



RESEARCH ARTICLE - SOCIAL ARTHROPODS

Flower Visitation by Bees, Wasps and Ants: Revealing How a Community of Flower-Visitors Establish Interaction Networks in a Botanical Garden

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Abstract

The Hymenoptera order includes several flower-visiting insects (e.g. ants, bees, and wasps) and the coexistence of many different species in the same community can generate interspecific competition. Notwithstanding shared communities, research which evaluates how these taxonomic groups influence a whole community of flower-visiting Hymenoptera is lacking. Moreover, abiotic factors can also impact these floral visits, because each organism responds differently to climatic variations. The goal of this study is to evaluate abiotic factors, specifically relative air humidity and air temperature, which may be able to impact the number and the frequency of interactions between hymenopterans and flowers and to assess the composition and niche organization, by making use of interaction networks, of the entire community of flower-visiting Hymenoptera at the botanical garden of the Universidade Federal Rural do Rio de Janeiro. For the duration of a year, we took samples in that botanical garden, compartmentalizing the collections temporally in accordance with the time of the insects' shift (morning or afternoon). We observed a positive influence of air temperature on the number of ant interactions and visits. It is also possible to observe that most of these interaction networks exhibited a nested and non-modular pattern and an average level of network specialization. In addition, bees stood out as the species with the highest frequency of visits and with the most generalist behavior. This study demonstrates how a botanical garden can sustain a diverse community of floral visiting Hymenoptera in an urban environment and why it consists in an important tool for biodiversity conservation.

Introduction

Bees, wasps and ants are insects that take part in various ecological interactions; among them, flower-visitation. The visitation of flowers by hymenopterans may result in plant pollination, although other phenomena, such as nectar robbing and competition with real pollinators, may also be observed. (Vizentin-Bugoni et al., 2018). Bees are key pollinators, responsible for the pollination of several botanical species and the absence or population decline of these animals is substantially risky for crops and the native flora, because,

since many species depend on these pollinators for sexual reproduction, it can lead plant species to extinction and affect food production (De Marco Jr. & Coelho, 2004; Klein et al., 2007). On the other hand, the role of wasps as plant pollinators may be considered unusual because certain wasps visit flowers to prey on other arthropods, to collect or to steal nectar collected by other hymenopterans or because they are attracted by hormones released by the plant (Toresan-Silingardi, 2012; Nagasaki, 2021). The importance of ants as plant pollinators is still a matter of debate while some ant species can contribute to the pollination process (González



et al., 2013; Wang et al., 2015), other species can chase away potential pollinators (Villamil et al., 2018; Nogueira et al., 2021). Notwithstanding shared communities, research which evaluates how these taxonomic groups influence the composition and the organization of a whole community of flower-visiting Hymenoptera is lacking.

When focusing on the interactions of Hymenoptera and flowers, several factors can impact the amount of these interactions and their frequency. Some of them are abiotic, such as relative air humidity. In another study on a community of floral-visitors, Barbosa et al. (2016) observed a negative correlation between relative air humidity and flower visits by Hymenoptera, which may be related to the fact that nectar changes its concentration and viscosity according to relative air humidity (Winkler et al., 2009). Another factor possibly related to the hymenopteran-flower interaction is air temperature. Air temperature can modulate the foraging behavior of hymenopterans, as the energy cost of foraging varies in accordance with changes in air temperature (Classen et al., 2015; Kovac et al., 2015). In warm environments, Hymenopterans tend to increase their foraging and, consequently, their floral visitation, what can change the community's characteristics (e.g. specialization, diversity, richness, resource supply) (Classen et al., 2015; Classen et al., 2020; Luna et al., 2021). However, because this community consists of organisms biologically and behaviorally unique, these factors can affect each of these taxonomic groups differently: ants are expected to respond better to increases in temperature once they are more resistant to high temperatures than bees and wasps are (Heinrich, 1993; Kovac et al., 2015). Therefore, assessing how abiotic factors relate to each taxonomic group separately may be a proper strategy to understand how these factors influence interactions in the community of flower-visitors.

When different species of flower-visitors interact with the same group of plants, they can be functionally redundant and end up increasing interspecific competition, which would reduce the diversity and richness of these visitors (Blüthgen & Klein, 2011). The co-occurrence of many species in the same community of flower visitors can be facilitated by the specialization of some groups and by the differentiation of niches (Blüthgen & Klein, 2011; Watts et al., 2016). To help us to understand how this particular community's organization and species composition, we can use a tool that has been widely employed to study insect-plant interactions: interaction networks (e.g. Dáttilo & Rico-Gray, 2018). Measures of specialization on the network level can show us the degree of niche division among species of floral visitors in the community studied (Blüthgen et al., 2006). Moreover, some other network metrics can help us understand community organization. To assess whether a group of selective species interact with a set of plants visited by generalist floral-visitors, we can calculate the nestedness of networks in that community (Fortuna, 2010; Dehling, 2018).

And to assess the tendency of a subset of species to relate more frequently to each other than to other species, constituting modules, we can calculate the modularity of the networks in that community (Fortuna, 2010; Dehling, 2018). We must be careful when treating insect-flower interactions as mutualistic networks because some visits have negative effects on plants (Vizentin-Bugoni et al., 2018). What usually happens in mutualistic plant-insect networks (e.g. flower visitors, extrafloral nectaries or seed removers) is that, due to the insects' behavior, they display low specialization, high nestedness and no modularity (Campos-Navarrete et al., 2013; Lange & Del-Claro, 2014; Anjos et al., 2018; Laviski et al., 2021). Although all hymenopteran networks follow the assumptions for insect-plant mutualistic networks, metric values are expected to be quite different for networks with each group of organisms, because they are different taxonomic groups (Campos-Navarrete et al., 2013). Bees, for instance, are responsible for the pollination of many botanical species and tend to be more generalist when it comes to flower visitation (De Marco Jr. & Coelho, 2004; Klein et al., 2007; Torezan-Silingardi, 2012). Thus, we expect the interaction networks which present bees to be more nested, less specialized and not to feature modularity (Blüthgen et al., 2006; Fortuna, 2010; Dehling, 2018).

While specialization indicates a niche division in a community, identifying its generalist species is of utmost importance, because they are crucial to the stability and operation of community organization, mainly because the core species interact with nearly all species in the community (Bascompte et al., 2003; Guimarães et al., 2006; Dáttilo et al., 2013a). We can evaluate the most generalist species in a community based on the analysis of core species in the network (Dáttilo et al., 2013a). As stated earlier, bees usually present generalist flower-visiting behavior, therefore they are commonly the species with the highest frequency of interactions in flower-visiting hymenopteran networks (Campos-Navarrete et al., 2013). Another factor for assessing similarities or differences between niches is time: observing the species composition and activities during a day, during a year or even over decades allows us to compare the species that interact during each interval and calculate the overlap of these temporal niches (Díaz-Castelazo et al., 2013; Dáttilo et al., 2014a). On an even smaller scale, we can evaluate how the temporal niche divides itself throughout the day. Some bees exhibit a peak behavior of flower visitation at different times (Tschoeke et al., 2015) and ant species can also have different peaks of activity in a 24-hour period (Fellers, 1989), as well as wasp species (Brito et al., 2020). However, there are no studies which consider the overlap of temporal niches during the day for a floral-visitor community with more than one hymenopteran group.

In this work, we used samplings of floral-visitors of a botanical garden's community collected over a year, both in the morning and in the afternoon, to understand how some abiotic factors correlate with the number and frequency

of floral visitation interactions and also to comprehend the organization and composition of this community by using floral-hymenopterans networks. Regarding the influence of abiotic factors on increased foraging and how these factors correlate with the number and frequency of floral visitations, we hypothesized that relative air humidity would negatively impact the number and frequency of floral visits, while air temperature would positively affect the interactions. Regarding the organization and composition of this community of floral-visitors, we also hypothesized that interaction networks would show patterns similar to other insect-plant mutualistic networks: they will be nested, lack modularity and have low specialization. In addition, we presumed that bee species would be most prevalent network core species. We also expect communities to be different according to the daily temporal niche: in the morning, with a higher frequency of bees in interactions, we expect the networks to be more nested, less specialized and non-modular; in the afternoon, with a higher frequency of ants, we expect the networks to be less nested, more specialized and non-modular.

Material and Methods

Study area

We conducted the study at the Botanical Garden of the Universidade Federal Rural do Rio de Janeiro (22°45'56"S; 43°41'33"W), a 16.5 hectare area, located in Seropédica, Rio de Janeiro State, Brazil. The site is located in a degraded region of the Atlantic Forest, where some botanical species, native and exotic, were planted, aiming to create a living botanical collection; the area has also a pond, a small secondary forest fragment and a separate area for crops (Cysneiros et al., 2011). Seropédica is located 26 meters above sea level, has an annual precipitation of 1294 mm and an average annual temperature of 23.9 °C (Oliveira Jr. et al., 2014). According to Köppen (1948), the region's climate is classified as 'Aw': tropical, with drier winters and rainy summers. The garden's local collection includes 125 dicotyledonous species, of which 94 are native (Cysneiros et al., 2011).

It is important to highlight that botanical gardens as urban parks are key instruments to preserve biodiversity in urban areas and maintain the community previously established in that area (Maruyama et al., 2019; Marín et al., 2020); also, they are unvaluable for scientific investigations (Chen & Sun, 2018), such as this one.

Sampling

We did the sampling of flower-visiting hymenopterans from December 2018 through December 2019, twice a month, when the weather conditions were favorable. We collected from 8:30 am to 11:00 am and from 1:30 pm to 3:00 pm, in accordance with the method established by Sakagami (1967). We chose these periods because the organisms studied are more active in them (Silveira et al., 2002; Barbosa et al., 2016).

We surveyed sixty-nine plant species inside the Botanical Garden. On the day before the sampling, we monitored flowering plants, regardless of each one's flowering stage. Then, we collected samples from the previously observed plants with an entomological net, tweezers and brush. From each plant individual, we sampled visiting Hymenoptera for ten minutes. In the case of ant collecting, an animal that recruits to dominate resources (Hölldobler & Wilson, 1990), we collected only one specimen per plant. At the beginning of each sampling period, we measured the air temperature and the relative air humidity at the time with a portable digital thermo hygrometer, THAR-300 - Instrutherm. We took the collected insects to the laboratory for mounting and subsequent identification.

We considered an interaction as every relationship between a flower-visiting Hymenoptera and a plant species, while visits are the frequency of the interactions.

Data Analysis

For each sample, we correlated the number of visits and interactions of bees, wasps and ants with the relative air humidity and air temperature at the time, separately, at the moment of sampling. We discarded the data relative to when there were no visits. Thereafter, we had 39 replicates for bee visits, 31 for wasp visits and 29 for ant visits. With the Kendall's rank correlation coefficient, we assessed the influence of relative air humidity and air temperature, independently from one another, on the number of visits and interactions, also independently from one another, for each sample. We previously tested the assumptions of normality and homogeneity of variances. We performed the test on the software R, version 4.1.0 (R Core Team, 2020).

With the data of all the collected hymenopterans and all the sampled plants, we built 12 networks of flower-visiting hymenopteran interactions. There were four groups: one consisting of ants and bees, another consisting of bees and wasps, another consisting of ants and wasps and another consisting of the three taxonomic groups. For each of those groups, we built three networks: one for the morning period, one for the afternoon period and one for the period of a whole day. We built the networks in this way to check how each group impacts the community of hymenopterans. For each network, we used weighted matrices to analyze specialization and discover the central species and binary matrices to analyze nestedness and modularity.

Primarily, on the software R version 4.1.0 (R Core Team, 2020), we evaluated specialization by employing the specialization index H_2' , which ranges from 0 (low specialization, generalist network and many overlapping interactions) to 1 (high specialization, specialist network and low or no overlapping interactions) (Blüthgen et al., 2006). Making use of null models, we calculated the significance of specialization by looking at the actual value of specialization

and comparing it to a sequence of values randomized a thousand times. The p-value reflects the position of the observed value in the probability distribution which was plotted (Mello et al., 2016). Next, to assess non-random patterns of hymenopteran-flower interaction, we measured nestedness. We calculated the nestedness of the network using the NODF metric in the ANINHADO software (Guimarães & Guimarães, 2006), using 1000 networks generated by null model II. Values range from 0 (not nested) to 100 (perfectly nested) (Bascompte et al., 2003). Then, we assessed whether there were groups of Hymenoptera that only associate with one plant set and are extremely specialized; to do this, we calculated the modularity of the networks. We used MODULAR software (Guimerà & Amaral, 2005) to verify the modularity of the networks. The modularity index ranges from 0 (no modules) to 1 (completely separated modules). We used a thousand networks randomized by the null model II with constant total margins (Bascompte et al., 2003). Thereafter, we used the methodology described by Dáttilo et al. (2013a) to discover the core species in that community. This allowed us to verify the flower visitors' species with the higher frequency of interactions, in other words, the most generalist species in the community. We also discovered the plant core species. Moreover, to measure the turnover in the hymenopteran community composition between the morning and the afternoon periods, we calculated the temporal niche overlap. We used Jaccard's similarity for the networks of

mixed assemblages and the networks of all communities; as follows: $A/(A + B + C)$, where A is the number of flower-visitor species shared between the two sampling periods, B is the number of flower-visitor species present only during the morning and C is the number of flower-visitor species present only during the afternoon (Dáttilo et al., 2014a).

Results

In our study, we found 10 different bee species, 9 different wasp species and 18 different ant species (Table 1) interacting with twenty different plant species (Table 2). The total number of visits by bees recorded over the whole sample period was 231, resulting in 49 different interactions with 17 plant species; visits by wasps were 77, distributed in 34 interactions with 13 plant species; and ants accounted for 175 recorded visits and 65 interactions with 16 plant species.

Average relative air humidity in samplings was $69.01 \pm 7.56\%$. The relative air humidity was not shown to impact the amount of visits or interactions of any hymenopteran. Neither the number of bee visits ($p = 0.2243$, $\tau = -0.1427$) nor the amount of bee interactions were influenced by relative humidity of air ($p = 0.2717$, $\tau = -0.1571$), as were not the number of wasp visits ($p = 0.7777$, $\tau = -0.0391$) and the amount of wasp interactions ($p = 0.3538$, $\tau = -0.1293$) or the number of ant visits ($p = 0.1359$, $\tau = -0.1982$) and interactions ($p = 0.1488$, $\tau = -0.1937$).

Table 1. The flower-visiting hymenopterans at the UFRRJ Botanical Garden, in Seropédica, Rio de Janeiro, Brazil; from December 2018 to December 2019.

ID	Family	Hymenoptera species	ID	Family	Hymenoptera species
#01	Apidae	<i>Plebeia</i> sp1	#20	Formicidae	<i>Pseudomyrmex</i> sp1
#02	Apidae	<i>Plebeia</i> sp2	#21	Formicidae	<i>Pseudomyrmex</i> sp2
#03	Apidae	<i>Apis mellifera</i> Linnaeus, 1758	#22	Formicidae	<i>Brachymyrmex heeri</i> Forel, 1874
#04	Halictidae	<i>Augochlora</i> sp1	#23	Formicidae	<i>Solenopsis invicta</i> Buren, 1972
#05	Halictidae	<i>Augochloropsis</i> sp1	#24	Formicidae	<i>Crematogaster</i> sp1
#06	Apidae	<i>Trigona spinipes</i> (Fabricius, 1793)	#25	Formicidae	<i>Camponotus crassus</i> Mayr, 1862
#07	Apidae	<i>Scaptotrigona</i> sp1	#26	Formicidae	<i>Wasmannia auropunctata</i> (Roger, 1863)
#08	Apidae	<i>Nomada</i> sp1	#27	Formicidae	<i>Cephalotes atratus</i> (Linnaeus, 1758)
#09	Apidae	<i>Bombus</i> sp1	#28	Formicidae	<i>Solenopsis</i> sp1
#10	Colletidae	<i>Actenosigynes</i> sp1	#29	Formicidae	<i>Brachymyrmex</i> sp1
#11	Vespidae	<i>Charterginus</i> sp1	#30	Formicidae	<i>Camponotus</i> sp1
#12	Vespidae	<i>Polybia paulista</i> von Ihering, 1896	#31	Formicidae	<i>Brachymyrmex admotus</i> Mayr, 1887
#13	Vespidae	<i>Angiopolybia</i> sp1	#32	Formicidae	<i>Crematogaster curvispinosa</i> Mayr, 1862
#14	Vespidae	<i>Polybia</i> sp1	#33	Formicidae	<i>Crematogaster limata</i> Smith, F., 1858
#15	Vespidae	<i>Ceramiopsis gestroi</i> Zavattari, 1910	#34	Formicidae	<i>Pseudomyrmex</i> sp3
#16	Vespidae	<i>Polybia</i> sp2	#35	Formicidae	<i>Camponotus novogranadensis</i> Mayr, 1870
#17	Vespidae	<i>Polybia</i> sp3	#36	Formicidae	<i>Brachymyrmex</i> sp3
#18	Vespidae	<i>Charterginus</i> sp2	#37	Formicidae	<i>Brachymyrmex</i> sp2
#19	Vespidae	<i>Charterginus</i> sp3			

Average air temperature during the sampling period was 27.65 ± 3.83 °C. Ambient temperature did not affect the number of bee visits ($p = 0.6062$, $\tau = -0.0605$) or interactions ($p = 0.3514$, $\tau = -0.1094$) or the number of wasp visits ($p =$

0.6592 , $\tau = -0.0610$) or interactions ($p = 0.7618$, $\tau = -0.0422$), but it did positively influence the number of ant visits ($p = 0.0010$, $\tau = 0.4360$, Fig 1) and the number of interactions ($p = 0.0010$, $\tau = 0.4420$, Fig 2).

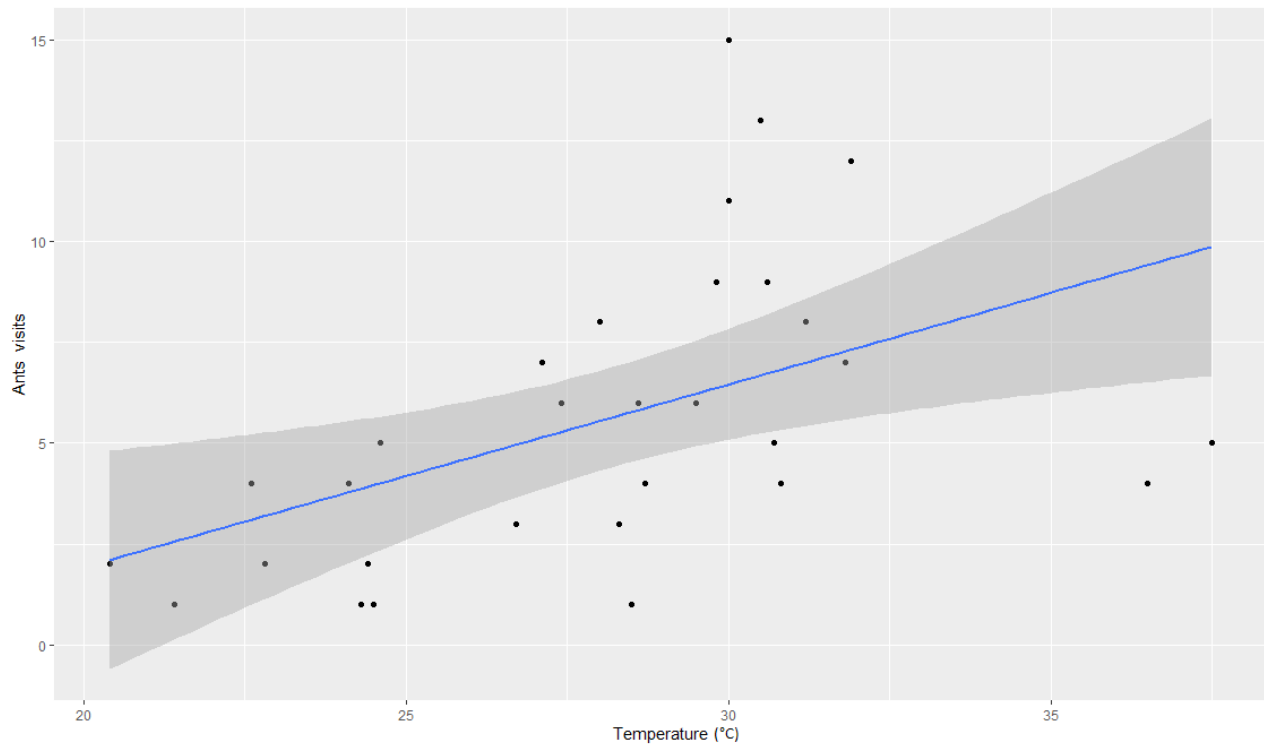


Fig 1. Kendall regression of temperature and number of ant visits to flowers at the UFRRJ botanical garden, in Seropédica, Rio de Janeiro, Brazil; from January 2019 to December 2019. The x-axis represents temperature and the y-axis represents the number of visits.

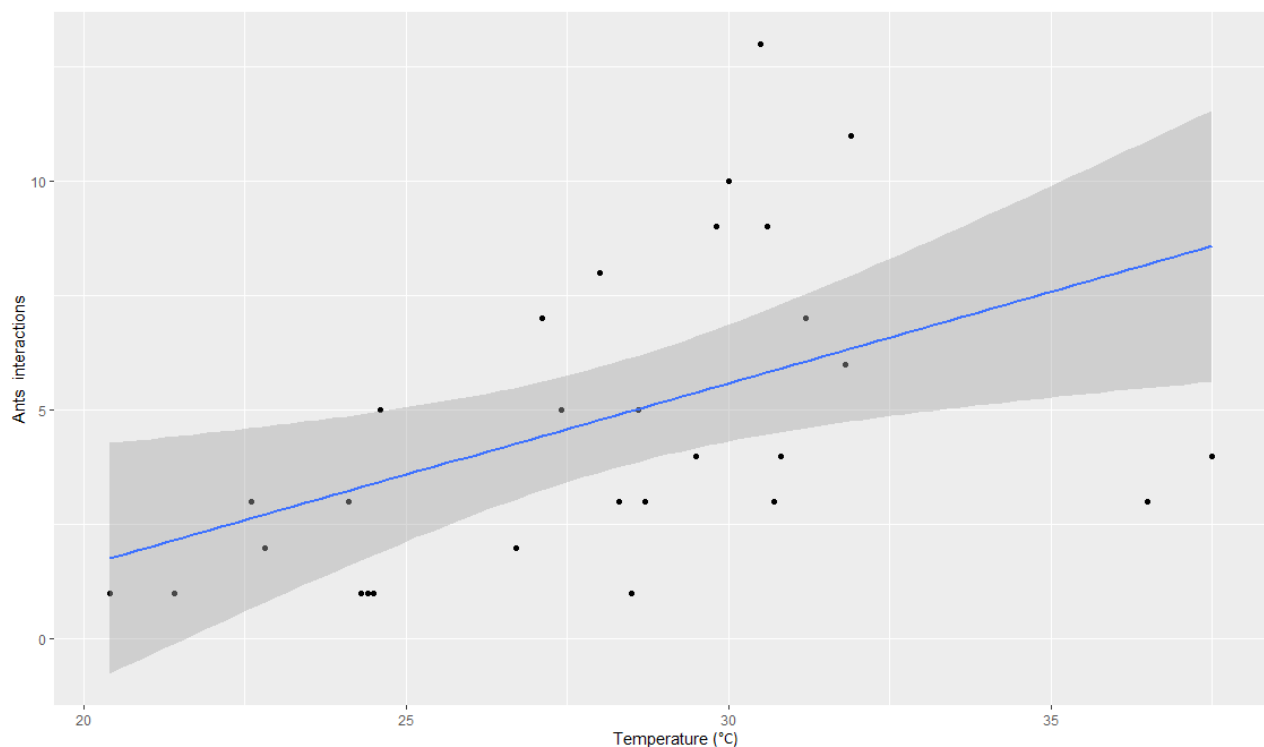


Fig 2. Kendall regression of temperature and number of ant interactions with flowers at the UFRRJ botanical garden, in Seropédica, Rio de Janeiro, Brazil; from January 2019 to December 2019. The x-axis represents temperature, and the y-axis represents the number of interactions.

In August, bees had the highest average number of visits and the highest average number of interactions (Fig 3; Fig 4), whereas the highest average number of wasp visits was observed in May and August (Fig 3), especially in the former (Fig 4); for ants, March had the highest average number of visits and interactions (Fig 3; Fig 4). In December 2019, the lowest average numbers of visits and interactions by bees (Fig 3; Fig 4) and no wasps foraging on any flowers were observed, while no ants visited any flowers in the period from September through October of that same year (Fig 3; Fig 4).

The networks of the community of flower-visiting Hymenoptera were nested during the morning (NODF = 23.17, $p = 0.03$), the afternoon (NODF = 19.96, $p = 0.01$) and all day (NODF = 25.41, $p < 0.001$). These networks exhibited no modularity and showed significant specialization (morning: $H_2' = 0.35$, $p < 0.001$; afternoon: $H_2' = 0.39$, $p < 0.001$; all day: $H_2' = 0.37$, $p < 0.001$) (Table 3). The Hymenoptera core species were: in the morning - *Apis mellifera*, *Plebeia* sp.1,

Plebeia sp.2, *Trigona spinipes*, and *Camponotus crassus*; in the afternoon - *Apis mellifera*, *Plebeia* sp.2, *Trigona spinipes*, *Camponotus crassus*, and *Wasmannia auropunctata*; on the whole day - *Apis mellifera*, *Plebeia* sp.1, *Plebeia* sp.2, *Trigona spinipes*, *Camponotus crassus*, and *Wasmannia auropunctata* (Table 3). The plant core species were: in the morning, in the afternoon and on the whole day, respectively: *Stiffia chrysantha*, *Clerodendrum x speciosum*, *Callistemon viminalis*, and *Antigonon leptopus* (Table 3).

The networks for ants and bees assemblages were nested during the afternoon (NODF = 19.31, $p = 0.05$) and during the whole day (NODF = 14.64, $p < 0.001$), but were not nested during the morning. These networks showed no modularity and displayed significant specialization (morning: $H_2' = 0.38$, $p < 0.001$; afternoon: $H_2' = 0.43$, $p < 0.001$; whole day: $H_2' = 0.40$, $p < 0.001$) (Table 3). The Hymenoptera and plant core species in these nets were the same as the core species obtained for the community nets (Table 3).

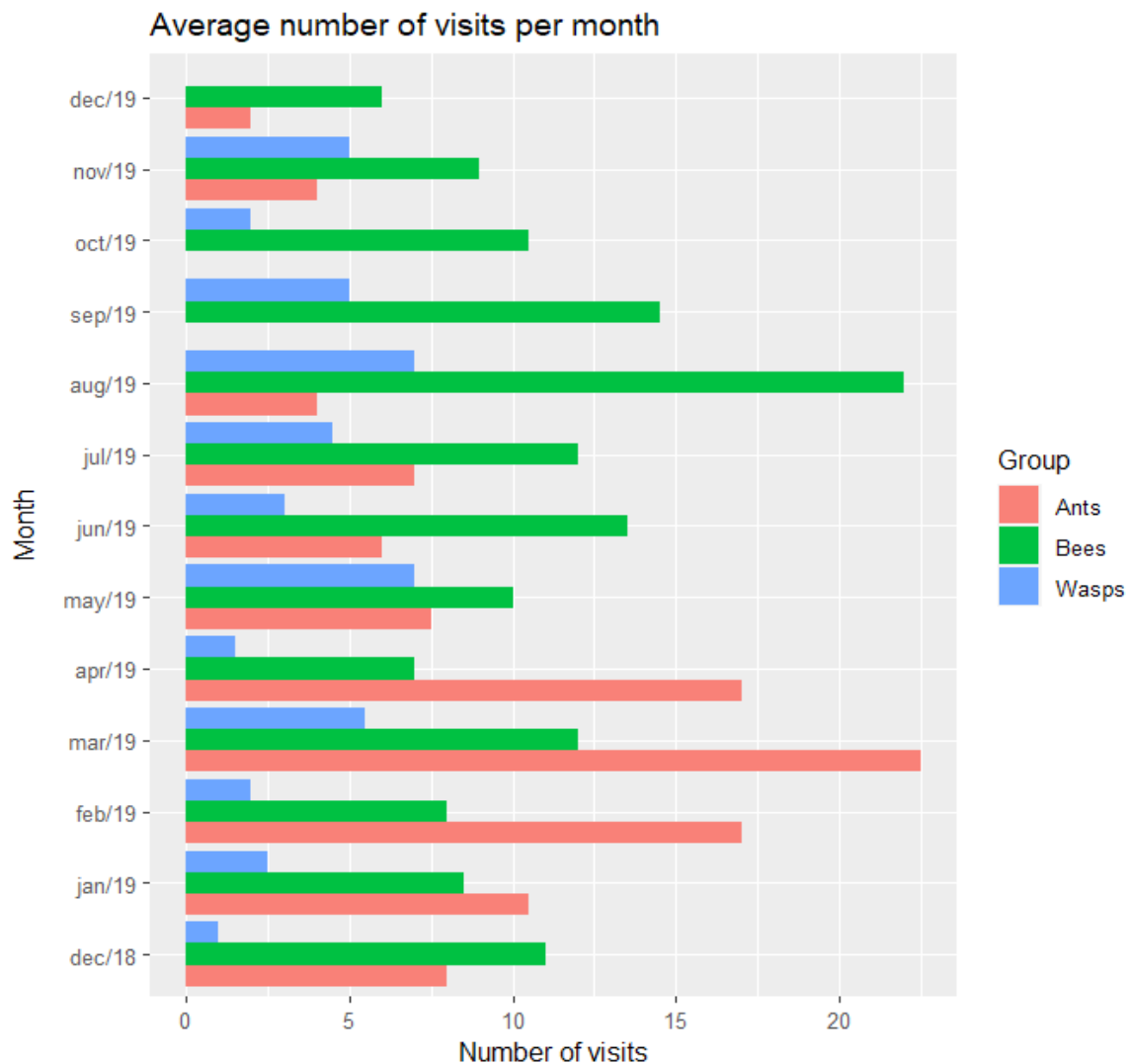


Fig 3. The average number of visits by groups of flower-visitors at the UFRRJ Botanical Garden, in Seropédica, Rio de Janeiro, Brazil; from December 2018 to December 2019. In red, the number of ant visits; in green, the number of bee visits; in blue, the number of wasp visits. The x-axis represents the average number of visits, and the y-axis represents the month of the sample.

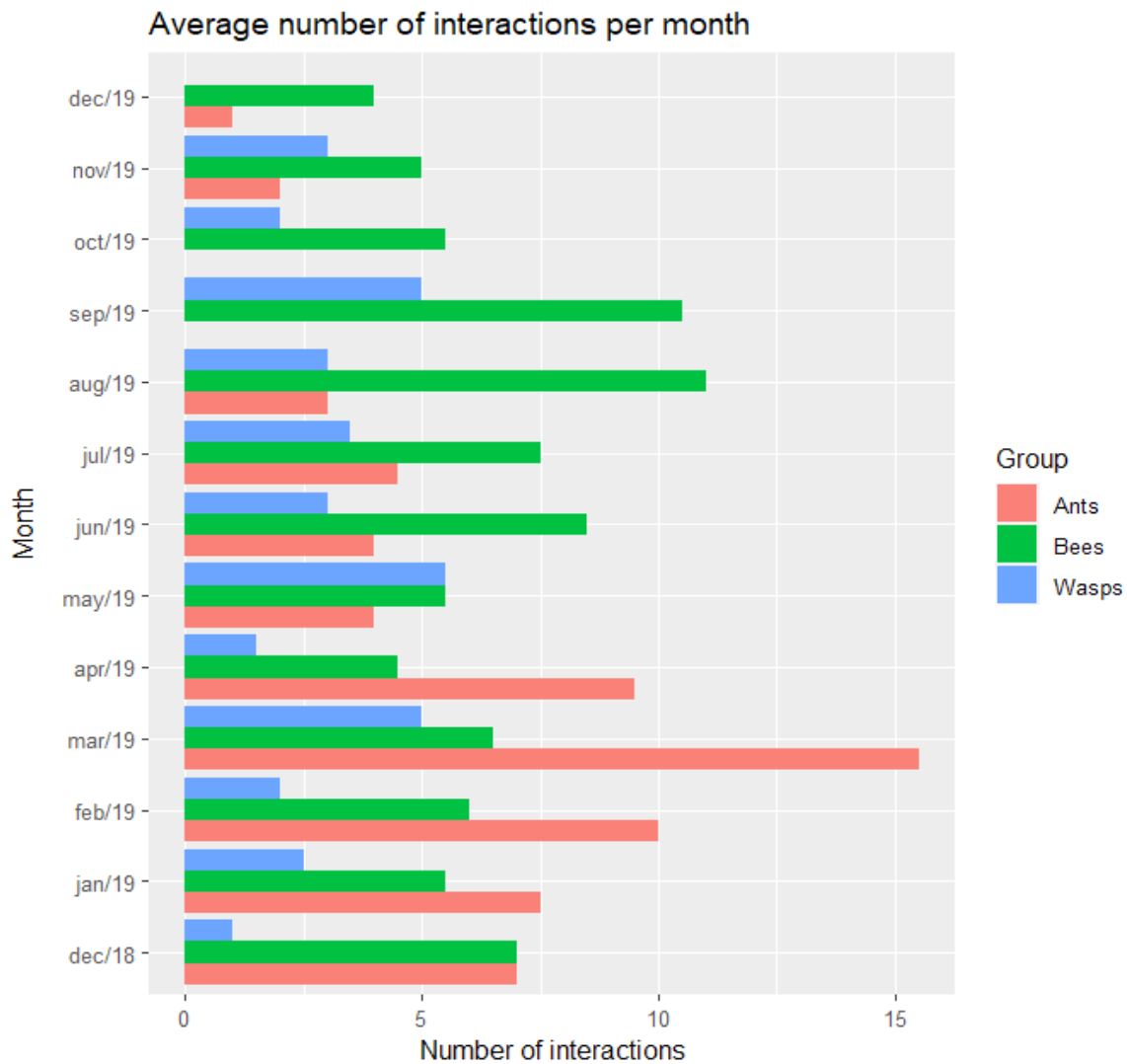


Fig 4. The average of interactions by groups of flower-visitors at the UFRRJ botanical garden, in Seropédica, Rio de Janeiro, Brazil; from December 2018 to December 2019. In red, the number of ant visits; in green, the number of bee visits; in blue, the number of wasp visits. The x-axis represents the average number of interactions and the y-axis represents the month of the sample.

Table 2. Plants involved in interactions of floral-visiting hymenoptera at the botanical garden of UFRRJ, in Seropédica, Rio de Janeiro, Brazil; from December of 2018 to December of 2019.

ID	Family	Plant species	n	ID	Family	Plant species	n
P01	Anacardiaceae	<i>Schinus terebinthifolia</i> Raddi	7	P11	Lamiaceae	<i>Clerodendrum x speciosum</i> W. Bull	5
P02	Arecaceae	<i>Phoenix</i> sp1	1	P12	Lamiaceae	<i>Clerodendrum speciosissimum</i> Drapiez	4
P03	Asteraceae	<i>Stiffia chrysantha</i> Mikan	9	P13	Lecythidaceae	<i>Couroupita guianensis</i> Aubl.	4
P04	Boraginaceae	<i>Cordia superba</i> Cham.	4	P14	Malvaceae	<i>Hibiscus</i> sp1	5
P05	Cactaceae	Cactaceae sp1	1	P15	Malvaceae	<i>Hibiscus</i> sp2	1
P06	Chrysobalanaceae	<i>Microdesmia rigida</i> (Benth.) Sothers & Prance	3	P16	Melastomataceae	<i>Tibouchina granulosa</i> (Desr.) Cogn.	1
P07	Ericaceae	<i>Rhododendron</i> sp1	2	P17	Myrtaceae	<i>Callistemon viminalis</i> G. Don ex Loud.	6
P08	Fabaceae	<i>Bauhinia variegata</i> L.	3	P18	Polygonaceae	<i>Antigonon leptopus</i> Hook. & Arn.	6
P09	Fabaceae	<i>Cassia fistula</i> L.	3	P19	Sapindaceae	<i>Sapindus</i> sp1	1
P10	Fabaceae	<i>Paubrasilia echinata</i> (Lam.) Gagnon & Lewis	1	P20	Verbenaceae	<i>Duranta repens</i> L.	2

The networks for bees and wasps assemblages were nested during the morning (NODF = 16.89, $p = 0.01$), the afternoon (NODF = 16.25, $p = 0.02$) and the whole day (NODF = 17.35, $p = 0.02$). These networks exhibited no modularity and the same specialization in every period ($H_2' = 0.29$, $p < 0.001$) (Table 3). The Hymenoptera core species were: in the morning and on the whole day – *Apis mellifera*, *Plebeia* sp.1, *Plebeia* sp.2, and *Trigona spinipes*; in the afternoon – *A. mellifera*, *Plebeia* sp.2, and *T. spinipes* (Table 3). The plant core species were: in the morning, in the afternoon and on the whole day, respectively – *Stiffitia chrysantha*, *Callistemon viminalis*, and *Antigonon leptopus* (Table 3). At last, the networks for wasps and ants

assemblages were nested during the afternoon (NODF = 11.43 $p = 0.02$) and during the whole day (NODF = 17.35, $p = 0.01$), but weren't nested during the morning. These networks showed no modularity and significant specialization (morning: $H_2' = 0.37$, $p < 0.001$; afternoon: $H_2' = 0.42$, $p < 0.001$; all day: $H_2' = 0.43$, $p < 0.001$) (Table 3). The Hymenoptera core species were the same in all networks: *Angiopolybia* sp1, *Camponotus crassus*, and *Wasmannia auropunctata*. The plant core species were: in the morning – *Clerodendrum x speciosum*, and *A. leptopus* (Table 3); in the afternoon and on the whole day – *Cordia superba*, *Clerodendrum x speciosum*, and *A. leptopus* (Table 3).

Table 3. Network metrics of all matrices obtained based on the observation of a community of flower-visiting hymenopterans at the botanical garden of the UFRRJ, in Seropédica, Rio de Janeiro, Brazil. During December of 2018 to December of 2019. Specialization = H_2' . Hymenoptera core species = Hymenoptera Core. Plant core species = Plant Core.

	H_2'	Modularity	Nestedness	Hymenoptera Core	Plant Core
All groups					
Morning	0.35 ($p < 0.001$)	0.30 ($p = 0.88$)	23.17 ($p = 0.03$)	#01; #02; #03; #06; #25	P03; P11; P17; P18
Afternoon	0.39 ($p < 0.001$)	0.33 ($p = 0.90$)	19.96 ($p = 0.01$)	#02; #03; #06; #25; #26	P03; P11; P17; P18
All day	0.37 ($p < 0.001$)	0.26 ($p = 0.91$)	25.41 ($p < 0.001$)	#01; #02; #03; #06; #25; #26	P03; P11; P17; P18
Ants + Bees					
Morning	0.38 ($p < 0.001$)	0.41 ($p = 0.30$)	13.11 ($p = 0.11$)	#01; #02; #03; #06; #25	P03; P11; P17; P18
Afternoon	0.43 ($p < 0.001$)	0.46 ($p = 0.32$)	19.31 ($p = 0.05$)	#02; #03; #06; #25; #26	P03; P11; P17; P18
All day	0.40 ($p < 0.001$)	0.35 ($p = 0.65$)	14.64 ($p < 0.001$)	#01; #02; #03; #06; #25; #26	P03; P11; P17; P18
Bees + Wasps					
Morning	0.29 ($p < 0.001$)	0.37 ($p = 0.66$)	16.89 ($p = 0.01$)	#01; #02; #03; #06	P03; P17; P18
Afternoon	0.29 ($p < 0.001$)	0.38 ($p = 0.65$)	16.25 ($p = 0.02$)	#02; #03; #06	P03; P17; P18
All day	0.29 ($p < 0.001$)	0.33 ($p = 0.86$)	17.35 ($p = 0.02$)	#01; #02; #03; #06	P03; P17; P18
Wasps + Ants					
Morning	0.37 ($p < 0.001$)	0.45 ($p = 0.27$)	12.65 ($p = 0.11$)	#13; #25; #26	P11; P18
Afternoon	0.42 ($p < 0.001$)	0.46 ($p = 0.32$)	11.43 ($p = 0.02$)	#13; #25; #26	P04; P11; P18
All day	0.43 ($p < 0.001$)	0.36 ($p = 0.79$)	14.15 ($p = 0.01$)	#13; #25; #26	P04; P11; P18

The organism code in the Hymenoptera central species column is in Table 1.
The organism code in the plant central species column is in Table 2.

The Jaccard similarity index of the networks of all taxonomic groups was 0.73, which means that 73% of observed hymenopteran species are the same in the morning and in the afternoon periods; networks of bees and wasps and of wasps and ants exhibited a higher similarity (Jaccard similarity index = 0.76; 0.79, respectively); ants and bees networks displayed the highest composition similarity among all networks (Jaccard similarity index = 0.80).

The morning network of all groups indicates a predominance of interactions made by ants; however, the number of visits made by bees was higher. Because of that, bee visits were the most often, mainly the visits made by *Apis mellifera* and *Trigona spinipes* (Fig 5a). The most visited plants in the morning were, respectively, *Antigonon leptopus*

and *Callistemon viminalis* (Fig 5a). In the afternoon network, *A. mellifera* occupied the position with the highest number of visits, in other words, a greater frequency of interaction, followed by the ant species *Camponotus crassus* (Fig 5b). It is remarkable that in the afternoon the frequency of ants became higher and they were still the group with more interactions. The plants with the highest number of visits also changed during the afternoon: species that occupied prominent positions were *C. viminalis* and *Stiffitia chrysantha* (Fig 5b). The all-day network showed similarities with both nets, in different aspects: regarding flower visitors, the all-day net was similar to the afternoon network, with a greater frequency of interaction of the species *A. mellifera*, but with a large frequency of interaction of ants; regarding the plants visited, the all-day

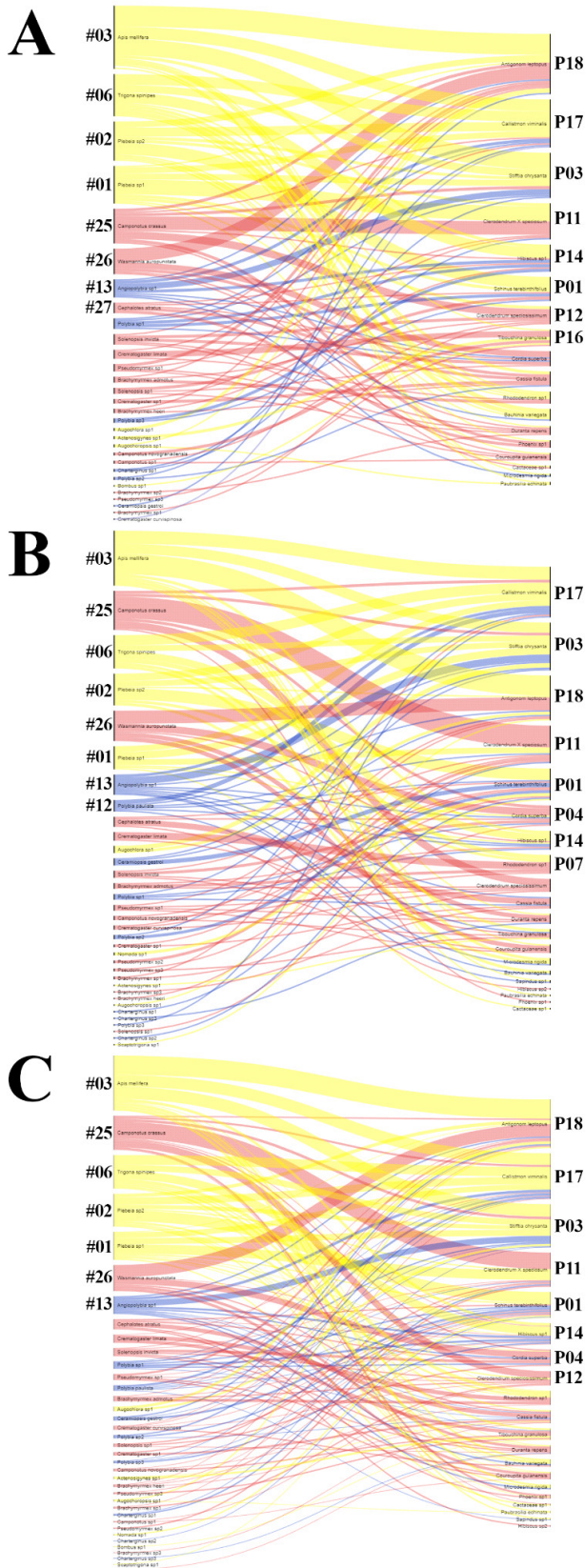


Fig 5. Networks of all groups of floral visiting hymenopterans at the UFRRJ botanical garden, in Seropédica, Rio de Janeiro, Brazil; from December 2018 to December 2019. The network is organized according to the frequency of interactions (visits). On the left are the visiting insect species and on the right are the plant species. In yellow are highlighted visits by bees, whereas visits made by wasps are highlighted in blue and visits made by ants are highlighted in red. A: Morning network; B: Afternoon network; C: All-day network.

network was closer to the result obtained by the morning network, with the species *A. leptopus* and *C. viminalis* being the plants with the highest number of visits (Fig 5c).

Discussion

In this study, we correlated the number of observed visits and interactions of each group of organisms with two abiotic factors – air temperature and relative air humidity. Our results showed that relative air humidity did not affect the number of visits or interactions of any of the assemblages and that air temperature did not affect the number of visits or interactions of bees or wasps; however, the higher the temperature, the more visits and interactions ants made. We also used the networks constructed from the floral-visitor community to assess the interaction pattern and composition of this community and the influence of each group of organisms on the community in different temporal niches. Our results showed that most networks exhibited the same interaction pattern in the morning and in the afternoon, except for the ant-bee and wasp-ant networks: these networks were nested, non-modular and of low specialization. On the other hand, in all networks, the core hymenopteran species changed when comparing the morning and the afternoon periods, which means that the composition of this community differed according to temporal niche. The assemblages also showed that the entire community of floral-visitors displayed different compositions and interaction patterns: the networks with bees displayed greater nestedness, while the networks with ants exhibited greater specialization; the morning ant-bee and wasp-ant networks were not nested; in addition, the central plant species visited in the wasp-ant network differed from the central plant species visited in the other networks.

Relative air humidity, despite influencing nectar composition (Winkler et al., 2009), did not impact the number of floral visits or interactions in any communities. Elements of the study area may have contributed to the the irrelevance of this factor to visits and interactions, such as the presence of a lake, irrigation and plant management (Cysneiros et al., 2011). Irrigation is one of the anthropogenic tools which can alter the microclimate, influencing not only plants but also the distribution of insect species (Federman et al., 2013). Air temperature had a positive role on the number of ant visits and interactions, exhibiting a strong correlation. Visits tended to be more frequent between 30-33° celsius, which is the air temperature range of highest insect activity (Paaijmans et al., 2013; Carvalho et al., 2014). Air temperature shapes the foraging behavior of ants and these are very heat resistant organisms, with activity recorded at air temperatures above 60 °C (Heinrich, 1993; Luna et al., 2021). Thus, a positive correlation of air temperature with ant visits and interactions had been expected and was duly confirmed, whereas air temperature had no effect on the number of bee and wasp visits and interactions. Bee and wasp visits and interactions may be affected by other abiotic factors which were not analyzed

in this work, such as rainfall, wind speed and solar radiation (Simões et al., 1985; Loyola & Martins, 2006; Oliveira et al., 2012; Kovac et al., 2015; Marinho & Vivallo, 2020).

Almost all networks showed low specialization, nestedness and no modularity, what points to the presence of highly generalist species which used the resources of several plants (Blüthgen et al., 2007; Blüthgen & Klein, 2011; Blüthgen, 2012). Low specialization also indicates that this network has a functional ecological niche redundancy; this may be due to the nestedness of niches among the present species or the fact that the species interacted with many different plant species, displaying generalism. Networks which present niche redundancy usually are observed in communities which are more stable in the face of adversity; however, as many species exploit the same resources, that can generate an increase in interspecific competition (Blüthgen & Klein, 2011; Blüthgen, 2012). Several factors may explain the nestedness and non-modular patterns of insect-plant community networks; some are abiotic (e.g. air temperature, rainfall, soil pH, elevation) and others are biotic (e.g. flower-visitor size, animal behavior, nectar characteristics) (Chamberlain et al. 2010; Rico-Gray et al., 2012; Lange et al., 2013; Dáttilo et al., 2013b; Dáttilo et al., 2014a; Santos et al., 2014; Giannini et al., 2015; Petanidou et al. 2017; Adedoja et al., 2018). Regarding the community studied, what possibly explains the nested pattern is the presence of super-generalist and dominant species (such as *Apis mellifera*, *Trigona spinipes*, *Camponotus crassus*, and *Wasmannia auropunctata*), which visit most of the plant species in the area and also interact with the set of plants visited by peripheral species (Dáttilo et al., 2014a; Dáttilo et al., 2014b; Giannini et al., 2015). Moreover, it is important to note that the ant-bee and wasp-ant networks did not achieve nestedness during the morning period, probably because the frequency of visitation of important super-generalist species (such as *Camponotus crassus*, and *Wasmannia auropunctata*) decreased, what promoted nestedness in the afternoon and all-day networks (Díaz-Castelazo et al., 2013), and because of a greater presence of peripheral species (Díaz-Castelazo et al., 2010; Lange & Del-Claro, 2014). The likely explanation for the non-modular pattern of these networks, besides a small specialization and a mostly generalist community, is the behavior of the flower-visiting Hymenoptera (Dáttilo et al., 2014a; Dáttilo et al., 2014b). Wasps and ants do not use only floral resources in their feeding; these organisms are occasional floral-visitors, often associated with the predation of other arthropods, the exploitation of other botanical resources (e.g. extrafloral nectary, fruits) and the consumption of other types of food sources, what makes their interaction more generalized and does not facilitate the constitution of modules in the networks (Brodmann et al., 2008; Rico-Gray & Oliveira, 2008; Mello et al., 2011; Dáttilo et al., 2014a; Brock et al., 2021; Lavisky et al., 2021). Bees, while exclusively floral-visitors, interact with different types of plants according to availability, which can even affect the density and abundance

of these organisms (Ebeling et al., 2011; Grass et al., 2016). The low diversity of vegetation in a botanical garden can affect these patterns too since vegetation structure is important for the composition of insect communities (Clemente et al., 2012; Junker et al., 2012; Rico-Gray et al., 2012). Although non-modular networks are a common pattern in generalist mutualistic networks (Del-Claro et al., 2018), the small number of plant species sampled may have impacted the result of this metric, because pollination networks with less than 50 plant species tend to lack modularity (Olesen et al., 2007).

When we looked at the metrics of the combined taxonomic group network, we found that most core species in the nets were bees and that the nestedness of bee-wasp and bee-ant networks was higher, except for the morning period of the bee-ant network. This may be explained by the behavior of the bees. Bees receive much attention for being crucial for the pollination of a large number of plants; their body is adapted to collect and store floral resources (Imperatriz-Fonseca et al., 2012) and they are the only animals capable of consuming all available floral resources (Torezan-Silingardi, 2012). Oligolectic bees visit either a restricted group of plants or only one type of plant, being highly specialized and performing pollination with great efficiency (Schlindwein, 2004; Imperatriz-Fonseca et al., 2012). No bee species found in the locality of this study are classified as oligolectic, which is probably caused by the low plant diversity, since no plants pollinated by these bees are found in the study area (Schlindwein, 2004). That can also explain why the specialization is lower in nets combined with bees. A higher specialization value in networks which feature ants may also be explained by the presence of peripheral species, but the value obtained was lower than that obtained for ant-plant interaction networks observed in other studies (Guimaraes et al., 2006; Junker et al., 2012). The networks were not highly specialized, as specialization is one of the strategies which may be adopted by organisms involved in floral visitation to decrease competition (Junker et al., 2012); another strategy which they can adopt is to perform visits at different times (Tschoeke et al., 2015). The similarity of community composition between the morning and the afternoon periods may be considered high, possibly indicating that this is not a strong strategy found in this community. However, there were differences between the morning and the afternoon networks and those differences may be greater according to the size of the community, the study area and the time discrepancy between niches (Díaz-Castelazo et al., 2013; Dáttilo et al., 2014). The difference which stands out the most is the change of some core species organisms when comparing the periods.

On the community level, the core species in the all-day network are four bee species and two ant species; although the greater presence of bees in this position is already expected, it is important to understand the biology and behavior of these animals to comprehend the important characteristics of the community and the study site. In the morning period,

there was a higher presence of bees as core species; in the afternoon, the frequency of visits by ants increases, adding one more ant species to the group of core species. *Apis mellifera*, a generalist bee, with an average size of 11-13 mm, which has a high foraging and pollination efficiency, having a very large foraging range for an arthropod (Beekman & Ratnieks, 2001; Costa et al., 2015) was firstly observed as the species with the highest number of visits, being the main key species of the community studied. Despite being an important species in the network, linked to several plant species, this bee is an exotic species, which has been pointed out as a risk to the conservation of native species (Paini, 2004; Russo et al., 2021). The genus *Plebeia* had two species pointed as core species. The genus belongs to the Meliponini tribe of stingless bees and includes species native to Brazil. The bees of the genus are small, with an average size of 3-4 mm, generalists and responsible for the pollination of several native plants (Pick & Blochtein, 2002; Wittmann, 2008). *Trigona spinipes* was also considered a key bee species. It is also from the Meliponini tribe, measuring approximately 7 mm, a native pollinator capable of pollinating several plant species, super-generalist and associated with improved fruit production (Chalegre et al., 2020; Tschoeke et al., 2015). Highlighting the core species of ants, *Camponotus crassus* belongs to the Formicidae subfamily and is a species which measures 20 mm and has no metapleural gland, being unable to produce harmful substances in the pollen (Del-Claro et al., 2019); it is a dominant forager in vegetation, exploits resources which do not come from flowers alone (Lange et al., 2019) and has already been associated with effective pollination (De Vega et al., 2014; Del-Claro et al., 2019). Finally, *Wasmannia auropunctata* is an ant from the subfamily Myrmicinae; the smallest of the key species, measuring 1.5 mm, it is invasive, commonly found in urban areas, often involved in cases of environmental impact and may have medical importance (Azevedo et al., 2022; Gruber et al., 2022). There are no studies relating this species to pollination, so it competes with pollinators once it recruits massively to dominate resources (Azevedo et al., 2022). Wasps had occasional interactions with flowers and were not often observed (except for *Angiopolybia* sp.1) having a greater presence as a peripheral species (Díaz-Castelazo et al., 2010; Lange & Del-Claro, 2014); therefore, no wasp species was considered core in the all-group networks. In almost all the other networks, the species core remained the same, except for the wasp-ant networks, which featured a wasp as a key species. *Angiopolybia* is one of the genera of Polistinae and presents native representatives from Brazil; this genus is abundant in Atlantic forest areas and, despite adaptations to the necrophagic habit, consumes other resources (Lima et al., 2010; Togni et al., 2014), as observed in this study.

In addition to the core species of floral visitors, the core species of plants visited also reveal to us important characteristics of this community. In the community nets and the ant-bee nets, the core plant species were the same, not

varying according to time of day. In the bee-wasp networks, the composition was very similar to the general network, minus one core plant species – *Clerodendrum x speciosum*. However, for the wasp-ant networks, the composition was different from the community network and there were differences between the most visited plants according to the time of day. Only in the networks with bees, *Stiffia chrysantha* and *Callistemon viminalis* were part of the core species, indicating a greater interaction of bees with these species. *S. chrysantha* is a native tree, which can reach 5 meters in height, has inflorescence of tubular flowers, displays shades of orange and is most frequently pollinated by hummingbirds, while rarely by bees (Nishida et al., 2014; Lorenzi, 2020; Gobatto et al., 2021). *C. viminalis* is an exotic species, one of the several honey trees pollinated by bees; it reaches up to 7 meters in height, has terminal, pendulous and spike-like inflorescence and flowers of numerous red stamens (Latif et al., 2016; Lorenzi, 2018; Guallpa-Calva et al., 2019). In the case of *Clerodendrum x speciosum*, it is a core species only in networks with ants. It is a woody shrub, a hybrid of exotic species, with inflorescence in terminal racemes and red flowers whose genus' species are commonly pollinated by bees; herbivorous ants, plunderers and attendant ants have already been associated with these plants (Carver et al., 2003; Rohitash, 2010; Lorenzi, 2015; Groutsch et al., 2018; Mukhopadhyay & Quader, 2018). It is noticeable that in the wasp-ant networks there was a smaller amount of plants in the core species and also a plant which was not present in any core species of any other networks: *Cordia superba*. This native tree can reach up to 10 meters high, has large white flowers, is pollinated by small insects and bees and is not uncommonly visited by nectar pillagers (Agostini & Sazima, 2003; Vale et al., 2013; Silva & Rossa-Feres, 2016; Lopes et al., 2015; Lorenzi, 2020; Gobatto et al., 2021). One of the plants was in the core species of all the community networks, indicating that it is a well-visited plant by all three organisms: *Antigonon leptopus*, a semi-herbaceous climber from Mexico with inflorescence of many durable flowers in pink or white colors (Lorenzi, 2015); it is a flower species visited frequently by bees, decently by wasps and rarely by ants (Raju et al., 2001; Lorenzi, 2015; Gobatto et al., 2021; Lima et al., 2021).

Studies on plant-pollinator networks in the tropics have been conducted more often in forests than in open habitats, with sampling concentrated over a single season (Vizentin-Bugoni et al., 2018). However, deforestation in the tropics has created an increasing proportion of open habitats (e.g. in the Atlantic forest domain) (Hirota, 2003) and it is crucial to assess information about ecological interactions in this kind of habitat, now predominant in most landscapes. The loss of green areas can impact the richness and abundance of flower-visitor communities in cities, what can jeopardize the biodiversity and functional richness of that community (Spiesman & Inouye, 2013; Geslin et al., 2016). Controlled environments may be critical for the preservation of flower-

visiting species in urban areas (Smith, 2006; Larson, 2014; Twerd & Banaszak-Cibicka, 2019; Twerd et al., 2021), what demonstrates that even small green areas are important for insect conservation. However, urban administrators should ideally plan to create urban parks which support, attract and maintain flower-visitors and have a large vegetation cover and a high variety of plant species, preferably with different morphologies (Garbuzov & Ratnieks, 2014; Banaszak-Cibicka et al., 2016; Hall et al., 2017). In this context, botanical gardens stand out as a good tool for the conservation of flower-visitor communities, as they serve as ecological corridors, shelter and foraging sites (Hall et al., 2017; Maruyama et al., 2019; Marín et al., 2020; Gobatto et al., 2021). Our study endorses that a botanical garden can sustain a diverse community of flower-visiting Hymenoptera in an urban environment (Ito et al., 2001; Mazzeo & Torretta, 2015; Marinho & Vivallo, 2020), being an important tool for biodiversity conservation (Hall et al., 2017; Maruyama et al., 2019; Marín et al., 2020; Gobatto et al., 2021). When it comes to botanical gardens in Atlantic Forest areas, especially in the state of Rio de Janeiro, it is clear that our results corroborate other studies already conducted, as the botanical garden studied clearly supports a diverse community of floral-visiting Hymenoptera, whose composition, which includes many pollinating species, is very similar to communities observed by other researchers (Pimentel & Rangel, 2017; Santos et al., 2017; Silva et al., 2018; Marinho e Vivallo, 2020; Gobatto et al., 2021). Being close to an area of forest fragments, the botanical garden studied has the potential to be an ecological corridor, as well as the Botanical Garden of Rio de Janeiro (Gobatto et al., 2021). However, future work is necessary to prove that this urban park is effectively an ecological corridor. Moreover, the current study can serve as a comparison for following works that investigate the response of flower-visiting Hymenoptera to climate change (Hofmann et al., 2018).

From the above, our study can contribute by showing that there is a correlation between the number and frequency of ant floral interactions and ambient temperature and by strengthening data on network patterns of flower-visitor communities. Moreover, it highlights the importance of botanical gardens for the maintenance of flower-visiting hymenopteran communities in urban environments. Future studies can further explore whether pollination is performed by floral-visitors and their niche in their communities.

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Authors' Contribution

MRM: Conceptualization; formal analysis; investigation; data curation; writing-original draft; writing-review and editing; resources.

BFSL: Conceptualization; formal analysis; investigation; writing-original draft; writing-review and editing.

APLS: Methodology; validation; data curation.

ECBF: Methodology; validation; data curation; organism identification.

MSM: Methodology; validation; data curation.

RC-N: Methodology; validation; formal analysis.

JMQ: Methodology; validation; writing-review and editing; supervision; project administration; funding acquisition.

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