Urban Ecosystems
https://doi.org/10.1007/s11252-024-01556-8

Ant-plant networks exhibit distinct species diversity but similar organization in urban and wild areas of neotropical savannas

Samira Rosa de Oliveira Lima[1] · Edvânia Costa de Oliveira Sá[1] · Poliane Neres Morais[1] · Tatianne Gizelle Marques Silva[2] · Wesley Dáttilo[3] · Walter Santos de Araújo[4]

Accepted: 4 May 2024

Abstract

Interactions between ants and plants can form complex ecological networks, which may have their structure affected by human-induced habitat modification, such as urbanization. In this study, we investigated if the species diversity and the network topology of ant-plant co-occurrence networks (facultative associations between plants and ants) differs between remnants of Neotropical savannas. We sampled 12 savanna fragments (cerrado *sensu stricto*) in wild, rural and urban areas of Minas Gerais, Brazil. In total, the 12 ant-plant interaction networks were composed by 65 ant species, 83 plant species and 432 distinct interactions. We observed that in addition to variations in species composition, wild areas exhibited higher richness and abundance of ants compared to urban areas. However, our results show no variation in the specialization, modularity, and nestedness of ant-plant co-occurrence networks among urban, rural, and wild areas. Despite changes in species diversity, ant-plant interactions maintain consistent organization across studied environments, showcasing resilience to anthropogenic disturbances similar to that observed in wild remanants.

Keywords Ant-plant interactions · Cerrado · Formicidae · Habitat disturbance · Network topology

Introduction

Ecological networks formed by the relationships between ants and plants are recognized for their remarkable diversity and complexity, both in terms of species composition and the nature of interactions involved (Juárez-Juárez et al. 2023). Ant-plant networks are commonly encountered in tropical regions and encompass a variety of biotic interactions, ranging from facultative to obligate myrmecophily (Rico-Gray and Oliveira 2007). These interactions include mutualism (such as ant–plant protection systems, pollination, and seed dispersion), neutralism (where ants use plants solely as substrates for foraging and patrolling), antagonism (including seed predation and leaf-cutter ants), and complex indirect associations that can exhibit both positive and negative aspects (Bascompte et al. 2006; Guimarães et al. 2007; Rico-Gray and Oliveira 2007; Del-Claro et al. 2018). Consequently, ant-plant networks can vary widely in their organization and species composition depending on the intimacy of the interaction involved, ranging from higly modular structure to symbiotic ant-myrmecophyte interactions to nested structure in ant-plant interactions mediated by extrafloral nectaries (Guimarães et al. 2007). However, most of ant-plant network types tend to have generalized structures with a cohesive central core of highly interacting species (Guimarães et al. 2006; Dáttilo et al. 2014a). While research on ant-plant networks in tropical ecosystems has made significant advances (reviewed by Del-Claro et al. 2018 and Juárez-Juárez et al. 2023), only few studies have focused on understanding how anthropogenic impacts affect the diversity and structure of ant-plant networks (Miranda et al. 2022; Juárez-Juárez et al. 2023). Therefore,

---

✉ Walter Santos de Araújo
walterbioaraujo@gmail.com

[1] Programa de Pós-Graduação em Biodiversidade e Uso dos Recursos Naturais, Universidade Estadual de Montes Claros, Montes Claros, Minas Gerais, Brazil

[2] Instituto Federal do Norte de Minas Gerais, SalinasCampus Salinas, Minas Gerais, Brazil

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

[4] Departamento de Biologia Geral, Centro de Ciências Biológicas e da Saúde, Universidade Estadual de Montes Claros, Montes Claros, Minas Gerais, Brazil

further elucidating this topic is essential to comprehensively understand the implications of human activities on ant-plant networks.

Several evidence suggests that anthropogenic modification of natural habitats can significantly impact ecological networks by reducing species diversity and altering ecological interactions, primarily due to habitat loss, fragmentation, pollution, and the introduction of invasive species (Fortuna and Bascompte 2006; Dormann et al. 2017; Tylianakis and Morris 2017; Del-Claro and Dirzo 2021). However, the extent of anthropogenic impacts varies depending on the ecological and evolutionary characteristics of interacting species (Tylianakis et al. 2010). For instance, in ant-plant mutualistic networks, the weak and asymmetric dependencies make the entire ensemble more resistant to anthropogenic impacts (Miranda et al. 2022). Moreover, the level of specialization and tolerance to anthropogenic disturbance can vary widely among ant communities (Andersen 2019), influencing the organization of ant-plant networks based on species composition and interaction types (Plowman et al. 2017). Specialized ant-plant networks, involving species with few interacting partners, are expected to be more sensitive to anthropogenic modifications (Dáttilo 2012), potentially leading to the loss of specialized species and the dominance of more generalist species (Dáttilo et al. 2014b), consequently altering network organization. Thus, higher levels of human impact and greater species specialization are likely to lead ant-plant networks more sensitive to anthropogenic disturbances.

The intricate relationship between species diversity and the organization of ant-plant networks is intricately connected to the characteristics of plant communities (Sampaio et al. 2023). Empirical evidence suggests that ant species richness is strongly influenced by the diversity and composition of plant communities (Achury et al. 2022), as the variability in resource availability among different plant species shapes the dynamics of ant-plant interactions (Dröse et al. 2019). These findings suggest that the richness and abundance of plants can also impact the structure of ant-plant networks, potentially serving as a primary mechanism through which anthropogenic impacts influence ant community structure (Andersen 2019).

Urbanization is considered one of the primary types of anthropogenic impacts affecting biodiversity across multiple dimensions (McKinney 2006; Grimm et al. 2008), often creating fragmentation of natural vegetation, creating isolated patches surrounded by urban infrastructure (McKinney 2002). Previous studies have reported that urbanization have negative effects on interaction organization in plant–animal networks, suggesting that in urban environments, networks are more connected and less specialized than in natural environments, for example, for plant-herbivore (Araújo et al. 2024) and plant-pollinator interactions (Santis et al. 2023). Moreover, urbanization exerts a substantial influence on ant-plant interactions, leading to notable changes in the richness and abundance of ant communities (Sanford et al. 2009). Previous studies also indicate that urban expansion can lead to loss of plant diversity and the simplification of habitat structure (Walker et al. 2009; Freitas et al. 2020), indirectly affecting ant populations which rely on plants for food resources and shelter (Andersen 2019). Habitat degradation associated to urbanization often leads to a decrease in ant species richness, with specialized species particularly vulnerable to local extinction (Rocha and Fellowes 2020). Despite an extensive body of literature on ant community responses to disturbance (reviewed in Andersen 2019), empirical studies on the impacts of urbanization on ant-plant interactions remain limited (Dáttilo et al. 2017; Juárez-Juárez et al. 2023).

In this study, we aimed to investigate the diversity of interactions between ants and plants in remnants of Neotropical savannas situated in urban, rural, and wild areas. Our approach involved describing the structure of ant-plant co-occurrence networks utilizing ant richness and abundance, along with various network descriptors of species relationships such as specialization, modularity, and nestedness of the networks. The ant–plant co-occurrence networks represent facultative associations composed by multiple types of possible interactions and the high degree of complexity involving ants occurring and patrolling on plants (Corro et al. 2019). Specifically, we have postulated that landscape urbanization influences the diversity and structure of interactions between ants and plants. Our expected that land use intensification would decrease ant species richness and abundance, potentially negatively impacting habitat specialist species while favoring generalists. Consequently, the network structure would exhibit greater generalization (e.g., lower specialization and modularity) and nestedness in urban environments compared to wild ones. Additionally, we explored whether plant species richness and abundance influence the species diversity and topology of ant-plant networks. In this case, we expected that higher diversity and abundance of plant communities would correlate with greater ant richness and abundance, as well as increased specialization in ant-plant networks.

Materials and methods

Study area

The study was conducted in different Neotropical savannas (cerrado *sensu stricto*) located in the Northern region of the state of Minas Gerais, Brazil (Fig. 1). The region has a tropical dry climate (*Aw* in the Köppen system), characterized by well-defined precipitation periods (October to April), an average temperature of 24.2 °C, and an annual precipitation of 1,000 mm (Alvares et al. 2014). Neotropical savanna is the main vegetation of the Brazilian Cerrado, being a vegetation dominated by sclerophyllous plants that occur in nutrient-poor soils with limited water availability (Ribeiro and Walter 2008). In the studied region, remnants of Neotropical savannas exhibit varying levels of conservation, being founded both in urban and in wild environments (Freitas et al. 2020).

In total, we sampled 12 areas of Neotropical savannas located in regions with different land uses, including four urban, three rural, and five wild areas (Fig. 1). The definition of the categories of land use was based on a buffer zone of 1 km from the center of each fragment, where we assessed the composition of the neighboring landscape using the Geographic Information System (QGIS) version 3.4 (QGIS Development Team 2020). Urban areas are situated within the urban matrix of the city of Montes Claros, surrounded by buildings and structures, making them susceptible to intense and frequent anthropogenic pressures such as waste deposition, wildfires, tree cutting, and the presence of domestic animals. Rural areas are located more than 10 km away the center of Montes Claros and exhibit minimal anthropogenic interference, with only the presence of livestock and occasional wildfires observed. On the other hand, wild areas are well-preserved remnants of Neotropical savannas located within the boundaries of the conservation units of Serra do Cabral State Park and Veredas do Peruaçu State Park.

Sampling of ant-plant interactions

In each sampling area, five plots of 100 m² (10 × 10 m) were established, totaling 60 plots across the 12 areas. Minimum distance between plots in each area was 20 m. Within the

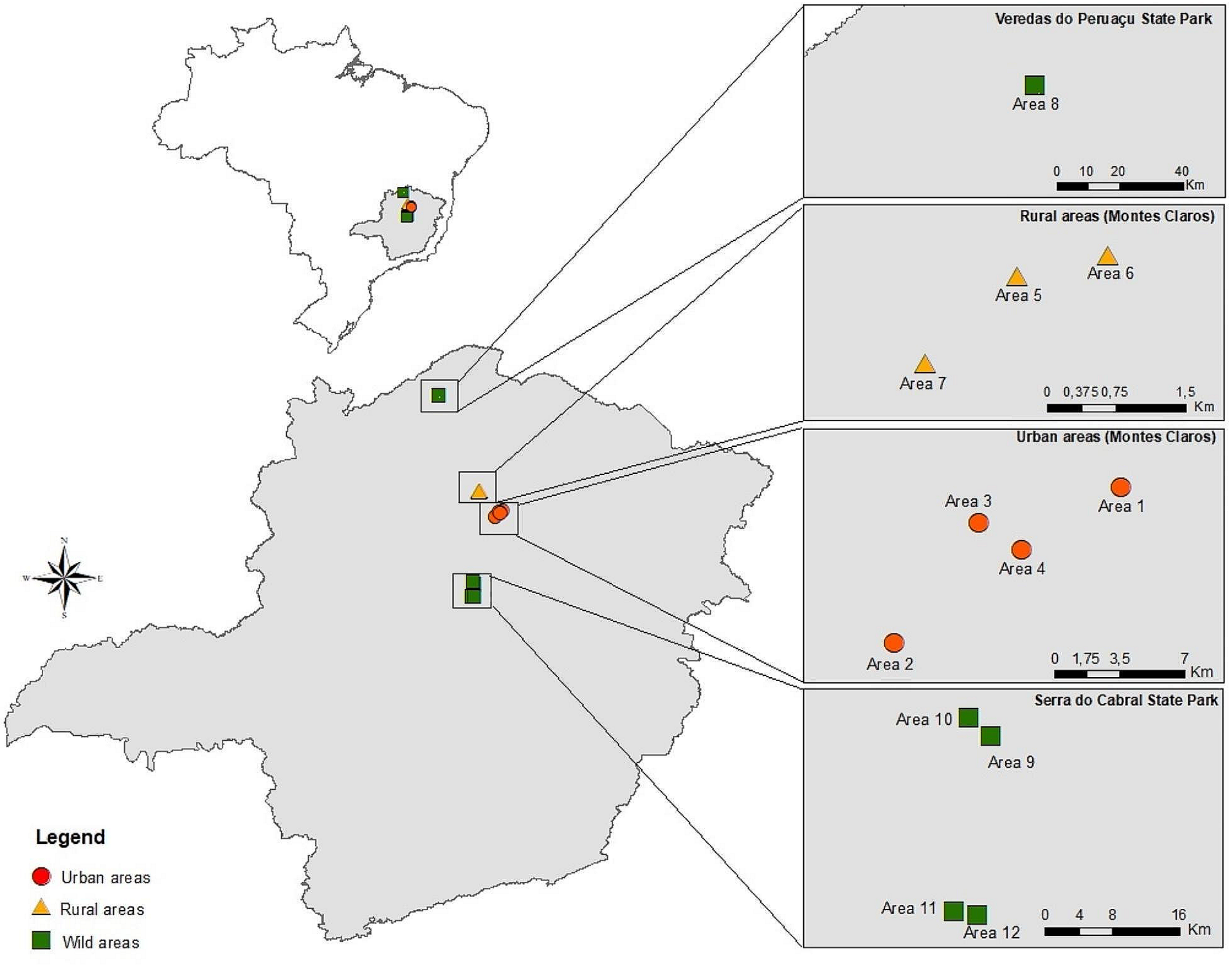

Fig. 1 Location of the 12 Neotropical savanna areas sampled in the Northern Region of Minas Gerais, Brazil. Red circles represent urban areas within the city of Montes Claros, orange triangles represent rural areas located approximately 50 km from the urban zone of Montes Claros, and green squares represent wild areas located in the Serra do Cabral State Park and Veredas do Peruaçu State Park

plots, all live woody individuals were inventoried following the methodology described in Freitas et al. (2023). From this inventory, the richness and abundance of plant species were determined for each area, as indicators of vegetation structure. Ant sampling in each area was conducted during two collection events in the years 2018 and 2019, covering both the dry period (July to August) and the rainy period (October to December). All inventoried plants had three randomly selected branches, on which 10 beatings were performed, and ants were collected using a modified entomological umbrella. The collected ants were preserved in 70% alcohol and taken to the laboratory for sorting and identification. Ant identification was conducted based on the guide for ant genera in Brazil (Baccaro et al. 2015), and after genus identification, ants were morphospeciated (from now on, referred to as species). Only data from plant species that showed associations with ants were used to construct the networks. We used incidence data recording the presence of a particular ant species on a specific plant species, and summing these incidences to determine ant abundances for each area.

Network descriptors and statistical analyses

Quantitative adjacency matrices were created from the collected data, with plant species in the rows and ant species in the columns, to construct interaction networks. The interactions were quantified by the frequency of records of ant species on each plant species. For each area, a network was built, considering all plant and ant species sampled in the two collection events, resulting in a total of 12 ant-plant networks (Fig. 2). In addition to ant richness and abundance, we utilized the topological descriptors specialization (Blüthgen et al. 2006), modularity (Beckett 2016), and nestedness (Almeida-Neto et al. 2008), calculated using the *bipartite* package (Dormann et al. 2008), to describe the structure of the networks. Specialization for each network was calculated using the H_2' index, which describes how species of ants and plants distribute their interactions based on partner availability throughout the community (Blüthgen et al. 2006). The H_2' index varies from 0 (no specialization) to 1 (total specialization). The modularity index was used to quantify the prevalence of interactions within subsets of species in the network. This indicates whether there are modules in the network formed by ant species that interact more frequently with the same set of plant species in the community (Dormann et al. 2017). The modularity index was calculated using the DIRTLPAwb + algorithm (Beckett 2016), ranging from 0 (non-modular) to 1 (perfectly modular), which takes into account the frequency of interactions, using the *computeModules* function (Dormann et al. 2008). We calculated nestedness using the NODF metric based on

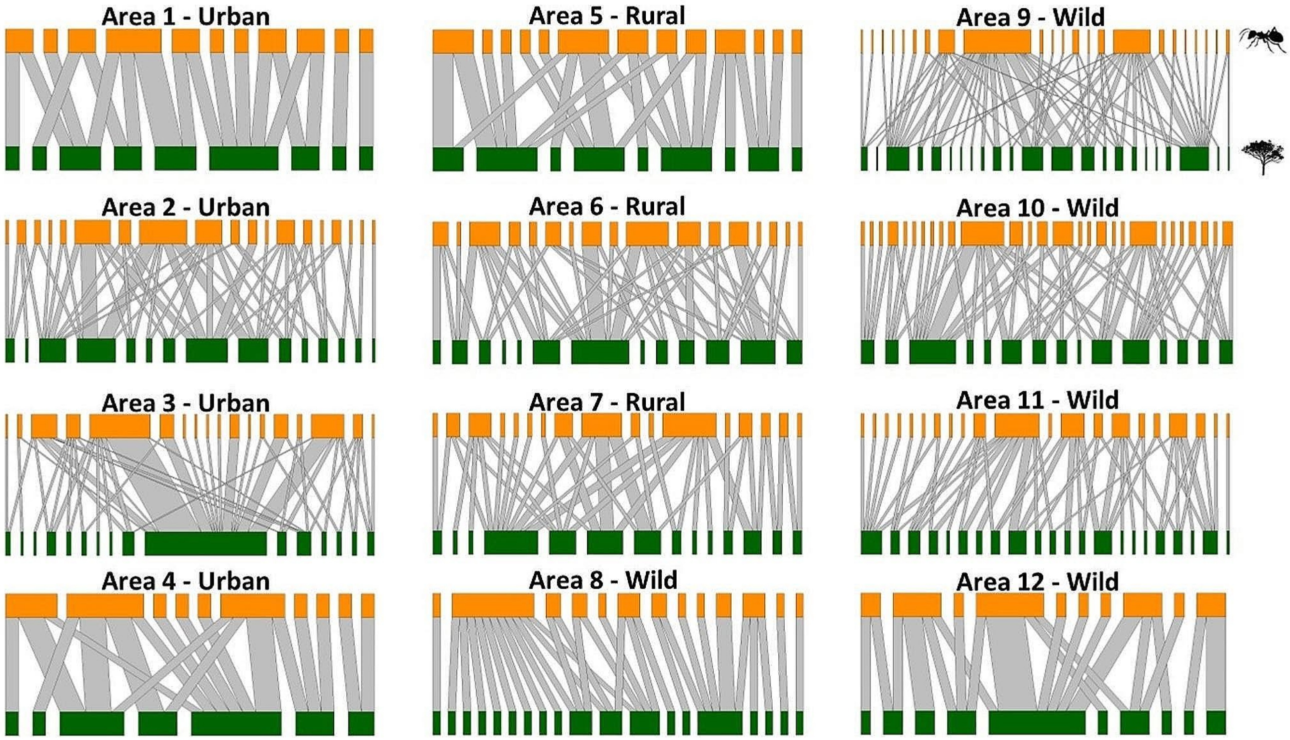

Fig. 2 Ant-plant networks constructed for urban, rural and wild areas of Neotropical savannas. The upper orange bars represent ant species; the lower green bars represent plant species, and the gray lines indicate interactions between the species. The width of the lines represents the number of interactions (quantified by frequency of records of ant species on each plant species)

overlap and decreasing fill (Almeida-Neto et al. 2008). The NODF takes values between 0 (perfectly non-nested) and 100 (perfectly nested). We calculated NODF using function *nested* (NODF2 method) seems to make more sense for comparisons across different networks (because it is independent of the initial presentation of the matrix) (Dormann et al. 2008). Although our data are quantitative, we used the NODF2 method instead of WNODF because studies on ant-plant networks suggest that binary data are more effective in detecting nested patterns in these networks (Dáttilo et al. 2014c; Miranda et al. 2019; Juárez-Juárez et al. 2023). For nestedness and modularity, we calculated standardized *z*-scores to enable comparison across communities (Pellissier et al. 2018), using 500 null networks built from the *r2d* null model in the *bipartite* package (Dormann et al. 2008).

To test the effects of the anthropization level (wild, rural, and urban areas) on ant species richness and abundance, as well as on the network descriptors (specialization, modularity, and nestedness), we used generalized linear mixed-effects models (GLMM's). In each model, the collection region (Montes Claros city, Veredas do Peruaçu State Park, and Serra do Cabral State Park) was used as a random effect variable to control for potential intrinsic differences between regions that may affect ant-plant interaction diversity and structure. Because the plant diversity can affect the insect diversity in ecological networks (Freitas et al. 2023), we included plant species richness and plant abundance recorded in each area as additional explanatory variables in the GLMM's. All explanatory variables were included in the GLMM's as fixed-effect variables. Model residuals were checked for distribution, and appropriate error distributions were employed. The *lme4* package (Bates et al. 2015) was used for constructing the mixed-effects models. To compare differences between types of areas (wild, rural, and urban), post-hoc analyses for mixed-effect models were conducted using the *phia* package (Martinez 2015).

Furthermore, multivariate analyses were employed to test differences in ant species composition among the studied areas (wild, rural, and urban). Initially, a non-metric multidimensional scaling (NMDS) analysis was used to ordinate the samples based on Bray-Curtis similarity index. Subsequently, a non-parametric permutation-based Analysis of Similarities (ANOSIM) with 999 permutations was conducted to test the significance of the groupings formed in the NMDS. The same procedure was employed to analyze the variation in plant species composition. These analyses were performed using the *vegan* package (Oksanen et al. 2017). All statistical analyses were conducted in R version 4.2.3 (R Development Core Team 2023).

Results

The ant-plant interaction networks (Fig. 2) were represented by 65 ant species, 83 plant species and 432 distinct interactions. The most representative ant genera were *Camponotus* with 12 species, *Pseudomyrmex* with 11 species, and *Cephalotes* with 10 species. On the other hand, the most abundant species belonged to the genus *Crematogaster*, namely *Crematogaster* sp. 1 with 619 individuals, *Crematogaster* sp. 2 with 258, and *Crematogaster* sp. 5 with 134. On the other hand, 14 ant species had only one recorded individual each (singletons). For plants, the most important genera were *Aspidosperma* (Apocynaceae) and *Vochysia* (Vochysiaceae), each with four species. As for the most abundant plant species, they were *Myracrodruon urundeuva* (Anacardiaceae) with 62 individuals, *Machaerium acutifolium* (Fabaceae) with 54, and *Qualea grandiflora* (Vochysiaceae) with 39 individuals recorded.

In the wild networks, the most representative ant genus was *Pseudomyrmex* with nine species, and the most abundant species were the ant *Crematogaster* sp.1 with 614 individuals and the plant *Machaerium acutifolium* with 30 individuals. In the rural networks, the highlighted ant genus was *Camponotus* with eight species, and the ant species *Camponotus* sp.4 stood out with 57 individuals and the plant species *Hymenaea stigonocarpa* (Fabaceae) with 21 individuals. In the urban networks, the richest ant genera were *Camponotus* and *Pseudomyrmex* with seven species each, while the most abundant species were *Brachymyrmex* sp.1 with 108 individuals for ants and the *Myracrodruon urundeuva* with 62 individuals for plants.

The number of ant species recorded in each network varied from 10 to 28 species (mean 16.7 ± SD 5.6; Table 1). Ant species richness varied significantly among areas (Table 2), with higher richness in wild areas compared to others (Fig. 3A). Ant abundance (incidence data) ranged from 19 to 109 records (52.8 ± 29.0; Table 1). Similar to species richness, ant abundance was also higher in wild areas compared to others (Table 2; Fig. 3B). Studied areas also varied in the species composition of both plants (ANOSIM: Stress $= 0.074$; $R = 0.862$, $P < 0.001$) and ants (ANOSIM: Stress $= 0.174$; $R = 0.263$, $P = 0.042$). For plants, the composition was distinct among urban, rural, and wild environments (Fig. 4A), while for ants, the greatest contrast occurred between urban and wild environments (Fig. 4B).

The specialization of networks ranged from 0.00 to 0.33 (0.19 ± 0.08; Table 1) and did not differ among the different studied areas (Table 2). Overall, the networks exhibited modularity values ranging between -0.67 and 2.28 (0.36 ± 0.85; Table 1) and nestedness values ranging from -1.98 to 2.37 (-0.19 ± 1.12; Table 1). The analyses indicate that neither modularity nor nestedness of networks differed

Table 1 Values for the different network parameters obtained for the 12 ant-plant networks sampled in urban, rural and wild areas of Neotropical savannas

Area	Anthropization level	Ant species richness	Ant abundance	Network specialization	Network modularity	Network nestedness
1	Urban	11	19	0.125	0.202	0.018
2	Urban	19	73	0.234	-0.093	-1.988
3	Urban	18	90	0.208	1.137	-0.683
4	Urban	10	22	0.251	-0.299	0.032
5	Rural	13	26	0.181	0.005	-0.064
6	Rural	17	60	0.224	1.160	-0.209
7	Rural	17	50	0.206	-0.386	-0.090
8	Wild	13	31	0.000	-0.107	2.373
9	Wild	23	109	0.144	0.189	0.865
10	Wild	28	66	0.176	-0.677	-0.537
11	Wild	21	62	0.242	2.287	-1.758
12	Wild	10	26	0.334	0.971	-0.299
Mean	-	16.7	52.8	0.194	0.366	-0.195
SD	-	5.6	29.0	0.082	0.853	1.123

Table 2 Results of GLMM's assessed the effects of anthropization level, plant species richness and plant abundance on the ant species richness, ant abundance, specialization, modularity and nestedness of ant-plant networks in Neotropical savannas

Response variables	Explanatory variables	$\chi2$	DF	*p*
Ant species richness	Anthropization level	19.37	2	<0.001
	Plant species richness	17.69	1	<0.001
	Plant abundance	2.97	1	0.085
Ant abundance	Anthropization level	9.35	2	0.009
	Plant species richness	14.55	1	<0.001
	Plant abundance	11.94	1	0.001
Network specialization	Anthropization level	1.56	2	0.458
	Plant species richness	3.51	1	0.060
	Plant abundance	0.03	1	0.854
Network modularity	Anthropization level	0.30	2	0.860
	Plant species richness	0.01	1	0.903
	Plant abundance	1.35	1	0.244
Network nestedness	Anthropization level	0.71	2	0.772
	Plant species richness	0.80	1	0.086
	Plant abundance	1.67	1	0.165

among urban, rural, and wild areas (Table 2). Additionally, the results indicate that plant diversity variables in the sampled areas influenced ant diversity but did not affect the network structure (Table 1). We observed that the greater the plant species richness, the lower the ant species richness (Fig. 5A), and the ant abundance (Fig. 5B). On the other hand, our results show that networks with higher plant abundance also had a greater abundance of ants (Fig. 5C).

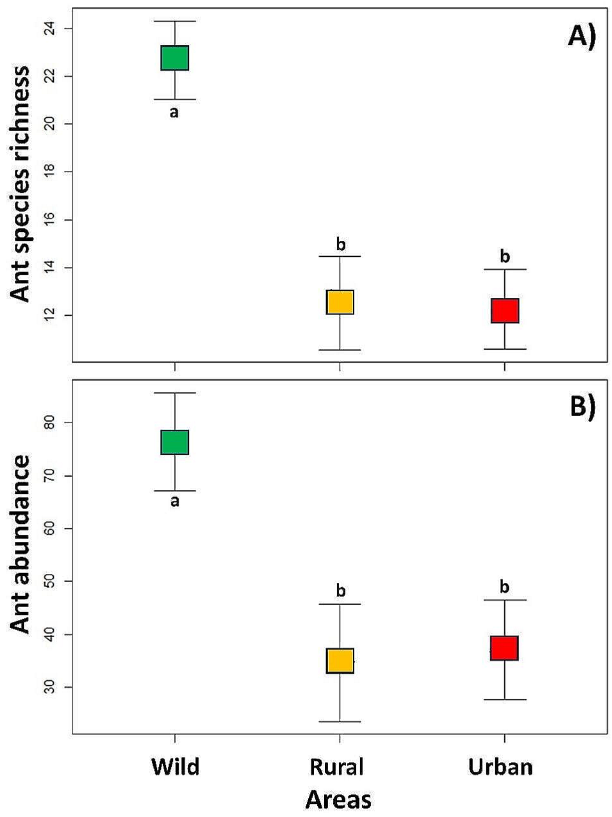

Fig. 3 Comparison of (**a**) ant richness and (**b**) ant abundance among wild, rural, and urban areas of Neotropical savannas. Letters indicate significant differences ($p<0.05$)

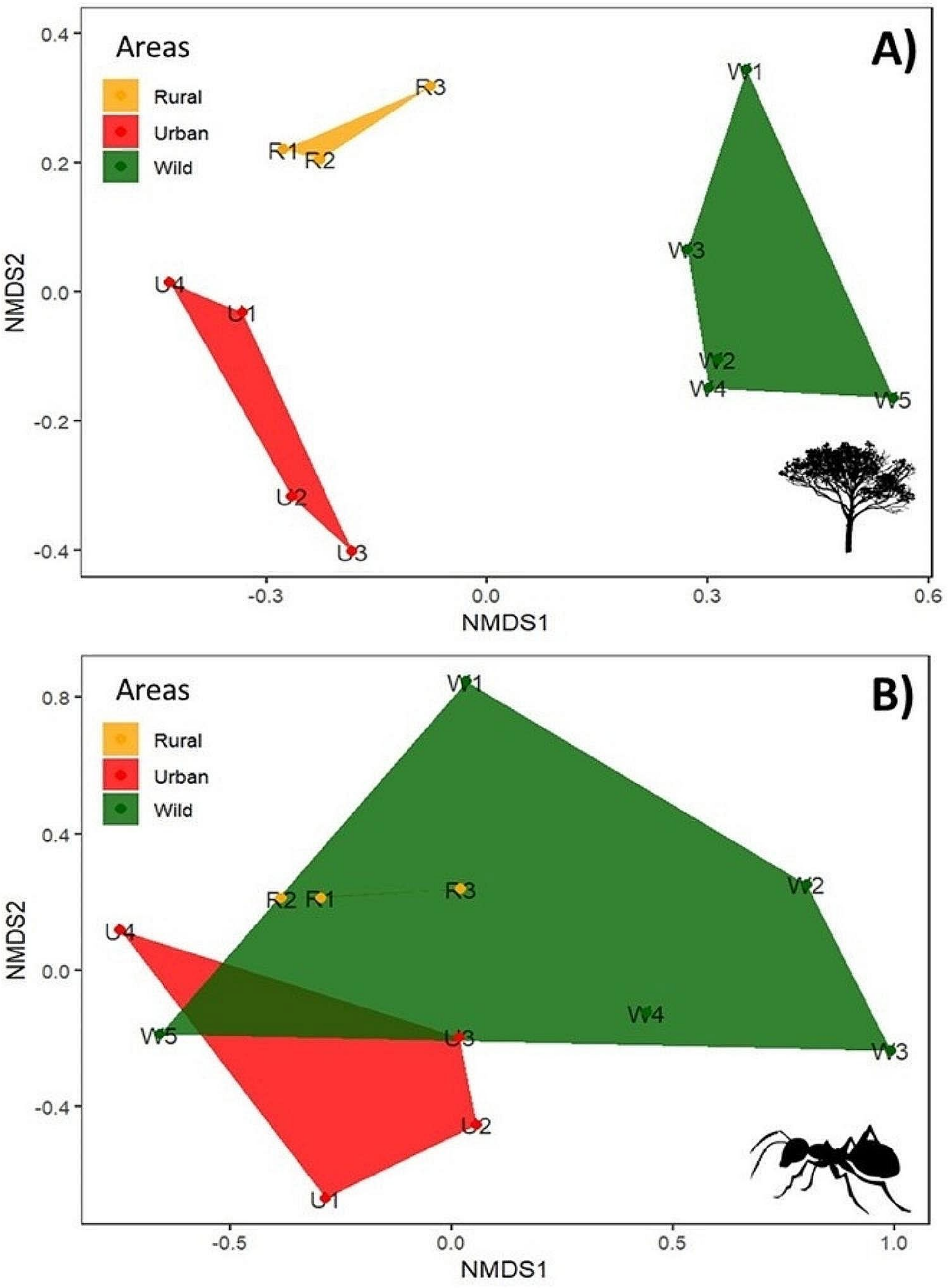

Fig. 4 Non-metric multidimensional scaling (NMDS) showing the species composition arrangement of (**a**) plants and (**b**) ants between wild, rural, and urban areas of Neotropical savannas

Discussion

Our study provides a novel contribution to understanding how urbanization impacts the diversity and organization of ant-plant co-occurrence networks. Interestingly, we found that while ant-plant networks exhibit differences in species diversity between urban and wild areas, the organization of these networks remains similar across these contrasting environments. Specifically, we observed higher richness and abundance of ants in neotropical savannas located in wild areas, with distinct species compositions between urban and wild areas, with urban areas being the most dissimilar. However, the specialization, modularity, and nestedness of the networks were consistent among wild, rural, and urban areas, suggesting a high structural stability of such networks.

Corroborating our expectations, we observed that both ant species richness and abundance were higher in wild areas than in other locations. These areas provide a conducive environment for a high diversity of ant species, offering distinct ecological niches that cater to the varied needs of these social insects (Apolinário et al. 2019).

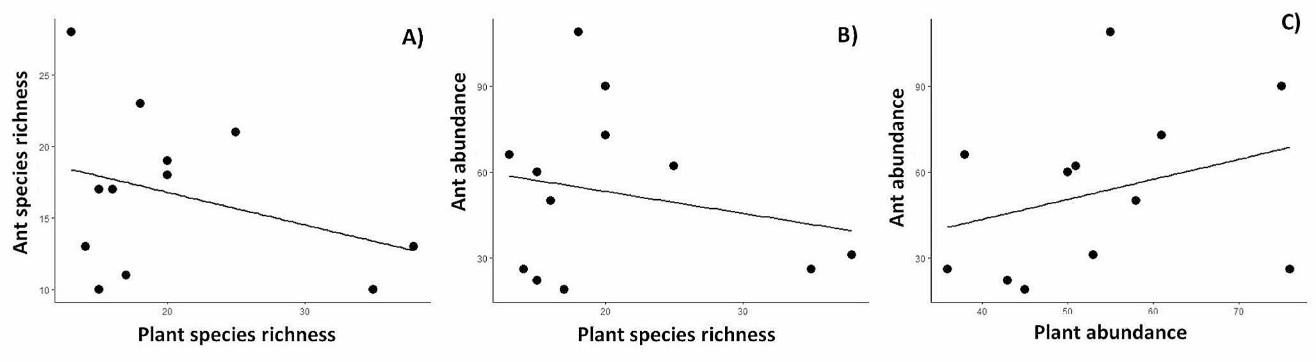

Fig. 5 Effects of plant diversity on the ant diversity in ant-plant networks. (**a**) Relationship between plant species richness and ant species richness. (**b**) Relationship between plant species richness and ant abundance. (**c**) Relationship between plant abundance and ant abundance

Preserved vegetation provides abundant food resources for ants, ranging from flower nectar, extrafloral nectaries and other resources (Andersen 2019). Additionally, the complex structures of vegetation, such as leaves, branches, and trunks, create microhabitats and nesting opportunities, fostering the coexistence of different ant species (Li et al. 2017). Wild areas also can play a fundamental role in maintaining ecological balance, contributing to the regulation of ant populations and promoting species co-occurrence. Additionally, our results also demonstrate that the composition of ant fauna varied among the studied areas, indicating that different species occur in wild and urban environments. This aligns with changes in the composition of plant species along the urbanization gradient in neotropical savannas (Freitas et al. 2023).

Despite detecting changes in species diversity, our results indicate that the structure of ant-plant co-occcurrence networks remained similar across wild, rural, and urban areas. The consistent network specialization observed across diverse environments suggests a notable stability in the functional aspects of ant-plant interactions (Dáttilo et al. 2013). In a recent study by Dáttilo and Vasconcelos (2019), it was found that ant-plant networks maintain an invariant structure, including specialization, nestedness, and modularity, along environmental gradients in savannas. Surprisingly, our study also revealed this invariant structure, highlighting the pervasive connectivity within the networks and indicating the adaptability of species to shifting environmental conditions (Miranda et al. 2022). These network characteristics align with previous research suggesting that resistance and resilience are common features in ant-plant ecological networks (Sánchez-Galván et al. 2012; Dáttilo et al. 2013; Fagundes et al. 2018; Miranda et al. 2022). It is important to emphasize that most of these previous studies were characterized by networks with interactions between plants with extrafloral nectaries and ants, whereas our study consisted of ant-plant co-occurrence interactions, indicating the generality of the pattern for different types of ant-plant interactions.

Recent studies involving different types of animal-plant interactions (e.g., plant-herbivore and plant-pollinator interactions) have reported a significant effect of urbanization on network structure and specialization (Geslin et al. 2013; Santis et al. 2023; Araújo et al. 2024). The differences in response patterns of ant-plant networks to these other types of ecological interaction networks may lie in the level of biological association of ecological interactions (Mazziotta et al. 2017). Considering that our networks involve facultative interactions (Cockle and Martin 2015; Mazziotta et al. 2017), networks of these interactions tend to have a more robust structure in the face of anthropogenic disturbances (Dáttilo 2012). However, it is important to highlight that even though the findings of our study suggest that ant-plant co-occurrence networks have similar topology between urban and wild areas, the alterations in species composition along the different habitats could have implications for the structure of interactions among these species. This suggests that the roles of species within the networks may vary due to species turnover (Poisot et al. 2015), and more intriguingly, that the same species may have distinct roles in networks located in different habitats. For example, it is possible that ant and plant species occurring in both urban and wild areas may have different interactions in these contrasting environments. Thus, the role of species may vary in environments with different levels of disturbance (Falcão et al. 2017), but for ant-plant interactions in urbanized savannas, this still needs to be investigated in future studies.

Another result obtained is that plant diversity affects ant diversity in the ant-plant networks. We found a positive correlation between plant abundance and ant abundance. Areas with higher plant abundance can provide more resources for ants, including abundant food and nesting sites (Li et al. 2017). However, contrary to expectations, we observed that the increase in plant richness leads to a decrease in species richness and ant abundance. One possible explanation is that the sampled ant fauna also includes epigaeic ants (e.g., some species of *Camponotus*, which were the most abundant group). These ants may occasionally forage on trees and were therefore sampled at the time of collection. Previous studies on ant assemblages composed by epigaeic species are usually not explained by vegetation variables (Marques et al. 2017). This epigeic fauna may be associated with factors other than tree vegetation diversity, such as soil types, presence of litter, and/or presence of grasses (Costa et al. 2010). These results are in line with previous studies that found a negative relationship between ant diversity and habitat diversity/complexity (e.g. Lassau and Hochuli 2004; Achury et al. 2022; Kuchenbecker et al. 2022).

The ant species composition differed significantly among urban, rural, and wild areas. We recorded different dominant ant groups in each type of environment, such as *Crematogaster* in wild areas, *Camponotus* in rural areas, and *Brachymyrmex* in urban areas, although these three genera were found in all types of areas (urban, rural, and wild). On the other hand, the genera *Gnamptogenys*, *Megalomyrmex*, and *Solenopsis*, occurred exclusively in wild areas, while the genus *Atta*, occurred exclusively in rural areas, but no ant genus was exclusive to urban areas. The genus *Camponotus* was more diverse in the present study. Most species within this genus are arboreal or epigaeic, primarily foraging during the night, displaying a generalist feeding habit, and seeking carbohydrates and proteins (Hölldobler and Wilson 1990; Silvestre et al. 2003). Ants of this genus can be observed on extrafloral nectaries (Junqueira et al. 2001) and may play a role in pollinating certain plant species (Gómez et al. 1996). Another important genus was *Pseudomyrmex*, which is widely distributed in tropical and subtropical ecosystems and establishes significant mutualistic associations with various plant species (Silvestre et al. 2003). Often, they provide protection against herbivores to host plants in exchange for shelter or food sources (Sanchez and Bellota 2015). Finally, the third most diverse genus in the present study was *Cephalotes*, which is characterized by predominantly arboreal species that specialize in canopy habitats (Silvestre et al. 2003). Their interactions with plants involve exploring plant surfaces, such as leaves and branches, in search of food resources, and the formation of colonies in arboreal environments (Silvestre et al. 2003). Some ant species found in Brazilian savannas are also territorial, capable of dominating interactions with many plant species in their foraging areas (Del-Claro et al. 2018), which could also explain the observed results.

Interactions between ants and plants can be formed by different types of interactions (Del-Claro et al. 2018). Among the plants recorded in the field in our study, no species with domatia, i.e., myrmecophytes, were registered. On the other hand, some species of plants with extrafloral nectaries were recorded, such as *Qualea grandiflora* (which was the third most abundant plant species in the study as a whole) and *Hymenaea stigonocarpa* (which was the most abundant species in rural areas). Although species with extrafloral nectaries can accumulate many interactions in the locations where they occur (Miranda et al. 2022), in the present study, they represented less than 10% of the species recorded. Thus, the vast majority of plant species recorded in the savanna areas studied do not present any known attractant for ants. Future studies may investigate whether the occurrence of plants with extrafloral nectaries and consequently their interactions with ants vary between urban and wild areas.

In conclusion, our study reveals that urbanization leads to a reduction in both the richness and abundance of ants, along with alterations in species composition. However, despite these changes, we found that the organization of ant-plant interactions remains unchanged along the different studied environments. This suggests a high level of resilience in ant-plant networks to anthropogenic disturbances, maintaining their structure in urban environments similarly to what is observed in wild environments. Future studies could investigate the role of different ant species in in shaping these networks, and whether these roles remain unchanged in networks located in urban and wild areas.

Acknowledgements The authors thank to Odirlei Simões and Santos D'Angelo (in memoriam) for their help in plant identification; Flávio Camarota for help in ant identification; the colleagues of the Laboratory of Ecological Interactions and Biodiversity - LIEB for their help in field collections, and the Instituto Estadual de Florestas – IEF team for the collection permit and support in field activities, and the financing agencies FAPEMIG, FAPESP, CAPES, and CNPq for financial support.

Author contributions All authors contributed to the study conception and design. Material preparation and data collection were performed by Samira Rosa de Oliveira Lima, Edvânia Costa de Oliveira Sá and Poliane Neres Morais. Data analysis was performed by Samira Rosa de Oliveira Lima and Walter Santos de Araújo. The first draft of the manuscript was written by Samira Rosa de Oliveira Lima and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Funding This research was funded by FAPEMIG (APQ-00394-18; APQ-03236-22) and CNPq (423915/2018-5; 308928/2022-9). Sampling in the Veredas do Peruaçu State Park was financed by PELD-VERE, a project supported by CNPq/CAPES/FAPEMIG-Brazil (CNPq 441440/2016-9; CAPES 88887.136273/2017–00; FAPEMIG APQ-04816-17).

Data availability Data is provided within the manuscript or supplementary information files.

Declarations

Competing Interests The authors have no relevant financial or non-financial interests to disclose.

References

Achury R, Clement L, Ebeling A, Meyer S, Voigt W, Weisser WW (2022) Plant diversity and functional identity alter ant occurrence and activity in experimental grasslands. Ecosphere 13:e4252

Almeida-Neto M, Guimaraes P, Guimaraes PR, Loyola RD, Ulrich W (2008) A consistent metric for nestedness analysis in ecological systems: reconciling concept and measurement. Oikos 117:1227–1239

Alvares CA, Stape JL, Sentelhas PC, Gonçalves JLM, Sparovek G (2014) Koppen's climate classification map for Brazil. Meteorol Z 22:711–728

Andersen AN (2019) Responses of ant communities to disturbance: five principles for understanding the disturbance dynamics of a globally dominant faunal group. J Anim Ecol 88:350–362

Apolinário LCMH, Almeida ÂAD, Queiroz JM, Vargas AB, Almeida FS (2019) Diversity and guilds of ants in different land-use systems in Rio De Janeiro State. Brazil Floran 26:e20171152

Araújo WS, Costa KCS, Freitas ÉVD, Santos JC, Cuevas-Reyes P (2024) Species richness and network topology patterns in neotropical plant-galling communities changes along an urbanization gradient. J Insect Conserv 28:191–200

Baccaro FB, Feitosa RM, Fernández F, Fernandes IO, Izzo TJ, Souza JLP, Solar RRC (2015) Guia para os gêneros de formigas do Brasil. INPA, Manaus

Bascompte J, Jordano P, Olesen JM (2006) Asymmetric coevolutionary networks facilitate biodiversity maintenance. Science 312:431–433

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

Beckett SJ (2016) Improved community detection in weighted bipartite networks. R Soc Open Sci 3:140536

Blüthgen, N., Menzel, F., & Blüthgen, N. (2006). Measuring specialization in species interaction networks. BMC ecology, 6, 1-12

Cockle KL, Martin K (2015) Temporal dynamics of a commensal network of cavity-nesting vertebrates: increased diversity during an insect outbreak. Ecology 96:1093–1104

Corro EJ, Ahuatzin DA, Jaimes AA, Favila ME, Ribeiro MC, López-Acosta JC, Dáttilo W (2019) Forest cover and landscape heterogeneity shape ant–plant co-occurrence networks in human-dominated tropical rainforests. Landsc Ecol 34:93–104

Costa CB, Ribeiro SP, Castro PT (2010) Ants as bioindicators of natural sucession in savanna and riparian vegetation impacted by dredging in the Jequitinhonha River Basin, Brazil. Restor Ecol 18:148–157

Dáttilo W (2012) Different tolerances of symbiotic and nonsymbiotic ant-plant networks to species extinctions. Netw Biol 2:127

Dáttilo W, Vasconcelos HL (2019) Macroecological patterns and correlates of ant–tree interaction networks in neotropical savannas. Glob Ecol Biogeogr 28:1283–1294

Dáttilo W, Guimarães PR Jr, Izzo TJ (2013) Spatial structure of ant–plant mutualistic networks. Oikos 122:1643–1648

Dáttilo W, Marquitti FM, Guimarães PR Jr, Izzo TJ (2014a) The structure of ant–plant ecological networks: is abundance enough? Ecology 95:475–485

Dáttilo W, Díaz-Castelazo C, Rico-Gray V (2014b) Ant dominance hierarchy determines the nested pattern in ant–plant networks. Biol J Linn Soc 113:405–414

Dáttilo W, Sánchez-Galván I, Lange D, Del-Claro K, Rico-Gray V (2014c) Importance of interaction frequency in analysis of ant-plant networks in tropical environments. J Trop Ecol 30:165–168

Dáttilo W, Ahuatzin-Flores DA, Corro-Mendez EJ, Escobar F, MacGregor-Fors I (2017) Redes complexas no estudo das interações ecológicas entre formigas e plantas em ambientes urbanos: um novo modelo conceitual. In: Bueno OC, Campos AEC, Morini MSC (eds) Formigas em Ambientes Urbanos do Brasil. Canal 6 Editora, Bauru, pp 265–284

Del-Claro K, Dirzo R (2021) Impacts of Anthropocene defaunation on plant-animal interactions. In: Del-Claro K, Torezan-Silingardi HM (eds) Plant-animal interactions: source of Biodiversity. Springer, Cham, pp 333–345

Del-Claro K, Lange D, Torezan-Silingardi HM, Anjos DV, Calixto ES, Dáttilo W, Rico-Gray V (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, Frund J (2008) Introducing the bipartite package: analysing ecological networks. R News 8:8–11

Dormann CF, Frund J, Schaefer HM (2017) Identifying causes of patterns in ecological networks: opportunities and limitations. Annu Rev Ecol Evol Syst 48:559–584

Dröse W, Podgaiski LR, Dias CF, Mendonca MS Jr (2019) Local and regional drivers of ant communities in forest-grassland ecotones in South Brazil: a taxonomic and phylogenetic approach. PLoS ONE 14:e0215310

Fagundes R, Lange D, Anjos DV, Lima FP, Nahas L, Corro E, Silva PBG, Del-Claro K, Ribeiro SP, Dáttilo W (2018) Limited effects of fire disturbances on the species diversity and structure of ant-plant interaction networks in Brazilian Cerrado. Acta Oecol 93:65–73

Falcão JC, Dáttilo W, Díaz-Castelazo C, Rico-Gray V (2017) Assessing the impacts of tramp and invasive species on the structure and dynamic of ant-plant interaction networks. Biol Conserv 209:517–523

Fortuna MA, Bascompte J (2006) Habitat loss and the structure of plant–animal mutualistic networks. Ecol Let 9:278–283

Freitas ÉVD, Veloso MM, Araújo WS (2020) Urbanization alters the composition, but not the diversity and structure, of neotropical savanna woody plant communities. Folia Geobot 55:95–108

Freitas ÉVD, Maracahipes L, Araújo WS (2023) Plant richness and vegetation structure drive the topology of plant-herbivore networks in neotropical savannas. Acta Oecol 121:103961

Geslin B, Gauzens B, Thébault E, Dajoz I (2013) Plant Pollinator networks along a gradient of urbanisation. PLoS ONE 8:e63421

Gómez JM, Zamora R, Hódar JA, García D (1996) Experimental study of pollination by ants in Mediterranean high mountain and arid habitats. Oecologia 105:236–242

Grimm NB, Faeth SH, Golubiewski NE, Redman CL, Wu J, Bai X, Briggs JM (2008) Global change and the ecology of cities. Science 319:756–760

Guimarães PR, Rico-Gray V, Dos-Reis SF, Thompson JN (2006) Asymmetries in specialization in ant–plant mutualistic networks. Proc R Soc Lond B 273:2041–2047

Guimarães PR Jr, Rico-Gray V, Oliveira PS, Izzo TJ, Dos Reis SF, Thompson JN (2007) Interaction intimacy affects structure and coevolutionary dynamics in mutualistic networks. Curr Biol 17:1797–1803

Hölldobler B, Wilson EO (1990) The ants. Harvard University Press, Cambridge

Juárez-Juárez B, Dáttilo W, Moreno CE (2023) Synthesis and perspectives on the study of ant-plant interaction networks: a global overview. Ecol Entomol 48:269–283

Junqueira LK, Diehl E, Diehl-Fleig E (2001) Formigas (Hymenoptera: Formicidae) visitantes de *Ilex paraguariensis* (Aquifoliaceae). Neotrop Entomol 30:161–164

Kuchenbecker J, Cuevas-Reyes P, Fagundes M (2022) Community structure of ants (Hymenoptera: Formicidae) in an open habitat: the importance of environmental heterogeneity and interspecific interactions. Rev Mex Biodivers 93:e933900

Lassau SA, Hochuli DF (2004) Effects of habitat complexity on ant assemblages. Ecography 27:157–164

Li Q, Hoffmann BD, Lu ZX, Chen YQ (2017) Ants show that the conservation potential of afforestation efforts in Chinese valley-type savanna is dependent upon the afforestation method. J Insect Conserv 21:621–631

Marques TG, 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 64:261–275

Martinez HDR (2015) Analysing interactions of fitted models. CRAN-R Project

Mazziotta A, Vizentin-Bugoni J, Tottrup AP, Bruun HH, Fritz O, Heilmann-Clausen J (2017) Interaction type and intimacy structure networks between forest-dwelling organisms and their host trees. Basic Appl Ecol 24:86–97

McKinney ML (2002) Urbanization, biodiversity, and conservation. Bioscience 52:883–890

McKinney ML (2006) Urbanization as a major cause of biotic homogenization. Biol Conserv 127:247–260

Miranda PN, Silva Ribeiro JEL, Luna P, Brasil I, Delabie JHC, Dáttilo W (2019) The dilemma of binary or weighted data in interaction networks. Ecol Complex 38:1–10

Miranda PN, Silva Ribeiro JEL, Corro EJ, Brasil I, Delabie JHC, Dáttilo W (2022) Structural Stability of ant-plant Mutualistic Networks mediated by Extrafloral nectaries: looking at the effects of Forest Fragmentation in the Brazilian Amazon. Sociobiology 69:e8261

Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGlinn D et al (2017) vegan: Community Ecology Package. R package version 2.4-4

Pellissier L, Albouy C, Bascompte J, Farwig N, Graham C, Loreau M, Gravel D (2018) Comparing species interaction networks along environmental gradients. Biol Rev 93:785–800

Plowman NS, Hood AS, Moses J, Redmond C, Novotny V, Klimes P, Fayle TM (2017) Network reorganization and breakdown of an ant–plant protection mutualism with elevation. Proc R Soc B Biol Sci 284:20162564

Poisot T, Stouffer DB, Gravel D (2015) Beyond species: why ecological interaction networks vary through space and time. Oikos 124:243–251

QGIS Development Team (2020) QGIS 3.4 Geographic Information System user guide. Open Source Geospatial Foundation Project

R Development Core Team (2023) R: a language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna

Ribeiro JF, Walter BMT (2008) As principais fitofisionomias do bioma Cerrado. In: Sano SM, Almeida SP, Ribeiro JF (eds) Cerrado: ecologia e flora. Embrapa Cerrados, Brasília, pp 151–212

Rico-Gray V, Oliveira PS (2007) The Ecology and Evolution of ant-plant interactions. The University of Chicago, Chicago

Rocha EA, Fellowes MDE (2020) Urbanisation alters ecological interactions: ant mutualists increase and specialist insect predators decrease on an urban gradient. Sci Rep 10:6406

Sampaio RC, Silva LBF, Souza Coelho RC, Queiroz JM (2023) Effects of Vegetation structure on ant diversity in different Seasonal periods in impacted fragments of Atlantic Forest. Sociobiology 70:e7949

Sanchez A, Bellota E (2015) Protection against herbivory in the mutualism between *Pseudomyrmex dendroicus* (Formicidae) and Triplaris americana (Polygonaceae). J Hymenopt Res 46:71–83

Sánchez-Galván IR, Díaz-Castelazo C, Rico-Gray V (2012) Effect of hurricane Karl on a plant–ant network occurring in coastal Veracruz, Mexico. J Trop Ecol 28:603–609

Sanford MP, Manley PN, Murphy DD (2009) Effects of urban development on ant communities: implications for ecosystem services and management. Conserv Biol 23:131–141

Santis AAA, Lomáscolo SB, Chacoff NP (2023) Effects of urbanization on the structure of plant-flower visitor network at the local and landscape levels in the northern Argentinian Yungas forest. Front Sustain Cities 5:1086076

Silvestre RC, Brandão RF, Silva RR (2003) Grupos funcionales de hormigas: El Caso De Los Gremios Del Cerrado. In: Fernández F (ed) Introducción a las hormigas de la región neotropical. Instituto de Investigación de Recursos Biológicos Alexander Von Humboldt, Bogotá, pp 101–136

Tylianakis JM, Morris RJ (2017) Ecological networks across environmental gradients. Annu Rev Ecol Evol Syst 48:25–48

Tylianakis JM, Laliberté E, Nielsen A, Bascompte J (2010) Conservation of species interaction networks. Biol Conserv 143:2270–2279

Walker JS, Grimm NB, Briggs JM, Gries C, Dugan L (2009) Effects of urbanization on plant species diversity in central Arizona. Front Ecol Environm 7:465–470