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Occurrence of Ants (Hymenoptera: Formicidae) in both Leaf Litter and Twigs in Atlantic Forest

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Abstract

Twigs in the litter derived from the fragmentation of tree branches form one microhabitat, where entire colonies of ants, both leaf litter and arboreal species, can be found. The objective was to survey ant species that are present in both the leaf litter and twigs simultaneously. We describe the nest type, the social structure of the colonies and the trophic guild membership of these species. Samples were collected from 10 preserved fragments of Brazilian Atlantic forest. We used Berlese funnels to collect leaf litter ants and manual collection for twig ants. We recorded 80 ant species; 60 species were in leaf litter samples and 35 species were in twigs. Of the total species, only 15 (20%) occurred simultaneously in the leaf litter and in twigs. Of these species, *Gnamptogenys striatula*, *Pheidole sarcina*, *P. sospes* and *Solenopsis* sp. 2 were the most frequent among leaf litter dwellers, and *Myrmelachista catharinae* was the most common arboreal species. Most of these belonged to generalist and predator guilds, with "polydomous nests" and colonies monogynous.

Introduction

Ants are one of the most diverse and abundant arthropods in tropical forests (Hölldobler & Wilson, 1990), where up to 50% of them may be associated with the leaf litter (Brandão et al., 2012). In this layer, ants are highly taxonomically diverse (Ward, 2000). Nine trophic (Delabie et al., 2000) and morphological guilds (Silva & Brandão, 2010) are found in the Atlantic forest.

In the leaf litter, ants use various microhabitats, such as those derived from vertebrates (Hölldobler & Wilson, 1990) or invertebrates (Leponce et al., 1999, Jahyny et al., 2007) and live branches (Hölldobler & Wilson, 1990) or dead branches and twigs (Souza et al., 2012, Castro et al., 2017) that are used for colony expansion (Carvalho & Vasconcelos, 2002) and nesting (Fernandes et al., 2012). The scarcity or absence of these resources is a limiting factor for ant diversity (Fowler et al., 1991).

In general, wood structures are frequently colonized by ants (Hashimoto et al., 2006; King et al., 2013), but twigs are the most sought-after resource in the leaf litter (Gomes et al., 2013). Twigs are derived from the fragmentation of tree branches (Fernández, 2003; Silva et al., 2009). Inside twig cavities there may be colonies comprised of hundreds of individuals (Nakano et al., 2012; King et al., 2018), with different feeding habits (Byrne, 1994). However, even if competition for nesting resources is high in the leaf litter (Delabie et al., 2007), due to the high species diversity (Silva & Brandão, 2010), not all of the available twigs are colonized (Sagata et al., 2010).

Twigs may be satellite structures, or temporary shelters, when only workers are present (Carvalho & Vasconcelos, 2002; Debout et al., 2007); or part of a polydomous colony, when it includes both workers and immatures (Kaspari et al., 1996). There are no descriptions of this kind of species found in both the leaf litter and twigs in the Brazilian Atlantic forest.

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Thus, in this work we analyse these ant communities, based on the hypothesis that twigs represent a satellite structure, because they are considered an ephemeral resource (Byrne, 1994). In addition, we describe the nest type, the social structure and the trophic guild membership. In this case, we assumed that twigs were colonized more often by generalist leaf litter species, because they belong to the most abundant guild in this layer (Silva & Brandão, 2010).

Materials and methods

Collection sites

In 2010, we conducted field expeditions in ten fragments of native Atlantic forest located in the state of São Paulo, Brazil (Figure 1). Fragment sizes ranged from 20 to 350 ha and were located at elevations between 600 and 850 m. According to the Köppen classification, the climate of this region is mesothermic with a dry winter (Cwb), and annual precipitation is 1,500 mm. Samples were collected in the months of September, October, November and December, which are between the end of the dry season and the middle of the rainy season according to CPTEC-INPE (Centre for Weather Prediction and Climate Studies/National Institute for Space Research, classification 2018).

Collection, colony characterization and ant identification

At each site a linear transect was established 100-200 m from the forest edge, depending on the size of the fragment. Six 16 m^2 plots 50 m apart were established in each fragment. At the centre of each 16 m^2 plot, 50 cm^2 was marked and all the leaf litter within it was scraped up. This material was placed in Berlese funnels for seven days. In the 16 m^2 plots, all twigs on the surface of the leaf litter were collected and placed in individual plastic bags, including those from the spot where the leaf litter was removed. In total, we processed 30 m^2 of leaf litter to collect ants and collected twigs from an area of 960 m^2 of leaf litter on the forest floor.

The twigs were opened and all colony components were removed, recorded and stored in 90% alcohol. Colony presence in twigs was defined by (*i*) the presence of ten or more workers, with or without a queen(s) or (*ii*) if less than ten workers were present, the presence of immatures or alates (Fernandes et al., 2012).

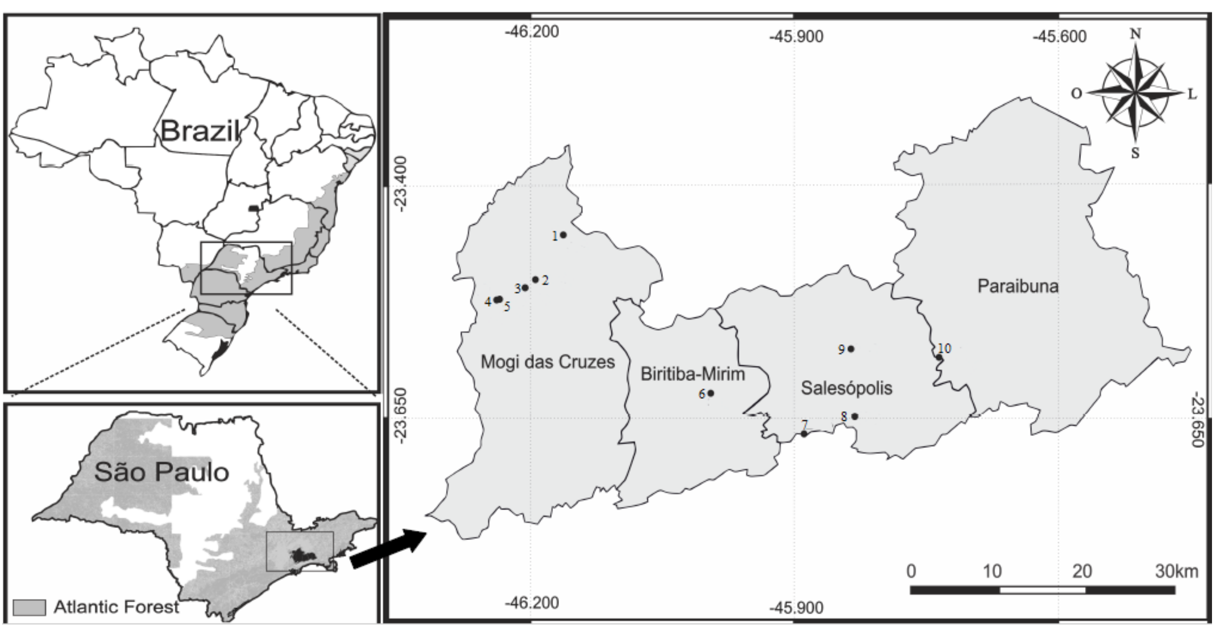

Fig 1. Brazilian Atlantic forest sites (1 to 10) where collections were conducted.

Nests were classified as a "satellite nest", when only workers were found in the twigs (Carvalho & Vasconcelos, 2002), or as a "polydomous nest", when they contained more than workers only and were likely part of a polydomous colony. In this case, there were two types of structure: workers and immatures (Debout et al., 2007), or workers plus alates, or workers plus immatures plus alates. The social structure of the colony was classified as monogynous or polygynous (Carvalho & Vasconcelos, 2002). The guilds were classified according to Brandão et al. (2012). Ants were identified based on Suguituru et al. (2015) and all morphospecies were numbered according to this literature. All vouchers were deposited at Laboratório de Mirmecologia do Alto Tietê (Myrmecology Laboratory of Alto Tietê) of University of Mogi das Cruzes, in the state of São Paulo, Brazil.

Results

We recorded 31 genera and 80 species/morphospecies of ants. Of these, 60 were in the leaf litter and 35 were inside twigs (Table 1). No twigs contained more than a single ant species. In the leaf litter there were 0.49 species per 50 cm^2. *Camponotus* sp. 10, *Gnamptogenys striatula* Mayr, 1884, *Myrmelachista catharinae* Mayr, 1887 *Pheidole sospes* Forel, 1908, *Solenopsis* sp. 2, and *Solenopsis* sp. 3 were the most frequent species.

We found 0.03 species/m² in 335 twigs; *Linepithema neotropicum* (Wild, 2007), *Pheidole sarcina* Forel, 1912, *Pheidole* sp. 43, and *Solenopsis* sp. 2 were the most frequent species. Among leaf litter dwellers, *G. striatula* and *Solenopsis* sp. 2 were the species that most often colonized both the leaf litter and the twigs at the same time. Among arboreal species, the most frequent colonizer was *Myrmelachista catharinae* Mayr, 1887 (Table 1). Out of all species, only 15 (20%) were simultaneously recorded in the leaf litter and in twigs, and most (63%) belonged to the generalist and predator guilds (Table 1, Figure 2). Despite the low richness, these species colonized most twigs (211 = 60%) In the remaining twigs (40%), five of the recorded species were arboreal (*Myrmelachista ruzskyi* Forel, 1903; two *Procryptocerus* species; and two *Pseudomyrmex* species), and six species were possibly arboreal (five *Camponotus* species and one *Crematogaster* species). *Pheidole flavens* Roger, 1863 was the most frequent species in twigs, but it was not recorded in the leaf litter.

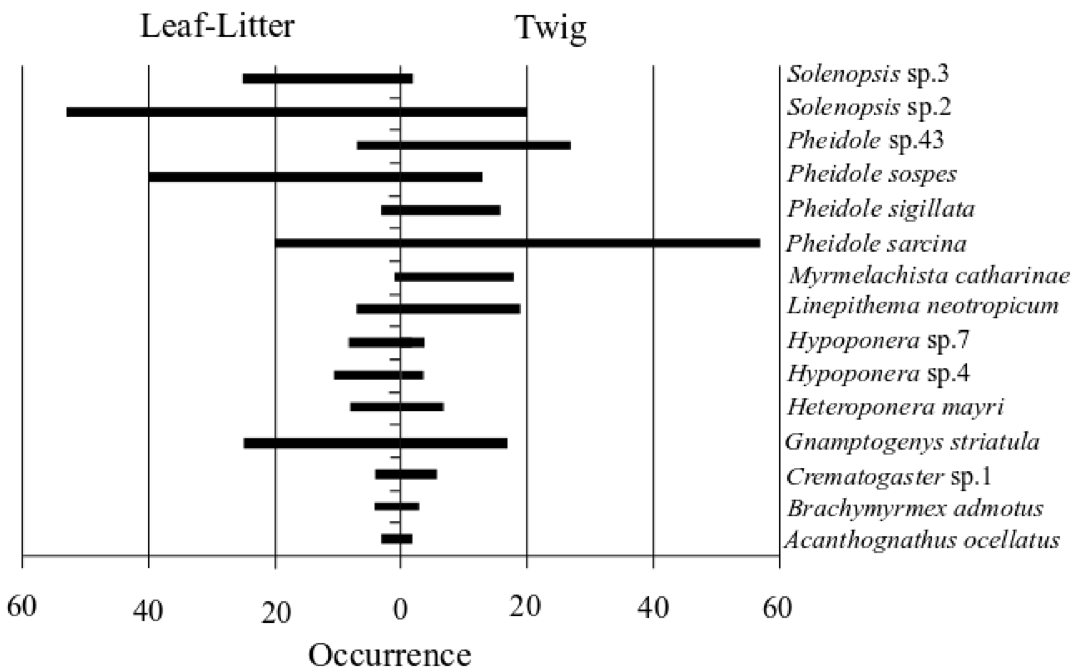

Fig 2. Total number of ant species colonizing both leaf litter and twigs.

We found 18 satellite nests (9 species, 57%) and 111 polydomous nests (14 species, 88%). The latter group included 96 nests with workers + immatures (14 species), 4 nests with workers + alates (3 species) and 11 nests with workers + immatures + alates (5 species). In addition, five species – *Brachymyrmex admotus* Mayr, 1887, *Camponotus* sp. 9, *P. sarcina*, *P. sospes*, and *Pheidole* sp. 43, formed polydomous and polygynous nests. Most colonies were monogynous (Figure 3). In total, we recorded 10 species with one queen and 5 species with more than one queen; four species had two queens (*B. admotus*, *Pheidole* sp. 43, *P. sarcina*, *P. sospes*) and one species had three (*Pheidole* sp. 43).

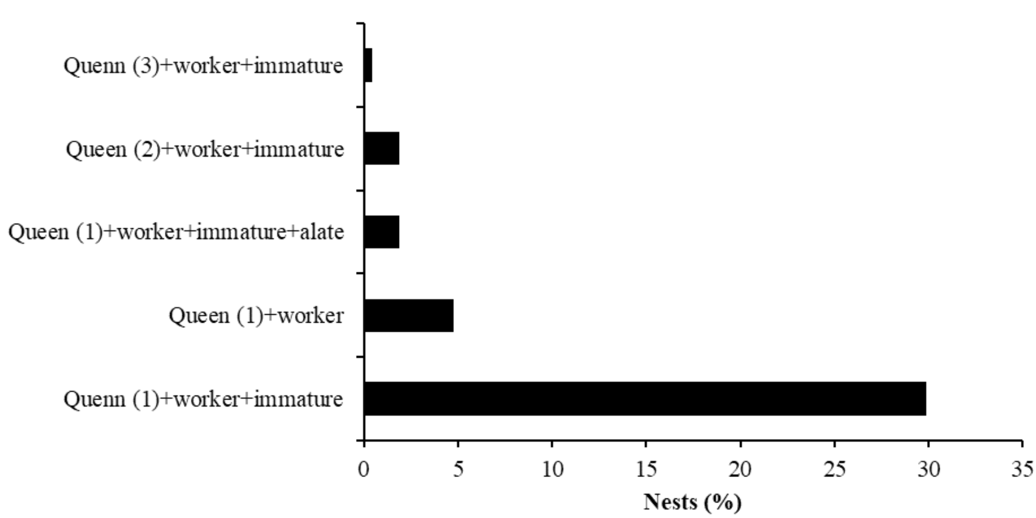

Fig 3. Proportion of nests of species found in both leaf litter and twigs with different colony component patterns. The number of queens is shown in parentheses.

Table 1. List of taxa recorded from leaf litter and twigs, with social structure of the colony, nest type, and guild membership. The total number of nests is shown in parentheses. Species in bold font were recorded both in the leaf litter and in twigs.

Taxon	Leaf Litter	Twig	Social Structure of the Colony	Nest Type	Trophic guild membership*
***Acanthognathus ocellatus* Mayr, 1887**	**3**	**2**	(0) Monogyny (0) Polygyny	(1) Satellite structure (1) Polydomy	Dacetini predators with kinetic mandibles
Acromyrmex diasi Gonçalves, 1893	1	-		-	Leaf cutters
Acromyrmex disciger Mayr, 1887	1	-		-	
Apterostigma sp. 1	2	-		-	Litter-Nesting Fungus Growers
Octostruma rugifera (Mayr, 1887)	15	-		-	Medium-sized epigeic generalist predators
Octostruma stenognatha Brown & Kempf, 1960	13	-		-	Dacetini predators
***Brachymyrmex admotus* Mayr, 1887**	**4**	**3**	(0) Monogyny (1) Polygyny	(1) Satellite structure (1) Polydomy	Generalist species
Brachymyrmex cordemoyi Forel, 1895	2	-		-	Dominant arboreal ants associated with carbohydrate-rich resources or domatia
Brachymyrmex heeri (Forel, 1874)	15	-		-	
Camponotus sp. 2	-	4	(0) Monogyny (0) Polygyny	(0) Satellite structure (4) Polydomy	Dominant arboreal ants associated with carbohydrate-rich resources or domatia
Camponotus sp. 5	-	2	(0) Monogyny (0) Polygyny	(0) Satellite structure (2) Polydomy	
Camponotus alboannulatus Mayr, 1887	-	20	(3) Monogyny (0) Polygyny	(0) Satellite structure (17) Polydomy	
Camponotus sp. 8	-	2	(0) Monogyny (0) Polygyny	(0) Satellite structure (2) Polydomy	
Camponotus sp. 9	-	2	(0) Monogyny (1) Polygyny	(0) Satellite structure (1) Polydomy	
Carebara sp. 1	4	-		-	Small-sized hypogeic generalist foragers
Neocerapachys splendens (Borgmeier, 1957)	3	-		-	Specialists predators living in the superficial layers of the soil
Crematogaster corticicola Mayr, 1887	1	-		-	Dominant arboreal ants associated with carbohydrate-rich resources or domatia
***Crematogaster* sp. 1**	**4**	**6**	(1) Monogyny (0) Polygyny	(2) Satellite structure (3) Polydomy	
Crematogaster sp. 7	1	-		-	
Crematogaster sp. 18	-	3	(0) Monogyny (1) Polygyny	(2) Satellite structure (0) Polydomy	
Cyphomyrmex rimosus (Spinola, 1851)	11	-		-	Litter-nesting fungus-growers
Cyphomyrmex transversus (Emery, 1894)	6	-		-	
Dyscothyrea sexarticulata (Borgmeier, 1954)	1	-		-	Specialist predators living in the superficial layers of the soil
Ectatomma edentatum Roger, 1863	2	-		-	Large epigeic generalist predators Arboreal predators
Gnamptogenys continua (Mayr, 1887)	2	-		-	Medium-sized epigeic generalist predators
***Gnamptogenys striatula* (Mayr, 1884)**	**25**	**17**	(0) Monogyny (0) Polygyny	(5) Satellite structure (12) Polydomy	Medium-sized hypogeic generalist predators

Table 1. List of taxa recorded from leaf litter and twigs, with social structure of the colony, nest type, and guild membership. The total number of nests is shown in parentheses. Species in bold font were recorded both in the leaf litter and in twigs. (Continuation)

Taxon	Leaf Litter	Twig	Social Structure of the Colony	Nest Type	Trophic guild membership*
Heteroponera dentinodis (Mayr, 1887)	-	3	(0) Monogyny (0) Polygyny	(0) Satellite structure (3) Polydomy	Medium-sized epigeic generalist predators
Heteroponera dolo (Roger, 1860)	-	1	(0) Monogyny (0) Polygyny	(0) Satellite structure (1) Polydomy	
***Heteroponera mayri* Kempf, 1962**	**8**	**7**	(0) Monogyny (0) Polygyny	(0) Satellite structure (7) Polydomy	
Hylomyrma balzani (Emery, 1894)	5	-		-	Medium-sized epigeic generalist predators
Hylomyrma reitteri (Mayr, 1887)	3	-		-	
Hypoponera sp. 1	10	-		-	Medium-sized hypogeic generalist predators
***Hypoponera* sp. 4**	**10**	**3**	(1) Monogyny (0) Polygyny	(1) Satellite structure (1) Polydomy	
Hypoponera sp. 5	2	-		-	
***Hypoponera* sp. 7**	**8**	**4**	(1) Monogyny (0) Polygyny	(0) Satellite structure (3) Polydomy	
Hypoponera sp. 10	-	2	(0) Monogyny (0) Polygyny	(0) Satellite structure (2) Polydomy	
Hypoponera sp. 11	3	-		-	
Linepithema iniquum (Mayr, 1870)	-	2	(0) Monogyny (0) Polygyny	(0) Satellite structure (2) Polydomy	Generalist species
***Linepithema neotropicum* (Wild, 2007)**	**7**	**18**	(3) Monogyny (0) Polygyny	(1) Satellite structure (14) Polydomy	
Megalomyrmex goeldii Forel, 1912	1	-		-	Medium-sized epigeic generalist predators
Mycetarotes parallelus (Emery, 1906)	-	1	(1) Monogyny (0) Polygyny	(0) Satellite structure (0) Polydomy	-
Mycetarotes senticosus Kempf, 1960	2	-		-	
***Myrmelachista catharinae* Mayr, 1887**	**1**	**18**	(0) Monogyny (0) Polygyny	(2) Satellite structure (16) Polydomy	-
Myrmelachista ruzskyi Forel, 1903	-	14	(0) Monogyny (0) Polygyny	(1) Satellite structure (13) Polydomy	
Neoponera crenata (Roger, 1861)	-	1	(0) Monogyny (0) Polygyny	(0) Satellite structure (1) Polydomy	-
Nylanderia sp. 1	11	-		-	-
Odontomachus affinis Guérin-Méneville, 1844	1	-		-	Large epigeic generalist predators
Odontomachus meinerti Forel, 1905	3	-		-	
Oxyepoecus myops Alburquerque & Brandão, 2009	4	-		-	Medium-sized epigeic generalist predators Generalist species
Pachycondyla harpax Fabricius, 1804	2	-		-	Large epigeic generalist predators
Pachycondyla striata Smith, 1858	4	-		-	Medium-sized hypogeic generalist predators Arboreal predator
Pheidole flavens Roger, 1863	-	13	(8) Monogyny (0) Polygyny	(0) Satellite structure (5) Polydomy	Medium-sized epigeic generalist predators

Table 1. List of taxa recorded from leaf litter and twigs, with social structure of the colony, nest type, and guild membership. The total number of nests is shown in parentheses. Species in bold font were recorded both in the leaf litter and in twigs. (Continuation)

Taxon	Leaf Litter	Twig	Social Structure of the Colony	Nest Type	Trophic guild membership*
Pheidole gertrudae (Forel, 1886)	1	-		-	Generalist species
***Pheidole sarcina* Forel, 1912**	**20**	**56**	(28) Monogyny (1) Polygyny	(2) Satellite structure (25) Polydomy	Medium-sized epigeic generalist predators
***Pheidole sigillata* Wilson, 2003**	**3**	**16**	(10) Monogyny (0) Polygyny	(0) Satellite structure (6) Polydomy	
***Pheidole sospes* Forel, 1908**	**40**	**13**	(6) Monogyny (1) Polygyny	(3) Satellite structure (3) Polydomy	
Pheidole subarmata Mayr, 1884	5	-		-	Generalist species
Pheidole sp. 9	-	3	(1) Monogyny (0) Polygyny	(0) Satellite structure (2) Polydomy	
Pheidole sp. 12	8	-		-	
Pheidole sp. 15	1	-		-	
Pheidole sp. 16	4	-		-	
Pheidole sp. 18	5	-		-	
Pheidole sp. 20	1	-		-	
Pheidole sp. 28	2	-		-	
***Pheidole* sp. 43**	**7**	**26**	(16) Monogyny (2) Polygyny	(2) Satellite structure (6) Polydomy	
Procryptocerus adlerzi (Mayr, 1887)	-	6	(0) Monogyny (0) Polygyny	(0) Satellite structure (6) Polydomy	Pollen-feeding arboreal ants
Procryptocerus sp. 2	-	2	(0) Monogyny (0) Polygyny	(0) Satellite structure (2) Polydomy	
Pseudomyrmex phyllophilus (Smith, 1858)	-	3	(0) Monogyny (0) Polygyny	(0) Satellite structure (3) Polydomy	Arboreal predators
Pseudomyrmex gr. pallidus	-	6	(1) Monogyny (0) Polygyny	(0) Satellite structure (5) Polydomy	
***Solenopsis* sp. 2**	**53**	**20**	(9) Monogyny (0) Polygyny	(0) Satellite structure (11) Polydomy	Small-sized hypogeic foragers
***Solenopsis* sp. 3**	**25**	**2**	(2) Monogyny (0) Polygyny	(0) Satellite structure (0) Polydomy	Small-sized hypogeic foragers
Solenopsis sp. 4	3	-		-	
Solenopsis sp. 5	-	4	(0) Monogyny (0) Polygyny	(0) Satellite structure (4) Polydomy	Small-sized hypogeic foragers Small-sized hypogeic foragers
Strumigenys appretiata (Borgmeier, 1954)	2	-			Dacetini predators with static pressure mandibles
Strumigenys cosmostela Kempf, 1975	2	-		-	
Strumigenys crassicorns Mayr, 1887	9	-		-	
Strumigenys denticulata Mayr, 1887	17	-		-	
Strumigenys sanctipauli Kempf, 1958	1	-		-	
Strumigenys schmalzi Emery, 1906	2	-		-	
Wasmannia affinis Santschi, 1929	20	-		-	Generalist species
Richness	61	36		-	-

* According to Brandão et al. (2012)

Discussion

The richness of ants that exploit both the leaf litter and twigs is small relative to the diversity of species that inhabit the leaf litter (20% of total species). In this work, we observed that not all twigs had ant colonies, but 43% were colonized by species that were also present in the leaf litter. According to Sagata et al. (2010), the fact that most twigs are not colonized, despite the diversity of leaf litter ants (Silva & Brandão, 2010), is probably not related to the availability of this nesting resource. Souza-Campana et al. (2017) showed that diameter explained the richness of ant communities in twigs. Some species even colonize same-diameter twigs, regardless of habitat (Fernandes et al., 2018).

We observed that most ant species present in both the leaf litter and in twigs were inhabitants of the Atlantic forest leaf litter (Brandão et al., 2012). However, species that forage sporadically in the leaf litter (Delabie et al., 2000), such as exclusively arboreal species (for instance, *M. catharinae*), were also recorded by us both in the leaf litter and in twigs. Arboreal species exploit a habitat that is constrained in terms of nesting and feeding resources (Wilson & Hölldobler, 2005) and provides a drier environment relative to the leaf litter (Davidson & Patrell-Kim, 1996; Yanoviak & Kaspari, 2000). Thus, we suggest that the leaf litter and the twigs may help maintain the colony, especially during the dispersal of reproductive forms, a period of great energy expenditure (Frank, 1987).

For *M. catharinae*, along with alates, we found workers and immatures, but never any queens. In contrast, Nakano et al. (2013) found colonies of *M. catharinae*, *M. nodigera* Mayr, 1887 and *M. ruszkyi* Roger, 1863 that included queens, demonstrating that twigs can contain all colony components and that this nesting site must be part of the life cycle of these arboreal species. In contrast to *Myrmelachista* species, *P. flavens* is a leaf litter dweller (McGlynn & Owen, 2002) that is rarely found in this layer in Atlantic forest areas (Pacheco et al., 2009; Suguituru et al., 2011; 2013), but is very frequent in twigs (Fernandes et al., 2012). Here we only detected this species in twigs. Given these reports, we suggest that this species is arboreal and forage sporadically in the leaf litter, in the same way as *M. catharinae* (Nakano et al., 2013), *Azteca* and *Crematogaster* (Delabie et al., 2000).

Conflicting with our hypothesis, most nests appeared to be from polydomous colonies and had workers and immatures, but no queen. The polydomous colony is a functional and cooperative unit (Ellis et al., 2017), because it increases the probability of colony survival (Silvestre et al., 2003; Santos & Del-Claro, 2009) by expanding the foraging area (Robinson, 2014) and the space for colony development (Byrne, 1994) in the competitive environment of the leaf litter (Yanoviak & Kaspari, 2000). In addition, it protects the colony against predators (Debout et al., 2007) by facilitating information sharing, such as mass recruitment (Hamidi et al., 2017) and transfer of immatures and the queen (Stroeymeyt et al., 2017). A polydomous colony structure is a strategy to reduce mortality, because this risk increases when there is only one nest (Hölldobler & Wilson, 1990; Debout et al., 2007). The presence of immatures also increases the level of defence deployed by the colony (Debout et al., 2007).

Species that colonize ephemeral habitats, such as twigs (Byrne, 1994), tend to be polygynous (Hölldobler & Wilson, 1990), but our results showed that monogyny was more frequent. Normally, a monogynous colony disperses farther away (Hamidi et al., 2017) because they have larger energy supplies compared to polygynous colonies (DeHeer et al., 1999). Given that the soil and the leaf litter are rich in ants (Delabie et al., 2007; Silva et al., 2017) and other invertebrates (Decaëns, 2010; Morais et al., 2010), the colony dispersal to more distant habitats may be a strategy to avoid competition; the twigs would act as a protective environment during this stage, when a higher accumulation of energy is needed.

Here we observed concurrent polydomy and polygyny in 6% of the species, which may indicate an influence of the environment over the strategy of colonization and colony dispersal of certain species. Martins Segundo et al. (2017) reported that colonies of *Crematogaster pygmaea* Forel, 1904 in environments subject to human disturbance and adverse and unstable climatic conditions had a higher rate of polydomous and polygynous colonies than *Crematogaster abstinens* Forel, 1899 recorded in a preserved environment.

Twigs host many ant genera that have different foraging habits, ranging from generalists to predators, which correspond to two of the nine most common guilds in the Atlantic forest leaf litter (Silva & Brandão, 2010). This has also been observed in the Amazon forest (Carvalho & Vasconcelos, 2002) and in different habitats within the Atlantic forest region (Souza-Campana et al., 2017). Predatory ants may feed on various arthropods that also colonize twigs, such as springtails (Castaño-Meneses et al., 2015), other ant species (Brandão et al., 2012), isopods, beetles (Baccaro et al., 2015) and larvae (Ogogol et al., 2017), which makes this an attractive resource due to the presence of potential prey (Lanan et al., 2014).

Our study presents biological information that contributes to the knowledge about ants that occupy the leaf litter and colonize twigs in the Brazilian Atlantic forest, since we show that most species are polydomous and monogynous. Species survival strategies in a competitive habitat may be linked to the type of nest and social structure of the colony. The monogynous status suggests that a new colony may be founded in a site that is more distant than the origin site, a strategy that was unknown for twig-colonizing species until now.

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Authors' Contributions

Tae Tanaami Fernandes: contribution to data collection, contribution to data analysis and interpretation, contribution to manuscript preparation.

Rogério Rosa Silva: Contribution to data analysis and interpretation; contribution to manuscript preparation; contribution to critical revision, adding intelectual content.

Débora Rodrigues de Sousa-Campana: Substantial contribution in the concept and design of the study, contribution to data analysis and interpretation; contribution to manuscript preparation.

Nathalia Sampaio da Silva: contribution to data collection, contribution to manuscript preparation, contribution to critical revision.

Otávio Guilherme Morais da Silva: contribution to data collection, contribution to data analysis and interpretation, contribution to manuscript preparation.

Maria Santina de Castro Morini: Substantial contribution in the concept and design of the study; contribution to manuscript preparation; contribution to critical revision, adding intelectual content.

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