



Contents lists available at ScienceDirect

Acta Oecologica

journal homepage: www.elsevier.com/locate/actoec

Insights into the structure of plant-insect communities: Specialism and generalism in a regional set of non-pollinating fig wasp communities

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ARTICLE INFO

Keywords:

Agaonidae

Community ecology

Food web

Interaction network

Modularity

Moraceae

ABSTRACT

Insects show a multitude of symbiotic interactions that may vary in degree of specialization and structure. Gall-inducing insects and their parasitoids are thought to be relatively specialized organisms, but despite their ecological importance, the organization and structure of the interactions they establish with their hosts has seldom been investigated in tropical communities. Non-pollinating fig wasps (NPFW) are particularly interesting organisms for the study of ecological networks because most species strictly develop their offspring within fig inflorescences, and show a multitude of life history strategies. They can be gall-makers, cleptoparasites or parasitoids of pollinating or of other non-pollinating fig wasps. Here we analysed a set of non-pollinating fig wasp communities associated with six species of *Ficus* section *Americanae* over a wide area. This allowed us to investigate patterns of specialization in a diverse community composed of monophagous and polyphagous species. We observed that most NPFW species were cleptoparasites and parasitoids, colonizing figs several days after oviposition by pollinators. Most species that occurred in more than one host were much more abundant in a single preferential host, suggesting specialization. The food web established between wasps and figs shows structural properties that are typical of specific antagonistic relationships, especially of endophagous insect networks. Two species that occurred in all available hosts were highly abundant in the network, suggesting that in some cases generalized species can be more competitive than strict specialists. The Neotropical and, to a lesser extent, Afrotropical NPFW communities seem to be more generalized than other NPFW communities. However, evidence of host sharing in the Old World is quite limited, since most studies have focused on particular taxonomic groups (genera) of wasps instead of sampling the whole NPFW community. Moreover, the lack of quantitative information in previous studies prevents us from detecting patterns of host preferences in polyphagous species.

1. Introduction

Interaction networks arise in a multitude of contexts such as social sciences (Burt, 1976; Friedkin and Johnsen, 1997), communication (Dorogovtsev and Mendes, 2003), molecular biology (Ma'ayan, 2011), and ecology (Bascompte and Jordano, 2006; Jordano, 1987; Memmott, 1999). Although network analysis is applied to different disciplines, organization levels and organisms, general patterns and unifying concepts can be used to describe their structure, such as centrality, connection intensity, interaction strength and modularity (Barrat et al.,

2004; Brandes et al., 2003; Dunne et al., 2002; Olesen et al., 2007). In an ecological perspective, the characteristics of interaction networks have been investigated to detect emergent patterns in areas such as food webs, pollination ecology, seed dispersal and parasitic interactions. They allow addressing important questions such as vulnerability to extinction, ecological specialization, and pollination efficiency (Bascompte et al., 2006; Blüthgen et al., 2007; Memmott, 1999; Memmott et al., 2004; Taudiere et al., 2015). In the context of plant-animal interactions, ecological network analysis contributes to the recognition of generalism and specialization patterns among species.

Abbreviations: NPFW, non-pollinating fig wasps; PDI, paired difference index

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<https://doi.org/10.1016/j.actao.2018.02.006>

Received 15 February 2017; Received in revised form 2 February 2018; Accepted 7 February 2018

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Such patterns may allow detecting the presence of underlying processes driving evolutionary diversification in symbiotic communities, concerning both antagonistic and mutualistic relationships (Forister and Feldman, 2011).

Plant-insect interaction networks vary in structure, yet some emerging patterns have been uncovered according to the type of interaction established. Mutualistic networks such as pollination and seed dispersal interactions tend to show nested structures that are cohesively organized around a central core of generalized interactions. This pattern has been hypothesized to arise from diffuse coevolution between plants and animals, and generates heterogeneous distributions of the number of interactions (Bascompte et al., 2003). On the other hand, specialized networks, organized around herbivorous insects and plants, or insects and their parasitoids, tend to show cohesive groups of animals associated with subsets of hosts, often called compartments or modules (Dormann and Strauss, 2014) which are generated by ecological or evolutionary trophic specialization (Olesen et al., 2007; Prado and Lewinsohn, 2004). Therefore, network structure may indicate the presence of underlying evolutionary mechanisms that generate the level of specialization/generalization observed within plant-insect communities.

The communities of micro-hymenoptera associated with fig trees (*Ficus*, Moraceae) may provide a powerful model to investigate processes driving the evolution of community structure. Indeed, these wasps include diversified sets of gall inducing wasps, cleptoparasites and parasitoids (Elias et al., 2012; Segar et al., 2013a). Further, most of these wasps breed exclusively within figs (the closed inflorescence of *Ficus*), and the adults of the different species emerge synchronously from their host fig. Therefore collecting whole communities is relatively easy. Furthermore, sampling the wasps emerging from all local *Ficus* species allows collection of the whole meta-community of fig wasps, and therefore they offer robust data for analysing the interconnections between the different communities using a network approach. Since each wasp utilizes a single fig flower ovary as oviposition site, and the cleptoparasites and parasitoids utilize a single larva to develop, it is straightforward to obtain a comparable quantitative measure of the degree of infestation for each species in each host. Therefore, we have a robust measure of the reproductive output of each wasp species in each host, and it is possible to obtain highly informative networks.

The relationship between fig trees and Agaonidae is a classic example of obligatory pollination mutualism. The fig is an urn-shaped inflorescence, which is lined inside by hundred(s) to thousands of uniovulate flowers depending on the *Ficus* species. Female pollinating wasps enter the fig by crawling through an aperture closed by bracts (the ostiole), oviposit in the ovaries of some pistillate flowers and pollinate others. The wasp larva develops instead of a would-be seed. Male offspring emerge into the fig cavity and mate with the females that are still enclosed in their galls. Then, female wasps emerge from their galls, leave the fig and fly to another fig to oviposit and pollinate (Galil and Eisikowitch, 1969). Global phylogenetic analyses of *Ficus* and Agaonidae show that these groups have broadly radiated in parallel (Cook and Segar, 2010; Cruaud et al., 2012; Machado et al., 2005). Generally, each *Ficus* species is pollinated by one or a few species-specific agaonid wasps (for exceptions see e.g. Cornille et al., 2012).

Besides pollinators, fig inflorescences host species-rich chalcid wasp communities. Indeed, several unrelated lineages of chalcid wasps develop exclusively or mainly on figs (Bouček, 1993; Rasplus et al., 1998). They interfere with the reproductive success of both *Ficus* and pollinating wasps in different ways, as they differ widely in feeding habits (Elias et al., 2007; Peng et al., 2005). Some non-pollinating fig wasps (NPFW) induce galls and their offspring develop in pistillate flowers as pollinators do (Elias et al., 2012; Jansen-Gonzalez et al., 2014); in some cases, they may even induce galls in other fig tissues or organs (Beardsley and Rasplus, 2001; Bronstein, 1999; Ghara et al., 2014; Müller, 1886). Some phytophagous NPFWs (known as inquillines or cleptoparasites) feed on galls induced by other wasps and eliminate

their larvae in the process (Joseph, 1958), while other groups are true parasitoids that feed directly on the larvae of phytophagous fig wasps (Tzeng et al., 2008). Finally, some wasps are facultative (Pereira et al., 2007) or obligatory seed eaters (Wang et al., 2014). Despite increasing interest in their biology and evolution (Cruaud et al., 2011a, 2011b; Elias et al., 2008), the communities of NPFW are poorly known (but see Compton and Hawkins, 1992; Compton and van Noort, 1992; Kerdelhué et al., 2000; Segar et al., 2013b). Information on host specificity of NPFW is scarce and limited by sampling effort and lack of taxonomic resolution (Cook and Segar, 2010; Darwell and Cook, 2017). Thus, the level of host specificity in NPFW is subject to debate. In some lineages, host specificity is supported by evidence for parallel cladogenesis between *Ficus* and NPFWs (Jousselin et al., 2006). However, in some other studies, co-phylogenies suggest considerable host switching during their evolutionary history (Jiang et al., 2006). Datasets on Neotropical and African fig wasps show some NPFW species colonizing several hosts (Marussich and Machado, 2007; McLeish et al., 2012). These results suggest that host specificity and strict-sense co-evolution may not satisfactorily explain the diversification of NPFW and their host species.

In this context, we analysed a set of NPFW communities associated with *Ficus* section *Americanae* in three areas of semi-deciduous forests in São Paulo state, Brazil. Large-scale sampling allowed us to thoroughly investigate patterns of specialization in a complex community composed of monophagous and polyphagous species with an array of life histories and a wide range of abundances in each *Ficus* host. As fig wasps have a delimited set of potential oviposition sites (one egg in each pistillate fig flower) and we measured the ovule occupancy rate of individuals belonging to each wasp species in the community in each host, our data allowed us to assess the ecological specialization of NPFW species with a quantitative network approach. Specifically, we aimed at answering the following questions: (1) how often do the offspring of a NPFW species develop in more than one host; (2) are NPFW communities specialized; (3) do NPFW communities present a structured pattern; (4) even if wasp species use several hosts, is the species composition of the community associated with each of these hosts different. Furthermore, extra-Amazonian Brazil in general – and São Paulo state in particular – has suffered from huge deforestation. Such a situation may have impacted NPFW communities. A simple prediction is that the communities associated with the least common *Ficus* species may be strongly affected, showing species-poor communities and a lack or imbalance in some trophic levels, while the community associated with the most abundant *Ficus* species may be more typical.

2. Material and methods

2.1. Studied species

We analysed the NPFW communities associated with six *Ficus* species belonging to the section *Americanae* in three locations in São Paulo state, Brazil. *Ficus* sect. *Americanae* is the most diverse *Ficus* section in the Neotropical region, with more than 120 described species (Berg and Villavicencio, 2004). The *Ficus* species present locally included seven species of section *Americanae* and two species of section *Pharmacosycea*. We verified that the NPFW genera associated with *Ficus* section *Americanae* and with section *Pharmacosycea* were distinct. The communities associated with the later group were not investigated in this study. Figs belonging to section *Americanae* are monoecious, and the studied species vary in average fig diameter from ~1 to ~2.5 cm when mature (Table 1).

Ficus section *Americanae* is a clade that only diversified recently between the Oligocene and Miocene (~20–25 Ma, Cruaud et al., 2012; Machado et al., 2018). The group is monophyletic, but phylogenetic relationships within section *Americanae* are not well established (Cruaud et al., 2012; Machado et al., 2018). Species may grow as hemiepiphytes or as free standing trees (Berg and Villavicencio, 2004).

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