Revista Brasileira de Entomologia 66(1):e20210101, 2022

SOCIEDADE BRASILEIRA
DE ENTOMOLOGIA
FUNDADA EM 1937

REVISTA BRASILEIRA DE
Entomologia
A Journal on Insect Diversity and Evolution

Community structure and specialization in fig wasps (Hymenoptera: Chalcidoidea) in a region of Cerrado

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ARTICLE INFO

Article history:
Received 28 September 2021
Accepted 25 January 2022
Available online 25 March 2022
Associate Editor: Marcelo Tavares

Keywords:
Insect-plant interactions,
Food web,
Pollination,
Agaonidae,
Multitrophic interactions

ABSTRACT

Ficus inflorescences host a species-rich chalcid wasp community, including pollinating fig wasps (Agaonidae: Tetrapusinae, Kradibiinae, and Agaoninae) and several species of non-pollinating fig wasps (NPFW), that show several life-history strategies, including gall-inducers, kleptoparasites (i. e. inquilines), and parasitoids. We analyzed the structure and degree of specialization of the fig wasp community associated with *Ficus* inflorescences in urbanized areas, agroecosystems, and on the edge of forest fragments in the state of Goiás (Brazil). We sampled 34 wasp species in four native *Ficus* tree species, from which four wasp species occurred in more than one host. Neotropical fig pollinators (*Pegoscapus* and *Tetrapus*) were the most abundant species, and they were host-specific, although two pollinator species were associated with *Ficus obtusifolia*. The Jaccard similarity index was higher in samples of fig wasps collected in the same host, indicating that the community composition was specific to each host species. Community structure indices indicate a specialized structure with low connectance, high bidimensional Shannon H_2' and low partner diversity. The communities present a modular web structure in which modules were represented by each host and its associated insect species. These results indicate that the fig wasp communities analyzed are highly specialized, despite a few not strictly host-specific species.

Introduction

Specialization is ubiquitous in living systems, as species may occupy only a subset of habitats or hosts available (Forister et al., 2012). Ecological specialization may be described as a species' variance in performance across a given range of resources or impact across ranges of environments (Devictor et al., 2010), and such frameworks are pervasive in interactions established among plants, herbivorous insects, and their enemies through geological time (Labandeira, 2021; Labandeira and Li, 2021). Such interactions are classic models for studies of host specialization in insects (Forister et al., 2012). They are examples of the importance of insects in natural communities and how they influence the ecosystem services (Schowalter et al., 2018).

The community of chalcid wasps associated with *Ficus* (Moraceae) is an interesting group for studying host specialization in multitrophic communities. Fig trees sustain a diverse community of associated arthropods (Palmieri and Pereira, 2018), and the interaction between fig wasps (Agaonidae; Tetrapusinae, Kradibiinae, and Agaoninae) and fig trees (*Ficus,* Moraceae) is one of the most well-known examples of specificity in insect-plant interactions. The wasps use the enclosed fig inflorescences as an oviposition site and pollinate the fig flowers (Weiblen, 2002; Cook and Rasplus, 2003). Figs and pollinating wasps establish a synchronous and specialized life cycle with well-defined phases (Galil and Eisikowitch, 1968). At the beginning of syconium development (phase A), figs are smaller, and flowers are immature; pistillate flowers mature and are receptive to pollination at phase B when pollinators arrive and enter the fig through a tiny pore called ostiole; "interfloral phase" (phase C) refers to the period between pollination and the maturation of male (staminate) flowers when wasp larvae develop; at the male phase (phase D) staminate flowers are mature, and wasps emerge from their galls and leave the figs in search of receptive flowers. In the post-floral stage (phase E), figs ripen after the emergence of fig wasps and become attractive to dispersers.

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https://doi.org/10.1590/1806-9665-RBENT-2021-0101

In addition to pollinators, several lineages of Chalcidoidea wasps use fig trees as an oviposition site but do not pollinate the flowers. These non-pollinating fig wasps (NPFW) develop as gall-inducers, kleptoparasites, or parasitoids. They mostly do not enter the fig as pollinators do, but oviposit from the outside by inserting their long ovipositors through the syconium wall, and usually oviposit in the pistillate flowers, without pollinating (Kerdelhue et al., 2000; Cook and Rasplus, 2003; Elias et al., 2008). Non-pollinating fig wasps oviposit in figs in different phases of fig development, according to their natural history (Elias et al., 2008). Several NPFW, known as early gall-inducers, oviposit at the beginning of fig development (phase A). They are relatively large wasps that induce large galls that may occupy a considerable portion of the fig lumen (Müller, 1886; Bronstein, 1999; Conchou et al., 2014). Receptive phase gall-inducers oviposit at the same stage as pollinators (phase B) but they oviposit through the fig wall; they may show complex oviposition mechanisms that imitate pollinators (Elias et al., 2012). Several groups of NPFW (kleptoparasites or parasitoids, but possibly also gall-inducers) may oviposit in fig pistillate flowers at interfloral phase (C phase), and their larvae develop at the expense of other wasps' larvae (Elias et al., 2008). Two sections of *Ficus* naturally occur in the neotropics: *Ficus* Section *Americanae* shows about 120 species, while section *Pharmacosycea* shows ca. 20 species (Berg, 1989), and each section shows different associated genera of both pollinating and NPFW (Bouček, 1993).

Specialization in pollinating and NPFW is much disputed. While pollinators tend to show a pattern of co-diversification with figs (Cruaud et al., 2012), cases of wasps co-occurring pollinators in the same fig are quite common (Rasplus, 1996; Molbo et al., 2003). For NPFW, several co-diversification and host switching patterns are described, which may be related to specialization and generalization in host-plant association (Jiang et al., 2006; Jousselin et al., 2006; Farache et al., 2018).

This study described the community of fig wasps associated with fig trees within the Cerrado areas in the south of the state of Goiás. We also estimated the similarity of the wasp fauna associated with different host *Ficus* species and analyzed the structure of the fig wasp community associated with fig trees.

Material and methods

This study was carried in Cerrado areas near the municipalities of Rio Verde (17.81°S 50.92°W), Caiapônia (16.95°S 51.81°W) and Maurilândia (17.97°S 50.33°W; Fig. 1). *Ficus* syconia were collected at the edge of forest fragments, urban areas, and agroecosystems between May 2019 and January 2020. All figs were sampled at the male phase (phase D) when the wasps emerge from the galls. Four *Ficus* species

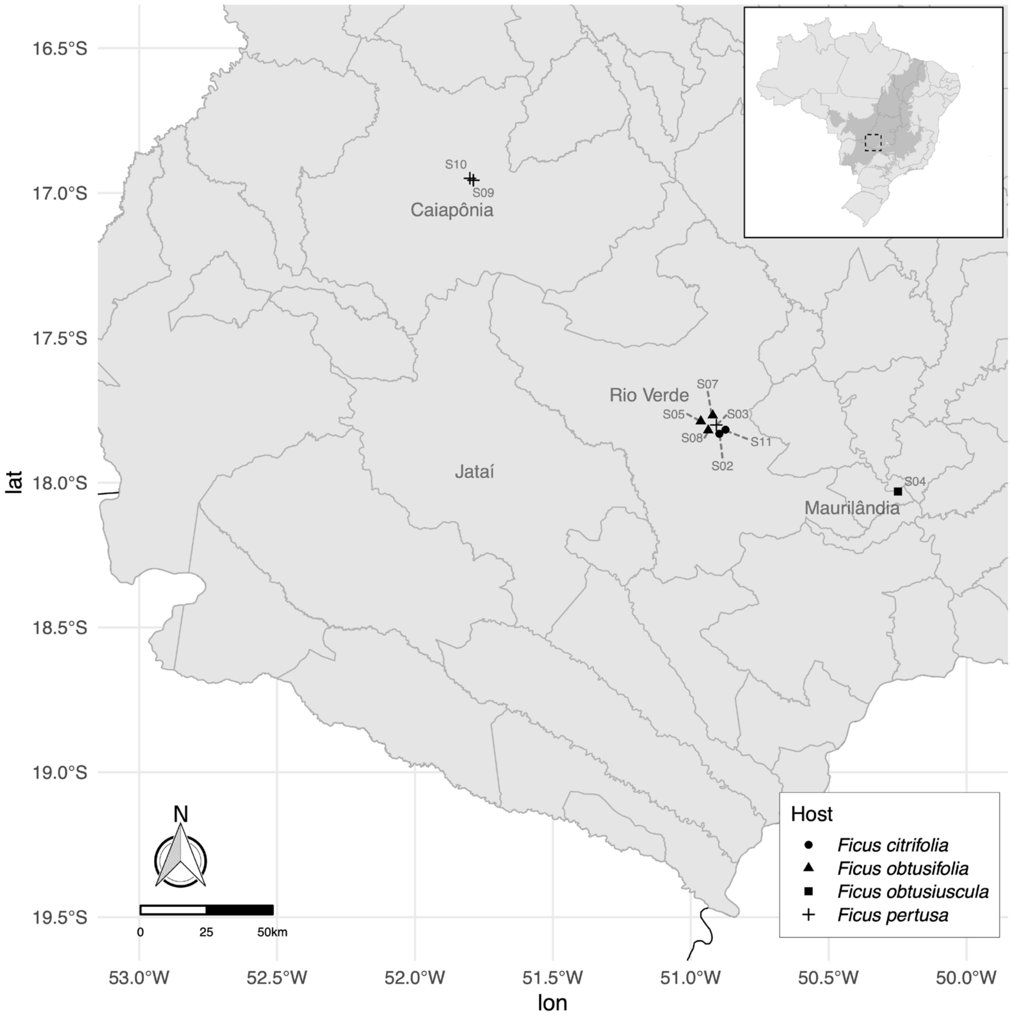

Figure 1 Map showing sampling localities and crops (reproductive episodes) from fig trees sampled in this study. The inset map shows the location of the sampling sites within Brazil and the state of Goiás, also highlighting the Cerrado. Points were jittered to facilitate visualization.

were sampled (Fig. S1), representing all species found during this study except *Ficus adathodifolia*, in which only a single tree was found but not in the reproductive phase. We sampled three species from the *Ficus* section *Americanae: Ficus citrifolia*, which are medium-sized trees with medium-sized figs; *Ficus obtusifolia,* which are larger trees with relatively large figs; and *Ficus pertusa*, which are usually small trees with smaller figs. We also sampled *Ficus obtusiuscula* from *Ficus* section *Pharmacosycea*, which are larger-freestanding trees with small figs (average fig diameters in Table 1; a taxonomic study providing further descriptive information on host species was published by Berg and Villavicencio 2004).

Fig wasps were sampled using two methods: (1) figs were collected and stored in fabric bags until the emergence of the wasps. Wasps were collected with a pooter, killed with ethyl acetate, and transferred to ethanol at 70%. Specimens were later transferred to ethanol 100% and stored at -20°C; (2) about 20 – 30 of the figs collected were individualized in plastic vials. The vials were kept in the laboratory for 24 – 48 hours for wasp emergence and then frozen at -20°C. Species richness and presence-absence data for wasps were estimated for each crop (reproductive episode of a fig tree) with both sampling methods; quantitative data for each crop was obtained with method 2. The wasps were identified to genera using identification keys by Bouček (1993), Rasplus and Soldati (2005) and then sorted into morphospecies. Figs collected with method two were then dissected under a stereomicroscope, and the total number of pistillate flowers for each fig was estimated by the quantification of (1) the total number of seeds; (2) the total number of unpollinated flowers; (3) the total number of undeveloped galls and (4) the total number of wasps. Wasps were identified, quantified, and kept in ethanol 70%. Wasps that did not emerge were removed from their galls and identified. As fig wasp larvae develop in pistillate fig flowers (a single wasp develops in each flower), and each fig species has different amounts of flowers depending on the size, we used the total number of pistillate flowers to standardize the sampling effort by dividing the number of wasps sampled in a host by the number of flowers, as described below.

Life history strategy terminology followed Conchou et al. (2014), Elias et al. (2008), Farache et al. (2018), and F. H. A. Farache (personal observation).

Some specimens from each morphospecies were dried and card-mounted following Noyes (1982). Vouchers (dried and in ethanol) are deposited at the Laboratório de Ecotoxicologia e Sistemática Animal (IFGoiano), Rio Verde, Goiás, Brazil and RPSP collection, FFCLRP, Universidade de São Paulo, Ribeirão Preto, São Paulo, Brazil.

Cluster analysis

To assess the fig wasp fauna similarity in samples collected from the same host species compared to samples from different hosts, we assembled a presence-absence matrix in which species were included as columns and crops as lines. We performed a hierarchical cluster analysis (UPGMA) on Jaccard dissimilarity indices (Legendre and Legendre, 1998). To test the hypothesis of whether the clustering occurred due to host species, we performed a Permutational Multivariate Analysis of Variance (PERMANOVA; Anderson, 2017) on the Jaccard Distance matrix, including the host species as the predictor variable, with 9,999 permutations, using adonis2 function. Analyses were performed in R (R Core Team, 2021) using the package vegan (Oksanen et al., 2019). This analysis allowed us to test whether the fauna associated with samples of the same species would show higher similarity, indicating host specialization.

Fig wasp community analysis

Bipartite interaction networks associating fig wasp species with their host figs were created using quantitative data. The sampling effort was standardized in two ways: (1) the links were weighed by the average number of individuals of each wasp species observed in each fig for each host (2) the total number of wasps belonging to each species for a given host was divided by the total number of pistillate flowers quantified in the syconia.

Besides the visual inspection of community structure, we analyzed diversity indices that indicate host specialization (connectance, H_2' and partner diversity) and food web structure (Nestedness and wNODF) (Bascompte et al., 2006; Dormann et al., 2009; Galeano et al., 2009).

In addition to these indices, the modularity of the community was analyzed using the QuanBiMo algorithm (Dormann and Strauss, 2014) in the quantitative bipartite interaction network. The algorithm has been iterated for 10^8 generations.

Table 1
Characterization of sampling effort in four *Ficus* species (nine crops with 20 figs in each crop) sampled in Cerrado regions in the south of Goiás.

	F. citrifolia (2 crops, 40 figs)	*F. obtusifolia* (3 crops, 60 figs)	*F. obtusiuscula* (1 crop, 20 figs)	*F. pertusa* (3 crops, 60 figs)
Diameter (cm)				
Mean (SD)	1.49 (0.109)	2.36 (0.185)	0.783 (0.0635)	0.713 (0.126)
Median [Min, Max]	1.47 [1.31, 1.78]	2.34 [1.80, 2.76]	0.773 [0.660, 0.983]	0.695 [0.487, 1.21]
Total of flowers				
Mean (SD)	418 (67.2)	634 (241)	86.5 (20.9)	169 (40.2)
Median [Min, Max]	428 [255, 568]	607 [249, 1220]	85.0 [49, 123]	167 [87, 266]
Total of seeds				
Mean (SD)	184 (44.3)	418 (179)	24.6 (13.0)	94.6 (42.3)
Median [Min, Max]	188 [92, 292]	428 [152, 756]	20.5 [4, 52.0]	95.0 [17, 177]
Total of wasps				
Mean (SD)	150 (40.2)	139 (113)	36.5 (16.2)	57.5 (18.3)
Median [Min, Max]	141 [59, 247]	135 [9, 529]	34.5 [13, 70]	57.5 [11, 91]
Total of pollinating wasps				
Mean (SD)	142 (42.4)	133 (114)	21.8 (16.4)	38.1 (22.9)
Median [Min, Max]	130 [51, 247]	125 [1, 529]	18.0 [3, 60]	33.5 [2, 86]
Total of NPFW				
Mean (SD)	7.83 (10.8)	5.45 (9.10)	14.7 (5.10)	19.4 (20.3)
Median [Min, Max]	1.50 [0, 41]	0 [0, 33]	14.0 [4, 23]	14.0 [0, 65]

To access significance for analyzed indices, null models were generated by randomizing the original quantitative network matrix. The null model created by Vázquez et al. (2007) was applied for H_2’, nestedness, wNODF partner diversity, and modularity Q (QuanBiMo) likelihood indices. This null model keeps marginal sums on the quantitative matrix and connectance constant. We applied the Patefield (Patefield, 1981) algorithm for connectance, which keeps the marginal sums constant but allows the connectance to variate. For each algorithm, we ran 1000 null models.

Results

Sampling effort

We have sampled 18,511 wasps from 180 collected figs in nine different crops from four *Ficus* species. The sampled figs varied in size and the number of pistillate flowers (Table 1). *F. obusiuscula* showed the lowest average number of flowers (86.5 ± 20.9, mean ± SD), whereas the highest number was observed in *F. obtusifolia* (634 ± 241). *Ficus citrifolia* showed the highest average number of wasps per syconium (150 ± 40.2) and pollinators per syconium (142 ± 42.4), whilst *F. pertusa* showed a larger average amount of NPFW per syconium (19.4 ± 20.3). Descriptive statistics about the samples are shown in Table 1.

Fig wasp diversity

Thirty-four fig wasp species belonging to 11 genera were collected (Table 2, Figs. S2-S5), from which 12 species were associated with *F. citrifolia*, 11 spp. with *F. obtusifolia*, three spp. with *F. obtusiuscula,* and 12 spp. with *F. pertusa*. Five collected species were pollinators, while four were identified as early gall-inducers. Three species belonging to *Idarnes flavicollis* species-group are considered receptive phase gall-inducers, and 22 species are considered kleptoparasites or parasitoids of other wasps. The life history of *Aepocerus* (3 spp.) and *Critogaster* (2 spp.) is still unclear. *Ficus* species from the *Americanae* section (*F. citrifolia, F. pertusa,* and *F. obtusifolia*) were pollinated by *Pegoscapus* species, while *F. obtusiuscula* (belonging to the *Pharmacosycea* section) was pollinated by *Tetrapus americanus*. *Ficus obtusifolia* presented two pollinating species: *Pegoscapus* sp. 3 and *P.* sp. 4. Eight genera of

Table 2
Fig wasps collected in four host species.

Family (subfamily)	Genus	Species (host)	Life history
Agaonidae (Agaoninae)	*Pegoscapus*	*P. aerumnosus* (*F. citrifolia*)	Pollinator
		P. sp. 2 (*F. pertusa*)	
		P. sp. 3 (*F. obtusifolia*)	
		P. sp. 4 (*F. obtusifolia*)	
Agaonidae (Tetrapusiinae)	*Tetrapus*	*Tetrapus americanus* (*F. obtusiuscula*)	Pollinator
Agaonidae (Sycophaginae)	*Anidarnes*	*A. dissidens* (*F. obtusifolia*)	Early gall-inducer
	Idarnes	*Idarnes carme* species group:	Kleptoparasite
		I. sp 1 (*F. citrifolia* & *F. pertusa*)	
		I. sp. 2 (*F. citrifolia*)	
		I. sp. 4 (*F. pertusa*)	
		I. sp. 9 (*F. citrifolia* & *F. obtusifolia*)	
		I. sp. 15 (*F. obtusifolia*)	
		Idarnes flavicollis species group:	Receptive phase gall-inducer
		I. flavicollis (*F. citrifolia* & *F. obtusifolia*)	
		I. sp. 3 (*F. citrifolia*)	
		I. sp. 5 (*F. pertusa*)	
		Idarnes incertus species group:	Early gall-inducer
		I. dimorphicus (*F. citrifolia*)	
		I. maximus (*F. obtusifolia*)	
Eurytomidae	*Sycophila*	*S.* sp. 1 (*F. pertusa*)	Parasitoid
Pteromalidae (Otitesellinae)	*Aepocerus*	*A. emarginatus* (*F. obtusifolia*)	Kleptoparasite/ parasitoid?
		A. sp. 1 (*F. citrifolia*)	
		A. sp. 9 (*F. obtusifolia*)	
	Heterandrium	*H. flavum* (*F. pertusa*)	Kleptoparasite/parasitoid
		H. sp. 1 (*F. pertusa*)	
		H. sp.2 (*F. pertusa*)	
		H. sp. 3 (*F. citrifolia*)	
Pteromalidae (Pteromalinae)	*Ficicola*	*F.* sp.2 (*F. citrifolia* & *F. pertusa*)	Early gall-inducer
Pteromalidae (Sycoryctinae)	*Critogaster*	*C.* sp. 1 (*F. obtusiuscula*)	Kleptoparasite/parasitoid?
		C. sp. 2 (*F. obtusiuscula*)	
Torymidae	*Physophorax*	*P.* sp. 1 (*F. citrifolia*)	Parasitoid
		P. sp. 2 (*F. pertusa*)	
		P. sp. 3 (*F. pertusa*)	
		P. sp. 4 (*F. obtusifolia*)	
		P. sp. 5 (*F. obtusifolia*)	
		P. sp. 6 (*F. pertusa*)	
	Incertae sedis	Torymidae sp. 1 (*F. citrifolia*)	Parasitoid

NPFW were collected in the *Ficus* section *Americanae*, while only one genus (*Critogaster*) was collected in the *Ficus* section *Pharmacosycea*.

Only four species occurred in more than one host (Table 2). The early gall-inducer *Ficicola* sp. 2 occurred in *F. citrifolia* and *F. pertusa*; *Idarnes* sp. 1 (belonging to *I. carme* species group) occurred in *F. citrifolia* and *F. pertusa*; *I.* sp. 9 (belonging to the *I. carme* sp. g.) occurred in *F. obtusifolia* and *F. citrifolia*, and *Idarnes flavicollis* (belonging to the *I. flavicollis* sp. g.) occurred in *F. obtusifolia* and *F. citrifolia*. *Idarnes* sp. 9 and *Ficicola* sp. 2 occurred in two host species on the qualitative (presence-absence) samples, but *Ficicola* sp. 2 was not observed in quantitative samples, and *Idarnes* sp. 9 was only observed in quantitative samples from *Ficus obtusifolia* (Table 2, Fig. 2).

Most wasp specimens were pollinators in all host species sampled, ranging from 96.1% in *F. obtusifolia* to 59.6% in *F. obtusiuscula*. Early gall-inducers were relatively rare, collected only in *F. citrifolia* (0.036% of the specimens) and *Ficus obtusifolia* (0.29%). Receptive phase gall-inducers were absent in *Ficus obtusiuscula* but represented 1.7% to 4.2% of collected individuals in the remaining *Ficus* species. Kleptoparasites and parasitoids were relatively abundant in *F. obtusiuscula* and *F. pertusa* (respectively 40.4% and 26.9% of collected specimens) but less abundant in *F. citrifolia* and *F. obtusifolia* (respectively 3% and 1.15% of collected specimens).

Cluster analyses

For presence-absence data on fig wasps in each sample, the UPGMA hierarchical grouping on Jaccard distances showed that the samples collected from the same host species clustered together. Faunas of different hosts were quite dissimilar, clustering at Jaccard distances close to 1 (Fig. 3). The PERMANOVA test on the community data matrix corroborated the tendency of samples to cluster by host species (DF = 3, SQ = 2.4, $R^2 = 0.69$, F = 3.66, $P < 10^{-3}$).

Fig wasp community analysis

We observed that pollinator species tended to be dominant in the bipartite networks, being the most abundant species both in the mean abundance network and in the network showing proportions of occupied pistillate flowers (Fig. 2). Only a few species were shared between hosts, and most species were exclusive to one host. The host samples from *Ficus* section *Americanae* and *Pharmacosycea* formed two separate compartments as observed in the qualitative network.

The community showed a significant low connectance index, a high H_2' index, and low partner diversity for both lower and higher levels, which indicate a specialized structure (Fig. 4, Table S1). Regarding community structure, the nestedness index was significantly high

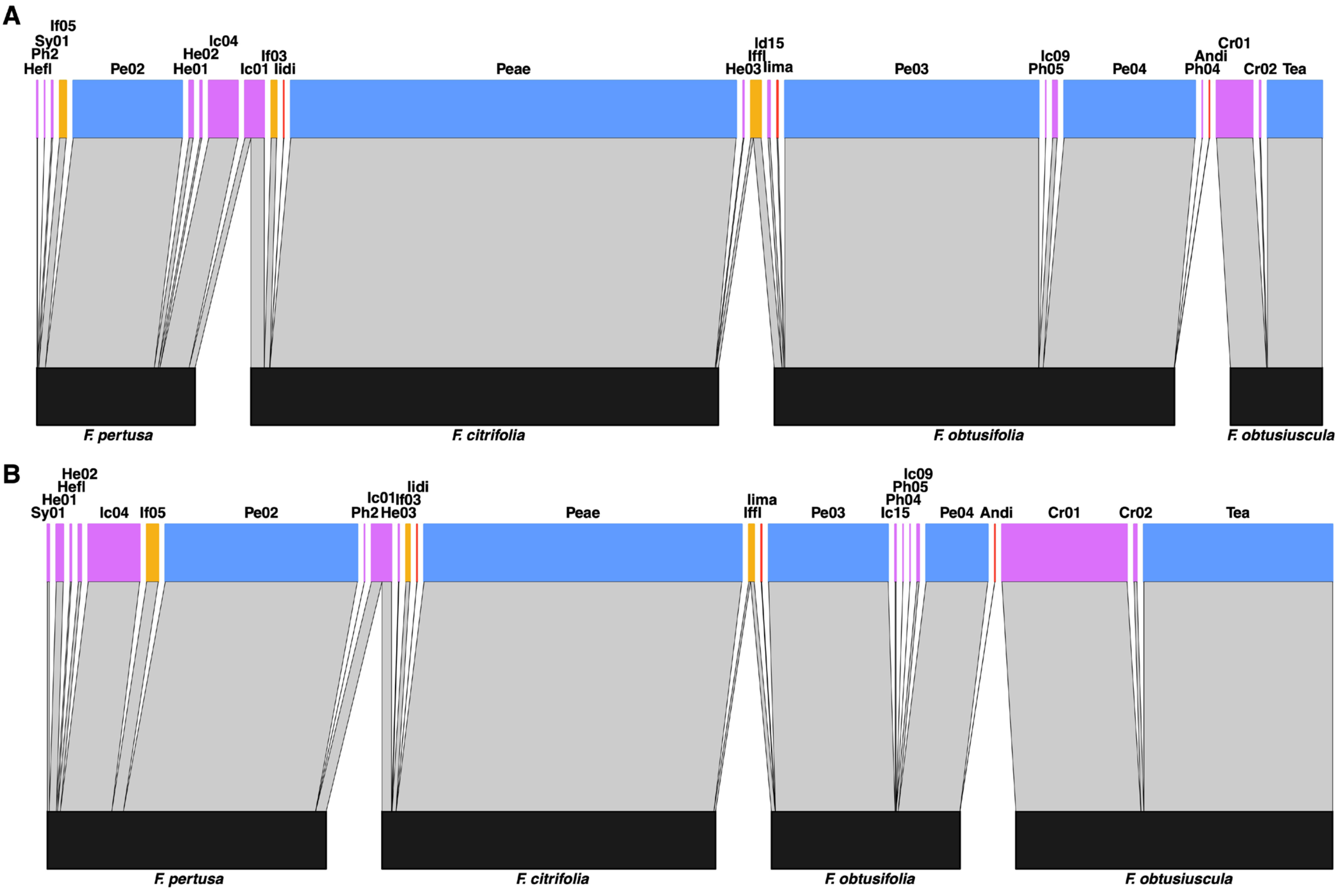

Figure 2 Bipartite quantitative trophic network associating wasps with their fig trees. Rectangles represent the species of wasps (upper level) and fig trees (lower level). Gray strokes represent the presence of interaction. A. Abundance calculated as the average number of individuals per fig analyzed. B Total wasps divided by the number of pistillate flowers. The colors of the upper level indicate the natural history: blue: pollinator; red: early gall-inducer; orange: receptive phase gall-inducer; purple: Kleptoparasite/parasitoid. An = *Anidarnes*; He = *Heterandrium*; Ic = *Idarnes* group *carme*; If = *Idarnes* group *flavicollis*; Ii = *Idarnes* group *incertus*; Cr = *Critogaster*; Pe = *Pegoscapus*; Te = *Tetrapus*; Ph = *Physothorax*; Sy = *Sycophila*; Tr = Torymidae. Species: Aeem = *Aepocerus emarginatus*; Andi = *Anidarnes dissidens*; Hefl = *Heterandrium flavum*; Iidi = *Idarnes dimorphicus*; Iffl = *Idarnes flavicollis*; Iima = *Idarnes maximus*; Peae = *Pegoscapus aerumnosus*.

whilst weighted NODF was non-significant, which indicates a lack of nestedness or failure to detect nestedness. Concerning modularity, the QuanBiMo algorithm Q index suggested that the structure was significantly modular (Figs. 4 and 5).

Discussion

We observed a higher generic diversity in hosts of *Ficus* section *Americanae* with eight genera of NPFW and the pollinator genus *Pegoscapus*, whereas *F.* section *Pharmacosycea* was exclusively associated with *Tetrapus* pollinators and the NPFW genus *Critogaster*. Thus, two independent compartments emerged in the network, represented by each section of *Ficus* and its associated wasps. Indeed, *Ficus* section *Americanae* shows a higher diversity of associated genera (Bouček, 1993), and the two *Ficus* sections seem to show distinct communities.

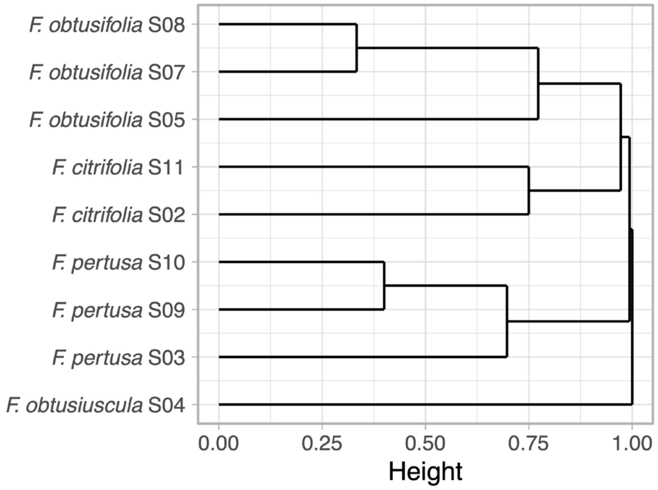

Figure 3 Hierarchical grouping (UPGMA) of the Jaccard distance matrix of the presence-absence data of fig wasps in the sampled crops.

The interaction network established between fig trees and wasps was highly specialized, and most species were exclusive to a single host. The most abundant species in the community were the specialist pollinating fig wasps, and the wasp species that occurred in more than one host were an early gall-inducer (*Ficicola* sp. 2), a receptive phase gall-inducer (*Idarnes flavicollis*), and two kleptoparasites (*Idarnes gr. carme* sp. 1 and sp. 9). This indicates that NPFW showing different life-history strategies may occur in more than one host. Pollinator species did not appear in more than one host. However, *F. obtusifolia* is associated with two pollinating species: *Pegoscapus* sp. 3 and *Pegoscapus* sp. 4. The occurrence of more than one pollinator in the same species of *Ficus* is not rare (Rasplus, 1996; Molbo et al., 2003), and pollinating wasps associated with the same host in the same region may show divergent life-history adaptations that allow coexistence by minimizing competition, such as different longevity and periods of activity (Conchou et al., 2014).

Fig wasp communities often exhibit a conserved structure over different geographic regions, with varying lineages of wasps that occupy similar niches across continents (Segar et al., 2013). These different guilds often present similar life-history strategies and convergent morphological traits. Pollinator species were present within all host species; early gall inducers were not sampled in *Ficus pertusa*, whereas a single early gall-inducer species were present in each other host. Receptive phase gall-inducers seem absent only in *Ficus obtusiuscula*, while kleptoparasites/parasitoids were present in all host species. The life

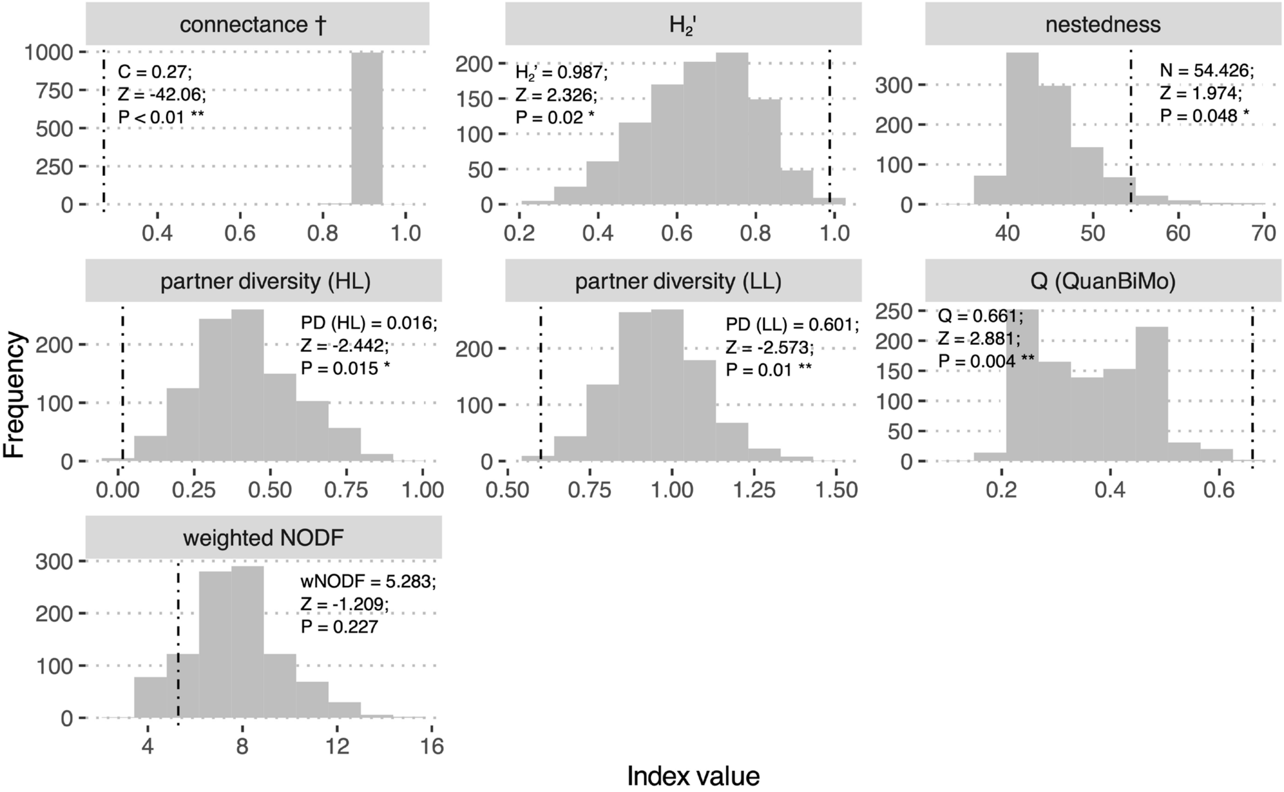

Figure 4 Histograms comparing the index values obtained in null models with the observed values (dashed lines). HL = higher level (wasps); LL = lower level (plants); † null models for connectance obtained using Patefield algorithm.

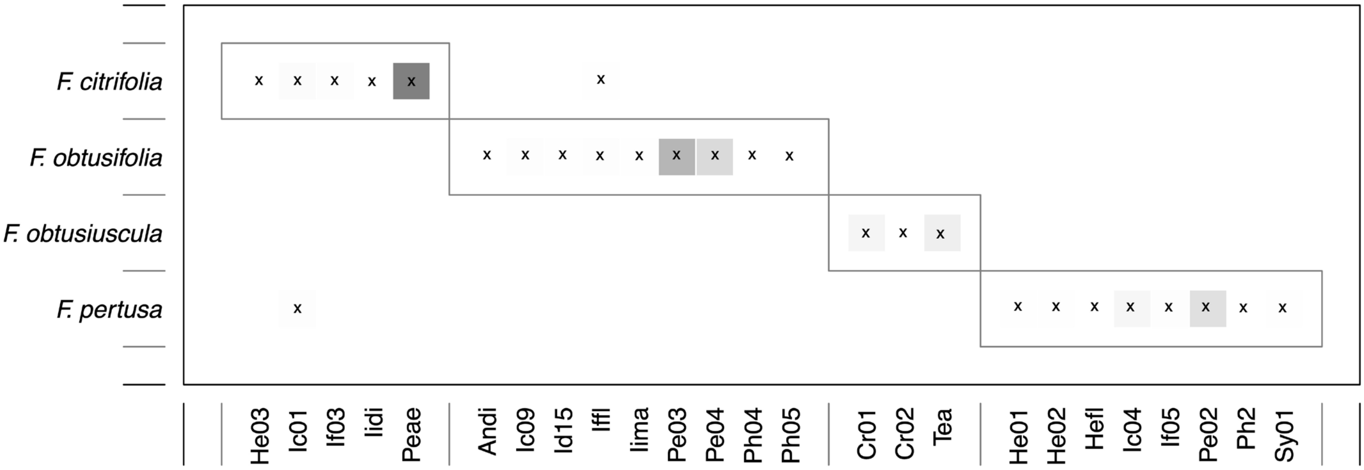

Figure 5 Structure of the quantitative network showing modules evidenced by the QuanBiMo algorithm; "x" indicates the presence of the species in quantitative samples. Wasp species acronyms follow Fig. 2.

history of *Critogaster* is particularly poorly known, yet the presence of species with very different ovipositor lengths (Bouček, 1993) indicate that they may show different life histories. The composition of the community observed here is generally similar to fig wasp communities from other the Brazilian biomes and regions (Pereira et al., 2000; Schiffler, 2002; Nazareno et al., 2007; Farache et al., 2018), though the comparison among fig wasp communities is constrained by the lack of taxonomic information for fig wasps.

A previous study on a Neotropical fig wasp community focused on NPFW species and observed de dominance of relatively generalist *Idarnes* species (Farache et al., 2018). However, in the present study, we observed that the interaction network established was dominated by pollinators, whilst groups showing other life histories were less abundant. Kleptoparasites/parasitoids were also relatively common, at least in *Ficus obtusiuscula* and *Ficus pertusa*. Overall, pollinators tend to be dominant in fig wasp communities (Segar et al., 2013). Nevertheless, figs can become highly infested with NPFW that may even occupy all oviposition sites and exclude pollinators, as observed in *Ficus citrifolia* in some localities, where kleptoparasites belonging to *Idarnes carme* sp. group may significantly affect the abundance of pollinating fig wasps (Elias et al., 2007).

Only 14% of the wasp species analyzed occurred in more than one host. In another study carried out in the neotropical region (Farache et al., 2018), about 45% of the fig wasp species occurred in more than one host; however, that study involved a long-term sampling of wasps over a more comprehensive geographic range which may have allowed observing rarer host associations. It also described a community with different host species composition, with two *Ficus* species, with several morphological affinities (i.e., *F. obtusifolia* and *F. crocata*), sharing an expressive portion of the community as evidenced by cluster and modularity analyses. This suggests that the phylogenetic relationship of the fig trees can, potentially, play a secondary role in the fig wasp community structure. Moreover, community structure indices indicate a specialized structure on the fig wasp community showing low connectance, high bidimensional Shannon H_2', and low partner diversity, indicating specialization. The community structure indices observed here are similar to indices observed in endophytic insect communities, with high modularity and low nestedness (Dormann and Strauss, 2014), indicating a specialized structure.

Conclusion

We described the community of wasps associated with four *Ficus* species within a region of Cerrado in the south of the state of Goiás, in which we found 34 wasp species. The studied community shows a high level of specialization, with only four species that occurred in more than one host. Pollinators were the most abundant species within the community, followed by kleptoparasites/parasitoids. We observed a modular and unnested community structure that seems characteristic of endophagous specialist insects. These results agree with previous knowledge of fig wasp communities worldwide, considered highly specialized, yet differ from studies on some Afrotropical and Neotropical communities, which show high host sharing by wasp species. The observed specialization may be related to the small number of host species, which show divergent fig sizes and habits. The degree of specialization in fig wasp communities may vary over different regions, yet further investigation is encouraged to establish how fig wasp communities and specialization vary geographically and over time.

Acknowledgments

This study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) - Finance Code 001. R.A.S.P. was supported by CNPq (grant # 305793/2018-7). We thank ICMBio/IBAMA for the permit to collect specimens (#69265). The authors thank Marco Antônio Guimarães, Nathan Lima, Rhayane Alves, Samara Ribeiro and Seixas Rezende for assistance in fieldwork.

Conflicts of interest

The authors declare no conflicts of interest.

Author contribution statement

NS, RASP, and FHAF conceived and designed the research; NS, JFA, and FHAF collected the specimens. N.S. and J.F.A. sorted the material. NS and FHAF identified the insect specimens; FHAF prepared the insect collection; NS and FHAF analyzed community data; NS and FHAF wrote the manuscript with major comments from RASP; All authors have approved the final manuscript.

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Supplementary material

The following online material is available for this article:
Figure S1 - Syconia of host Ficus species.
Figure S2 - Fig wasps associated with Ficus citrifolia.
Figure S3 - Fig wasps associated with Ficus obtusifolia.
Figure S4 - Fig wasps associated with Ficus obtusiuscula.
Figure S5 - Fig wasps associated with Ficus pertusa.
Table S1 - Network indices compared to null models.