Revisiting the ideas of trees as templates and the competition paradigm in pairwise analyses of ground-dwelling ant species occurrences in a tropical forest

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A B S T R A C T

A challenge for studies on the organization of ant assemblages in forest ecosystems is to disentangle the causal effects of species occurrences. The structural and functional attributes of trees can act as environmental filters for ground-dwelling ant species influencing resource availability and the microclimate. The biotic interactions, especially competition, can work together with plant characteristics influencing ant species occurrences. To test the importance of tree traits and species interactions on co-occurrence patterns of ants, we collected ground-dwelling ants, with pitfalls and litter sampling, beneath the canopies of four tree species during the rainy and dry seasons in a restored forest. We used five predictors (tree identity, crown size, trunk circumference, litter depth, and leaves density) to model the presence probabilities of ants. Hence, we applied habitat constrained null models in pairwise analyses to disentangle the causal effects of ants co-occurrences. The random pattern predominated in the assemblages, making up 96% of all possible species pairs combinations. Overall, 50% of the species pairs that showed nonrandomness in the ant occurrences were interpreted as resulting from environmental filters, 36% as negative associations and 14% as positive associations. Additionally, we found that the effects of season and the sampling technique on the ant assemblages were also important. We suggest that the ideas of the trees as templates and the paradigm of competition are both useful for understanding pairwise occurrence patterns in ant assemblages, and can be tested using tree traits as predictors in ant species distribution models for running constrained null models.

Introduction

The influence of vegetation characteristics and biotic interactions are usually considered two important factors behind the organization of local ant assemblages. In forest ecosystems, the trees can be used as templates due to the variations in their structural and functional attributes that affects the resource supplies and modify abiotic conditions for the ant species (Andersen, 1995; Ríos-Casanova et al., 2006; Lopes and Vasconcelos, 2008; Donoso et al., 2010, 2013). The litter is a resource for the ground-dwelling ant species, providing food and shelter (Blüthgen and Feldhaar, 2010), and its composition and quantity can vary depending on the tree species (Ehrenfeld, 2003; Donoso et al., 2010; Mejía-Domínguez et al., 2011; Donoso et al., 2013). The differences among tree species in the crown characteristics, such as size, leaves density, and leaf phenology can create microsite variations in solar radiation and soil humidity (Mejía-Domínguez et al., 2011), and is capable of influencing ant assemblages (Levings, 1983; Kaspari and Weiser, 2000). Therefore, the tree traits can be important for the environmental filtering of ground-dwelling ant species in local assemblages.

On the other hand, interspecific competition has been considered as the most important biotic interaction structuring ant assemblages (Parr and Gibb, 2010; Cerdá et al., 2013). Ants can compete for nesting space and food, with the species sometimes displaying a hierarchy of dominance (Pisarski and Vepsäläinen, 1989). Bait experiments have been used to measure the abundance and aggressiveness of ant species in order to assess the degree of species dominance (LeBrun, 2005; Baccaro et al., 2012). However, the presence of dominant species excluding other species from baits does not necessarily result in an assemblage structured by competition (Baccaro et al., 2012). Moreover, the competitive interactions between ant species can be affected by plants directly through differences in plant attractiveness for ant species
In general, biotic interactions would be expected to be more important to community assembly on a local scale, while environmental filters would operate on a regional scale. This is because environmental conditions tend to be spatially structured (Kristiansen et al., 2012). Here, we focus on ground-dwelling ant co-occurrence patterns in a reforested area. Ecological restoration projects are a great opportunity to investigate patterns and mechanisms in the process of assembling communities (Young et al., 2001). Reforestation areas represent environments with a known history, which can facilitate the design of field experiments. We hypothesized that even in a small spatial scale, ground-dwelling ant assemblage would be structured by both, biotic interactions and environmental filters. We worked with the premise that the species distribution on a small spatial scale would not be limited by dispersion, because most ground-dwelling species in tropical forests can frequently relocate their nests (McGlynn, 2006). We hypothesized that the differences in the attributes of the trees, and canopy openness, in a forest habitat, would act as environmental filters influencing ant species co-occurrence. We also hypothesized that competition between ant species would be detected through segregated species distribution patterns on a local scale, because competition tends to be an important factor structuring local ant assemblages (Cerdà et al., 2013). We adopted the Peres-Neto et al. (2001) approach to disentangle the biotic interactions and environmental filters, applying habitat constrained null models. Instead of analyzing the structure of the entire community, we adopted the pairwise analysis (Veech, 2014; Ellwood et al., 2016). This choice occurred because the analyses based on the entire data matrix patterns can hide important interactions between pairs of species (Camarota et al., 2016). We also checked if the results were dependent on the ant sampling techniques and seasons.

Material and methods

Study area

The study was carried out at the Reserva Ecologica de Guapiaçu (REGUA), located in the municipality of Cachoeiras de Macacu, State of Rio de Janeiro, southeastern Brazil (22° 27′3.41″ S, 42° 46′28.17″ W) (Fig. 1). The region has a rainy summer and a dry winter. Annual rainfall is 2,050 mm, ranging between 60 mm in July and 338 mm in February, with January being the hottest month (25.3 °C) and July the coldest (17.9 °C) (Azevedo et al., 2018). REGUA is in the Atlantic Forest biome, presenting phytophysionomies characteristic of Dense Ombrophilous forest, with altitudes varying from 20 to 2,000 m above sea level (Veloso et al., 1991). The forest cover of the low areas is quite fragmented, being interspersed with pastures, agricultural areas and areas under forest restoration (Rocha et al., 2007; Almeida-Gomes and Rocha, 2014; Azevedo et al., 2018).

Experimental design

Our study was conducted in a 12-years aged forest restoration area, 3.4 hectares in size (Azevedo et al., 2018). Herbicide pasture grass suppression was carried out before plowing the soil for planting forest seedlings. Pioneer, secondary and climax tree species were used in the forest restoration. Chemical control of leaf-cutting ants was carried out for two years since the tree planting (Azevedo, 2012). Three years after the planting the studied area had 73 tree species (Azevedo et al., 2018). We chose four tree species that are common in the Atlantic Forest of Rio de Janeiro state and are frequently used in forest restoration (Nóbrega et al., 2008; Sansevero et al., 2011; Azevedo et al., 2018). Our samples were distributed in 37 trees, with a minimum distance of 10 m
between individuals and with little or no crown overlap with surrounding trees. The tree individuals were distributed in the following species: *Guarea guidonia* (L.) Sleumer (GG) (n = 11); *Inga edulis* Mart (IE) (n = 9); *Nectandra membranacea* (Swartz) Giseb. (NM) (n = 8); and *Piptadenia gonoacantha* (Mart.) F. Marc. (PG) (n = 9) (Appendix 1, Supplementary material). We chose trees with a circumference at breast height greater than 30 cm to ensure that we measured the species-specific effects of trees on ant colonies, reducing the possibility of neighboring trees effects (Lameira et al., 2019). To ensure that most of the litter was composed of material from the focal tree, all ant samples were collected at a distance of 1 m from the tree trunk (Donoso et al., 2010). In the study area, the tree species had contrasting attributes (Table 1).

**The sampling of ants**

Ant collections were carried out in 2018, in periods of high and low rainfall (rainy and dry season, respectively). We used two techniques to sample ground-dwelling ants: pitfall traps and litter collection for mini-Winkler extraction. The pitfalls consisted of plastic cups with a capacity of 400 ml, 10 cm in height and 7.5 cm in diameter. The cups were buried with the upper part at ground level and half-filled with salt water (24 g/L) with a drop of detergent. Each sampling point received a pitfall for 48 hours. The litter samples were collected within a quadrat of 0.25 m² placed on the ground. The sifted litter samples were suspended in mini-Winkler sacks, during 48 hours, to extract the ants (following Bestelmeyer et al., 2000).

All the collected ants were taken to the laboratory for identification. The identification was carried out using the keys found in the literature (Kempf, 1951; Mayhè-Nunes and Meneguete, 2000; Longino, 2007; Sosa-Calvo and Schultz, 2010; Dash, 2011; Feitosa, 2011; Baccaro et al., 2015; Johnson, 2015; Ješovnik and Schultz, 2017).

**The environmental variables**

The circumference of the tree trunk and the diameters of the crown of each focal tree were measured with a tape; for the diameters, we took

![Figure 1](image-url) Location of REGUA in the State of Rio de Janeiro, Brazil.

| Tree identity          | Family    | Leaf-loss strategy | Crown size | Trunk circumference | Litter height |
|------------------------|-----------|--------------------|------------|--------------------|---------------|
| *Guarea guidonia*      | Meliaceae | Perenifolius       | Small      | Small              | Medium        |
| *Inga edulis*          | Fabaceae  | Perenifolius       | Large      | Large              | High          |
| *Nectandra membranacea*| Lauraceae | Perenifolius       | Small      | Large              | High          |
| *Piptadenia gonoacantha*| Fabaceae | Deciduous          | Small      | Large              | Low           |
two measurements for each crown. The size of the crown was estimated using the ellipse model, which consists of multiplying the minor axis by the major axis and then by the value of pi. The leaf area indexes (LAI) were calculated through hemispheric photography, which consisted in the photograph of the canopy at the height of one meter with the camera facing north (Denslow and Guzman, 2000). Subsequently, the photos were analyzed in Hemiview 2.1 software, to obtain the LAI values. At each sampling site, the litter height was measured at four points with the aid of a ruler. The litter depth values used in the subsequent analyzes was an average of the four values. The measuring of LAI and litter depth was carried out in the rainy and dry seasons.

Data preparation

Ant species presence/absence matrices were built to analyze the community's assembly pattern according to sampling technique and season; this means that we built four different matrices (2 techniques x 2 seasons). We analyze only the most frequent ground-dwelling ant species sampled in the area, i.e. those which were recorded in more than 10% of the samples for each technique and season. Fungus-growing ants were also removed because of their food diet specialization. The presence/absence matrices are generally used to avoid overestimating the abundance of certain species that may have a large representation of individuals in certain samples (Longino et al., 2002; Gotelli et al., 2011).

SDM analysis

We obtained probability values for each ant species in the samples for the four presence/absence matrices by fitting species distribution models (SDM). We used five environmental predictors (tree identity, crown size, trunk circumference, litter depth, and the leaf area index-LAI). We applied two modeling techniques indicated for presence/absence data (Qiao et al., 2015): Generalized Linear model and Random Forest, with 10 replications each. The resulting 20 projections were averaged based on AUC (area under the curve) statistics (values are provided in Appendix 2, supplementary material) to implement a single ensemble estimate of the probability of presence for each ant species in each sample. The analyses were performed using the SDM package for R (Naimi and Araújo, 2016). We used the probability values of ant presence in the constrained null models described below.

Null model analysis

The matrices containing ant species presence/absence data were subjected to co-occurrence analysis using the pairwise C-score index. The pairwise C-score index quantifies the degree of co-occurrence of each pair of species for the locations in the matrix (Stone and Roberts, 1990); it is appropriate for detecting non-randomness in the community, in addition to being less susceptible to type I and II errors (Gotelli, 2000). The pairwise C-score index is calculated for each pair of species using the equation \( C_{ij} = (r_i - S_{ij})(r_j - S_{ij})/(r_i^* r_j^*) \), where \( r_i \) represents the total sites that species \( i \) occurs in the matrix, \( S_{ij} \) is the total sites for species \( j \), \( S_{ij}^* \) is equivalent to the total number of sites that both species occur simultaneously. One C-score value is calculated for each species pair (observed index). The observed pairwise C-score is compared to a mean of simulated indices. To calculate the mean and variance of simulated indices, each of the four presence/absence matrices was randomized 1000 times.

We followed the methodology proposed by D’Amen et al. (2018) running unconstrained and constrained null models. The unconstrained model uses only presence/absence matrix, whereas the constrained null model uses the presence/absence matrix with the probability values of ant presence calculated by the SDMs. Given that we worked in a small spatial scale, in an area relatively homogeneous, we considered that ant species wouldn’t be limited by dispersion. We adapted the approach of D’Amen et al. (2018) in the following way: if we find a result for the pairwise occurrence that is nonrandom for the unconstrained model and random for the constrained model, it is interpreted as caused by the environmental filter. If the result is segregation for both models, it is interpreted as a negative association; and if the result is aggregation for both models, it is interpreted as a positive association. We used the algorithm fixed-equiprobable (FE) for the randomizations because it is less prone to Type I and II errors (Gotelli, 2000). In the FE algorithm, the number of ant species remains (fixed lines), because co-occurrence tests are very sensitive to variation in species occurrence frequencies (Gotelli, 2000), but ant occurrence in each sampling point is equiprobable (equiprobable columns) (Gotelli and Ellison, 2002). This algorithm is indicated for samples collected in homogeneous habitats (Gotelli, 2000), and can be biased towards detecting positive associations (Azevão et al., 2012). The analyzes were performed using the Open Source R version 3.6.1 statistical software (R Core Team, 2019), following the scripts provided by D’Amen et al. (2018).

Results

In the study, 82 ant species/morphospecies were collected, corresponding to 22 genera. However, after the removal of rare (less than 10% of records), arboreal species, and fungus-growing ants, the co-occurrence analyzes, by null models, were restricted to 459 records of 27 species/morphospecies of ants, corresponding to 11 genera and two trophic guilds (predators and omnivores). The most frequent ant species included Pheidole subarmata, Hypoponera parva, Linepithema neotropicum, Rogeria scobinata, and several species of Solenopsis and Strumigenys. Pheidole subarmata was collected either with pitfalls and Winkler samples, in the rainy or dry seasons. Hypoponera parva and Rogeria scobinata were both more frequent in Winkler samples, with the former increasing their presence in the dry season. Linepithema neotropicum was predominantly collected by pitfalls in the dry season; and species of Solenopsis or Strumigenys showed varied patterns. Pitfalls in the rainy season had the lower proportion of species records and richness (15.7%, 8 species), followed by pitfalls in the dry season (24.8%, 13 species), Winkler samples in the rainy season (25.9%, 12 species), and Winkler samples in the dry season (33.6%, 17 species). The species records increased by 58% for pitfall samples and 29% for Winkler samples during the dry season. Five ant species were present only in the pitfall data matrices, whereas nine species were exclusive of Winkler data matrices. Four species were exclusive of rainy season data matrices, whereas 11 species were exclusive of dry season data matrices (Table 2).

The random pattern of distribution of species pairs predominated in the assemblages, making up 96% of all possible species pairs in the four data matrices (n = 351 pairs) for the unconstrained null model. Fourteen species (52%) were involved in at least one nonrandom pairwise species association (significant C-scores values are provided in Appendix 3, supplementary material). The presence probabilities for the 14 species involved in nonrandom associations varied within and among tree species (Fig. 2). There was a reduction of 50% in the number of nonrandom species pairs for the habitat constrained null model in relation to the unconstrained model. The proportions of nonrandom pairs varied between seasons and sampling techniques (Table 3).

The numbers of nonrandom pairs in the unconstrained model were seven aggregated and seven segregated. For the constrained model, we observed two aggregated and five segregated pairs. All the segregated pairs, under either the constrained or unconstrained models, involved...
Table 2
Species composition and records (>10% of the samples) of ant assemblages sampled at REGUA during the rainy and dry season, with two sampling techniques, and used in null model analyses.

| Species                     | Pitfall | Winkler | Total |
|-----------------------------|---------|---------|-------|
|                             | Rainy season | Dry season | Rainy season | Dry season |
| Brachymyrmex adimnotus Mayr, 1887 | 7       |         |         |         |
| Ectoponera permagnum For., 1908 | 4       |         |         |         |
| Hypoponera parva (For., 1909) |         |         |         |         |
| Hypoponera sp3               |         |         |         |         |
| Linepithema neotropicum Wild, 2007 | 5       | 14      |         |         |
| Nylanderia fulva Mayr, 1862  | 5       |         |         |         |
| Nylanderia steinheili For., 1893 | 8       |         |         |         |
| Pachycondyla harpax (Fabricius, 1804) |         |         |         |         |
| Pachycondyla striata (Smith, 1858) | 4       |         |         |         |
| Pheidole sp1                 |         |         |         |         |
| Pheidole sp2                 |         |         |         |         |
| Pheidole sp5                 |         |         |         |         |
| Pheidole subarmata Mayr, 1884 | 24      | 26      |         |         |
| Rogeria germani Emery, 1894  |         |         |         |         |
| Rogeria scobinata Kluger, 1994 |         |         |         |         |
| Solenopsis invicta Buren, 1972 | 5       | 9       |         |         |
| Solenopsis sp1               |         |         |         |         |
| Solenopsis sp2               |         |         |         |         |
| Solenopsis sp3               |         |         |         |         |
| Solenopsis sp4               | 11      | 16      |         |         |
| Solenopsis sp5               | 14      | 6       |         |         |
| Solenopsis sp7               | 14      | 7       |         |         |
| Strumigenys denticulata Mayr, 1887 | 4       | 4       |         |         |
| Strumigenys eggersi Emery, 1890 |         |         | 10      | 7       |
| Strumigenys louisianae Roger, 1863 |         |         |         | 5       |
| Strumigenys subdentata Mayr, 1887 |         |         |         | 9       |
| Wasmannia auropunctata Roger, 1863 |         |         |         | 7       |
| Total                        | 72      | 114     | 119    | 154     |

Table 3
Percentages of nonrandom species pairs in the unconstrained (unc) and constrained (cons) models.

| Sampling method | Season | Model  | % of nonrandom species pairs |
|-----------------|--------|--------|-----------------------------|
| Pitfall         | Rainy  | unc    | 10.7                        |
|                 |        | cons   | 3.6                         |
|                 | Dry    | unc    | 1.3                         |
|                 |        | cons   | 1.3                         |
| Winkler         | Rainy  | unc    | 1.5                         |
|                 |        | cons   | 0.0                         |
|                 | Dry    | unc    | 5.9                         |
|                 |        | cons   | 3.7                         |

Discussion

The ant assemblages we analyzed were composed by species belonging to the genera that are commonly reported for ground samples in neotropical forests (McGlynn and Kirksey, 2000; Ward, 2000; Baccaro et al., 2012). Given that our study area was in the process of recovery from disturbance by active restoration with native trees (Azevedo, 2012) and because we have restricted the analyzes to the most frequent ant species, we worked with habitat generalists which are very common in disturbed areas elsewhere. For example, Pheidole subarmata, the most frequent species in our studied area, can be found in areas of pastures and crops (Perfecto and Vandermeer, 2011; Munhæ et al., 2014). Linepithema neotropicum, Solenopsis invicta and Wasmannia auropunctata are recorded in different types of agroecosystems or urban areas (Munhæ et al., 2014; Sinisterra et al. 2016; Santos et al., 2019). Hypoponera parva can be found in both mature and disturbed forests (California Academy of Sciences, 2020). The Strumigenys species are also found in disturbed ecosystems (Montone et al., 2011; Souza-Campana et al., 2016). Moreover, several species, although nesting and foraging on the ground, are also known to forage on trees, such as L. neotropicum, W. auropunctata, and species of Solenopsis (e.g. Schoereder et al., 2010; Sinisterra et al., 2016; Qin et al., 2019). Therefore, we believe that the results found here may apply to other generalist ant assemblages in forests with some degree of disturbance, such as naturally recovered secondary forests.

Our analyses showed that species pair co-occurrence patterns for ground-dwelling ants are influenced by environmental filter, even on a small spatial scale, although other studies have suggested that environmental filter operate more frequently at larger spatial scales or between different types of ecosystems (Gotelli and Ellison, 2002; King, 2007; Fichaux et al., 2019). When we ran the analyzes using the predictions of the ensemble models to create restricted null models (Peres-Neto et al., 2001), 50% of the pairs with nonrandom distribution
Figure 2 Presence probabilities of ant species in each tree species only for those one involved in nonrandom pairs for the two sampling techniques and seasons. PR: pitfall, rainy season; PD: pitfall, dry season; WR: Winkler, rainy season; WD: Winkler, dry season. GG = Guarea guidonia; IE = Inga edulis; NM = Nectandra membranacea; PG = Piptadenia gonoachanta.
became non-significant, being interpreted as environmental filter effects (D’Amen et al., 2018). Therefore, using the habitat restricted null models, we were able to confirm our hypothesis that the tree attributes act as environmental filters for ant species occurrences. We also demonstrated that the biotic interactions were as important as environmental filters in the observed nonrandom distribution of a small number of species pairs. However, despite the small spatial scale and the relatively homogeneous area where the work was done, our interpretation of the processes causing the co-occurrence pattern is dependent on our premise related to species dispersion. We have to consider that there is little information on the dispersion capacity of ant species (Hakala et al., 2019) and some of them may not fit the general pattern. Moreover, although model performances for most species were quite acceptable, there is room for substantial model improvement for a few species. We found that the effects of environmental filters generate more convergence than divergence on the occurrence of ant species. The results suggested that the selected tree species are able to cause patchiness in the distribution of a small number of generalist ants in the area, favoring the idea that trees can be used as templates for the study of ground-dwelling ants. For example, _L. neotropicum_, _Pachycondyla harpax_, and _S. invicta_ showed an aggregated distribution with higher presence probabilities under the canopies of _L. edulis_ and _P. gonoacantha_. Although the tree species have some differences in attributes (see Table 1), both have extrafloral nectaries (EFN) which can be tended by ants. Indeed, _L. neotropicum_ is known to visit EFN of _I. edulis_ and _P. gonoacantha_. The same can occur with _S. invicta_. Ant species that are frequent users of EFN are known to nest closer to EFN-producing plants (_Sinisterra et al., 2016_, _Silva et al., 2019_). However, _R. germaini_ and perhaps the _S. edulis_ and _I. invicta_), both have EFNs on trees needs to with higher presence probabilities under the canopies of _L. edulis_ and _P. gonoacantha_. Although the tree species have some differences in attributes (see Table 1), both have extrafloral nectaries (EFN) which can be tended by ants. Indeed, _L. neotropicum_ is known to visit EFN of _I. edulis_ and _P. gonoacantha_. The same can occur with _S. invicta_. Ant species that are frequent users of EFN are known to nest closer to EFN-producing plants (_Sinisterra et al., 2016_, _Silva et al., 2019_). However, _R. germaini_ and perhaps the _S. edulis_ and _I. invicta_), both have EFNs on _trees_ needs to

### Table 4

| Sp1 | Sp2 | Season | Model | P   | Pattern | Interpretation |
|-----|-----|--------|-------|-----|---------|----------------|
| _Pheidole subarmata_ (om) | _Linepithema neotropicum_ (om) | rainy | unc  | 0.04 | Segregated | Negative association |
| _Solenopsis sp3_ (om) | _Solenopsis sp5_ (om) | rainy | unc  | <0.01 | Segregated | Environmental filter |
| _Solenopsis sp5_ (om) | _Nylanderia fulva_ (om) | rainy | unc  | >0.05 | Random | Environmental filter |
| _Pheidole subarmata_ (om) | _Linepithema neotropicum_ (om) | dry   | unc  | 0.02 | Aggregated | Positive association |
| _Solenopsis invicta_ (om) | _Linepithema neotropicum_ (om) | dry   | unc  | 0.02 | Aggregated | Environmental filter |

### Table 5

| Sp1 | Sp2 | Season | Model | P   | Pattern | Interpretation |
|-----|-----|--------|-------|-----|---------|----------------|
| _Pheidole subarmata_ (om) | _Wasmannia auropunctata_ (om) | rainy | unc  | 0.04 | Segregated | Environmental filter |
| _Pachycondyla harpax_ (pr) | _Solenopsis invicta_ (om) | dry   | unc  | 0.04 | Aggregated | Environmental filter |
| _Pachycondyla harpax_ (pr) | _Linepithema neotropicum_ (om) | dry   | unc  | >0.05 | Random | Environmental filter |
| _Hypoponera sp3_ (pr) | _Hypoponera parva_ (pr) | dry   | unc  | >0.05 | Random | Segregated |
| _Hypoponera sp3_ (pr) | _Wasmannia auropunctata_ (om) | dry   | unc  | >0.05 | Random | Segregated |
| _Hypoponera parva_ (pr) | _Strumigenys eggersi_ (pr) | dry   | unc  | 0.01 | Segregated | Negative association |
| _Strumigenys denticulata_ (pr) | _Strumigenys eggersi_ (pr) | dry   | unc  | 0.03 | Segregated | Negative association |
| _Strumigenys eggersi_ (pr) | _Solenopsis sp2_ (om) | dry   | unc  | 0.03 | Segregated | Positive association |
| _Rogeria germaini_ (om) | _Solenopsis sp2_ (om) | dry   | unc  | 0.03 | Segregated | Negative association |
be further investigated. *Nylanderia fulva* and *Solenopsis* sp 5 is another case of aggregated distribution associated with *Inga edulis*, possibly involving the frequent visit to EFN (Wang et al., 2016). Among the few pairs that were segregated in distribution by environmental filters, the pair of *Solenopsis* species can also be explained by the divergence in the probability of occurrence under the canopies of the different trees. *Hypoponera* sp 3 and *W. auropunctata* had aggregated distribution because both had the occurrence more associated with trees where the litter was deeper, such as *Nectandra membranacea*. However, the segregation by environmental filters between *P. subarmata* and *W. auropunctata* cannot be linked to tree identity, because there was no clear trend on the probability of species presence among the tree species. Based on our results we can predict that other pairs of ant species occurring in the area, but not evaluated here, will also show nonrandom distributions caused by either aggregation or segregation in relation to tree species.

We found more negative than positive associations between species, thus differing from the pairwise analysis of Ellwood et al. (2016) with tropical ant assemblages. In relation to the species pairs negatively associated, but not by environmental filters, we had two pairs in the same genus and three pairs in the same guild (omnivores). Therefore, our results agree with Camarota et al. (2016), who also demonstrated that species pairs with segregated distribution had higher trait similarity. The first case of negative association was between *Strumigenys eggersi* and *S. denticulata*. *Strumigenys* species are very common in litter samples, and although, on some occasions, we have collected more than one *Strumigenys* species per sample, we never found *S. eggersi* and *S. denticulata* together. *Strumigenys denticulata* is the most frequent species in litter samples in the Atlantic Forest and has a morphology very similar to that of *S. eggersi* (Silva, 2014). We do not know of studies on interactions between species of this genus, but this may be because they are small in size and cryptic (Lattke et al., 2018). Species of *Strumigenys* nest in the litter and are recognized by their specialized habit of preying on Colembola (Silva, 2014; Lattke et al., 2018). The second case is between *Hypoponera parva* and *Hypoponera* sp 3; *Hypoponera parva* was one of the most frequent species in the studied site, whereas *Hypoponera* sp 3 was much less frequent. The case of *Hypoponera* is similar to *Strumigenys* in that the species are cryptic, nesting in the litter or soil, and although they are considered more generalist than *Strumigenys*, they can also be predators of collemboles (Baccaro et al., 2015). Although it is not uncommon to find *Hypoponera* species at the same spot (Soares and Schoereder, 2001; Brandão et al., 2012), we never found *H. parva* and *H. sp 3* together in our samples.

The segregation we observed between species from different genera, involved pairs in the same feeding guild. *Hypoponera parva* and *S. eggersi* were negatively associated and, because they both share feeding and nesting habits, it is possible to suggest competition as the cause of the segregated distribution. Our results suggested that *Rogeria germaini* could be displaced by *Solenopsis* sp 2, because the latter was much more frequent than the former. There is little information about *Rogeria* species besides they are cryptic omnivores, nesting in soil or litter (Baccaro et al., 2015; Koch et al., 2019). However, *Solenopsis* species are usually involved in competition with different ant groups (Hölldobler and Wilson, 1990; LeBrun et al., 2007; Perfecto and Vandermeer, 2011), since their colonies are bigger, being generalist in feeding and nesting habits, and dominant over resources (Baccaro et al., 2012, 2015).

The last case of segregation is somewhat dubious, and perhaps more interesting. *Pheidole subarmata* and *L. neotropicum* showed segregation in the rainy season and aggregation in the dry season for the pitfall sampling. *Linepithema neotropicum* was much less frequent in the rainy season, agreeing with the results of Munhae et al. (2014), whereas *P. subarmata* was highly frequent in both seasons. It is possible to assume that the rainy season negatively affects the foraging of *L. neotropicum* but not *P. subarmata*, perhaps because the latter forages predominantly on the ground. The negative effect of rainfall should be greater on vegetation than on the ground, since vegetation intercepts raindrops in the forest (Park and Cameron, 2008). Indeed, Hahn and Wheeler (2002) found that the effect of the rainy season on ant activity was higher for ants on plants than on the ground. If the foraging of *L. neotropicum* became more restricted to the ground during the rainy season, it is possible that it suffered more from competition with *P. subarmata*, thus explaining the segregated distribution during this season. Conceição et al. (2014) observed that *L. neotropicum* is behaviourally dominant at baits. On the other side, Perfecto and Vandermeer (2011) observed that *P. subarmata* discover fastly food resources on the ground, when nest density is high, but it is not dominant in interactions with *S. geminata*. Therefore, the rainy season may favor *P. subarmata* in the dispute with *L. neotropicum* for resources on the ground. During the dry season, the foraging of *L. neotropicum* workers is increased, and without the negative effects of raindrops on vegetation, the foraging on trees might be higher. Hence, in the dry season, the competitive interactions between *P. subarmata* and *L. neotropicum* on the ground would be reduced. We found only one other species pair with positive association between *Strumigenys eggersi* and *Solenopsis* Sp 2. Positive associations between species can be generated by consumer-resource and mutualistic interactions, but Ellwood et al. (2016) suggested that even competition between ant species may result in positive associations between species. Therefore, we need more information on species biology to uncover the mechanisms behind these positive associations.

Similar to our results, other studies, done in ecosystems with different levels of precipitation, have observed a negative effect of the rainy season on the abundance and richness of ants (e.g. Basu, 1997; Anu et al., 2009; Neves et al., 2010; Jacquemin et al., 2016). Different reasons were suggested to explain the seasonal pattern in ant assemblages, including the direct effect of rain (Anu et al., 2009) and the change in food supply (Neves et al., 2010; Jacquemin et al., 2016). Our results suggest that the direct effects of rainfall can be more important for the species that forage on the surface, e.g. *L. neotropicum*, and that are most captured in pitfall traps (Bestelmeyer et al., 2000). The drop in the number of records for pitfall traps was much greater than that observed in Winkler samples during the rainy season. Perhaps the rainy season affects less those species that forage in the interstices of the litter, and are sampled with the Winkler method, e.g. *Strumigenys* species (Parr and Chown, 2001; Farji-Brener et al., 2004). Seventy-one and sixty-four percent of the pairs with nonrandom distribution was observed, respectively, in the dry season and in the Winkler samples. The effects of both the season and the sampling technique on the co-occurrence patterns of ground-dwelling ants suggest that they should not be ignored in this kind of study.

Our work showed that most pairs of ant species were randomly distributed. The random distribution of ground-dwelling ant species also prevailed in studies done in the Amazon rainforest (Baccaro et al., 2012), the Atlantic forest (Hanisch et al., 2018), and Asian tropical forests (Fayle et al., 2013). Even for canopy ants the random pattern can prevail (e.g. Camarota et al., 2016). The predominance of random distribution of species pairs in ant assemblages may suggest that stochastic processes would be more important than deterministic processes (Ribas and Schoereder, 2002) or that we do not know the nonrandom causes behind the observed patterns (Vellend, 2017). For the species pairs showing nonrandom distribution, we suggest that the ideas of the trees as templates (Donoso et al., 2010, 2013) and the paradigm of competition (Cerdá et al., 2013) are both useful for understanding pairwise occurrence
patterns in ant assemblages. Advances in myrmecology, especially in Brazil, are providing increasingly taxonomic and ecological knowledge of neotropical ant species (e.g. Baccaro et al., 2015). This will allow a substantial improvement in species distribution models that can be used in the approach reported here to uncover the deterministic causes of species’ co-occurrence patterns.

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Conflicts of interest

The authors declare no conflicts of interest.

Author contribution statement

Conceived and designed experiments: JMQ; data sampling: RCN, ECFB, JMQ; organism identifications: ECFB, RMF; data analysis: RCN, JMQ; manuscript writing: RCN, JMQ; manuscript review: ECFB, RMF.

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Supplementary material

The following online material is available for this article:
Appendix 1 - Map of georeferenced distribution of ant sampling points in the studied area at REGUA, Cachoeiras de Macacu-RJ, Brazil. GG= Guarea guidonia; IE= Inga edulis; NM= Nectandra membranacea; PG= Piptadenia gonoachanta
Appendix 2 - AUC statistics for the SDMs of ant species used in the constrained null models.
Appendix 3 - SES_Cscore and p values for each nonrandom species pair