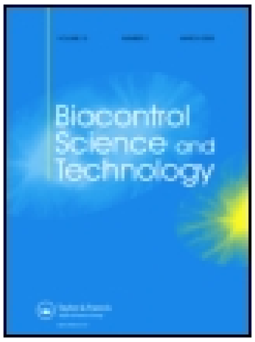


Taylor & Francis
Taylor & Francis Group

Biocontrol Science and Technology

ISSN: 0958-3157 (Print) 1360-0478 (Online) Journal homepage: http://www.tandfonline.com/loi/cbst20

Non-pollinator fig wasp impact on the reproductive success of an invasive fig tree: why so little?

Yue Kong, Rong Wang, Da-Rong Yang, Rachakonda Sreekar, Yan-Qiong Peng & Stephen G. Compton

To cite this article: Yue Kong, Rong Wang, Da-Rong Yang, Rachakonda Sreekar, Yan-Qiong Peng & Stephen G. Compton (2016): Non-pollinator fig wasp impact on the reproductive success of an invasive fig tree: why so little?, Biocontrol Science and Technology, DOI: 10.1080/09583157.2016.1214862

To link to this article: http://dx.doi.org/10.1080/09583157.2016.1214862

Publisher: Taylor & Francis & Informa UK Limited, trading as Taylor & Francis Group
Journal: *Biocontrol Science and Technology*
DOI: 10.1080/09583157.2016.1214862

Running head:

Fig tree and fig wasp interaction

Title:

Non-pollinator fig wasp impact on the reproductive success of an invasive fig tree: why so little?

Authors: Yue Kong [a, b], Rong Wang [c], Da-Rong Yang [a], Rachakonda Sreekar [a,b], Yan-Qiong Peng [a], Stephen G. Compton [c, d]

[a] Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Kunming, China

[b] University of Chinese Academy of Science, Beijing, China

[c] School of Biology, University of Leeds, Leeds, UK

[d] Department of Zoology and Entomology, Rhodes University, Grahamstown, South Africa.

(Received 13 January, 2016; Returned 11 April; Accepted 13 July, 2016)

Correspondence: Yan-Qiong Peng, email: pengyq@xtbg.ac.cn

Abstract

Classical biological control agents fail to achieve an impact on their hosts for a variety of reasons and an understanding of why they fail can help shape decisions on subsequent releases. Ornamental *Ficus microcarpa* is a widely planted avenue fig tree that is invasive in countries where its pollinator (*Eupristina verticillata*) is also introduced. This tree also supports more than 20 species of non-pollinating fig wasps (NPFW) that feed in the figs and have the potential to reduce the plant’s reproduction. *Odontofroggatia galili*, one of the most widely introduced NPFW, has larvae that develop in galled ovules that might otherwise develop into seeds or support pollinator larvae. We examined the distribution and relative abundance of the pollinator and *O. galili* on *F. microcarpa* in China, towards the northern limit of the tree’s natural range and in Italy, where the two species have been introduced. Where they co-existed, we also recorded the impact of varying densities of *O. galili* on *F. microcarpa* seed and pollinator production. *O. galili* and *E. verticillata* displayed contrasting habitat preferences in China, with *O. galili* almost absent from warmer sites. *O. galili* abundance and sex ratios varied between the natural and introduced ranges. Figs with more *O. galili* contained fewer seeds and pollinator offspring, but reproduction was rarely inhibited totally. Additional species with a greater impact in the figs they occupy are needed if biocontrol of *F. microcarpa* is to be effective.

Key words Biocontrol, fig wasps, fig trees, mutualism, gall, *Odontofroggatia*

1. Introduction

Classical biological control attempts to control weeds that have become invasive using plant-feeding insects or diseases that originate in the plant's natural range (Culliney 2005). Most biological control agents that are released become established, but only a proportion of these have any significant impact on their hosts (Julien, and Griffiths 1998; McFadyen 2003) and an understanding of why established species have little impact can help shape decisions on subsequent releases (Myers 2000). Low-efficacy agents may fail to reach sufficient densities or are otherwise insufficiently damaging to have a significant impact on host plant population dynamics. Reasons given for failure of biological control programs include interference by local natural enemies of agents, poor climate matching and a lack of complementary alternative hosts (Stiling 1993; Rand, Waters, and Shanower 2016). Alternatively, biological features of potential agents may mean that they are never likely to have a noticeable impact on their host plants (McClay, and Balciunas, 2005).

Fig trees (*Ficus*, Moraceae) are a species-rich group distributed in warmer countries throughout the Old and New Worlds (Harrison 2005). They are of great ecological significance because of the many animals that feed on their figs (syconia) (Shanahan, So, Compton, and Corlett 2001), but this wide range of seed dispersal agents also results in the rapid dispersal of any ripe figs produced by fig trees growing outside their natural range (Simberloff, and Von Holle, 1999). Mature figs (and fertile fig seeds) are produced after young figs are pollinated by a fig tree's host-specific pollinator fig wasps (Hymenoptera, Agaonidae). To achieve pollination, adult female fig wasps seek out receptive young figs, using volatile attractant cues (van Noort, Ware, and Compton 1989). Because fig crops are often synchronized within trees, this usual means that they must fly between trees, which can be tens or even hundreds of kilometers apart (Ahmed, Compton, Butlin, and Gilmartin 2009). Foundresses (reproductive female fig wasps) lose their wings and antennae when they enter a fig through its narrow ostiole (Janzen 1979). Once inside a suitable fig they can pollinate some of the flowers and at the same time they gall and lay eggs in some of their ovules. A single pollinator offspring develops inside each galled ovule. The next generation of fig wasps emerge from their galls a few weeks later and after mating and becoming loaded with pollen the female offspring disperse to find receptive figs (Weiblen 2002).

Figs are also exploited by a diverse community of non-pollinating fig wasps (NPFW) that almost never transfer pollen. NPFW exhibit a wide range of trophic relationships, with larvae that feed inside ovules and seeds or in the fig wall. They include gallers, seed predators, secondary gallers, parasitoids (that may also feed on some plant tissue) and specialist hyper-parasitoids (Compton, van Noort, Mcleish, Deeble, and Stone 2009; Chen, Yang, Gu, Compton, and Peng 2013; Wang et al. 2014). Most of these species will have a negative impact on the reproductive success of fig trees because they kill pollinators and reduce seed numbers (Kerdelhué, and Rasplus, 1996), and fig ovules may be particularly easy to be eaten because the plant cannot defend them chemically without harming its pollinators (Cook, and Rasplus, 2003).

Fig trees are widely planted as ornamental and avenue trees outside their native ranges. They can only reproduce sexually if their associated host-specific pollinators are also present, but this has not prevented them from becoming invasive in natural and semi-natural habitats (Stange, and Knight Jr, 1987; McKey 1989). *Ficus microcarpa* L. f.

is the most widely naturalised and invasive fig tree. An Asian native, it is grown in almost every tropical and sub-tropical country world-wide. Its pollinator fig wasp was deliberately introduced into Hawaii (Beardsley 1998) but unauthorised releases have led to pollinators becoming increasingly widely distributed and they are now present throughout most of their host's introduced range. Often the tree remains a minor urban pest, with its seedlings causing architectural damage, but after expansion into natural habitats it has become invasive in Hawaii, Florida, Bermuda and elsewhere (Hilburn, Marsh, and Schauff 1990; Nadel, Frank, and Knight Jr 1992; Simberloff, and Von Holle, 1999; Starr, Starr, and Loope 2003). Increasing numbers of NPFW species associated with *F. microcarpa* have also been introduced outside their natural range. The two most widely introduced NPFW are two species that gall the ovules, *Walkerella microcarpae* Bouček and *Odontofroggatia galili* Wiebes (both Pteromalidae). Interactions between *O. galili* and *F. microcarpa* were investigated by Kobbi et al. (1996) in Tunisia. They confirmed that this NPFW had a negative impact on the numbers of pollinators and seeds present in shared figs.

Biological control of fig trees using insects has never been attempted, though Miao et al. (2011) suggested that a gall midge (Cecidomyiidae) associated with *F. benjamina* might prove effective at reducing seed and pollinator production in that species. It is known that natural enemies with female-biased sex ratios can potentially increase their population sizes more rapidly than species with balanced sex ratios. *O. galili* of *F. microcarpa* has several characteristics that suggest it might be an effective control agent. This species is host specific, has female-biased populations and does not require pollinated figs for development, which should aid population persistence when pollinator numbers are low. Here we address the following questions that together seek to explain why *O. galili* does not have a more significant impact on the reproduction of its host plant. (1) Within and adjacent to the natural distribution of *F. microcarpa*, do *O. galili* and the tree's pollinator display different habitat preferences? (2) How abundant are *O. galili* galls and is their abundance similar in the native and introduced ranges? (3) What is the relationship between *O. galili* gall density and host plant reproductive success?

2. Materials and methods

2.1. Study species

F. microcarpa, the Indian laurel fig or Chinese banyan, (previously often referred to as *F. retusa* L. or *F. retusa* var *nitida* – see Corner 1960) is a medium to large sized tree with a wide natural distribution extending from Australia northwards to Japan and westwards to India, found growing as a hemi-epiphytic strangler or free-standing tree in coastal and riparian forests and on cliffs (Berg, and Corner 2005). *F. microcarpa* is also widely grown as an avenue tree, both in its native and introduced ranges. Within its natural range, *F. microcarpa* figs are produced year round, usually in discrete crops, but fewer crops are produced in colder seasons (Corlett 1984; Lin, Zhao, and Chen 2008; Yang, Tzeng, and Chou 2013). Its mature figs are pink or purple in colour and average 13 mm in diameter (SE = 0.08, n = 21 figs). They are mainly dispersed by birds (Shanahan, So, Compton, and Corlett 2001), with secondary seed dispersal by ants (Kaufmann, Mckey, Hossaert-Mckey, and Horvitz 1991). Large crops can number many thousands of figs. *F. microcarpa* is a monoecious species, with individual figs capable of supporting both seeds and pollinator fig wasps, as well as NPFWs. The tree's pollinator is recorded as *Euptistina verticillata* Waterston, but this taxon may be a complex of closely related species (Sun, Xiao, Cook, Feng, and Huang 2011). In Yunnan, China there is also an undescribed species of 'cheater' non-pollinating agaonid associated with *F. microcarpa* (Martinson et al. 2014)

F. microcarpa supports a diverse community of NPFW, comprising more than 20 species (Chen, Chuang, and Wu 1999; Wang et al. 2015), several of which have been introduced outside their natural ranges. Amongst these, *O. galili* (Pteromalidae, Epichrysomallinae) is now present in the Pacific (Beardsley 1998), the Americas (Bouček, 1993), Africa (van Noort,Wang, and Compton 2013), Europe (Compton 1989; Lo Verde, Porcelli, and Sinacori 1991) and the Middle East (Galil, and Copland 1991), including areas such as Hawaii where *F. microcarpa* is invasive. *O. galili* is probably restricted to *F. microcarpa*, though there is a single unconfirmed record from a distantly related fig tree (Bouček 1988). *O. galili* females lay their eggs into ovules while standing on the outside of the figs at about the time that pollinator females enter the figs to oviposit (Galil, and Copland 1981). Their larvae develop inside larger galls than pollinator larvae. *Sycophila* (Eurytomidae) species are NPFW with larvae that develop at the expense of epichrysomallines, including *Odontofroggatia* (Compton 1993). These specialist parasitoids have been introduced with *O. galili* into the USA and Greece (Beardsley, 1998; Wang R, unpublished data). One *Sycophila* larva develops inside each ovule galled by *O. galili* and their numbers were combined in some analyses to estimate pre-parasitism densities of *O. galili* in the figs.

2.2. Study sites

The relationship between *O. galili* and its host plant's reproductive success was compared on the basis of collections from Sicily, an island in the Mediterranean Sea where *F. microcarpa* was introduced (Lo Verde, Porcelli, and Sinacori 1991), and several sites in Yunnan Province, south-west China, at and probably beyond the northern limit of the natural distribution of the tree. NPFW in Yunnan are diverse, with around 15 species present, compared with three NPFW species that have been introduced into Sicily, two of which are rare (Wang et al. 2015). Locations of the Yunnan collection sites, with their altitudes and habitats, are given in Table S1. The ten Sicilian collections were all made in July 2012 from street trees in Palermo, at an altitude of approximately 29 m.

2.3. Fig wasp collections

F. microcarpa trees were sampled at times when almost mature figs, without exit holes, were present. The figs were collected haphazardly, then placed individually in netting bags to allow the adult fig wasps to emerge (China), or placed immediately into alcohol for storage (Italy). The figs were opened and the fig wasps and seeds that they had contained were identified using a binocular microscope.

2.4. Data analysis

The differences in number of female pollinator offspring and seeds with and without *O. galili* were determined using a non-parametric Wilcoxon rank sum test. The relationships between *O. galili* gall numbers and *F. microcarpa* reproduction were modeled using four zero-inflated generalized linear mixed models (GLMM) with negative binomial errors and log links. Crop effects may be present and we therefore included crop identity as a random effect in all the models. The first two models examined the effects of number of *O. galili* (combined with the number of its *Sycophila* parasitoids if present) and the number of non-pollinating fig wasps on seed numbers in China (first model) and Italy (second model). The third and fourth models examined the effects of the number of *O. galili* and the number of non-pollinating fig wasps, and their interaction, on female pollinator offspring numbers in China and Italy. In China, the number of *O. galili* was correlated with the number of non-pollinating fig wasps (r = 0.5, $P < 0.001$). Therefore we only included the number of *O. galili* into the model to avoid colinearity. We cannot distinguish males of the two *Eupristina* species morphologically. The males of each species were estimated in proportion to the number of females in figs where females of both species were present.

To determine whether the sex ratio of *O. galili* varied according to the numbers of offspring individuals sharing a fig, we modeled the effects of *O. galili* abundance on the proportion of males produced in China (first model) and Italy (second model) using binomial generalized linear mixed models (GLMM) with logit links. Figs that also contained *Sycophila* spp. were not included in these analyses. Crop identity was again included as a random effect in both models. All analyses were carried out using the statistical software R 3.01 (R Development Core Team 2013).

3. Results

3.1. The distribution of F. microcarpa *fig wasps in Yunnan and Sicily*

O. galili was the most common fig wasp in collections of *F. microcarpa* figs from Kunming, where it was present in six of the seven crops. Only one crop had the pollinator *E. verticillata*. In contrast, *O. galili* was rare or absent elsewhere in Yunnan, but the pollinator was common elsewhere (Table S1). In those crops where *O. galili* was present, about 7–100% of the figs were occupied by this species (Table S2). *O. galili* was present in nine of the 10 crops sampled in Sicily (n figs per crop = 10), where it was present in 20–100% of the figs of different crops (Table S2). The pollinator was present in all 10 of the crops sampled in Sicily. Two more species of NPFW were sometimes present in these figs, but in small numbers, occupying between 0% and 20% of the figs in different crops.

3.2. Impact on the pollinator and seed production of **O. galili** *in China and Italy*

In the absence of *O. galili, F. microcarpa* figs in Yunnan were capable of supporting the development of up to 110 female pollinator adult offspring and 137 seeds. Equivalent values for Sicily were 182 female pollinator offspring and 123 seeds. *Sycophila* parasitoids of *O. galili* were absent from the Sicilian fig collections, and were also rare in Yunnan (Table S2). *O. galili* reached high densities in some crops, with a maximum of 126 and 70 *O. galili* recorded from individual figs in Yunnan and Sicily respectively (Table S2). Mean densities of *O. galili* within the figs it occupied ranged from about 5 to over 88 in Yunnan (not including a crop where only one individual was recorded in total, Table S2). The range in densities was lower in Sicily, with crop means ranging between 8 and 54 *O. galili* per fig (Figure 1; Table S2).

Only three crops in Yunnan had both *O. galili* and *E. verticillata* present (Table S1). Taking these two crops together (not including the crop where only one individual was recorded in total, Table S2) mean ± SE = 9.9 ± 4.5 female pollinator offspring were present in figs shared by the two species (n = 46), compared with 45.5 ± 21.9 offspring in the remaining figs sampled from these crops (n = 6; W = 188.5, $P < 0.05$). The numbers of seeds in the figs shared with *O. galili* were 4.0 ± 1.65 (n = 46), whereas in figs without *O. galili* there were 19.83 ± 12.59 seeds (n = 6; W = 151, *P* = 0.67). In Sicily, the two species co-existed more frequently (9 from 10 crops) and the numbers of female pollinator offspring in figs shared with *O. galili* were 27.9 ± 3.7 (n = 62) compared with 59.6 ± 5.2 pollinator offspring in figs where *O. galili* was absent (n = 35; W = 1690, *P* < 0.001)). The numbers of seeds in the figs where *O. galili* was present were 14.56 ± 2.04 (n = 62), compared to 54.52 ± 5.13 (n = 35; W = 1892; *P* < 0.001)) in figs without *O. galili*. Despite this, figs containing *O. galili* could still release more than 120 female pollinator offspring and more than 60 seeds (Table S2; Figure 2 and 3).

The numbers of female pollinator adult offspring in China decreased significantly with increasing numbers of both *O. galili* (Figure 2A) and other non-pollinators (z = -4.08, *P* < 0.01). Similarly in Italy female pollinator offspring decreased with increasing numbers of *O. galili* (Figure 2B) and other non-pollinators (z = -2.31, *P* < 0.05). The numbers of seeds in the figs in China also decreased significantly with an increase in numbers of *O. galili* (Figure 3A) and with other non-pollinators (z = -4.77, *P* < 0.01). In Italy the numbers of seeds in the figs decreased significantly with an increase in numbers of *O. galili* only (Figure 3B). There were significant differences in seed and pollinator offspring numbers among crops in both countries.

3.3. Sex ratios of **O. galili** *in China and Italy*

Sex ratios in *O. galili* were investigated and were consistently female-biased in Yunnan (Table S2), with a mean proportion of 0.28 ± 0.02 (SE) males (n = 7485 *O. galili* from 222 figs). In Sicily most crops also contained female-biased collections, but a male bias was present in two collections (mean proportion males = 0.48 ± 0.03, n = 1911 *O. galili* from 62 figs, Table S2). The proportion of males decreased significantly with an increase in the number of *O. galili* sharing a fig in China (z = -3.87, *P* < 0.001; Figure 4A). However, the proportion of males in Italy did not show any significant difference in relation to density (z = -0.55, *P* = 0.58; Figure 4B). There were significant differences in sex ratios between crops in both countries.

4. Discussion

Our results confirm that *O. galili* has a detectable impact on female (seeds) and male (pollinator female) reproductive functions of *F. microcarpa* in both its natural and introduced ranges, but also that it rarely suppresses reproduction entirely. *O. galili* has become established in most of the countries where the pollinator of *F. microcarpa* is also established (Brazil is an exception, Farache, do O, and Pereira 2009), and also in South Africa, where the pollinator has not been recorded (van Noort, Wang, and Compton 2013). This suggests that the two fig wasps have similar climatic preferences, yet at the northern edge of the natural range of *F. microcarpa* in China, *O. galili* is rare or absent from warmer, lowland sites, but frequent in Kunming, a city located at a higher altitude than the other sites, with a cooler climate. Conversely, pollinators were generally absent in Kunming, suggesting that it is less successful than *O. galili* in more seasonal, cooler climates. Alternatively, the pollinator may suffer from competitive displacement in Kunming, because the 'cheater' fig wasp *Eupristina* sp. was common there. The absence of pollinators from Kunming may nonetheless have inflated the apparent fig occupancy rates of *O. galili*, because any figs not utilised by *O. galili* (or *Eupristina* sp.) are likely to have aborted at an early stage of development and only the remaining figs will have been sampled.

The contrasting distribution patterns of *O. galili* and the pollinator meant that they rarely co-existed inside the same figs at the edge of the tree's natural range. In Sicily, where the two species routinely co-existed, opportunities for interactions between the species were much greater. Larvae of *O. galili* and the pollinator of *F. microcarpa* both develop in galled ovules, and therefore compete for oviposition sites. In addition, *O. galili* galls grow quickly and if initiated before pollinator oviposition can distort the fig interior, making entry through the ostiole and oviposition more difficult for pollinator foundresses. Possibly there is also indirect competition for nutrients within the figs, as in other galled plants (Bagatto, Paquette, and Shorthouse 1995). Seed and pollinator offspring numbers in shared figs both declined equally with increasing numbers of *O. galili* galls. This contrasts with the pattern recorded by Segar and Cook (2012), who found that pollinator offspring are usually more greatly impacted by NPFW than seeds. Many NPFW are parasitoids that target pollinator larvae, whereas *O. galili*, as an ovule galler, is preventing ovules from supporting the development of both pollinator larvae and seeds.

O. galili has a demonstrable impact on the reproductive success of *F. microcarpa*, but to provide more effective and ecologically significant control it would need to be present at densities where the reproduction is inhibited more completely. This species often achieved high occupancy rates (the proportion of figs where it was recorded) but the densities required to eliminate host plant reproduction were rarely achieved, in either the natural or introduced ranges, even where the galler's *Sycophila* parasitoids were absent.

Factors that prevent *O. galili* from reaching high densities more frequently are unclear, but may include an oviposition strategy that favours the relatively wide dispersal of their eggs by females across several figs. This spreading of offspring across several figs can nonetheless cause mortalities among *O. galili* females in figs where pollinators are absent, because some female offspring develop in figs where no male *O. galili* fig wasps are present, and males are needed to chew the exit holes that allow female fig wasps to escape (Wang et al. 2015).

As well as being a poor use of resources, the release of ineffective agents can add to the potential risks of biological control, without providing benefits (McClay, and Balciunas 2005). Other species of NPFW associated with *F. microcarpa* may have a similarly limited individual impact on *F. microcarpa* reproduction because all fig wasp species have evolved in a close relationship with the fig inflorescence and the pollinator. Therefore, the populations of all NPFW species could be constrained by fig morphology and other features of the pollinator mutualism. As the resources provided by female flowers are limited, some NPFW species may be selected to spread their offspring in several figs, to decrease intra-specific competition (Weiblen 2012). These constraints could select for other NPFWs to disperse their eggs, as seen in *O. galili*. Despite this oviposition behaviour, *O. galili* did reduce both seed and pollinator offspring numbers and its impact could be additive with other NPFW if they are also present. Species, with a greater impact on the reproduction of *F. microcarpa* have been described. They include other species of NPFW, gall midges, beetles and hemipterans, all of which destroy its seeds and/or pollinator larvae (Mia, Yang, Liu, Peng, and Compton 2011).

Acknowledgements

Dr. Costas Zachariades provided valuable comments on this manuscript. We also thank Yi-Mei Ba and Teng-Chao Xu for assistance with fig wasp collections in Kunming. This work was funded by Candidates of the Young and Middle Aged Academic Leaders of Yunnan Province (2011HB041), the Chinese Natural Science Foundation (31372253), and the CAS 135 program (XTBG-F01).

Supplementary materials

Table S1 Locations (North-South) and contents of *F. microcarpa* figs in Yunnan. Each collection comprised figs from a single tree, collected on the same date. Kunming is located at N 24º 53', Jinghong at N 22º 00'.

Table S2 The proportion of figs occupied by *O. galili* and its densities within occupied figs in Yunnan (collections 1–6, 19, 16) and Sicily (collections 21–29). *Sycophila* spp. are parasitoids of *O. galili*. Palermo (Sicily) is located at 38º 07' N.

References

Ahmed, S., Compton, S.G., Butlin, R.K., and Gilmartin, P.M. (2009) Wind borne insects mediate directional pollen transfer between desert fig trees 160 kilometers apart. *Proceedings of the National Academy of Sciences USA*, 106, 20342–20347.

Bagatto, G., Paquette, L.C., and Shorthouse, J.D. (1995) Influence of galls of *Phanacis taraxaci* on carbon partitioning within common dandelion, *Taraxacum officinale. Entomologia Experimentalis et Applicata*, 79, 111–117.

Beardsley, J.W. (1998) Chalcid wasps (Hymenoptera: Chalcidoidea) associated with fruit of *Ficus microcarpa* in Hawai'i. *Proceedings of the Hawaiian Entomological Society,* 33, 19–34.

Berg, C.C., and Corner, E.J.H. (2005) Moraceae - *Ficus*. Flora Malesiana Series I (Seed Plants) Volume 17/Part 2. National Herbarium of the Netherlands, Leiden.

Bouček, Z. (1988) Australasian Chalcidoidea (Hymenoptera). A biosystematic revision of genera of fourteen families, with a reclassification of species. pp. 1–832. CAB International, Wallingford, UK**.**

Bouček, Z. (1993) The genera of chalcidoid wasps from *Ficus* fruit in the New World. *Journal of Natural History*, 27, 173–217.

Chen, H.H., Yang, D.R., Gu, D., Compton, S.G., and Peng, Y.Q. (2013) Secondary galling: a novel feeding strategy among ‘non-pollinating’ fig wasps from *Ficus curtipes*. *Ecological Entomology*, 38, 381–389.

Chen, Y.R., Chuang, W.C., and Wu, W.J. (1999) Chalcid wasps on *Ficus microcarpa* L. in Taiwan (Hymenoptera: Chalcidoidea). *Journal of Taiwan Museum,* 52, 39–79.

Compton, S.G. (1989) The fig wasp *Odontofroggatia galili* in the Greek Isles. *Entomologist's Gazette,* 40, 183–184.

Compton, S.G. (1993) An association between epichrysomallines and eurytomids (Hymenoptera: Chalcidoidea) in Southern African fig wasp communities. *African Entomology*, 1, 123–125.

Compton, S.G., van Noort, S., Mcleish, M., Deeble M., and Stone V. (2009) Sneaky African fig wasps that oviposit through holes drilled by other species. *African Natural History,* 5, 9–15.

Cook, J.M., and Rasplus, J.Y. (2003) Mutualists with attitude: coevolving fig wasps and figs. *Trends in Ecology* & *Evolution*, **18**, 241–248.

Corlett, R.T. (1984) The phenology of *Ficus benjamina* and *Ficus microcarpa* in Singapore. *Journal of the Singapore Academy of Science*, 13, 30–31.

Corner, E.J.H. (1960) Taxonomic notes on *Ficus* Linn., Asia and Australasia. I Subgen. Urostigma (Gasp.) Miq. The Garden's Bulletin, Singapore, 17, 368–404.

Culliney, T.W. (2005) Benefits of classical biological control for managing invasive plants. *Critical Reviews in Plant Sciences*, 24, 131–150.

Farache, F.H.A. do O, V.T., and Pereira, R.A.S. (2009) New occurrence of non-pollinating fig wasps (Hymenoptera: Chalcidoidea) in *Ficus microcarpa* in Brazil. *Neotropical Entomology*, 38, 683–685.

Galil, J., and Copland, J.W. (1981) *Odontofroggatia galili* Wiebes in Israel, a primary fig wasp of *Ficus microcarpa* L. with a unique ovipositor mechanism (Epichrysomallinae, Chalcidoidea). *Proceedings Koninklijke Nederlandse Akademie van Wetenschappen, Amsterdam* (C), 84, 183–195.

Harrison, R.D. (2005) Figs and the diversity of tropical rainforests. *Bioscience*, 55, 1053–1064.

Hilburn, D.J., Marsh, P.M., and Schauff, M.E. (1990) Hymenoptera of Bermuda. *Florida Entomologist*, 73, 161–176.

Janzen, D.H. (1979) How to be a fig. *Annual Review of Ecology, Evolution, and Systematics*, 10, 13–51.

Julien, M.H., and Griffiths, M.W. (1998) Biological Control of Weeds: A World Catalogue of Agents and Their Target Weeds (Fourth ed.). CAB International, Wallingford, UK.

Kaufmann, S., McKey, D.B., Hossaert-McKey, M., and Horvitz, C.C. (1991) Adaptations for a two-phase seed dispersal system involving vertebrates and ants in a hemiepiphytic fig (*Ficus microcarpa*: Moraceae). *American Journal of Botany*, 78, 971–977.

Kerdelhué, C., and Rasplus, J.Y. (1996) The evolution of dioecy among *Ficus* (Moraceae): an alternative hypothesis involving non-pollinating fig wasp pressure on the fig-pollinator mutualism. *Oikos*, 77, 163–166.

Kobbi, M., Edelin, C., Michaloud, G., and Chaieb, M. (1996) Relationship between a mutualist and a parasite of the laurel fig, *Ficus microcarpa* L. *Canadian Journal of Zoology*, 74, 1831–1833.

Lin, S.L., Zhao, N.X., and Chen, Y.Z. (2008) Phenology and the production of seeds and wasps in *Ficus microcarpa* in Guangzhou, China. *Symbiosis*, 45, 101–105.

Lo Verde, G., Porcelli, F., and Sinacori, A. (1991) Presenza di *Parapristina verticillata* (Waterst.) e *Odontofroggatia galili* Wiebes (Hymenoptera: Chalcidoidea Agaonidae) in Sicilia. *Atti della Congresso Nazionale Italiana Di Entomologia*, 16, 139–143.

Martinson E.O., Jander K.C., Peng Y.Q., Chen H.H., Machado C.A., Arnold A.E., and Herre E.A. (2014) Relative investment in egg load and poison sac in fig wasps: implications for physiological mechanisms underlying seed and wasp production in figs. *Acta Oecologica*, 57, 58–66.

McFadyen, R.E. (2003) Does ecology help in the selection of biocontrol agents? *Improving the Selection, Testing and Evaluation of Weed Biological Control Agents* (ed. by H.S. Jacob and D.T. Briese) pp. 5–9. CRC for Australian Weed Management, Glen Osmond, Australia.

McKey, D. (1989) Population biology of figs: Applications for conservation. *Experientia*, 45, 661–673.

McClay, A.S., and Balciunas, J.K. (2005) The role of pre-release efficacy assessment in selecting classical biological control agents for weeds – applying the Anna Karenina principle. *Biological Control*, 35, 197–207.

Miao, B.G., Yang, D.R., Liu C., Peng, Y.Q. and Compton S.G. (2011) The impact of a gall midge on the reproductive success of *Ficus benjamina*, a potentially invasive fig tree. *Biological Control*, 59, 228–233.

Myers, J.H. (2000) What can we learn from biological control failures. *Proceedings of the X international symposium on biological control of weeds*. pp. 151–154. Montana State University, Bozeman, Montana, USA.

Nadel, H., Frank, J.H., and Knight Jr., R.J. (1992) Escapees and accomplices: the naturalization of exotic *Ficus* and their associated faunas in Florida. *Florida Entomologist*, 75, 29–38.

Rand T.A., Waters D.K., and Shanower T.G. (2016) Preliminary evaluation of the parasitoid wasp, *Collyria catoptron*, as a potential biological control agent against the wheat stem sawfly, *Cephus cinctus*, in North America. *Biocontrol Science and Technology*, 26(1):61–71.

Segar, S.T. and Cook, J.M. (2012) The dominant exploiters of the fig/pollinator mutualism vary across continents, but their costs fall consistently on the male reproductive function of figs. *Ecological Entomology*, 37, 342–349.

Shanahan, M., So, S., Compton, S.G. and Corlett, R. (2001) Fig-eating by vertebrate frugivores: a global review. *Biological Reviews*, 76, 529–572.

Simberloff, D. and Von Holle, B. (1999) Positive interactions of nonindigenous species: invasional meltdown? *Biological Invasions*, 1, 21–32.

Stange, L.A. and Knight Jr, R.J. (1987) Fig pollinating wasps of Florida. Florida Department of Agriculture and Consumer Services, Division of Plant Industry. Entomology Circular, 296.

Starr, F., Starr, K. and Loope, L. (2003) *Ficus microcarpa* Chinese Banyan, Moraceae. United States Geological Survey, Biological Resources Division Haleakala Field Station, Maui, Hawai'I, 1–8.

Stiling, P. (1993) Why do natural enemies fail in classical biological control programs? Amer. *Entomologist*, 39, 31–37.

Sun, X.J., Xiao, J.H., Cook, J.M., Feng, G. and Huang, D.W. (2011) Comparisons of host mitochondrial, nuclear and endosymbiont bacterial genes reveal cryptic fig wasp species and the effects of *Wolbachia* on host mtDNA evolution and diversity. *BMC Evolutionary Biology*, 11, 86.

van Noort, S., Ware, A.B. and Compton, S.G. (1989) Release of pollinator-specific volatile attractants from the figs of *Ficus burtt-davyi*. *South African Journal of Science*, 85, 323–324.

van Noort, S., Wang R. and Compton, S.G. (2013) Fig wasps (Hymenoptera: Chalcidoidea: Agaonidae, Pteromalidae) associated with Asian fig trees (*Ficus*, Moraceae) in southern Africa: Asian followers and African colonists. *African Invertebrates*, 54, 381–400.

Wang, R., Matthews, A., Ratcliffe, J., Barwell, L., Peng, Y.Q., Chou, L.S., Yu, H., Yang, H.W. and Compton, S.G. (2014) First record of an apparently rare fig wasp feeding strategy: obligate seed predation. *Ecological Entomology*, 39, 492–500.

Wang, R., Aylwin R., Barwell, L., Chen X.Y., Chen Y., Chou L. X. Cobb J., Collette D., Craine L., Giblin-Davis R., Ghana S., Harper M., Harrison R.D., McPherson J. R., Peng, Y.Q., Pereira R.A.S., Reyes-Betancort, A., Rodriguez L.J.V., Strange E., van Noort S., Yang H. W. and Compton, S.G. (2015) The fig wasp followers and colonists of a widely introduced fig tree, *Ficus microcarpa*. *Insect Conservation and Diversity*, 8(4): 322–336.

Weiblen, G.D. (2002) How to be a fig wasp. *Annual Review of Entomology*, 47, 299–330.

Yang, H.W., Tzeng, H.Y. and Chou, L.S. (2013) Phenology and pollinating wasp dynamics of *Ficus microcarpa* L.f.: adaptation to seasonality. *Botanical Studies*, 54, 11.

Figure legends

Figure 1 The numbers of *O. galili* present in figs of *F. microcarpa* from A) Yunnan and B) Sicily. *Sycophila* spp. are parasitoids of *O. galili*.

Figure 2 The relationship between densities of *O. galili* and *E. verticillata* pollinators in shared figs of *F. microcarpa* in A) Yunnan ($z = -6.88$, $P < 0.001$), and B) Sicily ($z = -3.34$, $P < 0.01$). Only figs that contained *O. galili* and pollinator offspring or seeds are included. Solid lines indicate lines of best fit, dashed lines indicate 95% probabilities.

Figure 3 The relationship between densities of *O. galili* and numbers of seeds in shared figs of *F. microcarpa* in A) Yunnan ($z = -2.88$, $P < 0.01$) , and B) Sicily ($z = -6.32$, $P < 0.01$) . Only figs that contained *O. galili* and pollinator offspring or seeds are included. Solid lines indicate lines of best fit, dashed lines indicate 95% probabilities.

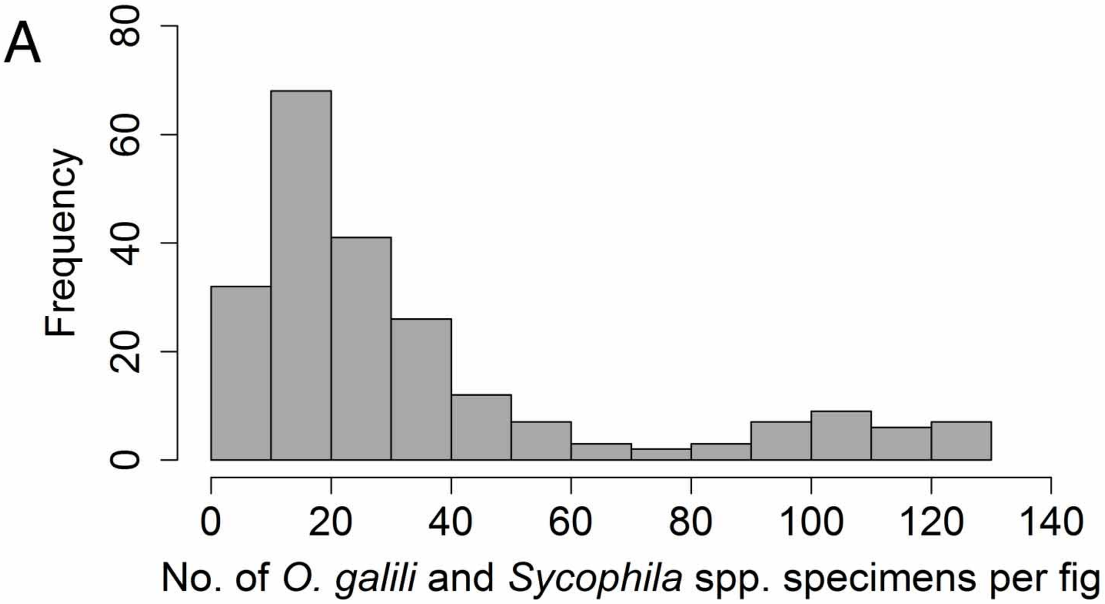
Figure 4 Sex ratios of *O. galili* in relation to densities of this species in figs of *F. microcarpa* in A) Yunnan, and B) Sicily. No figs containing *Sycophila* spp. are included. Solid lines indicate lines of best fit, dashed lines indicate 95% probabilities.

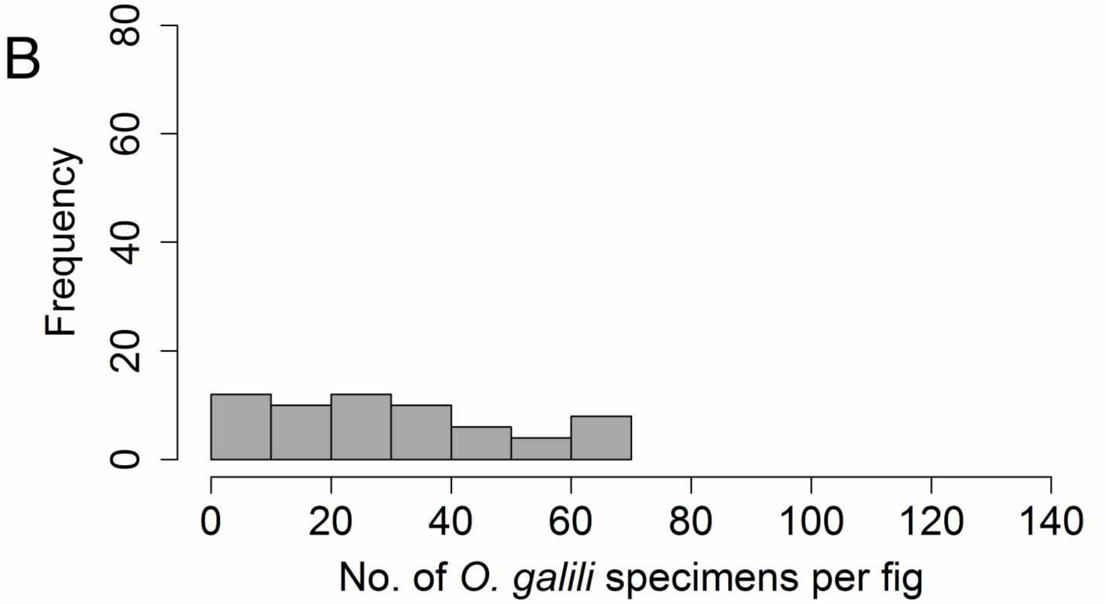
Table S1 Locations (North-South) and contents of *F. microcarpa* figs in Yunnan. Each collection comprised figs from a single tree, collected on the same date. Kunming is located at N 24º 53', Jinghong at N 22º 00'.

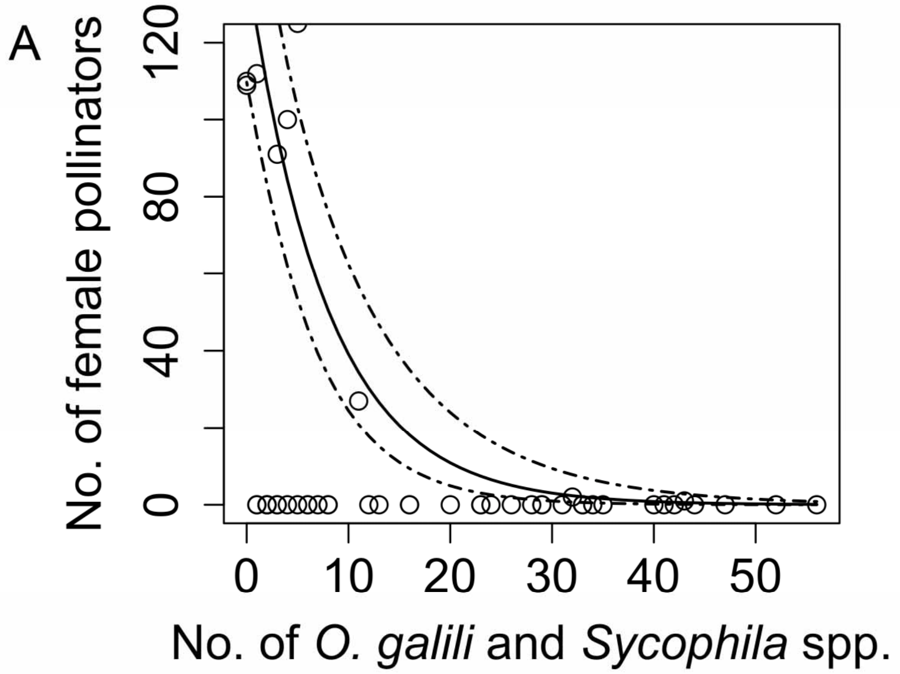
Crops	Date	Site	Altitude (m)	Habitat	Sample size (figs)	Pollinator	*O. galili*	Figs with other NPFW
1	Jan 2013	Kunming	1900	Street tree	31	-	+	3
2	Mar 2013	Kunming	1902	Street tree	30	-	+	0
3	Mar 2013	Kunming	1902	Street tree	39	-	+	1
4	Mar 2013	Kunming	1902	Street tree	37	-	+	2
5	Jan 2013	Kunming	1900	Street tree	30	+	+	20
6	Aug 2012	Kunming	1902	Street tree	40	-	+	38
7	Mar 2013	Kunming	1902	Street tree	30	-	-	14
8	Oct 2012	Yanhe	1665	Street tree	30	+	-	29
9	Oct 2012	Mengzi	1292	Street tree	22	+	-	18
10	Oct 2012	Mengzi	1292	Street tree	23	+	-	16
11	Oct 2012	Jianshui	1310	Street tree	22	+	-	2
12	Oct 2012	Jianshui	1310	Street tree	21	+	-	1
13	Dec 2012	Puer	1305	Street tree	30	+	-	1
14	Oct 2012	Hekou	104	Street tree	25	-	-	25
15	Oct 2012	Hekou	104	Street tree	22	-	-	22
16	Aug 2012	Xishuangbanna	553	Street tree	30	+	+	13
17	Sept 2012	Xishuangbanna	553	Street tree	30	+	-	15
18	Dec 2012	Xishuangbanna	553	Street tree	25	+	-	12
19	Dec 2012	Xishuangbanna	569	Garden tree	32	+	+	5
20	Nov 2012	Xishuangbanna	580	Garden tree	30	+	+	6

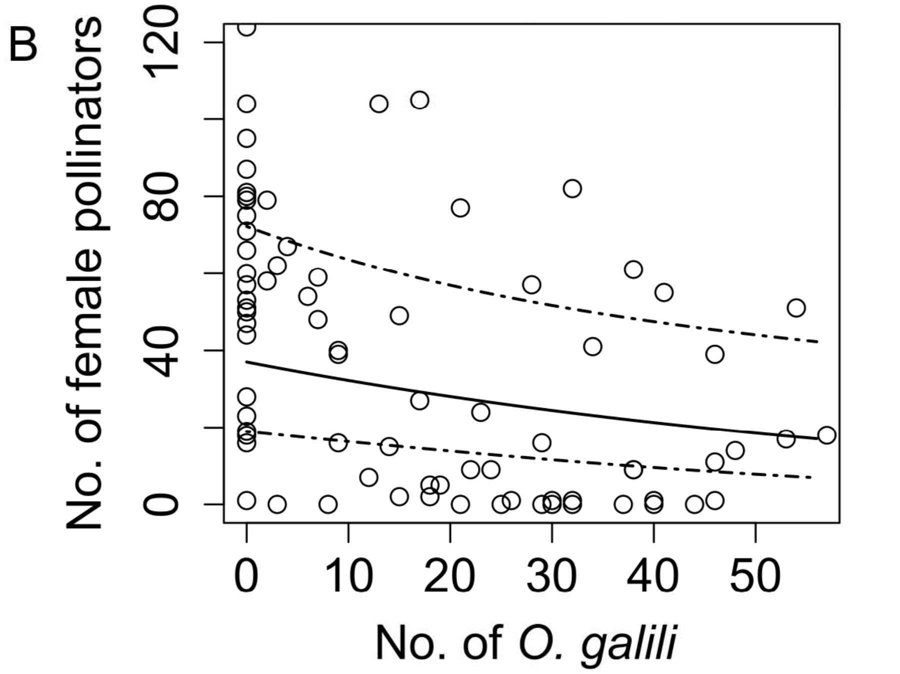
Table S2 The proportion of figs occupied by *O. galili* and its densities within occupied figs in Yunnan (collections 1–6, 19, 16) and Sicily (collections 21–29). *Sycophila* spp. are parasitoids of *O. galili.* Palermo (Sicily) is located at 38º 07' N.

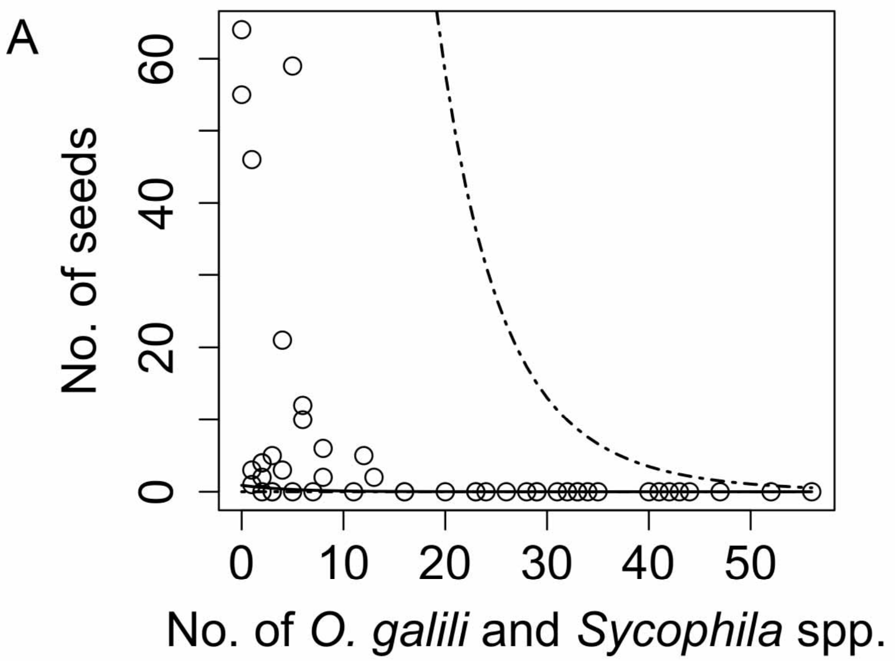
Crops	Frequency occupied	N (figs)	Female wasps of *O. galili*		Male wasps of *O. galili*		Total wasps of *O. galili*		*Sycophila* spp.
			Average (mean±SE)	Range	Average (mean±SE)	Range	Average (mean±SE)	Range	
1	0.97	30	12.63 ± 1.24	1-34	3.47 ± 0.64	0-17	16.10 ± 1.23	7–39	0
2	0.97	29	18.34 ± 1.47	8-35	5.00 ± 0.92	1-22	23.17 ± 1.63	9–40	0
3	1.00	39	22.59 ± 1.88	5-49	6.10 ± 0.88	1-23	28.69 ± 1.93	13–59	0
4	1.00	37	18.19 ± 1.71	1-47	4.11 ± 0.75	1-5	22.30 ± 1.71	6–53	0
5	0.90	27	18.11 ± 2.28	3-36	10.41 ±1.61	2-33	28.52 ± 2.64	2–56	1.07 ± 0.45
6	1.00	40	49.70 ± 2.49	20-79	39.00 ± 2.10	3-63	88.70 ± 3.79	27–126	1.06 ± 0.24
19	0.59	19	3.68 ± 0.78	1-17	1.79 ± 0.30	0-5	5.47 ± 0.10	1–16	0
16	0.07	2	1	0	1	0	1	1–1	0
21	0.40	4	16.75 ± 9.36	2-41	3.75 ± 1.11	1-6	20.50 ± 9.72	3–46	0
22	1.00	10	17.10 ± 4.23	2-47	12.60 ± 1.46	6-21	29.70 ± 4.71	15–64	0
23	0.20	2	14.00 ± 11.00	3-25	1.50 ± 1.50	0-3	15.50 ± 12.50	3–28	0
24	0.20	2	16.50 ± 14.50	2-31	5.00 ± 5.00	0-10	21.50 ± 19.50	2–41	0
25	0.90	9	26.67 ± 4.35	2-45	13.11 ± 3.16	2-28	39.78 ± 6.65	4–66	0
26	1.00	10	13.10 ± 1.64	6-21	22.90 ± 3.46	15-50	36.00 ± 4.62	22–70	0
27	1.00	10	23.60 ± 2.00	10-30	30.80 ± 2.42	18-45	54.40 ± 3.82	32–67	0
28	0.60	6	6.70 ± 4.38	0-13	1.50 ± 0.73	1-9	8.20 ± 4.88	2–17	0
29	0.90	9	17.10 ± 4.23	0-18	12.60 ± 1.46	4-21	29.70 ± 4.71	9–38	0

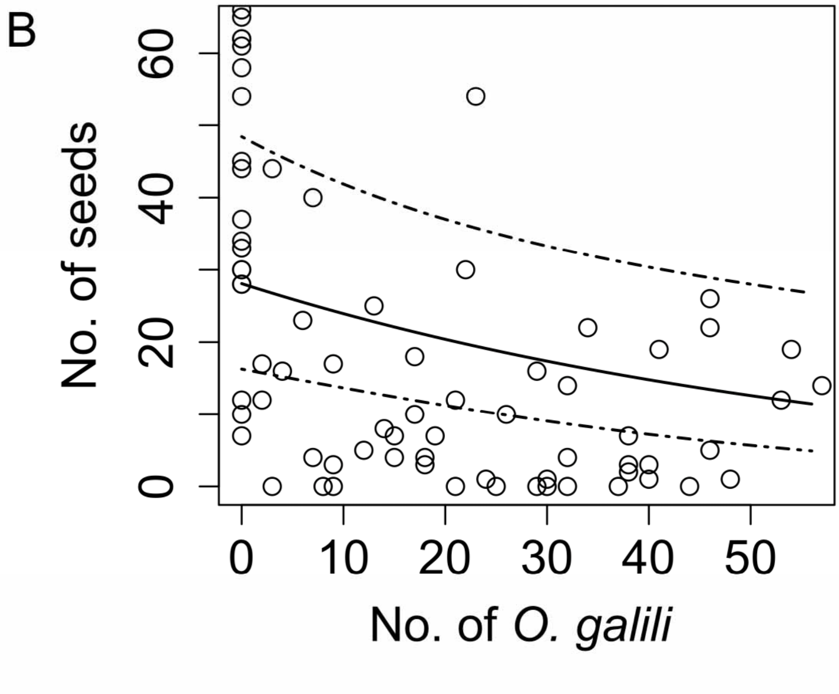

A
Frequency
0
20
40
60
80
0
20
40
60
80
100
120
140
No. of *O. galili* and *Sycophila* spp. specimens per fig

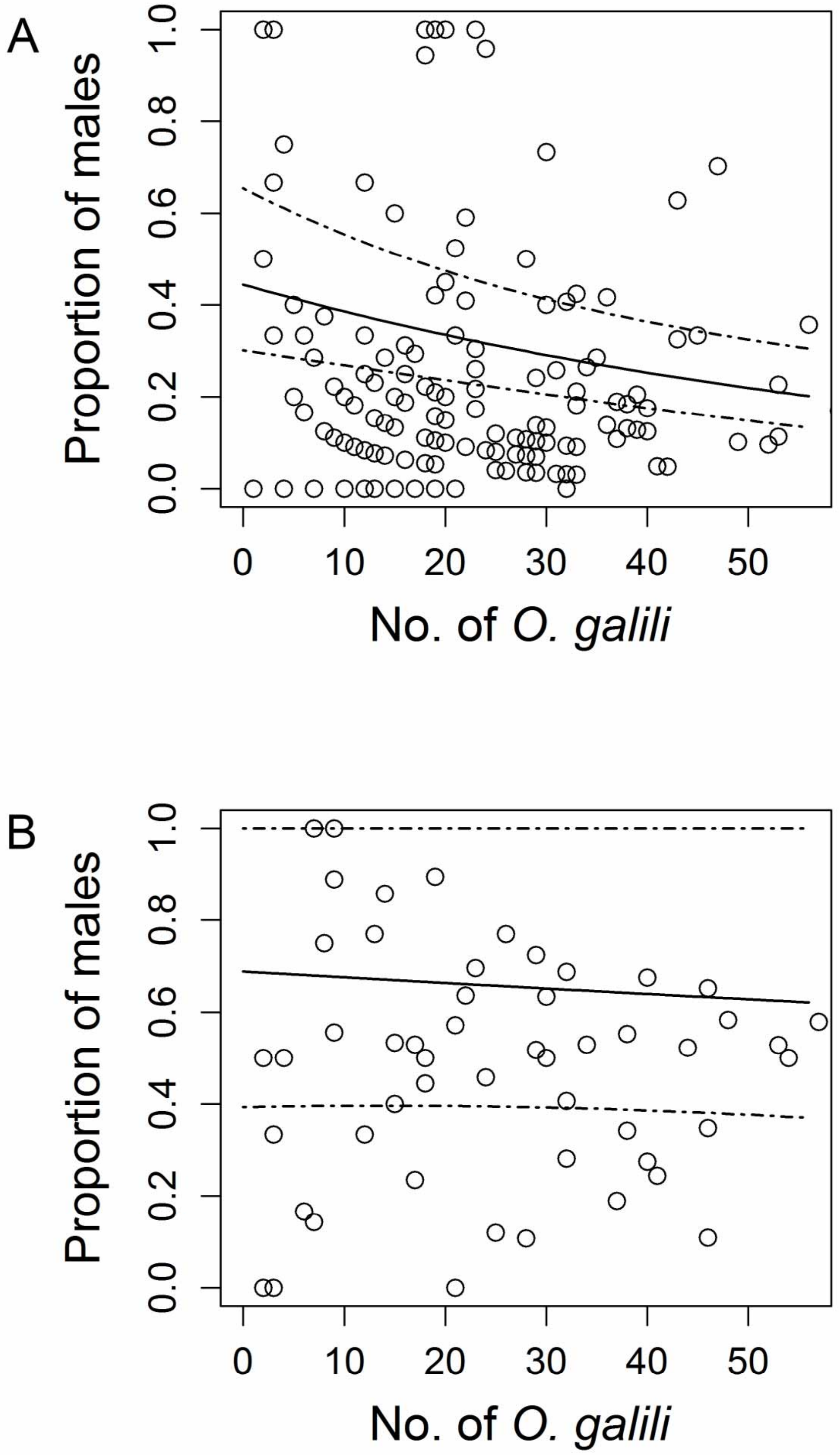

B
Frequency
0
20
40
60
80
0
20
40
60
80
100
120
140
No. of *O. galili* specimens per fig


A
No. of female pollinators
0
40
80
120
0
10
20
30
40
50
No. of *O. galili* and *Sycophila* spp.


B
No. of female pollinators
0
40
80
120
0
10
20
30
40
50
No. of *O. galili*


A
No. of seeds
0
20
40
60
0
10
20
30
40
50
No. of *O. galili* and *Sycophila* spp.


B
No. of seeds
0
20
40
60
0
10
20
30
40
50
No. of *O. galili*


A
Proportion of males
0.0
0.2
0.4
0.6
0.8
1.0
0
10
20
30
40
50
No. of *O. galili*
B
Proportion of males
0.0
0.2
0.4
0.6
0.8
1.0
0
10
20
30
40
50
No. of *O. galili*