Nesting stratum and habitat affinity matter in ant assemblage response to forest-pasture shifting

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Abstract. Ants have been extensively used as bioindicators, however ants from different nest stratum and habitat affinity groups could distinctly respond to a same ecological process and environmental impact. In this study, we evaluated if nest stratum and habitat affinity matter in the response of ant assemblages to forest-pasture shifting. We tested the response of number of species in entire ant assemblages (soil surface and subterranean) and in each ant fauna stratum (only soil surface and only subterranean). In both cases, we also tested the response of number of ant species of each habitat affinity groups (forest specialist, open-habitat specialist and generalist). Ants were sampled in three plots for each habitat type in Southwestern Brazilian Amazon. We sampled 124 ant species. Only for soil surface ant assemblages, the number of species was different between the two habitats types, among habitat affinity ant groups and their number of species also changed with habitat shifting. Therefore, we corroborate the inclusion of samplings in different nest stratum and recommend the classification of ants according to their habitat affinity in monitoring programs that use ants as bioindicator. However, efforts must be done to improve the information availability on habitat affinity of ant species.

Keywords: Amazon; biodiversity; bioindication; Formicidae; land-use change.

Considering the difficulty of assessing the response of all biodiversity to different types of human impacts, the use of bioindicators has been proposed because they provide clear and predictable responses of their diversity patterns and ecological interactions to these impacts (McGeoch 1998). Ants have been extensively used as bioindicators due to their high diversity and key ecological functions (Philpott *et al.* 2010) and besides being easily sampled, their diversity patterns predictably respond to anthropogenic disturbances (Philpott *et al.* 2010; Schmidt *et al.* 2013).

However, there are some limitations in the use of ants as bioindicators, for example, ant assemblages present a great vertical stratification regarding to nest stratum, ranging from underground soil layer to tree canopies. Besides the difficulty to sample ants in all these strata (Bestelmeyer *et al.* 2000), ant assemblages from each stratum could present different response to the same ecological process and environmental impacts (Bihn *et al.* 2008; Ribas *et al.* 2012a; Schmidt *et al.* 2013).

Moreover, ant fauna can be classified according to the habitat affinity, such as, open or forest habitats specialist and habitat generalist which can live in both habitats (Vasconcelos *et al.* 2018). Andersen (2018) has argued that ant species responses to disturbance are to a large degree determined by their responses to habitat openness, leading these habitat affinity ant groups respond distinctly to the same ecological process (Vasconcelos *et al.* 2018) and environmental impacts (Paolucci *et al.* 2017).

Negative effects on biodiversity and ecosystem functions have been promoted by intense human-induced land use changes (Fahrig *et al.* 2019; Zambrano *et al.* 2019). One of the most prominent changes is forest-pasture shifting which resulted in an highly distinctly human-modified habitat (Fearnside 2005; Araújo *et al.* 2011). This is happing at high levels in Acre, Southwestern Brazilian Amazon, which already achieved 13% of its territory as human-modified landscapes, which the most part (nearly 80%) is pasture areas (Acre 2010).

Although most species respond to the forest-pasture substitution, measures of diversity (*e.g.*, number of species and species composition) of whole ant assemblages do not necessarily respond in a clear and predictable way to this change (Nakamura *et al.* 2003, 2007). Thus, considering separately the response of ant assemblage from different nest stratum and from different habitat affinity groups could offer a more predictable response of ants to forest-pasture shifting. Furthermore, changes in the landscape and, consequently, ecosystems affect the availability of resources for myrmecofauna, whether used for foraging or nesting. Here, we evaluated if nest stratum and habitat affinity matter in the response of ant assemblages to forest-pasture shifting. Thus, we verified the response of number of species in entire ant assemblages (soil surface and subterranean) and in each ant fauna stratum (only soil surface and only subterranean). In both cases above, we also verified the response of number of ant species of each habitat affinity groups

(forest specialist, open-habitat specialist and generalist). In this way, we expected to identify which stratum provides the clearest response to forest-pasture shifting and the different responses of habitat affinity ant groups to it.

MATERIAL AND METHODS

Study area. The ants were collected inside and around Fazenda Experimental Catuaba - FEC (10º04'S and 67°37'W), in Senador Guiomard, Acre state in Southwestern Brazilian Amazon. FEC is a nature reserve of Universidade Federal do Acre - UFAC. FEC is 214 m of average altitude and has a forest fragment with an area of 1,200 ha, whose vegetation is classified as open ombrophilous forest, with the presence of palms, bamboo, lianas, wild banana and open canopy (Daly & Silveira 2008; Medeiros *et al.* 2013). The surroundings of the FEC consist of vast areas of pastures made up mainly by the exotic grass *Urochloa brizantha* (Hochst. Ex A. Rich) RD Webster, with scattered presence of palm trees and Brazil nut tress (Araújo & Lani 2012).

According to the Köppen classification, the characteristic climate of the Western Amazon is (Am), with average annual temperatures of 25 ºC. Additionally, the State of Acre has two distinct seasons: dry (from May to September) and rainy (from October to April). This present average monthly rainfall of less than 60 mm, with an average temperature of 24.5 ºC, and 110 mm/month, with an average temperature of 25.9 °C, respectively (Duarte 2006; Acre 2012). Furthermore, the average annual precipitation is 1,973 mm (Duarte 2006).

Sampling and identification of ants. We collected the ants in three plots of forest and three plots of pasture (Figure 1), hereinafter called of forest 1, forest 2, forest 3, pasture

1, pasture 2 and pasture 3 respectively. Forest plots were established inside the forest fragment of FEC along the permanent sampling transect of the Biodiversity Research Program module (PPBio), which the distance among them was 1 km. Pasture plots, were established in pastures surrounding FEC (Figure 1).

In each plot, we distributed 10 sampling points at a 20 m interval along 200 m transect. In each sampling point, we installed four pitfall traps on soil surface level (Bestelmeyer *et al.* 2000) and four at soil underground (Schmidt & Solar 2010). Soil surface pitfall traps consist of plastic cup (height: 12 cm, diameter: 8 cm) containing inside a solution composed of water, neutral detergent and salt in order to kill and conserve ants. Small roofs were installed under the soil surface traps to prevent unwanted objects from falling and to prevent direct entry of rainwater. Moreover, in the pasture plots, aluminum screens were attached under the traps and immediately below their roofs to avoid the removal of the traps by cattle. Subterranean traps also consist of plastic cup (height: 12 cm, diameter: 8 cm) with water, neutral detergent and salt, however, they contain four radial holes (1 cm - diameter) made at 6 cm height, which allow ants to access the trap. Subterranean traps were closed with plastic caps to prevent soil from entering and buried to a depth of 20 cm (Schmidt & Solar 2010). A string with a colored ribbon was tied to the pitfall to help find the place where it was buried. Finally, all trap types remained in the field for 48 hours and we put sampled ants in vials containing alcohol 90%. Afterward, we sorted and mounted the sampled ants in "Laboratório de Ecologia de Formigas" - UFAC.

We identified ants at genera level using the taxonomic key of Baccaro *et al.* (2015). When possible, species-level identification
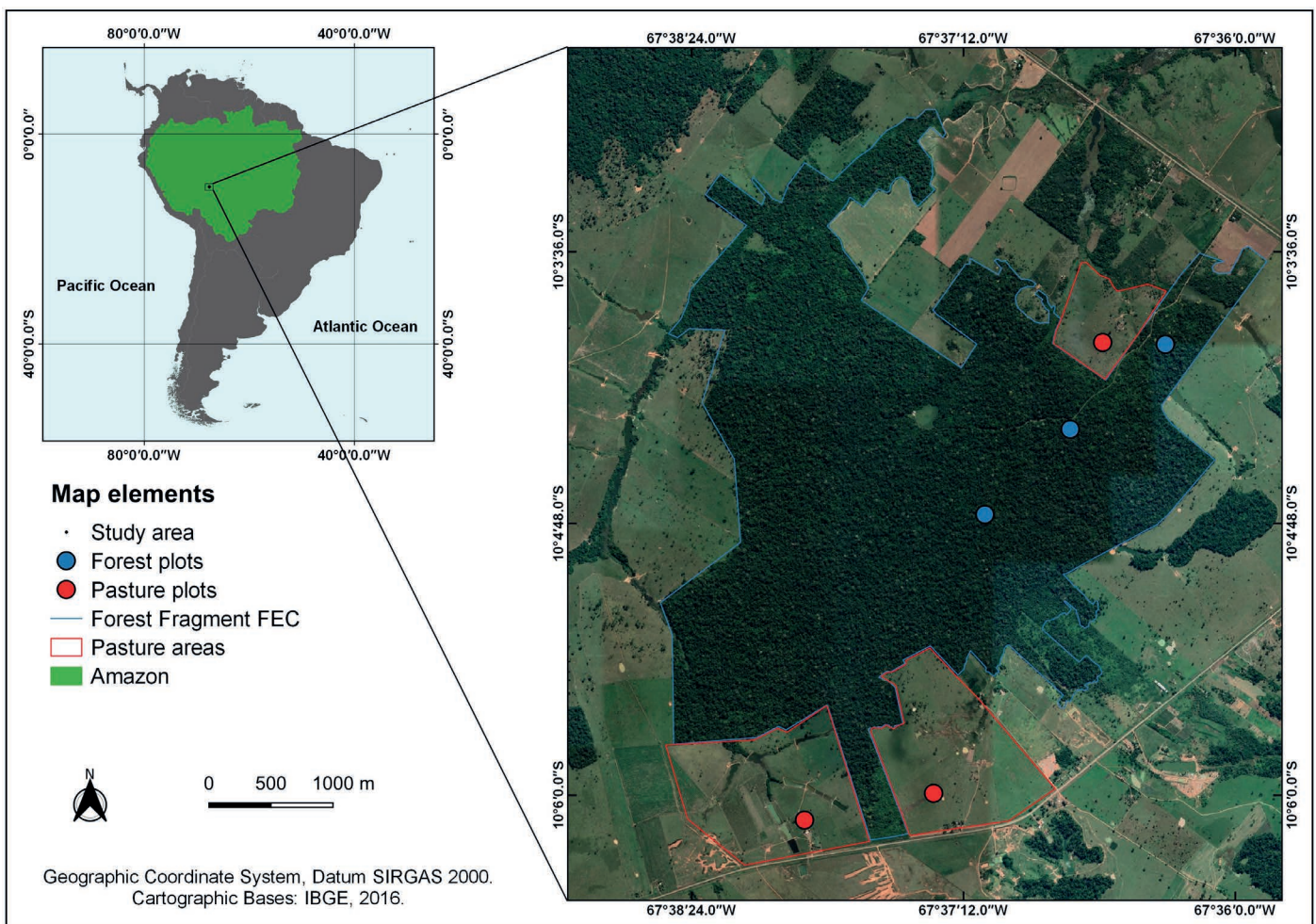

Figure 1. Study area with three forest plots inside forest fragment of Fazenda Experimental Catuaba (FEC) and three pasture plots in surrounding pastures in Acre state, Southwestern Brazilian Amazon.

was made through comparisons with specimens from the ant collection of "Laboratório de Ecologia de Insetos" - UFAC, where the voucher specimens were deposited. Ants that could not be identified at the species level were sorted into morphospecies according their external morphology similarity.

Ant classification according to habitat affinity. In order to sort the ant fauna sampled in the groups of habitat affinity (forest specialists, generalists, and open-habitat specialists), we used as reference the classification presented by Vasconcelos *et al.* (2018). To ant species that Vasconcelos *et al.* (2018) do not provide information on habitat affinity, we consulted Oliveira & Hölldobler (1991), AntWeb (2020) and Wilson (2003).

We proceeded this consult to further references at a conservative approach, which means to assign a species as forest specialist or open specialist, all records found should be associated only to one of these habitats, if we found for a species, records associated for both habitats (forest and open-habitat), this was assigned as generalist. Finally, ant species that we did not find any data on habitat affinity were excluded from analyses in the same way morphospecies were not considered.

Data analysis. All analyzes were performed using R 3.2.2 R Development Core Team (2019) software. When necessary specific packages were used and are cited below.

To evaluated how nest stratum and habitat affinity matter in the response of ant assemblages to forest-pasture shifting, we constructed generalized linear models with mixed effects - GLMM (Bolker *et al.* 2009), using the package lme4 (Bates *et al.* 2020), which number of ant species was the response variable and habitat type (forest and pasture) and habitat affinity (forest-specialist, generalist and open-habitat specialist) were the explanatory variables. Sampling plot was identified as random effect to control pseudo-replication (Pinheiro & Bates 2000).

We verified the significance of explanatory variables using the package car (Fox *et al.* 2020) and non-significant terms were removed to obtain the final model containing only significant terms (Crawley 2013). The model followed the Poisson distribution errors, since number of species is count data and we performed a residual analysis on the final model to evaluate the adequacy of error distribution (Crawley 2013). Finally, we ran this analyses protocol to entire ant assemblage involving both nest stratum (soil surface and subterranean) and to each nest stratum separately (only soil surface and only subterranean).

RESULTS

Ant fauna. In total, we collected 124 ant species, of which 38.7% were identified at species level and 61.3% were separated into morpho-species. The collected ants belong to 40 genera and are distributed in eight subfamilies (Supplemental File 1). The most speciose subfamily was Myrmicinae (70 species), followed by Formicinae (24), Dolichoderinae and Ponerinae (7), Dorylinae (6), Ectatomminae (5), Pseudomyrmecinae (4) and Paraponerinae (1) (Supplemental File 1).

We sampled 95 ant species along the three forest plots, 71 of which occurred exclusively on this habitat. In the three pasture plots, we sampled 53 species, 29 of which occurred exclusively on this habitat. We sampled 24 species in both habitat types (Supplemental File 1). The forest soil surface was the stratum with the highest number of ant species (82 species) followed by the pasture soil surface (45 species), forest subterranean (30 species) and pasture subterranean (24 species) (Supplemental File 1).

We were able to access the habitat affinity of 47 ant species, which correspond to 38% of the total ant species/morpho-species sampled (124). Of these 47 species, 21 are forest-specialists, 20 generalists and six open-habitat specialists (Table 1).

Regarding the total number of species of each group of habitat affinity sampled in each habitat type, along the forest plots, we collected 18 forest-specialist species, 17 generalists and two open-habitat specialists. In pasture habitat, we found only four ant species as forest-specialists, six were open-habitat specialists and 10 generalists.

Response of ant assemblages to forest-pasture shifting. In this analysis, only ants identified at the species level were used. Considering the entire ant assemblage (surface and underground), the number of ant species was not different between forest and grassland habitats (χ^2 = 2.99; p = 0.08) (Figure 2), however, the habitat affinity groups show a significant difference in the number of ant species (χ^2 = 30.97; p < 0.01) (Figure 2), with generalist being the most specious, followed by forest specialist and habitat specialist open. Furthermore, the interaction between a habitat affinity group and habitat type was significant (χ^2 = 36.49; p < 0.01), which means that these habitat affinity groups present different numbers of ant species according to the type of habitat (Figure 2).
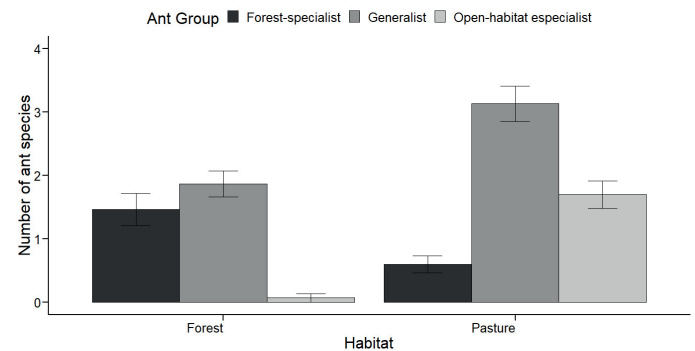

Figure 2. Relationship between number of ant species of entire ant assemblage with habitat type (forest and pasture) (p = 0.08), habitat affinity group (forest specialist, open-habitat specialist and generalist) (p < 0.01) and the interaction between them (p < 0.01) in Acre state, Southwestern Brazilian Amazon.

Regarding to the response of the ant assemblage of each nest stratum to forest-pasture shifting, we observed distinct patterns to soil surface and subterranean stratum. The number of species of soil surface ant assemblage was lower in forest than in pasture habitat (χ^2 = 5.40; p < 0.01) (Figure 3), however, the number of species of each group of habitat affinity was also different (χ^2 = 17.81; p < 0.01) (Figure 3) following the same pattern of entire ant assemblage. The interaction between group of habitat affinity and habitat type was significant (χ^2 = 39.78; p < 0.01) (Figure 3), which forest-specialist decreased the number of species and generalist and open-habitat specialist increased with forest-pasture shifting. In the subterranean ant assemblage, forest and pasture did not differ on the number of species (χ^2 = 1.26; p = 0,26) (Figure 4), but the number of species of each group of habitat affinity was also different (χ^2 = 35.93; p < 0,01) (Figure 4) following the same pattern of entire ant assemblage. The interaction between group of habitat affinity and habitat type was non-significant (χ^2 = 0.67; p = 0,71) (Figure 4).

Table 1. List of ant species sorted according to their habitat affinity: forest-specialist (forest), generalist, open-habitat specialist (open-habitat), Senador Guiomard, Acre, Southwestern Brazilian Amazon.

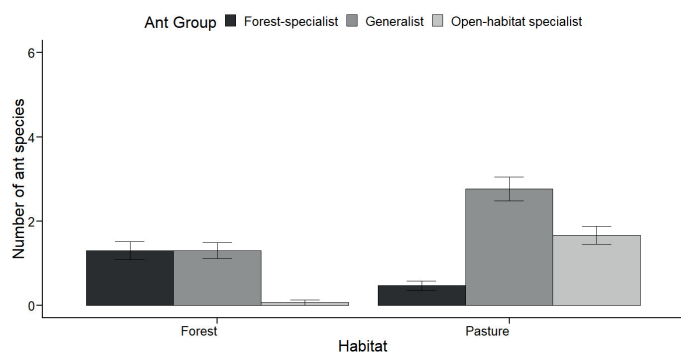| Species	Habitat affinity	Source
Acromyrmex coronatus (Fabricius)	Forest	AntWeb 2020
Acropyga goeldii (Forel)	Forest	Vasconcelos (2018)
Apterostigma auriculatum (Wheeler)	Forest	AntWeb 2020
Atta sexdens (Linnaeus	Open-habitat	Vasconcelos (2018)
Camponotus ager (Smith)	Forest	AntWeb 2020
Camponotus blandus (Smith)	Generalist	Vasconcelos (2018)
Camponotus cacicus (Emery)	Forest	AntWeb 2020
Camponotus crassus (Mayr)	Generalist	AntWeb 2020
Camponotus depressus (Mayr)	Forest	AntWeb 2020
Camponotus leydigi (Forel)	Open-habitat	Vasconcelos (2018)
Camponotus novogranadensis (Mayr)	Generalist	Vasconcelos (2018)
Crematogaster tenuicula (Forel)	Forest	AntWeb 2020
Cyphomyrmex laevigatus (Weber)	Forest	AntWeb 2020
Cyphomyrmex minutus (Mayr)	Generalist	AntWeb 2020
Cyphomyrmex rimosus (Spinola)	Generalist	Vasconcelos (2018)
Dolichoderus bidens (Linnaeus)	Forest	AntWeb 2020
Dolichoderus bispinosus (Olivier)	Generalist	Vasconcelos (2018)
Dolichoderus septemspinosus (Emery)	Forest	AntWeb 2020
Dorymyrmex brunneus (Forel)	Open-habitat	Vasconcelos (2018)
Ectatomma brunneum (Smith)	Generalist	Vasconcelos (2018)
Ectatomma edentatum (Roger)	Generalist	Vasconcelos (2018)
Ectatomma tuberculatum (Olivier)	Generalist	Vasconcelos (2018)
Gnamptogenys regularis (Mayr)	Forest	AntWeb 2020
Gracilidris pombero (Wild & Cuezzo)	Open-habitat	Vasconcelos (2018)
Labidus praedator (Smith)	Forest	Vasconcelos (2018)
Linepithema neotropicum (Wild)	Generalist	AntWeb 2020
Mayaponera constricta (Mayr)	Forest	Vasconcelos (2018)
Megalomyrmex ayri (Brandão)	Forest	AntWeb 2020
Mycocepurus smithii (Forel)	Generalist	Vasconcelos (2018)
Neoponera commutata (Roger)	Generalist	Vasconcelos (2018)
Ochetomyrmex neopolitus (Fernández)	Forest	AntWeb 2020
Odontomachus bauri (Emery)	Generalist	Vasconcelos (2018)
Pachycondyla crassinoda (Latreille)	Forest	Vasconcelos (2018)
Pachycondyla harpax (Fabricius)	Generalist	Vasconcelos (2018)
Pachycondyla obscuricornis (Emery)	Forest	Oliveira & Hölldobler (1991)
Paraponera clavata (Fabricius)	Forest	Vasconcelos (2018)
Pheidole capillata (Emery)	Generalist	Wilson (2003)
Pheidole fimbriata (Roger)	Forest	AntWeb 2020
Pheidole radoszkowskii (Mayr)	Generalist	Vasconcelos (2018)
Pheidole subarmata (Mayr)	Generalist	Vasconcelos (2018)
Pogonomyrmex naegelli (Emery)	Open-habitat	Vasconcelos (2018)
Pseudomyrmex tenuis (Fabricius)	Generalist	Vasconcelos (2018)
Pseudomyrmex termitarius (Smith)	Open-habitat	Vasconcelos (2018)
Strumigenys zeteki (Brown)	Forest	AntWeb 2020
Trachymyrmex bugnioni (Forel)	Forest	Vasconcelos (2018)
Tranopelta gilva (Mayr)	Generalist	Vasconcelos (2018)
Wasmannia auropunctata (Roger)	Generalist	Vasconcelos (2018)

Figure 3. Relationship between number of ant species of soil surface ant assemblage with habitat type (forest and pasture), habitat affinity group (forest specialist, open-habitat specialist and generalist) and the interaction between them (p < 0.01) in Acre state, Southwestern Brazilian Amazon.
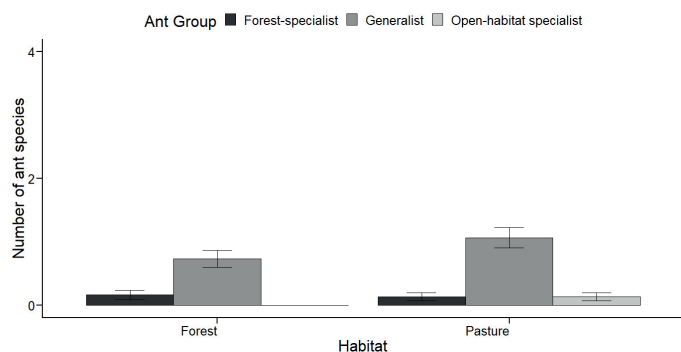

Figure 4. Relationship between number of ant species of subterranean ant assemblage with habitat type (forest and pasture) (p = 0.26), habitat affinity group (forest specialist, open-habitat specialist and generalist) (p < 0.01) and the interaction between them (p = 0.71) in Acre state, Southwestern Brazilian Amazon.

DISCUSSION

Our study was restricted by sampling efforts and on the classification of ant species on groups of habitat affinity, possibly leading to more limited perspective on ant assemblage diversity. However, our results are consistent with the findings of other studies on the response of ant assemblages to shifting of natural habitats into human modified habitats (Ribas *et al.* 2012a; Oliveira & Schmidt 2019; Paolucci *et al.* 2017; Menezes & Schmidt 2020).

Despite these considerations, we demonstrated that nest stratum and habitat affinity matter in the response of ant assemblages to forest-pasture shifting, which soil surface ants offer a clearest response and forest-specialist are the most hampered group. In the sections below, we offer possible explanations for these results and discuss their implications to the use of ant assemblages as bioindicators in environments under different levels of human-activities pressure. Moreover, the use of these to guilds (nest stratum and habitat affinity) as other ant guilds offer a clearer and more predictable response of ant assemblages to human impacts and ecosystem changes (Assis *et al.* 2018; Kwon *et al.* 2014).

Ant fauna. The classification of ants according to their habitat affinity allowed us to realize that generalist ants present a similar number of species than forest-specialist in forest habitat and these groups respond distinctly to forest-pasture shifting. Furthermore, this similar number of species between forest-specialist and generalist ants in forest habitat also highlight that forests in Southwestern Brazilian Amazon due to be under a relative low level of precipitation (Davidson *et al.* 2012) which has effects on forest structure and leads to more open canopy (Acre 2010; Arruda *et al.* 2017) could offer similar condition opportunities for both groups of ants (*i.e.*, forest specialist and generalist) In this way, considering the habitat

openness is a key driver of variation in ant assemblages (Andersen 2018), we can expected that forest ecosystems in central Amazon under higher levels of precipitation and with closer canopy (Fisch *et al.* 1998; Davidson *et al.* 2012; Arruda *et al.* 2017) probably affect differently these group of habitat affinity of ants, which forest-specialists could have higher number of species than generalists. However, to confirm this assumption ant survey at regional scale comparing border and central region of Amazon are necessary.

Regarding to open-specialist ant species seems that forest-pasture shifting offer a great opportunity to them expand their home range from natural open-habitats (*e.g.*, Cerrado - Brazilian Savanna) to the Amazon forest region. This process has been called as Amazon forest conversion into derived savanna (Silvério *et al.* 2013) where repeated burning in forest habitat have led to forest-by-savanna replacement on plant and animal communities. In our study, six open-specialist ant species (*i.e.*, *Atta sexdens* Linnaeus, *Camponotus leydigi* Forel, *Dorymyrmex brunneus* Forel, *Gracilidris pombero* Wild & Cuezzo, *Pogonomyrmex naegelli* Forel e *Pseudomyrmex termitarius* Smith) which has their home range associated to *Cerrado* (Vasconcelos *et al.* 2018) occur exclusively in pasture plots and this number of ant species is three times higher than in forest plots. These ants probably have expanded their distribution to Amazon region thanks to the increasing of agricultural landscapes in Amazon-Cerrado transition region (Morton *et al.* 2013; Marques *et al.* 2019), which pasture is the most conspicuous component (12.7%) (MapBiomas 2018) and have achieved the countryside of the biome, such as in Southwestern Brazilian Amazon (Acre 2010).

Response of ant assemblages to forest-pasture shifting. The most part of studies on ant assemblages as bioindicators, of environmental impacts and ecosystems changes, have used number of species and species composition (Ribas *et al.* 2012a) with non-consideration to ant groups that explore different niche types (but see Paolucci *et al.* 2017). Our results corroborate the importance to sample ants in more than one nest stratum, to allow the identification of which ant fauna segment is more sensitive to a common impact (Ribas *et al.* 2012b; Schmidt *et al.* 2013; Paolucci *et al.* 2017; Queiroz *et al.* 2017) which in our study was soil surface ant assemblages. The clear changes on diversity patterns of soil surface ant assemblages to forest-pasture shifting (Nakamura *et al.* 2007; Queiroz *et al.* 2017; Schmidt *et al.* 2013) could be due that the replacement of original forest-vegetation by grass and the consequent opening of vegetation cover leads to severe changes on conditions and resource availability to soil surface ants (Schmidt *et al.* 2013; Paolucci *et al.* 2017; Queiroz *et al.* 2017).

Thus, the non-response of number of species in subterranean ant assemblages to forest-pasture shifting could means that the changes on conditions and resource availability aboveground is not transmitted to underground. Subterranean ant assemblages are affected when some impact effectively reduce the free space for ants move at the underground soil pore system (Marques *et al.* 2017; Schmidt *et al.* 2017), which in our study area seems not happen. Thus, the trampling promoted by cattle at to soil surface seems not achieve high depths, maybe associated to the soil type in the region or the low amount of cattle in the sampled pastures.

The classification of ants in groups of habitat affinity, allowed us to identify which ant groups are disturbance-adapted - 'winners', and which are disturbance-sensitive - 'losers' (McKinney & Lockwood 1999; Tabarelli *et al.* 2012) regarding to forest shift into pastures, which has great implications to the use of ant assemblages as bioindicators of human-induced disturbances. Usually when entire ant assemblage is used in bioindication studies, the number of species non respond to human-induced disturbances and only species composition

changes (Ribas *et al.* 2012a). Approaching ant assemblages according habitat affinity of ants allow us to realize that changes on species composition between forest and pasture (Nakamura *et al.* 2007) is due to a high replacement among different habitat affinity ant groups. Thus, habitat affinity ant groups could offer a much more predictable use of ants as bioindicators of human-induced disturbances in forest ecosystems because once we know which ant groups are the winners and losers in conserved forest and in human-induced disturbed habitats, we could safe infer if a habitat under restoration is closer to a forest or to an open-cover habitat induced by human activity, such as pastures.

According to our results, forest-specialists could be considered the losers and generalists and open-habitat specialists, the winners in the forest-pasture shifting, once their number of species presented opposite responses, which is more evident in entire ant assemblage and soil surface ant assemblage. Thus, include different habitat affinity ant groups could offer a much more predictable use of ant assemblages in monitoring programs about the response of biodiversity to human-induced disturbances in forest ecosystems.

Although ant assemblages of forest are very sensitive to disturbances that promote habitat openness (Andersen 2018), we demonstrated that nest stratum and habitat affinity matter in the response of ant assemblages to forest-pasture shifting, which soil surface ants offer a clearest response and forest-specialist are the most hampered group. Therefore, we corroborate the inclusion of samplings in different nest stratum (Ribas *et al.* 2012b; Schmidt *et al.* 2013; Paolucci *et al.* 2017; Queiroz *et al.* 2017) and recommend the classification of ants according to their habitat affinity in monitoring programs that use ants as bioindicator. However, specifically regarding to habitat affinity, our study allowed us identified three critical drawbacks to be overcome: i) lack of information on habitat affinity of several ant species; ii) easy-friendly access to this information; iii) difficulty in identifying ants at the species level due to taxonomic impediments. We understand that much efforts are desirable to improve the information on habitat affinity and to make available it on online open databases.

ACKNOWLEDGMENTS

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