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Host-parasitoid relationships within figs of an invasive fig tree: a fig wasp community structured by gall size

Running head: Food web of fig wasps in a fig tree

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Abstract

1. Species in a community interact to food webs, whose stability plays a critical role in the maintenance of biodiversity. Host specificity of top predators/parasitoids may determine the stability of food webs, but this is unclear for most insect communities.

2. *Ficus microcarpa* is a native in Asia and Australasia and is becoming increasingly invasive in some tropical and subtropical areas. Besides its species-specific pollinator, its figs also support many ovule-galling and parasitoid non-pollinating fig wasps.

3. Here, based on a global collection of fig wasps associated with *F. microcarpa* figs, we used path analysis, supplemented by within-fig spatial distributions and natal gall sizes to reveal food web structure of its associated fig wasps and the factors forming host ranges of parasitoids.

4. The fig wasp community was species-rich, and parasitoids were far rarer in the plant's introduced range. Parasitoids exhibited some host specificity, and four specific natural enemies of the plant's pollinator were identified with various intensities of effects on pollinator abundance. Parasitoid host ranges were consistent in both ranges of the plant, and mainly restricted by the size and the locations of host galls. No parasitoids were found associated with a unique seed predator.

5. Our results identify how a large number of fig wasp species partition one host fig tree's

figs and identify those species that have potential to control the sexual reproduction of F. microcarpa.

Key words: Ficus, fig wasps, food web, host specificity, parasitoid, gall size

Introduction

Species located at different trophic levels within ecological communities form food webs linking those species that are eaten with those that do the eating. Food webs underpin community structure (Heath et al. 2014, Terborgh 2015) as well as providing a convenient way of summarising trophic interactions within communities, through which top-down regulation contributes to the sustainability of biodiversity and ecosystem function (O'Corner et al. 2009, Estes et al. 2011, Wallach et al. 2015). Species at higher trophic levels prey on those at lower levels, providing regulation that can control prey density and reduce intra-guild competition, with trophic cascades then influencing the abundance of species at even lower trophic levels (Estes et al. 2011). The stability of food webs tends to increase with their complexity, and generalist feeders that have increased connectance may also generate more stability than specialists interacting with fewer species (Pillar et al. 2011, Rooney & McCann 2012). However, the host ranges of predators/parasitoids are still unknown in many insect communities, especially those in the tropics and subtropics, where food webs are often characterized by high local species richness and contribute significantly to global biodiversity. This is partly a consequence of the difficulties involved with describing trophic interactions in more complex food webs, and the issue of cryptic diversity.

Modification and simplification of food webs by human activities can cause the collapse of local communities (Tylianakis et al. 2007; Estes et al. 2011) and can facilitate biological invasions (Dickie et al. 2010; Gurevitch et al. 2011). Utilizing host-specific predators/parasitoids from the native ranges of invasive species is the basis for classical biological control projects, and an understanding of their host ranges and relationships with other species based on the food web structure is a prerequisite when assessing the suitability of agents for deliberate introduction (Keane & Crawley 2002). Furthermore, host ranges of predators/parasitoids are likely to vary in communities with different species compositions (Keane & Crawley 2002), and thus it is necessary to evaluate the consistency of host specificity of candidate biological agents and gain an understanding of the factors restricting their host ranges.

The species-rich genus Ficus is a significant contributor to the sustainability and biodiversity of tropical and subtropical forest ecosystems (Herre et al. 2008; Compton et al. 2010), but a small number of Ficus species have also been introduced outside their natural ranges and become invasive (Richardson 2000; Caughlin et al. 2012). The wider significance of fig trees results from the large number of vertebrates that feed on their figs and disperse their seeds (Shanahan et al. 2001). Figs are complex hollow inflorescences containing tiny male and female flowers on their inner surfaces. Sexual reproduction of the plants relies on adult female pollinating fig wasps (Agaonidae), whose offspring develop in galled ovules in figs (Cook & Rasplus 2003; Liu et al. 2015). Pollinators are almost always host-tree-specific and one or a small number of fig wasp species typically pollinate each tree (Chen et al. 2012; Cruaud et al. 2012).

Besides pollinating agaonids, figs are also exploited by large numbers of non-pollinating fig wasps (NPFW) belonging to Agaonidae and other families of Chalcidoidea (Eurytomidae, Ormyridae, Pteromalidae and Torymidae) (Cook & Rasplus 2003; Cook & Segar 2010; Wang et al. 2015a). Like pollinating fig wasps, most NPFW are believed to have one or only a few host fig tree species (Cook & Segar 2010; Li et al. 2010; Zhou et al. 2012). Females of most NPFW lay their eggs from outside the figs, and their offspring develop in galled ovules and emerge from the figs at the same time as those of the pollinators. NPFW can be allocated into two trophic levels comprising phytophages with larvae that only feed on plant tissues and do not directly kill other fig wasps and parasitoids with larvae that develop at the expense of other species. In addition to killing other wasp larvae, some parasitoid larvae may also consume plant tissue and can be considered as inquilines (Segar & Cook 2012). Most species in Pteromalidae subfamilies Epichrysomallinae and Otitesellinae are believed to be gall formers (Bouček 1988), and Eurytomidae and Sycoryctinae (Pteromalidae) species are generally regarded as parasitoids of epichrysomallines and agaonids, respectively (Compton 1993b; Segar & Cook 2012; Suleman et al. 2013), but exceptions to broad taxonomic generalizations are likely (Pereira et al. 2007; Compton et al. 2009; Chen et al. 2013; Wang et al. 2014; Krishnan et al. 2015). Nevertheless, the exact extent of parasitoid host specificity within each fig wasp community associated with a particular fig tree is poorly understood.

Related fig trees are often pollinated by related agaonids, suggesting that they share long co-evolutionary histories (Cruaud et al. 2012). Some gall-forming NPFW show similar patterns, but parasitoids often appear to be more likely to display host or niche shifts (Segar & Cook 2010; Segar et al. 2013). Nonetheless, niche conservatism induced by morphological characters such as fig size, ovipositor length (reflected by locations of galls inside figs) and gall size contributes to the matches between parasitoids and their hosts, indicating the role of evolutionary constraints in the structuring of fig wasp communities (Dunn et al. 2008; Segar & Cook 2012; Segar et al. 2013).

Ficus microcarpa is a monoecious fig tree that has been widely planted outside its native range. Where the plant's pollinator is also introduced, it has increasingly become invasive (Wang et al. 2015b). Numerous NPFW species can exploit its figs and some can significantly reduce the plant's seed production (Wang et al. 2014; Wang et al. 2015a & b), but their value as potential biocontrol agents depends on an understanding of their trophic relationships. To address this, we sampled the fig wasps associated with the figs of F. microcarpa throughout much of the plant's native and introduced ranges and recorded the sizes and spatial locations of their natal galls within individual figs with the aims of (1) detecting and comparing host ranges of parasitoid fig wasps between the two ranges of F. microcarpa and (2) testing the factors that contribute to fig wasp community structure. Specifically, we asked (1) whether parasitoids are restricted to particular hosts, (2) whether parasitoid host ranges varied between different ranges of the plant, (3) whether the size of galled ovules determines which parasitoids utilize them and generates partially or complete compartments within the food webs and (4) whether the fig wasps that develop in seeds, rather than galls, support a distinct suite of parasitoids.

Materials and methods

Study system

F. microcarpa is a monoecious fig tree with a natural distribution in tropical and subtropical forests of SE Asia and Australasia, where it grows as a strangler or from bare rocks (Berg & Corner 2005). During the last 200 years it has also been transplanted widely as an ornamental and shade tree into many tropical and warm temperate urban areas (Wang et al. 2015a & c). A crop of F. microcarpa can consist of up to several thousand small figs located in the leaf axils, and mature figs are eaten by a wide range of bird species that aid rapid expansion of F. microcarpa populations (Shanahan et al. 2001; Caughlin et al. 2012). It has been regarded as invasive in Bermuda, Florida, and Hawaii and is an expanding nuisance species in urban environments elsewhere (Wang et al. 2015b).

As with other fig trees, sexual reproduction of F. microcarpa is recorded as depending on a host specific pollinating fig wasp, namely Eupristina verticillata Waterston. However, within the native range this taxon represents a complex of several cryptic pollinating species and also one species (Eupristina sp. ‘cheater’) that no longer pollinates the plant (Sun et al. 2011; Wang et al. 2014). Only one of these is known to have been introduced outside the native range (R. Wang, unpublished).

Figs of F. microcarpa are exploited by a large community of NPFW comprising at least 42 species (Wang et al. 2015a). Except for the non-pollinating agaonid, all the known NPFW belong to families of Chalcidoidea other than Agaonidae and lay their eggs in the ovules or seeds via the outer wall of the fig by utilising their long ovipositors (Cook & Segar 2010). Like the agaonids, a single NPFW larva typically completes development inside each ovule. Philotrypesis taiwanensis (Sycoryctinae) is an exception as it is an obligate seed predator, with larvae that consume seeds rather than hosts in galled ovules (Wang et al. 2014). The NPFW are generally specific to F. microcarpa, but a few species may be associated mainly with closely-related Ficus species and only occasionally utilise this host (Zhou et al. 2012; Wang et al. 2015a).

Sample sites and fig wasp faunas

Fig crops were sampled in both the introduced and native ranges of F. microcarpa, with 7 native-range sites located in East and Southeast Asia and 20 sites in the plant's introduced range (Tables S1, Fig. 1a). From December 2010 to July 2013, several F. microcarpa crops were sampled at each site, with each sample comprising at least 10 mature figs that were haphazardly selected from all available heights of the target trees and were stored in 70% ethanol. When dissecting figs, all flowers were identified under a binocular microscope, and were sorted into the following categories: male flowers, seeds, unfertilized and undeveloped female flowers, galls containing wasps, and failed, empty galls. All fig wasps were identified morphologically using primarily Chen et al. (1999) and Feng & Huang (2010), or scored as morpho-species where necessary (Wang et al. 2015a). The higher taxonomy of fig wasps was based on the information shown in figweb (http://www.figweb.org).

Gall sizes

We randomly selected 105 figs (from 22 crops) collected from Panzhihua, Xichang, Xishuangbanna, Taibei and Manila. At least five galls with adult fig wasp offspring were sub-sampled in each fig and their lengths and widths were measured to the nearest 0.04 mm under a dissecting microscope using an eyepiece graticule. Fig wasps inside the measured galls were then identified. The volumes of the galls were calculated assuming their shape to be an ellipsoid.

Spatial stratification of fig wasps

Pedicels elongate after their associated ovules are galled and their lengths can be used to delineate the spatial distribution of the galls in mature figs. Ovules with longer pedicels are located closer to the centre of a fig (Dunn et al. 2008; Yu & Compton 2012). We recorded pedicel lengths in 33 figs from seven F. microcarpa crops collected in Xichang, Xishuangbanna, Bangkok and Kanchanaburi. Pedicel lengths and the contents of their associated ovules were recorded from all the flowers that either developed seeds or were galled. Each fig contained at least three galls occupied by putative parasitoids. Pedicel lengths were measured to the nearest 0.02 mm under a dissecting microscope using an eyepiece graticule and the adult fig wasps inside the galls were then identified.

Statistics

Path analysis

We assigned the fig wasps associated with F. microcarpa into two trophic levels, putative phytophages with larvae that feed exclusively on plant tissue: (mainly ovule-gallers but including the obligate seed-feeder, P. taiwanensis) and putative parasitoids with larvae that develop at the expense of gall forming species (Wang et al. 2015a). The hypothesized relationships between different fig wasp species and seeds in the path analysis model were set as follows (Fig. 1b):

(1) Putative parasitoids were selected initially on the basis of their long ovipositors, supported where possible by experimental data (Rodriguez 2015). This indicates that they lay their eggs into older, larger figs that had been pollinated some time before (Compton et al. 1994; Segar et al. 2013). Parasitoids were expected to negatively influence their host fig wasps (one or more phytophagous species) in the path analysis without affecting seed numbers (Kerdelhué et al. 2000). If any putative parasitoids were found to reduce seed production in the path analysis, then this would suggest they were atypical late-ovipositing phytophages rather than parasitoids. Their negative effects on seed production could then be indicative of either their galls competing with seeds for nutrients, of seed-feeding species that utilise pollinated ovules, or of species with a mixed feeding strategy that combines utilisation of both gall-forming fig wasps and seeds as hosts (Pereira et al. 2007).

(2) Depending on the relative timing of their oviposition, early-ovipositing ovule gallers could potentially have negative effects on other phytophages because they are competing for ovules to utilize and later through competition for nutrients (Wang et al. 2015b). The pollinator clearly facilitates the seed predator. Pollinators were especially

likely to be adversely affected by the ‘cheater’ Eupristina sp. in shared figs and vice versa, because individual females of these species concentrate their oviposition within a single fig after the females enter to oviposit.

(3) All non-pollinating phytophages have the potential for negative impacts on seed production via both competition for oviposition sites and later for competition between galls and seeds for nutrition, while pollinator offspring abundance was expected to be positively linked to seed production.

We only included putative parasitoids appearing in more than 20 figs in either the native or introduced ranges of F. microcarpa into the path analysis. For each putative parasitoid species, only figs containing that species were used. Any other fig wasp species that emerged from less than 30% of these figs were excluded. We did not test for evidence of secondary parasitism in the model (parasitoids developing at the expense of other parasitoids) because two parasitoid species seldomly shared the same fig.

Co-association

Path analysis was unlikely to detect interactions involving less common fig wasp species. We therefore also examined the co-occurrence of parasitoids and their putative hosts within individual figs as a supplementary approach. In a fig occupied by only one species of phytophage and one species of parasitoid it can be assumed that the phytophage is the likely host, thereby allowing rarer associations between parasitoids and phytophages to be identified. This nonetheless assumes that all individuals of alternative phytophagous hosts have not been killed by the parasitoid. In order to avoid such 'false positive' interactions, we only considered species-pairs that were recorded from at least three figs. Figs collected from both ranges were combined together because they were seldomly occupied only by a parasitoid-phytophage pair, and rare species that occurred in less than 10 figs were not considered.

Data analyses

All statistical analyses were carried out using R 3.3.3 setting a hierarchical random effect (figs nested in crops nested in study sites) (R Development Core Team 2017). Likelihood ratio (LR) tests and multiple tests with Bonferroni corrections were used to estimate the significance of fixed effects and pairwise comparisons, respectively. Response variables were square root or natural logarithm transformed where necessary.

We compared the differences in species richness of fig wasps and fig wasp abundance per fig at different trophic levels and parasitoid prevalence between the native and introduced range of F. microcarpa, using Generalized Linear Mixed Models (GLMMs) in R package lme4 version 1.0-5 (Bates et al. 2013), assuming either Poisson or binomial distribution of residuals.

We tested food web structure of fig wasps in the two ranges of the plant based on the path analysis model (Fig. 1b) using Structural Equation Modeling (SEM) in R package piecewiseSEM version 1.2.1 (Lefcheck 2016), assuming Poisson distribution of residuals.

At both species and the generic levels, niche differentiation among phytophages and parasitoids with different hosts was examined by comparing the sizes and pedicel lengths of galls occupied by different fig wasp species/genera using Linear Mixed Models (LMMs) in R package nlme version 3.1 (Pinheiro et al. 2013). Micranisa and Walkerella (Otitesellinae) are closely related genera and were combined, and the seed predator P. taiwanensis was not included in the Philotrypesis spp. Data from both ranges was combined due to limited sample size of parasitoids in the plant's introduced range.

Results

Fig wasp community

We recorded the contents of 2681 figs from 192 crops, including 857 and 1824 figs in the native and introduced ranges of F. microcarpa, and a total of 99038 adult fig wasp offspring were present. We identified a total of 1 pollinating and 31 NPFW morpho-species with 14 and 18 species provisionally identified as phytophages and parasitoids, respectively (Table S2). All morpho-species were detected in figs within the native range of F. microcarpa except three species (Sycobia sp., Bruchophagus sensoriae Chen and Ormyrus sp.). Whereas only 8 parasitoid species were present in the plant's introduced range, most of the phytophagous species were recorded there. The only absences were Walkerella nigrabdomina Ma & Yang and Walkerella sp. (Table S2).

The mean species richness per fig in the plant's native range was significantly higher than that in the introduced range (Table 1). The mean phytophagous species richness was similar in both ranges, but a far higher parasitoid species richness was recorded in the plant's native range (Table 1; Fig. S1). In addition, parasitoids were absent in most figs in the plant’s introduced range, while less than half of the figs did not contain parasitoids in the native range of F. microcarpa, indicating a significant difference in prevalence (Table 1; Fig. S1). There was no significant difference in both total fig wasp abundance and abundance of phytophages between the two ranges, whereas parasitoids in the plant’s native range were much more abundant than those in its introduced range (Table 1).

Path analysis

In the plant’s native range, the four common Sycoryctinae putative parasitoids had specific negative correlations with the pollinating agaonids, and in addition Philotrypesis okinavensis Ishii and Sycoscapter gajimaru Ishii were also negatively associated with Walkerella microcarpae Bouček and Eupristina sp., respectively. Philotrypesis emeryi Grandi imposed the strongest negative effect on the pollinator based on path coefficients (Table S3; Fig. 2a). Another Sycoryctinae species, Sycoryctes sp., which has a very limited geographical distribution, only negatively correlated with the ‘cheater’ Eupristina sp. (Table S3; Fig. 2a). Odontofroggatia spp. were the specific hosts of Sycophila spp. Odontofroggatia galili Wiebes and Odontofroggatia corneri Wiebes were negatively correlated with three Sycophila parasitoids (Sycophila maculafacies Chen, Sycophila maculafacies ‘pale’ and Sycophila petiolata Chen) (Table S3; Fig. 2a). We failed to detect any negative associations between putative parasitoids and seeds and between putative parasitoids and the seed predator, P. taiwanensis, which had a strong negative impact on seed production (Table S3; Fig. 2a).

Only four of the eight parasitoids analyzed in the plant's native range were available for path analysis in the introduced range, and we failed to detect any variation in their host ranges (Table S3; Fig. 2b). Between the two Sycoryctinae species, S. gajimaru exhibited a stronger negative effect on the pollinator than P. okinavensis (Table S3; Fig. 2b). In addition, the parasitoid Bruchophagus sensoriae Chen, which was only recorded outside the plant's native range, was exclusively negatively associated with the epichrysomallid gall former Meselatus bicolor Chen (Table S3; Fig. 2b).

Evidence for both inter-specific competition and facilitation among putative phytophages were present, but these were not consistent throughout all analyses in both ranges (Table S3; Fig 2a & b).

Species associations

Using the figs that contained combinations of one parasitoid and one phytophage species, we identified a total of 15 parasitoid-phytophage associations including two extra trophic interactions, i.e. S. maculafacies and Odontofroggatia quinifuniculus Feng & Huang, and S. gajimaru and W. microcarpae (Table S4).

Gall sizes

The volumes of 1261 galls occupied by 18 fig wasp species were obtained from 105 F. microcarpa figs (Tables S6 & S7). Significant variations in natal gall size were detected among the galls occupied by different genera of phytophages and parasitoids (Table S8). M. bicolor and B. sensoriae were reared from extremely large galls with volumes at least

2.5 times those containing any other species (Table S6; Fig. 3a). We detected no within-genus variation in gall size in any of the phytophages and parasitoids (Table S9). Support for our identified associations between parasitoids and their particular hosts was provided by a lack of any differences in the sizes of galls containing phytophages and their putative parasitoids (Tables S10 & S11; Fig. 3a).

Spatial stratification of fig wasps within figs

Pedicel lengths of 2203 flowers from 33 figs were measured. They included 544 seeds, 98 failed galls, 31 seeds occupied by P. taiwanensis and 1530 galled ovules containing 15 other fig wasp species (Tables S6 & S7). No within-genus variation in host gall pedicel length was detected in any of the phytophages and parasitoids (Table S9). Agaonids and their parasitoids (Philotrypesis spp., Sycoryctes spp. and S. gajimaru) and Otitesellinae spp. and their parasitoids (Philotrypesis spp.) emerged mainly from the more central galls with longer pedicels, while Odontofroggatia spp. and their parasitoids (Sycophila spp.) tended to occupy ovules nearer to the fig wall (Tables S6-S8; Fig. 3b). Similar pedicel lengths of natal galls were found in each parasitoid-host pair (Tables S10 & S11; Fig. 3b).

Discussion

This study has revealed the food web of fig wasps associated with F. microcarpa in both its native and introduced ranges and tested the factors contributing to the formation of the parasitoid host ranges. Path analysis and species associations revealed the major trophic links within the fig wasp community, with most parasitoids being specific at host genus level. Our results also offered evidence for competitive and facilitative interactions among phytophages. Parasitoids associated specifically with the pollinator were present, with the pollinator aggregate (and 'cheater' agaonid) from F. microcarpa being the hosts of five sycoryctine species, as has been recorded for pollinators associated with fig trees native to Africa, Australasia and South America (Compton 1993a; Segar & Cook 2012; Segar et al. 2013). The smaller range of the Eupristina sp. 'cheater' meant that fewer interactions with parasitoids were detected, but its suite of parasitoids was otherwise similar to that of the pollinator. In addition, as recorded by Compton et al. (1993b) in Africa, epichrysomallines were the exclusive hosts of eurytomids. The apparent absence from the plant's native range of B. sensoriae, a specific parasitoid of M. bicolor, requires further investigation, but may reflect a species that is rare, but not absent, there. No parasitoids were detected in association with P. taiwanensis. It is an example of a major shift to phytophagy from parasitoid ancestors, and utilisation of this novel resource appears to have provided it with 'enemy-free space' within the figs (e.g. Rodriguez et al. 2015).

All parasitoids that are common to both ranges of F. microcarpa displayed consistent host ranges, suggesting that factors independent of locally-varying environments play a role in determining these host-parasitoid relationships. Body size differences among fig wasps reflect the size of their galls, and size has been identified previously as a potential driver of galler-parasitoid specificity inside figs (Segar et al. 2013). In the present study, all genera of phytophages with different gall sizes supported distinct groups of parasitoids except for the Otitesellines. Otiteselline species produce galls that are slightly (though significantly) larger than those of agaonids, and were acting as hosts for some sycoryctines that usually develop inside the galls of agaonids. Given the high species richness of some Sycoryctinae genera (e.g. Zhou et al. 2012) and their known trophic diversity (e.g. Wang et al. 2014), it is likely that some species are moderately flexible in their host relationships.

Parasitoid host specificity to particular higher taxa has been described in previous fig wasp community studies (Dunn et al. 2008), and suggests a co-evolutionary history between parasitoids and their hosts (Segar & Cook 2010; Segar et al. 2013). Hoever, insofar as related species tend to generate similar sized galls, it is hard to separate gall size effects from phylogenetic history. Within groups with similar-sized galls, host specificity was not evident. For example, there was no evidence for particular Sycophila species being associated with individual Odontofroggatia species, whereas the related species (M. bicolor) that produce exceptionally large galls appears to evade Sycophila species. The widespread breakdown of host specificity at the host species level indicates a lack of niche differentiation within each gall-size group and suggests that gall size, rather than taxonomic affiliation per se is the main driver of host relationships in F. microcarpa figs. This pattern exists in some other fig wasp communities (Segar et al. 2013), but exceptions have also been reported, such as the Apocrypta parasitoid from F. sur, which utilizes galls with varying sizes and displays a strikingly wide range of body sizes (Compton & Robertson 1988).

Galls of different sizes are not distributed randomly within F. microcarpa figs. The concentration of larger galls towards the periphery and smaller galls towards the centre reflects variations in ovule selection by ovipositing females belonging to different species and possibly also differences in the extent to which they stimulate pedicel extension (Dunn et al. 2008; Yu & Compton 2012). For parasitoids that oviposit at developing stages of figs, species associated with smaller galls therefore require longer ovipositors than those that utilise larger galls. Such spatial stratification of galls is therefore indicative of niche diversification of different fig wasps.

There is a rising awareness of the importance of mutualistic organisms in biological invasions (Richardson et al. 2000; Dickie et al. 2010). However, the host-specific species that can attack mutualists are still seldom considered for biological control. Parasitoids of pollinating agaonids can regulate pollinator populations (e.g. Suleman et al. 2013) and indirectly affect seed production by reducing the number of female pollinators entering figs, but in general they release greater impact on pollinator offspring density than on seed production (Dunn et al. 2008; Segar & Cook 2012). All the four Sycoryctinae species that utilised E. verticillata showed the same host ranges in both geographical ranges of F. microcarpa, but P. okinavensis and S. gajimaru were less specific to the pollinator, and P. emeryi imposed a stronger impact on the pollinator than Sycoryctes moneres based on path coefficients and is a potential candidate for aiding biological control of the tree. In addition, P. taiwanensis has the potential to be utilized together with the pollinator’s natural enemies because this seed predator can significantly reduce seed production and is independent of parasitoids. Though our results provided a species pool for the biological control of F. microcarpa, it is essential to carry out risk assessments for all potential biocontrol agents, which includes rigorous pre-introduction testing and the reconstruction of their phylogenies to evaluate their adaptations, effects and invasiveness in the sites where F. microcarpa is invasive.

In conclusion, we have constructed the food web of common fig wasps associated with a widespread invasive fig species. The host ranges of parasitoid fig wasps were consistent in both native and introduced ranges of the plant and were compartmented by both the size and the locations of host galls. Based on their host specificity and effects on pollinator abundance and seed production, some species exhibited the potential to act as useful biocontrol agents though further studies are needed to ensure their safety and effectiveness.

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Table 1. Comparisons of species richness of fig wasps and fig wasp abundance per fig (mean ± S.E.) at different trophic levels and parasitoid prevalence between the native and introduced ranges of F. microcarpa based on likelihood ratio (LR) tests using GLMMs assuming either Poisson or binomial distribution of residuals.

	Overall	Native range	Introduced range	Native vs. Introduced range	
				df	LR
Total species richness	1.96 ± 0.02	2.65 ± 0.05	1.64 ± 0.02	1	7.47 **
Species richness of phytophages	1.55 ± 0.02	1.79 ± 0.03	1.44 ± 0.02	1	1.49 NS
Species richness of parasitoids	0.41 ± 0.01	0.86 ± 0.03	0.20 ± 0.01	1	9.68 **
Total fig wasp abundance	36.94 ± 0.64	50.14 ± 1.27	30.74 ± 0.68	1	3.43 NS
Phytophage abundance	2.41 ± 0.11	4.79 ± 0.25	1.29 ± 0.09	1	1.91 NS
Parasitoid abundance	34.16 ± 0.65	45.18 ± 1.32	28.99 ± 0.68	1	9.41 **
Parasitoid prevalence (%)	29.32	53.44	17.98	1	10.40 **

NS: not significant; **: $p<0.01$.

Figure legends

Fig. 1. Distribution of sample sites (a) and path analysis model used to test the host-parasitoid relationships for each parasitoid species (b). (a) Triangles and squares represent sites in the plant's native and introduced ranges, respectively. (b) Arrows represent the directions of effects, with black and open arrows indicating potential negative and positive effects respectively.

Fig. 2. Food web diagrams of the fig wasp community in the native (a) and introduced (b) range of F. microcarpa based on the results of SEM. Black and grey arrows represent significant and insignificant effects which were assumed as shown in Fig. 1, and path coefficients (mean ± S.E.) were provided for all effects.

Fig. 3. Volumes (a) and pedicel lengths (b) of galls containing fig wasp species or genera. Line, box, whiskers, black squares and black triangles represent the median, the range from the first to third quartile, 1.5 times lower and upper quartiles, mean and minimum and maximum values of pedicel lengths in each utilization type. **EP** Eupristina spp.; **MS** Meselatus; **OD** Odontofroggatia spp.; **OT** Otitesellinae spp.; **BC** Bruchophagus; **SP** Sycophila spp.; **PL** Philotrypesis spp. excluding P. taiwanensis; **SR** Sycoryctes spp.; **SS** Sycoscapter.

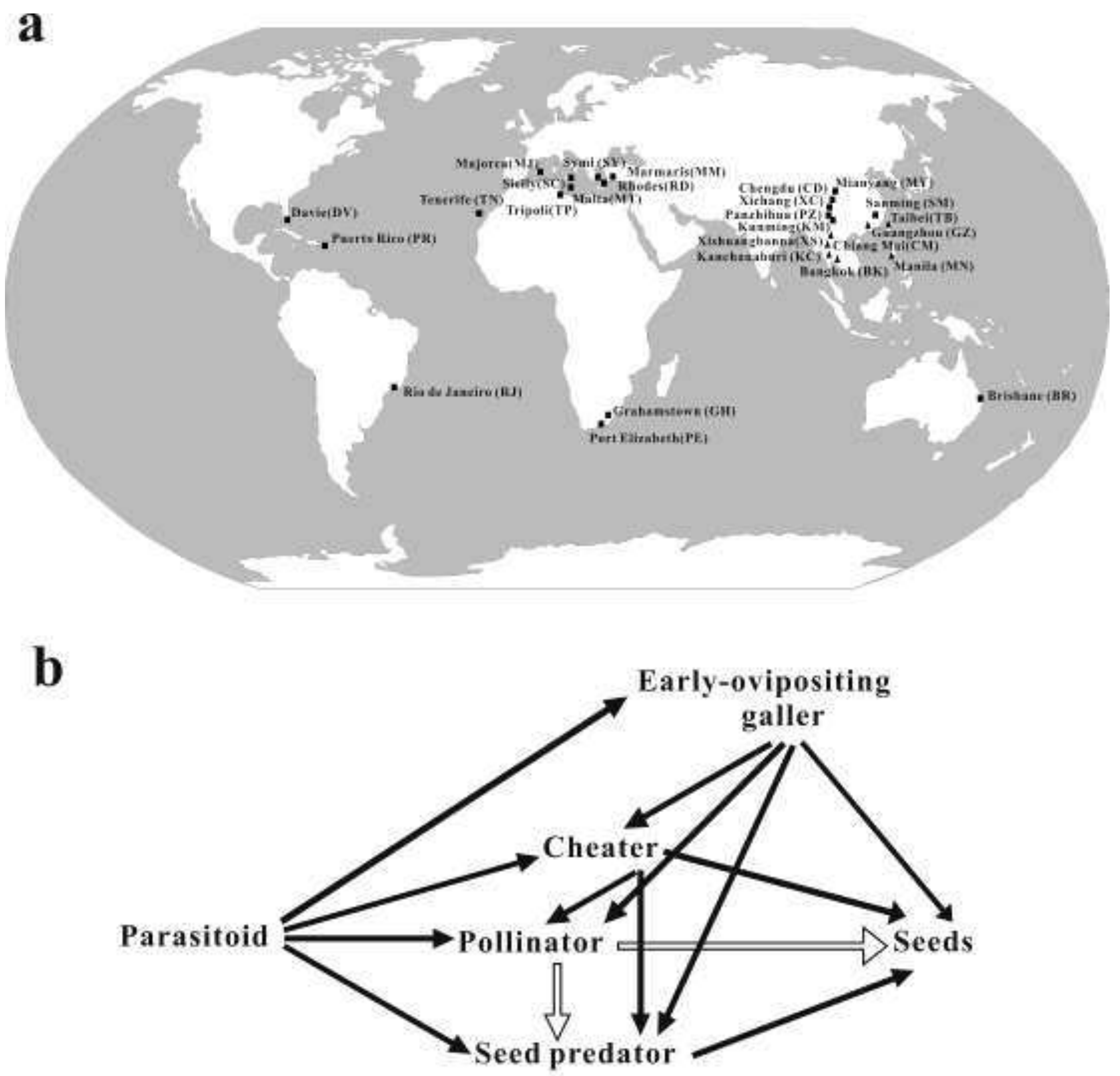
a
Majorca(MJ)
Symi (SY)
Marmaris(MM)
Sicily(SC)
Rhodes(RD)
Malta(MT)
Tenerife(TN)
Tripoli(TP)
Davie(DV)
Puerto Rico (PR)
Chengdu (CD)
Mianyang (MY)
Xichang (XC)
Panzhihua (PZ)
Kunming(KM)
Sanming (SM)
Taibei(TB)
Guangzhou (GZ)
Xishuangbanna(XS)
Chiang Mai(CM)
Kanchanaburi (KC)
Bangkok (BK)
Manila (MN)
Rio de Janeiro (RJ)
Grahamstown (GH)
Port Elizabeth(PE)
Brisbane (BR)
b
Early-ovipositing galler
Cheater
Parasitoid
Pollinator
Seeds
Seed predator

Fig. 1.

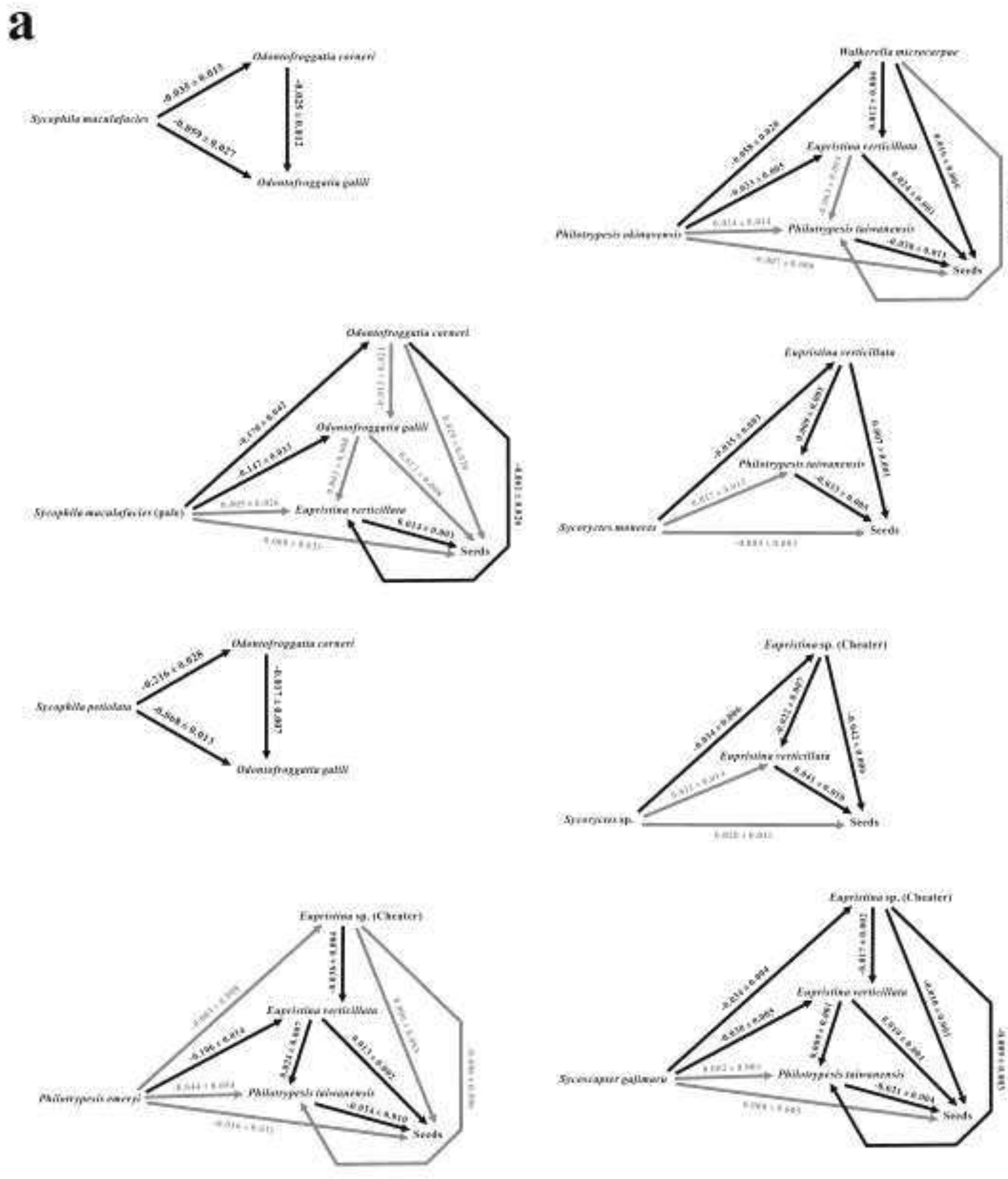
a
Sycophila maculafacies
Odontofroggatia corneri
Odontofroggatia galili
-0.035 ± 0.015
-0.059 ± 0.027
-0.025 ± 0.011
Walkerella microcarpae
Eupristina verticillata
Philotrypesis okinavensis
Philotrypesis taiwanensis
Seeds
-0.058 ± 0.028
-0.033 ± 0.004
-0.012 ± 0.004
0.016 ± 0.005
0.024 ± 0.003
-0.038 ± 0.011
0.014 ± 0.014
Sycophila maculafacies (gals)
Odontofroggatia corneri
Odontofroggatia galili
Eupristina verticillata
Seeds
-0.176 ± 0.042
-0.147 ± 0.033
0.014 ± 0.003
Eupristina verticillata
Philotrypesis taiwanensis
Sycoryctes moneta
Seeds
-0.035 ± 0.003
0.009 ± 0.003
0.007 ± 0.001
-0.033 ± 0.004
Sycophila petiolata
Odontofroggatia corneri
Odontofroggatia galili
-0.216 ± 0.028
-0.068 ± 0.013
-0.037 ± 0.007
Eupristina sp. (Cheater)
Eupristina verticillata
Sycoryctes sp.
Seeds
-0.034 ± 0.006
-0.022 ± 0.007
-0.042 ± 0.009
0.041 ± 0.019
Eupristina sp. (Cheater)
Eupristina verticillata
Philotrypesis emeryi
Philotrypesis taiwanensis
Seeds
-0.036 ± 0.004
-0.106 ± 0.024
0.032 ± 0.007
-0.013 ± 0.002
-0.034 ± 0.010
Eupristina sp. (Cheater)
Eupristina verticillata
Sycoscapter gajimaru
Philotrypesis taiwanensis
Seeds
-0.034 ± 0.004
-0.030 ± 0.005
-0.017 ± 0.002
0.019 ± 0.001
-0.016 ± 0.005
-0.021 ± 0.004

Fig. 2a.

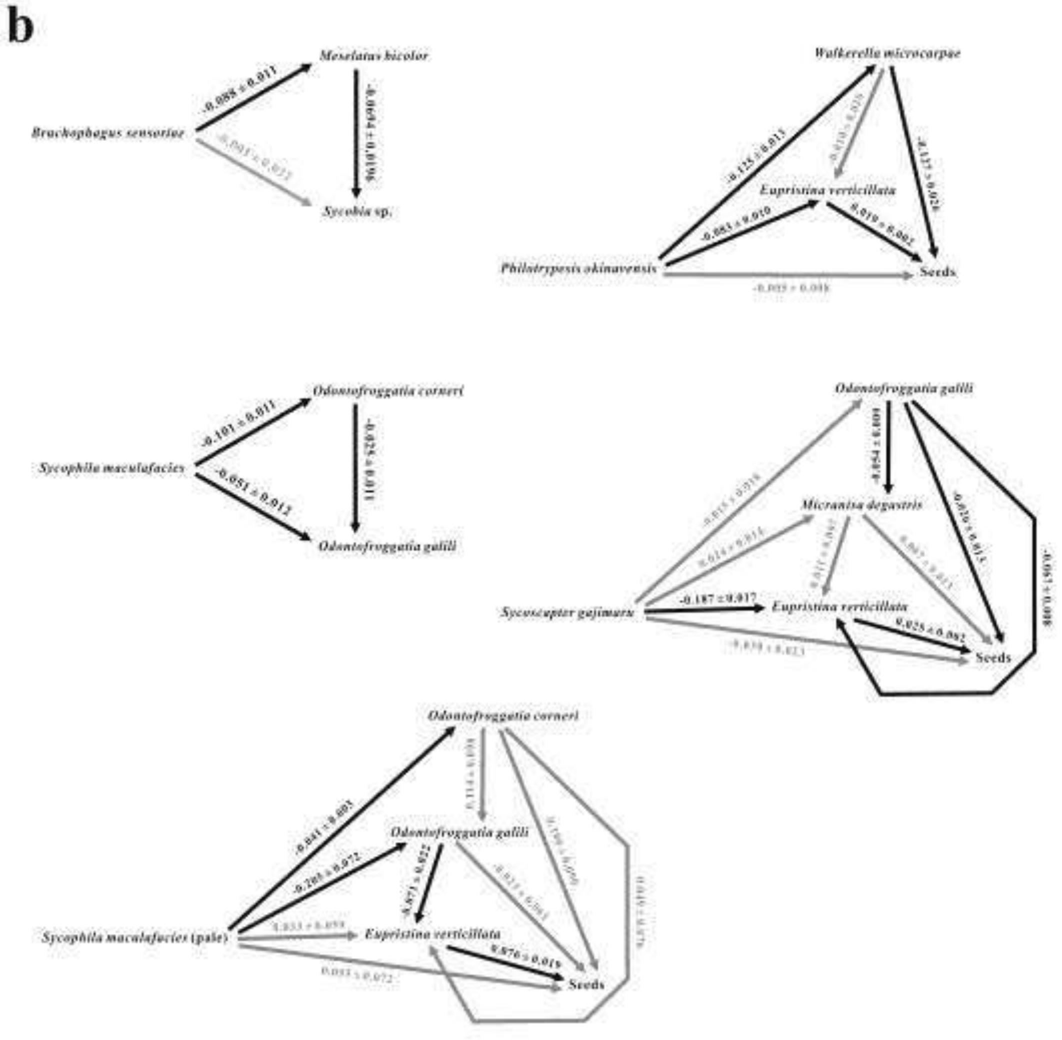
b
Meselatus bicolor
Bruchophagus sensoriae
Sycobia sp.
-0.088 ± 0.011
-0.0694 ± 0.0106
Walkerella microcarpae
Eupristina verticillata
Philotrypesis okinavensis
Seeds
-0.125 ± 0.013
-0.083 ± 0.010
0.019 ± 0.002
-0.127 ± 0.026
Odontofroggatia corneri
Sycophila maculafacies
Odontofroggatia galili
-0.101 ± 0.011
-0.051 ± 0.012
-0.025 ± 0.011
Odontofroggatia galili
Micranisa degastris
Sycoscapter gajimaru
Eupristina verticillata
Seeds
-0.054 ± 0.004
-0.020 ± 0.013
-0.061 ± 0.008
-0.187 ± 0.017
0.025 ± 0.002
Odontofroggatia corneri
Odontofroggatia galili
Sycophila maculafacies (pale)
Eupristina verticillata
Seeds
-0.041 ± 0.003
-0.205 ± 0.072
-0.071 ± 0.022
0.076 ± 0.019

Fig. 2b.

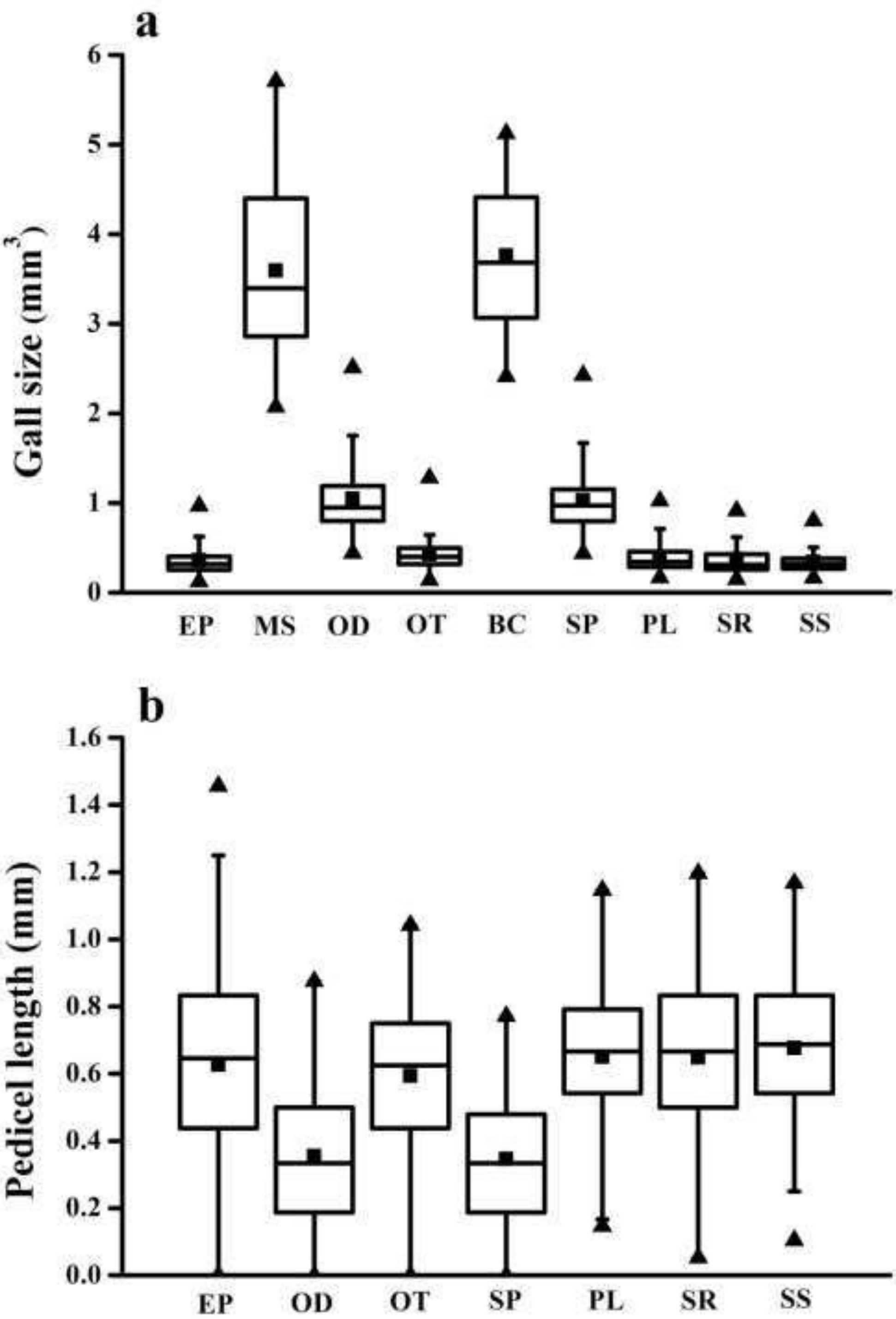
a
Gall size (mm³)
0
1
2
3
4
5
6
EP
MS
OD
OT
BC
SP
PL
SR
SS
b
Pedicel length (mm)
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
EP
OD
OT
SP
PL
SR
SS

Fig. 3.