Journal of Insect Conservation
https://doi.org/10.1007/s10841-023-00544-1

ORIGINAL PAPER

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

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Received: 29 May 2023 / Accepted: 29 November 2023

Abstract

Ant assemblages have been used as bioindicators of biodiversity response to different types of anthropogenic disturbances. However, usual diversity metrics (e.g., ant species richness and composition) sometimes seem limited in showing an overall panorama of human impacts. Thus, we checked habitat-use guilds of ants as a complementary predictable parameter, based on the ant fauna reported in thirteen forest fragments and pastures in the southwestern Brazilian Amazon. Specifically, we hypothesized that forest specialist, open-habitat specialist, and generalist ants would have distinct responses to forest-pasture shifting. We expected that forest-pasture shifting would cause a decrease in 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 little change. This indicates that human-induced open habitats (e.g., pastures) are essentially comprised of generalist ants and open-habitat ant specialists, which 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, which might ensure a higher species richness of forest-specialist ants than other habitat-use guilds.

Implications for insect conservation: Habitat-use ant guilds (forest specialists, open-habitat specialists, and generalists) have been used as a complementary parameter on bioindication. Here, we provided a standard protocol to classify the ant fauna in these habitat-use guilds, which allows for objective, reproducible and broad use in monitoring programs that consider ant assemblages as bioindicators.

Keywords Biodiversity · Biological Conservation · Bioindication · Formicidae · Land Use Change

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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 highly human-modified landscapes (Tscharntke et al. 2012). The use of bioindicators has been proposed due to the difficulty in assessing biodiversity response to different types of human impacts (McGeoch 1998). Bioindicators are groups of organisms whose diversity patterns and ecological functions clearly and predictably respond to anthropogenic impacts (McGeoch 1998; Del Toro et al. 2012).

Published online: 16 December 2023

Ants are excellent bioindicators as they have high biomass in almost all terrestrial habitats, they 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). On the other hand, among diversity patterns, species richness and diversity indexes have had a coarse relationship with human impacts (Ribas et al. 2012). Thus, several studies have highlighted that ant species composition provides the clearest and most predictable response to several natural and human-induced impacts (Gollan et al. 2011; Ribas et al. 2012; Schmidt et al. 2013).

Ant species differ from each other regarding habitat preference, which allows for classifying them into habitat-use guilds, e.g. either 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 disturbances, generally manifested by a decreasing in species richness, abundance, and biomass in disturbed habitats (Sales and Schmidt 2023). On the other hand, open-habitat and generalist ants have high values in highly disturbed environments, such as in low forest cover landscapes (Paolucci et al. 2017; Martins et al. 2022). This distinct response in 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 ant 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 addressed (Paolucci et al. 2017; Vasconcelos et al. 2018; Martins et al. 2022), there is no standard way to assign ants in these guilds, which hampers the reproducibility and broad use 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 setting, the state of Acre in the southwestern Brazilian Amazon has experienced significant changes in landscape dynamics over the last four decades, mainly through forest-pasture shifting (Acre 2010; INPE 2020; Mapbiomas 2021). Human-modified landscapes represent 13% of Acre's territory (Azevedo 2021), with 80% of that modified land represented by pastures. Thus, this land-use shift in Acre could be seen as a model of human impacts on Amazon ecosystems and biodiversity mainly in the region called the "Arc of Deforestation" (Nogueira et al. 2007, 2008).

Most studies on ant assemblages as bioindicators in the Amazon biome have addressed 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 provide a clearer understanding of ant assemblage response to forest shifting, which can be applied to all kinds of land use changes that cause 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). Aside from the use of standard assemblage parameters (i.e., species richness and species composition), we checked habitat-use ant guilds as a complementary predictable parameter of the use of ant assemblages as bioindicators. Specifically, we hypothesized that forest specialists, open-habitat specialists, and generalist ants would have distinct responses to forest-pasture shifting. We expected that forest-pasture shifting would lead to a decrease in species richness of forest specialists and an increase in open-habitat specialists, while the generalists would have little change in species richness because they can live in both habitats (Paolucci et al. 2017; Martins et al. 2022). We have these expectations because previous studies have reported that these habitat-use ant guild respond distinctly to a common disturbance and land-use change (Paolucci et al. 2017; Martins et al. 2022; Sales and Schmidt 2023).

Materials and methods

Data sampling

Information on ant species occurrence was recovered from the ant database of the state of Acre available in Schmidt et al. (2020), who compiled 17 studies that address ant fauna surveys or ecological questions on ant assemblages in the state of Acre in Brazil and reported the occurrence of 389 ant species in 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 (Federal University of Paraná) (DZUP), ant collection of the Museu de Zoologia da Universidade de São Paulo (MZSP – Zoology Museum of the University of São Paulo), and Myrmecology Laboratory of Centro de Pesquisa do Cacau, Comissão Executiva do Plano da Lavoura Cacaueira (CEPLAC – Center for Research of Cocoa, Executive Commission of Cocoa Farm Plan). Corrections and updates in ant species nomenclature reported by Schmidt et al. (2020) were also performed based on recent taxonomic contributions (Ladino and Feitosa 2020; Longino and Branstetter 2020; Oliveira et al. 2021; Ulysséa and Brandão 2021; Camacho et al. 2022).

Habitat-use ant guild classification

To classify habitat-use guilds, we first checked this information in Vasconcelos et al. (2018). For species with no habitat-use information in Vasconcelos et al. (2018), their habitat types are 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 of 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%. The value of 80% as threshold on guild determination was considered because both habitat-use ant guilds (forest and open-habitat specialist) can be occasionally sampled in a non-expected habitat type or even transition zones. Therefore, if we limit species classification in guilds based on 100% of their occurrence for a habitat type, we will probably underestimate the potential occurrence of habitat specialists and overestimate the generalist ants. 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 the records derived from collections.

Statistical analyses

To verify habitat-use ant guilds as a complementary predictable parameter on the use of ant assemblages as bioindicators, we used two studies on the response of ant assemblage to forest-pasture shifting (Fontenele and Schmidt 2021; Sales and Schmidt 2023) and one about the response of ant diversity to forest cover gradient (Costa and Schmidt 2022). All these studies were carried out in Acre River basin, southwestern Brazilian Amazon (Fig. 1) and the ants were sampled in forest and pasture areas. Thus, these studies provided 13 pairs of comparisons between ant assemblages from forest fragments and pasture areas. Most of these pairs (12 pairs) are located around Rio Branco, the capital of Acre state, with another pair located in Assis Brazil, Acre, near the border with Bolivia and Peru (Fig. 1). Ants sampled in these studies were collected using pitfall traps in soil and through artificial attractive seeds. We only considered the ants identified at the species level in these studies.

We evaluated the response of ant species richness using two models, one with overall species richness as the response variable and the other with species richness per habitat-use guild as the response variable. In the model of overall species richness, the explanatory variable was habitat type (forest and pasture), and in the model of species richness per habitat-use ant guilds, habitat-use ant guild was an explanatory variable as well as habitat type, and the interaction between them was also considered. Both models were generalized linear mixed-effects models - GLMM (Bolker et al. 2009), using the lme4 package (Bates et al. 2020), where sampling plot was identified as a random effect to control pseudo-replication (Pinheiro and Bates 2000). We checked the significance of explanatory variables using the car package (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 a Principal Coordinate Analysis (PCoA) (Legendre and Legendre 2012). For this, we used a matrix of species presence and absence and checked 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 assigned symbols representing habitat-use guild to each ant species in the ordination plot, were the grey, black and brown asterisks represent forest specialists, open-habitat specialists and generalists, respectively. We performed a Permutation Multivariate Analysis of Variance (PERMANOVA) (Anderson 2001), with 9,999 permutations and Jaccard's 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 394 ant species in Acre, belonging 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.

Concerning corrections and updates in the nomenclature of ant species reported by Schmidt et al. (2020), three

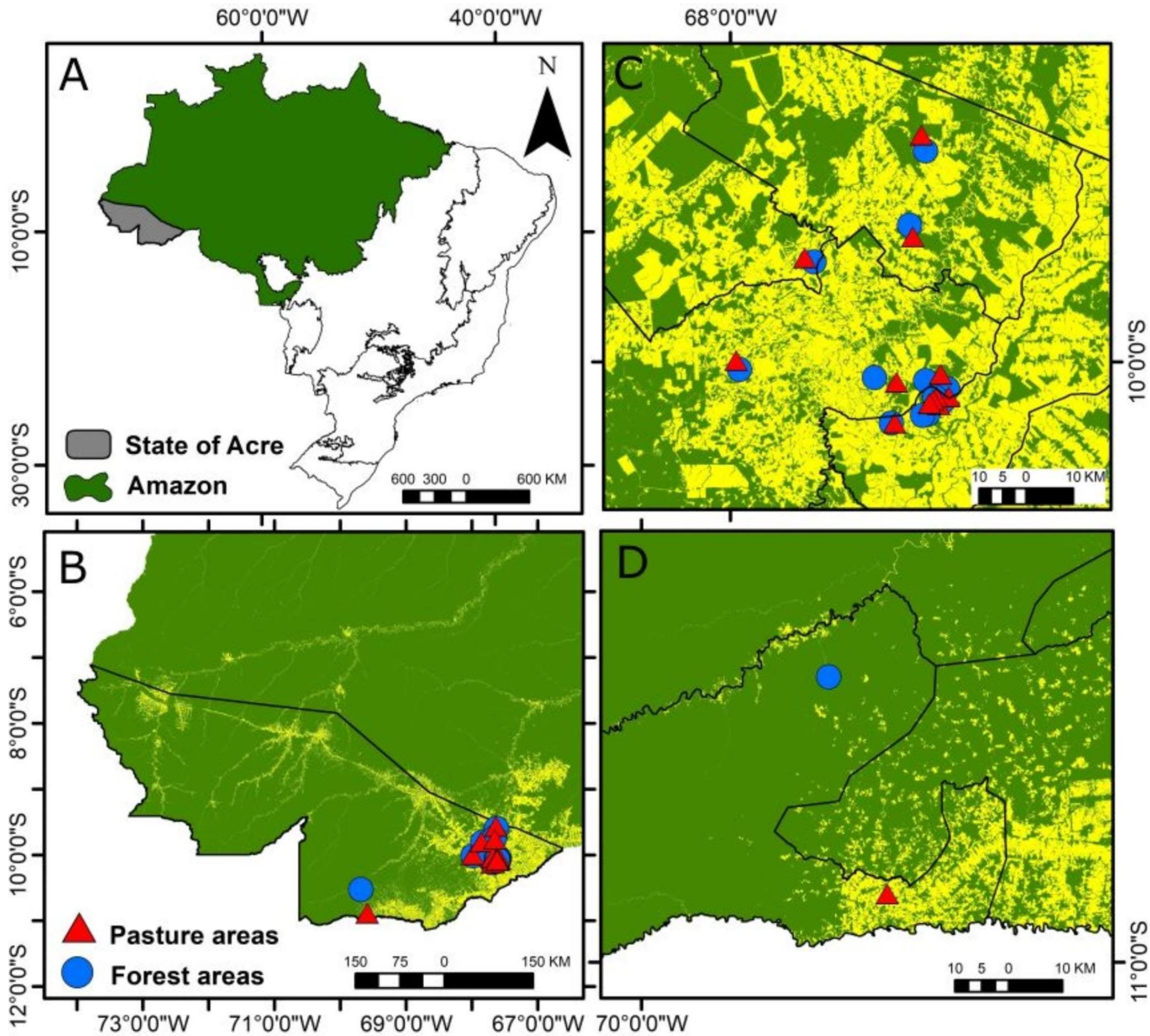

Fig. 1 Pasture (red) and forest (blue) areas where samplings were carried out. (**A**) The state of Acre in Brazil; (**B**) Study area in the state of Acre; (**C**) Ant sampling points in pastures and forests surrounding Rio Branco, AC, and in (**D**) Assis Brazil, AC

species (*Neoponera metanotalis* Luederwaldt, 1918, *Crematogaster dorsidens* Santschi, 1925, and *Brachymyrmex gaucho* Santschi, 1917) were excluded because they were incorrectly reported as found in Acre according to 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, there were 16 additional records of ant species based on literature and collections (Supplementary Material – Table A3).

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

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

Overall ant species richness was higher in forest habitat than in pasture ($\chi^2_{(1.24)} = 18.27$; $p<0.01$) (Fig. 2).

The response of species richness per habitat-use guild to forest-pasture shifting was associated with habitat type ($\chi^2_{(1.37)} = 5.95$; $p = 0.01$), habitat-use guild ($\chi^2_{(1.23)} = 30.67$; $p<0.01$), and with the interaction between these terms ($\chi^2_{(1.7)} = 48.84$; $p<0.01$). This means that forest specialist

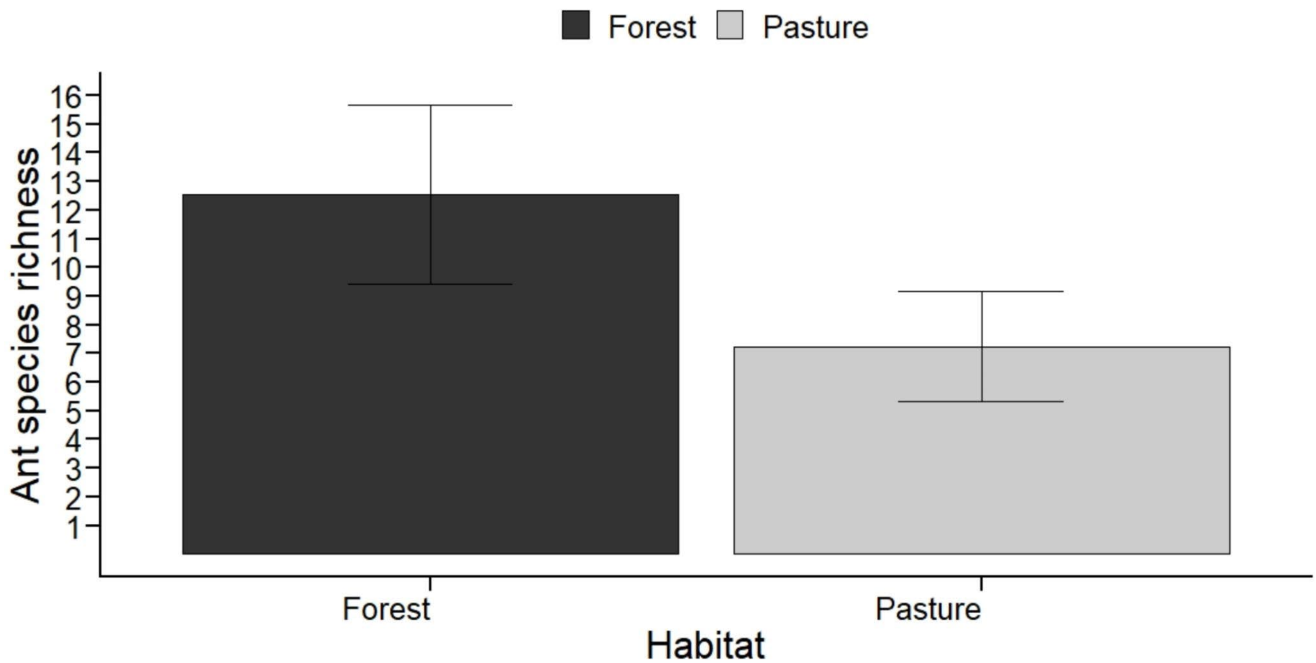

Fig. 2 Relationship between overall ant species richness and habitat type (forest and pasture) ($\chi^2_{(1,24)} = 18.27$; $p<0.01$) in Acre state, Southwestern Brazilian Amazon

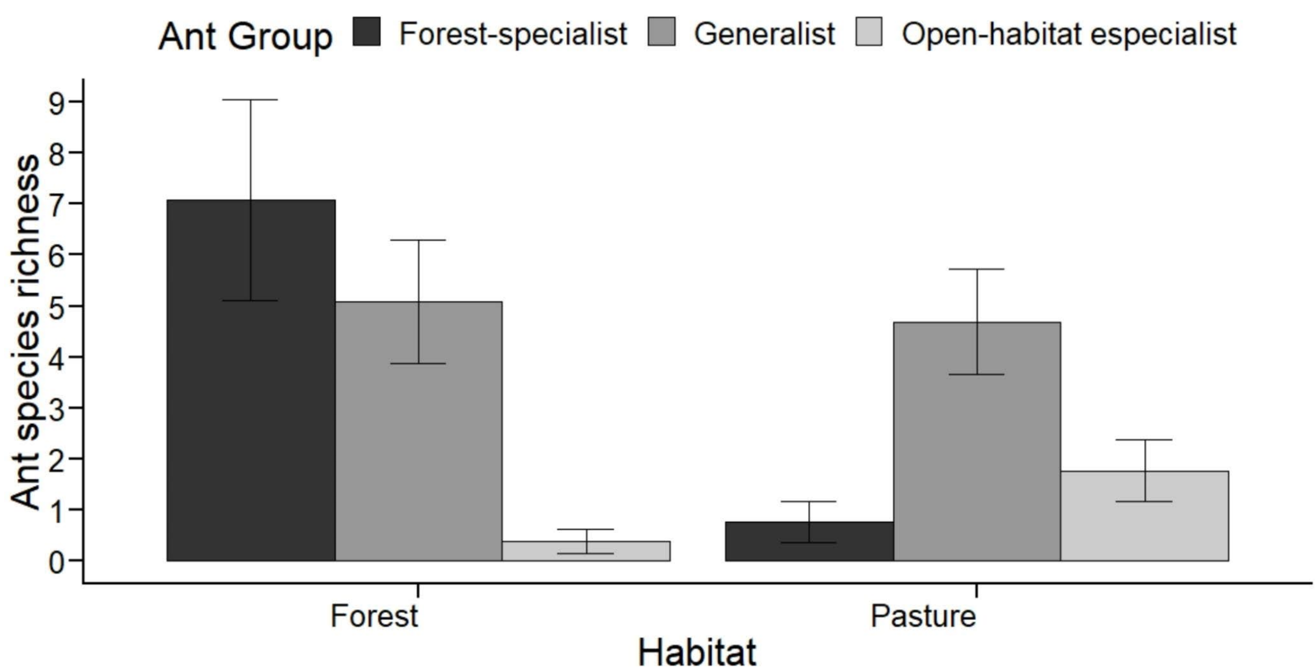

Fig. 3 Relationship between Ant species richness and habitat type (forest and pasture) ($\chi^2_{(1.37)} = 5.95$; $p = 0.01$), habitat-use ant guild (forest specialist, open-habitat specialist, and generalist) ($\chi^2_{(1.23)} = 30.67$; $p<0.01$,) and the interaction between them ($\chi^2_{(1.7)} = 48.84$; $p<0.01$) in the state of Acre, Southwestern Brazilian Amazon

ants have the highest species richness in forest habitat, followed by generalist and open-habitat specialist ants (Fig. 3). Otherwise, forest specialist ants have the lowest species richness in pasture habitat and generalist ants are the most speciose, although with a small difference in the forest habitat (Fig. 3). Finally, there is a significant increase in species richness of open-habitat specialist ants from forest to pasture habitat (Fig. 3).

The PCoA represented approximately 38.9% of the dissimilarity in ant species composition. Forest specialist ants had a higher number of species than the other habitat-use guilds in forest habitat. Open-habitat ants were the most speciose habitat-use guild in pasture habitat. Generalists had a similar number of species in both habitats. Furthermore, we found that this dissimilarity in 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 in 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 for the response of biodiversity to several types of land use changes.

Ant fauna in Acre

The total number of species reported in Acre (394 species) could be higher considering that in the few published studies related to this region, a great part of ants has been sorted only into 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 Acre River basin. Thus, it would be interesting to carry out additional ant sampling in other regions of Acre, e.g. the ant samplings provided by the project Insect Biodiversity in Amazon (Schmidt et al. 2020), which potentially will increase the number of ant species in the state of Acre.

As expected, forest specialist ants had the highest number of species in forest habitats; generalist ants also had 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 leads to predominance of thinner and smaller trees resulting in a more open canopy in Acre's forested ecosystems (Acre 2010; Arruda et al. 2017), thus offering similar condition opportunities for both ant groups (i.e., forest specialists and generalists). Therefore, given 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 trees and more closed 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 Amazon edge and its central region is necessary. Finally, canopy gaps in forest could allow the occurrence of open-habitat ant specialists, although with relatively low species richness.

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

Although ant species richness decreased from forest to pasture (Fontenele and Schmidt 2021; Sales and Schmidt 2023), but see Nakamura et al. (2003, 2007), this response became much clearer when analyzed by the habitat-use guilds (Fig. 3). This distinct response of species richness of habitat-use guilds to forest-pasture shifting can be best understood through the lens 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

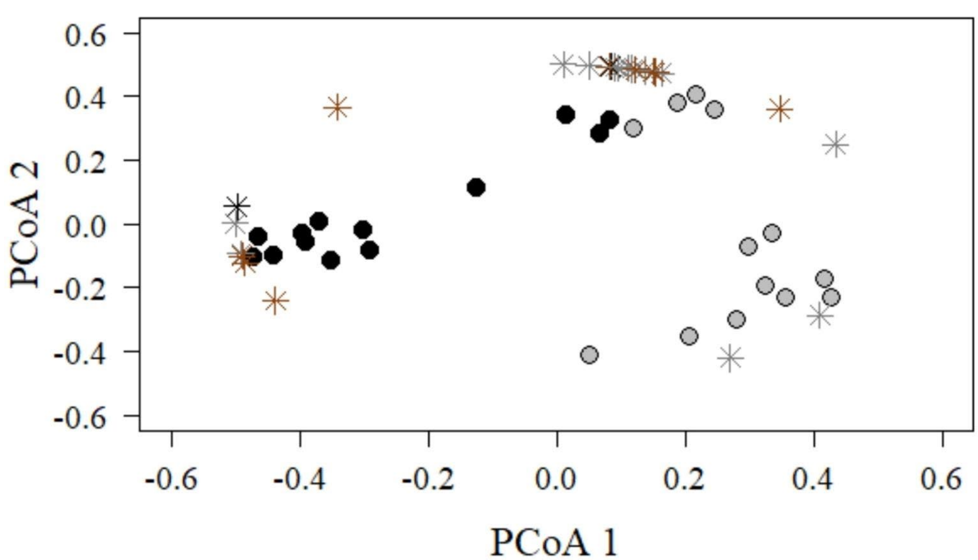

Fig. 4 Ant species composition ordering by Principal Coordinate Analysis (PCoA). Forest areas are represented by black circles and pasture areas by grey circles. The asterisks represent the different habitat-use ant guilds, were forest specialists, open-habitat specialists and generalists are grey, black and brown respectively

forest-pasture shifting. This distinct response of ant habitat-use guilds offers a better understanding of how species composition changes due to land-use shifting. Such conspicuous changes in species composition 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 influence 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 generalists and open-habitat specialists in these 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. First, considering community assembly rules of ant assemblages, we could propose that a hypothetical ant assemblage is primarily comprised of generalist species, and once there is an increase in forest cover, this allows the survival of ant forest-specialist species. Otherwise, if this ant assemblage is under low or no forest cover, open-habit species could replace forest-specialist species (Andersen 2019). Second, in a 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 if a habitat under restoration is closer to a forest or to an open-cover habitat induced by human activity (i.e., pastures) based on species richness variation in these habitat-use guilds.

Conclusion

Our results corroborate previous studies on habitat-use guilds as complementary predictor parameters regarding the use of ant assemblages as bioindicators (Paolucci et al. 2017; Martins et al. 2022).

In addition, we provided a standard protocol to access habitat-use guild classification which was lacking in previous studies. Therefore, a future step is to quantify the limits of forest cover clearing in human-induced land use to preserve the species richness of forest-specialist ants over the other habitat-use guilds. To tackle to this issue, efforts on classifying habit-use guild at a broad scale should be made and ant assemblages at several types (i.e., ranging in forest cover) of land uses should be considered, as well.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10841-023-00544-1.

Acknowledgements We thank Higher Conselho Nacional de Desenvolvimento Científico e Tecnológico - Brazil (CNPQ) by PROPEG-UFAC nº. 07-2020- for its financial support to Dhâmyla Bruna during her undergraduate course. We also thank the Federal University of Acre - UFAC. We are very grateful to the colleagues of Laboratório de Ecologia de Formigas for the emotional support. We are deeply indebted to C. Lasmar and the anonymous referee for the reviewing of a previous version of the manuscript.

Author contributions All authors contributed to the study conception and design. Material preparation, data collection were performed by D. B. Dhâmyla, and analysis F. (A) Schmidt, R. M. Feitosa, T. T. Jory, F. M. Sales, L. K. Fontenele, M. M. Marília. The first draft of the manuscript was written by D. (B) Dhâmyla and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Funding RMF was funded by the Conselho Nacional de Desenvolvimento Científico e Tecnológico - CNPq (grant 301495/2019-0). DBSD has scholarship from Coordenação de Aperfeiçoamento de Pessoal de Nível Superior—Brasil (CAPES)—Finance Code 001.

Data Availability All data and material that are requested will be provided by the authors.

Code Availability Not applicable.

Declarations

Ethics approval Not applicable.

Consent for publication All authors approve the publication of this manuscript.

Consent from the authors All persons who meet this manuscript's authorship are listed as authors, and all authors certify that they have participated sufficiently in this work to assume public responsibility for the content, including participation in the list, analysis, writing, and proofreading.

Competing interests The authors declare no competing interests.

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