Sociobiology 71(2): e9286 (June, 2024)
DOI: 10.13102/sociobiology.v71i2.9286

Sociobiology
An international journal on social insects

RESEARCH ARTICLE - ANTS

By the Way, Does the Presence of Ants in Flowers Interfere with Floral Visitation, or Not? A community Ecology Study

Gabriela Santana de Oliveira, José Enéas Schramm Júnior, Tamires Bastos dos Santos, Gilberto Marcos de Mendonça Santos

Biological Sciences Department, Feira de Santana State University, Feira de Santana - BA, Brazil

Article History

Edited by
?

Received	16 March 2023
Initial acceptance	09 May 2023
Final acceptance	04 February 2024
Publication date	28 May 2024

Keywords
Antagonism, Ants, Mutualistic Interactions, Ecological Networks, Floral Visitors, Community Ecology

Corresponding author
José Enéas Schramm Júnior
Departamento de Ciências Biológicas
Universidade Estadual de Feira de Santana (UEFS)
Av. Transnordestina s/nº, Novo Horizonte - CEP 44036-900,
Feira de Santana, Bahia, Brasil.
E-Mail: eneaschr@gmail.com

Abstract

Several mutualistic interactions occur in natural communities that, in some cases, present antagonistic functions happening simultaneously and even within the same interaction, so both mutualistic and antagonistic partners present direct and indirect interactions reflecting the system's whole structure. The mutualistic interaction some ants have with plants – based on which defense is offered in exchange for another benefit (such as food and/or shelter) – raises doubts about its likely effect on floral visitors that account for pollination processes. The current study uses the complex network approach to assess whether these divergent interactions affect each other at the community level. We adopted interactions' connectedness as a response metric to highlight the strength of interactions within a given community. We tested the hypothesis that ants' presence in flowers interferes with floral visitation by other animal species, influences floral visitors' network structure, and, consequently, reduces networks' connectedness. According to the current results, ants' presence in flowers did not change floral visitors' network structure. Although it had some impact on certain floral visitors, such as bees, as also evidenced in studies conducted at the population level, it was not significant enough to change the community's structure. The findings in the present study maintained the concept of mutualism, according to which benefits outweigh the losses. Yet, they did not show antagonism in the ants/plants association.

Introduction

Most past studies about interactions in ecological communities have focused on investigating antagonistic interactions, such as predation or competition (Holt, 1977; Kotler, 1984). Most recently, several studies have focused on mutualistic interactions and their role in structuring natural communities (Boucher, 1988; Stachowicz, 2001; Santos et al., 2006 and 2007; Bascompte, 2010; Bluthgen & Klein, 2011).

Several studies based on the complex network approach have been carried out to assess how mutualistic interactions affect different communities after the study conducted by Jordano (1987). These studies use different investigation models, such as fish-cleaner (Guimarães et al., 2007; Floeter et al., 2007), ants-plants with extrafloral nectaries (EFNs) (Guimarães et al., 2006; Schramm Júnior et al., 2023), bees-plants (Pigozzo et al., 2010) and wasps-plants (Mello et al., 2011a) partners.

Robust studies conducted with large data sequences, even meta-analyses, helped to improve the knowledge about the ecology of natural communities and mutualistic interaction networks. Despite presenting their specificities (Olesen et al., 2010a), communities structured based on reciprocal relationships also show universal properties shared by all mutualistic networks (Barabasi et al., 2002; Bascompte et al., 2007).

Studies based on ecological network analysis have significantly contributed to understanding both the dynamics (Vázquez, 2009) and the structure of ecological communities. Thus, they are essential to help explain important aspects, such

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ISSN: 0361-6525

as species' stability and coexistence, coevolution processes, as well as temporal and spatial patterns (Jordano et al., 2006; Bascompte, 2007; Nuismer et al., 2012; Dáttilo, 2013; Santos et al., 2014; Schramm Júnior et al., 2023).

The complex set of ecological interactions taking place in natural communities is quite chaotic. It often involves more than two partners, a fact that leads to mutualistic and agonistic interactions taking place at the same time. This interaction involving more than two partners often results in simultaneous direct and indirect interactions between mutualistic and agonistic partners. Consequently, it significantly impacts the structure of natural communities (Bronstein, 2012; Romero & Vasconcelos-Neto, 2012).

Ants/plants mutualism is one of the most investigated interaction types (Beattie, 1985; Oliveira & Brandão, 1991; Freitas & Oliveira, 1996; Oliveira, 1997; Oliveira & Pie, 1998; Oliveira & Freitas, 2004; Dáttilo et al., 2009; Byk & Del-Claro, 2010), because ants are occasional floral visitors, although frequent and abundant. They can interact with plants as mutualistic agents in different ways, such as pollinators (Beattie, 1985; Ashman & King, 2005), seed dispersers (Marques, 2006; Leal, 2003), and protectors against herbivores (Del-Claro et al., 1996; Horvitz & Schemske, 1984). On the other hand, plants provide ants with shelter and/or food (nectar, pollen, oils, resins, and even hunting areas to find prey in plants' reproductive and vegetative structures) (Rico-Gray & Oliveira 2007, Byk & Del-Claro, 2010).

Community structures based on mutualistic bee-plant interactions are also widely investigated. Bees provide pollination services to partner plants in these systems, and consequently, they are rewarded with food, oils, and resins (Jordano, 1987; Memmott et al., 2004; Vázquez & Aizen, 2004; Bezerra et al., 2009; Santos et al., 2010b).

According to studies carried out with focal plants, the initially mutualistic ants/plants interaction can cause damage when ants defend plants against herbivores since they can scare away other mutualistic partners, such as pollinating bees, and it can make this interaction's cost higher than its benefit (Romero & Vasconcelos-Neto, 2012; Gaume, 2005; Ness, 2006; Bronstein, 2012).

Thus, if some visitors avoid certain plants with ants in their flowers, one could expect it to affect the network structure due to connectance metrics issues (Jordano, 1987), since network connectance can decrease as the number of interactions decreases.

The cost of the association between different mutualistic partners and these interactions remains relatively poorly explored in scientific studies (Bronstein, 2001a; Bronstein, 2001b; Bronstein, 2012). Conflicts between mutualistic guilds will always exist in widespread systems. Some of these arthropods can interact with each other in such a way that some aggressive species can discourage visitation by legitimate pollinators (Gaume, 2005; Ness, 2006; Romero & Vasconcelos-Neto, 2012) and, consequently, reduce pollination by some spider species, for example (Louda, 1982).

Pollination and protection against herbivores are important functions, although they present different interaction strengths, intimacy, and specialization levels. The current study used interaction network metrics to assess the effect of ants' presence in flowers on bees' visitation to them. The herein-tested hypothesis advocates that bees and ants have agonistic interaction and that ants' presence in flowers significantly affects the structure of bee communities. Assumingly, ants' presence in flowers makes the plant-bee network less cohesive, reduces connectance, and increases modularity and specialization.

Material and methods

Study site

The study was conducted at Sempre-Viva Municipal Park, Mucugê County, (12°59`31.43` S, 41°20`32.15" W; 980 m above sea level), Bahia State, Brazil. The climate in the study site is of the humid subtropical type (Cwa, according to Koppen's classification system), and prevalent vegetation comprises rupestrian grasslands featured by rocky outcrops associated with herbaceous-shrubby phytophysiognomy (Harley, 1995; Conceição et al., 2005).

Sampling

Six sampling procedures were conducted at 30-day intervals between each field campaign (from May to October 2013). Data were collected within a 2,000 m transect comprising twenty 100 m^2 plots (10x10m) arranged 50 m apart (Figure 1).

Each plot was inspected by two collectors from 7:00 am to 7:00 pm (daytime), at 2-hour intervals between samplings, and from 7:00 pm to 7:00 am (nighttime), and at 2-hour intervals between samplings. All flowering plants in each plot were inspected to check on the presence of ants and/or other associated floral visitors. Two collectors monitored each plot for 24 minutes to standardize the sampling process (method adapted from Sakagami et al., 1967), regardless of the number of individuals or visitor species in the assessed plots.

Each observed plant was considered a sampling unit. Plant species exsiccates were assembled and deposited in HUEFS's herbarium. Bees, ants, and other floral visitors were manually collected with the aid of tweezers, entomological vacuum devices, and entomological nets, as well as deposited in Prof. Johann Becker Entomological Collection at the Zoology Museum of State University of Feira de Santana.

Data analysis

Data were analyzed using complex network metrics. Matrices were mounted based on three spreadsheets: 1) all original visitor/plant interaction data, 2) data on the interaction between bees and plants with ants in flowers, and

3) data on the interaction between bees and plants without ants in flowers. Plant species presenting more than two ant records in their flowers were considered “plants with ants”.

Interaction frequency data were used to build a weighted interaction network to assess the hypothesis that ants’ presence in flowers interferes with floral visitors’ network structure. Each floral visitors’ network was analyzed as a binary adjacency matrix, wherein lines represented visitor species (bees and/or ants), and columns represented plant species. It was done to assess interaction effects at the community level.

Networks were thoroughly analyzed based on 5-month data, whereas specific networks were assessed based on data referring to each collection month. Networks were analyzed based on the following metrics: connectance (C), network specialization index (H “and d´) (Blüthgen et al., 2006, 2007), NODF-based nestedness (Almeida-Neto et al., 2008) and modularity (M) (Marquitti et al., 2013). Calculations were performed in R software, version 2.13.2 (R Core Team 2014), based on using bipartite (Darmann et al., 2008) and SNA (Butts, 2013) packages. IGRAPH Software (CSARDI G, Nepusz T 2006) was used to plot network graphs based on the visitor-plant species interaction frequencies matrix.

A paired t-test was used to assess differences in metrics in the different analyzed networks and to test the significance level of the results. Ants’ presence or absence was used as the explanatory variable.

Results

Seventy-five (75) visitor species interacted with flowers belonging to 36 plant species. In total, 14 of them had ants in their flowers, whereas 22 plants did not (Tables 2 and 3).

Thirty-nine (39) of 75 visitor species only interacted with plants that had ants in their flowers, 18 visitor species interacted with plants that did not have ants in their flowers, and 17 visitor species interacted with both plants that had and did not have ants in their flowers. The network with ants recorded 89 interactions, whereas the network without ants recorded 67 interactions (Fig. 2 A and B). These two network types presented similar connectance patterns (t = 0.4293, df = 4, p = 0.68). The network with ants recorded a connectance index equal to 0.11, whereas the ant-free network recorded a connectance index equal to 0.08 (Table 1).

There was no significant variation in the specialization index (H2´) between networks with and without ants (t = 0.67, df = 4, p = 0.54). Both network types presented H2´ with low specialization value. The specialization index observed for the visitor-plant with ants’ network reached 0.40, whereas that for the ant-free network reached 0.46 (Table 1).

Networks with ants presented a nestedness rate similar to those without ants – 19.13% and 16.99%, respectively. Nestedness variation between them was not significant (t = 2.66, df = 4, p = 0.06) (Table 1).

Modularity (m) values did not show significant variation (t = 1.78, df = 4, p = 0.15) between networks: 0.54 for networks with ants and 0.59 for networks without ants (Table 1).

Table 1. Results of both calculated network metrics and paired t-test.

Metrics	Network with ant on the flower	Network without ant on the flower	Paired t-test		
Connectance (C)	0.11	0.08	t = 0.429	df = 4	p = 0.68
Specialization (H2’)	0.40	0.46	t = 0.673	df = 4	p = 0.54
Nestedness (NODF)	19.13	16.99	t = 2.656	df = 4	p = 0.06
Modularity (M)	0.54	0.59	t = 1.775	df = 4	p = 0.15

Discussion

The resemblance between connectance values observed for networks with and without ants has indicated that ants’ presence in flowers did not influence values recorded for this index in floral visitor-plant networks since they were consistently low in both network types (Figure 3). This finding explains these networks’ modular nature since the higher the connectance level, the more generalized the community-level interactions. However, connectance is often low in mutualistic networks since only some potential interspecific interactions occur (Vázquez et al., 2009), and connectance exponentially decreases in species-rich networks (Olesen & Jordano, 2002).

All networks presented a higher trend towards modularity than towards nestedness (Figure 3); nevertheless, they were mixed networks. Nowadays, the combined nested/modular structure is the most acknowledged and investigated in studies highlighting this topology type for facultative mutualism networks (Fortuna et al., 2010). Fortuna also stated that the less connected the communities, the more they tend to present a combined structure. This fact was also observed in the current study.

The investigated networks did not show high specialization levels (H2'). It may have happened due to the

Table 2. Recorded floral visitors’ species and specialization level in the network (d’), Mucugê municipality, Chapada Diamantina region-BA.

FLORAL VISITORS	SPECIALIZATION (d’)	
	WITH ANT ON THE FLOWER	WITHOUT ANT ON THE FLOWER
APIDAE		
Apis mellifera	0.18	0.55
Bombus sp	0.40	0.54
Centris caxiensis	-	0.31
Centris fuscata	0.85	0.00
Centris spilopoda	-	0.00
Eulaema nigrita	-	0.50
Frieseomelitta sp	0.07	0.37
Trigona spinipes	0.21	0.33
Xylocopa cearensis	0.15	0.39
Xylocopa frontalis	-	0.50
Xylocopa suspecta	0.00	-
Arctiidae sp1	0.46	-
Ascia monuste orseis	-	0.00
Bibionidae sp	0.51	-
Bombiliidae sp1	0.39	-
Bombiliidae sp2	-	0.83
Bombiliidae sp3	-	0.50
Carabidae sp	0.21	-
Chalcidoidea sp	0.15	-
Chrysomelidae sp1	0.27	-
Chrysomelidae sp10	-	0.37
Chrysomelidae sp11	0.31	-
Chrysomelidae sp12	0.15	-
Chrysomelidae sp13	0.00	-
Chrysomelidae sp14	0.15	-
Chrysomelidae sp15	0.39	-
Chrysomelidae sp2	0.85	0.37
Chrysomelidae sp3	-	0.33
Chrysomelidae sp4	0.68	-
Chrysomelidae sp5	0.15	0.31
Chrysomelidae sp6	0.27	-
Chrysomelidae sp7	-	1.00
Chrysomelidae sp8	0.21	0.57
Chrysomelidae sp9	-	0.55
Curculionidae sp1	0.14	-
Curculionidae sp2	0.30	-
Curculionidae sp3	0.17	0.50
Curculionidae sp4	0.31	-
Curculionidae sp5	0.12	-
Curculionidae sp6	0.31	-
Curculionidae sp7	0.07	-
Curculionidae sp8	0.00	-
Curculionidae sp9	0.04	-
Curtonotidae sp1	0.31	-
Curtonotidae sp2	0.00	-
Erotylidae sp1	0.17	0.50
Erotylidae sp2	0.00	-
Euptoieta hegesia meridiania	-	1.00
Junonia evarete evarete	-	0.00
Libytheana carinenta	0.39	-
Lycaenidae *Hemiargus hanno hanno*	1.00	0.31
Lycaenidae *Strymon rufofusca*	0.00	-
Noctuidae sp1	-	0.60
Noctuidae sp2	0.54	0.83
Noctuidae sp3	-	0.50
Noctuidae sp4	0.39	0.50
Pieridae Aphrissa statira statira	-	0.00
Polistes canadenis	0.36	0.69
Polybia sp	0.15	-
Pompilidae sp1	-	0.50
Pompilidae sp2	0.15	-
Pyralidae sp1	0.19	-
Riodinidae *Ariconias glaphyra*	0.31	-
Sarcophagidae sp1	0.00	-
Sarcophagidae sp2	0.71	-
Sarcophagidae sp3	0.00	-
Scarabaeidae sp1	0.22	0.83
Scarabaeidae sp2	-	0.73
Syrphidae sp1	0.71	-
Syrphidae sp2	0.71	0.65
Tachinidae sp	0.71	-
Tenebrionidae sp1	0.31	-
Tenebrionidae sp2	0.77	-
Theclinae sp	0.39	-
Urbanus dorantes dorantes	-	0.00
Urbanus proteus proteus	-	0.00

number of generalist species, such as *Apis mellifera* (Linnaeus, 1758), which is a quite common visitor that, consequently, interacts with many of the plants available in these networks, as well as *Bombus* sp and *Trigona spinipis* (Fabricius, 1793), which are highly abundant at the investigated site and present high frequency of interactions with several plants growing in it. Thus, these species play a key functional role since they connect subgroups of different species within each network.

Table 3. Recorded plant species and specialization level (d`) in Mucugê municipality, Chapada Diamantina region-BA

PLANT SPECIES	SPECIALIZATION (d')	
	WITH ANT	WITHOUT ANT
Myrtaceae sp	1.00	-
Periandra mediterrânea	1.00	-
Calliandra mucugeana	1.00	-
Calliandra viscidula	0.48	-
Acritopappus confertus	0.51	-
Syagrus harleyi	0.45	-
Paralychnophora harleiy	0.42	-
Gaylussacia virgata	0.44	-
Manihot jacobinensis	0.44	-
Agarista pulchella	0.39	-
Senna cana	0.36	-
Chamaecrista blanchetii	0.30	-
Vellozia harleyi	0.24	-
Baiantus viscosus	0.06	-
Cuphea ericoides	-	0.22
Marcetia taxifolia	-	0.18
Diplusondo ulei	-	0.59
Eriope exaltata	-	0.21
Microlicia giulietti	-	0.12
Ditassa retusa	-	0.97
Stachytarpheta crassifólia	-	0.61
Lepidaploa cotoneaster	-	0.34
Evolvulus sp	-	0.48
Lamiaceae sp	-	0.07
Humiria balsamifera	-	0.81
Phyllanthus klotzschianus	-	0.86
Calliandra sp	-	0.52
Serbastiana bronquite		0.91
Marcetia velutina	-	0.00
Tenstroensoria carnosa	-	0.16
Mikania sp	-	0.00
Estrutatus sp	-	1.00
Esterhazya splendida	-	0.58
Clusia burlemarxii	-	0.00
Jachemontia montana	-	1.00
Manihot reniformes	-	0.00
Estrutatus sp		1.00

Another interesting finding is that bees substantially impacted ant-free networks since they participated in many interactions with plants without ants in their flowers. This finding confirmed the assumption that effective pollinators tend to either avoid or be scared away by the presence of some ant types, as corroborated by some population studies (Gaume et al., 2005; Ness, 2006; Onã & Lachmann, 2011; Tabatinga-Filho & Leal, 2007). These studies were carried out at the population level, using one plant species and specific pollinators. This effect was also herein observed at the community level. Studies always focus on the benefits associated with these partners (Bronstein 2001 a,b). However, it is acknowledged that these benefits may have a cost, although some studies consider that these relationships' indirect costs remain relatively low and recent (Assunção et al., 2014). Thus, benefits must overcome losses so these relationships can be mutualistic (Bronstein, 2012). However, it does not rule out that conflicts of interest are at the root of these seemingly cooperative associations (Bronstein, 2012). Nevertheless, it does not make much biological/evolutionary sense for a plant to invest in biotic defense that, in the present case, is the ant, just for it to turn into a liability by forcing plant-visitor interactions to distance themselves from mutualism and to move towards antagonism literally.

According to Del-Claro et al. (2013), the positive and negative impacts of predators who scare away floral visitors depend on the visitor type. For example, they may have a positive impact if they scare away nectar robbers rather than effective pollinators (Assunção et al., 2014). Overall, future studies should investigate visitor types that can be scared away by ants since these studies may show that, although ants' presence has some impact on certain floral visitors, it is not strong enough to change the community structure. Therefore, we can conclude that ants' presence in flowers does not affect services provided by partners with divergent functions (protector ants x pollinators) at the community level. However, it can inhibit specific pollinator species' visitation at the population level.

Authors' contribution

GSO: Conceptualization, Methodology, Formal analysis, Investigation, Resources, Project administration, Data Curation and Writing.
JESJr: Methodology, Formal analysis, Investigation, Writing and Writing-Review & Editing.
TBS: Investigation and Writing-Review & Editing.
GMMS: Writing-Review & Editing, Resources and Supervision, Project administration, Funding acquisition.

Acknowledgment

The authors would like to thank the Post-Graduation Program in Zoology/PPGZOO and the Entomology Laboratory (LENT) of the State University of Feira de Santana/UEFS for the institutional support; the PELD/CNPq Program for the logistical and financial support; Sempre-Viva Project, for welcoming us during collection procedures; to FAPESB, for granting the scholarship, as well as to all friends who contributed to the current research.

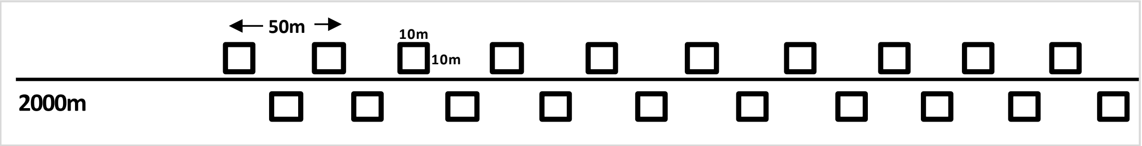

Fig 1. Image depicting the transect partitioned into 20 plots (10x10m, each) located 50 m apart. It was adopted to sample communities of floral visitors and ants in the investigated area.

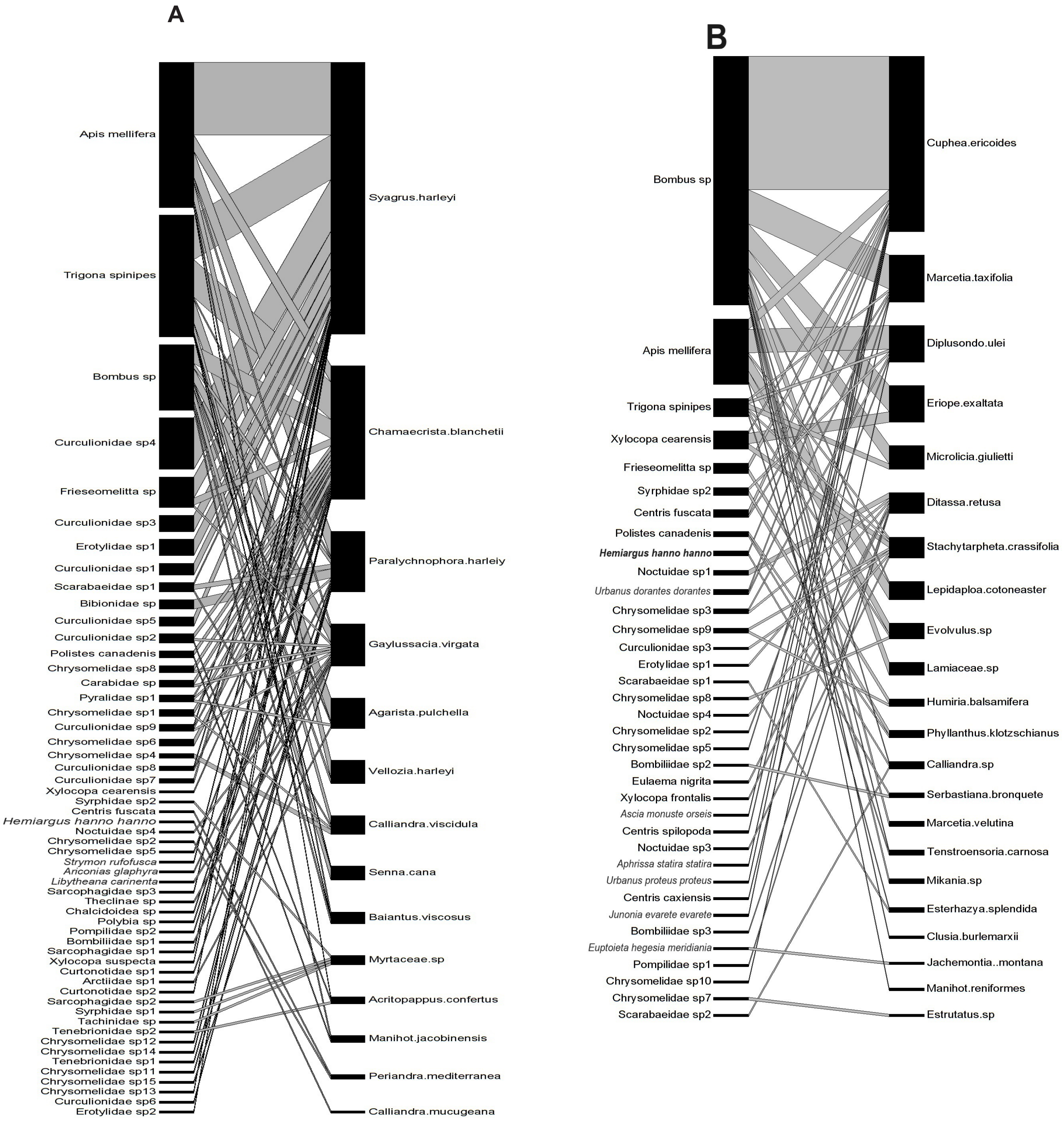

Fig 2. A and B: Floral-plant visitor interaction networks in Mucugê municipality – Chapada Diamantina region-BA, wherein (A) are plants with ants and (B) are plants without ants in their flowers. Data were collected from May to October 2013. Nodes to the right represent plant species, whereas nodes to the left correspond to floral visitor species. Lines represent floral visitor/ plant interactions. Each interaction network is based on combined data from all five collection months.

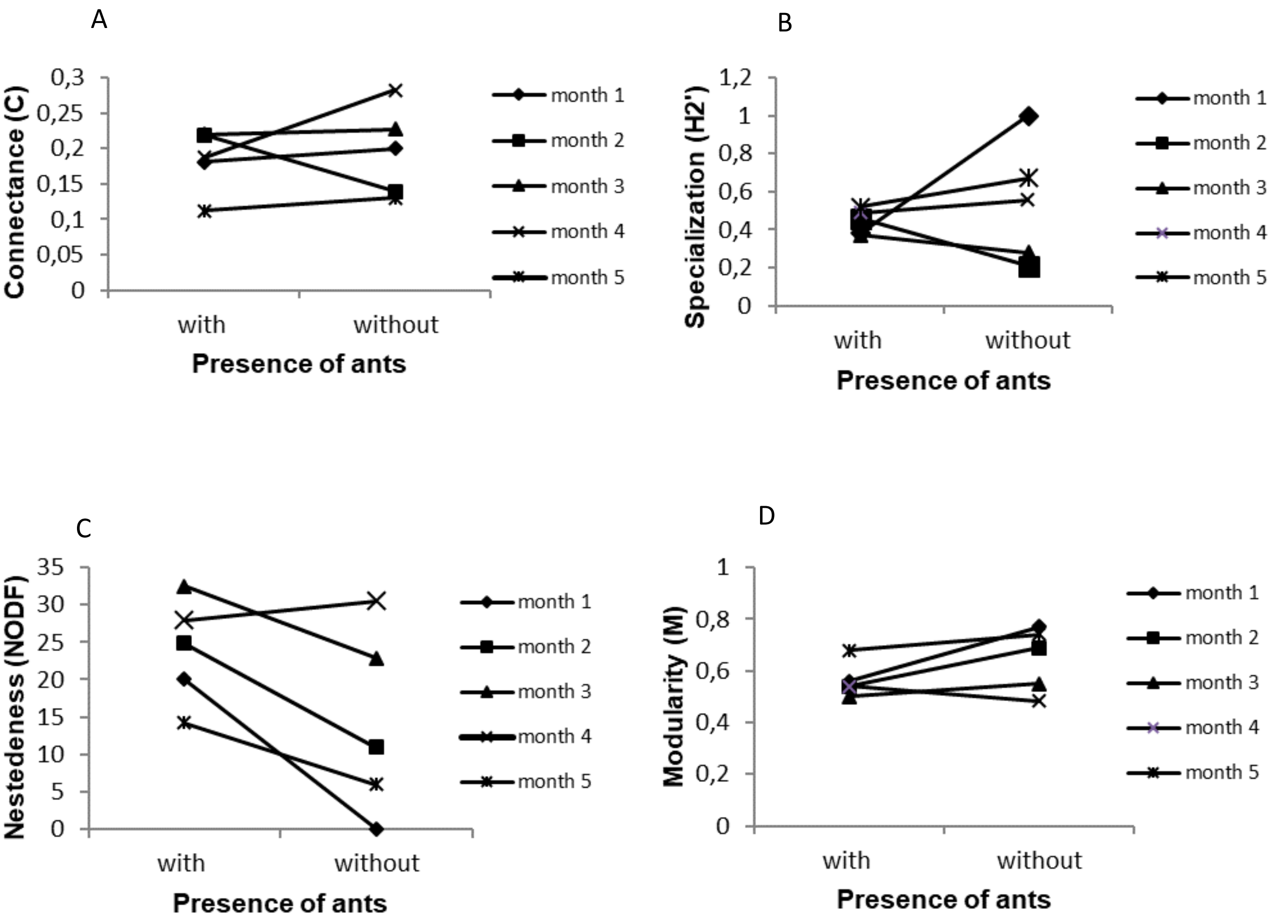

Fig 3. Values recorded for connectance (A), specialization (B), nestedness (C), and modularity (D) in floral visitor-plant networks comprising plant species with or without ants in flowers. Straight lines connect values observed for networks in the same sampling period.

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