected 20 landscapes covering a forest cover gradient (Fig 1) using the patch-landscape approach (Tischendorf & Fahrig, 2000). All landscapes were mapped for land use using satellite imagery (RapidEye, 2009-2010; QuickBird; and WorldView, 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 et al., 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 forest cover to be 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 involves pruning branches of plants and wrapping them in plastic collection bags (40 x 60 cm) to capture invertebrates in the foliage (Cooper & Whitmore, 1990). For the application of the method, five (5) transects of 25 m each were allocated at each sampling site, with a minimum distance of 25 m between transects (Fig 1). In each transect, we randomly selected five (5) plants in the forest understory with a 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, with a minimum distance of 10 m between traps; there were three pitfalls per transect, totaling 15 traps per sampling site. The pitfalls were set for a total period of 48 hrs. 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 to species level whenever possible; otherwise, they were classified as morphospecies. Identifications were performed by comparison with the reference collection of the Myrmecology Laboratory at CEPEC/CEPLAC. Voucher specimens are deposited in the CEPEC Myrmecology Laboratory Collection.

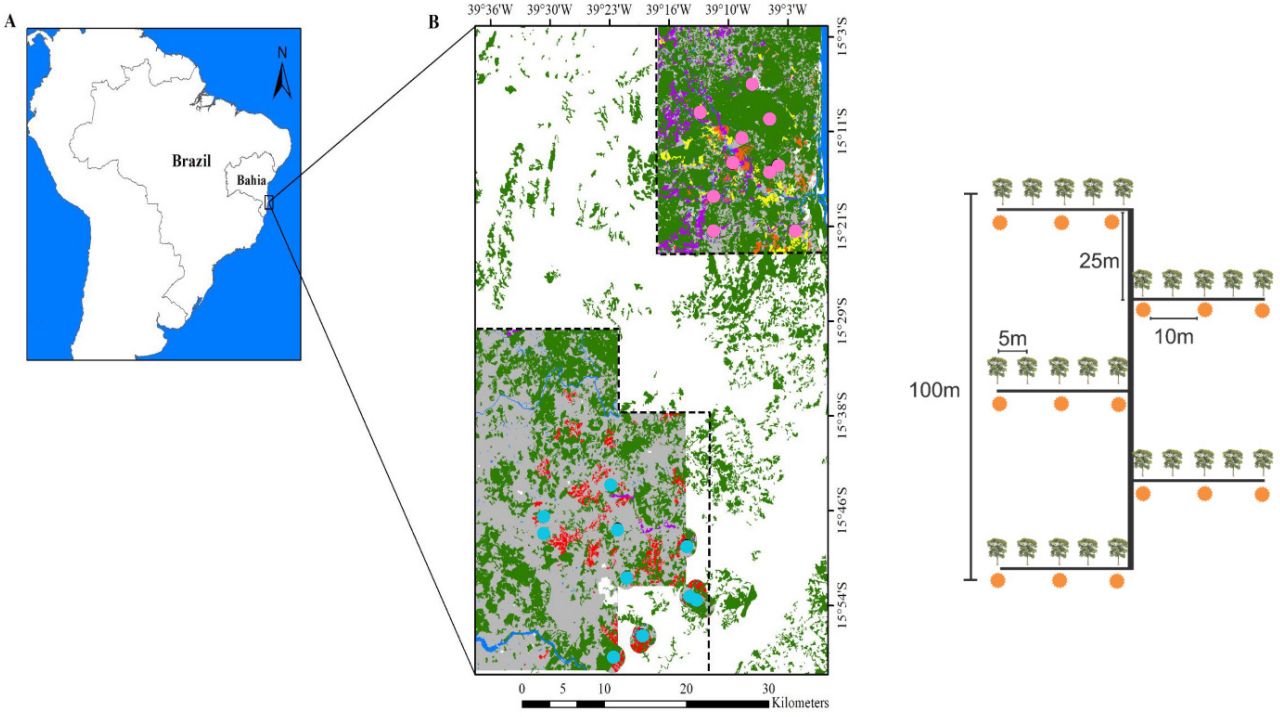


Fig 1. Location of the 20 sampled forest landscapes in southeastern Bahia, Brazil, and their land-cover classification used to calculate landscape descriptors. Black points indicate sampling sites. Blue dots correspond to the region with low forest cover (LFC), while pink dots represent sites in the region with high forest cover (HFC). Ants were collected on trees and on the ground using branch clipping and pitfall traps, respectively. Orange circles represent pitfall traps; each landscape included 25 sampled plants and 15 pitfalls.

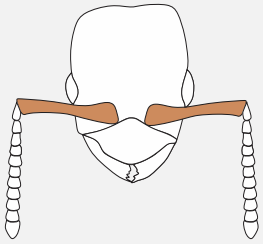
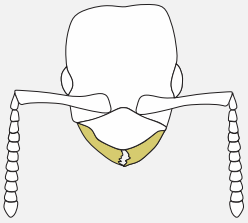
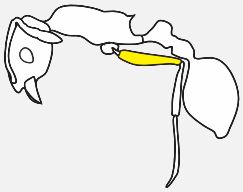
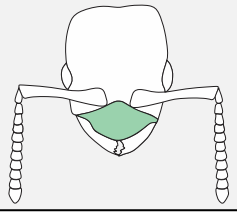
Functional traits

We measured eight morphological characteristics (Table 2). We selected those traits because they are strongly associated with a species' capacity to use and explore available resources and 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 was adopted to avoid confounding environmental effects with morphological variation associated with worker polymorphism (major and minor workers). We measured the ants using an ocular micrometer, accurate to 0.01 mm, mounted on a Leica M80 stereomicroscope (Leica Microsystems, Ilhéus, Brazil). The functional traits were standardized using Weber's measure (trait value/Weber's length), the longest rigid length on an ant's body, to reduce errors in measuring body size. All features were standardized by Weber's length, except for the mandible, which was standardized by head width (see Fowler et al., 1991; Bishop et al., 2015; Guilherme et al., 2019).

Data Analysis

We used forest cover and edge density as predictor variables. The study region (HFC or LFC) comprised an interaction factor in the models; the differences between land-use in both regions were taken into account. It is well known that decreases in habitat availability and increases in edge density are frequently correlated patterns in the complex processes of habitat loss and fragmentation driven by human land use (Fahrig et al., 2003). Then, we tested the correlation between forest cover and edge density using a concurvity analysis within generalized additive models (GAMs), where

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

VARIABLES	FOREST COVER	EDGE DENSITY	EXPLANATION
Antennal scape 	↓	↑	Ants depend on chemical markers (e.g., pheromones and kairomones) for communication, foraging, and orientation. Because the antennae contain the sensory receptors involved in chemo-sensory and tactile perception, variation in antennal morphology is associated with differences in sensory capacity. Thus, scape length is not a causal factor per se, but is widely used as a morphological proxy for antennal size and sensory performance in ants (Weiser & Kaspari, 2006). We expect that in environments where the ground surface is more heterogeneous and sensorially complex, ants with shorter antennal scapes are more likely to be sensory-limited, which may reduce their foraging efficiency. Forest fragments with higher edge density tend to present a more irregular three-dimensional configuration of the soil surface due to the accumulation of coarse woody debris and litter, increasing both physical barriers and chemical noise.
Mandible 	↑	↓	Predatory species, on average, have larger mandibles, here assessed as mandible length, which is commonly used as a proxy for mandible size and predatory ability. Sites in landscapes with greater forest cover and lower anthropogenic disturbance may harbor a higher quantity and diversity of potential prey, making them more suitable environments for predatory ants and increasing their probability of persistence. Therefore, we expect that ants in areas with higher forest cover and lower edge density will exhibit longer mandibles.
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 ants. In general, species that feed on extrafloral nectaries and on the sugary secretions of hemipterans tend to have a larger clypeus, here assessed as clypeus length. Forest fragments embedded in more deforested landscapes tend to show higher edge representation and a higher proportion of pioneer plants, which usually invest more in extrafloral nectaries. Therefore, we expect that landscapes with higher edge density and lower forest cover will harbor ant species with longer clypeus.

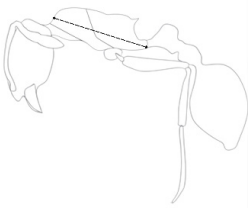
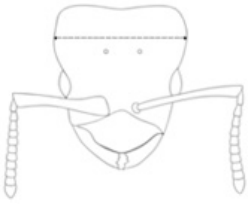
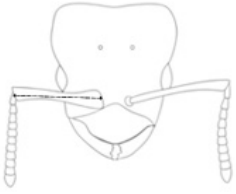
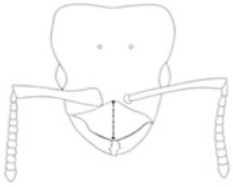
concurvity values range from 0 (no collinearity) to 1 (perfect collinearity), allowing us to evaluate potential nonlinear dependencies between predictor variables.

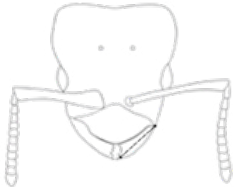
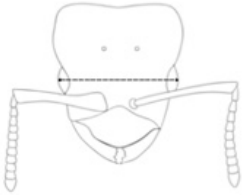
Our response variables were the mean values of mandible, antennal scape, clypeus, and femur lengths of ants collected using pitfall and branch-clipping methods. To analyze how traits are affected, we calculated the community-trait mean (CTM) in each landscape: (summed mean of trait values in co-occurring species/number of species) (Guilherme et al., 2019). We used only the traits most closely related to feeding, foraging mode, and sensory ability to calculate the CTM (mandible, femur, clypeus, and antennal scape lengths). Our unit of analysis was the landscape level.

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 radii around each sampling site to identify species response to multiple scales (Huais, 2018). We selected the best buffer size for each response variable using the smallest Akaike Information Criterion corrected for small samples (AICc) (supplementary material). All models were fitted using Additive Models (GAM).

We used generalized additive models (GAMs) to test the relationships between the response variables (functional traits) and the predictors (forest cover, edge density, and region).

Table 2. 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 based on or using liquid resources (Davidson et al. 2004)

Traits	Ecological functions
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 (Kaspari and Weiser, 1999; Hurlbert et al., 2008; 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 et al., 2003)

Different models were fitted (see Table 3) after determining the most appropriate buffer size for each response variable. For all smooth terms, we set a maximum basis dimension (k) of 4, which defines the upper limit of model complexity. This value was chosen a priori to limit the number of parameters and avoid overfitting, given the relatively small sample size. The effective degree of smoothing was then automatically estimated by the model during fitting. Then, based on our initial hypotheses (Table 1), we contrasted different models (Table 3). 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, Forest Cover and Edge. The AICc was used for model selection (Burnham & Anderson, 2002). Models with $\Delta AICc < 2.0$ 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 (R Core Team, year), supported by the packages mgcv (Wood, 2006), visreg (Breheny & Burchett, 2017), gamm4 (Wood & Scheipl, 2017), bbmle (Bolker, 2013), mgcViz (Fasiolo et al., 2018), and tidymv (Coretta, 2020).

Results

We sampled 123 ant species from 39 genera and 8 subfamilies (Supplementary Material, Table 1). The subfamilies Myrmicinae (64 species) and Ponerinae (20 species) were the best-represented in the samples. The most frequent species were Crematogaster limata (Smith, 1858) and Ectatomma tuberculatum (Olivier, 1792). A total of 4,021 ant morphological measurements were performed in different gradients of forest cover and edge density. The selected spatial scales ranged from 200 to 1000 m, depending on the response variable, and represent the spatial extents at which landscape metrics showed the strongest relationships with each response variable (Supplementary Material, Table 2). Edge density and forest cover were not correlated (Supplementary Material, Table 3).

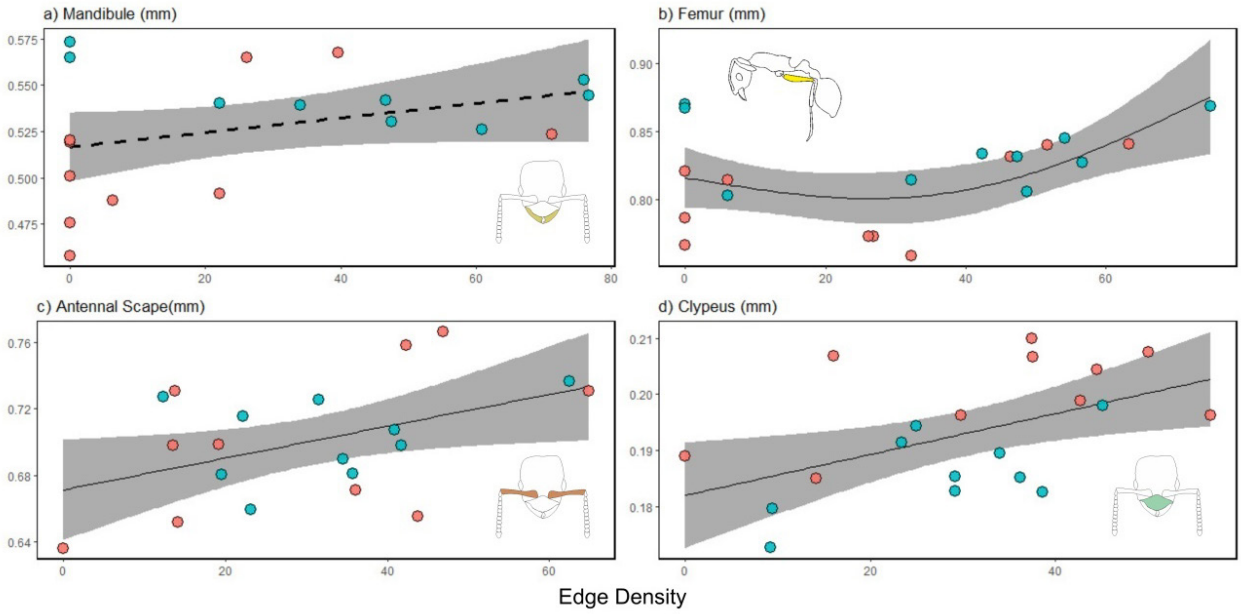


Fig 2. Relationship between edge density within 1-km landscape buffer at 20 surveyed forest sites and functionals traits. Blue dots correspond to the region with low forest cover (LFC), while pink dots represent sites in the region with high forest cover (HFC). When a null model was selected (without the effects of edge density), we represent it by the dashed line.

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.
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.
Forest Cover and Edge	Forest cover and edge density joinly affects the response variable.

Landscapes with higher edge densities had ants with significantly larger femora, antennal scapes, and clypeae (Fig 2b, c, d). We also detected significant differences in trait sizes between the two regions. In the High Forest Cover (HFC) region (i.e., more connected fragments and low contrast matrices), forest cover was negatively related with mandible and clypeus size (Fig 3a, d). Although the average size of mandible and clypeus was smaller in the other region, no relationship with forest cover was detected.

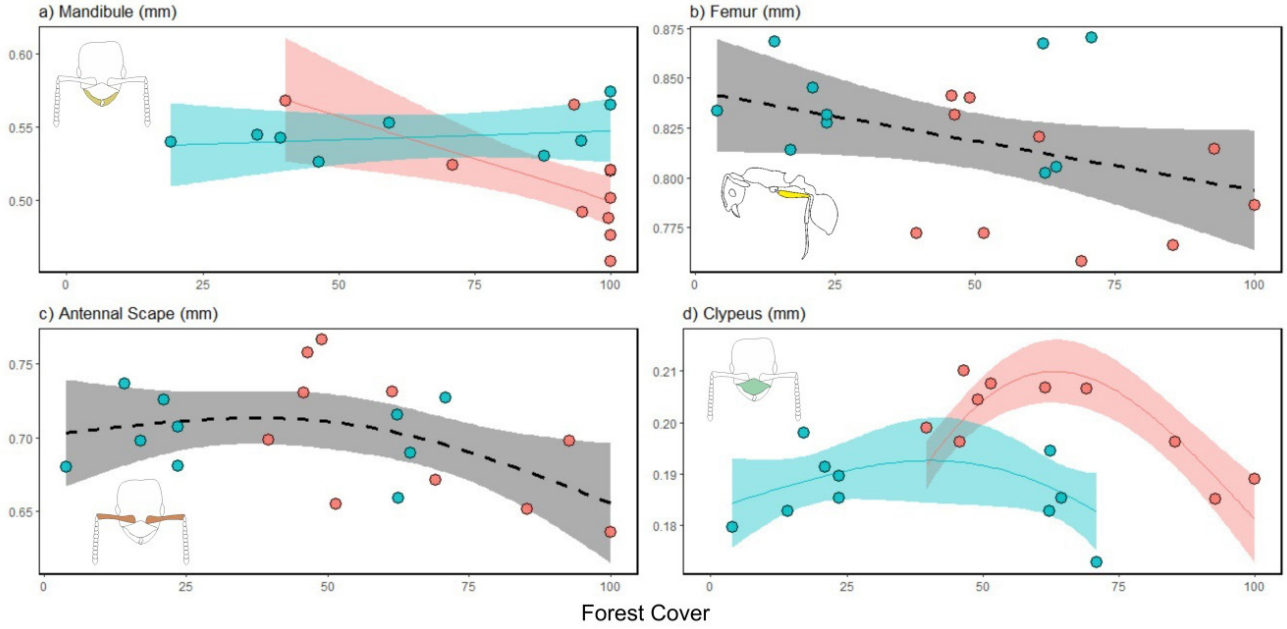


Fig 3. Relationships between mandible (a), femur (b), antennal scape (c) and clypeus (d) according to forest cover loss at the landscape-scale. Blue dots correspond to the region with low forest cover (LFC), while pink dots represent sites in the region with high forest cover (HFC). When a null model was selected (without the effects of forest cover), we represent it by the dashed line.

Discussion

Our study showed how landscape changes can significantly alter 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 appendices (leg, antenna) and clypeus. Furthermore, we show the pervasive role of deforestation at the landscape scale in shaping important functional traits, as demonstrated by differences in mandible and clypeus size between two nearby regions, one less forested and the other more forested.

The morphological characters favored by increased edge density (larger antennal scape, clypeus, and legs) are typical of habitat-generalist ant species with an omnivorous diet (Silva & Brandão, 1999). The presence of generalist species is commonly associated with landscapes highly exposed 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 (Murcia, 1995; Harper et al., 2005). These factors together directly interfere with the ants' nesting and foraging strategy. Small-legged ants generally prefer to nest in twigs on the ground or in leaf litter, with little exposure to direct sunlight, and rarely cover distances greater than 1 m 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, reducing the distance between their bodies and warmer air surfaces (Sommer & Wehner, 2012), which can be a valuable strategy in environments more exposed to solar radiation. A good example of this is the genus *Dorymyrmex,* which is virtually the only ant genus in the Neotropical Region that can forage at midday on beaches (Jaffe, 1993).

The positive relationship between antennal scape length and increased edge exposure may be related to changes in the three-dimensional configuration of the ground surface within forest fragments. As ants forage mainly on the ground, the arrangement of elements on the soil surface, such as fallen branches and coarse woody debris, can act as physical and sensory barriers. The spatial configuration of these elements differs between fragmented and continuous forests. In tropical environments, sites with stronger edge influence may present up to 60% more fallen woody litter than areas with lower edge exposure. This dense and heterogeneous ground cover may interfere with the dispersion of semiochemical cues, making

the olfactory environment more complex and potentially favoring ants with longer antennal scapes, which may be more efficient in chemical and tactile perception. In addition, ant trails may be more easily disrupted in edge-exposed areas, since higher solar radiation increases the evaporation and degradation rates of trail pheromones, as commonly observed in 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, such as those in the Ponerinae subfamily, in fragments with less forest cover in the less anthropized region. In this region, the remnants have a low-contrast matrix, such as agroforestry systems, and are relatively less isolated. This indicates that species that can capture large prey can establish themselves in landscapes with less forest cover, where the remaining patches are more connected and embedded in more "friendly" matrices (Dias et al., 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 landscapes with lower forest cover and fragments with higher edge density, tended to harbor ants with larger clypeus. Ants with a larger clypeus are generally associated with nectarivorous habits, commonly feeding on sugary liquids secreted by homopterans or on plants bearing extrafloral nectaries (Fowler et al., 1991). Thus, clypeus size is often hypothesized to be related to the use of liquid resources in ants. Extrafloral nectaries are typical of pioneer plant species, which present high growth rates and are associated with high-light environments (Bentley, 1976). Forest cover loss and increased exposure to edge effects may favor the establishment of such plants and, consequently, increase the availability of liquid resources at these sites, thereby attracting nectarivorous ant species, such as those in the subfamilies Dolichoderinae and Formicinae (Bentley, 1976; Pereyra et al., 2015).

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 across traits reveal that this tool can help us decide which ant species may be most vulnerable to the effects of changes in tropical rainforests. Here, we encourage the study of effects generated by changing landscapes in other taxonomic groups using a functional approach.

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Authors' Contribution

B.C.: Conceptualization, formal analysis, writing-original draft.
P.D.: Supervision, conceptualization, formal analysis, data curation, writing-review & editing.
I.M.: Investigation, conceptualization, methodology, writing-review and editing.
D.F.: Supervision, conceptualization, methodology, funding acquisition, writing-review & editing.
J.H.C.D.: Supervision, conceptualization, writing-review & editing.

References

Arnan, X., Cerdá, X., Rodrigo, A. & Retana, J. (2013). Response of ant functional composition to fire. Ecography, 36: 1182-1192. https://doi.org/10.1111/j.1600-0587.2013.00155.x

Benchimol, M., Mariano-Neto, E., Faria, D., Rocha-Santos, L., de Souza Pessoa, M., Gomes, F. S., Talora, D.C. & Cazetta, E. (2017). Translating plant community responses to habitat loss into conservation practices: Forest cover matters. Biological Conservation, 209: 499-507. https://doi.org/10.1016/j.biocon.2017.03.024

Bentley, B.L. (1976). Plants bearing extrafloral nectaries and the associated ant community: Interhabitat differences in the reduction of herbivore damage. Ecology, 57: 815-820. https://doi.org/10.2307/1936195

Bishop, T.R., Robertson, M.P., van Rensburg, B.J. & Parr, C.L. (2015). Contrasting species and functional beta diversity in montane ant assemblages. Journal of Biogeography, 42: 1776-1786. https://doi.org/10.1111/jbi.12537

Blüthgen, N., Stork, N.E. & Fiedler, K. (2004). Bottom-up control and co-occurrence in complex communities: Honeydew and nectar determine a rainforest ant mosaic. Oikos, 106: 344-358. https://doi.org/10.1111/j.0030-1299.2004.12687.x

Bolker, B. (2013). bbmle: Tools for General Maximum Likelihood Estimation. R package version 1.0.25.1.

Bolton, B. (2003). Synopsis and classification of Formicidae. Gainesville: American Entomological Institute.

Bolton, B. (2016). New General Catalogue of the Ants of the World, and Synopsis of Taxonomic Publications on Formicidae.

Breheny, P. & Burchett, W. (2017). Visualization of regression models using visreg. The R Journal, 9: 56-71. https://doi.org/10.32614/rj-2017-046

Burnham, K.P. & Anderson, D.R. (2002). Model selection and multi-model inference: A practical information-theoretic approach. New York: Springer.

Caitano, B., Chaves, T.P., Dodonov, P. & Delabie, J.H.C. (2020). Edge effects on insects depend on life history traits: A global meta-analysis. Journal of Insect Conservation, 4: 233-240. https://doi.org/10.1007/s10841-020-00227-1

Cianciaruso, M.V., Silva, I.A. & Batalha, M.A. (2009). Diversidades filogenética e funcional: Novas abordagens para a ecologia de comunidades. Oecologia Brasiliensis, 9: 93-103. https://doi.org/10.1590/s1676-06032009000300008

Cleary, D.F.R., Boyle, T.J.B., Setyawati, T. et al. (2007). Bird species and traits associated with logged and unlogged forest in Borneo. Ecological Applications, 17: 1184-1197. https://doi.org/10.1890/05-0878

Cooper, R. & Whitmore, R.C. (1990). Arthropod sampling methods in ornithology. In D.M. Power (Ed.), Current Ornithology. New York: Plenum Press. pp. 29-37.

Coretta, S. (2020). tidymv: Tidy Model Visualisation for Generalised Additive Models. R package version 3.0.0. Retrieved from: https://CRAN.R-project.org/package=tidymv https://doi.org/10.32614/cran.package.tidymv

Davidson, D.W., Cook, S.C. & Snelling, R.R. (2004). Liquid-feeding performances of ants (Formicidae): Ecological and evolutionary implications. Oecologia, 139: 255-266. https://doi.org/10.1007/s00442-004-1508-4

Del Toro, I., Ribbons, R.R. & Pelini, S.L. (2012). The little things that run the world revisited: A review of ant-mediated ecosystem services and disservices (Hymenoptera: Formicidae). Myrmecological News, 17: 133-146.

Delabie, J.H.C., Feitosa, R.M., Serrão, J.E., Mariano, C.S.F. & Majer, J.D. (2015). As formigas poneromorfas do Brasil: Introduction: the poneromorph ants of Brazil. In J.H.C. Delabie, R.M. Feitosa & J.D. Majer (Eds.), As formigas poneromorfas do Brasil. Ilhéus: Editus. pp. 447-462 https://doi.org/10.7476/9788574554419.0001

Dias, N.S., Zanetti, R., Santos, M.S. et al. (2008). Interação de fragmentos florestais com agroecossistemas adjacentes de café e pastagem: Respostas das comunidades de formigas (Hymenoptera, Formicidae). Iheringia Série Zoologia, 98: 136-142. https://doi.org/10.1590/s0073-47212008000100017

Fahrig, L. (2013). Rethinking patch size and isolation effects: The habitat amount hypothesis. Journal of Biogeography, 40: 1649-1663. https://doi.org/10.1111/jbi.12130

Fasiolo, M., Nedellec, R. & Wood, S.N. (2018). mgcViz: Visualizations for generalized additive models. R package.

Fichaux, M., Béchade, B., Donald, J. et al. (2019). Habitats shape taxonomic and functional composition of Neotropical ant assemblages. Oecologia, 189: 501-513. https://doi.org/10.1007/s00442-019-04341-z

Fichaux, M., Vleminckx, J., Courtois, E.A. et al. (2020). Environmental determinants of leaf litter ant community composition along an elevational gradient. Biotropica, 53: 97-109. https://doi.org/10.1111/btp.12849

Fittkau, E.J. & Klinge, H. (1973). On biomass and trophic structure of the Central Amazonian rain forest ecosystem. Biotropica, 5: 2-14. https://doi.org/10.2307/2989676

Fletcher, R.J. Jr., Didham, R.K., Banks-Leite, C. et al. (2018). Is habitat fragmentation good for biodiversity? Biological Conservation, 226: 9-15. Result score too low

Fowler, H.G., Forti, L.C., Brandão, C.R.F. & Delabie, J.H.C. (1991). Ecologia nutricional de formigas. In A.R. Panizzi & J.R.P. Parra (Eds.), Ecologia nutricional de insetos e suas implicações no manejo de pragas. São Paulo: Manole. pp. 131-223. https://doi.org/10.1590/s0102-311x1993000100013

Gibb, H., Stoklosa, J., Warton, D.I. et al. (2014). Does morphology predict trophic position and habitat use of ant species and assemblages? Oecologia, 177: 519-531. https://doi.org/10.1007/s00442-014-3101-9

Guilherme, D.R., Souza, J.L.P., Franklin, E. et al. (2019). Can environmental complexity predict functional trait composition of ground-dwelling ant assemblages? A test across the Amazon Basin. Acta Oecologica, 99: 103434. https://doi.org/10.1016/j.actao.2019.05.004

Hanski, I. (2015). Habitat fragmentation and species richness. Journal of Biogeography, 42: 989-993. https://doi.org/10.1111/jbi.12478

Harper, K.A., Macdonald, S.E., Burton, P.J. et al. (2005). Edge influence on forest structure and composition in fragmented landscapes. Conservation Biology, 19: 768-782. https://doi.org/10.1111/j.1523-1739.2005.00045.x

Huais, P.Y. (2018). multifit: An R function for multi-scale analysis in landscape ecology. Landscape Ecology, 33: 1023-1028. https://doi.org/10.1007/s10980-018-0657-5

Hurlbert, A.H., Ballantyne, I.V.F. & Powell, S. (2008). Shaking a leg and hot to trot: The effects of body size and temperature on running speed in ants. Ecological Entomology, 33: 144-154. https://doi.org/10.1111/j.1365-2311.2007.00962.x

Jaffe, K. (1993). Surfing ants. Florida Entomologist, 76: 182-183. https://doi.org/10.2307/3496029

Kaspari, M. (1993). Body size and microclimate use in Neotropical granivorous ants. Oecologia, 96: 500-507. https://doi.org/10.1007/bf00320507

Kaspari, M. & Weiser, M.D. (1999). The size-grain hypothesis and interspecific scaling in ants. Functional Ecology, 13: 530-538. https://doi.org/10.1046/j.1365-2435.1999.00343.x

Kotze, J. & O'Hara, R.B. (2003). Species decline – but why? Explanations of carabid beetle (Coleoptera, Carabidae) declines in Europe. Oecologia, 135: 138-148. https://doi.org/10.1007/s00442-002-1174-3

Laurance, W.F. (2007). Have we overstated the tropical biodiversity crisis? Trends in Ecology and Evolution, 22: 65-70. https://doi.org/10.1016/j.tree.2006.09.014

Laurance, W.F., Sayer, J. & Cassman, K.G. (2014). Agricultural expansion and its impacts on tropical nature. Trends in Ecology and Evolution, 29: 107-116. https://doi.org/10.1016/j.tree.2013.12.001

Leal, I.R., Filgueiras, B.K.C., Gomes, J.P. et al. (2012). Effects of habitat fragmentation on ant richness and functional composition in Brazilian Atlantic forest. Biodiversity and Conservation, 21: 1687-1701. https://doi.org/10.1007/s10531-012-0271-9

Leong, C.M., Wang, R., Cheung, S.C. et al. (2022). Are thermal constraints shaping foraging ant assemblages in tropical regions? Integrating thermal and morphological traits to understand consequences of land-use transformation. Insect Conservation and Diversity, 16: 254-265.

https://doi.org/10.1111/icad.12619

Lindell, C.A., Riffel, S.K., Kaiser, S.A. et al. (2007). Edge responses of tropical and temperate birds. The Wilson Journal of Ornithology, 119: 205-220. https://doi.org/10.1676/05-133.1

Manhães, M.A. & Dias, M.M. (2011). Spatial dynamics of understorey insectivorous birds and arthropods in a southeastern Brazilian Atlantic woodlot. Brazilian Journal of Biology, 71: 1-7. https://doi.org/10.1590/s1519-69842011000100003

McGarigal, K. & Marks, B.J. (1995). FRAGSTATS: Spatial pattern analysis program for quantifying landscape structure. Portland: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. https://doi.org/10.2737/pnw-gtr-351

Morante-Filho, J.C., Arroyo-Rodriguez, V. & Faria, D. (2016). Patterns and predictors of β-diversity in the fragmented Brazilian Atlantic forest: A multiscale analysis of forest specialist and generalist birds. Journal of Animal Ecology, 85: 240-250. https://doi.org/10.1111/1365-2656.12448

Morante-Filho, J.C., Benchimol, M. & Faria, D. (2020). Landscape composition is the strongest determinant of bird occupancy patterns in tropical forest patches. Landscape Ecology, 36: 105-117. https://doi.org/10.1007/s10980-020-01121-6

Mouchet, M.A., Villéger, S., Mason, N.W.H. & Mouillot, D. (2010). Functional diversity measures: An overview of their redundancy and their ability to discriminate community assembly rules. Functional Ecology, 24: 867-876. https://doi.org/10.1111/j.1365-2435.2010.01695.x

Murcia, C. (1995). Edge effects in fragmented forests: Implications for conservation. Trends in Ecology and Evolution, 10: 58-62. https://doi.org/10.1016/s0169-5347(00)88977-6

Nooten, S.S., Schultheiss, P., Rowe, R.C. et al. (2019). Habitat complexity affects functional traits and diversity of ant assemblages in urban green spaces (Hymenoptera: Formicidae). Myrmecological News, 29: 67-77.

Pereyra, M., Pol, R.G. & Galetto, L. (2015). Does edge effect and patch size affect the interaction between ants and Croton lachnostachyus in fragmented landscapes of Chaco forest? Arthropod-Plant Interactions, 9: 175-186. https://doi.org/10.1007/s11829-015-9361-4

Püttker, T., Crouzeilles, R., Almeida-Gomes, M. et al. (2020). Indirect effects of habitat loss via habitat fragmentation: A cross-taxa analysis of forest-dependent species. Biological Conservation, 241: 108368.

R Core Team. (2020). R: A language and environment for statistical computing. Vienna: R Foundation for Statistical Computing. Retrieved from: https://www.r-project.org/

Rainio, J. & Niemela, J. (2003). Ground beetles (Coleoptera: Carabidae) as bioindicators. Biodiversity and Conservation, 12: 487-506. https://doi.org/10.1023/a:1022412617568

Ries, L., Fletcher, R.J. Jr., Battin, J. & Sisk, T.D. (2004). Ecological responses to habitat edges: Mechanisms, models, and variability explained. Annual Review of Ecology, Evolution, and Systematics, 35: 491-522. https://doi.org/10.1146/annurev.ecolsys.35.112202.130148

Rocha-Santos, L., Pessoa, M.S., Cassano, C.R. et al. (2016). The shrinkage of a forest: Landscape-scale deforestation leading to overall changes in local forest structure. Biological Conservation, 196: 1-9. https://doi.org/10.1016/j.biocon.2016.01.028

Rodrigues, P.J. & Nascimento, M.T. (2006). Fragmentação florestal: Breves considerações teóricas sobre efeitos de borda. Rodriguésia, 57: 63-74. https://doi.org/10.1590/2175-7860200657105

Sanabria, C., Barot, S., Fonte, S.J. & Dubs, F. (2022). Do morphological traits of ground-dwelling ants respond to land use changes in a neotropical landscape? Geoderma, 418: 115841. https://doi.org/10.1016/j.geoderma.2022.115841

Silva, R.R. & Brandão, C.R.F. (1999). Formigas (Hymenoptera: Formicidae) como indicadores da qualidade ambiental e da biodiversidade de outros invertebrados terrestres. Biotemas, 12: 55-73.

Silvestre, R., Brandão, C.R.F. & Silva, R.R. (2003). Grupos funcionales de hormigas: El caso de los gremios del Cerrado.

In F. Fernández (Ed.), Introducción a las hormigas de la región Neotropical. Bogotá: Instituto de Investigación de Recursos Biológicos Alexander von Humboldt. pp. 113-148. https://doi.org/10.25100/socolen.v32i1.9373

Sommer, S. & Wehner, R. (2012). Leg allometry in ants: Extreme long-leggedness in thermophilic species. Arthropod Structure and Development, 41: 71-77. https://doi.org/10.1016/j.asd.2011.08.002

Thier, O. & Wesenberg, J. (2016). Floristic composition and edge-induced homogenization in tree communities in the fragmented Atlantic rainforest of Rio de Janeiro, Brazil. Tropical Conservation Science, 9: 852-876. https://doi.org/10.1177/194008291600900217

Thomas, W.W., De Carvalho, A.M.V., Amorim, A.M.A. et al. (1998). Plant endemism in two forests in southern Bahia, Brazil. Biodiversity and Conservation, 7: 311-322. https://doi.org/10.1023/a:1008825627656

Tischendorf, L. & Fahrig, L. (2000). On the usage and measurement of landscape connectivity. Oikos, 90: 7-19. https://doi.org/10.1034/j.1600-0706.2000.900102.x

Turner, I.M. (1996). Species loss in fragments of tropical rain forest: A review of the evidence. Journal of Applied Ecology, 33: 200-209. https://doi.org/10.2307/2404743

Vasconcelos, H.L., Neves, K.C., Vieira, J. et al. (2024). Land-use intensification has extensive effects on the functional and phylogenetic diversity of Neotropical ant communities. Biodiversity and Conservation, 33: 2487-2502. https://doi.org/10.1007/s10531-024-02866-1

Van Oudenhove, L., Billoir, E., Boulay, R. et al. (2011). Temperature limits trail following behaviour through pheromone decay in ants. Naturwissenschaften, 98: 1009-1017. https://doi.org/10.1007/s00114-011-0852-6

Weiser, M.D. & Kaspari, M. (2006). Ecological morphospace of New World ants. Ecological Entomology, 31: 131-142. https://doi.org/10.1111/j.0307-6946.2006.00759.x

Wood, S.N. (2008). Fast stable direct fitting and smoothness selection for generalized additive models. Journal of the Royal Statistical Society Series B: Statistical Methodology, 70: 495-518. https://doi.org/10.1111/j.1467-9868.2007.00646.x

Wood, S.N. (2006). Generalized additive models: An introduction with R. Boca Raton: Chapman and Hall/CRC.

Wood, S. & Scheipl, F. (2017). gamm4: Generalized additive mixed models using “mgcv” and “lme4”. R package version 0.2-5. https://doi.org/10.32614/cran.package.gamm4

Yates, M.L., Andrew, N.R., Binns, M. & Gibb, H. (2014). Morphological traits: Predictable responses to macrohabitats across a 300 km scale. PeerJ, 2: e271. https://doi.org/10.7717/peerj.271

Zhang, X., Lu, Z.X., Zhang, N.N. & Chen, Y.Q. (2022). Data of ant community compositions and functional traits responding to land-use change at the local scale. Biodiversity Data Journal, 10: e85119. https://doi.org/10.3897/bdj.10.e85119.suppl1