Ant habitat-use guilds response to forest-pasture shifting in southwestern Amazon

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Abstract

Ant assemblages have been used as bioindicators of the response of biodiversity to different types of anthropogenic disturbances. However, usual diversity metrics (e.g., ant species richness and composition) sometimes seem fair limited to show a general panorama of human impacts. Thus, we verified habitat-use ant guilds as a complementary predictable parameter, based on the ant fauna reported to thirteen forest fragments and pastures in southwestern Brazilian Amazon. Specifically, we hypothesized that forest specialist, open-habitat specialist, and generalist ants would present distinct responses to forest-pasture shifting. We expected that the forest-pasture shifting promotes a decrease in the species richness of forest specialists and an increase in open-habitat specialists, while the generalists would have few changes in their richness because they can live in both habitats. As expected, the species richness of forest specialist ants decreased, and open-habitat ants increased with forest-pasture shifting, while generalists had few changes. This indicates that in human-induced open habitats (e.g., pastures) are essentially made up by generalist ants and open-habitat ant specialists that replace forest specialists. Additionally, considering the plasticity of generalist ants, they can be considered as primary elements of ant assemblages. Therefore, a future step is to quantify the limit of forest cover clearing in human-induced land uses that assure a higher species richness of forest-specialist ants than other habitat-use guilds.

Introduction

Human activities have been responsible for huge impacts on natural ecosystems (Oliver et al. 2016). Fragmentation, habitat loss and habitat degradation are the main sources of biodiversity loss and ecosystem function hampering (Fahrig 2013; Oliver et al. 2016) in high human-modified landscapes (Tscharntke et al. 2012). Considering the difficulty of assessing the biodiversity response to different types of human impacts, the use of bioindicators has been proposed (McGeoch 1998). Bioindicators are groups of organisms which diversity patterns and ecological functions clearly and predictably respond to anthropogenic impacts (McGeoch 1998; Del Toro et al. 2012).

Ants are excellent bioindicators because they have a large biomass in almost all terrestrial habitats, participate in several ecosystem functions (predation, seed dispersal, pollination, and others) (Leal et al. 2015), have mutualistic associations with other organisms (Del Toro et al. 2012; Parker 2022; Hojo 2022), are relatively easy to sample and identify (Agosti et al. 2000), and predictably respond to human impacts (Underwood and Fisher 2006; Philpott et al. 2010). However, among diversity patterns, species richness and diversity indexes have presented a coarse response to human impacts (Ribas et al. 2012). Thus, several studies have highlighted that ant species composition clearest and most expected answer to several natural and human-induced impacts (Gollan et al. 2011; Ribas et al. 2012; Schmidt et al. 2013).

Ant species differ regarding their habitat preference, which allows for classifying them into habitat-use guilds, such as: forest or open habitats specialists or habitat generalists (Leal et al. 2017; Vasconcelos et al. 2018; Andersen 2019). These ant guilds respond distinctly to human-induced impacts (Martins et al.

2022). For example, forest specialists are very sensitive to disturbance, which generally presents a low number of species richness, abundance, and biomass. On the other hand, open habitat and generalist ants have elevated values in highly disturbed environments, such as in low forest cover landscapes (Paolucci et al. 2017; Martins et al. 2022). This distinct response of habitat use by ant guilds can be understood as a winner-loser approach (McKinney and Lockwood 1999; Filgueiras et al. 2021), where there are many specialist ant losers and few generalist and open-habitat specialist ants winners in response to anthropogenic disturbances (Paolucci et al. 2017; Martins et al. 2022). Although the response of habitat use guilds to ecological and environmental changes has been accessed (Paolucci et al. 2017; Vasconcelos et al. 2018, Martins et al. 2022), a standard way to assign ants in these guilds is lacking, which hampers the reproducibility and broad using of habitat use ant guilds in ant diversity studies and monitoring programs.

Forest-pasture shifting is a major land use change in Brazil (Mapbiomas 2021), leading to negative impacts on biodiversity and ecosystem services (Fearnside 2005; Imazon 2021). In this sense, the state of Acre in the southwestern Brazilian Amazon has experienced expressive changes in landscape dynamics over the last four decades, mainly by forest-pasture shifting (Acre 2010; INPE 2020; Mapbiomas 2021). Human-modified landscapes represent 13% of Acre territory (Azevedo 2021), with 80% represented by pastures. Thus, these land-use shifting in Acre could be seen as a model of human impacts on Amazonian ecosystems and biodiversity mainly in the region called as “Arc of Deforestation” (Nogueira et al. 2007, 2008).

Most studies on ant assemblages as bioindicators in Amazon biome have approached the effects of forest-pasture shifting on ant diversity (e.g., Oliveira and Schmidt 2019; Menezes and Schmidt 2020). The addition of habitat use ant guilds can give a clearer understanding of ant assemblages response to forest shifting, which can be applied to all kinds of land use changes that promote deforestation (Andersen 2019).

In this study, we propose a standard protocol to classify the ant fauna in habitat-use guilds (forest specialists, open-habitat specialists, and generalists). Besides the use of standard assemblage parameters (i.e., species richness and species composition), we verified habitat-use ant guilds as a complementary predictable parameter on the use of ant assemblages as bioindicators. Specifically, we hypothesized that forest specialists, open-habitat specialists, and generalist ants would present distinct responses to forest-pasture shifting. We expected that the forest-pasture shifting promotes a decrease in the species richness of forest specialists and an increase in open-habitat specialists, while the generalists would have few changes in species richness because they can live in both habitats (Paolucci et al. 2017; Martins et al. 2022).

Material and Methods

Data sampling

Information on ant species occurrence was recovered from the database of the ants of the state of Acre available in Schmidt et al. (2020), which compiled 17 studies dealing with ant fauna surveys or ecological questions on ant assemblages in Acre state in Brazil and reported the occurrence of 389 ant species to the state. We updated that list by searching for records based on the species deposited at the Entomological Collection Padre Jesus Santiago Moure – Universidade Federal do Paraná (DZUP), ant collection of the Museu de Zoologia da Universidade de São Paulo (MZSP) and Myrmecology Laboratory of the Centro de Pesquisa do Cacau, Comissão Executiva do Plano da Lavoura Cacaueira (CEPLAC). Corrections and updates in the nomenclature of the ant species reported by Schmidt et al. (2020) were also performed based on recent taxonomic contributions (Ladino & Feitosa (2020); Longino & Branstetter (2020); Oliveira et al. (2021), Ulysséa & Brandão (2021); Camacho et al. (2022)).

Habitat-use ant guilds classification

To carry out the habitat-use guilds classification, we first checked this information in Vasconcelos et al. (2018). For species with no habitat-use information in Vasconcelos et al. (2018), we accounted their habitat types as listed in the "Habitat summary" topic on AntWeb.org. We considered an ant species as a forest or open habitat specialist when the occurrence for one of these habitat types was equal to or higher than 80%. We assigned species as generalists when records in a specific habitat were lower than 80%. Additionally, we also searched for habitat records of ant species based on the labels of specimens deposited at DZUP, CEPLAC and MZSP. We also applied the habitat-use assignment described above for these records from collections.

Statistical analyses

To verify habitat-use ant guilds as a complementary predictable parameter on the use of ant assemblages as bioindicators, we chose three studies reported by Schmidt et al. (2020) that provided ant species occurrence in forest and pasture habitats. These studies totalized 13 forest fragments and 13 pasture areas (Fig. 1). Ants sampled in these studies were collected by pitfall traps in soil and through artificial attractive seeds. We only considered ants identified at species level in these studies.

We evaluated the response of ant species richness using two models, one considering the general species richness as response variable and the other considering the species richness per habitat-use guilds as response variable. In the model of general species richness, the explanatory variable was habitat type (forest and pasture) and in the model of species richness per habitat-use ant guilds, besides habitat type, the habitat-use ant guild was also an explanatory variable and the interaction between them was also considered. Both models were generalized linear mixed-effects models - GLMM (Bolker et al. 2009), using the package lme4 (Bates et al. 2020), where sampling plot was identified as a random effect to control pseudo-replication (Pinheiro and Bates 2000). We verified the significance of explanatory variables using the package car (Fox et al. 2020). The models followed the Poisson distribution errors since species richness is count data. We performed a residual analysis on the final model to evaluate the adequacy of error distribution (Crawley 2013).

To investigate the effect of forest-pasture shifting on ant species composition, we used Principal Coordinate Analysis (PCoA) (Legendre and Legendre 2012). For this, we utilized a matrix of species presence and absence and verified the contribution of ant species to the PCoA ordering with the “envfit” function, using 9,999 permutations (Oksanen et al, 2019). Thus, we considered only the species that significantly contributed to the model. In addition, we inserted symbols into the visual model that highlighted to which habitat-use guild each ant species presented on ordination (Fig. 4). We performed a Permutation Multivariate Analysis of Variance (PERMANOVA) (Anderson 2001), with 9,999 permutations and Jaccard dissimilarity index to analyze the significance of the visually explored model in PCoA. To perform PERMANOVA, we used the vegan package (Oksanen et al. 2019), applying the “adonis” function. For this analysis, we also considered only the species that significantly contributed to the model generated on the PCoA.

Results

Ant fauna updates and habitat-use ant guilds

We recorded a total of 394 ant species to Acre, which belong to 77 genera and 10 subfamilies (Supplementary Material – Table A1). The most speciose subfamily was Myrmicinae (190 species), followed by Ponerinae (48), Formicinae (46), Dolichoderinae (33), Pseudomyrmecinae (27), Dorylinae (23), Ectatomminae (23), Amblyoponinae (two species) and Paraponerinae and Proceratiinae (both with only one species). The genus with the highest species richness was *Pheidole* (Myrmicinae) with 47 species, followed by *Camponotus* (Formicinae) with 35 species, and *Pseudomyrmex* (Pseudomyrmecinae), with 27 species.

Regarding corrections and updates in the nomenclature of ant species reported by Schmidt et al. (2020), three species (*Neoponera metanotalis* Luederwaldt, 1918, *Crematogaster dorsidens* Santschi, 1925 and *Brachymyrmex gaucho* Santschi, 1917) were excluded because they were incorrectly recorded to Acre according our recent taxonomic validation. Sixteen of the ant species reported by Schmidt et al. (2020), had their taxonomic status updated due to new combinations and synonymies in recent taxonomic studies (Supplementary Material - Table A2) Finally, 16 additional records of ant species were made based on the literature and collections (Supplementary Material – Table A3).

All the ant species were classified according to the habitat-use guilds. A total of 236 ant species were identified as forest specialists, 29 as open-habitat specialists and 129 as generalists (Supplementary Material – Appendix).

Response of habitat-use ant guilds to forest-pasture shifting

Considering the general species richness, this was higher in forest habitat than in pasture ($^{2}_{(1,24)} = 18.27$; $p < 0.01$) (Fig. 2).

Regarding the response of species richness per habitat-use guilds to forest-pasture shifting, this was associated with habitat type ($^2_{(1,37)}$ = 5.95; p = 0.01), habitat-use guild ($^2_{(1,23)}$ = 30.67; p < 0.01) and to the interaction between these terms ($^2_{(1,7)}$ = 48.84; p < 0.01). This means that in forest habitat, forest specialist ants present the highest species richness followed by generalist and open-habitat specialist ants (Fig. 3). Otherwise, in pasture habitat, forest specialist ants present the lowest species richness and generalist ants are the most speciose, although with small difference in relation to forest habitat (Fig. 3). Finally, open-habitat specialist ants expressive increased their species richness from forest to pasture habitat (Fig. 3).

The PCoA represented about 38.9% of the dissimilarity in the ant species composition. Forest specialist ants presented a higher number of species than the other habitat-use guilds in forest habitat. Open-habitat were the most species habitat-use guild in pasture habitat. Generalists presented a similar number of species in both habitats. Furthermore, we found that this dissimilarity on ant species composition was consistent (PERMANOVA $F_{(1.25)}$ = 8.95, R2 = 0.27, p = 0.001) (Fig. 4).

Discussion

We were able to classify all ant species reported to Acre in habitat-use guilds. Moreover, our results supported the use of habitat-use guilds as a complementary predictable parameter on the use of ant assemblages as bioindicators. Below, we highlight the implications of our results and discuss the potential use of habitat-use guilds in monitoring programs that consider ants as surrogates of the response of biodiversity to several types of land use changes.

Ant fauna of Acre

The total number of species reported to Acre (394 species) could be higher considering that in the few published studies reported to the region, a great part of ants has been sorted only in morphospecies (44.6%) (Schmidt et al. 2020). Additionally, this number of ant species is a result of ant surveys and ecology-oriented studies carried out almost exclusively in the Rio Acre basin. Thus, it is desirable to carry additional ant samplings throughout other regions within Acre, such as the ant samplings provided by the project Insect Biodiversity in Amazon (Schmidt et al. 2020), that potentially will improve the number of ant species in Acre state.

Although, as expected, forest specialist ants presented the highest number of species in forest habitats, generalist ants also present a high number of species inside forests. The high number of generalists in forests could be associated with the low level of precipitation in the Southwestern Brazilian Amazon (Davidson et al. 2012), which promotes the predominance of thinner-smaller trees and opener canopy in forested ecosystems (Acre 2010; Arruda et al. 2017) offering similar condition opportunities for both groups of ants (i.e., forest specialists and generalists). In this way, considering that habitat openness is a key driver of variation in ant assemblages (Andersen 2019) we expect that forest ecosystems in central Amazon under higher levels of precipitation and consequently thicker-taller tress and closer canopy

(Arruda et al. 2017; Davidson et al. 2012; Fisch et al. 1998) could probably harbor a higher number of species of these two habitat-use guilds. However, to confirm this assumption, an ant survey at a regional scale comparing the border and central region of Amazon is necessary. Finally, the opens in forest canopy could allow the occurrence of open-habitat ant specialists, although at low species richness.

Response of habitat-use ant guilds to forest-pasture shifting

Although ant species richness decreased expressively from forest to pasture, this does not usually happen in the response of ant assemblage to forest-pasture shifting (Nakamura et al. 2003, 2007). Nevertheless, this response became much clearer when it was analyzed considering the habitat-use guilds (Fig. 3).

This distinct response of species richness of habitat-use guilds to forest-pasture shifting can be understood under the approach of winner and loser species, in which winners are disturbance-adapted species and losers are disturbance-sensitive (McKinney and Lockwood 1999; Tabarelli et al. 2012). Thus, we can clearly identify forest specialists as losers and generalists and open-habitat specialists as winners in the forest-pasture shifting. This distinct response of ant habitat-use guilds offers a better understanding of how species composition changes occur due to land-use shifting. Thus, the conspicuous species composition changes between ant assemblages of forest and pasture (Nakamura et al. 2003, 2007; Fontenele and Schmidt 2021) could be due to a replacement of ant forest specialists by generalists and open-habitat specialists (Martins et al. 2022). However, the low impact of pasture on ant species composition in open-habitat biomes (i.e., savanna like-vegetation) (Queiroz et al. 2017) could be due to the predominance of generalist and open-habitat specialists in this biome types (Andersen 2019; Vasconcelos et al. 2018).

Furthermore, the use of habitat-use guilds could allow at least two approaches to the study of ant assemblages and their use as bioindicators: i) at assembly-community rules of ant assemblages, we could propose that a hypothetical ant assemblage is primarily made up of generalist species, once there is an increase on forest cover this allows the survival of ant forest-specialist species, otherwise, if this ant assemblage is under low or none forest cover, open-habit species could replace forest-specialist species (Andersen 2019). ii) At bioindication context, once we know which ant groups are the winners and losers in conserved forest and in human-induced disturbed habitats (Martins et al. 2022), we could safely infer, based on species richness variation of these habitat-use guilds, if a habitat under restoration is closer to a forest or to an open-cover habitat induced by human activity (i.e., pastures).

Conclusion

Our results corroborate previous studies on habitat-use guilds as a complementary predictable parameter on the use of ant assemblages as bioindicators (Paolucci et al. 2017, Martins et al. 2022), but additionally offer a standard protocol to access habitat-use guild classification which was lacking in these previous studies. Therefore, we understand that a future step is to quantify the limit of forest cover clearing in human-induced land use to preserve the species richness of forest-specialist ants higher than other habitat-use guilds. To attend to this issue, efforts on habit-use guild classification at a broad scale should be made and considering the ant assemblages at several types (i.e., ranging in forest cover) of land uses.

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Figures

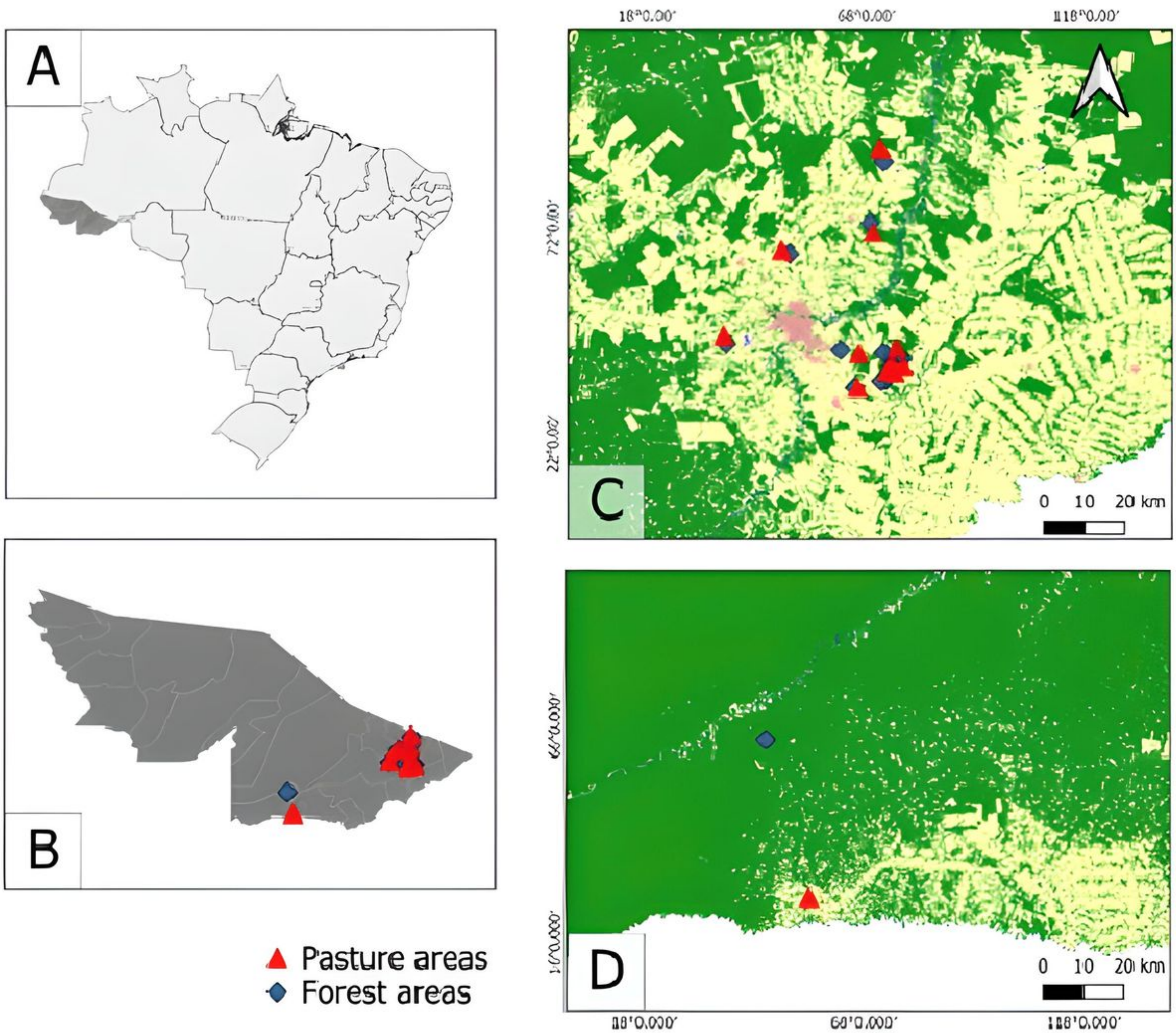

Figure 1

Pasture (red) and forest (blue) areas where collections were carried out. (A) The state of Acre in Brazil; (B) Study area in the state of Acre; (C) Ant collection points in pastures and forests surrounding Rio Branco, AC and in (D) Assis Brasil, AC.

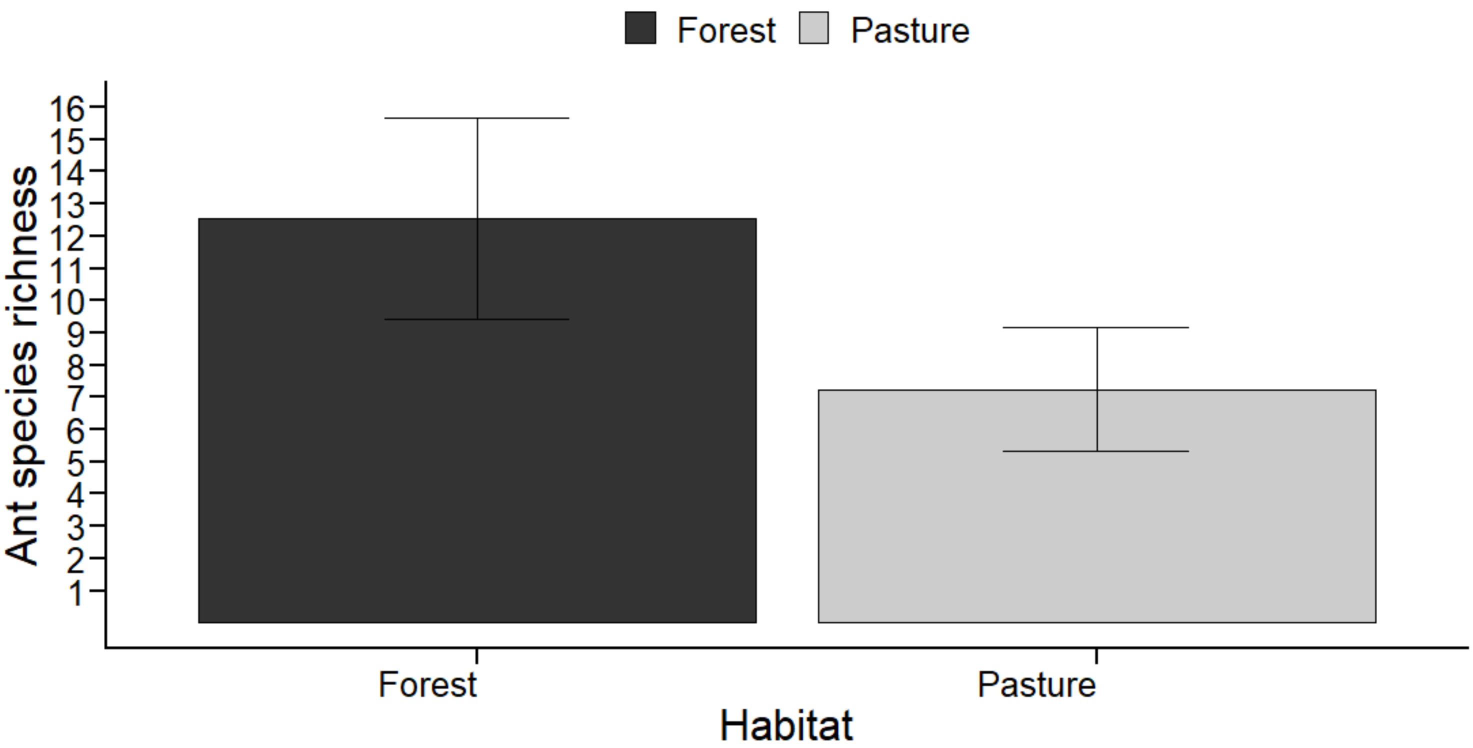

Figure 2

Relationship between general Ant species richness and habitat type (forest and pasture) ($^{2}_{(1,24)}$ = 18.27; p <0.01) in Acre state, Southwestern Brazilian Amazon.

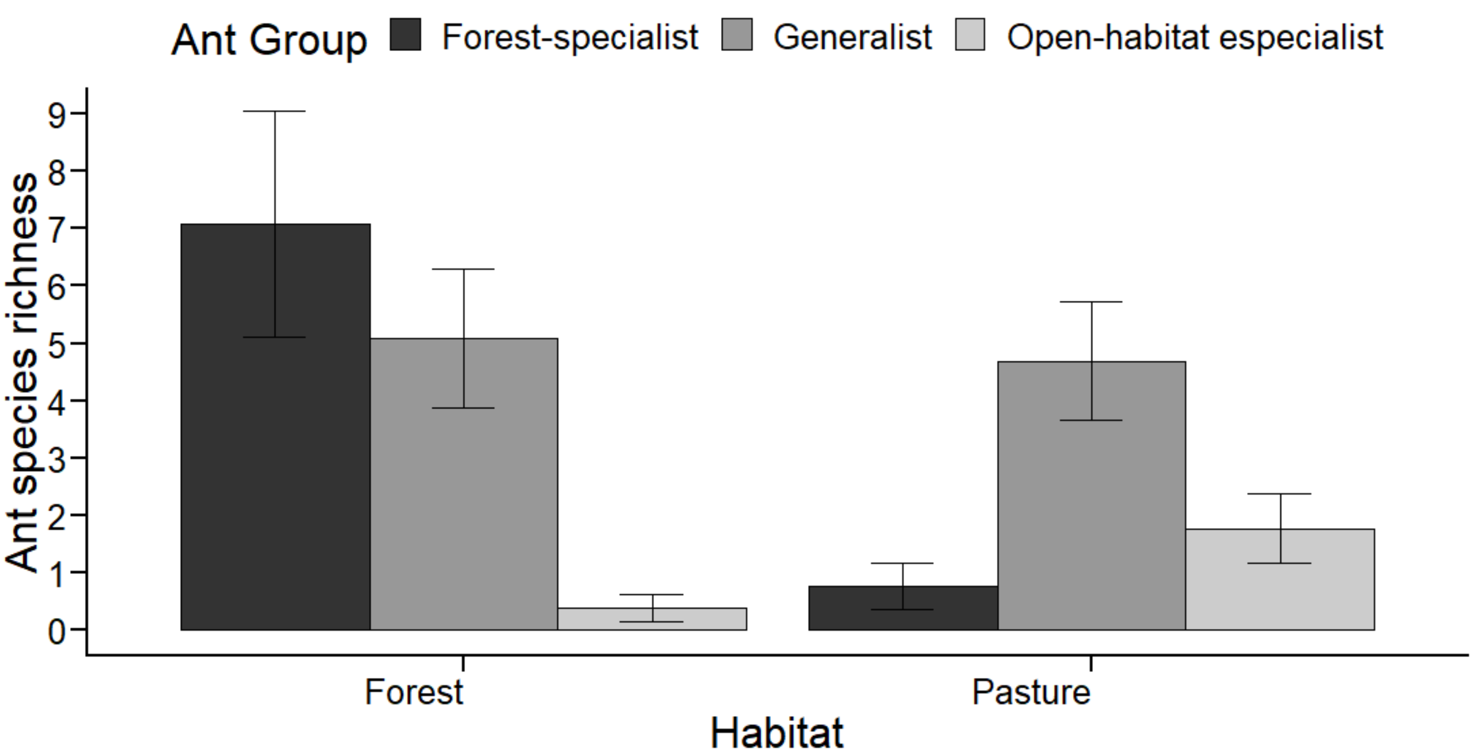

Figure 3

Relationship between Ant species richness with habitat type (forest and pasture) ($^{2}_{(1,37)}$ = 5.95; p = 0.01), habitat-use ant guild (forest specialist, open-habitat specialist and generalist) ($^{2}_{(1,23)}$ = 30.67; p <0.01) and the interaction between them ($^{2}_{(1,7)}$ = 48.84; p <0.01) in Acre state, Southwestern Brazilian Amazon.

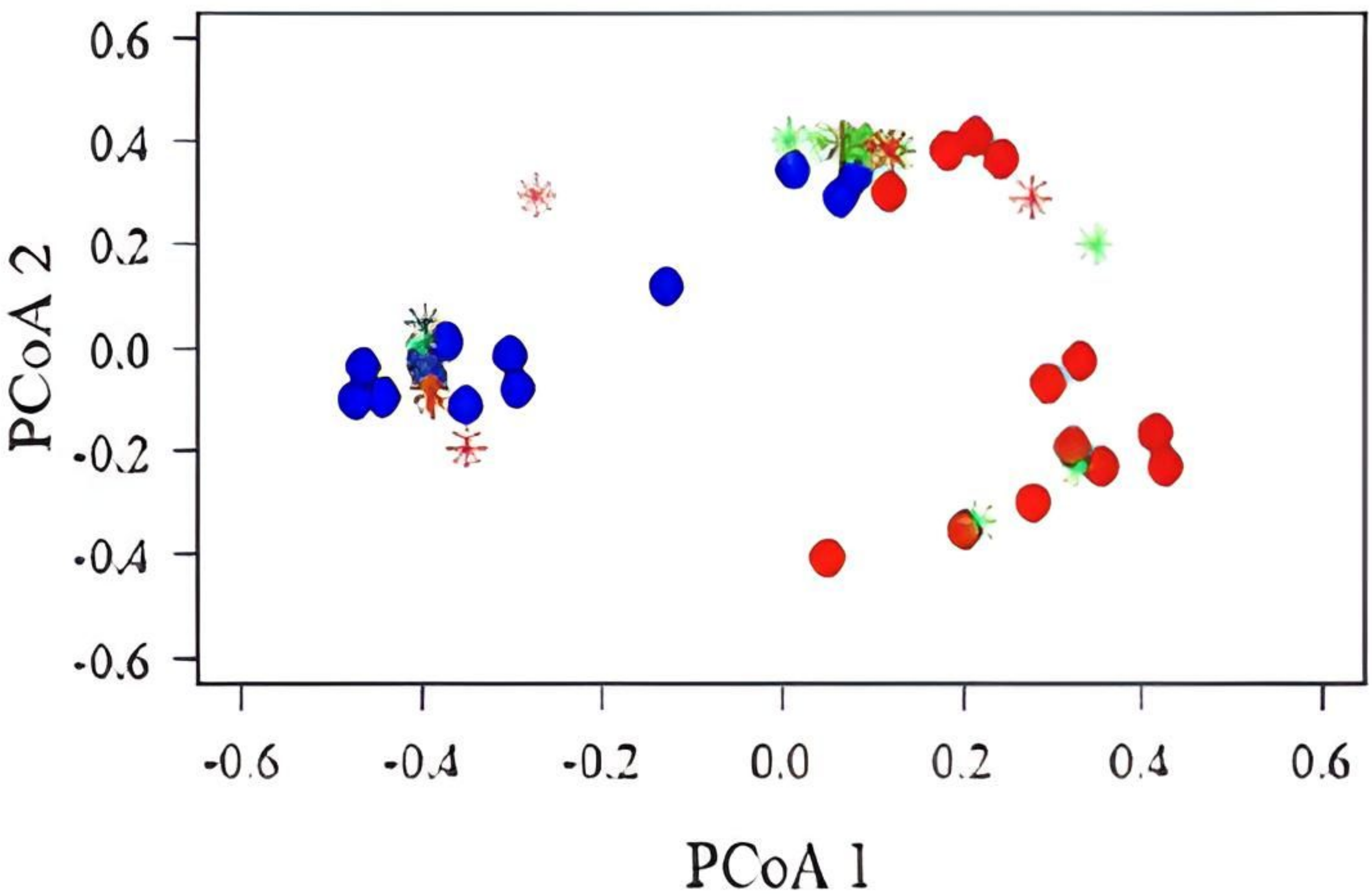

Figure 4

Ant species composition ordering by Principal Coordinate Analysis (PCoA). Forest areas are represented by blue circles and pasture areas by red circles. The asterisks represent the different habitat-use ant guilds, were forest specialists, open-habitat specialists and generalists are green, red and black respectively.

Supplementary Files

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