



RESEARCH ARTICLE - ANTS

Effects of Vegetation Structure on Ant Diversity in Different Seasonal Periods in Impacted Fragments of Atlantic Forest

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Abstract

The destruction of forest habitats generates extremely fragmented areas and changes in vegetation structure. That changes the characteristics of microhabitats and the availability of resources and affects the diversity of animal species such as ants, which are a large group with an important ecological role. As ants forage on trees and shrubs, the vegetation structure can affect the presence of these organisms. Abiotic factors such as seasonality can also influence the diversity of the ant community. Based on that, this study aimed to investigate the distribution of the diversity of ant species that forage on plants in different seasonal periods. The study was carried out in eight secondary forest fragments of the Atlantic Forest. We used additive partitioning of diversity, partitioning of β diversity and canonical correspondence analysis to measure the effect of seasonality and vegetation structure on the distribution of ant species diversity. The rainy season positively influences the diversity of ants that forage on plants. Composition was affected by shrub leaf density in the rainy season and by tree circumference in the dry. Each fragment preserved a different pool of ant species, and the vegetation structure positively influenced ant diversity. These results highlight the importance of conserving the majority of forest fragments to better preserve the pool of ant species regionally.

Introduction

Anthropic action on land use is one of the most important drivers of change in natural environments. Habitat destruction for conversion of land use to intensive agriculture and for urban expansion generates fragmented areas and drastically reduces the population of thousands of species, representing a serious threat to biological diversity (Wilson, 1989; IPBES, 2019). Fragmented areas present different shapes, sizes, and distances between them vary greatly. As the availability of habitats and the adaptive capacity of species physiology influence the species distribution in geographic space, fragmented areas can undergo biogeographic changes (Saunders et al., 1991; Ribas et al., 2005; Zhao et al., 2021).

Since forest degradation changes the microclimate, destabilizes supporting ecosystems, and affects the trophic web, some species, especially specialists, can be vulnerable to extinction (Myers, 1988). This is the case of the Atlantic Forest biome in Brazil, which is considered a biodiversity hotspot, that is, it presents a high degree of species richness and endemism of plants and animals but has suffered an exceptional loss of habitat (Myers et al., 2000). Only about 12% of the original Atlantic Forest vegetation remained, with a prevalence of small forest fragments (< 50 ha) (Ribeiro et al., 2009).

Diversity partitioning has been used effectively to assess changes in species distribution in response to habitat changes (Crist et al., 2003; Ribeiro et al., 2008; Costa & Schmidt, 2022). When multiple spatial scales are studied,



patterns of species diversity distribution can change. The additive partitioning of diversity is an approach that allows analyzing the patterns of species diversity distribution at different hierarchical scales. This approach allows the use of species richness as a metric to measure diversity and also decomposes the total species diversity (γ) into additive components representing the average number of species within the samples (α) and the average number of species that vary between samples (β). As additive diversity partitioning expresses the α and β components in the same units of species richness, it allows the contributions of α and β to γ to be compared at different spatial scales (Crist et al., 2003; Ribeiro et al., 2008). In a hierarchy of different scales, total diversity can be expressed as $\gamma = \alpha + \beta_1 + \beta_2 + \beta_3 + \dots + \beta_n$, where n is the number of scales (Veech et al. 2002; Ribeiro et al., 2008). Another analysis of species diversity is the partitioning of β diversity, which differs from the previous approach, uses metrics based on species dissimilarity and reflects turnover phenomena, the substitution of species that occur in one area with different species in another area, as well as nestedness phenomena, where one area has a subset of the species present in a richer area (Baselga, 2010; Baselga & Orme, 2012).

Among insects, ants (Hymenoptera: Formicidae) are an important group and perform several ecological functions, such as seed dispersal and predation of herbivorous insects (Elizalde et al., 2020). Present in most terrestrial habitats, ants are easy to observe and have the study of their biology well developed. They are accessible study models and stand out for their high diversity, richness, and abundance of species (Hölldobler & Wilson, 1990).

Ant species can be found nesting and foraging from the underground to the top of the trees (Lucky et al., 2013). The vegetation is important for ants because it can affect environmental conditions, such as temperature and humidity, and resources for different species. Many ant species nest and forage on plants searching for food resources such as extrafloral nectar, secretions of Hemiptera, and prey (Yanoviak & Kaspari, 2000; Ribas et al., 2003; Blüthgen et al., 2003; Blüthgen & Feldhaar 2010). Some ant species that nest in the ground also foraging on plants in search of food sources (Martinez., 2015; Lange et al., 2019).

Ant species richness can be positively associated with vegetation structure (Oliveira et al., 2014), that is, more heterogeneous vegetation can have a higher variety of food resources and nesting sites for ant species (Ribas et al., 2003; Rico-Gray et al., 2012). On a regional scale, habitat fragments can be in different successional stages and have a different history of impacts, which influences the richness and composition of ant species (Leal et al., 2012). The dispersal limitation of ants can also influence the distributional pattern of species in fragmented landscapes (e.g. Zhao et al., 2021). Many studies have shown that forest cover alters the microclimate and influences ant diversity (Perfecto & Vandermeer, 1996; Ahuatzin et al., 2019; Ahuatzin et al., 2022; Costa & Schmidt, 2022). Abiotic factors such as

seasonality can also influence ant community diversity (Rico-Gray et al., 2012; Marques et al., 2017; Calixto et al., 2021).

Within the Atlantic Forest biome, the Vassouras region is one of the areas that has suffered great alterations over time due to land use changes. Habitat destruction has generated extremely fragmented areas and altered the structure of the vegetation (Stein, 1990; Drummond, 1997; Pereira et al., 2017). The change in vegetation structure can alter the microclimate and affect habitat quality which can affect the species in the community (Myers, 1988). However, the effect of the influence of these changes can vary according to particular characteristics of each fragment (Saunders et al., 1991).

In this study, we investigated the distribution of the diversity of ant species that forage on plants in different seasonal periods in impacted fragments of the Atlantic Forest. We test the following hypotheses: H1) Seasonality modulates the distribution of the diversity of ant species that forage on plants. H2) The distance between fragments influences the species composition of ants that forage on plants. H3) Vegetation structure modulates ant species composition in forest fragments. We expect that the diversity of ants that forage on plants will be positively correlated to the rainy season, and the similarity of ant species composition will be greater between closer fragments. We also expect that ant species diversity will be positively correlated with the environmental variables used to characterize the vegetation structure: Tree richness, tree density, shrub leaf density, and average circumference at breast height (CBH) of trees.

Material and methods

Study area

The fieldwork was conducted in eight forest fragments in the municipality of Vassouras, Rio de Janeiro state, southeastern Brazil (22°24'14"S; 43°39'45"W). Vassouras is located between the Serra do Mar and Mantiqueira mountain ranges and is at an altitude of 418 m above sea level (AGEVAP, 2018). Based on Köppen's climate classification, the climate is CWA - humid subtropical, dry winter with dominant summer rainfall (Köppen, 1948; Peel et al., 2007). In the coldest month, the average temperature is 18 °C; and 23 °C in the warmest month. Annual rainfall is 1280 mm (Francelino et al., 2012). The region is an area of ecological interest as it belongs to the Atlantic Forest biome. This region has suffered continuous environmental degradation since the 19th century, mainly due to the removal of forest cover for coffee plantation (Stein, 1990; Drummond, 1997). A recent study of the Vassouras region reveals a landscape with a predominance of pastures, very fragmented forest cover and the absence of large forest remnants (Pereira et al., 2017).

Selection of sampling sites

We selected eight fragments belonging to the secondary forest of the Atlantic Forest, which had undergone alterations

over time by land use change. The fragments were at different distances among themselves. We used the geographic coordinates to obtain the geographic proximity of the fragments. The mean distance was 1365.53 ± 331.82 m (SD). The largest distance between the fragments was 1854.46 m and the smallest distance was 908.83 m. The largest chosen fragment was 780 ha and the smallest was 3.55 ha.

Sampling methods

A 30 m x 40 m plot was demarcated in each fragment, 50 m from the edge. In each plot, 20 trees were marked with at least 10 m distance between them to avoid bait domination by workers from the same colony (Baccaro et al., 2010; Baccaro et al., 2011). The trees had circumference at breast height (CBH) between 15 and 40 cm. In addition, we also selected a shrub at 1-2 m from each marked tree, totaling 40 sampling points (20 trees and 20 shrubs) per fragment. Ant sampling was performed at each sampling point during the winter (dry season) of 2009 and during the summer (rainy season) of 2010 (Coelho, 2011).

The ant sampling method followed Freitas et al. (2003), in which the same number of baits (sardines) was placed at each sampling point for one hour. The bait was placed directly into the trunk of the trees at a height of 1.30 m above the ground. In the shrubs, the bait was placed on white paper (measuring 10 cm x 12 cm) at a height of approximately one meter. The baits were placed between 10:30 and 11:00 am. After one hour, the visiting ants on the baits were collected for one minute. In total, each fragment received 20 baits on shrubs (1 per shrub) and 20 baits on trees (1 per tree) per season, totaling 40 baits in the rainy season and 40 baits in the dry season per fragment.

The collected ant specimens were preserved in 70% alcohol. Taxonomic keys were used to identify ants at the level of subfamilies and genus in the laboratory (Bolton, 1994; Palacio & Fernández, 2003). The morphospecies were identified by comparison with the Coleção Entomológica Costa Lima, from the Instituto de Ciências Biológicas e da Saúde of the Universidade Federal Rural do Rio de Janeiro, where the specimens were deposited (Coelho, 2011).

Vegetation structure

To characterize the vegetation structure, we assessed different measures. The shrub leaves density was estimated using a vertical one-meter graduated stick and counting the number of times the leaves of a marked shrub touched the stick (Mantovani & Martins, 1990). We repeated the procedure on all 20 shrubs in each forest fragment. All trees with CBH above 15 cm in a plot were counted and separated in morpho species to obtain their density of individuals and species (Moro & Martins, 2011). The density of trees and shrub leaves represented the quantity of available resources.

Tree richness represented an indicator of environmental heterogeneity because each tree species may represent a different set of food and shelter (Ribas et al., 2003; Campos et al., 2006).

Data analyses

To test if seasonality modulates the distribution of the diversity of ant species that forage on plants (*Hypotheses 1*), we compared ant diversity at different spatial scales and seasons. We used additive partitioning of diversity to evaluate the proportion of the total diversity (γ) found in different samples, strata (trees or shrubs), and fragments separately for the rainy and dry seasons. We used species occurrence data per bait. In a hierarchy of different scales, total diversity was expressed as $\gamma = \alpha_1 + \beta_1 + \beta_2 + \beta_3$, where the additive components are in the same units of species richness, representing the average number of species within the samples (α_1), the average number of species that vary among samples (β_1), the average number of species that vary among strata (β_2), and the average number of species that vary among fragments (β_3). The average values obtained by observation at each hierarchical scale were compared with the expected average values obtained by randomization, and the null hypothesis that the observed values could have been obtained by the random distribution of individuals was tested at all hierarchical scales (Crist et al., 2003; Ribeiro et al., 2008). We used partitioning of β diversity to assess the dissimilarity of species composition of ants that forage on plants among different samples, strata, and fragments. In this approach, β diversity was partitioned into the turnover and nestedness components. The Sørensen index was used as a measure of dissimilarity. The analysis returns three values, which are the total dissimilarity (β_{SOR}) and the turnover (β_{SIM}) and nestedness (β_{SNE}) components. β_{SOR} reflects the total difference in species composition between the evaluated communities and can be expressed as $\beta_{\text{SOR}} = \beta_{\text{SIM}} + \beta_{\text{SNE}}$ (Baselga, 2010; Baselga & Orme, 2012). The values of β_{SIM} and β_{SNE} range from 0 to β_{SOR} , with values closer to β_{SOR} indicating a greater contribution of the component to dissimilarity.

To test whether the distance between fragments affects the species composition of ants that forage on plants (*Hypotheses 2*), a Mantel test was conducted using Euclidean distance. The geographic coordinates of the fragments were used to examine the relationship between geographic proximity and species composition.

To investigate whether vegetation structure modulates ant species composition in forest fragments (*Hypotheses 3*), we investigated the relationships among environmental variables (tree richness, tree density, shrub leaf density, and average CBH of trees) and ant species composition, canonical correspondence analysis (CCA) was used. Analyses were performed separately for the rainy and dry seasons. The species matrix consisted of species presence data per fragment, which

was transformed to logarithmic base 10 and analyzed with Bray-Curtis distance. Tree richness, tree density, shrub leaf density, and average CBH of trees in the fragment were used as environmental variables. A CCA was carried out for each rainy and dry season.

All analyses were performed in R Language 4.1.0 (R Development Core Team, 2021), using the packages *vegan* (Oksanen et al., 2018) and *betapart* (Baselga & Orme, 2012).

Results

A total of 68 ant species were collected, distributed in 19 genera and 7 subfamilies: Myrmicinae (30), Dolichoderinae (15), Formicinae (10), Pseudomyrmecinae (7), Ponerinae (3), Ectatomminae (2) and Dorylinae (1) (Table 1; Table 3). The subfamily Myrmicinae showed the highest species richness (30). *Pheidole* was the genus with the highest species

Table 1. Size of the eight forest fragments and number of records of ant species sampled on baits in fragments in the rainy (R) and dry (D) seasons in the Atlantic Forest study area.

	Fragment (size in ha)								Total (ha)	Season
	1 (780)	2 (53.4)	3 (35.5)	4 (31.2)	5 (27.9)	6 (6)	7 (5.9)	8 (3.5)		
									943.4	
Dolichoderinae										
<i>Azteca</i> sp1	1	1	0	1	0	0	1	1	5	D R
<i>Azteca</i> sp2	0	0	0	1	0	0	0	0	1	D
<i>Azteca</i> sp3	0	0	0	0	0	0	0	1	1	R
<i>Dolichoderus attelaboides</i> (Fabricius, 1775)	0	0	0	0	1	0	0	0	1	R
<i>Linepithema iniquum</i> (Mayr, 1870)	1	1	1	0	1	0	0	1	5	D R
<i>Linepithema</i> sp1	1	0	0	0	0	1	0	0	2	R
<i>Linepithema</i> sp2	1	0	0	0	1	1	0	0	3	D R
<i>Linepithema</i> sp3	0	0	1	0	1	0	1	0	3	D R
<i>Linepithema</i> sp4	0	0	1	0	0	0	0	0	1	D
<i>Linepithema</i> sp5	0	0	0	0	1	1	0	0	2	D R
<i>Linepithema</i> sp6	0	0	0	0	1	0	0	0	1	D
<i>Linepithema</i> sp7	0	0	0	0	0	0	1	0	1	D
<i>Linepithema</i> sp8	0	0	0	0	0	0	1	0	1	R
<i>Tapinoma atriceps</i> Emery, 1888	0	0	0	0	1	0	0	1	2	D
<i>Tapinoma melanocephalum</i> (Fabricius, 1793)	0	0	0	0	0	1	0	0	1	D
Dorylinae										
<i>Labidus</i> sp	1	0	0	0	0	0	0	0	1	D
Ectatomminae										
<i>Ectatomma edentatum</i> Roger, 1863	0	0	0	0	0	1	1	0	2	R
<i>Gnamptogenys</i> sp	1	0	0	0	0	0	0	0	1	R
Formicinae										
<i>Brachymyrmex</i> sp1	1	0	0	0	0	1	1	1	4	D R
<i>Brachymyrmex</i> sp4	0	0	1	0	0	0	0	0	1	R
<i>Brachymyrmex</i> sp5	0	0	1	0	0	0	0	0	1	D R
<i>Brachymyrmex</i> sp6	0	0	0	0	0	1	0	0	1	D
<i>Camponotus crassus</i> Mayr, 1862	1	1	0	1	1	0	1	1	6	D R
<i>Camponotus fastigatus</i> Roger, 1863	1	1	1	1	1	1	0	1	7	D R
<i>Camponotus sericeiventris</i> (Guérin-Méneville, 1838)	1	1	1	1	1	0	0	0	5	D R
<i>Camponotus striatus</i> (Smith, 1862)	0	1	0	0	0	0	0	0	1	R
<i>Camponotus</i> sp3	1	1	0	1	1	0	1	1	6	D R
<i>Myrmelachysta catharinae</i> Mayr, 1887	1	1	0	1	0	1	1	1	6	D R
Myrmicinae										
<i>Cephalotes atratus</i> (Linnaeus, 1758)	0	1	0	1	1	0	1	0	4	D R
<i>Cephalotes notatus</i> (Mayr, 1866)	0	0	0	0	0	0	0	1	1	D
<i>Cephalotes pusillus</i> (Klug, 1824)	0	0	0	1	1	0	0	0	2	D R

Table 1. Size of the eight forest fragments and number of records of ant species sampled on baits in fragments in the rainy (R) and dry (D) seasons in the Atlantic Forest study area. (Continuation)

	Fragment (size in ha)								Total (ha)	Season
	1 (780)	2 (53.4)	3 (35.5)	4 (31.2)	5 (27.9)	6 (6)	7 (5.9)	8 (3.5)		
									943.4	
Myrmicinae										
<i>Crematogaster evallans</i> Forel, 1907	0	0	0	1	1	0	1	1	4	D R
<i>Crematogaster</i> sp2	1	0	0	0	0	0	0	0	1	R
<i>Crematogaster</i> sp4	0	0	0	1	0	0	0	0	1	R
<i>Crematogaster</i> sp5	0	0	0	0	0	0	0	1	1	R
<i>Pheidole gertrudae</i> Forel, 1886	0	0	1	0	1	0	0	0	2	D R
<i>Pheidole</i> sp1	0	0	0	1	0	0	1	0	2	D R
<i>Pheidole</i> sp3	1	0	0	0	0	0	0	0	1	D
<i>Pheidole</i> sp4	1	0	0	0	0	1	0	0	2	D R
<i>Pheidole</i> sp5	1	1	0	0	1	1	1	0	5	D R
<i>Pheidole</i> sp6	0	1	0	0	0	0	0	0	1	R
<i>Pheidole</i> sp8	0	0	1	0	0	0	0	0	1	R
<i>Pheidole</i> sp9	0	0	0	1	0	1	0	0	2	R
<i>Pheidole</i> sp10	0	0	0	0	1	1	0	0	2	D
<i>Pheidole</i> sp11	0	0	0	0	0	1	0	0	1	R
<i>Pheidole</i> sp12	0	0	0	0	1	0	0	0	1	R
<i>Pheidole</i> sp13	0	0	0	0	0	1	0	0	1	R
<i>Procryptocerus montanus</i> Kempf, 1957	1	0	0	0	0	0	0	0	1	D
<i>Procryptocerus</i> sp1	0	0	0	1	0	0	0	0	1	D R
<i>Solenopsis</i> sp1	0	0	0	0	0	1	0	0	1	D
<i>Solenopsis</i> sp2	1	1	1	0	0	1	1	0	5	D R
<i>Solenopsis</i> sp3	0	1	0	1	1	1	1	0	5	D R
<i>Solenopsis</i> sp4	0	0	0	0	0	0	1	1	2	R
<i>Solenopsis</i> sp5	0	0	0	0	0	1	0	0	1	R
<i>Solenopsis</i> sp6	0	1	0	0	0	0	0	0	1	R
<i>Solenopsis</i> sp7	0	0	0	0	0	1	0	0	1	R
<i>Solenopsis</i> sp8	0	0	0	0	0	0	1	0	1	R
<i>Wasmannia auropunctata</i> (Roger, 1863)	1	0	0	0	1	1	0	0	3	R
Ponerinae										
<i>Neoponera venusta</i> Forel, 1912	0	0	0	1	0	0	0	0	1	R
<i>Neoponera villosa</i> (Fabricius, 1804)	0	0	0	1	0	0	0	0	1	R
<i>Odontomachus chelifer</i> (Latreille, 1802)	0	0	0	0	0	1	0	0	1	R
Pseudomyrmecinae										
<i>Pseudomyrmex schuppi</i> (Forel, 1901)	0	1	1	1	0	0	0	1	4	D R
<i>Pseudomyrmex tenuis</i> (Fabricius, 1804)	0	0	0	0	0	0	0	1	1	R
<i>Pseudomyrmex</i> sp1	1	0	0	1	0	0	0	0	2	D R
<i>Pseudomyrmex</i> sp2	1	0	1	0	0	0	0	0	2	R
<i>Pseudomyrmex</i> sp3	0	1	0	0	0	0	0	0	1	R
<i>Pseudomyrmex</i> sp5	0	1	0	0	0	0	0	0	1	D
<i>Pseudomyrmex</i> sp6	0	0	0	1	1	0	0	1	3	D R

richness (12), followed by *Linepithema* (9), *Solenopsis* (8), *Pseudomyrmex* (7) and *Crematogaster* (4). Among the most frequent identified species, *Camponotus sericeiventris*, *C. fastigatus*, and *Myrmelachista catharinae* (Table 1).

During the rainy season, the total diversity (γ) was 55 species, with the respective observed and expected values for the additive components (Fig 1, Table 2): within samples (α_1): 1.38 and 1.36 ($p = 0.05$); among samples (β_1): 8.31 and

11.88 ($p = 0.01$); among strata (β_2): 4.56 and 7.96 ($p = 0.01$); and among fragments (β_3): 40.75 and 33.80 ($p = 0.01$). During the dry season, the total diversity (γ) was 38 species, with the respective observed and expected values for the additive components: within samples (α_1): 1.21 and 1.20 ($p = 0.67$); among samples (β_1): 3.85 and 4.93 ($p = 0.01$); among strata

(β_2): 3.44 and 4.75 ($p = 0.01$); and among fragments (β_3): 29.50 and 27.11 ($p = 0.01$).

In the rainy season, the analysis resulted in the following values: among samples ($\beta_{SIM} = 0.989$; $\beta_{SNE} = 0.005$; $\beta_{SOR} = 0.994$), among strata ($\beta_{SIM} = 0.236$; $\beta_{SNE} = 0.072$; $\beta_{SOR} = 0.309$), and among fragments ($\beta_{SIM} = 0.800$; $\beta_{SNE} = 0.026$; $\beta_{SOR} = 0.827$).

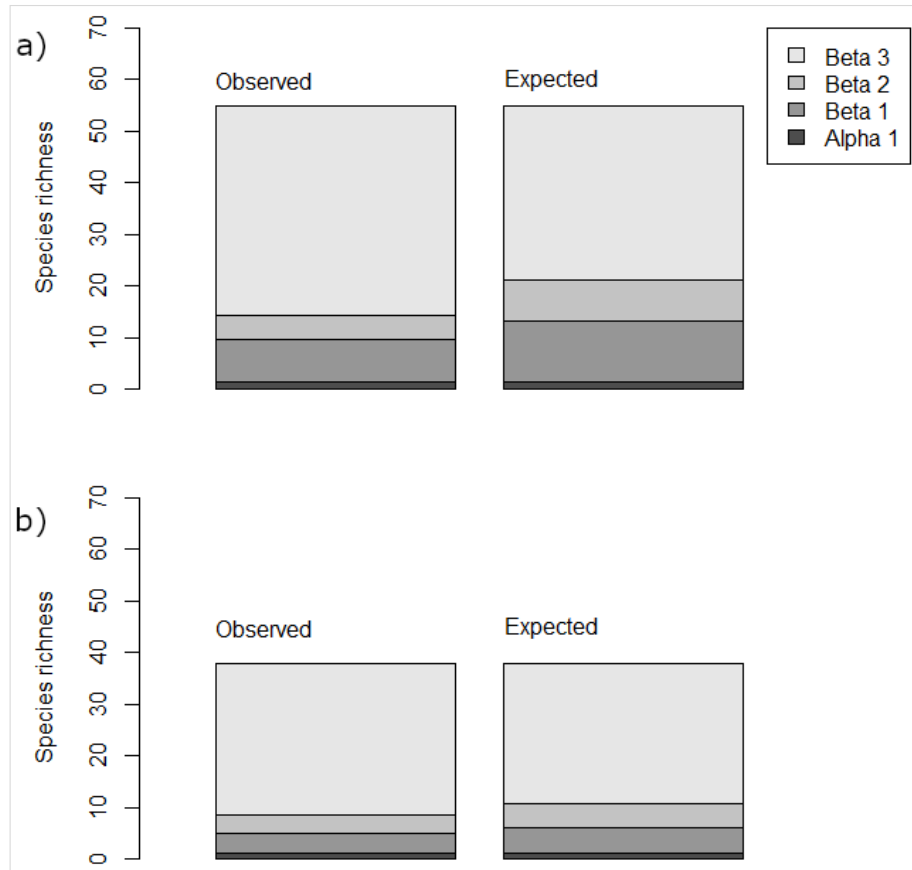


Fig 1. Total of ant species explained by alpha diversity and beta diversity on four spatial scales in the rainy (a) and dry (b) season. β_3 - average number of species that vary among fragments; β_2 - average number of species that vary among strata; β_1 - average number of species that vary among samples; α_1 - average number of species within the samples. The contributions to the total diversity of ant species for each scale were determined by the additive partitioning of diversity and expressed as proportions of the total diversity. The observed partition is compared to the expected value from random distribution.

Table 2. Statistical significance of the spatial partitioning of ant species diversity for rainy and dry seasons at different scales in fragments of Atlantic Forest, Vassouras-RJ, Brazil. Comparison of observed and expected values at different hierarchical scales. A p-value less than or equal to 0.05, indicate that the observed diversity significantly differed from the expected values in a random distribution.

Diversity	Scale	Observed	(%)	Expected	P
Rainy season					
α_1	Sample	1.38	2.5	1.36	0.05
β_1	Among samples	8.31	15.1	11.88	0.01
β_2	Among strata	4.56	8.3	7.96	0.01
β_3	Among fragments	40.75	74.1	33.80	0.01
γ		55	100	55	
Dry season					
α_1	Sample	1.21	3.2	1.20	0.67
β_1	Among samples	3.85	10.1	4.93	0.01
β_2	Among strata	3.44	9.1	4.75	0.01
β_3	Among fragments	29.50	77.6	27.11	0.01
γ		38	100	38	

In the dry season, the analysis resulted in the following values: among samples ($\beta_{SIM} = 0.982$; $\beta_{SNE} = 0.013$; $\beta_{SOR} = 0.995$), among strata ($\beta_{SIM} = 0.300$; $\beta_{SNE} = 0.161$; $\beta_{SOR} = 0.461$), and among fragments ($\beta_{SIM} = 0.833$; $\beta_{SNE} = 0.027$; $\beta_{SOR} = 0.861$).

Mantel tests showed that there was no relationship in the distance among the fragments and species composition of

the ant community in the fragments (rainy season - $r = 0.14$, $p = 0.253$; dry season - $r = 0.24$, $p = 0.109$).

In the rainy season, CCA showed that shrub leaves density affects ant species composition ($F = 1.41$, $df = 1$, $p = 0.04$, Fig 2a), with axis 1 explaining 19.08% of the variance. In the dry season, CCA showed that average tree CBH affects

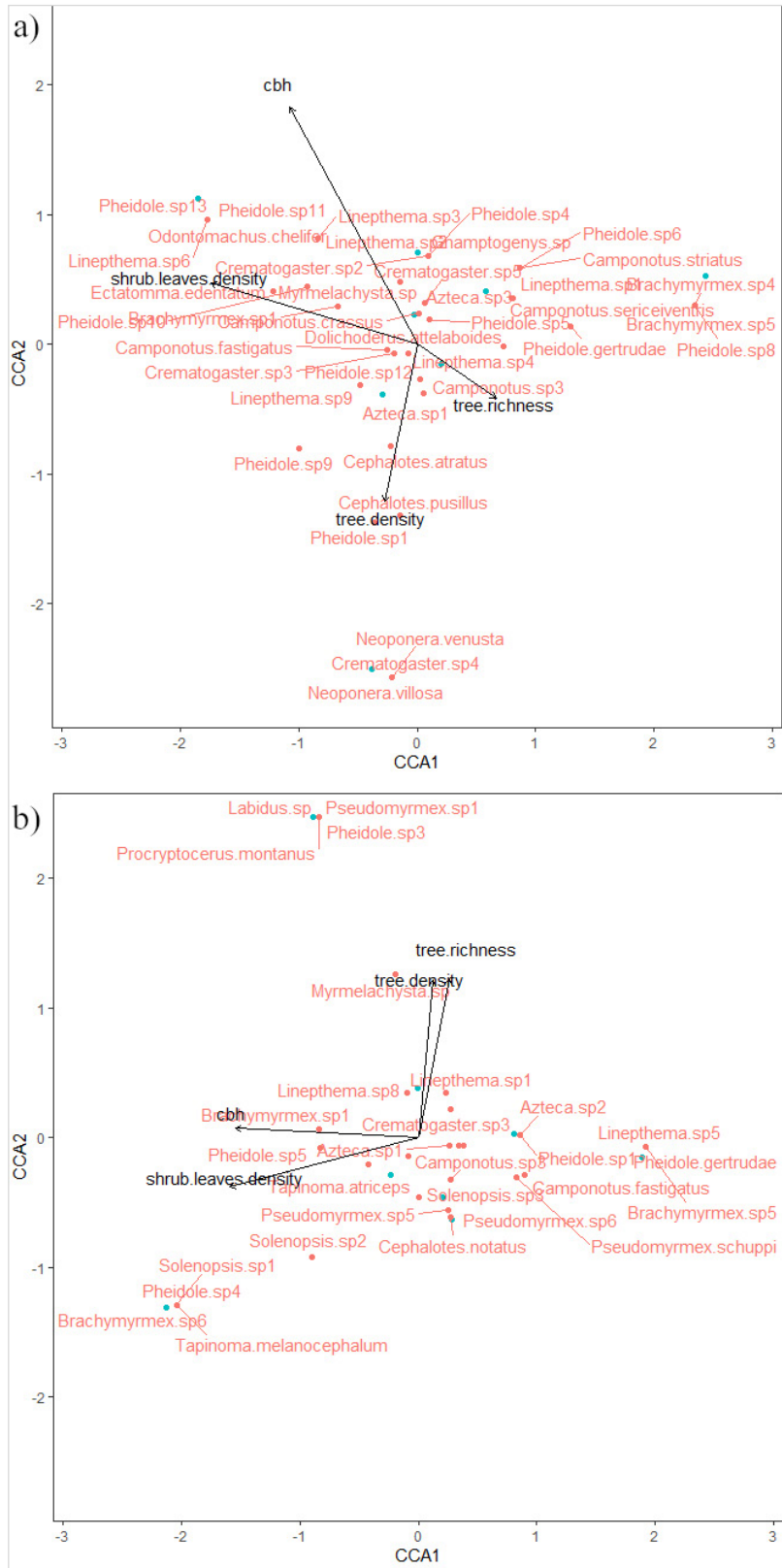


Fig 2. Canonical correspondence analysis with axes 1 and 2 showing the organization of species according to environmental variables (tree density; tree richness; shrub leaves density; average circumference at breast height (cbh) in the rainy (a) and dry (b) season.

Table 3. Total richness of species per stratum per season.

Fragment	Rainy Season		Dry Season	
	Tree	Shrub	Tree	Shrub
1	12	10	4	5
2	7	6	8	6
3	9	5	5	2
4	10	10	8	8
5	14	11	9	2
6	12	10	4	3
7	12	8	4	5
8	9	10	5	3

ant species composition ($F = 1.34$, $df = 1$, $p = 0.004$, Fig 2b), with axis 1 explaining 18.30% of the variation. Tree richness and tree density were not statistically significant.

Discussion

Our results show that the diversity of ant species that forage on plants was positively correlated with the rainy season. Additionally, the dissimilarity in ant species composition reflected the substitution of species that occur in one area with different species in another area (turnover). The ant species composition was not influenced by the distance between fragments. Furthermore, ant species diversity was positively correlated with the shrub leaf density and the average circumference at breast height (CBH) of trees.

In this study, we collected 68 ant species distributed in 19 genera. Although the richness of ants foraging on plants in tropical forests is variable, our results are similar to previous studies (Majer, 1990; Klimes et al., 2015). These results vary according to the sampling effort and conservation status of the area, with areas of secondary forest harboring less diversity (Majer, 1990; Klimes et al., 2015).

Water availability is correlated with plant phenophases (e.g., sprouting leaves, flowering and fruiting) of many tropical plant species (Van Schaik et al., 1993; Novaes et al., 2020; Calixto et al., 2021) and, therefore, the resources offered by these plants to the fauna. The diet of ant species that forage on plants is mainly based on plant-derived resources or indirectly as excretion from honeydew-producing insects and prey (Blüthgen & Feldhaar, 2010). The rainy season favors the abundance of resources (Morellato et al., 2013; Calixto et al., 2021). The availability of resources promotes higher foraging intensity of ant colonies and eventual control of the resource by dominant species. This dominance influences the behavioral response of other ant species, affecting the ant community in terms of species distribution and activity (Baccaro et al., 2010).

In the additive partitions of diversity, α_1 had low values, being slightly higher in the rainy season (1.38 and 1.36 ($p = 0.05$)) than in the dry season (1.21 and 1.20 ($p = 0.67$)). The observed value of α_1 was not significant in relation

to the expected value in the dry season, may be due to the higher scarcity of resources during this season (Morellato et al., 2013; Calixto et al., 2021). The observed β_1 was significantly lower than expected in the rainy season (8.31 and 11.88 ($p = 0.01$)) and in the dry season (3.85 and 4.93 ($p = 0.01$)). The low α_1 and β_1 values are found in other works and can be explained by the dominance behavior of ants in protecting and monopolizing baits (Yanoviak & Kaspari, 2000; Baccaro et al., 2010, 2011). The sardine bait used may have contributed to the low diversity values of the sample. Although ant species have different preferences for food sources, vitamins, minerals, and proteins are essential to meet the nutritional needs of immatures and egg production, while carbohydrates are important for adult nutrition (Fowler et al., 1991). It is important to note that although many ant species have a varied diet, including both plant and animal sources, some species have a mainly plant-based diet (Blüthgen & Feldhaar, 2010). The observed β_2 was significantly lower than expected in the rainy season (4.56 and 7.96 ($p = 0.01$)) and in the dry season (3.44 and 4.75 ($p = 0.01$)). This result may be due to the same ant species exploiting the resources of both strata in the rainy and dry seasons. As many species found were generalists and with soil nestings, such as the genera *Pheidole*, *Linepithema* and *Solenopsis* (Baccaro et al., 2015), these ants end up exploring all available resources, foraging on both strata: arboreal and shrubby. The observed β_3 was significantly higher than expected in the rainy season (40.75 and 33.80 ($p = 0.01$)) and in the dry season (29.50 and 27.11 ($p = 0.01$)) indicating that the high diversity found is due to the variation in richness among the fragments. The observed β_3 was higher in the rainy season than in the dry season. The significant results showed that the null hypothesis that the observed values could have been obtained by the random distribution of individuals was rejected.

The results of the β diversity partitioning analysis showed that the turnover component (β_{SIM}) had a greater contribution to the differences in ant species composition among different samples, strata (shrub or tree), and fragments for both the rainy and dry seasons. This means that each fragment preserved a different pool of ant species, which is potentially caused by the variation in vegetation structure among the fragments.

Each fragment has its characteristics acquired in space and time: they have different phytophysiognomies, sizes and distances from areas of continuous forests. Forest fragments are more susceptible to edge effects and habitat loss has a negative effect on biodiversity (Fahrig, 2003). Trees distinctly alter microhabitat and can influence invertebrate diversity (Yanoviak & Kaspari, 2000). Being more specialized organisms, insects are more susceptible to loss of vegetation and habitats (Perfecto & Vandermeer, 1996). The availability of habitat and resources affects the diversity of ants and influences the distribution and interactions of species (Fahrig, 2003; Ribas et al., 2003; Rico-Gray et al., 2012).

In the rainy season, plants have higher water availability, which favors the growth and differentiation of new plant tissues and higher activity of extrafloral nectaries, for example (Calixto et al., 2021). Shrubs offers a higher quantity and variety of resources in this period. In the dry season, resource production is lower (Morellato et al., 2013; Calixto et al., 2021) and it is the trees that sustain resource production and promotes specialization (Yanoviak & Kaspari, 2000). In the rainy season, CCA showed that the shrub leaf density affects the composition of ant species. A potential explanation is that in these regions leaves sprout during rainy season increasing the food resources to ants. Therefore, more resources more ants. In the dry season, CCA showed that CBH affects the composition of ant species. CBH is used to measure variation in density, basal area and tree size (Moro & Martins, 2011) and is also an indicator of forest successional stage (Oliveira et al., 1997; Lorenzoni-Paschoa et al., 2019). Forest fragments with higher CBH indicate that they are in a more advanced successional stage, which can affect the ant community (Campos et al., 2006). In the dry season, trees sustain the production of resources, and an area with more developed trees would promote more resources. This could explain why the diversity of ant species was positively affected by CBH.

We found differences in the species composition of the ant community in forest fragments of the Atlantic Forest biome in the municipality of Vassouras. The results showed that the rainy season positively influences the diversity of ant species that forage on plants, and that each fragment preserved a different pool of ant species, which is potentially caused by different vegetation structure among fragments. These findings highlight the importance of conserving the majority of forest fragments to better preserve the pool of ant species regionally, which could also contribute positively to the preservation of other organisms, species interactions, and ecosystem maintenance. Therefore, it is necessary to conduct additional studies in the region to evaluate other taxonomic groups in different seasonal periods, as well as to better understand the intensity of interactions between ants and other organisms. These studies can provide valuable information to develop more effective environmental conservation policies.

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References

AGEVAP. (2018). Plano municipal de gestão integrada de resíduos sólidos. Vassouras, Rio de Janeiro: Associação Pró-

Gestão das Águas da Bacia Hidrográfica do Rio Paraíba do Sul – AGEVAP e Keyassociados, 92 p

Ahuatzin, D. A., Corro, E. J., Jaimes, A. A., Valenzuela González, J. E., Feitosa, R. M., Ribeiro, M. C., ... & Dáttilo, W. (2019). Forest cover drives leaf litter ant diversity in primary rainforest remnants within human-modified tropical landscapes. *Biodiversity and Conservation*, 28: 1091-1107. doi: 10.1007/s10531-019-01712-z

Ahuatzin, D. A., González-Tokman, D., Silva, R. R., González, J. E. V., Escobar, F., Ribeiro, M. C., ... & Dáttilo, W. (2022). Forest cover modulates diversity and morphological traits of ants in highly fragmented tropical forest landscapes. *Biodiversity and Conservation*, 1-21. doi: 10.1007/s10531-022-02428-3

Baccaro, F.B., Ketelhut, S.M. & De Morais, J.W. (2010) Resource distribution and soil moisture content can regulate bait control in an ant assemblage in central Amazonian Forest. *Austral Ecology*, 35: 274-281. doi: 10.1111/j.1442-9993.2009.02033.x

Baccaro, F. B., Ketelhut, S. M. & Morais, J. W. (2011). Efeitos da distância entre iscas nas estimativas de abundância e riqueza de formigas em uma floresta de terra-firme na Amazônia Central. *Acta Amazonica*, 41: 115-122. doi: 10.1590/s0044-59672011000100013

Baccaro, F.B., Feitosa, R.M., Fernández, F., Fernandes, I.O., Izzo, T.J., de Souza, J.L.P. & Baselga, A. (2010). Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography*, 19: 134-143. doi: 10.1111/j.1466-8238.2009.00490.x

Baselga, A. & Orme, C.D.L. (2012). Betapart: An R package for the study of beta diversity. *Methods in Ecology and Evolution*, 3: 808–812. doi: 10.1111/j.2041-210X.2012.00224.x

Blüthgen, N., & Feldhaar, H. (2010). Food and shelter: How resources influence ant ecology. In L. Lach., C.L. Parr & K.L. Abbott (Eds.), *Ant Ecology* (pp.115-136). Oxford: Oxford University Press.

Blüthgen, N., Gebauer, G. & Fiedler, K. (2003). Disentangling a rainforest food web using stable isotopes: Dietary diversity in a species-rich ant community. *Oecologia*, 137: 426-435. doi: 10.1007/s00442-003-1347-8

Bolton, B. (1994). Identification guide to the ant genera of the world. Massachusetts: Harvard University Press, 222p

Calixto, E.S., Novaes, L.R., Santos, D.F.B., Lange, D., Moreira, X. & Del-Claro, K. (2021). Climate seasonality drives ant-plant-herbivore interactions via plant phenology in an extrafloral nectary-bearing plant community. *Journal of Ecology*, 109: 639-651. doi: 10.1111/1365-2745.13492

Campos, R.I., Vasconcelos, H.L., Ribeiro, S.P., Neves, F.S. & Soares, J. P. (2006). Relationship between tree size and insect assemblages associated with *Anadenanthera macrocarpa*. *Ecography*, 29: 442-450. doi: 10.1111/j.2006.0906-7590.04520.x

- Coelho, R.C. de S. (2011). Comunidades de formigas (Hymenoptera: Formicidae) do estrato arbustivo-arbóreo em fragmentos florestais de Mata Atlântica no Rio de Janeiro. Instituto de Florestas. Dissertação (Mestrado em Ciências Ambientais e Florestais). Seropédica: Universidade Federal Rural do Rio de Janeiro, 59 p
- Costa, M.M.S.D. & Schmidt, F.A. (2022). Gamma, alpha, and beta diversity of ant assemblages response to a gradient of forest cover in human-modified landscape in Brazilian Amazon. *Biotropica*, 54: 515-524. doi: 10.1111/btp.13073
- Crist, T.O., Veech, J.A., Gering, J.C. & Summerville, K.S. (2003). Partitioning species diversity across landscapes and regions: A hierarchical analysis of α , β , and γ diversity. *The American Naturalist*, 162: 734-743. doi: 10.1086/378901
- Drummond, J.A. (1997). Devastação e preservação ambiental no Rio de Janeiro. Niterói: EDUFF, 306p
- Elizalde, L., Arbetman, M., Arnan, X., Eggleton, P., Leal, I.R., Lescano, M.N., Saez, A., Werenkraut, V. & Pirk, G. (2020). The ecosystem services provided by social insects: Traits, management tools and knowledge gaps. *Biological Reviews*, 95: 1418-1441. doi: 10.1111/brv.12616
- Fahrig, L. (2003). Effects of Habitat Fragmentation on Biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, 34: 487-515. doi: 10.1146/annurev.ecolsys.34.01
- Francelino, M.R., Rezende, E.M.C. & Silva, L.D.B. (2012). Proposta de metodologia para zoneamento ambiental de plantio de eucalipto. *Cerne*, 18: 275-283.
- Fowler, H.G., Forti, L.C., Brandão, C.R.F., Delabie, J.H.C. & Vasconcelos, H.D. (1991). Ecologia Nutricional de formigas. In A.R. Panizzi & J.R.P. Parra (Eds.), *Ecologia Nutricional de Insetos e suas Implicações no Manejo de Pragas* (pp. 131-223). São Paulo: Editora Manole e CNPq.
- Freitas, A.V.L., Francini, R.B. & Brown, J.R.K.S. (2003). Insetos como indicadores ambientais. In J.R.L. Cullen., C. Valladares-Pádua & R. Rudran (Eds.), *Métodos de estudos em biologia da conservação e manejo da vida silvestre* (pp. 125-151). Curitiba, Brasil: Editora UFPR.
- Hölldobler, B. & Wilson, E.O. (1990) *The ants*. Cambridge: Harvard University Press, 732 p
- IPBES (2019). Summary for policymakers of the global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. Díaz, S., Settele, J., Brondízio, E.S., Ngo, H.T., Guèze, M., Agard, J., Arneth, A.P., ... & Zayas, C.N. (Eds.). IPBES secretariat, Bonn, Germany. 56 pages.
- Klimes, P., Fibich, P., Idigel, C. & Rimandai, M. (2015). Disentangling the Diversity of Arboreal Ant Communities in Tropical Forest Trees. *PLOS ONE*, 10: e0117853. doi: 10.1371/journal.pone.0117853
- Köppen, W. (1948). *Climatología: Con un estudio de los climas de la tierra*. (Es) Traducido del alemán. México, D.F: Fondo de Cultura Económica, 474 p
- Lange, D., Calixto, E. S., Rosa, B. B., Sales, T. A. & Del-Claro, K. (2019). Natural history and ecology of foraging of the *Camponotus crassus* Mayr, 1862 (Hymenoptera: Formicidae). *Journal of Natural History*, 53: 1737-1749. doi: 10.1080/00222933.2019.1660430
- Leal, I. R., Filgueiras, B.K.C., Gomes, J.P., Iannuzzi, L. & Andersen, A.N. (2012). Effects of habitat fragmentation on ant richness and functional composition in Brazilian Atlantic Forest. *Biodiversity and Conservation*, 21: 1687-1701. doi: 10.1007/s10531-012-0271-9
- Lorenzoni-Paschoa, L. de S., Abreu, K.M.P. de, Silva, G. F. da, Dias, H.M., Machado, L.A. & Silva, R. de D. (2019). Estágio sucessional de uma floresta estacional semidecidual secundária com distintos históricos de uso do solo no sul do Espírito Santo. *Rodriguésia*, 70. doi: 10.1590/2175-7860 201970028
- Lucky, A., Trautwein, M.D., Guénard, B.S., Weiser, M.D. & Dunn, R.R. (2013). Tracing the rise of ants - Out of the ground. *PLoS ONE*, 8: e84012. doi: 10.1371/journal.pone.0084012
- Majer, J.D. (1990). The Abundance and Diversity of Arboreal Ants in Northern Australia. *Biotropica*, 22: 191. doi: 10.2307/2388412
- Mantovani, W. & Martins, F.R. (1990) O método de pontos. *Acta Botanica Brasilica*, 4: 95-122. doi: 10.1590/s0102-33061 990000300011
- Marques, T., Espírito-Santo, M., Neves, F. & Schoereder, J. (2017). Ant Assemblage Structure in a Secondary Tropical Dry Forest: The Role of Ecological Succession and Seasonality. *Sociobiology*, 64: 261. doi: 10.13102/sociobiology.v64i3.1276.
- Martinez, J.-J.I. (2015). Monopolization of resources by ground-nesting ants foraging on trees in Mediterranean forests. *Acta Oecologica*, 65-66: 11-16. doi: 10.1016/j.actao.2015.03.002
- Morellato, L.P.C., Camargo, M.G.G. & Gressler, E. (2013). South and Central America: phenology overview and perspectives. Pages 91-113 In: Schwartz, M.D. (Ed.), *Phenology: An Integrative Environmental Science*. Springer, Dordrecht.
- Moro, M.F. & Martins, F.R. (2011). Métodos de levantamento do componente arbóreo-arbustivo. In J.M. Felfili., P.V. Eisenlohr., M.M.R.F. Melo., L.A. Andrade. & J.A.A. Meira-Neto (Org.), *Fitossociologia no Brasil: Métodos e estudos de casos*. volume 1. (pp. 174-212). Viçosa, MG: Editora UFV.
- Myers, N. (1988). Threatened biotas: "Hot spots" in tropical forests. *The Environmentalist*, 8: 187-208. doi: 10.1007/bf02240252
- Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B. & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, 403: 853-858. doi: 10.1038/35002501

- Noaes, L.R., Calixto, E.S., de Oliveira, M.L., Alves-de-Lima, L., de Almeida, O. & Torezan-Silingardi, H.M. (2020). Environmental variables drive phenological events of anemocoric plants and enhance diaspore dispersal potential: a new wind-based approach. *Science of The Total Environment*, 730: 139039. doi: 10.1016/j.scitotenv.2020.139039
- Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlenn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E. & Wagner, H. (2018). *Vegan: Community Ecology Package*. R package version, 2.
- Oliveira-Filho, A. T. & Márcio de Mello, J. (1997). Effects of past disturbance and edges on tree community structure and dynamics within a fragment of tropical semideciduous forest in south-eastern Brazil over a five-year period (1987-1992). *Plant Ecology Formerly 'Vegetatio'*, 131: 45-66. doi: 10.1023/a:1009744207641
- Oliveira, M.A.de., Gomes, C.F.F., Pires, E.M., Marinho, C.G.S. & Della Lucia, T.M.C. (2014). Bioindicadores ambientais: Insetos como um instrumento desta avaliação. *Revista Ceres*, 61: 800-807. doi:10.1590/0034-737x201461000005
- Palacio, E.E. & Fernández, F. (2003). Claves para las subfamilias y géneros. In F. Fernández, *Introducción a las hormigas de la region neotropical* (pp. 233-260). Bogotá: Instituto de Investigación de Recursos Biológicos Alexander von Humboldt.
- Peel, M.C., Finlayson, B.L. & McMahon, T.A. (2007). Updated world map of the Köppen-Geiger climate classification. *Hydrology and Earth System Sciences*, 11: 1633-1644. doi: 10.5194/hess-11-1633-2007
- Pereira, M.P.dos S., Francelino, M.R. & Queiroz, J.M. (2017). A cobertura florestal em paisagens do Médio Vale do Rio Paraíba do Sul. *Floresta e Ambiente*, 24: e00134115. doi: 10.1590/2179-8087.134115
- Perfecto, I. & Vandermeer, J. (1996). Microclimatic changes and the indirect loss of ant diversity in a tropical agroecosystem. *Oecologia*, 108: 577-582. doi: 10.1007/BF00333736
- R Development Core Team (2021). *A language and environment for statistical computing*. R Foundation for Statistical Computing. <http://www.r-proje.ct.org/>
- Ribas, C.R., Schoederer, J.H., Pic, M. & Soares, S.M. (2003). Tree heterogeneity, resource availability, and larger scale processes regulating arboreal ant species richness. *Austral Ecology*, 28: 305-314. doi: 10.1046/j.1442-9993.2003.01290.x
- Ribas, C. R., Sobrinho, T. G., Schoederer, J. H., Sperber, C. F., Lopes-Andrade, C. & Soares, S. M. (2005). How large is large enough for insects? Forest fragmentation effects at three spatial scales. *Acta Oecologica*, 27: 31-41. doi: 10.1016/j.actao.2004.08.008
- Ribeiro, D.B., Prado, P.I., Brown Jr, K.S. & Freitas, A.V.L. (2008). Additive partitioning of butterfly diversity in a fragmented landscape: Importance of scale and implications for conservation. *Diversity and Distributions*, 14: 961-968. doi: 10.1111/j.1472-4642.2008.00505.x
- Ribeiro, M.C., Metzger, J.P., Martensen, A.C., Ponzoni, F.J. & Hirota, M.M. (2009). The Brazilian Atlantic Forest: How much is left, and how is the remaining forest distributed? Implications for conservation. *Biological Conservation*, 142: 1141-1153. doi:10.1016/j.biocon.2009.02.021
- Rico-Gray, V., Díaz-Castelazo, C., Ramírez-Hernández, A., Guimarães, Jr., P.R. & Holland, J.N. (2012). Abiotic factors shape temporal variation in the structure of an ant-plant network. *Arthropod-Plant Interactions*, 6: 289-295. doi: 10.1007/s11829-011-9170-3
- Saunders, D.A., Hobbs, R.J. & Margules, C.R. (1991). Biological Consequences of Ecosystem Fragmentation: A Review. *Conservation Biology*, 5: 18-32. doi: 10.1111/j.1523-1739.1991.tb00384.x
- Stein, S.J. (1990). *Vassouras: Um município brasileiro do café, 1850-1900*. Tradução de Vera Bloch Wrobel. Rio de Janeiro: Nova Fronteira, 364p
- Van Schaik, C.P., Terborgh, J.W. & Wright, S.J. (1993). The Phenology of Tropical Forests: Adaptive Significance and Consequences for Primary Consumers. *Annual Review of Ecology and Systematics*, 24: 353-377. doi: 10.1146/annurev.es.24.110193.002033
- Veech, J. A., Summerville, K. S., Crist, T. O. & Gering, J. C. (2002). The additive partitioning of species diversity: recent revival of an old idea. *Oikos*, 99: 3-9. doi: 10.1034/j.1600-0706.2002.990101.x
- Wilson, Edward O. "Threats to Biodiversity." *Scientific American*, vol. 261, no. 3, Scientific American, a division of Nature America, Inc., 1989, pp. 108-17. <http://www.jstor.org/stable/24987402>.
- Yanoviak, S.P. & Kaspari, M. (2000). Community structure and the habitat templet: Ants in the tropical forest canopy and litter. *Oikos*, 89: 259-266. doi: 10.1034/j.1600-0706.2000.890206.x
- Zhao, Y., Sanders, N. J., Liu, J., Jin, T., Zhou, H., Lu, R., ... Si, X. (2021). β diversity among ant communities on fragmented habitat islands: the roles of species trait, phylogeny and abundance. *Ecography*, 44: 1568-1578. doi: 10.1111/ecog.05723

