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Social Wasp-Flower Visiting Guild Interactions in Less Structurally Complex Habitats are More Susceptible to Local Extinction

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Abstract

Several studies have shown that habitat complexity is an important factor for the dynamic and stability of interacting species. However, it is not known how the habitat complexity may affect the tolerance of wasp-flower interactions to local extinction. Based on this perspective, in this study, we aimed to compare the tolerance of wasp flower visiting guild to local extinction in two different types of vegetation (Riparian Forest and Rocky Grassland). Through observations made during one year, we verified that the structure of the plant-wasp interaction network differed between the two areas, as well as that the robustness to cumulative extinctions had different patterns. The simulations of cumulative removal of species showed that the network in the Riparian Forest is more robust against the removal of both plants and wasps than that network in Rocky Grassland, since their extinction curves declined more slowly. Therefore, in our study area, we demonstrate that social wasp-plant interactions in areas with lower structural complexity are less tolerant to extinction (i.e. more fragile). We therefore suggest that studies that aim at biodiversity conservation should focus not only in areas where diversity is high, but also in area with lower species richness for the conservation of ecological roles within communities.

Introduction

The importance of species interactions for the maintenance of biodiversity has been widely recognized (Thompson, 2013; Del-Claro & Torezan-Silingardi, 2009). These interactions vary from mutualistic to antagonistic and affect populations and individuals in different ways, since all species establish ecological interaction at some point in their lifetime. It is also recognized that ecological interactions vary in time and space (Thompson, 2013; Del-Claro et al., 2013) and that structurally more heterogeneous and complex environments have a higher species richness and diversity. Alternatively, more homogeneous environments are simpler in their structure and less diverse (Santos et al., 2007; Tews et al., 2004).

Currently, network analysis has been widely used for ecological interaction studies. This tool enables conclusions concerning the structure, stability and robustness of ecological interactions involving two or more groups of organisms to be reached (Montoya et al., 2006; Thébault & Fontaine, 2010; Hernández-Yáñez et al., 2013). Our current understanding about how ecological networks might have different patterns in distinct habitats has, in general, been limited to few studies (see Clemente et al., 2012; Dáttilo et al., 2013a). From this, we can infer that structurally different habitats might have different patterns of ecological networks and consequently vary in their tolerance to species loss.

Studies on species extinction have been the focus of conservation ecologists who aim to preserve biodiversity, however, such studies approach only the loss of species, without considering the loss of the functional role that species exert (Memmott et al., 2007; Dyer et al., 2010). In natural systems, each species performs specialized functions or those complementary to its partners (Blüthgen & Klein, 2011). In interactions among species specialists (i.e. with a narrow

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niche breadth), each species is extremely important for interactive pair and the loss of one species results in the loss of the interaction and the extinction of one of its associates (Blüthgen & Klein, 2011). Alternatively, the extinction of generalist species (i.e. with a wide niche), causes fewer effects on its associates, because complementary functions are provide by other species. However, regardless of the ecological function, the extinction of an interaction between two species can influence the structure of the ecological network within an entire community (Olesen & Jain, 1994).

According to Santos et al. (2007), interactions established among social wasps and plants (e.g. Torezan-Silingardi 2011) are a good system to study the issues of co-extinction in ecological networks and the effect of abiotic factors on them, since they have certain requirements from the environment, for example, the habitat might provide a nesting substrate (Santos & Gobbi, 1998; Cruz et al., 2006), food resources (e.g. nectar) (Santos et al., 1998; Silva-Pereira & Santos, 2006; Santos et al., 2006), material for nest building (e.g. plant fiber) (Machado, 1982; Marques & Carvalho, 1993) and prey (Santos et al., 1998).

Thus, the floristic composition, vegetation structure and complexity are determinants of the composition and community structure of social wasps (Santos et al., 2007). Additionally, some wasp species build their nests only under specific structural conditions of vegetation (Sinzato et al., 2011), which can be open or closed landscapes, as well as morphological conditions of the plant species; the size and shape of leaves, stem diameter and/or the presence of thorns (Henriques et al., 1992; Santos & Gobbi, 1998; Cruz et al., 2006). Thus, the complexity of the vegetation is determinant for the composition and community structure of social wasps and its fundamental and realized niche (Santos et al., 2007; Carvalho et al., 2013). Therefore, environments with different complexities of vegetation might hypothetically have interaction networks with different compositions and topological properties, and consequently have different degrees of tolerance to species extinction. In this study, we compared the tolerance of the interaction network between flower-visiting social wasps and plants to extinction, in two distinct areas with different types of vegetation in the Brazilian Savanna (Riparian Forest and Rocky Grassland), to analyze in which vegetation physiognomy the wasp-plant interactions are more fragile.

Materials and Methods

We collected data in the Parque Estadual do Ibitipoca (Unidade de Conservação) (PEIB - 21º40'44"S and 43º52'55"W), southeastern Brazil, from November 2007 to October 2008. The PEIB is managed by the Forestry Institute, organ of the Environment Agency of the State of Minas Gerais. Moreover, the area is composed of several vegetation types that form different phytophysiognomies. Riparian Forest and Rocky Grassland are the most abundant phytophysiognomies of the PEIB. The Riparian Forest exhibits a profile of transition vegetation from high-altitude savannas to ombrophilous forests, with a physiognomy sequence from shrubby-arboreal to predominantly arboreal and a great heterogeneity of plant species (Durigan et al., 2000), with a predominance of cloudiness (i.e. high moisture) (Fontes, 1997). The Rocky Grassland exhibits a xeromorphic aspect, with a wide diversity of herbs and shrubs distributed over quartzite outcrops (Rodela, 1998). This area is dominated by plants tolerant to water stress, due to the high incidence of light and wind (Giulietti et al., 1997).

At each of the two studied sites, which were 1,200 m distant from each other, we used one transect of 800 x 4 m, where we carried out monthly observations on two consecutive days between 7:00 - 17:00 h, during this period, we observed each plant that had flowers for 10 min and collected one individual of each wasp species that visited the flowers. Capture was performed using entomological sweep net, according to the method of Sakagami et al. (1967).

Data Analysis

Initially, we built two quantitative wasp-plant adjacency matrices (one for each vegetation type), c_{ij} = number of interactions between wasp species *i* and plant species *j* inside in transects. In order not to overestimate the plant species with more number of flowers, we considered as interaction frequency only the interactions among individuals within transects. To test whether the composition of plants and wasps shifts along the core-periphery gradient of the networks in each area, we defined the core of generalist species according to Dáttilo et al. (2013b). The species that exhibit a $Cp > 1$ are species with a higher proportion of interactions in relation to other species of the same group and are therefore considered core species of the network. The species with a $Cp < 1$ are species with a lower proportion of interactions and are considered periphery species.

We calculated the robustness to extinction for both wasp-plant interaction networks (Riparian Forest and Rocky Grassland), based on the cumulative removal of species from the network at random (sensu Burgos et al., 2007; Dáttilo et al., 2012). We also calculated the area under the extinction curve (*R*) according to Burgos et al. (2007), as a measure of the robustness of the networks, which varied from 1.0 (a more robust network) to 0 (a less robust network).

We ran 100 randomizations for each network to simulate species removal and we chose the *R* index because it is more robust and is not sensitive to the shape of the curve, in contrast to the index proposed by Memmott et al. (2004). We used the Network 3D Software (Williams, 2010) to create the graphical representations of social wasp–plant networks, and the Attack Tolerance Curve (ATC) to calculate the *R* index.

Results

In this study, we recorded 15 wasp species in associations with 27 plant species (or morphospecies) (Table 1). A list of all wasp–plant interactions recorded can be viewed in the supplementary material (Appendix 1). The social wasp-plant interaction networks of two Cerrado physiognomies showed different structure (Fig 1). The network in the Riparian Forest had a greater number of species (18 plant species and 15 wasp species) and a fourfold greater number amount of connections between them (83 associations) compared to the Rocky Grassland (11 plant species, eight wasp species, and 20 associations). The percentage of plant and wasp core species was also different between the two landscapes, with a greater number of wasp species belonging to the principal core in the Riparian Forest (16.6 % for plants and 20% for wasps in Riparian Forest, and 37.5% for plants and 9.1% for wasps in Rocky Grassland). The average degree of plant and wasp species was also different between areas (2.44 for plants and 2.93 for wasps in Riparian Forest, and 1.27 for plants and 1.75 for wasps in Rocky Grassland).

The robustness to cumulative extinctions showed different pattern at each site (Fig 2). The simulations of the cumulative removal of species showed that the network in the Riparian Forest is more robust against the removal of both plants and wasps than the network in the Rocky Grassland, since their extinction curves declined more slowly. The robustness of the network in the Riparian Forest was relatively high, both for plants (R = 0.914) and wasps (R = 0.706) (see Fig 2C, D). In the Rocky Grassland network, the robustness was lower for plants (R = 0.799) and wasps (R = 0.658) (see Fig 2A, B).

Discussion

Our results show that interactions between social wasps and flowers have a different tolerance to species extinction in habitats with a distinct vegetation structure. Furthermore, we showed that in the Brazilian Cerrado, a more heterogeneous habitat exhibit plant-social wasp networks that are more tolerant to the extinction of interactions.

Table 1. Code of plant and wasp species exhibited in Figure 1.

Code	Plant Species	Code	Wasp Species
MSE	*Mandevilla sellowii* (Müll. Arg.) Woodson	AMU	*Agelaia multipicta* (Haliday, 1836)
DLA	*Ditassa laevis* Mart.	APA	*Apoica pallens* (Fabricius, 1804)
AS1	Asteraceae sp1	BLE	*Brachygastra lecheguana* (Latreille, 1824)
AS2	Asteraceae sp2	COM	*Mischocyttarus confusus* Zikán, 1935
AS3	Asteraceae sp3	MDR	*Mischocyttarus drewseni* Saussure, 1857
AS4	Asteraceae sp4	PBI	*Polistes billardieri* Fabricius, 1804
AS5	Asteraceae sp5	PCI	*Polistes cinerascens* Saussure, 1854
AS6	Asteraceae sp6	PFE	*Polistes ferreri* Saussure, 1853
VE1	*Vernonia* sp1	PO1	*Polistes* sp1
BAC	*Baccharis* sp1	PFF	*Polybia fastidiosuscula* Saussure, 1854
VER	*Vanillosmopsis erythropappa* (DC.) Sch. Bip.	PIG	*Polybia ignobilis* (Haliday, 1836)
WEI	*Weimmannia* sp1	PPA	*Polybia paulista* (Von. Ihering, 1896)
EGO	*Erythroxylum gonocladum* (C. Martius) O. E. Schulz	PSC	*Polybia sericea* (Oliver, 1791)
PER	*Periandra* sp1	PB1	*Polybia* sp1
CUP	*Cuphea* sp1	PSY	*Protonectarina sylveirae* (Saussure, 1854)
MEL	Melastomataceae sp1		
TPA	*Trembleya parviflora* (D. Don) Cogn.		
MFA	*Myrcia fallax* (Rich.) DC		
CCO	*Calyptranthes concinna* DC.		
OUR	*Ouratea* sp1		
PVE	*Prosthechea vespa* (Sw.) W.E.Higgins		
TSP	*Trachypogon spicatus* (L. F.) Kuntze		
PLA	*Posoqueria latifolia* (Rudge) Schult.		
BAR	*Barreria* sp1		
GFR	*Gordonia fruticosa* (Schrad.) H. Keng		
BFL	*Barbacenia flava* Mart. ex Schult. F.		
VAL	*Vellozia albiflora* Pohl		

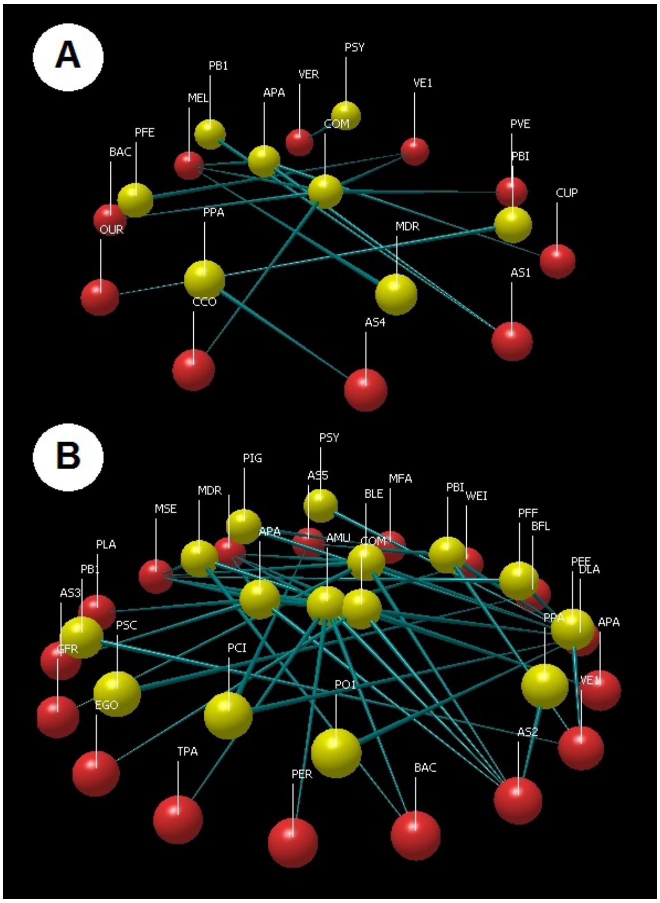

Fig 1. Graphical representation of social wasp–plant networks of two phytophysiognomies (A) Rocky Grassland and (B) Riparian Forest of a Brazilian Savanna in the period from November 2007 to October 2008. The red nodes represent different plant species, and the yellow nodes correspond to wasp species that interact with plants. Lines represent wasp–plant interactions. Plant and wasp species codes are presented in Table 1.

Vegetation complexity is positively related to species diversity in many groups of organisms (see Tews et al., 2004) including social wasps (see Lawton, 1983; Santos et al., 2000, 2007). According to Santos et al. (2007), vegetation is the main substrate for the foundation of social wasp nests, so more heterogeneous environments increase the quantity and variety of sites for nesting, and consequently, the coexistence of wasp species in these locations becomes greater.

In our study, this finding was confirmed in the Riparian Forest, which showed the greatest number of wasp and plant species, number of associations and interaction degree between plant-wasp species. A greater complexity in forest than in grassland areas has also been demonstrated in other studies (see review in Tews et al., 2004).

Previous studies have shown that wasp-plant networks are highly generalists (Mello et al., 2011; Aguiar & Santos, 2007). Here, we show that that despite the generalization of these networks, this pattern can vary between habitats with different complexity. Environments with a greater availability of resources (food or nesting sites) have lower levels of species competition (Markwell et al., 1993; Harris et al., 1994), mainly among wasps, where the competition for floral resources is rare (De Souza et al., 2010). The lower competition, or lack thereof, contributes to the increase in species coexistence and local biodiversity (Henriques et al., 1992; Bastolla et al., 2009). Although, the social interaction between wasps and flowers in the Riparian Forest is more generalist that in the Rocky Grassland, most wasp species of both networks established an association with only one plant species. This result might relate to limitations in resource collection by wasps from plants with a specific floral morphology (i.e. length corollas) (see Heithaus, 1979a), because the mouthpart of wasps is short. Several authors have suggested that this is one of the main factors limiting of the niche breadth in wasps (Heithaus, 1979a; Johnson & Steiner, 2000; Shuttleworth & Johnson, 2006).

Nectar is an important resource for Hymenoptera development and survivorship (e.g. Byk & Del-Claro, 2011), and despite nectar being considered an accessory food in the diet of wasps (Faegri & Van der Pijl, 1979), they tend to preferentially visit plants that produce higher amounts of nectar (Gess & Gess, 1993), which leads to an increase in the coexistence between of wasp species in a particular plant species. Since the competition for food in wasps is rare (De Souza et al., 2010), this factor poorly explains the specialization in this interaction, because the specialization observed in this study might be explained by a low abundance and richness of wasps and not by the coevolution of the associates.

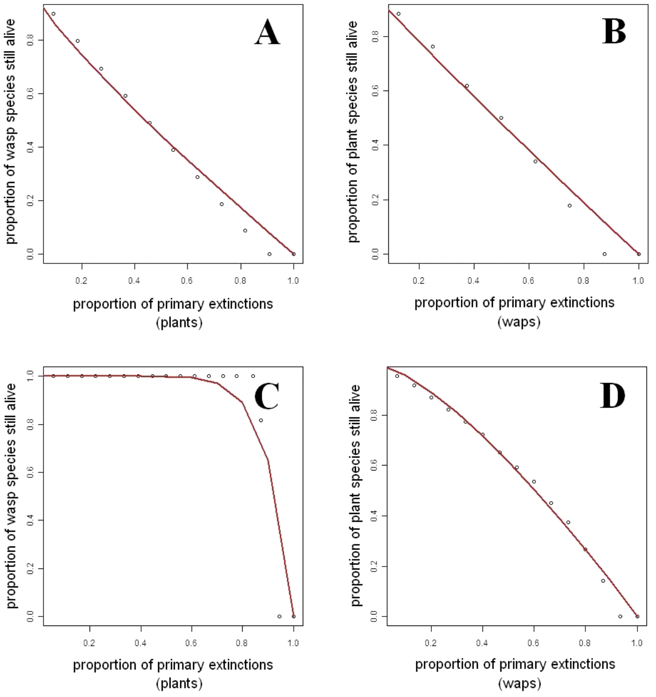

Fig 2. Robustness to cumulative species removal of plants (A) and wasps (B) in the Rocky Grassland, and plants (C) and wasps (D) in the Riparian Forest network.

In addition to the aforementioned factors, abiotic components might also explain the variation in specialization of the social wasp-flower interaction. Some social wasp species such as *euriecias* have a wide ecological valence, nesting in every type of habitat (Wenzel, 1991; Marques & Carvalho, 1993; Santos & Gobbi, 1998). However, the species *estenoecias* exhibits a narrow limit of ecological valence, only nesting in specific locations (Silva-Pereira & Santos, 2006; Santos et al., 2007, Souza et al., 2010), which might result in local extinction as an outcome of variations in habitat conditions. For example, wasp species such as *Angiopolybia pallens* (Lepeletier, 1836) and *Synoeca cyanea* (Fabricius, 1775) are only found in environments with specific substrate conditions (Marques, 1996; Santos et al., 2007), whereas *Polistes canadensis* (Linnaeus, 1758), and *Polybia ignobilis* (Haliday, 1836) can alter their nesting habits according to the available environmental conditions and substrates (Santos & Gobbi, 1998; Santos et al., 2007). Thus, the ecological valence of wasp species might influence species diversity in an environment and major change in its microclimate might cause the extinction or migration of species at higher rates than in an environment where climatic conditions are more stable (Wilson, 1988).

The factors mentioned above might have been decisive in the differentiation of the specialization and variation in the tolerance to extinction of the species interaction in the social wasp-flower networks studied. The Rocky Grassland area, which has less dense vegetation with strong winds and a high light incidence, might experience a large variation in microclimates, which might have contributed to a lower species diversity in this area (see Elpino-Campos et al., 2007). Unlike the Riparian Forest, which has a greater availability of resources, species coexistence, and a more generalist social wasp-flower interaction network. In fact, the more generalist networks tend to be functionally redundant and more robust to species extinction (Dáttilo et al., 2012). Furthermore, the presence of trees in this area maintains the stability of the local microclimate, as shown by Hernandes et al. (2004).

The importance of interaction conservation between social wasps and flowers has been only recently recognized (Shuttleworth & Johnson, 2009), because wasps were previously considered as thieves of floral resources (Hunt et al., 1991; Elpino-Campos et al., 2007). Recent studies have shown that some species can contribute to pollination (Sühs et al., 2009). According to Heithaus (1979a, b), the guild of wasps that visit flowers surpasses that of bees in terms of exploitation of nectar in various ecosystems. Some species, such as *Polistes versicolor* (Olivier, 1791), *Polistes simillimus* Zikán, 1951, *Polybia sericea* (Olivier, 1791), and *Polybia ignobilis* (Haliday, 1836), can be more representative in richness and abundance than bee species and are efficient pollinators (see Sühs et al., 2009). Despite that social wasp-plant interactions be considered as non-obligatory mutualistic associations and leans to generalization rather than to specialization (Santos et al., 2010; Mello et al., 2011), as other interactions involving plants and pollinators (see Hernández-Yáñez et al., 2013), the extinction of this interaction might result in the loss of part of the ecological function of pollination and cause damages to the community (see Blüthgen & Klein, 2011), especially in environments where this interaction is more specialized (Olesen & Jain, 1994). In these cases, the extinction of a pollinator (even an eventual pollinator) might trigger the loss of plant species and begin a 'cascade of linked extinctions' (Myers, 1986).

Although studies containing greater number of networks are needed to confirm these results, our data show that social wasp-flower interactions in areas with low structural complexity might be less tolerant to extinction, (i.e. they are more fragile). Thus, we suggest that studies that aim at biodiversity conservation should focus not only on areas where diversity is high, but also in areas with lower species richness, because the dependence among species partners is greater in these areas.

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This article has supplementary material that can be downloaded in electronic format (data set spreadsheet).

Appendix 1. Interaction matrix between social wasps-flowers

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