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Ant Occupation of Twigs in the Leaf Litter of the Atlantic Forest: Influence of the Environment and External Twig Structure

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Abstract

Twig cavities are microhabitats that may be used by different ant species for nesting and colony expansion. However, ants do not colonize all twigs available in the leaf litter, pointing to the existence of environmental or twig-related filters. In this study, we analyzed which environmental and twig attributes affected twig occupation by ants. We surveyed seven plots in six Atlantic forest sites in southeastern Brazil. To characterize the environmental filters, we quantified canopy cover and leaf litter moisture and depth. At the twig level, we measured twig length and diameter and the area and circumference of all holes in each twig. Ant colonies occupied 13.42% of the 4,805 twigs surveyed, and we recorded a total of 52 twig-nesting ant species. *Brachymyrmex admotus* was the most frequent species. Ant species richness increased with canopy cover and leaf litter moisture and with the relative number of occupied twigs. In addition, we found that ant species richness increased with length and diameter of the twigs, and that twigs with smaller holes were more frequently occupied by ants, regardless of the availability of larger diameter holes. Our work demonstrates that both environmental characteristics and twig morphology can structure occupation of twigs by ants. In addition, we demonstrated that certain species show a preference for certain twig types. We highlight the importance of twigs for maintaining ant diversity and for colony expansion of arboreal species and species inhabiting the leaf litter.

Keywords

Atlantic forest, ant communities, tropical diversity, ant nesting, conservation

Introduction

Tropical forest leaf litter is formed primarily by the deposition of plant (e.g., leaves, flowers, fruits, seeds and twigs; Pagano & Durigan, 2000; Pereira, Menezes, & Schultz, 2008) and animal organic matter (e.g., larvae and feces) (Schumacher, Brun, Rodrigues, & Santos, 2003). The deposition of these materials on the soil surface is temporally and spatially heterogeneous, affecting the structure and dynamics of plant (Facelli & Pickett, 1991; Molofsky & Augspurger, 1992) and invertebrate (Morais, Oliveira, Dambros, Tapia-Coral, & Acioli, 2010) communities. More specifically, the leaf litter is important for the diversity and survival of invertebrate species (Bieber, Corrêa, & Leal, 2011; Campos, Schoederer, & Sperber, 2003; Theunis, Gilbert, Roisin, & Laponce, 2005) by providing favorable microclimate conditions and nesting and feeding sites (Carvalho &

Vasconcelos, 1999; Fowler, Forti, Brandão, & Delabie, 1991; Philpott & Foster, 2005).

In tropical forests, ants colonize all habitats (Wilson, 1959), from the soil to the canopy (Hölldobler & Wilson, 1990), but a large proportion of the ant diversity is found in the leaf litter. In the Brazilian Atlantic forest, for instance, 1 m² of leaf litter may contain up to 35 ant

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species (Silva & Brandão, 2010). Some litter ants expand their colonies into twigs (Byrne, 1994; Soares & Schoereder, 2001), seeds (Pizo, 2008; Silva et al., 2009), and fruits (Castaño-Meneses et al., 2015). Ants also nest in cavities and structures created by other animals (Almeida, Santos, & Carneiro, 2014; Jahyny, Lacau, Delabie, & Fresneau, 2007; Leponce, Roisin, & Pasteels, 1999; Zara, Morini, & Kato, 2003). However, of all the leaf litter components, twigs are the most used by ants for nesting (Gomes, Almeida, Vargas, & Queiróz, 2013). But, twigs are commonly used by small-sized ants because they allow entire colonies to nest and defend themselves (Pratt & Pierce, 2001) and provide stable abiotic conditions (Booher, Macgown, Hubbell, & Duffield, 2017; Wilson, 1959).

Through the occupation of twigs, ants are indirect but essential agents for dead-wood decomposition in the leaf litter, because they inhabit stem and twig cavities, modifying the physical properties (e.g., durability) of the wood and facilitating the action of decomposers, such as fungi and bacteria (King, Andersen, & Cutter, 2018). Most twig-occupying ant species come from the leaf litter (Armbrecht & Perfecto, 2003; Delabie, Lacau, Nascimento, Casimiro, & Casorla, 1997; Fernandes, Silva, Souza, Araújo, & Morini, 2012). Although twigs may be abundant in the leaf litter, not all twigs are occupied by ants (Carvalho & Vasconcelos, 2002), despite the high diversity of this taxon in the leaf litter (Delabie, Agosti, & Nascimento, 2000).

Why so many twigs are vacant, and therefore available for ant occupation, remains an unanswered question in ant ecology (Sagata, Mack, Wright, & Lester, 2010). In addition, despite the availability of twigs, different ant species colonize the same twig (Byrne, 1994), which may indicate they have the same preferences.

Ant species assemblages strongly respond to macrohabitat and to several microhabitat variables (Yates, Gibb, & Andrew, 2012). Souza-Campana et al. (2017) evaluated the effect of macrohabitat on twig availability in the leaf litter and concluded that availability is primarily determined by vegetation structure. Studies have shown that ant richness on twig is influenced, respectively, by the degree of decay, which is related to relative humidity in the environment (Carvalho & Vasconcelos, 2002) and a greater variety of twigs (Armbrecht, Perfecto, & Vandermeer, 2004). In relation to the microhabitat, twigs with visible woodborer holes had a higher probability of being occupied by ants (Sagata et al., 2010), and the number of twig-nesting ant colonies was correlated with the number of hollow twigs (Boucher, Hérbet, Francoeur, & Sirois, 2015; De La Mora, Murnen, & Philpott, 2013). The results of these studies suggest the existence of environmental filters (e.g., vegetation structure), filters at the occupation site itself (e.g., twig structure), or some combination of these.

This work investigated the environmental and the external characteristics of leaf-litter twigs that were occupied by ants in the Brazilian Atlantic forest. We studied twigs that had been naturally perforated (e.g., by wood borers) and asked the following questions: (a) Which environmental characteristics (canopy cover and leaf litter moisture and depth) determine the number of ant species in twigs? (b) Which external physical characteristics (length and diameter of the twig and area and circumference of holes in twigs) determine ant occupation? (c) Do different ant species share twigs with the same characteristics?

Methods

Collection Sites

Twigs were collected from six Atlantic forest sites in southeastern Brazil (Supplementary Figure 1), with elevations ranging from 600 m to 850 m asl. All collection sites are located in preserved areas of Atlantic forest. The climate is humid temperate, with warm summers and cool winters. Average annual temperature is approximately 20°C. Annual precipitation is around 1,500 mm, uniformly distributed throughout the year (Cptec-Inpe, 2018).

Experimental Design and Environmental Variables

Twigs were collected in January, March, April, August, September, and November 2015 after a week without rain, to avoid collecting moist twigs. At each site, we established seven 4 m × 4 m plots ($N=42$ and 672 m² of leaf litter) 10 m apart, along a linear transect, placed randomly. Distance between plots was based on the study by Carvalho and Vasconcelos (2002). The distance between sites ranged from 5 to 66 km, and each site was sampled only once. It is worth to mention that we worked within an understory of a tropical rainforest where the GPS system used by us has an error value associated of ~7 m, which made it difficult to register the exact location of each site and plot. Collections were made from 100 m from the edge. All twigs in each plot were collected, regardless of length and diameter and stored individually in plastic bags (Supplementary Figure 2A and B). Twigs were taken to the lab to check for the presence of ant colonies.

We measured leaf litter depth (in mm) using a manual caliper and moisture content with a digital thermohygrometer. These variables were used to characterize the environment. To measure canopy cover, we took photographs of the canopy 1.5 m above the soil with a fish-eye lens attached to a Nikon D80 digital camera. These images were later analyzed in Gap Light Analyzer version 2.0 (Frazer, Canham, & Lertzman, 1999).

Images were transformed into binary archives to remove artifacts and tonalities that were not needed for the analyses.

Twig Structure and Hole Measurements

We measured length (cm) and diameter (mm) of all twigs in the lab using a digital caliper and a ruler, respectively (Supplementary Figure 2C and D). The entire surface of the twig was examined under a Motic SMZ-168 stereoscope and carefully inspected for holes, using a rotating support and a no. 0 entomological pin. All holes were photographed, and the software Motic Images Plus 2.0^{ML} was used to measure the area (mm²) and circumference (mm) of each. These variables were used to quantitatively describe twig characteristics.

Ants

Twigs were opened in the lab to search for ant colonies (Supplementary Figure 3). We classified twigs as occupied if they contained ≥ 10 workers; if fewer than 10 workers were present, twigs were considered occupied if they contained immatures, queens, or winged males (Fernandes et al., 2012). Ants were identified to species or morphospecies based on Suguituru, Morini, Feitosa, and Silva (2015) and by comparison to specimens deposited in the Formicidae reference collection for the Upper Tietê watershed. We deposited all vouchers in the Myrmecology lab of University of Mogi das Cruzes (Brazil).

Data Analysis

To test the relationship between environmental variables and species richness, we fitted a generalized linear mixed model with a Poisson error distribution and a log link function (Crawley, 2012). We used leaf litter depth and moisture and canopy cover as the fixed effects, and the response variable was the observed ant species richness. Plots nested within sites were included as random effects. Furthermore, we employed a generalized mixed model with Poisson error distribution and log link function (Crawley, 2012). In this analysis, we used the occupied twigs as independent variable and ant species richness as response variable, and we considered the plots nested within sites as random effects. For all models, we applied a Wald χ^2 test to measure the deviance and significance of each factor. All analyses were carried out using the *lme4* (Bates, Maechler, & Bolker, 2001) and *car* (Fox & Weisberg, 2011) packages in R version 3.1.1 (R Core Team, 2016).

To test if twigs occupied by ants differed from unoccupied twigs in diameter and length, we used nonparametric Wilcoxon tests for each variable. However, due to

the remarkable difference between the number of occupied ($N=575$) and unoccupied ($N=4,230$) twigs by ants, we randomly selected unoccupied twigs for the analyses using a bootstrap procedure. For this, we randomly sampled 575 unoccupied twigs and subsequently we tested if there were statistical differences between the occupied and randomly unoccupied twigs. We repeated this procedure 500 times and then we estimated the p value based on the number of times that we found the statistical differences between diameter and length of occupied and unoccupied twigs.

A graphical display (density plots) was used to describe the distribution shape of the length and diameter of colonized twigs and the area and circumference of the holes. An ordination matrix including twig characteristics (twig length and diameter and hole area and circumference) and species presence was constructed using the *gplots* package (Warnes, Bolker, & Bonebakker, 2016) in R. This matrix was used to (a) analyze which twig characteristics were shared between different ant species and (b) evaluate the external structure of the twigs that were most frequently occupied by ants. For this analysis, only species found in 10 or more twigs were included, because these may be considered common inhabitants of this resource (Carvalho & Vasconcelos, 2002).

Results

We collected 4,805 twigs, with lengths ranging between 6 and 671 cm and diameters ranging between 1.62 and 143.70 mm, in 672 m² of leaf litter (7.15 twigs per m²). Of these, only 13.4% (575 twigs, or 0.95 twigs per m²) were occupied by ants. These ants belonged to 8 subfamilies, 22 genera, and 52 species or morphospecies (Supplementary Table 1). The family with most species was Myrmicinae, with 10 genera and 29 species or morphospecies. The richest genus was *Pheidole*, with 11 species or morphospecies. Of all species, 17 (33%) were considered common, because they were found in 10 or more twigs. Although most species were not present in all sites, all sites had at least one species occupying more than 10 twigs, that is, considered a common inhabitant (see species highlighted in bold font in Table 1 of the Supplementary Material).

Brachymyrmex admotus was the most frequent species (14.7%), followed by *P. sarcina* (11.2%) and *Solenopsis* sp.2 (9.0%) (Supplementary Figure 4). Species that were considered common occupied 536 twigs (84% of the total). Of these, we found holes in 453 (84%), and 83 (16%) had no holes based on our inspection technique.

Ant community richness was influenced by canopy cover ($\chi^2=4.94$, $df=1$, $p < 0.05$) and leaf litter moisture ($\chi^2=13.66$, $df=1$, $p < 0.05$) (Supplementary Table 2). Specifically, we found that species richness of

communities occupying twigs increased as the canopy became more closed and the leaf litter became more humid (Figure 1(a) and (b)). However, leaf litter depth did not affect ant richness ($\chi^2=0.05$, $df=1$, $p<0.824$; Supplementary Table 2). We also observed that ant community richness increased with the number of occupied twigs ($\chi^2=10.32$, $df=1$, $p<0.001$; Supplementary Table 2, Figure 1(c)). In addition, twigs occupied by ants were longer (54.44 ± 1.04 cm [mean \pm standard error]; bootstrap p value = 0.039) and thicker (16.26 ± 0.59 mm; bootstrap p value = 0.043) than unoccupied twigs (length: 46.98 ± 1.55 cm; diameter: 11.21 ± 0.57 mm) (Figure 2).

Most occupied twigs (483 twigs, or 84%) had holes and were occupied by 52% of the species (27 species). Only 92 occupied twigs (16%) had no holes, but we found 25 ant species; in these twigs (48%), the tiny *Solenopsis* sp.5 among them (see image in Suguituru et al., 2015). The highest occupation rate (77.7%) was observed in twigs with smaller holes, with areas ranging from 0.1 to 8 mm² and circumferences ranging from 1.5 to 15 mm (Figure 3).

Ant species that were considered common inhabitants of twigs in the leaf litter were more frequently associated with holes of up to 7 mm² in area and circumference of 13 mm (Figure 4(a) and (b), respectively). Regardless of

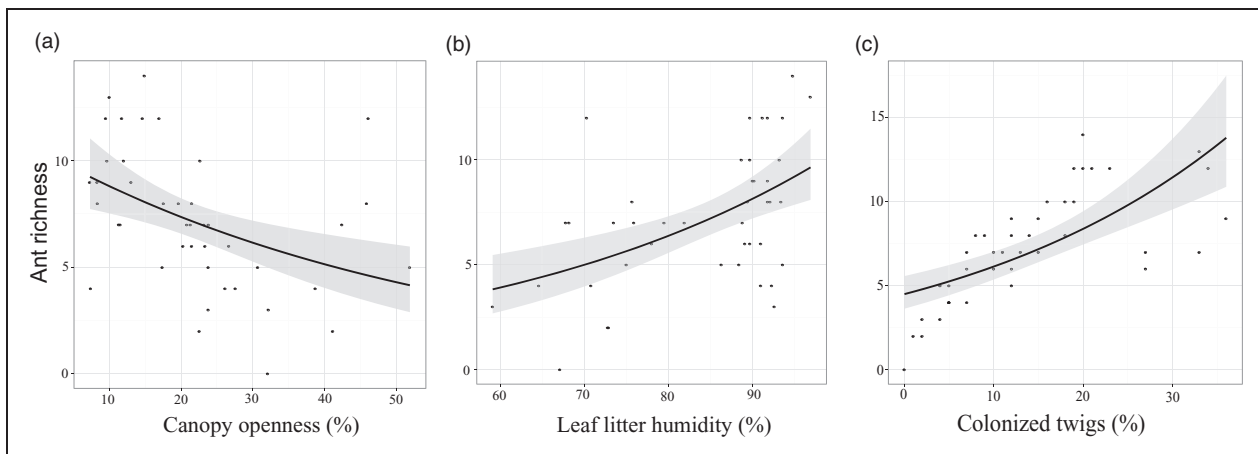


Figure 1. Ant richness in relation to (a) canopy openness, (b) leaf litter moisture, and (c) proportion of occupied twigs. The shaded area shows the 95% confidence interval of the best-fit line of the generalized mixed linear model. Because these graphics represent generalized linear mixed models, it is worth to mention that they represent the relationship between the variables (fixed effects) and the ant richness, the effect of the random factors is not included in these representations, but it was considered when the models were built and reported.

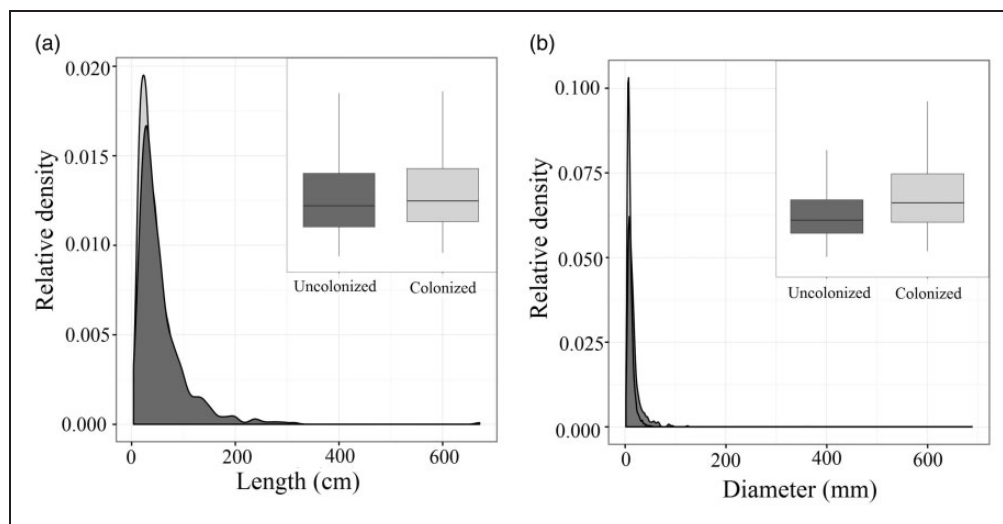


Figure 2. Frequency distributions of (a) length and (b) diameter of occupied and unoccupied twigs. Occupied twigs = light gray; unoccupied twigs = dark gray.

the size of the hole, most occupied twigs were 100 cm long (Supplementary Figure 5A) and had a diameter of 35 mm (Supplementary Figure 5B). *Pheidole sarcina*, *P. sospes*, and *P. sigillata* occupied twigs with similar morphology (area and circumference of the twig hole) (Figure 4).

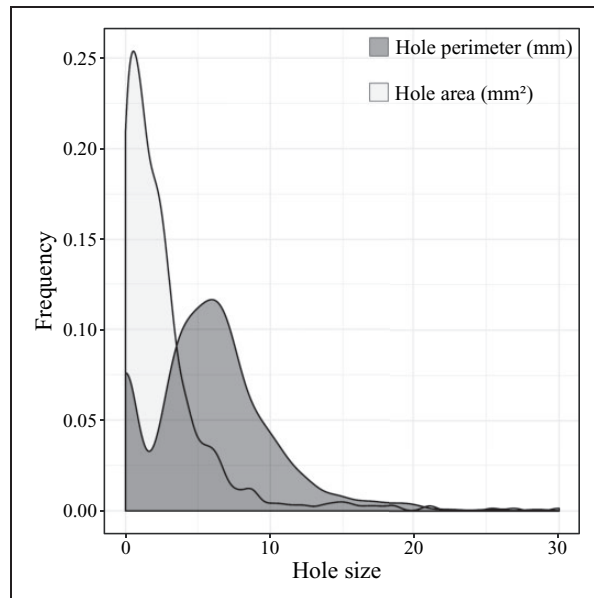


Figure 3. Frequency distributions of area (mm², light gray) and circumference (mm, dark gray) of the holes in ant-occupied twigs.

Discussion

In our study, the richness of twig-occupying ant communities was correlated with just two environmental variables, canopy cover and leaf litter moisture. Sites where the canopy was more open and the moisture content in the leaf litter was lower had fewer twig-nesting ant species on average, perhaps because they lacked shade and had fewer microhabitats within the leaf litter (Kaspari, O'Donnell, & Kercher, 2000; Philpott & Foster, 2005) and inside twigs (Souza-Campana et al., 2017). Our results corroborate the large study carried out by Souza-Campana et al. (2017) in urban parks, *Eucalyptus* plantations, and Atlantic forests, in which the depth of the leaf litter did not affect ant richness on twigs. However, studies of litter-inhabiting ants in tropical forests show that the richness of hypogeic (Silva et al., 2011) and epigeic communities (Queiróz, Ribas, & França, 2013) is influenced by structure of the leaf litter and its components, since that is where ants find resources for nesting (e.g., amount of leaves) and foraging (e.g., potential prey) (Fowler et al., 1991).

Our results also indicate that richness is directly modulated by twig occupation, particularly by length and diameter. We should mention that twigs were collected along a single linear transect in each site, which may have affected our results. However, Carvalho and Vasconcelos (2002) and Souza-Campana et al. (2017)

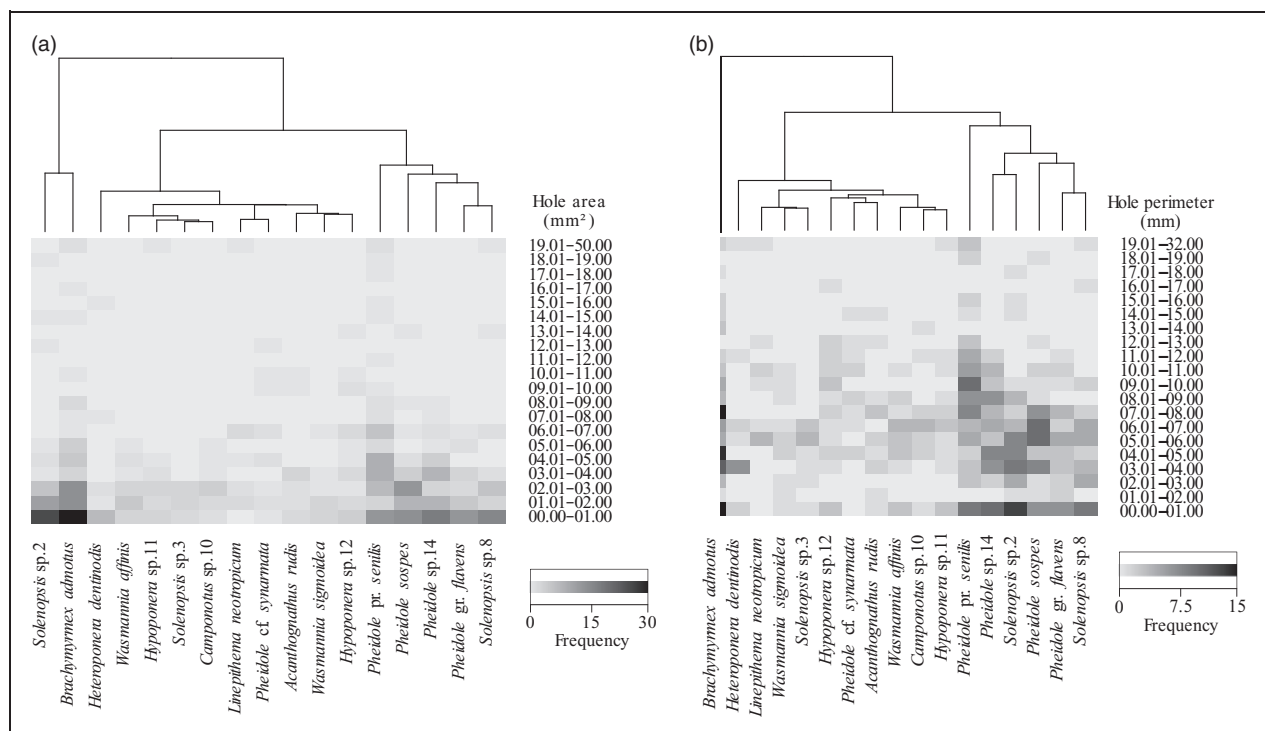


Figure 4. Ordination matrix of ant species that colonized 10 or more twigs in relation to (a) area and (b) circumference of the twig hole. Darker cells indicate higher nest frequencies.

also showed that diameter is a variable that influences the richness of ants occupying twigs.

The influence of twig structure over ant community richness may explain why we found that 7.15 twigs were available per m² of leaf litter, but only 0.95 twigs/m² were occupied by ants inhabitants of leaf litter. Although the leaf litter in the Atlantic forest had more twigs available and higher rates of ant occupation than the Amazon (6.2 twigs/m² and 0.22 twigs/m², respectively; Carvalho & Vasconcelos, 2002), we confirmed a low occupation rate of twigs by ants inhabiting the leaf litter relative to the availability of this resource in the Atlantic Forest. The same pattern was observed in other forest types (Byrne, 1994; Kaspari, 1996a, 1996b), suggesting that the availability of twigs alone is unlikely to strongly shape litter ant communities (Sagata et al., 2010). A twig may be available but not occupied by ants because it is very hard (Carvalho & Vasconcelos, 2002) or very decomposed (Rocha-Ortega & García-Martínez, 2018). A lack of cavities in the twig (Carvalho & Vasconcelos, 2002) also makes it hard to occupy (De La Mora et al., 2013). Only a few ant species, such as *Melissotarsus* (Khalife et al., 2018; Peeters, Imre, Danièle, & Brian, 2017) and some species of *Camponotus* (King et al., 2018), are able to excavate living wood (McGlynn, 2012).

In addition to these characteristics, in this work, we show that twig morphology also seems to determine ant occupation, because larger twigs (length >100 mm and diameter >35 mm) with holes were the most often occupied. Thus, in the leaf litter of the Brazilian Atlantic forest, twig occupation by ants is also related to twig morphology, likely because these twigs have more room to house ant colonies with a larger number of individuals (Byrne, 1994; Nakano et al., 2012; Souza-Campana et al., 2017).

The presence of holes reduces the cost of occupation, because it requires lower investment by ants (McGlynn, 2012). The size of the holes also affected twig occupation by ants, since the most frequently occupied twigs had smaller holes (0.1–8 mm², with a circumference of 1.5–15 mm). Most of the ant fauna recorded here is also found in leaf litter samples (Pacheco, Silva, Morini, & Brandão, 2009; Suguituru, Souza, Munhae, Pacheco, & Morini, 2013), which may explain this pattern. The litter fauna is characterized by small- to medium-bodied species (0.2–10 mm long; Brandão, Silva, & Delabie, 2009; Silva & Brandão, 2010). Thus, twigs with smaller holes seem to support occupation by a greater richness of small ants, which occupy the leaf litter. In this study, we found that most occupied twigs had relatively small holes, which were comparable to the body sizes of leaf litter species (Brandão et al., 2009). Therefore, even if twigs with larger holes were available to ants foraging in the leaf litter, these ants occupied twigs with smaller holes. We posit that ants use twigs with small entrance

holes more often because they provide greater defensibility and crypsis; indeed, when ants colonize twigs with larger holes, the size of the hole entrance is often further reduced by ant activity, with the addition of soil particles and leaf-litter material (Pratt & Pierce, 2001).

The existence of different hole sizes (i.e., hole diversity) may contribute to an increase in the richness of species that use twigs for nesting (Jiménez-Soto & Philpott, 2015). For arboreal species, cavity diversity appears to greatly affect new colony founding (Powell, Costa, Lopes, & Vasconcelos, 2011). However, our results show that the presence of holes on the surface did not determine community species richness, because we found the same number of species in twigs with and without holes (27 and 25, respectively). It is possible that the ants used perforations or areas derived from pith decay (Yamaguchi, 1992) and cracks (Arruda et al., 2015) that were not detected through the technique used in our study. In those cases, only minute ants had access to the interior of the twigs, which could be the case of *Solenopsis* sp.5.

Our work is the first analysis of the correlation between ant community composition and natural hole morphology in twigs. Our results are consistent with twig-nesting ants selecting larger twigs in more shaded, humid locations. The presence of twigs is important for maintaining ant diversity and for colony expansion, because most species that nest in twigs may be considered common inhabitants of this resource (Carvalho & Vasconcelos, 2002). Decision-making in ants often involves nest-site selection (Pratt & Pierce, 2001), but we cannot conclude that all species in the same genus occupied the same type of nest, since only 3 (27%) out of 11 *Pheidole* species were found in twigs that shared the same areas and twig hole circumferences. Of these, *P. sospes* also showed preference for twig diameter, regardless of habitat (Fernandes, Souza-Campana, Silva, & Morini, 2018).

Implications for Conservation

In our study, we found numerous ant colonies occupying twigs on the forest floor, and most species were native inhabitants of the leaf litter and the top layers of the soil surface. However, we also detected several arboreal species colonizing twigs in the forest floor, which is important for the conservation of the diversity of this ant guild. We found that tree cover and leaf litter moisture were determining factors of twig occupation by ants, along with twig length and diameter and hole size. Thus, our results indicate the presence of environmental and twig-related filters, with some species showing preference for a given type of twig, advancing the current knowledge about the biology of twig-colonizing ants. The knowledge of biology allows a better understanding

of interactions between species and local diversity. This is fundamental when the biome is extremely threatened and still undervalued, as is the case of the Brazilian Atlantic forest (May, Veiga-Neto, & Pozo, 2000).

The Brazilian Atlantic domain includes many forest fragments in different stages of succession (Ribeiro, Metzger, Martensen, Ponzoni, & Hirota, 2009), and several strategies have been developed to restore degraded areas (Almeida, 2016). The results obtained here may help ant communities that colonize twigs. For instance, if the technique of transferring leaf litter to degraded areas is used, twigs with specific traits may be selected in detriment of others. Even if the ant communities that occupy twigs are not very rich and abundant, they are part of the ecological interaction processes in the leaf litter that aid in the recovery of degraded areas. Twigs are also part of the life cycle of arboreal species (Fernandes, Silva, Souza-Campana, Silva, & Morini, 2019), which includes ants that naturally control pests (Choate & Drummond, 2011), an important ecological function during the process of restoration of a degraded area.

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Declaration of Conflicting Interests

The author(s) declared that there is no conflict of interest with respect to the research, authorship, and/or publication of this article.

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