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ECOLOGY, BEHAVIOR AND BIONOMICS

Effect of Bamboo Dominance on Leaf-Litter Ant Assemblages in the Southwestern Amazon Forest

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Abstract
Bamboo density is a primary driver of changes in vegetation structure in the southwestern Brazilian Amazon, also affecting the forest litter, a significant and diverse component of which is ants. Here, we investigated the impact of bamboo dominance on litter ant assemblages with the following hypotheses: (i) bamboo patches have a more homogeneous and denser litter layer, (ii) which reduces the number of ant species, (iii) alters species composition, and (iv) results in smaller body sizes and simpler structures in litter ants. Additionally, bamboo patches are expected to have (v) a more open canopy, leading to (vi) a higher number of generalist and open-habitat specialist species compared to forest specialists. To test these hypotheses, we established 30 paired plots along the boundary between bamboo and non-bamboo habitats in an Amazon Forest fragment in Acre, Brazil. In each plot, we collected a 1 m^2 sample of the litter layer for ant sampling using a mini-Winkler extractor. We also measured litter density, litter heterogeneity, and canopy openness in each plot. Our findings showed that bamboo habitats present less dense litter layers, that heterogeneity did not differ, a higher number of ant species, and smaller ants. Species composition weekly differed between the habitats. In conclusion, the dominance of bamboo primarily affects ants through morphological filtering rather than species composition. Given that climate and land-use changes may promote the expansion of bamboo patches in the region, this could have significant impacts on ant assemblage composition and their ecosystem functions.

Keywords Biodiversity · Ecological filters · Habitat use · Morphology · Neotropical region

Introduction

The species pool that comprises a local community varies in time and space and is determined by ecological and evolutionary processes (Ricklefs and Schluter (1993). For a given species to join a local community, it needs to overcome several ecological filters (Hillebrand and Blenckner 2002). There are three ecological filters currently recognized, all acting at the same time: (i) species dispersion ability (Padial et al. 2014); (ii) the physiological capacity of species to tolerate the conditions imposed by the physical environment and availability of resources (Gibb et al. 2015); and (iii) the results from interactions with other species (Sexton et al. 2009, Wiens 2011). The limitations posed by abiotic conditions and by the availability of resources can illustrate the filtering action related to tolerance to environmental conditions, because species that arrive in a local community will only be able to survive if they tolerate the spectrum of conditions present in the local community and if they find

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the resources they need (Sobral & Cianciaruso 2012). Thus, solar radiation, temperature, humidity, and physical and chemical aspects of the soil (Larcher 2000, Calixto 2001) are some of the abiotic factors that work in the selection of species that comprise ecological communities in terrestrial ecosystems (Duellman, and Trueb, 1994, McDiarmid 1994, Gonzalez et al. 2010, Watling and Orrock 2010). The availability of resources is another key aspect for the persistence of a species in a local community. Some plants, for example, have high nutritional requirements for adequate productivity (Severino et al. 2006). Similarly, fauna needs food resources such as fruits, seeds, prey, and others to occur in a given local community (Piratelli and Pereira 2002).

Moreover, species dominance is also a determining factor for the presence of species in local communities. In the southwestern Amazon, bamboos of the genus *Guadua* (Poaceae) dominate huge forest areas, which makes this region the largest area of bamboo-dominated forests throughout the Neotropical region (Griscom et al. 2007). Bamboos show a high ecological amplitude in response to canopy disturbances and can become dominant in the understory, particularly due to their abundance and the potential effect on forest regeneration in gaps (Gonzalez et al. 2002). Consequently, bamboo population density creates wide openings in the canopy (Carvalho et al. 2013) and changes vegetation structure and dynamics (Zaninovich et al. 2017). Their aggressive growth capacity (Griscom and Ashton 2006) and the plasticity in functional traits, such as photosynthetic capacity, can explain their success in disturbed areas and provide a competitive advantage over trees in the forests (Montti et al. 2014).

As bamboo dominance changes drastically, the flora composition and vegetation structure in forests, litterfall, and the litter layer are also affected (Zaninovich et al. 2017). Areas with bamboo dominance may have litter essentially formed by deciduous plant materials from bamboos, which arguably affects the heterogeneity of the litter and its ecological function. Moreover, bamboo-dominated forests in the Amazon may show lower litterfall, due to the replacement of trees by bamboo culms, while at the same time accumulating a layer of litter above the soil (Dantas et al. 2020). The effects of bamboo dominance on litter dynamics in the Amazon are so pronounced that they appear even at small spatial scales (Dantas et al. 2020).

Litter layer dominated by material from bamboo also puts pressures on invertebrate assemblages (Zanoli & Morato 2015) since the bamboos increase litter layer thickness and decrease decomposition rate and the quality of this litter in nutritional terms (Zaninovich et al. 2017). A very abundant invertebrate group with high species diversity in the litter is the ants (Schutte et al. 2007, Silva and Brandão 2010, Gomes et al. 2013). Among the habitats used by ants, litter is the stratum with the highest species diversity (Marinho et al. 2002, Santos et al. 2006, Silva & Brandão 2014). Ants can live and move inside as well as outside the litter because of the high variability of life histories, shapes, and body sizes of species (Kaspari & Weiser 1999).

Therefore, changes in litter constitution and density caused by bamboo dominance can change the substrate for ant nesting and foraging, which affects ant species dispersal (Nooten et al. 2019). The role of filter played by bamboos can be reflected in ant morphology and in species composition of ant assemblages (Schofield et al. 2016, Guilherme et al. 2019). Moreover, high canopy openness in bamboo areas (Lima and Gandolfi 2009) may affect the species composition of litter ant assemblages. In the Neotropical region, the evolution and diversification of ant species are associated with forest ecosystems (Moreau and Bell 2013). The ant fauna of ecosystems with highly open vegetation has been reported essentially as originating from forest ecosystems (Branstetter et al. 2017); however, these ant species tolerate conditions of high temperature and aridity (Leal et al. 2017). Thus, in the Neotropical ant fauna, it is possible to identify specialist species of forest habitats, species that are capable of living in highly open environments as well as in forest, being thus designated as generalists, and finally, a few numbers of ant species are considered open-habitat specialists (Vasconcelos et al. 2018). Therefore, these different groups of ants can respond differently to canopy openness in bamboo areas, leading to changes in the species composition of litter ant assemblages.

In this study, we investigated the effect of bamboo dominance on leaf-litter ant assemblages in the southwestern Amazon Forest. We tested the following hypotheses: (i) forests under bamboo dominance should have a homogeneous and dense litter, which causes a (ii) reduction in the number of ant species and a selective (iii) change in species composition leading to an ant assemblage comprised of (iv) species with small body sizes and structures; (v) forests under bamboo dominance should have an open canopy, which can thus select ant species that tolerate open habitats. Considering projections in climatic changes for the future of the southwestern Brazilian Amazon, bamboo-dominated forests could expand their distribution area (Perz et al. 2008). Thus, our study could provide perspectives about the response of ant assemblages to potential forest structure shifting.

Materials and methods

Study area

The study was carried out in the forest fragment of Fazenda Experimental Catuaba, which belongs to Universidade Federal do Acre (UFAC), located in the municipality of Senador Guiomard, Brazil, at coordinates 10°04′S and 67°37′W and a

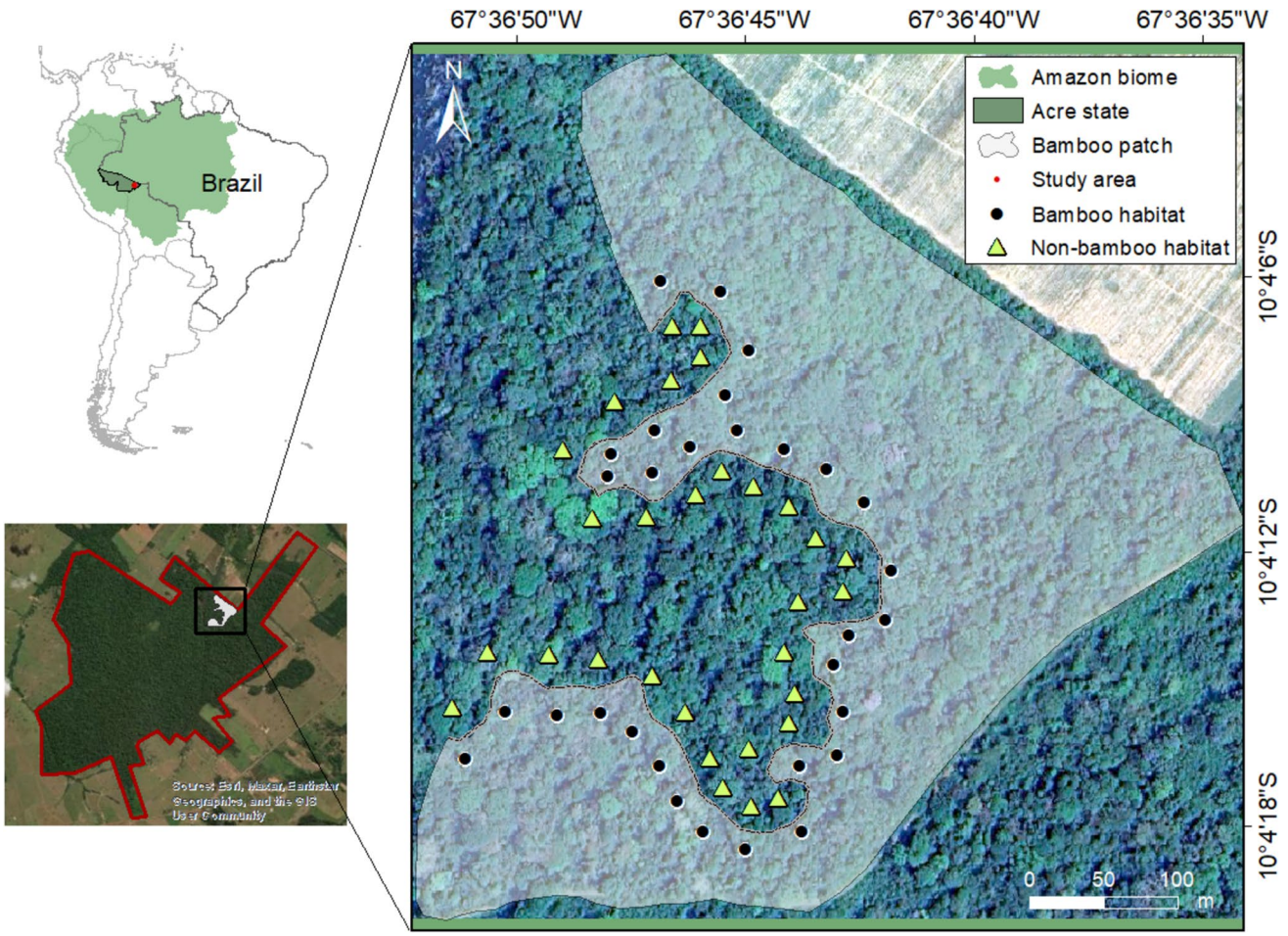

Fig. 1 Sampling area at Fazenda Experimental Catuaba (FEC/UFAC), state of Acre, southwestern Brazilian Amazon. Black points are bamboo habitats and yellow triangles are non-bamboo habitats

mean altitude of 214 m (Fig. 1). The forest fragment has an area of 1200 ha, which is covered by ombrophilous open forest, characterized by an open canopy, the presence of palm trees, vines, and extensive bamboo areas (Daly, and Silveira, 2008, Medeiros et al. 2013).

Sampling design

To evaluate if the bamboo dominance acts as an ecological filter on leaf-litter ant assemblages, we used the sampling design proposed by Bona et al. (2020) and Dantas et al. (2020), which includes the boundaries of a large bamboo area inside the forest fragment, to obtain a contact area between a bamboo habitat and a non-bamboo habitat with approximately 1600 m. In this contact area between the two habitat types, there are 30 sets of plots of 10 × 10 m paired, separated ca. 30 m inside each habitat and ca. 50 m between habitats, totaling 60 plots (total of 6000 m^2). The plots of bamboo habitat have 10 or more bamboo culms per 100 m^2 (density equal to or greater than 0.1 culm/m^2), which is the minimum density to be considered a bamboo-dominated forest (Griscom and Ashton 2003). In contrast, the plots of non-bamboo habitat have from zero to two bamboo culms per 100 m^2 (bamboo density less than 0.1 culm/m^2).

Ant collection and identification

We sampled 1 m^2 of litter layer in the plots of each habitat type, which was sieved and placed in a mini-Winkler extractor for 72 h to collect the ants (Bestelmeyer et al. 2000). The ants were identified at the genera level using taxonomic keys according to Baccaro et al. (2015). The identification at the species level was performed by comparing with specimens from the ant collection of Laboratório de Ecologia de Insetos of Universidade Federal do Acre, where the voucher specimens were deposited. Additionally, ants were identified at the species level at Laboratório de Biologia e Sistemática of Universidade Federal do Paraná using proper taxonomic literature (see Appendix 1, as digital supplementary material to this article, at the journal's web pages). Finally, ants

that could not be identified at the species level were sorted into morphospecies according to their external morphology similarity.

Ant morphology measurements

For each sample, we photographed up to three ants per species using a Leica M125 stereomicroscope camera. Ants were measured from the photos using the software Leica Application Suite, Version: 4.8.0. Specifically, we measured the following structures: head width (HW), head length (HL), posterior femur length (FL), and Weber length (WL) (Nooten et al. 2019). According to Silva and Brandão (2010) and Silva and Brandão (2014), the width and length of the head are related to the size of the mandible musculature, the length of the femur is related to the distribution of species in the litter, and Weber length is an indicator of ant body size. As the measurements of HW and HL are less informative than the general head shape (Holley et al. 2016), they were analyzed as Head Index (HI), calculated as: HI = 100 HW/HL.

Habitat-use ant guild classification

To all ants identified to species level, habitat-use guilds were obtained from the application program Brazilian Ant Habitat-use guilds (Bah 2023). Morphospecies and species with no information found were not included.

Litter data collection

We collected four samples of litter in each plot using a metal square sampler (10 × 10 × 10 cm). The litter samples were removed from the corners of each plot. To estimate litter heterogeneity in each plot, the items comprising dry litter samples were classified into seven categories: bamboo leaves, leaves in general, flowers and inflorescences, diaspores (fruits and seeds), thin branches (diameter ≤ 2 mm), thick branches (> 2 mm), and miscellaneous (all items not assigned to the above categories). Shannon Diversity Index (Magurran 2011) was calculated for each litter sample considering the item categories described above. The mean value of the four samples was used as the Shannon Index of the plot, which was considered the surrogate of litter heterogeneity. To estimate litter density, we obtained the dry weight of the samples present in the metal square sampler (volume = 1000 cm^3). Mean litter density for each plot was obtained considering four litter samples and was considered the litter density of the plot. Considering that the higher the density of a material is, the smaller the space between the particles that constitute it, the mean litter density of each plot was used as an operational variable to quantify the existing space between litter items, which is the space available for the ants to nest and forage.

Canopy openness measurement

The physical canopy openness was quantified with a spherical canopy densiometer (Lemmon 1957), using the average of four measurements (north, south, east, and west) in relation to the center of the plot. The percentage of canopy openness of the plot was the average of these four values.

Data analysis

All analyses were performed with a 5% probability, using the R v. 3.6.1. (R Core Team, 2019). For all statistical tests, residual analyses were performed to check the adequacy of the error distributions (Crawley 2013).

To test whether the bamboo habitat had a more homogeneous, dense litter, and a more open canopy, an analysis of variance (ANOVA) was performed using linear models (LMs). Litter heterogeneity, density, and canopy openness were used as response variables, and habitat type was used as a predictor variable. Models followed normal distribution when litter heterogeneity and density were the response variables and binomial distribution when canopy openness was the response variable.

To check the effects of litter heterogeneity and density on the number of ant species, we ran an analysis of covariance (ANCOVA) using generalized linear models (GLMs) with a Poisson distribution. The number of ant species was used as a response variable, litter density and heterogeneity were used as predictor variables, and habitat type was used as a covariable. We checked the significance of the predictor variables, and non-significant terms were removed to obtain the final model containing only significant terms (Crawley 2013)**.**

To assess whether the litter of bamboo-dominated forest leads to a selective change in species composition of ant assemblages, we performed a non-metric dimensional scale (NMDS) with Jaccard distance, based on a species presence and absence matrix. The robustness of the groups formed by NMDS was confirmed by a permutational multivariate variance (PERMANOVA) with the *adonis* function from the *vegan* R-package and Jaccard distance, using 999 permutations. Finally, we checked the homogeneity of the variances between groups using permutational multivariate dispersion analysis (PERMDISP), with the *anosim* function from the *vegan* R-package and Jaccard distance, using 1000 permutations.

To check if ants from bamboo and non-bamboo habitats showed differences in body size and structures, we ran an analysis of covariance (ANCOVA) using generalized linear models (GLMs) with a normal distribution. Weber length,

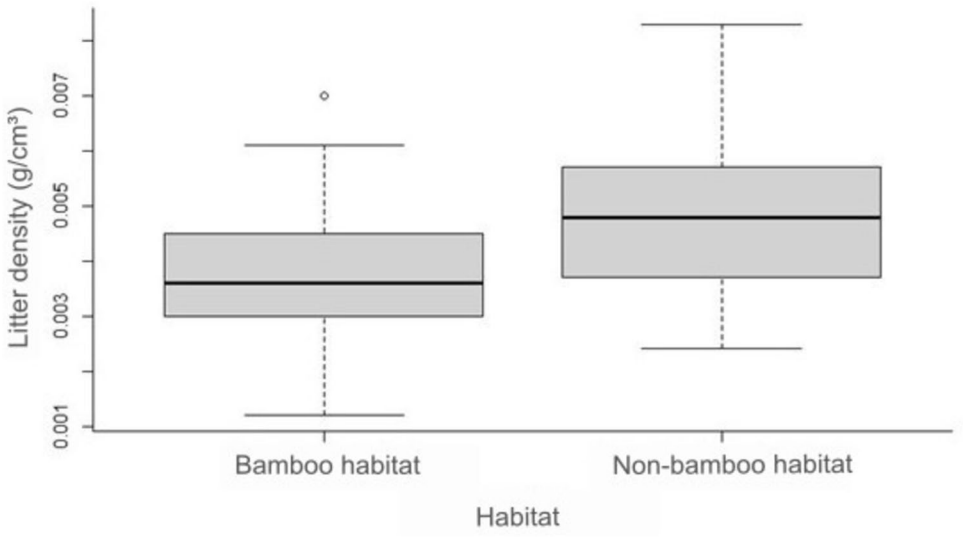

Fig. 2 Litter density in bamboo habitat and non-bamboo habitat at Fazenda Experimental Catuaba (FEC), southwestern Brazilian Amazon

Head Index, and femur size were used as response variables in the models. Heterogeneity, litter density, and habitat type were used as predictor variables. The interaction between litter heterogeneity and density with habitat type was also considered in the models. We checked the significance of the predictor variables, and non-significant terms were removed to obtain the final model containing only significant terms (Crawley 2013)**.**

To test the effects of canopy openness on the number of species of habitat-use ant guilds, we ran an analysis of covariance (ANCOVA) using generalized linear models (GLMs), with a Poisson distribution. The number of ant species was used as a response variable, canopy was the predictor variable, and habitat type and habitat-use guilds were covariates, and the interaction between them was considered. We checked the significance of the predictor variables, and non-significant terms were removed to obtain the final model containing only significant terms (Crawley 2013).

Results

Ant fauna

We sampled 149 ant species (e.g., 149 ant species, of which 61 were identified to species level and 88 were sorted into morphospecies), with 116 (56.58%) occurring in the bamboo habitat and 89 (43.41%) occurring in the non-bamboo habitat. The ants identified at species level are listed in Appendix 2, as digital supplementary material to this article, at the journal's web pages. Sixty ant species were exclusive to the bamboo habitat, 56 are exclusive to the non-bamboo habitat, and 33 occurred in both habitats. The sampled ant species belong to 36 genera and are distributed in eight subfamilies: Amblyoponinae (1), Dolichoderinae (1), Dorylinae (4), Ectatomminae (6), Formicinae (10), Myrmicinae (109), Ponerinae (16), and Proceratiinae (2). Regarding genera, *Pheidole* had the highest number of species (33), followed by *Wasmannia* (12), *Strumigenys* (11), and *Solenopsis* (10).

Effects of bamboo dominance on litter and canopy openness

The bamboo and non-bamboo habitats did not differ regarding litter heterogeneity ($F_{(1.58)} = 1.07$; $p = 0.3$) and canopy openness ($F_{(1.58)} = 0.74$; $p = 0.23$), but bamboo habitat had a less dense litter layer than non-bamboo habitat ($F_{(1.58)} = 9.33$; $p = 0.003$) (Fig. 2).

Ant assemblage structure

Number of ant species responded only to habitat type and litter density ($\chi^2_{(1.59)} = 159.95$; $p < 0.001$). Thus, bamboo habitat had a higher number of ant species than non-bamboo habitat ($\chi^2_{(1.57)} = 88.75$; $p < 0.001$) (Fig. 3). In both habitats, with increasing litter density, the number of ant species decreased ($\chi^2_{(1.58)} = 146.83$; $p = 0.0002$) (Fig. 3).

Ant assemblages from bamboo and non-bamboo habitats differed in species composition (PERMANOVA $F_{(1.59)} = 2.94$; $R^2 = 0.04$; $p = 0.001$). However, inside each group formed by NMDS, there was a significant variation in ants species composition between the plots (PERMDISP $F_{(1.58)} = 4.27$; $p = 0.04$), which indicates a lack of homogeneity inside each group (Fig. 4).

Morphology of leaf-litter ant species

Mesosoma length responded to habitat type ($F_{(1.56)} = 19.75$; $p < 0.001$) (Fig. 5). Bamboo habitat had smaller mesosoma length ants than non-bamboo habitat.

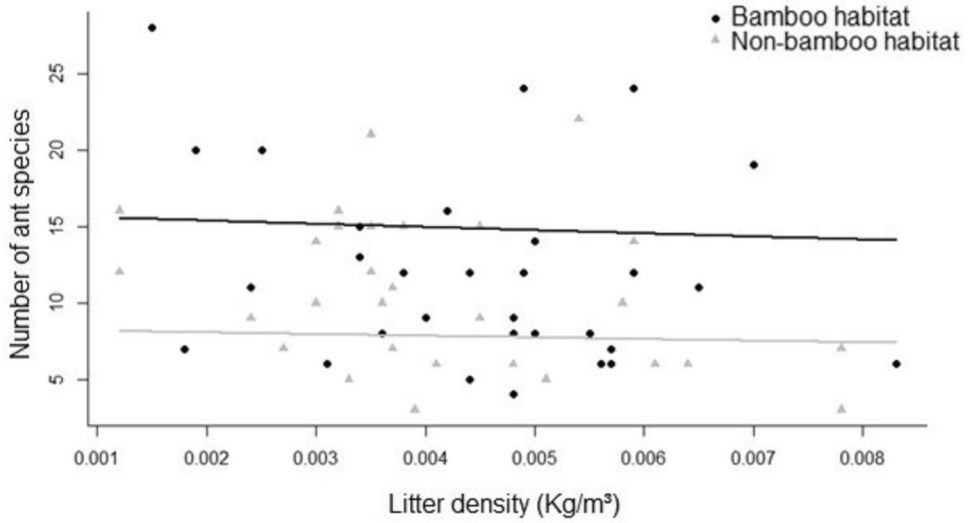

Fig. 3 Relationship between the number of ant species with litter density in bamboo habitat and non-bamboo habitat at Fazenda Experimental Catuaba (FEC), southwestern Brazilian Amazon

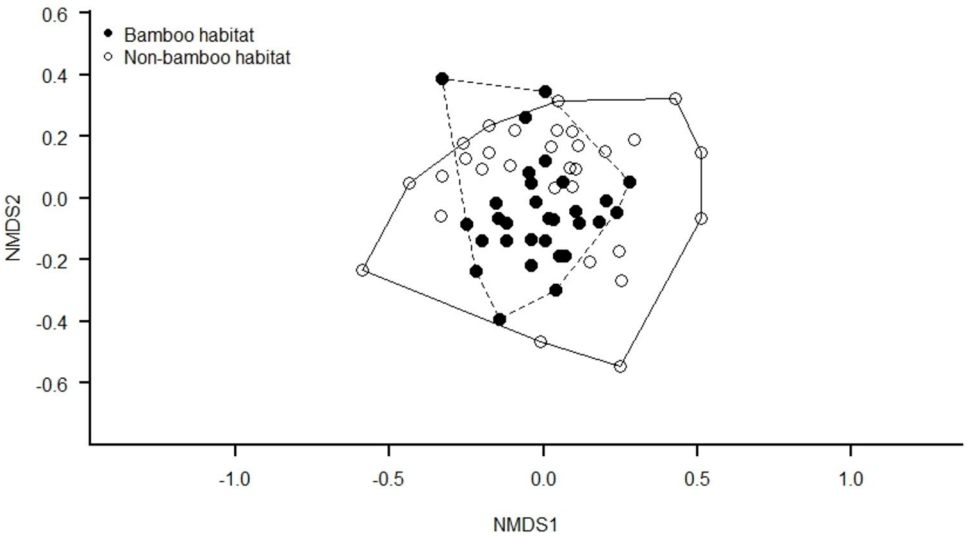

Fig. 4 Non-metric multidimensional scale ordination (NMDS) illustrating litter ant species composition in bamboo habitat and non-bamboo habitat at Fazenda Experimental Catuaba (FEC), southwestern Brazilian Amazon

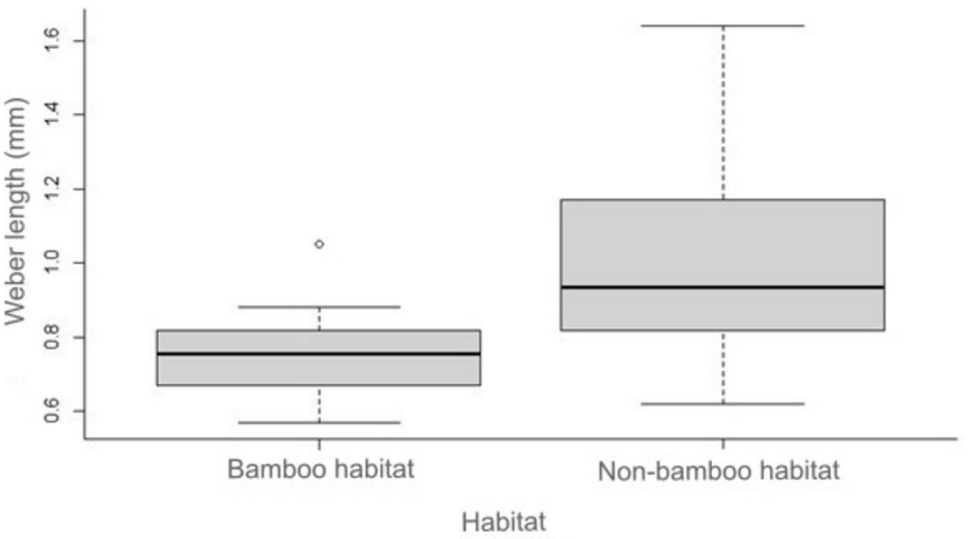

Fig. 5 Relationship of mesosoma size with habitat type (bamboo habitat and non-bamboo habitat) at Fazenda Experimental Catuaba (FEC), southwestern Brazilian Amazon

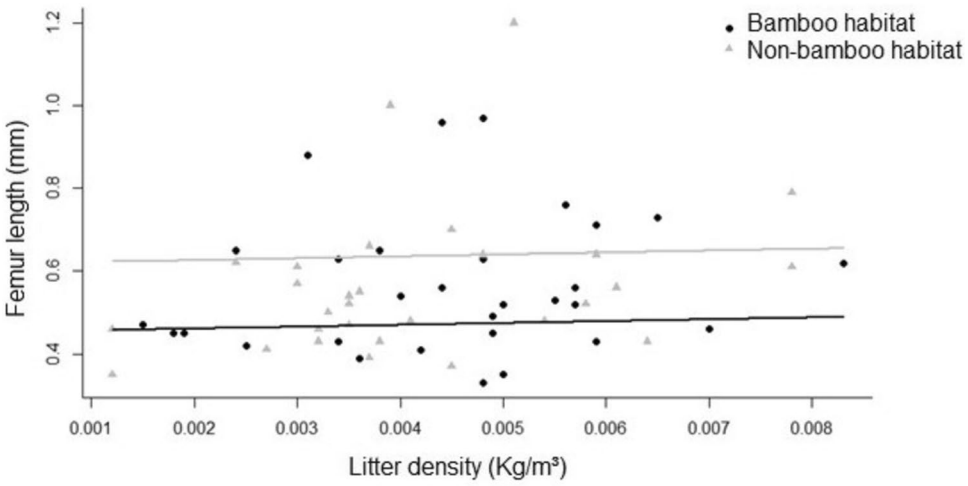

Fig. 6 Relationship of litter ant femur size with litter density in bamboo habitat and non-bamboo habitat at Fazenda Experimental Catuaba (FEC), southwestern Brazilian Amazon

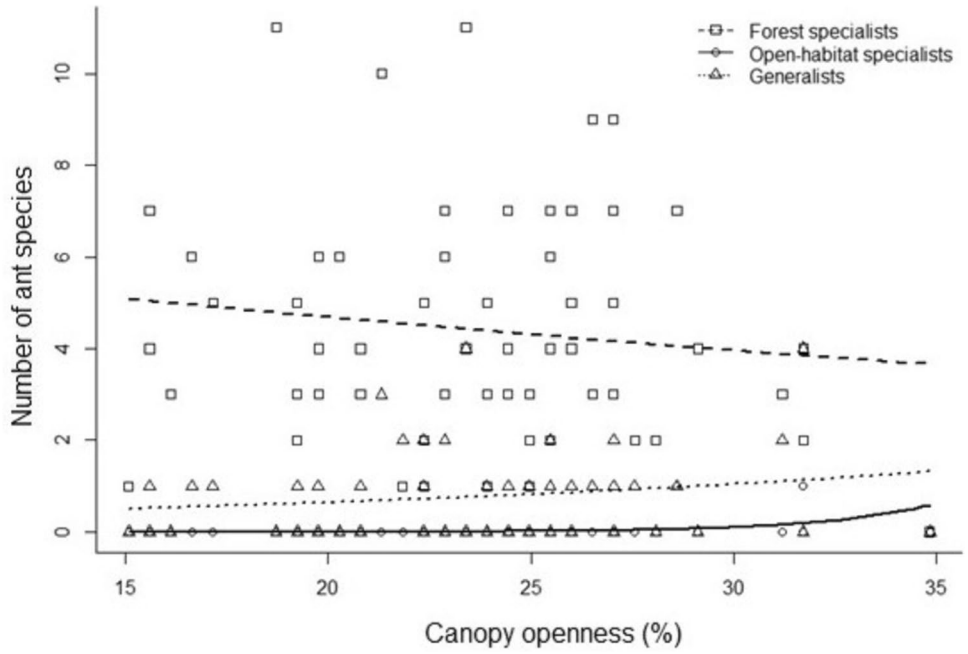

Fig. 7 Relationship between the number of ant species belonging to the habitat-use ant guilds (forest specialists, open-habitat specialists, and generalists) with the canopy openness (%) in bamboo habitat and non-bamboo habitat, at Fazenda Experimental Catuaba (FEC), southwestern Brazilian Amazon

Femur length responded to habitat type and litter density ($F_{(2.59)} = 4.98$; $p < 0.001$) (Fig. 6). Thus, the ants from non-bamboo habitat had a larger femur than those from bamboo habitat. In both habitats, increasing litter layer density leads to increased femur length. Finally, the Head Index did not respond to any of the litter variables and habitat types ($F_{(1.674)} = 0.85$; $p = 0.5$).

Effects of canopy openness on ant habitat-use guilds

Number of ant species responded to habitat-use ant guilds ($\chi^2_{(1.176)} = 169.2$; $p < 0.001$) and the interaction between canopy openness and habitat-use ant guilds ($\chi^2_{(1.174)} = 161.98$; $p < 0.05$). When canopy openness increases, the number of ant species of open-habitat specialists and generalists increases, but the number of forest specialist ant species decreased (Fig. 7).

Discussion

Our study provides unprecedented information on the interference of the dominance of native bamboo populations in the structure of ant assemblages in the southwestern Amazon. In this study, we found out that bamboo-dominated habitats have less dense litter, which hosts a larger number of ant species. Although bamboo dominance leads to a weak

selective change in species composition of litter ant assemblages, the ants from bamboo habitats are smaller (i.e., mesosoma and femur length). Finally, although canopy openness did not differ between habitat types, the canopy openness among plots determines the number of ant species per habitat-use guilds. In the following sections, we presented explanations for these findings and reports on potential implications for the structure of leaf-litter ant assemblages.

Ant assemblage structure

In bamboo-dominated habitats, contrary to our expectations, the litter layer was less dense and hosted a higher number of ant species. This can be explained considering the long time for bamboo leaf decomposition due to the high concentration of fibers (Zaninovich et al. 2017). Thus, space among bamboo leaves can persist for a longer time, which leads to a decrease in litter density and promotes more space (Marques et al. 2017) for a higher number of ant species to nidify and move inside the litter.

Although the ant assemblages from bamboo-dominated and non-bamboo habitats differed in ant species composition, the result groups lack homogeneity, which indicate a low dissimilarity between the ant assemblages from the two habitats due to a high number of shared species. Thus, we can infer that the role of bamboo as a local ecological filter on the regional species pool is weak because ants can disperse between the two habitats without strong restrictions in the same way that tree seeds can in the study area (Bona et al. 2020). This is in accordance with the findings of Schmidt et al. (2017), which have reported that at a local scale, ant species have a high dispersal ability, leading to a high number of species and low differences in species composition.

However, when the effect of plot canopy openness on the number of species of ant habitat-use guilds is considered, we can realize an ecological filter acting. Although, in all plots, the number of species of forest specialist ants is higher than that of generalists and open-habitat specialists, these guilds presented contrary trends with canopy openness (Fig. 7). Canopy openness or habitat openness has been reported as the main driver of ant assemblages (Andersen 2019) and disturbs the forest ecosystem, which leads to canopy opening, consequently promptly affecting the number of these habitat-use guilds, decreasing the number of species of forest specialist ants and increasing generalists and open-habitat specialists (Martins et al. 2022, Dutra et al. 2023). The lack of differences regarding habitat type (bamboo-dominated and non-bamboo habitats) might have occurred due to the proximity of the forest, which maintained the bamboo stands' canopy with still low openness on fine spatial scales. However, studies conducted on larger spatial scales indicate a high impact of bamboos on forest structure, resulting in greater canopy openness (Griscom and Ashton 2006; Carvalho et al. 2013). Therefore, we encourage future studies to evaluate the habitat-use guilds of ants in bamboo-dominated areas on larger spatial scales to understand how bamboo influences these communities beyond diversity.

Ant morphology

The less dense litter in habitats with bamboo potentially offers a great variability of space within litter debris, allowing ants with small body size and femur length to access this stratum. On the other hand, in non-bamboo habitats, the litter is sparse, which favors ants with large body size and femur length. Thus, our results corroborate previous findings that complex habitats (e.g., non-bamboo-dominated habitat) host ants with larger body size and appendices length (Nooten et al. 2019, Guilherme et al. 2019). Therefore, we could highlight that the ecological filter played by bamboo dominance is expressed essentially in ant morphology, promoting a replacement of body size and femur length among ants in southwestern Brazilian Amazon. These findings uncover another mechanism by which bamboo populations can maintain themselves within forests and expand geographically. This is because larger ants disperse more seeds and with higher quality for the dispersal process (Leal et al. 2014a, b). Therefore, in addition to the dominance of bamboos acting in filtering for seed species arriving in bamboo-dominated areas (Bona et al., 2020), it also interferes with a crucial characteristic of an important dispersing agent, which reduces the chances that the few seed species arriving will be dispersed.

Conclusion

Our study present implications for the effects of forest management in the southwestern Brazilian Amazon, which is the home of the largest area of bamboo-dominated forests throughout the Neotropical region (Griscom et al. 2007). Forests under selective logging in the region have the risk of being dominated by bamboo after wood exploitation, which drawback forest regeneration (Carvalho et al. 2007) and, according to our findings, could lead to ant assemblages, although rich in number of species, composed of smaller and generalist and open-habitat specialist ants. These changes also could have effects on ecosystem functions played by ant species, once small ants have been associated with low-quality potential seed dispersion because they consume seeds or remove them to short distances (Leal et al. 2014a, b), which is a hamper for plant population dynamics. Finally, the effect observed here can be intensified by climate change, with projections predicting a drier and warmer climate for the

Amazon (PBMC 2014) favoring the expansion of bamboo patches (Perz et al. 2008).

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Author contribution Fabiana Oliveira, Fernando Augusto Schmidt formulated the main questions and hypothesis. Ketlen Bona and Henrique Augusto Mews made the sampling design. Material preparation and data collection were performed by Fabiana Oliveira, Kelsy Ellen da Silva Vale, Francisco Matheus da Silva Sales, and Rodrigo Machado Feitosa. Analysis was performed by Fabiana Oliveira, Fernando Augusto Schmidt, Luane Karoline Fontenele, and Ketlen Bona. The first draft of the manuscript was written by Fabiana Oliveira, and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Declarations

Ethical approval Not applicable.

Conflict of interest The authors declare no competing interests.

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