Scattered Trees as Crucial Elements in Maintaining Urban Diversity: A Case Study with Canopy ants in a Biodiversity Hotspot

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Abstract

Urban environments are under a high degree of human disturbance, which profoundly changes their abiotic characteristics, affecting the biotic communities. A conspicuous element in cities are scattered trees, often included in urban planning around the world. These trees are key elements for urban ecological processes and services and act as islands of resources (i.e., food and shelter) for a considerable arthropod's diversity, such as ants. Studies involving ants in urban environments often focus on ground-dwelling ants, and few studies seek to glimpse the ants that occupy scattered trees and, even less, how these ants and trees interact within cities. This study aimed to investigate the ant communities foraging day and night on trees in an urban area inside a biodiversity hotspot, the Brazilian Atlantic Forest. Specifically, we investigated how tree characteristics (tree size, tree isolation, presence of extrafloral nectaries, and the tree origin, i.e., native and exotic) modulate ant diversity and ant-plant interactions. We found that the species composition is different between day and night, as well as the central core of generalist ant species of day and night interaction networks. The tree size increases beta-diversity among trees only of the nocturnal ant community, while none of the tree characteristics shaped the ant community. This study is the first to address the role of scattered trees in maintaining the diversity of arboreal ants in urban landscapes, focusing on species diversity and their interaction networks. Overall, we provide insights supporting the conservation value of scattered trees in maintaining urban biodiversity.

1. Introduction

Urbanization can significantly impact on communities of all kinds of organisms, including plants and animals, both vertebrates and invertebrates (Gibb and Hochuli 2002; Mckinney 2008). At a regional level, the reduction of natural vegetation cover and spatial heterogeneity led to changes in the composition and functional diversity of organisms (Aronson et al. 2017; Nooten et al. 2019). At a local level, urbanization often has a direct influence on biota due to changes in microclimatic conditions (e.g., habitat complexity, light availability, soil nutrient composition) and a decrease in resource availability (i.e., food and shelter) (Byrne 2007; Friedrich and Philpott 2009; Threlfall et al. 2016). Thus, summing regional and local factors, urban ecosystems can provide unique environmental templates that might lead to the assembly of novel ecological communities with distinct taxonomic and functional diversities (Aronson et al. 2017; Fournier et al. 2020).

Despite urbanization being a significant threat to global biodiversity (Seto et al. 2012), cities can be critical for native biodiversity conservation (Ives et al. 2016). A significant part of urban biodiversity lives within urban green spaces (UGS) that include a range of habitats, like remnant patches of native vegetation, gardens, and yards (Aronson et al. 2017). While UGS retained the focus on urban biodiversity studies, it is also important to consider the organisms inhabiting the green patches outside UGS. For example, there is an increasing recognition of the importance of scattered trees, which can be found anywhere in a city, from public areas to private lands (Prevedello et al. 2018). In this sense, scattered trees can provide a range of ecosystem services, such as providing shelter and food resources for animals and enhancing landscape connectivity (Prevedello et al. 2018; Bhullar and Majer 2000). Therefore, understanding the role of scattered

trees and their resident biodiversity can reveal important aspects of conservation, ecology, and human well-being in cities.

Scattered trees may act as islands in the urban matrix, and their size, shape, and connectivity with the surrounding vegetation might constrain the diversity and abundance of their inhabiting organisms (Stagoll et al. 2012). While there is an increasing number of studies focusing on the potential effects of different factors on urban community assemblies of several organisms, most of them focused on the traditional species diversity patterns (McKinney 2008). However, the ecological associations between species, a crucial component in the origin and maintenance of biodiversity (Andresen et al. 2018), are often neglected in studies made in urban environments. Additionally, it is known that ecological associations between species are highly influenced by habitat conditions, including urbanization (Wood and Pullin 2002). Although there is much progress in understanding how urbanization affects diversity, it is not clear how isolated trees in an urban matrix can guarantee the integrity of the associated fauna.

Ants are an important part of urban biodiversity, both in species diversity and biomass (Lessard and Christopher 2005; Sanford et al. 2009). Ants are also considered ecological indicators, responding rapidly to habitat changes (Lawes et al. 2017). Ants play key ecological roles in urban ecosystems, such as soil modification, predation, seed dispersal, and plant defense against herbivores (Sanford et al. 2009; Del Toro et al. 2012). Not surprisingly, some studies have assessed the role of urbanization in ant communities. Although it was often detected an overall negative effect of urbanization on ant diversity (e.g., Thompson and McLachlan 2007; Uno et al. 2010; Dáttilo et al. 2011; García-Martínez et al. 2019), this is not a consensus (Savitha et al. 2008; Cross et al. 2016). Moreover, previous studies have suggested that ground-dwelling and arboreal ants respond differently to urban habitat changes (Estrada et al. 2014; Santiago et al. 2018). However, how arboreal ants living in scattered trees across the urban landscape are affected by urbanization remains unknown.

Arboreal ants comprise a significant part of overall ant diversity in tropical ecosystems (Floren et al. 2014; Longino and Colwell 2020) and are often involved in many interactions, mostly with other arthropods and their host trees (Rico-Gray and Oliveira 2007; Blüthgen and Feldhaar 2010). Additionally, distinct ant species forage in distinct periods of the day, with a shift in community composition between day and night (e.g., Cros et al. 1997; Cerdá et al. 1998b; Dáttilo et al. 2014a). Often, factors related to the host trees can be critical for arboreal ants' diversity and species interactions (e.g., Klimes et al. 2012; Antoniazzi et al. 2019). For example, higher connectivity between trees can increase species diversity, as the colonization of new trees by different species is facilitated (Powell et al. 2011; Adams et al. 2017). Tree size can increase the number of resident species in a given tree (Campos et al. 2006; Koch et al. 2016), as larger trees often have more available resources, like nesting sites. Food resources can also be quite variable among different tree species, as some species present extrafloral nectaries (EFNs), which are readily used by a diverse array of ant species (Rico-Gray and Oliveira 2007). Although some of these effects on the ant community are predictable in conserved habitats, it is less understood how they can act in urban environments. Additionally, many scattered trees on urban landscapes are from exotic species, which may directly influence the community of herbivores inhabiting them, which can indirectly impact the ants interacting with the herbivores (Tallamy 2004; Urghardt et al. 2010). Thus, arboreal ants raise as an exciting model system to

understand the factors shaping species organization and biotic interactions in urban areas, especially in highly diverse environments, such as the tropics.

This study aimed to evaluate the factors shaping the local communities of arboreal ants in scattered trees within urban ecosystems. For this, we studied a community of tropical arboreal ants living in scattered trees of a city in a Brazilian Atlantic Forest, a biodiversity hotspot, *sensu* Mittermeier et al. (2005). Also, we assessed potential factors related to the host trees that may shape the ant community and ant-plant interactions. Specifically, we asked the following questions: 1) Is there an influence of different factors associated with the trees (i.e., tree size, isolation, exotic species, and presence of EFNs) on resource-dominant ant assemblages? 2) Do different factors associated with the trees influence the structure of ant-tree individual-based networks?

2. Material And Methods

2.1. Study area

We performed this work inside the campus of the Federal University of Sergipe (UFS), at the city of *São Cristóvão*, located in the mid-east of Sergipe state, Northeastern Brazil (10° 55' 31" S, 37° 06' 08" W). The university campus comprises about 65 hectares of building constructions, parking lots, compact exposed soil, and car and pedestrian paths. The studied area comprises about 35 ha within the limits of the university campus (Fig. 1). There are different densities of trees in this area, from isolated to clustered trees at different distances from a large fragment of secondary vegetation and the most urbanized areas around the university campus (Fig. S1). The original vegetation of the university campus is Atlantic Forest, and it is still surrounded by some small forest fragments and riparian forests of a tributary of the *Poxim* river (Gomes et al. 2017; Malta et al. 2012; Santos et al. 2007).

2.2. Sampling design

Inside the study area, we labeled all trees with a circumference at breast height above 15 cm with numbered metal tags and obtained their coordinates (Fig. S1). We mapped a total of 1,484 trees, and from that, we randomly spotted 30 trees *in silico*, with a minimum distance of at least 80 m among them, using the *discrete.sample* function of *PrevMap* package (Giorgi and Diggle 2017) in R software (R Core Team 2020). This function draws a sub-sample from a set of units spatially located irregularly over some defined geographical region by imposing a minimum distance between any two sampled units.

2.3. Tree variables

We determined the sampled trees to species level using Ferreira et al. (2013), which previously cataloged and described all tree species found on the university campus. For valid plant species names, we used the online repository "The Plants List" (<http://www.theplantlist.org/>, accessed January 2019). As a proxy of tree size, we used the circumference at breast height (CBH) using a three-meter-long tape-measurer. We measured tree isolation based on all trees marked and computed the distance from each tree to its nearest neighbor, using the *nndist* function of *spatstat* package (Baddeley and Turner 2005) in R software (R Core

Team 2020). We separated the trees between native and exotic based on Ferreira et al. (2013), and for the presence/absence of extrafloral-nectaries, we used the guide 'World List of Angiosperm Species with Extrafloral Nectaries' (Weber et al. 2015).

2.4. Ant sampling

We focused on the dominant species (i.e., resource-dominant) on trees and used sampling methods accordingly. We used a ground-based technique for ant sampling, adapted from the “arboreal bait line technique” (Delabie et al. 2021), previously used in other ecological studies (Leponce et al. 2019; Antoniazzi et al. 2020, 2021). On each of the 30 trees, we put three nylon ropes with five millimeters diameter over different tallest branches and with the maximum distance as possible between each other within the same tree, using notch throw weight tied at the ropes, forming a loop. The baiting started between 8:00–9:00 during the day and between 20:00–21:00 during the night. We suspended a mixed bait of honey and sardine with oil and fixed the ropes when the bait touched the branch. After three to four hours of exposure on tree branches, we pulled down the baits, capturing all ants foraging on them (Fig. S2). We collected all ants found on the baits, placed them in vials with 70% ethanol, and transported them to the laboratory at Federal University of Sergipe. We sorted, mounted, and identified the ants to the level of species or morphospecies, first at genus level following Baccaro et al. (2015), and posteriorly determined with the aid of experts and based on the Formicidae collection of *Centro de Pesquisas do Cacau* (Brazil) (Delabie et al. 2020). For valid names, we used the “AntCat repository” (Bolton 2012). Despite the possibility of a turnover of ant species during the baiting trials, we focused on the species that would effectively dominate the resource, i.e., after four hours left at the tree branches. Moreover, the turnover of species on baits is relatively small, and in many cases, the first species to arrive at a food bait would also be the one to dominate it (Camarota et al. 2018).

2.5. Ant community description

First, we built sample size- and coverage-based rarefaction and extrapolation curves to describe the collected ant species richness in each of the distinct sampling periods (i.e., day and night) using tree individuals as sampling units. Confidence intervals were determined by using 999 bootstraps in order to effectively estimate the total species richness (Chao et al. 2014). Afterward, we assessed the differences in ant species composition between day and night by performing a generalized linear multivariate model (GLMmv) (Wang et al. 2012), with the data following a binomial distribution. We plotted the results of GLMmv in a graphic of principal coordinates analysis (PCoA), using the presence-absence matrix and the similarity distance of Jaccard. Additionally, to identify the ant species that were more associated with a given period of the day, we performed a multinomial species classification method (CLAM) (Chazdon et al. 2011). We used the CLAM approach classifying the species from the two periods (day and night) in four different groups: *i*) diurnal specialists (A); *ii*) nocturnal specialists (B); *iii*) generalists; and *iv*) species that are extremely rare to be classified as either specialist or generalist. To perform the CLAM, we applied the constraints of a $p < 0.05$ and a specialization threshold of 0.67, considered by Chazdon et al. (2011) as a conservative value.

2.6. Predictions test

To test whether ant species diversity is affected by different factors associated with the trees, we used an approach based on multi-model inference, following the Akaike information criteria (Burnham and Anderson 2002). In order to avoid pseudo-replication issues, once we sampled the same trees at day and night, we built separated models for each period, using three proxies of diversity as our response variables: *i*) ant species incidence at the baits; *ii*) ant species richness; *iii*) average β -diversity. The β -diversity was calculated based on the Sorensen index and followed Anderson et al. (2011) approach of directional dissimilarity in community structure. Thus, the beta-diversity of ant community in each tree is the average of differentiation of the *ith* tree among all trees. Each model had one response variable in relation to the following predictor variables: *i*) Tree circumferences at breast height (CBH); *ii*) Tree distances from the nearest-neighbor (isolation); *iii*) Exotic or native tree species; *iv*) Presence of extrafloral nectaries (EFNs). The candidate models were based on the concurrent biological hypotheses that ant species diversity would depend on: *i*) a single factor (i.e., models containing only a predictor variable) or *ii*) action of two simultaneous factors (i.e., models containing a group of predictor variables). For this, we initially built a global model to include all candidate models into a given response variable. The effects of the predictor variables were inferred based on the set of 11 models (i.e., one null model, four models of a single factor, and six models of two factors) for each response variable that differed by two or fewer units of AICc from the best model (ΔAICc), capturing greater uncertainty in the final set of candidate variables (Burnham and Anderson 2002). Model averaging was applied to make biological inferences about the variables of which the averaged estimates did not include zero within their standard-error range. This strategy is important to identify uninformative parameters in statistical models applying model selection in ecology. An uninformative parameter is a predictor with no relationship with the response variable, making little to no improvement in the log-likelihood of a model (i.e., model fit), but can be included in a model ranked close to models with informative parameters based on confidence intervals (Leroux 2019). We also calculated the relative importance value (RIV) of each predictor on the full model. The RIV is the sum of the Akaike weights (probability of a model to be the most plausible one) for the models in which each predictor appears. Therefore, a predictor included in models with high Akaike weights will receive a higher RIV value. These values can be considered as the general support for each predictor variable in all models. The 50% cut-off threshold is arbitrary and was defined to differentiate important and unimportant predictors (Burnham and Anderson 2002; Terrer et al. 2016; Deschutter et al. 2017; Everaert et al. 2018).

2.7. Ant-tree interactions network

We used the individual-based ant-plant approach, considering tree individuals and ant species associations (Dáttilo et al. 2014a; Antoniazzi et al. 2019; Carvalho et al. 2021). We analyzed the properties of three interaction networks, day, night, and both day and night together from incidence matrices A , where A_{ij} was the number of records in which the plant species i and the ant species j occurred together. The ant-tree interaction was defined as the number of times in which a tree individual interacts with an ant species, in which various ant workers of the same ant species on one of the baits were considered as only one record of that ant species (Miranda et al. 2019). As on each tree we placed three baits, for each tree individual the maximum interaction frequency for a given ant species was three and the minimum was zero. For each ant-tree interaction network, we calculated the following network descriptors (network level): network size, specialization, interaction diversity, modularity, and nestedness. The network size was obtained from the

product of the number of ant and tree individuals of each network. Network specialization was calculated using the specialization index (H_2') (Blüthgen et al. 2006), which ranges from 0 (extreme generalization) to 1 (extreme specialization). This index is derived from the Shannon diversity index and is based on the deviation from the expected probability distribution of interactions of network links (Blüthgen et al. 2006). To estimate the interaction diversity, we used the interaction diversity index (H_i) (Dyer et al. 2010). To test whether there were groups of ant species strongly associated with a particular set of tree individuals, we used the QuanBiMo modularity algorithm (Q) (Dormann and Strauss 2014). This index ranges from minimum ($Q = 0$) to maximum ($Q = 1$) modularity. Also, we evaluated the hierarchical arrangement of networks by testing whether species with fewer links interacted with a subset of species with more links using the *WNODF* (weighted nestedness) metric (Almeida-Neto and Ulrich 2011). The *WNODF* metric ranges from 0 (no nestedness) to 100 (perfect nestedness) and uses quantitative rather, weighting the nestedness contribution of different frequencies. For the four indices: specialization (H_2'), interaction diversity (H_i), modularity (Q), and nestedness (*WNODF*), we generated random matrices to test for significance using the “Patefield” null model, which preserves the marginal totals of each row (lower trophic level, i.e., tree individuals) and column (higher trophic level, i.e., ant species) (Patefield 1981; Miklós and Podani 2004) and 1,000 random matrices. We also defined the central core of highly interacting species (generalist core), i.e., ant species with more interactions in relation to other species of the same trophic level (Dáttilo et al. 2013), for each ant-plant network. All these network analyses and metrics were carried out using the *bipartite* (Dormann et al. 2009) and *vegan* (Oksanen et al. 2015) in R software (R Core Team 2020).

3. Results

3.1. Tree and ant community description

The tree community is comprised of 13 tree species from seven different plant families. Fabaceae was the most speciose family, with five species and ten individuals, followed by Anacardiaceae, Myrtaceae, Meliaceae, Combretaceae, Moraceae, and Malvaceae (Table 1). Of all tree species, seven belong to species that had EFNs, and six ones did not have EFNs. Among the 13 tree species, five were identified as exotic species from the Atlantic Forest biome, and eight were classified as native species (Table 1). The tree's size varied between 33.5 and 357.0 centimeters in circumference at breast height (CBH), with an average of 126.4 ± 73.4 cm (mean $\pm$ SD). The average isolation of each tree was 6.4 ± 6.1 m, with a range between 0.00 and 22.5 meters.

We recorded 19 ant species belonging to five subfamilies and 11 genera (Table 2). The subfamilies Formicinae and Myrmicinae presented the highest species richness (seven species each), followed by Dolichoderinae and Pseudomyrmecinae (two species each), and Ponerinae (one species). Only three ant species were exotic (15.8 %): *Tapinoma melanocephalum*, *Cardiocondyla obscurior*, and *Monomorium floricola*. Of the 19 ant species, 11 were collected during the day and 13 at night, being eight species exclusively sampled at the daytime and six species at the nighttime (Table 2). The incidence-based rarefaction curves almost reached the asymptote (Fig. 2a). The estimated sample coverage (over 80% for all assemblies, i.e., day, night, and both together) suggested that the ant species richness was well represented

(Fig. 2b). The composition of the arboreal ant communities was significantly different between day and night (GLM_{MV} Deviance = 88.43, $p < 0.001$; Fig. 2c). The species *Camponotus blandus* was classified as a diurnal specialist according to CLAM analysis, while the species *Camponotus melanoticus*, *Camponotus atriceps*, and *Dolichoderus lutosus* were considered as a nocturnal specialist. The ant species *Cephalotes pusillus* was considered as generalist on both day and nighttime. All the other ant species were considered rare due to their low incidence at the baits (Table 2 and Fig. S3).

3.2. Influence of tree characteristics on the ant community

We found that only the β -diversity of the nocturnal ant community was affected by structural (size), spatial (isolation), and biological (native or exotic, with/ without EFN's) characteristics of trees (Table 3). Although nine models had substantial empirical evidence concerning the β -diversity of nocturnal ants (Table 3), only tree size (CBH) did not present zero within its standard-error range (Fig. 3a), and more than 50% of relative importance value (RIV, Fig. 3b), with a relationship significantly positive with this response variable (Fig. 3c).

3.3. Ant-tree interaction networks

In our bait sampling, we observed 1.5 ± 0.8 (mean $\pm$ SD) ant species during the daytime, 1.5 ± 0.7 in the nighttime, and 2.5 ± 1.4 in the day and night together per tree individual. The network specialization levels were above average in both diurnal and nocturnal networks (Diurnal: $H_2' = 0.58$. Nocturnal: $H_2' = 0.63$). However, when considering day and night together, the network specialization level was below average ($H_2' = 0.45$) (Table 4). Moreover, the interaction diversity was quite similar between the diurnal and nocturnal networks and larger on the diurnal and nocturnal networks considered together (Table 4). In addition, all networks were modular, compared with the neutral patterns of ant-plant interactions (null models) (QuanBimo values, Z-score > 2) (Table 4). Evaluating the non-random patterns of ant-tree interactions of each individual-based network, only the network of day and night together exhibited a significantly nested network topology ($WNODF$ values, $p < 0.05$) (Table 4). This suggests that the interactions recorded for tree individuals with fewer interactions by ants are a cohesive subset of the interactions found on the most visited individuals. The ant species that were part of the generalist core differed between diurnal and nocturnal networks, following the differences in ant species composition. The species *Camponotus blandus* and *Cephalotes pusillus* were the generalist core ant species of the diurnal network, while the species *Camponotus melanoticus* and *C. atriceps* were the core in the nocturnal network (Fig. 4a). Considering the diurnal and nocturnal networks together, the species *Camponotus blandus*, *Cephalotes pusillus*, and *Camponotus melanoticus* were the core of the generalist species (Fig. 4b).

4. Discussion

In the present study, we assessed different factors associated with the host trees (i.e., size, isolation, exotic species, and presence of EFNs) that would influence the community of arboreal ant foraging in scattered trees in an urban landscape. We found a significant shift in the ant community composition between day and night and, accordingly, a different core of interacting species between these periods. The tree size was

the only tree factor that influenced the ant diversity, and importantly, this was true only for the nocturnal ant community. In relation to ant species associations with their hosting trees, we observed high levels of network specialization and modular networks. Only the nocturnal network of ant-plant interactions followed a nested pattern, and there was no relationship of tree individual specialization to any predictive variable, i.e., size, isolation, exotic species, and presence of EFNs. This study is the first to assess the effects of different factors on communities of arboreal ants in urban ecosystems, focusing on diversity patterns as well as in the species interaction networks. Our work provides valuable insights into the conservation value of scattered trees to urban biodiversity, specifically ants.

Of all factors tested, namely tree size, isolation, native/exotic tree species, and presence of EFNs, only tree size has substantial empirical evidence related to ant diversity patterns. This result is in concordance with prior studies in preserved forests, showing an increase in arthropod diversity with tree size in the Brazilian Atlantic forest (Campos et al. 2006) and Papua New Guinea (Klimes et al. 2012). Indeed, larger trees possess a higher number of essential resources, mainly shelter (Klimes et al. 2012; Klimes 2017). Arboreal ants rely heavily on existing cavities produced by wood-boring beetles as shelter resources (Blüthgen and Feldhaar 2010) and presumably, larger trees would have a higher availability of such resources (Koch et al. 2016). Additionally, larger trees often have a large number of structures and microhabitat availability in their crowns, which might allow a higher amplitude of available nesting sites, from small cavities in twigs to large ones in the main branches. The strong influence of tree size we found in our study highlights that resource use patterns in an urban area are similar to previous findings for arboreal ants from natural ecosystems. Finally, larger trees might also support a richer community of herbivores and other insects, which are important food items for arboreal ants, either as prey (Floren et al. 2002) or by producing sugar-liquid resources, i.e., honeydew (Styrsky and Eubanks 2007). Overall, in urban ecosystems, resource partitioning and limitation might also play an essential role in defining species coexistence, especially in areas with a higher concentration of scattered trees.

Tree isolation and the presence of EFNs did not have a detectable effect on our focal ant communities. While the lack of effect of tree isolation on arboreal ant species diversity seems to contradict prior studies (e.g., Gove and Majer 2006; Powell et al. 2011), it is important to stress that in our study, all trees were relatively isolated (about 6 meters apart). Thus, it was much more a situation of comparing the distance between trees than connectivity per se. Most ant species that forage on trees also nest on the same tree, or at least in adjacent ones, rarely using the ground layer for foraging between trees (Camarota et al. 2016). Instead of increasing or decreasing the diversity, the distance might effects the species pool that use the cluster of closer than distant trees. In our study, all trees were located within a range of 35 ha, and thus, the arboreal ant species pool is likely to be the same for all sampled trees. Extrafloral nectaries are important resources for arboreal ants, and many ant species are involved in protective interactions with plant-bearing EFNs (Rico-Gray and Oliveira 2007). However, the role of EFNs in structuring ant composition at the community level is not clear and is probably much more limited than initially proposed (Camarota et al. 2015; Antoniazzi et al. 2019). Additionally, the spatial scale of the study might influence the detection of any effect of EFNs on ant communities (Ribeiro et al. 2018). Potentially, EFNs are important for ant community composition but in a much more supplementary way than as a primary food resource (Camarota et al. 2015;

Pacelhe et al. 2019). Moreover, these resources are seasonal, and their importance may be much higher in the peak of EFN productivity (Lange et al. 2013, but see Camarota et al. 2015).

Interestingly, the ant species foraging on exotic trees were similar to the community foraging on native trees. Notably, urban trees support a significant number of herbivorous arthropods, which in turn influence their importance for higher trophic levels, such as predators (Tallamy 2004; Urghardt et al. 2010). Ants comprise a significant part of this higher trophic level, and presumably, the community of herbivores supported by a given tree would influence the arboreal ant community. An excess of herbivores can damage scattered trees' important properties for urban well-being by reducing photosynthesis, tree growth, and the structural condition of the tree (Dreistadt et al. 1990; Christie and Hochuli 2005). Thus, our results on arboreal ants reassure the need for balanced management of urban trees (Frank et al. 2019), focusing on the beneficial effects of native trees in hosting native arthropods and the potential of exotic trees to perform essential ecosystem services.

We observed a significant shift between the diurnal and nocturnal ant communities and detected higher than average values of specialization at the network level for a given period, as well as a different core of interacting species. While one ant species, *Cephalotes pusillus*, was frequent at both periods of the day, the ant species that were part of the generalist core were completely different between day and night, with *Camponotus blandus* and *Cephalotes pusillus* during the day and *Camponotus melanoticus* and *Camponotus atriceps* at night. Interestingly, in a study in a natural habitat, at the Brazilian Cerrado, Camarota et al. (2016) found the same core of ant species. We also found that both diurnal and nocturnal ant networks were modular, indicating some specialization of the ants to a given set of trees. Similar to our results, a previous study showed that disturbance did not change the topology of plant-herbivorous networks, being modular in forest interior and anthropogenic edges (Carvalho et al. 2021). Perhaps the high values of modularity are more related to stochastic factors, as the distance between the sampled trees, than any other factor related to tree and ant specializations, such as a given food reward or nesting site. We also found that only the nocturnal ant network was significantly nested, with a cohesive subset of each tree's overall interacting species. A candidate explanation for this finding might be that nocturnal ant communities have more dominant ant species than diurnal ones, competing by valuable resources under less harsh abiotic conditions (Bestelmeyer 2008). Therefore, there would be some foraging species hierarchy, ultimately leading to a more predictable distribution of foraging ant species (Dáttilo et al. 2014b).

While the shift in ant communities between day/night communities has been extensively documented in the literature, most studies have focused on natural areas (e.g., Anjos et al. 2017; Dáttilo et al. 2014a, 2015). Urban habitats can provide exciting insights into the temporal partition of food resources. Such temporal partition might reflect either the ant species' physiological constraints or competitive abilities (Cerdeira et al. 1997, 1998a; Wittman et al. 2010). Thus, different levels of urbanization can result in different temporal patterns of food resource use. For example, in trees located in more exposed environments, like less wooded areas inside the cities, desiccation risk is much higher (Menke et al. 2011). Thus, in such drier areas, eco-physiological constraints may be the main factor between temporal variation in resource use, if any. However, in scattered trees located in less exposed areas, such as our focal wooded university campus, competition between ant species might be stronger than a physiological limitation in defining the species

foraging times. Further studies would be essential to disentangle the main factor associated with ant species temporal food partitioning in urban ecosystems, and scattered trees provide a useful template for such studies.

5. Conclusions

This study is the first to assess the effects of different factors on communities of arboreal ants in urban ecosystems focused on diversity patterns and interaction networks. Our work provides valuable insights into the conservation value of scattered trees on overall urban biodiversity. First, tree size plays an essential role in maintaining the diversity of ecologically dominant ants and ant-tree interactions. Second, we need to consider both the diurnal and nocturnal ant communities, as there are different species and different network patterns between ants foraging at different periods of the day. Thirds, there are some similarities of our focal ant communities to those found in pristine areas, such as the Neotropical savannas. Future studies should incorporate both local and macroscale effects for understanding the role of scattered trees in keeping ant diversity and ant-plant interactions in urban environments. For example, we need further understanding of the role of resource-use in ant-tree interactions in urban areas. Moreover, we need to consider a strong urbanization gradient, from scattered trees in avenues to scattered trees in urban green areas. Only then will we have a deeper understanding of the habitat use by ants on trees in the urban landscape. Our results highlight that it is essential to consider the local biota and its interactions for better planning and decision-making on urban growth and development.

Declarations

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Availability of data and material

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Author contribution

RGM: Data Curation, Investigation. RA and ABVJ: Conceptualization, Formal analysis. RGM and ABVJ: Writing - Original Draft, RGM, RA, FC, ABVJ: Writing - Review & Editing, YTR and ABVJ: Supervision, Project administration. All authors made substantial contributions to the interpretation of results, writing, and the editing of the manuscript.

Ethics approval

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Consent to participate

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Consent for publication

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Tables

Table 1. Structural and biological characteristics of 30 trees randomly sampled and the frequency of ant species found by bait/tree individual in the Federal University of Sergipe (UFS), São Cristóvão, Sergipe state. Tree species code refers to a code used in Figures 4. EFN = extra-floral nectary presence, CBH = circumference at breast height in centimeters.

Family	Tree species		Tree species code	Native/ Exotic	EFN	CBH	Ant frequency	
							Day	Night
Anacardiaceae	<i>Anacardium occidentale</i>	L.	Ana_occ	Nat	Yes	106	0	2
	<i>Anacardium occidentale</i>	L.	Ana_occ	Nat	Yes	124	2	3
	<i>Anacardium occidentale</i>	L.	Ana_occ	Nat	Yes	129	3	1
	<i>Anacardium occidentale</i>	L.	Ana_occ	Nat	Yes	143	2	2
	<i>Anacardium occidentale</i>	L.	Ana_occ	Nat	Yes	200	1	2
	<i>Anacardium occidentale</i>	L.	Ana_occ	Nat	Yes	41	2	2
	<i>Anacardium occidentale</i>	L.	Ana_occ	Nat	Yes	82	4	2
	<i>Schinus terebinthifolius</i>	Raddi	Sch_ter	Nat	No	33.5	1	3
	<i>Schinus terebinthifolius</i>	Raddi	Sch_ter	Nat	No	93	3	1
	<i>Schinus terebinthifolius</i>	Raddi	Sch_ter	Nat	No	93	3	1
Combretaceae	<i>Terminalia catappa</i>	L.	Ter_cat	Exo	Yes	137	1	1
	<i>Terminalia catappa</i>	L.	Ter_cat	Exo	Yes	210	3	4
	<i>Terminalia catappa</i>	L.	Ter_cat	Exo	Yes	357	2	0
Fabaceae	<i>Clitoria fairchildiana</i>	R. A. Howard	Cli_fai	Nat	No	155	1	1
	<i>Clitoria fairchildiana</i>	R. A. Howard	Cli_fai	Nat	No	78	3	3
	<i>Clitoria fairchildiana</i>	R. A. Howard	Cli_fai	Nat	No	231	3	6
	<i>Hymenaea courbaril</i>	L.	Hym_cou	Nat	Yes	46	2	3
	<i>Inga laurina</i>	(Sw.) Willd.	Ing_lau	Nat	Yes	50	2	4
	<i>Inga laurina</i>	(Sw.) Willd.	Ing_lau	Nat	Yes	77	0	3
	<i>Libidibia ferrea</i>	(Mart. ex	Lib_fer	Nat	Yes	144.5	2	2

	<i>Pithecellobium dulce</i>	(Roxb.) Benth.	Pit_dul	Exo	Yes	120	0	3
	<i>Pithecellobium dulce</i>	(Roxb.) Benth.	Pit_dul	Exo	Yes	152	4	3
	<i>Pithecellobium dulce</i>	(Roxb.) Benth.	Pit_dul	Exo	Yes	259	1	0
Malvaceae	<i>Pachira aquatica</i>	Aubl.	Pac_aqu	Nat	No	186	4	1
Meliaceae	<i>Azadirachta indica</i>	A. Juss.	Aza_ind	Exo	No	124.5	2	0
	<i>Azadirachta indica</i>	A. Juss.	Aza_ind	Exo	No	47.5	3	3
	<i>Azadirachta indica</i>	A. Juss.	Aza_ind	Exo	No	55	2	3
	<i>Azadirachta indica</i>	A. Juss.	Aza_ind	Exo	No	71.5	5	1
Moraceae	<i>Ficus retusa</i>	L.	Fic_ret	Exo	No	59	2	1
Myrtaceae	<i>Myrcia obovata</i>	Lam.	Myr_obo	Nat	No	154	3	0
	<i>Syzygium cumini</i>	(L.) Skeels	Syz_cum	Exo	Yes	136	0	2

Table 2. Ant species sampled in tree crowns in the Federal University of Sergipe (UFS), São Cristovão, Sergipe state. Ant species code refers to a code used in Figures 4 and Table 4. Ants species native or exotic in the study area are indicated (Native/ Exotic), of frequency of ants in day-night periods (Incidence) and results of Multinomial Species Classification Method (CLAM results).

Subfamily	Ant species	Ant species	Native/	Incidence		CLAM
		code	Exotic	Day	Night	results
Dolichoderinae	<i>Dolichoderus lutosus</i> (Smith, 1858)	Dol_lut	Native	0	9	Specialist night
	<i>Tapinoma melanocephalum</i> (Fabricius, 1793)	Tap_mel	Exotic	0	1	Rare
Formicinae	<i>Camponotus arboreus</i> (Smith, 1858)	Cam_arb	Native	4	2	Rare
	<i>Camponotus atriceps</i> (Smith, 1858)	Cam_atr	Native	0	11	Specialist night
	<i>Camponotus blandus</i> (Smith, 1858)	Cam_bla	Native	20	0	Specialist day
	<i>Camponotus crassus</i> Mayr, 1862	Cam_cra	Native	2	1	Rare
	<i>Camponotus melanoticus</i> Emery, 1894	Cam_mel	Native	1	15	Specialist night
	<i>Camponotus vittatus</i> Forel, 1904	Cam_vit	Native	0	7	Rare
	<i>Nylanderia</i> sp1	Nyl_sp1	Native	0	4	Rare
Myrmicinae	<i>Cardiocondyla obscurior</i> Wheeler, 1929	Car_obs	Exotic	1	0	Rare
	<i>Cephalotes clypeatus</i> (Fabricius, 1804)	Cep_cly	Native	7	0	Rare
	<i>Cephalotes pusillus</i> (Klug, 1824)	Cep_pus	Native	15	4	Generalist
	<i>Crematogaster stollii</i> Forel, 1885	Cre_sto	Native	3	3	Rare
	<i>Crematogaster victima</i> Smith, 1858	Cre_vic	Native	0	3	Rare
	<i>Monomorium floricola</i> (Jerdon, 1851)	Mon_flo	Exotic	3	0	Rare
	<i>Pheidole flavens</i> Roger, 1863	Phe_fla	Native	0	1	Rare
Ponerinae	<i>Neoponera inversa</i> (Smith, 1858)	Neo_inv	Native	0	1	Rare
Pseudomyrmicinae	<i>Pseudomyrmex gracilis</i> (Fabricius, 1804)	Pse_gra	Native	5	0	Rare
	<i>Pseudomyrmex pallidus</i> (Smith, 1855)	Pse_pal	Native	2	0	Rare

Table 3. Models with substantial empirical evidence ($\Delta < 2$) for ant community parameters (response variables) between different periods of the day at the Federal University of Sergipe Campus, São Cristovão, Sergipe. Predictors variables include the breast height circumference (CBH), the distance from the nearest neighboring tree (ISO), whether the plant was an exotic species (EXO) and whether the plant had extra-floral nectaries (EFN). k = number of parameters of the model; logLik = log-likelihood; AICc = second-order Akaike information criterion; Δ = AICc difference between the model under concern and the best model; Weight = Akaike weight, that is, the probability that the current model is the best among the set of candidates. Full model includes: $y \sim \text{CBH} + \text{ISO} + \text{EXO} + \text{EFN}$.

Response	Period	Models	k	logLik	AICc	Δ	Weight
Incidence (<i>Poisson</i>)	Day	NULL	1	-50.05	102.25	0.00	0.32
		EFN	2	-49.80	104.04	1.79	0.13
		ISSO*	2	-50.01	104.46	2.21	0.10
	Night	CBH+EFN	3	-48.34	103.61	0.00	0.17
		EFN	2	-49.74	103.92	0.31	0.15
		NULL	1	-50.91	103.95	0.35	0.14
		CBH	2	-50.11	104.66	1.05	0.10
		EXO	2	-50.41	105.26	1.65	0.07
		EXO+EFN*	3	-49.53	105.98	2.37	0.05
Richness (<i>Poisson</i>)	Day	NULL	1	-39.82	81.80	0.00	0.28
		ISO	2	-39.52	83.50	1.71	0.12
		CBH	2	-39.53	83.50	1.72	0.12
		EXO	2	-39.73	83.90	2.12	0.10
	Night	NULL	1	-39.41	80.97	0.00	0.21
		EFN	2	-38.55	81.54	0.57	0.16
		CBH	2	-39.00	82.45	1.48	0.10
		CBH+EFN	3	-37.77	82.46	1.49	0.10
		EXO	2	-39.13	82.71	1.74	0.09
Average β -diversity (<i>Gaussian</i>)	Day	ISO	3	27.48	-48.03	0.00	0.17
		NULL	2	26.11	-47.77	0.25	0.15
		EXO	3	26.98	-47.04	0.99	0.10
		EXO+ISO	4	28.29	-46.99	1.04	0.10
		CBH+ISO	4	28.04	-46.49	1.54	0.08
		ISO+EFN	4	28.04	-46.48	1.55	0.08
		EXO+ISO+EFN	5	29.36	-46.22	1.81	0.07
		EFN*	3	26.32	-45.71	2.32	0.05
	Night	CBH	3	34.49	-62.07	0.00	0.14
		EXO+CBH	4	35.69	-61.78	0.29	0.12

CBH+EXO	4	35.67	-61.73	0.33	0.12
EXO+ISO	4	35.39	-61.18	0.89	0.09
EXO	3	33.90	-60.89	1.18	0.08
EXO+CBH+ISO	5	36.36	-60.22	1.85	0.06
EXO+CBH+EFN	5	36.33	-60.15	1.91	0.06
CBH+ISO	4	34.87	-60.15	1.92	0.06
CBH+ISO+EXO	5	36.30	-60.11	1.96	0.05
NULL*	2	32.17	-59.90	2.16	0.05

*Models included to demonstrate the $\Delta AICc$ values between models with and without substantial empirical evidence.

Table 4. Networks descriptors for individual-based ant-plant networks for day, night, and both together.

	Networks		
	Day	Night	Both day and night
Tree individuals sampled	26	26	26
Ant species (exclusive)	11 (6)	13 (8)	19
Mean of ant richness per individual tree	1.54 ± 0.76	1.5 ± 0.71	2.5 ± 1.39
Generalist core of ant species	Cam_bla, Cep_pus	Cam_mel, Cam_atr	Cam_bla, Cam_mel, Cep_pus
Network size	286	338	570
Specialization (H2)	0.58*	0.63**	0.45*
Interaction diversity (Hi)	3.58***	3.54***	4.17***
Modularity (QuanBimo)	0.61***	0.69***	0.56**
Nestedness (<i>WNODF</i>)	4.4	3.8	4.59*

“*” $p < 0.05$; “**” $p < 0.01$; “***” $p < 0.001$

Figures

Figure 1

Location of the study area, the campus of Federal University of Sergipe (UFS) (a, b), northeast Brazil (c), showing the sampling locations of the trees (d).

Figure 2

Sample size-based rarefaction (solid lines) and extrapolation curves (dashed lines) (a) and coverage-based rarefaction (solid lines) and extrapolation (dashed lines) curves up to the corresponding coverage value (b). The 95% confidence intervals (shaded areas) are obtained by a bootstrap method based on 999 simulations. Principal coordinates analysis (PCoA) of arboreal-dwelling ants community composition between day and night (c), each point represents the tree sampled, and the ellipses indicate 70% confidence intervals.

Figure 3

Full model average coefficients for beta-diversity of arboreal-dwelling ant community nocturnal after applying model averaging. (a) Averaged coefficients $\pm$ standard-errors for each predictor variable; (b) relative importance values (RIV) of each predictor variable; (c) relationship between the average beta-diversity of nocturnal ants and the tree sizes.

Figure 4

Individual-based ant–plant networks, using the diurnal and nocturnal ant communities (a), and both together (b). Nodes represent ant species or plant individuals, and lines represent ant–tree interactions. The nodes are arranged according to their number of interactions. The rectangle height is proportional to the frequency of interactions of each species or tree individuals. Red rectangles denote ant species that were part of the generalist core of ant species. Species codes are presented in Table 2.

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