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ORIGINAL PAPER

Ant species richness and interactions in canopies of two distinct successional stages in a tropical dry forest

Reuber Antoniazzi[1,2] · Raphael N. S. L. Garro[2] · Wesley Dáttilo[1] · Sérvio P. Ribeiro[3] · Frederico S. Neves[2,4]

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Abstract

Canopy ecology is a fast-growing field, but still a scientific frontier in many ecological aspects. For instance, the hypothesis that tree traits shape patterns in ant-plant interactions lacks data, notably for tropical canopies in different successional stages. In this study, we investigated canopy traits, such as tree height, the presence of extrafloral nectaries (EFNs), connectivity among tree crowns, and successional stage, structure ant-tree interactions in a tropical dry forest (TDF), examining whether these are the determinant factors for ant species richness. We collected ants on trees in early and late successional stages over 2 years, in rainy and dry seasons. In the late successional stage, ant species richness was greater in the taller trees; in the early successional stage, the smallest trees had a greater ant species richness than the taller trees. The EFNs and connectivity among treetops had no effect on ant species richness. We obtained a tree-ant network of the early successional stage, involving 786 interactions among 57 ant species and 75 trees; in the late successional stage, the network had 914 interactions among 60 ant species and 75 trees. There were 27 species of trees in our study, 11 of which (40.7% of all individual trees) had EFNs. The ant-plant interactions were not randomly distributed, suggesting that various biotic factors structured the ant assemblies. This study presents new insights into ant-tree interactions, showing that both tree height and successional stage influence the occurrence of many species of ants in tree canopies of tropical dry forests.

Keywords Arboreal ants · Territoriality ants · Crown connectivity · Extrafloral nectaries · Ant-plant interactions · Network analysis

Introduction

Tropical forest canopies support a high diversity of organisms and life forms (Wardhaugh 2014) and may contain half of the diversity within a forest (Stork and Grimbacher 2006; Basset et al. 2012). Among the insects that occupy canopies, ants stand out, representing 20–40% of the arthropod biomass recorded in that habitat (Tobin 1995). Canopy ant species can display major dominance and territoriality on canopies (Majer 1972; Majer et al. 1994), resulting in well-defined territories of dominant and aggressive ant species (Dejean et al. 2015). These dominant ant species patrol and occupy areas without overlapping territories that, however, could be pervaded by subdominant species (Majer 1972; Majer and Delabie 1993; Majer et al. 1994; Dejean et al. 2007). Furthermore, epigeic ant species can also forage on vegetation (Rico-Gray and Oliveira 2007; Marques et al. 2017).

Ant species foraging patterns are associated with the distribution and the type of available resources (Gordon 2012; Klimes et al. 2015), related to vegetation traits, for instance, tree height (Campos et al. 2006; Dejean et al. 2008; Janda and Konečná 2011; Klimes et al. 2012) and canopy stratum (i.e., luminosity) (Blüthgen and Stork 2007; Ribeiro et al. 2013). Therefore, it is expected that taller trees may favor an increase in the number of microhabitats, as they have more space that can be used as nesting sites (Powell et al. 2011; Klimes et al.

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✉ Reuber Antoniazzi
reuberjunior@gmail.com

[1] Red de Ecoetología, Instituto de Ecología A.C., Xalapa, Veracruz, Mexico

[2] Programa de Pós-Graduação Stricto Sensu em Ciências Biológicas, Universidade Estadual de Montes Claros, Montes Claros, Minas Gerais, Brazil

[3] Laboratório de Ecohealth e Ecologia de Insetos de Dossel e Sucessão Natural, Instituto de Ciências Biológicas, Universidade Federal de Ouro Preto, Ouro Preto, Minas Gerais, Brazil

[4] Laboratório de Ecologia de Insetos, Departamento de Genética, Ecologia e Evolução, Universidade Federal de Minas Gerais, Belo Horizonte, Minas Gerais, Brazil

2015). Furthermore, taller trees may also offer more sheltering sites and food (Campos et al. 2006; Tanaka et al. 2010; Yusah and Foster 2016), for instance, extrafloral nectaries (EFN), allowing the establishment of ant species related to the use of these feeding structures by the ants (Schoereder et al. 2010; Fagundes et al. 2016). Another important characteristic of the plant community in forests related to the ant fauna is the connectivity among treetops in the canopy, which increases the foraging area and potential territories for dominant ants (Majer and Delabie 1999; Yanoviak 2015).

The literature on canopy insect ecology has shown that any pattern in insect distribution in forests depends on the forest vertical size scale as well as the canopy strata (Basset et al. 2015). In a study of Amazonian understory, Falcão et al. (2015) found that the diversity of ant-plant interactions increased along different successional stages. In a study in Neotropical montane forest canopies, ant species dominance was more frequent in highly disturbed sites, and this pattern differed among tree crowns of the entire canopy (Lourenço et al. 2015). In a tropical forest in New Guinea, Klimes et al. (2012) found a greater species richness and a different ant species composition in late than in early successional stages. In summary, our knowledge about the relationships between canopy ants and successional stages lacks data, since previous studies have been restricted to the understory, to montane forest, or to evergreen forest. Furthermore, some studies have not considered the persistent ant foraging patterns on the canopy over time.

The lack of knowledge about canopy ants is especially evident in tropical seasonal environments, such as tropical dry forests (TDFs) (Castaño-Meneses 2014; Vergara-Torres et al. 2017). TDF plant communities present strong seasonality changes, shedding up almost of their leaves during the dry season (Pezzini et al. 2014). In addition, these forests are subject to prominent levels of anthropogenic perturbation (Arroyo-Mora et al. 2005), forming landscapes in different successional stages (Arroyo-Mora et al. 2005). Previous studies in tropical dry forests found changes in ant community compositions along different successional stages (Neves et al. 2010; Sousa-Souto et al. 2016; Marques et al. 2017) and regions (Silva et al. 2017), but were restricted to the tree trunks, the understory, or the ground level. Thus, further investigation is needed to understand the dynamics of canopy ant species, the trees they inhabit, and how they interact.

Ants interact with plants in different ways, such as protecting the plant from some herbivorous insects (Rico-Gray and Oliveira 2007), and the innumerable possibilities of these interactions can produce complex networks between ants and plants (Del-Claro et al. 2018). Based on studies of such networks, it is possible to assess properties at both the species level and in the community as a whole (Bascompte 2007; Antoniazzi et al. 2018). However, measuring the interaction networks in canopy habitats is not a trivial task (Lowman et al. 2012) due to the difficulty in accessing and sampling high above the ground. Although the knowledge of insect diversity, species distributions, and herbivory in the canopy has increased tremendously in the past years (Ribeiro et al. 2013; Neves et al. 2014; Basset et al. 2015; Leal et al. 2016; Nakamura et al. 2017), there have not yet been similar efforts to measure the interaction networks in canopy ant communities (DaRocha et al. 2016).

This study aimed to evaluate how canopy traits (i.e., tree height, tree connectivity, presence of EFNs, and successional stage) structure the ant assemblage in a TDF canopy. Hence, we postulated that taller trees, with more connected crowns, with EFNs, and located in advanced successional stages will have a higher ant species richness, as there are more available resources, a higher possibility of locomotion between tree crowns, and distinct kinds of microhabitats at the canopy. In addition, since arboreal-dwelling ants dominate and defend canopy resources, certain ant species could distribute in a set of trees, in territories across tree crowns; thus, we expected that interaction networks involving individual trees and ant species should be characterized by a low co-occurrence of certain ant species on a set of trees.

Material and methods

Study area

The study was conducted in the Parque Estadual da Mata Seca (PEMS; 14° 48′ 36″–14° 56′ 12″ S and 43° 55′ 12″–44° 04′ 12″ W; 493 m a.s.l.) in SE Brazil, in the transition zone between three important Brazilian biomes: *Cerrado* (Brazilian savanna), *Caatinga* (spiny-dry forest), and *Mata Atlântica* (Brazilian Atlantic Forest). Inserted in a mosaic of pristine (*sensu* undisturbed for a long time) and secondary forests (previously used for agriculture and livestock activities), the PEMS covers a total area of 15,466 ha (Madeira et al. 2009). The climate of the region is tropical semi-arid (*Aw* in Köppen's classification) (Alvares et al. 2013), characterized by a severe dry season during the winter (May through September). The average annual temperature is 25.1 °C, with an average annual precipitation of 818 ± 242 mm (mean ± SD), concentrated between November and April (Pezzini et al. 2014).

The original vegetation in the area is a tropical dry forest on fertile soils and mostly flat terrains. In this region, the tropical dry forest (TDF) is dominated by deciduous vegetation, losing between 90 and 95% of its leaves during the dry season (Pezzini et al. 2014). We chose areas in two successional stages, henceforth early and late stage, with striking differences in their structure and land-use history (Madeira et al. 2009; Pezzini et al. 2014). The early stage was a pasture in recovery for about 15 years and composed of trees < 8 m in height, with an understory of herbs and grasses, without a distinguishable vertical stratification. The later stage had experienced little or no anthropogenic intervention for at least 60 years. There were emergent trees that exceeded 20 m in height, a distinct canopy and understory strata, with light input at the soil level only during the dry season. In this area, there were fewer new trees and lianas when compared with other adjacent areas at different levels of regeneration (for a detailed description of the study areas, see Madeira et al. (2009)).

Sample design

Along a 7-km transect, we established 10 rectangular plots of 20 × 50 m, at least 200-m apart, five in the early and five in the late successional stages (Madeira et al. 2009; Marques et al. 2017). In each corner and in the center of each plot, we selected three of the taller trees with a CBH (circumference at breast height) of at least 15 cm, forming five clusters. In each plot, we sampled 15 trees, with 75 trees in each successional stage, resulting in a total of 150 sampled trees.

Ant sampling

We performed the samplings during four consecutive periods, two in the dry season (September 2010 and September 2011) and two in the wet season (February 2011 and February 2012). To sample ants, we reached the canopy using a ladder for trees up to a height of 8 m; in trees taller than 8 m, we used the "single rope climbing technique" (Perry 1978). We used two complementary techniques for sampling the ants: arboreal pitfall trap and entomological beating technique (Campos et al. 2006). Arboreal pitfall traps consisted of plastic pots of 15 cm in diameter, filled with water and soap that we left active for 48 h. On each tree, we placed two arboreal pitfall traps tied to the trunk with a thin string, with 30 pitfalls per plot, 300 pitfalls per sample period, and a total of 1200 pitfalls. The entomological beating technique consisted of an entomological umbrella made by an inverted cloth funnel, with a surface of 1 × 1 m, and a plastic bag attached to the bottom. For ant sampling, we placed this apparatus under tree branches and beat the branches above (Campos et al. 2006). We beat the same trees on which pitfalls were placed, with 10 beatings on three branch groups, with the greatest possible distance between them on the treetop. We obtained one entomological beat sample per tree, with 75 samples per successional stage, 150 samples in each sample period, and a total of 600 samples. Throughout the four sampling periods (two dry and two rainy seasons simultaneously), we performed 1800 samplings among the arboreal pitfall traps and entomological beatings on the 150 trees of the early and late successional stages.

All the sampled materials were transported to the laboratory for sorting, mounting, and identification to the lowest taxonomic level. For ant species identification, we used the following resources: Baccaro et al. (2015), "AntWeb" (Fisher 2002), "AntCat" (Bolton 2012), "Ants of Costa Rica" (Longino 2007), and determination by experts. All materials are deposited in the Laboratório de Ecologia de Insetos (LEI), Universidade Federal de Minas Gerais (UFMG), Brazil.

Tree structure

Trees were identified to morphospecies, or species when possible, with the help of experts from the Universidade Estadual de Montes Claros (Unimontes). For each of the 150 sampled trees, 75 per successional stage, we estimated the tree height, using a ladder or ropes as length reference, and measured the connectivity among treetops. Connectivity among treetops was measured as the total number of times that a tree was connected to another tree either by its own structures (leaves, branches, trunk) or by structures associated to the tree (epiphytes and lianas). To determine the presence of extrafloral nectaries (EFNs) on the tree species, we used the guide "World List of Angiosperm Species with Extrafloral Nectaries" (Weber et al. 2015) and published data (Rivera 2000; Gonzalez 2011, 2013) for those trees we could identify (27 were not identified).

Statistical analysis

Comparisons of different successional stages could be potentially biased by variation in the habitat structure. To circumvent this issue, we developed ant species accumulation curves to determine whether the species was well represented by our collection effort, using rarefaction and extrapolation curves (the number of samples was extrapolated to double the sample size, as suggested by Chao et al. (2014). We implemented these methods within the package iNEXT (Hsieh et al. 2016), using the R software (R Core Team 2017).

To assess the relationship among ant species richness and canopy traits, we used the generalized linear mixed model (GLMM) procedure (Bolker et al. 2009), with tree height, tree connectivity, presence/absence EFNs, and successional stage as the fixed effect variables. Due to hierarchical sampling, we used the plot within the successional stage (p) and the tree within the plot within the successional stage (t) as random effects ($1|\text{successional\_stage}/p/t$; *see* Crawley (2013)). Additionally, we performed a model for each successional stage separately, which we tested for seasonal effect (dry and wet seasons), considering the presence of EFNs, in relation to ant activity. Thus, we avoided mistakes when presenting the results of the relationship between EFN and ant activity in the trees among different seasons, because the samples of each season of the year (two dry and two rainy seasons) were initially combined. For the GLMMs, we first performed the complete model and then excluded the non-significant terms from

Table 1 Sampled ant species in the tropical dry forest, Parque Estadual da Mata Seca (PEMS), Minas Gerais, southeast Brazil. "Species code" is an abbreviation used in the graphs of Fig. 4. "Number of Interactions" refers to the number of interactions of each ant species on each one of the successional stages ("Early," "Late") and both together ("Both"). The dominant ant species are marked with an asterisk

Ant taxa	Species code	Number of Interactions		
		Early	Late	Both
Formicidae				
Dolichoderinae				
Azteca instabilis Smith, 1862	Aztins	–	20	20
Azteca sp1	Aztsp1	–	1	1
Dolichoderus lutosus Smith, 1858	Dollut	1	20	21
Dolichoderus sp1	Dolsp1	4	–	4
Dolichoderus sp2	Dolsp2	–	1	1
Dorymyrmex sp1	Dorsp1	3	1	4
Forelius brasiliensis Forel, 1908	Forbra	6	–	6
Linepithema sp1	Linsp1	1	–	1
Tapinoma sp1	Tapsp1	2	6	8
Tapinoma sp2	Tapsp2	–	1	1
Dorylinae				
Eciton sp1	Ecisp1	2	–	2
Labidus praedator Smith, 1858	Labpra	2	–	2
Ectatomminae				
Ectatomma muticum Mayr, 1870	Ectmut	5	1	6
Gnamptogenys striatula Mayr, 1884	Gnastr	1	–	1
Gnamptogenys sulcata Smith, 1858	Gnasul	3	–	3
Formicinae				
Brachymyrmex sp1	Brasp1	1	1	2
Brachymyrmex sp2	Brasp2	2	–	2
Camponotus arboreus Smith, 1858	Camarb	3	106*	109
Camponotus atriceps Smith, 1858	Camatr	2	59*	61
Camponotus blandus Smith, 1858	Cambla	162*	10	172
Camponotus bonariensis Mayr, 1868	Cambon	1	6	7
Camponotus melanoticus Emery, 1894	Cammel	44*	108*	152
Camponotus renggeri Emery, 1894	Camren	93*	3	96
Camponotus senex Smith, 1858	Camsen	16	23	39
Camponotus vittatus Forel, 1904	Camvit	1	77*	78
Camponotus sp1	Camsp1	4	4	8
Myrmelachista bambusarum Forel, 1903	Myrbam	5	3	8
Myrmelachista sp2	Myrsp2	–	2	2
Heteroponerinae				
Acanthoponera mucronata Roger, 1860	Acamuc	1	1	2
Myrmicinae				
Acromyrmex sp1	Acrsp1	1	1	2
Cephalotes atratus Linnaeus, 1758	Cepatr	–	48*	48
Cephalotes betoi (De Andrade & Baroni Urbani, 1999)	Cepbet	11	2	13
Cephalotes maculatus Smith, 1876	Cepmac	20	22	42
Cephalotes minutus Fabricius, 1804	Cepmin	38	1	39
Cephalotes pellans De Andrade and Baroni Urbani, 1999	Ceppel	6	4	10
Cephalotes persimilis De Andrade and Baroni Urbani, 1999	Cepper	–	2	2
Cephalotes pusillus Klug, 1824	Ceppus	98*	49	147
Cephalotes sp1	Cepsp1	–	6	6

Table 1 (continued)

Ant taxa	Species code	Number of Interactions		
		Early	Late	Both
Cephalotes sp2	Cepsp2	–	4	4
Cephalotes sp3	Cepsp3	–	1	1
Crematogaster goeldii Forel, 1903	Cregoe	63*	120*	183
Crematogaster quadriformis Roger, 1863	Crequa	3	–	3
Crematogaster sp1	Cresp1	11	9	20
Crematogaster sp2	Cresp2	–	5	5
Crematogaster sp3	Cresp3	5	–	5
Crematogaster sp4	Cresp4	–	1	1
Cyphomyrmex sp1	Cypsp1	3	–	3
Nesomyrmex costatus Emery, 1896	Nescos	1	1	2
Nesomyrmex vicinus Mayr, 1887	Nesvic	1	–	1
Pheidole flavens Roger, 1863	Phefla	2	3	5
Pheidole radoszkowskii Mayr, 1884	Pherad	9	8	17
Pheidole sp1	Phesp1	1	2	3
Pheidole sp6	Phesp6	–	1	1
Pheidole sp7	Phesp7	–	1	1
Pheidole sp8	Phesp8	1	–	1
Pheidole sp10	Phsp10	1	1	2
Rogeria sp1	Rogsp1	0	1	1
Solenopsis sp1	Solsp1	1	–	1
Solenopsis sp2	Solsp2	1	–	1
Solenopsis sp3	Solsp3	1	–	1
Solenopsis sp4	Solsp4	–	1	1
Wasmannia auropunctata Roger, 1863	Wasaur	5	1	6
Wasmannia lutzi Forel, 1908	Waslut	1	3	4
Ponerinae				
Neoponera villosa Fabricius, 1804	Neovil	–	8	8
Odontomachus bauri Emery, 1892	Odobau	1	–	1
Pseudomyrmecinae				
Pseudomyrmex elongatus Mayr, 1870	Pseelo	1	1	2
Pseudomyrmex gracilis Fabricius, 1804	Psegra	35*	33	68
Pseudomyrmex lizeri Santschi, 1922	Pseliz	21	11	32
Pseudomyrmex maculatus Smith, 1855	Psemac	18	9	27
Pseudomyrmex oculatus Smith, 1855	Pseocu	10	25	35
Pseudomyrmex pallidus Smith, 1855	Psepal	41*	4	45
Pseudomyrmex schuppi Forel, 1901	Psesch	2	60*	62
Pseudomyrmex tenuis Fabricius, 1804	Pseten	–	1	1
Pseudomyrmex termitarius Smith, 1855	Pseter	7	–	7
Pseudomyrmex unicolor Smith, 1855	Pseuni	–	5	5
Pseudomyrmex sp1	Psesp1	1	3	4
Pseudomyrmex sp2	Psesp2	–	1	1
Pseudomyrmex sp3	Psesp3	–	1	1
Total		786	914	1700

the model until we obtained the simplest model with minimal model adequacy (Crawley 2013), with only the interaction between tree height and successional stages. The GLMM was made using the packages nlme (Pinheiro et al. 2014), lme4 (Bates et al. 2015), and hnp (Moral et al. 2017) in the statistical program R 3.1.1 (R Core Team 2017).

To examine the variation in species composition, we used the permutation multivariate analysis of variance (PERMANOVA) to test for significant clustering of successional stages and the height of the trees. We computed 999 permutations to account for successional stage and tree height effects. Subsequently, we used non-metric multidimensional scaling (NMDS), using presence/absence data and Jaccard's dissimilarity index, to examine the extent to which there were successional stage and tree height in the ordination.

To study the interaction patterns between ants and trees, we initially built two A weighted matrices (for both early and late successional stages), in which A_{ij} represents an interaction between a tree (individual) i and an ant species j (Bascompte et al. 2003) from 0 (absent) to 4 (ant species occurrences accumulated over the four sampling periods). Then, we calculated the level of specialization in the networks (H_2'), using a metric derived from the Shannon diversity index, and performed 10,000 randomizations in comparison with random matrices. This index is based on the probability deviation expected from the distribution of interactions and varies from 0 (low degree of specialization) to 1 (high degree of specialization); it is a quantitative index and extremely robust to variations in sampling intensity and in the number of interacting agents (Blüthgen et al. 2006). For these analyses, we used the package bipartite (Dormann et al. 2008) in the statistical program R 3.1.1 (R Core Team 2017).

To determine if the ant species settle into a consistent pattern with low co-occurrence patterns, we used the co-occurrence index (C-score) (Stone and Roberts 1990) for each successional stage, which is based on the average number of interactions for each unique pair of species and varies from 0 to 1. High C-score values indicate that the interactions between species are highly exclusive and not randomly distributed within the network, while low C-score values indicate that the two species involved co-occur more frequently than expected at random (Gotelli 2000). We generated null models by applying Patefield's algorithm (Patefield 1981) according to the "r2dtable" method, using 10,000 simulations and confronted with the index obtained by the data matrix. The C-score and the bipartite network graphs were generated using the packages bipartite (Dormann et al. 2008) and vegan (Oksanen et al. 2015) in the statistical program R 3.1.1 (R Core Team 2017).

We explored which ant species have the most interactions with individuals of trees, as proposed previously (Dáttilo et al. 2013), defining ant species (network components) as either core or peripheral for each of the successional stages. This classification is based on $G_c = (k_i - K_{mean})/\sigma_k$, in which k_i = "average number of links for a tree/ant species," k_{mean} = "average number of links for all tree individuals/ants," and σ_k = "standard deviation of number of links for tree individuals/ant species." Species with a value of $G_c > 1$ are represented by a higher number of interactions in relation to other species of the same trophic level and are therefore considered as species that constitute a generalist core. On the other hand, $G_c < 1$ classifies species with fewer interactions in relation to other species of the same trophic level, and these species are therefore considered as species that constitute a periphery of networks. It should be noted that, for this analysis, we considered that the interaction was counted for each ant worker; thus, the ant individual presence was the replicate level of relevance, regardless of the colony of origin. Considering that most of the ant canopy community is based on extremely large dominant colonies, to assume those as replicates would basically flatten the results. Moreover, ant individuals are the actual source of interactive links, and regardless of belonging to common territories and groups, they are the interaction component that makes ecological sense.

Results

The ant fauna

We found 78 ant species belonging to 26 genera and eight subfamilies in the tropical forest canopies studied (Table 1). The sampling effort was sufficient to characterize the ant fauna sampled for the early successional stage, with a sampling coverage (SC) of 96.08%, and for the late successional stage

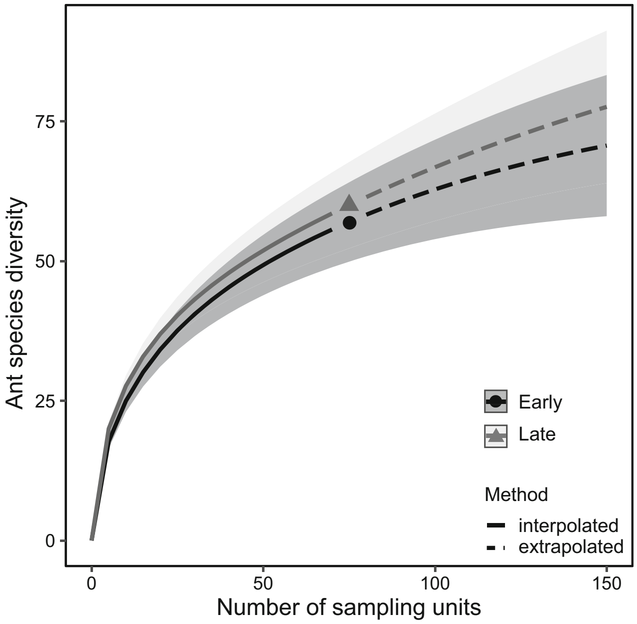

Fig. 1 Sample-size-based rarefaction (solid lines) and extrapolation (dashed lines, up to double the sample size) curves of ant species diversity for the early (black lines) and late (gray lines) successional stages of a tropical dry forest. Gray-shaded regions represent the 95% confidence intervals. Sample sizes are denoted by a solid circle (early successional stage) and a solid triangle (late successional stage)

Table 2 Tree species sampled in the tropical dry forest of Parque Estadual da Mata Seca (PEMS), Minas Gerais, Southeast Brazil. "Abundance" represents the number of individual trees for each species in each successional stage and in both; "EFN" indicates species that possess extrafloral nectaries; "Freq." represents the frequency (%) of tree species sampled in relation to total trees sampled ($n = 150$)

Tree taxa	Abundance			EFN	Freq.
	Early	Late	Both		
Anacardiaceae					
Myracrodruon urundeuva Allemão	17	8	25		16.67%
Schinopsis brasiliensis Engl.	1	–	1		0.67%
Spondias tuberosa Arruda	–	1	1		0.67%
Apocynaceae					
Aspidosperma parvifolium A. DC.	3	–	3	x	2.00%
Aspidosperma polyneuron Müll. Arg.	–	3	3	x	2.00%
Aspidosperma pyrifolium Mart.	1	–	1	x	0.67%
Bignoniaceae					
Handroanthus chrysotrichus (Mart. ex A. DC.) Mattos	–	27	27	x	18.00%
Handroanthus heptaphyllus (Vell.) Mattos	–	2	2	x	1.33%
Handroanthus ochraceus (Cham.) Mattos	13	2	15	x	10.00%
Tabebuia reticulata A.H. Gentry	–	1	1		0.67%
Boraginaceae					
Auxemma oncocalyx (Allemão) Baill.	–	1	1		0.67%
Patagonula bahiensis Moric.	–	1	1		0.67%
Burseraceae					
Commiphora leptophloeos (Mart.) J.B. Gillett	–	3	3		2.00%
Combretaceae					
Combretum duarteanum Cambess.	1	5	6		4.00%
Terminalia fagifolia Mart.	–	1	1	x	0.67%
Fabaceae					
Chloroleucon foliolosum (Benth.) G.P. Lewis	2	–	2	x	1.33%
Goniorrhachis marginata Taub.	–	1	1		0.67%
Machaerium acutifolium Vogel	2	–	2		1.33%
Mimosa hostilis (Mart.) Benth.	1	–	1		0.67%
Piptadenia sp.	1	–	1		0.67%
Plathymenia reticulata Benth.	–	2	2	x	1.33%
Platymiscium blanchetii Benth.	3	–	3		2.00%
Prosopis sp.	3	–	3	x	2.00%
Senegalia polyphylla (DC.) Britton	11	–	11	x	7.33%
Senna spectabilis (DC.) H.S. Irwin & Barneby	4	–	4		2.67%
Flacourtiaceae					
Casearia selloana Eichler	–	1	1		0.67%
Malvaceae					
Pseudobombax marginatum (A. St.-Hil.) A. Robyns	–	1	1		0.67%
Unidentified	12	15	27	NA	18.00%
Total			150	70	

(SC = 96.22%). Rarefaction analysis showed that ant species diversity was similar in the early and successional stages, since the 95% confidence intervals overlapped (Fig. 1).

The trees

Of the 150 sampled trees, 123 were identified to the genus or species level, with a total of 27 morphospecies distributed in nine families. The richest arboreal families in terms of species were Fabaceae (10 species), Bignoniaceae (four species), Anacardiaceae, and Apocinaceae (three species each; Table 2). Although Fabaceae had the highest richness, only 20% of the sampled trees belonged to this family, while Bignoniaceae represented 30% and Anacardiaceae 18% of the total sampled trees. These three families together represented 68% of the total trees sampled. Out of all trees, 27 individuals were *Handroanthus chrysotrichus* (Bignoniaceae), 25 were *Myracrodruon urundeuva* (Anacardiaceae), 15 were *Handroanthus ochraceus* (Bignoniaceae), and 11 were *Senegalia polyphylla* (Fabaceae). We verified that 11 tree species sampled and identified (47% of the total) had EFNs (Table 2).

Ant species richness and composition related to canopy traits

The subfamily Myrmicinae had the highest species richness (34 species), followed by Formicinae and Pseudomyrmecinae (13 species), Dolichoderinae (10 species), Ectatomminae (three species), Dorylinae and Ponerinae (two species each), and Heteroponerinae (one species; Table 1). We found 13 species of the genus *Pseudomyrmex*, 10 species of the genus *Camponotus* and *Cephalotes*, seven *Pheidole* species, and six *Crematogaster* species (Table 1).

Although the mean species richness did not differ between the early (mean ± SE = 57 ± 2.21) and late (60 ± 2.30) successional stages, we verified that tree height affects ant species richness; however, this effect interacted with the successional stage (Table 3). Thus, tree height had a negative effect on the ant species richness in trees in the early successional stage and a positive effect on ant species richness in trees in the late successional stage (Fig. 2). Treetop connectivity and EFN-bearing plants did not affect ant species richness on trees, and the EFN-bearing plants were not related to the seasonality (Table 3). Moreover, we found distinct ant species compositions in relation to tree height (NMDS, Fig. 3; PERMANOVA $F_{1,147} = 9.21$, $P < 0.001$), and between successional stages (NMDS, Fig. 3, PERMANOVA $F_{1,147} = 26.31$, $P < 0.001$).

Ant-tree interactions

We found 786 independent interactions among the 57 ant species and the 75 individual trees in the early stage throughout the four sampling periods (Fig. 4). For the late stage, there were 914 independent interactions among the 60 ant species and the 75 individual trees. We found a low complementarity of interactions at the community level of early ($H_2' = 0.15$, $P < 0.05$) and late ($H_2' = 0.17$, $P < 0.0001$) successional stages. Furthermore, we found that the interactions between ant species were not exclusive and non-randomly distributed in the trees of early (*C*-score = 0.77, $P < 0.001$) and late successional stages (*C*-score = 0.76, $P = 0.002$), indicating that a high degree of interspecific interactions determined the species distribution through the sampled trees. Additionally, we found no relationship between the tree specialization index (*d*′) and tree species both in the early and late successional stages (Table 3).

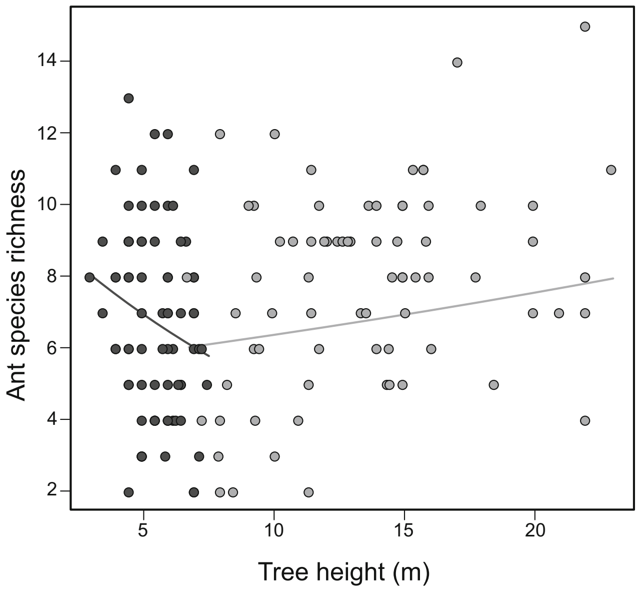

Fig. 2 Ant richness as a function of tree height in early (black circles) and late (gray circles) successional stages (Table 2) of the tropical dry forest of the Parque Estadual da Mata Seca (PEMS), northern Minas Gerais, Southeast Brazil

Based on the core-peripheral species analyses, we found seven core ant species for the early stage: *Camponotus blandus*, *Camponotus renggeri*, *Cephalotes pusillus*, *Crematogaster goeldii*, *Camponotus melanoticus*, *Pseudomyrmex gracilis*, and *Pseudomyrmex pallidus* (Table 1; Fig. 4, left). For the late successional stage, the core

Table 3 Analyses of the deviance of the minimal adequate models showing the effects of tree traits and successional stage on ant richness; seasonality on ant species richness; and tree specialization on tree species, for the tropical dry forest of Parque Estadual da Mata Seca (PEMS), Minas Gerais, Southeast Brazil

Analysis	Successional stage	Terms	df	Deviance (χ^2)	*P*
Tree traits and ant species richness	Both together	Tree height	1	4.19	0.04*
		Successional stage	1	0.09	0.75
		Tree height: successional stage	1	4.80	0.02*
EFN (per season) and ant species richness	Early	EFN (per season)	1	0.65	0.41
	Late	EFN (per season)	1	0.30	0.57
Tree Specialization index (*d*′) and tree species richness	Early	Tree species	13	2.44	0.74
	Late	Tree species	15	2.03	0.40

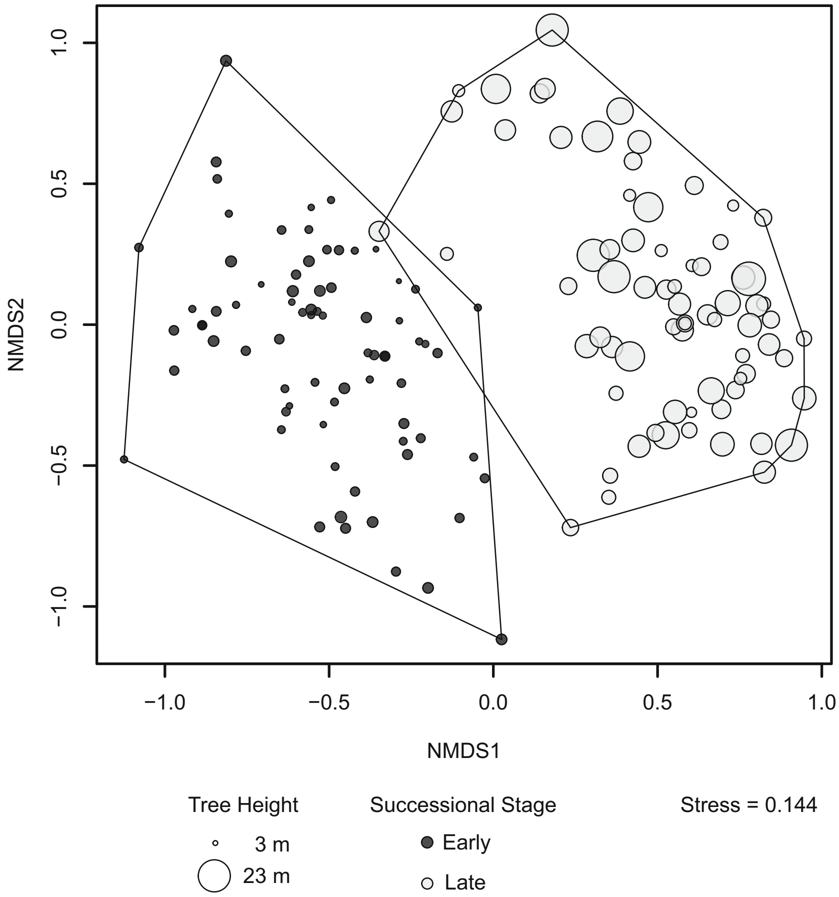

Fig. 3 NMDS plot of species composition according to tree height (point sizes) and early (dark gray) and late (light gray) successional stages in a tropical dry forest, Southeast Brazil

ant species were *Crematogaster goeldii*, *Camponotus arboreus*, *C. melanoticus*, *C. vittatus*, *C. atriceps*, *Pseudomyrmex schuppi*, and *Cephalotes atratus* (Table 1, Fig. 4, right). Only *C. goeldii* and *C. melanoticus* were core species in both successional stages (Table 1, Fig. 4), following the remarkable differences in species composition between the two successional stages presented above.

Discussion

Based on our results, tree height is an important driver for ant species richness in the tropical dry forest canopies studied, and this effect is dependent upon the successional stage. Furthermore, we found that core ant species in the ant species–tree networks have low spatial co-occurrence, which means that these ant species establish in sets of trees. Increasing tree height decreased the ant species richness in trees in the early successional stage, and we found a greater ant species richness in the smallest trees within this stage. This is most likely due to the foraging habitat of the ant species. In a TDF in Mexico, Vergara-Torres et al. (2017) found epigeic ant species foraging on trees, which has also been reported by Marques et al. (2017) in our study area. We found a particular ant fauna in each successional stage, in which only trees of the early successional stage were mainly used by epigeic ants for foraging. Examples of this include the typically predatory epigeic species *Ectatomma muticum* and *Odontomachus bauri*, some generalist myrmicines (e.g., *Pheidole* spp., *Solenopsis* spp., *Wasmannia* spp., *Rogeria* spp.), army ants such as *Labidus praedator* and *Eciton* sp1 (Brandão et al. 2012), and a typical fungus-grower ant genus that nests in the soil, represented by the ant species *Cyphomyrmex* sp1 (Mackay et al. 2014).

In the late successional stage, the effect of tree height on ant species richness followed the expected pattern, i.e., increased height resulted in greater ant species richness. A positive correlation between tree height and ant species richness has also been reported in other studies in the Brazilian savanna (Costa et al. 2011; Koch et al. 2016) and semi-deciduous and wet forests (Campos et al. 2006; Lourenço et al. 2015; Yusah and Foster 2016). In our study, the genus *Azteca* occurred exclusively in the late successional stage. It is a common arboreal ant genus (Brandão et al. 2012), especially *Azteca instabilis*, forming patches around shade trees (Philpott 2006). Taller trees are associated with the increase in available microhabitats or nest sites (Klimes et al. 2012), creating more opportunities for shelter and resource use (Campos et al. 2006; Klimes et al. 2012). In our study area, trees with similar

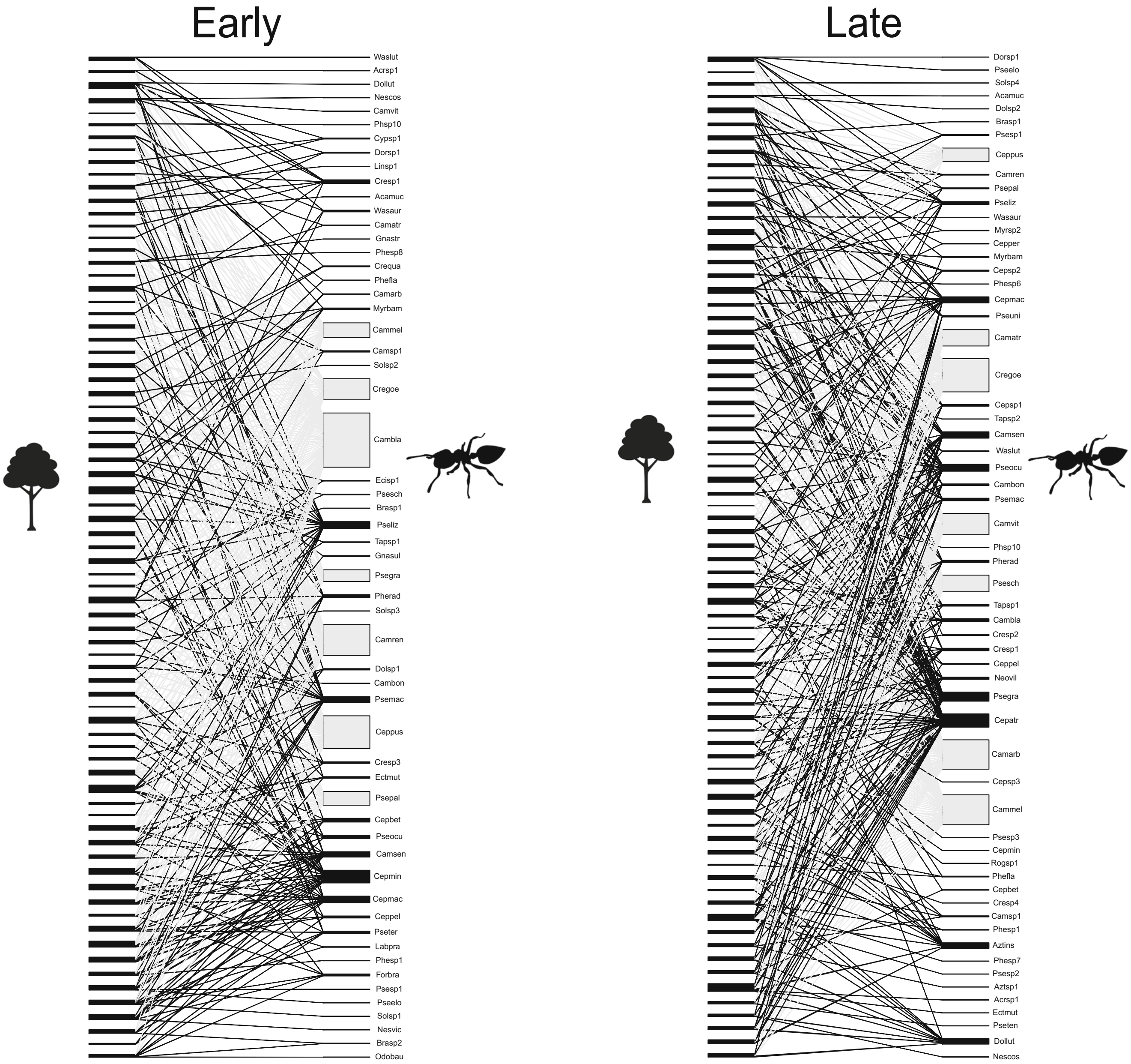

Fig. 4 Tree-ant interaction networks in different successional stages, early (left) and late (right), in a tropical dry forest, Southeast Brazil. The boxes on the left-hand side represent individual trees, while the boxes on the right-hand side represent the ant species (nodes). The thickness of the boxes represents the centrality per degree of each node and the core ant species are in gray

heights of both successional stages were subjected to different environmental conditions. Specifically, while trees of the early successional stage tended to be more exposed to solar radiation, trees of the late successional stage with similar height were mostly located in the understory, with limited radiation. Therefore, to control sun exposition on the trees, we sampled ants on trees with different tree heights in both successional stages. This approach allowed us to infer about our specific initial hypothesis, focused on the importance of tree height under similar sun exposition levels, for the maintenance of ant diversity and the interactions in an individual-based network approach in the two successional stages. Our results raised main issues related to the importance of the successional stage and tree height to canopy ant diversity, a key issue for conservation and ecology.

In many systems, the connectivity among treetops is a determining factor for arboreal ant fauna, as it can promote movement and increase available resources (Majer and Delabie 1999; Powell et al. 2011; Yanoviak 2015; Adams et al. 2017). In our study, however, this factor did not explain ant species richness. Although the trees were in contact with each other via their branches, leaves, and lianas, our findings may be related to the paucity of lianas in the late successional stage in the tropical dry forest studied (Madeira et al. 2009).

Besides, we found that ant species richness was not related to the distribution of the EFNs, in accordance with studies previously performed in the low woody vegetation, in which the authors found that EFNs have a limited effect on ant communities (Camarota et al. 2015; Sendoya et al. 2016). Most likely, this is because EFN secretion is seasonally restricted, with a significant emission of exudates being associated with the production of new buds and leaves, increasing ant foraging activity (Blüthgen and Reifenrath 2003; Melo et al. 2010; Schoereder et al. 2010; Lange et al. 2013). Indeed, environmental seasonality influences plant phenology (Pezzini et al. 2014) and insect diversity (Neves F de et al. 2013; Novais et al. 2016). In addition, as expected in a species-area relationship, in tropical forests, higher trees should have greater connectivity with neighboring trees and a greater amount of EFNs (Villamil et al. 2013; Dáttilo et al. 2014). Although we measured only the vertical height of the trees, we consider that the explanatory variables that we used (i.e., tree height, tree connectivity, the presence of EFNs) were sufficient to support our hypothesis. Nevertheless, we acknowledge that other canopy traits, such as cavities or other spaces formed by suspense gardens that accumulate litter, e.g., epiphytes (Powell et al. 2011; DaRocha et al. 2016; Klimes 2017), crown size, number of ramifications, growth units, and foliage (Campos et al. 2006; Blüthgen and Stork 2007; Lourenço et al. 2015), or tree density (Ribas et al. 2003), may contribute to ant occurrence and distribution and thereby to the network interactions found in this study.

We found a low co-occurrence (as expressed by the *C*-score index) between ant species and trees in each successional stage, suggesting that particular ant assemblages are associated with specific sets of trees (individuals). Additionally, in our ant-plant co-occurrence networks, individual trees were not influenced by tree species in terms of specialization (given by *d*′). Although we did not find an influence of the tree species in our networks, other factors related to habitat requirements could explain our results, such as food and shelter availability (Philpott and Foster 2005; Houadria et al. 2015), which were not measured in our study. Thus, in addition to the habitat requirement, we propose that biotic forces may be structuring the ant communities in our study, for example, species competition. According to this, in a study of ant-tree relationships in the Brazilian savanna (Camarota et al. 2016), the authors found that competition better explained co-occurrence patterns than habitat requirements. More detailed studies evaluating competition or habitat requirements could definitively conclude which factor most interferes with tree foraging in tropical dry forest canopies. Another exciting avenue of research is related to the physiological tolerance of ant species and the implications related to the persistence of these ant species in such environments (Bestelmeyer 2008; Spicer et al. 2017).

We conclude that the effects of tree height on ant species richness are dependent on the successional stage and may be related to the ant species composition and their functional role. We evidenced a high number of some arboreal ant species in the canopies, since the generalist core ant species with a low spatial-temporal co-occurrence established specific territories persistent over time (i.e., four samples over the course of 2 years analyzed together). Based on this, and because the ant-plant interactions were non-randomly distributed, our findings strongly suggest that ants play a key role in the structure of the associated fauna on the studied tropical dry forest canopies.

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References

Adams BJ, Schnitzer SA, Yanoviak SP (2017) Trees as islands: canopy ant species richness increases with the size of liana-free trees in a Neotropical forest. Ecography 40:1067–1075. https://doi.org/10.1111/ecog.02608

Alvares CA, Stape JL, Sentelhas PC, de Moraes Gonçalves JL, Sparovek G (2013) Köppen's climate classification map for Brazil. Meteorol Zeitschrift 22:711–728. https://doi.org/10.1127/0941-2948/2013/0507

Antoniazzi R, Dáttilo W, Rico-Gray V (2018) A useful guide of main indices and software used for ecological networks studies. In: Ecological networks in the tropics. Springer, Cham, pp 185–196

Arroyo-Mora JP, Sánchez-Azofeifa GA, Kalacska MER et al (2005) Secondary forest detection in a Neotropical dry forest landscape using Landsat 7 ETM+ and IKONOS imagery. Biotropica 37:497–507. https://doi.org/10.1111/j.1744-7429.2005.00068.x

Baccaro FB, Feitosa RM, Fernandez F et al (2015) Guia para os gêneros de formigas do Brasil, 1st edn. Editora INPA, Manaus

Bascompte J (2007) Networks in ecology. Basic Appl Ecol 8:485–490. https://doi.org/10.1016/j.baae.2007.06.003

Bascompte J, Jordano P, Melián CJ, Olesen JM (2003) The nested assembly of plant–animal mutualistic networks. Proc Natl Acad Sci USA 100:9383–9387. https://doi.org/10.1073/pnas.1633576100

Basset Y, Cizek L, Cuénoud P et al (2012) Arthropod diversity in a tropical forest. Science 338:1481–1484. https://doi.org/10.1126/science.1226727

Basset Y, Cizek L, Cuénoud P, Didham RK, Novotny V, Ødegaard F, Roslin T, Tishechkin AK, Schmidl J, Winchester NN, Roubik DW, Aberlenc HP, Bail J, Barrios H, Bridle JR, Castaño-Meneses G, Corbara B, Curletti G, Duarte da Rocha W, de Bakker D, Delabie JHC, Dejean A, Fagan LL, Floren A, Kitching RL, Medianero E, Gama de Oliveira E, Orivel J, Pollet M, Rapp M, Ribeiro SP, Roisin Y, Schmidt JB, Sørensen L, Lewinsohn TM, Leponce M (2015) Arthropod distribution in a tropical rainforest: tackling a four dimensional puzzle. PLoS One 10:e0144110. https://doi.org/10.1371/journal.pone.0144110

Bates D, Mächler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. J Stat Softw 67:1–48

Bestelmeyer BT (2008) The trade-off between thermal tolerance and behavioural dominance in a subtropical South American ant community. J Anim Ecol 69:998–1009. https://doi.org/10.1111/j.1365-2656.2000.00455.x

Blüthgen N, Reifenrath K (2003) Extrafloral nectaries in an Australian rainforest : structure and distribution. Aust J Bot 51:515–527. https://doi.org/10.1071/bt02108

Blüthgen N, Stork NE (2007) Ant mosaics in a tropical rainforest in Australia and elsewhere: a critical review. Austral Ecol 32:93–104. https://doi.org/10.1111/j.1442-9993.2007.01744.x

Blüthgen N, Menzel F, Blüthgen N (2006) Measuring specialization in species interaction networks. BMC Ecol 6:9. https://doi.org/10.1186/1472-6785-6-9

Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Stevens MHH, White JSS (2009) Generalized linear mixed models: a practical guide for ecology and evolution. Trends Ecol Evol 24:127–135. https://doi.org/10.1016/j.tree.2008.10.008

Bolton B (2012) AntCat: an online catalog of the ants of the world. Online publication: URL: http://antcat.org. [Accessed January 2015]

Brandão C, Silva R, Delabie J (2012) Neotropical ants (Hymenoptera) functional groups: nutritional and applied implications. In: Panizzi AR, Parra JRP (eds) Insect bioecology and nutrition for integrated pest management. CRC Press, Boca Raton, pp 213–236

Camarota F, Powell S, Vasconcelos HL, Priest G, Marquis RJ (2015) Extrafloral nectaries have a limited effect on the structure of arboreal ant communities in a Neotropical savanna. Ecology 96:231–240. https://doi.org/10.1890/14-0264.1

Camarota F, Powell S, Melo AS, Priest G, Marquis RJ, Vasconcelos HL (2016) Co-occurrence patterns in a diverse arboreal ant community are explained more by competition than habitat requirements. Ecol Evol 6:8907–8918. https://doi.org/10.1002/ece3.2606

Campos RI, Vasconcelos HL, Ribeiro SP, Neves FS, Soares JP (2006) Relationship between tree size and insect assemblages associated with *Anadenanthera macrocarpa*. Ecography 29:442–450. https://doi.org/10.1111/j.2006.0906-7590.04520.x

Castaño-Meneses G (2014) Trophic guild structure of a canopy ants community in a Mexican tropical deciduous forest. Sociobiology 61:35–42. https://doi.org/10.13102/sociobiology.v61i1.35-42

Chao A, Gotelli NJ, HSieh TC et al (2014) Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. Ecol Monogr 84:45–67. https://doi.org/10.1890/13-0133.1

Crawley MJ (2013) The R book, 2nd edn. John Wiley & Sons, Chichester

Costa FV, Neves F de S, Silva J de O, Fagundes M (2011) Relationship between plant development, tannin concentration and insects associated with *Copaifera langsdorffii* (Fabaceae). Arthropod Plant Interact 5:9–18. https://doi.org/10.1007/s11829-010-9111-6

DaRocha WD, Neves FS, Dáttilo W, Delabie JHC (2016) Epiphytic bromeliads as key components for maintenance of ant diversity and ant-bromeliad interactions in agroforestry system canopies. For Ecol Manag 372:128–136. https://doi.org/10.1016/j.foreco.2016.04.011

Dáttilo W, Guimarães PR, Izzo TJ (2013) Spatial structure of ant–plant mutualistic networks. Oikos 122:1643–1648. https://doi.org/10.1111/j.1600-0706.2013.00562.x

Dáttilo W, Fagundes R, Gurka CAQ, Silva MSA, Vieira MCL, Izzo TJ, Díaz-Castelazo C, del-Claro K, Rico-Gray V (2014) Individual-based ant–plant networks: diurnal-nocturnal structure and species-area relationship. PLoS One 9:e99838. https://doi.org/10.1371/journal.pone.0099838

Dejean A, Corbara B, Orivel J, Leponce M (2007) Rainforest canopy ants: the implications of territoriality and predatory behavior. Funct Ecosyst Commun 1:105–120

Dejean A, Djiéto-Lordon C, Céréghino R, Leponce M (2008) Ontogenetic succession and the ant mosaic: an empirical approach using pioneer trees. Basic Appl Ecol 9:316–323. https://doi.org/10.1016/j.baae.2007.03.001

Dejean A, Ryder S, Bolton B, Compin A, Leponce M, Azémar F, Céréghino R, Orivel J, Corbara B (2015) How territoriality and host-tree taxa determine the structure of ant mosaics. Sci Nat 102:33. https://doi.org/10.1007/s00114-015-1282-7

Del-Claro K, Lange D, Torezan-Silingardi HM et al (2018) The complex ant–plant relationship within tropical ecological networks. In: Dáttilo W, Rico-Gray V (eds) Ecological networks in the tropics: an integrative overview of species interactions from some of the most species-rich habitats on earth. Springer, Cham, pp 59–71

Dormann CF, Gruber B, Fründ J (2008) Introducing the bipartite package: analysing ecological networks. R News 8:8–11

Fagundes R, Dáttilo W, Ribeiro SP, Rico-Gray V, del-Claro K (2016) Food source availability and interspecific dominance as structural mechanisms of ant–plant–hemipteran multitrophic networks. Arthropod Plant Interact 10:207–220. https://doi.org/10.1007/s11829-016-9428-x

Falcão JCF, Dáttilo W, Izzo TJ (2015) Efficiency of different planted forests in recovering biodiversity and ecological interactions in Brazilian Amazon. For Ecol Manag 339:105–111. https://doi.org/10.1016/j.foreco.2014.12.007

Fisher BL (2002) Antweb. Online Publication: URL: http://www.antweb.org. [Accessed January 2019]

Gonzalez AM (2011) Domacios y nectarios extraflorales en Bignoniáceas: componentes vegetales de una interacción mutualística. Bol la Soc Argentina Bot 46:271–288

Gonzalez AM (2013) Indumento, nectarios extraflorales y anatomía foliar en bignoniáceas de la Argentina. Bol la Soc Argentina Bot 48:221–245. https://doi.org/10.1103/PhysRevE.49.2192

Gordon DM (2012) The dynamics of foraging trails in the tropical arboreal ant *Cephalotes goniodontus*. PLoS One 7:e50472. https://doi.org/10.1371/journal.pone.0050472

Gotelli NJ (2000) Null model analysis of species co-occurrence patterns. Ecology 81:2606–2621. https://doi.org/10.1890/0012-9658(2000)081[2606:NMAOSC]2.0.CO;2

Houadria M, Salas-Lopez A, Orivel J, Blüthgen N, Menzel F (2015) Dietary and temporal niche differentiation in tropical ants—can they explain local ant coexistence? Biotropica 47:208–217. https://doi.org/10.1111/btp.12184

Hsieh TC, Ma KH, Chao A (2016) iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). Methods Ecol Evol 7:1451–1456. https://doi.org/10.1111/2041-210X.12613

Janda M, Konečná M (2011) Canopy assemblages of ants in a New Guinea rain forest. J Trop Ecol 27:83–91. https://doi.org/10.1017/S0266467410000623

Klimes P (2017) Diversity and specificity of ant–plant interactions in canopy communities: insights from primary and secondary tropical forests in New Guinea. In: Oliveira PS, Koptur S (eds) Ant-plant interactions: impacts of humans on terrestrial ecosystems. Cambridge University Press, Cambridge, pp 26–51

Klimes P, Idigel C, Rimandai M, Fayle TM, Janda M, Weiblen GD, Novotny V (2012) Why are there more arboreal ant species in primary than in secondary tropical forests? J Anim Ecol 81:1103–1112. https://doi.org/10.1111/j.1365-2656.2012.02002.x

Klimes P, Fibich P, Idigel C, Rimandai M (2015) Disentangling the diversity of arboreal ant communities in tropical forest trees. PLoS One 10:e0117853. https://doi.org/10.1371/journal.pone.0117853

Koch EBA, Camarota F, Vasconcelos HL (2016) Plant ontogeny as a conditionality factor in the protective effect of ants on a Neotropical tree. Biotropica 48:198–205. https://doi.org/10.1111/btp.12264

Lange D, Dáttilo W, Del-Claro K (2013) Influence of extrafloral nectary phenology on ant–plant mutualistic networks in a Neotropical savanna. Ecol Entomol 38:463–469. https://doi.org/10.1111/een.12036

Leal CRO, Silva JO, Sousa-Souto L, de Siqueira Neves F (2016) Vegetation structure determines insect herbivore diversity in seasonally dry tropical forests. J Insect Conserv 20:979–988

Longino JT (2007) Ants of costa rica. In: Online Publ. URL http://academic.evergreen.edu, accessed January, 2015

Lourenço GM, Campos RBF, Ribeiro SP (2015) Spatial distribution of insect guilds in a tropical montane rainforest: effects of canopy structure and numerically dominant ants. Arthropod Plant Interact 9:163–174. https://doi.org/10.1007/s11829-015-9359-y

Lowman MD, Schowalter T, Franklin J (2012) Methods in forest canopy research, 1st edn. University of California Press, Berkeley

Mackay WP, Maes J-M, Fernández PR, Luna G (2014) The ants of North and Central America: the genus *Mycocepurus* (Hymenoptera: Formicidae). J Insect Sci 4(27):1–7. https://doi.org/10.1093/jis/4.1.27

Madeira BG, Espírito-Santo MM, Neto SD et al (2009) Changes in tree and liana communities along a successional gradient in a tropical dry forest in South-eastern Brazil. Plant Ecol 201:291–304. https://doi.org/10.1007/s11258-009-9580-9

Majer JD (1972) The ant mosaic in Ghana cocoa farms. Bull Entomol Res 62:151–160

Majer JD, Delabie JHC (1993) An evaluation of Brazilian cocoa farm ants as potential biological control agents. J Plant Prot Trop 10:43–49

Majer JD, Delabie JHC (1999) Impact of tree isolation on arboreal and ground ant communities in cleared pasture in the Atlantic rain forest region of Bahia, Brazil. Insect Soc 46:281–290. https://doi.org/10.1007/s000400050147

Majer JD, Delabie JHC, Smith MRB (1994) Arboreal ant community patterns in Brazilian cocoa farms. Biotropica 26:73–83. https://doi.org/10.2307/2389112

Marques T, Espírito-Santo MM, Neves FS, Schoereder JH (2017) Ant assemblage structure in a secondary tropical dry forest: the role of ecological succession and seasonality. Sociobiology 64(3):261–275. https://doi.org/10.13102/sociobiology.v64i2.1276

Melo Y, Machado SR, Alves M (2010) Anatomy of extrafloral nectaries in Fabaceae from dry-seasonal forest in Brazil. Bot J Linn Soc 163:87–98. https://doi.org/10.1111/j.1095-8339.2010.01047.x

Moral RA, Hinde J, Demétrio CGB (2017) Half-normal plots and overdispersed models in R: the hnp package. J Stat Softw 81:1–23. https://doi.org/10.18637/jss.v081.i10

Nakamura A, Kitching RL, Cao M, Creedy TJ, Fayle TM, Freiberg M, Hewitt CN, Itioka T, Koh LP, Ma K, Malhi Y, Mitchell A, Novotny V, Ozanne CMP, Song L, Wang H, Ashton LA (2017) Forests and their canopies: achievements and horizons in canopy science. Trends Ecol Evol 32:438–451. https://doi.org/10.1016/j.tree.2017.02.020

Neves F de S, Silva JO, Marques T et al (2013) Spatiotemporal dynamics of insects in a Brazilian tropical dry forest. In: Sanchez-Azofeifa A, Powers JS, Fernandes GW, Quesada M (eds) Tropical dry forests in the Americas. CRC Press, New York, pp 225–239

Neves FS, Araújo LS, Espírito-Santo MM, Fagundes M, Fernandes GW, Sanchez-Azofeifa GA, Quesada M (2010) Canopy herbivory and insect herbivore diversity in a dry forest-savanna transition in Brazil. Biotropica 42:112–118. https://doi.org/10.1111/j.1744-7429.2009.00541.x

Neves FS, Silva JO, Espírito-Santo MM, Fernandes GW (2014) Insect herbivores and leaf damage along successional and vertical gradients in a tropical dry forest. Biotropica 46:14–24. https://doi.org/10.1111/btp.12068

Novais SMA, Evangelista LA, Reis-Júnior R, Neves FS (2016) How does dung beetle (Coleoptera: Scarabaeidae) diversity vary along a rainy season in a tropical dry forest? J Insect Sci 16:81. https://doi.org/10.1093/jisesa/iew069

Oksanen J, Blanchet FG, Kindt R, et al (2015) Vegan: community ecology package. R Packag version 23–0. 2015

Patefield WM (1981) Algorithm AS 159: an efficient method of generating random R × C tables with given row and column totals. J R Stat Soc Ser C (Appli Stat) 30:91–97. https://doi.org/10.2307/2346669

Perry DR (1978) A method of access into the crowns of emergent and canopy trees. Biotropica 10:155–157. https://doi.org/10.2307/2388019

Pezzini FF, Ranieri BD, Brandão DO, Fernandes GW, Quesada M, Espírito-Santo MM, Jacobi CM (2014) Changes in tree phenology along natural regeneration in a seasonally dry tropical forest. Plant Biosyst 148:965–974. https://doi.org/10.1080/11263504.2013.877530

Philpott SM (2006) Ant patchiness: a spatially quantitative test in coffee agroecosystems. Naturwissenschaften 93:386–392. https://doi.org/10.1007/s00114-006-0123-0

Philpott SM, Foster PF (2005) Nest-site limitation in coffee agroecosystems: artificial nests maintain diversity of arboreal ants. Ecol Appl 15:1478–1485. https://doi.org/10.1890/04-1496

Pinheiro J, Bates D, DebRoy S, Sarkar D (2014) R Core Team (2014) nlme: linear and nonlinear mixed effects models. R package version 3.1–117. https://CRANR-project.org/package=nlme

Powell S, Costa AN, Lopes CT, Vasconcelos HL (2011) Canopy connectivity and the availability of diverse nesting resources affect species coexistence in arboreal ants. J Anim Ecol 80:352–360. https://doi.org/10.1111/j.1365-2656.2010.01779.x

R Core Team (2017) R: a language and environment for statistical computing. R Found Stat Comput Vienna, Austria

Ribas CR, Schoereder JH, Pic M, Soares SM (2003) Tree heterogeneity, resource availability, and larger scale processes regulating arboreal ant species richness. Austral Ecol 28:305–314. https://doi.org/10.1046/j.1442-9993.2003.01290.x

Ribeiro SP, Espírito Santo NB, Delabie JHC, Majer JD (2013) Competition, resources and the ant (Hymenoptera: Formicidae) mosaic: a comparison of upper and lower canopy. Myrmecol News 18:113–120

Rico-Gray V, Oliveira PS (2007) The ecology and evolution of ant-plant interactions. University of Chicago Press, Chicago

Rivera GL (2000) Nectarios Extranupciales Florales en Especies de Bignoniaceae de Argentina. Darwiniana 38:1–10

Schoereder J, Sobrinho T, Madureira M et al (2010) The arboreal ant community visiting extrafloral nectaries in the Neotropical cerrado savanna. Terr Arthropod Rev 3:3–27. https://doi.org/10.1163/187498310X487785

Sendoya SF, Blüthgen N, Tamashiro JY, Fernandez F, Oliveira PS (2016) Foliage-dwelling ants in a Neotropical savanna: effects of plant and insect exudates on ant communities. Arthropod Plant Interact 10:183–195. https://doi.org/10.1007/s11829-016-9423-2

Silva LF, Souza RM, Solar RRC, Neves F de S (2017) Ant diversity in Brazilian tropical dry forests across multiple vegetation domains. Environ Res Lett 12:35002. https://doi.org/10.1088/1748-9326/aa5f2a

Sousa-Souto L, Figueiredo PMG, Ambrogi BG, Oliveira A, Ribeiro GT, Neves F (2016) Composition and richness of arboreal ants in fragments of Brazilian Caatinga: effects of secondary succession. Sociobiology 63:762–769. https://doi.org/10.13102/sociobiology.v63i2.909

Spicer ME, Stark AY, Adams BJ, Kneale R, Kaspari M, Yanoviak SP (2017) Thermal constraints on foraging of tropical canopy ants. Oecologia 183:1007–1017. https://doi.org/10.1007/s00442-017-3825-4

Stone L, Roberts A (1990) The checkerboard score and species distributions. Oecologia 85:74–79. https://doi.org/10.1007/BF00317345

Stork NE, Grimbacher PS (2006) Beetle assemblages from an Australian tropical rainforest show that the canopy and the ground strata contribute equally to biodiversity. Proc R Soc B Biol Sci 273:1969–1975. https://doi.org/10.1098/rspb.2006.3521

Tanaka HO, Yamane S, Itioka T (2010) Within-tree distribution of nest sites and foraging areas of ants on canopy trees in a tropical rainforest in Borneo. Popul Ecol 52:147–157. https://doi.org/10.1007/s10144-009-0172-2

Tobin J (1995) Ecology and diversity of tropical forest canopy ants. In: Lowman MD, Nadkarni NM (eds) Forest canopies. Academic Press, San Diego, CA, pp 129–147

Vergara-Torres CA, Vásquez-Bolaños M, Corona-López AM, Toledo-Hernández VH, Flores-Palacios A (2017) Ant (Hymenoptera: Formicidae) diversity in the canopy of a tropical dry forest in Tepoztlán, Central Mexico. Ann Entomol Soc Am 110:197–203. https://doi.org/10.1093/aesa/saw074

Villamil N, Márquez-Guzmán J, Boege K (2013) Understanding ontogenetic trajectories of indirect defence: ecological and anatomical constraints in the production of extrafloral nectaries. Ann Bot 112:701–709. https://doi.org/10.1093/aob/mct005

Wardhaugh CW (2014) The spatial and temporal distributions of arthropods in forest canopies: uniting disparate patterns with hypotheses for specialisation. Biological Reviews 89(4):1021–1041. https://doi.org/10.1111/brv.12094

Weber MG, Porturas LD, Keeler KH (2015) World list of plants with extrafloral nectaries. www.extrafloralnectaries.org. [Accessed January 2015]

Yanoviak SP (2015) Effects of lianas on canopy arthropod community structure. In: Schnitzer SA, Bongers F, Burnham RJ, Putz FE (eds) Ecology of lianas. John Wiley & Sons, Ltd, Hoboken, pp 343–361

Yusah KM, Foster WA (2016) Tree size and habitat complexity affect ant communities (Hymenoptera: Formicidae) in the high canopy of Bornean rain forest. Myrmecol News 23:15–23