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Loss of top-down biotic interactions changes the relative benefits for obligate mutualists

Running head: Changes in benefits to mutualists

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Abstract

The collapse of mutualisms due to anthropogenic changes is contributing to losses of biodiversity. Top predators can regulate biotic interactions between species at lower trophic levels and may contribute to the stability of such mutualisms, but they are particularly likely to be lost after disturbance of communities. We focused on the mutualism between the fig tree *Ficus microcarpa* and its host-specific pollinator fig wasp and compared the benefits accrued by the mutualists in natural and translocated areas of distribution. Parasitoids of the pollinator were rare or absent outside the natural range of the mutualists, where the relative benefits the mutualists gained from their interaction were changed significantly away from the plant's natural range due to reduced seed production rather than increased numbers of pollinator offspring. Furthermore, in the absence of the negative effects of its parasitoids, we detected an oviposition range expansion by the pollinator, with the use of a wider range of ovules that could otherwise have generated seeds. Loss of top-down control has therefore resulted in a change in the balance of reciprocal benefits that underpins this obligate mutualism, emphasising the value of maintaining food web complexity in the Anthropocene.

Key words

Trophic cascades, fig-fig wasp mutualism, parasitoids, interspecific interactions

Introduction

The collapse of mutualisms is a major force driving Anthropocene losses of biodiversity [1-3]. The continued stability of mutualisms depends on the interplay between changing environments and the evolutionary histories of the interacting species [1,4], and in a world where anthropogenic change is increasing, both abiotic and biotic environments are being fundamentally altered [5,6]. These changes can rapidly alter critical traits of host plants, causing mismatches with the animals and microorganisms that are their partners in mutualisms [2,7,8]. Highly specific mutualistic associations are often considered to be less likely to respond to changing environments because the key traits that link the species together are under strong evolutionary constraints [9,10], but these mutualisms rarely occur in isolation from other species that may be more responsive to environmental change and other human activities [4]. The importance of overall networks of interactions for the stability of mutualisms has been demonstrated in some severely degraded ecosystems, where alterations in food web structure have even shifted some generalist mutualistic relationships towards antagonism [1]. Changes in biotic environments may have similar consequences for highly specific mutualisms.

Food webs including mutualistic species comprise competitors and predators of one or more mutualists. The presence of competitors is unlikely to stabilise the relative benefits obtained by the partners in a mutualism, because interspecific competition is expected to exclude species or enable their persistence only at reduced densities. Predators however can regulate the abundance of species at lower trophic

levels and facilitate the persistence of interspecific interactions through top-down control [11,12]. This suggests that the loss of top predators has the potential to destabilise even highly specific mutualisms.

Fig trees (*Ficus*, Moraceae) and their pollinating fig wasps (Hymenoptera, Agaonidae) are a well-known example of host-specific obligate mutualism [13-15]. Figs (syconia) are enclosed inflorescences that contain many ovules. In monoecious *Ficus* species, each ovule can potentially develop into a seed or form a gall that supports a single pollinator offspring. This leads to a conflict of interest between the host plant and its pollinators [16,17]. Mechanisms that restrict the extent of pollinator oviposition in monoecious figs vary among species [13]. These include (1) closure of the entrance tunnel (ostiole) to limit the number of fig wasp foundresses that enter each fig [18], (2) host sanctions at either whole fig or ovule levels [19,20], (3) physical limitations of agaonids such as their ovipositor lengths [18] and (4) optimal oviposition strategies that favour oviposition in certain ovules but not others [21,22].

In addition to the pollinators, figs support a wider fig wasp community. These non-pollinating fig wasps (NPFWs, Chalcidoidea) [23-25], include parasitoids of pollinator offspring that can have significant impacts on pollinator abundance [26-28]. Moreover, because those parasitoids oviposit from the outside surface of figs, they may help stabilize fig-pollinator mutualisms by reducing the benefits to pollinator foundresses of ovipositing in ovules located nearer to the outside surface [17]. This is because pollinator offspring developing in the ovules nearer the periphery of figs are more likely to be attacked [16,29,30]. In conjunction with other factors influencing

pollinator oviposition preferences, this results in the spatial stratification of fig wasp galls and fig seeds within figs, with ovules located towards the periphery less likely to host pollinator offspring and more likely to become seeds (figure 1).

We hypothesized that in situations where parasitoids that attack pollinator larvae are rare or absent there will be reduced selection pressure on pollinator oviposition site preferences that will result in a spatial expansion of the ovules they use. Any such shift could change the relative benefits gained by host fig trees and their pollinator mutualists, because if more pollinator offspring are generated, this can be at the cost of fewer seeds, with potential consequences for the long-term stability of the mutualism.

Our study mutualism comprised *Ficus microcarpa* L. and its associated fig wasps. *Ficus microcarpa* is monoecious and has a natural distribution across Asia and Australasia [31] but has also been widely planted outside of its natural range [25,32]. Translocated *F. microcarpa* can set viable seed because of the widespread colonisation of its pollinator [25]. Outside the plant's natural range, some NPFWs have also colonised the plant, but parasitoids of pollinator offspring are rare or absent [25,33].

Here, we compare the fig wasp faunas and seed production of *F. microcarpa* figs in its native and translocated ranges to answer two questions: (1) Do pollinators gall more flowers, and are fewer seeds produced where parasitoids are rare or absent? and (2) Does the spatial distribution of ovules supporting pollinator development change in the absence of selection pressure from parasitoids?

Materials and methods

Ficus microcarpa and its associated fig wasps

The natural distribution range of *F. microcarpa* encompasses a variety of tropical and sub-tropical climates, and the tree has also been translocated into some localities with seasonal, Mediterranean climates world-wide [34,35]. *Ficus microcarpa* is a natural lithophyte or ‘strangler’ of other trees, but outside its native range occurs mainly as a planted street tree or as a colonizer of buildings [36]. It produces synchronized crops of up to several thousand figs [37], each reaching about 1cm in diameter. Reproduction of *F. microcarpa* relies on its host specific pollinating agaonid, *Eupristina verticillata* (Agaonidae), a morphospecies that contains several genetically differentiated taxa of uncertain status (R. Wang, unpublished data).

Across its native range, *F. microcarpa* supports at least 40 NPFW species. These include an obligate seed predator, *Philotrypesis taiwanensis* Chen (Pteromalidae) [30] and several species of Eurytomidae, Ormyridae and Pteromalidae that parasitise ovule-galling fig wasps, including the pollinators [25]. *Eupristina* species enter figs to lay their eggs, whereas these NPFW oviposit from outside of figs using their long ovipositors to reach the ovules [38]. Several NPFWs have become established in translocated populations of *F. microcarpa* [25,39]. Agaonids are the major hosts of NPFWs from the subfamily Sycoryctinae (Pteromalidae), and the host ranges of these parasitoids do not vary between the native and the translocated ranges of *F. microcarpa* [33].

Sampling strategy and sample sites

To assess the difference in fig traits and community structure of fig wasps among the natural and translocated locations of *F. microcarpa*, we collected its figs from a total of 134 trees at 24 sites between 2010 and 2016 (table S1). We chose trees planted on roadsides at all sites, to keep the microhabitats of all sampled trees the same, in case of potential differences in some critical but plastic fig traits. At each site, we sampled mature crops from trees separated by a minimum interval of 30 m, and at least five mature figs were collected from all available heights of each sampled tree (table S1). In addition, we tried to collect several immature figs from each sampled tree to record the number of pollinator foundresses entering figs at different sites.

The samples comprised 7 sites within the plant's natural range, 4 sites within the plant's translocated range that extended from its Chinese natural range, and 13 sites where the plant has been translocated outside of Asia (table S1). The fig wasps in the Chinese extension range may have dispersed from the natural range or have been moved by human activities, whereas those in the non-Asian translocation range required human transportation [36,39]. Nevertheless, we combined data from the two translocated ranges because the characters of the figs and fig wasp communities were consistent across these two ranges (see electronic supplementary material for comparative results). *Eupristina verticillata* was first recorded from the areas of host translocation at least ten years prior to our fig collections, and each population will have been present locally for at least thirty generations given that the fig wasp averages three annual generations [37].

Fig contents

We dissected our sampled figs to describe the characters of both the figs and their associated fig wasp communities. From each sampled fig, we recorded the numbers of male florets, seeds, unused ovules (neither pollinated nor galled by fig wasps), galls containing adult fig wasp offspring, and failed galls that contained no adult fig wasp offspring. Each gall that contained an adult fig wasp was opened and it was identified to species. We assigned the fig wasps to one of four categories [33]: (1) pollinating agaonids, (2) parasitoids of the pollinator offspring, (3) the seed predator *Philotrypesis taiwanensis*; and (4) ‘other NPFWs’, which included other gall-making NPFWs and their parasitoids (table S2). We also recorded the number of pollinator foundresses in each immature fig by identifying their remains (table S3).

Oviposition sites of fig wasps

Pollinator fig wasp foundresses lay their eggs into ovules after inserting their ovipositors along the styles, which vary greatly in length in monoecious figs, and most eggs are laid into the ovules with shorter styles [16,18]. Ovules with shorter styles have longer pedicels, and in maturing figs the ovules with short pedicels are located towards the periphery, while those with longer pedicels are situated towards the centre (figure 1). Pedicel lengths can thus be used to measure the spatial distribution of galls containing fig wasp offspring and seeds within the figs, relative to the fig wall [17].

To examine whether the oviposition behavior of pollinators altered between the natural and the translocated ranges of *F. microcarpa*, the locations of ovules and their contents were recorded at 12 sites in a sub-sample of 136 randomly selected figs from 26 trees where numerous mature figs had been collected (table S4). In these figs we recorded the pedicel lengths of all the ovules and their contents. Ovipositor length sets an upper limit to utilization of flowers with longer styles, and we randomly selected 450 adult female pollinators yet to emerge from figs from most of the sub-samples in both ranges (table S4) and measured their ovipositor lengths [18]. The lengths of pedicels and ovipositors were measured to the nearest 0.02 mm using a binocular microscope eyepiece graticule.

Statistical analyses

Comparisons of fig contents and benefits of mutualists

Differences in the reproductive investment of figs and the colonisation success of fig wasps between different ranges of *F. microcarpa* were compared by setting the numbers of male florets and ovules, seed number, the abundance of total fig wasps and pollinators (per fig), ovule occupancy rates (the proportion of ovules containing adult fig wasp offspring in each fig), and gall failure rates (the proportion of galled ovules in each fig where no offspring completed development) as response variables and different ranges of *F. microcarpa* as a fixed effect (predictor variable). In addition, we set the number of pollinator foundresses and sex ratios of pollinator offspring (the proportion of male pollinator offspring in each fig) as response variables and different

ranges as a fixed effect to test if the variation in pollinator abundance was the result of varying foundress numbers in different ranges, because offspring sex ratio varies with foundress numbers [40].

We used the ratio of pollinator abundance to the sum of pollinator abundance and seeds per fig ('P:S ratio') as a response variable and different ranges as fixed effects, to examine if the relative benefits for the two mutualists differed between ranges.

All the analyses mentioned above were conducted in R 3.4.3 [41] using generalized linear mixed models (GLMMs) in package 'lme4' version 1.0-5 [42], assuming either Poisson or binomial distributions of residuals and setting tree identities nested in sites as random effects due to our hierarchical sampling strategy. Likelihood ratio (LR) tests were used to evaluate the significance of fixed effects.

Comparisons of NPFW communities and their effects

We assessed differences in NPFW communities by setting the prevalence (proportion of figs where a category of NPFWs (parasitoids of pollinator offspring, seed predator or 'other NPFWs') was present), the abundance and the species richness of each category of NPFWs as response variables and different ranges as a fixed effect.

To test whether variation in NPFW communities contributed to changes in benefits gained by the two mutualists, we first evaluated the relationships between each NPFW category (fixed effect) and pollinator abundance, seed numbers and the P:S ratio (response variables), and then examined whether the strengths of these

relationships (represented by the slopes of regression functions) varied between ranges by analysing the interactions between the abundance of each category of NPFWs and range (fixed effects) on pollinator abundance, seed numbers and the P:S ratio (response variables). When analysing the relationships between a category of NPFWs and benefits for the two mutualists, we only included figs from the sites where this category was present (see table S1, S5).

All analyses were carried out using GLMMs assuming either Poisson or binomial distributions of residuals and setting tree identities nested in sites as random effects. Z-tests and LR tests were used to assess the significance of slopes and fixed effects (including interactions), respectively.

Alterations in pollinator oviposition preferences

To assess whether the key morphological traits of the two mutualists varied between different ranges, we used linear mixed models (LMMs) in R package ‘nlme’ version 3.1 [43] and set pedicel lengths and ovipositor lengths of female pollinator offspring as response variables and different ranges as a fixed effect.

To test if pollinator oviposition preferences altered in the plant’s translocated range, we first described the spatial distributions of pollinator offspring and seeds by evaluating relationships between the proportion of pollinator galls/seeds to total ovules (response variable) and their pedicel lengths (fixed effect), and then tested the difference in the strengths of these relationships (represented by the slopes of regression functions) between ranges by analysing the interactions between pedicel

length and range (fixed effects) on the proportion of pollinator galls/seeds to total ovules (response variable). These analyses were conducted using GLMMs assuming binomial distributions of residuals and setting fig identities nested in tree identities nested in sites as random effects. Z-tests and LR tests were used to assess the significance of slopes and fixed effects (including interactions), respectively.

Each parasitoid of a pollinator offspring develops at the expense of a single pollinator, and most failed galls are likely to originally have contained eggs of the pollinator [44]. We therefore combined the galls of pollinator offspring and parasitoids of pollinator offspring and failed galls as a representation of the initial oviposition/galling sites of pollinator foundresses. Similarly, the numbers of seed predators, one of which develops in each ovule, were combined with seed counts to determine initial seed numbers. We then ran the analyses using GLMMs again to test for differences in oviposition preferences between ranges.

Results

Comparisons of fig contents and benefits of mutualists

We recorded the contents of 1,492 figs that contained *E. verticillata* (table S1). Each fig contained about 17 male florets and 178 ovules, with no significant differences between ranges (table S6; figure 2a). Both occupancy rate and gall failure rate did not vary between the two range types (table S6; figure 2b), and the pollinator was the predominant species, with similar offspring abundance, foundress numbers and sex ratios of pollinator offspring in the two ranges (table S3, S6; figure 2a, b).

These results suggested that both the plant's initial reproductive investment to each fig and the colonisation success of fig wasps were consistent across different ranges.

However, figs from the natural range contained on average about 28% more seeds than those from the translocated range (table S6; figure 2a) and this led to an apparent change in the relative benefits for the two mutualists as shown by a significantly higher P:S ratios in the translocated range (table S6; figure 2b).

Comparisons of NPFW communities and their effects

We recorded a total of 24 NPFW morphospecies in the figs (table S5). The parasitoids of pollinator offspring, and the seed predator, were absent from most sample sites in the translocated range (table S5), and their prevalence, abundance and species richness in the natural range were significantly higher than in the translocated range (table S7; figure S1a-c). In contrast, prevalence and species richness of 'other NPFWs' were similar in both ranges (table S7; figure S1a-c).

Within the natural range of *F. microcarpa*, the abundance of parasitoids of pollinator offspring had significant negative relationships with both pollinator abundance and the P:S ratio (table S8; figure 3a, c), while parasitoid abundance did not negatively affect either measure in the translocated range (table S8; figure 3a, c), showing that the rarity of parasitoids of pollinator offspring benefited pollinator populations and consequently facilitated the alteration of relative benefits for the two mutualists. Parasitoids of pollinators had no effects on the number of seeds in figs, irrespective of location (table S8; figure 3b).

The seed predator and ‘other NPFWs’ had no significant impacts on the P:S ratio (table S8; figure S2c, f), though ‘other NPFWs’ had significant negative relationships with pollinator abundance and seed number in both ranges (table S8; figure S2d, e).

Alterations in pollinator oviposition preferences

We measured the pedicel lengths of a total of 20,969 ovules from 136 figs (table S9). Mean pedicel and pollinator ovipositor lengths did not differ between the two ranges (table S3, S10), showing that the key morphological traits of both mutualists had not changed after translocation. The parasitoids of pollinator offspring and the seed predator were rare in the translocated range, while ‘other NPFWs’ were relatively common throughout (table S9).

The proportion of ovules galled by pollinators (and containing either pollinator offspring, parasitoids of pollinator offspring or were empty) increased with increasing pedicel length, i.e. towards the central area of the figs (table S10; figure 4a). This trend was significantly stronger in the plant's natural range than in the translocated range (table S10; figure 4a) and reflects an apparent alteration in pollinator oviposition preferences. Conversely, ovules with longer pedicels (located towards the central area of the figs) were less likely to contain seeds or the offspring of the seed predator, and this trend was significantly stronger in the translocated range than the natural range (table S10; figure 4b), indicating that the expanded oviposition range of pollinators restricted the distribution of seeds. In addition, pedicels of pollinator-galled ovules (containing pollinators, parasitoids of pollinator offspring or as failed

galls) were significantly longer in figs from the natural range than in those from the translocated range (table S3, S10), further confirming that pollinator foundresses were more willing to oviposit in ovules closer to the fig wall in the translocated range. When only galls that produced pollinator offspring or seeds were considered, we detected similar spatial patterns (table S10; figure S3a, b).

Discussion

Host-specific mutualisms are often the product of long periods of coevolution and are widely considered to be highly stable [45,46]. Despite this, our results have shown that the anthropogenic translocation of a pair of mutualists outside of their native range, where there was a lower diversity and abundance of parasitoids, has altered the relative reproductive benefits in favour of the pollinating fig wasp. Moreover, consistent with the selection-relaxation hypothesis [17], we found a within-fig oviposition range expansion by the pollinating wasps in the areas where its parasitoids were rare, an effect analogous to competitive release, that has occurred in response to the availability of enemy-free space [29,47-49]. Such an oviposition range expansion utilised some ovules that might otherwise have become seeds, therefore further restricting seeds to the places closer to the fig wall and causing a decline in the number of seeds.

We failed to detect any increase in the number of pollinator offspring in the areas where they had been translocated. This may reflect a tradeoff between oviposition range expansion and the time taken for individual eggs to be laid by the short-lived

pollinators. Although ovipositor length, a key trait for oviposition [10,16], did not change within the short time after translocation, oviposition range expansion is likely to be at the cost of increased handling time of oviposition because ovules closer to fig wall have longer styles and require more time to penetrate. Adult female pollinators however have only a few hours to lay their eggs [13].

Contrasting likelihoods of translocation among the different groups of fig wasps may reflect their relative native-range distributions and abundance, ability to survive in seasonal environments and variation in their ability to establish successfully. This is likely to depend on their trophic level [27,28,33]. Pollinators of monoecious fig trees can independently disperse long distances [50,51], and some NPFW may be equally mobile. Human agency is nonetheless responsible for extra-continental transport [52], and this is facilitated by the many pollinator and gall-forming NPFW fig wasp larvae that routinely develop inside a single fig. In contrast, the relatively low densities and prevalence of parasitoids of both the pollinator and gall-makers in the native range of *F. microcarpa* [25,33] suggest that they are less likely to be transported by un-sanctioned human activities. Parasitoid NPFWs also need suitable hosts to already be present at a translocation site if they are to become established.

The mean style lengths of ovules galled by pollinator foundresses increases as oviposition progresses and if multiple foundresses compete for oviposition sites [53]. We found no differences in pollinator foundress numbers, pollinator offspring and galling/oviposition rates per fig between the natural and translocated ranges, suggesting that foundress number variation is unlikely to explain our results. The

climate in the translocated ranges of *F. microcarpa* is less tropical and more seasonal than in its native range and the initiation and development of figs become more seasonal there [37]. This might have influenced pollination rates or seed set, but our data provide no evidence that relevant morphological traits within figs, such as style and pedicel lengths or the numbers of flowers, vary according to range type. Given the relatively long generation times of the plant, and their often-horticultural origins, this is not surprising.

Our results emphasise the important role of their natural enemies in reducing the value of the more peripheral ovules inside figs to ovipositing pollinator foundresses and thus facilitating seed production, because pollinator offspring in these ovules suffer higher rates of parasitism. Together with other factors, this selection pressure contributes to the oviposition decisions made by the pollinators. In the longer term, this may act as an agent of selection on pollinator morphological characters such as ovipositor length [10,17], which is correlated with the lengths of the styles of the particular host *Ficus* species [18]. Selection may favour longer ovipositor lengths when the value of oviposition in longer-styled flowers (those with shorter pedicels; figure 1) increases. We failed to find evidence in support of this, possibly because of the relatively short time after translocations (only several tens of generations in many translocated sites), and because the small number of foundresses that enter each fig also reduces the intensity of competition for oviposition sites, so the advantages of being able to oviposit into additional ovules is weak. Changes in behavior appear to have been more labile and rapidly responsive to selection than morphological

characters [17].

The reluctance or inability of pollinators to oviposit in the longer-styled ovules has consequences for the long-term relationship between the host trees and their wasp mutualists, because it helps ensure that a certain proportion of the ovules become seeds and promotes long-term mutualism stability. The benefits for the plant from the activities of parasitoid fig wasps might be argued to constrain the evolution of defenses favouring pollinators [16], but these benefits must be weighed against direct losses to individual trees of the male component of their reproductive function, which is related to the number of pollen-carrying female fig wasp offspring they generate [13,54].

Anthropogenic activities are posing increasingly serious threats to the maintenance of biodiversity and ecosystem functions. The resulting declines in the complexity of food webs and loss of top-down controls are likely to have cascading effects [1,55]. Our results show that they can alter the relative benefits to mutualists even in a long-established plant-insect pollinator system. Such changes may already be ubiquitous, but are seldom sufficiently understood to be detected [1,4].

Data accessibility. The data used in this paper can be accessed via Dryad:

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Authors' Contributions. XYZ and SGC designed the experiments, RW, WG, DWD, RJQ and SGC analyzed data, RW, YC and SGC collected the data. All authors contributed to paper writing and approved the manuscript.

Competing interests. The authors declare that they have no competing interests.

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Figure legends

Figure 1. Schematic spatial stratification pattern of fig contents (a & b). (a) After entering figs, pollinator foundresses prefer to oviposit in ovules close to the center of a fig, but pollinate flowers irrespective of their style lengths. Conversely, parasitoids lay eggs from the outside of figs and are more likely to attack hosts located in ovules nearer the fig wall. (b) After pollination and oviposition, galls of pollinator offspring are aggregated towards the center of the figs and developing seeds and galls containing parasitoid larvae are mainly located nearer the fig wall.

Figure 2. Comparisons of fig contents, gall failure rates, occupancy rates, pollinator sex ratios and pollinator abundance to seed number ratio (P:S ratio) between different ranges of *F. microcarpa* (a-c). Different letters indicate significant differences based on the results from GLMMs (see table S5).

Figure 3. Relationships between the numbers of parasitoids of pollinator offspring and pollinator abundance, seed number and the P:S ratio in different ranges of *F. microcarpa* (a-c). Solid and dashed lines represent significant and nonsignificant relationships based on the results from GLMMs, with different letters indicating significant differences in the strength of effects (as reflected by the slopes of GLMMs) between ranges (see table S8).

Figure 4. The relationships between pedicel length and the proportions of ovules

developing as galls of pollinator fig wasps and their parasitoids (a) and those becoming seeds or containing seed predators (b). Trends in different ranges are displayed separately, and the proportions of total ovules with different contents (means \pm S.E.) are shown for every 0.1 unit of LN(x+1)-transformed pedicel length. Different letters indicate significant differences in the strength of effects (as reflected by the slopes of GLMMs) between ranges (see table S10).

Electronic supplementary material

Journal name: Proceedings of the Royal Society B

Title: Loss of top-down biotic interactions changes the relative benefits for obligate mutualists

Authors: Rong Wang, Xiao-Yong Chen, Yan Chen, Gang Wang, Derek W. Dunn, Rupert J. Quinnell, Stephen G. Compton

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Table S1. Sample sizes of *F. microcarpa* figs at each site. We recorded the contents of 1,492 figs that contained *E. verticillata* (additional figs, which contained only NPFWs were not included). The sample consisted of 608 and 884 figs from the natural and the translocated ranges of *F. microcarpa*, respectively.

Area	Site (abbreviation)	Location	Year(s)	N trees	N figs
Natural range					
China	Guangzhou (GZ)	N 23°11', E 113°22'	2012, 2015	11	127
China	Xishuangbanna (XS)	N 22°00', E 100°48'	2011, 2016	17	279
China	Taibei (TB)	N 25°01', E 121°33'	2012	8	104
Thailand	Bangkok (BK)	N 13°44', E 100°33'	2012, 2015	4	43
Thailand	Chiang Mai (CM)	N 18°46', E 98°59'	2012	4	47
Thailand	Kanchanaburi (KC)	N 14°04', E 99°32'	2013	5	48
The Philippines	Manila (MN)	N 14°40', E 121°04'	2012	2	40
Total	--	--	--	51	608
Translocated range					
Chinese extension range					
China	Chengdu (CD)	N 30°40', E 104°06'	2012, 2015	3	21
China	Panzhihua (PZ)	N 26°35', E 101°43'	2012	4	31
China	Sanming (SM)	N 26°16', E 117°38'	2013	4	71
China	Xichang (XC)	N 27°53', E 102°17'	2012	2	23
Total	--	--	--	13	146
Non-Asian translocation range					
Australia	Brisbane (BR)	S 27°29', E 153°06'	2012	3	48
Bermuda	Bermuda (BM)	N 32°18', W 64°47'	2016	3	25
Brazil	Rio de Janeiro (RJ)	S 22°53', W 43°34'	2012	6	101
Canary Islands	Tenerife (TN)	N 28°29', W 16°19'	2013	1	30
Florida	Davie (DV)	N 26°04', W 80°14'	2012	4	75
Greece	Rhodes (RD)	N 36°10', E 27°58'	2011, 2012	11	67
Greece	Symi (SY)	N 36°35', E 27°50'	2012	2	19
Italy	Sicily (SC)	N 38°07', E 13°22'	2012	10	87
Libya	Tripoli (TP)	N 32°51', E 13°12'	2012	7	75
Malta	Malta (MT)	N 35°56', E 14°23'	2011	9	57
Puerto Rico	Puerto Rico (PR)	N 18°23', W 66°04'	2013	7	64
Spain	Majorca (MJ)	N 39°35', E 2°40'	2012	6	80
Turkey	Marmaris (MM)	N 36°51', E 28°15'	2013	1	10
Total	--	--	--	70	738
Overall total	--	--	--	134	1492

Table S2. Species belonging to different categories of fig wasps based on Wang et al. (2015a) and Compton et al. (2018).

Categories of fig wasps	Wasp taxon (abbreviation)
Pollinating agaonids	Agaonidae, Agaoninae Eupristina verticillata Waterston (Ev)
Parasitoids of pollinator offspring	Pteromalidae, Sycoryctinae Philotrypesis emeryi Grandi (Pe) Philotrypesis okinavensis Ishii (Po) Philotrypesis sp.1 (Ps1) Philotrypesis sp.2 (Ps2) Philotrypesis sp.3 (Ps3) Sycoryctes moneres Chen (Srm) Sycoryctes sp. (Srs) Sycoscapter gajimaru Ishii (Scg) Sycoscapter sp. (Scs)
Seed predator	Pteromalidae, Sycoryctinae Philotrypesis taiwanensis Chen (Pt)
'Other NPFWs'	Agaonidae, Agaoninae Eupristina sp. ('Cheater') (Es) Pteromalidae, Epichrysomallinae Acophila quinata Zhang & Xiao (Aq) Meselatus bicolor Chen (Mb) Odontofroggatia corneri Wiebes (Oc) Odontofroggatia galili Wiebes (Og) Odontofroggatia ishii Wiebes (Oi) Odontofroggatia quinifuniculus Feng & Huang (Oq) Sycobia sp. (Sbs) Pteromalidae, Otitesellinae Micranisa degastris Chen (Md) Walkerella microcarpae Bouček (Wm) Walkerella nigrabdomina Ma & Yang (Wn) Walkerella sp. (Ws) Eurytomidae Bruchophagus sensoriae Chen (Bs) Sycophila curta Chen (Sc) Sycophila maculafacies Chen (Sm) Sycophila maculafacies ('pale') (Smp) Sycophila petiolata Chen (Sp) Sycophila sp. (Ss) Ormyridae Ormyrus lini Chen (Ol) Ormyrus sp. (Os) Pteromalidae, Pireninae

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Table S3. Pollinator foundress number, pedicel lengths of all ovules and the ovules becoming galls of pollinators and parasitoids of pollinator offspring and failed galls, and ovipositor lengths of pollinators in different ranges.

	Natural range				Translocated range			
	N crops	N figs	N ovules	Mean \pm S.E.	N crops	N figs	N ovules	Mean \pm S.E.
Number of pollinator foundresses	30	216	--	1.47 \pm 0.06	51	266	--	1.44 \pm 0.06
Pedicel lengths of all ovules (mm)	11	57	9488	0.246 \pm 0.003	15	79	11481	0.247 \pm 0.002
Pedicel lengths of ovules becoming galls of pollinators and parasitoids of pollinator offspring and failed galls (mm)	11	57	2477	0.484 \pm 0.006	15	79	3146	0.427 \pm 0.005
Ovipositor lengths of pollinators (mm)	11	32	150	0.681 \pm 0.011	15	50	300	0.732 \pm 0.006

Table S4. Sample sizes of *F. microcarpa* figs used in the oviposition preference study and for measuring the ovipositor lengths of female pollinator offspring. Order and abbreviations of sample sites are as in Table S1.

Range	Site	N trees	N figs	N trees for ovipositor length	N figs for ovipositor length
Natural range					
	GZ	2	12	2	10
	XS	3	11	3	8
	BK	3	11	3	6
	KC	3	23	3	8
Total	--	11	57	11	32
Translocated range					
Chinese extension range					
	PZ	2	6	2	5
	SM	2	10	2	10
	XC	2	6	2	5
Total	--	6	22	6	20
Non-Asian translocation range					
	DV	2	12	2	5
	RD	2	11	2	10
	TP	3	18	3	10
	MJ	2	16	2	5
Total	--	9	57	9	30

Table S6. Comparisons of different fig contents, pollinator foundress number, gall failure rate, occupancy rate, pollinator sex ratio and pollinator abundance : seed number ratio (the P:S ratio) (per fig) between different ranges of *F. microcarpa*, using GLMMs that assumed either binomial (B) and Poisson (P) distributions of residuals. A total of 79,846 fig wasps were present within the figs, comprising 58,023 pollinators and 21,823 NPFWs. A total of 88996 ovules had been galled by pollinators or a galler NPFW, with $10.5\% \pm 0.3\%$ of these galls failing to support the full development of fig wasp offspring (failed galls).

Response variable	Fixed effect	Model	df	LR test		
				df	LR	p
Male floret number	Range	GLMMs (P)	1488	1	0.23	0.634 ^{NS}
Ovule number	Range	GLMMs (P)	1488	1	0.01	0.923 ^{NS}
Abundance of total fig wasps	Range	GLMMs (P)	1488	1	0.10	0.747 ^{NS}
Pollinator abundance	Range	GLMMs (P)	1488	1	<0.01	0.986 ^{NS}
Seed number	Range	GLMMs (P)	1488	1	6.39	0.011 [*]
Number of pollinator foundresses	Range	GLMMs (P)	478	1	0.11	0.744 ^{NS}
Gall failure rate	Range	GLMMs (B)	1488	1	2.56	0.110 ^{NS}
Occupancy rate	Range	GLMMs (B)	1488	1	0.33	0.567 ^{NS}
Pollinator sex ratio	Range	GLMMs (B)	1488	1	0.77	0.380 ^{NS}
P:S ratio	Range	GLMMs (B)	1488	1	13.37	0.001 ^{***}

^{NS}: not significant; ^{*}: $p < 0.05$; ^{**}: $p < 0.01$; ^{***}: $p < 0.001$.

Table S7. Comparisons of the prevalence, abundance and species richness of total NFPWs and three component categories of fig wasps between different ranges of *F. microcarpa*, using GLMMs that assumed either binomial (B) and Poisson (P) distributions of residuals.

Response variable	Fixed effect	Model	df	LR test		
				df	LR	p
Prevalence of total NFPWs	Range	GLMMs (B)	1488	1	0.39	0.531 ^{NS}
Prevalence of parasitoids of pollinator offspring	Range	GLMMs (B)	1488	1	12.01	<0.001 ^{***}
Prevalence of seed predator	Range	GLMMs (B)	1488	1	9.92	0.002 ^{**}
Prevalence of 'other NFPWs'	Range	GLMMs (B)	1488	1	2.13	0.145 ^{NS}
Abundance of total NFPWs	Range	GLMMs (P)	1488	1	0.02	0.893 ^{NS}
Abundance of parasitoids of pollinator offspring	Range	GLMMs (P)	1488	1	11.27	<0.001 ^{***}
Abundance of seed predator	Range	GLMMs (P)	1488	1	10.35	0.001 ^{**}
Abundance of 'other NFPWs'	Range	GLMMs (P)	1488	1	4.90	0.027 [*]
Species richness of total NFPWs	Range	GLMMs (P)	1488	1	2.29	0.131 ^{NS}
Species richness of parasitoids of pollinator offspring	Range	GLMMs (P)	1488	1	12.31	<0.001 ^{***}
Species richness of seed predator	Range	GLMMs (P)	1488	1	9.37	0.002 ^{**}
Species richness of 'other NFPWs'	Range	GLMMs (P)	1488	1	1.82	0.177 ^{NS}

NS: not significant; *: p<0.05; **: p<0.01; ***: p<0.001.

Table S8. Comparisons of the strengths of effects of different categories of fig wasps on pollinator abundance, seed number and the P:S ratio between different ranges of *F. microcarpa*, using GLMMs that assumed either binomial (B) and Poisson (P) distributions of residuals.

Response variable	Fixed effect	Model	df	LR test			Z-test			
				df	LR	p	Range	Slope (mean \pm S.E.)	z value	p
Pollinator abundance	Abundance of the parasitoids of pollinator offspring \times Range	GLMMs (P)	1117	1	91.10	<0.001 ***	Natural	-0.07 \pm 0.01	-8.05	<0.001 ***
							Translocated	0.09 \pm 0.01	6.40	<0.001 ***
Seed number	Abundance of the parasitoids of pollinator offspring \times Range	GLMMs (P)	1117	1	0.48	0.490 NS	Natural	-0.02 \pm 0.01	-1.93	0.053 NS
							Translocated	-0.03 \pm 0.02	-1.74	0.082 NS
P:S ratio	Abundance of the parasitoids of pollinator offspring \times Range	GLMMs (B)	1117	1	41.79	<0.001 ***	Natural	-0.07 \pm 0.01	-5.13	<0.001 ***
							Translocated	0.12 \pm 0.03	4.58	<0.001 ***
Pollinator abundance	Abundance of the seed predator \times Range	GLMMs (P)	873	1	0.81	0.369 NS	Natural	-0.001 \pm 0.01	-0.07	0.948 NS
							Translocated	-0.02 \pm 0.02	-1.05	0.293 NS
Seed number	Abundance of the seed predator \times Range	GLMMs (P)	873	1	0.02	0.901 NS	Natural	-0.02 \pm 0.01	-1.99	0.047 *
							Translocated	-0.02 \pm 0.02	-0.85	0.395 NS
P:S ratio	Abundance of the seed predator \times Range	GLMMs (B)	873	1	0.20	0.658 NS	Natural	0.03 \pm 0.01	1.82	0.053 NS
							Translocated	0.01 \pm 0.03	0.51	0.612 NS
Pollinator abundance	Abundance of 'other NPFWs' \times Range	GLMMs (P)	1436	1	2.68	0.101 NS	Natural	-0.16 \pm 0.01	-21.84	<0.001 ***
							Translocated	-0.18 \pm 0.01	-34.58	<0.001 ***
Seed number	Abundance of 'other NPFWs' \times Range	GLMMs (P)	1436	1	3.56	0.059 NS	Natural	-0.14 \pm 0.01	-17.98	<0.001 ***
							Translocated	-0.16 \pm 0.01	-25.39	<0.001 ***
P:S ratio	Abundance of 'other NPFWs' \times Range	GLMMs (B)	1436	1	0.62	0.431 NS	Natural	-0.002 \pm 0.01	-0.18	0.859 NS
							Translocated	0.01 \pm 0.01	1.07	0.287 NS

NS: not significant; *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$; \times : interaction.

Table S9. Contents in the figs where pedicel lengths of all ovules were measured for analyzing the oviposition preferences of fig wasps. Order and abbreviations of species are as in Table S2, and clustering of fig wasps are as in Table S5.

Content	Unused ovules	Failed galls	Seeds	Pollinating agaonids	Parasitoids of pollinators						Seed predator	'Other NPFWs'										Total ovules
Species				Ev	Pe	Po	Srm	Srs	Seg	Sum	Pt	Es	Oc	Og	Oi	Md	Wm	Sm	Smp	Sp	Sum	
Natural range	4778	468	1500	1772	71	17	55	21	73	237	250	130	71	66	114	12	52	18	11	9	483	9488
Translocated range	5412	487	2013	2647	0	5	0	0	7	12	0	0	73	571	0	98	99	34	19	16	910	11481
Total	10190	955	3513	4419	71	22	55	21	80	249	250	130	144	637	114	110	151	52	30	25	1393	20969

Table S10. Comparisons of lengths of ovule pedicels and pollinator ovipositors (mm) and trends in the proportions of ovules containing different contents in relation to increasing pedicel lengths in the figs used in the oviposition preference study between different ranges of *F. microcarpa*, using LMMs and GLMMs assuming binomial distributions of residuals.

Response variable	Fixed effect	Model	df	LR test			Z-test			
				df	LR	p	Range	Slope (mean \pm S.E.)	z value	p
Pedicel lengths of all ovules	Range	LMMs	1, 20833	1	3.12	0.077 ^{NS}	--	--	--	--
Pedicel lengths of ovules becoming galls of pollinators and parasitoids of pollinator offspring and failed galls	Range	LMMs	1, 5487	1	8.24	0.004 ^{**}	--	--	--	--
Ovipositor lengths of pollinators	Range	LMMs	1, 366	1	2.71	0.100 ^{NS}	--	--	--	--
Proportion of ovules becoming galls of pollinators, parasitoids of pollinator offspring and failed galls	Pedicel length \times Range	GLMMs (B)	20962	1	108.26	<0.001 ^{***}	Natural	7.22 \pm 0.16	44.66	<0.001 ^{***}
							Translocated	5.14 \pm 0.12	41.58	<0.001 ^{***}
Proportion of ovules becoming seeds and galls of seed predator	Pedicel length \times Range	GLMMs (B)	20962	1	176.74	<0.001 ^{***}	Natural	-0.50 \pm 0.14	-3.52	<0.001 ^{***}
							Translocated	-3.37 \pm 0.17	-20.34	<0.001 ^{***}
Proportion of ovules containing pollinating agaonids	Pedicel length \times Range	GLMMs (B)	20962	1	115.43	<0.001 ^{***}	Natural	6.96 \pm 0.17	40.41	<0.001 ^{***}
							Translocated	4.72 \pm 0.13	37.66	<0.001 ^{***}
Proportion of ovules becoming seeds	Pedicel length \times Range	GLMMs (B)	20962	1	178.75	<0.001 ^{***}	Natural	-0.42 \pm 0.15	-2.81	0.005 ^{**}
							Translocated	-3.38 \pm 0.17	-20.35	<0.001 ^{***}

^{NS}: not significant; *: p<0.05; **: p<0.01; ***: p<0.001; \times : interaction.

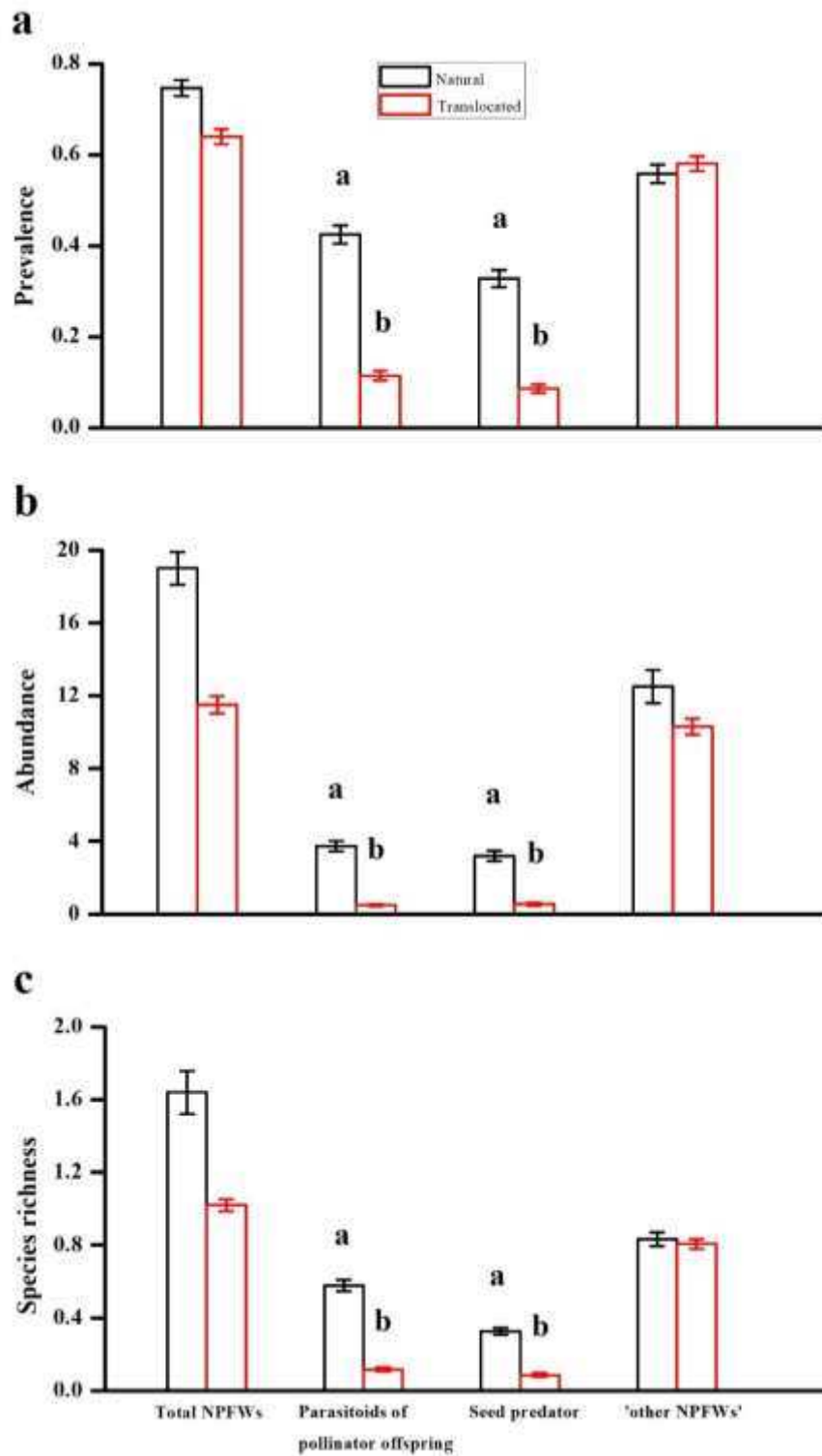


Figure S1. Comparisons of prevalence, abundance and species richness of all NPFW species and the three categories of NPFWs between two ranges of *F. microcarpa* (a-c). Groupings of NPFW species are as shown in Table S5, and different letters indicate significant differences based on the results from GLMMs (see table S7).

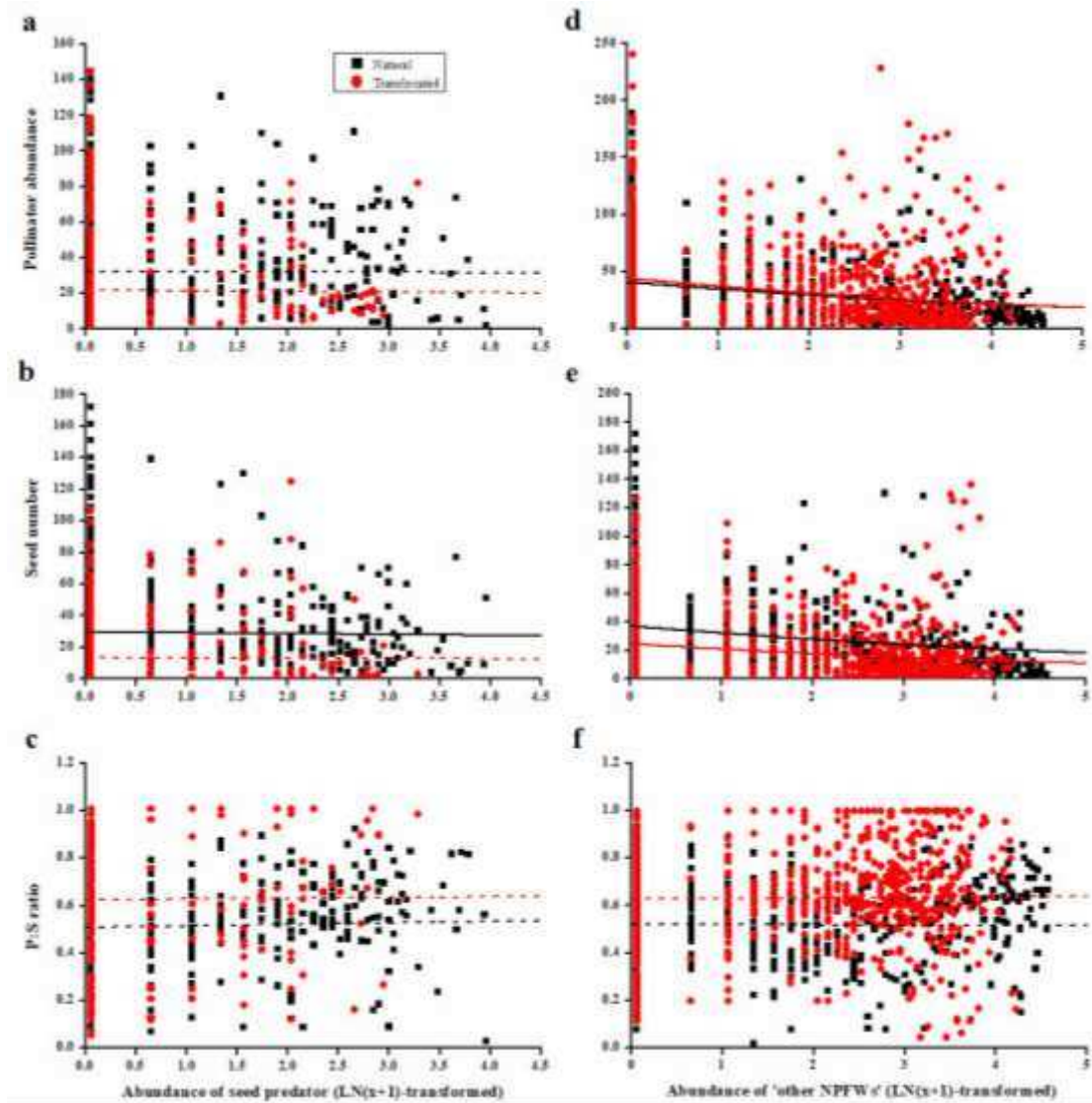


Fig. S2. Effects of the seed predator (a-c) and 'other NPFWs' (d-f) on pollinator abundance, seed number and the P:S ratio in different ranges of *F. microcarpa*. Black curves with squares, red curves with circles and blue curves with triangles represent the regression functions and the data points (per fig) in the natural and the translocated ranges of *F. microcarpa*. Solid and dashed curves represent significant and nonsignificant relationships, respectively (see Table S8).

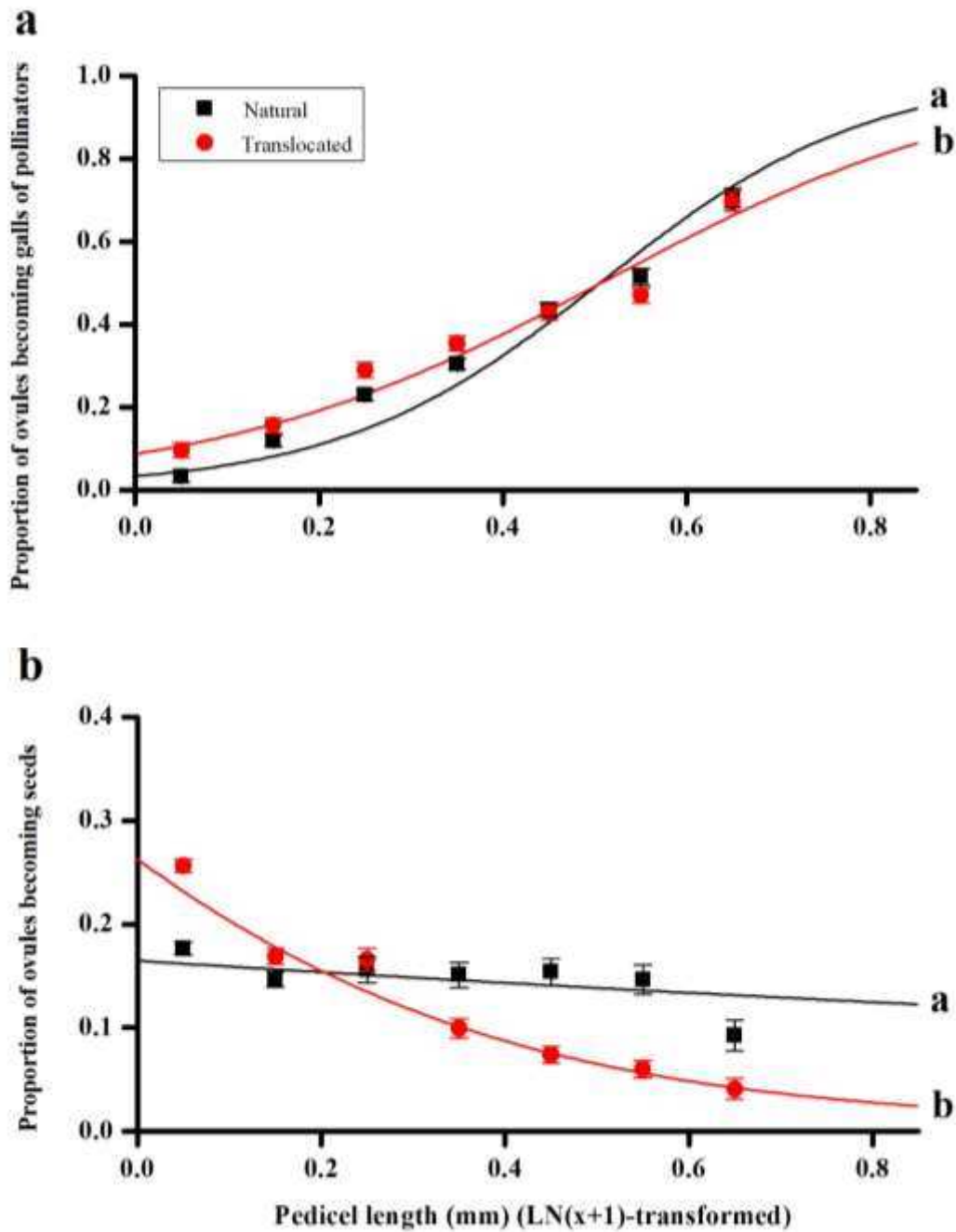


Figure S3. Trends of the proportions of ovules containing pollinator offspring (a) and those becoming seeds (b) towards increasing pedicel lengths in different ranges of *F. microcarpa*. The proportion of ovules containing each of the two contents to total ovules (mean \pm S.E.) is shown for every 0.1 unit of LN(x+1)-transformed pedicel length except for the last one, which includes all ovules with pedicel lengths larger than 0.6 unit (shown at 0.65 unit). Different letters indicate significant differences in the strength of effects (reflected by the slopes of GLMMs) between two ranges (see Table S10).

Electronic supplementary material for comparative results (three ranges)

Comparisons of fig contents and benefits of mutualists

We recorded the contents of 1,492 figs that contained *E. verticillata* (table S1). Each fig contained about 17 male florets and 178 ovules, with no significant differences among the three ranges (table S11; figure S4a). Both occupancy rate and gall failure rate did not vary across the three range types (table S11; figure S4b), and the pollinator was the predominant species, with similar abundance, foundress numbers and sex ratios of pollinator offspring in all three ranges (table S11; figure S4a, b). These results suggested that the plant's initial reproductive investment to each fig and the colonisation success of fig wasps were consistent across different ranges.

Figs from the natural range however contained on average about 25% more seeds than those from the two translocated ranges (table S11; figure S4a) and consequently led to a significant change in the relative benefits for the two mutualists mirrored by significantly higher P:S ratio in both translocated ranges (table S11; figure S4b).

Comparisons of NPFW communities and their effects

We recorded a total of 24 morphospecies of NPFWs in the figs (table S5), and their overall prevalence, abundance and species richness did not vary significantly among different ranges (table S12; figure S5a-c). However, the parasitoids of pollinator offspring and the seed predator were absent from most sample sites in both translocated ranges (table S5), and their prevalence, abundance and species richness in the plant's natural range were significantly higher than in the two translocated ranges

(table S12; figure S5a-c). In contrast, prevalence, abundance and species richness of ‘other NPFWs’ were similar in all three ranges (table S12; figure S5a-c).

Within the natural range of *F. microcarpa*, the abundance of parasitoids of pollinator offspring had significant negative relationships with both pollinator abundance and the P:S ratio within individual figs (table S13; figure S6a-c), while parasitoid abundance failed to negatively affect either measure in the two translocated ranges (table S13; figure S6a-c), showing that the rarity of parasitoids of pollinator offspring benefited pollinator populations and consequently facilitated the change of relative benefits for the two mutualists. This category of NPFWs had no effects on the number of seeds in figs, irrespective of location (table S13; figure S6a-c).

The seed predator and ‘other NPFWs’ had no significant effects on the P:S ratio (table S13; figure S7c, f), though ‘other NPFWs’ had significant negative relationships with both pollinator abundance and seed number in any of the three ranges (table S13; figure S7d, e).

Alterations in pollinator oviposition preferences

We measured the pedicel lengths of a total of 20,969 ovules from 136 figs (table S14). Mean pedicel and pollinator ovipositor lengths did not differ among the three ranges (table S15), showing that key morphological traits of both mutualists did not change after translocation. The parasitoids of pollinator offspring and the seed predator were rare in both translocated ranges, while ‘other NPFWs’ were relatively common throughout (table S14).

The proportion of ovules galled by pollinators (and containing either pollinator offspring, parasitoids of pollinator offspring or were empty) increased with increasing pedicel length, i.e. towards the central area of the figs (table S15; figure 8a). This trend was significantly stronger in the plant's natural range than in the two translocated ranges (table S15; figure 8a) and reflects an apparent alteration in pollinator oviposition preferences. Conversely, ovules with longer pedicels (located towards the central area of the figs) were less likely to contain seeds or the offspring of the seed predator, and this trend was significantly stronger in the two translocated ranges than the natural range (table S15; figure 8b), indicating that the expanded oviposition range of pollinators restricted the availability of seeds. In addition, pedicels of pollinator-galled ovules (containing pollinators, parasitoids of pollinator offspring or as failed galls) were significantly longer in figs from the natural range than in those from translocated ranges (table S15), further confirming that pollinator foundresses were more willing to oviposit in ovules closer to the fig wall in the two translocated ranges. We detected similar spatial distribution patterns when only galls containing pollinators or seeds were considered (table S15; figure 9a, b).

Table S11. Comparisons of different fig contents, pollinator foundress number, gall failure rate, occupancy rate, pollinator sex ratio and pollinator abundance : seed number ratio (P:S) (per fig) among different ranges of *F. microcarpa*, using GLMMs that assumed either binomial (B) and Poisson (P) distributions of residuals. A total of 79,846 fig wasps were found within the figs, comprising 58,023 pollinators and 21,823 NPFWs. A total of 88996 ovules had been galled by pollinators or galler NPFWs, with $10.5\% \pm 0.3\%$ of these galls failing to support the full development of fig wasp offspring (empty galls). Bonferroni corrections were used to evaluate the significance of multiple pair-wise tests among different ranges, and the corrected significance was presented as ^{NS}: not significant; *: $p < 0.05$; **: $p < 0.01$ and ***: $p < 0.001$.

Response variable	Fixed effect	Model	df	LR test			Pair-wise comparison		
				df	LR	p	Comparison pair (mean value (mean \pm S.E.))	z value	p
Male floret number	Range	GLMMs (P)	1487	2	2.94	0.230 ^{NS}	Natural vs. Chinese extension	0.87	0.383 ^{NS}
							Natural vs. Non-Asian translocation	-0.98	0.326 ^{NS}
							Chinese extension vs. Non-Asian translocation	-1.68	0.092 ^{NS}
Ovule number	Range	GLMMs (P)	1487	2	0.11	0.944 ^{NS}	Natural vs. Chinese extension	0.16	0.870 ^{NS}
							Natural vs. Non-Asian translocation	-0.19	0.852 ^{NS}
							Chinese extension vs. Non-Asian translocation	-0.32	0.745 ^{NS}
Abundance of total fig wasps	Range	GLMMs (P)	1487	2	0.44	0.803 ^{NS}	Natural vs. Chinese extension	0.64	0.519 ^{NS}
							Natural vs. Non-Asian translocation	0.15	0.884 ^{NS}
							Chinese extension vs. Non-Asian translocation	-0.58	0.563 ^{NS}
Pollinator abundance	Range	GLMMs (P)	1487	2	0.20	0.907 ^{NS}	Natural vs. Chinese extension	0.34	0.733 ^{NS}
							Natural vs. Non-Asian translocation	-0.11	0.915 ^{NS}
							Chinese extension vs. Non-Asian translocation	-0.44	0.658 ^{NS}
Seed number	Range	GLMMs (P)	1487	2	7.07	0.029 [*]	Natural vs. Chinese extension	2.41	0.016 [*]
							Natural vs. Non-Asian translocation	2.48	0.013 [*]
							Chinese extension vs. Non-Asian translocation	-0.82	0.411 ^{NS}
Number of pollinator foundresses	Range	GLMMs (P)	477	2	3.87	0.144	Natural (1.47 \pm 0.06) vs. Chinese extension (1.74 \pm 0.19)	-1.38	0.167 ^{NS}
							Natural vs. Non-Asian translocation (1.37 \pm 0.06)	0.93	0.353 ^{NS}
							Chinese extension vs. Non-Asian translocation	1.99	0.047 ^{NS}
Gall failure rate	Range	GLMMs (B)	1487	2	2.59	0.274 ^{NS}	Natural vs. Chinese extension	-0.94	0.349 ^{NS}

							Natural vs. Non-Asian translocation	-1.64	0.100 ^{NS}
							Chinese extension vs. Non-Asian translocation	-0.16	0.870 ^{NS}
Occupancy rate	Range	GLMMs (B)	1487	2	0.83	0.661	Natural vs. Chinese extension	0.92	0.358 ^{NS}
							Natural vs. Non-Asian translocation	0.36	0.718 ^{NS}
							Chinese extension vs. Non-Asian translocation	-0.71	0.478 ^{NS}
Pollinator sex ratio	Range	GLMMs (B)	1487	2	2.33	0.312 ^{NS}	Natural vs. Chinese extension	0.32	0.746 ^{NS}
							Natural vs. Non-Asian translocation	-1.25	0.213 ^{NS}
							Chinese extension vs. Non-Asian translocation	-1.26	0.206 ^{NS}
P:S ratio	Range	GLMMs (B)	1487	2	13.81	0.001 ^{**}	Natural vs. Chinese extension	-3.26	0.001 ^{**}
							Natural vs. Non-Asian translocation	-3.99	<0.001 ^{***}
							Chinese extension vs. Non-Asian translocation	0.66	0.507 ^{NS}

Table S12. Comparisons of the prevalence, abundance and species richness of total NFPWs and three component categories of fig wasps among different ranges of *F. microcarpa*, using GLMMs that assumed either binomial (B) and Poisson (P) distributions of residuals. Bonferroni corrections were used to evaluate the significance of multiple pair-wise tests among different ranges, and the corrected significance was presented as ^{NS}: not significant; *: p<0.05; **: p<0.01 and ***: p<0.001’.

Response variable	Fixed effect	Model	df	LR test			Pair-wise comparison		
				df	LR	p	Comparison pair	z value	p
Prevalence of total NFPWs	Range	GLMMs (B)	1487	2	0.40	0.818 ^{NS}	Natural vs. Chinese extension	0.35	0.725 ^{NS}
							Natural vs. Non-Asian translocation	0.64	0.522 ^{NS}
							Chinese extension vs. Non-Asian translocation	0.10	0.920 ^{NS}
Prevalence of parasitoids of pollinator offspring	Range	GLMMs (B)	1487	2	12.02	0.002 ^{**}	Natural vs. Chinese extension	2.41	0.016 [*]
							Natural vs. Non-Asian translocation	3.38	0.001 ^{**}
							Chinese extension vs. Non-Asian translocation	0.06	0.956 ^{NS}
Prevalence of seed predator	Range	GLMMs (B)	1487	2	9.93	0.007 ^{**}	Natural vs. Chinese extension	2.33	0.016 [*]
							Natural vs. Non-Asian translocation	2.60	0.009 [*]
							Chinese extension vs. Non-Asian translocation	0.12	0.906 ^{NS}
Prevalence of ‘other NFPWs’	Range	GLMMs (B)	1487	2	2.35	0.308 ^{NS}	Natural vs. Chinese extension	-1.35	0.178 ^{NS}
							Natural vs. Non-Asian translocation	-1.27	0.205 ^{NS}
							Chinese extension vs. Non-Asian translocation	0.48	0.633 ^{NS}
Abundance of total NFPWs	Range	GLMMs (P)	1487	2	0.78	0.678 ^{NS}	Natural vs. Chinese extension	-0.55	0.582 ^{NS}
							Natural vs. Non-Asian translocation	0.38	0.706 ^{NS}
							Chinese extension vs. Non-Asian translocation	0.87	0.387 ^{NS}
Abundance of parasitoids of pollinator offspring	Range	GLMMs (P)	1487	2	11.28	0.004 ^{**}	Natural vs. Chinese extension	2.53	0.014 [*]
							Natural vs. Non-Asian translocation	3.28	0.001 ^{**}
							Chinese extension vs. Non-Asian translocation	0.08	0.935 ^{NS}
Abundance of seed predator	Range	GLMMs (P)	1487	2	10.38	0.006 ^{**}	Natural vs. Chinese extension	2.52	0.014 [*]
							Natural vs. Non-Asian translocation	2.88	0.004 [*]
							Chinese extension vs. Non-Asian translocation	0.14	0.891 ^{NS}

Abundance of 'other NPFWs'	Range	GLMMs (P)	1487	2	5.56	0.062 ^{NS}	Natural vs. Chinese extension	-2.20	0.028 ^{NS}
							Natural vs. Non-Asian translocation	-2.01	0.042 ^{NS}
							Chinese extension vs. Non-Asian translocation	0.81	0.417 ^{NS}
Species richness of total NPFWs	Range	GLMMs (P)	1487	2	2.82	0.244 ^{NS}	Natural vs. Chinese extension	0.57	0.570 ^{NS}
							Natural vs. Non-Asian translocation	1.73	0.084 ^{NS}
							Chinese extension vs. Non-Asian translocation	0.73	0.463 ^{NS}
Species richness of parasitoids of pollinator offspring	Range	GLMMs (P)	1487	2	12.31	0.002 ^{**}	Natural vs. Chinese extension	2.45	0.014 [*]
							Natural vs. Non-Asian translocation	3.45	0.001 ^{**}
							Chinese extension vs. Non-Asian translocation	0.05	0.957 ^{NS}
Species richness of seed predator	Range	GLMMs (P)	1487	2	9.39	0.009 ^{**}	Natural vs. Chinese extension	2.33	0.016 [*]
							Natural vs. Non-Asian translocation	2.56	0.011 [*]
							Chinese extension vs. Non-Asian translocation	0.12	0.906 ^{NS}
Species richness of 'other NPFWs'	Range	GLMMs (P)	1487	2	2.50	0.287 ^{NS}	Natural vs. Chinese extension	-1.53	0.125 ^{NS}
							Natural vs. Non-Asian translocation	-1.06	0.289 ^{NS}
							Chinese extension vs. Non-Asian translocation	0.82	0.411 ^{NS}

Table S13. Comparisons of the strengths of effects of different categories of fig wasps on pollinator abundance, seed number and the P:S ratio among different ranges of *F. microcarpa*, using GLMMs that assumed either binomial (B) and Poisson (P) distributions of residuals. Note that we only compared the strengths of effects of the seed predator between the Natural and the Non-Asian translocation ranges because only 8 figs contained the seed predator in the extension to the Chinese range. Bonferroni corrections were used to evaluate the significance of multiple pair-wise tests among different ranges, and the corrected significance was presented as ^{NS}: not significant; *: p<0.05; **: p<0.01 and ***: p<0.001’.

Response variable	Fixed effect	Model	df	LR test			Pair-wise comparison		
				df	LR	p	Comparison pair (slope (mean ± S.E.))	z value	p
Pollinator abundance	Abundance of the parasitoids of pollinator offspring × Range	GLMMs (P)	1115	2	94.67	<0.001 ***	Natural (-0.07 ± 0.01 ***) vs. Chinese extension (0.04 ± 0.04 ^{NS})	-3.01	0.003 **
							Natural vs. Non-Asian translocation (0.11 ± 0.02 ***)	-9.68	<0.001 ***
							Chinese extension vs. Non-Asian translocation	-1.87	0.061 ^{NS}
Seed number	Abundance of the parasitoids of pollinator offspring × Range	GLMMs (P)	1115	2	1.86	0.394 ^{NS}	Natural (-0.02 ± 0.01 ^{NS}) vs. Chinese extension (-0.09 ± 0.05 ^{NS})	1.34	0.181 ^{NS}
							Natural vs. Non-Asian translocation (-0.02 ± 0.02 ^{NS})	0.24	0.808 ^{NS}
							Chinese extension vs. Non-Asian translocation	-1.17	0.244 ^{NS}
P:S ratio	Abundance of the parasitoids of pollinator offspring × Range	GLMMs (B)	1115	2	41.95	<0.001 ***	Natural (-0.07 ± 0.01 ***) vs. Chinese extension (0.10 ± 0.06 ^{NS})	-2.52	0.012 *
							Natural vs. Non-Asian translocation (0.12 ± 0.03 ***)	-6.14	<0.001 ***
							Chinese extension vs. Non-Asian translocation	-0.38	0.703 ^{NS}
Pollinator abundance	Abundance of the seed predator × Range	GLMMs (P)	842	1	1.42	0.234 ^{NS}	Natural (-0.01 ± 0.01 ^{NS}) vs. Non-Asian translocation (-0.02 ± 0.02 ^{NS})	1.19	0.235 ^{NS}
Seed number	Abundance of the seed predator × Range	GLMMs (P)	842	1	1.63	0.202 ^{NS}	Natural (-0.02 ± 0.01 *) vs. Non-Asian translocation (-0.01 ± 0.02 ^{NS})	-1.28	0.201 ^{NS}
P:S ratio	Abundance of the seed predator × Range	GLMMs (B)	842	1	2.29	0.130 ^{NS}	Natural (0.03 ± 0.01 ^{NS}) vs. Non-Asian translocation (-0.02 ± 0.03 ^{NS})	1.51	0.130 ^{NS}
Pollinator abundance	Abundance of ‘other NPFWs’ × Range	GLMMs (P)	1434	2	3.48	0.175 ^{NS}	Natural (-0.16 ± 0.01 ***) vs. Chinese extension (-0.17 ± 0.01 ***)	0.46	0.647 ^{NS}
							Natural vs. Non-Asian translocation (-0.18 ± 0.01 ***)	1.83	0.068 ^{NS}
							Chinese extension vs. Non-Asian translocation	0.90	0.370 ^{NS}
Seed number	Abundance of ‘other NPFWs’ × Range	GLMMs (P)	1434	2	6.09	0.055 ^{NS}	Natural (-0.14 ± 0.01 ***) vs. Chinese extension (-0.18 ± 0.01 ***)	1.94	0.041 ^{NS}
							Natural vs. Non-Asian translocation (-0.16 ± 0.01 ***)	1.82	0.068 ^{NS}
							Chinese extension vs. Non-Asian translocation	-1.37	0.171 ^{NS}
P:S ratio	Abundance of ‘other NPFWs’ × Range	GLMMs (B)	1434	2	0.62	0.734 ^{NS}	Natural (-0.01 ± 0.01 ^{NS}) vs. Chinese extension (0.01 ± 0.02 ^{NS})	-0.55	0.581 ^{NS}
							Natural vs. Non-Asian translocation (0.01 ± 0.01 ^{NS})	-0.73	0.464 ^{NS}
							Chinese extension vs. Non-Asian translocation	0.07	0.947 ^{NS}

Table S14. Contents in the figs where pedicel lengths of all ovules were measured for analysing the oviposition preferences of fig wasps. Order and abbreviations of species are as in Table S2, and clustering of fig wasps are as in Table S5.

Content	Unused ovules	Failed galls	Seeds	Pollinating agaonids	Parasitoids of pollinators						Seed predator	'Other NPFWs'										Total ovules
					Ev	Pe	Po	Srm	Srs	Scg		Sum	Pt	Es	Oc	Og	Oi	Md	Wm	Sm	Smp	
Natural	4778	468	1500	1772	71	17	55	21	73	237	250	130	71	66	114	12	52	18	11	9	483	9488
Chinese extension	1555	104	891	1044	0	0	0	0	0	0	0	0	73	109	0	21	87	23	19	16	348	3942
Non-Asian translocation	3857	383	1122	1603	0	5	0	0	7	12	0	0	0	462	0	77	12	11	0	0	562	7539
Total	10190	955	3513	4419	71	22	55	21	80	249	250	130	144	637	114	110	151	52	30	25	1393	20969

Table S15. Comparisons of lengths of ovule pedicels and pollinator ovipositors (mm) and trends in the proportions of ovules containing different contents in relation to increasing pedicel lengths in the figs used in the oviposition preference study among different ranges of *F. microcarpa*, using LMMs and GLMMs assuming binomial distributions of residuals. Bonferroni corrections were used to evaluate the significance of multiple pair-wise tests among different ranges, and the corrected significance was presented as ^{NS}: not significant; * : p<0.05; ** : p<0.01 and *** : p<0.001’.

Response variable	Fixed effect	Model	df	LR test			Pair-wise comparison		
				df	LR	p	Comparison pair (mean value/slope (mean ± S.E.))	t/z value	p
Pedicel lengths of all ovules	Range	LMMs	2, 20833	2	3.29	0.193 ^{NS}	Natural (0.246 ± 0.003) vs. Chinese extension (0.243 ± 0.004)	1.76	0.093 ^{NS}
							Natural vs. Non-Asian translocation (0.250 ± 0.003)	1.55	0.137 ^{NS}
							Chinese extension vs. Non-Asian translocation	-0.41	0.690 ^{NS}
Pedicel lengths of ovules becoming galls of pollinators and parasitoids of pollinator offspring and failed galls	Range	LMMs	2, 5487	2	10.68	0.005 **	Natural (0.484 ± 0.006) vs. Chinese extension (0.396 ± 0.008)	4.67	0.002 **
							Natural vs. Non-Asian translocation (0.445 ± 0.007)	3.54	0.008 *
							Chinese extension vs. Non-Asian translocation	-1.60	0.149 ^{NS}
Ovipositor lengths of pollinators	Range	LMMs	2, 366	2	4.08	0.130 ^{NS}	Natural (0.681 ± 0.011) vs. Chinese extension (0.725 ± 0.010)	-1.37	0.184 ^{NS}
							Natural vs. Non-Asian translocation (0.736 ± 0.008)	-2.04	0.054 ^{NS}
							Chinese extension vs. Non-Asian translocation	-0.49	0.631 ^{NS}
Proportion of ovules becoming galls of pollinators, parasitoids of pollinator offspring and failed galls	Pedicel length × Range	GLMMs (B)	20960	2	108.29	<0.001 ***	Natural (7.22 ± 0.16 ***) vs. Chinese extension (5.01 ± 0.22 ***)	8.14	<0.001 ***
							Natural vs. Non-Asian translocation (5.20 ± 0.15 ***)	9.91	<0.001 ***
							Chinese extension vs. Non-Asian translocation	-0.69	0.489 ^{NS}
Proportion of ovules becoming seeds and galls of seed predator	Pedicel length × Range	GLMMs (B)	20960	2	181.37	<0.001 ***	Natural (-0.50 ± 0.14 ***) vs. Chinese extension (-2.96 ± 0.25 ***)	8.45	<0.001 ***
							Natural vs. Non-Asian translocation (-3.67 ± 0.22 ***)	12.08	<0.001 ***
							Chinese extension vs. Non-Asian translocation	2.12	0.034 ^{NS}
Proportion of ovules containing pollinating agaonids	Pedicel length × Range	GLMMs (B)	20960	2	114.56	<0.001 ***	Natural (6.95 ± 0.17 ***) vs. Chinese extension (4.82 ± 0.22 ***)	7.65	<0.001 ***
							Natural vs. Non-Asian translocation (4.67 ± 0.15 ***)	9.92	<0.001 ***
							Chinese extension vs. Non-Asian translocation	0.57	0.567 ^{NS}
Proportion of ovules becoming seeds	Pedicel length × Range	GLMMs (B)	20960	2	183.75	<0.001 ***	Natural (-0.42 ± 0.15 *) vs. Chinese extension (-2.97 ± 0.25 ***)	8.67	<0.001 ***
							Natural vs. Non-Asian translocation (-3.68 ± 0.22 ***)	12.25	<0.001 ***
							Chinese extension vs. Non-Asian translocation	2.12	0.034 ^{NS}

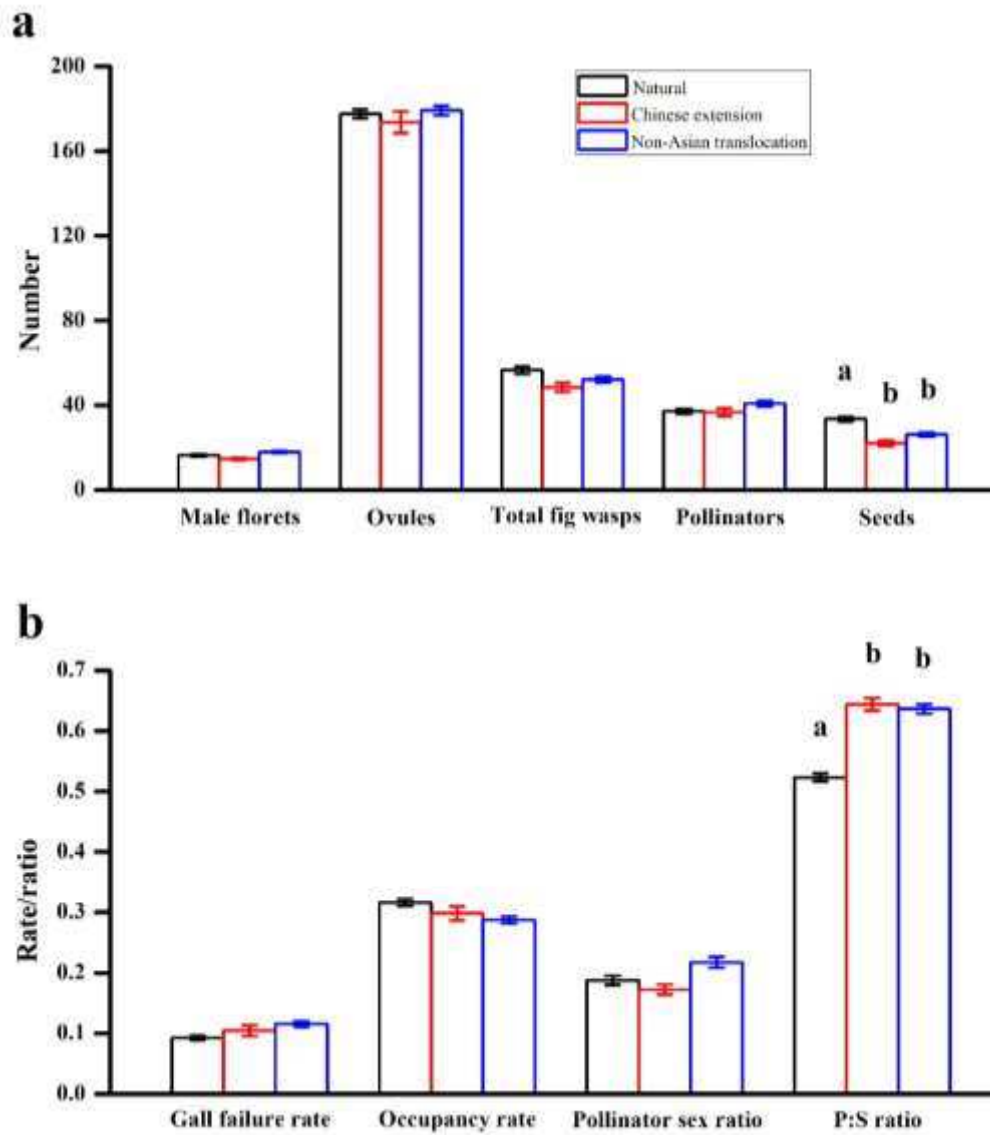


Figure S4. Comparisons of fig contents, gall failure rates, occupancy rates, pollinator sex ratios and the P:S ratio among different ranges of *F. microcarpa* (a-c). Different letters indicate significant differences (see table S11).

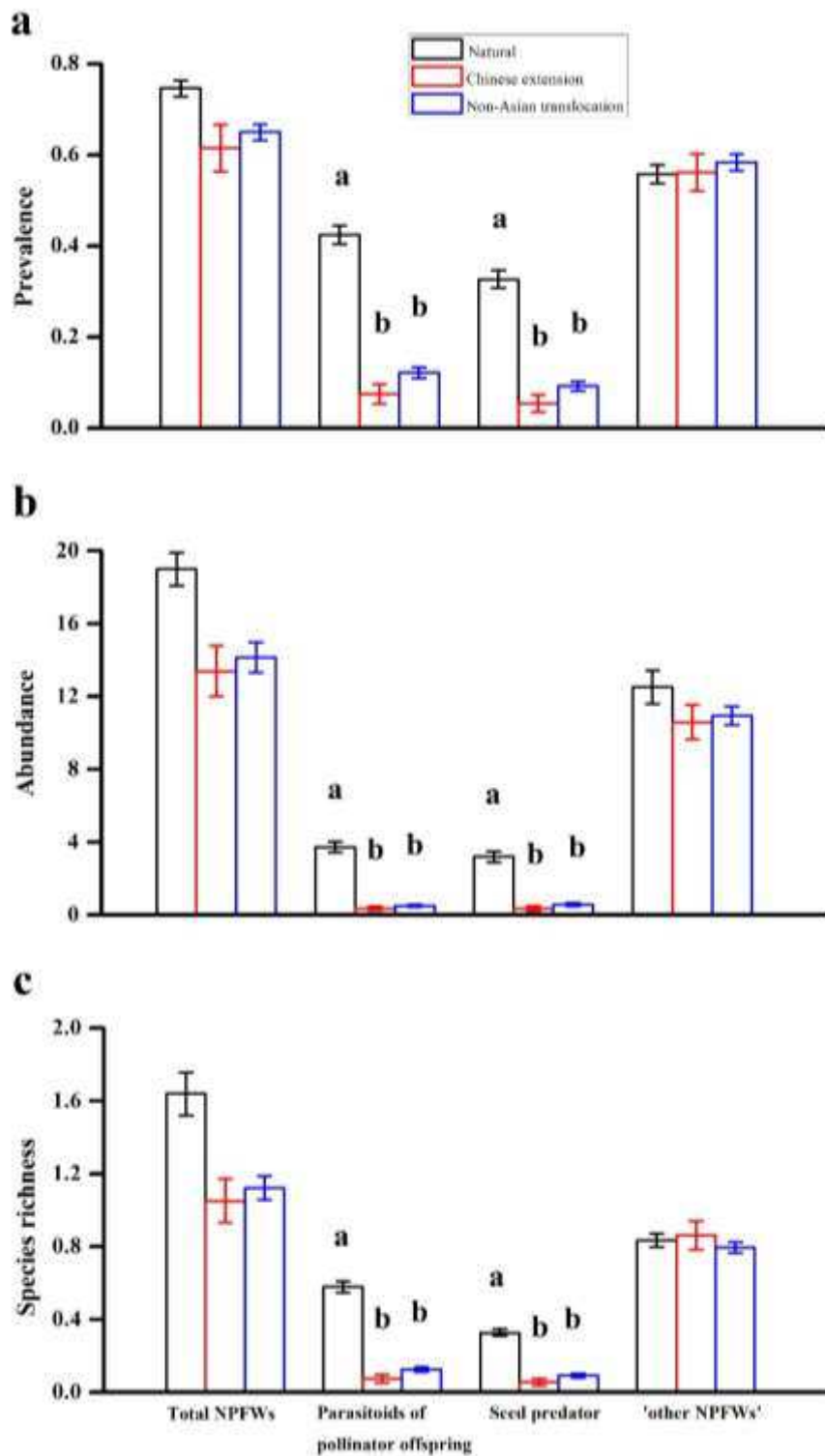


Figure S5. Comparisons of the prevalence, abundance and species richness of all NPFW species and the three categories of NPFWs in different ranges (a-c). Groupings of NPFW species are as shown in Table S5, and different letters indicate significant differences (see table S12).

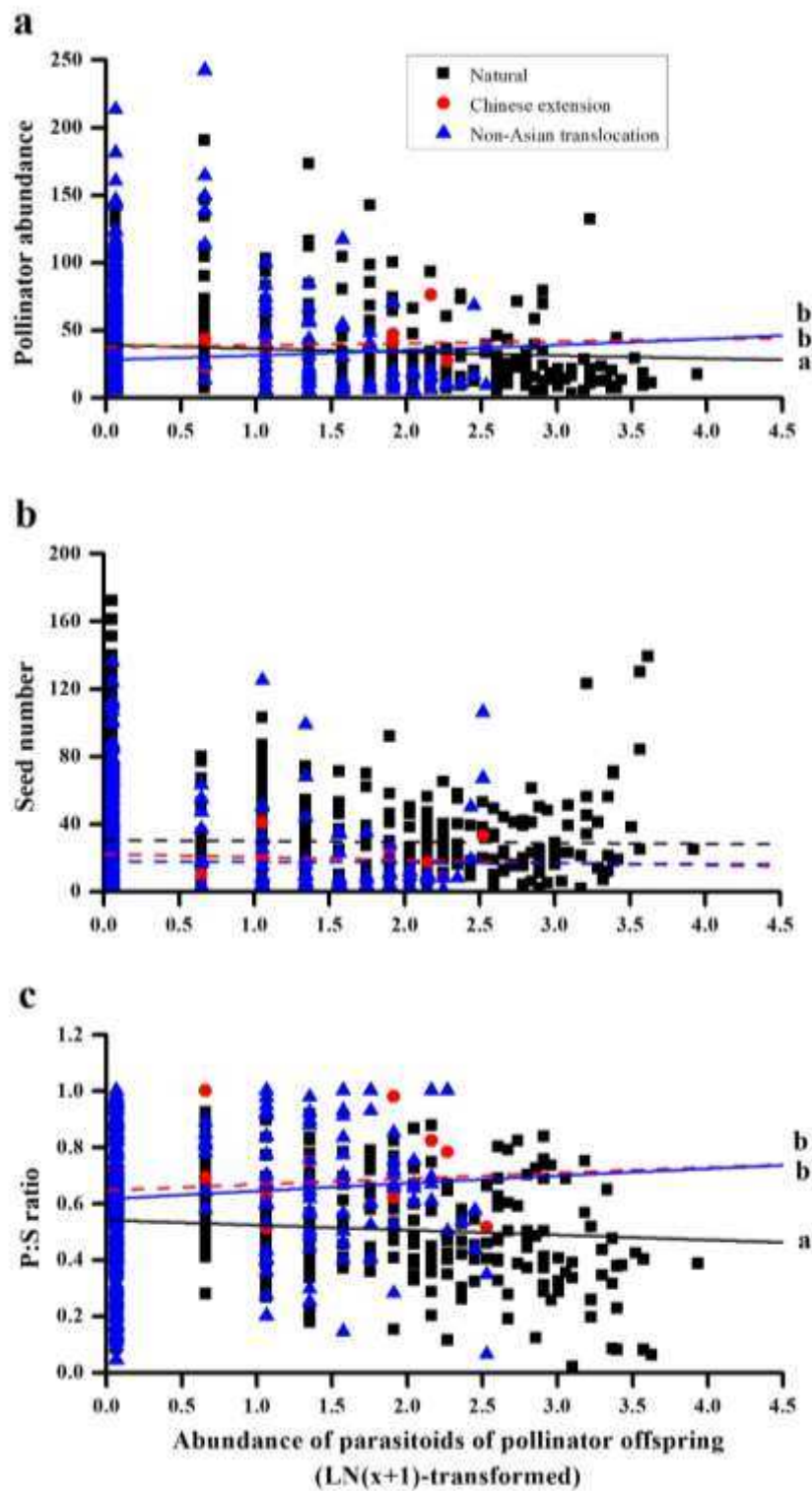


Figure S6. Relationships between the abundance of parasitoids of pollinator offspring and pollinator abundance, seed number and the P:S ratio in different ranges (a-c). Solid and dashed lines represent significant and nonsignificant relationships, with different letters indicating significant differences in the strength of relationships (as reflected by the slopes of GLMMs) among different ranges (see table S13).

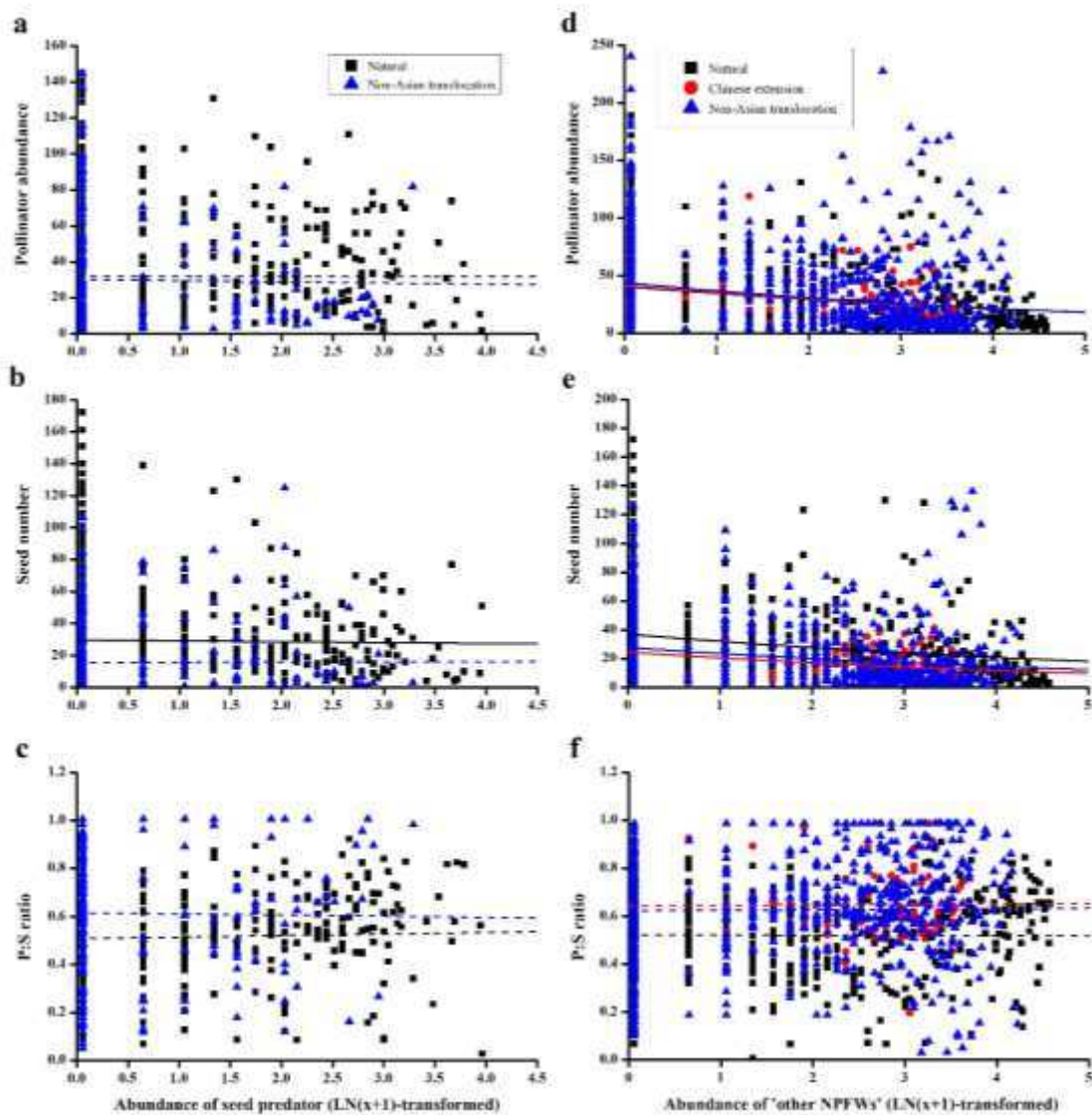


Figure S7. Effects of the seed predator (a-c) and ‘other NPFWs’ (d-f) on pollinator abundance, seed number and the pollinator abundance : seed number ratio (P:S) in different ranges of *F. microcarpa*. Solid and dashed curves represent significant and nonsignificant relationships, respectively (see Table S13). We only tested and compared the effects of the seed predator in the natural and the non-Asian translocation ranges because only 8 figs contained seed predators in the Chinese extension range.

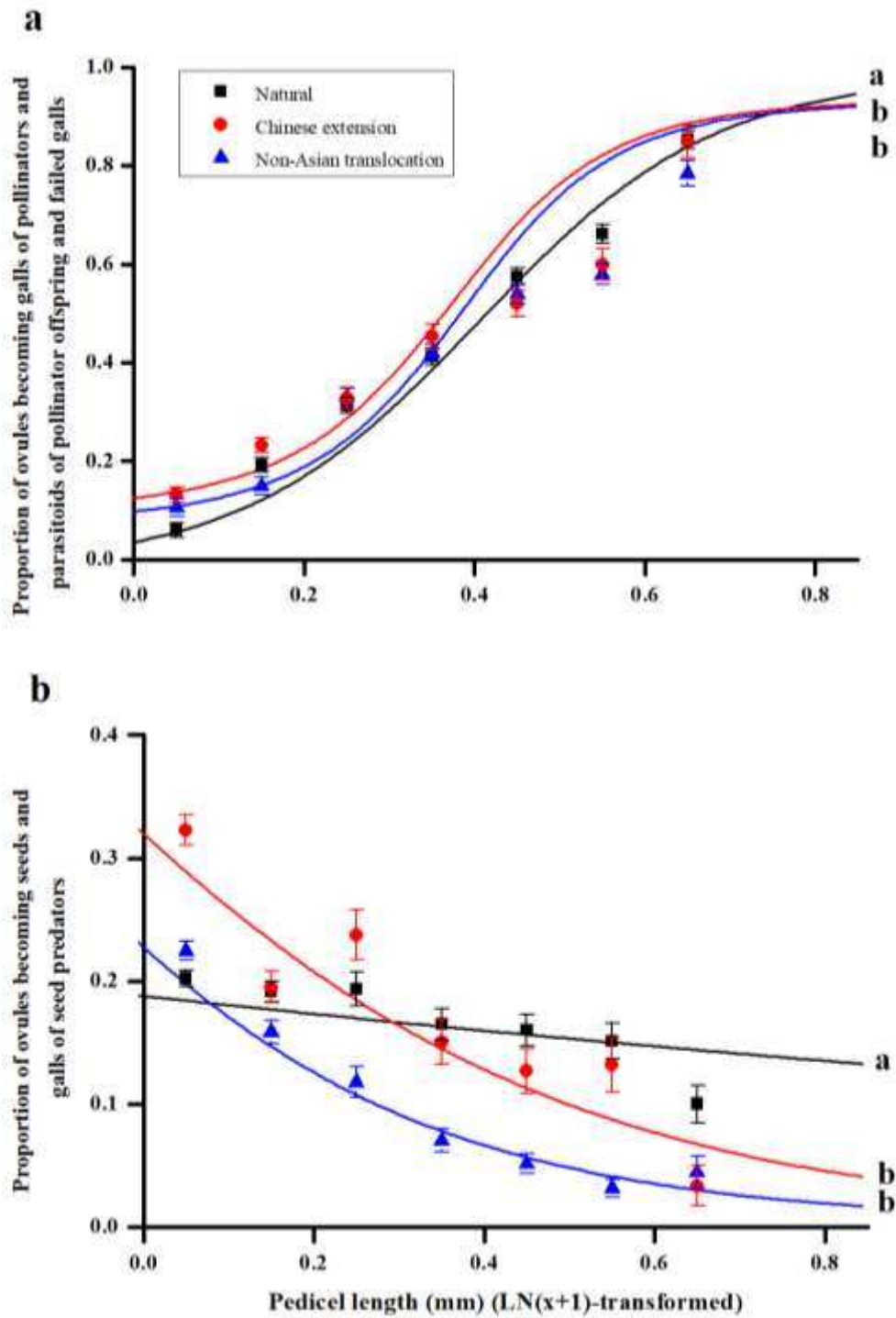


Figure S8. The relationships between pedicel length and the proportions of ovules developing as galls of pollinator fig wasps and their parasitoids (a), and those becoming seeds or containing seed predators (b). Trends in different ranges are displayed separately, and the proportions of total ovules with different contents (means \pm SE) are shown for every 0.1 unit of LN(x+1)-transformed pedicel length. Different letters indicate significant differences in the strength of relationships (as reflected by the slopes of GLMMs) among different ranges (see table S15).

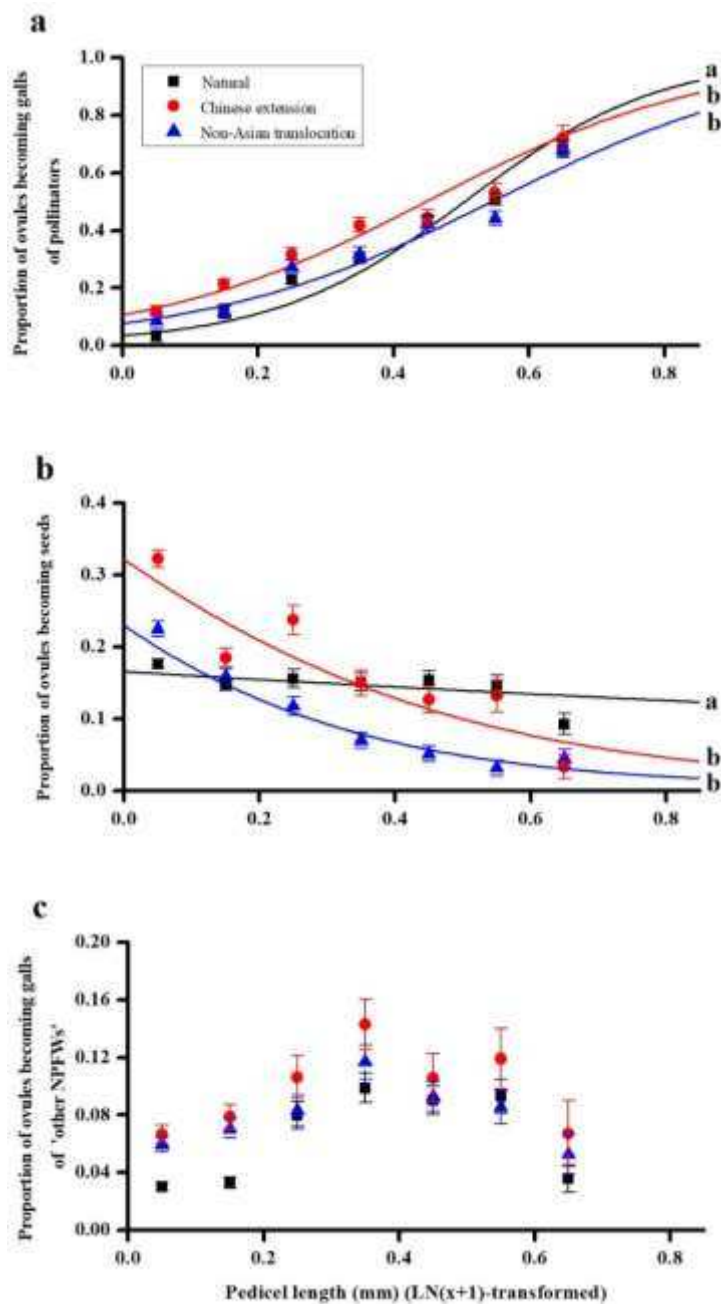
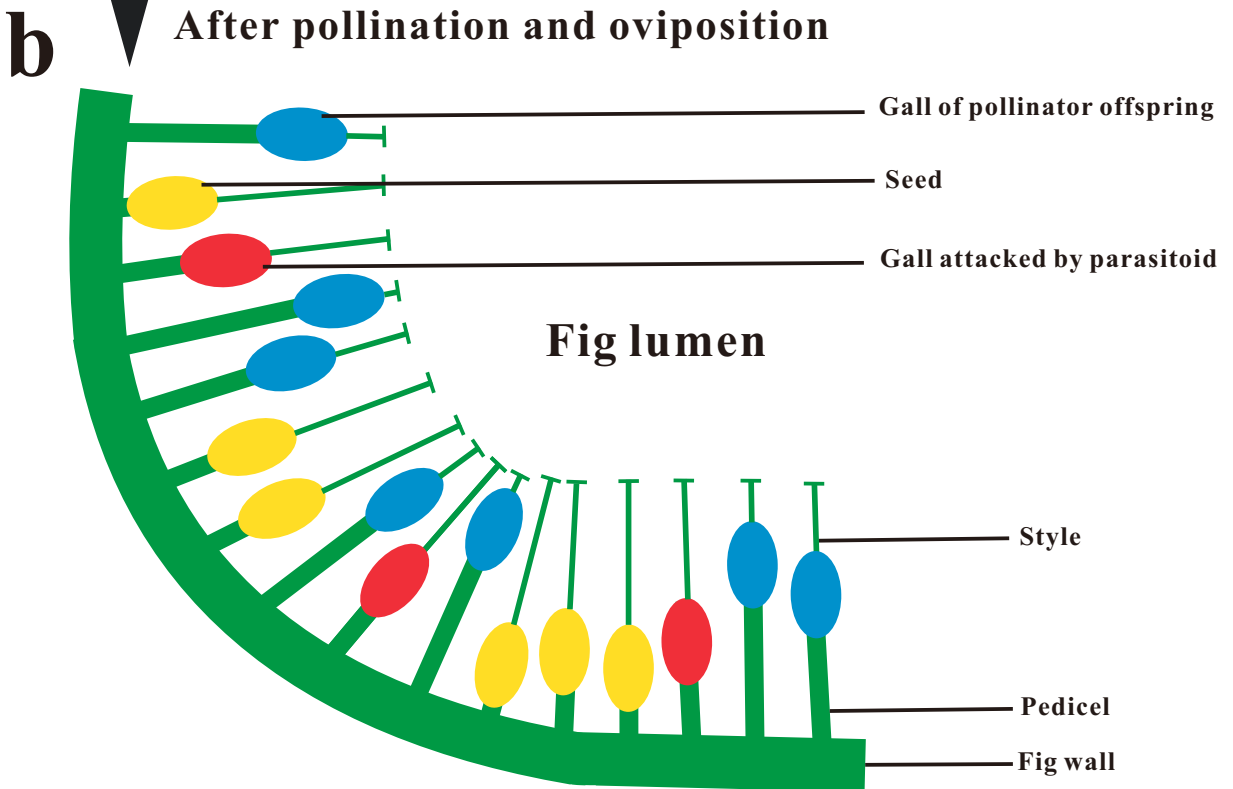
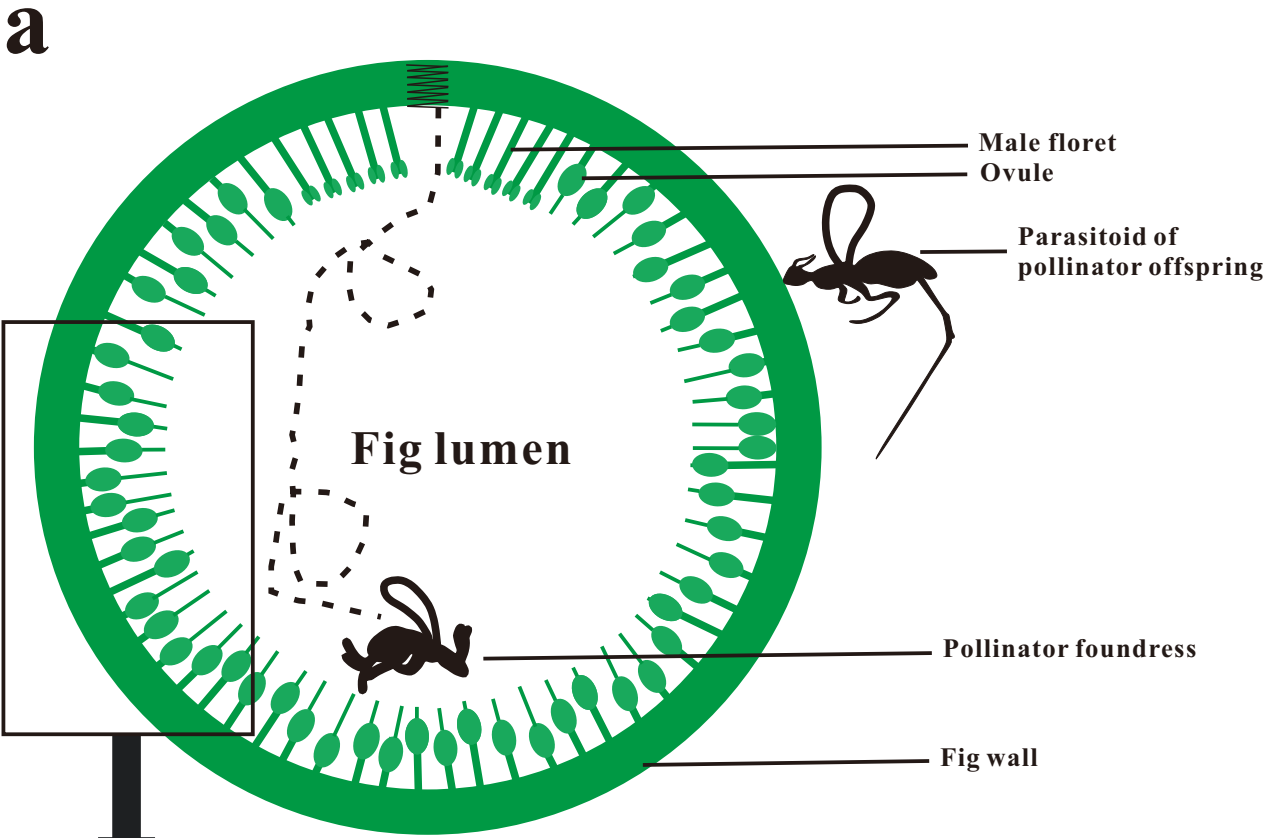
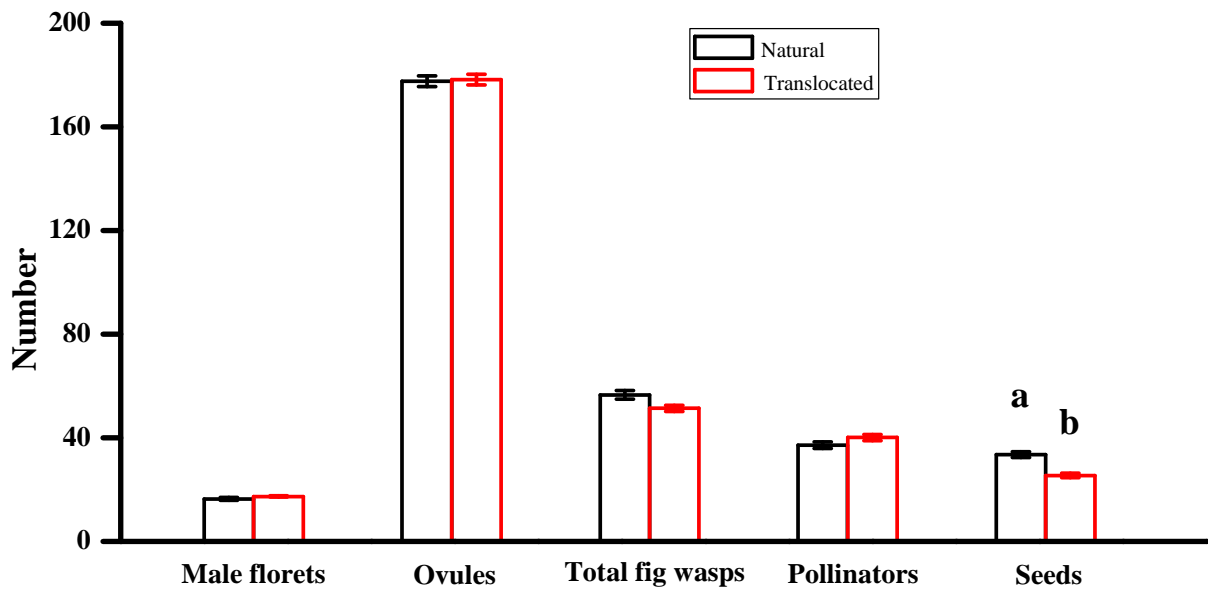


Figure S9. Trends of the proportions of ovules containing pollinator offspring (a) becoming seeds (b) and those containing 'other NPFWs' (c) towards increasing pedicel lengths in different ranges of *F. microcarpa*. The proportion of ovules containing each content to total ovules (mean \pm S.E.) is shown for every 0.1 unit of LN(x+1)-transformed pedicel length except for the last one, which includes all ovules with pedicel lengths larger than 0.6 unit (shown at 0.65 unit). Different letters indicate significant differences in the strength of effects (as reflected by the slopes of GLMMs) among different ranges (see table S15). We did not test the trends of 'other NPFWs' because the overall proportion (6.64%) of ovules containing this category was very low, and it also is composed of many NPFW species with contrasting differences in oviposition time and behaviour.



a**b**