



RESEARCH ARTICLE - ANTS

Mechanisms of species coexistence and functional diversity of ant assemblages in forest and pasture habitats in southwestern Brazilian Amazon

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Abstract

In this study, we investigated the mechanisms behind species coexistence and the relationships between functional diversity and species richness in ant assemblages in both forest and pasture habitats in the southwestern Brazilian Amazon. We addressed the specific question: What is the primary mechanism for species coexistence in forest and pasture habitats? According to the identified mechanism in each habitat, we had the following alternative expectations: (i) niche partitioning – we expected to observe a positive linear relationship between functional diversity and species richness, indicating a complementary relationship; or (ii) niche filtering – a positive constant asymptotic relation between functional diversity and species richness, indicating a functional redundant relationship. In total, we sampled 91 ant species, 82 species in a forest habitat and 16, in a pasture habitat. In the forest habitat, we identified niche filtering as the structuring mechanism of the ant assemblage, but we were unable to identify a clear mechanism in the pasture habitat. Although the relationship between functional diversity and species richness was positive in both habitats, the relationship was weaker in the forest habitat, indicating a greater functional redundancy among the ant species in this habitat. Our results reinforce the divergence of species coexistence mechanisms and ant assemblage structures in both natural and human-modified habitats in the Southwestern Brazilian Amazon.

Introduction

Niche partitioning has often been used to explain ant species coexistence as well as ant community assemblages (Blüthgen & Feldhaar, 2010; Camarota et al., 2016). However, the high number of ant species at the local scale (e.g., 86 species in 0.13 ha in northwestern Australia and 30 species in 1 m² of leaf litter in Atlantic Forest, Brazil) (Andersen, 1983; Silva & Brandão, 2010) has led ant ecologists to question the role of interspecific competition in ant species coexistence and propose alternative mechanisms for community ant assemblages (Ribas & Schoereder, 2002; Cerdá et al., 2013).

Andersen (2008) proposed alternative explanations for the high diversity of ants at the local scale, based on sociability and modularity of their nests, which protect species

against environmental harm (Hölldobler & Wilson, 2009). Additionally, competitive interactions between species are highly variable depending on both temporal and spatial environmental variations. The dominance of resources and space by dominant ant species occurs in patches, which makes it possible to use these resources by subordinate species (Andersen, 2008). Thus, ant species could overcome the negative effects of interspecific competition. In this way, recent studies have suggested that niche filtering (similarities regarding the use of the resource) is the mechanism responsible for the coexistence of species in ant assemblages (Arnan et al., 2011; Fowler et al., 2013).

Ants are responsible for various functions in terrestrial ecosystems, which can be demonstrated by their morphological diversity that reflect their life histories such



as resource use, habitat preference, and foraging strategies (Kaspari & Weiser, 1999; Silva & Brandão, 2010; Silva & Brandão, 2014; Schofield et al., 2016). Thus, several studies have focused on functional diversity in ant assemblages based on the measurement of functional traits (Bihn et al., 2010; Arnan et al., 2014; Silva & Brandão, 2014; Schofield et al., 2016; Martello et al., 2018).

Given that niche partitioning promotes species coexistence that differ in the use of limiting resources and that niche filtering promotes the coexistence of species with similar niches, we can deduce specific expectations about the relationship between functional diversity and species richness in ant assemblages. First, in ant assemblages structured by niche partitioning, we expect there to be a linear and positive relationship between functional diversity and species richness. Second, for ant assemblage structured by niche filtering, we expect the relationship between functional diversity and species richness to be positive, but when the relationship levels off, it achieves a constant asymptotic relationship. This has been interpreted to be a functionally redundant relationship (Naeem et al., 2002).

The selective action of the range of physical conditions, resources, and ecological interactions on the species set that make up an ecological community is reflected in the morphology and physiology of the species and on the assembly's functional diversity (Schofield et al., 2016). Thus, we expect that ant species living in different environments will have distinct morphologies and physiologies, and consequently will exhibit different patterns of functional diversity (Wiesher et al., 2012).

Besides forest habitats, the Amazon region, due to conversion and fragmentation processes, contains large area of pastures. Pastures are very different from forest habitats, specifically in relation to the abiotic conditions and resources available such as land cover, leaf litter soil cover, moisture, and biodiversity (Fearnside, 2005; Imazon, 2010; Araújo et al., 2011). This is the case in the southwestern Brazilian Amazon, where ant assemblages in both forest and pasture habitats present very distinctive patterns in both fauna and species diversity (Oliveira & Schmidt, 2019).

In this study, our main aim is to understand the mechanism (niche partitioning or niche filtering) for ant species coexistence and the implications of this mechanism for the relationship between functional diversity and species richness in two contrasting habitats (forest and pasture) in the southwestern Brazilian Amazon. Therefore, we addressed the main question: What is the primary mechanism for species coexistence in forest and pasture habitats? According to the mechanism identified for each habitat, we had the following alternative expectations: (i) niche partitioning – we expected to observe a positive and linear relationship between functional diversity and the species richness, indicating a complementarity relationship; or (ii) niche filtering - an asymptotic relationship between functional diversity and species richness, indicating a functional redundant relationship.

Material and Methods

Study Area

The study was carried out in a forest fragment inside Fazenda Experimental Catuaba (FEC/ UFAC, 10°04'S e 67°37'W) and in an adjacent pasture (Fig 1). FEC/UFAC is 27 km away from Rio Branco, the capital of Acre state. The size of the forest fragment is 1,200 ha, with vegetation of open rainforest with palm trees, bamboos and vines (Medeiros et al., 2013). The surrounding area of FEC/UFAC is composed of pasture areas with exotic grasses and sparse remnants of palm and Brazil nut trees (Araújo & Lani, 2012).

Sample design and ant identification

Ant sampling was carried out during the dry season (Cemaden, 2016), from July to August 2016, when the average rainfall was 50 mm (INMET, 2015). In each habitat (forest and pasture), we employed 20 plots of 10 x 12 m, 60 meters apart from each other. The plots in the forest habitat were placed along the permanent sampling transect of Biodiversity Research Program module (PPBio), while the plots distributed in the pasture habitat were 500 meters from the edge of the forest fragment (Fig 1).

In each plot, we offered five types of liquid food resources to the ants: 10 mL with H₂O (distilled water), 20% amino acid (unflavored whey protein isolate), 20% carbohydrate (crystal sugar), 20% lipid (extra virgin olive oil), 1 % NaCl, and dry cotton (control). We offered the resources to the ants using a cotton swab soaked in each type of resource and inserted in a 50 mL plastic centrifuge tube. Each tube was arranged horizontally on the soil surface. We used liquid resources because observed patterns of resource use were not affected by the texture, shape or size of the resource, but depended only on the type of resource (Fowler et al., 2013; Kaspari et al., 2008).

In each plot, we used five replicates of each resource type and control, creating a total of 30 centrifuge tubes. In each plot, we established transect lines every 2 m resulting in 30 subplots. At the vertices of each subplot, we randomly placed one of the 30 tubes with resources. We stored the resources in a Styrofoam box (8 L) in order to avoid evaporation of the solution during the experiment.

We placed the tubes at 08:30 a.m. and collected them after 3 hours of exposure (Fowler et al., 2013). We transferred all ants present in the centrifuge tubes to 5 mL plastic tubes containing 96% alcohol, and subsequently separated, mounted and identified the ants in the laboratory.

We conducted ant identification at the genus level using the taxonomic keys sourced from Baccaro et al. (2015) and later sorted the ants into morpho-species. We identified ants at the species level by comparing our ants with specimens from the ant collection of the Insect Ecology Laboratory of Federal University of Acre and with specimens from the ant collection of the Ant Systematic and Biology Laboratory of

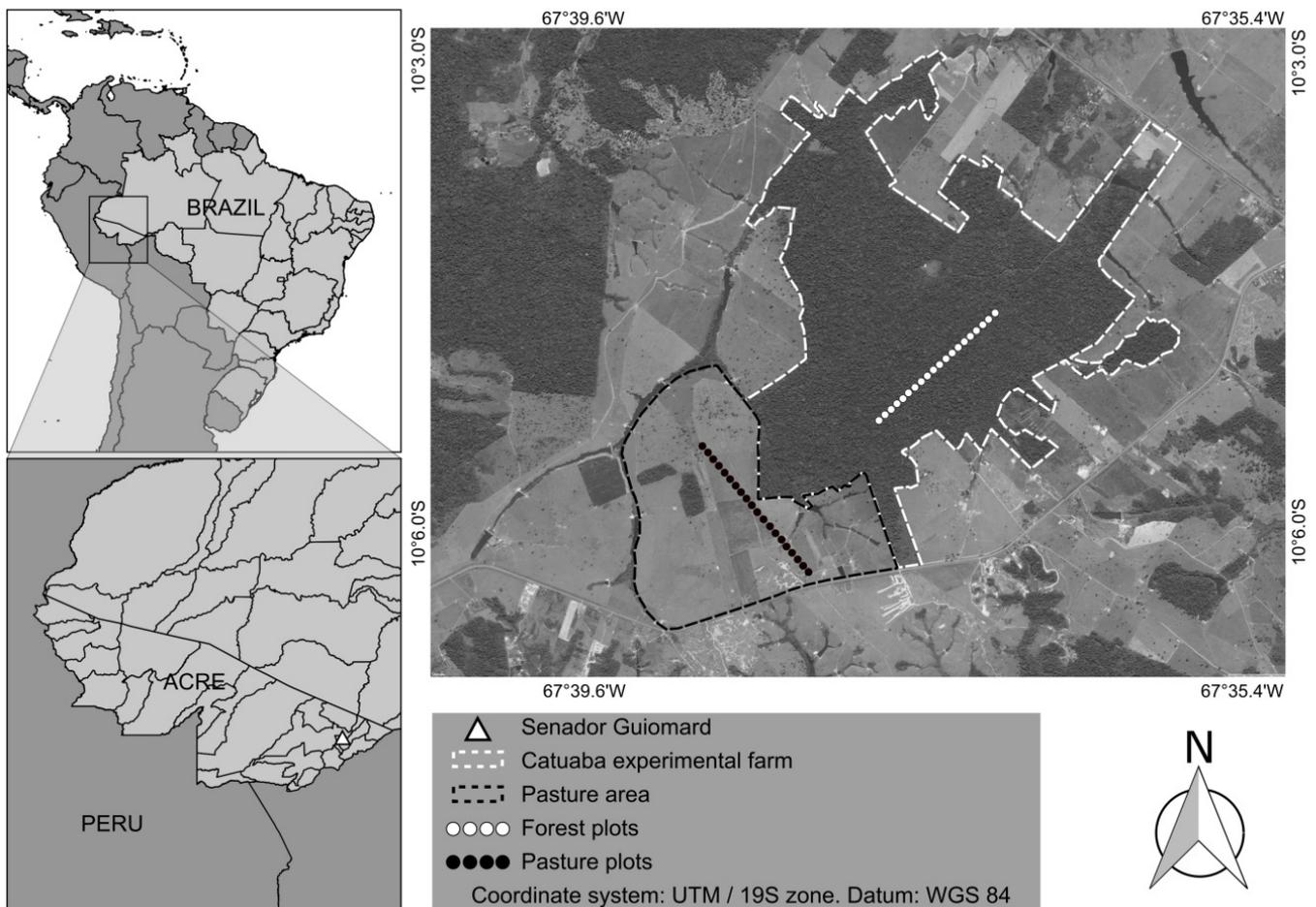


Fig 1. Catuaba Experimental Farm - UFAC and São Francisco Farm, with 20 plots in each habitat type (forest and pasture), in the southwestern Brazilian Amazon.

Federal University of Paraná under the support provided by Prof. Dr. Rodrigo Feitosa and his research group. We deposited all voucher ant specimens in the ant collection of the Insect Ecology Laboratory at UFAC.

Statistical Analysis

We performed all analyses using the programming software R v. 3.2.2 (R Development Core Team, 2015). We used specific packages as needed, which we describe below.

What is the primary mechanism for species coexistence in forest and pasture habitats?

To discern whether ant species coexistence in each habitat type is determined by niche partitioning or filtering, we tested whether niche overlap was greater among species that rarely co-occur or among species that frequently co-occur. For this, we used two matrices: one for niche overlap and one for species co-occurrence. In the niche overlap matrix, columns corresponded to the different types of resources offered (6), and the lines listed the species. The input values in the matrix recorded the ant species occurrence (number of tubes) in each resource category ($n = 6$).

Afterward, we ran a null model analysis using the EcoSimR R package (Gotelli et al., 2015). We compared the mean of the observed niche overlap to the expected mean of niche overlap, as obtained from 1000 randomized trials. Thus, we tested the null hypothesis that the average of the observed niche overlap is lower than the average of the expected niche overlap at random (overlap below 5%) (Gotelli & Entsminger, 2004). We employed Pianka's index to obtain the niche overlap in resource use among paired species (Pianka, 1973):

$$O_{jk} = \frac{\sum p_{ij} \cdot p_{ik}}{\sqrt{\sum p_{ij}^2 + \sum p_{ik}^2}}$$

where, p_{ij} and p_{ik} represent the proportion of resource i in relation to the total resources used by species j and species k . This index estimates the symmetric overlap of the categories (by habitat and resource) for each pair of species whose values range from 0 (no overlap) to 1 (total overlap) (Pianka, 1973).

We then compared the observed overlap index to the values obtained by the randomization of the original matrix (1,000) using the Ra3 algorithm, that retains the observed niche width and randomizes the allocation of each use value for each different niche category (Winemiller & Pianka, 1990).

We also constructed a species co-occurrence matrix for each habitat type (forest and pasture), calculating the number of combinations arranged in checkerboard space

(Checkerboard Units – CU) of a presence-and-absence matrix (Gotelli, 2000), in the following way: $CU = (ri - S)(rj - S)$, where S corresponds to the number of shared sites (containing both species), and ri and rj are the sum of the lines for species i and j . A higher C-Score indicates that the species pair is more segregated with fewer shared sites (Stone & Roberts, 1990). We obtained the C-Score Index using the *bipartite* Rpackage (Dormann et al., 2008).

Next, for each species pair, we obtained the relationship between co-occurrence and niche overlap by applying a Mantel's test (Douglas & Endler, 1982), available in the *Vegan* R-package (Oksanen et al., 2017). We compared the observed value of the correlation coefficient (r) to the values obtained from 1,000 randomizations, using a 5% significance threshold. Negative values of (r) indicate that species with similar niches are less likely to co-occur, suggesting that niche partitioning is the mechanism responsible for the coexistence of species in ant assemblages for each habitat type. On the other hand, positive values of (r) indicate that species with similar niches are more likely to co-occur, suggesting that niche filtering is the determinant factor of species coexistence in ant assemblages in each habitat type (Fowler et al., 2013).

Alternative expectations for the relationship between functional diversity and species richness

To evaluate the relationship between functional diversity and species richness, we measured eight morphological structures based on ant resource use and habitat preferences. According to Silva and Brandão (2010, 2014), trait indicators include: (i) Weber length (WL) a body size indicator; (ii) head width (HW) based on the size of the mandible musculature; (iii) eye length (EL) as important to search for food; (iv) interocular distance (ID) since generalist species tend to have more distant eyes, positioned laterally; (v) posterior femoral length (FL) assuming that leg size can determine species distributions in leaf litter; (vi) scape length (SL) an important behavioral function; (vii) mandible length (ML) related to resource size; and (viii) clypeus length (CL) since species that depend on liquid resources tend to have a more developed clypeus.

We conducted all measurements with a Leica S8 APO stereomicroscope and using a micrometer lens. We used up to six workers per species (when available), to measure each morphological trait and obtain an average. However, for species with less than six workers sampled, we measured the number of workers available (from 1 to 5) (Silva & Brandão, 2010; Martello et al., 2018). For polymorphic species, we only measured the smaller workers (Del Toro et al., 2015).

We used an abundance matrix for each habitat (forest and pasture), where the lines corresponded to the plots, the columns indicated ant species identities, and the input values referred to the number of tubes that the species of ants visited in each plot. We also constructed a second matrix, which

contained the traits in the columns and the species in the rows. After obtaining the averages for each morphological trait, we standardized the traits by dividing each by the Weber's length to reduce correlations with body size (Martello et al., 2018). We transformed the distance measure between the eyes into a position measurement (HW-ID) and then standardized the WL.

We used the *SYNCSA* R-package (Debastiani, 2018) to calculate the functional diversity index, using the rao diversity function (Rao's quadratic entropy), based on a Gower dissimilarity matrix calculated for rational values traits (Pavoine et al., 2009) and equally weighted (Swenson, 2014). This function calculates the square root of the one-complement Gower's similarity index in order to keep the dissimilarity matrix with Euclidean metric properties (Debastiani, 2018). We used the Rao quadratic diversity index as a metric to aggregate species abundance data and the functional differences between them (Arnan et al., 2014). Rao's Q varies between 0 and 1, where higher values indicate greater dissimilarity in community traits (Arnan et al., 2014).

We verified the relationship between species richness (explanatory variable) and functional diversity (response variable) through a simple linear model. In this model, we interpreted a high slope coefficient to be indicative of the niche partition expectation leading to a functional complementarity between species and interpreted a low slope coefficient as indicative of niche filtering expectation leading to functional redundancy.

Results

Ant fauna

In total, 91 ant species were collected, belonging to 24 genera and distributed into six subfamilies. Of all the subfamilies, only Ponerinae was not recorded in pasture habitat. Myrmicinae contained the highest number of species (61 species), followed by Formicinae (17 species), Dolichoderinae and Ectatomminae (both with four species), Ponerinae (three species), and Pseudomyrmecinae (two species) (see Table S1 at <http://periodicos.ufrpe.br/index.php/sociobiology/rt/suppFiles/4552/0>). The genera with the highest number of species was *Pheidole* (28 species), followed by *Camponotus* and *Crematogaster* (both with 12 species), and *Solenopsis* (eight species).

In the forest habitat, 82 species of ants visited the centrifuge tubes, 75 of which were exclusive to this habitat. In the pasture habitat, only 16 species were recorded, of which only 9 were exclusive to it. Only seven species of ants were recorded in both habitats: *Crematogaster tenuicula* Forel, *Dolichoderus inermis* MacKay, *Ectatomma brunneum* Smith, *Solenopsis invicta* Buren, *S. saevissima* (Smith), *S. sp. 2* and *Wasmannia auropunctata* (Roger).

What is the primary mechanism for species coexistence in forest and pasture habitats?

By employing Pianka's index and the C-Score index,

we verified that the niche overlap is greater among species that frequently co-occur than those that do not frequently co-occur.

In the results for paired ant species in the pasture habitat, many species did not have a niche overlap for resource use. In the forest habitat, many paired ant species overlapped, such as *Acromyrmex coronatus* x *Pheidole* sp. 17 and *Camponotus heathi* x *Pheidole* gr. *Dilligens* sp. 3, with an overlap of (> 0.70), but there were other species such as *Camponotus heathi* x *Pheidole biconstricta* or *Pachycondyla crassenoda* x *Pheidole* sp. 16 that had a low overlap. The C-score index was between 0.001 to 0.05 in the pasture and 0.0014 to 0.05 in the forest, indicating that the co-occurrence between paired species is relatively high.

The correlation between co-occurrence and niche overlap in the pasture was not significant ($r = 0.047$ and $p = 0.308$), while in the forest the correlation was positive and significant ($r = 0.147$ and $p = 0.001$) (Fig 2).

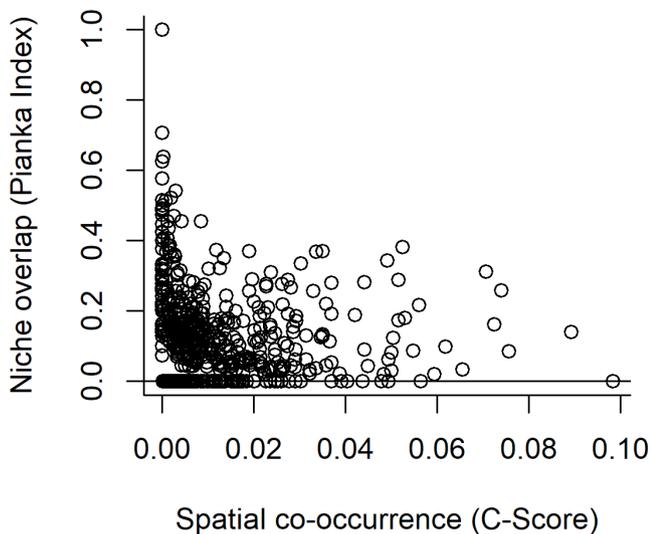


Fig 2. Relationship between niche overlap (Pianka Index) and spatial co-occurrence (C-Score Index), ($p = 0.001$, $r = 0.147$) for pairs of ant species sampled in the forest fragment at Catuaba Experimental Farm- UFAC, AC, Brazil.

Alternative expectations for the relationship between functional diversity and species richness

The species of ants in the pasture habitat had, on average, smaller morphological traits (except eye length) than those of ants in the forest environment (Table S2 at <http://periodicos.uefs.br/index.php/sociobiology/rt/suppFiles/4552/0>). The relationship between functional diversity and species richness was positive in both habitats (forest and pasture). However, the slope of the relationship between functional diversity and species richness differed in each environment (Fig 3).

In the forest habitat, the relationship between species richness and functional diversity had a low slope, highlighting that an increase in ant species richness among plots is not tightly associated with an increase in functional diversity (Rao's Q). In the pasture habitat, the coefficient of variation of the relationship between ant species richness and functional diversity was higher

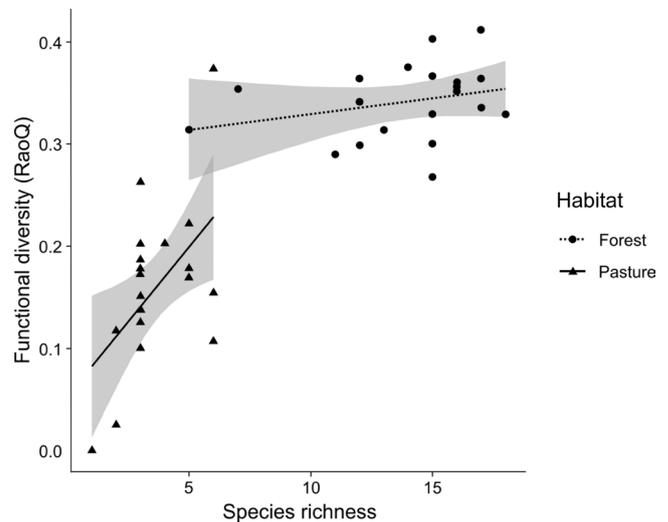


Fig 3. Relationship between functional diversity (Rao's Q) and observed species richness in the plots of each habitat type (forest: intercept value = 0.29927, slope value = 0.00304 and pasture: intercept value = 0.05334, slope value = 0.02929), in southwestern Brazilian Amazon.

than in the forest habitat. Therefore, in the pasture habitat there is a greater increase in functional diversity (Rao's Q) with increasing of number of ant species than in the forest habitat.

Discussion

Our study was restricted by the timing of the sampling period (mornings) and the use of attractive baits, which can restrict the ant fauna, possibly leading to more limited perspective on ant species coexistence and functional diversity. However, our results are consistent with the findings of other studies on species coexistence (Ribas & Schoereder, 2002; Cerdá et al., 2013) and niche partitioning *versus* niche filtering (Fowler et al., 2013) in ant assemblages.

Despite these considerations, we demonstrate that in forest habitats (and not in pastures) the mechanism responsible for ant species coexistence is niche filtering. Furthermore, the relationships between functional diversity and species richness are very different in forest vs. pasture ant assemblages. In the sections below, we offer possible explanations for these results and discuss their implications to ant assemblage structures in both habitat types.

What is the primary mechanism for species coexistence in forest and pasture habitats?

In the forest habitat, we identified niche filtering as the process responsible for the coexistence of ant assemblage species. Still, ant assemblages in this habitat have similarities in resource use with high niche overlap, as co-occurring species can survive and remain in the assemblage. Recent studies have indicated the importance of environmental filters for ant assemblages as an alternative explanation for the niche partitioning and the possible coexistence of species that have similar niches (Wiescher et al., 2012; Fowler et al., 2013).

Wiescher et al. (2012) reported that ant assemblages are governed by environmental conditions, and that adaptations to these conditions determine differences in the morphology and physiology of ant species. The modularity of ant nests, as well as ant sociality, protects them from possible adverse events since the caste division causes the queen to be fully protected in the nest, making her immune to external disturbances (Andersen, 2008; Hölldobler & Wilson, 2009). In addition, species competition may cause ants to have different strategies regarding the use of similar resources that allow their coexistence in space, as well as at sites that dominant ants do not occupy (Andersen, 2008).

In the pasture habitat, we did not find a significant correlation between spatial co-occurrence and niche overlap. Compared to forest habitat, we found few species of ants visiting the liquid resource tubes (16 species only). Therefore, it is still unclear whether niche partitioning or filtering are the predominant structures for ant species in pasture habitat. Our spatial co-occurrence data show that these few species are highly co-occurring and therefore they are not segregated in space.

Alternative expectations for the relationship between functional diversity and species richness

Functional redundancy is related to the stability of ecological communities (Naeem et al., 2002), since high levels could either allow for ecosystem recovery or for random extinctions or disturbances when species loss does not translate to a loss in ecosystem functioning (Naeem et al., 1995; Fonseca & Ganade, 2001; Pillar et al., 2013; Arnan et al., 2019). Differences in the relationship between species richness and functional diversity by habitat type shows that functional redundancy is potentially higher in forest habitat. Furthermore, the forest-pasture shifting to pasture not only has an effect on species richness but also on species functional role.

Therefore, we found that the high diversity of ant species in tropical forests leads to high functional redundancy for ant assemblages. As summarized above, in addition to being an important factor in the maintenance of ecological functioning, functional redundancy also indicates the existence of environmental filters in ecological communities (Del Toro et al., 2015).

Conclusion

This study fills a gap in the research on the mechanisms behind ant species coexistence in forest and pasture habitats, contributing to knowledge on the relationship between functional diversity and ant species richness. In the forest habitat, niche filtering emerged as a key mechanism responsible for ant species coexistence. Land cover change, such as forest-pasture shifting in southwestern Brazilian Amazon, has been a serious environmental problem. In this study, we demonstrated that species loss led to a lack of functional redundancy, which is a key variable for managing ecosystem stability.

However, for a more accurate understanding of the mechanism responsible for ant species coexistence, it is necessary to further analyze which environmental variables could act as ecological selective filters on ant species from regional pools to make up species set of ant assemblages at local scales.

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