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ARTICLE

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# Parasites and investment to host inflorescences in a fig tree–fig wasp mutualism

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## Abstract

Most mutualisms are parasitized by third-party species that inflict costs to the mutualists. How such parasites affect mechanisms that help maintain mutualism stability is poorly understood, even in well-studied systems. Angiosperm plants tend to invest most resources in tissue that yields high net benefits. In mutualisms with plant hosts, reduction in such investment can function as a key stability-promoting mechanism, such as in fig–wasp mutualisms. Here, uncooperative symbiont wasps that fail to pollinate incur "sanctions" via reduced host investment to unpollinated figs, realized via fig abortion, killing all wasp offspring, or via elevated offspring mortality within unaborted figs. We experimentally exposed host *Ficus racemosa* figs to parasitic wasps *Sycophaga fusca,* which convert fig flowers into offspring without benefitting host trees, with or without uncooperative (pollen-free) or cooperative (pollen-laden) symbiont pollinator wasps *Ceratosolen fuscipes.* Pollen-free *C. fuscipes* were still able to convert fig flower ovaries into wasp offspring, whereas those naturally pollen laden were prevented from reproducing by experimental manipulation. Independent of the effects of pollination and reproduction by pollinators, increased exposure to *S. fusca* parasites resulted in reduced rates of fig abortion and gall failure in unaborted figs. Although *S. fusca* convert flower ovaries that could otherwise become beneficial pollinator offspring or fig seeds into parasite offspring, figs with intermediate levels of parasite exposure received high levels of investment. Our results suggest that *S. fusca* parasite oviposition/larval activities can result in host trees boosting investment to figs, even when this may counter the tree's interests. We suggest that oviposition/larval activity by these parasites may mimic the biochemical pathways of pollinator gall formation and seed production.

KEYWORDS
Agaonidae, cooperation, *Ficus*, host investment, host sanctions, mutualism stability, symbiosis, third-party species

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Chun Chen and Derek W. Dunn should be considered co-first authors and authors of equal contribution.

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# INTRODUCTION

Mutualisms are interspecific interactions in which individuals of different species trade resources or services (Herre et al., 1999; Shapiro & Addicott, 2004; West et al., 2007). Mutualisms underpin most ecosystems, and understanding how they evolve and remain stable over the long term has fundamental importance to global biodiversity conservation (Kiers et al., 2010). All mutualisms support other species that effectively parasitize one or both mutualists (Bronstein, 2004; Sachs, 2015; Yu, 2001). However, although mechanisms promoting system stability have been identified in several different model systems (Jandér & Herre, 2010; Kiers et al., 2003; Pellmyr & Huth, 1994), how costs imposed by third-party species affect such mechanisms remains relatively poorly understood, even in well-studied mutualisms (but see Dunn et al., 2008; Wang et al., 2019).

Each fig-tree species (*Ficus*) has an obligate mutualism with one or very few agaonid wasp species, their sole pollinators who can only reproduce within the characteristic globular, enclosed inflorescences (figs) of *Ficus* (Cook & Rasplus, 2003; Weiblen, 2002). In monoecious *Ficus* (~350 spp.), adult female agaonids (hereafter "pollinators") find and enter a fig receptive to pollination. Once inside, "foundresses" oviposit sequentially into some flower ovaries with each ovary receiving a single egg while simultaneously spreading pollen carried from their natal fig, thus pollinating the many flowers within. Flowers that receive a wasp egg become galls that house and feed developing larvae, whereas ungalled pollinated flowers become seeds (Cook & Rasplus, 2003; Dunn, 2020; Herre et al., 2008; Janzen, 1979).

To reproduce, monoecious *Ficus* must produce both seeds and female pollinator offspring to disperse their pollen (Cook & Rasplus, 2003; Dunn, 2020; Dunn et al., 2025; Herre et al., 2008; Janzen, 1979). Pollination by wasps is clearly a prerequisite to seed production, but pollinator reproduction is not dependent on pollination (Dunn, 2020; Jandér & Herre, 2010; Jousselin et al., 2003; Wang et al., 2014; Zhang et al., 2019). However, pollination behavior in wasps is under strong positive selection due to host "sanctions" to unpollinated figs (sensu Denison, 2000). Sanctions work via host trees investing most in figs likely to offer the highest net benefits, with trees tending to withhold or reduce resources directed to unpollinated figs (Dunn, 2020; Frederickson, 2013; Jandér & Herre, 2010, 2016; Jansen-Gonzalez et al., 2012; Zhang et al., 2019). This results in "cheater" foundresses (Ghoul et al., 2013) that fail to pollinate incurring high costs due to their offspring being all killed either if figs are aborted by the tree (Jandér & Herre, 2010; Wang et al., 2014) or if figs remain unaborted, produced in fewer numbers (Jandér & Herre, 2010; Jousselin et al., 2003; Wang et al., 2014), with less female-biased brood sex ratios (Wang et al., 2014) of reduced body size (Jandér et al., 2016; reviewed by Dunn, 2020).

In addition to their mutualist pollinators, all *Ficus* species support a community of non-pollinating fig wasps (NPFWs) that obligately use figs in order to reproduce (Borges, 2015, 2021; Herre et al., 2008; Segar et al., 2014; Weiblen, 2002). Unlike the pollinators, most NPFWs oviposit into figs from outside of the host fig but are of similar small size. Dependent on their reproductive biology, NPFWs can broadly be categorized into four groups (Borges, 2015): (a) wasps that are able to independently convert fig ovaries into galls and have herbivorous larvae, (b) kleptoparasitic "gall thieves" (inquilines) that are unable to independently gall fig ovaries that usurp galls made by pollinators or type (a) NPFWs, (c) wasps that are unable to independently gall fig ovaries that are parasitoids of the larvae of pollinators or type (a) and (b) NPFWs, and (d) hyperparasitoids, parasitoids of the larvae of type (c) NPFWs.

In order to successfully reproduce, each small NPFW offspring relies on the use of an individual fig ovary that could otherwise produce a pollen-dispersing female pollinator offspring or a seed, thus inflicting costs to the *Ficus* host (Borges, 2015; Weiblen, 2002; but see Dunn et al., 2008; Wang et al., 2019). These costs are likely to add to those associated with a lack of pollination in determining patterns of resource investment to individual figs by host trees. Furthermore, many gall-inducing insects have evolved mechanisms enabling them to circumvent host plant responses to the costs they inflict and/or to manipulate plant responses to galling in their favor (Borges, 2018, 2021). For example, some insects inject chemicals that result in the diversion of host resources from neighboring tissue to galls (Borges, 2021). Host plants may also be able to discriminate between different insect galler species that are either beneficial or costly to hosts, for instance, by differences in gall size (Borges, 2015, 2021). Both processes have the potential to affect patterns of plant resource investment to specific tissues infested by parasites.

To date, no study has formally quantified the effects of any third-party parasite species on patterns of host plant resource investment known to function as mechanisms that sanction uncooperative "cheater" insect pollinators. Fig–wasp mutualisms are ideal systems to fill this knowledge gap. Both the mutualists and the NPFW parasites have to use the same resource to reproduce, fig flower ovaries, which are compartmentalized within the enclosed figs. In addition to facilitating host tree control over their symbiont pollinators (Chomicki et al., 2020), this compartmentalization also enables straightforward field experimental manipulation and the direct measurement of reproductive costs and benefits to host trees, pollinator symbionts, and NPFW parasites. We conducted field experiments using *Ficus racemosa*, its pollinator *Ceratosolen fusciceps*, and the parasite NPFW herbivorous galler *Sycophaga fusca* (a "type a" NPFW as described above). We partitioned costs and benefits to host trees that can be attributed to pollination and flower galling by both pollinators and parasites, and then, we estimated host investment to individual figs via rates of fig abortion and variation in reproduction for pollinators, parasites, and host trees in unaborted figs. This was achieved by introducing into figs variable numbers of pollen-free *C. fusciceps* pollinators that were able to convert fig ovaries into galls or naturally pollen-laden pollinators that were experimentally manipulated to prevent galling while also exposing figs to variable numbers of *S. fusca* parasites (Table 1).

# METHODS

## Study site

The study was performed in the Xishuangbanna Tropical Botanical Garden (XTBG), Chinese Academy of Sciences, Yunnan, southern China (21°41′ N, 101°25′ E). This garden is ~600 m above sea level. Yearly average rainfall is ~1560 mm, with 80% falling during May to October, with November to April as the dry season (Yang et al., 2001). The mean annual temperature and humidity are 21°C and 87%, respectively (Wang et al., 2014).

## Study system

*Ficus racemosa* resides in the *Sycomorus* section of *Ficus* (Cruaud et al., 2012) and is widely distributed in moist habitats throughout Southeast Asia, the Indian subcontinent, New Guinea, and northern Australia (Kobmoo et al., 2010). *Ficus racemosa* is monoecious and thus produces fig wasps, pollen, and seeds in each of its figs (Cook & Rasplus, 2003; Dunn, 2020; Janzen, 1979). Mature trees can reach up to 30 m in height and bear large crops of cauliflorous figs, which are attached to racemes growing from the trunk and larger branches.

At XTBG, *F. racemosa* is pollinated by *C. fusciceps* Mayr (Agaonidae), an actively pollinating wasp species (Wiebes, 1994), and has five associated species of NPFWs: (1) *Sycophaga testacea*, (2) *S. fusca*, (3) *Sycophaga agraensis*, (4) *Apocrypta* sp.2. (undescribed), and (5) *A. westwoodi*. Unlike female pollinators that enter the fig inner cavity

**TABLE 1** Experimental design detailing the wasps used and measurements taken from figs in each of the three experiments.

| Factor | Experiment 1 | Experiment 2 | Experiment 3 | Description |
|---|---|---|---|---|
| Wasps | | | | |
| Parasites | Presence vs. absence | Presence vs. absence | Variable numbers vs. absence | Non-pollinating fig wasps (NPFWs) *Sycophaga fusca* |
| Gall-only pollinators | Variable numbers vs. absence | Not applicable | Not applicable | Pollen-free (P−) ovipositor intact (OI) *Ceratosolen fusciceps* |
| Pollen-only pollinators | Not applicable | Variable numbers vs. absence | Presence vs. absence | Ovipositor-excised (OE) naturally pollen-laden (P+) *C. fusciceps* |
| Measurements | | | | |
| Fig abortion | Yes | Yes | Yes | The major component of host sanctions. Total disinvestment from an individual fig results in it dropping from the tree |
| Flower occupancy | Yes | Yes | Yes | Estimates total host investment to each unaborted fig |
| Gall failure | Yes | Yes | Yes | A major component of sanctions, revealing host investment to wasp offspring in unaborted figs |
| Number of pollinator offspring | Yes | No | No | As a supplement to gall failure, show benefits and costs of pollinator/parasite offspring production, respectively, to host trees |
| Number of parasite offspring | Yes | Yes | Yes | |
| Number of seeds | No | Yes | Yes | The most direct benefit to hosts in maintaining investment to individual figs |

(lumen) in order to pollinate and oviposit, these NPFWs insert their long ovipositors into figs from the outside. Depending on larval biology, NPFW species oviposit at different fig developmental stages (Borges, 2015, 2021; Cruaud et al., 2011; Ghara & Borges, 2010; Segar et al., 2014; Wang & Zheng, 2008; Yadav & Borges, 2018). For *F. racemosa* at XTBG, two *Sycophaga* species, *S. testacea* and *S. fusca*, oviposit before or at the same stage as *C. fusciceps*, respectively, have herbivorous larvae, and are thus parasites of the host tree ("type a" NPFWs as described previously). *Sycophaga agraensis* and both *Apocrypta* species are parasitoids or kleptoparasites (Borges, 2015; Dunn et al., 2008) of other fig wasps (Wang & Zheng, 2008) and thus oviposit later than *C. fusciceps*, *S. testacea*, and *S. fusca*. Importantly, both *S. testacea* and *S. fusca* can independently convert fig flower ovaries into wasp galls (Borges, 2021; Ghara et al., 2014; Yadav & Borges, 2018).

We conducted field experiments involving *S. fusca* and *C. fusciceps* because both species oviposit at the same fig developmental stage and can independently gall fig ovaries. We exposed individual *F. racemosa* figs to different numbers of field-collected female *S. fusca* parasites, in conjunction with or without the introduction of different numbers of two groups of female *C. fusciceps* pollinators: (1) those that were naturally pollen laden (P+) with their ovipositors excised (OE) or (2) experimentally pollen free (P−) with ovipositors intact (OI). This enabled us to independently quantify the effects of flower galling by both *C. fusciceps* pollinators and *S. fusca* parasites on investment to figs independent of the effects of pollination (Table 1).

## Experimental wasp collection

To obtain all experimental wasps, we first collected mature (D-stage; Galil & Eisikowitch, 1968) figs from several *F. racemosa* trees. Several figs were placed into a fine-mesh bag in the laboratory until the fig wasps within emerged, which occurred within 24 h. The wasps were then sorted by species using an entomological aspirator (pooter) and a collecting jar in order for individual *C. fusciceps* and *S. fusca* to be allocated ad hoc to different experimental treatments (Table 1). When identifying wasps, *C. fusciceps* cannot be confused with any other species; *S. fusca* and *S. testacea* females are similar, but *S. fusca* can be distinguished due to its longer ovipositor but slender thorax and abdomen.

To collect pollen-free (P−) *C. fusciceps* pollinators (gall-only pollinators), D-stage figs were collected. On return to the laboratory, each fig was bisected laterally. The male flowers were removed, the two halves of the fig were put back together and held using adhesive tape, and then, the fig was left for the wasps to emerge (see Wang et al., 2014).

Ovipositor-excised *C. fusciceps* pollinators (pollen-only pollinators) were obtained by the removal of the ovipositor and ovipositor sheath just prior to introduction to an experimental fig (see below). This was achieved by the experimenter preventing the individual wasp from moving by lightly pressing with a fingernail and then removing the ovipositor and sheath with a small scalpel. Ovipositor-excised *C. fusciceps* pollinate as effectively as unmanipulated wasps (Wang et al., 2014).

## Experimental figs

We used five *F. racemosa* trees for experimentation (Appendix S1: Table S1). When a tree exhibited a crop of pre-receptive (A-stage) figs (Galil & Eisikowitch, 1968), we covered several racemes with fine mesh bags (50 × 40 cm) to prevent infestation by free-ranging wasps and to exclude green tree ants (*Oecophylla smaragdina*). Each bag covered ~30 figs on a single raceme.

All figs were checked daily until they were receptive to pollination (B-stage; Galil & Eisikowitch, 1968). Then, the initial bags were removed so as each fig could be individually enclosed in a new, smaller bag (20 × 15 cm) and subjected to a single treatment depending on the experiment (see below). Experimental introductions involved from one to seven *C. fusciceps* foundresses, which reflects actual foundress numbers for *F. racemosa* at XTGB (mean = ~4.5: Wang et al., 2014). At XTGB, individual *F. racemosa* figs are typically attacked by variable densities of simultaneously ovipositing NPFWs, especially *S. fusca*, meaning that our experimental exposure treatments of 5, 20, or 80 *S. fusca* regularly occur in nature. Whenever possible, all treatments were spread across at least two different trees. Each raceme was protected from heavy rain and strong sunlight by a plastic-sheeting "umbrella."

After treatment, figs were monitored daily. If a fig fell off its raceme during development, the fig was designated as having aborted (Wang et al., 2014). All unaborted figs were collected just prior to wasp emergence (D-stage). Each fig was measured and placed into a fine mesh bag to catch the wasps that emerged. Because small fig wasps require exit holes dug by male pollinators in order to leave their natal fig (Suleman et al., 2012), before being placed into the bag, each fig for treatments using only *S. fusca* parasites had its ostiole bracts opened with sharp tweezers to enable the *S. fusca* offspring within to disperse. All emerged wasps were counted. Then, each fig was bisected twice, and the fig quarters were dissected so that wasps loose in the cavity, wasp galls, vacant flowers, and any seeds could be counted (Wang et al., 2014).

## Controls

For base controls, we bagged as described above 30 A-stage figs across three trees. These figs were thus not exposed to any *S. fusca* nor did they receive any pollinator foundresses. All 30 figs were aborted prior to maturity.

## Experiment 1

Our first experiment used a total of 210 unpollinated figs spread across four trees (Appendix S1: Table S1). Each fig was exposed to either 0 or 20 *S. fusca*. For both of these two groups, figs had 0, 1, 2, or 7 foundress pollinators introduced. All pollinators (gall-only) had their OI, so they were able to gall fig ovaries but were pollen free (P−) so seeds could not be produced. The figs that were exposed to 20 *S. fusca*, except those that received zero pollinators, were therefore galled by a consistent number of *S. fusca* parasites but variable numbers of *C. fusciceps* pollinators; figs exposed to zero *S. fusca* were only galled by variable numbers of pollinators.

This experiment enabled us to measure the effects of *S. fusca* on host investment to figs while simultaneously assessing the effects of variation in galling by pollinators. Host trees could only benefit via pollen vectoring by pollinator offspring, which were likely to be higher with more pollinator foundresses. Exposing figs to *S. fusca* could only inflict costs on host trees.

## Experiment 2

This experiment used 230 figs spread across four trees (Appendix S1: Table S1). Again, each fig was exposed to either 0 or 20 *S. fusca*. Within these two blocks, figs received 0, 1, 3, or 5 naturally pollen laden (P+) but OE pollen-only pollinator foundresses. Therefore, the only figs that were galled by wasps and produced wasp offspring were those exposed to 20 *S. fusca*, but with the exception of those that received zero pollinators, all figs produced seeds.

This experiment enabled the effect of *S. fusca* on host investment to figs to be assessed while controlling for variable levels of pollination in the absence of galling by pollinators. Host trees could only benefit from producing seeds that would likely increase with increasing numbers of (P+) pollen-only pollinators. Again, exposing figs to *S. fusca* could only inflict costs to host trees.

## Experiment 3

Our third experiment involved 317 figs spread across four trees (Appendix S1: Table S1) that each had either zero or three naturally pollen laden (P+) but OE pollen-only pollinator wasps introduced. Within these two blocks, figs were exposed to 0, 5, 20, or 80 *S. fusca*. All galls and wasp offspring were thus only produced by *S. fusca*; figs with zero exposure to *S. fusca* produced no galls/wasp offspring. Only figs that received pollinators produced seeds.

This experiment enabled us to quantify the effects of exposure to variable numbers of *S. fusca* on host investment to pollinated and unpollinated figs. Host trees could only benefit from seed production in pollinated figs but incurred costs of exposure to variable numbers of *S. fusca*.

## Statistical analyses

For each of our three experiments, we used several host tree, symbiont pollinator, and *S. fusca* traits as response variables for statistical analysis, with their variation serving as an indicator of investment to figs by hosts (see *Introduction* and *Methods*; Table 1). First, we used whether individual figs aborted or not prior to maturity. For unaborted figs retained by the tree, we subsequently used: (1) the rate of flower occupancy ([gall number + seed number]/total flower number), (2) the rate of wasp gall failure (1 − [total wasp offspring/total galls]), (3) the total number of pollinator or *S. fusca* offspring, and (4) the total number of seeds (Table 1).

We used generalized linear models (GLMs), generalized linear mixed models (GLMMs), and linear mixed models (LMMs). In all models, "pollinator number" and "*S. fusca* number" were included as fixed factors along with their interaction, except when only one of these fixed factors was appropriate. In each mixed model, "tree" was included as a random factor. When the random factor failed to explain any variance in the response variable, we instead used a GLM. For models in which the response variable was binary (i.e., a fig aborted [1] or was retained by the tree until collection [0]), binomial errors were assumed and a logit link function was used. For count data, data were over-dispersed so quasi-Poisson or negative binomial errors were assumed along with a log link function for GLMs or GLMMs, respectively. Finally, for continuous data, we used either GLMs or GLMMs with Gaussian errors and a log link or LMMs after appropriate transformation in order to normalize the error variances. All statistical analyses were conducted using R version 4.1.2 for the Macintosh computer (R Core Team, 2021). Mixed models were built using the package "lmerTest" (Kuznetsova et al., 2017).

# RESULTS

## Experiment 1

Fig abortion declined when figs were exposed to 20 *S. fusca* ($\chi^2_{1,202} = 31.55$, $p < 0.001$) and with increasing numbers of pollinator wasps ($\chi^2_{3,202} = 80.55$, $p < 0.001$). Importantly, the effect of pollinator numbers on fig abortion increased with exposure to 20 *S. fusca* (*S. fusca* exposure × pollinator number interaction: $\chi^2_{3,202} = 11.20$, $p = 0.01$). In figs that received zero pollinators, exposure to 20 *S. fusca* clearly reduced fig abortion rates. The presence of seven pollinators resulted in the cessation of fig abortion irrespective of *S. fusca* exposure (Figure 1A).

For this experiment, flower occupancy represents the proportion of galls per flower because all figs were unpollinated, so seeds could not be produced. It is also noteworthy that figs that contained zero pollinator wasps but were also exposed to 20 *S. fusca* were only galled by *S. fusca*. Flower occupancy rates of figs exposed or not to 20 *S. fusca* did not differ significantly ($\chi^2_{1,114} = 1.23$, $p = 0.27$) but did vary significantly according to pollinator foundress numbers, with high rates of galling as numbers increased, especially with seven pollinators present ($\chi^2_{3,114} = 174.91$, $p < 0.001$). Importantly, a significant *S. fusca* × pollinator number interaction ($\chi^2_{2,114} = 8.91$, $p = 0.012$) reflected compensatory flower occupancy by *S. fusca* when occupancy levels by pollinators were absent (zero pollinators) or low (one pollinator); with likely increased occupancy by pollinators (two or seven pollinators) overall, flower occupancy rates between figs exposed or not to 20 *S. fusca* were similar (Figure 1B).

Gall failure rate did not differ significantly between figs either exposed or not to 20 *S. fusca* ($\chi^2_{1,114} = 0.38$, $p = 0.54$). Gall failure significantly varied according to pollinator foundress numbers ($\chi^2_{3,114} = 17.52$, $p < 0.001$) primarily due to high failure rates in figs with no pollinators and hence containing only *S. fusca* galls. Gall failure rates in figs containing seven pollinator foundresses were low. Overall, the presence of pollinators resulted in reduced gall failure, but the underlying trends did not covary according to exposure to 20 *S. fusca* (*S. fusca* exposure × pollinator number interaction: $\chi^2_{2,114} = 0.90$, $p = 0.64$; Figure 1C).

Significantly fewer pollinator offspring were produced in figs exposed to 20 *S. fusca* than those unexposed ($F_{1,72} = 13.16$, $p < 0.001$), with more pollinator offspring, as expected, produced as pollinator foundress numbers also increased ($F_{2,72} = 240.68$, $p < 0.001$), an effect that did not vary according to exposure to *S. fusca* (*S. fusca* × pollinator number interaction: $F_{2,72} = 0.61$, $p = 0.55$; Figure 1D). *Sycophaga fusca* offspring were clearly only produced in those figs exposed to 20 *S. fusca* and declined significantly as pollinator numbers increased ($F_{3,66} = 5.88$, $p < 0.025$; Figure 1E).

## Experiment 2

In experiment 2, all figs with the exception of controls received pollen and thus were able to produce seeds. However, pollinator foundresses were all OE, so any effects of galling by pollinators were excluded. Fig abortion rates were significantly reduced when exposed to 20 *S. fusca* ($\chi^2_{1,222} = 30.02$, $p < 0.001$) and declined with increased numbers of pollinator foundresses ($\chi^2_{3,222} = 83.05$, $p < 0.001$), an effect enhanced by exposure to 20 *S. fusca* ($\chi^2_{3,222} = 13.42$, $p < 0.01$; Figure 2A).

Flower occupancy consisted of the sum of only *S. fusca* galls and seeds because pollinator foundresses were ovipositor excised and could not create galls. Occupancy rates did not vary according to *S. fusca* exposure ($\chi^2_{1,137} = 0.65$, $p = 0.42$) but increased as foundress numbers also increased ($\chi^2_{3,137} = 68.22$, $p < 0.001$), a trend unaffected by *S. fusca* (*S. fusca* exposure × pollinator number interaction: $\chi^2_{3,137} = 0.61$, $p = 0.74$; Figure 2B). Galling by *S. fusca* was consistent across different pollinator treatments ($\chi^2_{3,108} = 3.87$, $p = 0.28$). This shows that variation in flower occupancy reflects seed production, which did not vary according to exposure to *S. fusca* ($\chi^2_{1,93} = 2.52$, $p = 0.11$) and increased with pollinator numbers ($\chi^2_{2,93} = 25.32$, $p < 0.001$), a trend consistent according to *S. fusca* exposure (*S. fusca* × pollinator number interaction: $\chi^2_{2,93} = 0.54$, $p = 0.76$; Figure 2C).

Gall failure rates (*S. fusca* galls only) significantly varied according to the number of (ovipositor-excised) pollinators ($F_{3,104} = 4.60$, $p < 0.001$), with failure in unpollinated, zero pollinator figs higher than that in pollinated figs (Figure 2D). Adult *S. fusca* offspring production did not vary according to the number of pollinators ($F_{3,111} = 1.04$, $p = 0.38$).

## Experiment 3

Figs used for this experiment were only galled by *S. fusca* because pollinator foundresses were all ovipositor excised (OE). Abortion rates of figs that received three pollen-laden (P+) pollinator foundresses were significantly lower than that of the unpollinated figs that received no foundresses ($\chi^2_{1,309} = 100.57$, $p < 0.001$). As *S. fusca* numbers increased, fig abortion rates tended to decline

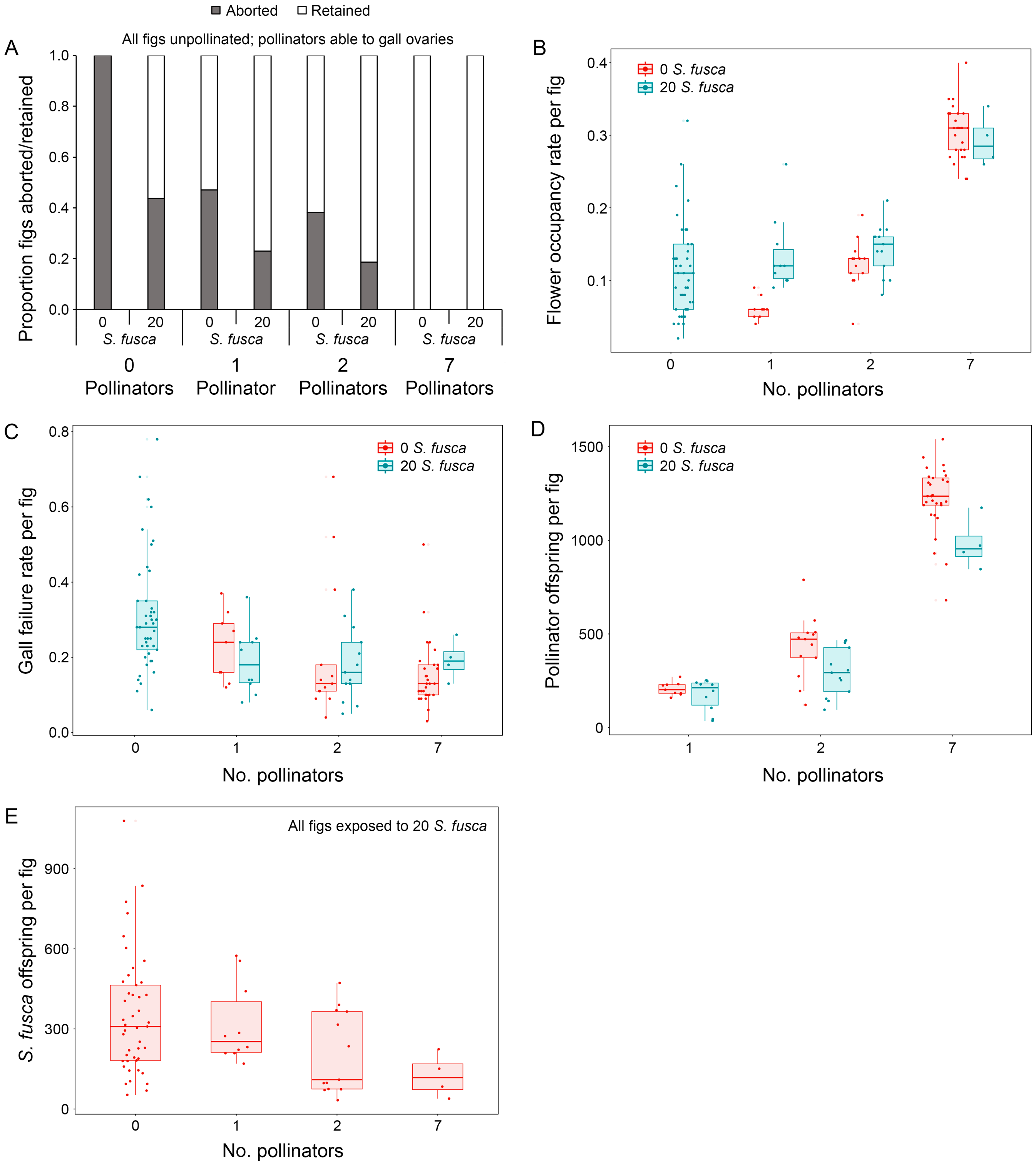

**FIGURE 1** Results for experiment 1, in which unpollinated figs were galled by variable numbers of pollinator foundresses and also exposed or not to galling by 20 *Sycophaga fusca* parasites. Trends shown are (A) fig abortion, (B) flower occupancy, (C) gall failure, (D) pollinator offspring production, and (E) *S. fusca* offspring production. (B–E) Raw data as dots. Lower and upper limits to boxes show first and third quartiles, respectively, with medians in-between. Vertical lines (whiskers) represent lower and upper adjacent values (1.5× the interquartile range).

($\chi^2_{3,309} = 54.79$, $p < 0.001$), an effect particularly pronounced in figs that were pollinator free ($\chi^2_{3,309} = 27.10$, $p < 0.001$; Figure 3A).

Flower occupancy rates reflected both seed and *S. fusca* galling in figs that received three pollinator foundresses but were constrained to only *S. fusca* galling

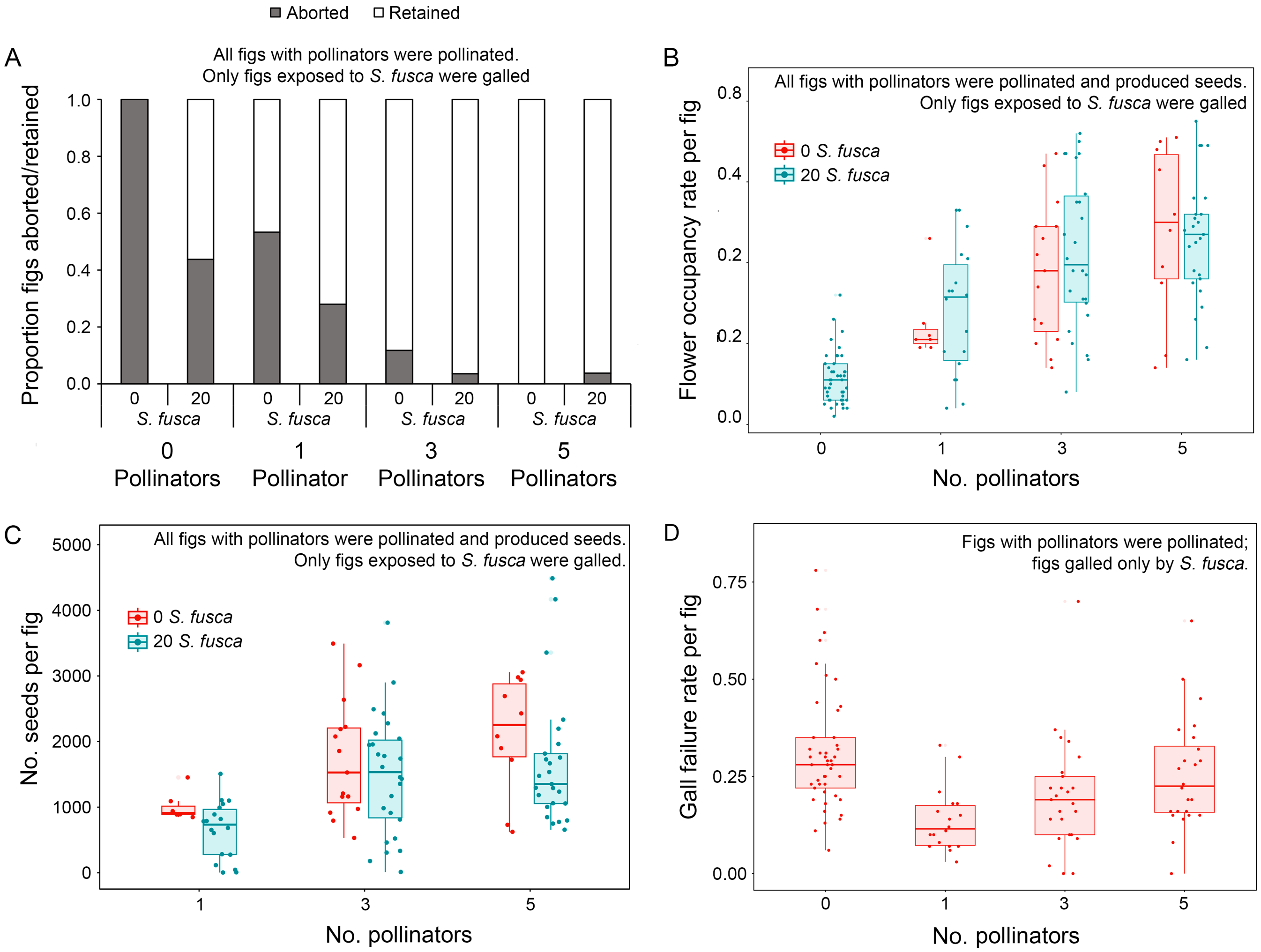

**FIGURE 2** Results for experiment 2, in which figs received variable numbers of pollen-laden foundress pollinators that were unable to create galls and also exposed or not to galling by 20 *Sycophaga fusca* parasites. Trends shown are (A) fig abortion, (B) flower occupancy, (C) seeds, and (D) gall failure. (B–D) Raw data and trends as for Figure 1B–E.

in figs that remained pollinator free. Occupancy was thus significantly higher in figs containing three pollinator foundresses ($\chi^2_{1,146} = 51.94$, $p < 0.001$) but also varied according to *S. fusca* exposure ($\chi^2_{3,146} = 9.64$, $p = 0.02$), with figs exposed to 20 *S. fusca* having high rates of occupancy. The pollination × *S. fusca* number interaction was not significant ($\chi^2_{3,146} = 1.76$, $p = 0.42$; Figure 3B).

Gall failure rates (*S. fusca* galls only) did not vary according to pollinator number ($F_{1,131} = 2.65$, $p = 0.11$) but did significantly vary according to the numbers of *S. fusca* to which figs were exposed ($F_{2,131} = 5.11$, $p < 0.01$); gall failure tended to decline as *S. fusca* numbers increased, a trend relatively consistent between the two pollinator treatments (pollinator number × *S. fusca* interaction: $F_{1,131} = 2.19$, $p = 0.12$; Figure 3C). Adult *S. fusca* offspring production also did not vary according to pollinator treatment ($F_{1,135} = 0.03$, $p = 0.85$) but tended to increase with increasing numbers of *S. fusca* ($F_{2,135} = 30.04$, $p < 0.001$). Lower offspring production in pollinated figs exposed to five *S. fusca* and increased production in unpollinated figs exposed to 80 *S. fusca* resulted in a significant *S. fusca* × pollinator treatment interaction ($F_{2,135} = 8.57$, $p < 0.001$; Figure 3D).

In figs that received three pollinators, seed production significantly varied according to *S. fusca* numbers, with figs exposed to 80 *S. fusca* producing fewer seeds than those exposed to 0, 5, or 20 *S. fusca* ($F_{3,80} = 4.37$, $p < 0.01$; Figure 3E).

## DISCUSSION

Our experiments show that in the *F. racemosa*–*C. fusciceps* fig–wasp mutualism, *S. fusca*, a third-party parasite NPFW galler, can affect patterns of fig abortion

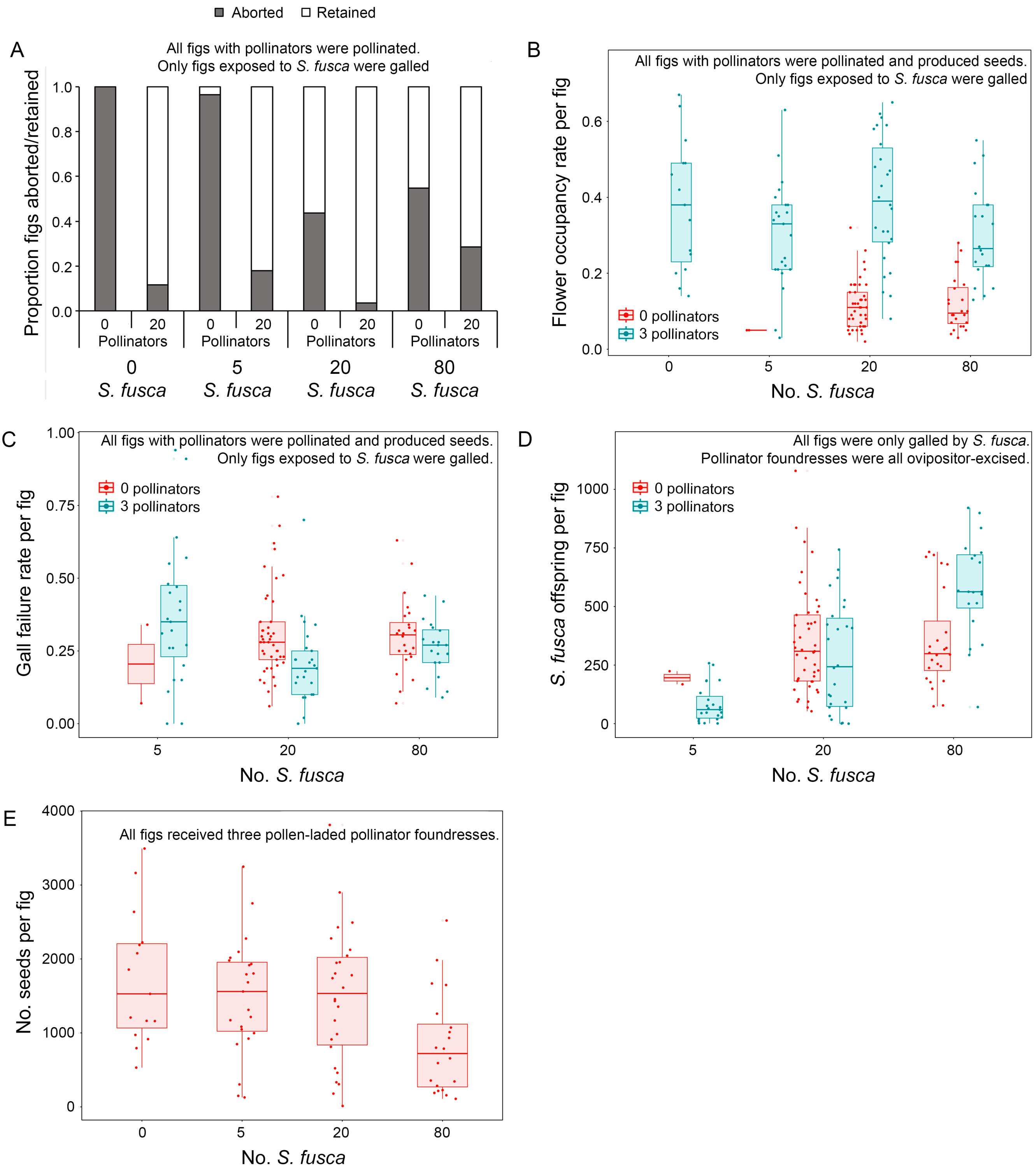

**FIGURE 3** Results for experiment 3, in which figs received either zero or three pollen-laden foundress pollinators that were unable to pollinate and also exposed to galling by variable numbers of *Sycophaga fusca* parasites. Trends shown are (A) fig abortion, (B) flower occupancy, (C) gall failure, (D) *S. fusca* offspring production, and (E) seed production. (B–E) Raw data and trends as for Figure 1B–E.

and, to a lesser extent, pollinator brood reduction. Both factors are likely associated with variation in host investment to figs and function as "sanctions" to pollinators that fail to pollinate (Dunn, 2020; Frederickson, 2013; Jandér & Herre, 2010, 2016; Wang et al., 2014; Zhang et al., 2019). Furthermore, we show that *S. fusca* affects variation in host sanctions independent of benefits to hosts associated with pollination and galling by pollinator wasps. We suggest that this is likely due to parasite adaptations that affect host investment to figs and/or due to parasite galling processes that are incompletely distinguishable by hosts from those of beneficial pollinators.

## Experiment 1: *S. fusca*, host investment to figs, and variation in galling by pollinators

In experiment 1, it appears that resource investment by host trees to individual figs does not align with variation in the potential benefits of galling by pollinators, or the likely costs of exposure to *S. fusca* parasites. This is clear in patterns for fig abortion. Host trees divested completely from control figs, resulting in ubiquitous abortion. However, when zero-pollinator figs were exposed to 20 *S. fusca*, abortion rates declined (Figure 1A). Paradoxically, this suggests that exposure to costly parasites resulted in increased investment to individual figs. Notably, when figs were galled by only a single (pollen-free) pollinator, abortion rates were also lower than those of control figs, being similar to zero-pollinator figs exposed to 20 *S. fusca*. Moreover, increasing numbers of pollinators and exposure to 20 *S. fusca* resulted in further reductions in fig abortion, until with seven pollinator foundresses, fig abortion ceased completely regardless of parasite exposure. Independent of benefits associated with pollination, host investment to inflorescences was clearly enhanced by increased numbers of pollinator foundresses and exposure to parasites. We suggest that the most parsimonious explanation is that host investment is associated with flower galling and/or early-stage larval presence, the activities most closely shared by both pollinators and *S. fusca*, with galling/larvae stimulating resource investment. This concurs with our previous work with *F. racemosa* at XTBG, which found that abortion in figs containing seven or more pollinator foundresses ceased regardless of pollination and that galling by pollinators independently reduced rates of fig abortion (Wang et al., 2014). Our new data suggest that galling by *S. fusca* has similar effects on investment to figs by host trees, but these effects are of reduced magnitude to variation in galling by pollinators. For instance, there is clearly reduced investment by host trees to figs that received two pollinator foundresses compared with figs that received seven pollinators. Mechanistic differences in the galling of flowers between NPFW gallers and pollinators may contribute to these patterns (see below; Elias et al., 2012; Jansen-Gonzalez et al., 2014).

In figs that remained unaborted, flower ovary occupancy rates, as could be expected, increased with the overall level of exposure to wasps by both pollinator foundresses and *S. fusca*. Gall failure rates, however, declined with increasing wasp numbers, again suggesting that resource investment to figs was higher as the number of flower ovaries galled increased. Patterns of offspring production are suggestive of inter-specific competition for the same subset of ovaries between the two wasp species (see also Ghara et al., 2014). Pollinators are much more fecund than small NPFW gallers such as *S. fusca* (Ghara & Borges, 2010), and unlike these small NPFWs that spread their reproductive activities across several different figs (Ghara et al., 2014), pollinators are usually reproductively tied to a single fig (Cook & Rasplus, 2003; Dunn, 2020; Weiblen, 2002). This explains the large effect of pollinator numbers on *S. fusca* offspring production (Figure 1E) and the large differences in total offspring production between the two species (Figure 1D,E).

## Experiment 2: *S. fusca*, host investment to figs and variable levels of pollination by pollinators

By the use of ovipositor-excised foundresses, our second experiment eliminated any effects of pollinator reproduction and hence any benefits to host trees of pollinator offspring vectoring pollen. However, foundresses were naturally pollen laden, so considerable benefits to host trees from seed production were present. Overall, rates of fig abortion declined with pollinator (pollen) presence and exposure to *S. fusca*, consistent with trees investing most in pollinated figs, with *S. fusca* oviposition/galling/reproduction further enhancing this investment.

In figs that reached maturity, flower occupancy rates (*S. fusca* galls + seeds) increased according to a corresponding increase in pollinator numbers and hence likely elevated rates of pollination. Increased pollinator foundress numbers therefore resulted in more seeds. Although *S. fusca* exposure tended to reduce seed production, suggesting that *S. fusca* uses flowers that would otherwise become seeds, their effects were not significant (Figure 2C). This suggests that pollination overwhelmed galling/larval activities by *S. fusca* in determining any host investment to figs that may affect variation in seed production. Gall failure rates (*S. fusca* only) declined significantly in pollinated figs, with relatively consistent adult *S. fusca* offspring production across different pollinator foundress treatments. Galling by some other NPFW species has been shown to be independent of pollination (Jansen-Gonzalez et al., 2014), whereas flowers galled by pollinators tend to have been pollinated (Jansen-Gonzalez et al., 2012). The galling process of different NPFW species can also vary interspecifically (Galil et al., 1970; Ghara et al., 2014; Jansen-Gonzalez et al., 2014). However, even though some NPFW gallers deposit their eggs in a similar location in the fig ovary as do the pollinators (Jansen-Gonzalez et al., 2012; Jansen-Gonzalez et al., 2014), there may be important differences in the process of gall formation and ovary exploitation (Jansen-Gonzalez et al., 2014). This in turn may result in subtle differences in the signals given to hosts in figs harboring variable numbers of NPFW and pollinator gallfs, resulting in corresponding variation in host responses and hence resource investment to individual figs.

Our data show that *S. fusca* can produce viable galls in both unpollinated and pollinated figs, as does the neotropical *Idarnes* (group *flavicollis* species) galler associated with *F. citrifolia* whose galling/larvae also reduce the likelihood of unpollinated fig abortion (Jansen-Gonzalez et al., 2014). The structure and niche partitioning of the wasp communities associated with *Ficus* converge across *Ficus* clades that diverged ~50 million years ago and are currently endemic to different continents (Segar et al., 2013). Extending this principle, we suggest that small galler NPFWs may also share some similarities in their effects on host investment to figs in different monoecious *Ficus*, as we have found in *F. racemosa*. This can only be confirmed by extending the approach used in this study to fig–wasp mutualisms from different clades on different continents in order to perform formal comparative analyses (sensu Dunn et al., 2025; Jandér & Herre, 2010).

## Experiment 3: Variable numbers of *S. fusca* and host investment to pollinated and unpollinated figs

Our first two experiments showed that exposing figs to 20 *S. fusca* resulted in enhanced investment to figs, over and above the effects of galling and pollination by pollinators. We therefore conducted a third experiment, exposing both pollinated and unpollinated figs to *S. fusca* to mimic variation in the numbers of these small galler NPFWs that oviposit into *F. racemosa* figs at XTGB (Wang et al., 2005). When only exposed to five *S. fusca*, fig abortion rates were high and only marginally lower than controls, only declining markedly when exposed to either 20 or 80 *S. fusca*. It is also noteworthy that abortion rates were lower in figs exposed to 20 *S. fusca* than in those exposed to 80 *S. fusca*, suggesting that an optimal density of between 5 and 20 *S. fusca*, or between 20 and 80 *S. fusca*, may result in high levels of investment to figs. Host trees may thus be reducing investment to individual figs as a reaction to increased costs of high densities of simultaneously ovipositing small-galler NPFWs such as *S. fusca*. For example, the fig outer wall suffers physical damage caused by the ovipositors of these wasps, eventually resulting in the formation of “scars” in unaborted figs (see also Ghara & Borges, 2010). Any effects of physical damage by NPFWs on investment to figs can only be confirmed with additional field experiments.

For figs retained by trees, flower occupancy rates tended to reflect mainly pollinator presence with significantly higher occupancy in pollinated figs that produced seeds. In unpollinated figs, occupancy predictably increased as *S. fusca* exposure also increased. However, in pollinated figs, exposure to *S. fusca* failed to increase overall levels of flower occupancy. Only exposure to 20 *S. fusca* resulted in levels of flower occupancy similar to pollinated figs unexposed to these parasites; with exposure to only 5 or 80 *S. fusca*, occupancy rates were lower than those in figs unexposed or exposed to 20 *S. fusca*. This is also consistent with an optimal density of *S. fusca* exposure resulting in host trees maintaining high levels of investment to individual figs, which requires further experimentation in order to test. For experiment 3, gall failure rates are only applicable to *S. fusca*. Contrary to overall predictions that host investment should be highest to pollinated figs, we found no significant variation in gall failure between figs that received zero or three pollinator foundresses, but a significant effect for *S. fusca* numbers. Gall failure tended to be lowest when figs were exposed to 5 *S. fusca* compared to exposure to 20 or 80 *S. fusca* (Figure 3C), but overall, patterns of costs to *S. fusca* offspring in figs retained by trees were not as pronounced as for fig abortion. In pollinated figs, seed production tended to decline with increasing numbers of *S. fusca*, especially when figs were exposed to 80 *S. fusca*. This tends to correspond to the opposite trend for *S. fusca* offspring production, especially in pollinated figs exposed to 80 *S. fusca*. This suggests that *S. fusca* converts fig ovaries that could have produced seeds into wasp offspring, a clear cost to trees. We discuss further potential mechanisms that may result in the observed counterintuitive phenomenon of continued host investment in figs that confer trees few or no benefits due to exposure to *S. fusca* parasites.

## Mechanistic interpretations of fig mediated costs to wasps via differential investment to figs

Our data show that exposing figs to *S. fusca* results in variation in patterns of host investment to figs that do not consistently align with variation in potential costs to host trees. We also found differences in patterns of fig abortion and in metrics associated with costs to wasps in figs retained by trees in each of our experiments. These results suggest that different mechanisms are triggered in hosts by exposure to *S. fusca* that affect either fig abortion or variation in wasp offspring performance in retained figs.

Exposing figs to *S. fusca* tends to reduce the likelihood of fig abortion, even though these parasites offer host trees no benefits for continued investment to individual inflorescences. We suggest that at least two factors may be at play: (1) galling by *S. fusca* may be similar to that of the pollinators, which may also share some of the biochemical processes underlying seed formation post-pollination, with trees reacting accordingly. (2) *S. fusca* may, during oviposition, inject chemicals that directly manipulate host investment to figs to benefit individual *S. fusca*, even though host trees may incur costs.

Galling of plant tissue by insect herbivores such as pollinating fig wasps and small galler NPFWs is the result of insect-mediated manipulation of the biochemical pathways underpinning resource investment to plant tissue to favor the insect offspring (Miller & Raman, 2018; Oliveira et al., 2016). After gall formation, larval activities such as feeding and respiration can also independently stimulate similar pathways, resulting in resource investment being maintained even though this may be costly to the host plant (Miller & Raman, 2018). Our results here are consistent with both mechanisms operating but *S. fusca* being more effective at manipulating fig abortion than within figs retained by the tree. Fig abortion has been shown to be the main component of host sanctions to uncooperative agaonid foundresses that fail to pollinate (Dunn, 2020; Jandér et al., 2012; Jandér et al., 2016; Jandér & Herre, 2010; Wang et al., 2014). If widespread, this suggests that small NPFW gallers may play an important role in mediating the stability of fig–wasp systems, mutualisms known to underpin much biodiversity in tropical and subtropical forests (Kiers et al., 2010; Shanahan et al., 2001).

Gall formation is the result of insect adaptations to plants and vice versa (Oliveira et al., 2016); galling costly to host plants will thus likely act as agent of selection for mechanisms in hosts that minimize these costs (sensu Schmid-Hempel, 2011). During each oviposition event, pollinator fig wasps and some NPFWs inject fluid that induces rapid enlargement of the nucleus cells and galling of the ovary, fluid that is stored in a "poison sac" (Martinsen et al., 2014). In two species of Panamanian *Ficus*, NPFWs that are able to independently gall fig ovaries invest less in their poison sacs than the pollinators, suggesting that NPFWs may have reduced galling efficacy than pollinators (Martinsen et al., 2014). Assuming that secretions of equal doses from either NPFWs or pollinators have similar effects on host plants, a higher volume of poison sac secretion may thus be required per oviposition event in order for NPFWs to create a gall. If so, host fig trees may thus be more "resistant" to galling from NPFWs than from pollinators, and/or NPFWs may have to inject higher volumes of secretions in order to manipulate host trees to maintain investment to figs with relatively high proportions of NPFW-galled ovaries. Wang et al. (2021) recently reported in dioecious *Ficus pumila* var. *pumila* that individual flower ovaries that have either become seeds or pollinator wasp galls have similar chemical profiles, with contraction of gene families associated with detoxification of plant defense chemicals in wasps being upregulated during the larval stage. If small gallers such as *S. fusca* similarly manipulate flower ovaries to "mimic" seeds (by investing more in the individual galling process than in pollinators), then this would clearly be beneficial to these wasps and at least partially explain why exposure to these gallers appears to enhance investment to individual figs. Investigations extending the methods used by Wang et al. (2021) to NPFWs in monoecious *Ficus* are thus required.

## Concluding remarks

Our results are consistent with *S. fusca* reproduction enhancing investment to individual figs, the clearest effect being reduced rates of fig abortion. Exposing figs to *S. fusca* thus tended to reduce "sanctions" to figs in which uncooperative pollinator foundresses had reproduced, even though their positive effects may be compensated for by competition for the same flowers for both seeds and beneficial pollinator wasps. However, under some circumstances in pollinated figs exposure to high densities of *S. fusca* resulted in reduced investment by hosts. Our results are consistent with *S. fusca* oviposition/galling/larval activities within galls affecting biochemical mechanisms that determine levels of resource investment to individual figs. Consistent with galling insects in general, *S. fusca* has likely evolved the ability to manipulate in its favor mechanisms resulting in variable investment to host plant reproductive tissue. These mechanisms have evolved to ensure that pollinated inflorescences receive adequate nutrients in order to produce maximum net reproductive benefits to hosts. Our results therefore do not show evidence of host plants consistently and accurately discriminating between figs infested with *S. fusca* parasites that offer them no direct reproductive benefits.

Other insect nursery pollination mutualisms harbor third-party parasites that inflict costs on both mutualists such as *Yucca* tree–*Yucca* moth systems (e.g., Bronstein & Ziv, 1997), mutualisms known to be stabilized by host sanctions (Pellmyr & Huth, 1994). An important contrast between fig–wasp mutualisms is that *Yucca* moths do not create galls, their larvae being seed predators, direct consumers of their natal host plant's reproductive tissue (Pellmyr, 2003) as are the other species of specialist seed predators of these systems (Bronstein & Ziv, 1997). Plants have evolved multiple adaptive defenses against insect herbivores, which have evolved counter adaptations to minimize the costs of these defenses (Waser & Ollerton, 2006). Mechanisms used by both plants and herbivores are likely to differ markedly from those involved in insect galling of plant tissue and insect manipulation of resource investment by plants to specific tissues in order to benefit the insects. Broadening studies into insect pollination mutualisms whose pollinator symbionts and parasites are insect herbivores, such as *Yucca* tree–*Yucca* moth systems, would make a tangible contrast to systems in which symbionts and parasites are gallers of host plants. This would make an ideal next step in furthering our understanding of how parasites affect mechanisms promoting stability in well-known mutualisms.

## AUTHOR CONTRIBUTIONS

All authors conceived the ideas and designed the methodology. Chun Chen collected the data. Chun Chen and Derek W. Dunn analyzed the data and led the paper writing. All authors finalized the paper writing.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

## DATA AVAILABILITY STATEMENT

Data (Chen et al., 2025) are available on Dryad at https://doi.org/10.5061/dryad.q83bk3jv5.

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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