

Kate Pereira Maia

Insetos sociais e a estrutura de redes de polinização

Social insects and the structure of pollination
networks

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Prof(a). Dr(a).

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Dedicatória

Aos meus pais, por seu amor e
dedicação.

Epígrafe

“If you can’t love yourself, how in the hell you’re gonna love somebody else?”

RuPaul

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Resumo

Mutualismos entre plantas e polinizadores estão organizados em redes de interação que envolvem muitas espécies. Em última instância, o que determina a ocorrência das interações entre plantas e polinizadores são as características dos dois grupos de espécies. O comportamento social pode ser uma das características chave na organização das interações em sistemas de polinização. Investigamos se a presença de polinizadores com comportamento social em redes de polinização está associada a diferentes padrões estruturais, e se polinizadores com níveis crescentes de complexidade no comportamento social são mais importantes pra estrutura dessas redes. Encontramos que a variação na proporção de espécies sociais não altera a estrutura de redes de polinização. Encontramos também que espécies com comportamento social são, em média, mais importantes para a estrutura de redes de polinização do que espécies solitárias. Nossos resultados corroboram resultados anteriores que sugerem que redes mutualísticas tem estruturas invariantes. Nossos resultados sugerem ainda que o papel estrutural mais proeminente das espécies sociais está associado à sua maior abundância. Incluir aspectos da história natural das espécies e das interações em estudos de redes ecológicas, nos permitirá fazer inferências cada vez mais assertivas sobre a importância funcional das espécies em comunidades.

Abstract

Mutualisms between plants and pollinators are organized in interaction networks that involve many species. Ultimately, what determines the occurrence of interactions among plants and pollinators are the traits of both groups of species. Social behavior can be a key trait on the organization of interactions between plants and pollinators. Here, we investigated if the presence of pollinators with social behavior in pollination networks is associated to different structural patterns, and if pollinators with increasing levels of complexity in social behavior are more important for network structure. We found that the presence of social pollinator species does not affect the structure of pollination networks. We also found that species with social behavior are, on average, more important for network structure than solitary species. Our results reinforce past studies that suggested that the structure of mutualistic networks has invariant structural properties. Our results also suggest that the more prominent role occupied by pollinators with social behavior is associated to these species' large abundances. Including natural history information about species and about species interactions on the study of ecological networks will allow us to make more assertive inferences on the functional roles species occupy in ecological communities.

Introdução Geral

Mutualismos são interações ecológicas interespecíficas que aumentam a aptidão de seus participantes (Bronstein 1994). Alguns exemplos de potenciais interações mutualistas são a dispersão de sementes por animais (Willson & Traveset 2000), a defesa de plantas contra herbivoria por meio de interações com formigas (Rico-Gray & Oliveira 2007), a remoção de ectoparasitas por peixes e camarões limpadores (Floeter et al. 2007), e a polinização de plantas por insetos (Waser & Ollerton 2006). Mutualismos são ubíquos e podem ser observados nos mais variados tipos de ambientes terrestres e aquáticos (Hay et al. 2004; Memmott et al. 2004). Mutualismos podem ter tido um papel importante na geração e manutenção da biodiversidade (Thompson 2005, 2009; Bascompte & Jordano 2007). De fato, muitos mutualismos evoluíram há muito tempo e essas interações podem estar associadas a diferentes eventos-chave na história da vida, como a origem da célula eucariótica, a radiação das angiospermas (Stachowicz 2001) e a maior diversidade em algumas famílias de plantas polinizadas por animais quando comparadas com seus grupos irmãos, polinizados por agentes abióticos (Dodd et al. 1999).

No mutualismo entre plantas e polinizadores, os animais visitam flores com o intuito de obter alimento e, ao mesmo tempo, realizam a reprodução das plantas (Fægri & Pijl 1979, mas veja Genini et al. 2010). Apesar da polinização beneficiar tanto plantas quanto polinizadores, essa interação pode ser desigual em importância para os dois grupos de espécies envolvidas

(Vázquez et al. 2012). Polinizadores necessitam visitar plantas uma única vez para se beneficiarem da interação e obter alimento. No entanto, a interação, geralmente, só resulta em benefícios para as plantas quando ocorrem ao menos duas visitas: uma visita que resulte na coleta de pólen pelo polinizador, e uma segunda visita que resulte na deposição do pólen coletado na flor de outra planta co-específica. Este é um dos exemplos das diferenças entre os benefícios associados aos mutualismos e que, por conseguinte, podem levar à evolução de diferentes modos de vida em grupos de espécies que interagem. Esses modos de vida incluem desde polinizadores e plantas altamente generalistas que interagem entre si, até interações extremamente específicas, nas quais certas espécies de plantas são polinizadas exclusivamente por uma espécie de polinizador (Waser et al. 1996). Em última instância, o que determina a ocorrência da interação para espécies generalistas, definidas aqui como espécies que interagem com muitas espécies, e especialistas, espécies que interagem com poucas espécies, são os atributos fenotípicos, ecológicos e comportamentais dos organismos envolvidos (Rezende et al. 2007a; Stang et al. 2009; Chamberlain et al. 2010; Hossaert-McKey et al. 2010).

Os atributos de uma espécie podem influenciar tanto a identidade de seus parceiros mutualistas, quanto o número de parceiros mutualistas com os quais a espécie irá interagir (Stang et al. 2006). Exemplos de atributos fenotípicos que influenciam a ocorrência de interações de polinização são a profundidade e a largura de tubos florais, que restringem o número de possíveis visitantes às flores (Stang et al. 2006). A compatibilidade entre a

morfologia de uma planta e de seu polinizador pode limitar o número de espécies que interagem com as duas espécies, aumentando a especialização da interação e, possivelmente, as chances de que o pólen da planta seja carregado até o estigma de uma planta da mesma espécie (Pellmyr 2002). Fatores ecológicos, como a abundância, também estão associados com o número de parceiros mutualistas de uma espécie (Vázquez & Aizen 2004; Lewinsohn et al. 2006; Vázquez et al. 2007; Krishna et al. 2008). Quanto aos atributos comportamentais, um exemplo que impõe limitações à identidade e quantidade de parceiros mutualistas de uma espécie é o período de atividade da espécie (Olesen et al. 2008; Chacoff et al. 2012). Algumas interações podem não ocorrer simplesmente por que o período de floração de uma espécie de planta não coincide com o período de atividade de um polinizador (Olesen et al. 2011; Vizentin-Bugoni et al. 2014).

Um outro atributo comportamental que pode estar associado à ocorrência das interações entre plantas e polinizadores é a eussocialidade, presente principalmente em alguns táxons de insetos. Insetos são considerados eussociais quando: 1) indivíduos da mesma espécie cooperam no cuidado dos jovens; 2) o trabalho da colônia é dividido e alguns indivíduos são responsáveis exclusivamente pela reprodução, enquanto outros não se reproduzem; 3) ocorre sobreposição de gerações (Wilson 2000). Níveis de pré-socialidade ocorrem quando espécies apresentam uma ou duas das três características que definem eussocialidade (Wilson 2000). Insetos sociais, definidos aqui como espécies de insetos que apresentem qualquer nível de comportamento social, especialmente abelhas e vespas, são organismos

frequentemente envolvidos em mutualismos com plantas (Thompson 1982). Por exemplo, as abelhas do mel (*Apis mellifera*, Apidae) dependem quase exclusivamente dos recursos florais obtidos durante a polinização para sobreviver (Pellmyr 2002). Já vespas sociais interagem com plantas por meio de tipos diferentes de interações positivas: atuam como polinizadores, mas também predam insetos presentes nas plantas, protegendo a planta contra herbivoria (Beggs 2011). Neste sentido, é possível que as características comuns aos insetos sociais possam explicar a relevância desses animais em mutualismos e, particularmente, como polinizadores.

As colônias de diversas espécies de insetos sociais são compostas por muitos indivíduos, e encontram-se ativas durante períodos prolongados do ano (Thompson 1982). Existem indícios de que tanto a abundância (Jordano 1987; Vázquez et al. 2007, 2009) quanto a amplitude fenológica (Olesen et al. 2008; Rasmussen et al. 2013) de uma espécie são positivamente correlacionadas com o número de interações estabelecidas por esta espécie em uma localidade. A divisão do trabalho por diferentes castas de indivíduos pode ser outra característica a facilitar o estabelecimento de muitas interações por espécies sociais, já que castas particulares podem se dedicar exclusivamente à procura de alimento e, conseqüentemente, às interações (Thompson 1982). Por exemplo, algumas operárias da abelha *Exoneura bicolor* dedicam-se exclusivamente à proteção da colônia permitindo às outras operárias apenas forragear (Melná & Schwarz 1994). Como consequência da divisão de trabalhos em castas, o tempo gasto por indivíduo interagindo com

plantas deve ser maior em castas especializadas em forrageamento do que em indivíduos de uma espécie solitária.

As interações entre plantas e polinizadores raramente envolvem um único par de espécies, mas estão organizadas em redes de interação compostas por conjuntos muito maiores de espécies de plantas e insetos (Jordano et al. 2003; Memmott et al. 2004). Assim, a abordagem de redes complexas é uma ferramenta fundamental para investigar se e como características das espécies, como a socialidade, estão associadas à organização desses sistemas de interação. A abordagem de redes complexas permite a caracterização quantitativa da estrutura das interações entre espécies em uma localidade, baseando-se na representação de conjuntos de espécies e de suas interações por meio de grafos (Figura 1). Nesses grafos, plantas e polinizadores são representados por pontos, enquanto as interações entre eles são representadas por linhas. Com essa representação é possível determinar, por exemplo, qual a distância, medida em número de interações, entre duas espécies, e conseqüentemente, quais são as espécies que estão em média mais próximas de todas as outras espécies da rede. Essa medida de proximidade das espécies é um exemplo de como o uso da abordagem de redes permite a quantificação de componentes da estrutura que não podem ser observados em seus elementos isoladamente, mas que emergem das interações entre esses elementos (Proulx et al. 2005). Dessa forma, a abordagem de redes é uma ferramenta essencial para a compreensão dos processos ecológicos e evolutivos que envolvem muitas espécies (Proulx et al. 2005).

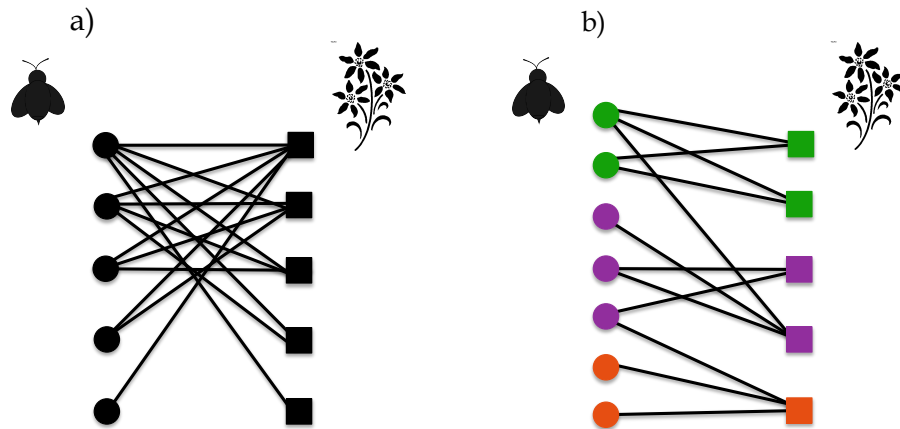


Figura 1: Exemplos hipotéticos de a) uma rede bipartida aninhada; b) uma rede bipartida modular. Círculos representam espécies de polinizadores, quadrados representam espécies de plantas e linhas representam interações polinizador-planta.

Na última década, diversos estudos foram realizados com o objetivo de descrever a estrutura de redes mutualistas. Alguns padrões vêm sendo descritos consistentemente para redes que envolvem polinizadores e plantas. Sabe-se que redes de polinização são aninhadas e podem ser modulares (Bascompte et al. 2003; Jordano et al. 2003; Olesen et al. 2007; Fortuna et al. 2010). Em uma rede perfeitamente aninhada (Figura 1a), as interações estabelecidas por espécies especialistas são um subconjunto das interações estabelecidas por espécies generalistas (Bascompte et al. 2003; Jordano et al. 2006). Uma rede modular (Figura 1b) é caracterizada pela presença de grupos de espécies (módulos) que interagem mais entre si do que com outras espécies da rede (Olesen et al. 2007; Bascompte 2009). Padrões como aninhamento e modularidade têm sido associados a diferentes processos ecológicos e evolutivos. O aninhamento é um padrão estrutural que pode facilitar a manutenção da alta diversidade de espécies geralmente observada em redes

mutualistas (Bascompte et al. 2006; Bastolla et al. 2009 mas veja Allesina & Tang 2012). Já a modularidade pode ser um componente estrutural importante para a estabilidade de comunidades, sendo os módulos unidades básicas onde podem ocorrer processos coevolutivos (Olesen et al. 2007).

Com base na abordagem de redes, os resultados de alguns trabalhos já sugerem que abelhas sociais (*Apis* e *Bombus*) são espécies centrais em redes de polinização, interagindo com muitas espécies de plantas (Memmott et al. 2004; Olesen et al. 2007; Vázquez & Aizen 2003). Santos e colaboradores (2012) estudaram o papel da abelha-do-mel *Apis mellifera*, uma abelha eussocial e invasora, na estrutura de redes de polinização e demonstraram que essa espécie geralmente ocupa papéis funcionais importantes nas redes da caatinga. Por outro lado, a natureza generalista das interações entre plantas e vespas sociais faz com que os módulos que incluem vespas sociais em redes de polinização sejam menos especializados do que as redes de polinização completas (Mello et al. 2011). Esses estudos levantaram a importância de investigar o papel da socialidade na organização das interações entre plantas e polinizadores. Isso pode apenas ser realizado em um estudo que inclua diferentes grupos de insetos nos quais o comportamento social evoluiu. Além disso, esse trabalho irá contribuir para o estudo de redes ecológicas investigando o impacto que o comportamento das espécies pode ter na organização de redes de interação.

Objetivos

O objetivo geral deste trabalho é investigar se a socialidade é um atributo chave associado à organização de redes de interação entre polinizadores e plantas. Nessa dissertação abordamos duas questões específicas: 1) A proporção de espécies de polinizadores com comportamento social em redes de interação polinizador-planta está associada a alguma estrutura específica dessas redes? Dadas as evidências de que espécies com comportamento social são importantes em redes de polinização, nós esperamos que a proporção crescente dessas espécies aumente os índices de aninhamento e centralidade das redes. Também esperamos que, por possuírem muitas interações, espécies com comportamento social conectem diferentes módulos, diminuindo a modularidade da rede. 2) O aumento em complexidade do comportamento social de espécies de polinizadores está associado ao aumento de contribuição dessas espécies para a estrutura de redes de polinização? Esperamos que a crescente complexidade no comportamento social dos polinizadores esteja associada a maiores números de interação, maiores índices de contribuição para o aninhamento, de centralidade e conectividade das espécies. Para responder às duas perguntas, combinamos conhecimento sobre o comportamento social de polinizadores, dados empíricos sobre interações entre plantas e polinizadores e ferramentas de redes ecológicas.

Does sociality shape the organization of plant-pollinator networks?

Kate P. Maia¹, Claus Rasmussen² and Paulo R. Guimarães Jr^{1*}

¹Departamento de Ecologia, Instituto de Biociências, Universidade de São Paulo, 05508-900 São Paulo, SP, Brazil

²Department of Biological Sciences, Aarhus University, DK-8000 Aarhus C, Denmark

*Author for correspondence (prguima@usp.br).

Abstract

Structural patterns commonly observed in ecological networks emerge because not all species play similar roles in interacting assemblages. Differences in patterns of interaction are related to species traits and therefore a central question in the study of species interactions is to understand which and how traits modulate the organization of ecological networks. We hypothesize that social insects, due to its higher abundance, temporal constancy and labor specialization, are likely to be the highly connected species in pollination networks. Here we investigated if social behavior of some floral visitors shapes pollination networks, and how the increasing complexity on species social behavior relates to patterns of interaction of individual species. We found that network-level patterns such as nestedness, closeness and betweenness centralization and modularity are not affected by the variation in the proportion of social species in the network. In contrast, species with social behavior are, on average, more important in structuring pollination networks than solitary species. Our analysis suggests that the larger abundance of social insects may explain their greater role on network structure. Our results point out the importance of sociality as a trait determining patterns of interaction in pollination networks. More broadly, our results suggest that the evolution of some traits, such as sociality, may impact the role of interacting species within networks even if not changing the overall network organization.

Introduction

Mutualisms are interactions between individuals of different species that result in benefits for both interaction partners (Bronstein 1994). A well-studied form of mutualism is the interaction between plants and pollinators in which animals visit flowers to obtain resources, and consequently pollinate flowers facilitating plant reproduction. At the community level, the interactions between plants and pollinators are organized in networks comprising many species (Bascompte & Jordano 2007). These networks present particular structural patterns that may facilitate species coexistence and maintain species diversity (Bascompte et al. 2006; Bastolla et al. 2009). Such structural patterns emerge because not all species play similar roles in the networks (Jordano et al. 2003; Vázquez & Aizen 2004; Guimarães Jr et al. 2006; Olesen et al. 2007). For instance, there is a large variation in the number of interactions across species in pollination networks (Jordano et al. 2003), so that just a few species have many interactions.

Highly connected species can be defined as species having a very wide pollination niche (Olesen et al. 2002), interacting with a disproportional diversity of plant species. Just a few pollinator species in pollination networks are highly connected species (Jordano et al. 2003) and therefore, highly connected species are the center of many ecological networks (Sazima et al. 2010). These species may be important for the functioning of ecological communities since they connect otherwise isolated subgroups of interacting species, i.e., modules (Olesen et al. 2007), and increase network nestedness, the overlap in patterns of interaction between species. Moreover, highly

connected species were also hypothesized to mediate evolution and coevolution in mutualistic networks, favoring the complementarity and convergence of traits in species-rich mutualisms (Guimarães Jr et al. 2011). Due to the potential importance highly connected species have on ecological and evolutionary processes, it is important to identify what factors allow the emergence of this kind of lifestyle that relies upon a diversity of mutualistic partners to persist (Thompson 2005).

Many factors may influence the occurrence of interactions between species, such as climate and species distribution (Gathmann & Tschardt 2002; Hegland et al. 2009; Blois et al. 2013). However, ultimately, what determines the patterns of interactions plants and pollinators establish at local communities are the traits of these species (Stang et al. 2006; Vizentin-Bugoni et al. 2014). Examples of phenotypic traits that may influence the occurrence of interactions between plants and pollinators are the length and width of corolla tubes that restrict the number of flower visitors (Stang et al. 2006). Plant species with extremely long corolla tubes will be able to interact with only few pollinator species that have long proboscis (Inouye 1980). Different lines of evidence, such as the fitting of assembly models to empirical data (Pires et al. 2011), the analysis of the dimensionality of complex networks (Eklöf et al. 2012), and the study of traits that constrain the occurrence of interactions (“forbidden links”, Olesen et al. 2011), suggest that a few, statistically-independent traits are keystone to understand the organization of ecological networks. A central question in the study of ecological networks is to identify which are these traits.

In pollination systems, a potentially important trait modulating the patterns of interaction of pollinator species is sociality. Social species, species that present any level of social behavior, such as the honey bee (*Apis mellifera*), are often important floral visitors in disparate ecological communities (Vázquez & Aizen 2003; Memmott et al. 2004; Olesen et al. 2007). Thompson (1982) hypothesized that the potentially preeminent role of some social insects in pollination interactions is related to three aspects of the natural history of sociality. First, the colonies of social insects are generally composed of many individuals, what could lead to higher abundances within local communities and, consequently, higher species-level interaction rates and higher number of interaction partners than observed for solitary species. In fact, the number of individuals is correlated to the number of interactions, at species level, in some mutualistic assemblages (Jordano 1987; Krishna et al. 2008; Vázquez et al. 2009). Second, colonies of many social insects are active throughout the entire year, increasing the opportunity for interacting with multiple plant species. Indeed, there is evidence that phenological amplitude is positively related to the number of interactions species establish in pollination networks (Olesen et al. 2008; Chacoff et al. 2012). Third, the division of labor among castes in eusocial species, the higher complexity level of sociality, could favor the establishment of many interactions, since particular castes are specialized in foraging. Therefore, sociality could be one underlying factor explaining why social insects are usually perceived as highly connected species in pollination networks (Memmott et al. 2004; Olesen et al. 2007). If so, we could

even expect that an overrepresentation of social insects could change network organization.

Here we investigate if social behavior of animal species shapes the structure of pollination networks formed by plants and their floral visitors. Specifically we address two questions: 1) Do pollination networks with larger proportions of social pollinator species present different structural patterns than networks with smaller proportions of social species? Our prediction is that the larger the proportion of species with social behavior, the more nested, centralized and less modular is the structure of pollination networks. 2) Do pollinator species with increasing complexity in social behavior have increasing importance in interaction patterns when compared to solitary species? Our prediction is that, with increasing complexity in social behavior, pollinators have more interactions, are more central and more important for the structural patterns observed in pollination networks than solitary species.

Materials and Methods

We analyzed 23 presence-absence pollination networks, found in the literature (Appendix A). For a subset of these networks (14 networks, 60%) we have information on the frequency of interactions between species. All networks comprised solitary and social pollinator species. Social pollinators included several groups of bees, wasps and ants. To investigate the role of social insects on network organization, we first classified the social behavior of every pollinator species present in the networks in four categories, which represent an order of the complexity of social behavior (Table 1): solitary (S),

communal (C), primitively social (PS) and eusocial (E) (Michener 2007). Eusociality is defined by the presence of three traits: 1) individuals of the same species cooperate in caring for the young; 2) there is reproductive division of labor, with sterile individuals working on behalf of fecund nestmates; and 3) there is overlap of generations in life stages capable of contributing to colony labor (Wilson 2000). According to Michener (2007), both solitary and communal species lack all three traits that define eusociality, but females of communal species can nest together (Table 1). Primitively social species present all three traits that define eusociality, and are not perennial (Michener 2007). In our analysis, we lumped all non-perennial species with other levels of presociality, i.e., that present one to the three traits that define eusociality (Wilson 2000) in the category “primitively social”. Finally, eusocial species present the three traits that define sociality and are perennial (Table 1).

Table 1: Classification of pollinator species sociality level according to Michener (2007).

Sociality level	Cooperative brood care	Castes	Overlap of generations	Observations
Solitary	-	-	-	Females do not nest together
Communal	-	-	-	Females can nest together
Primitively social	+	+	+	Seasonal activity
Eusocial	+	+	+	Perennial activity

Proportion of social species and structure of the networks

We characterized the structure of the networks to evaluate if higher proportions of social species in networks are associated to higher nestedness and centralization, and to lower modularity levels. We chose metrics that characterize the network-level aspects of the organization of mutualistic assemblages that are likely to be affected by the presence of highly connected species. We used ANINHADO to quantify the level of nestedness (NODF), the R package “bipartite” for quantifying closeness centralization (CC) and betweenness centralization (BC), and NETCARTO for quantifying modularity (M). Nestedness is a common structural pattern in pollination networks (Bascompte et al. 2003), according to which species have interactions with a subset of the species with which highly-connected species interact (Almeida-Neto et al. 2008). Closeness and betweenness centralization are based on the shortest path between nodes, so that the shortest path is the minimum number of interactions between two species (de Nooy et al. 2005). Networks have high closeness centralization when there is a large variation in the number of direct and indirect pathways connecting species in the network (de Nooy et al. 2005). Networks have high betweenness centralization when there is a large variation in how frequently species are part of the shortest paths connecting pairs of species (de Nooy et al. 2005). A network is modular when there are modules (groups) of species that interact more among themselves than with species in other modules (Olesen et al. 2007; Bascompte 2009). We tested the significance of all four metrics calculated for each network using a null model that controls for the effects of species richness, number of recorded

interactions, and heterogeneity in the number of interactions across species (null model 2 - Bascompte et al. 2003). Network metrics are considered significant if empirical networks present higher metric values than expected by the null model, indicating that the structural pattern observed (e.g., nestedness) is stronger than expected for a random network with similar species richness and heterogeneity in number of interactions per species

For every network we computed the proportion of social pollinators, $I_1=(E+PS+C)/P$, and the proportion of eusocial pollinators, $I_2=E/P$, in which E is number of eusocial species, PS is number of primitively social species, C is number of communal species and P is the total number of pollinator species. We excluded ants from the computation of both indexes, since there is empirical evidence they rarely visit flowers and are often poor pollinators when they do (Janzen 1977; Beattie & Hughes 2002). We emphasize that including ants in the analysis does not change the final results (Appendix E). Using general linear models, we tested if the increasing proportion of social (I_1) and eusocial (I_2) pollinators in the network were related to increasing nestedness, closeness centralization and betweenness centralization, and to decreasing modularity. Network metrics often depend on basic network properties such as species richness and number of interactions (Almeida-Neto et al. 2008). To allow across-networks comparisons, we standardized all network metrics using z-scores, defined as

$$z = \frac{e - \bar{n}}{\sigma_n} \quad (1)$$

where e is the metric value of the empirical network, \bar{n} is the mean metric value of the null networks (generated by null model 2), and σ_n is the standard

deviation of the metric values of the null networks. We used the Akaike Information Criteria (AIC) to select among three models the one that best describes each of the four network metrics: 1) no explanatory variable; 2) proportion of social pollinators (I_1) as explanatory variable and; 3) proportion of eusocial pollinators (I_2) as explanatory variable.

Interaction patterns of social and solitary species

We characterized the role of all pollinator species in the networks with metrics that describe how important for network organization species are. This characterization allows us to evaluate if with increasing complexity in social behavior species have more interactions, are more central and more important for network structure. We quantified the number of interactions or degree (k), contribution to nestedness (cn), closeness (cc) and betweenness centrality (bc), among-module connectivity (c) and standardized within-module degree (z) of every pollinator species, and *strength* only for the species present in the networks that had quantitative information. The degree (k) is the number of species with which each pollinator species interacts. The contribution to nestedness of a given species, cn , is a metric derived from NODF that describes the overlap in the interacting assemblages of focal pollinators and all other pollinators (Almeida-Neto et al. 2008). The closeness centrality, cc , is related to closeness centralization, so that the higher cc , the shorter are the pathways connecting the species to other species in the network (Martín-González et al. 2010). The betweenness centrality, bc , is related to betweenness centralization, so that the higher bc , the more in-

between network shortest paths a given pollinator is (Martín-González et al. 2010). The among-module connectivity, c , and the standardized within-module degree, z , are related to modularity, and species that are important for connecting the different modules of the network have high c , and species important for connecting species inside its own module have high z (Olesen et al. 2007). Finally, the *strength* of a pollinator species is the sum of the dependences every plant species has on this pollinator, in which the dependence of species i on j is defined as the proportion of interaction events of species i that were performed with species j (Bascompte et al. 2006).

Using general linear mixed models (GLMM) we tested if an increase in social behavior complexity was related to changes in all species level metrics. For each metric, there were four competing models with the following fixed effects: 1) no fixed effect (no effect of social behavior); 2) a categorical variable that separated pollinator species in two groups, solitary versus social species, in which communal, primitively social and eusocial species were lumped together; 3) pollinator species categorized in two groups, eusocial versus non-eusocial species, in which primitively social, communal and solitary species were lumped together; 4) and a categorical variable with the four levels of social behavior. In the four models, the identity of the network was specified as a random effect to control for network-specific effects on species-level metrics. We used the Akaike Information Criteria (AIC) to select which model best describes species metrics. For the two zero-inflated metrics, betweenness centrality (bc) and among-module connectivity (c), species were divided in two groups: species with bc or c values equal zero, and species with non-zero

bc or *c* values. For the GLMM, regarding *bc* and *c*, only species with non-zero metric values were used. We used chi-squared tests to investigate if species with social behavior had metrics *bc* and *c* different from zero more often than expected by chance.

Results

General characterization of the networks

The mean richness of pollinators on networks was 98.87 ± 138.99 species (mean \pm SD, min=12, max=679, median=62). Hymenopterans, which include all social insects in these networks, are a major component of these networks being on average one third of the floral visitors ($36.95 \pm 24.31\%$, mean \pm SD). Nevertheless, there is a wide variation in the relative contribution of hymenopterans to pollinator richness (from 5.56% to 100%). Considering only hymenopterans (ants excluded), most species were solitary ($78.65 \pm 22.67\%$, min=0%, max=96.77%), followed by primitively social ($11.52 \pm 21.77\%$, min=0%, max=100%), eusocial ($9.58 \pm 10.52\%$, min=0%, max=33.33%) and communal ($0.24 \pm 0.81\%$, min=0%, max=3.42%). Most networks (18 out of 23, 78.26%) had degrees of nestedness higher than expected by the null model (mean NODF= 30.99 ± 17.63 for empirical networks, mean NODF= 20.88 ± 13.14 for null networks, $P < 0.05$), while only two networks had significant closeness centralization (mean CC= 0.23 ± 0.08 for empirical networks, mean CC= 0.24 ± 0.08 for null networks, $P < 0.05$) and modularity (mean M= 0.43 ± 0.12 for empirical networks, mean M= 0.43 ± 0.1 for null networks, $P < 0.05$) values. Finally, only four networks had significant

betweenness centralization (mean BC=1154.94 \pm 3997.89 for empirical networks, mean BC=868.56 \pm 2962.26 for null networks, $P < 0.05$).

Proportion of social species and structure of the networks

We found no trend relating the proportion of social (I_1) or eusocial (I_2) pollinators to network-level structural patterns, as evidenced by model selection (Appendix B, Figure 2). For closeness centralization only the model assuming no relationship between network-level structure and the proportion of social or eusocial insects (null model) was selected (Appendix B). For betweenness centralization, besides the null model, the model assuming that I_2 affects network-level structure was also selected. For nestedness and modularity all three models, the null model and the models that assume I_1 and I_2 affect network-level structure, were selected. Collectively, these results suggest that there is weak evidence, if any, that the proportion of social or eusocial pollinators can impact the network-level organization of interacting assemblages.

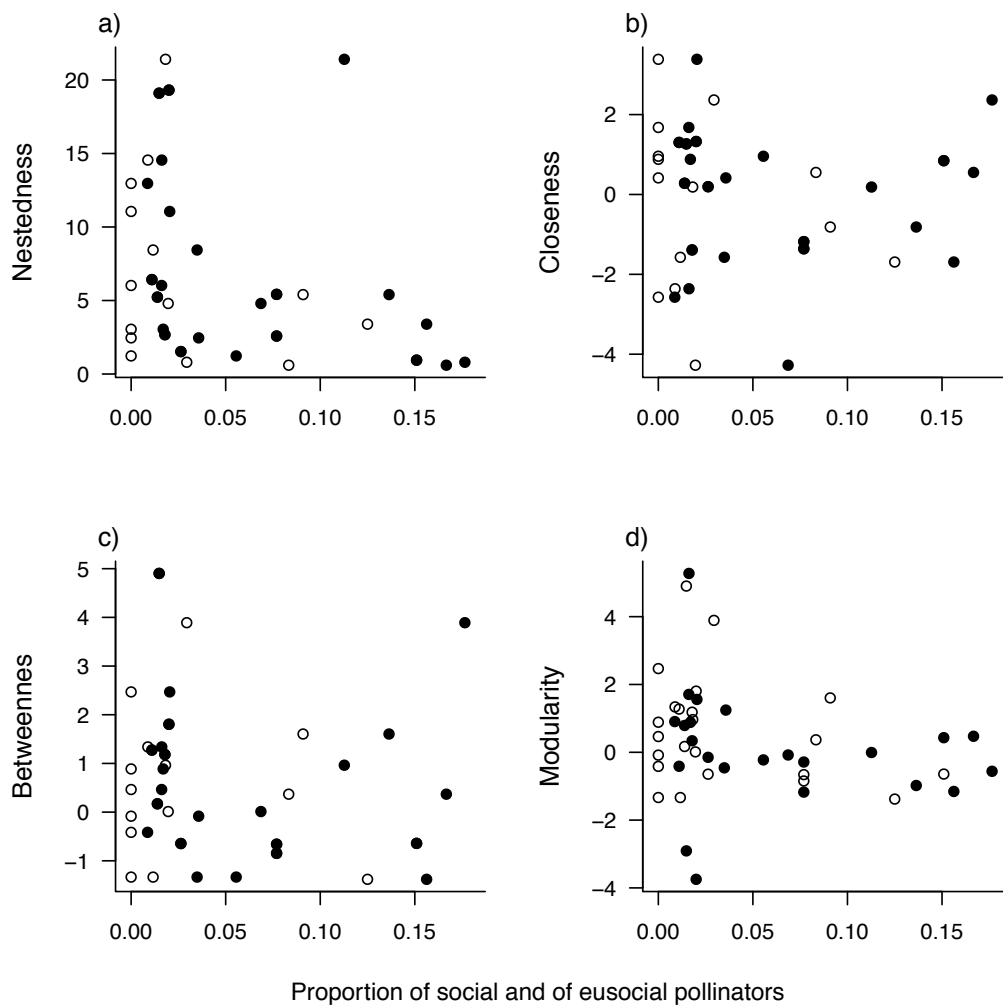


Figure 2: Relationship between the proportion of social pollinators (I_1 , closed circles) and proportion of eusocial pollinators (I_2 , open circles) and the z-scores of a) nestedness, b) closeness centralization, c) betweenness centralization and d) modularity.

Interaction patterns of social and solitary species

Species with any level of social behavior, on average, have higher values of species-level metrics than solitary species, despite the large variation in the interaction patterns of solitary species (Figure 3). In fact, species with social behavior often show a higher frequency of nonzero values for betweenness centrality and among-module connectivity than solitary

species (Table 2). The differences among different levels of sociality, however, are less clear, since an increase in the complexity of social behavior is not always related to an increase on the values of the metrics. As a consequence, social insects often contribute more to nestedness (cn), show higher closeness centrality (cc), and have higher among-module connectivity (c), but no differences among classes of social behavior were detected for these metrics (Appendix C, Figure 3). In contrast, for the number of interactions (k), betweenness centrality (bc) and within-module degree (z), the model selected assumes that all four categories of social behavior differ in their patterns of interaction (Appendix C, Figure 3). For *strength* both models were selected: the one that assumes social species have higher *strength* than solitary species, but species with all levels of social behavior have similar interaction patterns, and the one that assumes that all four categories of social behavior (including solitary) differ in their patterns of interaction (Appendix C, Figure 3).

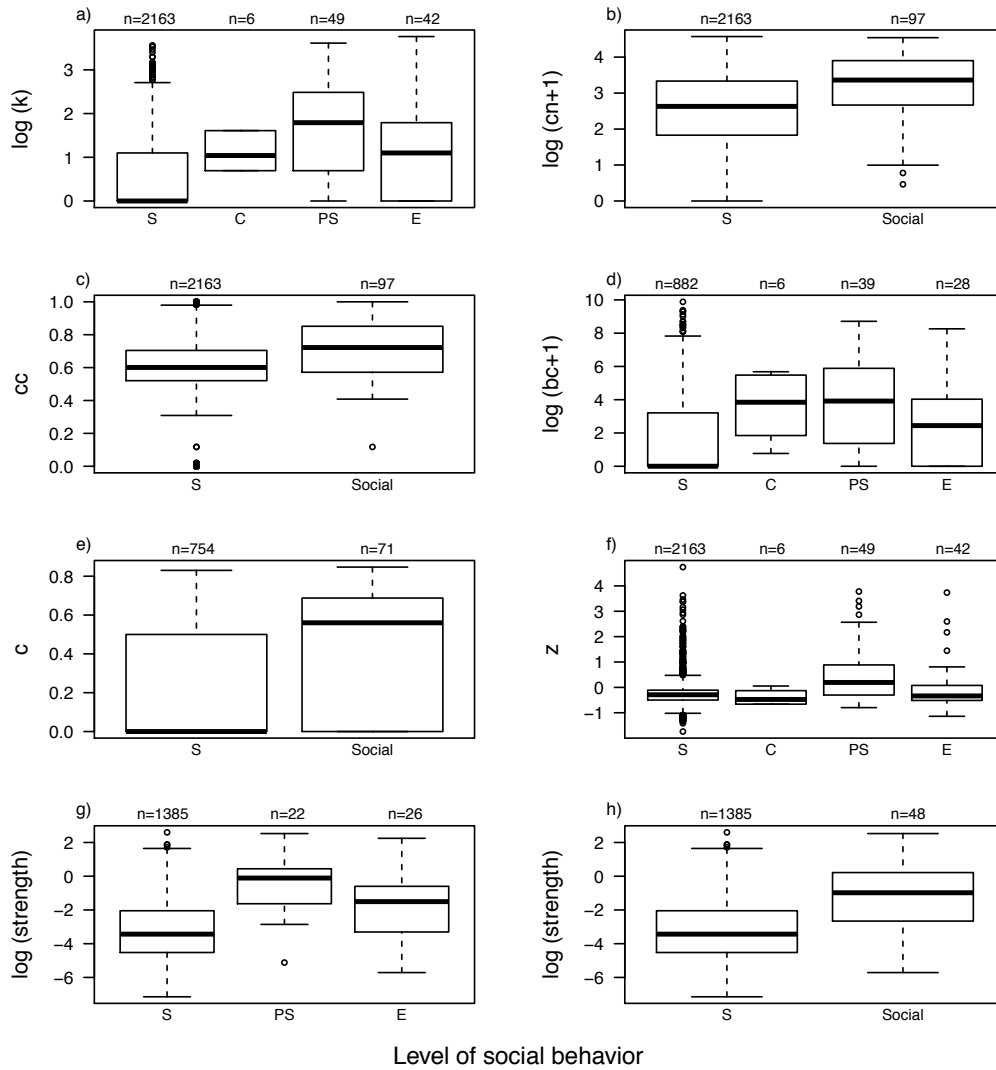


Figure 3: Boxplots of species level metrics per level of social behavior. Selected models are shown. Each plot represents the model that was selected for each metric: a) number of interactions or degree (k), b) contribution to nestedness (cn), c) closeness centrality (cc), d) betweenness centrality (bc), e) among-module connectivity (c), f) within-module degree (z), g) and h) *strength*. Coding for explanatory variables: solitary (S), communal (C), primitively social (PS), eusocial (E), Social (E+PS+C) species.

Table 2: Chi-squared tests comparing values of betweenness centrality (bc) and among-module connectivity (c) between solitary and social species. The chi-squared values presented are for the comparisons between solitary (S) versus social species (communal, primitively social and eusocial), $S \times (C+PS+E)$, eusocial versus primitively social, communal and solitary species, $E \times (PS+C+S)$, and between the four levels of social behavior, $S \times C \times PS \times E$. One asterisk (*) represents significant values, and two (**) represent significant levels beyond 0.001.

Metric	$S \times (C+PS+E)$	$E \times (PS+C+S)$	$S \times C \times PS \times E$
bc	43.83**	9.46*	48.39**
c	57.22**	13.05**	61.44**

Discussion

How traits shape the interaction patterns of individual species is a fundamental question for our understanding on how networks are organized and, consequently, on the ecological and evolutionary processes that depend on network organization. Social species were many times pointed out to be key components in pollination networks due to the prevalence of some social insects in several studied systems (Mello et al. 2011, Santos et al. 2010, 2012), and to the natural history aspects of sociality that could favor higher interaction rates (Thompson 1982). We found that the increasing proportion of social pollinator species in a network is not associated with patterns of nestedness, centralization, and modularity at network-level in multiple plant-pollinator assemblages. In contrast, at species-level, we found evidence that social species have, on average, a more preeminent role than solitary species in pollination networks.

We hypothesized that social species, by establishing multiple interactions, would lead to higher network nestedness and centralization patterns, whereas to lower network modularity, by interconnecting otherwise isolated modules of species. However, our analysis showed that models assuming no effect of the proportion of social insects on network metrics performed better (for closeness centralization) or as good (for nestedness, betweenness centralization and modularity) as models assuming that the proportion of social insects on network matters. In these sense, we concluded that the presence of social species does not change the overall network patterns studied. In the last decade, ecologists have put effort to find and understand the biological basis of the structural patterns that repeatedly appear in mutualistic networks (Rezende et al. 2007a; Guimarães Jr. et al. 2007b; Gómez et al. 2010; Donatti et al. 2011). The structural patterns found were invariant to different species composition, environment or interaction type (Bascompte et al. 2003; Jordano et al. 2003; Guimarães Jr et al. 2006, 2007a). The structure of ecological networks is also robust to the never-ending changes in species abundances across time (Olesen et al. 2008; Dupont et al. 2009; Rasmussen et al. 2013), to species loss and re-wiring of interactions (Memmott et al. 2004; Kaiser-Bunbury et al. 2010). The invariance in structure suggests that some aspects of network structure are shaped by general aspects of ecological systems, such as patterns of niche overlap among species (Pires et al. 2011) or species abundance distributions (Krishna et al. 2008), and not by other traits, such as sociality, that do not affect the organization of interacting species at network level.

At species level, solitary species present a wider variation in their interaction patterns when compared to social species. This variation is expected due to the enormous diversity of evolutionary lineages of solitary pollinators, which includes bees, flies, butterflies and birds. Consequently, there is also an enormous diversity of lifestyles among solitary pollinators, and some solitary pollinators are highly connected species. In contrast, social pollinators are a much more homogeneous group, formed essentially by species from three families of bees and one family of wasps. On average, we found evidence that social species have a more preminent role than solitary species in pollination networks. Social behavior was reported to be important in explaining the preminent role of some species within interacting assemblages in multiple types of ecological interactions. For instance, avian species that forage in groups were reported to be important in connecting modules in seed dispersal networks (Schleuning et al. 2014). Accordingly, social predators such as wolves, hyenas, hunting dogs, and lions are often among the highly connected species in predator-prey networks (Sinclair et al. 2003; Yeakel et al. 2012, 2013). Here, we suggest that for pollination networks sociality played a similar role, leading to the emergence of highly-connected species.

The relationship between levels of social behavior and species structural roles, however, is neither strong nor monotonic, suggesting there is no clear relationship between the complexity of social behavior and species' patterns of interaction. The selected models for species contribution to nestedness, closeness centrality and among-module connectivity indicate that

sociality *per se*, and not the different levels of complexity in social behavior, is relevant in making these species contribute more to these species-level metrics than solitary species. When differences between levels of sociality matter, as for degree, betweenness centrality and within-module degree, it is interesting to observe that in none of these three metrics eusocial species were the ones with the highest metric values. This indicates that having perennial colonies (the main trait that distinguishes primitively social from eusocial species) may be not as important as having colony organization and large number of individuals to make pollinator species central in networks.

One of the first steps in the evolution of social behavior is communal nesting, that may be present in some species even before the traits that define eusociality evolve (Wilson 2000). Therefore, an immediate consequence of the evolution of social organization is the numerical effect of having many individuals living together. Actually, large abundance is one of the reasons why social species are hypothesized to occupy central positions in pollination networks (Thompson 1982). We tested if abundance of pollinator species is important to explain species interaction patterns, using estimated colony size as a proxy for species abundance (Appendix D). For all but one species-level metrics (within-module degree), colony size was more important or as important as social behavior to explain species interaction patterns, indicating that abundance is important to explain the role social species play in pollination networks. Abundance was already demonstrated to be an important factor in organizing species interactions (Krishna et al. 2008; Vázquez et al. 2009; Suweis et al. 2013; Vizentin-Bugoni et al. 2014). We

hypothesize that sociality, by favoring large abundance of individuals, shapes the role of individual species in the network. In this case, abundance is a biological attribute of the studied species and not a matter of sampling or a factor to be controlled when investigating the biological correlates of network organization (Fontaine 2013).

Our study supports the notion that other traits, besides sociality, may influence patterns of interaction at network and species level in pollination systems. It also shows the potential and the limitations that behavioral traits have in organizing species interactions. Some social insect species occupy important roles in pollination networks, but the presence of social species does not change the network organization of the interacting assemblages. It is possible that the same is true for other traits in other types of ecological interactions, and future work should investigate which traits are driving the roles of species within ecological networks and which traits are shaping the general organization of ecological networks. The next step in the analysis of the role of social insects in pollination networks is to assess accurately their efficiency as pollinators. For instance, some abundant and highly connected flower visitor species, such as the invasive *A. mellifera*, are poor pollinators when compared with native pollinators (Aebi & Newmann 2011; Aebi et al. 2012; Ollerton et al. 2012). We suggest that future studies should investigate which are the ecological and evolutionary implications if species identified as the keystones in pollination networks are not efficient pollinators.

Conclusões

Mutualismos são interações importantes para a organização da biodiversidade (Bascompte & Jordano 2007). No entanto, durante a história da Ecologia, a relevância de mutualismos para a estruturação de comunidades ecológicas foi negligenciada, principalmente quando comparada a interações antagonistas como competição e predação (Bronstein 1994). Nas últimas duas décadas, ecólogos passaram a ressaltar a importância de mutualismos, o que pode ser exemplificado pelo grande foco dado ao estudo de redes mutualistas (Bascompte 2009). Particularmente, interações entre polinizadores e plantas têm ainda importância econômica, dada a necessidade dos serviços ecossistêmicos providos por polinizadores (Montoya et al. 2012). Esta dissertação contribui de duas formas principais para a compreensão de quais fatores são importantes para moldar as interações entre plantas e polinizadores.

Em primeiro lugar, nesse trabalho nós relacionamos a descrição do papel topológico das espécies de uma rede a um aspecto da história natural dessas espécies, o comportamento social. Redes de interação são representações matemáticas da complexidade encontrada na natureza, e essa ferramenta nos permite descrever, por exemplo, quem são as espécies importantes para a estrutura dessas comunidades. Para podermos inferir importância funcional com base em importância estrutural mais assertivamente, é necessário que essas redes incorporem cada vez mais informações relevantes sobre a biologia das espécies e das interações. Dessa forma, nesse trabalho nós incorporamos informações sobre um aspecto da

história natural das espécies envolvidas para compreender a estrutura, e inferir sobre funcionalidade. Um próximo passo é entender como, ao incorporar aspectos da história natural das espécies, processos dinâmicos nessas redes podem ser alterados.

Em segundo lugar nós investigamos a potencialidade de um comportamento em organizar as interações entre plantas e polinizadores. Diversos atributos das espécies já haviam sido estudados com o intuito de entender como se organizam redes de interação: filogenia, abundância, morfologia e mesmo comportamento (Stang et al. 2006; Rezende et al. 2007b; Vázquez et al. 2009). No entanto, o comportamento das espécies foi geralmente estudado como um fator limitante para a ocorrência de interações, os chamados “forbidden links” (Olesen et al. 2011; Vizentin-Bugoni et al. 2014). Esses estudos demonstraram que interações que não ocorrem devido aos períodos de atividade das espécies que não se sobrepõem, representam uma grande parcela das interações não observadas em redes de interação. Nesse trabalho nós encontramos que o comportamento social dos polinizadores pode ser o motivo pelo qual espécies sociais ocupam posições centrais em redes de polinização. Dessa forma, nós queremos motivar a importância que comportamentos das espécies podem ter em organizar interações, não apenas impedindo temporalmente sua ocorrência.

Essas duas contribuições, que resultaram da combinação de análises de dados empíricos, de métodos derivados da teoria de redes complexas e de informações sobre a história natural das espécies envolvidas, se inserem em um corpo teórico que visa compreender como podemos incorporar história

natural no estudo de redes ecológicas. Futuramente, mais informações biológicas sobre as espécies, assim como informações sobre a história natural das interações, poderão ser incorporadas em estudos de dinâmica de redes. É importante ressaltar que não só as espécies exibem aspectos da sua biologia que necessitam ser incorporados no estudo de redes ecológicas. A maioria dos estudos trata diversos tipos de interação diferentes de uma mesma forma, por exemplo, como se todas as interações entre visitantes florais e plantas fossem positivas (Genini et al. 2010). Já sabemos que o resultado das interações para os parceiros mutualistas pode variar, por exemplo, geograficamente ou com a presença de uma terceira espécie (Thompson 2005; Chamberlain et al. 2014). Dessa forma, investigar as consequências ecológicas e evolutivas de incorporar diferentes aspectos da história natural dos organismos e das interações permitiria uma maior compreensão sobre como as interações estão organizadas na natureza.

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Anexos

Appendix A) Empirical networks used in the study

Table S1: Dataset used in the paper (source: Interaction Web Database), including the locality, habitat type and number of plants and pollinators.

Reference	Locality	Habitat type	Plants	Pollinators
Arroyo et. al 1982 - 1	Chile	Andean scrub	87	98
Arroyo et. al 1982 - 2	Chile	Andean scrub	43	62
Arroyo et. al 1982 - 3	Chile	Andean scrub	41	28
Barrett & Helenurm 1987	Canada	Boreal forest	12	102
Bezerra et al. 2009	Brazil	Caatinga	13	13
Clements & Long 1923	USA	Montane forest and grassland	96	275
Dupont et al. 2003	Tenerife, Canary Islands	High altitude desert	11	38
Elberling & Olesen 1999	Sweden	Alpine subarctic community	23	118
Hocking 1968	Canada	Arctic community	29	86
Kaiser-Bunbury et al. 2009 - 1	Mauritius	Heathland heavily invaded by introduced plants	73	135
Kaiser-Bunbury et al. 2009 - 2	Mauritius	Heathland from which introduced plants were removed	58	100
Kato et al. 1990	Japan	Beech forest	91	679
Kevan 1970	Canada	High arctic community	32	115

Inouye & Pyke 1988	Australia	Montane forest	42	91
Medan et al. 2002	Argentina	Woody riverine vegetation and xeric scrub	23	72
Mosquin & Martin 1967	Canada	Arctic community	11	18
Motten 1982	USA	Deciduous forest	13	44
Olesen et al. 2002 - 1	Mauritius Islands	Coastal forest	14	13
Olesen et al. 2002 - 2	Azores Islands	Rocky cliff and open herb community	10	12
Ollerton et al. 2003	South Africa	Upland grassland	9	56
Ramirez & Brito 1992	Venezuela	Palm swamp community	28	53
Schemske et al. 1978	USA	Maple -oak woodland	7	32
Small 1976	Canada	Peat bog	13	34

Appendix B) Model selection to investigate the effect of the proportion of social species on network structure

The proportion of social (I_1) and eusocial (I_2) pollinators were compared in order to clarify if the putative effect of social behavior on network structure was due to the presence of pollinators with every level of social behavior, in this case the model I_1 would be selected, or only due to the presence of eusocial pollinators, and in this case the model I_2 would be selected. Ants were excluded in both indexes of sociality. The AIC tables are presented below.

Table S2: Model selection results for network nestedness (NODF). The competing models were GLM with Gaussian errors, z-scores of NODF as response variable, and proportion of social (I_1) and proportion of eusocial (I_2) pollinators as predictor variables. Ants were excluded in this analysis. The selected models ($\Delta AIC < 2$) are shaded. AIC = Akaike's Information Criterion and $\Delta AIC = AIC$ of each model - AIC best model.

Models	Explanatory variables	AIC	ΔAIC
Null	_____	154.2	0.4
I_1	Proportion of social pollinators	153.9	0.1
I_2	Proportion of eusocial pollinators	153.8	0.0

Table S3: Model selection results for network closeness centralization (CC). The competing models were GLM with Gaussian errors, z-scores of CC as response variable, and proportion of social (I_1) and proportion of eusocial (I_2) pollinators as predictor variables. Ants were excluded in this analysis. The selected model ($\Delta AIC < 2$) is shaded. AIC = Akaike's Information Criterion and $\Delta AIC = AIC$ of each model - AIC best model.

Models	Explanatory variables	AIC	ΔAIC
Null	_____	95.3	0.0
I_1	Proportion of social pollinators	98.0	2.7
I_2	Proportion of eusocial pollinators	97.4	2.1

Table S4: Model selection results for network betweenness centralization (BC). The competing models were GLM with Gaussian errors, z-scores of BC as response variable, and proportion of social (I_1) and proportion of eusocial (I_2) pollinators as predictor variables. Ants were excluded in this analysis. The selected models ($\Delta AIC < 2$) are shaded. AIC = Akaike's Information Criterion and $\Delta AIC = AIC$ of each model - AIC best model.

Models	Explanatory variables	AIC	ΔAIC
Null	_____	90.8	0.0
I_1	Proportion of social pollinators	93.4	2.6
I_2	Proportion of eusocial pollinators	91.6	0.8

Table S5: Model selection results for network modularity (M). The competing models were GLM with Gaussian errors, z-scores of M as response variable, and proportion of social (I_1) and proportion of eusocial (I_2) pollinators as predictor variables. Ants were excluded in this analysis. The selected models ($\Delta AIC < 2$) are shaded. AIC = Akaike's Information Criterion and $\Delta AIC = AIC$ of each model - AIC best model.

Models	Explanatory variables	AIC	ΔAIC
Null	_____	93.6	0.0
I_1	Proportion of social pollinators	95.4	1.9
I_2	Proportion of eusocial pollinators	95.0	1.4

To investigate how robust were our results facing other measures of the frequency of species with social behavior in the network, we defined I_3 as the proportion of social hymenopterans, $(E+PS+C)/H$, and I_4 as the proportion of eusocial hymenopterans, E/H , where E is number of eusocial species, PS is number of primitively social species, C is number of communal species and H is total number of hymenopteran species. We excluded ants of these analyses. The AIC tables are presented below.

Table S6: Model selection results for network nestedness (NODF). The competing models were GLM with Gaussian errors, z-scores of NODF as response variable, and proportion of social pollinators (I_1), proportion of eusocial pollinators (I_2), proportion of social hymenopterans (I_3) and proportion of eusocial hymenopterans (I_4) as predictor variables. Ants were excluded in this analysis. The selected models ($\Delta AIC < 2$) are shaded. AIC = Akaike's Information Criterion and $\Delta AIC = AIC$ of each model - AIC best model.

Models	Explanatory variables	AIC	ΔAIC
Null	_____	154.2	0.4
I_1	Proportion of social pollinators	153.9	0.1
I_2	Proportion of eusocial pollinators	153.8	0.0
I_3	Proportion of social hymenopterans	154.4	0.7
I_4	Proportion of eusocial hymenopterans	156.2	2.5

Table S7: Model selection results for network closeness centralization (CC). The competing models were GLM with Gaussian errors, z-scores of CC as response variable, and proportion of social pollinators (I_1), proportion of eusocial pollinators (I_2), proportion of social hymenopterans (I_3) and proportion of eusocial hymenopterans (I_4) as predictor variables. Ants were excluded in this analysis. The selected model ($\Delta AIC < 2$) is shaded. AIC = Akaike's Information Criterion and $\Delta AIC = AIC$ of each model - AIC best model.

Models	Explanatory variables	AIC	ΔAIC
Null	_____	95.3	0.0
I_1	Proportion of social pollinators	98.0	2.7
I_2	Proportion of eusocial pollinators	97.4	2.1
I_3	Proportion of social hymenopterans	97.7	2.4
I_4	Proportion of eusocial hymenopterans	97.7	2.4

Table S8: Model selection results for network betweenness centralization (BC). The competing models were GLM with Gaussian errors, z-scores of BC as response variable, and proportion of social pollinators (I_1), proportion of eusocial pollinators (I_2), proportion of social hymenopterans (I_3) and proportion of eusocial hymenopterans (I_4) as predictor variables. Ants were excluded in this analysis. The selected models ($\Delta AIC < 2$) are shaded. AIC = Akaike's Information Criterion and $\Delta AIC = AIC$ of each model - AIC best model.

Models	Explanatory variables	AIC	ΔAIC
Null	_____	90.8	0.0
I_1	Proportion of social pollinators	93.4	2.6
I_2	Proportion of eusocial pollinators	91.6	0.8
I_3	Proportion of social hymenopterans	92.2	1.4
I_4	Proportion of eusocial hymenopterans	93.2	2.4

Table S9: Model selection results for network modularity (M). The competing models were GLM with Gaussian errors, z-scores of M as response variable, and proportion of social pollinators (I_1), proportion of eusocial pollinators (I_2), proportion of social hymenopterans (I_3) and proportion of eusocial hymenopterans (I_4) as predictor variables. Ants were excluded in this analysis. The selected models ($\Delta AIC < 2$) are shaded. AIC = Akaike's Information Criterion and $\Delta AIC = AIC$ of each model - AIC best model.

Models	Explanatory variables	AIC	ΔAIC
Null	_____	93.6	0.7
I_1	Proportion of social pollinators	95.4	2.6
I_2	Proportion of eusocial pollinators	95.0	2.1
I_3	Proportion of social hymenopterans	95.6	2.7
I_4	Proportion of eusocial hymenopterans	92.8	0.0

Appendix C) Model selection to investigate the difference between the interaction patterns of social and solitary species

Here we show the AIC tables regarding the model selection for species-level metrics. The specified fixed effects were chosen in order to investigate in which level of social behavior - if any - different interaction patterns appear: if sociality has no effect on species interaction patterns, the null model would be selected; if social species, regardless of the level of complexity in social behavior (eusocial, primitively social or communal), have similar interaction patterns among them, but different interaction patterns compared to solitary species, model 1 would be selected; if different interaction patterns only appear on eusocial species, model 2 would be selected; and if every level of complexity in social behavior present different interaction patterns, than model 3 would be selected. The AIC tables are presented below.

Table S10: Model selection results for species degree (k). The competing models were GLMM with Gaussian errors, the log transformation of k as response variable, (E+PS+C) versus S (model 1), E versus (PS+C+S) (model 2), and S versus C versus PS versus E (model 3) as fixed effects, and the identity of the network as random effect. Ants were excluded in this analysis. The selected model ($\Delta AIC < 2$) is shaded. AIC = Akaike's Information Criterion and $\Delta AIC = AIC$ of each model - AIC best model. Coding for explanatory variables: solitary (S), communal (C), primitively social (PS), eusocial (E).

Models	Fixed effects	AIC	ΔAIC
Null	_____	5147.6	122.2
Model 1	S x (C+PS+E)	5031.8	6.4
Model 2	E x (PS+C+S)	5128.4	103.0
Model 3	S x C x PS x E	5025.3	0.0

Table S11: Model selection results for species contribution to nestedness (*cn*). The competing models were GLMM with Gaussian errors, the log transformation of *cn*+1 as response variable, (E+PS+C) versus S (model 1), E versus (PS+C+S) (model 2), and S versus C versus PS versus E (model 3) as fixed effects, and the identity of the network as random effect. Ants were excluded in this analysis. The selected model ($\Delta\text{AIC} < 2$) is shaded. AIC = Akaike's Information Criterion and $\Delta\text{AIC} = \text{AIC of each model} - \text{AIC best model}$. Coding for explanatory variables: solitary (S), communal (C), primitively social (PS), eusocial (E).

Models	Fixed effects	AIC	ΔAIC
Null	_____	5364.2	21.9
Model 1	S x (C+PS+E)	5342.3	0.0
Model 2	E x (PS+C+S)	5363.7	21.4
Model 3	S x C x PS x E	5345.4	3.1

Table S12: Model selection results for species closeness centrality (*cc*). The competing models were GLMM with Gaussian errors, *cc* as response variable, (E+PS+C) versus S (model 1), E versus (PS+C+S) (model 2), and S versus C versus PS versus E (model 3) as fixed effects, and the identity of the network as random effect. Ants were excluded in this analysis. The selected model ($\Delta\text{AIC} < 2$) is shaded. AIC = Akaike's Information Criterion and $\Delta\text{AIC} = \text{AIC of each model} - \text{AIC best model}$. Coding for explanatory variables: solitary (S), communal (C), primitively social (PS), eusocial (E).

Models	Fixed effects	AIC	ΔAIC
Null	_____	-3138.1	26.9
Model 1	S x (C+PS+E)	-3164.9	0.0
Model 2	E x (PS+C+S)	-3137.9	27.0
Model 3	S x C x PS x E	-3153.6	11.3

Table S13: Model selection results for species betweenness centrality (*bc*). The competing models were GLMM with Gaussian errors, the log transformed non-zero values of *bc*+1 as response variable, (E+PS+C) versus S (model 1), E versus (PS+C+S) (model 2), and S versus C versus PS versus E (model 3) as fixed effects, and the identity of the network as random effect. Ants were excluded in this analysis. The selected model ($\Delta\text{AIC} < 2$) is shaded. AIC = Akaike's Information Criterion and $\Delta\text{AIC} = \text{AIC of each model} - \text{AIC best model}$. Coding for explanatory variables: solitary (S), communal (C), primitively social (PS), eusocial (E).

Models	Fixed effects	AIC	ΔAIC
Null	_____	3391.2	18.6
Model 1	S x (C+PS+E)	3377.9	5.3
Model 2	E x (PS+C+S)	3391.8	19.2
Model 3	S x C x PS x E	3372.6	0.0

Table S14: Model selection results for species among-module connectivity (*c*). The competing models were GLMM with Gaussian errors, the non-zero values of *c* as response variable, (E+PS+C) versus S (model 1), E versus (PS+C+S) (model 2), and S versus C versus PS versus E (model 3) as fixed effects, and the identity of the network as random effect. Ants were excluded in this analysis. The selected model ($\Delta\text{AIC} < 2$) is shaded. AIC = Akaike's Information Criterion and $\Delta\text{AIC} = \text{AIC of each model} - \text{AIC best model}$. Coding for explanatory variables: solitary (S), communal (C), primitively social (PS), eusocial (E).

Models	Fixed effects	AIC	ΔAIC
Null	_____	-1148.5	9.0
Model 1	S x (C+PS+E)	-1157.5	0.0
Model 2	E x (PS+C+S)	-1143.9	13.6
Model 3	S x C x PS x E	-1146.6	10.9

Table S15: Model selection results for species standardized within-module degree (z). The competing models were GLMM with Gaussian errors, z as response variable, (E+PS+C) versus S (model 1), E versus (PS+C+S) (model 2), and S versus C versus PS versus E (model 3) as fixed effects, and the identity of the network as random effect. Ants were excluded in this analysis. The selected model ($\Delta\text{AIC} < 2$) is shaded. AIC = Akaike's Information Criterion and $\Delta\text{AIC} = \text{AIC of each model} - \text{AIC best model}$. Coding for explanatory variables: solitary (S), communal (C), primitively social (PS), eusocial (E).

Models	Fixed effects	AIC	ΔAIC
Null	_____	3696.7	107.5
Model 1	S x (C+PS+E)	3613.9	24.7
Model 2	E x (PS+C+S)	3692.1	102.9
Model 3	S x C x PS x E	3589.2	0.0

Table S16: Model selection results for species *strength*. The competing models were GLMM with Gaussian errors, the log transformation of *strength* as response variable, (E+PS) versus S (model 1), E versus (PS+ S) (model 2), and S versus PS versus E (model 3) as fixed effects, and the identity of the network as random effect. Ants were excluded in this analysis. The selected models ($\Delta\text{AIC} < 2$) are shaded. AIC = Akaike's Information Criterion and $\Delta\text{AIC} = \text{AIC of each model} - \text{AIC best model}$. Coding for explanatory variables: solitary (S), primitively social (PS), eusocial (E).

Models	Fixed effects	AIC	ΔAIC
Null	_____	5651.6	49.7
Model 1	S x (PS+E)	5603.5	1.6
Model 2	E x (PS+S)	5638.2	36.3
Model 3	S x PS x E	5601.9	0.0

Appendix D) Model selection to investigate the difference between the interaction patterns of social and solitary species – what about colony size?

We also investigated if colony size, as a proxy of the effect of sociality on species abundance, is a better predictor of species interaction patterns than sociality. We estimated every pollinator species colony size based on the literature and empirical knowledge on species' natural history. We allocated each species in one of the following colony size ranges: between 1 and 10, between 11 and 100, between 101 and 1000, between 1001 and 10000 and between 10001 and 100000 individuals. In these sense, solitary species were included in the range of until 10 individuals. We log transformed the colony size ranges, and used it as a fixed effect in a new model that competed with the other models that describe species level-metrics. The AIC tables are presented below.

Table S17: Model selection results for species degree (k). The competing models were GLMM with Gaussian errors, the log transformation of k as response variable, (E+PS+C) versus S (model 1), E versus (PS+C+S) (model 2), S versus C versus PS versus E (model 3) and the log transformed ranges of colony size (model 4) as fixed effects, and the identity of the network as random effect. Ants were excluded in this analysis. The selected model ($\Delta AIC < 2$) is shaded. AIC = Akaike's Information Criterion and $\Delta AIC = AIC$ of each model - AIC best model. Coding for explanatory variables: solitary (S), communal (C), primitively social (PS), eusocial (E).

Models	Fixed effects	AIC	ΔAIC
Null		5147.6	130.5
Model 1	S x (C+PS+E)	5031.8	14.7
Model 2	E x (PS+C+S)	5128.4	111.3
Model 3	S x C x PS x E	5025.3	8.3
Model 4	Colony size	5017.1	0.0

Table S18: Model selection results for species contribution to nestedness (*cn*). The competing models were GLMM with Gaussian errors, the log transformation of *cn*+1 as response variable, (E+PS+C) versus S (model 1), E versus (PS+C+S) (model 2), S versus C versus PS versus E (model 3) and the log transformed ranges of colony size (model 4) as fixed effects, and the identity of the network as random effect. Ants were excluded in this analysis. The selected models ($\Delta AIC < 2$) are shaded. AIC = Akaike's Information Criterion and $\Delta AIC = AIC$ of each model - AIC best model. Coding for explanatory variables: solitary (S), communal (C), primitively social (PS), eusocial (E).

Models	Fixed effects	AIC	ΔAIC
Null	_____	5364.2	21.9
Model 1	S x (C+PS+E)	5342.3	0.0
Model 2	E x (PS+C+S)	5363.7	21.4
Model 3	S x C x PS x E	5345.4	3.1
Model 4	Colony size	5343.8	1.4

Table S19: Model selection results for species closeness centrality (*cc*). The competing models were GLMM with Gaussian errors, *cc* as response variable, (E+PS+C) versus S (model 1), E versus (PS+C+S) (model 2), S versus C versus PS versus E (model 3) and the log transformed ranges of colony size (model 4) as fixed effects, and the identity of the network as random effect. Ants were excluded in this analysis. The selected models ($\Delta AIC < 2$) are shaded. AIC = Akaike's Information Criterion and $\Delta AIC = AIC$ of each model - AIC best model. Coding for explanatory variables: solitary (S), communal (C), primitively social (PS), eusocial (E).

Models	Fixed effects	AIC	ΔAIC
Null	_____	-3138.1	27.3
Model 1	S x (C+PS+E)	-3164.9	0.4
Model 2	E x (PS+C+S)	-3137.9	27.5
Model 3	S x C x PS x E	-3153.6	11.7
Model 4	Colony size	-3165.4	0.0

Table S20: Model selection results for species betweenness centrality (*bc*). The competing models were GLMM with Gaussian errors, the log transformed non-zero values of *bc*+1 as response variable, (E+PS+C) versus S (model 1), E versus (PS+C+S) (model 2), S versus C versus PS versus E (model 3) and the log transformed ranges of colony size (model 4) as fixed effects, and the identity of the network as random effect. Ants were excluded in this analysis. The selected models ($\Delta\text{AIC} < 2$) are shaded. AIC = Akaike's Information Criterion and $\Delta\text{AIC} = \text{AIC of each model} - \text{AIC best model}$. Coding for explanatory variables: solitary (S), communal (C), primitively social (PS), eusocial (E).

Models	Fixed effects	AIC	ΔAIC
Null	_____	3391.2	19.5
Model 1	S x (C+PS+E)	3377.9	6.2
Model 2	E x (PS+C+S)	3391.8	20.1
Model 3	S x C x PS x E	3372.6	0.9
Model 4	Colony size	3371.7	0.0

Table S21: Model selection results for species among-module connectivity (*c*). The competing models were GLMM with Gaussian errors, the non-zero values of *c* as response variable, (E+PS+C) versus S (model 1), E versus (PS+C+S) (model 2), S versus C versus PS versus E (model 3) and the log transformed ranges of colony size (model 4) as fixed effects, and the identity of the network as random effect. Ants were excluded in this analysis. The selected models ($\Delta\text{AIC} < 2$) are shaded. AIC = Akaike's Information Criterion and $\Delta\text{AIC} = \text{AIC of each model} - \text{AIC best model}$. Coding for explanatory variables: solitary (S), communal (C), primitively social (PS), eusocial (E).

Models	Fixed effects	AIC	ΔAIC
Null	_____	-1148.5	9.0
Model 1	S x (C+PS+E)	-1157.5	0.0
Model 2	E x (PS+C+S)	-1143.9	13.6
Model 3	S x C x PS x E	-1146.6	10.9
Model 4	Colony size	-1156.4	1.1

Table S22: Model selection results for species standardized within-module degree (z). The competing models were GLMM with Gaussian errors, z as response variable, (E+PS+C) versus S (model 1), E versus (PS+C+S) (model 2), S versus C versus PS versus E (model 3) and the log transformed ranges of colony size (model 4) as fixed effects, and the identity of the network as random effect. Ants were excluded in this analysis. The selected model ($\Delta\text{AIC} < 2$) is shaded. AIC = Akaike's Information Criterion and ΔAIC = AIC of each model - AIC best model. Coding for explanatory variables: solitary (S), communal (C), primitively social (PS), eusocial (E).

Models	Fixed effects	AIC	ΔAIC
Null	_____	3696.7	107.5
Model 1	S x (C+PS+E)	3613.9	24.7
Model 2	E x (PS+C+S)	3692.1	102.9
Model 3	S x C x PS x E	3589.2	0.0
Model 4	Colony size	3594.2	5.0

Table S23: Model selection results for species *strength*. The competing models were GLMM with Gaussian errors, the log transformation of *strength* as response variable, (E+PS) versus S (model 1), E versus (PS+ S) (model 2), S versus PS versus E (model 3) and the log transformed ranges of colony size (model 4) as fixed effects, and the identity of the network as random effect. Ants were excluded in this analysis. The selected model ($\Delta\text{AIC} < 2$) is shaded. AIC = Akaike's Information Criterion and ΔAIC = AIC of each model - AIC best model. Coding for explanatory variables: solitary (S), primitively social (PS), eusocial (E).

Models	Fixed effects	AIC	ΔAIC
Null	_____	5651.6	56.6
Model 1	S x (PS+E)	5603.5	8.5
Model 2	E x (PS+S)	5638.2	43.2
Model 3	S x PS x E	5601.9	6.9
Model 4	Colony size	5595.0	0.0

Appendix E) Sensitivity analysis – accounting ants as pollinators

The results presented in this appendix are equivalent to the results presented on appendices B, C and D, however in this section ant species are also accounted as pollinator species having eusocial behavior. Ant species were only present in four of the networks: Kaiser-Bunbury et al. 2009 - 1 and 2 that had 3 ant species each, Kato et al. 1990 that had 7 ant species and Olesen et al. 2002 - 2 that had one ant species. The results in the subsection *“Proportion of social species and network structure”* are qualitatively similar to the ones presented in appendix B, since only the proportion of social species in four networks changed by the presence of ant species. The results in this section reinforce the absence of effect proportion of social species has on network structure. The results in the subsection *“Interaction patterns of social and solitary species”* are qualitatively similar to the ones presented in appendix C since we added just a few ant species to a much larger species pool that includes all 2260 pollinator species in the 23 networks. However, in subsection *“Interaction patterns and colony size”* the results of four metrics (closeness centrality, betweenness centrality, among-module connectivity and within-module degree) are qualitatively different from the ones from appendix D. For closeness centrality, betweenness centrality and within-module degree, the only model selected after the inclusion of ant species is the model that has colony size as fixed effect. This is probably due to the presence of two ant species that had estimated colony sizes bigger than the biggest colony size every other pollinator had, creating a new range of colony size. Therefore, these two species might have a large effect in the model.

Proportion of social species and network structure

Table S24: Model selection results for network nestedness (NODF). The competing models were GLM with Gaussian errors, z-scores of NODF as response variable, and proportion of social (I₁) and proportion of eusocial (I₂) pollinators as predictor variables. Ants were included as species with eusocial behavior in this analysis. The selected models ($\Delta\text{AIC} < 2$) are shaded. AIC = Akaike's Information Criterion and $\Delta\text{AIC} = \text{AIC of each model} - \text{AIC best model}$.

Models	Explanatory variables	AIC	ΔAIC
Null	_____	154.2	0.0
I ₁	Proportion of social pollinators	154.8	0.7
I ₂	Proportion of eusocial pollinators	154.9	0.8

Table S25: Model selection results for network closeness centralization (CC). The competing models were GLM with Gaussian errors, z-scores of CC as response variable, and proportion of social (I₁) and proportion of eusocial (I₂) pollinators as predictor variables. Ants were included as species with eusocial behavior in this analysis. The selected model ($\Delta\text{AIC} < 2$) is shaded. AIC = Akaike's Information Criterion and $\Delta\text{AIC} = \text{AIC of each model} - \text{AIC best model}$.

Models	Explanatory variables	AIC	ΔAIC
Null	_____	95.3	0.0
I ₁	Proportion of social pollinators	97.9	2.6
I ₂	Proportion of eusocial pollinators	97.8	2.5

Table S26: Model selection results for network betweenness centralization (BC). The competing models were GLM with Gaussian errors, z-scores of BC as response variable, and proportion of social (I₁) and proportion of eusocial (I₂) pollinators as predictor variables. Ants were included as species with eusocial behavior in this analysis. The selected models ($\Delta\text{AIC} < 2$) are shaded. AIC = Akaike's Information Criterion and $\Delta\text{AIC} = \text{AIC of each model} - \text{AIC best model}$.

Models	Explanatory variables	AIC	ΔAIC
Null	_____	90.8	0.0
I ₁	Proportion of social pollinators	93.5	2.7
I ₂	Proportion of eusocial pollinators	92.7	1.9

Table S27: Model selection results for network modularity (M). The competing models were GLM with Gaussian errors, z-scores of M as response variable, and proportion of social (I₁) and proportion of eusocial (I₂) pollinators as predictor variables. Ants were included as species with eusocial behavior in this analysis. The selected models ($\Delta\text{AIC} < 2$) are shaded. AIC = Akaike's Information Criterion and $\Delta\text{AIC} = \text{AIC of each model} - \text{AIC best model}$.

Models	Explanatory variables	AIC	ΔAIC
Null	_____	93.6	0.0
I ₁	Proportion of social pollinators	95.3	1.7
I ₂	Proportion of eusocial pollinators	94.7	1.2

Table S28: Model selection results for network nestedness (NODF). The competing models were GLM with Gaussian errors, z-scores of NODF as response variable, and proportion of social pollinators (I₁), proportion of eusocial pollinators (I₂), proportion of social hymenopterans (I₃) and proportion of eusocial hymenopterans (I₄) as predictor variables. Ants were included as species with eusocial behavior in this analysis. The selected models ($\Delta\text{AIC} < 2$) are shaded. AIC = Akaike's Information Criterion and $\Delta\text{AIC} = \text{AIC of each model} - \text{AIC best model}$.

Models	Explanatory variables	AIC	ΔAIC
Null	_____	154.2	0.0
I ₁	Proportion of social pollinators	154.8	0.7
I ₂	Proportion of eusocial pollinators	154.9	0.8
I ₃	Proportion of social hymenopterans	156.3	2.1
I ₄	Proportion of eusocial hymenopterans	156.5	2.4

Table S29: Model selection results for network closeness centralization (CC). The competing models were GLM with Gaussian errors, z-scores of CC as response variable, and proportion of social pollinators (I₁), proportion of eusocial pollinators (I₂), proportion of social hymenopterans (I₃) and proportion of eusocial hymenopterans (I₄) as predictor variables. Ants were included as species with eusocial behavior in this analysis. The selected models ($\Delta\text{AIC} < 2$) are shaded. AIC = Akaike's Information Criterion and $\Delta\text{AIC} = \text{AIC of each model} - \text{AIC best model}$.

Models	Explanatory variables	AIC	ΔAIC
Null	_____	95.3	0.0
I ₁	Proportion of social pollinators	97.9	2.6
I ₂	Proportion of eusocial pollinators	97.8	2.5
I ₃	Proportion of social hymenopterans	97.3	2.0
I ₄	Proportion of eusocial hymenopterans	97.9	2.6

Table S30: Model selection results for network betweenness centralization (BC). The competing models were GLM with Gaussian errors, z-scores of BC as response variable, and proportion of social pollinators (I_1), proportion of eusocial pollinators (I_2), proportion of social hymenopterans (I_3) and proportion of eusocial hymenopterans (I_4) as predictor variables. Ants were included as species with eusocial behavior in this analysis. The selected models ($\Delta AIC < 2$) are shaded. AIC = Akaike's Information Criterion and $\Delta AIC = AIC$ of each model - AIC best model.

Models	Explanatory variables	AIC	ΔAIC
Null	_____	90.8	0.0
I_1	Proportion of social pollinators	93.5	2.7
I_2	Proportion of eusocial pollinators	92.7	1.9
I_3	Proportion of social hymenopterans	93.3	2.6
I_4	Proportion of eusocial hymenopterans	92.9	2.1

Table S31: Model selection results for network modularity (M). The competing models were GLM with Gaussian errors, z-scores of M as response variable, and proportion of social pollinators (I_1), proportion of eusocial pollinators (I_2), proportion of social hymenopterans (I_3) and proportion of eusocial hymenopterans (I_4) as predictor variables. Ants were included as species with eusocial behavior in this analysis. The selected model ($\Delta AIC < 2$) is shaded. AIC = Akaike's Information Criterion and $\Delta AIC = AIC$ of each model - AIC best model.

Models	Explanatory variables	AIC	ΔAIC
Null	_____	93.6	3.0
I_1	Proportion of social pollinators	95.3	4.7
I_2	Proportion of eusocial pollinators	94.7	4.2
I_3	Proportion of social hymenopterans	94.1	3.6
I_4	Proportion of eusocial hymenopterans	90.6	0.0

Interaction patterns of social and solitary species

Table S32: Model selection results for species degree (k). The competing models were GLMM with Gaussian errors, the log transformation of k as response variable, (E+PS+C) versus S (model 1), E versus (PS+C+S) (model 2), and S versus C versus PS versus E (model 3) as fixed effects, and the identity of the network as random effect. Ants were included as species with eusocial behavior in this analysis. The selected model ($\Delta\text{AIC} < 2$) is shaded. AIC = Akaike's Information Criterion and $\Delta\text{AIC} = \text{AIC of each model} - \text{AIC best model}$. Coding for explanatory variables: solitary (S), communal (C), primitively social (PS), eusocial (E).

Models	Fixed effects	AIC	ΔAIC
Null	_____	5210.9	130.3
Model 1	S x (C+PS+E)	5087.9	7.3
Model 2	E x (PS+C+S)	5182.9	102.3
Model 3	S x C x PS x E	5080.6	0.0

Table S33: Model selection results for species contribution to nestedness (cn). The competing models were GLMM with Gaussian errors, the log transformation of $cn+1$ as response variable, (E+PS+C) versus S (model 1), E versus (PS+C+S) (model 2), and S versus C versus PS versus E (model 3) as fixed effects, and the identity of the network as random effect. Ants were included as species with eusocial behavior in this analysis. The selected model ($\Delta\text{AIC} < 2$) is shaded. AIC = Akaike's Information Criterion and $\Delta\text{AIC} = \text{AIC of each model} - \text{AIC best model}$. Coding for explanatory variables: solitary (S), communal (C), primitively social (PS), eusocial (E).

Models	Fixed effects	AIC	ΔAIC
Null	_____	5405.7	25.8
Model 1	S x (C+PS+E)	5379.9	0.0
Model 2	E x (PS+C+S)	5401.8	21.9
Model 3	S x C x PS x E	5383.6	3.7

Table S34: Model selection results for species closeness centrality (*cc*). The competing models were GLMM with Gaussian errors, *cc* as response variable, (E+PS+C) versus S (model 1), E versus (PS+C+S) (model 2), and S versus C versus PS versus E (model 3) as fixed effects, and the identity of the network as random effect. Ants were included as species with eusocial behavior in this analysis. The selected model ($\Delta\text{AIC} < 2$) is shaded. AIC = Akaike's Information Criterion and $\Delta\text{AIC} = \text{AIC of each model} - \text{AIC best model}$. Coding for explanatory variables: solitary (S), communal (C), primitively social (PS), eusocial (E).

Models	Fixed effects	AIC	ΔAIC
Null	_____	-3152.2	30.3
Model 1	S x (C+PS+E)	-3182.5	0.0
Model 2	E x (PS+C+S)	-3155.4	27.1
Model 3	S x C x PS x E	-3171.2	11.4

Table S35: Model selection results for species betweenness centrality (*bc*). The competing models were GLMM with Gaussian errors, the log transformed non-zero values of *bc*+1 as response variable, (E+PS+C) versus S (model 1), E versus (PS+C+S) (model 2), and S versus C versus PS versus E (model 3) as fixed effects, and the identity of the network as random effect. Ants were included as species with eusocial behavior in this analysis. The selected model ($\Delta\text{AIC} < 2$) is shaded. AIC = Akaike's Information Criterion and $\Delta\text{AIC} = \text{AIC of each model} - \text{AIC best model}$. Coding for explanatory variables: solitary (S), communal (C), primitively social (PS), eusocial (E).

Models	Fixed effects	AIC	ΔAIC
Null	_____	3422.2	21.8
Model 1	S x (C+PS+E)	3404.7	4.3
Model 2	E x (PS+C+S)	3419.8	19.4
Model 3	S x C x PS x E	3400.4	0.0

Table S36: Model selection results for species among-module connectivity (c). The competing models were GLMM with Gaussian errors, the non-zero values of c as response variable, (E+PS+C) versus S (model 1), E versus (PS+C+S) (model 2), and S versus C versus PS versus E (model 3) as fixed effects, and the identity of the network as random effect. Ants were included as species with eusocial behavior in this analysis. The selected model ($\Delta\text{AIC} < 2$) is shaded. AIC = Akaike's Information Criterion and ΔAIC = AIC of each model - AIC best model. Coding for explanatory variables: solitary (S), communal (C), primitively social (PS), eusocial (E).

Models	Fixed effects	AIC	ΔAIC
Null	_____	-1157.9	8.9
Model 1	S x (C+PS+E)	-1166.8	0.0
Model 2	E x (PS+C+S)	-1153.5	13.3
Model 3	S x C x PS x E	-1156.2	10.7

Table S37: Model selection results for species standardized within-module degree (z). The competing models were GLMM with Gaussian errors, z as response variable, (E+PS+C) versus S (model 1), E versus (PS+C+S) (model 2), and S versus C versus PS versus E (model 3) as fixed effects, and the identity of the network as random effect. Ants were included as species with eusocial behavior in this analysis. The selected model ($\Delta\text{AIC} < 2$) is shaded. AIC = Akaike's Information Criterion and ΔAIC = AIC of each model - AIC best model. Coding for explanatory variables: solitary (S), communal (C), primitively social (PS), eusocial (E).

Models	Fixed effects	AIC	ΔAIC
Null	_____	3810.9	117.6
Model 1	S x (C+PS+E)	3712.9	19.6
Model 2	E x (PS+C+S)	3793.2	99.9
Model 3	S x C x PS x E	3693.3	0.0

Table S38: Model selection results for species *strength*. The competing models were GLMM with Gaussian errors, the log transformation of *strength* as response variable, (E+PS) versus S (model 1), E versus (PS+ S) (model 2), and S versus PS versus E (model 3) as fixed effects, and the identity of the network as random effect. Ants were included as species with eusocial behavior in this analysis. The selected models ($\Delta\text{AIC} < 2$) are shaded. AIC = Akaike's Information Criterion and $\Delta\text{AIC} = \text{AIC of each model} - \text{AIC best model}$. Coding for explanatory variables: solitary (S) , primitively social (PS), eusocial (E).

Models	Fixed effects	AIC	ΔAIC
Null	_____	5735.3	64.9
Model 1	S x (PS+E)	5671.1	0.7
Model 2	E x (PS+S)	5706.9	36.5
Model 3	S x PS x E	5670.4	0.0

Interaction patterns and colony size

Table S39: Model selection results for species degree (*k*). The competing models were GLMM with Gaussian errors, the log transformation of *k* as response variable, (E+PS+C) versus S (model 1), E versus (PS+C+S) (model 2), S versus C versus PS versus E (model 3) and the log transformed ranges of colony size (model 4) as fixed effects, and the identity of the network as random effect. Ants were included as species with eusocial behavior in this analysis. The selected model ($\Delta\text{AIC} < 2$) is shaded. AIC = Akaike's Information Criterion and $\Delta\text{AIC} = \text{AIC of each model} - \text{AIC best model}$. Coding for explanatory variables: solitary (S), communal (C), primitively social (PS), eusocial (E).

Models	Fixed effects	AIC	ΔAIC
Null	_____	5210.9	141.6
Model 1	S x (C+PS+E)	5087.9	18.6
Model 2	E x (PS+C+S)	5182.9	113.6
Model 3	S x C x PS x E	5080.6	11.3
Model 4	Colony size	5069.3	0.0

Table S40: Model selection results for species contribution to nestedness (*cn*). The competing models were GLMM with Gaussian errors, the log transformation of *cn*+1 as response variable, (E+PS+C) versus S (model 1), E versus (PS+C+S) (model 2), S versus C versus PS versus E (model 3) and the log transformed ranges of colony size (model 4) as fixed effects, and the identity of the network as random effect. Ants were included as species with eusocial behavior in this analysis. The selected models ($\Delta AIC < 2$) are shaded. AIC = Akaike's Information Criterion and $\Delta AIC = AIC$ of each model - AIC best model. Coding for explanatory variables: solitary (S), communal (C), primitively social (PS), eusocial (E).

Models	Fixed effects	AIC	ΔAIC
Null	_____	5405.7	27.5
Model 1	S x (C+PS+E)	5379.9	1.6
Model 2	E x (PS+C+S)	5401.8	23.5
Model 3	S x C x PS x E	5383.6	5.3
Model 4	Colony size	5378.3	0.0

Table S41: Model selection results for species closeness centrality (*cc*). The competing models were GLMM with Gaussian errors, *cc* as response variable, (E+PS+C) versus S (model 1), E versus (PS+C+S) (model 2), S versus C versus PS versus E (model 3) and the log transformed ranges of colony size (model 4) as fixed effects, and the identity of the network as random effect. Ants were included as species with eusocial behavior in this analysis. The selected model ($\Delta AIC < 2$) is shaded. AIC = Akaike's Information Criterion and $\Delta AIC = AIC$ of each model - AIC best model. Coding for explanatory variables: solitary (S), communal (C), primitively social (PS), eusocial (E).

Models	Fixed effects	AIC	ΔAIC
Null	_____	-3152.2	33.5
Model 1	S x (C+PS+E)	-3182.5	3.2
Model 2	E x (PS+C+S)	-3155.4	30.3
Model 3	S x C x PS x E	-3171.2	14.5
Model 4	Colony size	-3185.7	0.0

Table S42: Model selection results for species betweenness centrality (*bc*). The competing models were GLMM with Gaussian errors, the log transformed non-zero values of *bc*+1 as response variable, (E+PS+C) versus S (model 1), E versus (PS+C+S) (model 2), S versus C versus PS versus E (model 3) and the log transformed ranges of colony size (model 4) as fixed effects, and the identity of the network as random effect. Ants were included as species with eusocial behavior in this analysis. The selected model ($\Delta\text{AIC} < 2$) is shaded. AIC = Akaike's Information Criterion and $\Delta\text{AIC} = \text{AIC of each model} - \text{AIC best model}$. Coding for explanatory variables: solitary (S), communal (C), primitively social (PS), eusocial (E).

Models	Fixed effects	AIC	ΔAIC
Null	_____	3422.2	24.2
Model 1	S x (C+PS+E)	3404.7	6.7
Model 2	E x (PS+C+S)	3419.8	21.8
Model 3	S x C x PS x E	3400.4	2.4
Model 4	Colony size	3398.0	0.0

Table S43: Model selection results for species among-module connectivity (*c*). The competing models were GLMM with Gaussian errors, the non-zero values of *c* as response variable, (E+PS+C) versus S (model 1), E versus (PS+C+S) (model 2), S versus C versus PS versus E (model 3) and the log transformed ranges of colony size (model 4) as fixed effects, and the identity of the network as random effect. Ants were included as species with eusocial behavior in this analysis. The selected model ($\Delta\text{AIC} < 2$) is shaded. AIC = Akaike's Information Criterion and $\Delta\text{AIC} = \text{AIC of each model} - \text{AIC best model}$. Coding for explanatory variables: solitary (S), communal (C), primitively social (PS), eusocial (E).

Models	Fixed effects	AIC	ΔAIC
Null	_____	-1157.9	8.9
Model 1	S x (C+PS+E)	-1166.8	0.0
Model 2	E x (PS+C+S)	-1153.5	13.3
Model 3	S x C x PS x E	-1156.2	10.7
Model 4	Colony size	-1163.9	3.0

Table S44: Model selection results for species standardized within-module degree (z). The competing models were GLMM with Gaussian errors, z as response variable, (E+PS+C) versus S (model 1), E versus (PS+C+S) (model 2), S versus C versus PS versus E (model 3) and the log transformed ranges of colony size (model 4) as fixed effects, and the identity of the network as random effect. Ants were included as species with eusocial behavior in this analysis. The selected model ($\Delta AIC < 2$) is shaded. AIC = Akaike's Information Criterion and $\Delta AIC = AIC$ of each model - AIC best model. Coding for explanatory variables: solitary (S), communal (C), primitively social (PS), eusocial (E).

Models	Fixed effects	AIC	ΔAIC
Null	_____	3810.9	126.1
Model 1	S x (C+PS+E)	3712.9	28.1
Model 2	E x (PS+C+S)	3793.2	108.4
Model 3	S x C x PS x E	3693.3	8.5
Model 4	Colony size	3684.8	0.0

Table S45: Model selection results for species *strength*. The competing models were GLMM with Gaussian errors, the log transformation of *strength* as response variable, (E+PS) versus S (model 1), E versus (PS+ S) (model 2), S versus PS versus E (model 3) and the log transformed ranges of colony size (model 4) as fixed effects, and the identity of the network as random effect. Ants were included as species with eusocial behavior in this analysis. The selected model ($\Delta AIC < 2$) is shaded. AIC = Akaike's Information Criterion and $\Delta AIC = AIC$ of each model - AIC best model. Coding for explanatory variables: solitary (S), communal (C), primitively social (PS), eusocial (E).

Models	Fixed effects	AIC	ΔAIC
Null	_____	5735.3	73.1
Model 1	S x (PS+E)	5671.1	8.9
Model 2	E x (PS+S)	5706.9	44.7
Model 3	S x PS x E	5670.4	8.2
Model 4	Colony size	5662.2	0.0