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Research Article

Twigs in the Leaf Litter as Ant Habitats in Different Vegetation Habitats in Southeastern Brazil

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Abstract

Vegetation structure and microhabitat availability and diversity affect ant assemblage diversity, growth, and dispersal. In this study, we described assemblages of ants nesting in twigs found in the leaf litter, comparing nest characteristics and ant colony sizes among different vegetation habitats at a regional scale. Twigs were collected in urban parks, *Eucalyptus* plantations, and preserved areas of native Atlantic Forest. We measured the twigs, counted the number of ant colonies, and estimated canopy openness. A total of 51,213 ants from 22 genera and 61 species were recorded. We collected 74, 141, and 283 nests in urban parks, *Eucalyptus* plantations, and native forest areas, respectively. The richest genera were *Pheidole*, *Camponotus,* and *Solenopsis*. *Linepithema neotropicum*, *Gnamptogenys striatula,* and *Solenopsis* sp.2 were recorded in all study areas. We found only one invasive species, *Cardiocondyla wroughtonii*. Typically, the canopy in urban park areas was more open, and these areas had lower species richness, lower rate of twig occupancy, and smaller diameter twigs occupied by smaller colonies compared to *Eucalyptus* plantations or native forest. Ant assemblages were determined mainly by vegetation habitat, followed by twig characteristics. As many ant species use twigs as nest site, twigs are critical habitats for maintaining ant diversity in the leaf litter of areas with varying degrees of complexity in the vegetation structure. However, the availability of twigs as nest resource depended on vegetation structure. In addition, twigs may increase the area occupied by the colonies of some ant species, including *Wasmannia auropunctata*, which was very frequent in urban parks.

Keywords

polydomy, urban areas, cultivated forests, native forest, silviculture

One of the goals of community ecology studies is to understand the relationship between species diversity (communities, homogeneity, and inter- and intraspecific interactions) and abiotic components (Begon, Townsend, & Harper, 2007). Species richness and composition are ecological parameters directly related to environmental (Martins, Almeida, Mayhé-Nunes, & Vargas, 2011), especially to microhabitats (Buczkowski & Richmond, 2012) and complexity of soil (Ossola, Nash, Christie, Hahs, & Livesley, 2015).

In soils, much of the biodiversity is represented by arthropods, which correspond to approximately 85% of the fauna in this stratum (Bagyaraj, Nethravathi, & Nitin 2016). In tropical soils, ants are considered as a dominant group in richness, biomass, and functional diversity (Brown et al., 2015; Korasaki, Morais, & Braga, 2013). One of the reasons for the ecological success of this insect group is the diversity of exploitation and competition mechanisms they use in different microhabitats, particularly those related to food and nesting resources (Hölldobler & Wilson, 1990).

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Many ant species nest in the soil, inside chambers connected by tunnels, modifying the physical properties of this stratum, and resource availability to other organisms (Bagyaraj et al., 2016; Lavelle et al., 2006). Other species nest under flat rocks (Hölldobler & Wilson, 1994) or termite nests (Leponce, Roisin, & Pasteels, 1999), in tree trunks (Schütte, Queiroz, Mayhé-Nunes, & Pereira, 2007), around roots (Adams & Longino, 2007), in the canopy of living trees (Longino & Nadkarni, 1990; Schütte et al., 2007), or in other plant parts (Oliveira et al., 2015). However, ants may also occupy structures created by vertebrates (Hölldobler & Wilson, 1990) or invertebrates, such as gastropods (Jahyny, Lacau, Delabie, & Fresneau, 2007), termites (Leponce et al., 1999), and flies (Almeida, Santos, & Carneiro, 2014). This behavior is often observed in the leaf litter, where there are many microhabitats suitable for nest building and colonization, allowing ants to gradually specialize in different substrates, including dry fruits, seeds, twigs, and decomposing trunks (Brandão, Silva, & Delabie, 2009; Castaño-Meneses et al., 2015; Nakano et al., 2012).

The availability and diversity of nesting sites are limiting factors for the diversification, growth, and dispersal of ant populations (Arruda et al., 2015; Benson & Harada, 1988; Fowler et al., 1991). Therefore, increases in nesting site diversity may influence species richness and composition (Armbrecht, Perfecto, & Vandermeer, 2004). Vegetation structure is of fundamental importance, since microhabitats are directly affected by plant materials deposited on the ground (Bieber, Oliveira, Wirth, Tabarelli, & Leal, 2011; Schumacher et al., 2004).

Twig-nesting ants are probably nest-site limited (Jimenez-Soto & Philpott, 2015), but up to 70 ant species have been observed in this type of cavity in tropical forests (Amazon and Atlantic; Carvalho & Vasconcelos, 2002; Fernandes, Silva, Souza, Araújo, & Morini, 2012; Souza, Fernandes, Nascimento, Suguituru, & Morini, 2012), including ant colonies with hundreds of workers and immature ants (Fernandes et al., 2012). However, compared to litter, the diversity in twigs is low (Delabie, Agosti, & Nascimento, 2000; Vasconcelos, Leite, Vilhena, Lima, & Magnusson, 2008) and residence time in the nests is short, ranging from 35 to 146 days depending on the species (Byrne, 1994). Nonetheless, since predators and seed dispersers also use this resource (Levey & Byrne, 1993), changes in its abundance and composition can affect vegetation regeneration (Carvalho & Vasconcelos, 1999). Additionally, owing to the ephemeral nature of twigs as nesting sites, the study of ant assemblages that occupy this resource is a good indicator of habitat conditions (Byrne, 1994) and ant species diversity and distribution indicator (Powell, Costa, Lopes, & Vasconcelos, 2011).

On a local scale, understanding the relationship between ants and their microhabitats may help to elucidate the feeding and nesting ecology of this highly diverse group. The purpose of this article is to describe the ecology of twig-nesting ant assemblages and compare the structure and colony sizes of nests in different vegetation habitats within the Brazilian Atlantic Forest domain. In this work, we studied whether twig characteristics and canopy structure determine which ant species nest in twigs. We tested the hypothesis that vegetation habitats with a more open canopy have smaller twigs and, therefore, smaller ant nests.

Method

Study Site and Sampling

Samples were collected in 27 sites representing a gradient in vegetation structure complexity. Nine sites were urban parks (13–26 ha) with exotic and native vegetation; nine were *Eucalyptus* plantations (25 ha) with a dense understory, in a timber production region that had been abandoned for 28 years; and the remaining nine were preserved placed in native Atlantic Forest areas (20–350 ha; Figure 1). The study area has a tropical rainforest (Af) climate, with annual precipitation over 2000 mm and no clearly defined seasonality. Elevations ranged from 780 to 840 m.

At each site, we established six 16 m^2 plots 50 m apart along a linear transect, for a total of 864 m^2 of leaf litter inspected per vegetation cover. Only twigs found on the surface were collected, since they are the most recent resources in the leaf litter. The sampling effort was the same in all sites (three collectors and 30 min of collection per plot).

The diameter of each twig was measured with a digital caliper (within 300 mm). Twigs were opened and the number of adult and immature ants (eggs and larvae) was recorded. Only species with ≥ 10 workers in the nest were recorded; when the number of workers in the twig was lower, we recorded the presence of gynes, males, and immature ants (eggs and larvae; Fernandes et al., 2012).

In each plot, five hemispherical images were acquired with a Nikon D80 digital camera, placed 1.50 m above the ground and coupled with a fisheye (hemispherical) lens. Images were processed in Gap Light Analyzer version 2.0 (Frazer, Canham, & Lertzman, 1999) and transformed into binary files for the removal of artifacts. The images were then transformed to count the percentage of black (canopy cover) pixels.

Ants were sorted, separated into subfamilies, and identified to genus level following (Baccaro et al., 2015) and to species and morphospecies accordingly (Suguituru, Morini, Feitosa, & Silva, 2015). Voucher specimens were deposited at University of Mogi das Cruzes (São Paulo).

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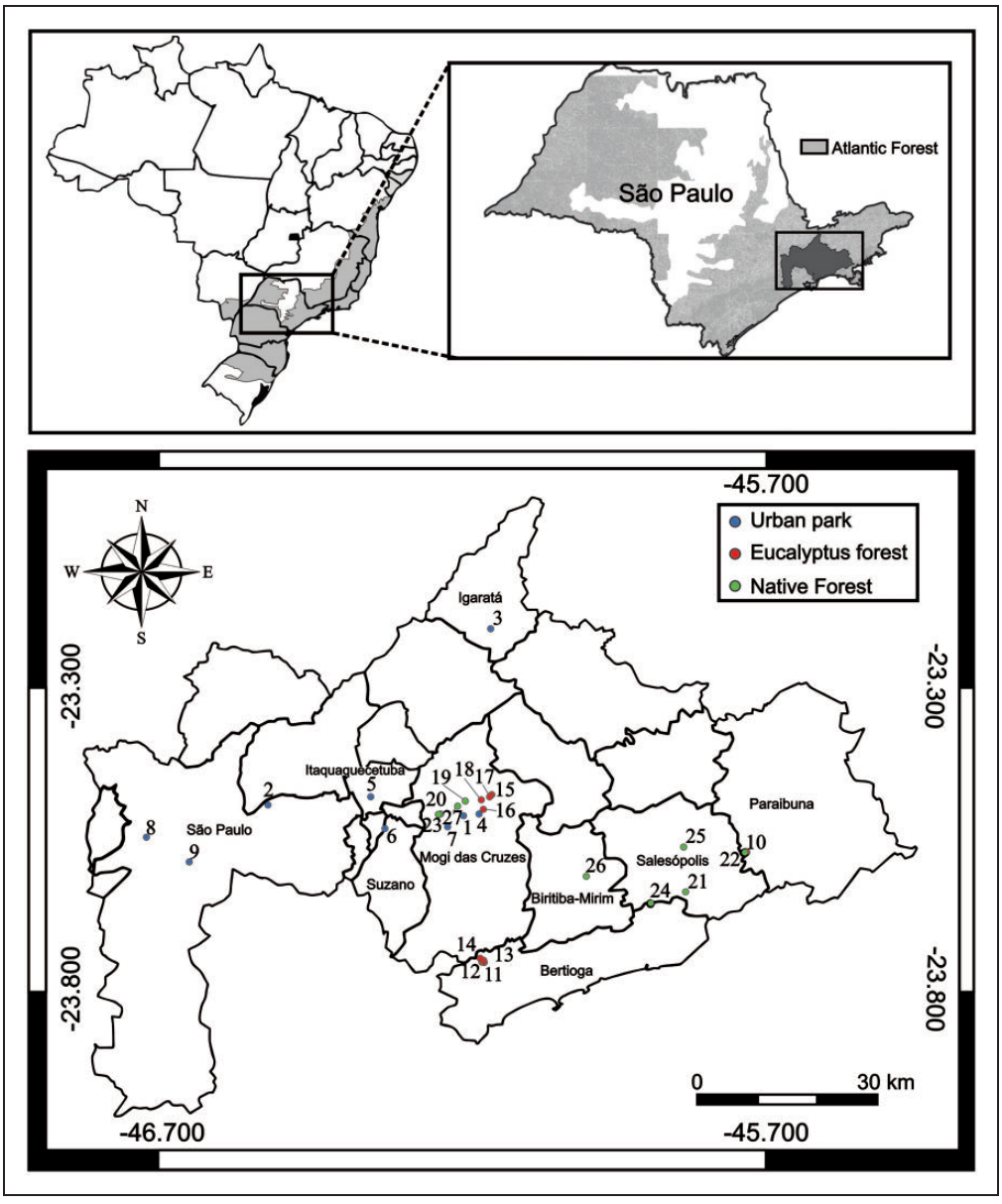


Figure 1. Study sites. Urban parks: 1–9; *Eucalyptus* plantation: 10–18; secondary native forest: 19–27.

Data Analysis

The complete data set contained 54 observations (nine sites with six plots each) per vegetation habitat, for a total of 162 plots surveyed (one twig per plot). As a first step, we visualized data structure by inspecting boxplots and Cleveland dotplots. We considered values that were considerably higher or lower than the rest of the observations to be outliers and excluded them from the data set. The final data set used in the statistical analyses (i.e., the sampling unit used in all statistic models) comprised 147 observations: 45 in the urban park, 51 in *Eucalyptus* plantation, and 51 in native forest).

We used linear mixed effect models (LMMs) to evaluate differences in richness of twig-nesting ant species, number of nests, abundance of adult and immature stages, twig diameter, leaf-litter depth, and canopy openness among vegetation habitats; the sampled sites were added to the model as a random effect. Further, because our data were strongly heterogeneous, we used the variance structure varPower in the LMM to allow for an increase (or decrease) of the residual variation of the vegetation habitat data along a continuous variance covariate (leaf-litter depth). We used the *lme* function in the *nlme* R package (Pinheiro, Bates, DebRoy, Sarkar,

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Table 1. Richness of Ant Species Nesting in Twigs in the Litter of Different Vegetation Habitats of Atlantic Forest, São Paulo State, Brazil, Grouped by Subfamily and Genus.

Subfamily and genus	Urban park	*Eucalyptus* plantation	Native forest	Total no. species
Dolichoderinae				
Linepithema Mayr, 1866	2	3	2	3
Ectatomminae				
Gnamptogenys Roger, 1863	1	1	1	1
Formicinae				
Brachymyrmex Mayr, 1868	2	1	1	2
Camponotus Mayr, 1861	1	3	4	7
Heteroponerinae				
Heteroponera Mayr, 1887	—	1	3	3
Nylanderia Emery, 1906	1	1	—	1
Myrmicinae				
Acanthognathus Mayr, 1887	—	1	1	1
Cardiocondyla Emery, 1869	1	—	—	1
Cephalotes Latreille, 1802	1	—	—	1
Crematogaster Lund, 1831	3	2	1	5
Hylomyrma Forel, 1912	—	1	—	1
Megalomyrmex Forel, 1885	—	1	—	1
Mycetarotes Emery, 1913	—	1	1	1
Myrmelachista Roger, 1863	1	3	2	3
Pheidole Westwood, 1839	8	3	8	12
Procryptocerus Emery, 1887	1	2	3	3
Solenopsis Westwood, 1840	1	3	3	5
Strumigenys Smith, 1860	1	—	—	1
Wasmannia Forel, 1893	1	—	—	1
Ponerinae				
Hypoponera Santschi, 1938	1	2	3	3
Neoponera Emery, 1901	—	1	—	1
Pseudomyrmecinae				
Pseudomyrmex Lund, 1831	2	4	2	4
Total species richness	28	34	35	61

& R Core Team, 2016) to build the models. R^2 values were estimated for the models using the *r.square* Generalized linear mixed models (*GLMMs*) function in the *MuMIn* package (Bartoń, 2016). We performed multiple comparisons of means (Tukey contrasts) of the mixed effects model using the *glht* function in the *multcomp* package (Hothorn, Bretz, & Westfall, 2008). Correlations among variables were described by Spearman's rank correlation coefficients.

The relationships between ant assemblage abundance or species richness and twig and site characteristics were described using GLMMs. The response variables were species richness, number of workers, or number of nests; the full model used a Poisson distribution with fixed terms defined by a quadratic twig diameter trend, leaf-litter depth, vegetation habitat, and the interaction between twig diameter and vegetation habitat as predictor variables; the random term of the model was area. We chose a quadratic model for twig diameter because the data suggested a convex relationship between this parameter and species richness. We found overdispersion in the Poisson GLMMs, and we implemented a negative binomial GLMM, a distribution that can be used for overdispersed count data. We used the *glmmADMB* package (Fournier et al., 2012) for the negative binomial GLMM. Nonsignificant terms were removed from the full model, and the model was refitted until all remaining terms were significant; we defined the significant p value at conventional levels, with a cutoff at $p \leq .05$. Model validation was based on visual analysis of normalized residuals against all predictor variables (included in the model or not).

Nonmetric multidimensional scaling (NMDS) was used to compare species composition among vegetation

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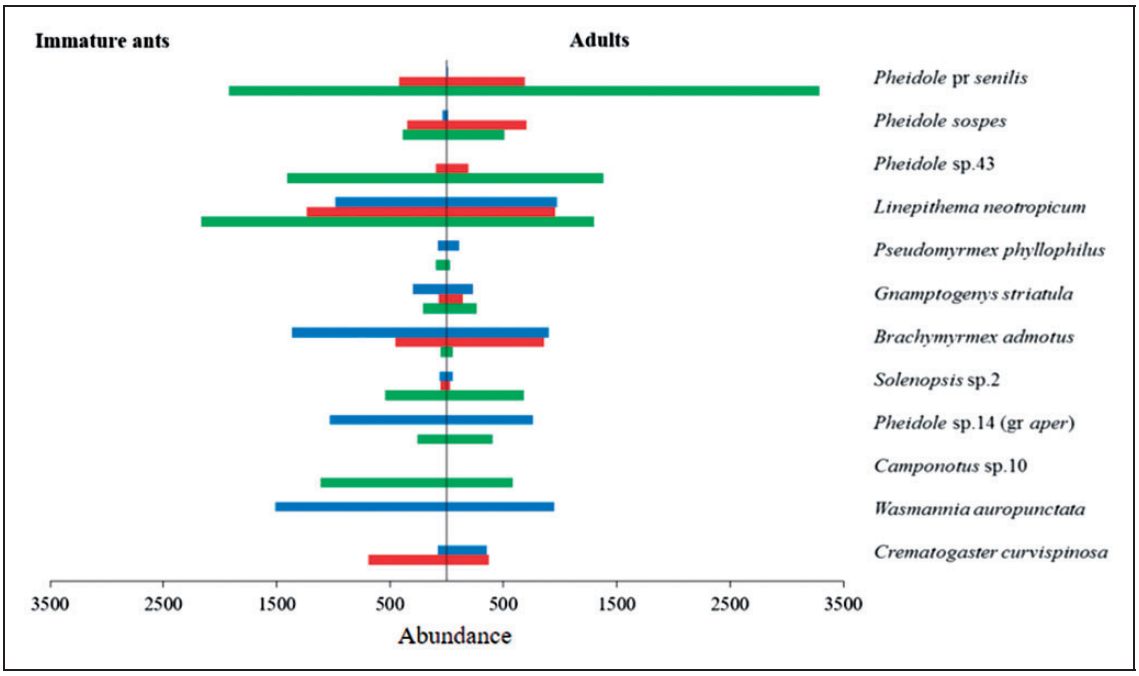


Figure 2. Abundance of immature stages and adults of the most common species in each vegetation habitat. Urban Park = blue bar; *Eucalyptus* plantation = red bar; native forest = green bar.

habitats, using the *metaMDS* function in the *vegan R* package (Oksanen et al., 2016). We carried out a permutational analysis of variance (PERMANOVA) using the *adonis* function in *vegan* to examine the differences among ant assemblages nesting in twigs, using vegetation habitat as explanatory variables. To test for differences in dispersion between groups (permutational multivariate analysis of dispersion [PERMDISP] was significant), we used the *betadisper* function in *vegan*. In addition, we used pairwise PERMANOVAs to examine which vegetation habitats were driving significant differences using the *pairwise.perm.manova* function in the *RVAideMemoire* package (Hervé, 2017).

Results

We found 51,213 ants (adult and immature stages) in 498 colonies, distributed in seven subfamilies, 22 genera, and 61 species. *Pheidole*, *Camponotus,* and *Solenopsis* were the richest genera (Table 1). They were also the most frequent and had the largest colonies (Figure 2). *Linepithema neotropicum* Wild, 2007, *Gnamptogenys striatula* Mayr, 1884, and *Solenopsis* sp.2 were found in all vegetation habitats, but *L. neotropicum* had the largest colonies (Figure 2). *Wasmannia auropunctata* (Roger, 1863) was collected only in urban parks and was very frequent (Figure 2). Only one invasive species, *Cardiocondyla wroughtonii* (Forel, 1890) was recorded in this study (Figure 2).

Total species richness (Table 1) was similar between *Eucalyptus* plantations and native forests. *Eucalyptus* plantations and native forests shared 21 species, while urban parks had more specific species (19.67%), including *Strumygenys crassicornis* Mayr, 1887 and *Cephalotes pusillus* Klug, 1824. Only 14.75% of the species were found in all study areas, including *Linepithema iniquum* (Mayr, 1870); *L. neotropicum*; *Brachymyrmex admotus* Mayr, 1887; *Pseudomyrmex phyllophilus* Smith, 1858; *Pheidole sospes* Forel, 1908; *Pheidole* pr. *senilis*; *G. striatula*; *Myrmelachista catharinae* Mayr, 1887; and *Solenopsis* sp.2.

The numbers of twigs colonized by ants in urban parks, *Eucalyptus* plantations, and native forest were 74 (0.5 nests/m^2 of leaf litter), 141 (0.98 nests/m^2 of leaf litter), and 283 (1.96 nests/m^2 of leaf litter), respectively. Thus, native forest sites had twice the number of colonized twigs of *Eucalyptus* plantations. In addition, 84%, 92%, and 69% of the twigs in urban parks, *Eucalyptus* plantations, and native forests, respectively, contained only colonies with immature stages and workers (i.e., without gynes).

In urban parks, the canopies were more open, ant assemblages occupied fewer twigs in the leaf litter, and species assemblage richness was lower compared to other areas. At the plot level, twigs in native forests had higher species richness, ant nests, and number of individuals and a more closed canopy than urban parks or *Eucalyptus* plantations (Table 2).

The analysis of assemblage structure by NMDS suggests that plots in urban parks, *Eucalyptus* plantations, and native forests were all different from each other (Figure 3). Indeed, there were significant differences in

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Table 2. Linear Mixed Effect Models for the Relationship Between Vegetation Type (Variable With Three Levels: Forest, Eucalyptus, and Park) and Ant Species Richness, Ant Abundance, Number of Individuals, Twig Diameter, Canopy Openness or Leaf-Litter Depth.

Model: Ant species richness ~ vegetation type					
	df_{num}	df_{den}	F	P	R^2 (conditional)
(Intercept)	1	120	352.46	<.0001	.58
Vegetation type	2	24	37.84	<.0001	
Multiple comparisons					
		Estimate	*SE*	*Z*	*p*
Forest × *Eucalyptus*		1.50	0.31	4.79	<.0001
Park × *Eucalyptus*		−0.93	0.32	−2.91	.0100
Park × Forest		−2.43	0.32	−7.6	<.0001
Model: Ant abundance (nests) ~ vegetation type					
	df_{num}	df_{den}	F	p	R^2 (conditional)
(Intercept)	1	120	199.86	<.0001	.5
Vegetation Type	2	24	25.32	<.0001	
Multiple comparisons					
		Estimate	*SE*	*Z*	*p*
Forest × *Eucalyptus*		2.51	0.53	4.71	.0001
Park × *Eucalyptus*		−1.26	0.54	−2.33	.05
Park × Forest		−3.77	0.54	−6.96	<.0001
Model: Number of individuals ~ vegetation type					
	df_{num}	df_{den}	F	P	R^2 (conditional)
(Intercept)	1	120	90.89	< 0.0001	0.38
Vegetation type	2	24	10.02	< 0.0001	
Multiple comparisons					
		Estimate	*SE*	*Z*	*p*
Forest × *Eucalyptus*		245.66	74.99	3.28	.003
Park × *Eucalyptus*		−79.94	76.32	−1.05	.546
Park × Forest		−325.61	76.32	−4.27	<.0001
Model: Twig diameter ~ vegetation type					
	df_{num}	df_{den}	F	P	R^2 (conditional)
(Intercept)	1	120	938.31	<.0001	.11
Vegetation type	2	24	1.67	.21	
Model: Canopy openness ~ vegetation type					
	df_{num}	df_{den}	F	P	R^2 (conditional)
(Intercept)	1	120	813.13	<.0001	.57
Vegetation type	2	24	56.17	<.0001	
Multiple comparisons					
		Estimate	*SE*	*Z*	*p*
Forest × *Eucalyptus*		−2.44	0.6824	−3.580	<.0001
Park × *Eucalyptus*		−4.14	0.6919	−5.995	<.0001
Park × Forest		−1.7	0.6919	−2.465	.0367
Model: Leaf-litter depth ~ vegetation type					
	df_{num}	df_{den}	F	P	R^2 (conditional)
(Intercept)	1	120	277.09	<.0001	.57
Vegetation type	2	24	18.23	<.0001	
Multiple comparisons					
		Estimate	*SE*	*Z*	*p*
Forest × *Eucalyptus*		−2.44	0.6824	−3.580	<.0001
Park × *Eucalyptus*		−4.15	0.6919	−5.995	<.0001
Park × Forest		−1.71	0.6919	−2.465	.04

Note. The random term was defined as ~ 1 | Area (i.e., the surveyed sites with six plots each). df_{num} = degrees of freedom in numerator; df_{den} = degrees of freedom in denominator; *SE* = standard error.

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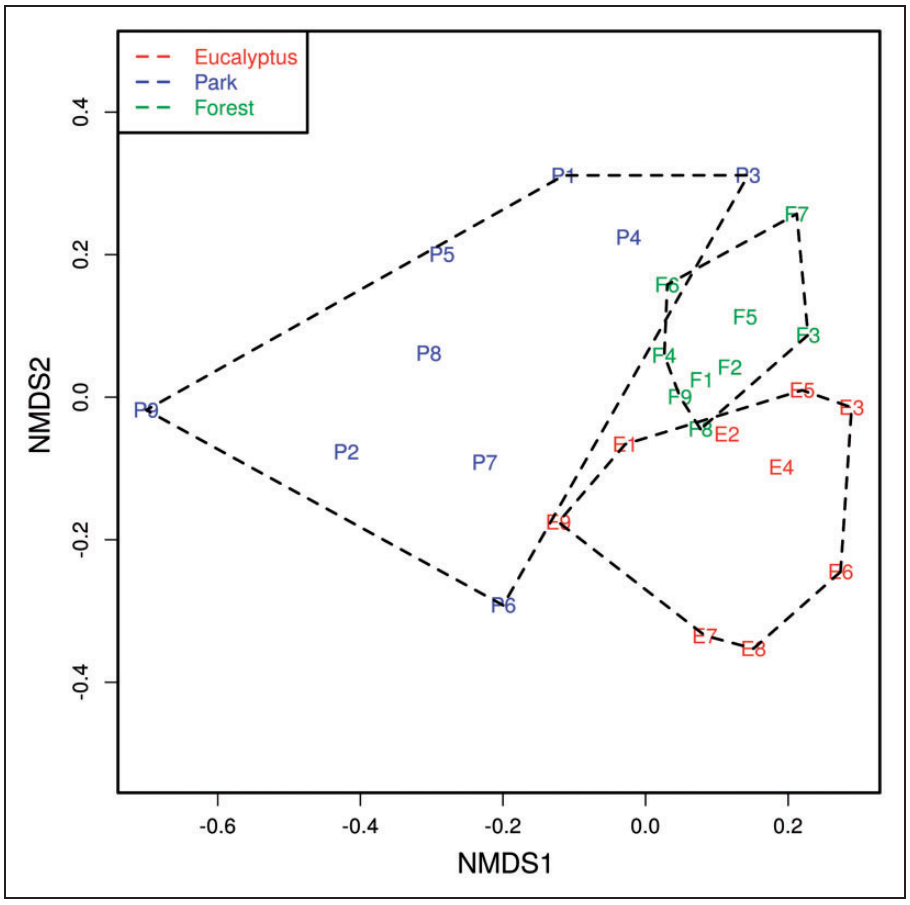


Figure 3. Nonmetric multidimensional scaling (NMDS) analysis based on the composition of ant species collected in urban parks, *Eucalyptus* plantation, and native forest. NMDS stress = .17.

ant fauna composition among vegetation habitats (PERMANOVA pseudo-$F = 3.95$, $p = .0001$), and all pairwise comparisons were significant ($p < .001$, 999 permutations). The PERMDISP was significant ($F = 11.47$, $p = .0003$), indicating unequal variances among vegetation habitats.

The best model to explain the relationship between species richness, number of workers, and number of ant nests in twigs retained the quadratic twig diameter term and vegetation habitat as predictors (Table 3). In all models, richness or abundance measurements had a quadratic relationship with twig diameter (Figure 4); the interaction between twig diameter and vegetation habitat was not significant in any of the models. Nonetheless, the effect of vegetation habitat was stronger than the effect of twig diameter in all models. We observed positive correlations between twig diameter and the number of individuals, particularly for *Pheidole* pr. *senilis* ($r_s = .294$, $p = .020$), *Pheidole* (Gr. Aper) sp.14 ($r_s = .448$, $p = .041$), *Pheidole* sp.43 ($r_s = .478$, $p = .006$), *Procryptocerus* sp.1 ($r_s = .767$, $p = .016$), and *Pseudomyrmex* sp.8 ($r_s = .821$, $p = .023$).

Discussion

Our results suggest that the number of twigs available in the leaf litter is determined by vegetation habitat. The abundance and species richness of ants occupying twig cavities were determined primarily by the vegetation habitat and secondarily by twig diameter. Species composition was markedly different across all vegetation habitats.

The positive influence of number of twigs available on ants communities has been showing by previous studies, which demonstrated that species richness of twig-nesting ants is variable (Byrne, 1994; Carvalho & Vasconcelos, 2002; Kaspari, 1996; Pereira, Queiroz, Souza, & Mayhé-Nunes, 2007). Environmental complexity, expressed as plant community richness and composition, affects the assortment of available microhabitats (Hoffman, 2000; Ribas, Schoereder, Pic, & Soares, 2003). An increase in nesting site diversity results in higher species richness and composition (Armbrecht et al., 2004).

Ant diversity is low in urban parks (Munhae, Bueno, Morini, & Silva, 2009; Pacheco & Vasconcelos, 2007; Souza-Campana et al., 2016), and twig-colonizing

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Table 3. Summary of Generalized Linear Mixed Models Examining the Relationship Between Twig Diameter, Vegetation Type, Ant Nests (Number of Workers and Number of Nests), and Ant Species Richness.

	df	AIC	LRT	*P*
Model: Ant species richness ~ poly (twig diameter, 2) + vegetation type				
Null		458.31		
Twig diameter	2	462.90	8.592	.0136
Vegetation type	2	489.55	35.246	<.0001
Model: Number of workers ~ poly (twig diameter, 2) + area				
Null		1778.7		
Twig diameter	2	1797.5	22.910	<.0001
Vegetation type	2	1784.5	9.896	.0071
Model: Number of nests ~ poly (twig diameter, 2) + area				
Null		545.92		
Twig diameter	2	555.05	13.138	.0014
Vegetation type	2	575.95	34.030	<.0001

Note. *df* = degrees of freedom; AIC = Akaike information criterion; LRT = likelihood-ratio test.

communities are less diverse. In these areas, the vegetation structure is often simpler (Rosa & Schiavini, 2006), and the canopy is more open. Compared to native forests, the soil is more exposed to sunlight, humidity is lower, and the rate of litter decomposition is slower (Louzada, Schoereder, & De Marco, 1997). These characteristics influence ant communities through changes in microhabitat availability (Kaspari, Alonso, & O'Donnell, 2000; Kaspari, Yanoviak, & Dudley, 2008; Silva, Bieber, Corrêa, & Leal, 2011), which is essential to increase the number of colonized nests and to expand ant colonies (Fowler et al., 1991).

The phytophysiognomy of an *Eucalyptus* forest is homogeneous (Ferreira & Marques, 1998), which affects both ant diversity (Marinho, Zanetti, Delabie, Schlindwein, & Ramos, 2002) and the diversity of twigs that are deposited in the leaf litter and available for colonization. We found twice as many colonized twigs in native forests than in *Eucalyptus* plantations. Armbrecht et al. (2004) showed that a diverse array of twigs attracted more species of twig-nesting ants than a monospecific collection of twigs, increasing community diversity in ecosystems. In addition, twigs from *Eucalyptus* species are harder (Pereira et al., 2007), which should make it more difficult for ants to colonize them.

Several studies have shown that tree identity does not affect twig colonization by ants, but that the rate of decomposition is crucial (Armbrecht et al., 2004; Kaspari, 1996). Ants prefer decayed twigs, where the softer wood facilitates access to the cortex and to cavities (Carvalho & Vasconcelos, 2002). In addition, moisture, one of the limiting factors for colony survival (Kaspari, 1996), is higher in decayed tissue (Carvalho & Vasconcelos, 2002). The size and diversity of holes in twigs are also relevant for colonization and for colony growth (Jiménez-Soto & Philpott, 2015; Powell et al., 2011).

Some genera observed in this study seem particularly well-adapted to nesting inside twigs, such as *Pheidole*, *Crematogaster*, *Solenopsis,* and *Camponotus*. *Camponotus renggeri* Emery, 1894, for instance, nests preferentially in hollowed-out and decaying fallen trunks (Ronque, Azevedo-Silva, Mori, Souza, & Oliveira, 2015). These genera were found by Carvalho and Vasconcelos (2002); Pereira et al. (2007); Fernandes et al. (2012); Souza et al. (2012); Ramalho, Santos, Fernandes, Morini, and Bueno (2016); and Silva, Fernandes, Silva, Souza-Campana, and Morini (2016) in a range of different vegetation habitats.

When the space available inside the twig is too small, a strategy observed in ants is to expand the colony to additional twigs, forming polydomous nests (Hölldobler & Wilson, 1990). In the present work, we found queenless colonies, which had only workers and immatures, in all vegetation habitats. That is one of the signs of polydomy (Debout, Schatz, Elias, & Mckey, 2007; Lanan, Dornhaus, & Bronstein, 2011). Generally, polydomous nests were more common in urban parks and *Eucalyptus* forests, although the diameters of the colonized twigs were similar to those in native forests. Polydomy is a common behavior in leaf-litter ants (Hölldobler & Wilson, 1990), especially because occupying additional twig cavities does not require a high investment by the colony (McGlynn, 2012). Even arboreal ants, such as *C. pusillus*, *Crematogaster* spp., *Myrmelachista* spp., *P. phyllophlus,* and *Procryptocerus* sp.1 exhibit this behavior as a way to expand their nests (Carvalho & Vasconcelos, 2002).

Twigs represent an important nesting resource for several leaf-litter and arboreal ant species. However, the diversity of the communities colonizing this resource seems related to vegetation habitat. If the environment is structurally diverse in terms of plant composition and

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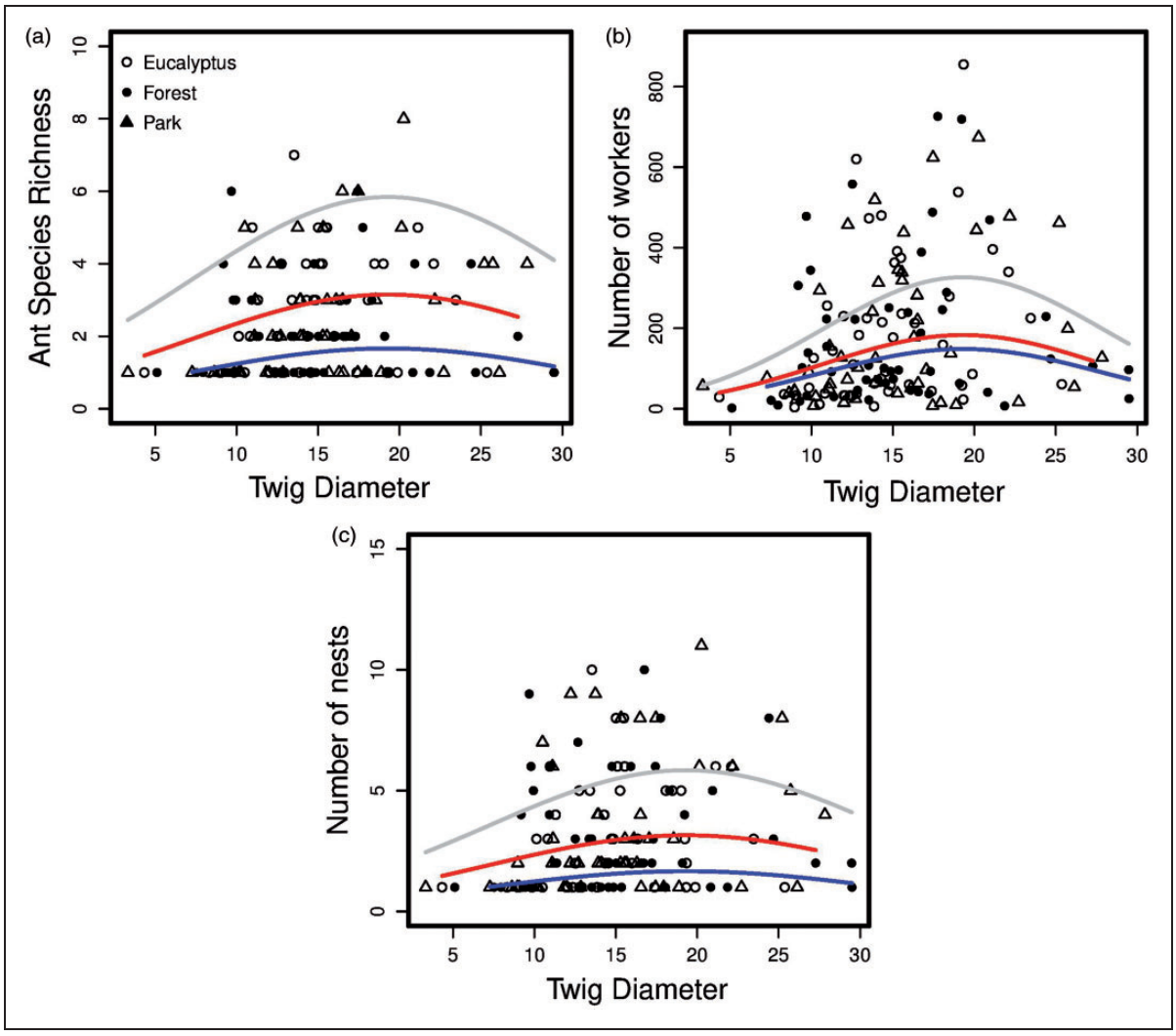


Figure 4. Generalized linear mixed model regression models used to evaluate the relationship between twig diameter and species richness (a), number of workers (b), and number of nests (c). Blue line = urban park; red line = *Eucalyptus* plantation; gray line = native forest.

ant fauna in the soil-litter system, twig-nesting communities will also be diverse. However, even if the environment is not structured, the very existence of this nesting resource may help maintain ant community diversity in these ecosystems over time.

Implications for Conservation

The Atlantic Forest is one of the most important ecosystems in the world for biodiversity conservation, but agricultural and urban expansion have left this biome increasingly fragmented (Tabarelli, Pinto, Silva, Hirota, & Bedê, 2005). Currently, it consists of a complex mosaic of vegetation habitats with different degrees of conservation. In the Brazilian Atlantic domain, *Eucalyptus* is commonly cultivated within native vegetation and near native forest remnants (Baptista & Rudel, 2006; Ribeiro, Metzger, Martensen, Ponzoni, & Hirota, 2009). In addition, forest fragments in the outskirts of cities and within urban areas create urban parks with native vegetation (Mello-Théry, 2011). At a landscape scale, preserving these areas is essential because they can act as corridors between fragments of native forest. Connectivity is a vital element for species survival and population dynamics (Tischendorf & Fahrig, 2000), and urban parks are essential in this regard. So much in this work we observed many species shared between native forest and urban parks, denoting the importance of these sites for the dispersion of ant communities.

Ant species richness and community composition are both affected by fragmentation (Leal, Filgueiras, Gomes, Iannuzzi, & Andersen, 2012; Vasconcelos et al., 2008), but population diversification depends on microhabitat use (Fowler et al., 1991). Thus, twigs used for nesting

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are an important source to maintain ant diversity in fragments of preserved native forest within urban areas and in *Eucalyptus* plantations. Many ant species that forage in the leaf litter use twigs to expand their colonies, increasing the area used for foraging and protection (Byrne, 1994). Arboreal ants also use twigs in the leaf litter as a resource for nesting (Carvalho & Vasconcelos, 2002; Nakano et al., 2012).

But how important are ants for these fragments or plantations? Ants are essential for the flow of energy and biomass; they affect the community structure of other invertebrates, exerting a strong impact at all trophic levels, due to their diet and different types of interactions with animals, plants, and fungi (Hölldobler & Wilson, 1990; Tobin, 1995). In addition, they are part of a select group of organisms known as ''ecosystem engineers,'' whose activity creates galleries, nests, chambers, and fecal pellets, that is, biogenic structures, that modify the physical and chemical properties of the soil and affect resource availability to other components of the soil fauna (Brown et al., 2015). Ants also control pests (Del Toro, Ribbons, & Pelini, 2012; Offenberg, 2015) and are as important as earthworms to maintain the fertility of tropical soils (Korasaki et al., 2013).

Our results indicate that vegetation habitats have a strong effect on twig colonization by ants. Therefore, the maintenance of this resource in the leaf litter may be a good strategy for the conservation or restoration of ant assemblage diversity in anthropic environments. Biodiversity conservation in urban environments requires improving the climate, reducing temperatures, controlling for erosion, and protecting watersheds, among other essential ecosystem services.

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