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Inflorescence size predicts host–symbiont conflict in monoecious fig–wasp mutualisms

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ABSTRACT

In monoecious fig–wasp mutualisms (*Ficus*; ~350 spp.), tiny wasps obligately pollinate fig-tree inflorescences ('figs'). Although pollination enables seed production, wasp symbionts also oviposit into flowers, replacing potential seeds with wasp offspring. Consistently across *Ficus*, ~40–60% of developed flowers produce seeds. Although several processes are probably involved, a general explanation for why wasps do not exploit more flowers has been elusive. However, interspecific scaling between host–symbiont reproductive traits suggests that as figs become larger across *Ficus*, the increase in wasp-eggs-per pollen-receptive fig will fail to match the increase in flower numbers. The potential for wasps to exploit hosts should thus decline due to an increasing excess of flowers. We tested these predictions, which were upheld, using data from 23 fig–wasp mutualisms from four continents. As fig size increases across *Ficus*, wasp egg-to-flower ratios, a measure of host–symbiont conflict of interest, declines, but the likelihood of a wasp egg successfully becoming an adult offspring increases. Host–symbiont conflict of interest thus varies systematically across *Ficus* due to variable relationships between key mutualist reproductive traits and fig size. We suggest that mutualism stability is more dependent upon mechanisms curtailing wasp flower exploitation in systems with small figs, and on preventing high foundress numbers in those with large figs.

Keywords: allometric scaling; mutualism; cooperation; conflict resolution

INTRODUCTION

Mutualisms are interactions in which interspecific individuals trade resources or services, and are fundamentally important for ecosystem function (Kalko *et al.* 1996, Shanahan *et al.* 2001, Kiers *et al.* 2010, Leigh 2010, Wilkins *et al.* 2019, Leray *et al.* 2021). While their ecological benefits are clear, because the benefits of mutualism (e.g. defence, pollination, nutrition) often result from the exploitation of costly resources provided by the other mutualist (Shapiro and Addicott 2004), the long-term stability of mutualisms can be puzzling. What prevents some mutualists from over-exploiting these resources, increasing their fitness relative to more cooperative conspecifics and potentially destabilizing a mutualism?

Mutualisms are highly diverse, and the resources and services exchanged by mutualists also vary greatly (Bronstein 1994, Herre *et al.* 1999, 2008, Ferdy *et al.* 2002, West *et al.* 2007, Dunn *et al.* 2008a, b, Ibanez *et al.* 2009, Wang *et al.* 2009, 2014, Goto *et al.* 2010, Kawakita 2010, Leigh 2010, Kiers *et al.* 2011, Thrall *et al.* 2011, Jandér *et al.* 2016, Zhang *et al.* 2021). Attempting to identify general mechanistic patterns promoting system stability across mutualisms can thus be daunting. However, mechanisms resulting in system stability broadly fall into two categories: (i) system characteristics that ensue little conflict between hosts and symbionts (Leigh 2010, West *et al.* 2021, see also Frederickson 2013, 2017), or (ii) host traits that promote interactions with the most beneficial symbionts, and/or limit the success and spread of nonbeneficial symbiont lineages (Pellmyr and Huth 1994, Herre *et al.* 1999, Kiers *et al.* 2003, Jandér and Herre 2010, Leigh 2010, West *et al.* 2021, Zhang *et al.* 2021). Until this study, the relative importance of each category has so far not been measured across systems in any single mutualism type.

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Monoecious fig tree–fig wasp mutualisms are a model system in which it is straightforward to identify and quantify variation in host–symbiont fitness as a function of measurable traits in both mutualists (Herre 1989). Each tree species (*Ficus*; ~350 spp.) is only pollinated by one or very few agaonid wasp species (Weibes 1979, Berg 1989, Weiblen 2002, Cook and Rasplus 2003, Molbo *et al.* 2003, Herre *et al.* 2008, Cruaud *et al.* 2012, Rasplus *et al.* 2021). Newly emerged pollen-laden female wasps (foundresses) locate and enter a receptive, enclosed inflorescence ('fig'; Fig. 1), and then pollinate the numerous tiny pistillate flowers (hereafter 'flowers') within (Ganeshaiah *et al.* 1995, 1999). During pollination, foundresses oviposit individually into some flower ovaries. Flowers receiving only pollen usually become seeds, whereas most that also receive an egg become galls that each support a developing wasp offspring (Verkerke 1989, Jansen-González *et al.* 2012; Martinson *et al.* 2014). Importantly, each flower can potentially produce either a seed or a wasp but not both (Janzen 1979, Herre 1989, Herre and West 1997, Anstett 2001, Herre *et al.* 2008, Dunn 2020). Pollinator offspring therefore develop in flowers at the expense of potential seeds (Janzen 1979, Herre 1989, Herre and West 1997, Weiblen 2002, Wang *et al.* 2011). Because seed production would be eliminated if all flowers were utilized by pollinators, there is a clear host–symbiont conflict over flower fates (Herre 1989, Anstett *et al.* 1996, Herre and West 1997, Anstett 2001). Nevertheless, despite within- and between-species variation in foundress numbers, in nature ~40–60% of developed flowers within individual figs become seeds (e.g. Herre 1989).

Mechanisms explaining why pollinators fail to exploit all fig flowers (Dunn 2020) fall into two groups: (i) those that act before foundresses enter receptive figs and come into contact with flowers ('pre-entry'), and (ii) those that act after entry, when foundresses are in direct contact with flowers ('post-entry'; Table 1). The main 'pre-entry' mechanism is 'insufficient (wasp) eggs' (Nedft and Compton 1996); wasps cannot fully exploit flowers because the total wasp eggs present in individual figs is less than the number of flowers. This can be realized by several factors, such as mechanisms restricting the number of foundresses entering figs (Wang *et al.* 2009). If 'insufficient eggs' applies, and pollination occurs, seed production is guaranteed and little or no host–symbiont conflict occurs. Alternatively, when pollinator wasps within receptive figs collectively carry enough eggs to enable the exploitation of all flowers, additional 'post-entry' mechanisms are required to ensure a subset of flowers become seeds,

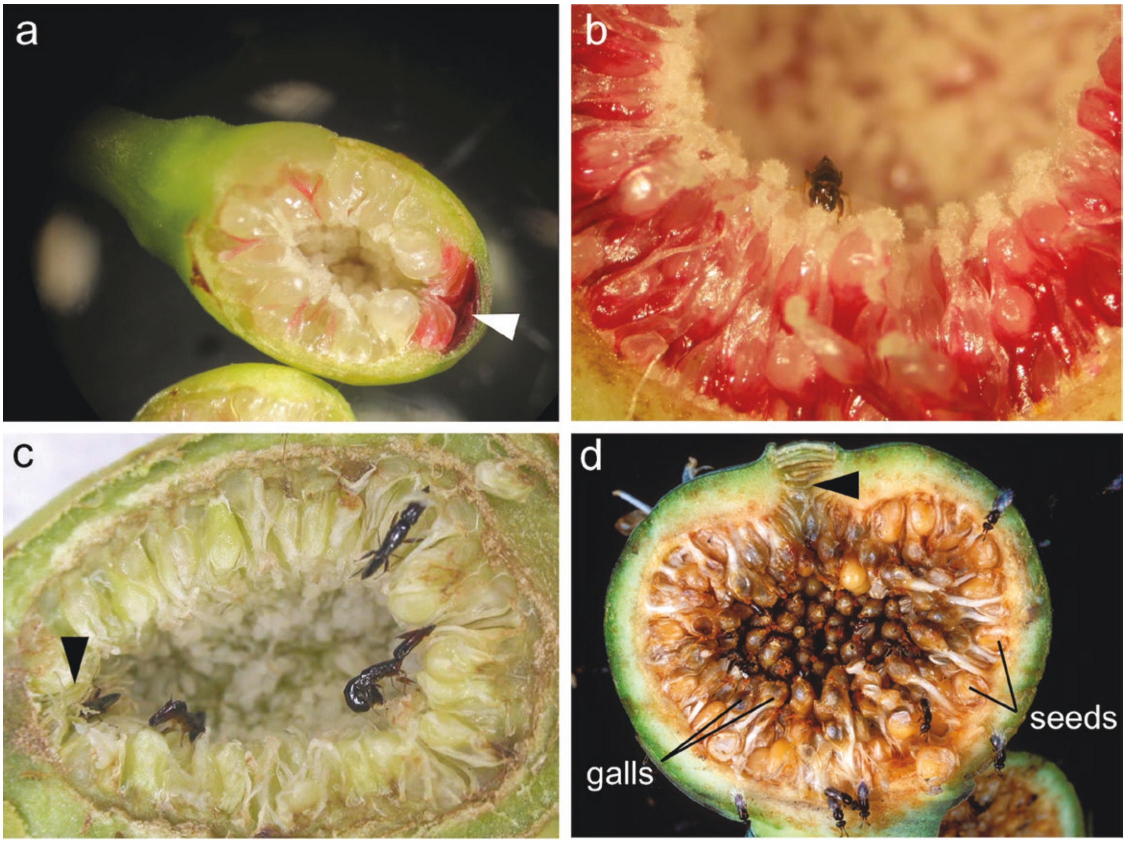

Figure 1. *Ficus* inflorescences (figs) vary greatly in size and hence flower number. Using four species included in this study, we illustrate with bisected pollen-receptive (flowering; interfloral phase) figs of: A, *F. americana* with male flower phase figs (diameter 8.5 mm) containing on average 168 flowers; B, *F. affinis crocata* with male flower phase figs (diameter 19.7 mm) containing on average 1476 flowers; and C, *F. macrophylla* with male flower phase figs (diameter 17.2 mm) containing on average 630 flowers. The flowers line the inner surface of the fig. One or several female pollinator wasps (foundresses) enter through the ostiole (arrows) to lay eggs and pollinate the flowers. D, some flowers develop into seeds, while others are converted by wasps into galls that each nourish a single wasp offspring. Here we show a bisected mature (male flower phase; diameter 25 mm) *F. obtusifolia* fig with female wasp offspring emerging to collect pollen. Photographs: A, B, K.C. Jandér; C, J.M. Cook; D, C. Ziegler.

Table 1. Potential pre- and post-entry mechanisms that limit flower exploitation of fig flowers by foundress wasps.

Mechanism	References
Pre-entry	
Restricting foundress numbers	Nefdt and Compton (1996), Wang *et al.* (2009)
Constraining fecundity by restricting size of developing wasps	Herre (1989), Nefdt and Compton (1996)
Constraining fecundity by restricting size of wasps that enter the fig (narrow ostiole)	Nefdt and Compton (1996), Lui *et al.* 2011
Post-entry	
Promoting competitive interactions among wasps by ensuring simultaneous pollinator presence within figs	Yu *et al.* (2004), Wang *et al.* (2009), Dunn *et al.* (2015)
Providing a variable floral environment that reflects variable costs/benefits to wasps ovipositing in different flowers	Yu *et al.* (2004), Dunn *et al.* (2008a and b)
Shortening wasp lifespans with a hostile microhabitat	Patiño *et al.* (1994), Wang *et al.* (2009)
Restricting wasp access by having a subset of flower ovaries resistant to wasp galling	West and Herre (1994), Wang *et al.* (2013), Martinson *et al.* (2015)
Restricting wasp access by having some flower ovaries inaccessible due to long styles	Nefdt and Compton (1996), Al-beidh *et al.* (2012)

such as physical or chemical barriers to oviposition or providing an oviposition environment that reduces rates of oviposition and hence rates of flower exploitation (*sensu* West and Herre 1994, Anstett 2001, Yu *et al.* 2004, Dunn *et al.* 2008a, b, 2015, Wang *et al.* 2009, 2013, Martinson *et al.* 2015; Table 1). Therefore, when host–symbiont conflict is high, i.e. when egg-to-flower ratios consistently enable pollinators to exploit flowers at very high rates, post-entry mechanisms will have enhanced functional significance in promoting system stability.

The several mechanisms constraining flower exploitation by pollinators (Table 1) have been identified using only a few fig–wasp mutualisms. However, to assess their systemic relevance, and to identify the probable significance of pre- or post-entry mechanisms in contributing to stability in these mutualisms, a wider comparative study of mutualist traits underpinning host–symbiont conflict of interest is required. In *Ficus* such a trait is fig size, due to its probable strong positive correlation with flower numbers (Fig. 1) and pollinator wasp sizes, fecundities, and foundress numbers (Herre 1989, Cook and Rasplus 2003, Dunn 2020). Interspecifically, fig size exhibits very high variation (~5–70 mm in diameter; Cook and Rasplus 2003), with flower numbers ranging from <10 to 20 000+ per fig (Herre 1989, Kjellberg *et al.* 2001, Cook and Rasplus 2003, Dunn 2020). There is much lower interspecific variation in wasp body size [e.g. ~3.5× in body length within genera (=~43× for volume; Lopez-Vaamonde *et al.* 2002)], which will probably correlate with wasp fecundity (the egg load of an adult female) (*sensu* Honèk 1993), and also foundress numbers (one to five per fig among host *Ficus* spp.; Herre 1989). As fig size increases the corresponding rate of increase in total wasp eggs (foundress number × fecundity) is thus unlikely to match the corresponding several-orders-of-magnitude increase in flower numbers (Dunn 2020). Therefore, across fig–wasp mutualisms, we predict that host–symbiont conflict over flower fates (the total number of wasp eggs relative to the total number of flowers) will decrease as fig size increases (see also Dunn 2020).

We tested our predictions using 23 monoecious *Ficus* species that capture much of the variation in fig sizes, geographical distributions, and phylogenetic relationships. Furthermore, if *Ficus* with small figs have high host–symbiont conflict (wasp egg-to-flower ratios), in order to maintain seed production post-entry mechanisms that prevent some wasp eggs from ultimately translating into adult wasp offspring must be present (Fig. 2). However, in large-fig species even if all wasp eggs successfully become adult offspring, host seed production will be maintained due to a surplus of flowers. Across *Ficus*, the likelihood of a wasp egg in a pollen-receptive fig later becoming an adult wasp offspring should thus increase with fig size.

METHODS

Fig tree–fig wasp natural history (see also Fig. 1)

With a few known exceptions (e.g. Gibernau *et al.* 1996), foundresses usually enter, pollinate, and oviposit into only one pollen-receptive fig. Pollinating fig wasps are pro-ovigenic, with their entire egg load mature on emergence as adults (Copland *et al.* 1973, Ghara and Borges 2010, Dunn *et al.* 2011). Therefore, the lifetime reproductive success of each foundress is generally tied to the fig it pollinates, predicting strong selection for wasps to lay eggs in as many flowers as possible during their brief adult lifespans (up to 48 h; Dunn *et al.* 2008a, b, Jevanandam *et al.* 2013, Dunn 2020).

In addition to their pollinating wasps, all *Ficus* support a community of from three to 30 nonpollinating fig wasp (NPFW) species (Weiblen 2002, Borges 2015, 2021). Most NPFWs are of similar small size to the pollinators, use an individual galled flower ovary to produce each offspring, and can be categorized into four groups: (i) gallers, (ii) kleptoparasitic inquilines, (iii) parasitoids of pollinators or other NPFWs, and (iv) hyperparasitoids (for details see Borges 2015). Unlike the pollinators, most NPFWs oviposit from the outside surface of the fig.

NPFWs can affect the reproduction of both mutualists due to their usage of flower ovaries that could potentially become pollinator offspring or seeds. However, NPFWs have been shown to mainly affect pollinators (e.g. Pereira and do Prado 2005, Segar and Cook 2012, Borges 2021), with NPFW parasitoids of pollinators in several systems paradoxically promoting mutualism

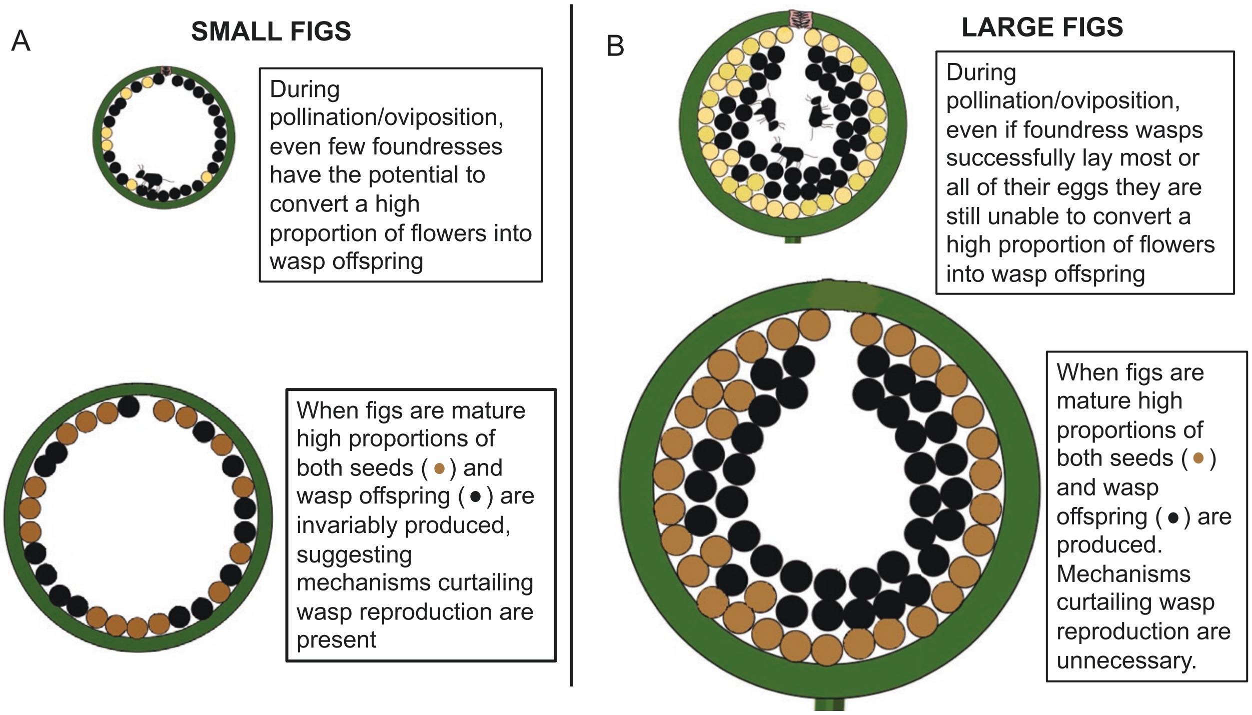

Figure 2. Schematic diagram illustrating the potential wasp exploitation of flowers in individual figs in: A, host *Ficus* with small figs; and B, host *Ficus* with large figs. Although small figs contain few foundresses of low fecundity, they have high flower exploitation potential due to few flowers per fig. This suggests that post-entry mechanisms reducing flower exploitation by wasps have adaptive significance in ensuring that both wasp offspring and seeds are produced. In large figs, high flower numbers reduce the exploitation potential of wasps even though multiple foundresses of relatively high fecundity are present. Even if most or all wasp eggs are laid, both wasp offspring and seeds are produced.

stability by acting as a post-entry mechanism preventing high rates of flower exploitation by pollinators (see Dunn *et al.* 2008b, Al-beidh *et al.* 2012, Wang *et al.* 2019). It is thus important to emphasize that despite the activities of NPFWs, including galler species that directly convert fig ovaries into offspring, under natural conditions among monoecious *Ficus* ~40–60% of developed flowers still consistently produce seeds.

Depending on the *Ficus* species and local environmental conditions, from several weeks to months after pollination and oviposition (interfloral phase; i.e. female anthesis), monoecious figs reach the male flower phase (male anthesis) in which mature seeds, adult wasp offspring (pollinators and NPFWs), and pollen are simultaneously produced (Galil and Eisikowitch 1968).

Study species

The 23 host *Ficus* species studied are native to four continents—Asia (one species: section Conosycea), Australia (five species: sections Malvanthera and Sycomorus), Africa (three species: sections Galoglychia and Sycomorus), and Central and South America (14 species: sections Americanae and the distantly related Pharmacosycea) (Supporting Information Table S1). Data for each fig–wasp species pair are presented in Table S2.

Measuring mutualist traits

For each of the 23 systems, to test our core predictions, we had to obtain reproductive and size trait measurements for both mutualists. To do this we used both interfloral (B-stage) and male-flower stage (D-stage) figs, and also data from published sources. For host trees, we calculated the average flower and foundress numbers in figs receptive to pollination/oviposition by pollinators, and the average seed numbers and fig sizes (mL) for mature figs. For wasp symbionts, we calculated average adult female wasp sizes (head widths), fecundities (egg counts), and total adult offspring produced. With the exception of wasp fecundity versus wasp size, we used each trait as a response variable in a separate statistical model with fig size as the explanatory variable (see Supporting Information Tables S4 and S5).

Composite variables

Variation in conflict

We first calculated for each *Ficus* species the average total number of wasp eggs-per-fig (foundress number × fecundity) to compare its relationship with fig size, with the relationship between average flower number and fig size.

For each *Ficus* species on average, we then calculated host–symbiont conflict as the total number of pollinator eggs relative to the total number of flowers within figs (mean foundress number × mean fecundity)/mean flower number. This estimates the flower exploitation potential of pollinators, the maximum proportion of flowers that wasps can convert into offspring (Herre 1989, Dunn 2020). When equal to or exceeding 1, wasps can potentially exploit all flowers.

We also calculated the proportion of individual figs for each *Ficus* species (sampled for foundress numbers) that contained sufficient foundresses, and hence wasp eggs, to enable wasps to exploit all flowers. We did this by using field-measured foundress number distributions (Supporting Information Table S3), after first calculating the number of foundresses of average (mean) fecundity required to exploit all flowers (Table S2). Both composite variables were used as a response variable in two statistical models, each with fig size as the explanatory variable (see Tables S4 and S5).

Conflict resolution

Any host–symbiont conflicts should be resolved across stable mutualisms with both partners consistently reproducing successfully. To test realized reproductive outputs for each mutualist across the 23 systems, we calculated for mature (male-flower phase) figs: (i) the number of seeds per adult pollinator offspring (mean seed number/mean pollinator offspring), (ii) the number of seeds-per-flower (mean seed number/mean flower number), and (iii) the number of adult pollinator offspring per flower (mean pollinator offspring/mean flower number).

Finally, to test our prediction that post-entry mechanisms of conflict resolution, i.e. processes preventing pollinators from exploiting fig flowers at high rates when they have the potential to do so, will be more likely in *Ficus* with smaller figs (Fig. 2), we calculated (iv) the average number of adult pollinator offspring (from male-flower phase figs) per wasp egg (in interfloral phase figs) [mean wasp offspring/mean total eggs (foundress × fecundity)]. Each of these composite variables was used in a separate statistical model that had as its explanatory variable fig size (see Supporting Information Tables S4 and S5).

To calculate species-level composite variables, different figs at different developmental stages had to be used. When presented as figures and in tables estimates for variation around composite variables are therefore absent.

Data analysis

Closely related species share traits via common descent (Felsenstein 1985, Harvey and Pagel 1991). To test our predictions independent of host phylogenetic effects we performed phylogenetic least-squares regression (PGLS) using two alternative methods to incorporate covariance: (i) a Brownian correlation structure and (ii) a correlation structure under Pagel's Lambda (estimated from the data) using R 4.1.2. (R Core Team 2021). Results were similar among methods (PGLS using either Brownian or Lambda correlation structures, and when using noncorrected least-squares regressions). We thus only present Brownian PGLS results in the main text. Details for data preparation and the phylogenies used, and results for Pagel's Lambda correlation structures and uncorrected data, are presented in the Supporting Information.

RESULTS

Variation in conflict

As predicted, foundress numbers ($b \pm \mathrm{SE} = 0.39 \pm 0.10$, $F_{1,21} = 13.89$, $P < .001$), wasp sizes ($b \pm \mathrm{SE} = 0.44 \pm 0.10$, $F_{1,21} = 18.70$, $P < .001$), and flower numbers ($b \pm \mathrm{SE} = 0.90 \pm 0.12$, $F_{1,21} = 50.27$, $P < 0.001$; Fig. 3A) all increased significantly with fig size, with wasp fecundity also increasing with wasp size ($b \pm \mathrm{SE} = 0.41 \pm 0.11$, $F_{1,21} = 13.57$, $P < .001$; Supporting Information Fig. S2). Total wasp egg number (foundress number × foundress fecundity) was thus a significant positive function of fig size ($b \pm \mathrm{SE} = 0.54 \pm 0.13$, $F_{1,21} = 15.28$, $P < .001$; Fig. 3B). Consistent with our prediction, the regression slope for flowers against fig size was steeper than that for total eggs on fig size (*t*-test: $t_{42} = 2.05$, $P < .05$; Zar 1984, Bland 1995).

Host–symbiont conflict, i.e. on average the total number of wasp eggs relative to the total number of flowers, varied widely across species and taxonomic sections of *Ficus* (Fig. 4A) and as predicted was a significant negative function of fig size ($b \pm \mathrm{SE} = -0.12 \pm 0.05$, $F_{1,21} = 5.71$, $P = .026$; Fig. 4B). On average, within figs the total number of wasp eggs exceeded flower numbers in only two host *Ficus* species (9%; *F. rubiginosa* and *F. citrifolia*; Fig. 4A). However, in six species (26%; *F. rubiginosa*, *F. macrophylla*, *F. citfrifolia*, *F. dugandii*, *F. pertusa*, and *F. yoponensis*), there were on average enough eggs to enable wasps to extensively exploit flowers, i.e. to convert ≥60% of flowers into wasp offspring. In the remaining 17 species (74%), wasps only had the potential to exploit flowers at lower rates, with 11 of these (48%) only having the potential to exploit less than 40% of flowers (Fig. 4A).

Across all 23 host species, the proportion of individual figs that contained sufficient foundresses to potentially exploit all flowers ranged from zero (nine species) to 57% (*F. dugandii*; Supporting Information Table S2). Nonetheless, 20% or more of all figs from five species (*F. rubiginosa*, *F. macrophylla*, *F. dugandii*, *F. citrifolia*, and *F. pertusa*) contained enough foundresses to exploit all flowers (Table S2). Across species, as figs become larger, fewer figs overall contain sufficient foundresses to exploit all flowers ($b \pm \mathrm{SE} = -0.27 \pm 0.12$, $F_{1,21} = 5.67$, $P = .027$).

Conflict resolution

Across all 23 *Ficus* species, there were on average 0.41 (± SE = 0.034; range: 0.13–0.71) seeds-per-flower, showing a very slight decline as fig size increased ($b \pm \mathrm{SE} = -0.04 \pm 0.02$, $F_{1,21} = 5.12$, $P = .03$). On average 0.33 (± 0.028; range: 0.12–0.53) wasp offspring were produced per flower, showing no relationship with fig size ($b \pm \mathrm{SE} = -0.02 \pm 0.03$, $F_{1,21} = 0.53$, $P = .48$). Similarly, on average 0.91 (± 0.11; range: 0.16–2.49) wasp offspring were produced per seed, again showing no relationship with fig size ($b \pm \mathrm{SE} = 0.04 \pm 0.06$, $F_{1,21} = 0.54$, $P = .47$). These results suggest that across these systems and independent of fig size and hence conflict between mutualists, the reproductive output of both mutualists is generally consistent.

Consistent with host *Ficus* with small figs and high host–symbiont conflict exhibiting post-entry mechanisms limiting flower exploitation by wasps, the likelihood of a wasp egg in a pollen-receptive fig later successfully becoming an adult wasp offspring (i.e. the number of adult offspring produced per egg) increased with fig size ($b \pm \mathrm{SE} = 0.11 \pm 0.05$, $F_{1,21} = 5.54$, $P = .028$; Fig. S3).

DISCUSSION

Many mutualisms are underpinned by host–symbiont conflict (Herre *et al.* 1999), such as that over flower fates in monoecious fig–wasp systems (Janzen 1979, Herre and West 1997, Anstett 2001, Dunn 2020). We show that relationships between key host–symbiont traits not only provide a general framework for

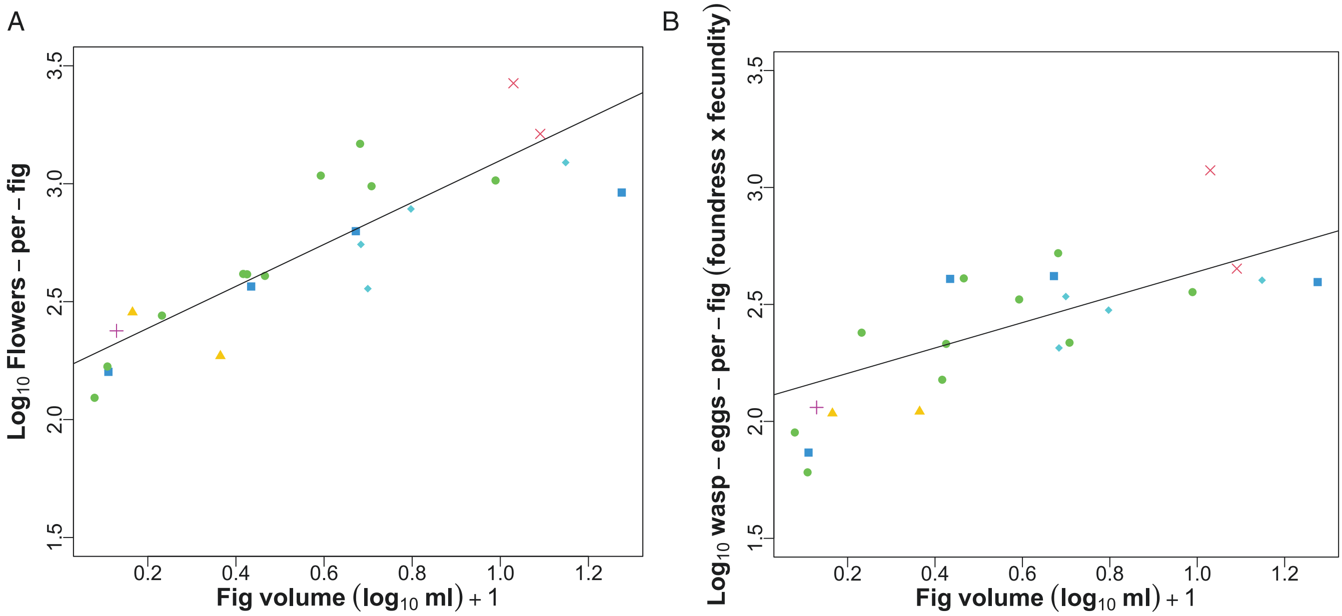

Figure 3. A, the relationship between flower number (log transformed) and fig size (volume in mL + 1, log-transformed). B, the relationship between the total number of wasp eggs (wasp fecundity × foundress number) (log-transformed) and fig size (volume in mL + 1, log-transformed). As figs become larger both flower numbers and the total number of wasp eggs increase. However, the rate of increase for flower numbers (b ± SE = 0.90 ± 0.12) is significantly higher than that for wasp eggs (b ± SE = 0.54 ± 0.13; *t*-test $t_{42} = 2.05$, $P < .05$), explaining the negative relationship between host–symbiont conflict and fig size (B). The lines of best-fit are calculated from each PGLS analysis and are thus independent of the effects of phylogeny. Data point types and colours represent different *Ficus* clades: Conosycea: +; Malvanthera: ▪; Galoglychia: ▲; Americanae: ●; Sycomorus: ×; Pharmacosycea: ⬩.

assessing host–symbiont conflict but also enable predictions of mechanisms promoting system stability. Specifically, large-fig host *Ficus* exhibit lower host–symbiont conflict than small-fig species. This is because too few foundresses, and hence wasp eggs, are present in large pollen-receptive figs to enable the wasps to consistently exploit flowers at very high rates, despite these figs being pollinated by higher numbers of relatively fecund foundresses. Importantly, as fig size increases interspecifically, the increase in total wasp eggs (foundress number × fecundity) fails to match the rise in fig flowers, providing a clear mechanistic explanation for among-species variation in this long-recognized host–symbiont conflict (Janzen 1979, Herre 1989, Ansett 2001, Cook and Rasplus 2003, Yu *et al.* 2004, Dunn *et al.* 2008a, b, Herre *et al.* 2008, Wang *et al.* 2009, Dunn 2020).

Despite much variation in host–symbiont conflict, we found relatively consistent rates of seeds-per-flower, wasp offspring-per-flower and wasp offspring-per-seed across all 23 mutualisms, i.e. those with or without clear conflict between mutualists. This concurs with effective host mechanisms across systems limiting the potential for wasps to convert would-be seeds into offspring (Table 1). We suggest this is probably due to pre-entry mechanisms in large-fig systems (low conflict) and post-entry mechanisms in those with smaller figs (high conflict) having increased adaptive significance.

Fig–wasp systems exhibiting low conflict

In ~74% of the *Ficus* species examined, individual receptive figs rarely, if ever, contained enough foundresses and hence eggs to enable wasps to exploit flowers at high rates (>60%; Fig. 4A; Nefdt and Compton 1996). This is consistent with 'shared interests' between mutualists (Frederickson 2017, West *et al.* 2021). A lack of clear conflict suggests that, within these mutualisms, current selection for 'post-entry' mechanisms that reduce flower exploitation by wasps will be relatively weak, because such 'enforcement' mechanisms (West *et al.* 2021; see 'post-entry' mechanisms, Table 1) would confer few net benefits to hosts: even if every foundresses laid all of its eggs, which in turn all successfully converted fig flowers into wasp galls, wasps would still be unable to exploit enough flowers to reduce seed production. In such systems, we suggest that 'pre-entry' mechanisms are more likely, those that operate before wasps come into contact with the flowers. For example, a narrow ostiole (the tract through which wasps enter figs) can limit the sizes, and hence the fecundities, of wasps that enter a fig (van Noort and Compton 1996, Lui *et al.* 2011), and by restricting the number of foundresses that enter figs by reducing the duration the ostiole remains open (Nedft and Compton 1996, Wang *et al.* 2009, Dunn 2020; Table 1).

Fig–wasp systems exhibiting high conflict

In each of the remaining 26% of the study *Ficus* species there is clearly potential for host–symbiont conflict. Within these species, at the time of pollination/oviposition there are often sufficient foundresses and hence wasp eggs present within figs to enable the wasps to exploit most, if not all, flowers (Fig. 4A). Indeed, in five *Ficus* species (*F. rubiginosa*, *F. dugandii*, *F. citrifolia*, *F. pertusa*, and *F. yoponensis*), pollen-receptive figs regularly contain enough wasp eggs to nearly or fully eliminate seed production (Supporting Information Tables S2 and S3). Nevertheless, this does not occur, suggesting the presence of post-entry

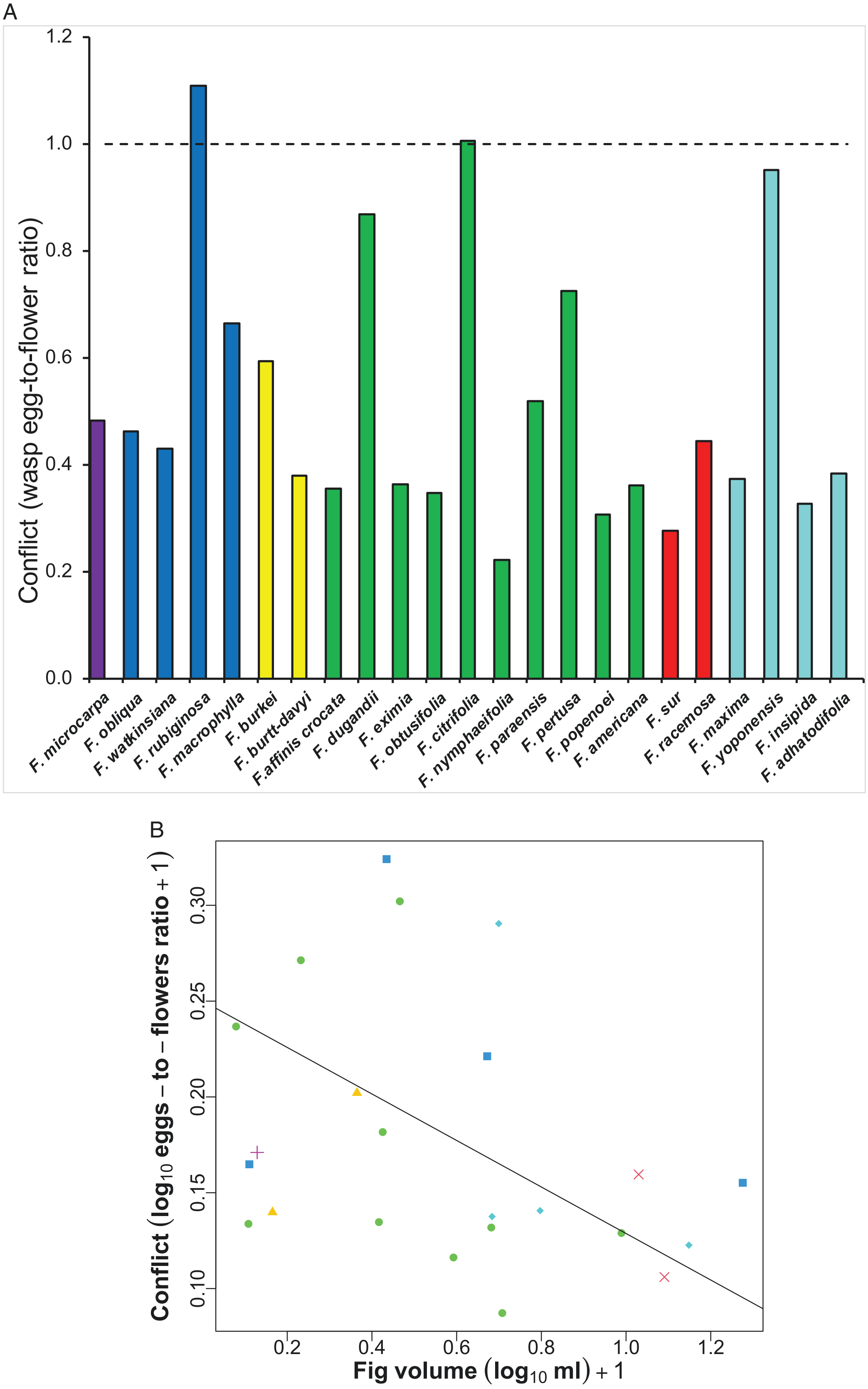

Figure 4. A, bar chart showing average host–symbiont conflict (the average number of wasp eggs relative to the number of flowers per fig) for each of the 23 *Ficus* species. Species are arranged according to taxonomic sections of *Ficus* captured by the study, each of which is represented by a different colour. The dashed horizontal line represents the point where on average the number of wasp eggs equals the number of flowers within a receptive fig for each species. B, the relationship between conflict between mutualists, the ratio of wasp eggs to flowers [(fecundity × foundress number/flower number) + 1, log-transformed], and fig size (volume in mL + 1, log-transformed). As fig size increases across host species the potential that symbiont wasps have to exploit flowers declines. The line of best-fit is calculated from PGLS analysis and is thus independent of the effects of phylogeny. Data point types and colours are as Figure 3.

mechanisms curtailing wasp flower exploitation rates, i.e. that ultimately prevent some wasp eggs from successfully developing into adult wasp offspring (Fig. 2). Consistent with this interpretation, the likelihood of a wasp egg successfully becoming an adult offspring increases with host fig size. The pollinators of small-fig *Ficus* thus appear to routinely realize less of their potential fitness than the pollinators of large-fig *Ficus*. These high-conflict, small-fig species contain relatively few flowers so only few foundresses are required to result in high host–symbiont conflict. Such host species are therefore unlikely to deploy 'pre-entry' mechanisms to restrict the number of foundresses entering figs.

We suggest that small-fig *Ficus* are more likely than those with larger figs to rely on 'post-entry' 'enforcement' mechanisms to limit flower exploitation by wasps (*sensu* West *et al.* 2021; Table 1). There is evidence for such mechanisms in several fig–wasp mutualisms (reviewed by Dunn 2020), such as barriers to oviposition in some flowers (West and Herre 1994, Nefdt and Compton 1996, Wang *et al.* 2013, Martinson *et al.* 2015), fig/flower morphology indirectly reducing foundress lifespans (Patiño *et al.* 1994, Dunn *et al.* 2008a) that may also facilitate competition among foundresses (Bronstein *et al.* 1998, Yu *et al.* 2004, Dunn *et al.* 2008b, 2015, Wang *et al.* 2009), and via NPFW parasitoids affecting pollinator flower preferences (Dunn *et al.* 2008b, Al-beidh *et al.* 2012, Wang *et al.* 2019). It is noteworthy that small-fig *Ficus* tend to show lower variation in foundress numbers than those with large figs (Supporting Information Table S3.). We thus also expect the pollinating wasps of small-fig hosts to exert relatively consistent selection on post-entry 'enforcement' mechanisms in hosts.

The compartmentalization of host resources in figs (Chomicki *et al.* 2021), the flowers accessible only via the ostiole, enables host trees to 'enforce' symbiont cooperation (*sensu* West *et al.* 2021) in two ways: (i) promoting pollination via host sanctions (Denison 2000), by which foundresses incur high fitness costs due to reduced host investment to unpollinated figs (Jandér and Herre 2016), and (ii) by limiting the rate by which wasps exploit fig flowers (both reviewed by Dunn 2020). The main component of host sanctions is fig abortion, by which unpollinated figs have increased propensity to drop off the tree prior to maturity, thus killing all wasp offspring (Dunn 2020). Unlike in some other brood-site pollination systems (e.g. *Yucca*–yucca moths; Pellmyr and Huth 1994), there is currently no evidence of sanctions to pollinated *Ficus* inflorescences with high rates of flower exploitation by pollinators. Therefore, in *Ficus* species with small figs, foundresses that enter and pollinate still have the potential to subsequently be uncooperative and exploit flowers at high rates.

Future research

In order to conduct detailed phylogenetic analyses to identify any trend for small-fig systems to evolve larger figs towards becoming 'shared interest' systems (*sensu* West *et al.* 2021), the selective agents maintaining interspecific fig size variation require further cross-species investigations. For instance, producing large figs due to increased evapotranspiration (Patiño *et al.* 1994, Herre 1996) and/or the strong correlation between fig and leaf sizes (Harrison *et al.* 2012) may be costly, or there may be seed dispersal–fig size trade-offs due to variation in vertebrate frugivore communities (Kalko *et al.* 1996, Shanahan *et al.* 2001). Intraspecific competition for oviposition sites results in some foundresses failing to lay their entire egg loads (see Kathuria *et al.* 1999, Moore and Greeff 2003, Yu *et al.* 2004, Dunn *et al.* 2008a, b, 2011, 2015, Dunn 2020), which should be most likely in large-fig *Ficus* due to multifoundress entry to figs. However, trends across *Ficus* due to interfoundress competition may be partially offset in large-fig hosts by an abundance of flowers and in small-fig hosts by the presence of post-entry mechanisms reducing wasp oviposition rates (Table 1). Larger wasp species may also produce relatively larger eggs, which may contribute to increased egg-to-offspring survival. The molecular regulation of important mutualist traits, including some likely to be associated with conflict between mutualists such as pollinator gall and seed development, has been recently identified and quantified (e.g. Zhang *et al.* 2020, Wang *et al.* 2021). Expansion of such studies to target traits known to underpin conflict between mutualists, such as variation in both wasp egg and fig flower numbers and sizes, and variation in fig sizes, will enable more in-depth understanding of how stability in fig–wasp mutualisms is maintained.

CONCLUDING REMARKS

Across brood-site pollination mutualisms there is much variation in the degree of potential conflict of interest between mutualists over host flower fates [e.g. *Yuccas* (Pellmyr and Huth 1994); Phyllanthaceae (Goto *et al.* 2010); *Ficus* (Dunn 2020); *Trollius* (Ibanez *et al.* 2009)]. Unsurprisingly, mechanisms preventing symbiont pollinating insects from overexploiting host flowers also vary (Herre *et al.* 1999). Here, we demonstrate systematic variation in host–symbiont conflict in 23 fig–wasp mutualisms. As fig size increases, host–symbiont conflict of interest declines due to differences in relationships between key mutualist reproductive traits associated with fig size. This variation provides a systematic framework for predictions as to the relative importance of different mechanisms in promoting mutualism stability according to fig size. We suggest that similar considerations be included in comparative studies designed to identify and measure mechanisms that limit host exploitation by symbionts both among and within different mutualism types.

SUPPLEMENTARY DATA

Supplementary data are available at *Evolutionary Journal of the Linnean Society* online.

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CONFLICT OF INTEREST

No authors have any conflicts of interest.

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DATA AVAILABILITY

The data used for this study are available on Dryad (https://doi.org/10.5061/dryad.547d7wmjw).

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