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Insect sociality plays a major role in a highly complex flower-visiting network in the neotropical savanna

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Abstract – Mutualistic networks between plants and their flower visitors provide information about the ecological dynamics and coevolutionary processes shaping species interactions. Sociality in insects has recently been considered a predictor for topological patterns in such networks. However, the effects that social and solitary species impose upon network topologies are still poorly understood. We evaluated the effects of social and solitary species within a tropical savanna flower visitor insect network in southeastern Brazil. We recorded a highly complex flower visitor network, with Hymenoptera as the most abundant and rich insect order in the samples. A total of 172 (48%) species were characterized as generalists and 183 (52%) as peripherals. Social species (54, ~ 15%) were the most abundant and solitary species (301, ~ 85%) represented the higher richness for all taxonomic groups. Most social species (~ 87%) and 41% of the solitary species were generalists. Social species played central roles in network structure, representing the most species with higher abundance and intensity of interaction with visited flowers. Finally, the sociality of Vespidae and Apidae is explained by different sets of metrics, which may reflect their different behaviors.

hymenoptera / species-level / interaction / centrality / mutualistic network / species importance

1. INTRODUCTION

Network approaches to evaluate mutualistic interactions between plants and animals are an important tool to identify non-random interaction patterns among species (Olesen et al., 2007). Revealing network structures and their mechanisms is a critical part of any biodiversity investigation (Olesen et al., 2007; Lau et al., 2017; Pedroso et al., 2021). Recently, Harvey et al.

(2017) argued about the importance of shifting the focus from individual species to interaction networks for conservation, management, restoration, and ecosystem services analyses. Indeed, given the current levels of biodiversity loss, the network approach may better explain and predict the effects of changes in the environment and species interactions on biodiversity, ecosystem structure, and function (Harvey et al., 2017).

Considering how links are arranged in a given network instead of the simple use of taxonomic diversity may offer an in-depth understanding of the importance of species regarding its structure and function (Bascompte and Jordano

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2007; Bascompte 2009). However, the role of the species traits relative to the structure, stability, and dynamics of the mutualistic networks is still poorly understood (Olesen et al., 2007; Vázquez et al. 2009a; Santos et al. 2010; Genini et al. 2010; Mello et al. 2013; Kaiser-Bunbury et al. 2014). Recent studies suggest that network topology is strongly linked to the species' functional identity, which in turn is determined by their traits, their dependence upon the way species interact and the ecosystem functions they perform (Vázquez et al. 2009a, b; Mello et al. 2013; Vizentin-Bugoni et al. 2014; Kaiser-Bunbury et al. 2014; Maruyama et al. 2015). Therefore, conservancy of the ecosystems and ecological services provided by the species may rely more on trait diversity than on taxonomic diversity.

Gathering knowledge on species traits that affect interaction patterns has been an obstacle to developing predictive theories regarding species effects upon network topology (Vázquez et al. 2007, 2009a; Kaiser-Bunbury et al. 2014). These efforts become even more challenging due to the lack of knowledge about the biology of the species involved in a given network, since they present distinct evolutionary histories, exploration patterns, and variable levels of dependence upon floral resources (Rezende et al. 2007; Olesen et al. 2007; Bezerra et al. 2009; Santos et al. 2010; Genini et al. 2010). The dependency on floral resources has been pointed out as a critical driver of network properties of the ant-plant network in the Brazilian savanna (Lange et al., 2013, 2014; Dáttilo, et al., 2014). On the other hand, species roles, such as generalists, did not change over time, which demonstrates different effects on network structure and species importance (Lange et al., 2013).

Network ecology metrics are usually approached in three levels: network-level metrics attempt to integrate the structure and patterns of the entire community and describe the overall complexity, such as modularity or nestedness (Allesina and Tang, 2012; Lau et al., 2017); sub-network-level metrics focus on identifying particular subsets in the entire network—e.g., modules or motifs—such as the interplay between topological properties and population dynamics

predicting subset occurrences (Monteiro and Faria, 2016), food web stability (Monteiro and Faria, 2017), and roles displayed by species in each subset (Olesen et al., 2007); finally, species-level metrics evaluate the relative importance of each species in the network, identifying critical species transmitting diseases, secondary extinctions (Lau et al., 2017), generalization level of the species (Martin Gonzalez, 2010), their functional roles in the network (Olesen et al., 2007), and sociality traits (Maia et al., 2019).

Eusocial insects (hereafter social insects) exhibit specialized foraging castes, longer activity periods, and an efficient communication system, enhancing their foraging capacity in both flight range and resource exploration, adding to their higher abundance compared to solitary species (Biesmeijer et al. 2005; Biesmeijer and Slaa 2006; Santos et al. 2010; Maia et al. 2019). Therefore, the social behavior displayed by several flower-visiting insects may impose different outcomes on network topologies associated with the effects of the traits ascribed above, such as modularity, nestedness, and connectance (Bezerra et al. 2009; Santos et al. 2010; Mello et al. 2011, 2013; Maia et al. 2019). Social bees (Apidae) and wasps (Vespidae) tend to produce similar general patterns in network-level topologies, even though their roles are different (Santos et al. 2010). On the other hand, solitary insects are more prone to seasonal fluctuations, where larval development, quiescence, or diapause processes determine their abundance in the environment (Wolda 1988; Roubik 1989; Martins and Barbeitos 2000).

Regarding network effects of solitary species, to the best of our knowledge, only a few studies are available in the literature (Bezerra et al. 2009; Maia et al. 2019; Romero et al. 2020). All of them point out the importance of solitary species on network structure; however, only one study compared social and solitary traits directly and concluded that both resulted in similar patterns for the network-level structural organization, such as nestedness and modularity (Maia et al. 2019).

Not all species—i.e., nodes—in a network are equally important for its structure and

function, and the higher the importance of the node, the more significant its impact on network stability (Memmott et al., 2004). Social species present a higher number of connections and frequency in comparison to solitary species (Maia et al. 2019), suggesting their higher importance, regarding species roles, for the network structure and function.

In this study, we evaluated social and solitary species importance in the network structure, using species network-level metrics. First, we estimated the general relationships among the importance metrics. Then, we tested the sociality explanation relative to the importance metrics to answer the question: do social species of floral visitors present higher importance values than solitary species? We hypothesized that social species would have greater importance than solitary species in the network structure and function. A potential reason would be associated with biological characteristics of the social species depicting a higher number of individuals, perennial colonial activity (in some cases), and specialized foraging castes (Thompson 1982), leading to a higher number of interactions (Fort et al. 2016). In addition, the greater the number of connections of a species, the more likely there will be, on average, shorter distances among the other species (Memmott et al., 2004), and the more likely the species is to act as a connector within modules or between modules (Olesen et al., 2007; Martín Gonzáles et al., 2010).

2. METHODS

2.1. Study area

The study was conducted in the Unilavras-Boqueirão Biological Reserve (RBUB) (21° 20' 47" S e 44° 59' 27" W), Minas Gerais, Brazil. The reserve comprises 159 ha with altitude between 1100 and 1250 m. The mean annual temperature ranges between 19 and 25 °C, and the mean annual precipitation is 1411 mm, with a rainy season between November and February. The winter is dry, with a hydric shortage of about 4 months (10–30 mm). The

vegetation is dominated by Cerrado *sensu stricto*, although high-altitude grasslands, rupestrian grasslands, and riparian forests are also part of the landscape. Also, part of the area is composed of the introduced *Brachiaria* sp. (Poaceae) (Pires et al. 2012).

2.2. Sampling

Interactions between plants and flower-visiting insects were recorded every 15 days from July 2015 to July 2016, except when sampling had to be postponed due to rain. Insect sampling was carried out in three areas of 100×50 m each with transects splitting them in half: area 1 (21° 20' 53" S/44° 59' 23" W), area 2 (21° 21' 01" S/44° 59' 29" W), and area 3 (21° 20' 51" S/44° 59' 58" W). For each transect, 10 plots of 20×25 m were delimited (Figure 1 in Appendix 3 depicts a schematic field design). The plots were numbered from 1 to 10 sequentially. Sampling order was determined based on 3 draws to select: first, which of the 3 areas to start; second, which side of the area should the collector start from; and finally, which plot (1 or 2, or 10 or 9) to begin with. Insects were sampled with entomological sweeping nets from 7:30 am to 4:30 pm, and each area was sampled twice a day, in the morning and in the afternoon.

The collector walked through the plots within each area, and for each blooming plant found, the collector would spend 5-min sampling. Only insects in direct contact with the plant's reproductive parts were collected, as this indicated they might be pollinators. Despite the difference in total sampling time among plots, selecting only insects in contact with the flowers ensured that most potential pollinator species would be collected. Even though it could potentially affect the network's structure, a systematic and robust sampling through the whole field was reached with this protocol. Thus, at the end of the day, all 10 plots of the 3 areas would have been observed and sampled, and if blooming plant species were present, they would have been sampled twice. The expression "flower-visiting species" is adopted here since pollination efficiency was not measured (Alves-dos-Santos et al. 2016).

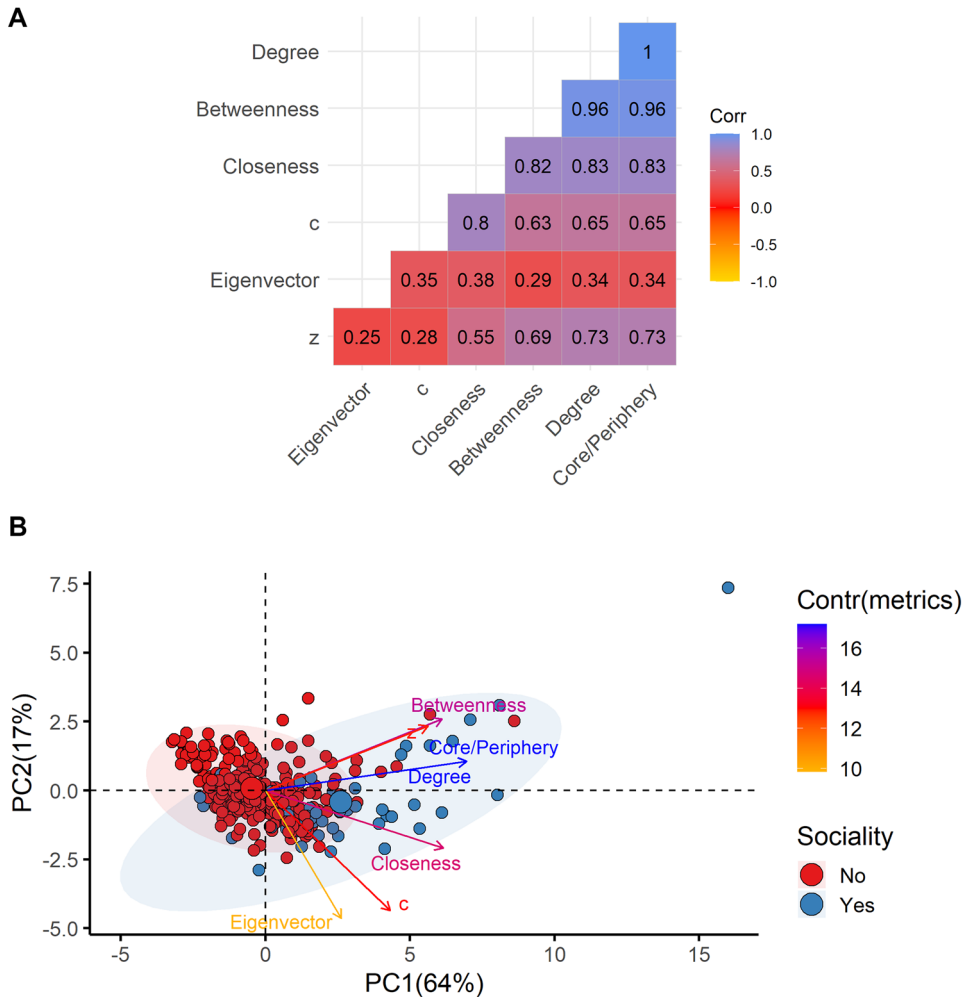


Figure 1. Correlation among six species-network-level metrics **A** showing that degree, betweenness and core/periphery are highly correlated ($r^2 \geq 0.96$). Principal components analyses (PCA) of six network metrics — connectivity degree, betweenness connectivity, closeness connectivity, between-module connectivity (c), within-module connectivity (z), core/periphery — on the sociality trait of the species **B**. Arrow colors represent the contribution of each network metrics on component axes. Contribution is a scaled representation of the squared correlation between variables and component axes. Core/periphery and degree had the same importance values explaining the variance and thus the arrows are overlapping.

All collected insects are deposited at the Entomological Collection at Universidade Federal de Lavras (CEUFLA). For plant identification, we collected part of the visited individuals with their reproductive organs. This material is deposited at the Herbarium (ESAL) of the same institution. Insect and plant identification were performed using specialized literature and the aid of systematists (see the “Acknowledgements” section).

2.3. Network construction

We constructed interaction matrices with the sampling data listing plants in the rows and insects in the columns, and each matrix cell representing the number of recorded visits (Bascompte and Jordano 2014). The results from the three transects were grouped, producing a complex network, since our focus was on the social insect roles in the general network.

We evaluated modularity by testing against a null model (1000 × Patefield model – Patefield, 1981; *bipartite* package (Dormann et al. 2009)), and the network assortativity range (i.e., $-1 \leq r \leq 1$) through a correlation coefficient (Newman 2002).

We estimated seven metrics regarding species-level networks to evaluate species roles: degree, eigenvector, betweenness and closeness centrality, connectivity between modules and within modules, and core/periphery composition. Degree centrality represents the primary network structural properties for the number of interactions of each species, (the more links a species has, the more important the node). Eigenvector centrality also measures the number of links of each species; however, it is weighted by the importance of its neighbor (i.e., a neighbor with a high number of connections depicts higher importance). Betweenness centrality ascribes the importance of a species as a connector between distinct parts or modules of the network, (therefore, the dependence of other species relative to a given species, and then, network cohesiveness). Closeness centrality measures the proximity of a node to all other nodes in the network, in which species with high values can quickly affect other nodes or be affected (*igraph* package (Csárdi and Nepusz 2020)). Hence, the higher the values estimated, the greater the importance of the species in the network structure.

We evaluated the connectivity between modules (c) and connectivity within the module (z). The connectivity between the modules describes how much each species contributes to connecting modules within the network, while the connectivity within the module (z) represents the standardized number of links that a given species has within its own module, compared to the remaining species in the same module (*bipartite* package (Dormann et al. 2009)). Thus, species that have high values of c and z are involved in many interactions in the network and described as generalists, playing an important role in connecting species within and between modules (Olesen et al. 2007; Laurindo et al. 2020).

To evaluate the core and the periphery network composition of the species, we used the

formula $G_c = (k_i - k_{average}) / \sigma k$ (Dáttilo et al. 2013), where k_i is the number of visited plants by each visiting insect species, $k_{average}$ is the average number of visited plants, and σk is the standard deviation. Values of $G_c > 1$ imply that a given visitor established comparatively more interactions than others of the same trophic niche, being considered as part of the generalist core. Values of $G_c < 1$ mean visitors established fewer interactions than others (from the same trophic niche) and, therefore, were assumed as a part of the network periphery (Dáttilo et al. 2013).

We organized the species according to their taxonomy groups: all species of Hymenoptera, Coleoptera, Lepidoptera, Diptera, Thysanoptera, Neuroptera, and Hemiptera composing the entire network and for species of Apidae and Vespidae, combined and separately. We did not include Formicidae because it includes only social species, while Apidae and Vespidae present both social and solitary species for comparison. Social and solitary species were categorized for all groupings indicated above. For the social species, we focused on stingless bees (Hymenoptera, Apidae, Meliponina), *Bombus mori* (Swederus, 1787), *Bombus atratus* Franklin, 1913 (Hymenoptera, Apidae, Bombina) and *Apis mellifera* (Hymenoptera, Apidae, Apina), paper wasps (Hymenoptera, Vespidae, Polistinae), and ants (Hymenoptera, Formicidae). Ant pollination is assumed to be rare (Peakall and Beattie, 1991), although it has been previously recorded (Domingos-Neto et al., 2017; Del-Claro et al., 2019). Therefore, we assumed that species of ants in this study could act as pollinators of some plant species. All visitor species included in this study were collected only in the reproductive parts of the flowers. The solitary species network comprised the remainder of the species. We tested social and solitary species visitor frequency (hereafter abundance) for the networks employing Mann–Whitney U test between the groups.

Next, we ascribed the general metrics variance considering all species in four steps. First, we tested the Spearman correlation among the seven metrics. Then, we ran a principal component analyses (PCA) among variables. PCA is a

helpful tool to visualize and summarize/reduce the social and solitary species variation with the six species-level variables estimated. The first component (PC1 or first dimension) captures the largest covariance among variables, maximizing the variance. Then, we computed the importance of species as the covariance among all six variables and the contribution of each variable to the variance explained (analysis and figure were produced using the *factoextra* package, Kassambara and Mundt, 2020). We plotted the metrics distributions categorized by the sociality trait. Lastly, we have built five networks considering degree, eigenvector, closeness centrality, and between-module and within-module connectivity as weights to floral visitor node sizes. These analyses provide general descriptions of the relationships between the metrics and sociality of the community of floral visitors as a whole.

To characterize the species role distribution in the network, we plotted between- and within-module values (*zc-plot*, sensu Olesen et al., 2007) for the entire network and for Vespidae and Apidae in separate. The following terminology is used to describe species conditions within a network: peripheral species have few links within their module and rarely with other modules; connector species are important to keep network structure linking modules; module hubs are important to keep the structure of their module; network hubs are important for both the network and its modules. Thus, in this context, connectors, module hubs, and network hubs are termed generalists.

Finally, we tested whether the species-network-level metrics could explain the sociality trait. We employed generalized linear models (GLM) assuming the binomial distribution of errors for all 4 models, i.e., the taxonomic organization described above. Our first model uses the entire network and framework and the metrics as explanatory variables. The second model assumes Vespidae and Apidae as frameworks and employs the metric and each taxon as explanatory variables. Our third and fourth models have Vespidae or Apidae species as frameworks and the metrics to explain sociality. Highly correlated metrics ($r^2 \geq 0.96$, sensu

Zuur et al., 2009) and those depicting high variance inflation factor ($VIF \geq 5$, Akinwande et al. 2015) were excluded from the final models. We performed an automated model selection with the *dredge* function, considering that models under $AIC \leq 2$ have an equal adjustment to the data. In this case, we performed a multimodel inference (Burnham and Anderson 2002), estimating the mean effect of the variables in the best models with the *MuMIn* package (Barton, 2016). We evaluated the importance of each variable by counting the number of times they occurred in comparison to the best models, again weighted by the value of w in the models where they occurred (Burnham et al. 2011). All analyses were carried out in the R 4.0.2 environment (R Core Development Team 2021).

3. RESULTS

Our sampling effort after 13 months totaled 36 field trips, in which we sampled blooming plant species in all 10 plots for each area at least once. The interaction network resulting from our effort was inferred from 11,531 collected insect specimens, belonging to 355 species and 116 species of flowering plants. The modularity of the network shows higher values than the null model ($M_{obs} = 0.33$; $M_{null} = 0.09 \pm 0.001$, $p < 0.001$) and 7 modules. In addition, the first 29 species with high values of hubs and local authority are composed by plant species, and they tend to link to small modules, i.e., disassortative, with $r = -0.40$.

The flower-visiting insects belonged to seven orders: Hymenoptera, Coleoptera, Diptera, Lepidoptera, Hemiptera, Neuroptera, and Thysanoptera. Hymenoptera, with 197 species (~55%), and Diptera, with 66 species (~19%), were the most sampled groups. Social species were represented by 54 insect species (~15%) and solitary species by 301 insect species (~85%). The social species belonged to three families: Apidae, with 19 species (~35%), Vespidae, with 31 species (~57%), and Formicidae, with four species (~8%). Among the visitors, only *Apis mellifera* is exotic (Appendix 1). The 116

plant species belong to 32 families, Asteraceae and Malvaceae being the most sampled, with 37 and 10 species (~28% and ~9%), respectively (Appendix 2). Among these, only *Brachiaria* sp. is exotic. The complete list of insect and plant species is available as supplementary material (Appendices 1 and 2). Social species represented a significantly higher abundance, i.e., frequency of flower visits ($p < 0.001$).

The correlation analyses among the six metrics (Figure 1A) pointed out that degree, betweenness, and core/periphery values are highly correlated ($|\rho| = 0.97$, $p < 0.001$; $|\rho| = 0.97$, $p < 0.001$; and $|\rho| = 1$, $p < 0.001$). It also indicated that all metrics have a positive correlation among them. Further, degree, core/periphery, and betweenness had equivalent contributions in explaining the variance.

PCA indicated two groups, corresponding to social and solitary species, and a clear correlation in which an increase in the species importance metrics for the network was associated with social species traits. The first dimension explained 64% of the variance, and the second dimension 17% (Figure 1B). Metrics dispersions demonstrate that sociality affects the frequency of the metrics values and increases the values of all of them when the social trait is assumed (Figure 2A–F). Assuming the correlation ascribed above we produced four networks (Figure 3 — Appendix 3 depicts the network colored by modules and nodes weighted by eigenvalues degree) having the nodes weighted by each network metric — e.g., degree, eigenvector, closeness, between-module (c), and within-module (z).

To better understand the modularity and the species roles linking other species or modules, we produced a z - c -plot (sensus Olesen et al., 2007). Figure 4A shows the distributions of the species regarding their role and insect order. A total of 172 (48%) species were generalists (e.g., connectors, module hubs, and network hubs), and 183 (52%) were peripherals. Among the most frequent insect orders, coleopteran (63%), and dipteran (81%) species had more generalist species than peripherals. On the other hand, hymenopteran (38%) and lepidopteran (43%) species had a lower proportion of generalists

than peripherals. Figure 4B shows the species distributions regarding their roles and sociality traits for Apidae and Vespidae. Social Apidae species presented 84% of the species and solitary species, 10%, of generalists. Vespidae social species also had most of its species described as generalists (90%), against 44% in solitary species. Finally, module and network hubs corresponded mostly to bee species, solitary, and social, respectively.

Four models were built and analyzed, considering the sociality trait as the response variable and the metrics as explanatory variables. Correlation and multicollinearity tests among the explanatory variables were used to avoid effects on the outcomes of the analyses. The first one, considering the entire network, had degree, eigenvector, closeness, and between-within-module as explanatory variables (VIF < 5: degree = 3.64, eigenvector = 1.04, closeness = 4.24, $c = 2.26$, $z = 2.00$). The model selection provided two models under the $AIC \leq 2$. Degree, eigenvector, between-module (c), and within-module (z) variables were selected and had a positive correlation with social traits; within-module did not present significant influence (Table I). For the second model, we used Vespidae and Apidae species, and had as explanatory variables degree, eigenvector, c , z , and family (VIF < 5: degree = 4.11, eigenvector = 1.06, family = 1.56, $c = 1.77$, $z = 2.76$). The model selection provided five models under the $AIC \leq 2$. All variables selected depicted a positive influence explaining social traits, except within-module connectivity. Degree, eigenvector, and family had a significant effect; between-module was marginally significant and within-module, non-significant (Table II). Lastly, the third and fourth models were built and analyzed for Apidae and Vespidae, respectively. Apidae model selection provided two models under the Akaike criterion (VIF < 5: eigenvector = 1.07, $c = 1.10$, $z = 1.16$), and eigenvector, c and z , showed a positive effect on explaining social species, even though within-module was non-significant (Table III). The Vespidae model selection indicated three models considering the four metrics (VIF < 5: degree = 3.89, eigenvector = 1.04,

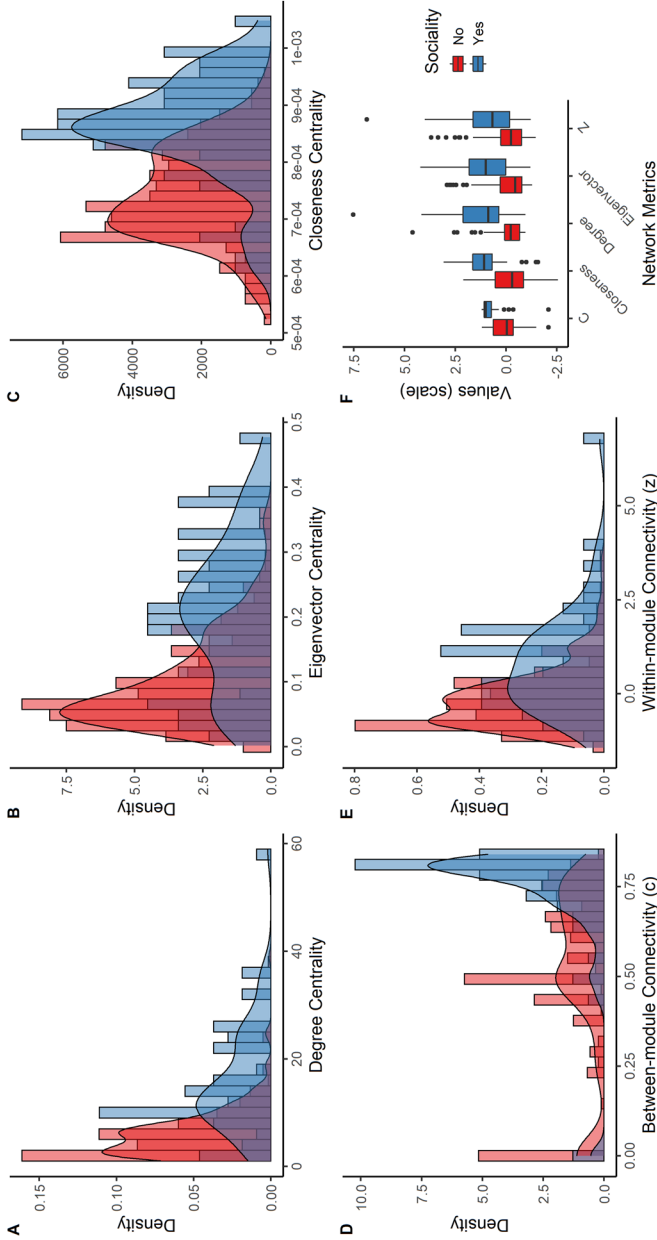


Figure 2. Metrics dispersions demonstrate the effects of sociality in the frequencies of the values. Histograms and densities distributions are categorized by sociality trait: degree centrality (A), eigenvector degree (B), closeness centrality (C), between-module connectivity (D), within-module connectivity (E). Boxplot distributions for the metrics and categorized by sociality trait (F). Note that core/periphery metric is not shown here, assuming its total correspondence with degree centrality.

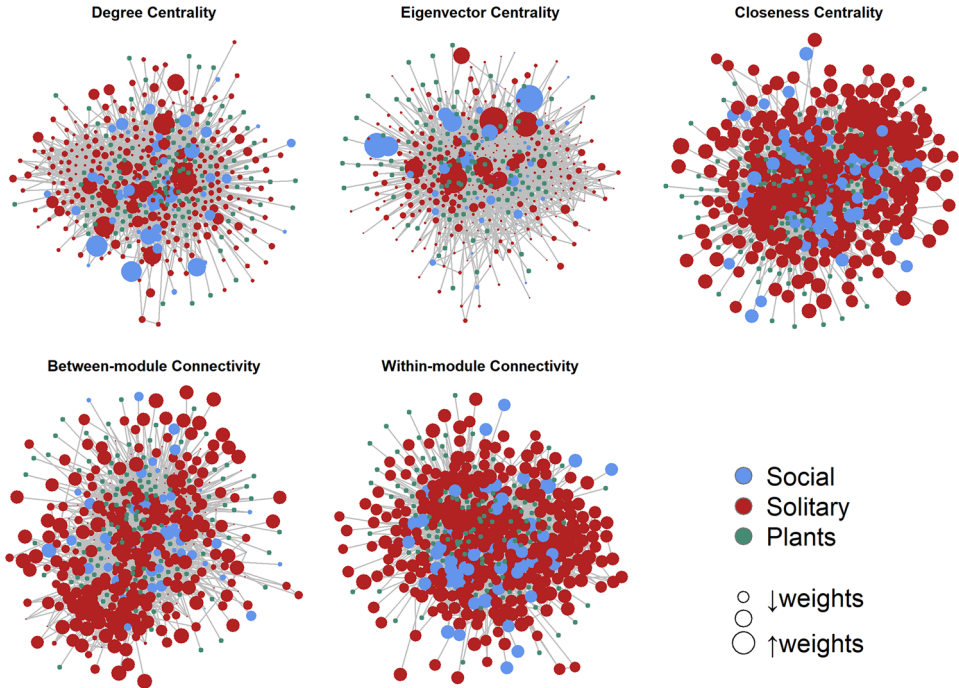


Figure 3. Network of plants and their insect visitors: Network degree centrality weights (top-left); Network weighting for the Eigenvector centrality (top-middle); Network assuming closeness centrality of visitors’ species as weight (top-right); Network with between-module (c) of visitor species as weight (bottom-left); Network assuming within-module (z) of visitor species as weight (bottom-middle). Green, blue and red circles represent plants, social and solitary insect visitors, respectively. The greater the node size, the higher the weight values.

$c = 2.61$, $z = 1.89$). Degree and eigenvector influenced positively the social trait for Vespidae species, and c and z demonstrated a negative influence, although not significant (Table III).

4. DISCUSSION

We recorded a highly complex flower-visiting network during 13 months, with Hymenoptera species representing the most abundant and rich composition among the insect orders. Social species were the most abundant, and solitary species, the richest, regardless of the taxonomic Order. Our results suggest that social and solitary species play different roles in plant–insect network topologies, in which most of the social species display generalist roles — i.e., connectors, module hubs, and network hubs — and also higher

numbers of connections, while solitary species act mostly as peripherals. It clearly shows differences in the properties of the social and solitary species within networks (Bezerra et al. 2009; Mello et al. 2011; Maia et al. 2019).

Many social insects have perennial colonies and are generalist flower visitors, interacting with several different plant species and floral types, being among the most abundant flower-visiting organisms in the Neotropics (Biesmeijer et al. 2005; Biesmeijer and Slaa 2006; Santos et al. 2010). Indeed, social species are proportionally more abundant and depict a higher degree of connections than solitary species (Maia et al. 2019). For that reason, they have been described as “supergeneralists” and considered key species in interaction networks, since they connect important subsets of species that otherwise would not be connected (Olesen et al. 2002, 2007; Biesmeijer et al. 2005;

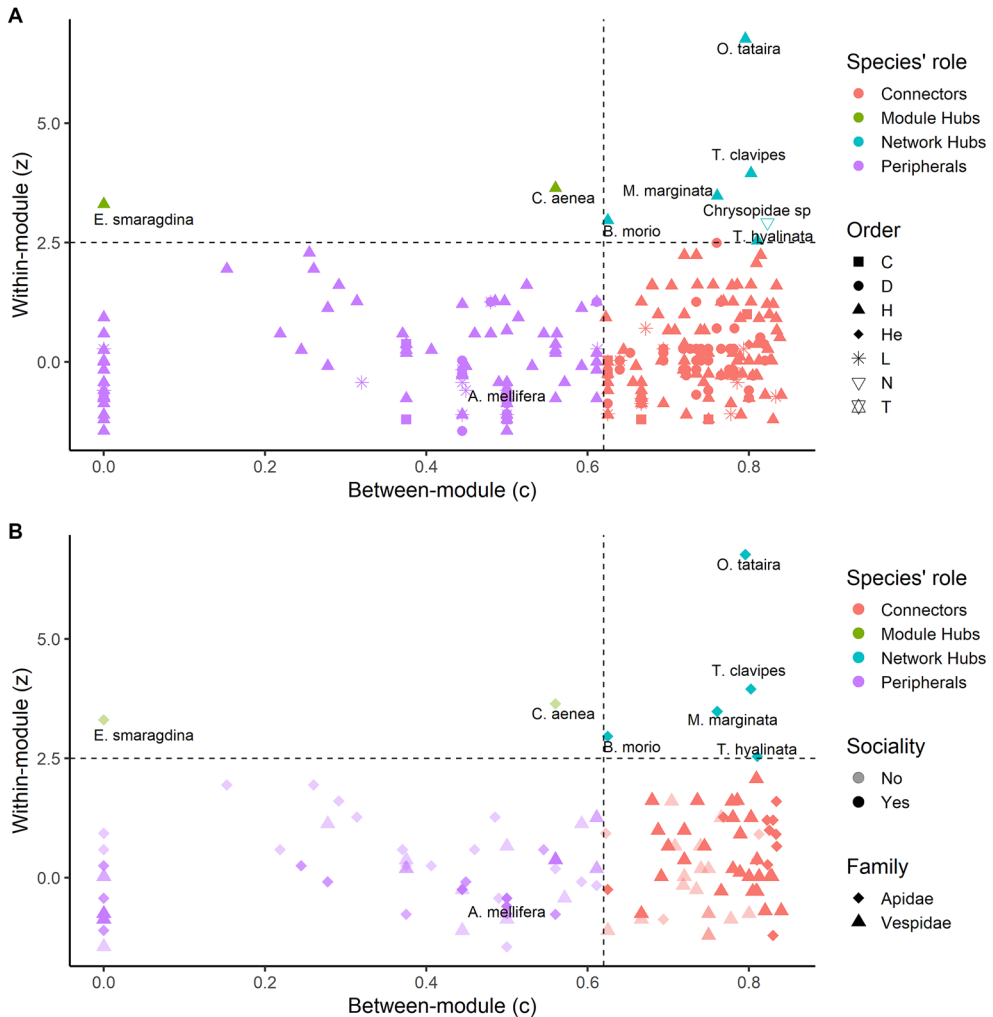


Figure 4. Distribution of species roles through the zc -plot (i.e., relationship between c and z metrics and the four-phase plane). **A** Entire network by species orders and role. **B** Vespidae and Apidae network by sociality, taxonomic family and species role. C: Coleoptera; D: Diptera; H: Hymenoptera; He: Hemiptera; L: Lepidoptera; N: Neuroptera; T: Thysanoptera. Different colors represent species roles. Sociality is represented by washed color dots (solitary) and solid color dots (social). Species labels were added to hub species and for the two most frequent species (e.g., *A. mellifera* and *Trigona spinipes*).

Mello et al. 2011; Datillo et al. 2014; Giannini et al. 2015). On the other hand, solitary insects present sparse and less abundant populations, susceptibility to seasonal variations, and are mass provisioners, that is, they may be more severely affected when resources are scarce (Roubik 1989; O'Neill 2001; Michener 2007).

A heterogeneous organization is a frequent characteristic of networks, depicting nodes either highly connected or slightly connected to other nodes (Barabási and Albert, 1999). The most highly connected central nodes are the most influential in the network, and the perturbations — caused by species abundance variations,

Table I

Model average and importance for models evaluating the effect of the species-network-level metrics on sociality for the entire network (SE: standard error; CI_{1%} confidence interval)

Parameters	Estimate	SE	CI _{2.5%}	CI _{97.5%}	Importance	p-value
Intercept	-6.606	0.958	-8.491	-4.721		<0.001
Degree	0.150	0.039	0.073	0.227	1	<0.001
Eigenvector	11.351	2.244	6.937	15.764	1	<0.001
Between-Module (c)	2.753	1.404	-0.008	5.515	1	=0.051
Within-module (z)	0.203	0.273	-0.335	0.741	0.32	=0.459

extinctions, invasive species, among others — can easily spread through the network from them than from the less central nodes (Kitsak et al., 2010). In addition, modularity increases the robustness of the network to secondary extinctions. A modular structure is expected to be found in complex ecological networks (Olesen et al., 2007), and is also characterized as disassortative (Newman, 2002). We evaluated the modular structure and pointed out seven communities with plants and social species occupying the most central nodes in a disassortative system, suggesting evident importance to the network structure and function.

Maia et al. (2019) recently addressed the differences between social and solitary species on pollination network-level and species-level metrics and suggested that the sociality trait did not affect the structure at the network level, but it did at the species-network level. We found here that most of the seven species-network level metrics were correlated with each other. Degree, core/periphery, and betweenness are highly

correlated, structuring a cluster. Closeness centrality, between-module, and within-module also showed some correlation, but at a lower level. Eigenvector centrality was the metric that had the lowest correlation among the studied metrics. The cluster structured by degree, core/periphery, and betweenness can also be observed in the dimension reduction tests where they contributed more to explain the most variance of the metrics. Finally, despite the differences between the raw values evaluated to degree and core/periphery, their distribution was overlapping, suggesting that they are equivalent. Further investigation is needed to understand the relationship between them under different conditions or networks.

Different importance metrics explained sociality traits in Apidae and Vespidae, besides the eigenvector centrality, which was present for both families. Between-module connectivity contributed to explaining sociality in Apidae and degree in Vespidae. Both families depicted species very connected to other species that also presented numerous links, which suggests high

Table II

Model average and importance for models evaluating the effect of the species-network-level metrics on sociality for Apidae and Vespidae together (SE: standard error; CI_{1%} confidence interval)

Parameters	Estimate	SE	CI _{2.5%}	CI _{97.5%}	Importance	p-value
Intercept	-5.959	1.043	-8.022	-3.897		<0.001
Degree	0.192	0.076	0.0414	0.343	1	<0.05
Eigenvector	10.756	2.797	5.224	16.287	1	<0.001
Between-Module (c)	3.216	1.810	-0.356	6.789	0.69	=0.077
Within-module (z)	-0.366	0.411	-1.79	0.446	0.27	=0.377
Family (Vespidae)	1.423	0.717	0.006	2.840	0.78	<0.05

Table III

Model average and importance for models evaluating the effect of the species-network-level metrics on sociality for Apidae and Vespidae (SE: standard error; CI_{i%} confidence interval)

Family	Parameters	Estimate	SE	CI _{2.5%}	CI _{97.5%}	Importance	p-value
Apidae							
	Intercept	-9.044	2.304	-13.639	-4.449		<0.001
	Eigenvector	8.617	4.277	0.087	17.147	1	<0.05
	Between-Module (c)	11.821	3.545	4.758	18.885	1	<0.01
	Within-module (z)	0.424	0.339	-0.252	1.102	0.44	=0.219
Vespidae							
	Intercept	-4.439	1.142	-6.719	-2.158		<0.001
	Degree	0.385	0.118	0.149	0.621	1	<0.01
	Eigenvector	9.498	4.060	1.391	17.605	1	<0.05
	Between-Module (c)	-0.368	0.512	-5.751	2.930	0.22	=0.479
	Within-module (z)	-1.410	2.173	-1.391	0.654	0.23	=0.524

quality of the interactions and similar roles in the network structure. Otherwise, differences among the variables explaining sociality may be associated with their different behavior. Social bees and wasps are frequent flower visitors collecting resources. However, while social bees have morphological adaptations for pollen collection and transportation, social wasps do not. Indeed, social wasps visit plants to hunt insects associated with the plants, and use nectar as an energy resource, and thus are considered potential pollinators. Further, our study's most connected plant species are those with flowers with most of the reproductive parts exposed, such as *Stryphnodendron adstringens* (Asteraceae) and others. The lack of specialization constraints by the flower traits may influence the interaction, by releasing potential filters that could limit visitor access, mainly for the social vespidae species, which are not as specialized in collecting pollen as the social bees.

The interplay between network structure and function is critical to understanding the mechanisms that affect network cohesiveness, network stability, and predicting future impacts (Strogatz, 2001; Bascompte et al., 2003; Monteiro and Faria 2017). Characterization of species roles in the network can indicate where species are positioned in the network and how they interact. Further,

central species affect the network stability negatively and faster when deleted (Memmott et al., 2004). We observed that most of the social species were recovered here as generalists. Five social and two solitary bees are network and module hubs among the generalist species. *Centris aenea* is a solitary bee that forages through the plants, not only after nectar and pollen but also oil and other substances. Oil bees tend to form robust and cohesive modules within the network (Olesen et al., 2007; Bezerra et al., 2009). *Exaerete smaragdina* is kleptoparasitic on other Euglossini bees, with females lacking a pollen collecting apparatus, and were most likely collected on flowers while foraging for nectar.

Regarding network hub species, we recovered five social bees in this role, and four of them are stingless. Bee species are among the most frequent flower visitors in many ecosystems (Santos et al., 2010 and 2013). Besides the social behavior, which is associated with a large number of individuals and ensuring a wide range of plant species visited (Thompson 1982; Santos et al., 2010; Fort et al. 2016; Maia et al, 2019), other complex and more elaborate behaviors can be assumed regarding stingless bee species, such as aggressiveness and territorialism (Johnson and Hubbell, 1974; Hubbell and Johnson 1978), interception of odor trails from foreign workers and

even from different species, flying directly to the source (Nieh et al. 2004; Schorkopf et al. 2009), and mechanisms to avoid trails from more aggressive species and possible encounters, preventing others from foraging (Hubbell and Johnson 1978).

Identifying the role of a given species within a network is important for the conservation of the network and the community, for the higher its importance connecting modules or species, the greater their effects on network structure and function. Further, knowing the species importance allows for management plans to be implemented, decreasing the risk of unsuccessful conservation efforts. We demonstrated that in the studied system, social species can affect a highly complex network more than solitary ones (although ant species should be treated with caution), in which centrality and connectivity metrics were higher, indicating the more significant role played by them regardless of the taxon (Thompson 1982; Maia et al. 2019). Social species played central roles in network structure, being represented by the most species with higher abundance and intensity of interaction with flowers. This is in agreement with our hypothesis that social and solitary species influence topological network properties differently. Finally, more studies approaching seasonality and time scales and how they affect networks are necessary to better understand how they mediate network topology according to species roles.

SUPPLEMENTARY INFORMATION

The online version contains supplementary material available at <https://doi.org/10.1007/s13592-022-00923-8>.

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AUTHOR CONTRIBUTION

EPP, LDBF, and MGH conceived and designed the experiments. EPP performed the experiments with advice and assistance from MGH and LDBF. EPP and MGH identified most of the insects. DQD and MEM provided identification of plants. LDBF analyzed the data. EPP, MGH, DQD, MEM, ABM, and LDBF wrote the manuscript.

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DATA AVAILABILITY

All data generated or analyzed during this study are included in this published article (and its supplementary information files as Appendices 1, 2, and 3). Also, the datasets and codes generated and analyzed during the current study are available in the <https://github.com> repository at <https://github.com/lfaria-ufba/apidologie>.

DECLARATIONS

Ethics approval Not applicable.

Consent to participate Not applicable.

Consent for publication Not applicable.

Competing interests The authors declare no competing interests.

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